Hooded seals (*Cystophora cristata*) in the Northwest Atlantic Ocean: Uncovering movement patterns, habitat selection and diving behaviour throughout the annual migration.

by

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ABSTRACT

How animals change their movement patterns in response to their environment is a central topic in ecology. The northwest (NW) Atlantic hooded seals occupy areas on the borderline between the North Atlantic- and high Arctic Ocean. By investigating these large predators' movement patterns through the marine landscape, we can obtain a better understanding of the seasonal dynamics of habitat selection and use. This will improve the knowledge needed for good ecosystem management of critical habitat. This is especially important for highly vulnerable regions increasingly exposed to the oil and shipping industry, as well as global warming.

NW Atlantic hooded seals rely on ice for two months of the year, when they reproduce and moult (March and July). Factors that influence the distribution at other times of the year are unknown. Here, 67 hooded seals (33 females, 18 males and 16 juveniles) were equipped with Satellite Relay Data Loggers (SRDLs) during the breeding or moulting season in the period 2004-2008. The study revealed that seals used areas of high topographic relief during migration. Such areas include the Labrador shelf, Davis Strait and Baffin Bay during the post-moult/pre-breeding period (August-February) and the area off the Grand Banks of Newfoundland, Flemish Cap, the Gulf of St. Lawrence and the southeast Greenland shelf during the post-breeding/pre-moult period (April-June). They exhibit sexual and age related segregation in terms of environmental habitat variables (sea surface temperature, surface chlorophyll concentration, bottom depth, bottom topography and ice concentration) and first passage time (FPT) at the area restricted search (ARS) scale. Furthermore, males and females demonstrated differences in diving strategies and fluctuations in the relative change of buoyancy over time. Females used areas with greater water depths than males and displayed an off-shelf, dynamic habitat use while males spent more time on top of the shelf and in areas of high topographic relief. I suggest that hooded seals exhibit a resource partitioning strategy to avoid competition between sexes, or that the geographic segregation and different patterns of timing and magnitude of lipid energy acquisition reflect a difference in energy requirements in relation to fasting periods.

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CHAPTER 1: INTRODUCTION AND OVERVIEW

1.1. *Habitat and the spatial dimensions of foraging*

Animals are ecologically influenced by the spatial heterogeneity of their habitat (e.g., Turner 1989, Johnson et al. 1992). The definition of habitat is "the conditions and resources present in an area that produce occupancy (including survival and reproduction) by an organism" (Hall et al. 1997, p. 175) and habitat selection is in turn defined as "the process whereby individuals preferentially use, or occupy, a non-random set of available habitats" (Morris 2003, p. 2). Different regions of the landscape are expected to vary in suitability according to differing levels of resource availability, and an animal's movements through a patchy environment will influence its dispersal rates and foraging behaviours (e.g., Milne et al. 1989, Turner 1989, Johnson et al. 1992). The interactions of the animal's movement patterns with landscape features produce spatial patterns in individual space-use, population dynamics and dispersion (Johnson et al. 1992).

An important factor influencing habitat selection is the availability of resources, particularly prey. Synoptic information on prey and predator presence is difficult to obtain for wide ranging marine animals occupying a three dimensional environment. However, observing the movement patterns of the predator through the landscape using satellite telemetry can offer indications of prey availability. It is generally thought that the dispersal and movement of predators are affected by the occurrence of high density patches within low density distributions, resulting in non-random search strategies for critical levels of prey (e.g., MacArthur and Pianka 1966, Charnov 1976, Kareiva and

Odell 1987, Senft et al. 1987, Johnson et al. 1992). Predators may also use proxies associated with prey abundance during wide range searches, such as temperature, salinity or upwelling of nutrients influenced by bottom topography (e.g., Smith et al. 1986, McConnell et al. 1992, Croll et al. 1998, Plötz et al. 2001, Burns et al. 2004, Baumgartner and Mate. 2005, Pinaud and Weimerskirch 2005, Breed et al. 2006, Bailleul et al. 2007, Biuw et al. 2007; 2010, Freitas et al. 2008, Harvey et al. 2008, Maxwell et al. 2012, Nordstrom et al. 2013).

The ability of highly mobile top predators to locate and exploit patchily distributed prey, especially in a changing environment, is crucial to their reproductive success and survival (e.g., Stephens and Krebs 1986). Optimal foraging theory states that a foraging activity should increase as long as the resulting gain in time spent per unit food exceeds the loss (MacArthur and Pianka 1966). Thus, the predator needs to make a decision as to which patch types it will visit and when it will leave to search for a new patch (Charnov 1976). The arrangement of resources further affects the clustering of animals in the landscape as high density locations will not be used by animals if the net energetic gain from visiting them is marginal (e.g., Charnov 1976, Milne et al. 1989). This could further result in interspecific or intraspecific competition for habitat and prey (e.g., Connell 1983, Mysterud 2000, Spina 2000, Chase et al. 2002). Differences in foraging strategies or spatial segregation by sex, size and/or age within the same species are thought to occur due to the different energetic needs in relation to metabolic rates, differences in morphology and/or reproductive costs (e.g., Mysterud et al. 2000, Breed et al. 2006, Muelbert et al. 2013). Such ecological segregation has been found to be higher amongst sexually dimorphic animals (Mysterud et al. 2000).

How marine mammals alter their movement pattern in relation to habitat has resulted in the development of various analytical methods such as resource selection functions (e.g., Boyce and McDonald 1999), Cox proportional hazard models (e.g., Freitas et al. 2008, Nordstrom et al. 2013) and state-space models (e.g., Breed et al. 2012, Patterson et al. 2008; 2009). These methods have contributed new knowledge in marine mammal ecology. However, this thesis has focussed analysis of transitions in movement patterns (travelling vs. feeding) and habitat selection on the application of a combined approach using First Passage Time (FPT; e.g., Fauchald and Tveraa 2003; 2006, Bailleul et al. 2008, Freitas et al. 2008, Thums et al. 2011, Nordstrom et al. 2013) and Generalized Additive Models (GAMs; Hastie and Tibshirani 1990). GAMs can offer a potential advantage through the ability to account for correlation among variables, include interactions among variables, make quantitative predictions of abundance or probability of occurrence at given flows and identify sharp thresholds in habitat selection (Jowett and Davey 2007).

FPT is defined as the time required to cross a circle of a given radius, and is implemented as a scale-dependent measure of search effort (Fauchald and Tveraa 2003). The size of the area in which an animal focuses its search effort is called the Area Restricted Search (ARS) scale. The observed ARS scale, is related to individual foraging patterns as well as the spatial distribution of resources (Pinaud and Weimerskirch 2005). By analysing FPT at the ARS scale the geographic positions of detectable shifts in movement patterns along the migration path can be identified. Large-scale patches of prey often reflect the boundaries of preferable habitat (Fauchald and Tveraa 2006) and by implementing FPT in habitat models, high-use areas with long passage time and areas of travelling with shorter passage times can be identified. This type of analysis can offer valuable information in regard to habitat use, habitat selection and migration dynamics.

1.2. Assumptions of spatial scales and sample representation

The range of spatial and temporal scales of ecological events is an ongoing issue in ecology (Turner et al. 1989). Parameters and processes important at one scale are frequently not important at another scale, and information is lost as spatial data are considered at coarser scales of resolution (Henderson-Sellers et al. 1985). However, the essence of modelling should facilitate understanding of the system studied, by abstracting and incorporating just enough detail to produce observed patterns (Levins 1992). The model should ask how much detail can be ignored without producing results that contradict specific sets of observations, on particular scales of interest (Levins 1992).

In studies where we strive to understand more about a population's movement patterns and habitat use we normally have to start our investigation at the level of the individual. Detailed observation of the movement of individuals is a fundamental unit in ecological studies (Grimm and Railsback 2005) and offers the potential to understand spatial population processes such as the ultimate consequence of individual behaviour, physiological constraints and fine-scale environmental influence (Patterson et al. 2008). In the process of constructing a model we are forced to incorporate what we know about how the landscape may influence the distribution of a species, thereby formalising our understanding and identifying gaps in our knowledge (Starfield 1997). We then use models to scale up data from an individual to reflect the total population (e.g., Johnsen et al. 2005; 2006, Boyce and McDonald 1999, Freitas et al. 2008, Nordstrom et al. 2013, Breed et al. 2012, Patterson et al. 2008; 2009).

1.3. The study area

Identifying the spatial and temporal scales at which marine predators forage is important for understanding oceanic ecosystems (Boyd 1997, Bailleul et al. 2008). The area of this study is located at the border zone between the Northwest Atlantic Ocean and the high Arctic. The Arctic is a key region in the planet's climate system, both as a sensitive responder and as an active player in global climate change (Johannessen and Miles 2011). The region is also a conduit for the relatively swift passage of very cool and fresh surface water of Nordic and Arctic origin to the sub polar ocean via the East Greenland Current, the West Greenland Current and the Labrador Current (Grist et al. 2011). The Newfoundland and Labrador Shelf are influenced by several factors including the Labrador Current, cross shelf exchange with warmer continental slope water, and bottom topography (DFO 2006). The Labrador Sea is characterised by high convection activity driven by winter cooling and wind creating deep surface mixed layers, directly linking the atmosphere and the deep ocean, sometimes mixing as deep as to 2,000 m (Ross and Harrison 2007). Inter-annual variability in water properties and changes in the balance of inflows of fresh water from northern sources and warm, saline waters from southerly latitudes impact the marine ecosystems of the Labrador region (Ross and Harrison 2007) and Baffin Bay. These dynamics result in numerous microhabitats which, in turn, may result in a high abundance of Arctic and subarctic wintering animals, including many species of seabirds (e.g., king eiders (*Somateria spectabilis*), common eiders (*Somateria mollissima*), thick-billed murres (*Uria lomvia*)), cetaceans (narwhal (*Monodon monoceros*), beluga (*Delphinapterus leucas*) and bowhead whale (*Balaena mysticetus*)), pinnipeds (bearded seal (*Erignathus barbatus)*, ringed seal (*Phoca hispida*), harp seal (*Pagophilus groenlandicus*), hooded seal (*Cystophora cristata*), walrus (*Odobenus rosmarus*)) and polar bears (*Ursus maritimus*) (Sergeant 1965; 1976, Kovacs and Lavigne 1986, Heide-Jørgensen and Laidre 2004). Thus, the high Arctic and subarctic waters constitute an area of critical habitat for a number of species, making this an ecosystem vulnerable to change (e.g., Heide-Jørgensen and Laidre 2004, Arctic Council 2007).

Climate change can impose detrimental effects on species adapted to the unique and cold conditions of the Arctic and adjacent waters (e.g., Heide-Jørgensen and Laidre 2004, Learmonth et al. 2006, Johnston et al. 2012). Animals occupying these areas are geographically restricted, with little or no opportunity for range expansion (Learmonth et al 2006). Climate change in the marine environment will result in an increase in temperature, rise of sea levels and a decrease in ice cover, affecting prey availability and thus predator distribution, abundance and migration patterns, reproductive success and survival (Learmonth et al. 2006). For pagophilic ("ice-loving") seals (e.g., harp, hooded, ringed and bearded seals), a decrease in ice cover can have serious implications for female reproductive success, pup survival and food availability for weaned pups (e.g., Johnston et al. 2005, Learmonth et al. 2006, Friedlander et al. 2007). Johnston et al. (2005) found that the ice conditions off the east coast of Canada during the breeding period for harp and hooded seals (February/March) fluctuated over a 6 year cycle. This was linked to the North Atlantic Oscillation (NAO), a large scale fluctuation in atmospheric pressure causing the dominant mode of winter climate variability in the North Atlantic region (Hurrell et al. 2003, Johnston et al. 2005). However, research shows that this cyclic system has been breaking up, creating longer periods of poor ice conditions (Friedlander et al. 2007). A modelled assessment of the long term trends in sea ice cover in the breeding regions for harp and hooded seals revealed that the sea ice has been declining up to 6% per decade (Johnston et al. 2012). Ice conditions in the Gulf of St. Lawrence and southern Newfoundland coast during 2010 and 2011 was the lowest recorded in 40 years (Bajzak et al. 2011, ICES 2011).

In addition to the threat of habitat loss and population decline through global warming, there is an even more direct anthropogenic threat emerging in the Arctic. As sea ice is diminishing, large areas of seasonally open water are becoming available for human interference. Many nations share an economic interest in terms of the continued development of oil and gas activities and increased ship traffic in arctic regions (Arctic Council 2007). Arctic plants and wildlife may be exposed to compounds released by oil and gas activities in a number of ways, but oil spills are thought to be the biggest threat (Arctic Council 2007). This is because of increased environmental persistence of petroleum hydrocarbons, the slow recovery of highly seasonal ecosystems and the difficulty of organising a clean-up in remote regions (Peterson et al. 2003, Arctic Council 2007). The ice edge is seasonally considered particularly vulnerable as the marine animals inhabiting these areas have limited means of escape in the event of an oil spill. The pack ice is important as breeding substrate for several pinniped species, whales and birds use leads and polyneas for seasonal migration and foraging, and polar bears use the ice edge as a feeding ground (Arctic Council 2007).

The study of habitat selection by animals dependent on the Arctic and subarctic regions can therefore provide information on the environmental characteristics necessary for the area dependent species. This can offer essential knowledge needed in the development of wildlife management and conservation policies as the consequences of climate change and increased human industrial activities in the Arctic and subarctic ecosystems are being assessed

1.4. The hooded seal

The hooded seal occupies the subarctic and Arctic areas of the North Atlantic Ocean ecosystem (Sergeant 1974, Folkow and Blix 1995, 1999; Hammill and Stenson 2006). It is a pelagic, deep-diving species that remains submerged 80% of the time during migration (Stenson et al. 1993). Hooded seals are capable of making repeated dives to more than 1,000 m lasting more than 50 min (Folkow and Blix 1995) feeding on benthopelagic species, including a variety of redfish species (*Sebastes* spp.), Atlantic argentine (*Argentina silus*), herring (*Clupea harengus*), capelin (*Mallotus villosus*), Greenland halibut (*Reinhardtius hippoglossoides*), Atlantic cod (*Gadus morhua*), Arctic cod (*Boreogadus saida*) and squid (*Gonatus fabricii*) (Hammill and Stenson 2000, Haug et al. 2004, 2007, Tucker et al. 2009).

The scientific and common names for hooded seals originate from the males' inflatable sac or "hood" located on top of their nose and their ability to inflate their nasal septum, forming a red balloon that emerges from their left nostril (*Cystophora* = bladder-carrying, *cristata* = crested, Lavigne and Kovacs 1988). They are sexual dimorphic with males measuring about 2.5 meters and weighing on average 250 kg, and females measuring about 2 meters and weighing 190 kg; although, they can weigh up to as much as 450 kg for males and 300 kg for females (Sergeant 1976, Lavigne and Kovacs 1988, Hammill and Stenson 2000, Fig. 1.1).

Figure 1.1: Drawing of a male and female hooded seal (Illustration © Pieter A. Folkens (1989)).

Hooded seals use pack ice as their whelping substrate during a period of 3-4 weeks in March and early April (Sergeant 1974, 1976; Folkow et al. 1996, Hammill and Stenson 2006, Stenson et al. 2006). The combined metabolic demands of lactation and fasting, the polar climate, and the instability of drifting ice during storms favour abbreviation of lactation in phocids that bear young on the pack ice (Bowen et al. 1985). Hooded seals have adapted to these conditions, and have the shortest lactation period known for any mammal (Bowen et al. 1985). They wean their pups after an average of only 4 days and during this short period the pups double their weight (from ~20 kg to ~40 kg; at a rate of ~7 kg per day; Bowen et al. 1985, Iverson et al. 1995, Kovacs and Lavigne 1992, Lydersen et al. 1997). Females do not forage during lactation and lose approximately 10 kg per day while feeding their pups the most energy-rich milk known for any mammal (61% fat; Oftedal et al. 1988, Kovacs and Lavigne 1992). They enter oestrus at the time of weaning, and copulation occurs in the water (Øritsland 1964) before the female leaves the whelping area. Although female hooded seals have high daily energetic costs, their total cost of lactation, relative to body reserves, has been found to be substantially less than in other phocids (Mellish et al. 1999).

Large body size is important to the breeding success of polygamous hooded seal males (Boness et al. 1988, Kovacs 1990). The short nursing period but extended breeding period enable males to secure multiple mates, and they fight, both on ice and in the water to gain and maintain proximity to a female (Kovacs 1990). Kovacs (1990) hypothesised that a male could attend three or more mother pup pairs during the breeding period, during which time they lose approximately 2.5 kg per day (Kovacs et al. 1996). This weight loss is similar to other pinniped species, such as the harbour seal (*Phoca vitulina*) (Coltman et al. 1998) and the grey seal (*Halichoerus grypus*) (Lidgard et al. 2005).

Many phocids reduce or cease to forage during the moult, and this period is considered to be an energetically expensive period (e.g., harbour seals, (Paterson et al. 2012), grey seals, (Boily 1996), southern elephant seals (*Mirounga leonina*; Boyd et al. 1993, Hindell et al. 1994)). Hooded seals moult during July (Rasmussen 1960; Sergeant 1974, 1976, Folkow et al. 1996) but there are few data on their energy expenditure during this fasting period. However, Rasmussen (1960) reported that the annual moult lasts for approximately one month (time period when the maximum number of animals was present), although the exact time required for an individual to finish the moult is unknown. Thordason et al. (2007) showed that male hooded seals lost 14% of their total body mass between May and August and Rasmussen (1960) reported a reduction in blubber mass ranging from 18-26% in 16-23 days (depending on condition at arrival), although the sex of the seals were not reported. Thordason et al. (2007) further found that hooded seals were in the poorest condition in August, directly after the moult.

Information that can shed light on how the body condition of hooded seals vary in accordance to fasting periods and where these changes occur is important to better understand the locations of critical habitat and their annual energetic budget.

1.5. Tracking methods

Individual animals pursuing their normal movements and activities are naturally difficult to identify in the wild without some form of marking or tagging (Cyr and Nebel 2013). As a solution to this problem, animal ecologists developed telemetry tracking systems in the late 1950s - early 1960s using collars or tags emitting very high frequency (VHF) radio signal pulses (see Clark et al. 2006). However, monitoring wide ranging wild animals was costly, time consuming and often posed risks to personnel safety (Clark et al. 2006). In marine environments, tracking was further complicated by the animals' very large home ranges, deep diving, and the visually obscure nature of aquatic habitats (Cyr and Nebel 2013). With the launch of the Nimbus 3 satellite in 1964 and the Advanced Research and Global Observation Satellite (ARGOS) in 1982, it became possible to automatically collect and transmit location data from widely ranging or migrating animals using satellite communication technology (see examples in Fancy et al. 1988). Since the first successful satellite telemetry tagging in approximately 1970 (e.g., Elk (*Cervus Canadensis*); Craighead et al. 1972), knowledge of the spatial distribution of wide ranging vertebrates has been greatly improved and lead to rapid advancements in the development of more sophisticated tags, especially in the marine environment (e.g., Bograd et al. 2010).

Telemetry can be used to record the animal's position, behaviour, information about physiology and condition and/or send measurements about the animal's environment (Fedak et al. 2002). Marine mammals present one of the most challenging situations for telemetry and effective field study as they spend little time ashore; they spend most of their time at sea, under water; they range over global distances and their streamlined, hydrodynamic shape make attachment of devices difficult (Fedak et al. 2002). In this study, seals were equipped with Satellite Relay Data Loggers (SRDLs). They were glued to the fur at the back of their head or neck where they remained until the next moult. The size of the SRDL is 10.5 x 4 cm and it weighs ~ 370 grams (Fig. 1.2). The potential effects on an animal's normal behaviour must be considered, and a "rule of thumb" for instrumentation dictates that they weigh no more than 2-5% of the animals total body weight (Cochran 1980 as cited in Boehme et al. 2009). The SRDL tag is designed to minimize the hydrodynamic drag and thereby minimize the effect to the animal (Boehme et al. 2009). Assessments of possible adverse effects on elephant seals using similar tags have shown no detectable harm in terms of loss of body mass or survival probability (McMahon et al. 2008).

Figure 1.2: Hooded seals with Satellite Relay Data Loggers (SRDLs) attached to the back of their necks. Left: male in the water after recovery from the tagging procedure. Right: female under sedation directly after the tag was attached (source: Dr. Garry Stenson, Science Branch, Department of Fisheries and Oceans (DFO), Canada).

The SRDLs collect a range of behavioural information about marine mammals at sea that is compressed and transmitted via the global ARGOS satellite system (Fedak et al. 2001, 2002, Service Argos). A transmitter's location is calculated by using the Doppler Effect on transmission frequency and requires at least 3 successive transmissions during a single satellite pass (Service Argos). ARGOS assigns a quality index to each position (Location classes (LC)) that varies between the most common, low-quality locations (Argos classes A, 0, B and Z) and standard-quality animal tracking locations (Argos classes 3, 2 and 1). Positions are reported with a 68th percentile spatial error ranging from 0.5 km - to 10 km (Service Argos). However, variable LCs combined with irregular uplinks can potentially result in large errors of the calculated positions.

The accuracy of the ARGOS locations received from pinnipeds has been examined under a number of conditions (e.g., Vincent et al. 2002, White and Sjöberg 2002, Costa et al. 2010). Costa et al. (2010) found error measurements that were larger than that reported by ARGOS, but they were within the range of other studies on other species. They found that species that make short duration dives and spend extended periods at the surface (e.g., sea lions (*Zalophus* spp.) and fur seals (*Arctocephalus* spp)) had less error than species such as elephant seals (*Mirounga* spp.) that spend more time underwater and have shorter surface intervals (similar to hooded seals). Spatial error can be problematic for many analyses for far ranging species, such as the determination of ARS (Costa et al. 2010). However, filtering techniques remove most of the erroneous positions (e.g., Freitas et al. 2008), and consequently, transmissions from free ranging animals will reflect the general behaviour of the individual (e.g., diving and turning rates) which can be used to make inferences about habitat selection and use.

1.6. Diving capability and foraging success

Satellite telemetry can provide data that make it possible to investigate the diving behaviour and lipid body condition of pinniped species (e.g., Weddell seal (*Leptonychotes weddellii*; Sato et al. 2003), Baikal seal (*Phoca sibirica*; Watanabe et al. 2006), northern elephant seal (*Mirounga angustirostris*; e.g., Crocker et al. 1997, Biuw et al. 2003), southern elephant seal (e.g., Bailleul et al. 2007), grey seal (Beck et al. 2000), harbour seal (*Phoca vitulina*; Baechler et al. 2002), crabeater seal (*Lobodon carcinophaga*; McDonald et al. 2008)).

Air breathing predators in the marine environment face the challenge of feeding underwater while managing their oxygen stores (Kramer 1988). Optimal diving behaviour predicts that breath-hold divers should adjust time allocation within their dives to the distance separating prey from the surface (Kramer 1988). Hooded seals have the highest capability to store oxygen in blood and skeletal muscles measured for any pinniped (Burns et al. 2007) and therefore have the ability to make repeatedly long and deep dives while feeding on bethopelagic prey.

The difference in morphology and reproductive investment in sexual dimorphic species is likely to influence the level of energetic needs for each sex (Mysterud 2000). These differences may be reflected in differing food requirements, foraging strategies and habitat choices (e.g., Mysterud 2000, Breed et al. 2006). Differences in foraging strategies and habitat use have been found for other sexually dimorphic pinnipeds such as grey seals (Beck et al. 2003a; 2003b; 2003c; 2007, Breed et al. 2006), northern elephant seals (Le Boeuf et al. 1993; 2000), southern elephant seals (McIntyre et al. 2010a; 2010b), New Zealand fur seals (*Arctocephalus forsteri*; Page et al. 2005) and hooded seals belonging to the Gulf of St. Lawrence breeding stock (Bajzak et al. 2009). For instance, sexually dimorphic elephant seals have been found to be horizontally and vertically segregated by sex, age and size during foraging migrations in relation to season, temperature, salinity, bathymetry and sea ice cover (e.g., Le Boeuf et al. 1993; 2000, Field et al. 2005, Bailleul et al. 2007, McIntyre et al. 2010a; 2010b, Muelbert et al. 2013). Although there is some variability between populations and season (summer or winter foraging migrations), adult males have been found to spend extended periods of time foraging on the continental margin, carrying out benthic dives where they are assumed to forage on demersal prey items (Le Boeuf et al. 1993; 2000, Hindell et al. 1991, Campagna et al. 1999). In comparison, adult females are normally found to range across a wider area offshore or at the outer margins of the sea ice, where they are thought to forage pelagically on vertically migrating prey (Le Boeuf et al. 1993; 2000, Hindell et al. 1991, Campagna et al. 1995).

Male and female hooded seals in the Gulf of St. Lawrence have been found to be vertically segregated during the post-breeding/pre-moult period, foraging at different depths (Bajzak et al. 2009). Males were found to dive deeper post-breeding, and females dived deeper pre-moult (Bajzak et al. 2009).

Spatial and temporal separation of foraging, reproduction and moulting result in large seasonal changes in the seals' body mass and composition (e.g., Beck et al. 2000, Sparling et al. 2006, Aoki et al. 2011). In order to ensure sufficient energy during periods of reduced energy intake (i.e., the moult and breeding seasons), seals store energy obtained at other times of the year, primarily as blubber. This change in body fat over time results in a change in buoyancy during dives (e.g., Beck et al. 2000, Bailleul et al. 2007, Biuw et al. 2003; 2007, Mitani et al. 2010, Aoki et al. 2011). Buoyancy is determined by the ratio of lipid to lean body tissue and by the mass of the individual, where lipid tissue is positively buoyant and lean tissue is negatively buoyant (Beck et al. 2000, Biuw et al. 2003). Mass affects buoyancy since the force of gravity is related to the mass of an object (Beck et al. 2000). The buoyancy of free diving seals can be measured through the investigation of drift dives, which is a dive type described as drifting passively through the water column (Le Boeuf et al. 1993, Crocker et al. 1997, Biuw et al. 2003, Mitani et al. 2010). The vertical drift rate is related to the body condition of the animal where a fatter seal (i.e., higher ration of lipids) will "sink" more slowly than a thin seal (Le Boeuf et al. 1993, Crocker et al. 1997, Biuw et al. 2003, Mitani et al. 2010). This means that a higher drift rate (faster speed) reflects a thinner seal (or a seal investing energy intake in building lean tissue) and vice versa. By analysing diving data, drift rates can be measured continuously along a seal track and the daily change in drift rates can be used to identify spatial and temporal patterns of feeding success (e.g., Bailleul et al. 2007, Biuw et al. 2007, Thums et al. 2008, Robinson et al. 2010).

1.7. Annual distribution patterns:

Information on the spatial locations of successful foraging habitat can provide information on how animals interact with their environment, identify critical habitat for the species and offer insight in the distribution of their prey. Hooded seals' wide ranging, pelagic behaviour makes them unavailable for direct observation during migrations, so little is known about their spatial distribution throughout the year. Historical knowledge of hooded seal distribution and movement patterns was based primarily on direct observation (mostly by Inuit along the coastal areas) and catch diaries from annual hunts (Allen 1880, Rasmussen 1960). However, since the 1950s, data from coded flipper tags have provided information on seasonal movements (9500 hooded seals tagged in 1951-1992; reviewed in Kapel 1996). Although the results were biased by a high representation from the hunt, they still revealed that the North Atlantic hooded seals were divided into two separate stocks. The two stocks inhabit different geographical areas during most of the year (west or east of Greenland) and are managed separately. Seals whelping and breeding near Jan Mayen ("West Ice") constitute the Northeast (NE) Atlantic or Greenland Sea population while hooded seals whelping and breeding in Davis Strait, Gulf of St. Lawrence (the "Gulf") and off southern Labrador and/or northern Newfoundland (the "Front") belong to the Northwest (NW) Atlantic population (Anonymous 2006a, Fig. 1.3). The total NW Atlantic population has been estimated at approximately 600,000 animals (593,500 SE=67,200; Hammill and Stenson 2006), of which 90% are estimated to whelp at the Front (Stenson et al. 2006). The population abundance of the Greenland Sea indicates that there has been a steady decrease in numbers over the last 60 years (ICES 2011). The most current assessment from 2011 reports a population size of 85,000 - 106,000 animals which is only 10-15% of the population level observed 60 years ago (ICES 2011).

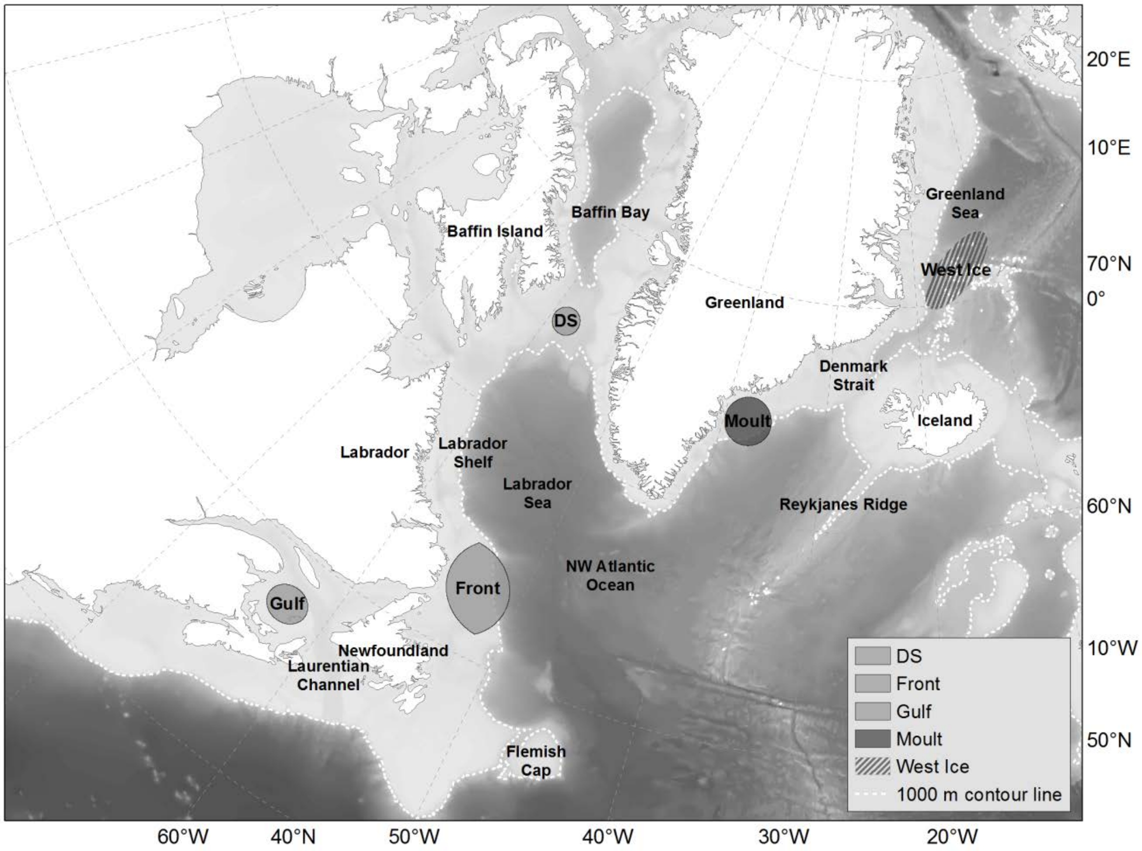

Fig. 1.3: Map of the study area: moulting area for the NW Atlantic stock in southeast (SE) Greenland (dark grey) and breeding areas in Davis Strait (DS), the Front and the Gulf (grey). The “West Ice” indicates the main moulting/breeding area for the Greenland Sea stock. Bathymetry of the study area is presented as backdrop in grey scale. Dashed white line is the 1000 m contour.

The NW Atlantic stock moults off the southeast (SE) coast of Greenland in the general area of the Denmark Strait each July while the Greenland Sea stock moults off northeast Greenland (Øritsland 1959, Rasmussen 1960, Sergeant 1974; 1976, Folkow and Blix 1996). Although these stocks are considered to belong to two putative populations for management purposes (Hammill and Stenson 2006), comparison of morphometric data (Wiig and Lie 1984) and genetic analyses (Coltman et al. 2007, Sundt et al. 1994) suggest that they are one panmitic population. Hooded seals appear to have recolonised much of their range relatively recently after the last glacial period and have had either insufficient time or sufficient gene flow and population mixing for genetic differentiation to occur (Coltman et al. 2007).

The distribution of NW Atlantic hooded seals outside of the whelping and moulting periods is poorly understood. The general hypothesis has been that most of the NW Atlantic population disperses across the NW Atlantic (southern limit being the Scotian shelf) and up to Davis Strait and Baffin Bay before migrating southward to the whelping areas (e.g., Øritsland 1959, Rasmussen 1960, Sergeant 1976). A recent satellite telemetry study has described the movement of hooded seals during the post-breeding/pre-moult period (March-July) (Bajzak et al 2009, Anonymous 2006b). Hooded seals breeding in the Gulf spend time in the Laurentian Channel for a period of 1-2 months before migrating to the moulting grounds, while Front breeding animals have been found to be more variable in their movement patterns (Bajzak et al 2009, Anonymous 2006b). After breeding, most seals remained in Newfoundland waters, dispersing along the Grand Banks and Flemish Cap, as well as along the southern part of the Labrador Shelf, before heading towards SE Greenland in June to moult (Anonymous 2006b).

Juvenile hooded seals have been reported to wander long distances outside their normal distribution area. They have been observed as far south as the Caribbean (sightings reviewed in Mignucci-Giannonni and Odell 2001) while infrequent sightings have been reported around the Canadian Arctic and a few animals have made it all the way through the Northwest Passage to the Beaufort Sea and even as far south in the Pacific Ocean as outside San Diego (Burns and Gavin 1980, Lavigne and Kovacs 1988, Dudley 1991). They may also wander east into the Barents Sea (Stenson pers. com.).

1.8. Rationale

Five basic principles form the base for fundamental questions asked in ecology: 1) all organisms consume resources, 2) all organisms require space in which to live, 3) all organisms interact, at some scale in space and time, with individuals of the same, and other, species, 4) all organisms live in dynamic environments that vary across scales in space and time and, 5) all organisms strive to copy their genes (Morris 2003). This thesis addresses the first four topics through the investigation of hooded seal movement, habitat selection, sexual and age related segregation and foraging success in relation to important life history events such as whelping/breeding and moulting. By investigating these central questions, we can gain insight into the biological patterns and structure of ecological systems occupied by hooded seals during their annual migration. This new information is important in developing hooded seal management and conservation policies, particularly when a changing environment is restricting their optimal habitat.

1.9. Thesis Overview

The thesis objective is to obtain new understanding about how large marine predators may select their habitat. I use Geographic Information Systems (GIS) and existing spatial data to sample environmental factors (e.g., bottom depth, bottom topography, sea surface temperature (SST), ice concentration and productivity) that may be of importance to hooded seals' habitat selection. I apply environmental data, data on diving behaviour and FPT to develop multiple statistical habitat models. Model selection is used to understand what inferences the data support, and to select between competing models.

Because little was known about the post-moult/pre-breeding migration period; I begin by describing the geographic movement patterns for 21 hooded seals tagged directly after the moult (*Chapter 2*). This is a period that lasts for seven months from August – February (*Chapter 2*).

I continue to investigate the annual habitat selection by hooded seals in relation to oceanographic and environmental variables using a combined approach of FPT and GAMs (*Chapter 3*). In order to investigate the diving behaviour within the high use areas of assumed foraging (i.e., long FPT) identified in Chapter 3, diving behaviour along the migration tracks is analysed in relation to additional habitat variables, applying similar models to that in Chapter 3, to explain habitat selection and use in more detail (*Chapter 4*).

Chapters 2-4 identify and describe areas where seals spend extended periods of time. In Chapter 5, I test the hypothesis that these locations overlap with areas where the seals experience an improved lipid body condition (increased buoyancy). I also explore the annual spatial and temporal fluctuations in lipid body condition in relation to reproduction and moulting. Chapter 6 is a summary where I revisit and briefly discuss some of the main findings within the thesis.

The sample sizes will differ between chapters due to the datasets used (diagnostic or diving) and if juveniles were included or not. The diagnostic dataset provided sufficient data for 32 females, 17 males and 16 juveniles (*Chapter 3*), of which chapter 2 included individuals tagged during the moult (July) and consisted of data from 21 seals (9 females, 8 males and 4 juveniles). The dataset containing the dive files provided sufficient data for 33 females and 18 males. No juveniles were included in these analyses (*Chapter 4 and 5*).

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CO-AUTHORSHIP STATEMENT

The following four manuscripts/chapters of this thesis were all co-authored by Dr. Garry Stenson (DFO), Dr. Yolanda F. Wiersma (Memorial University), Dr. Mike Hammill (DFO) and Dr. Aqqulu Rosing-Asvid (Greenland Institute of Natural Resources). Chapters 3, 4 and 5 were also co-authored by Dr. Mette Skern-Mauritzen (IMR), and Chapters 4 and 5 also included Dr. Lars Boehme (Scottish Oceans Institute) as a co-author. I was the principal contributor to the ideas for, and execution of, data analyses as well as manuscript preparation for all chapters of the thesis. Garry Stenson, Mike Hammill and Aqqulu Rosing-Asvid contributed design and implementation of hooded seal data collection, ecological knowledge of hooded seals in the North West Atlantic Ocean and constructive feedback regarding project design and manuscript drafts. Yolanda Wiersma and Garry Stenson provided critical support in the form of research guidance, throughout the process from initial design through to manuscript completion. This includes contributions towards ideas and research questions and constructive feedback at all levels of the work during the manuscript writing process. Dr. Skern-Mauritzen provided critical support with data extraction and modelling, as well as valuable support in terms of research guidance. Dr. Boehme provided valuable discussion as well as data extraction and some handling in relation to the dive data. All co-authors provided constructive feedback on manuscript drafts.

All chapters are written for publication; chapters 2 and 3 are already published (in the Journal of Northwest Atlantic Fishery Science and the ICES Journal of Marine Science respectively), however the versions printed here contain some differences compared to the published versions. In Chapter 2 the changes are minor changes of wording, while Chapter 3 contains some new analyses which have resulted in changes to the text as well as figures. Chapters 4 and 5 are in review at PLOS One and will probably, after revisions, change somewhat compared to the versions printed here. Thus, there will be some repetition of information between chapters, as well as slight differences in style and format to meet individual journal guidelines.

CHAPTER 2: Movement patterns of hooded seals (*Cystophora cristata*) in the Northwest Atlantic Ocean during the post-moult and pre-breeding seasons

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2.1. ABSTRACT

Movement patterns of hooded seals (*Cystophora cristata*) in the Northwest Atlantic in the period following moulting and prior to breeding are not well known. Here, we describe the movement patterns of 21 seals for this period based on information gathered from Satellite Relay Data Loggers (SRDLs). This study provides important baseline information necessary to understand the ecological requirements and patterns in habitat selection for the species. Adult and sub-adult hooded seals were tagged with SRDLs directly after moulting in Southeast Greenland during July 2004, 2005 and 2007. Due to variation in the date of tagging and arrival date to the breeding grounds, data between Aug 1st – Feb 28th were used which gave all seals a track duration of 211 days (212 in 2005) except for one juvenile where the tag lasted for only 154 days. The tags yielded 36,107 locations (mean = 1719.4 ± 410.6). Although there was individual variation between seal trajectories during migration, the population shared a similar overall pattern of distribution. After moulting in July individuals travelled along the continental shelf to Davis Strait and Baffin Bay, thereafter moving southwards along the Labrador shelf until they arrived at the breeding grounds by March. Females tended to transit the Labrador Sea and arrived at the Labrador shelf before travelling up to the Baffin Bay area, while males travelled via the western Greenland Shelf. The majority of the seals were Front breeders (off Newfoundland and Southern Labrador) arriving there by March, although a few of the tagged seals may have belonged to the Davis Strait breeding population and one male belonged to the Gulf of St. Lawrence breeding population. Seven seals migrated east after the moult and might have overlapped with the Greenland Sea population. This would support the theory of a panmitic population structure.

Keywords: Hooded seals; *Cystophora cristata*; distribution; movement patterns; Northwest Atlantic Ocean

2.2. INTRODUCTION

The hooded seal (*Cystophora cristata*) is an abundant, pelagic, deep-diving pinniped distributed throughout the North Atlantic and adjacent Arctic Oceans (Sergeant, 1974; Folkow and Blix 1995, 1999; Hammill and Stenson, 2006). They breed synchronously during mid-to late March on the pack ice around Jan Mayen ("West Ice"), in Davis Strait between Baffin Island and western Greenland, in the Gulf of St. Lawrence (the "Gulf") and off southern Labrador and/or northern Newfoundland (the "Front") (Fig. 2.1) (Sergeant, 1974, 1976; Hammill, 1993; Folkow *et al.,* 1996). These four breeding herds are considered to belong to two putative populations (Hammill and Stenson, 2006). Hooded seals whelping near Jan Mayen are thought to constitute the population belonging to the Northeast (NE) Atlantic, known as the Greenland Sea population, while hooded seals whelping and breeding in Davis Strait, the Gulf and at the Front are all thought to belong to the Northwest (NW) Atlantic population (Hammill and Stenson, 2006). The total NW Atlantic population has been estimated to consist of approximately 600,000 animals (593,500 SE=67,200, Hammill and Stenson, 2006), of which 90% are estimated to whelp at the Front (Stenson *et al.,* 2006). The Greenland Sea population is likely to number between 70,000 and 90,000 animals, although there is considerable uncertainty around these estimates (Anonymous, 2006).

Coltman *et al.,* (2007) carried out a genetics study of the two populations and found that the Greenland Sea breeding herd was genetically most distant from the NW Atlantic breeding areas; however, the difference was statistically non-significant. The results indicated that the world's hooded seals belong to a single panmitic genetic population, thereby suggesting that there is some overlap in distribution between the

Greenland Sea and the NW Atlantic populations. The Greenland Sea herd, whelping around Jan Mayen, disperses to sea after breeding in March and some individuals return to the pack ice in the same area in July to moult (Øritsland, 1959; Rasmussen, 1960), while the majority moult further north (Folkow *et al.,* 1996). Following breeding, NW Atlantic hooded seals leave the whelping areas to feed and eventually migrate to the ice off southeast (SE) Greenland where they moult in July (Stenson*, unpublished data*; Sergeant, 1974). After moulting, the general hypothesis has been that most of these animals disperse across the NW Atlantic and up to Davis Strait (Rasmussen, 1960) before migrating southward to the whelping areas.

Preliminary studies have indicated that hooded seals spend much of their time along the edges of the Canadian and Greenland continental shelves or sea mounts (e.g., Flemish Cap, Reykjanes Ridge) where they dive to depths of over 1,500 m (Stenson *et al., unpublished data*). Due to their pelagic distribution and the lack of knowledge regarding their prey selection at various times of the year, the extent of their fish consumption is difficult to assess (Folkow *et al.,* 1996). However, diet studies indicate that adult hooded seals forage mainly on benthopelagic species (Ross, 1992; Hammill and Stenson, 2000; Haug *et al.,* 2007). To a great extent, the role of hooded seals in the marine ecosystem is virtually unknown. However, satellite telemetry allows us to monitor movements of free ranging pinnipeds throughout the year, providing data that have previously been difficult to obtain.

Data from satellite tags provide us with valuable knowledge of the general movement pattern for hooded seals during the post-moult and pre-breeding period, which has not been possible to obtain previously. Historical information on marine mammal distributions was provided by shore-based observations, incidental observations from commercial hunting and capture of branded or tagged individuals (Rasmussen, 1960; Sergeant, 1974, 1979; Hammill and Stenson, 2006). Although useful, these observations provide more information about the observer effort then the actual distribution of the animals. Satellite telemetry is therefore very valuable in terms of providing distribution information throughout the year which can be projected onto a population level. Here the movement patterns of 21 seals equipped with satellite transmitters were examined during the post-moult and pre-breeding period (July-March).

2.3. METHODS

Adult and sub-adult hooded seals were tagged with Satellite Relay Data Loggers (SRDLs) directly after moulting in July in SE Greenland (2004, 2005 and 2007; Fig. 2.1) (approx. 65°N, 37°W). The animals were captured using a net, weighed, and tranquilized using tiletamine hydrochloride and zolazepam hydrochloride (Telazol, AH. Robins Company, Richmond, VZ, USA) administered intramuscularly ($1 \mathrm{mg} \cdot \mathrm{kg}_{(\mathrm{body\ mass})}^{-1}$). The SRDLs were designed by the Sea Mammal Research Unit (SMRU) in St. Andrews, Scotland, and collect a range of behavioural information about marine mammals at sea which is compressed and transmitted via the ARGOS satellite system (Fedak et al. 2001, 2002, CLS/Service Argos). The data used for this study included the diagnostic information provided by Argos, along with the spatial location of the seal and a time/date stamp for each transmission. Transmissions were attempted every 80 seconds when the seal was surfacing. The transmitters were attached to the head or neck of the seal, using quick drying epoxy glue (Cure 5, Industrial Formulators of Canada Ltd. Burnaby, BC Canada) and the seals were released immediately upon recovery from the tranquilizer. The tag may last up to a year, and is lost when the seal moults.

2.3.1 Seal Locations

Locations at the surface were determined by the Argos system, and subsequently filtered to remove outliers by using an algorithm based on the travelling speed of the tracked animal, distance between successive locations and turning angle (Freitas *et al.* 2008). We used a maximum swim speed of 2 m/s between successive locations which was similar to that used for grey seals (Austin et al. 2003).

Distribution maps were created using ArcGIS 9.3 (Environmental Systems Research Institute, Redlands, CA) where the points are represented by filtered locations of seal transmissions at the surface throughout their migration. Kernel density maps (20 km resolution) were created using the package "spatstat" in R (version 2.8.0, The R Foundation for Statistical Computing) and are based on the total number of filtered locations. These density plots are created using an isotropic Gaussian kernel to create smoothed histograms where "sigma" determines the bandwidth of the kernel. Narrower bandwidths yield more extreme density values and broader bandwidths narrow the interquartile range. The bandwidth used for this study was a sigma value of 0.75. The darker areas of figures represent locations where the presence of seals caused a higher number of transmissions indicating more time spent in those areas. Due to different tag dates and arrival to the breeding ground, the study period was selected to run from 1 August to 28 February.

2.4. RESULTS

A total of 26 seals with a post-moulting body mass (BM) range of 73.5-194 kg were caught at approximately at 65°N, 37°W in SE Greenland in July 2004, 2005 and 2007. Of the 26 seals tagged, 5 were excluded due to tag malfunction within one month of the actual tag date, yielding a sample size of 21 seals (9 adult females, 8 adult males and 4 juveniles (3 females and 1 male), 2004: n = 5, 2005: n = 13 and 2007: n = 3). Data on the individual seals are presented in Table 2.1 together with individual tagging locations. Figure 2.2 presents combined tracks for the entire study period. One tag transmitted for 154 days, whereas the rest lasted the entire study period (18 tags = 211 days, 2 tags = 212 days (2005)). The tags had a combined transmission period of 4,376 days and provided (after filtering) 36,107 location fixes, (SD = 411), for an average number of 173 locations each day per seal. The mean total travel distance throughout the period was 14,142 ± 2,039 km.

The majority of the seals (15) fanned out quite widely once they left the moulting grounds in southern Greenland, but in similar directions (across the Labrador Sea) (Fig. 2.3). Females moved across the Labrador Sea to the Labrador Shelf and Front area, while males chose a more direct route up to the Davis Strait and Baffin Bay area along the continental shelf off western Greenland. Seven animals stayed behind in Greenland for a longer period of time: one female juvenile (#44443) stayed in the moulting area throughout the migration period apart from a few shorter trips along the SE Greenland coast and into the Denmark Strait. This female did not migrate to the breeding areas. A young male (#44487) stayed behind in the moulting areas until November, at which point he started to move south, crossing the Labrador Sea towards the Front in December. The signal was lost on January 3rd 2005 when the male was mid basin. Female #44488 moved northeast into the Denmark Strait and did not migrate across the Labrador Sea towards the Front until December. This female then stayed in the Front area until breeding. Male #44489 was the only seal to head straight northeast through the Denmark Strait following the Greenland shelf all the way up to the area off Danmark Havn (~ 75º7`N, 13º3`W). This male increased travel speed in October when it moved south across the Labrador Sea to the Front. Male #44503 migrated north following the same pattern as #44489, but turned around and migrated south of Iceland, along the Faeroe-Iceland ridge and back on the north side of Iceland, ending up in the Denmark Strait by the end of February. Male #49537 stayed in the moulting area until February when it abruptly migrated to the Front. Only one of the tagged seals was a Gulf breeder (#49540) and was the only male to cross the Labrador Sea to the Front after moulting before travelling northwards along the continental shelf area. This seal returned to the Front by the end of November and from there travelled to the south of Newfoundland and arrived in the Gulf of St. Lawrence by the end of December. Males #44450 and #44419 ended up in Davis Strait by the end of February indicating that they were either not breeding or they may have belonged to the Davis Strait breeding herd.

Although the seals spread out in various directions in August, 15 of them gathered in Baffin Bay and Davis Strait by October and November (Fig. 2.3). The Labrador shelf, the Front and SE Greenland may also be important habitat locations for this species based on movement- and kernel density patterns (Fig. 2.4 and Fig. 2.5).

2.5. DISCUSSION

This study is the first to illustrate the movement patterns of the NW Atlantic hooded seals during their post-moult, pre-breeding migration. To date, there has been limited information about the annual migration of this species, but this study reveals that they travel large distances during this time. Although there is variation based on the individual and by sex in trajectories chosen, the overall picture of how these animals move throughout the NW Atlantic seem to be similar throughout the population. This differs somewhat to Folkow *et al.*'s (1996) findings for the Greenland Sea population's migration pattern. They found that the migrations to distant waters by these seals were not synchronized in time, and that they did not display a general seasonal migration pattern (Folkow *et al.,* 1996). However, individuals within the NW Atlantic population did demonstrate similarities in habitat selection, and there was general synchrony, with some individual variation. The seals all started their migration after their annual moult and seemed to travel in various directions. However, most of them start to gather along the continental shelf, Davis Strait and in Baffin Bay in September (Fig. 2.3), presumably for feeding as this is an important period for them to put on weight after the moult and prepare themselves for the whelping and breeding season. The choice of habitat appear to be closely related to areas of high topographic relief as the seals tend to stay close to the 1,000m contour line along the Labrador shelf area as well as in the Baffin Bay basin. Baffin Bay and the eastern Canadian High Arctic have a complex coastline, an influx of warm Atlantic water along the West Greenland coast, and a restricted opening to the polar basin through Robeson Channel (Heide-Jørgensen and Laidre, 2004) in the north. This results in numerous microhabitats in the region which may result in the high abundance of animals overwintering there (Heide-Jørgensen and Laidre, 2004). Some species which overlap with the range of hooded seals in this area include marine mammals such as beluga (*Delphinapterus leucas*), narwhal (*Monodon monoceros*) and bowhead whales (*Balaena mysticetus*) as well as various species of seabirds (Heide-Jørgensen and Laidre 2004; Laidre *et al.,* 2003, 2004, 2007). There may be some overlap in prey preference between beluga, narwhal and hooded seals (e.g., Greenland halibut (*Reinhardtius hippoglossoides*)) (Richard *et al.,* 1998; Laidre *et al.,* 2004) in these areas. The aspects of how oceanographic processes and prey distribution may drive hooded seal habitat use (including their diving behaviour throughout their migration) will be the subject of future research.

The sinuosity of the tracks and the number of location fixes suggest that areas along the Labrador shelf and the Baffin Bay basin are important habitat, while the Labrador Sea and the west coast of Greenland appear to be areas where the seals move through quickly (Fig. 2.4). Even though the seals may have a wide movement range during certain months (Fig. 2.3), the high-use areas are quite small (Fig. 2.5). Some of the high-use areas could be biased due to a higher number of seals moving through a specific location during the month resulting in a higher number of location fixes point (e.g., Fig. 2.5: August post-moult). It is not expected that hauling out on ice will bias the results too much due to the fact that the tags will stop transmitting if dry for more than 6 hours. By September the seals arrived on the shelf in southern Davis Strait and in the southern Baffin Bay. In October the seals appeared to spend more time in the latter, while the movement range of the seals during that month was very wide (Fig. 2.3). During November the seals displayed a more general use of Baffin Bay and Davis Strait, and they started to move south; by December they were all south of Baffin Bay spending time in Davis Strait and on the Labrador Shelf. This movement may be influenced by the build-up of ice in the area forcing the seals southwards. Another possibility could be due to colder water temperatures forcing prey to deeper depths thereby increasing the cost of feeding.

January appears to be a month when the seals are more localised in their habitat use (Front and in the Davis Strait) which could also be due to ice conditions. In February seals started to move over somewhat longer distances towards the breeding ground, perhaps to obtain a good position for whelping. A high-use area in southern Denmark Strait was caused by one seal's intense use of a small area. This seal did probably not participate in the breeding.

There appears to be a difference between sexes in the initial choice of feeding areas. Females crossed the Labrador Sea and arrived earlier onto the continental shelf area off Labrador (Fig. 2.3, August), while males took a more direct route up to Davis Strait and Baffin Bay. Because the hooded seal is a sexually dimorphic phocid, the different choice in feeding area may be due to different dietary requirements (Hammill and Stenson, 2000) after the moult. Recent studies have shown that although there is an overlap between males and females on a horizontal plane during feeding migrations after the breeding season, they display differences in foraging depths. Females tended to make more shallow dives than males during the post-breeding migration and deeper dives during the pre-moult migration (Bajzak *et al.,* 2009). The feeding behaviour and diving during post-moult and pre-breeding seasons has not yet been investigated; however this study indicates that there is initially less horizontal overlap between sexes during this period.

Two female juveniles (#49539 and #44417) migrated to Baffin Bay by the end of September, moving south with the rest of the animals and ending up at the Front by end of February. They may possibly be first time breeders or they could have left before the breeding started. Female #44486 arrived at the Front by the beginning of February, but migrated back across the Labrador Sea to Cape Farewell by the end of the month, prior to the start of the breeding season. This may have been a detour, or perhaps this female did not breed that year. There is also a possibility that this female continued up to the "West Ice", located in the area around Iceland and Jan Mayen, where the Greenland Sea population breeds in late March (e.g., Øritsland, 1959; Rasmussen, 1960). The seven seals which stayed behind in Greenland for a longer period of time executing migrations up to the Denmark Strait and #44503 who travelled to Faroese waters before ending up back in Denmark Strait by the end of February offers a strong indication that there is an overlap between the two hooded seal populations, as has been suggested in earlier studies (Rasmussen, 1960; Coltman *et al.,* 2007). The Greenland Sea population spends longer periods of time in the Denmark Strait and in the West Ice, and are found to be present in waters off the Faeroe Islands during all months of the year (Folkow *et al.,* 1996). The findings in this study therefore support the genetic study carried out by Coltman *et al.,* (2007), who suggested that North Atlantic hooded seals consists of one panmitic population.

This study provides new and valuable information on the possible locations of important habitat for hooded seals. Further investigation of the telemetry data will include exploring how the physical environment affects hooded seal migrations and their diving behaviour throughout the full year. Such studies will improve our understanding of the role this species plays in the NW Atlantic ecosystem.

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2.8. TABLES

Table 2.1: Year, Argos PTT identification number, sex, body mass (Wt) at tag date, start and end dates for study period, days transmitted and tagging location of Northwest (NW) Atlantic hooded seals.

Year	**PTT #**	**Sex**	**Wt (kg)**	**Start**	**End**	**Days transmitting**	**Latitude tagged**	**Longitude tagged**
2004	44444	F	116	01.aug	28.feb	211	66°15’	34°17’
2004	44487	M	155	01.aug	03.jan	154	66°08’	34°35’
2004	44443	F	85	01.aug	28.feb	211	66°10’	34°27’
2004	44489	M	172	01.aug	28.feb	211	66°09’	34°30’
2004	49539	F	81	01.aug	28.feb	211	66°15’	34°17’
2005	44486	F	112	01.aug	28.feb	211	65°28’	36°13’
2005	44450	M	127	01.aug	28.feb	211	65°31’	36°21’
2005	44448	F	90	01.aug	28.feb	211	65°29’	37°00’
2005	44488	F	138	01.aug	28.feb	211	65°30’	36°19’
2005	49540	M	194	01.aug	28.feb	211	65°31’	36°14’
2005	49530	M	146	01.aug	28.feb	211	65°25’	36°37’
2005	49533	F	138	01.aug	28.feb	211	65°20’	37°03’
2005	49531	F	95	01.aug	28.feb	211	65°20’	37°06’
2005	49537	M	174	01.aug	28.feb	211	65°25’	37°01’
2005	49534	F	117	01.aug	28.feb	211	65°19’	37°11’
2005	49535	F	98	01.aug	28.feb	211	65°19’	37°11’
2005	49529	F	114	01.aug	28.feb	211	65°22’	37°20’
2005	44503	M	109	01.aug	28.feb	211	65°23’	37°22’
2007	44417	F	73.5	01.aug	29.feb	212	65°26’	37°18’
2007	44419	M	97.5	01.aug	29.feb	212	65°23’	37°48’
2007	44425	F	130	01.aug	29.feb	212	65°23’	37°55’

2.9. FIGURES

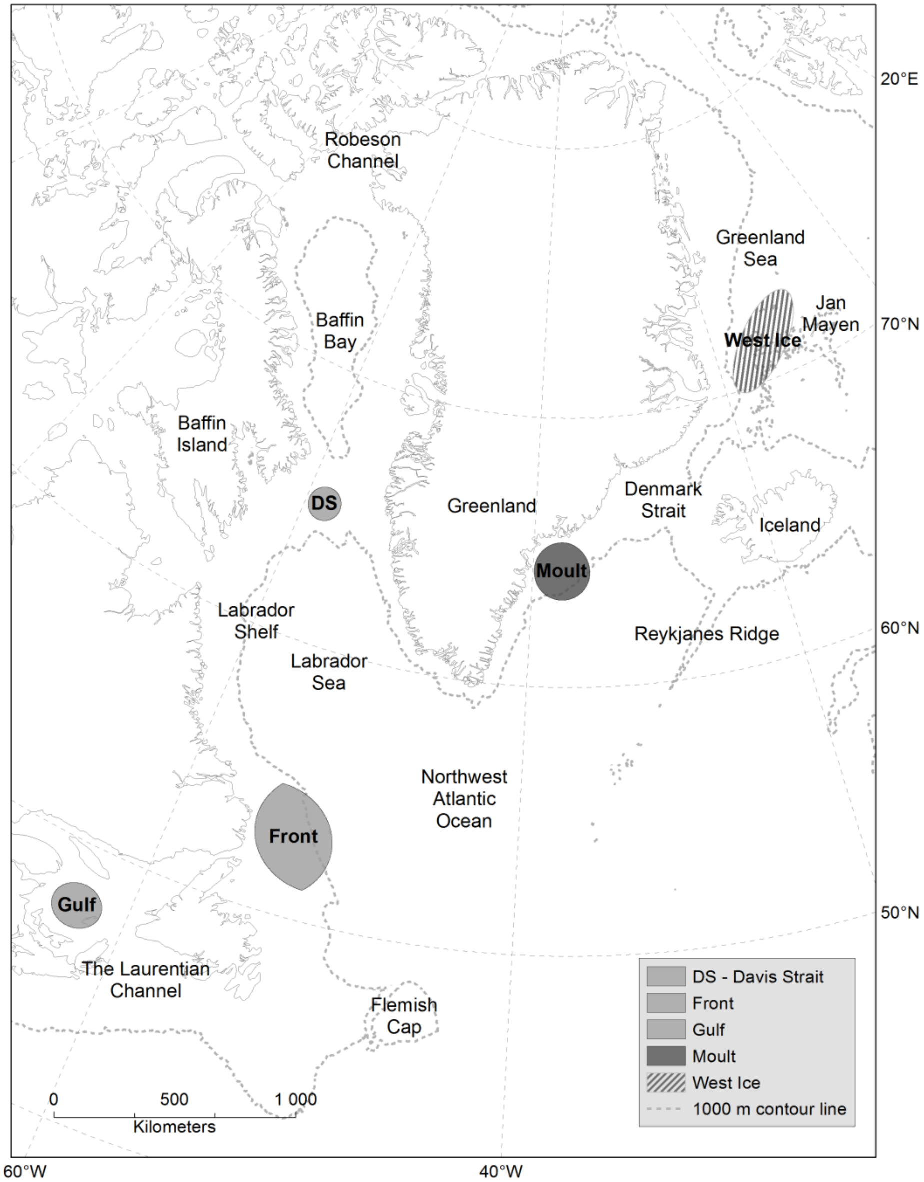

Figure 2.1: Reference map of the Northwest Atlantic Ocean showing place names, breeding locations (light grey colour) and moulting locations (dark grey colour). Dashed grey line represents the 1,000m contour line.

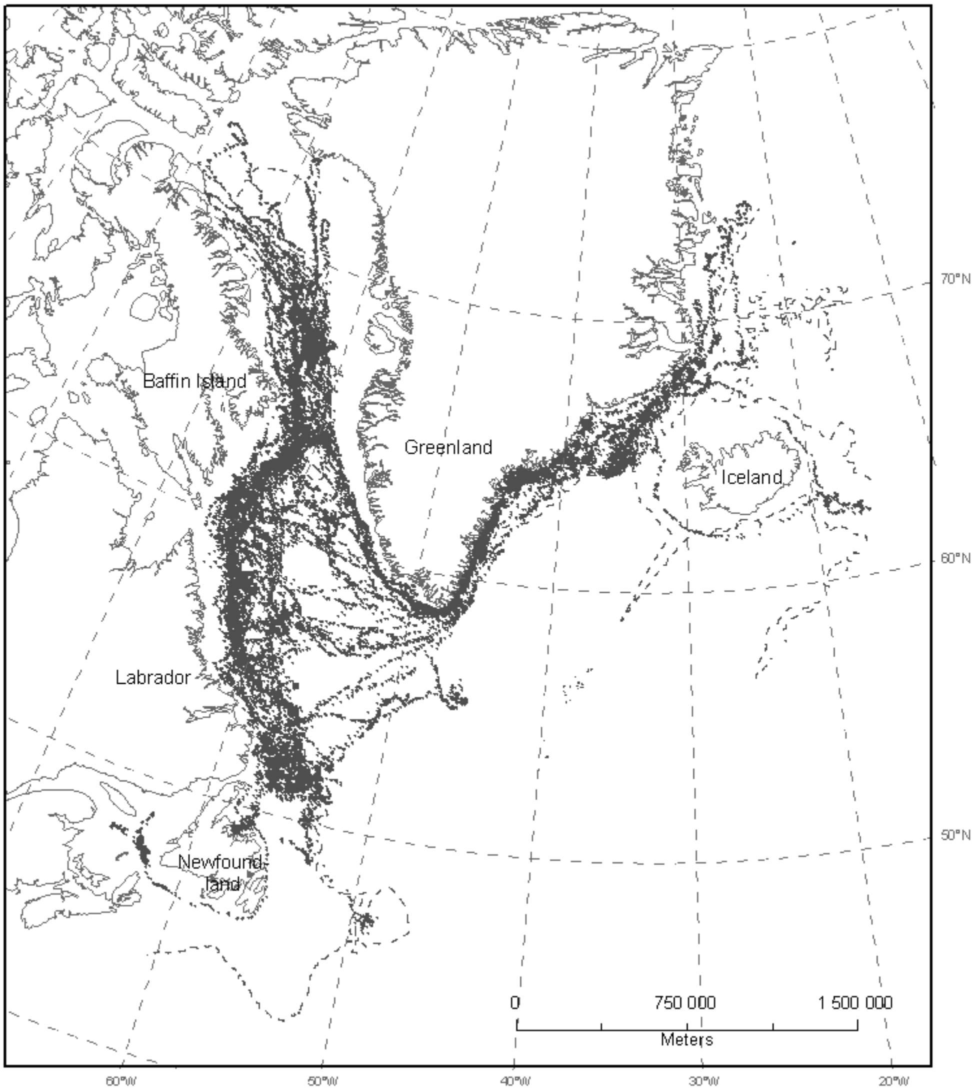

Figure 2.2: All 21 hooded seal tracks (filtered data) during the study period running from August 1st to February 28th which is the post-moult pre-breeding migration period for this species. Dashed contour line represents 1,000 m depth line.

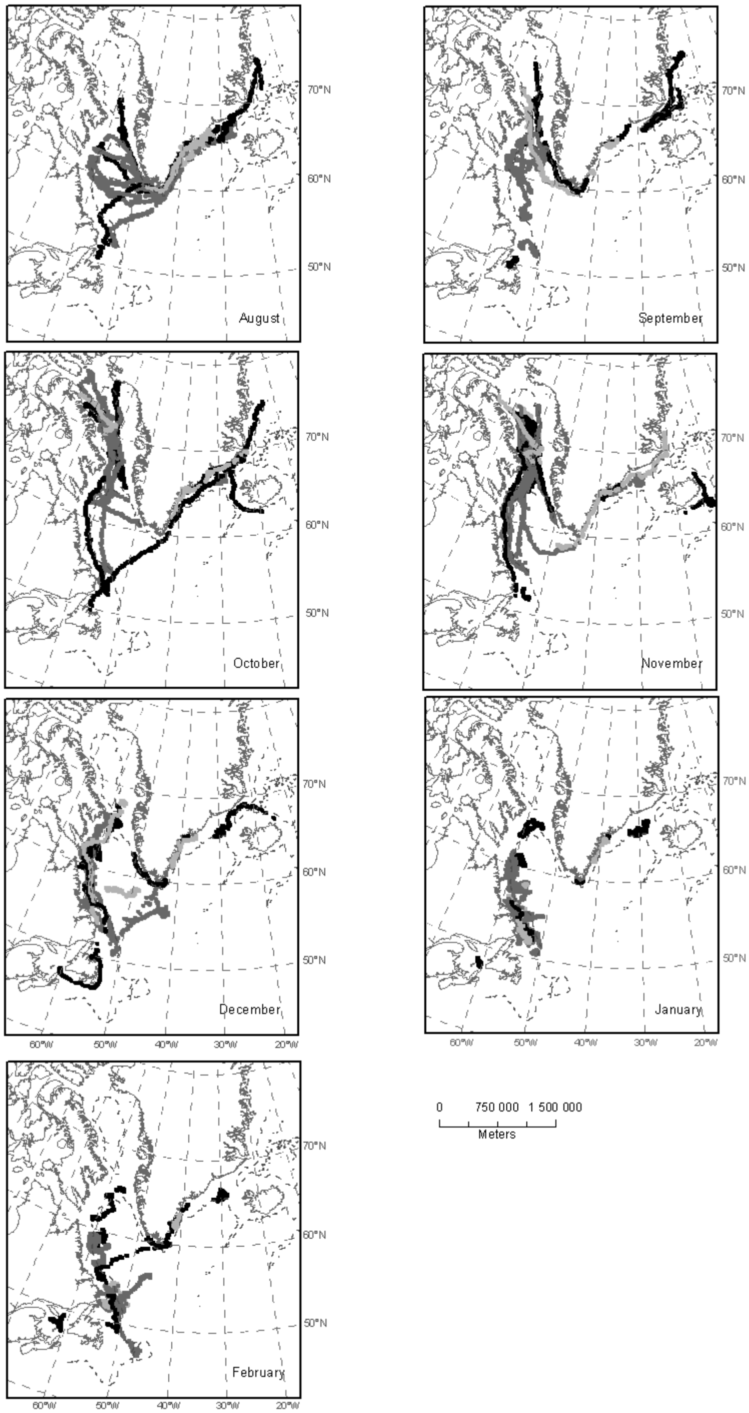

Figure 2.3: Monthly movements of satellite tagged hooded seals based on filtered locations. Juveniles = Light grey symbols, females = dark grey symbols and males = black symbols. Dashed line represents the 1,000 m contour line.

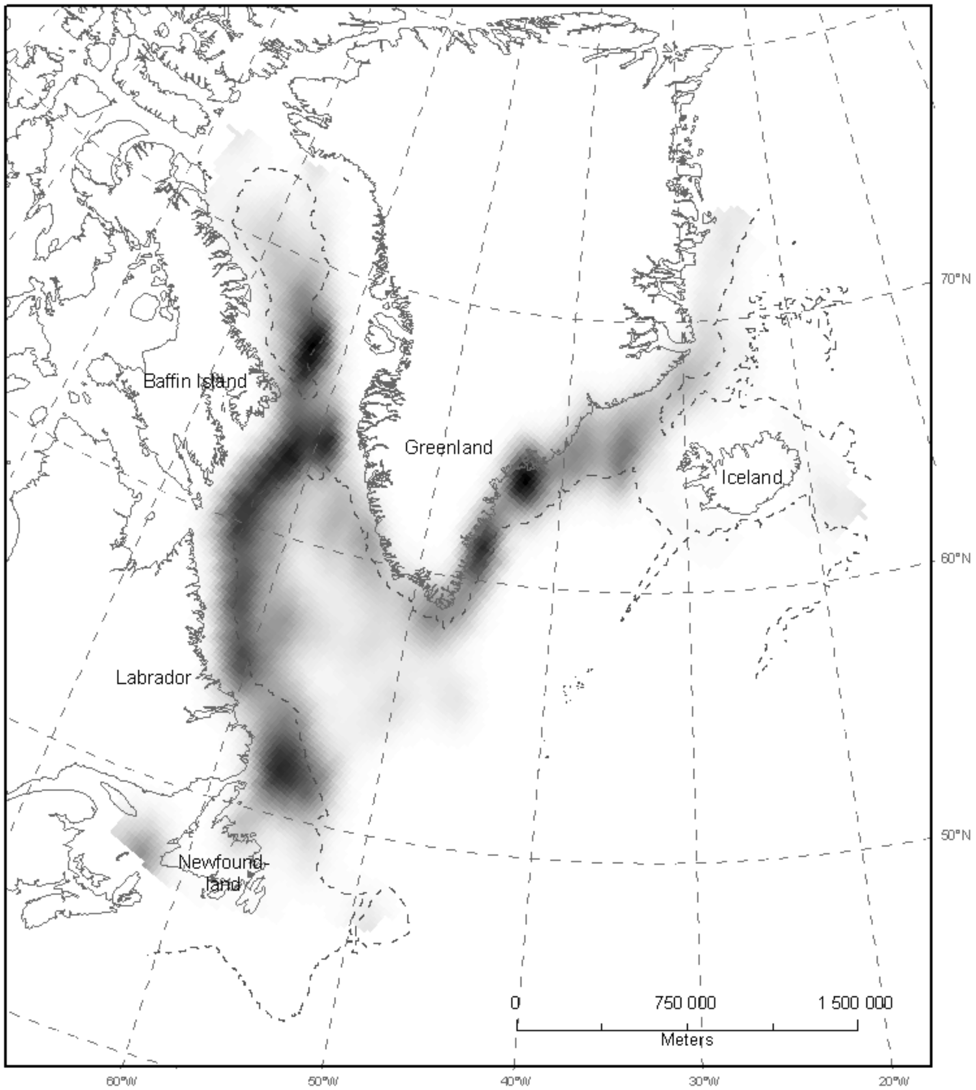

Figure 2.4: Kernel density surface map displaying the areas of high-use by hooded seals in the NW Atlantic Ocean during the full post-moult/pre-breeding migration period based on filtered locations. Dashed line represents the 1,000 m contour line. Resolution is 20 km.

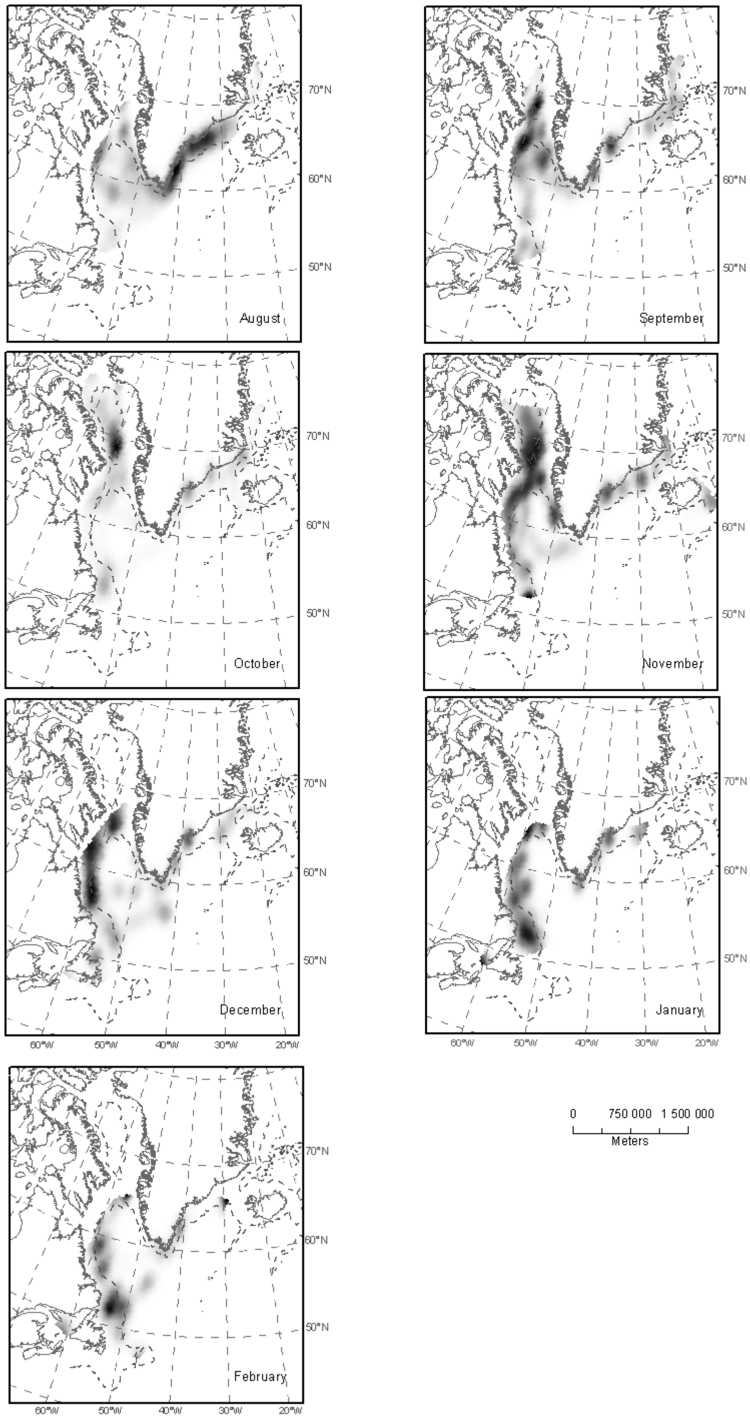

Figure 2.5: Kernel density surface maps displaying areas of high-use by hooded seals in the NW Atlantic Ocean per month during the post-moult/pre-breeding period (August-

February) based on filtered locations. Dashed line represents the 1,000 m contour line. Resolution is 20 km.

CHAPTER 3: Habitat selection by hooded seals (*Cystophora cristata*) in the Northwest Atlantic Ocean

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3.1. ABSTRACT

We examined annual habitat use of 65 hooded seals (32 adult females, 17 adult males, 16 juveniles) equipped with Satellite Relay Data Loggers (SRDLs) in spring or summer across five field seasons (2004-2008). A Generalized Additive Model (GAM) was applied to First Passage Time (FPT) to test for habitat selection in relation to depth, slope of sea floor, ice presence, sea surface temperature (SST) and chlorophyll concentration. Separate models were run on adult males, adult females and juveniles. The results identified SST, depth and chlorophyll as the most important factors influencing habitat selection across all seal groups (males, females and juveniles). Males and females preferred similar habitat conditions, but were separated geographically, and by depth, at various times of the year. Males appeared to be more localized in their habitat use, focusing their movements in areas such as Baffin Bay, Davis Strait and the Flemish Cap, while females concentrated their movements along ridges and shelf areas (e.g., the Labrador Shelf). Juveniles (born in March) spent time in the breeding areas and over the Grand Banks in the spring season, but started to follow a similar migration pattern as the rest of the adult population in the autumn/winter period, spending time in southeast (SE) Greenland, Davis Strait and Baffin Bay as well as on the Labrador Shelf.

Key words: hooded seal, *Cystophora cristata*, habitat use, habitat model, GAM, First Passage Time, sex and age differences, migration

3.2. INTRODUCTION

The hooded seal (*Cystophora cristata*) is an abundant, pelagic, deep-diving pinniped distributed throughout much of the North Atlantic and adjacent Arctic Ocean (Sergeant 1974, Folkow and Blix 1995, 1999, Hammill and Stenson 2006). Two management stocks, the Northwest (NW) Atlantic and Northeast (NE) Atlantic (also known as the Greenland Sea population) have been recognized, although they cannot be distinguished with genetic analyses (Coltman et al. 2007). NW Atlantic hooded seals have an annual migration pattern, with animals breeding in March off southern Labrador and/or the northern Newfoundland coast (The Front), the Gulf of St. Lawrence (The Gulf) and in Davis Strait (Sergeant 1974, 1976, Hammill 1993, Bajzak et al. 2009). They leave the breeding areas in early April to feed, and migrate to Southeast (SE) Greenland by late June early July to moult (Hammill 1993, Kapel 1996, Anon 2006, Fig 3.1). Following the moult, they migrate along the west coast of Greenland over to the Labrador Shelf, Davis Strait and Baffin Bay area where they remain prior to returning to the Newfoundland/Gulf areas in late autumn or early winter (*Chapter 2*).

The NW Atlantic hooded seal population inhabits the waters in marine systems at the border zone between the North Atlantic and the Arctic. These areas are highly dynamic, demonstrating pronounced seasonal and annual variation in ocean climate (e.g., Gulland 1974, Loeng 1991). The ocean environment in the Labrador Sea is influenced by a system subject to nutrient replenishment by some of the deepest mixing in the northern hemisphere, down to 2500 m (Frajka-Williams et al. 2009, Ross and Harrison 2007). Inter-annual variability in water properties and changes in the balance of inflows of fresh water from northern sources and warm, saline waters from the southerly latitudes impact the marine ecosystems of the Labrador region (Frajka-Williams et al. 2009, Ross and Harrison 2007) and Baffin Bay. These dynamics result in numerous microhabitats which, in turn, may result in a high abundance of overwintering animals (Heide-Jørgensen and Laidre 2004).

Habitat can be defined as the conditions and resources present in an area that result in occupancy by an organism (Hall et al. 1997). Habitat selection has been defined as the process where individuals preferentially use, or occupy, a non-random set of variable habitats (Morris 2003). Knowledge of the environmental features affecting habitat selection by animals is important for designing wildlife management and conservation policies (Calenge 2007). Following the groundfish fishery collapse in Atlantic Canada in the 1990s and the lack of recovery of what was historically the most important commercial species, interest into how predation by seals may influence groundfish stocks intensified (Mohn and Bowen 1996, Hammill and Stenson 2000, DFO 2008, 2009). Diet studies indicate that adult hooded seals forage primarily on benthopelagic species (Ross 1992, Anon. 2006, Haug et al. 2007, Tucker et al. 2009), and Hammill and Stenson (2000) estimated that hooded seals accounted for 10% of the combined total annual prey consumption by four common seal species in Atlantic Canada (harp seal (*Pagophilus groenlandicus*), hooded seal, grey seal (*Halichoerus grypus*), and harbour seal (*Phoca vitulina*)). Diet is, however, difficult to assess for free moving, pelagic marine mammals, but by using satellite telemetry to investigate habitat selection one can obtain valuable information about locations where the animals are spending extended periods of time (e.g., Bajzak et al. 2009, Biuw et al. 2007, Breed et al. 2006, Freitas et al. 2008, McIntyre et al. 2011, 2012, Thums et al. 2011). First Passage Time (FPT) is defined as the time it takes an animal to cross a circle of a given size, which is based on the animal's average Area Restricted Search (ARS) scale (Fauchald and Tveraa 2003). Optimal foraging theory predicts that an organism should spend more time in areas where resources are plentiful than in areas where resources are scarce (Fauchald and Tveraa 2003, Charnov 1976). ARS occurs when an animal responds to an abundant food source by slowing down and increasing its turning rate, and the animal will not be expected to continue on a wider ranging search until prey encounter rate decreases (Fauchald 1999, Kareiva and Odell 1987). FPT can therefore be used as a scale-dependent measure of habitat selection and as an indication of feeding effort as search effort can be expected to be higher in habitats of high prey encounter rate.

Being a sexual dimorphic animal (Sergeant 1976, Hammill and Stenson 2000; males: ~250 kg, females: ~190 kg), males and females may be expected to have different dietary needs throughout the annual migration (e.g., Bajzak et al. 2009, Beck et al. 2003, 2007, Breed et al. 2006, McIntyre et al. 2010, Page et al. 2005). Bajzak et al. (2009) found that although male and female adult hooded seals from the Gulf overlapped on a horizontal scale, they were segregated at a vertical scale during the post-breeding migration. A diet study carried out by Tucker at al. (2009) supports these findings by showing that male and female hooded seals forage on different benthopelagic prey. They also found a sexual difference in diet by seasons and geographical areas. These studies suggest that hooded seals segregate as part of a resource partitioning strategy to avoid competition for prey between the sexes, however, there may still be inter-species competition for prey for example with harp seals, beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*) (Richard et al.1998, Laidre et al. 2003, 2004) within important feeding areas for hooded seals.

Here, we hypothesize that hooded seals forage in areas of complex oceanographic conditions (defined by the slope of the sea floor and bottom depth). We expect that if complex seafloor relief concentrates prey, hooded seal movement patterns and long FPT will be associated with the continental shelf, deep basins and sea mounts. Variability in primary productivity and temperature observed at the surface (SST) are often reflected by underlying processes driven, in part, by topography. We therefore expect to see seals concentrate their search effort in areas of high chlorophyll concentrations, indicating highly productive areas, and where SST may be a reflection of optimal temperatures for hooded seal prey. Ice cover is important for hooded seals during whelping/breeding and moulting, but the ice edge is also known to be productive (e.g., Smith and Nelson 1986) and could represent a foraging habitat for this species. If hooded seals are following the ice edge, either for foraging, shelter or rest, we would expect to see seasonal shifts in movement in accordance with changes in ice extent. We predict that movement patterns and habitat use shift northward and southward throughout the annual migration in relation to seasonal changes in weather conditions and oceanographic processes such as ice extent, mixing and productivity. We tested these hypotheses with data obtained from multiple hooded seals of the NW Atlantic population tagged with Satellite Relay Data Loggers (SRDLs) and separated the data into groups of males, females and juveniles to look for segregation by season, age and sex.

3.3. METHODS

3.3.1 Study area

The study area is the NW Atlantic Ocean, extending from the Gulf of St. Lawrence northwards covering most of Baffin Bay, including Davis Strait, to SE Greenland (Fig. 3.1).

3.3.2 Deployment of Satellite Relay Data Loggers (SRDLs)

Satellite transmitters were deployed on 65 seals, of which there were 32 adult females, 17 adult males and 16 juveniles (10 female and 6 male, 11 of these were newborns). Both adult and juvenile hooded seals were captured using a V-shaped pole-net on the ice during July directly after moulting in SE Greenland (2004, 2005 and 2007; approx. 65°N, 37°W) and during March (2004, 2005, 2006 and 2008; approx 49°N, 52°W (the Front) and 46°50´N, 62°W (the Gulf)). They were weighed, and subsequently tranquilized using tiletamine hydrochloride and zolazepam hydrochloride (Telazol, AH. Robins Company, Richmond, VZ, USA) administered intramuscularly ($1\text{mg}\cdot\text{kg}_{(\text{body mass})}^{-1}$). Satellite Relay Data Loggers (SRDLs, Sea Mammal Research Unit (SMRU), St. Andrews, Scotland) were glued to the head or upper neck of the seal, using quick drying epoxy glue (Cure 5, Industrial Formulators of Canada Ltd. Burnaby, BC Canada) before the seals were released. The SRDLs collect a range of behavioural information about marine mammals at sea which is compressed and transmitted via the ARGOS satellite system (Fedak et al. 2001, 2002, CLS/Service Argos). The data used for this study included the diagnostic information provided by Argos, along with the spatial location of the seal and a time/date stamp for each transmission. Transmissions were attempted every

80 seconds when the seal was surfacing. Seal locations were subsequently filtered using an algorithm based on the travelling speed of the tracked animal, distance between successive locations, and turning angle (Freitas et al. 2008). We used a maximum swim speed of 2 m/s between successive locations which was similar to that used for grey seals (Austin et al. 2003).

3.3.3 Seal and habitat data

We used First Passage Time (FPT) and Generalized Additive Models (GAMs) to evaluate habitat preferences. Habitat selection was investigated by evaluating how individual annual movement patterns were associated with environmental variables such as water depth, ice concentration, chlorophyll concentration (primary productivity), SST and slope of the seafloor. The distribution patterns of male, female and juvenile hooded seals were compared to look for differences in habitat preference by sex and age. The year was separated into two periods: spring (April-June = post-breeding/pre-moult period) and autumn/winter (August-February = post-moult/pre-breeding period). March and July were excluded from the analysis as hooded seals spend most of their time during these two months hauled out on the ice for breeding and moulting, respectively.

Oceanographic information (SST and chlorophyll concentrations) was collected via remotely sensed satellite data (8-day composites at 4 km resolution) downloaded from NASA's oceancolor web database (http://oceancolor.gsfc.nasa.gov/). The data were imported to ArcGIS 9.3 and data values were extracted based on filtered seal locations.

Daily ice cover data (25 km resolution) were obtained from the National Snow and Ice Data Center in Colorado (http://nsidc.org/index.html). Depth, slope and the 1,000 m depth contours were derived using bathymetry data from the General Bathymetry Chart of the Ocean (GEBCO, http://www.gebco.net/).

Kernel maps were generated using the package "spatstat" (version 1.21-5; Baddeley and Turner 2005) in R (version 2.11.1, the R Foundation for Statistical Computing). The density plots used a Gaussian kernel to create smoothed histograms where "sigma" determines the bandwidth of the kernel. Extreme values are removed when increasing the bandwith, and this creates a smoother dataset for visual comparison. We used the bandwidth with sigma value 0.75. The kernel maps were then exported to ArcGIS 9.3 (Environmental Systems research Institute, Redlands, CA) and the raster cell resolution was set to 20 km.

First passage Time (FPT) is defined as the time required for an animal to cross a circle of a certain radius, hence, it is a measure of how much time an animal spends in a given area (Fauchald and Tveraa 2003). FPT was calculated using the "adehabitat" package (version 1.8-3; Calenge 2006) in R. By calculating FPT between each location for an animal we can identify the Area Restricted Search (ARS) scale which is the scale the animal focuses its search effort (Kareiva and Odell 1987, Fauchald and Tveraa 2003, 2006). The ARS scale for each seal group and season was derived by plotting a histogram of the variance of FPT vs. the radius, and by extracting the radii at the highest variance of FPT. The difference in sample sizes of seal groups (Table 3.1) was taken into account by employing a bootstrap routine to extract ARS for each group (a set number of individuals per season were randomly selected through 1,000 iterations; 7 in autumn/winter, and 10 in spring). The variance-scale function, and consequently the observed ARS scale, is related to individual foraging patterns and success as well as the spatial distribution of resources (Pinaud and Weimerskirch 2005). The purpose of the FPT is to capture the search effort at each point along the entire movement path (Fauchald and Tveraa 2003, 2006). With location data sampled independently of speed along a path, a larger number of location points will be sampled in areas of low speed compared to areas of high speed (Fauchald and Tveraa 2003). This gives a sampling bias toward search effort. In order to remove this bias, sampling points were made regular in space by spatial interpolation of locations (Fauchald and Tveraa 2003). Data points were placed 500 meters apart along each of the seal tracks and averaged per ARS scale step identified from the FPT, and consequently bootstrap routine, to obtain a trajectory based on the ARS scale. We then calculated the FPT between each new location. FPT at the ARS scale was then related to oceanographic variables using General Additive Models (GAMs).

3.3.4 Statistical analysis: GAM and AIC

We divided the tracks into steps equal to the ARS scale, and estimated the FPT for each step. FPT was used as a response in the GAMs (package "mgcv" in R; Wood 2011) with habitat variables as predictors in order to investigate how FPT was associated with habitat. To take into account individual variability, individual seal id was entered as a random factor using a smooth specifier. The model is given by:

```
gam(y ~ s(x) + s(z) + s(v)….. + s(w,bs="re"))
```

where y is the response variable and x, z, v etc. are the predictor variables.

A GAM can deal with simple random effects, by treating random effects as smooths (Wood 2008). This is implemented in the GAM by s(w, bs = ”re”) where w is the covariate of the smooth (here the individual seal id), bs is a basis penalty smoother, and the "re" class implements simple random effects (Wood 2008). The restricted/residual maximum likelihood estimation (REML) is used to correct for the degrees of freedom when there is an increased number of fixed parameters in the model (Wood 2006, Smyth and Verbyla 1996). It thereby produces an unbiased estimation of the variance parameters (Wood 2006).

The oceanographic habitat variables were log transformed to obtain normal distribution (except ice, which did not improve with transformation). SST was first converted to Kelvin to avoid problems with negative values when log transformed.

To select between competing models we applied an information-theoretic approach and examined parameter weightings using Akaike Information Criterion (AIC). Candidate models with ΔAIC < 2 are considered to have substantial support (Burnham and Anderson 2002) and only these are presented in this paper (full model results are available in supplementary material (Tables A3.4a, b, c)). AIC weights (*w*) per model indicate the weight of evidence that each model is the best approximating model giving the data and the set of candidate models. Parameter weights were calculated by summing the AIC weights for each model that contained the parameter of interest. These range from 0-1, where parameter values closer to 1 indicate higher importance as explanatory variables for hooded seal habitat selection (Burnham and Anderson 2002). Seemingly highly plausible models, with AIC values less than 2 units apart and an unchanged deviance explained, were deemed false, as they contained pretending variables (Anderson 2008). These model weights were removed prior to calculating the AIC weight and parameter weights in order to avoid bias.

The GAM predictive graphs were derived from the best model results and plotted using R. The data were first back transformed, and then the variables were plotted against the predicted mean FPT (days).

3.4. RESULTS

Satellite transmitters were deployed on 65 seals over a period of four years (2004-2008), and the annual coverage by seals per season is presented in Table 3.1. The FPT analysis showed that male and juvenile hooded seals exhibit one ARS scale throughout the year, while females had a smaller search radius during the spring period than the autumn/winter period (Table 3.2). The dataset yielded 4,011 locations based on these calculated search radii.

The kernel maps were created using the modified dataset based on ARS, and we only display FPT (circles) where they spent more than 2 days (based on average FPT at ARS scale; Fig. 3.2). Dark areas signify that the seals have spent time there, but crossed the ARS circle in less than 2 days. Our results showed that females spent shorter periods along the Labrador shelf and at the Reykjanes Ridge area (2-10 days), and longer periods in Greenland when preparing for the moult (>10 days; spring: Fig. 3.2a). Males did not spend much time along the Reykjanes Ridge during spring (Fig. 3.2c) compared to females (Fig. 3.2a). Females and males breeding in the Gulf tend to remain there before heading over to Greenland by July (Fig. 3.2a and c). Following the moult, females spent extended periods of time along the Labrador Shelf area (Fig. 3.2b) while the majority of males travelled to Baffin Bay and Davis Strait (Fig. 3.2d). A few animals remained along the east coast of Greenland prior to the transit across the Labrador Sea in time for breeding (Fig. 3.2b and d). In spring, newborns spent time in the breeding area before heading out to sea for their first migration. This seemed to especially be the case for young born in the Gulf (Fig. 3.2e). In autumn, juveniles started to show a similar migration pattern to adult seals, although they seemed to have a wider distribution pattern (Fig. 3.2f).

3.4.1 Model selection

Our results for model selection consisting of the best or most plausible models (ΔAIC < 2) per seal group and season are presented in Table 3.3. Some of our models were under the influence of pretending variables, and the models in question were removed prior to calculating the parameter weights to avoid bias. All the best models included SST and depth. Chlorophyll was present in all but one (males during the spring period). The ranking of the models' parameter weights are displayed in Table 3.4 and 3.5, and these results are presented below in more detail together with the predicted model results (Fig. 3.3 - 3.7). The model goodness of fit is given by the deviance explained (%) which were low for all models in this analysis (Table 3.3). The plots show the estimated effects as a solid line, and the standard error as thin dashed lines. The confidence of the standard error and the estimated line, at the point where the line passes through zero on the vertical axis, is a result of the identifiability constraints applied to the smooth terms (Wood 2006).

3.4.2 Chlorophyll

Our results suggest that chlorophyll is important in relation to habitat selection by female and juvenile hooded seals during their annual migration, although the AIC weights were highest in spring (Table 3.3). Our models did not identify chlorophyll as an important variable on its own for males during spring, and the parameter weight, calculated from all candidate models, was only 0.310 during this season (Table 3.4). However, chlorophyll was included in the best model for the autumn/winter period, when the findings indicate that males spent less time in areas of higher surface chlorophyll concentration (w_i = 0.744; Tables 3.3 and 3.5; Fig 3.3d). During spring, female and juvenile seals exhibited a decrease in FPT (moving faster) in areas of low concentrations of chlorophyll (0-0.5 mgm^3), and longer FPT from medium to high concentrations of chlorophyll (4 mgm^3-30 mgm^3, Fig. 3.3a, b). In autumn/winter, FPT increased (slowed down) with low chlorophyll concentrations (0.25-0.5 mgm^3) for both these seal groups, where passage time became faster towards the higher end of the range. However, females also slowed down across a slightly higher level of chlorophyll concentration (1-1.75 mgm^3).

3.4.3 Depth

The parameter weights for depth were very high across all categories during spring (females: parameter weight = 1, males: parameter weight = 0.999, juveniles: parameter weight = 0.999; Table 3.4), and during autumn/winter the values were slightly lower for males and females (males: parameter weight = 0.829, females: parameter weight = 0.825, juveniles: parameter weight = 0.991; Table 3.5). The best models identified this as an important variable for all three groups in terms of annual habitat selection (Table 3.3, Fig. 3.4). In spring, males and females slowed down towards 600 m depths, where they had the longest FPT (Fig. 3.4a, b). Juveniles had the longest FPT between depths of 0-600 m, but increased speed (faster FPT) towards 600 m depths (Fig. 3.4c). In autumn/winter, males and females had the longest FPT around 600 m, but females displayed a similar FPT across deeper waters, where males displayed shorter FPTs (Fig. 3.4d, e).The average bottom depth based on all tracks show that females crossed areas with bottom depths 30% deeper than males in spring (1387.17 m (SE = 339.45 m), 947.5 m (SE = 325.83 m), respectively) and 50% deeper than males in autumn/winter (1313.17 m (SE = 339.45 m), 656.43 (SE = 294.12 m), respectively). Juveniles used areas with bottom depths from 750 m, slowing down across deeper depths (Fig. 3.4f).

3.4.4 SST

Temperature at the surface seemed to influence all seals during their annual migration (Table 3.3) and the parameter weights were high for all seal groups in both seasons, except it was not the most important variable for females during the autumn/winter season (Table 3.5). Males and females were associated with a temperature range of -2 to +2°C during the spring season, decreasing FPT (moving faster) towards warmer temperatures (Fig. 3.5a, b). Juveniles used areas within the ranges of -2 - 0°C, also decreasing the time spent in an area as the temperature neared 0°C, however, they exhibited longer FPTs within the temperature range +3 - +9°C (Fig. 3.5c). The results further indicated that the preferred temperatures varied greatly during autumn/winter. Females did not show strong associations in terms of SST, although the results suggested that they displayed longest FPT at a temperature around -1°C (Fig. 3.5d). Males decreased FPT (moving faster) as the temperature neared +3°C, however, they were slowing down at high temperatures (10°C; Fig. 3.5e) Juveniles had the longest FPT in areas around -1°C, which was similar to that of females. (Fig. 3.5f).

3.4.5 Slope

Males and juveniles had a much higher parameter weight for slope during autumn/winter than for spring season (males autumn/winter: parameter weight = 0.744, spring: parameter weight = 0.310, juveniles autumn/winter: parameter weight = 0.881, spring: parameter weight < 0.001; Table 3.4 and 3.5). The predictive graphs did not support this high parameter weight, showing no relationship between FPT and slope in autumn/winter for juveniles, and males seemed to have the longest FPT in areas of 0 - 1 degree slope during the same period (Fig. 3.6b, c). In contrast, females had a much higher weight in the spring season compared to autumn/winter (not part of the best models), although the ranking placed it second to last of all variables for both seasons (spring: parameter weight = 0.999, autumn/winter: parameter weight = 0.124; Table 3.4 and 3.5). The predictive graph showed that females were associated with slopes varying from about 1-11 degrees in spring (Fig. 3.6a)

3.4.6 Ice

Ice was the least significant variable to explain habitat selection for hooded seals (Tables 3.4 and 3.5). However, the predictive graphs describe some association in spring, where females had the longest FPT in areas of 20% ice cover (Fig. 3.7a). We did not have enough data to test juveniles for ice associations during this season. However, the autumn/winter period showed that there was a clear positive association to ice by juveniles where they increased passage time (longer FPT) with increase in ice coverage.

3.5. DISCUSSION

This study supports our hypothesis and earlier findings that, in general, hooded seals are inclined to migrate along, and use the continental shelf and areas of high topographic relief, such as ridges and sea mounts (Folkow et al. 1996, Anon 2006, *Chapter 2*). However, sexually dimorphic animals are often found to differ in habitat use and feeding strategies (e.g., Le Boeuf et al. 1993, Mysterud 2000, Breed et al. 2006, Bailleul et al. 2007, McIntyre et al. 2010) and our results suggest that males and females from the largest part of the NW Atlantic population (Front breeders alone consist of about 90%) are separated on a horizontal scale during the annual migration. Females tended to use the Labrador Shelf more intensively than males, especially in the autumn/winter season (post-moult and pre-breeding; Fig. 3.2b, d) and the Reykjanes Ridge area during spring season (post-breeding and pre-moult; Fig. 3.2a, c). Males used the Baffin Bay and Davis Strait areas more frequently during autumn/winter (Fig. 3.2d), and in spring they spent time in SE Greenland as well as Davis Strait and the Gulf, for those who breed there (Fig. 3.2c). Furthermore, females used areas of 30% deeper bottom depths than males in spring and 50% deeper in autumn/winter. Other sexually dimorphic seals, such as northern elephant seals (*Mirounga angustirostris*, e.g., Le Boeuf et al. 1993, 2000), southern elephant seals (*Mirounga leonina*, e.g., Bailleul et al. 2007, McIntyre et al. 2010) and grey seals (e.g., Breed et al. 2006), share this segregation behaviour where males and females are separated geographically and McIntyre et al. (2010) also found that male southern elephant seals tended to dive in areas with 20% shallower bottom depths than females. In contrast to our findings, Bajzak et al. (2009) found that adult male and female hooded seals tagged in the Gulf of St. Lawrence during the breeding season overlapped geographically. However, they also investigated the diving behaviour and found that they were segregated on the vertical scale, targeting different depths. They suggested that both sexes needed to undergo some replacement of energy resources before undertaking the long migration to SE Greenland, and that the limited extent of the channel slope area in the Gulf and the possible abundance of resources would reduce opportunities for extensive geographic spatial separation. They further hypothesized that vertical segregation between male and female hooded seals could be due to intra-specific competition for prey, or that the larger males feed on larger prey found at deeper depths (Bajzak et al. 2009).

The NW and Greenland Sea hooded seal populations differ in their migration patterns, both on a population level and by sex. In the Greenland Sea population, Folkow et al. (1996) did not find any sexual segregation between males and females, nor did they observe any seasonal movement patterns as seen in the NW Atlantic population (*Chapter 2*). Seals of the Greenland Sea population tend to make unsynchronized, longer feeding trips to sea and return to the ice edge off the east coast of Greenland (Folkow et al. 1996), while the NW Atlantic population embarks on a more or less synchronized annual round-trip with the basin of the Labrador Sea in centre. The differences in migration behaviour between these two populations (and also between Gulf animals and the rest of the NW Atlantic population) may be a reflection of the differential patterns of energy availability within their habitats.

As capital breeders, hooded seals do not feed during nursing and mating (e.g., Houston et al. 2006, Trillmich and Weissing 2006). Females leave the breeding grounds to embark on their feeding migration as soon as they have weaned their pup and mated, while males stay behind to mate with more than one female (Kovacs 1989, Kovacs et al. 1996). Following mating, the seals need to replenish their energy stores and recover from the intensive, but short, lactation period and the period of competition for mates among males. Due to differences in size and the different rate of mass loss during breeding (males ~2.5 kg per day over a 2.5 week period (Kovacs et al. 1996), females: ~10 kg per day over a 4 day period (Kovacs and Lavigne 1992)), males and females may seek to recover using different strategies, either in visiting different geographic locations and/or feeding on different prey items (e.g., Bajzak et al. 2009). Beck et al. (2007) found sex differences in the feeding behaviour of grey seals where, during the post-breeding period (spring), females selected fewer and higher quality prey species than males. This behaviour is consistent with the nutritional-needs hypothesis (NNH) which predicts that when males are much larger than females males should accept a lower diet and habitat quality since high quality items are rare (Mysterud 2000). Tucker et al. (2009) found a significant annual difference in the diets of male and female hooded seals, where males consumed a higher concentration of redfish (*Sebastes* spp.) and Greenland halibut (*Reinhardtius hippoglossoides*) while females consumed a greater percentage of blue hake (*Antimora rostrata*) and white baraccudine (*Arctozenus rissoi)*. They further found a seasonal difference in diet composition where there was a higher composition of capelin (*Mallotus villosus*) and Atlantic argentine (*Argentina silus*) in the pre-breeding period, while the percentage of redfish was much higher in the post-breeding period. This supports our findings regarding the shift in hooded seal distribution patterns within these two seasons. Males spend more time in the breeding areas than females during the spring season (post-breeding and pre-moult), and cross over to SE Greenland and the moulting grounds in a more direct route (Fig 3.2a, c). We found that females leave the breeding area immediately after mating and spend time over the Reykjanes Ridge and the SE Greenland shelf break, which is an area with significant redfish fisheries (ICES 2010).

The distribution patterns of males and females indicate that males have a more specific, and northern, habitat preference than females during the post-moult/pre-breeding period (Fig. 3.2d). Females display a more southern distribution and use a larger area as they feed along the Labrador shelf (Fig. 3.2b). According to the reproductive-strategy hypothesis (RSH), when preparing for the breeding season, males should seek high-quality forage in order to improve body condition and growth, which would greatly increase their reproductive success (Mysterud 2000). However, Tucker et al. (2009) did not find a difference in the energy density of prey between sexes, nor between juvenile and adults. They also found that the energy density was higher during the pre-breeding period for all groups, not just for the males (Tucker et al. 2009). This could mean that the energy requirements for hooded seals are similar for both sexes when preparing for the short intense nursing and mating period. Thus, the observed spatial segregation and preferred bottom depths between males and females suggest a possible avoidance of inter-sexual competition (e.g., McIntyre et al. 2010). If they forage on prey of similar quality, spatial segregation behaviour may indicate that hooded seals use a resource partitioning strategy in their foraging behaviour.

GAMs have the ability to deal with highly non-linear and non-monotonic relationships between the response and the set of exploratory variables (Guisan et al. 2002). Like GLMs, the ability of this tool to handle non-linear data structures can aid in the development of ecological models that better represent the underlying data, and hence increase our understanding of ecological systems (Guisan et al. 2002). Although collinearity can cause a problem in GAMs, our data show only moderate correlations between some of the variables examined (<0.5) and the highest r values were between temperature and depth (Tables A3.2a and A3.3a; 0.48 and 0.50 respectively).

The parameter weightings showed that SST, depth and chlorophyll concentration were the most important parameters explaining habitat selection in both seasons (Tables 3.4 and 3.5) and this may indicate that the distribution of target prey in cold areas may be more influenced by oceanographic processes driven by topography and mixing in the water column. Both sexes seem to have the longest passage time in areas of 600 m depth, although females spend equal amounts of time over deeper water depths in autumn/winter, when no association to slope is observed. This could be due to the spatial shifts of oceanographic processes between the deep water depths to the seals locations at the surface. Slope was however, a significant factor for habitat selection by females in spring, when they were spending more time along the shelf break than over the deeper waters of the Labrador Basin. Males showed no association to slope during spring, but demonstrated a preference to a slope of about 1 degree during autumn/winter (Table 3.3 and 3.4; parameter weights = 0.310 and 0.744, respectively), A lack of importance for the combination of depth and slope during spring and the low level of slope preferred in autumn/winter could suggest that males actually feed on top of the shelf or sea mounts rather on the slopes. Tucker et al. (2009) found that redfish was one of the most prominent prey items in their diet, and this species is among the most dominant deep sea fishes in the Reykjanes Ridge area and on the Greenland shelf (Hareide and Garnes, 2001, ICES 2010). According to Hareide and Garnes (2001), redfish occupy depths between

500-1000 m and can be found close to the top of sea mounts and coral formations, which supports our theory that male hooded seals prefer flat surfaces for foraging during this time.

There was variation in SST preference among the seal groups, although there was some overlap. SST does not mirror the temperatures at depth, and we need to remember that hooded seals are excellent divers, mainly feeding on benthopelagic species. This means that the seals will dive past the thermocline to the cooler bottom waters to catch their prey. Thus SST itself may not be a very useful predictor of habitat use even though our best GAMs identified it as an important predictor.

Chlorophyll seem to have a significant influence on habitat selection for females and juveniles throughout the year (Tables 3.4 and 3.5; Fig 3.3 a, b, c, e), but according to the best GAM model and predictive graphs, male habitat choice does not appear to be influenced by chlorophyll at either times of the year. However, the parameter weights tell a different story (Table 3.4; parameter weight = 0.310 and Table 3.5; parameter weight = 0.766) and these findings suggest that chlorophyll can be an important predictor in combination with other environmental variables. Furthermore, oceanographic parameters, such as those presented in this study, may be acting as proxies for currently undefined processes important for hooded seal habitat selection. Areas with high chlorophyll concentrations are productive, and attract feeding organisms all along the food chain. However, these patches of prey congregations are very dynamic and of a transient nature (Fauchald and Tveraa 2006), which may cause a spatial shift in the actual feeding locations depending on where on the trophic level the predator targets its prey. Our results suggest that male and female hooded seals may be foraging on different prey during the annual migration. Incorporating dive behaviour and possible prey overlap for this population may allow us to clarify if this in fact occurs. Furthermore, integrating a Topographic Complexity Index (TCI) in the models as a predictor of basins and sea mounts could yield a better understanding of exactly what topographic properties male and female hooded seals hone in on when they select a feeding location.

Juveniles share the annual distribution pattern with adults (Fig. 3.2e, f), although they exhibit a slightly different ranking of parameter weights (Table 3.4 and 3.5). Folkow et al. (2010) suggest that juveniles (and especially young of the year) target different prey as they cannot yet dive to the same depths. Additional investigations show that hooded seals do not dive beyond 250 meters in their first year (Stenson; unpublished data). Studies on the development of diving abilities in Weddell seal (*Leptonychotes weddellii*) pups show that these do not have the physiological condition to remain submerged for as long as adults (Burns 1999, Burns and Castellini 1996, Burns et al. 1999). However, when they have passed one year of age, they have developed physiologically, and the diving ability now depends on body size and condition rather than age (Burns et al. 1997). Furthermore, Folkow et al. (2010) found that hooded seal pups from the Greenland Sea population seem to improve their diving abilities greatly in the first year. Our findings show that juveniles prefer bottom depths between 0-600 m in spring season, during their first months of life and > 750 m in autumn/winter (Fig. 3.5c, f), which could be due to increased confidence in diving and thereby venturing across deeper waters. Tucker et al. (2009) found that juvenile hooded seals mainly target pelagic prey, which coincides with findings by Beck et al. (2007) on the diet preferences of juvenile grey seals. They found that young grey seals had a broader niche breadth than adults and that the diets were of lower energy density. They suggested that juveniles display less selectivity as young and naïve predators, and it is therefore interesting that young hooded seals generally share the movement pattern of adults already in their first year. They follow the same route, but our results suggest that they use the oceanographic proxies or "triggers" differently than adults when locating a feeding habitat.

Juveniles also showed a higher affinity to ice than adults (autumn/winter; Table 3.5, Fig. 3.7b). This positive relationship between FPT and ice covered areas during autumn/winter (Fig. 3.7b) could have various explanations. For instance, ice edges are known to be productive and the parameter weights for juveniles show that chlorophyll is of great significance at all times of the year (Table 3.4 and 3.5). This could also mean that young seals initially target prey at a trophic level closer to primary production than adult seals (as supported by Tucker et al. 2009). Another reason why juveniles might spend more time in areas with more ice cover could be that they have a higher need for resting than adults, as diving might be more physiologically challenging for younger seals (Burns et al. 1997). Further study on haul-out behaviour on ice throughout the year could provide more information about how important ice itself is for hooded seals in general when searching for a feeding habitat.

Our models explain a low proportion of deviance in hooded seal habitat use, indicating that habitat variables other than those that are included in this study are important. As hooded seals forage at the top of the food chain, the relationship between habitat use and physical features may be indirect (Ballance et al. 2006). This is likely mediated by the responses of their prey or prey's resources to these physical features (Ballance et al. 2006). As a result, statistical associations between seals and any given set of oceanographic parameters may be weak relative to values for organisms feeding lower on the food chain (Ballance et al. 2006). Nevertheless, this study offers new insight into the associated conditions and habitat properties for hooded seals in the NW Atlantic Ocean, and will serve as a stepping stone towards finding the habitat variables, or combinations thereof, that will best explain hooded seals habitat selection and use.

Identifying the spatial scales of where marine predators forage is important for understanding marine ecosystems (Fauchald and Tveraa 2003, Bailleul et al. 2008). FPT analysis is especially useful to identify transitions in movement patterns (Bailleul et al. 2008) (e.g., between travelling, searching and feeding). We used FPT to identify the spatial scale at which hooded seals focus their search effort and linked this to environmental variables that could be influencing habitat selection. As the tracks were interpolated to fit the ARS scale, we lost fine-scaled information on the original track, but gained information about the areas of increased search effort, which was the goal of this paper. Further investigations will focus on the dive activity along the tracks in an attempt to provide more information on habitat use within the areas identified here.

3.5.1 Conclusion

This study supports our hypothesis that hooded seals associate with areas of complex topographic properties, such as the shelf and ridges. However, the seal groups differed in preferred habitat conditions. A geographic and/or vertical separation between males and females may indicate that they have different dietary needs and/or show competition avoidance as they may feed on similar quality prey. How competition with other species feeding in the same areas as hooded seals may influence habitat choice is yet to be investigated. Our work to date offers new insight into hooded seal habitat selection and how they use their environment. This is important information for making good management decisions and also to understand how environmental change may affect such an arctic species throughout the year as they prepare for important life history events.

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3.8. TABLES

Table 3.1: Number of hooded seals tagged with Satellite Relay Data Loggers (SRDLs) (n=65), 2004-2008 for which data were available for the spring (post-breeding/pre-moult) and autumn/winter (post-moult/pre-breeding) period (Season). Group represents seal group, and Number is the number of seals represented in each season (Details of the individuals are provided in the supplementary material (Table A3.1)).

Group	**Season**	**Number**
Females	Spring	28
Females	Autumn/winter	11
Males	Spring	12
Males	Autumn/winter	7
Juveniles	Spring	10
Juveniles	Autumn/winter	11

Table 3.2: Area Restricted Search (ARS) scale for all categories (sex, age (Group) and Season). ARS (km) is the search radius estimated per seal group per season and it was extracted using a bootstrap routine (radii at highest variance of FPT).

Group	**Season**	**ARS (km)**
Females	Spring (April-June)	27.5
Males	Spring (April-June)	37.5
Juveniles	Spring (April-June)	45
Females	Autumn/winter (August-February)	37.5
Males	Autumn/winter (August-February)	37.5
Juveniles	Autumn/winter (August-February)	45

Table 3.3: AIC table showing the best models calculated for each group (F: females, M: males, J: juveniles) per season. The best models are based on having a ΔAIC < 2. Loglik is the loglikelihood. K is the number of parameters in the model. AIC is the Akiake information criterion for each model and ΔAIC is the difference between the AIC of the best fitting model and each of the other candidate models. Exp(-0.5Δ_i) represent the relative likelihoods and the w_i is the Akiake weight. The percent deviance explained (DE (%)) is here presented as a measure of the models goodness of fit. The full list of models run can be viewed in the supplementary material (Tables A3.4).

Group	**Season**	**Model**	**loglik**	**K**	**AIC**	**ΔAIC**	**exp(0.5Δ_i)**	**w_i**	**DE (%)**
F	Spring	SST, ice, chlorophyll, slope and depth	-2729.23	6	5470.46	0	1	0.990	12.9
F	Autumn	SST, chlorophyll and depth	-691.46	4	1390.92	0	1	0.415	6.15
F	Autumn	Chlorophyll	-694.35	2	1392.70	1.77	0.412	0.171	4.99
M	Spring	SST and depth	-842.88	3	1691.76	0	1	0.690	15.6
M	Autumn	SST, chlorophyll, slope and depth	-436.79	5	883.58	0	1	0.744	21.3
J	Spring	SST, chlorophyll and depth	-512.18	4	1032.37	0	1	0.968	12.9
J	Autumn	SST, ice, chlorophyll, slope and depth	-410.38	6	832.76	0	1	0.843	18.1

Table 3.4: Parameter weightings for each seal group (Females, Males and Juveniles) per habitat variable for spring season (April-June). Weights are calculated by summarising the Akiake weights from each model containing the specific variable.

Females:		**Males:**		**Juveniles:**	
Variable	**Weight**	**Variable**	**Weight**	**Variable**	**Weight**
Depth	1	SST	0.999	Depth	0.999
Chlorophyll	1	Depth	0.999	SST	0.999
SST	1	Chlorophyll	0.310	Chlorophyll	0.970
Slope	0.999	Slope	0.310	Slope	<0.001
Ice coverage	0.989	Ice coverage	0.193		

Table 3.5: Parameter weightings for each seal group (Females, Males and Juveniles) per variable for autumn/winter season (August- February). Weights are calculated by summarising the Akiake weights from each model containing the specific variable.

Females:		**Males:**		**Juveniles:**	
Variable	**Weight**	**Variable**	**Weight**	**Variable**	**Weight**
Chlorophyll	0.850	SST	0.999	Chlorophyll	0.999
Depth	0.825	Depth	0.829	Depth	0.991
SST	0.689	Chlorophyll	0.766	SST	0.988
Slope	0.124	Slope	0.744	Slope	0.881
Ice coverage	0.124	Ice coverage	<0.001	Ice coverage	0.843

3.9. FIGURES

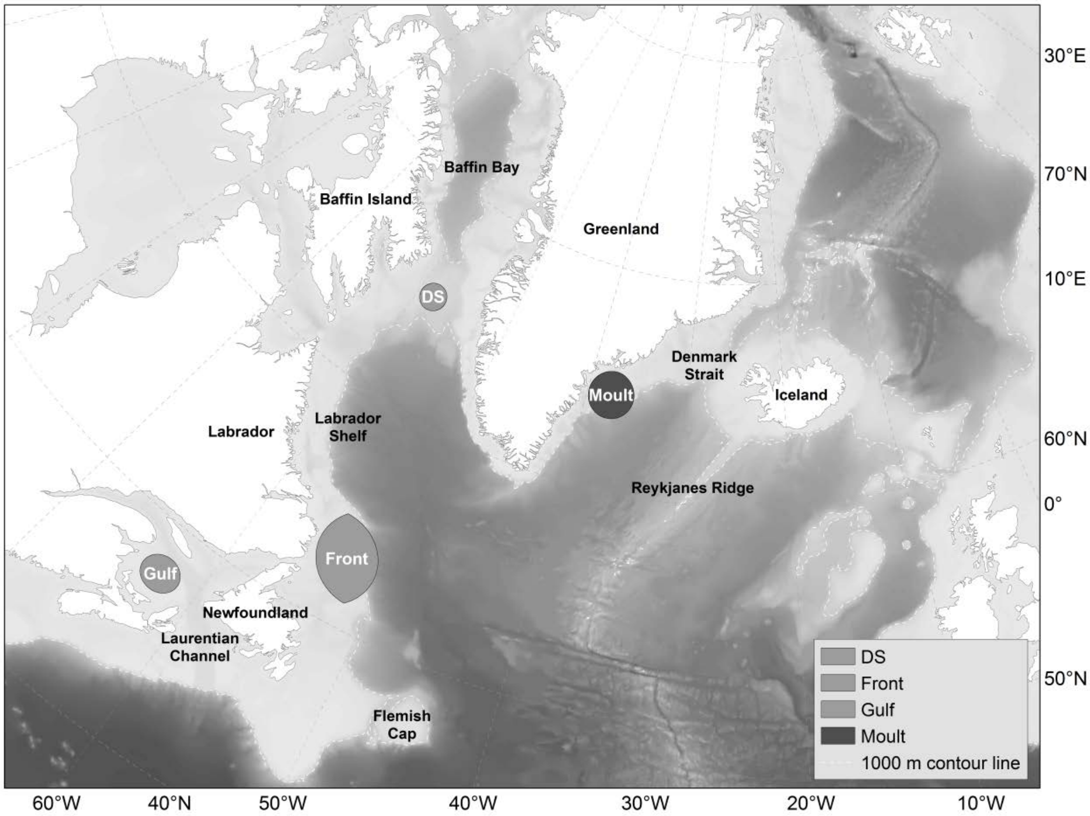

Figure 3.1: Map of the study area: Moulting area in southeast Greenland (dark grey) and breeding areas in Davis Strait (DS), The Front and The Gulf (grey). Bathymetry of the study area is presented as backdrop in grey scale. Dashed white line represents the 1,000 m contour line.

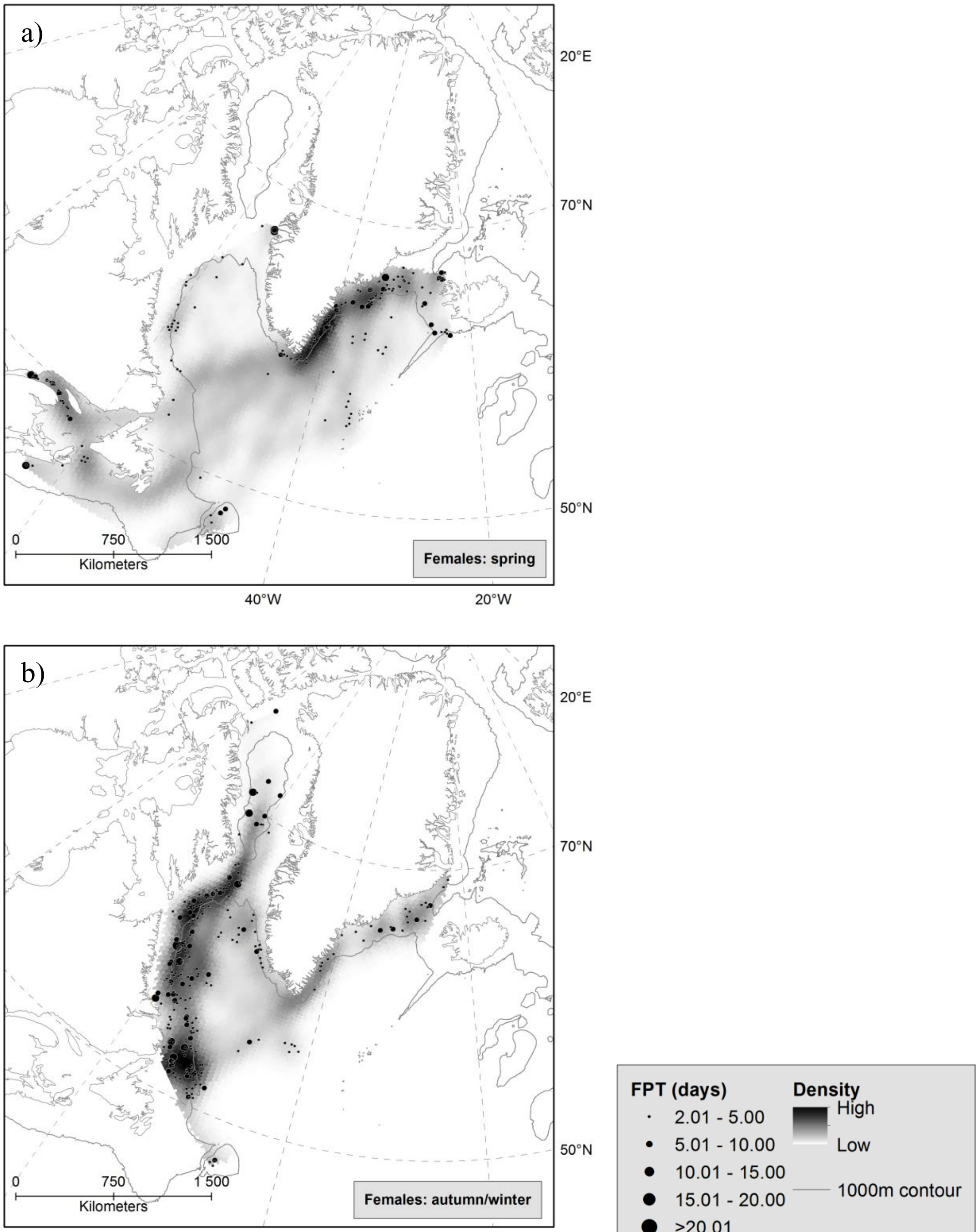

Figure 3.2a,b: Kernel density plots overlaid with FPT (>2 d; black circles) for a) females in the spring season, b) females in autumn/winter. The grey scale shadings represent locations where there was a higher concentration of uplinks. Dashed grey line represents the 1,000 m contour line.

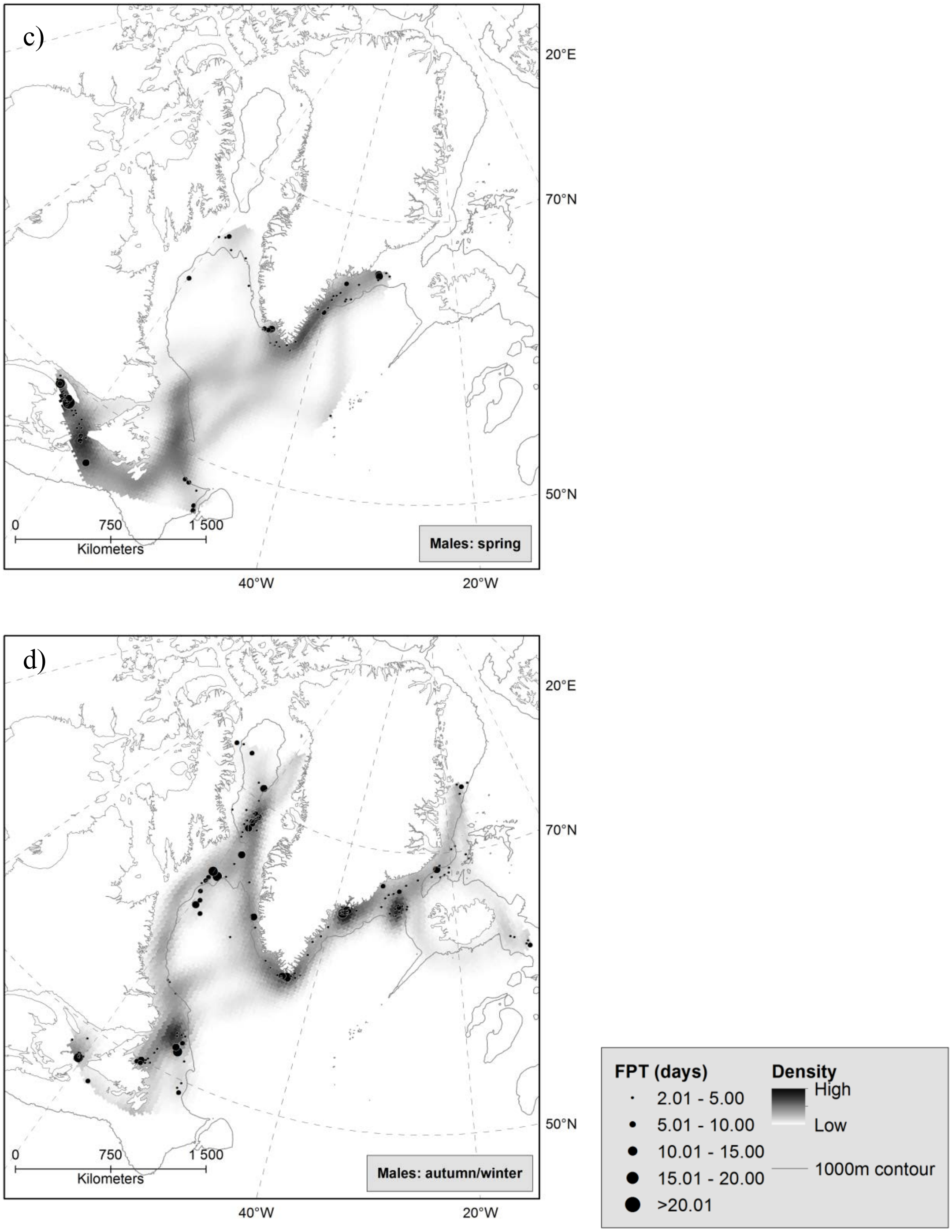

Figure 3.2c,d: Kernel density plots overlaid with FPT (>2 d; black circles) for c) males in spring, d) males in autumn/winter. The grey scale shadings represent locations where there was a higher concentration of uplinks. Dashed grey line represents the 1,000 m contour line.

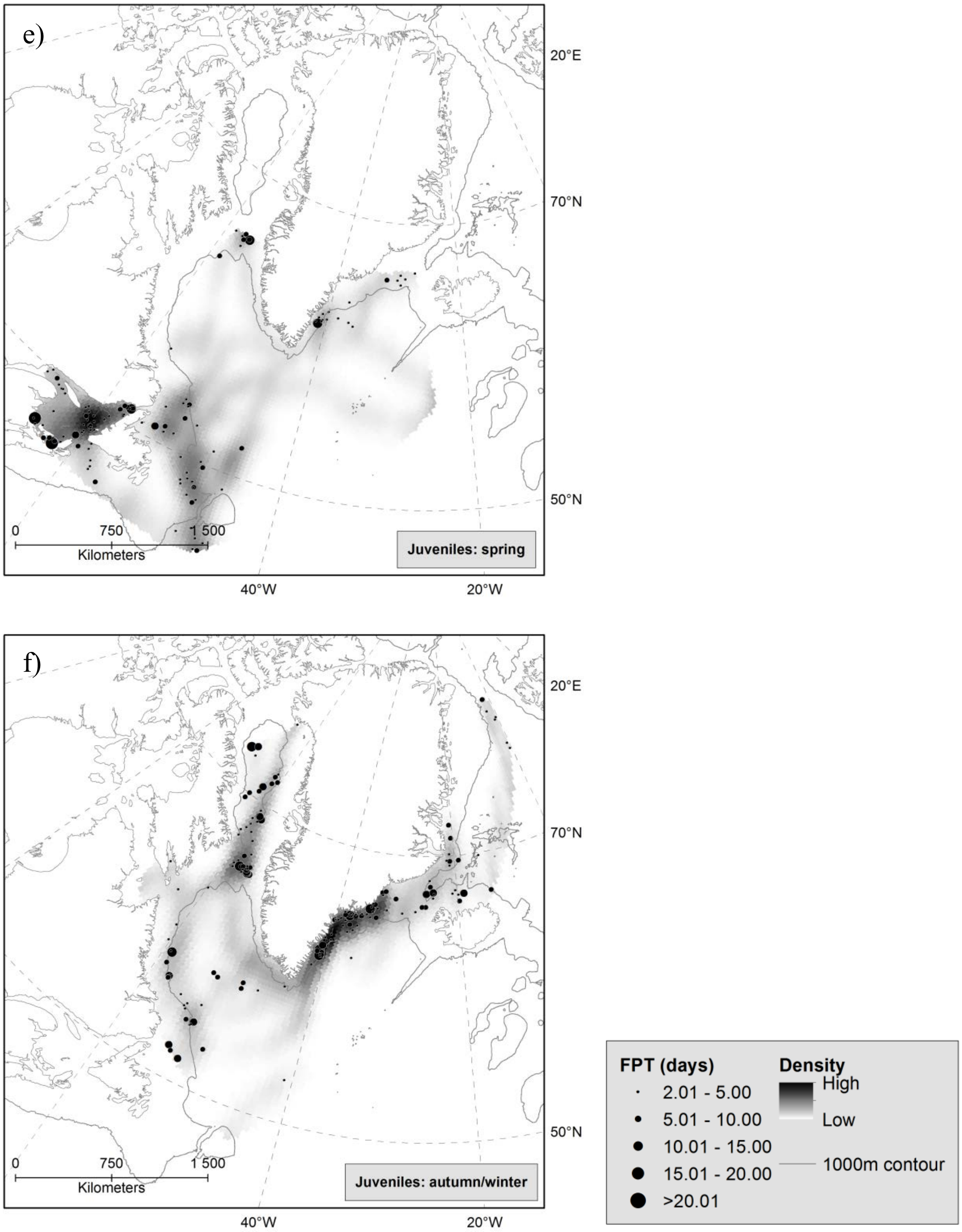

Figure 3.2e,f: Kernel density plots overlaid with FPT (>2 d; black circles) for e) juveniles in spring, f) juveniles in autumn/winter. The grey scale shadings represent locations where there was a higher concentration of uplinks. Dashed grey line represents the 1,000 m contour line.

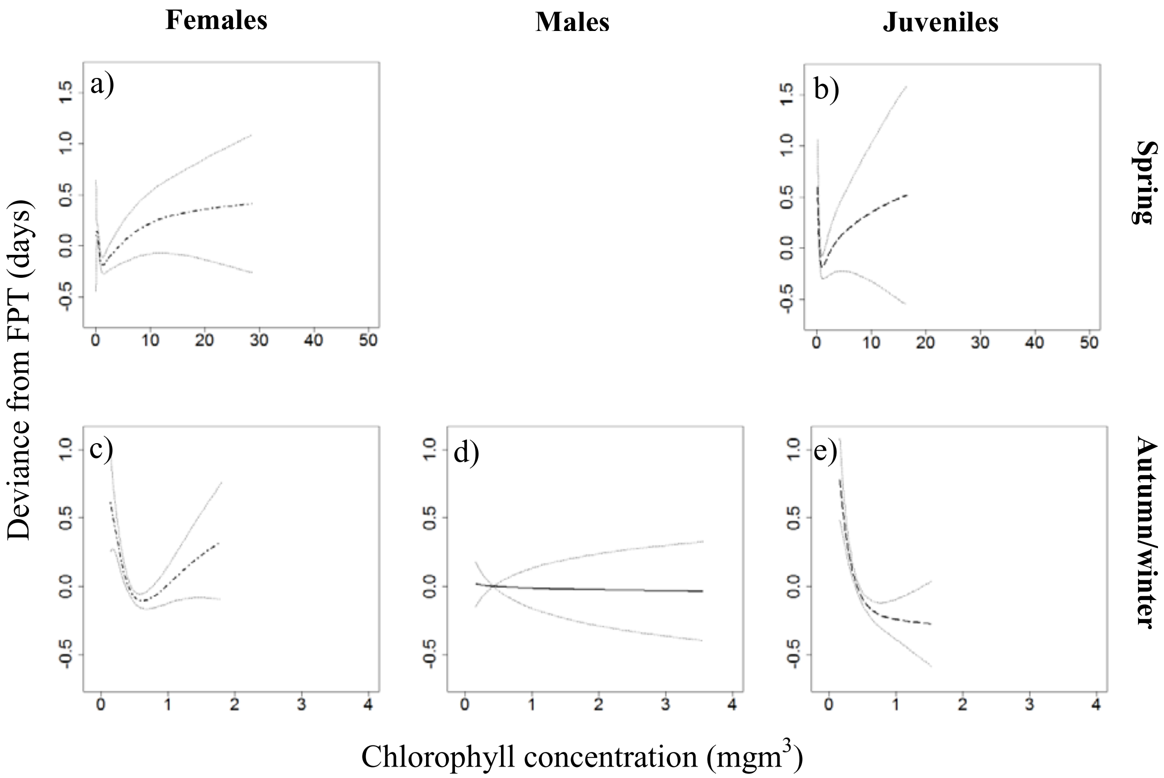

Figure 3.3: Chlorophyll concentration (mgm^3): Top row: Spring predicted GAM results for a) females and b) juveniles. Bottom row: Autumn/winter predicted GAM results for c) females, d) males and e) juveniles. Light grey lines represent the standard error.

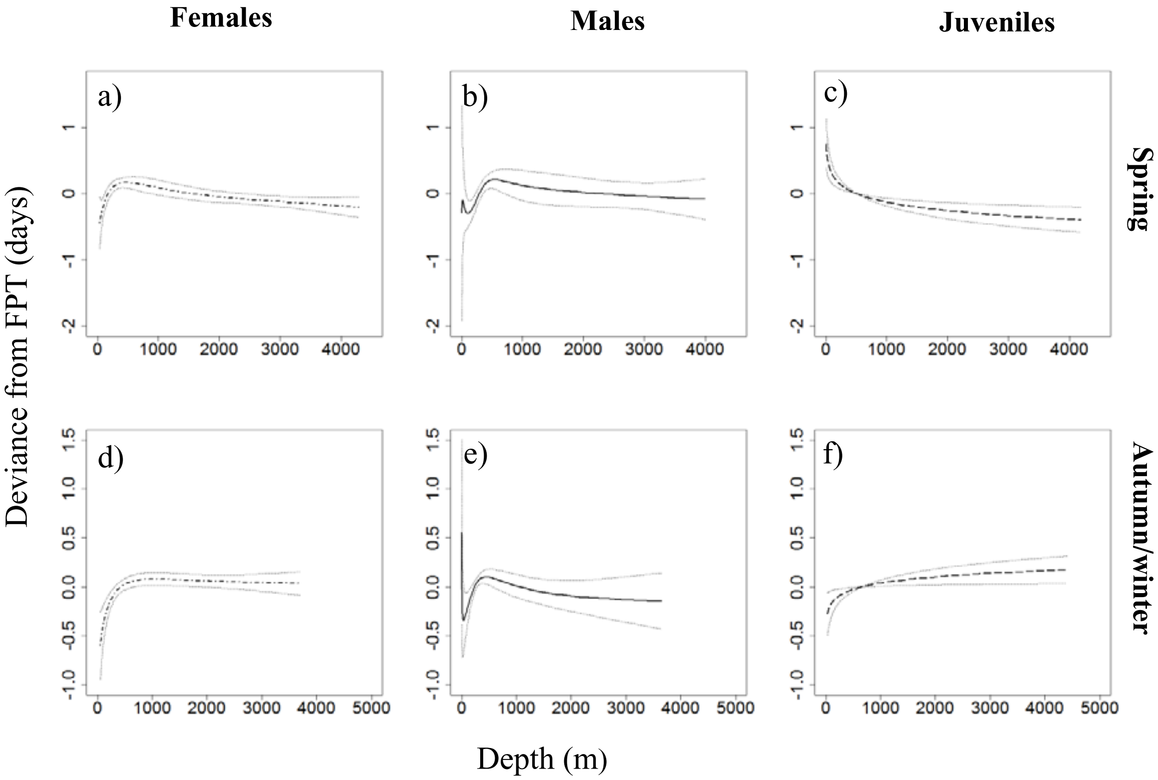

Figure 3.4: Bottom depth (m): Top row: Spring predicted GAM results for a) females, b) males and c) juveniles. Bottom row: Autumn/winter predicted GAM results for d) females, e) males and f) juveniles. Light grey lines represent the standard error.

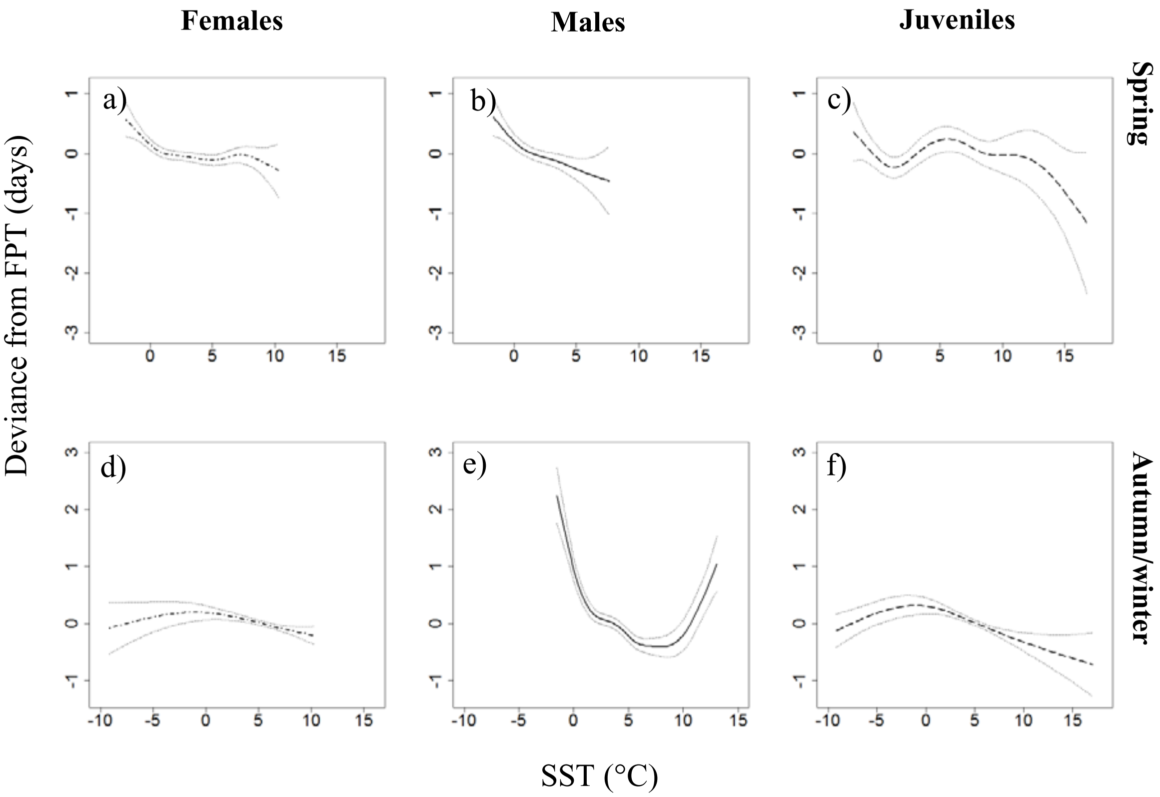

Figure 3.5: Sea surface temperature (SST): Top row: Spring predicted GAM results for a) females, b) males and c) juveniles. Bottom row: Autumn/winter predicted GAM results for d) females, e) males and f) juveniles. Light grey lines represent the standard error.

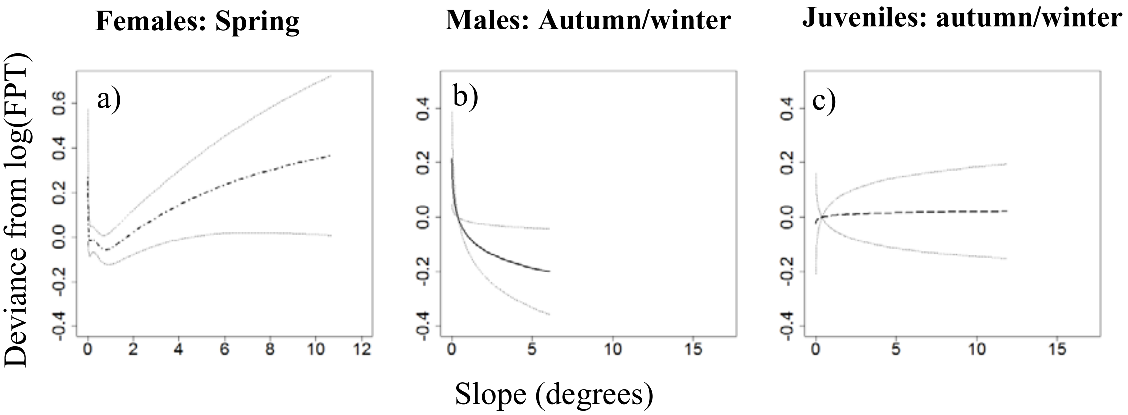

Figure 3.6: Slope (degrees): Spring predicted GAM results for a) females. Autumn/winter predicted GAM results for b) males and c) juveniles. Light grey lines represent the standard error.

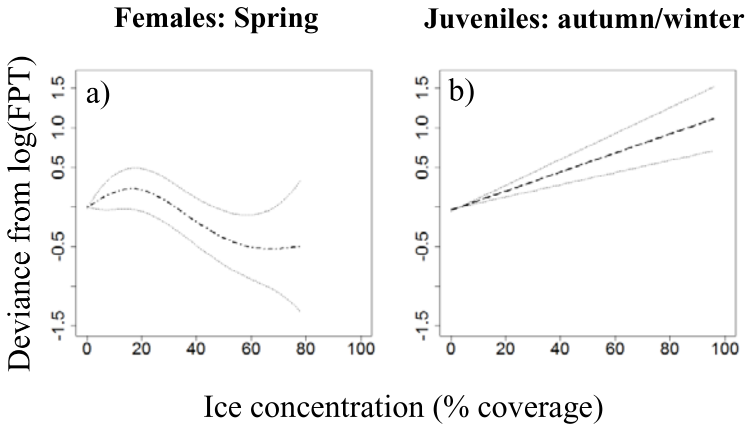

Figure 3.7: Ice concentration in a 25 km grid (% coverage): a) Spring predicted GAM results for females. b) Autumn/winter predicted GAM results for juveniles. There were not enough data to test ice affiliation for juvenile seals for the spring season. Light grey lines represent the standard error.

CHAPTER 4: Investigating annual diving behaviour by hooded seals (*Cystophora cristata*) within the Northwest Atlantic Ocean

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4.1. ABSTRACT

With the exception of relatively brief periods when they reproduce and moult, hooded seals, *Cystophora cristata,* spend most of the year in the open ocean where they undergo feeding migrations to either recover or prepare for the next fasting period. Valuable insights into habitat use and diving behaviour during these periods have been obtained by attaching Satellite Relay Data Loggers (SRDLs) to 51 Northwest (NW) Atlantic hooded seals (33 females and 18 males) during ice bound fasting periods (2004-2008). Using General Additive Models (GAMs) we describe habitat use in terms of First Passage Time (FPT) and analyse how bathymetry, seasonality and FPT influence hooded seals' diving behaviour described by maximum dive depth, dive duration and surface duration. Adult NW Atlantic hooded seals exhibit a change in diving activity in areas where they spend more than approximately 20 h by increasing maximum dive depth, dive duration and surface duration. This indicates that areas where they spend <20 h represent areas of travel and >20 h represent areas of restricted search. We found that male and female hooded seals are spatially segregated and that diving behaviour varies between sexes in relation to habitat properties and seasonality. Migration periods are described by increased dive duration for both sexes with a peak in May, October and January. Males demonstrated an increase in dive depth and dive duration towards May (post-breeding/pre-moult) and August–October (post-moult/pre-breeding) but did not show any pronounced increase in surface duration. Females dived deepest and had the highest surface duration between December and January (post-moult/pre-breeding). Our results suggest that the smaller females may have a greater need to recover from dives than that of the larger males. Horizontal segregation could have evolved as a result of a resource partitioning strategy to avoid sexual competition or that the energy requirements of males and females are different due to different energy expenditure during fasting periods.

Key words: hooded seal, *Cystophora cristata*, sexual segregation, habitat, diving
behaviour, topographic complexity index (TCI), First Passage Time (FPT)

4.2. INTRODUCTION

The Northwest (NW) Atlantic Ocean is a highly dynamic and productive oceanographic system that is influenced by a number of currents (the East Greenland Current, West Greenland Current and the Labrador Current) in conjunction with cross shelf exchange between warmer continental slope water and colder water via sea bottom topography (Grist et al. 2011, DFO 2006). The NW Atlantic hooded seal (*Cystophora cristata*) is distributed throughout these waters displaying a distinct annual migration pattern (*Chapter 2 and 3*). They leave their whelping grounds in the Davis Strait, off Newfoundland and Labrador (the Front) and the Gulf of St. Lawrence (the Gulf) by late March, and disperse along slope edges to feed (*Chapter 2*, Bajzak et al. 2009, Fig. 4.1). Toward the end of their post-breeding/pre-moult feeding period they arrive at the ice off southeast (SE) Greenland where they moult during July (*Chapter 2 and 3*, Bajzak et al. 2009, Sergeant 1974). After the moult, which is highly synchronous, they disperse northwards along the west Greenland shelf and across the Labrador Sea and Baffin Bay (post-moult/pre-breeding period) before returning to their respective whelping areas (*Chapter 2 and 3*).

Like most phocids, hooded seals are capital breeders, meaning that they fast during whelping and breeding, relying on energy reserves obtained during the post-moult/pre-breeding period (Trillmich and Weissing 2006). The moult is also a potentially energetically expensive fasting period for phocids (e.g., harbour seals (*Phoca vitulina*, Paterson et al. 2012), grey seals (*Halichoerus grypus*, Boily 1996), southern elephant seals (*Mirounga leonina*, Boyd et al. 1993, Hindell et al. 1994)) and the extent of total body mass loss in hooded seals during this period has been estimated to be as high as 14% (Thordason et al. 2007).

Hooded seals are sexually dimorphic animals where males weigh, on average, 250 kg and females 190 kg, although they can get much larger (up to 460 kg for males and 300 kg for females) (Hammill and Stenson 2000, Lavigne and Kovacs 1988, Sergeant 1976). Sexually dimorphic animals have been found to display differences in spatial distribution and diet preferences (e.g., Bajzak et al. 2009, Beck et al. 2003a, 2003b, 2003c, 2007, Breed et al. 2006, Le Boeuf et al. 1993, 2000, Mysterud 2000). Males must acquire more resources to attain, and maintain, their greater size (Le Boeuf et al. 1993, 2000), especially when preparing for the breeding season and competition for females. Males have been found to lose 14% of their mean body mass (~2.5 kg per day) over a breeding period lasting 2.5 weeks (Kovacs et al. 1996). In comparison, females need to attain energy stores to maintain pregnancy and prepare for a very short, but intense lactation period. Female hooded seals wean their pup in 3-5 days during which time they lose 16% of their mean body mass (~10 kg per day) (Bowen et al. 1985, Kovacs and Lavigne 1992). Thus, the total body mass of these animals fluctuates throughout the year in relation to important life history events.

Optimal foraging theory predicts that organisms should spend more time in areas where resources are plentiful than in areas where resources are scarce (Fauchald and Tveraa 2003, Charnov 1976). The same theory predicts that breath-hold divers should adjust time allocation within their dives to the distance separating prey from the surface (Kramer 1988). As hooded seals carry out their extensive migrations each year, the specific movement patterns and diving behaviour should, to some extent, reflect the distribution and availability of their prey (Biuw et al. 2007, Durant et al. 2009). Diet studies have shown that hooded seals mainly forage on benthopelagic prey consisting of species such as Atlantic halibut (*Hippoglossus hippoglossus*), Greenland halibut (*Reinhardtius hippoglossoides*), redfish (*Sebastes* spp.), squid (*Gonatus fabricii*), herring (*Clupea harengus*), capelin (*Mallotus villosus*), Atlantic cod (*Gadus morhua*), Arctic cod (*Boreogadus saida*), blue hake (*Antimora rostrata*), and white baraccudine (*Arctozenus rissoi,* (Hammill and Stenson 2000, Haug et al. 2004, 2007, Potelov et al. 2000, Tucker et al. 2009). Furthermore, diet variation by sex, age and season has been observed (Hammill and Stenson 2000, Tucker et al. 2009). Recent research on the highly sexually dimorphic southern elephant seal suggested that dive depth appears to be due to differences in prey selection between sexes (McIntyre et al. 2010). This indicates that southern elephant seals are using a resource partitioning strategy and that they may be displaying avoidance behaviours as a result of inter-sexual competition (McIntyre et al. 2010). Previous research on NW Atlantic hooded seals has shown that males and females are spatially segregated (*Chapter 3*, Bajzak et al. 2009) which could indicate that hooded seals also use a similar foraging strategy to avoid competition.

Satellite telemetry has proven to be an especially useful tool in monitoring pelagic marine mammals (e.g., Bajzak et al. 2009, Biuw et al. 2007, Folkow et al. 1996, 1999, Freitas et al. 2008, Heerah et al. 2013, Kuhn et al. 2009, McIntyre et al. 2010, Thums et al. 2008, 2011, 2013). The availability of data on the movements of free-ranging marine mammals has led to the adoption of powerful analytic approaches for the investigation of habitat use, which in turn allow for researchers to gain insights into possible foraging strategies (e.g., Bailleul et al. 2008, Biuw et al. 2010, Breed et al. 2012, Fauchald and

Tveraa 2003, 2006, Freitas et al. 2008, Robinson et al. 2010). One method to analytically investigate habitat selection and use is to incorporate First Passage Time (FPT) as part of habitat modelling (e.g., Bailleul et al. 2008, Fauchald and Tveraa 2003, 2006, Freitas et al. 2008). FPT is defined as the time it takes an animal to cross a circle of a given size, which is based on the animal's average Area Restricted Search (ARS) scale (Fauchald and Tveraa 2003). ARS occurs when an animal responds to an abundant food source by slowing down and increasing its turning rate (Fauchald 1999, Kareiva and Odell 1987). This simple behavioural response increases the likelihood that the animal can more fully exploit a patch of food as prey encounters will be more frequent (Kareiva and Odell 1987). The animal will not continue on a wider ranging search until prey encounter rate decreases (Kareiva and Odell 1987). FPT can therefore be used as a scale-dependent measure of habitat selection and as an indication of feeding effort as search effort can be expected to be higher in habitats of high prey encounter rate.

Habitat use by NW Atlantic hooded seals have previously been investigated in a 2 dimensional landscape. Andersen et al. (2013a) identified FPT along the migration track and related location data at the surface with environmental parameters such as bottom depth, slope, sea surface temperature, surface chlorophyll and ice concentrations (*Chapter 3*). However, marine environments are characterized by 3 dimensions, which are fully exploited by marine mammals. Analysing data on diving behaviour in areas of various FPTs can offer valuable indirect information on hooded seal habitat selection and foraging strategies in the NW Atlantic Ocean.

Andersen et al. (2013a) showed that hooded seals had longer FPT in SE Greenland (moulting area), the Gulf of St. Lawrence (high use area for animals breeding there) and in the Davis Strait area (*Chapter 3*). Males had longer FPT in Baffin Bay, while females had longer FPT along the Labrador shelf and Reykjanes Ridge area. Therefore, even though there was some spatial overlap between sex, spatial and temporal differences in habitat use and geographic locations were observed (*Chapter 2, Chapter 3*). Among females, long FPTs were associated with intermediate bottom depths along the shelf break and areas with high primary productivity. Males appeared to be more spatially restricted than females and were associated with complex seafloor relief and cool surface temperatures (*Chapter3*).

Here we will build on previous research to describe the diving behaviour of these same seals in relation to habitat. As a sexually dimorphic species we will investigate (i) if males and females show differences in seasonal diving behaviour and FPT in relation to spatial location and bathymetry and (ii) if these characteristics vary in relation to the annual breeding and moulting periods. This knowledge can improve our understanding of the overall habitat use and foraging strategies of hooded seals in the NW Atlantic Ocean, and thereby offer valuable information that can improve future management of the species.

4.3. METHODS

4.3.1 Ethics statement

The capture and tagging protocols have been reviewed and approved by the Canadian Council of Animal Care (Newfoundland Region). Capture and deployment of satellite transmitters was carried out under annual animal care permits and by experienced personnel with the Department of Fisheries and Oceans (DFO), Canada. The CCAC permit numbers are NAFC 2004-11 and NAFC 2008-04.

4.3.2 Study area and deployment of Satellite Relay Data Loggers (SRDLs)

The study area extends throughout the NW Atlantic Ocean from the Gulf of St. Lawrence and the Flemish Cap in the south to the Denmark Strait in the east and Baffin Bay to the north (Fig. 4.1).

Satellite transmitters were deployed directly after the annual moult in SE Greenland during three field seasons (2004, 2005 and 2007, 65°N, 37°W), and after the whelping and breeding period during three field seasons (The Front: 2004 and 2008, 49°N, 52°W, The Gulf: 2004, 2005 and 2008, 46°50´N, 62°W). In total, data from 51 tagged seals were used in this study (33 adult females and 18 adult males). The animals were captured using a net, weighed, and subsequently tranquilized using tiletamine hydrochloride and zolazepam hydrochloride (Telazol, AH. Robins Company, Richmond, VZ, USA) administered intramuscularly ($1\text{mg}\cdot\text{kg}_{(\text{body mass})}^{-1}$). Satellite Relay Data Loggers (SRDLs, Sea Mammal Research Unit (SMRU), St. Andrews, Scotland) were glued to the head or upper neck, using quick drying epoxy glue (Cure 5, Industrial Formulators of Canada Ltd. Burnaby, BC Canada).

The SRDLs collect a range of behavioural information about marine mammals at sea which is compressed and transmitted via the ARGOS satellite system (Fedak et al. 2001, 2002, CLS/Service Argos). The data collected included number of dives (dives deeper than 6 meters were recorded), dive depth, dive duration and surface intervals (Fedak et al. 2001, 2002). Transmissions were attempted every 80 seconds when the seal was at the surface.

4.3.3 Habitat data

Habitat use was investigated by evaluating the association of individual annual movement patterns (based on diving location data) with seasonality (represented by month) and environmental variables, such as geographic location, bottom depth and the topographic complexity index (TCI).

Bottom depths at dive locations were extracted using the 1 minute bathymetry raster data from the General Bathymetry Chart of the Ocean (GEBCO, http://www.gebco.net/). TCI was calculated based on methods described by Wolock and McCabe (1995) using GEBCO data, and an AML code in ArcInfo (version 9.3) by S. Wilds, modified by J. Young and F. van Manen, USGS LSC. The TCI model calculates (from each grid cell of one minute scale) the total upslope area, before calculating how much flow/drainage from the surrounding area that would accumulate in each grid cell, thereby offering a more realistic picture of the sea floor. The underlying formula of TCI = ln((A/tanB), where A is the surface area of each grid cell providing “drainage” and B is the surface slope of the grid cell (Shriner et al. 2002, Wolock and McCabe 1995). The TCI value of a grid cell is therefore dependent on the slope or shape of the sea floor in either direction (up or down) to the surrounding grid cells, which is represented by the term “flow” or “drainage”. TCI identifies basins and peaks where high numeric values represent peaks, and low values represent basins (our data ranged from 0.53-25.32, where values around 12.5 represent a flat surface). A map showing the TCI surface for the entire survey area is provided in the appendix (Fig. A4.1).

4.3.4 Variation in First Passage Time (FPT)

We calculated the FPT radius by using the “adehabitatLT” package in R (version R 2.14.1, (Calenge 2006)). The spatial dynamics of foraging areas can be studied by analysing the spatial distribution of FPT among individuals (Fauchald and Tveraa 2003). To do this it is necessary to select a scale on which the FPT is to be calculated (Fauchald and Tveraa 2006). By creating a histogram of the variance of FPT vs. radius, we derived the size of the area of which the animals focus their search effort (ARS). The variance-scale function, and consequently the observed ARS scale, is related to individual foraging patterns and success as well as the spatial distribution of resources (Pinaud and Weimerskirch 2005). In order to remove some of the noise due to stochastic and individual differences in ARS scales we chose to use a common spatial scale (see Fauchald and Tveraa 2006 for details). Andersen et al. (2013a) estimated a search radius of 37.5 km for males, and 27.5 km and 37.5 km for females (post-breeding/pre-moult, post-moult/pre-breeding, respectively; *Chapter 3*). Because high foraging success in some of the trips will mask a large-scale search pattern, we chose a spatial scale (40 km) in the upper range of individual ARS scales. The purpose of the FPT is to capture the search effort at each point along the entire movement path (Fauchald and Tveraa 2003, 2006).

With location data sampled independently of speed along a path, a larger number of location points will be sampled in areas of low speed compared to areas of high speed (Fauchald and Tveraa 2003). This gives a sampling bias toward search effort. In order to remove this bias, sampling points were made regular in space by spatial interpolation of locations (Fauchald and Tveraa 2003). Data points were placed 500 meters apart along each of the tracks and the data averaged per 80 km step (diameter of ARS circle) to obtain summary information about diving behaviour along the trajectory on the ARS scale.

FPT, extracted at the ARS scale, was used as a response variable in the GAM analysis (package "mgcv" in R, Wood 2011), with geographic location, bottom depth, month and TCI as predictors (we refer to this as the "habitat model"). This was done to investigate how FPT could be explained by these habitat properties, and how FPT fluctuated annually. March and July were excluded from the analysis as hooded seals spend most of their time during these two months hauled out on the ice for breeding and moulting, respectively. To take into account individual variability, individual seal id was entered as a random factor using a smooth specifier (Wood 2008). The model is given by:

gam(response ~ te(x_1)z_1 + s(x_2)z_2 + ... + s(w, bs = "re"), data, method="REML")

where FPT is the response variable and x_1, x_2 etc. are the predictor variables (geographic location, bottom depth, month and TCI). The models were run by including sex as an indicator variable (z) to look for segregation by sex in the data. Diving behaviours (maximum dive depth, dive duration and surface duration) were used as response variables in a separate GAM analyses to investigate how habitat, FPT and seasonality (month) might explain diving strategies (referred to as “diving behaviour models”).

A GAM can deal with simple random effects such as individual variability, by treating random effects as smooths (Wood 2008). This is implemented in the GAM by s(w, bs = "re") where w is the covariate of the smooth (here the individual seal id), bs is a basis penalty smoother, and the "re" class implements simple random effects (Wood 2008). The restricted/residual maximum likelihood estimation (REML) is used to correct for the degrees of freedom when there is an increased number of fixed parameters in the model (Wood 2006, Smyth and Verbyla 1996). It thereby produces an unbiased estimation of the variance parameters (Wood 2006).

Bottom depth, TCI, maximum dive depth and surface duration were square root transformed and FPT was log transformed to obtain normal distribution. To select between competing models we applied an information-theoretic approach and examined parameter weightings using Akaike’s Information Criterion (AIC). All possible models (30 for the FPT habitat model and 56 for each of the diving behaviour models) nested within the full model were assumed to be candidate models. Models with ΔAIC < 2 are considered to have substantial support and ΔAIC >10 have very little support (ΔAIC is the difference between the AIC of the best fitting model and that of model i, Burnham and Anderson 2002). If the addition of one predictor variable to a model resulted in an AIC of < 2 values from the model without this variable, and the model fit was not improved (deviance explained), the added variable was deemed a pretending variable and removed from the analysis (Anderson 2008).

The fitted values from the best habitat model (FPT as the response variable) were back transformed before plotting a predictive surface using ArcGIS 10 (ESRI® ArcMap^{TM} 10.0). The predicted graphs for each of the best models (both habitat and behavioural models) were created to present the fitted results for each of the predictor variables.

4.4. RESULTS

4.4.1 Dive statistics across all seals

Of a total of 352,438 dive locations, the summary data, aggregated at the ARS scale of 40 km, yielded 3,269 data points. Dive statistics of the non aggregated data are presented in Table 4.1. We found that 50% of the total number of dives recorded occurred in waters of less than 500 m deep (Fig. 4.2a). In addition, 90% of the maximum dive depths did not exceed 500 m and 35% of the total number of dives targeted a maximum dive depth between 150-300 m (Fig. 4.2b). We also found that females used waters with bottom depths 30% deeper in the post-breeding/pre-moult period (April-June; $F = 5.742$, $p<0.05$) and 40% deeper during the post-moult/pre-breeding period (August-February; $F = 6.804$, $p<0.05$) than males.

Spearman correlation statistics were run on the aggregated data between dive behaviours and bottom depth (Table 4.2). The relationship between the variables were significant, but showed relatively low levels of linear correlation ($df = 12$, $r_s = 0.05\text{-}0.36$, $p < 0.05$) except for a moderate positive correlation between maximum dive depth and dive duration ($df = 12$, $r_s = 0.58$, $p < 0.001$, Table 4.2).

4.4.2 Habitat model: Segregation by sex in relation to FPT

The GAM analysis of habitat relationships showed that hooded seals were segregated by sex in relation to geographic location, month and bottom depth in terms of FPT ($w_i = 0.832$, Table 4.3). The deviance explained was 31.4%. The next best model included predictor variables geographic location, month, bottom depth and TCI by sex

((ΔAIC = 3.2, w_i = 0.168, Table 4.3). The deviance explained for this model was also 31.4%, suggesting that TCI is a pretending variable. All other models had a ΔAIC > 10 and were highly implausible (Table A4.1). The map created on the back-transformed fitted values from the best habitat model (frequency histogram presented in Fig. 4.3) showed that males exhibited long FPTs along the shelf areas, especially the northern parts of the Labrador shelf and in Davis Strait (Fig. 4.4a). Females had long FPT mainly along the Labrador shelf and were also distributed over deeper waters than males (Fig. 4.4b, Fig. 4.5a). Some seals spent extended time in SE Greenland and Denmark Strait area, the Front, Flemish Cap and in the Gulf of St. Lawrence (Gulf breeding animals only, Fig. 4.4)).

The predicted results showed that seals spent most time in waters of approximately 700 m, exhibiting a decrease in passage time (shorter FPT) across shallower and deeper waters (Fig. 4.5a). Females spent longer time periods over all deeper bottom depths than males (Fig. 4.5a). FPT was longer in September during the post-moult period and through the winter during the pre-breeding period (December-February) for both sexes (Fig. 4.5b).

4.4.3 Behavioural models: Segregation by sex in relation to diving behaviour

4.4.3.1 Maximum dive depth

The GAM analysis of diving depth relationships showed highest support for the full model (geographic location, FPT, bottom depth, month and TCI) including a separation by sex per predictor variable (w_i = 0.9966, Table 4.3). The deviance explained was 57%. All other candidate models had a ΔAIC > 10 (Table A4.2). Males and females show similar patterns of fluctuation in terms of maximum diving behaviour, except in relation to TCI (Fig. 4.6d). Males increased dive depths towards areas where they spent >20 h while females initially decreased dive depth from 0-20 FPT prior to increasing dive depth towards areas where they spent >30 hours. Maximum dive depth then stabilised across longer FPT for both sexes (Fig. 4.6a, Fig. A4.2). The standard error was larger for females, and overlapped completely with that of males, which indicates a considerable amount of variability among females, and the apparent deeper diving by females across all bottom depths is not significant (Fig. 4.6a).

The maximum dive depth fluctuated across all months of the year and this behaviour was very similar between males and females. However, males displayed shallower dive depths directly before breeding (March) and moulting (July) (Fig. 4.6b). Dive depths increased following these periods reaching a peak in May and then again from August to October (Fig. 4.6b). Females underwent their deepest dives during the winter (December/January) with lower values prior to the moult (Fig. 4.6b).

Both males and females increased their maximum dive depths from bottom depths of 0-600 m (Fig. 4.6c). They appeared to reduce their dive depths as bottom depth increased from ~600 to 1,000 m, but both sexes stabilised their dive depth across all bottom depths of >1000 m (Fig.4.6c).

Female dive depths did not seem to be influenced by TCI, while males showed a slight positive relationship to a TCI value of ~7, above which no relationship to TCI was detected (Fig. 4.6d). The standard error was large for females, which means that there was considerable variability related to this variable.

4.4.3.2 Dive duration

The GAM analysis of dive duration relationships showed highest support for the full model (geographic location, FPT, bottom depth, month and TCI) including a separation by sex per predictor variable ($w_i = 0.7925$, Table 4.3). The deviance explained was 65.3%. The next best model included predictors geographic location, FPT, bottom depth and month and had a ΔAIC of 2.68, making this model less plausible ($w_i = 0.2075$). However, the deviance explained was the same as the best model (65.3%), suggesting that TCI was acting as a pretending variable, and we therefore present our predicted graphs from the next best model. All other candidate models had ΔAIC > 10 (Table A4.3).

Males exhibited a decrease in dive duration from 20-50 h FPTs and no relationship between dive duration and FPT with longer passage times was observed for either sex (Fig. 4.7a; Fig. A4.3). Both sexes showed variable dive durations across months. Dive durations increased in May and decreased towards the moult (Fig. 4.7b). Following the moult, dive duration increased with a peak in October and January (Fig. 4.7b).

Dive duration peaked for both sexes at bottom depths of 600 to 800 m (Fig. 4.7c). Males showed a decrease in dive durations as bottom depths increased to 1,000 m, before they increased again toward 3,000 m depth. Females did not change dive durations across deeper depths (Fig. 4.7c).

4.4.3.3 Surface duration

The GAM analysis of surface duration relationships showed highest support for the full model (geographic location, FPT, bottom depth, month and TCI) including a separation by sex per predictor variable (w_i = 0.6599, Table 4.3). The deviance explained was 39.8%. The next best model did not include TCI and had a ΔAIC of 1.33, making this model highly plausible (w_i = 0.3401, Table A4.3). The deviance explained was 39.7%, which again suggests that TCI in the best model acted as a pretending variable and we therefore plotted the results for the next best model. All other candidate models had a ΔAIC > 10 (Table A4.4).

Although there is considerable variation among females, they showed an increase in surface durations with increasing FPT up to approximately 50 h, while males continued to increase the time spent at the surface between dives up to approximately 150 h FPT from when it started to stabilise (Fig. 4.8a; Fig. A4.4).

There was no relationship between surface duration and season for males. Females showed longer surface durations during late winter, early spring and around the moult, although there was a high amount of variability in the data (Fig. 4.8b). Both males and females increased surface durations with increasing bottom depths to ~600 m (Fig. 4.8c). Males then had the same surface duration across all bottom depths, while females showed some fluctuation across deeper bottom depths (Fig. 4.8c).

4.5. DISCUSSION

Hooded seals have the highest capability to store oxygen in blood and skeletal muscles measured for any pinniped (Burns et al. 2007) with a maximum dive depth of 1,652.3 m for a male, and 1,592.3 m for a female, and maximum dive duration of 57.25 minutes (Table 4.1). Only males demonstrated a dive duration of more than 39.25 min, however, Folkow and Blix (1999) showed that females from the Greenland Sea population could dive for >52 min. Among the pinnipeds, this diving ability can probably only be matched by elephant seals (e.g., Hindell et al. 1991, Le Boeuf et al. 1989, McIntyre et al. 2010). For much of the year, hooded seals appear to utilize (i.e., have the longest passage time through) areas with mean bottom depths between 700-1,200 m (Fig. 4.5a, Table 4.1). In these areas they carry out dives into the mesopelagic zone (annual mean maximum dive depth was 255 ± 184.9 m), along the shelf break areas and areas of high topographic relief. These results are similar to what has been observed among the Greenland Sea population of hooded seals, which were found to regularly dive to depths between 100–600 m, although the dive depths varied between areas and seasons (Folkow and Blix 1999). Folkow and Blix (1999) also estimated the average dive durations for the Greenland Sea hooded seals of 5-15 min, while seals in our study showed mean dive durations at the high end of their range (13.5-14.5 min, Table 4.1). These differences are likely due to the fact that the data available to Folkow and Blix (1999) were binned into predefined periods, which did not allow for fine scale observations.

In this study, we demonstrated that hooded seals are segregated by sex in terms of FPT and diving behaviours. Our best habitat model identified geographic location, bottom depth and seasonality as the most important explanatory variables. Habitat selection was not influenced by TCI, which is consistent with the findings by Andersen et al. (2013a) who found a low level of importance by slope when this was applied as a measure of bathymetry in their habitat model (*Chapter 3*). These findings suggest that bathymetry alone may not be a good explanatory variable in terms of habitat selection and the time hooded seals spend in a particular location. In fact, our findings suggest that bathymetry acts as a pretending variable, which means that it does not improve the fit of the model (Anderson 2008). The complex topographic properties may serve as a weak proxy for other oceanographic processes, such as movements of currents, and thereby temperature and productivity at depth, which might be of higher importance.

Another parameter that is likely to be important, and whose distribution is driven by oceanographic processes, is a measure of prey availability. Prey availability is hard to measure in the marine environment (e.g., Hindell 2008) and more so in the high Arctic where suitable abundance estimates are limited, especially for non-commercially important species. Thus prey could not be included in the models here. However, some spatial inferences have previously been made from diet data. Hammill and Stenson (2000) found geographic variation in dominant prey species in the diet depending on sampling area. They also found that, although hooded seals foraged on benthic species such as Greenland halibut, redfish and Atlantic cod, most of these consisted of juveniles, which are often found higher in the water column than adult fish (e.g., Scott 1982). This suggests that hooded seals carry out pelagic feeding dives within their high use areas as mean dive depths were 255±184.9 m and mean bottom depths ranged from 700-1,200 m. Only 10% of the dives were deeper than 500 m. However, as hooded seals appear to be generalist feeders with a high diversity of prey species in their diet (e.g., Hammill and Stenson 2000, Haug et al. 2004, 2007, Potelov et al. 2000, Tucker et al. 2009), real time inferences about their diet requires spatial and temporal overlap in sampling of both diet data, (or at the least observed predator presence) and prey presence (including abundance estimates).

GAM models including an indicator variable (sex) were found to be the best models, thereby identifying sexual segregation in the data. A significant statistical difference in habitat selection and diving behaviour between male and female hooded seals was observed, but the diving behaviour models were described with considerable overlap of predicted results. This could be due to behavioural variation of the individuals or variability in terms of body size and diving capabilities. However, our results suggest that overall diving behaviour was influenced by FPT, geographic location, bottom depth and season. Similarly to the results from the habitat model, the behavioural models suggested that the surface duration and dive duration was not influenced by TCI. However, the model identified TCI as an important predictor of maximum dive depth. We observed a weak positive relationship with TCI by males to a value of ~7 (mean = 7.7 ± 2.7, Table 4.1). TCI for the entire study area ranges from 0.5-25, where a high number represents peaks and a low number represent basins. This suggests that male hooded seals adjust their dive depth according to topography representing a “downward slope” toward basins more than an “upward slope” toward peaks (TCI of ~12.5 represents a flat surface). Such areas could, for example, describe the shelf break where males spend extended periods of time at various times of the year. Females showed no (or a slightly negative) relationship between dive depth and TCI, and the results show very high variability. This lack of relationship could be linked to females preferring deeper water than males, where prey distribution may not be as affected by the topographic complexity of the sea floor as over the shelf (e.g., Pepin 2013).

Both migration periods are characterized by an increase in dive duration for both sexes (peak in May, October and January). This increase could indicate a higher foraging intensity in order to gain body mass and increase energy reserves after fasting periods to prepare for the next fasting period. Males also demonstrated an increase in maximum dive depth during these periods, but did not show a pronounced change in surface durations. This may be explained by hooded seals' high capability to store oxygen and recover quickly from diving (Burns et al. 2007). Females showed a less pronounced variability in dive depth throughout the year, but the deepest diving occurred during the winter months (December-January), and the surface duration seemed to fluctuate similarly to dive depth (Fig. 4.6b, Fig. 4.8b). There was a slight increase in surface duration from May with a peak in June prior to the moult, which is consistent with the increase in dive duration and a small increase in dive depth during the same time period. Females also showed an increase in surface duration over the winter months, and although these results are represented with some variability, the combined diving behaviour and longer FPT in between fasting periods suggest that the smaller females, especially if carrying a foetus, may have a greater need to recover from dives than that of the larger males. These findings differ somewhat from what has been found for the Greenland Sea hooded seal stock. Folkow and Blix (1999) observed no sexual segregation (4 males and 12 females), and the deepest and longest dives occurred in the winter months and not necessarily in relation to fasting periods as observed for the NW Atlantic stock. A difference in foraging behaviour between the two stocks may be explained by the differences in the environmental properties of their range.

Little has been known previously about hooded seal sexual segregation during the post-moult/pre-breeding period (August-February), although Bajzak et al. (2009) found sexual segregation by hooded seals in the Gulf of St. Lawrence during the post-breeding/pre-moult period (April-June) where females dived, on average, 70 m shallower than males prior to migration, and 40 m deeper than males following migration. They demonstrated vertical, but not horizontal segregation. We found that males and females were spatially segregated in relation to bottom depth (Fig. 4.5a), where females used areas with bottom depths 30% deeper post-breeding/pre-moult and 40% deeper during post-moult/pre-breeding than males, but no significant difference in dive depth was observed. The differences in the degree of spatial overlap within the Gulf breeding animals and within the Front (and Davis Strait) breeding animals during parts of the migration is probably due to the small numbers of the Gulf breeding herd and spatial limitations of the Laurentian Channel (~500 m deep, Fig. 4.1) compared to the areas available for Front breeding seals (Bajzak et al. 2009). The Front breeding herd comprises 90% of the NW Atlantic population which means that they may need to spread out more to access suitable feeding areas (Stenson et al. 2006). Thus, the Gulf may be able to sustain both males and females of this small herd residing there during the post-breeding period, but they segregate vertically instead of geographically. During the pre-moult period the segregation behaviour becomes more similar to the rest of the population.

Females occupying waters with deeper bottom depths than males may be targeting vertically migrating benthopelagic prey with diurnal cycles across deeper depths than species occupying less deep waters. Folkow and Blix (1999) found that the Greenland Sea hooded seal stock showed similar diurnal variations in diving depths, implying foraging on diurnally migrating prey, and there was no difference between males and females. Le Boeuf et al. (1993) found a similar difference in distribution patterns of northern elephant seals where females carried out consistent pelagic foraging while venturing across a broad expanse of the northeast Pacific Ocean, while males would target the continental margin. They suggested that males fed on food sources determined by spatial boundaries, while females were utilizing a food source determined by a fixed cyclical pattern of vertical prey movement in the pelagic and mesopelagic environment. Diets of NW Atlantic hooded seals differ between males and females, even within seasons (Tucker et al. 2007) and a difference in prey selection could account for the differences in habitat locations we observed, or the difference in habitat locations could explain differences in prey items available. Our findings are similar to those of Le Boeuf et al. (1993) in that male hooded seals have longer FPTs according to month than females (Fig. 4.5b), which suggest that males spend more time in profitable areas while females travel with shorter FPT, covering a larger area (hence more time spent over all bottom depths; Fig. 4.5a).

Spatial segregation and different diving behaviours between males and females could indicate that the energy requirements (and hence dietary needs) are different due to different energy expenditure during fasting periods (e.g., during the breeding period males lose ~14% of their mean body mass over ~2.5 weeks (Kovacs et al. 1996), while females lose ~16% mean body mass over 4 days (Bowen et al. 1985, Kovacs and Lavigne 1992)). A horizontal spatial segregation between sexes may have evolved as a result of a resource partitioning strategy to avoid sexual competition.

In summary, we have demonstrated that male and female hooded seals in the North Atlantic Ocean are spatially segregated in relation to the selection of habitat throughout the annual migration and by diving behaviour in relation to FPT, bathymetry and life history events such as whelping/breeding and moulting periods. According to the habitat model, NW Atlantic hooded seals have the highest dive frequency in areas where the FPT is approximately 20-40 h (Fig. 4.3) and this is also where they start to carry out deeper diving and exhibit longer dive durations. There is also a slight increase in surface duration during this time of restricted search and assumed foraging. These findings suggest that diving behaviours change with passage time according to the oceanographic properties of the ARS area, and that males and females differ in respect to these properties. This information adds valuable knowledge of the habitat selection of male and female hooded seals in the NW Atlantic Ocean. Changes in body condition associated with these areas of high use may confirm their importance as feeding areas, which can further improve our understanding of the ecology of the species.

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4.8. TABLES:

Table 4.1: Dive statistics (non aggregated data) of dive behaviours (surface duration (SuD), dive duration (DD), maximum dive depth (MDD)) and habitat variables (bottom depth (BD), TCI) as well as FPT throughout the year (March and July are excluded) across all seals (n = 352,438 dive locations). Mean is given with ±SD in parentheses.

	Sample size	SuD (min)	DD (min)	MDD (m)	BD (m)	TCI	FPT (h)
max all	352,438	9.45	57.25	1652.30	4293.0	22.80	952.60
mean all		1.8± (1.1)	13.9 ± (7.0)	255± (184.9)	1048.3± (1021.1)	7.5± (2.7)	167.3± (200.3)
max male	131,385	9.45	57.25	1652.30	3992.0	22.39	952.57
mean male		1.9± (1.1)	14.5± (7.6)	254.7± (196.6)	733.8± (774.7)	7.7± (2.7)	211.8± (251.2)
max female	221,053	9.45	39.25	1592.3	4293.0	22.80	718.08
mean female		1.7± (1.1)	13.5± (6.5)	255.1± (177.5)	1235.2± (1100.9)	7.5± (2.7)	140.8± (156.5)

Table 4.2: Spearman rank correlation table presenting the relationship between the surface duration (SuD), dive duration (DD), maximum dive depth (MDD) and bottom depth (BD) across all seals (n = 3,269). All r_s in the table are significant at $p < 0.05$.

	SuD	**DD**	**MDD**	**BD**
SuD		0.25	0.36	0.15
DD	0.25		0.58	0.05
MDD	0.36	0.58		0.36
BD	0.15	0.05	0.36	

Table 4.3: AIC table presenting the best models. The response variables (RV; FPT, maximum dive depth (MDD), dive duration (DD, surface duration (SuD)) were investigated in relation to geographic location (GL), bottom depth (BD), month (M) and TCI. The behavioural models included FPT as a predictor variable (P). Loglik is the loglikelihood, K is the number of parameters in the model. AIC_i is AIC for model *i*, and ΔAIC is the difference between the AIC of the best fitting model and that of model *i*. Exp($-0.5\Delta_i$) represent the relative likelihoods and the w_i is the Akiake weight. D.E (%) is the deviance explained by the model. Tables showing all candidate models are presented in the supplementary material (Tables A4.1-A4.4).

RV	**P**	**loglik**	**K**	**AIC_i**	**ΔAIC**	**exp($-0.5\Delta_i$)**	**w_i**	**DE (%)**
FPT	GL, BD and M by sex	-3293.69	7	66601.39	0	1	0.8323	31.4
	GL, BD, TCI and M by sex	-3293.30	9	6604.59	3.20	0.2014	0.1677	31.4
MDD	GL, FPT, BD, TCI and M by sex	-7380.97	11	14783.94	0	1	0.9966	57
DD	GL, FPT, BD, TCI and M by sex	-21741.35	11	43504.7	0	1	0.7925	65.3
	GL, FPT, BD and M by sex	-21744.69	9	43507.38	2.68	0.2618	0.2075	65.3
SuD	GL, FPT, BD, TCI and M by sex	-4488.28	11	8998.57	0	1	0.6599	39.8
	GL, FPT, BD and M by sex	-4490.95	9	8999.9	1.326	0.5153	0.3401	39.7

4.9. FIGURES

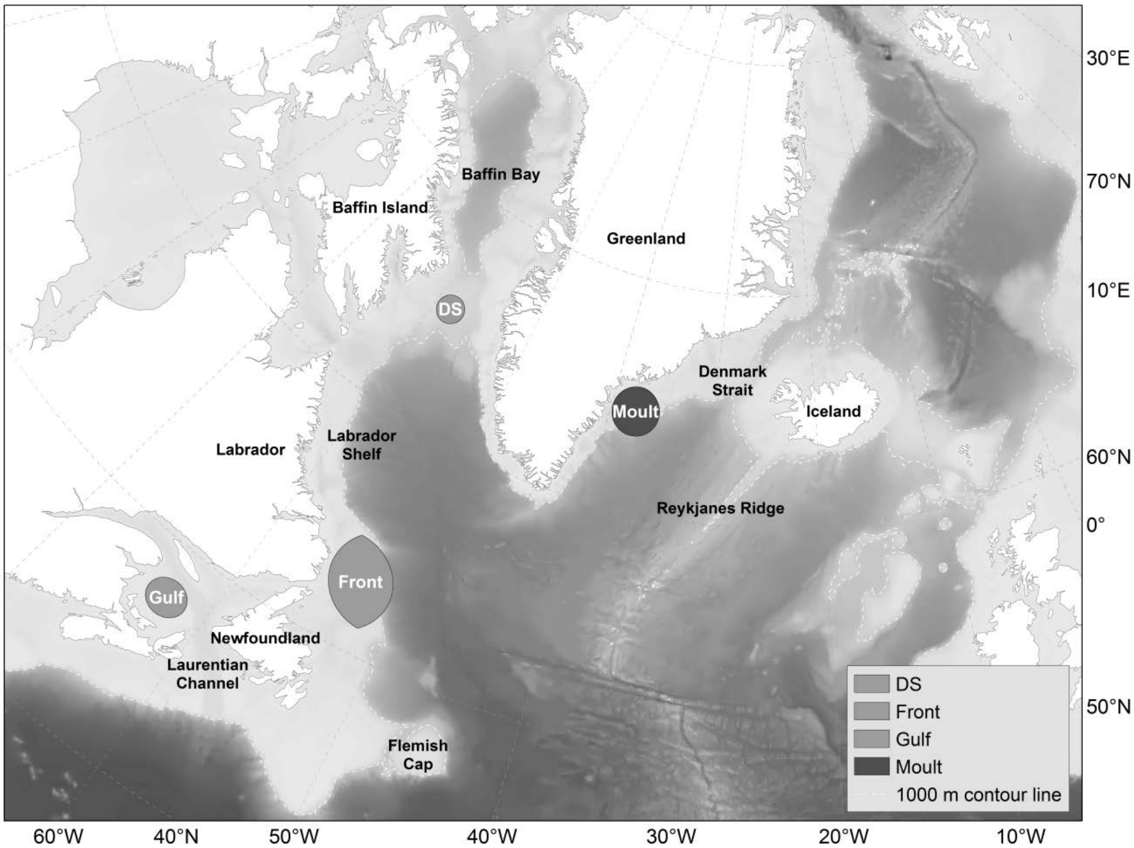
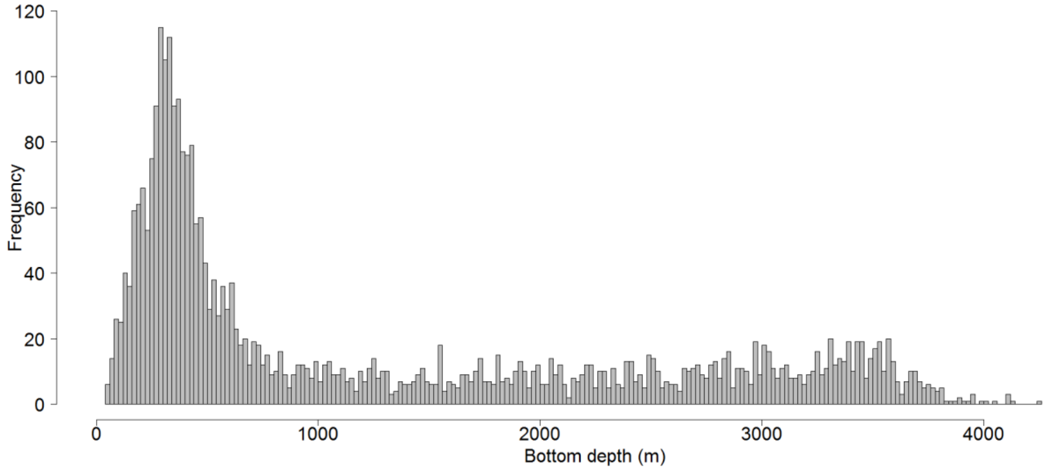


Figure 4.1: Map of the study area: Moulting area is located in southeast Greenland and breeding areas in Davis Strait (DS), off Labrador and Newfoundland (Front) and in the Gulf of St. Lawrence (Gulf). Bathymetry of the study area is presented as backdrop in grey scale. Dashed white line is the 1,000 meter contour.

a)



b)

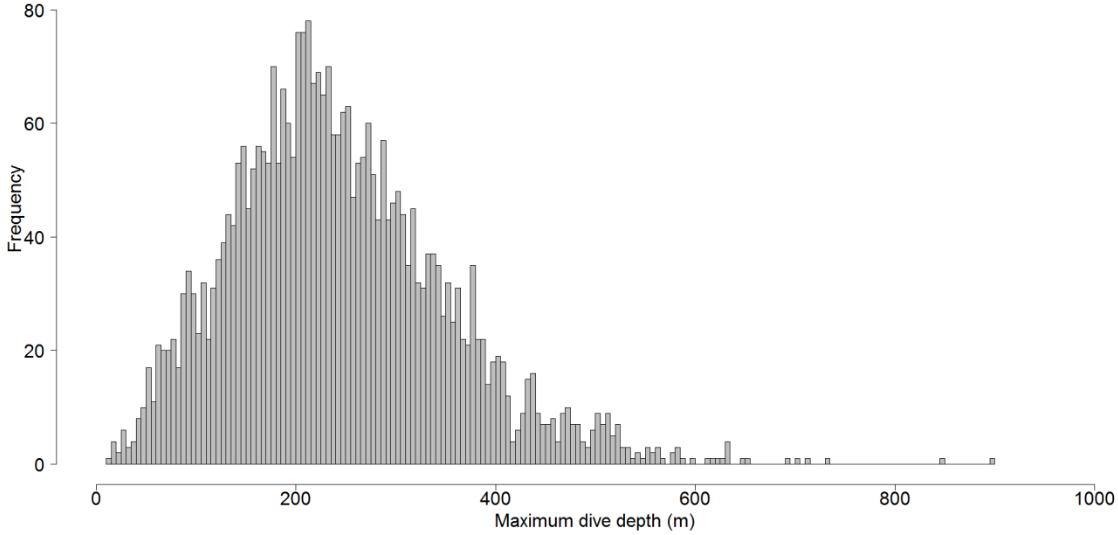


Figure 4.2: a) Frequency distribution of bottom depth across all seals based on the number of dive locations obtained from the SRDL tags (n = 3,269). b) Frequency distribution of maximum dive depth across all seals based on number of dive locations obtained from the SRDL tags (n = 3,269). The range on the y-axis differs between the two figures.

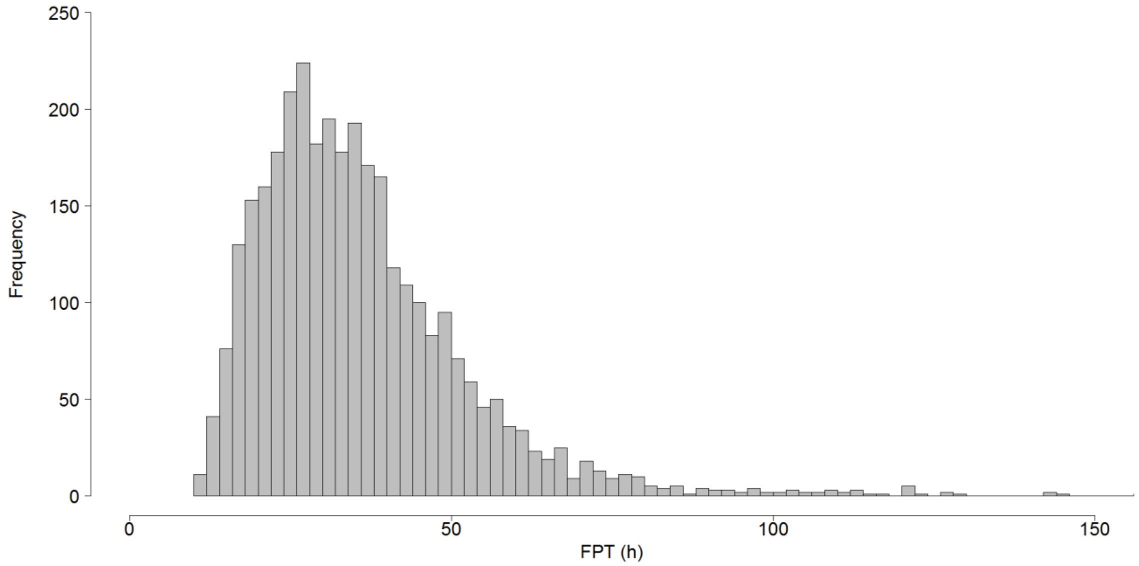


Figure 4.3: Histogram showing the fitted distribution of FPT across all seals (n = 3,269) from our best habitat model.

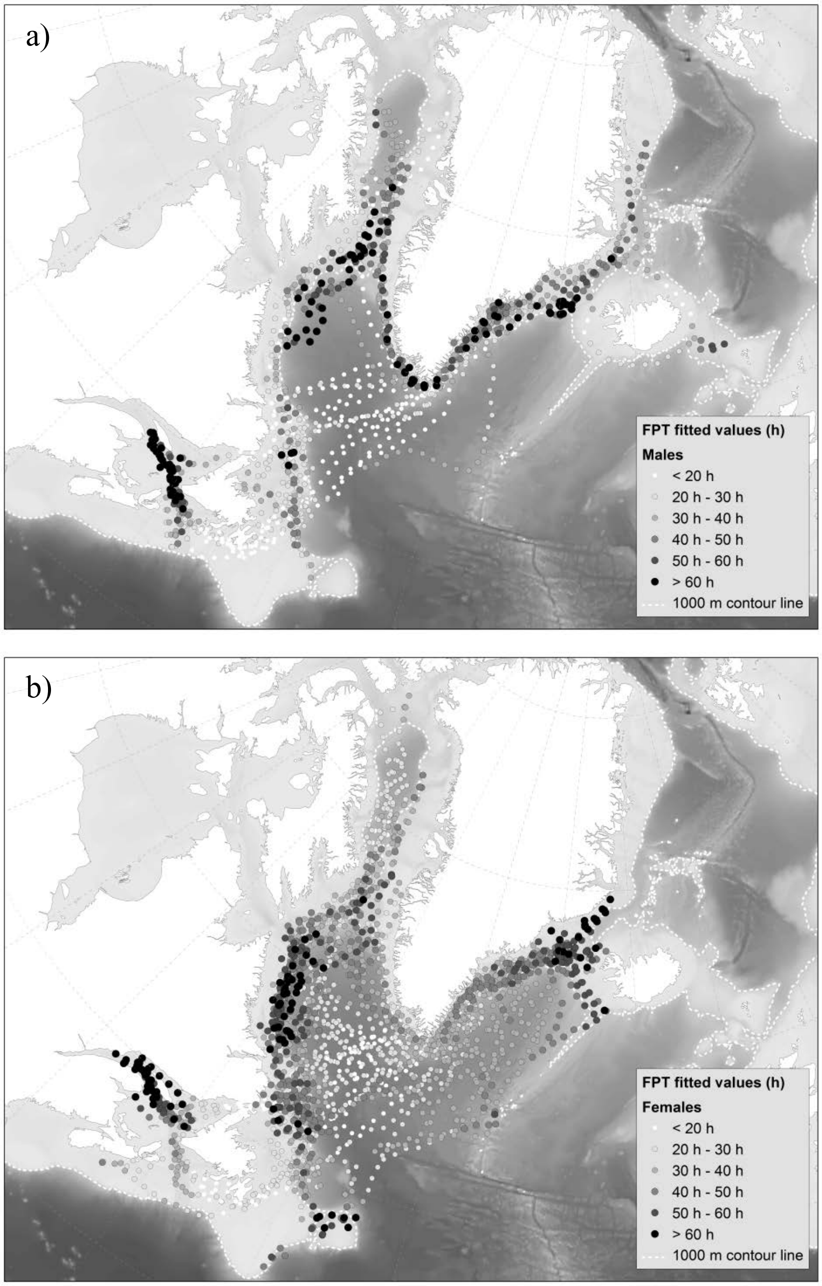


Figure 4.4: Fitted values from the best habitat model (Geographic location, Month, Bottom depth) for a) males (n=18) and b) females (n=33). Track is plotted on the 80 km ARS scale. Filled circles represent FPT from < 20 hours - > 60 hours (light to dark). The dashed white line is the 1,000 m contour line and the bathymetry is represented by the grey scale backdrop.

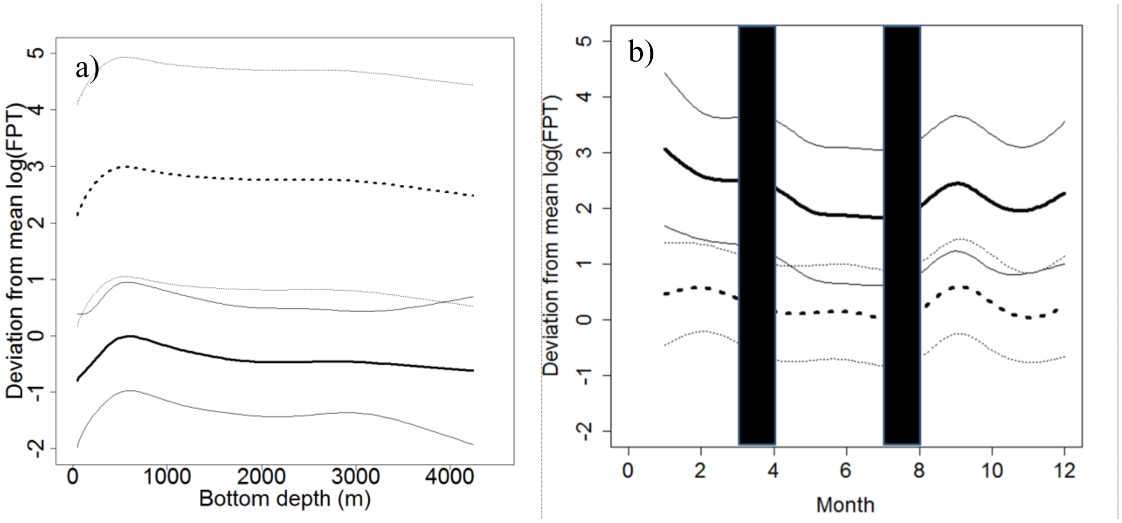


Figure 4.5: Habitat model results: Predicted results for a) Bottom depth (m) and b) Month (black columns represent approximate fasting periods) for male (n=18) and female (n=33) hooded seals. Solid black line represents males and hashed line represents females. Thin black lines represent the standard error.

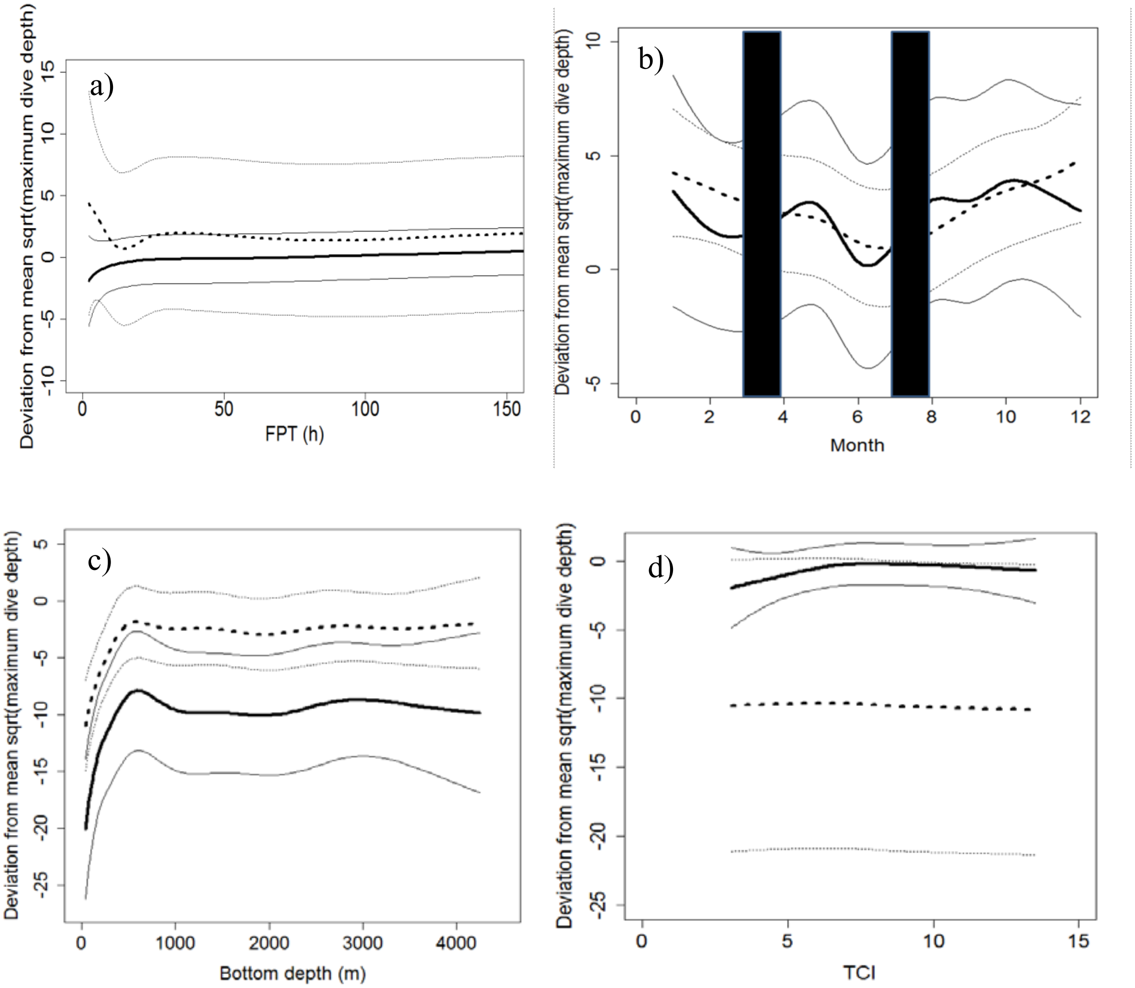


Figure 4.6: Maximum dive depth model results: Predicted results for a) FPT (h), b) Month (black columns represent approximate fasting periods), c) Bottom depth (m) and d) TCI for male (n=18) and female (n=33) hooded seals. Solid black line represents males and hashed line represents females. Thin black lines represent standard error.

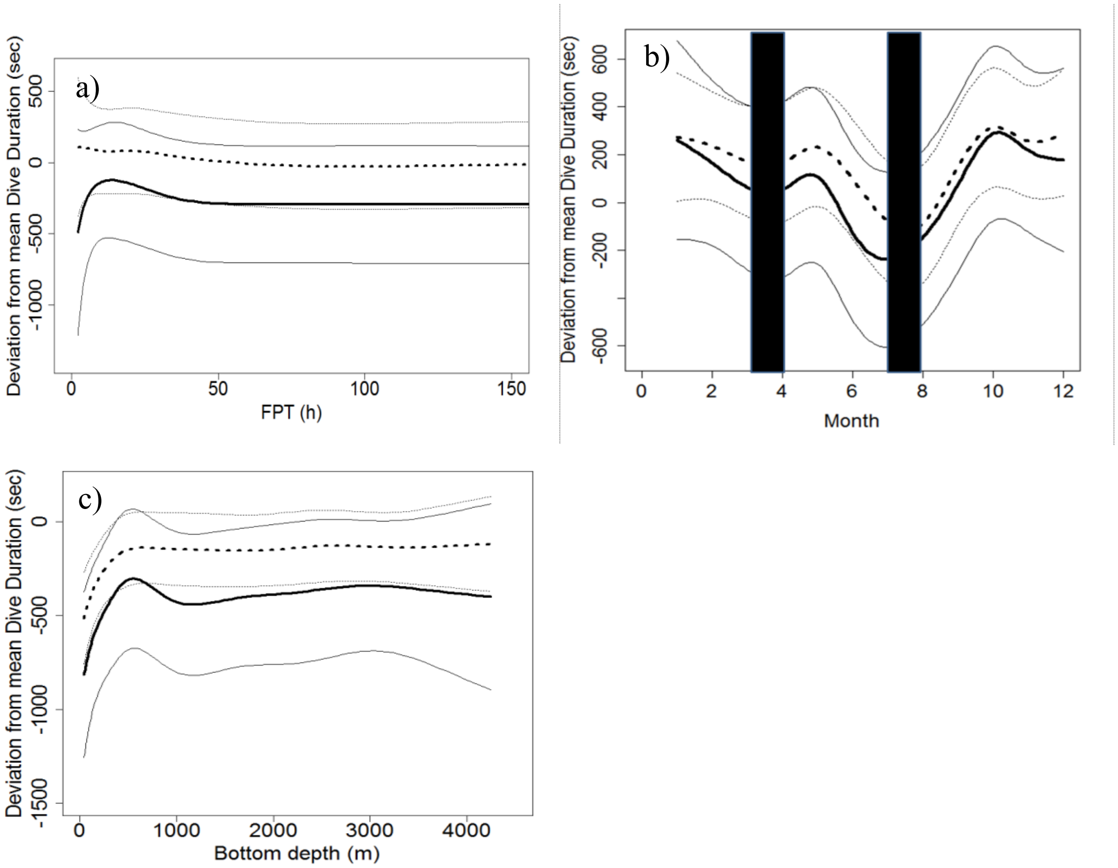


Figure 4.7: Dive duration model results: Predicted results for a) FPT (h), b) Month (black columns represent approximate fasting periods) and c) Bottom depth (m) for male (n=18) and female (n=33) hooded seals. Solid black line represents males and hashed line represents females. Thin black lines represent standard error.

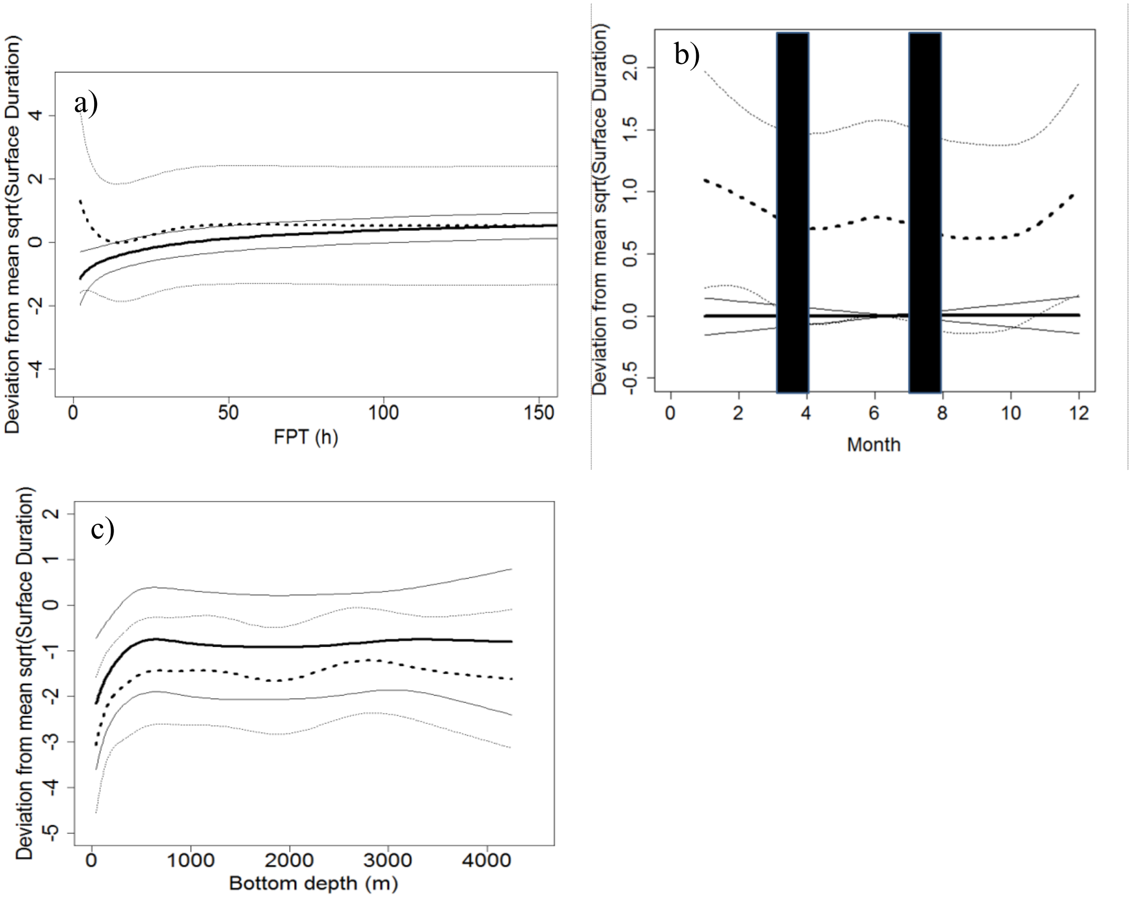


Figure 4.8: Surface duration model results: Predicted results for a) FPT (h), b) Month (black columns represent approximate fasting periods) and c) Bottom depth (m) for male (n=18) and female (n=33) hooded seals. Solid black line represents males and hashed line represents females. Thin black lines represent standard error.

CHAPTER 5: Drift diving by Hooded seals (*Cystophora cristata*) in the Northwest Atlantic Ocean

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5.1. ABSTRACT

Many pinniped species perform a specific dive type, referred to as a 'drift dive', where they drift passively through the water column. This dive type has been suggested to function as a resting/sleeping or food processing dive, and can be used as an indication of feeding success by calculating the daily change in vertical drift rates over time, which reflects the relative fluctuations in buoyancy of the animal as the proportion of lipids in the body change. Northwest Atlantic hooded seals perform drift dives at regular intervals throughout their annual migration across the Northwest Atlantic Ocean. We found that the daily change in drift rate varied with geographic location and the time of year and that this differed between sexes. Positive changes in buoyancy (reflecting increased lipid stores) were evident throughout their migration range and although overlapping somewhat, they were not statistically associated with high use areas as indicated by First Passage Time (FPT). Differences in the seasonal fluctuations of buoyancy between males and females suggest that they experience a difference in patterns of energy gain and loss during winter and spring, associated with breeding. The fluctuations in buoyancy around the moulting periods are similar between sexes.

Key words: Hooded seal, *Cystophora cristata*, sexual segregation, drift diving, migration

5.2. INTRODUCTION:

Pinniped life-history is often characterized by seasonal cycles of terrestrial (or ice bound) fasting (or reduced feeding) and at-sea foraging where energy reserves are replenished. Fasting periods coincide with periods of increased energy expenditure (whelping/breeding and moulting) and pinnipeds prepare for these periods by undertaking extensive foraging trips and feeding at depth (Houston et al. 2007). Such activities prevent direct observation of feeding and consequently information on feeding success and prey consumption is difficult to obtain. A variety of methods have been developed to indicate important areas for feeding, for example the use of stomach or oesophageal temperature tags to record when the seal consumes prey (e.g., Andrews 1998, Austin et al. 2006, Horsburgh et al. 2008, Kuhn and Costa 2006), and video and image recording instruments to record prey encounters (e.g., Davis et al. 1999, 2001, Watanabe and Takahashi 2013, Williams et al. 2000). Such devices can provide interesting information about foraging behaviour and intake rates, but often have limited sampling duration. A different method, offering long term (months) information of possible feeding success, is the investigation of pinniped diving behaviours by the use of satellite linked time-depth recorders (e.g., Asaga et al. 1994, Burns et al. 2004, Crocker et al. 1997, Fedak et al. 2002, Folkow et al. 1996, Le Boeuf et al. 1993, Martin et al. 1998, Thums et al. 2011, Webb et al. 1998). Indications of energy acquisition along the migration track can be observed through seasonal fluctuations in body composition, which should be reflected by changes buoyancy (e.g., Aoki et al. 2011, Bailleul et al. 2007, Beck at al. 2000, Biuw et al. 2003, Crocker et al. 1997, Mitani et al. 2010, Robinson et al. 2010, Webb et al. 1998). Seals do not have anatomical structures allowing them to regulate their buoyancy (below the depth where residual air in the lungs no longer has an effect (Biuw et al. 2003)) and consequently, buoyancy is determined by the ratio of lipid to lean body tissue (Beck et al. 2000). Blubber or lipid tissue is positively buoyant while lean tissue is negatively buoyant; hence an animal with a high ratio of lipid to lean tissue is more buoyant than an animal of similar mass but with a lower ratio of lipid tissue (Beck et al. 2000, Webb et al. 1998). Generally, seals store energy to be used during periods of fasting in an expanding layer of blubber, although they may also invest some of the energy attained during successful foraging by building core mass (i.e., muscles) (e.g., Le Blanc 2003). A particular dive profile, referred to as a "drift dive" has been identified in some pinniped species (e.g., northern elephant seals (*Mirounga angustirostris*) (Aoki et al. 2011, Asaga et al. 1994, Crocker et al. 1997, Mitani et al. 2010, Webb et al. 1998), southern elephant seals (*Mirounga leonina*) (Bailleul et al. 2007, Biuw et al. 2003, Thums et al. 2008) and New Zealand fur seals (*Arctocephalus forsteri*) (Page et al. 2005)). The shape of this dive type appears to be affected by changes in buoyancy, and therefore it can be used to provide information about where the seals are gaining relative lipid condition.

Drift dives are defined as a dive type with a direct descent to a depth at which point the descent rate decreases dramatically until the bottom of the dive, followed by a direct ascent to the surface (Asaga et al. 1994, Le Boeuf et al. 1993), Fig. 5.1). In the case of very fat (blubber rich) seals; a "positive" drift dive may occur. This is when the seal is positively buoyant and drifts upward during the drift phase. However, this is quite seldom observed in adult animals, apart from elephant seal females in the late stages of pregnancy and juveniles at the beginning and end of their first foraging migration (Crocker et al. 1997, Biuw et al. 2003), respectively). Furthermore, a high or low degree of buoyancy would increase energy expenditure during dives, and the optimal condition is probably at neutral buoyancy (Sato et al. 2013). During drift dives the seals are thought to drift passively through the water column (no active swimming) (Bailleul et al. 2007, Beck at al. 2000, Biuw et al. 2003, Crocker et al. 1997, Mitani et al. 2010, Webb et al. 1998), and the dives have been hypothesised to represent periods of physiological processing such as digesting recently ingested food or for rest/sleep (Asaga et al. 1994, Crocker et al. 1997, Le Boeuf et al. 1993). It has also been hypothesised that the form of this dive type, in addition to physiological functions, makes the seals less susceptible to predation, as the drift phase would start once they enter into the "safe zone" below possible predators' depth range (e.g., Mitani et al. 2010).

Regardless of the function of these dives, the buoyancy will be determined by the difference between the density of the seal and the surrounding sea water (Biuw et al. 2003). Sea water density varies with salinity and temperature, and in less saline, ice covered waters this could result in a lower density of seawater causing the seal to have a higher vertical speed than in more saline waters. However, Biuw et al. (2003) found that this only accounted for <1% of the overall bias when investigating drift diving in southern elephant seals. Drift rates will also be influenced by physiological and behavioural changes such as residual air in the lungs, drag and the orientation of the body in the water (Biuw et al. 2003; Mitani et al. 2010). Biuw et al. (2003) found that residual air in the lungs accounted for the highest bias, and that this would depend on the depth where the drift segment would occur. They also found variability in drift rate at shallow dives (< 100m) suggesting that the seals voluntarily adjusted the volume of residual air in the lungs to optimise buoyancy during shallower dives. Furthermore, Mitani et al. (2010)

found that juvenile elephant seals would roll over on their backs and sink like a "falling leaf" during the drift phase, reducing the vertical speed to a minimum. These factors might influence the accuracy of identifying drift dives, and once the dives have been identified, the interpretation of the fluctuations in buoyancy can be challenging. A seal can invest acquired energy to improve their condition through somatic growth (lean tissue) or storing it as lipid tissue. It can therefore be difficult to interpret what a decrease in buoyancy represents. It could mean that a seal is foraging successfully and improving body condition by building core mass, or the seal could be experiencing poor foraging conditions, and as a result become skinnier (less blubber). However, despite these aspects of uncertainty, research has documented drift diving as an informative method to investigate the relative change in body composition over time for free ranging pinnipeds (e.g., Aoki et al. 2011, Bailleul et al. 2007, Biuw et al. 2003, Crocker et al. 1997, McIntyre et al. 2011, Mitani et al. 2010, Robinson et al. 2010, Webb et al. 1998).

Hooded seals (*Cystophora cristata*) are sexually dimorphic, capital breeding pinnipeds distributed throughout much of the North Atlantic and adjacent Arctic Ocean (Hammill and Stenson 2006, Rasmussen 1960, Sergeant 1974). They spend two months of the year fasting on the sea ice during breeding and moulting (March and July, respectively), and display a distinct annual migration pattern during the remaining 10 months (e.g., *Chapter 2 and 3*, Bajzak et al. 2009, Folkow et al. 1996, Rasmussen 1960). North Atlantic hooded seals consist of two putative populations. Hooded seals whelping near Jan Mayen (the "West Ice") are considered to constitute the Greenland Sea population while the Northwest (NW) Atlantic population, and the subject of this study, is comprised of animals whelping in Davis Strait, the Gulf of St. Lawrence (the Gulf) and at the Front (off Northeast Newfoundland and Southern Labrador) (Hammill and Stenson 2006). After the breeding period the NW Atlantic population leaves the whelping areas to feed before they eventually arrive at the ice off Southeast (SE) Greenland in June, just prior to the July moult (*Chapter 3*, Bajzak et al. 2009, Rasmussen 1960, Sergeant 1974). Post moult they disperse across the NW Atlantic and Baffin Bay before returning to the respective whelping areas (*Chapter 2*, Fig. 5.2).

The annual migration cycle for capital breeding pinnipeds is heavily influenced by the preparation for, or recovery from, whelping/breeding and moulting. Reproduction represents a period of increased energy demand (of variable length depending on species) and the cost of (or patterns of) mass gain and loss in relation to reproduction differ between males and females (e.g., Beck et al. 2003, Breed et al. 2006, Lindenfors et al. 2002, Ralls 1977). Males must acquire more resources to attain, and maintain, their greater size (Le Boeuf et al. 1993, 2000), especially when preparing for the breeding season and competition for females. Male hooded seals lose approximately 14% of their mean body mass (~2.5 kg per day) over a breeding period lasting 2.5 weeks (Kovacs et al. 1996). In comparison, females need to obtain sufficient energy stores to maintain pregnancy and prepare for a short and very intense lactation period. They wean their pup in only 3-5 days, during which time the mother loses on average 10 kg per day (Bowen et al. 1985, Kovacs and Lavigne 1992). Thus, males and females lose a similar amount of energy during breeding, but females lose it in a much shorter time period than males, which can be expected to be more energetically demanding. The difference in energy expenditure over time and the change in total body composition could suggest that males and females have different foraging strategies in order to optimise their body conditions.

Males may have greater demands for resources that can build core tissue, whereas females may have greater demands for resources that can be a rapid energy source for themselves and their pups. These possible differences in energy acquisition may be reflected by differences in their fluctuations of drift rates over time.

Previous analyses have shown that there is geographic segregation between high use areas by male and female NW Atlantic hooded seals (*Chapter 3 and 4*). Andersen et al. (2013b) used First Passage Time (FPT, see (Fauchald and Tveraa 2003) and three habitat variables (geographic location, bottom depth and the Topographic Complexity Index (TCI) to identify such areas based on data from the same dataset as used in this study (*Chapter 4*). FPT is defined as the time an animal use to cross a circle of a given radius (Fauchald and Tveraa 2003), of which the scale of the circle is determined by calculating the animals' average Area Restricted Search (ARS) scale (see Kareiva and Odell 1987). Sex related segregation generally occurred during the post moult/pre breeding period in the northern areas of their range, where males had the longest FPT in the Davis Strait while females had their longest FPT along the Labrador shelf and over the Labrador basin (*Chapter 4*). All seals had a long FPT in SE Greenland, near the moulting area (*Chapter 4*). The Gulf breeding animals also exhibited a high degree of overlap between males and females in the Gulf of St. Lawrence during the post breeding period, but they mixed with the rest of the population in SE Greenland in time for the moult (*Chapter 4*).

The objective of this study was to determine if hooded seals exhibit drift dives and if so, to use this information to extract information about how these animals' buoyancy change over time. A difference in drift diving frequencies across months may be a reflection of different foraging strategies carried out by males and females. We can thereby learn about how males and females allocate energy resources differently to building relative lipid body mass in relation to important life history events such as whelping/breeding and moulting. A change in drift rate may further identify specific locations where they experience an increase in relative lipid tissue, i.e., foraging success. Also, if FPT correctly identify important seal foraging areas, we expect to observe a positive change in drift rate in areas with longer FPTs (i.e., more time spent in a limited area).

5.3. METHODS:

5.3.1 Ethics statement

The capture and tagging protocols were reviewed and approved by the Canadian Council of Animal Care. Capture and deployment of satellite transmitters on seals were carried out under appropriate animal care permits and by experienced personnel with the Department of Fisheries and Oceans (DFO), Canada. This project did not have any adverse effects on the environment. The permit numbers were NAFC 2004-11 and NAFC 2008-04.

5.3.2 Deployment of Satellite Relay Data Loggers (SRDLs)

The study area was the NW Atlantic Ocean, extending from the Gulf of St. Lawrence northwards covering most of Baffin Bay, including Davis Strait, and along the Greenland shelf to SE Greenland (Fig. 5.2). Satellite transmitters were deployed directly after moulting in SE Greenland during three field seasons (2004, 2005 and 2007; 65°N, 37°W), and after breeding/whelping during three field seasons (The Front: 2004 and 2008; 49°N, 52°W; The Gulf: 2004, 2005 and 2008; 46°50′N, 62°W). In total, 51 adult seals were tagged of which there were 33 adult females and 18 adult males. All hooded seals were captured using a V-shaped pole-net on the ice. They were weighed, and subsequently tranquilized using tiletamine hydrochloride and zolazepam hydrochloride (Telazol, AH. Robins Company, Richmond, VZ, USA) administered intramuscularly ($1\text{mg}\cdot\text{kg}_{(\text{body mass})}^{-1}$). Satellite Relay Data Loggers (SRDLs; Sea Mammal Research Unit (SMRU), St. Andrews, Scotland) were glued to the head or upper neck of the seal, using quick drying epoxy glue (Cure 5, Industrial Formulators of Canada Ltd. Burnaby, BC

Canada). The size of the SRDL is 10.5 x 4 cm, weighing approximately 370 grams. The seals were released as soon as they recovered from the tranquilizer.

The SRDLs collect a range of behavioural information about free ranging animals at sea. The data included number of dives, dive depth (deeper than 6 meters), dive duration and surface intervals, along with detailed information of the time-depth profile for each dive. Time and depth were recorded every 4 seconds throughout the duration of the dive and these full resolution profiles were compressed on-board using a broken-stick abstraction algorithm, resulting in four at-depth points plus two surface points (start and end) (Fedak et al. 2001, 2002). Finally, data were compressed before transmission via the ARGOS satellite system (Fedak et al. 2001, 2002, CLS/Service Argos). Transmissions were attempted every 80 seconds when the seals were at the surface. The data was filtered prior to analysis to remove outliers by using an algorithm based on the travelling speed of the tracked animal, distance between successive locations and turning angles (Freitas et al. 2008). We used a maximum swim speed of 2 m/s between successive locations which was similar to that used for grey seals (Austin et al. 2003).

5.3.3 Diving and drift dives:

Drift dives were identified by extracting vertical speeds from all time-depth profile segments having characteristics of drift dive segments (Gordine 2012). Dive profiles are reduced to four inflection points excluding surface points (e.g., Fedak et al. 2001). Two vertical speeds from the segments before and after the deepest point of the dive were extracted. A segment was classified as a possible drift segment when the maximum dive depth was deeper than 50 m, absolute vertical speed of the dive segment was between 0.6 and 0 m/s, the length of the segment was longer than 3 minutes and when the segment constituted more than 40% of the total dive duration (Fig. 5.1). Only descending segments (before the deepest point of the dive) fulfilled these criteria. A selection of dives, which included such potential drift dive segments, were also investigated visually, so that we could be certain that our selection would be representative of drift dives and reduce the likelihood of bias in selected dives.

The chosen inflection points do not represent true start or end points of linear time-depth segments; instead they rather represent points at which the dive profile changed its shape most significantly (Photopolou, 2012). Consequently, the true start and end of a drift fragment are not known, and the extracted vertical speed from the inflection points will have an error component. We therefore used a robust iterative smoothing method to remove outliers in our time series of extracted vertical speeds (e.g., Press et al. 1992) assuming that the drift rate changes slowly over time and not in sudden jumps. This method calculated a weighted running mean with a Gaussian kernel of sigma = 4 days for each time step. Vertical speeds deviating more than 0.15 m/s from the smoothed values were rejected from the time series and the process was repeated. After three to four steps no more outliers were found and the remaining vertical speeds were used to calculate a weighted running mean, which we assume to be representative of drift rates. These drift rates were then used to extrapolate daily drift rates and daily changes onto the complete time series. Every dive therefore had an associated drift rate and dives with a dive segment fulfilling the above criteria, as well as an associated vertical speed within 0.06 m/s of the daily drift rate value, were classified as potential drift dives.

The percent frequency (i.e., number per unit time) of drift dives throughout the 24 hour period and by month was investigated. The objective was to identify the timing and frequency of drift diving. The sunlight hours vary significantly at Arctic latitudes, and may affect diving behaviour more than the actual time of day. We therefore calculated the sun angle at the location of dive occurrence to investigate how sunlight affected dive behaviour on a diurnal basis. Random intercept models were used to investigate regular diving behaviour (dives with no drift component; maximum dive depth and dive durations) on a diurnal scale and drift diving frequencies on a diurnal and monthly scale. Individual seal id was implemented as the random factor in the models.

A GAM was fitted to generate spatial predictions of the daily change in drift rates throughout the annual migration. The models were run on two datasets (aggregated dataset based on ARS (FPT dataset), and the full drift dive dataset). The effects of FPT, geographic location and day of year were used as predictor variables, and the daily change in drift rate was set as the response variable. The FPT dataset was averaged across an 80 km step (based on a 40 km ARS scale used in Chapter 4) and FPT was calculated per step yielding 1,459 data locations. The GAM was implemented with the gam function in the mgvc library in R (Wood 2006, 2008) using restricted maximum likelihood (REML) as the fitting method. Random effects were implemented by using the "re" smoother option, which is appropriate for simple, independent random effects (Wood 2011). We were therefore running a GAM including random effects (individual seal id) instead of a mixed GAM (GAMM). Sexual segregation in the data was investigated by including sex as an interaction term.

To select between competing models we applied an information-theoretic approach and examined parameter weightings using Akaike's Information Criterion (AIC). All models (14) nested within the full model were assumed to be candidate models, and models with $\Delta_i < 2$ are considered to have substantial support while $\Delta_i > 10$ have very little support (Δ_i is the difference between the AIC of the best fitting model and that of model *i*; (Burnham and Anderson 2002)). If the addition of one predictor variable to a model resulted in an AIC of < 2 values from the model without this variable, and the model fit was not improved (deviance explained), the added variable was deemed a pretending variable and removed from the analysis (Anderson 2008).

All maps were created using ArcGIS Desktop 10 (Environmental Systems research Institute, Redlands, CA) and the bathymetric backdrop and 1000 m depth contour line was derived using bathymetry data from the General Bathymetry Chart of the Ocean (GEBCO; http://www.gebco.net/).

5.4. RESULTS:

In total, we examined 87,565 dives from 51 adult seals with complete dive records. Of these, 6,806 dives from 47 seals fitted our selection of criteria for drift dives (31 females and 16 males; Table A5.1). The number of drift dives extracted per seal ranged from 16 to 846 (Mean = 144.81±156.97) depending on tag survival time and individual variability in drift diving occurrence. The mean maximum drift dive depth across all seals was 199.25±95.10 m and the mean drift dive duration was 15.03±5.38 min.

5.4.1 Diurnal dive behaviour:

There was no clear diurnal pattern observed for regular dives (i.e., dives with no drift component) based on sun angle to dive locations (Fig. A5.1). In contrast, there was a clear diurnal pattern observed for drift dives where 80% occurred when the sun was below the horizon (Fig. A5.1) and no drift dives were observed during the day between 08:00 and 15:00 (Fig. 5.3).

A linear mixed model showed a significant difference in drift dive frequencies between hours within a 24 hour cycle (F = 6.59, $p<0.0001$, df = 17), and a significant level of sexual segregation was found (F = 1.71, $p<0.05$, df = 17) where males performed more drift dives than females between 01:00 and 08:00 and females performed more drift dives than males between 19:00 and 23:00 (Fig. 5.3).

Dive duration and maximum dive depth of regular dives were highly correlated ($r=0.74$, $p<0.001$) and both sexes dived significantly deeper and longer during mid day (F = 66.62, $p<0.001$, df = 23, F = 178.61, $p<0.001$, df = 23, respectively, Fig. A5.2 a, b).

5.4.2 Drift diving behaviour by month:

Using a linear mixed model we detected a significant difference in drift dive frequencies between months (F = 10.93, p < 0.0001, df = 11). Males and females carried out a similar amount of drift dives per month and there was a clear increase in drift dive occurrence after breeding in April and May, for both sexes (Fig. 5.4).

5.4.3 Daily change in drift rate:

Of a total of 6,806 drift dive locations, the averaged FPT data, aggregated at the ARS scale of 40 km, yielded 1,459 data points. We ran 14 candidate models on each of the datasets, identifying FPT as a pretending variable. We therefore disregarded the aggregated dataset and focussed this analysis on the full drift dive dataset of 6,806 dive locations. The best GAM model indicated that seasonality (represented by the day of year) and the geographic location of the seals best explained the variation in the daily change of drift rates ($AICw_i = 1$, deviance explained = 29.7%; Table A5.2, Fig. A5.3). All other models were highly implausible ($\Delta AIC > 10$). To further investigate the segregation between males and females identified in the best model, we decided to run the GAM model on males and females separately and found that the model investigating the daily change in drift rate by geographic location and day of year was a better fit for males than for females (deviance explained = 35.1% and 19% respectively, Fig. 5.5). A difference in the timing of relative lipid loss or gain (as represented by changes in drift rates) was observed, although, both males and females experienced a large negative change in drift rate (i.e., reduced buoyancy) directly after the moult (Fig. 5.5). Females experienced a loss of buoyancy in December, but regained lost buoyancy by February. They then exhibited some loss in relative lipid condition directly prior to the breeding period. Males showed level buoyancy through the winter, but a decrease occurred in January before a continued increase in relative lipid condition up to the start of the breeding period. They further experienced a large negative change in buoyancy directly after the breeding period was over, while females started to increase their relative lipid condition at an earlier stage than males. Both males and females experienced a gain in relative lipid condition at the end of June and beginning of July, immediately before the moult (Fig. 5.5).

We mapped the fitted values from our best GAM to identify and compare the geographic locations of increased relative lipid content as shown by the change in buoyancy for males and females (Fig. 5.5). Males experienced a positive change in drift rate (i.e., increased buoyancy) throughout their range (daily change 0-0.25 cm/s), although, 11 individuals in the southern part of the range experienced a higher positive change (the Gulf, southern Labrador Sea, Southwest and East Greenland (daily change of > 0.25 cm/s), Fig. 5.6a). Females seemed to experience a large positive change in buoyancy in the northern parts of the Labrador shelf and in the Davis Strait, but also around the Front and Flemish Cap area (daily change > 0.25 cm/s). However, positive change occurred on and off the Labrador shelf as well as in SE Greenland. Females exhibited a lower level of positive change in the Gulf than males (daily change < 0.25 cm/s, Fig. 5.6b).

5.5. DISCUSSION:

Drift diving has been identified in a number of other pinniped species and this study shows that hooded seals of the NW Atlantic Ocean also carry out this specific type of dive. Hooded seals exhibited a clear diurnal pattern in dive duration and depth of dives, where regular dives were longer and deeper during the day than at night (Fig. A5.2 a, b), although the frequency of dives were similar between night and day (Fig. A5.1). These findings are similar to what Folkow and Blix (1999) found for the Greenland Sea population and suggests that hooded seals are foraging on diurnally migrating prey that approach the surface at night and migrate down during the day. Drift dives occurred with highest frequency during the time of day when the seals exhibited the lowest dive duration and shallowest dives (i.e., night time; Fig. 5.3). Crocker et al. (1997) suggested that northern elephant seals would drift while processing food, thereby balancing the oxygen demands of foraging and locomotion while diving continuously and remaining within their aerobic limits. Seals have further been found to be able to delay costly physiological processes (e.g., digestion) that are incompatible with the physiological adjustments to diving until hours after periods of active foraging (Sparling et al. 2007). It is not possible for us to infer the function of drift dives for hooded seals based on diurnal diving behaviour without further analysis. Crocker et al. (1997) hypothesised that drift diving is a behavioural response to increased feeding success, however, the seals' ability to invest attained energy to somatic growth (resulting in decreasing buoyancy), makes the relationship between increased drift dive frequencies and foraging difficult to interpret with certainty.

Data on the exact timing and duration of the moult are scarce (Rasmussen 1960) but we found that the time period where no tags were active (lost as a result of the moult, or not attached because the moult was not yet finished), occurred between June 27th – July 20th, which suggests that the moult started at the end of June for some seals and ended towards the last week of July for others. After the moult, both sexes showed a large decrease in buoyancy, indicating increasingly poor body condition. Rasmussen (1960) reported that the total reduction in blubber mass during moulting would vary depending on the condition of the seals at arrival to the moulting grounds. Female hooded seals seemed to start to store lipid energy directly after breeding, steadily increasing their buoyancy towards the moult. Males showed an initial decrease in buoyancy, which may indicate that they use the first half of this same period to allocate ingested resources preferentially towards somatic growth, (i.e., relative lean body mass). According to our results males did not start to increase their relative lipid condition until late May (Fig. 5.5). These findings are supported by Thordason et al. (2007) who reported that males were heaviest in core mass (i.e., muscle) in May. They further found that core mass decreased with 14% between May and August and that the males were 10% heavier in October than August as a result of increased relative lipid content. These findings are reflected in our model results, where we found that males exhibit a negative change in buoyancy post moult, and increase buoyancy from mid September to November (Fig. 5.5).

The duration of the moult is similar for both males and females, as opposed to breeding when females invest on average 4 days (Bowen et al. 1985) and males' ~2.5 weeks (Kovacs et al. 1996). This suggests that, although the energy lost during fasting periods is similar between sexes, the timing of loss may be different during breeding, but similar during the moult. Males may also be freer to enter the water and occasionally feed during breeding, as opposed to the moulting period when both sexes fast for a similar amount of time. It has been suggested that the energetic costs associated with the immediate migration after breeding followed by reduced food intake during the moult must be met from energy stored prior to the breeding season or from what have been acquired during the migration between breeding and moulting (Mellish et al. 1999). The relatively poor body condition after the moult (or less relative lipid content) observed for both sexes suggests that the post moult migration marks the beginning of the build up of energy reserves to prepare them for breeding and consequently the moult.

Among sexually dimorphic pinnipeds, males store energy to last through the period of reduced intake during the breeding period and to improve their ability to compete for mates (e.g., Lindenfors et al. 2002). Due to the larger size of males, it is expected that they need to feed more than females if they are foraging on similar prey (Le Boeuf et al. 1993). Although the drift dive frequencies were similar directly after breeding, males have been previously found to perform slightly longer and deeper dives than females during the same time period (see *Chapter 4*). Our habitat model also showed that male and female NW Atlantic hooded seals have different movement patterns, using different geographical areas. These findings could indicate that males and females avoid competition by foraging on similar prey at different depths where males seek out larger prey of the same species found deeper in the water column, or that they feed on different prey. Tucker et al. (2009) found evidence of variation in diets, diet quality and breadth, reflecting different foraging strategies by males and females during the pre and post breeding periods. However, the most important prey item for both sexes post breeding were redfish.

After the moult, males appeared to recover relative lipid stores faster than females by exhibiting an increase in buoyancy from mid September, while females did not experience an increase in buoyancy until a month later (mid October, Fig. 5.5). Andersen et al. (2013b) found that males undertook longer dives during this period, but the dive depths were similar between sexes throughout the winter months (*Chapter 4*). This further suggests that hooded seals exhibit a resource partitioning strategy through spatial segregation. Our best model results (geographic location and day of year influencing the fluctuations buoyancy) also showed a higher deviance explained for males, supporting earlier findings that males seem to be more spatially localised in their habitat use than females (*Chapter 3 and 4*).

Females experienced two periods of negative change in buoyancy during the post moult/pre breeding period (December and February, Fig. 5.5). The buoyancy at these times may have been negatively influenced by the increasing lean weight of the growing foetus (e.g., Le Boeuf et al. 2000, Robinson et al. 2010, Webb et al. 1998). As the foetus is growing, the female would need to counteract the added relative lean mass by increasing her relative lipid condition to maintain neutral buoyancy, which may explain the decreased drift rate observed in December and January (Fig. 5.5). Robinson et al. (2010) reported a marked decline in the daily change in drift rates well before the return phase of the migration in female elephant seals. Although hooded seal pups have been found to be born with an average of 15.9 ± 3.10% fat (Mellish et al. 1999) which is higher than what has been found for elephant seals (~ 4%, Rea and Costa 1992), the negative influence on the female hooded seals' buoyancy may still be detectable. We would also expect females to show an initial negative change in drift rate post breeding due to the buoyancy lost during lactation (females have been found to lose on average 10 kg a day during the 4 days of lactation; (Kovacs and Lavigne 1992)). Thus the rapid loss of relative lipid content by females vs. the more gradual loss by males (2.5 weeks, 2.5 kg a day; (Kovacs et al. 1996) during breeding may trigger behavioural differences in feeding strategies which could be reflected in the dive behaviour.

In this study we explored the relationship between areas where seals spend more time (i.e. longer FPT) (see Andersen et al 2013a, b) presumably to feed, and areas where seals appeared to be successfully feeding, assuming that resources are allocated preferentially to lipid storage (which we know are not always the case). Although we observed some area overlap, FPT did not explain changes in hooded seals' buoyancy during migration. Hooded seals generally started their post fasting migration by transit to locations where they slowed down their passage time, which was reflected in an initial decrease in body condition (negative change in daily drift rate) after a fasting period (Fig. 5.5; Fig. A5.4 – A5.7). Elephant seals also show periods of decrease in body condition during migration, which has been linked to long travelling distances and short travel time (Biuw et al 2003, Bailleul et al. 2007). However, reasons for why FPT did not explain changes in buoyancy could be due to hooded seals' ability to forage successfully regardless of passage time (observed increased buoyancy). In addition, an observed decrease in buoyancy does not necessarily mean that the seal is experiencing poor foraging conditions. Seals have also been found to return to areas of successful foraging based on previous experience, where they slow down and increase their turning rate without, necessarily, an increase in prey encounters (Thums et al. 2011).

In summary, this study has shown that NW Atlantic hooded seals exhibit drift dives, as also observed in a number of other pinnipeds. Although it is difficult to directly observe hooded seals and how they interact with their environment, examining these dives have provided valuable information on where, and when, hooded seals experience seasonal changes in relative lipid content and allowed us to relate these changes to important life history events such as whelping/breeding and moulting. Differences in seasonal fluctuations of buoyancy between males and females suggest that they respond differently to the annual cycle of fasting periods and energy acquisition.

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5.8. FIGURES

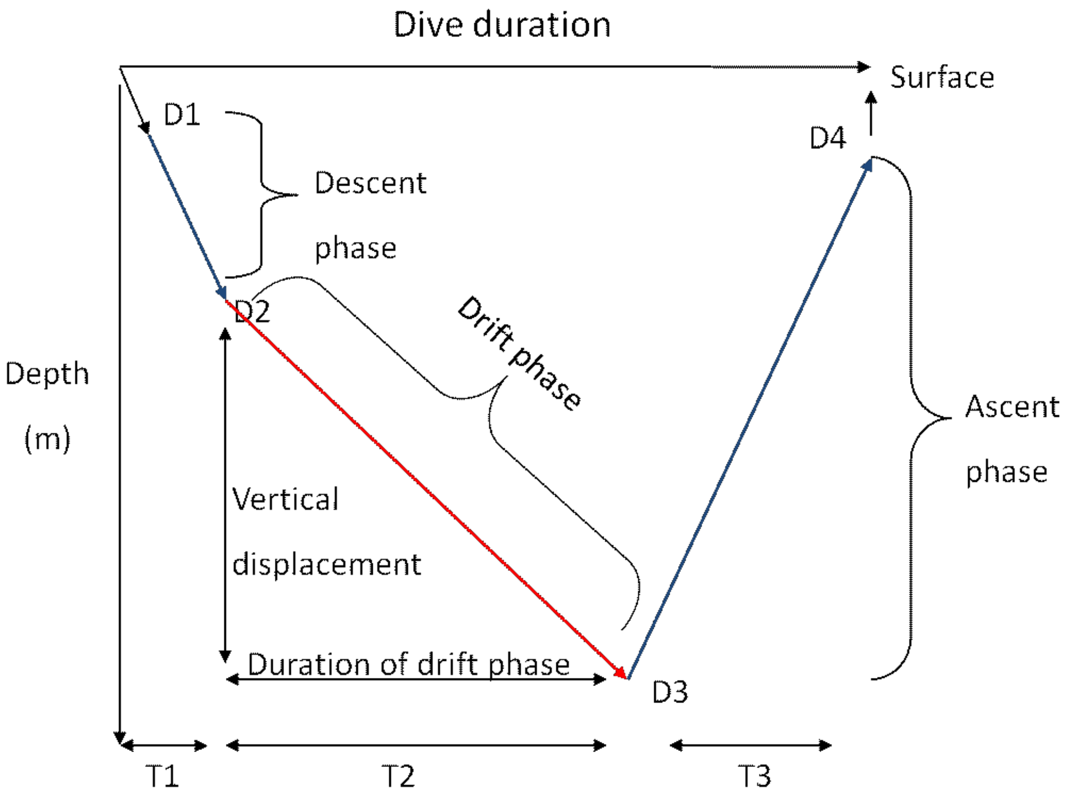


Figure 5.1: A description of a drift dive: time spent from point D1 to D2 represents fast descent with possibly active swimming, D2 to D3 represents a dramatic decrease in vertical speed, with no active swimming and is called the “drift phase”. D3 to D4 represents ascent with active swimming. T1 and T3 represent the duration of ascent and descent and T2 is the duration of the drift phase. T1 to T3 is the total duration of the dive.

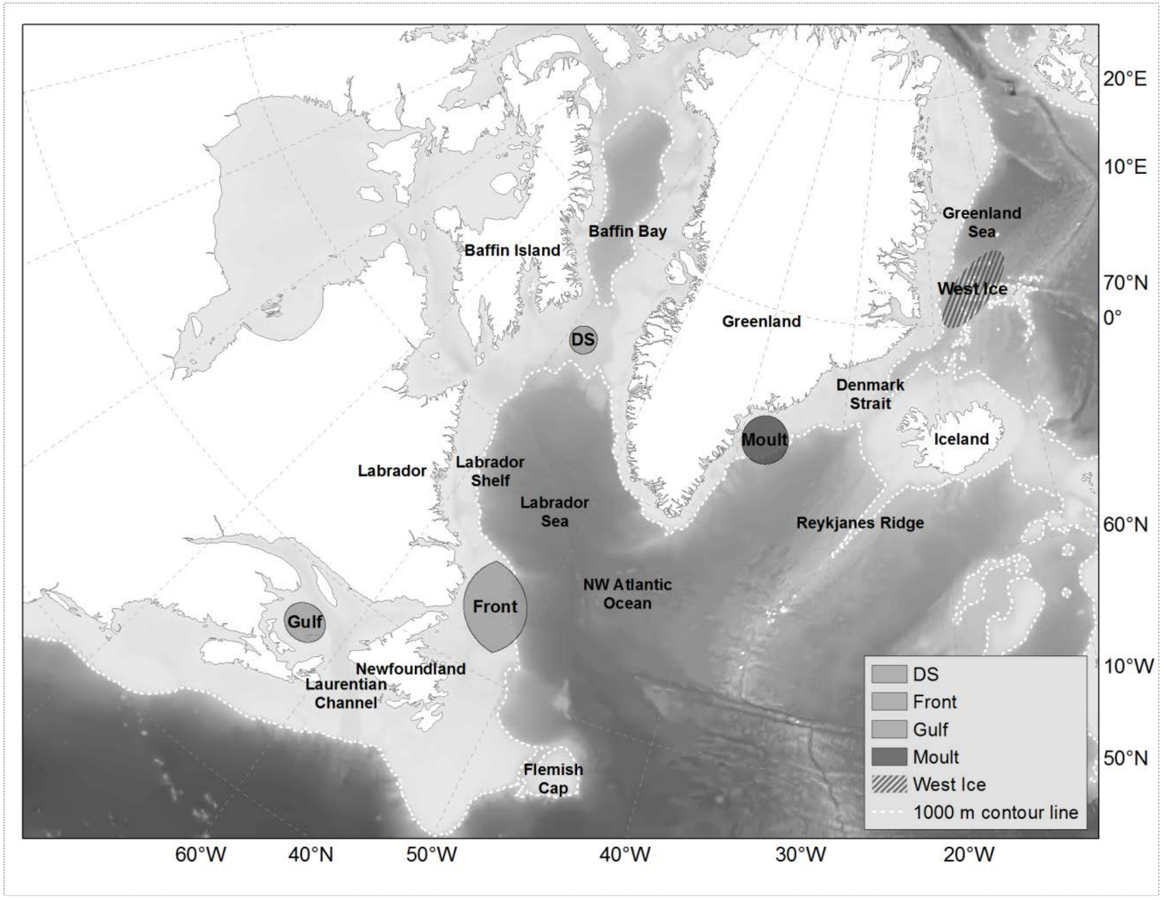


Figure 5.2: Map over the study area: Moulting area in southeast Greenland and breeding areas in Davis Strait (DS), The Front and The Gulf. Bathymetry of the study area is presented as backdrop in grey scale. Dashed grey line is the 1,000 m contour.

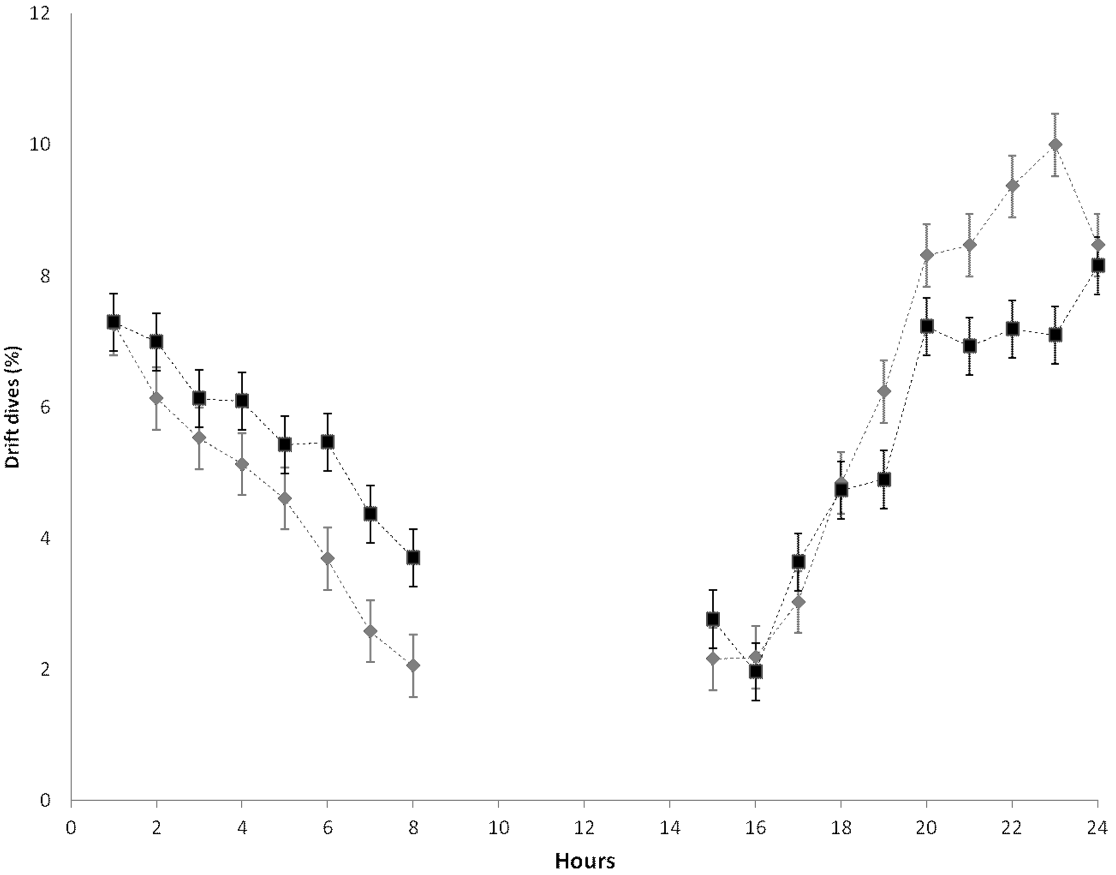
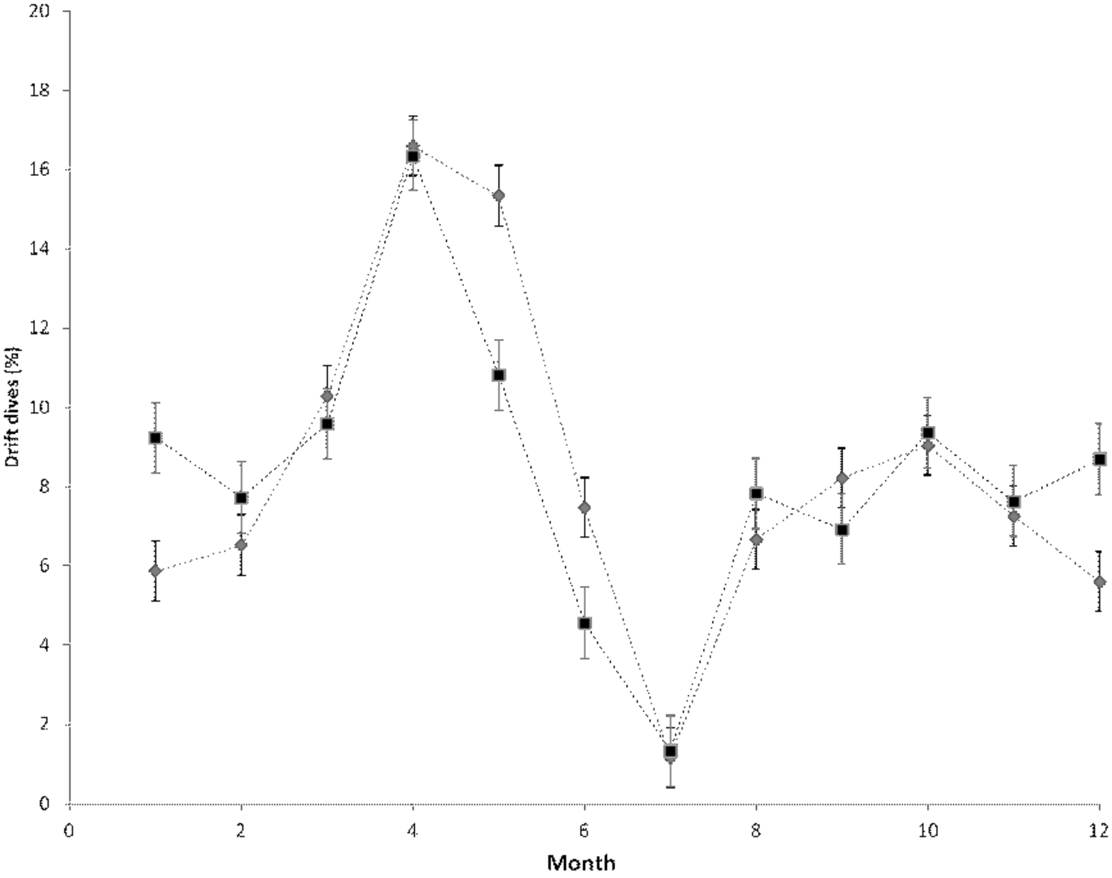


Figure 5.3: Percentage of drift dives as a function of time of day (1-24 = 01:00-24:00) across females (grey), and males (black). There were no drift dives observed between 08:00 and 15:00. Females: n=30, males: n=17. Error bars represent the standard error.



Months

Figure 5.4: Percentage of drift dives as a function of month (1-12 = January – December) across females (grey), and males (black). Females: n=30, males: n=17. Error bars represent the standard error.

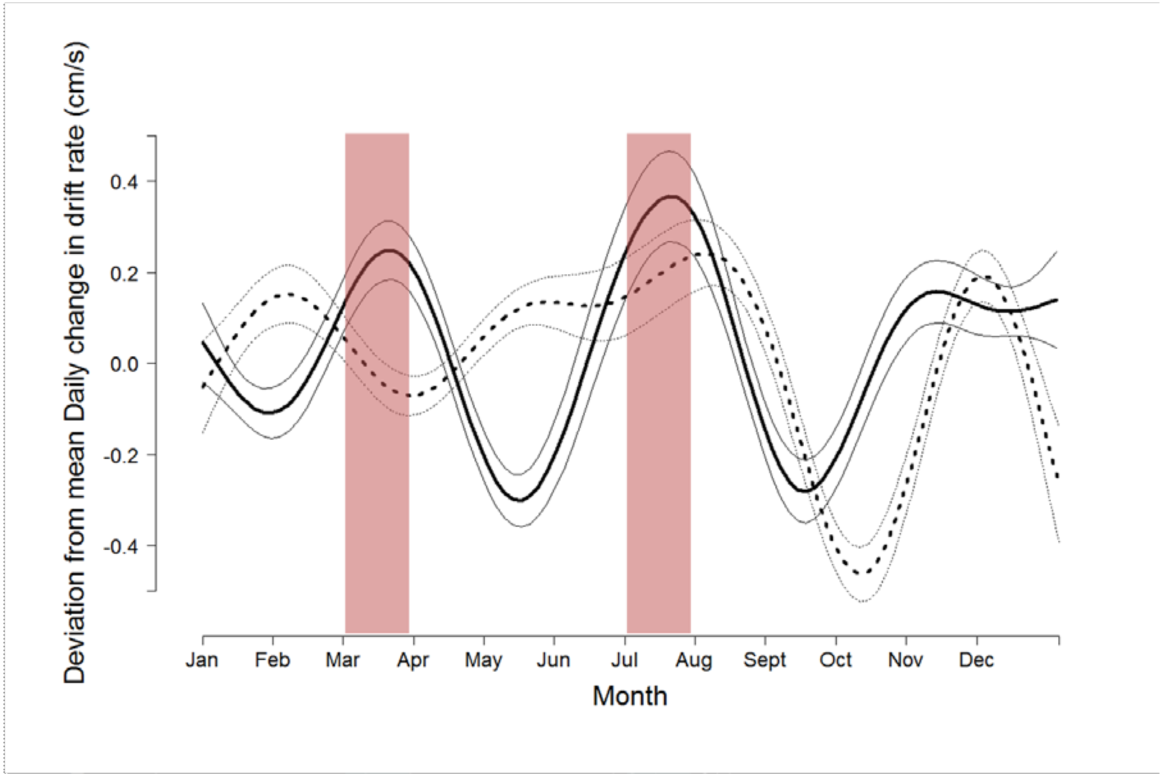


Figure 5.5: Predicted GAM results when only males and females were run in seperate models (males: solid black line (n=17) and female:s dashed line (n=30). The x-axis show the the month and y-axis show the deviation from the mean daily change in drift rate (cm/s) where the mean is at 0. Thin lines represent the standard error and red columns represent the annual fasting periods (breeding/whelping in March and moulting in July).

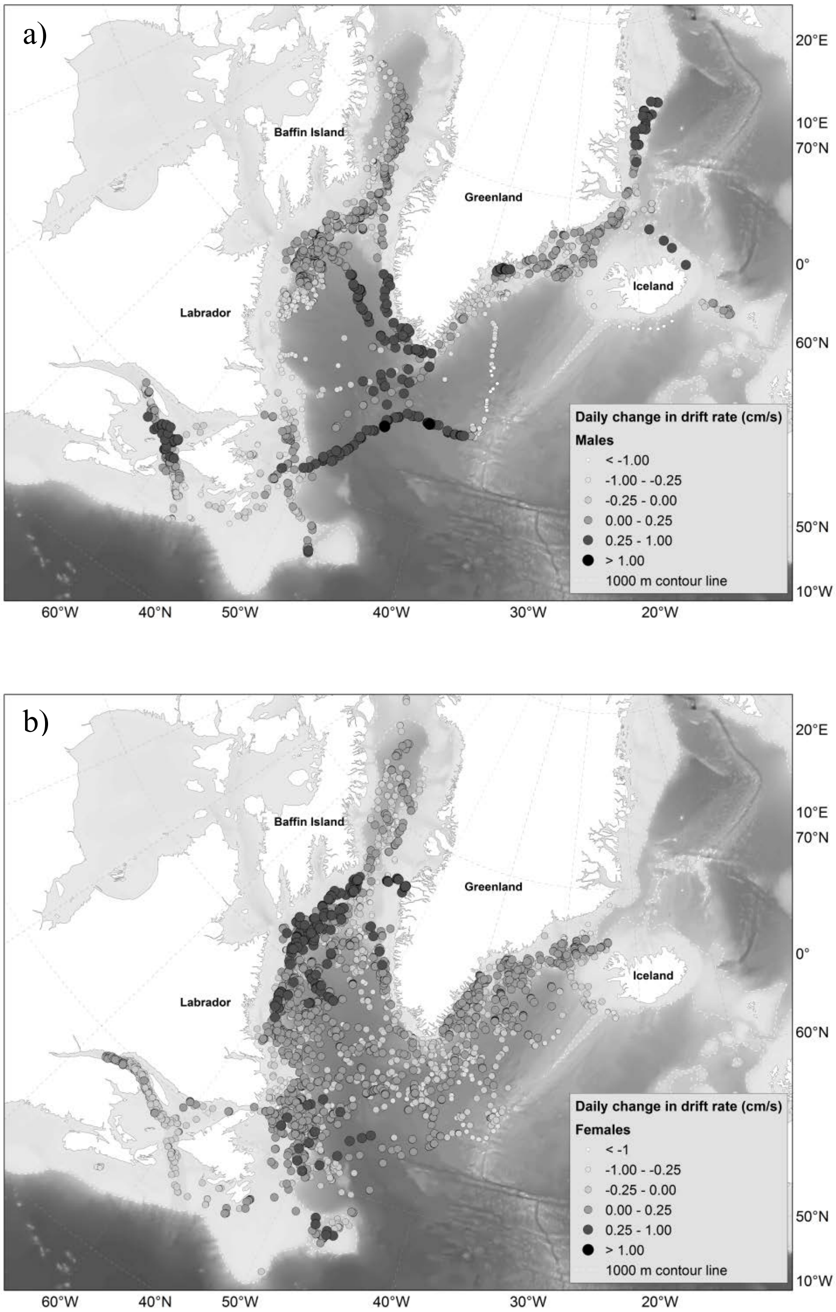


Figure 5.6: Plot of fitted values (daily change in drift rate cm/s) from the best GAM for a) males (n=17) and b) females (n=30). The darker the colour, the bigger the daily change in drift rate.

CHAPTER 6: Summary and conclusions

6.1. Habitat selection

This thesis has offered in-depth analyses of the annual distribution, movement patterns, habitat selection, diving behaviour and fluctuations of relative lipid body condition of the NW Atlantic hooded seals in relation to important life history events (whelping/breeding and moulting). One of the baseline assumptions was that the spatial distributions and availability of resources would influence the species' habitat selection and use. The information obtained from Chapter 2 helped develop research questions about the annual ecological requirements and patterns of habitat selection for the population. It further revealed the first signs of sex and age related spatial segregation through the description of monthly movements.

Highly mobile marine predators with a large distribution range are greatly dependent on locating patchily distributed prey in order to secure their reproductive success and survival (e.g., Stephens and Krebs 1986). It was therefore expected that NW Atlantic hooded seals' foraging effort would increase as long as the gain per unit food was higher than the energetic cost (optimal foraging theory: MacArthur and Pianka 1966). According to Charnov (1976), once the animal has located an acceptable patch, it needs to make the decision of when to leave. The ARS scale provided information on the spatial boundaries of this search range, and the amount of time the seals spent crossing that area (FPT) offered important information on its energetic profitability (i.e., prey availability; *Chapter 3 and 4*). FPT was incorporated into habitat models using oceanographic conditions as proxies for energetically attractive areas. High use areas were described by the habitat properties identified by the best habitat models (*Chapter 3*).

There was some spatial and temporal overlap in FPTs in relation to the various habitat predictors between the seal groups, but variability between sex and age, suggested from observations made in Chapter 2, was statistically confirmed (*Chapters 3 and 4*). Habitat models identified SST, depth and surface chlorophyll as the most important factors influencing habitat selection by NW Atlantic hooded seals, and juveniles showed a higher affinity towards ice than adults (*Chapter 3*). Males and females preferred similar conditions, but were separated geographically, and by bottom depth, at various times of the year (*Chapter 3 and 4*). Chlorophyll did not, however, seem to have a direct influence on male habitat selection, and they were more localised within their foraging habitat, focusing their search effort on top of shelves and sea mounts (*Chapter 3*). Females displayed a more dynamic, off-shelf distribution across deeper waters, foraging on vertically migrating prey (*Chapter 4*). This spatial segregation could be a result of a resource partitioning strategy or it could indicate that male and female hooded seals have different energetic needs associated with the fasting seasons. Adult hooded seals have been found to seasonally exhibit a difference in diets where males preferred higher proportions of redfish while females consumed greater proportions of benthopelagic fishes such as blue hake and white baraccudine (Tucker et al. 2009). The morphological differences between males and females may also be a reason for why they may target prey with different levels of energetic reward. Although pelagic prey tend to have a higher energy density than benthic prey, the cost of foraging on highly mobile pelagic prey for larger bodied hooded seal males may not be beneficial, making benthic resources increasingly attractive (Tucker et al. 2013).

Juvenile NW Atlantic hooded seals showed a higher affinity to ice than adults during the post-moult/pre-breeding period and shared with females a pattern of increased FPTs in relation to low levels of chlorophyll (*Chapter 3*). Young of the year, initially, spent time in shallower waters (e.g., Grand Banks and the Gulf) before they began to follow similar migration patterns as the adults (*Chapter 3*). Size segregation in juveniles may influence habitat selection as seen in e.g., Steller sea lions (*Eumetopias jubatus*) and elephant seals (Fadely et al. 2005, Field et al. 2005, Campagna et al. 2006, 2007, Muelbert et al. 2013), thus a comparison of immature juveniles of different known ages could reveal how habitat selection patterns and use change as they are getting closer to maturity and larger in size (e.g., Burns 1999, Field et al. 2005, Folkow et al. 2010).

The model fit (deviance explained) was low for the habitat models in Chapter 3. This could suggest that the oceanographic parameters included in the models (SST, chlorophyll, bottom depth, slope and ice concentration) are acting as proxies for currently undefined processes important for NW Atlantic hooded seal habitat selection. The increased model fit in Chapter 4 indicated that habitat use and diving in hooded seals were better explained by topography, season and the geographic location than by environmental parameters measured at the surface. Hooded seals mainly carried out dives into the mesopelagic zone (annual mean maximum dive depth was 255 m) along the shelf break and areas of high topographic relief with mean bottom depths between 700-1200 m (*Chapter 4*). Analysis of temperature data from within foraging zones have demonstrated to be useful predictors in studies of other pinniped species (e.g., Field et al. 2001, Biuw et al. 2007; 2010, Heerah et al. 2013), and may offer a useful description of habitat selection and use by hooded seals.

6.2. Distribution range

Spatial segregation between seal groups (males, females and juveniles) were implied based on the observed differences in movement patterns within the distribution range, but it became apparent that the population shared an overall similar migration area, across specific subarctic and Arctic parts of the NW Atlantic Ocean (*Chapter 2*). This distribution area and the observed common movement direction through the area according to month (or seasonality) may be influenced by spatial boundaries (*Chapters 2 and 3*). Baffin Bay was the northernmost limit of their range, the Gulf was the southwestern limit and SE Greenland was the eastern limit (although individual variability was observed; *Chapters 2 and 3*). None of the tagged seals entered into the Canadian archipelago or Hudson Bay, or ventured south into the Atlantic Ocean, except for one seal that made a trip to the Faeroe Islands. This distribution pattern indicates that the area surrounding the Labrador Basin (and north in Baffin Bay) and the Gulf of St. Lawrence offer optimal and critical habitat for hooded seals of the NW Atlantic population. It appears that, in particular, the Labrador shelf represents important habitat than the west Greenland shelf, which seemed to mainly be an area of transit. Although seals foraged successfully along the west Greenland shelf (especially males), but they did not use the shelf extensively as they did the Labrador shelf, Davis Strait and Baffin Bay (*Chapter 4 and 5*). Other areas which have been identified as important habitat for this species during the 10 months of migration are the SE Greenland shelf, the Front and the Gulf of St. Lawrence (*Chapters 2-4*).

The Greenland Sea population does not share similar synchrony in the migration route, and no sexual segregation has been observed (Folkow et al. 1996). However, their distribution during migration was similarly confined to waters of high topographic relief such as the shelf break and submarine ridges and sea mounts (Folkow et al. 1996). Resource availability in a heterogeneous environment is influenced by the geographic restrictions of the area in terms of topography and hydrographic properties. The variations in movement patterns and foraging strategies among hooded seals may therefore be a result of prey distribution associated with local oceanographic conditions. For example, the Gulf breeding herd showed a clear preference to seasonal foraging in the spatially restricted Laurentian Channel (< 500 m deep) rather than along the Labrador and Newfoundland shelf areas (Bajzak et al. 2009). Other species show similar variability in habitat selection. Different breeding populations of southern elephant seals differ in habitat use according to season and the properties of the surrounding habitat. Animals from Patagonia (Península Valdés), Macquarie Island, Kerguelen Island, Elephant Island and Bovetøya show distribution patterns related to the continental margin, ice margin and frontal zones in the open ocean where females generally forage pelagically while males generally forage benthically or display greater variation in foraging strategies, exhibiting both benthic and pelagic diving (e.g., Hindell et al. 1991, Campagna et al. 1999, Bailleul et al. 2007, Biuw et al. 2010, Muelbert et al. 2013). However, both males and females from Marion Island have been observed to display a pelagic distribution, although males dive deeper than females (McIntyre et al. 2012). Marion Island is surrounded by deep water, and although possible habitat in shelf areas is available within reasonable proximity, males do not seem to use them (McIntyre et al. 2012). In comparison to these findings for southern elephant seals, the proximity of available shelf habitat and productive upwelling zones in the Gulf may allow hooded seals from this breeding herd to travel short distances to find suitable foraging habitat. In contrast, seals breeding at the Front must move greater distances to find suitable areas to replenish their energy stores after the breeding period. In addition, approximately 90% of the NW Atlantic population breed at the Front which may require them to spread out over larger areas in order to avoid competition for resources.

6.3. Habitat vulnerability

The low level of ice association observed by hooded seals during migrations and the pelagic (and likely solitary) distribution during this time (*Chapter 2 and 3*) may suggest that loss of ice cover due to climate change and other anthropogenic disasters such as an oil spill, may not have large adverse effects on a population level. Increased fisheries pressure and marine transportation due to seasonally larger ice free areas as well as changes to the physical environment such as shifts in prey distribution or a decline in prey density as a result of increased ocean temperatures, could potentially have much more serious consequences (*Chapter 2-5*). However, the most serious threat to the hooded seal population is the loss of important breeding and moulting substrate (March and July). The breeding season is especially vulnerable as females may have problems finding a good birthing place, which can result in miscarriages, increased pup mortality by drowning or starvation due to lower levels of food availability (e.g., Johnston et al 2005, Learmonth et al. 2006, Friedlander et al. 2007, Kovacs and Lydersen 2008). Females normally whelp in a loose herd, located 50 m or more from each other (Kovacs and Lydersen 2008). Less good ice substrate may cause frequent ice breakup, increasing pup mortality through drowning, as well as females may have to whelp in closer proximity to each other which may increase the risk of conflict and disease, and they will become more vulnerable to anthropogenic disturbances.

6.4. *Diving and foraging success*

Hooded seals have impressive diving capabilities and spend 80% of the time below the surface during migration (Stenson et al. 1993). I have here shown how the various seal groups change their diving behaviour according to the FPT through an area, and that they do not, in spite of their ability, dive repeatedly to depths past 500 m (*Chapter 4*). The deepest dive recorded surpassed 1,650 m, but the mean dive depth was only 255±184.9 m and 50% of dives occurred in waters less than 500 m deep (*Chapter 4*). Both males and females had higher dive frequencies within FPTs of ~ 20-40 h at an ARS radius of 40 km (*Chapter 4*). This could mean that prey is distributed at a density making this timeframe from arrival to leaving the patch the most profitable. They increased dive durations and dive depths towards ~20 h FPT, and, with some variability, stabilised this behaviour across longer FPTs. They also displayed an increased surface duration at this scale of restricted search and assumed foraging, and mean bottom depths decrease in areas of increased FPT. Thus, the diving behaviour in areas of longer FPT is very different from areas with faster FPT (i.e., <20h). It is likely that areas of fast FPT represent areas of transit when seals travel towards more preferable habitat conditions.

In general, the diving behaviour seemed influenced by the habitat they resided in. This was reflected in dive depths vs. bottom depths (*Chapter* 4) and slope (*Chapter 3*). For example, females used areas of deeper bottom depths, and displayed association to steeper slopes than males and juveniles (*Chapters 3 and 4*). This indicates that they may prefer off-shelf habitat along the Labrador shelf break, while males and juveniles prefer habitat on top of the shelf in high use areas with very little or no slope. This behaviour is similar to what has been observed for elephant seals (Hindell et al. 1991, Campagna et al. 1999, Bailleul et al. 2007, Biuw et al. 2010, Muelbert et al. 2013).

6.5. Drift dives and First Passage Time (FPT)

The possible profitability of high use areas identified in Chapter 3 and 4 was investigated further by linking the daily changes in drift rates to areas of feeding success (measured by observing positive shifts in buoyancy; *Chapter 5*). The annual fluctuations of buoyancy differ between males and females, where a temporal difference in the investment of relative lipid body tissue is observed, as opposed to relative lean body tissue. An increase in relative lean tissue is not possible to measure using drift dives, although the spatial locations of low buoyancy can imply where the seals experience a poor body condition or offer an indication of when they may be investing energy to build core mass. Previous studies on body composition and observed body conditions of hooded seals at various times of the year (Rasmussen et al. 1960, LeBlanc 2003, Thordason et al. 2007) offered valuable information for interpreting the annual energy fluctuations observed in Chapter 5. Both sexes increase lipid growth prior to fasting periods which confirms that thick blubber is important during these periods (*Chapter 5*).

However, it is possible that relative lipid tissue accumulation is not preferential outside these periods because the cost of diving is higher with a high level of positive buoyancy. When negatively or positively buoyant, seals must use energy to maintain their place in the water column or to move in the direction opposite to the total force acting upon them (Beck et al. 2000). Hooded seals may therefore delay lipid growth until closer to fasting periods, when they need to burn energy from blubber and not lean tissue such as muscles. However, it has been suggested that seals need to balance this energy use from blubber and core mass, as blubber is also needed for thermal insulation (Ryg et al. 1988). Both sexes showed an increase in lipid body condition from October–December, but this could have occurred as a function of cold temperatures, when blubber is necessary as insulation, both for the individuals and as protection for a growing foetus.

Seals increase the time spent in areas according to oceanographic properties (*Chapter 3 and 4*). This suggests that FPT is very useful in identifying the high use areas which we expect is providing important feeding habitat (*Chapter 3 and 4*). By implementing FPT in the models investigating the daily drift rate change in relation to habitat, I wanted to determine if successful foraging was directly linked to the extended periods of time spent in an area (*Chapter 5*). However, the GAM models identified FPT as a pretending variable. Thus, FPT was valuable in terms of explaining species response to habitat parameters, and how this varied between seal groups in regard to movement patterns and diving behaviour (*Chapter 3 and 4*), but it did not explain changes in buoyancy throughout the annual migration. This suggests that FPT is a poor method to link the time an animal spend in an area to successful prey acquisition and relative lipid gain, which could be due to hooded seals' ability to find food along the migration path, when FPT is faster (*Chapter 5*). Studies of diving and foraging in northern elephant seals show that males concentrate their foraging to specific locations, while females would forage *en route* to the feeding grounds (Le Boeuf et al. 1993). A similar behaviour in hooded seals could distort the patterns of increased body condition in areas of long FPT vs. areas of shorter FPT. As with elephant seals, male hooded seals seem to forage in more localised areas than females, who are more dynamic in their movement patterns (*Chapters 2 and 3*). However, daily changes in drift rates show that males also feed *en route* to their feeding grounds where they then stay for longer periods of time (*Chapters 4 and 5*). Additionally, there is also expected to be a time lag of days between ingestion and a measurable increase in relative lipid body condition (e.g., Biuw et al. 2003; *Chapter 5*). These aspects might influence the relationship between relative lipid gain and FPT length as the animal could move out of the high use area prior to weight gain, resulting in an underestimate of the influence of passage time on drift rates in the model. Seals have an ability to invest energy to building core mass (lean tissue) and lipid mass in relation to the annual cycle (e.g., Thordason et al. 2007, Aoki et al. 2011). Thus, successful foraging may not always result in lipid energy accumulation but rather lean tissue accumulation. The study of changes in drift rates can therefore offer new and valuable information about the species' possible strategy of energy use in terms of building body mass (lean vs. lipid mass accumulation) according to the timing within the annual cycle. However, because poor body condition and increased core mass (and in females a growing foetus) cannot be differentiated using drift dives, this information can only be viewed as circumstantial and be interpreted in accordance with other studies on the species body composition.

6.6. Suitability of modelling methods

Using statistical models to predict the likely occurrence or distribution of species has become an important tool in conservation planning and wildlife management (Pearce and Ferrier 2000, Guisan et al. 2002, 2006). The selection of appropriate criteria and determination of habitat requirements for a particular ecosystem require a good understanding of the species' ecology, as the primary objective of habitat suitability modelling is to develop a model that is biologically realistic (Austin 2002). Correlation and interaction amongst habitat variables, as well as the identification of sharp thresholds in the data (e.g., transitions between slow and fast movement behaviour) have been challenging in modelling animal tracking data (e.g., Jowett and Davey 2007). Biologists are increasingly seeking appropriate flexible methods that can address these difficulties, such as generalized additive models (GAMs; e.g., Austin 2002, Guisan et al. 2002), generalized linear models (GLMs; e.g., Guisan et al. 2002) and Cox Proportional Hazard models (CPH models; Freitas et al. 2008, Nordstrom et al. 2013) to evaluate species-environment relationships in general.

6.6.1 Handling telemetry data:

I wanted to investigate the spatial and temporal habitat selection of hooded seals by identifying the locations and properties of high use areas. Animals move through various types of areas that may be more or less suitable with respect to current needs, but the profitable areas used may actually only be a subset of the whole set of suitable areas available and these are usually unknown (Barraquand and Benhamou 2008). By applying the FPT approach to a Geographic Information System (GIS) framework, I could identify areas where the seals were spending more time, and identify important environmental properties of their entire home range. The drawback of the procedure was, for example, that the hooded seals behavioural mechanisms could not be readily identified. Other methods that could be useful for this purpose include residence time (see Barraquand and Benhamou 2008) or state-space models (Jonsen et al. 2006, Patterson et al. 2008).

State-space models are time-series methods that allow unobserved states and biological parameters to be estimated from data observed with error, such as satellite telemetry data (Jonsen et al. 2006), by coupling an observation model with a process model (see Patterson et al. 2008). They allow a natural way to handle location error and behavioural changes and can reveal important behavioural patterns in complex, noisy movement data where conventional methods cannot (Jonsen et al. 2006, Patterson et al. 2008). Although this method is a broadly accepted method in the analyses of animal movement behaviour using wildlife telemetry (e.g., elk (*Cervus elaphus*; Morales et al. 2004), California sea lions (*Zalophus californianus*; Breed et al. 2012), grey seals (Breed et al. 2006), pigeons (Roberts et al. 2004) and leatherback turtles (*Dermochelys coriacea*; Jonsen et al. 2006)), it only uncovers hidden behaviour solely from the geometry of the movement path. It has not yet been applied (to my knowledge) in the investigation of preferred habitat through the incorporation of environmental covariates and subsequent model selection (Jonsen et al. 2006, Patterson et al. 2008). The FPT analysis is also based on the animal's behaviour along its movement path and the data is filtered *a priori* in order to remove unlikely uplink locations (see Austin et al. 2003, Freitas et al. 2008). This is a step that is incorporated into the state-space procedure and is argued to be more true to the animals' actual movements by keeping from elimination of biologically plausible locations. However, the filters by e.g., Austin et al. (2003) and Freitas et al. (2008) are based on the species' general behaviour such as turning angles and average travel speed. The elimination of biologically sound locations should therefore be at a minimum. Also, telemetry data, such as the Argos tracking data used here, offer locations that are observed irregularly through time. This means that locations need to be regularly spaced along the trajectory prior to analyses. State-space locations are distributed at regular time intervals along the trajectory before analyses can be carried out, while FPT locations are distributed at regular space intervals. An important asset of the FPT approach is that it can be brought one step further than state-space models by incorporation into habitat models investigating habitat selection based on known oceanographic properties.

Residence time simulation analyses of animal movement could certainly also be a method to explore in the future. It analyses the behavioural modes along an animals' movement path based on time spent in the vicinity of a given location instead of within (such as FPT), appearing more robust than FPT and state-space models. However, further investigation is needed. FPT offers the opportunity to investigate the movements of the animals based on ARS. The time spent within a circle of ARS scale can be used to identify profitable areas. This is based on the assumption that predators increase their turning rate and reduce travel speed as a response to increased intake rate (Fauchald and Tveraa 2003). By incorporating this information, together with data on known habitat features, into a robust statistical framework, I was able to gain valuable and new information about habitat selection and habitat use by hooded seals. Such information is important for increased species understanding and management. However, I did find that hooded seals were successfully feeding along their migration track regardless of passage time, which opens up for the idea of applying a different method of future analyses that has the ability to identify fine scale behavioural mechanisms. This study focussed on the large scale search patterns in order to identify important habitat, thereby establishing a necessary big picture of hooded seal habitat selection and use, which was previously unknown. Future analysis of movement behaviours, such as transit rates and diving behaviour, could benefit from the investigation of fine scale behavioural modes. However, this should include fine scale habitat modelling in order to identify the relationship between *in situ* habitat properties to movement behaviour, instead of properties averaged across the ARS scale, where possible important information on movement behaviour is lost.

6.6.2 Statistical framework:

One alternative method that could incorporate FPT into a statistical framework was CPH models. These models estimate the relative habitat preference, where the lower the hazard ratio (i.e., the lower the risk of leaving) the higher the preference (e.g., Freitas et al. 2008). This analysis has been applied in resource selection studies and to investigate patch leaving decisions in foraging studies (see references in Freitas et al. 2008). By incorporating random effect terms, these models become more suitable to perform analysis on telemetry data where it is essential to distinguish between random variation between and within individuals (e.g., Pankratz et al. 2005, Freitas et al 2008). I initially applied the mixed effects CPH models to my data. The analysis did identify seemingly realistic geographic locations of preference by hooded seals in the Northwest Atlantic Ocean, but they also showed an unrealistic habitat preference to, for example, all areas of very deep waters, also outside their range. I therefore started to look into other modelling possibilities. I found GAMs to be a much better and informative alternative for investigating the hooded seal telemetry data, averaged at the scale of their search effort (ARS). I also ran GLMs and GLMMs, but these models did not explain the data as well as the GAMs.

GAMs are extensions of generalized linear models (GLMs) that, in addition to allowing the response to follow any distribution from an exponential family, permit explanatory variables to be modelled as nonparametric smoothing functions (Hastie and Tibshirani 1990). Nonparametric smoothing relaxes the usual assumption of linearity by allowing the form of the relationship between the independent variables and the response variable to take any shape as defined by the data, ranging from a straight line to curves of increasing complexity (Jowett and Davey 2007). The amount of smoothing can be controlled by specifying the degrees of freedom for the smoothing function (Jowett and Davey 2007). This flexibility makes GAMs well suited to develop habitat suitability models that can be used to predict habitat selection, such as the non-linear data used in this study. GAMs are often referred to as data driven instead of model driven due to their ability to let the data determine the nature of the relationship between the response and the explanatory variables, and not assume a parametric relationship (Yee and Mitchell 1991). The ability of GAMs to deal with non-linear data structures can make it easier to develop ecological models that better represent the underlying data (Guisan et al. 2002), and thereby increase our understanding of the ecological systems driving hooded seal habitat selection. The best models assembled for this study revealed sound biological results explaining in more detail how the specific covariates, averaged at the ARS scale, could explain the habitat preference by seal groups (males, female sand juveniles) by the time spent along the trajectory.

The identification of which of several alternative models best explain the data is a key step in statistical modelling (Burnham and Anderson 2002). The Akaike Information Criteria (AIC) is based on the principle of parsimony by identifying the model that accounts for most of the variation with the fewest variables (Boyce et al. 2002). However, it is important to make sure that the model is not too complex (over fitted), because too many variables and too much structure introduces large uncertainties and interpretability may become challenging (Anderson 2008). Models should be built based on ecological principles that can be evaluated with data (Boyce et al. 2002). This requires a fundamental understanding of relevant theory to propose models that are most likely to direct our understanding of the system (Boyce et al. 2002), thus offering a good out-of-sample prediction performance (Anderson 20008). By being critical about the predictor variables that go into the model, one can ensure a biologically realistic output of the fitted values (e.g., Boyce 2001, Austin 2002, Anderson 2008).

In chapter 3, five possibly important oceanographic parameters were included in GAM models to see if they could explain an increase of time spent in specific areas along a seals trajectory (i.e., FPT). FPT was a preferred response variable to transit rates, because the focus was to identify areas were the seals increased or decreased time spent within an area of restricted search, and not just to identify an increase or decrease in travel speed between shorter, equal step distances of the track. The predictors were chosen based on the knowledge of biological processes that may influence oceanographic processes within an area by creating favourable conditions for arctic marine predators (ice presence, SST, primary productivity at the surface, depth to the sea floor and slope of the sea floor). The results show that most of the covariates probably represented areas of the water column that drive processes at a lower trophic level to what hooded seals home in on (i.e., Surface: ice, chlorophyll and SST; Bottom: depth of sea floor and slope), or they were acting as proxies for other unidentified important parameters, such as currents and prey presence (or prey of prey). However, important indications of preferences to habitat conditions by hooded seals were revealed and better habitat models were developed (*Chapter 4*).

Ideally, future covariates to include in a hooded seal habitat selection model would be temperature at depth, productivity at depth, current velocity and direction, information on time of prey ingestion (and if they ingest prey at depth or if they bring it up to the surface), and some data on real time overlap with prey to make inferences of the type of prey that is ingested in the different locations. This information, in addition to the identification and investigation of all other dive types, as well as to monitor the daily change in buoyancy (*Chapter 5*) would add valuable information of the critical habitat for hooded seals in the NW Atlantic Ocean, as well as reveal unknown information about their behaviour during migrations.

6.7. Conclusion and further research

Based on the main findings of this study, the following conclusions can be drawn:

i) NW Atlantic hooded seals carry out extensive foraging migrations extending from the moulting ground in SE Greenland, north into Baffin

Bay, and south to the breeding grounds at the Front (off Newfoundland and/or Labrador) and to the Gulf of St. Lawrence.

ii) There is geographic segregation between seal groups (males, females and juveniles) within their migration range, but in general, all groups prefer to spend time along the continental shelf break and areas of high topographic relief.

iii) Males and females exhibit differences in habitat selection and diving strategies. A horizontal segregation between sexes could have evolved as a result of a resource partitioning strategy to avoid sexual competition or that the energy requirements for males and females are different.

iv) The daily changes in drift rates showed that the patterns of relative mass gain and loss during the annual migration differ between males and females in relation to the two fasting periods. Males experienced the highest daily change in drift rates and thereby increased relative lipid mass in the Gulf, the east Greenland shelf and *en route* to Baffin Bay and the Front, however, Baffin Bay and Davis Strait also represent areas of relative lipid mass increase. Females did not show a high daily change in drift rates in the Gulf, but they showed a positive change throughout their range, with the largest change occurring in Davis Strait and the northern parts of the Labrador shelf, as well as off Newfoundland and Flemish Cap.

v) The daily change in drift rates are supposed to show where the seals are experiencing successful foraging, however, low buoyancy may not necessarily mean that the foraging is poor, but rather indicate where the seal is investing energy during successful foraging to building core mass (although this is circumstantial information).

vi) The function of drift dives in hooded seals seems to be linked to diving behaviour, which indicates that they represent rest and/or food processing dives after foraging bouts.

Further research should include a study of hooded seal haul out behaviour in relation to diving activity during migration periods. This could provide additional information about the behaviour of hooded seals in relation to their environment and offer further information about the function of drift diving. If there is an inverse relationship between the occurrence of drift dives and haul out behaviour, and if haul outs seem to be related to diving behaviour, then drift dives are most likely to be resting and/or food processing dives as suggested for elephant seals (Asaga et al. 1994, Crocker et al. 1997, Le Boeuf et al. 1993) and now hooded seals. Although ice cover was not found to be an important habitat predictor for adult hooded seals, we do know that they haul out at various times. It is therefore important for management purposes to gain additional knowledge of the importance of available ice cover for hooded seals during migration and not only during breeding in times of reduced ice concentrations.

The identification of various dive shapes would enable an investigation of any relationship between dive types and the intensity of feeding as determined by drift diving (e.g., Baechler et al. 2002, Beck et al. 2000, Crocker et al. 1997, Hassrick et al. 2007, Sala et al. 2011). Detailed information of dive shapes would aid in describing the different foraging strategies between males and females, as well as juveniles. A comparison of the occurrence of specific feeding dives and fluctuations in drift rates may offer a better understanding of when seals build lipid vs. lean tissue during migrations. This understanding could be improved further by investigating the energy requirements for both male and female hooded seals during the moulting period.

Overall, this thesis has shed new light on an important marine pinniped species where very little was previously known about its habitat selection and habitat use. It provides new and valuable information identifying the location of critical habitat, as well as describing the oceanographic properties of their habitat. In addition, I suggest that daily changes in drift rates during drift dives in conjunction with other studies on body composition can shed new light on how the seals are investing energy obtained from successful foraging to building body mass in relation to key life history events. The information obtained from this study offers important data that can improve wildlife management and further aid in the development of conservation policies for a species that is already experiencing an increased loss of seasonally crucial breeding substrate as a result of global warming.

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APPENDICES

CHAPTER 3: TABLES

Table A3.1: Summary table presenting tag data, including tag performance. The individual tags are named by “Seal Id”. “Sex” = Males (M), Females (F) and Juveniles (J). “Wt (kg)” is the weight of the animal at tagging. “Start” and “End” columns represent the dates the tags began and stopped transmitting. “Days transmitting” is the number of days the tag transmitted for. “Latitude” and “Longitude” represent the coordinates at tag location.

sort	Seal Id	Sex	Age	Wt (kg)	Year	Start	End	Days transmitting	Latitude tagged	Longitude tagged
1	hd1_9315_04	F	A	330	2004	14.mar	31.may	78	46°58	-62°40
2	hd1_9256_04	F	A	208	2004	14.mar	09.jul	117	46°64	-62°25
3	hd1_9338_04	F	A	195.5	2004	14.mar	13.jun	90	46°63	-62°24
4	hd1_9324_04	M	A	321	2004	16.mar	15.jun	91	46°60	-61°85
5	hd1_9335_04	M	A	326.5	2004	17.mar	08.jun	83	46°64	-61°87
6	hd1_9255_04	F	A	276	2004	17.mar	17.jun	92	46°62	-61°85
7	hd1_9336_04	M	A	192	2004	17.mar	21.jul	126	46°57	-61°82
8	hd1_9317_04	M	A	274	2004	19.mar	14.jun	87	46°47	-61°90
9	hd2f-9257-04	F	A	148	2004	20.mar	30.jun	103	51°78	-55°52
10	hd2f-9337-04	F	A	150	2004	20.mar	24.may	66	51°77	-55°52
11	hd2f-9350-04	F	A	182.5	2004	20.mar	23.jun	95	51°77	-55°52
12	hd2bb-9340-04	M	J	40.5	2004	20.mar	28.may	69	51°80	-55°44
13	hd2f-9343-04	F	A	162	2004	23.mar	17.jun	86	52°08	-55°15
14	hd2bb-9339-04	F	J	47.5	2004	23.mar	11.mar	353	52°09	-55°17
15	hd2f-9316-04	F	A	147	2004	23.mar	28.jun	97	52°07	-55°16
16	hd2f-9355-04	M	A	246	2004	25.mar	24.jun	92	51°87	-55°40
17	hd2g-9409-04	F	A	116	2004	24.jul	28.jun	340	66°23	-34°28
18	hd2g-9426-04	F	J	81	2004	24.jul	29.jun	340	66°21	-34°23
19	hd2g-9411-04	M	J	155	2004	24.jul	03.jan	163	66°24	-34°24
20	hd2g-9421-04	M	A	172	2004	24.jul	20.mar	239	66°20	-33°48
21	hd2g-9412-04	F	J	85	2004	24.jul	26.jun	337	66°38	-33°56
22	hd1_9397_04	M	A	338	2005	12.mar	16.jun	95	47°98	-61°84
23	hd1_9363_04	F	A	228	2005	13.mar	06.jun	86	48°03	-61°91
24	hd1_9351_04	F	A	188	2005	13.mar	23.jun	102	47°92	-61°99
25	hd1_9341_04	M	A	338.5	2005	14.mar	03.jul	111	47°77	-61°99
26	hd5g-9427-05	M	A	194	2005	20.jul	07.apr	261	65°50	-36°02
27	hd5g-9352-05	M	J	105	2005	20.jul	30.sep	72	65°52	-36°12
28	hd5g-9400-05	F	A	112	2005	20.jul	20.may	304	65°44	-36°29
29	hd5g-9422-05	M	A	253	2005	20.jul	07.sep	49	65°40	-36°28
30	hd5g-9420-05	F	A	138	2005	20.jul	13.jun	328	65°51	-36°37
31	hd5g-9410-05	M	J	127	2005	20.jul	23.jun	338	65°42	-36°34
32	hd5g-9413-05	F	A	90	2005	23.jul	27.jun	338	65°49	-37°09
33	hd5g-9344-05	F	A	108	2005	24.jul	25.aug	33	65°40	-36°64
34	hd5g-10204-05	M	A	146	2005	24.jul	13.jun	324	65°23	-36°83
35	hd5g-10207-05	M	A	174	2005	24.jul	12.jul	353	65°46	-37°23
36	hd5g-10219-05	F	A	117	2005	25.jul	14.jun	324	65°32	-37°47
37	hd5g-10222-05	F	A	98	2005	25.jul	18.jun	328	65°44	-37°14

38	hd5g-10188-05	M	A	109	2005	25.jul	22.mar	240	65°40	-37°46
39	hd5g-10227-05	F	A	114	2005	25.jul	26.may	305	65°46	-37°39
40	hd5g-10206-05	F	A	95	2005	25.jul	04.jul	343	65°50	-37°85
41	hd5g-10205-05	F	A	138	2005	25.jul	14.apr	263	65°38	-37°57
42	hd5bb-9318-05	F	J	51	2006	18.mar	20.nov	246	51°91	-55°20
43	hd5bb-9329-05	F	J	50	2006	18.mar	09.des	265	51°91	-55°19
44	hd5bb-9311-05	M	J	50	2006	25.mar	22.sep	180	51°14	-57°56
45	hd5bb-9304-05	M	J	45	2006	26.mar	21.jul	118	51°40	-55°44
46	hd6-D-06	F	A	73.5	2007	20.jul	02.jun	319	65°36	-37°25
47	hd6-E-06	F	A	98	2007	24.jul	06.sep	44	65°38	-37°92
48	hd6-F-06	M	A	97.5	2007	24.jul	24.jun	336	65°40	-37°82
49	ct18-L-06	M	A	130	2007	24.jul	07.apr	258	65°38	-37°97
50	MH4-10392-08	F	A	182.5	2008	14.mar	18.jun	96	47°69	-61°84
51	MH4-10423-08	F	A	251	2008	14.mar	01.jul	109	47°68	-61°83
52	MH4-10209-08	F	J	46	2008	14.mar	27.apr	43	47°39	-61°86
53	MH4-10348-08	F	A	251	2008	15.mar	26.jun	104	47°69	-61°81
54	MH4-10386-08	F	A	224.5	2008	15.mar	14.jun	91	47°69	-61°77
55	MH4-10349-08	F	J	39	2008	15.mar	25.apr	40	47°69	-61°78
56	MH4-10401-08	M	A	352.5	2008	16.mar	22.jun	98	47°66	-61°76
57	MH4-9391-08	F	J	51	2008	17.mar	11.aug	147	47°59	-61°87
58	hd3-CTD453-08	M	A	230	2008	24.mar	14.may	51	49°66	-52°62
59	hd3-80-08	F	A	155.5	2008	24.mar	11.jul	109	49°87	-52°32
60	hd3-81-08	F	A	158.5	2008	24.mar	02.jul	100	49°69	-52°16
61	hd3-82-08	F	A	139	2008	24.mar	23.jun	90	49°72	-52°18
62	hd3-79-08	F	A	149.5	2008	25.mar	19.jun	86	49°65	-52°30
63	hd3-78-08	F	A	229	2008	25.mar	21.jun	88	49°96	-51°87
64	hd3-76-08	F	J	42	2008	27.mar	18.may	52	49°21	-51°55
65	hd3-77-08	F	J	51.5	2008	28.mar	09.may	42	49°28	-51°33

Table A3.2a: Spearman correlation coefficients for the five prediction variables: Spring (April-June) dataset. The r values are presented here where “Group” represent the seal group: “J”= Juveniles, “M” = Males, “F” = Females.

Group	Variable	Temperature	Ice	Chlorophyll	Slope	Depth
J	Temperature	1.00	0.09	-0.07	-0.18	0.21
J	Ice	0.09	1	0.07	-0.06	-0.14
J	Chlorophyll	-0.07	0.07	1	-0.1	-0.24
J	Slope	-0.18	-0.06	-0.1	1	0.29
J	Depth	0.21	-0.14	-0.24	0.29	1
M	Temperature	1.00	-0.11	-0.35	0.03	0.28
M	Ice	-0.11	1	0.09	-0.04	-0.08
M	Chlorophyll	-0.35	0.09	1	-0.12	-0.37
M	Slope	0.03	-0.04	-0.12	1	0.21
M	Depth	0.28	-0.08	-0.37	0.21	1
F	Temperature	1.00	-0.18	-0.24	0.08	0.48
F	Ice	-0.18	1	0.03	0.05	-0.24
F	Chlorophyll	-0.24	0.03	1	-0.15	-0.29
F	Slope	0.08	0.05	-0.15	1	0.09
F	Depth	0.48	-0.24	-0.29	0.09	1

Table A3.2b: P-values explaining the significant degree of the Spearman correlation test (reported in Table A3.2a) between the predictor variables in the spring (April-June dataset). “Group” represents the seal group: “J”= Juveniles. “M” = Males. “F” = Females.

Group	Variable	Temperature	Ice	Chlorophyll	Slope	Depth
J	Temperature		0.0976	0.1738	0.0004	0
J	Ice	0.0976		0.2086	0.232	0.0067
J	Chlorophyll	0.1738	0.2086		0.0594	0
J	Slope	0.0004	0.232	0.0594		0
J	Depth	0	0.0067	0	0	
M	Temperature		0.005	0	0.4981	0
M	Ice	0.005		0.0198	0.3366	0.0412
M	Chlorophyll	0	0.0198		0.0037	0
M	Slope	0.4981	0.3366	0.0037		0
M	Depth	0	0.0412	0	0	
F	Temperature		0	0	0.0005	0
F	Ice	0		0.189	0.0435	0
F	Chlorophyll	0	0.189		0	0
F	Slope	0.0005	0.0435	0		0
F	Depth	0	0	0	0	

Table A3.3a: Spearman correlation coefficients for the prediction variables: Fall (Aug - Feb) dataset. The r values are presented here where “Group” represent the seal group: “J”= Juveniles. “M” = Males. “F” = Females.

Group	Variable	Temperature	Ice	Chlorophyll	Slope	Depth
J	Temperature	1.00	-0.04	0.13	0.1	0.46
J	Ice	-0.04	1	-0.06	-0.06	-0.13
J	Chlorophyll	0.13	-0.06	1	-0.04	-0.13
J	Slope	0.10	-0.06	-0.04	1	0.22
J	Depth	0.46	-0.13	-0.13	0.22	1
M	Temperature	1.00	-0.13	0.17	-0.05	0.16
M	Ice	-0.13	1	0.04	-0.11	-0.13
M	Chlorophyll	0.17	0.04	1	0.08	0.05
M	Slope	-0.05	-0.11	0.08	1	0.24
M	Depth	0.16	-0.13	0.05	0.24	1
F	Temperature	1.00	-0.22	0.46	-0.09	0.5
F	Ice	-0.22	1	-0.04	0.01	-0.18
F	Chlorophyll	0.46	-0.04	1	0.02	0.26
F	Slope	-0.09	0.01	0.02	1	-0.02
F	Depth	0.50	-0.18	0.26	-0.02	1

Table A3.3b: P-values explaining the significant degree of the Spearman correlation test (reported in Table A3.3a) between the predictor variables in the fall (Aug – Feb dataset). “Group” represents the seal group: “J”= Juveniles. “M” = Males. “F” = Females.

Group	Variable	Temperature	Ice	Chlorophyll	Slope	Depth
J	Temperature		0.5423	0.0226	0.0851	0
J	Ice	0.5423		0.3184	0.3142	0.0306
J	Chlorophyll	0.0226	0.3184		0.4992	0.03
J	Slope	0.0851	0.3142	0.4992		0.0002
J	Depth	0	0.0306	0.03	0.0002	
M	Temperature		0.027	0.0031	0.4141	0.0071
M	Ice	0.027		0.5368	0.0525	0.0226
M	Chlorophyll	0.0031	0.5368		0.1455	0.4101
M	Slope	0.4141	0.0525	0.1455		0
M	Depth	0.0071	0.0226	0.4101	0	
F	Temperature		0	0	0.0637	0
F	Ice	0		0.4343	0.7694	0.0001
F	Chlorophyll	0	0.4343		0.6652	0
F	Slope	0.0637	0.7694	0.6652		0.6523
F	Depth	0	0.0001	0	0.6523	

Table A3.4a: Full AIC table including all GAM model results for females (Group = F): Loglik is the loglikelihood. K is the number of parameters in the model. AIC_i is AIC for model *i*. and ΔAIC is the difference between the AIC of the best fitting model and that of model *i*. Exp(-0.5Δ-i) represent the relative likelihoods and the w_i is the Akiake weights.

Group	**Season**	**Best models per category and season**	**loglik**	**K**	**AIC_i**	ΔAIC	**exp(-0.5Δi)**	W_i
F	Spring	SST. ice. chlorophyll. slope and depth	-2729.23	6	5470.462	0	1	0.989492355
F	Spring	SST. chlorophyll. slope and depth	-2734.78	5	5479.564	9.102	0.010556642	0.010445717
F	Spring	SST. chlorophyll and depth	-2740.91	4	5489.82	19.358	6.25841E-05	6.19264E-05
F	Spring	Chlorophyll and depth	-2752.65	3	5511.302	40.84	1.35427E-09	1.34004E-09
F	Spring	SST and depth	-2754.58	3	5515.156	44.694	1.97161E-10	1.95089E-10
F	Spring	Slope and depth	-2763.28	3	5532.556	62.094	3.28442E-14	3.24991E-14
F	Spring	Depth	-2769.14	2	5542.284	71.822	2.53543E-16	2.50878E-16
F	Spring	SST	-2772.42	2	5548.84	78.378	9.55946E-18	9.45902E-18
F	Spring	Chlorophyll	-2793.15	2	5590.292	119.83	9.53336E-27	9.43319E-27
F	Spring	Slope	-2795.67	2	5595.342	124.88	7.63225E-28	7.55205E-28
F	Spring	Ice	-2799.69	2	5603.372	132.91	1.37708E-29	1.36261E-29
F	Fall	SST. chlorophyll and depth	-691.46	4	1390.9246	0	1	0.331680726
F	Fall	SST. chlorophyll. slope and depth	-690.97	5	1391.9376	1.013	0.602600996	0.199871136
F	Fall	Chlorophyll	-694.35	2	1392.6974	1.7728	0.412136778	0.136697826
F	Fall	SST and depth	-693.50	3	1393.0056	2.081	0.353277999	0.117175503
F	Fall	Chlorophyll and depth	-693.55	3	1393.0962	2.1716	0.337631573	0.111985885
F	Fall	SST. ice. chlorophyll. slope and depth	-690.67	6	1393.336	2.4114	0.299482289	0.099332503
F	Fall	SST	-698.17	2	1400.3376	9.413	0.00903635	0.002997183
F	Fall	Depth	-701.43	2	1406.8544	15.9298	0.000347446	0.000115241
F	Fall	Ice	-702.21	2	1408.4278	17.5032	0.000158208	5.24745E-05
F	Fall	Slope and depth	-701.34	3	1408.68	17.7554	0.000139465	4.62577E-05
F	Fall	Slope	-702.36	2	1408.7234	17.7988	0.000136471	4.52647E-05

Table A3.4b: Full AIC table including all GAM model results for males (Group = M): Loglik is the loglikelihood. K is the number of parameters in the model. AIC_i is AIC for model *i*. and ΔAIC is the difference between the AIC of the best fitting model and that of model *i*. Exp(-0.5Δ-i) represent the relative likelihoods and the w_i is the Akiake weights.

Group	**Season**	**Best models per category and season**	**loglik**	**K**	**AIC_i**	ΔAIC	**exp(-0.5Δi)**	W_i
M	Spring	SST and depth	-842.88	3	1691.76	0	1	0.540807744
M	Spring	SST. chlorophyll and depth	-842.80	4	1693.59	1.8318	0.400156323	0.216407639
M	Spring	SST. ice. chlorophyll. slope and depth	-841.15	6	1694.31	2.5468	0.279878416	0.151360415
M	Spring	SST. chlorophyll. slope and depth	-842.66	5	1695.32	3.5576	0.168840635	0.091310323
M	Spring	SST	-852.88	2	1709.76	17.9974	0.00012357	6.68278E-05
M	Spring	Depth	-853.87	2	1711.74	19.9796	4.58654E-05	2.48044E-05
M	Spring	Chlorophyll and depth	-853.66	3	1713.33	21.5698	2.07099E-05	1.12001E-05
M	Spring	Slope and depth	-853.68	3	1713.36	21.5972	2.04281E-05	1.10477E-05
M	Spring	Ice	-868.30	2	1740.60	48.8422	2.47771E-11	1.33997E-11
M	Spring	Chlorophyll	-871.68	2	1747.35	55.5928	8.47573E-13	4.58374E-13
M	Spring	Slope	-871.76	2	1747.52	55.7578	7.80454E-13	4.22076E-13
M	Fall	SST. chlorophyll. slope and depth	-455.14	2	914.27	0	1	0.582137986
M	Fall	SST. ice. chlorophyll. slope and depth	-455.01	3	916.03	1.7512	0.416611977	0.242525657
M	Fall	SST	-441.26	2	886.52	2.9386	0.230086489	0.132708287
M	Fall	SST and depth	-441.26	3	888.53	4.9444	0.084398977	0.048679276
M	Fall	SST. chlorophyll and depth	-441.29	4	890.57	6.9932	0.030300229	0.017476435
M	Fall	Slope and depth	-457.10	3	920.20	36.6162	1.11916E-08	6.45506E-09
M	Fall	Depth	-458.74	2	921.47	37.8908	5.91721E-09	3.41291E-09
M	Fall	Chlorophyll and depth	-458.41	3	922.81	39.2302	3.0288E-09	1.74694E-09
M	Fall	Slope	-462.89	2	929.79	46.208	9.24827E-11	5.33417E-11
M	Fall	Ice	-463.54	2	931.08	47.4996	4.84834E-11	2.7964E-11
M	Fall	Chlorophyll	-463.68	2	931.35	47.7692	4.23692E-11	2.44375E-11

Table A3.4c: Full AIC table including all GAM model results for juveniles (Group = J): Loglik is the loglikelihood. K is the number of parameters in the model. AIC_i is AIC for model *i*. and ΔAIC is the difference between the AIC of the best fitting model and that of model *i*. Exp(-0.5Δ-i) represent the relative likelihoods and the w_i is the Akiake weights.

Group	Season	Best models per category and season	loglik	K	AIC_i	ΔAIC	exp(-0.5Δi)	W_i
J	Spring	SST. chlorophyll and depth	-512.18	4	1032.37	0.00	1	0.681467
J	Spring	SST. chlorophyll. slope and depth	-512.02	5	1034.04	1.67	0.434874	0.296352
J	Spring	SST. chlorophyll and depth	-512.18	4	1032.37	0.00	1	0.681467
J	Spring	SST. chlorophyll. slope and depth	-512.02	5	1034.04	1.67	0.434874	0.296352
J	Spring	SST and depth	-516.62	3	1039.24	6.87	0.032242	0.021972
J	Spring	Chlorophyll and depth	-521.81	3	1049.62	17.25	0.00018	0.000123
J	Spring	SST	-523.19	2	1050.39	18.02	0.000122	8.33E-05
J	Spring	Depth	-527.19	2	1058.37	26.00	2.26E-06	1.54E-06
J	Spring	Chlorophyll	-527.28	2	1058.56	26.19	2.05E-06	1.4E-06
J	Spring	Slope and depth	-526.71	3	1059.43	27.06	1.33E-06	9.07E-07
J	Spring	Slope	-533.00	2	1070.00	37.64	6.72E-09	4.58E-09
J	Fall	SST. ice. chlorophyll. slope and depth	-410.38	6	832.76	0.00	1	0.8432
J	Fall	SST. chlorophyll. and depth	-414.45	4	836.91	4.15	0.125506	0.105827
J	Fall	SST. chlorophyll. slope and depth	-414.46	5	838.93	6.17	0.045721	0.038552
J	Fall	Chlorophyll	-418.96	2	841.92	9.17	0.010209	0.008608
J	Fall	Chlorophyll and depth	-418.98	3	843.96	11.20	0.00369	0.003111
J	Fall	SST and depth	-420.71	3	847.42	14.66	0.000655	0.000552
J	Fall	SST	-423.43	2	850.87	18.11	0.000117	9.83E-05
J	Fall	Ice	-424.14	2	852.28	19.52	5.77E-05	4.86E-05
J	Fall	Depth	-427.90	2	859.80	27.05	1.34E-06	1.13E-06
J	Fall	Slope	-428.14	2	860.27	27.52	1.06E-06	8.92E-07
J	Fall	Slope and depth	-427.87	3	861.75	28.99	5.07E-07	4.27E-07

CHAPTER 4: TABLES

Table A4.1: AIC table presenting all candidate GAM models with FPT as a response variable. The response variable was investigated in relation to geographic location (GL), bottom depth (BD), month (M) and TCI. Loglik is the loglikelihood, K is the number of parameters in the model. AIC$_i$ is AIC for model i, and ΔAIC is the difference between the AIC of the best fitting model and that of model i. Exp(-0.5Δ_i) represent the relative likelihoods and the w_i is the Akiake weights. D.E% is the deviance explained by the model.

model	**loglik**	**K**	**AIC$_i$**	**ΔAIC**	**exp(0.5Δ_i)**	**w_i**	**DE (%)**
GL, BD and M by sex	-3293.69	7	6601.39	0.00	1	0.833	31.4
GL, BD, TCI and M by sex	-3293.30	9	6604.59	3.20	0.20149	0.168	31.4
GL, BD, TCI and M	-3349.04	5	6708.08	106.69	6.8E-24	5.64899E-24	29
GL, BD and M	-3350.45	4	6708.90	107.51	4.5E-24	3.75646E-24	28.9
GL and M by sex	-3359.54	5	6729.07	127.68	1.9E-28	1.56333E-28	28.5
GL, BD and TCI by sex	-3372.67	7	6759.33	157.94	5.1E-35	4.20348E-35	28
GL and BD by sex	-3379.22	5	6768.44	167.05	5.3E-37	4.4286E-37	27.7
GL ,TCI and M by sex	-3390.54	7	6795.07	193.69	8.7E-43	7.27609E-43	27.2
GL ,BD and TCI	-3413.72	4	6835.44	234.05	1.5E-51	1.24891E-51	26.1
GL and BD	-3416.41	3	6838.81	237.43	2.8E-52	2.31141E-52	26
GL and M	-3421.33	3	6848.66	247.27	2E-54	1.68208E-54	25.8
GL, TCI and M	-3420.47	4	6848.95	247.56	1.7E-54	1.45649E-54	25.8
BD and M by sex	-3439.15	5	6888.29	286.91	5E-63	4.16325E-63	25
GL by sex	-3450.60	3	6907.20	305.81	3.9E-67	3.26623E-67	24.5
GL and TCI by sex	-3449.33	5	6908.67	307.28	1.9E-67	1.56931E-67	24.5
BD, TCI and M by sex	-3450.78	7	6915.56	314.17	6E-69	5.00184E-69	24.4
BD, TCI and M	-3464.51	4	6937.02	335.63	1.3E-73	1.09433E-73	23.8
BD and M	-3465.86	3	6937.72	336.33	9.2E-74	7.69624E-74	23.7
GL and TCI	-3490.45	3	6986.90	385.51	1.9E-84	1.61217E-84	22.6
GL	-3491.84	2	6987.69	386.30	1.3E-84	1.08826E-84	22.5
BD and TCI by sex	-3554.92	5	7119.83	518.44	3E-113	2.198E-113	19.5
BD by sex	-3563.63	3	7133.27	531.88	3E-116	2.6546E-116	19
BD and TCI	-3574.81	3	7155.62	554.23	4E-121	3.7145E-121	18.5
BD	-3575.82	2	7155.64	554.25	4E-121	3.6849E-121	18.4
M by sex	-3597.63	3	7201.27	599.88	5E-131	4.5498E-131	17.3
M	-3620.40	2	7244.80	643.41	2E-140	1.6038E-140	16.2
M and TCI	-3620.50	3	7246.99	645.61	6E-141	5.3545E-141	16.2
M and TCI by sex	-3667.61	5	7345.21	743.82	3E-162	2.5174E-162	13.7

TCI by sex	-3723.70	3	7453.41	852.02	1E-185	8.0709E-186	10.7
TCI	-3728.67	2	7461.33	859.95	2E-187	1.5324E-187	10.4

Table A4.2: AIC table presenting all candidate GAM models with maximum dive depth as a response variable. The response variable was investigated in relation to geographic location (GL), FPT, bottom depth (BD), month (M) and TCI. The behavioural models included FPT as a predictor variable. Loglik is the loglikelihood, K is the number of parameters in the model. AIC_i is AIC for model *i*, and ΔAIC is the difference between the AIC of the best fitting model and that of model *i*. Exp($-0.5\Delta_i$) represent the relative likelihoods and the w_i is the Akiake weights. D.E% is the deviance explained by the model.

model	**loglik**	**K**	**AIC_i**	**ΔAIC**	**exp(0.5Δ_i)**	**w_i**	**DE (%)**
GL, FPT, BD, TCI and M by sex	-7380.97	11	14783.94	0	1	0.996557126	57
GL, FPT, BD and M by sex	-7388.64	9	14795.27	11.336	0.003454768	0.003442874	56.8
GL, BD AND M by sex	-7434.44	7	14882.88	98.946	3.267E-22	3.25575E-22	55.6
GL, FPT, BD, TCI and M	-7480.61	6	14973.22	189.28	7.91353E-42	7.88628E-42	54.3
GL, FPT, BD and M	-7485.01	5	14980.01	196.074	2.64894E-43	2.63982E-43	54.2
GL, FPT, BD and TCI by sex	-7511.15	9	15040.29	256.354	2.15495E-56	2.14753E-56	53.5
GL, FPT and BD by sex	-7515.65	7	15045.29	261.356	1.76712E-57	1.76103E-57	53.3
GL, BD and M	-7518.94	4	15045.89	261.952	1.31173E-57	1.30722E-57	53.2
FPT, BD, TCI and M by sex	-7535.16	9	15088.31	304.378	8.03817E-67	8.01049E-67	52.8
FPT, depth and M by sex	-7545.15	7	15104.30	320.366	2.71273E-70	2.70339E-70	52.5
GL, BD and TCI by sex	-7557.85	7	15129.69	345.756	8.31838E-76	8.28974E-76	52.1
GL and BD by sex	-7564.26	5	15138.53	354.59	1.00406E-77	1.0006E-77	51.9
GL, FPT,BD and TCI	-7572.26	5	15154.51	370.578	3.38852E-81	3.37685E-81	51.7
GL, FPT and BD	-7574.46	4	15156.91	372.978	1.0206E-81	1.01709E-81	51.6
BD, TCI and M by sex	-7594.96	7	15203.91	419.978	6.35237E-92	6.3305E-92	51
BD and M by sex	-7606.22	5	15222.44	438.502	6.03254E-96	6.01178E-96	50.7
GL, BD and TCI	-7610.95	4	15229.90	445.962	1.44738E-97	1.4424E-97	50.5

GL and BD	-7613.92	3	15233.84	449.904	2.01645E-98	2.00951E-98	50.5
FPT, BD, TCI and M	-7618.62	5	15247.23	463.298	2.4895E-101	2.481E-101	50.3
FPT, BD and M	-7626.10	4	15260.19	476.258	3.8185E-104	3.8053E-104	50.1
BD, TCI and M	-7667.66	4	15343.32	559.384	3.3987E-122	3.387E-122	48.8
BD and M	-7675.26	3	15356.52	572.586	4.6188E-125	4.6029E-125	48.6
FPT, BD, and TCI by sex	-7746.70	7	15507.39	723.456	8.008E-158	7.9805E-158	46.3
FPT, and BD by sex	-7765.42	5	15540.84	756.906	4.3647E-165	4.3496E-165	45.6
FPT, BD, and TCI	-7788.73	4	15585.45	801.516	8.9745E-175	8.9436E-175	44.9
FPT and BD	-7795.48	3	15596.95	813.016	2.8564E-177	2.8466E-177	44.6
BD and TCI by sex	-7819.70	5	15649.39	865.456	1.1712E-188	1.1671E-188	43.8
GL ,FPT, TCI and M by sex	-7822.89	9	15663.79	879.85	8.77E-192	8.7398E-192	43.7
GL ,FPT and M by sex	-7832.73	7	15679.47	895.532	3.449E-195	3.4372E-195	43.4
BD by sex	-7841.80	3	15689.61	905.672	2.1668E-197	2.1594E-197	43
BD and TCI	-7854.29	3	15714.58	930.644	8.1889E-203	8.1607E-203	42.6
BD	-7860.79	2	15725.59	941.652	3.3332E-205	3.3218E-205	42.4
GL , TCI and M by sex	-7912.44	7	15838.88	1054.946	8.3442E-230	8.3155E-230	40.5
GL and M by sex	-7922.66	5	15855.31	1071.374	2.2599E-233	2.2521E-233	40.2
GL ,FPT and TCI by sex	-7931.19	7	15876.38	1092.442	6.015E-238	5.9943E-238	39.8
GL and FPT by sex	-7943.01	5	15896.02	1112.08	3.2726E-242	3.2614E-242	39.4
GL ,FPT, TCI and M	-7953.31	5	15916.62	1132.688	1.0963E-246	1.0925E-246	39
GL ,FPT and M	-7972.24	4	15952.48	1168.546	1.7925E-254	1.7863E-254	38.3
FPT and M by sex	-7978.57	5	15967.13	1183.196	1.181E-257	1.1769E-257	38.1
GL ,FPT and TCI	-8018.94	4	16045.89	1261.952	9.3456E-275	9.3134E-275	36.5
GL and TCI by sex	-8024.65	5	16059.31	1275.372	1.1389E-277	1.135E-277	36.3
GL by sex	-8036.59	3	16079.17	1295.234	5.54E-282	5.5209E-282	35.8
GL and FPT	-8038.12	3	16082.25	1298.312	1.1889E-282	1.1848E-282	35.8
FPT and M	-8039.42	3	16084.83	1300.894	3.2693E-283	3.2581E-283	35.7
GL , TCI and M	-8040.74	4	16089.48	1305.548	3.1905E-284	3.1795E-284	35.7
GL and M	-8060.80	3	16127.60	1343.666	1.6851E-292	1.6793E-292	34.9
TCI and M by sex	-8071.21	5	16152.42	1368.488	6.8645E-298	6.8408E-298	34.5
GL and TCI	-8115.82	3	16237.64	1453.704	0	0	32.6
TCI and M	-8127.95	3	16261.90	1477.968	0	0	32.1
FPT and TCI by	-8131.65	5	16273.30	1489.368	0	0	32

sex							
GL	-8136.48	2	16276.96	1493.026	0	0	31.8
FPT and TCI	-8159.14	3	16324.28	1540.346	0	0	30.8
FPT by sex	-8164.17	3	16334.35	1550.41	0	0	30.6
FPT	-8176.88	2	16357.75	1573.816	0	0	30.1
TCI by sex	-8256.20	3	16518.39	1734.458	0	0	26.6
TCI	-8274.49	2	16552.98	1769.044	0	0	25.8

Table A4.3: AIC table presenting all candidate GAM models with dive duration as a response variable. The response variable was investigated in relation to geographic location (GL), FPT, bottom depth (BD), month (M) and TCI. The behavioural models included FPT as a predictor variable. Loglik is the loglikelihood, K is the number of parameters in the model. AIC$_i$ is AIC for model *i*, and ΔAIC is the difference between the AIC of the best fitting model and that of model *i*. Exp(-0.5Δ$_i$) represent the relative likelihoods and the w_i is the Akiake weights. D.E% is the deviance explained by the model.

model	**loglik**	**K**	**AIC$_i$**	**ΔAIC**	**exp(0.5Δ$_i$)**	**w_i**	**DE (%)**
GL ,FPT, BD, TCI and M by sex	-21741.35	11	43504.7	0	1	0.79249	65.3
GL ,FPT, BD and M by sex	-21744.69	9	43507.38	2.68	0.261845669	0.20751	65.3
GL ,FPT, BD, TCI and M	-21813.7	6	43639.4	134.7	5.62687E-30	4.5E-30	63.8
GL ,FPT, BD and M	-21815.5	5	43641	136.3	2.52831E-30	2E-30	63.7
GL , BD and M by sex	-21826.68	7	43667.36	162.66	4.77342E-36	3.8E-36	63.5
GL , BD and M	-21892.79	4	43793.58	288.88	1.86425E-63	1.5E-63	62
GL ,FPT, TCI and M by sex	-21894.53	9	43807.06	302.36	2.20475E-66	1.7E-66	61.9
GL ,FPT and M by sex	-21897.02	7	43808.04	303.34	1.35069E-66	1.1E-66	61.9
FPT, BD, TCI and M by sex	-21919.33	9	43856.66	351.96	3.73987E-77	3E-77	61.4
FPT, BD and M by sex	-21927.48	7	43868.96	364.26	7.97895E-80	6.3E-80	61.2
GL ,FPT, TCI and M	-21951.89	5	43913.78	409.08	1.47709E-89	1.2E-89	60.6
GL ,FPT and M by sex and age	-21953.21	4	43914.42	409.72	1.07259E-89	8.5E-90	60.6
GL , TCI and M by sex	-21954.74	7	43923.48	418.78	1.15632E-91	9.2E-92	60.5
GL and M by sex	-21956.75	5	43923.5	418.8	1.14482E-91	9.1E-92	60.5
FPT, BD, TCI and M	-21975.78	5	43961.56	456.86	6.2246E-100	5E-100	60
FPT, BD and M	-21985.9	4	43979.8	475.1	6.8131E-104	5E-104	59.8
GL and M	-22004.24	3	44014.48	509.78	2.0076E-111	2E-111	59.3
GL , TCI and M	-22003.76	4	44015.52	510.82	1.1936E-111	9E-112	59.3
BD, TCI and M by sex	-22015.28	7	44044.56	539.86	5.9005E-118	5E-118	59
BD and M by sex	-22023.11	5	44056.22	551.52	1.7336E-120	1E-120	58.8
FPT and M by sex	-22041.97	5	44093.94	589.24	1.1173E-128	9E-129	58.4
BD, TCI and M	-22049.54	4	44107.08	602.38	1.5662E-131	1E-131	58.2
BD and M	-22059.64	3	44125.28	620.58	1.7489E-135	1E-135	57.9
GL ,FPT, BD and TCI by sex	-22075.7	9	44169.4	664.7	4.5944E-145	4E-145	57.5
GL ,FPT and BD by sex	-22079.39	7	44172.78	668.08	8.4776E-146	7E-146	57.4
FPT and M	-22084.58	3	44175.16	670.46	2.5791E-146	2E-146	57.3
TCI and M by sex	-22123.71	5	44257.42	752.72	3.5394E-164	3E-164	56.2
GL ,FPT, BD and TCI	-22126.85	5	44263.7	759	1.5319E-165	1E-165	56.1
GL ,FPT and BD	-22128.06	4	44264.12	759.42	1.2418E-165	1E-165	56.1

GL , BD and TCI by sex	-22138	7	44290	785.3	2.9804E-171	2E-171	55.8
GL and BD by sex	-22140.23	5	44290.46	785.76	2.368E-171	2E-171	55.8
TCI and M	-22145.36	3	44296.72	792.02	1.0352E-172	8E-173	55.6
GL , BD and TCI	-22182.96	4	44373.92	869.22	1.7835E-189	1E-189	54.6
GL and BD	-22184.16	3	44374.32	869.62	1.4602E-189	1E-189	54.6
GL ,FPT and TCI by sex	-22213.19	7	44440.38	935.68	6.6019E-204	5E-204	53.8
GL and FPT by sex	-22216.15	5	44442.3	937.6	2.5278E-204	2E-204	53.7
GL ,FPT and TCI	-22247.33	4	44502.66	997.96	1.9758E-217	2E-217	52.8
GL and FPT	-22250.11	3	44506.22	1001.52	3.3319E-218	3E-218	52.7
GL and TCI by sex	-22258.83	5	44527.66	1022.96	7.3631E-223	6E-223	52.4
GL by sex	-22260.84	3	44527.68	1022.98	7.2898E-223	6E-223	52.4
GL and TCI	-22287.16	3	44580.32	1075.62	2.7045E-234	2E-234	51.6
GL	-22288.98	2	44581.96	1077.26	1.1911E-234	9E-235	51.6
FPT, BD, and TCI by sex	-22419.45	7	44852.9	1348.2	1.7462E-293	1E-293	47.5
FPT, and BD by sex	-22423.32	5	44856.64	1351.94	2.6913E-294	2E-294	47.4
FPT, BD, and TCI	-22440.6	4	44889.2	1384.5	2.289E-301	2E-301	46.8
FPT, and BD	-22443.19	3	44892.38	1387.68	4.6678E-302	4E-302	46.8
BD and TCI by sex	-22474.67	5	44959.34	1454.64	0	0	45.7
BD by sex	-22477.02	3	44960.04	1455.34	0	0	45.7
BD and TCI	-22484.16	3	44974.32	1469.62	0	0	45.4
BD	-22486.18	2	44976.36	1471.66	0	0	45.3
FPT and TCI by sex	-22520.55	5	45051.1	1546.4	0	0	44.2
FPT by sex	-22525.01	3	45056.02	1551.32	0	0	44
FPT and TCI	-22531.84	3	45069.68	1564.98	0	0	43.8
FPT	-22534.06	2	45072.12	1567.42	0	0	43.7
TCI by sex	-22572.49	3	45150.98	1646.28	0	0	42.4
TCI	-22574.71	2	45153.42	1648.72	0	0	42.3

Table A4.4: AIC table presenting all candidate GAM models with surface duration as a response variable. The response variable was investigated in relation to geographic location (GL), FPT, bottom depth (BD), month (M) and TCI. The behavioural models included FPT as a predictor variable. Loglik is the loglikelihood, K is the number of parameters in the model. AIC_i is AIC for model *i*, and ΔAIC is the difference between the AIC of the best fitting model and that of model *i*. Exp(-0.5Δ_i) represent the relative likelihoods and the w_i is the Akiake weights. D.E% is the deviance explained by the model.

model	**loglik**	**K**	**AIC_i**	**ΔAIC**	**exp(0.5Δ_i)**	**w_i**	**DE (%)**
GL ,FPT, BD, TCI and M by sex	-4488.285	11	8998.57	0	1	0.65993	39.8
GL ,FPT, BD and M by sex	-4490.948	9	8999.896	1.326	0.515303104	0.34007	39.7
GL ,FPT, BD and TCI by sex	-4511.57	9	9041.14	42.57	5.70219E-10	3.8E-10	38.9
GL ,FPT and BD by sex	-4514.329	7	9042.658	44.088	2.66939E-10	1.8E-10	38.8
GL ,FPT, BD and M	-4539.919	5	9089.838	91.268	1.51847E-20	1E-20	37.8
GL ,FPT, BD, TCI and M	-4539.45	6	9090.9	92.33	8.92884E-21	5.9E-21	37.9
GL ,FPT, TCI and M by sex	-4547.553	9	9113.106	114.536	1.34531E-25	8.9E-26	37.5
GL ,FPT and M by sex	-4551.636	7	9117.272	118.702	1.67567E-26	1.1E-26	37.4
GL ,FPT and BD	-4556.861	4	9121.722	123.152	1.81085E-27	1.2E-27	37.2
GL ,FPT, BD and TCI	-4556.408	5	9122.816	124.246	1.04791E-27	6.9E-28	37.2
GL ,FPT and TCI by sex	-4575.254	7	9164.508	165.938	9.26875E-37	6.1E-37	36.5
GL and FPT by sex	-4579.898	5	9169.796	171.226	6.58789E-38	4.3E-38	36.3
GL , BD and M by sex	-4578.906	7	9171.812	173.242	2.40424E-38	1.6E-38	36.3
FPT, BD, TCI and M by sex	-4591.158	9	9200.316	201.746	1.55386E-44	1E-44	35.9
GL , BD and TCI by sex	-4600.521	7	9215.042	216.472	9.85604E-48	6.5E-48	35.5
GL and BD by sex	-4604.899	5	9219.798	221.228	9.14008E-49	6E-49	35.3
FPT, BD and M by sex	-4605.893	7	9225.786	227.216	4.57797E-50	3E-50	35.3
GL ,FPT, TCI and M	-4609.506	5	9229.012	230.442	9.12337E-51	6E-51	35.1
GL ,FPT and M by sex and age	-4612.925	4	9233.85	235.28	8.12077E-52	5.4E-52	35
GL , BD and M	-4622.709	4	9253.418	254.848	4.57573E-56	3E-56	34.6
GL ,FPT and TCI	-4626.091	4	9260.182	261.612	1.55481E-57	1E-57	34.5
FPT, BD, and TCI by sex	-4624.424	7	9262.848	264.278	4.09979E-58	2.7E-58	34.5
GL and FPT	-4628.951	3	9263.902	265.332	2.42041E-58	1.6E-58	34.4
FPT, BD, TCI and M	-4628.436	5	9266.872	268.302	5.48228E-59	3.6E-59	34.4
FPT, BD and M	-4631.077	4	9270.154	271.584	1.06239E-59	7E-60	34.3
FPT, and BD by sex	-4639.022	5	9288.044	289.474	1.38522E-63	9.1E-64	33.9
GL and BD	-4649.384	3	9304.768	306.198	3.23556E-67	2.1E-67	33.5
GL , BD and TCI	-4648.794	4	9305.588	307.018	2.14728E-67	1.4E-67	33.6
FPT, BD, and TCI	-4654.025	4	9316.05	317.48	1.1484E-69	7.6E-70	33.3

FPT, and BD	-4655.413	3	9316.826	318.256	7.7909E-70	5.1E-70	33.3
GL , TCI and M by sex	-4656.792	7	9327.584	329.014	3.5935E-72	2.4E-72	33.2
GL and M by sex	-4660.979	5	9331.958	333.388	4.03381E-73	2.7E-73	33.1
BD, TCI and M by sex	-4677.404	7	9368.808	370.238	4.01643E-81	2.7E-81	32.4
BD and M by sex	-4691.562	5	9393.124	394.554	2.10711E-86	1.4E-86	31.8
GL and TCI by sex	-4695.683	5	9401.366	402.796	3.41948E-88	2.3E-88	31.6
GL by sex	-4700.846	3	9407.692	409.122	1.44639E-89	9.5E-90	31.4
BD, TCI and M	-4707.913	4	9423.826	425.256	4.53767E-93	3E-93	31.1
BD and M	-4710.42	3	9426.84	428.27	1.00543E-93	6.6E-94	31
FPT and M by sex	-4715.398	5	9440.796	442.226	9.37226E-97	6.2E-97	30.8
GL , TCI and M	-4719.769	4	9447.538	448.968	3.21986E-98	2.1E-98	30.6
GL and M	-4724.456	3	9454.912	456.342	8.0648E-100	5E-100	30.4
FPT and M	-4733.409	3	9472.818	474.248	1.0432E-103	7E-104	30
FPT and TCI by sex	-4732.54	5	9475.08	476.51	3.3664E-104	2E-104	30.1
BD and TCI by sex	-4739.305	5	9488.61	490.04	3.883E-107	3E-107	29.8
FPT by sex	-4748.021	3	9502.042	503.472	4.7038E-110	3E-110	29.4
BD by sex	-4749.697	3	9505.394	506.824	8.8017E-111	6E-111	29.3
GL and TCI	-4750.362	3	9506.724	508.154	4.5265E-111	3E-111	29.3
GL	-4754.213	2	9512.426	513.856	2.6157E-112	2E-112	29.1
FPT and TCI	-4753.513	3	9513.026	514.456	1.9378E-112	1E-112	29.2
FPT	-4758.385	2	9520.77	522.2	4.0338E-114	3E-114	28.9
BD	-4760.847	2	9525.694	527.124	3.4394E-115	2E-115	28.8
BD and TCI	-4760.017	3	9526.034	527.464	2.9017E-115	2E-115	28.9
TCI and M by sex	-4799.557	5	9609.114	610.544	2.6427E-133	2E-133	27.1
TCI and M	-4824.061	3	9654.122	655.552	4.4534E-143	3E-143	26
TCI by sex	-4864.148	3	9734.296	735.726	1.7343E-160	1E-160	24.2
TCI	-4877.226	2	9758.452	759.882	9.8564E-166	7E-166	23.6

CHAPTER 5: TABLES

Table A5.1: Tagging information for the 47 seals. ID = individual tag numbers, Sex = males (M) or females (F), Wt = weight in kg at the time of tagging, Start = tag date, End = date when tag stopped transmitting, Days = number of days of transmissions, Latitude and Longitude = tag location.

sort	ID	Sex	Wt (kg)	Year	Start	End	Days	Latitude	Longitude
1	hd1_9315_04	F	330	2004	14.3.	31.5.	78	46°58	-62°40
2	hd1_9256_04	F	208	2004	14.3.	9.7.	117	46°64	-62°25
3	hd1_9338_04	F	195.5	2004	14.3.	13.6.	90	46°63	-62°24
4	hd1_9255_04	F	276	2004	17.3.	17.6.	92	46°62	-61°85
5	hd2f-9257-04	F	148	2004	20.3.	30.6.	103	51°78	-55°52
6	hd2f-9337-04	F	150	2004	20.3.	24.5.	66	51°77	-55°52
7	hd2f-9350-04	F	182.5	2004	20.3.	23.6.	95	51°77	-55°52
8	hd2f-9343-04	F	162	2004	23.3.	17.6.	86	52°08	-55°15
9	hd2f-9316-04	F	147	2004	23.3.	28.6.	97	52°07	-55°16
10	hd2g-9409-04	F	116	2004	24.7.	28.6.	340	66°23	-34°28
11	hd1_9363_04	F	228	2005	13.3.	6.6.	86	48°03	-61°91
12	hd1_9351_04	F	188	2005	13.3.	23.6.	102	47°92	-61°99
13	hd5g-9400-05	F	112	2005	20.7.	20.5.	304	65°44	-36°29
14	hd5g-9420-05	F	138	2005	20.7.	13.6.	328	65°51	-36°37
15	hd5g-9413-05	F	90	2005	23.7.	27.6.	338	65°49	-37°09
16	hd5g-9344-05	F	108	2005	24.7.	25.8.	33	65°40	-36°64
17	hd5g-10222-05	F	98	2005	25.7.	18.6.	328	65°44	-37°14
18	hd5g-10227-05	F	114	2005	25.7.	26.5.	305	65°46	-37°39
19	hd5g-10206-05	F	95	2005	25.7.	4.7.	343	65°50	-37°85
20	hd5g-10205-05	F	138	2005	25.7.	14.4.	263	65°38	-37°57
21	hd6-D-06	F	73.5	2007	20.7.	2.6.	319	65°36	-37°25
22	MH4-10392-08	F	182.5	2008	14.3.	18.6.	96	47°69	-61°84
23	MH4-10423-08	F	251	2008	14.3.	1.7.	109	47°68	-61°83
24	MH4-10348-08	F	251	2008	15.3.	26.6.	104	47°69	-61°81
25	MH4-10386-08	F	224.5	2008	15.3.	14.6.	91	47°69	-61°77
26	hd3-80-08	F	155.5	2008	24.3.	11.7.	109	49°87	-52°32
27	hd3-81-08	F	158.5	2008	24.3.	2.7.	100	49°69	-52°16
28	hd3-82-08	F	139	2008	24.3.	23.6.	90	49°72	-52°18
29	hd3-79-08	F	149.5	2008	25.3.	19.6.	86	49°65	-52°30
30	hd3-78-08	F	229	2008	25.3.	21.6.	88	49°96	-51°87
31	hd1_9324_04	M	321	2004	16.3.	15.6.	91	46°60	-61°85
32	hd1_9335_04	M	326.5	2004	17.3.	8.6.	83	46°64	-61°87
33	hd1_9336_04	M	192	2004	17.3.	21.7.	126	46°57	-61°82
34	hd1_9317_04	M	274	2004	19.3.	14.6.	87	46°47	-61°90
35	hd2f-9355-04	M	246	2004	25.3.	24.6.	92	51°87	-55°40
36	hd2g-9421-04	M	172	2004	24.7.	20.3.	239	66°20	-33°48
37	hd1_9397_04	M	338	2005	12.3.	16.6.	95	47°98	-61°84

38	hd1_9341_04	M	338.5	2005	14.3.	3.7.	111	47°77	-61°99
39	hd5g-9427-05	M	194	2005	20.7.	7.4.	261	65°50	-36°02
40	hd5g-10204-05	M	146	2005	24.7.	13.6.	324	65°23	-36°83
41	hd5g-10207-05	M	174	2005	24.7.	12.7.	353	65°46	-37°23
42	hd5g-10188-05	M	109	2005	25.7.	22.3.	240	65°40	-37°46
43	hd6-F-06	M	97.5	2007	24.7.	24.6.	336	65°40	-37°82
44	ct18-L-06	M	130	2007	24.7.	7.4.	258	65°38	-37°97
45	MH4-10401-08	M	352.5	2008	16.3.	22.6.	98	47°66	-61°76
46	hd3-CTD453-08	M	230	2008	24.3.	14.5.	51	49°66	-52°62
47	hd1_9354_04	M	301	2005	12.3.	23.6.	103	47°98	-61°84

Table A5.2: AIC table. The response variable, daily change in drift rate, was investigated in relation to geographic location and day of year. Loglik is the loglikelihood, K is the number of parameters in the model. AIC$_i$ is AIC for model *i*, and ΔAIC is the difference between the AIC of the best fitting model and that of model *i*. Exp(-0.5Δ_i) represent the relative likelihoods and the w_i is the Akiake weights. D.E% is the deviance explained by the model. Models were run with and without a differentiation by sex to look for sexual segregation.

model	**loglik**	**K**	**AIC**	**ΔAIC**	**exp(0.5Δ_i)**	**w_i**	**DE(%)**
Geographic location and day of year, by sex	-3876.8	**5**	7763.59	0	1	1	**27**
Geographic location, by sex	-4197.61	3	8401.23	637.64	3.4602E-139	3.4602E-139	19.8
Geographic location and day of year	-4368.03	3	8742.06	978.47	3.3724E-213	3.3724E-213	15.7
Day of year, by sex	-4457.23	3	8920.46	1156.87	6.1438E-252	6.1438E-252	13.4
Geographic location	-4560.29	2	9124.58	1360.99	2.9159E-296	2.9159E-296	10.8
Day of year	-4611.98	2	9227.97	1464.38	0	0	9.4

CHAPTER 4: FIGURES

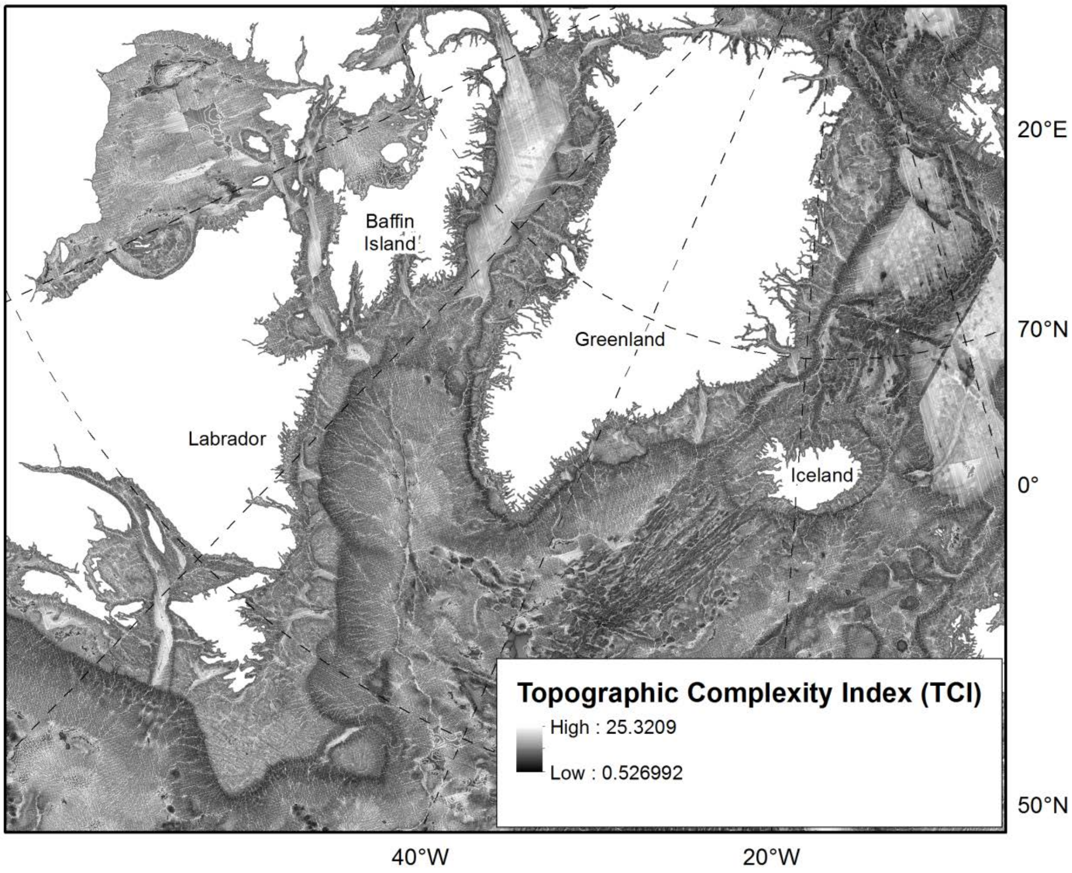


Figure A4.1: Map showing the calculated Topographic Complexity Index (TCI) surface for the Northwest Atlantic Ocean. High numeric values (and light colour) represent peaks, and low numeric values (and dark colour) represent basins. The data ranged from 0.53-25.32, where values around 12.5 represent a flat surface.

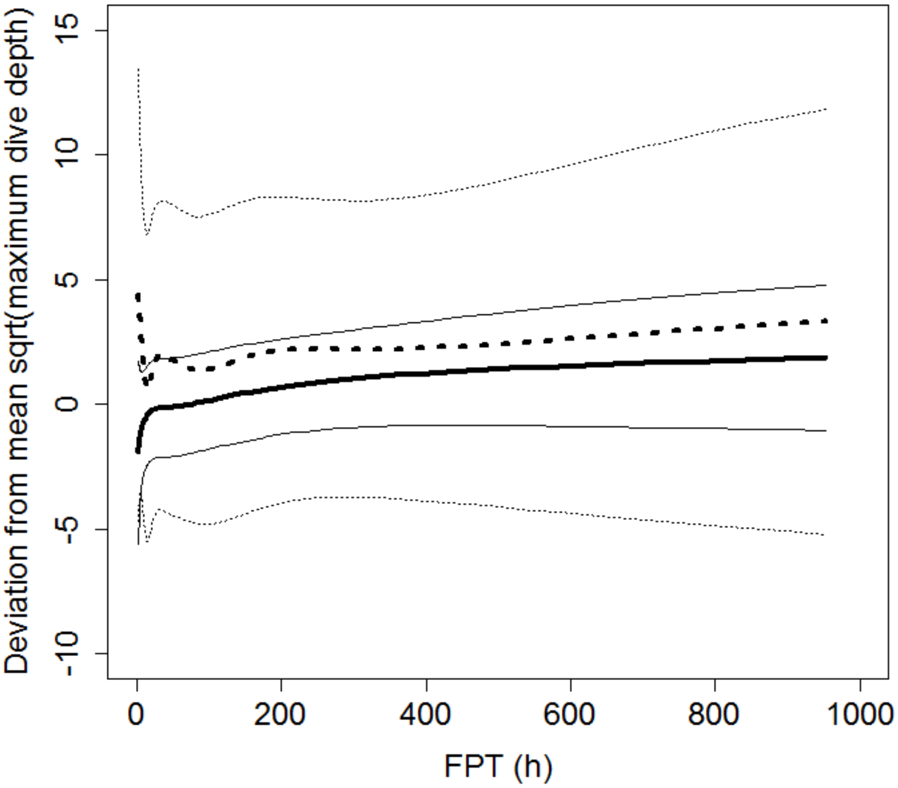


Figure A4.2: Full predicted maximum dive depth model results for FPT as seen in figure 4.6a across all hours of FPT. Solid black line represents males (n=18) and the hashed line represents females (n=33). Thin black lines represent the standard error.

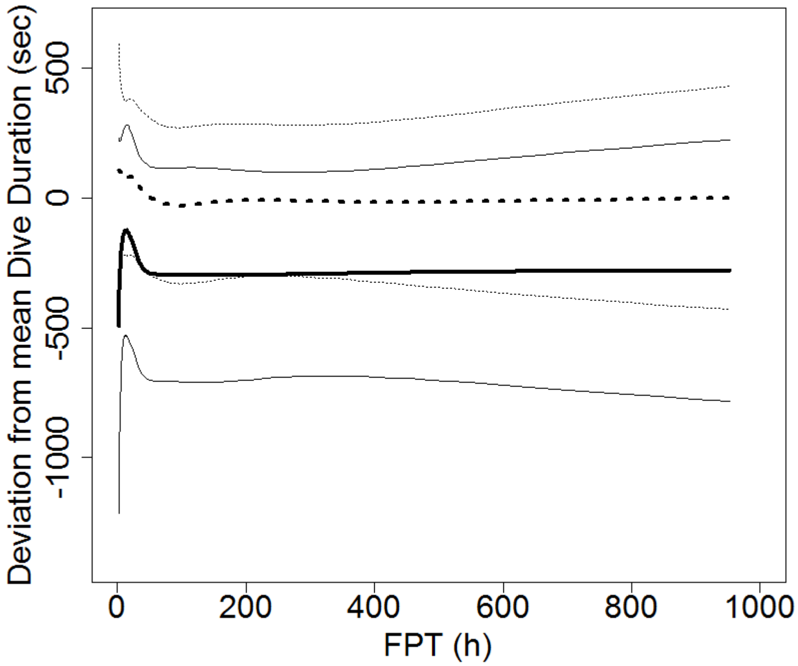


Figure A4.3: Full predicted dive duration model results for FPT as seen in figure 4.6a across all hours of FPT. Solid black line represents males (n=18) and the hashed line represents females (n=33). Thin black lines represent the standard error.

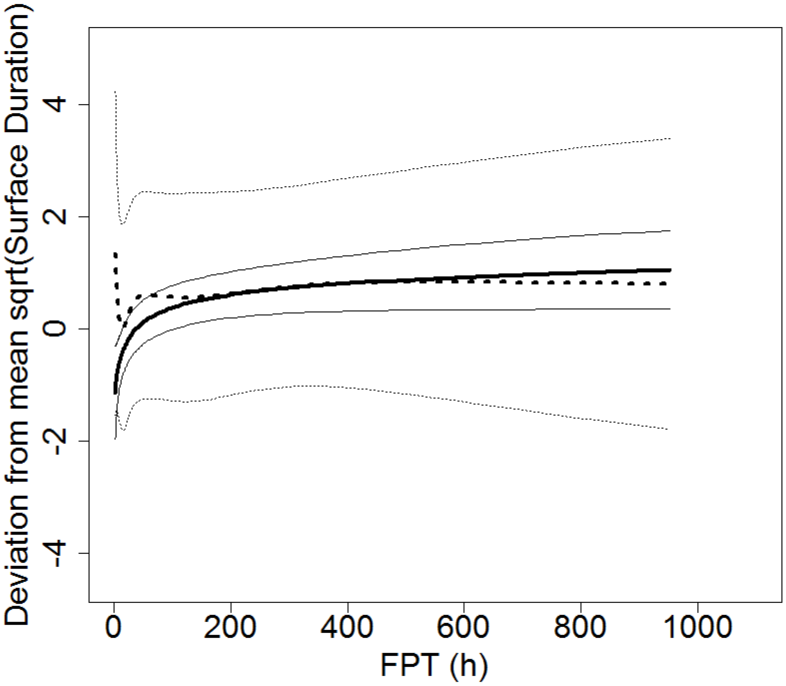


Figure A4.4: Full predicted surface duration model results for FPT as seen in figure 4.6a across all hours of FPT. Solid black line represents males (n=18) and the hashed line represents females (n=33). Thin black lines represent the standard error.

CHAPTER 5: FIGURES

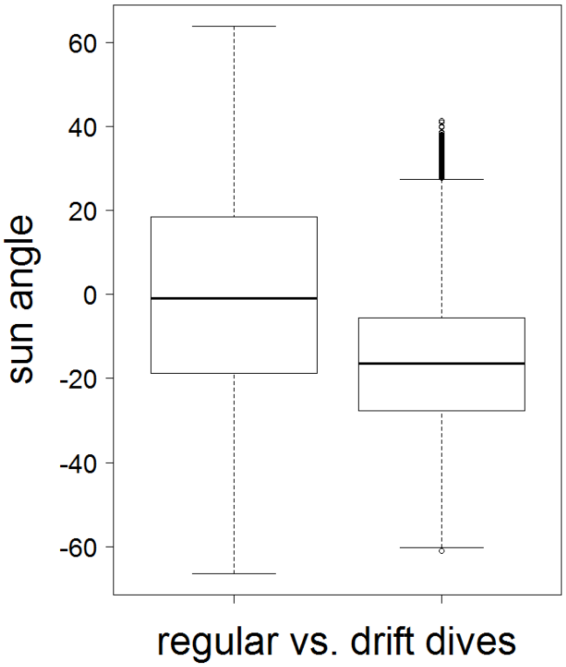


Figure A5.1: Occurence of regular dives (i.e., dives with no drift component) to the left (n = 87,565) and drift dives to the right (n = 6,806) in realtion to the suns angle to the dive location throughout the day.

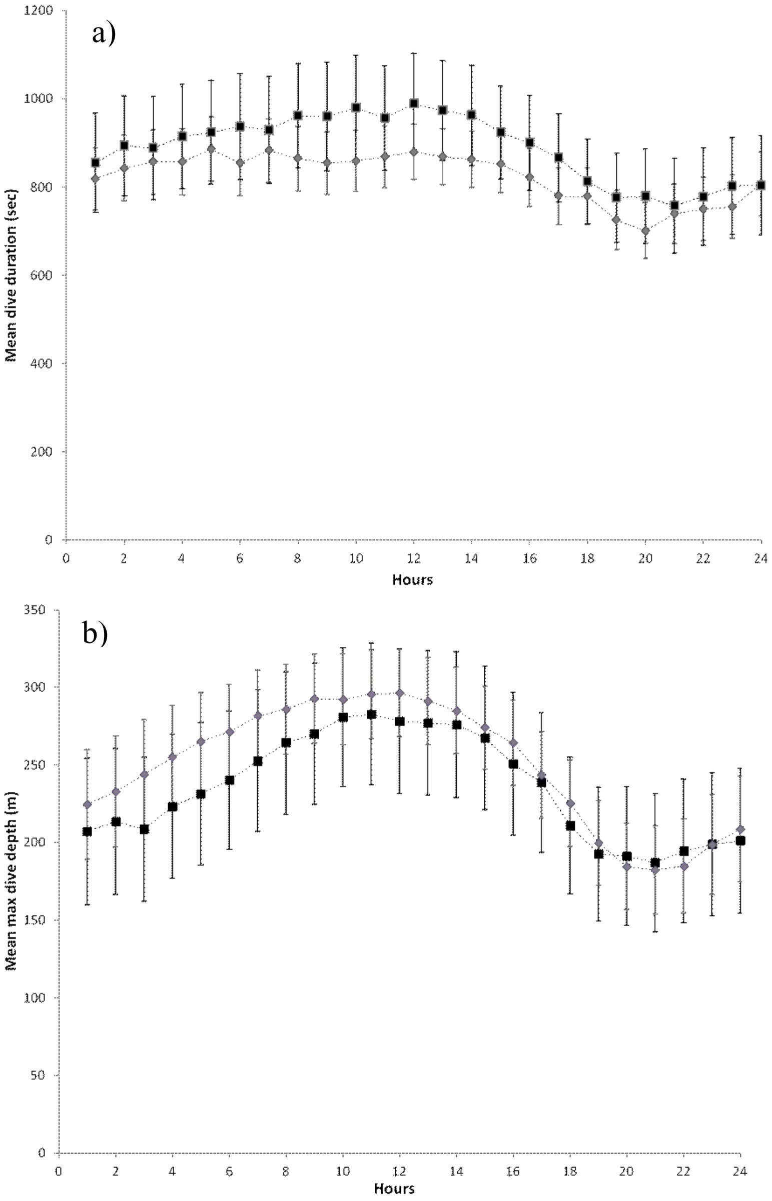


Figure A5.2: a) Dive durations (seconds) during regular dives as a function of time of day (01:00-24:00) across females (grey lines), and males (black lines). b) Mean maximum dive depths (meters) during regular dives as a function of time of day (01:00-24:00) across females (grey lines), and males (black lines). Females: n=30, males: n=17. Error bars represent the standard error.

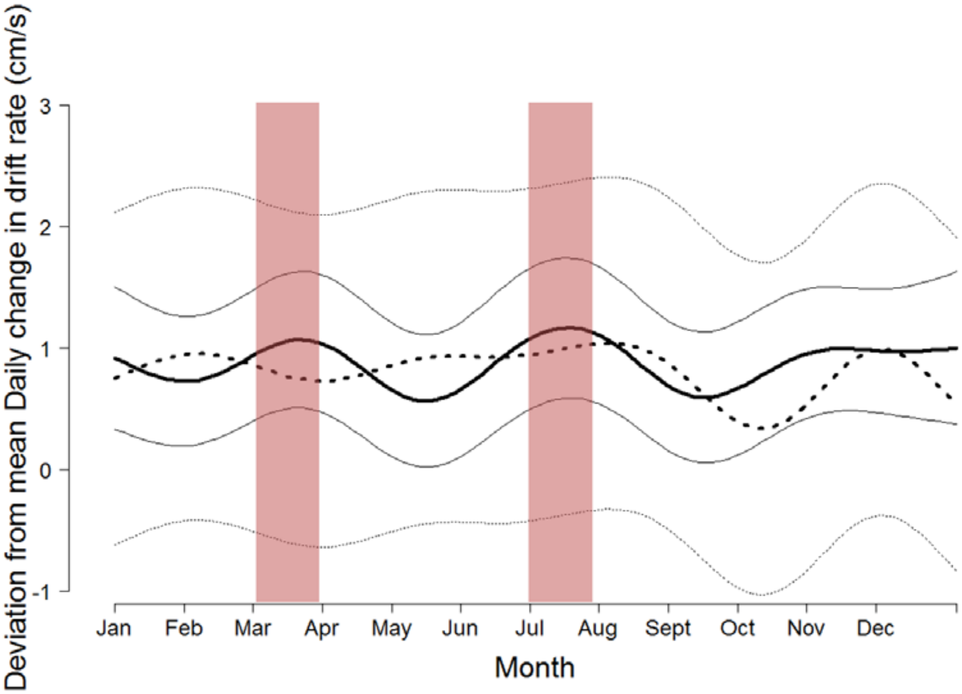
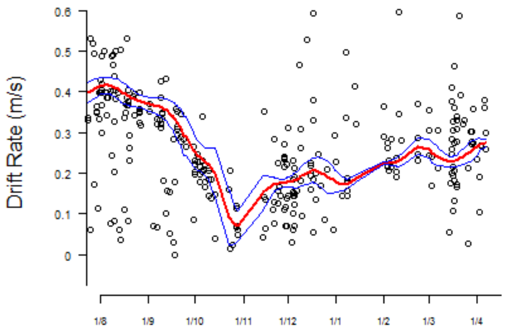
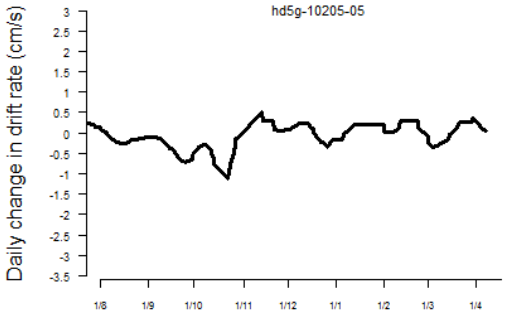
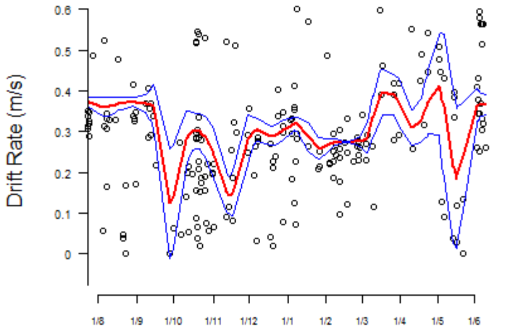
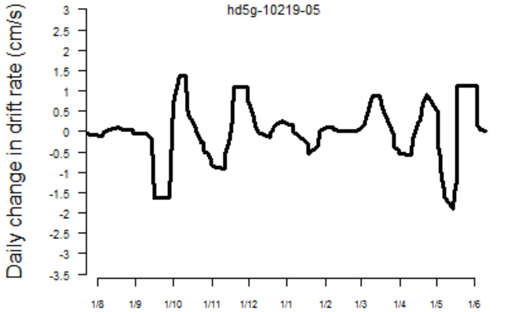


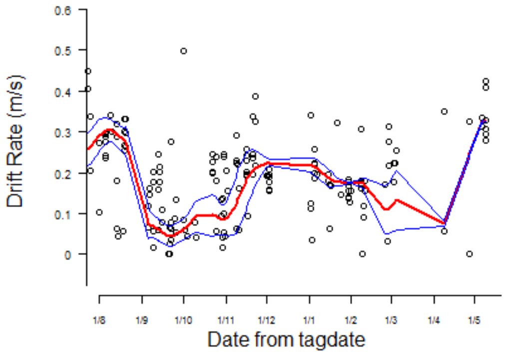
Figure A5.3: Predicted graphs from the best GAM model (males: solid black line (n=17) and females dashed line (n=30). Columns represent the fasting periods (March = breeding/whelping and July = moult).

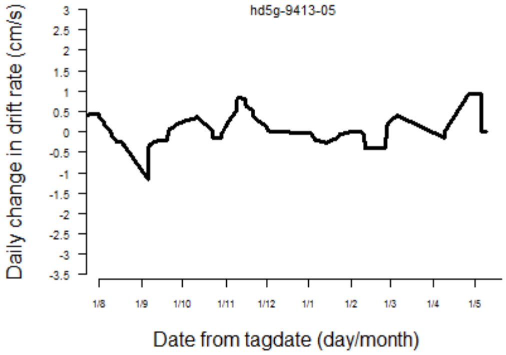

Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4

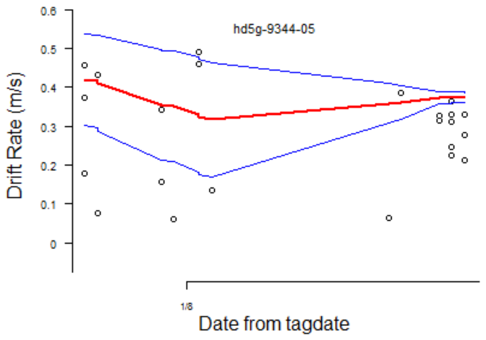

hd5g-10205-05
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4

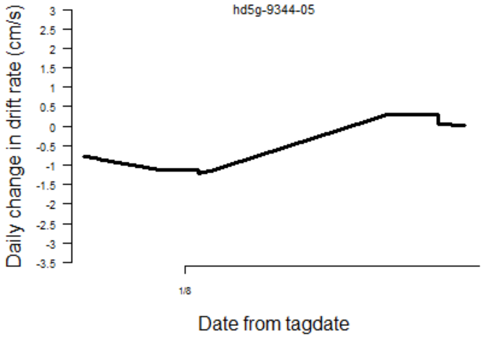

Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6

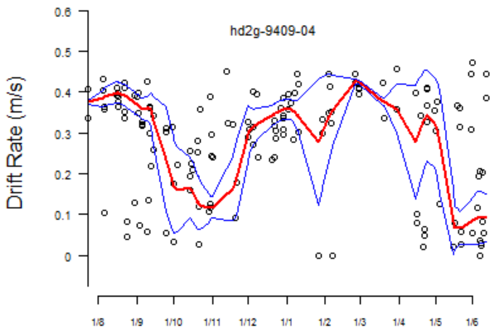

hd5g-10219-05
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6

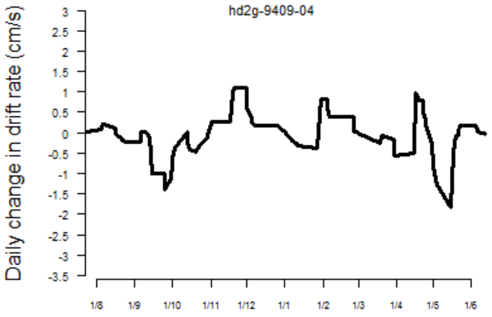

Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
Date from tagdate

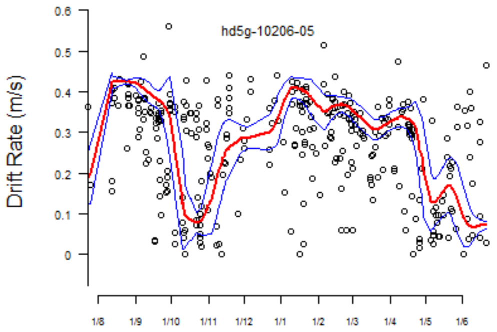

hd5g-9413-05
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
Date from tagdate (day/month)

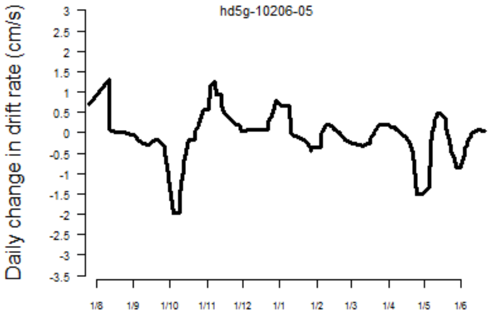

hd5g-9344-05
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
Date from tagdate

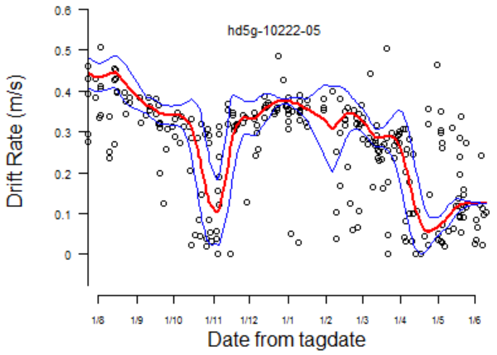

hd5g-9344-05
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
Date from tagdate

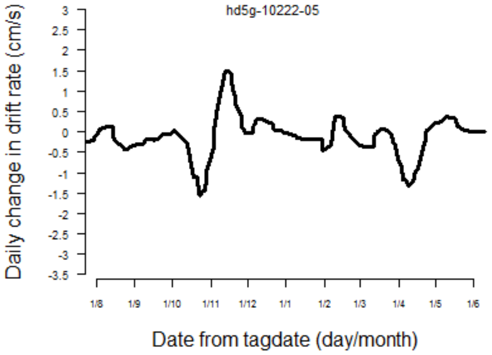

hd2g-9409-04
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6

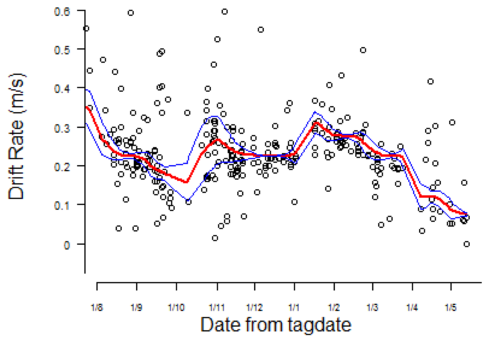

hd2g-9409-04
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6

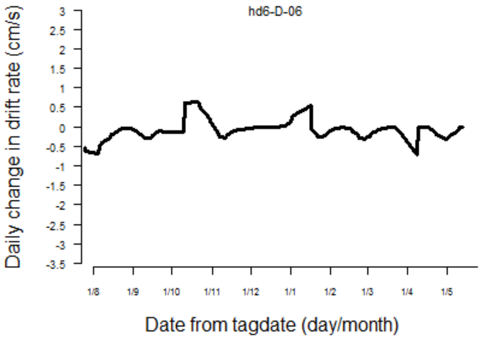

hd5g-10206-05
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6


hd5g-10206-05
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6


hd5g-10222-05
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6
Date from tagdate


hd5g-10222-05
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6
Date from tagdate (day/month)


Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
Date from tagdate


hd6-D-06
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
Date from tagdate (day/month)

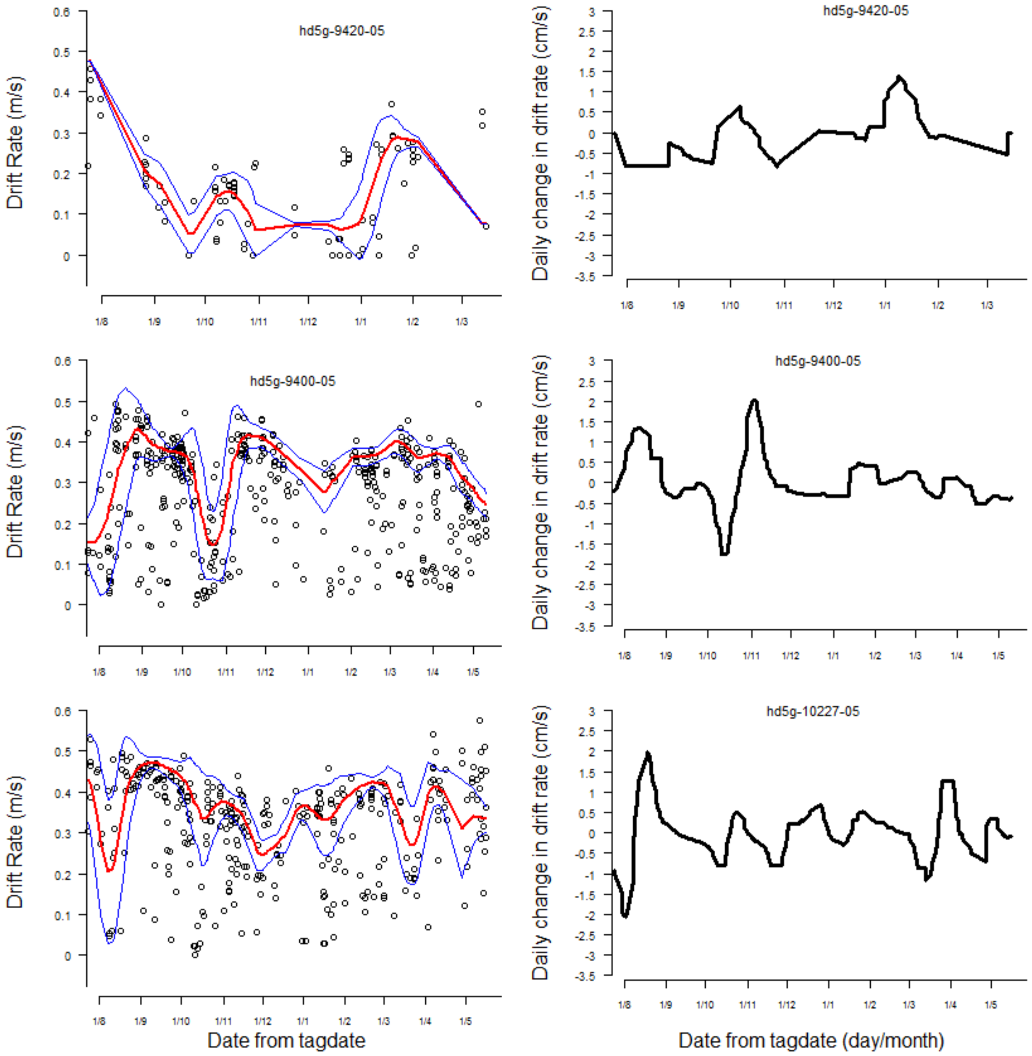
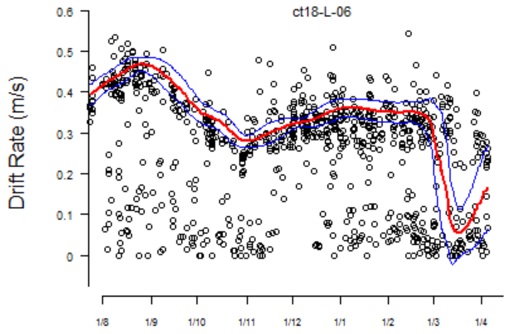
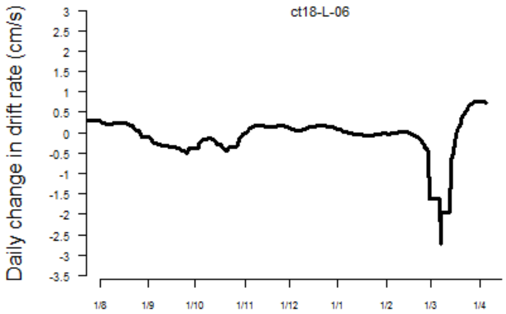
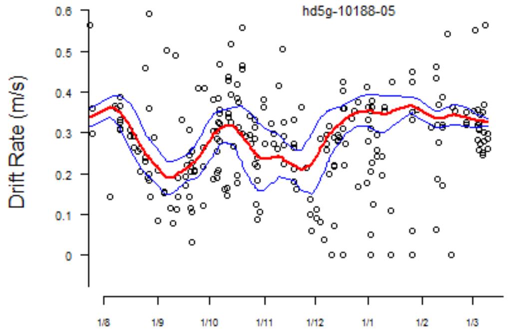
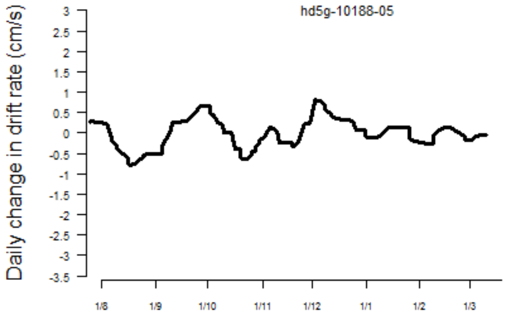


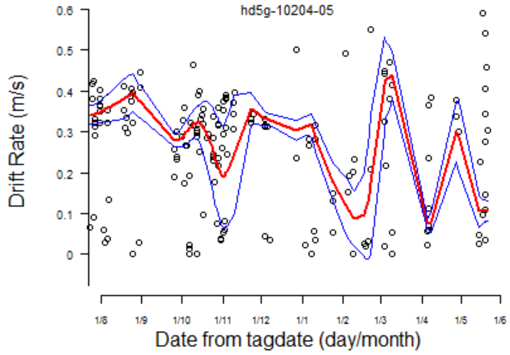
Figure A5.4: All individual females tagged in July (n=11). Left hand panels show the fluctuation in drift rate (m/s), fitted with a smooth line. Blue lines represent 1 standard error from the smooth. The right hand panel shows the daily change in drift rate (cm/s) over the same period. The title of each plot is the individual seal id.

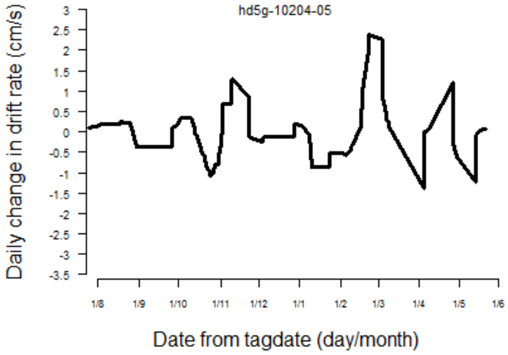

ct18-L-06
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4

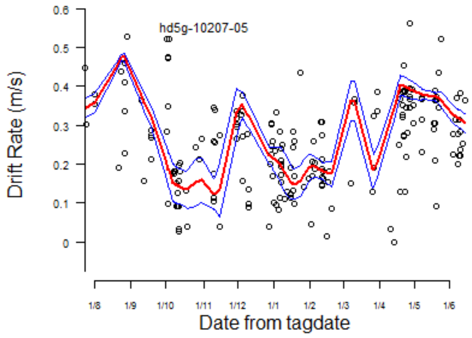

ct18-L-06
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4

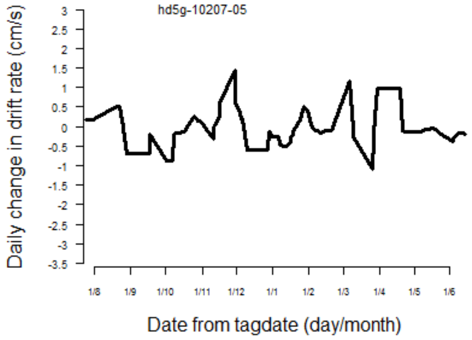

hd5g-10188-05
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3


hd5g-10188-05
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3


hd5g-10204-05
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6
Date from tagdate (day/month)


hd5g-10204-05
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6
Date from tagdate (day/month)


hd5g-10207-05
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6
Date from tagdate


hd5g-10207-05
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/8
1/9
1/10
1/11
1/12
1/1
1/2
1/3
1/4
1/5
1/6
Date from tagdate (day/month)

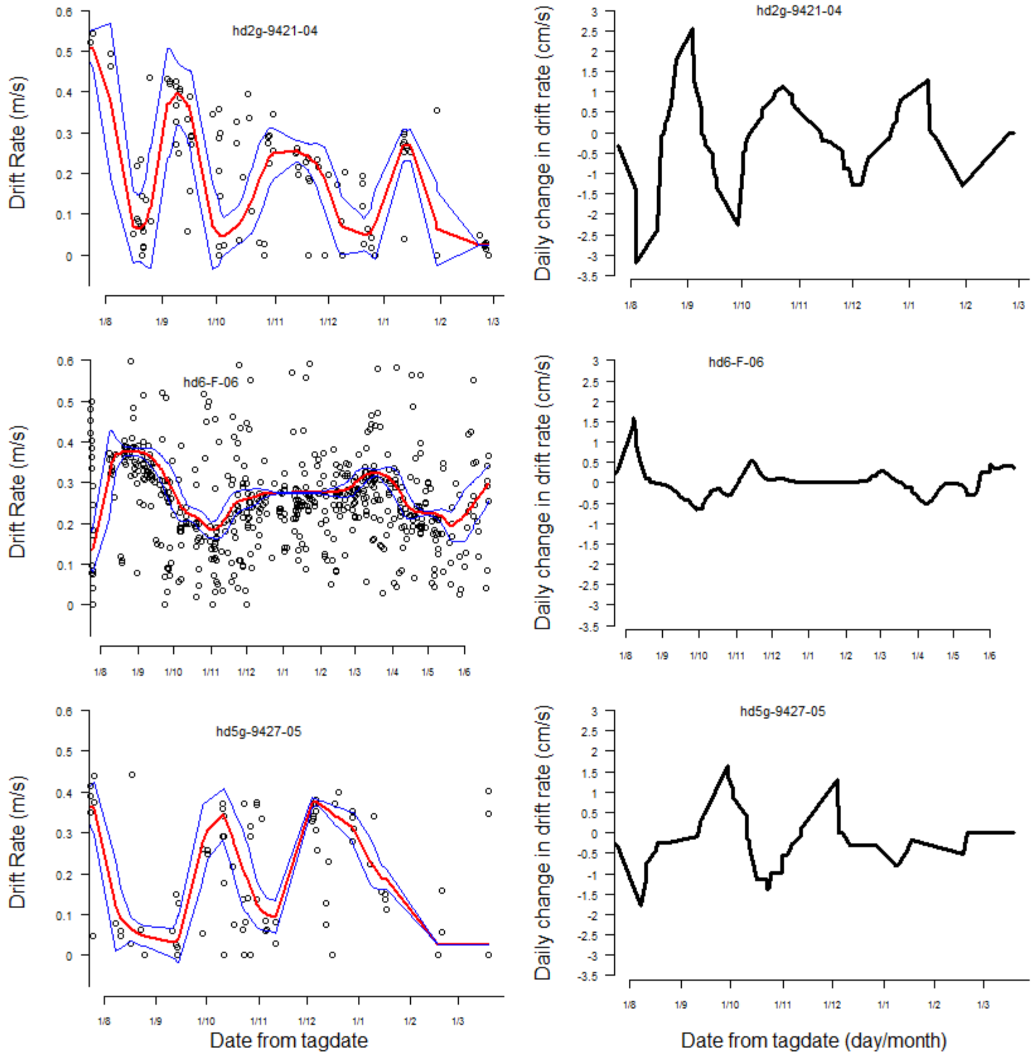
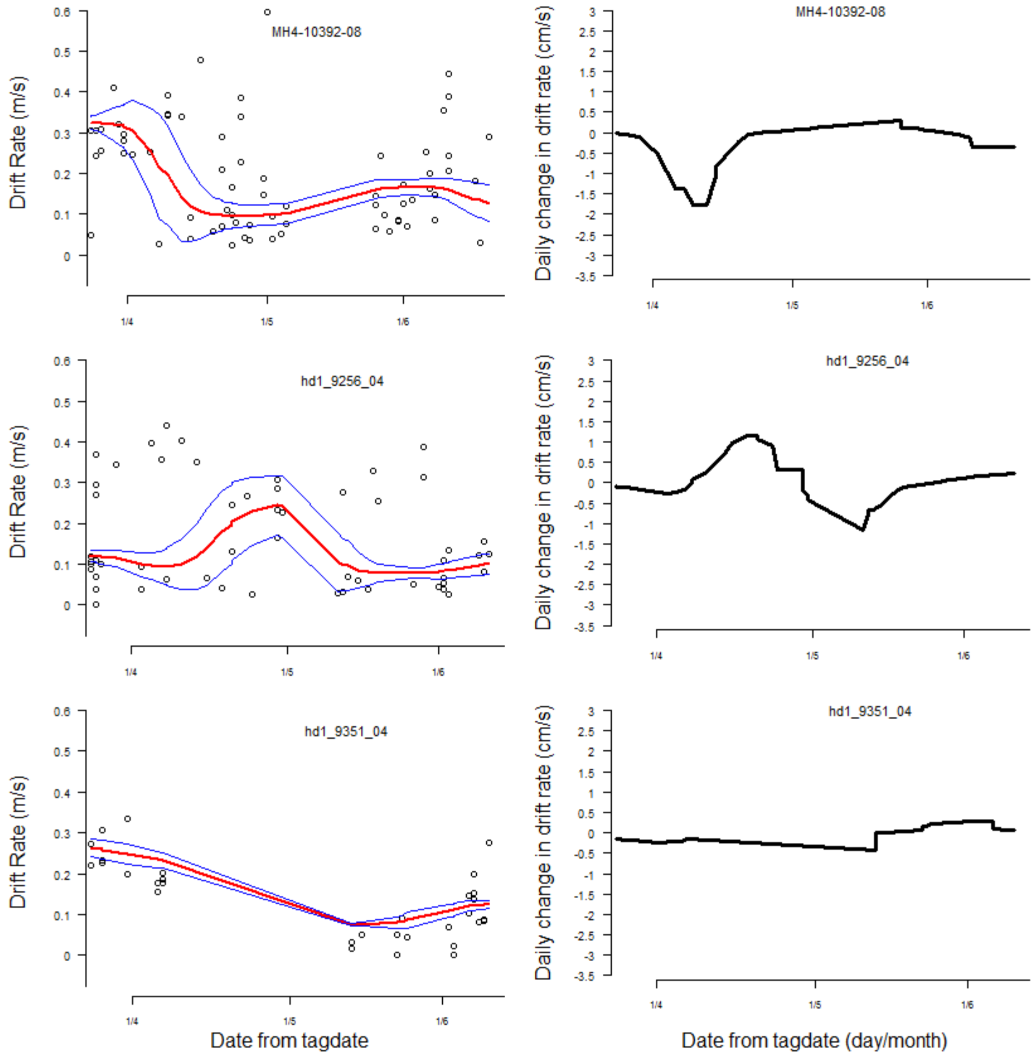
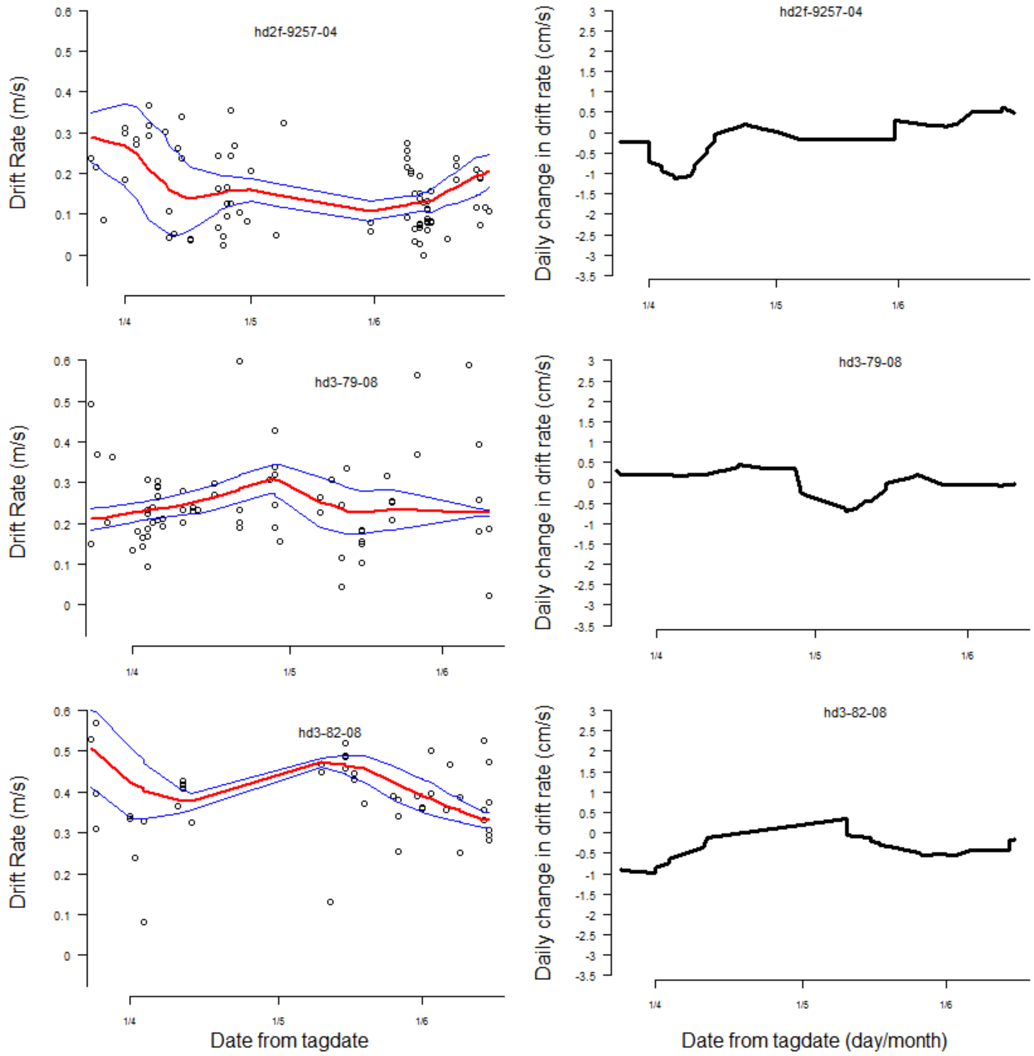
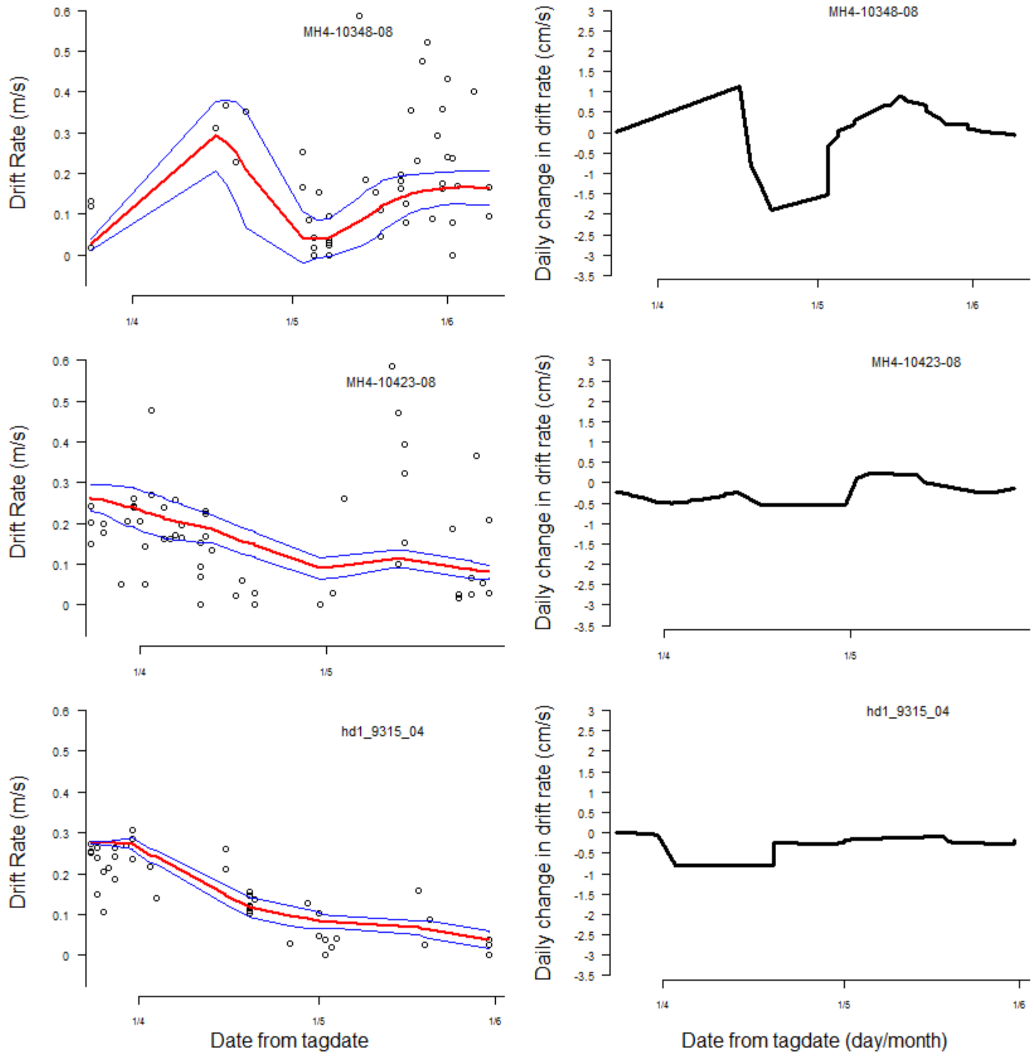
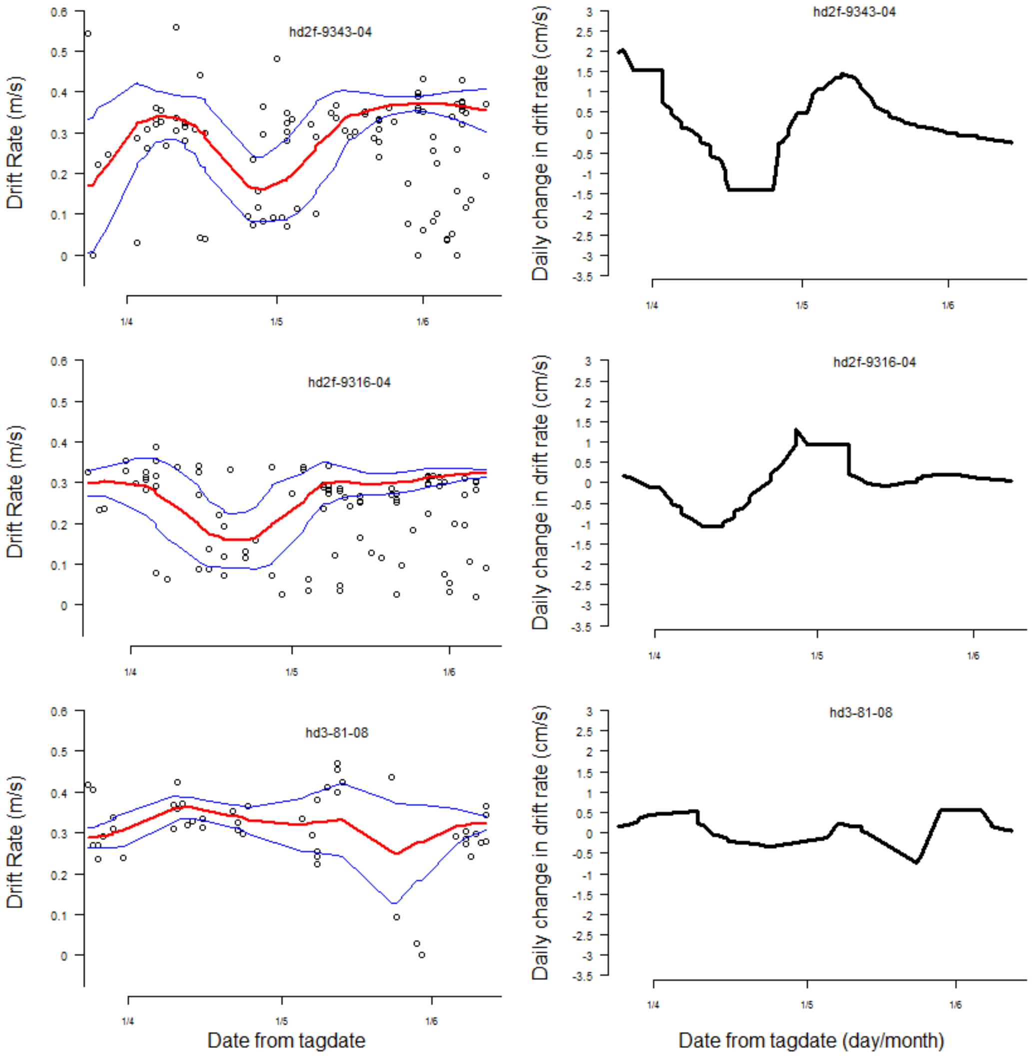


Figure A5.5: All individual males tagged in July (n = 7). Left hand panels show the fluctuation in drift rate (m/s), fitted with a smooth line. Blue lines represent 1 standard error from the smooth. The right hand panels show the daily change in drift rate (cm/s) over the same period. The title of each plot is the individual seal id.

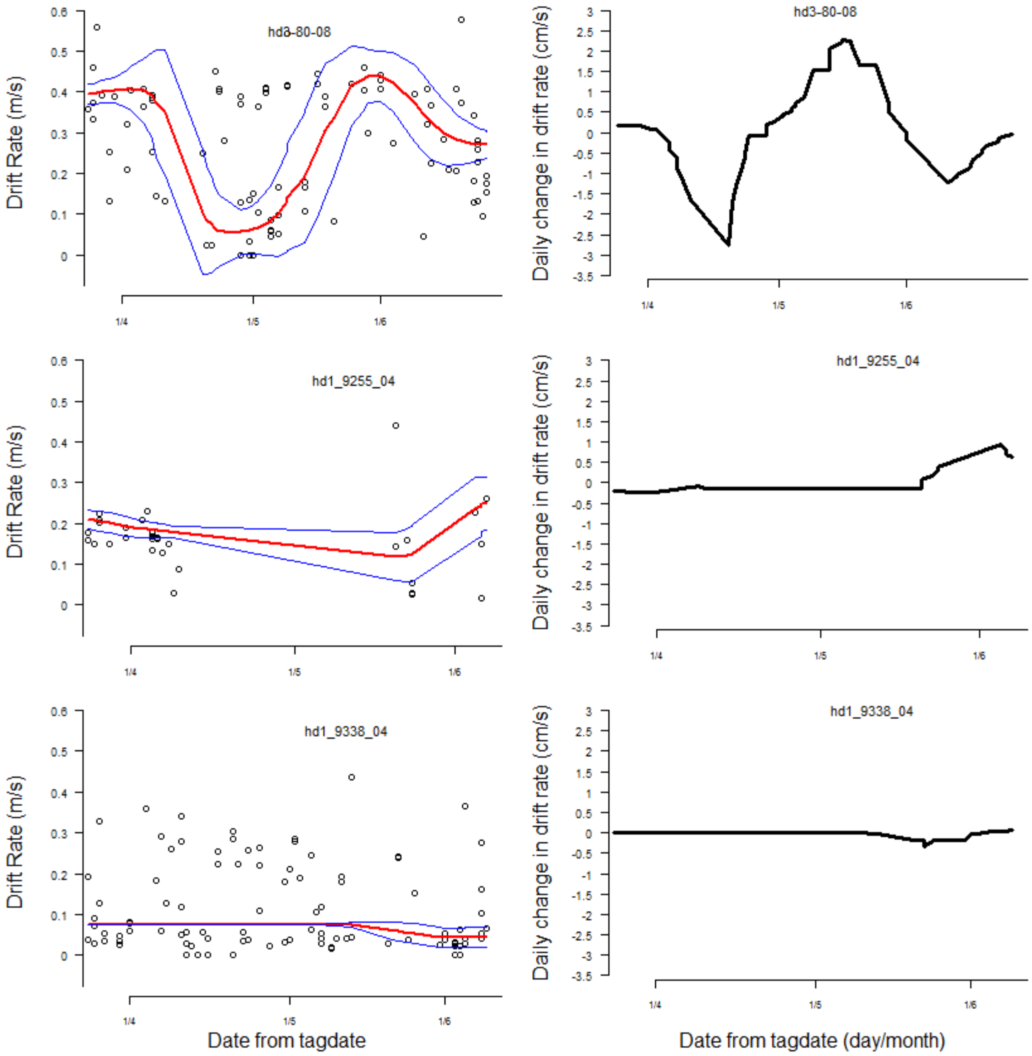

MH4-10392-08
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/4
1/5
1/6
MH4-10392-08
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
hd1_9256_04
hd1_9351_04
Date from tagdate
Date from tagdate (day/month)

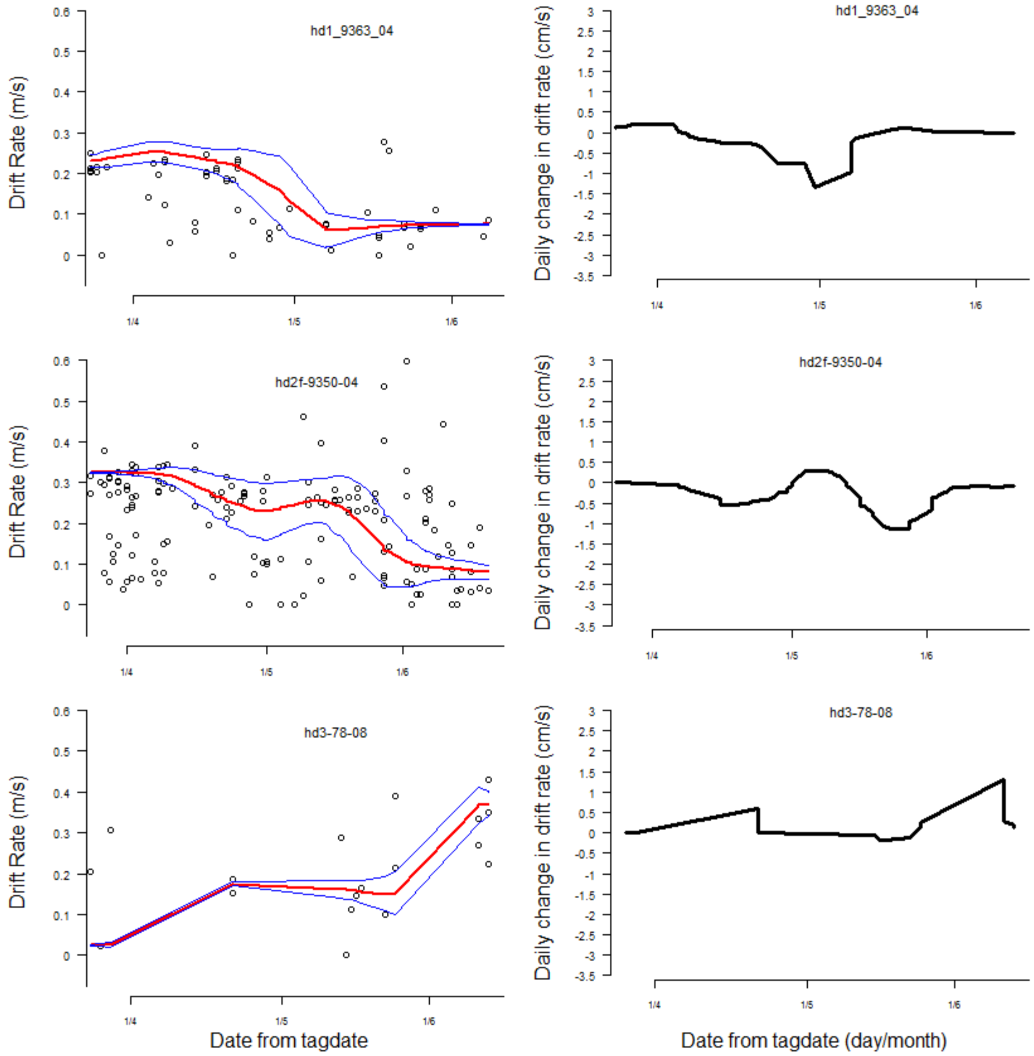

hd2f-9257-04
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/4
1/5
1/6
hd2f-9257-04
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
hd3-79-08
hd3-79-08
hd3-82-08
hd3-82-08
Date from tagdate
Date from tagdate (day/month)


MH4-10348-08
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/4
1/5
1/6
MH4-10348-08
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/4
1/5
1/6
MH4-10423-08
Drift Rate (m/s)
1/4
1/5
MH4-10423-08
Daily change in drift rate (cm/s)
1/4
1/5
hd1_9315_04
Drift Rate (m/s)
1/4
1/5
1/6
Date from tagdate
hd1_9315_04
Daily change in drift rate (cm/s)
1/4
1/5
1/6
Date from tagdate (day/month)



hd2f-9343-04
hd2f-9343-04
hd2f-9316-04
hd2f-9316-04
hd3-81-08
hd3-81-08
Drift Rate (m/s)
Daily change in drift rate (cm/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/4
1/5
1/6
Date from tagdate
Date from tagdate (day/month)


hd3-80-08
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/4
1/5
1/6
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
hd1_9255_04
hd1_9338_04
Date from tagdate
Date from tagdate (day/month)


hd1_9363_04
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/4
1/5
1/6
hd1_9363_04
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/4
1/5
1/6
hd2f-9350-04
Drift Rate (m/s)
1/4
1/5
1/6
hd2f-9350-04
Daily change in drift rate (cm/s)
1/4
1/5
1/6
hd3-78-08
Drift Rate (m/s)
1/4
1/5
1/6
Date from tagdate
hd3-78-08
Daily change in drift rate (cm/s)
1/4
1/5
1/6
Date from tagdate (day/month)

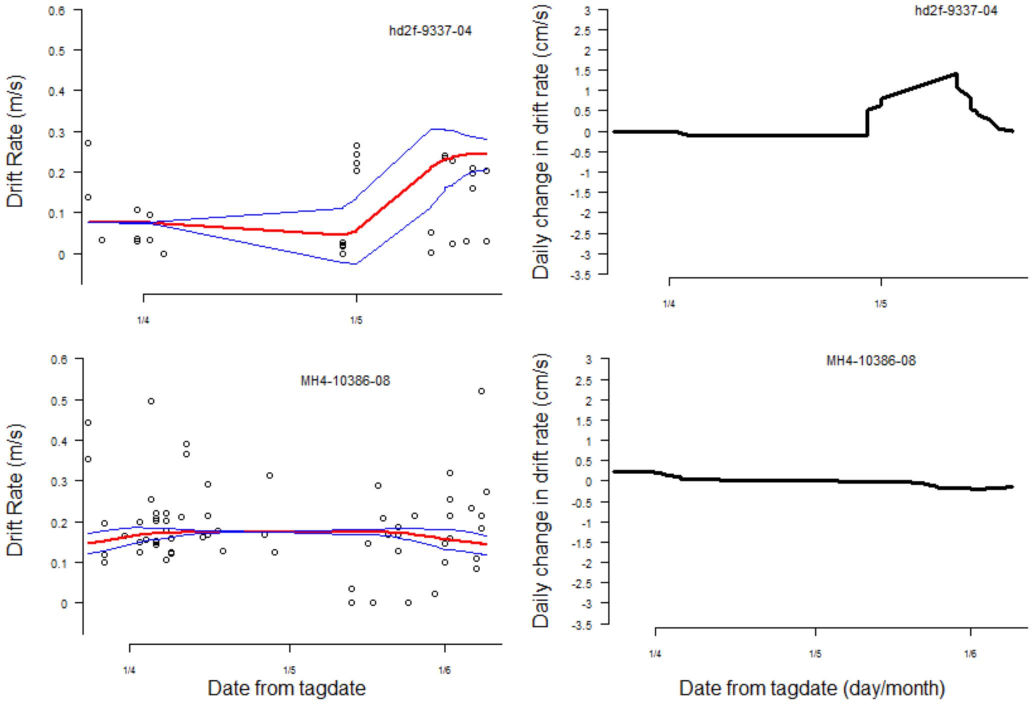
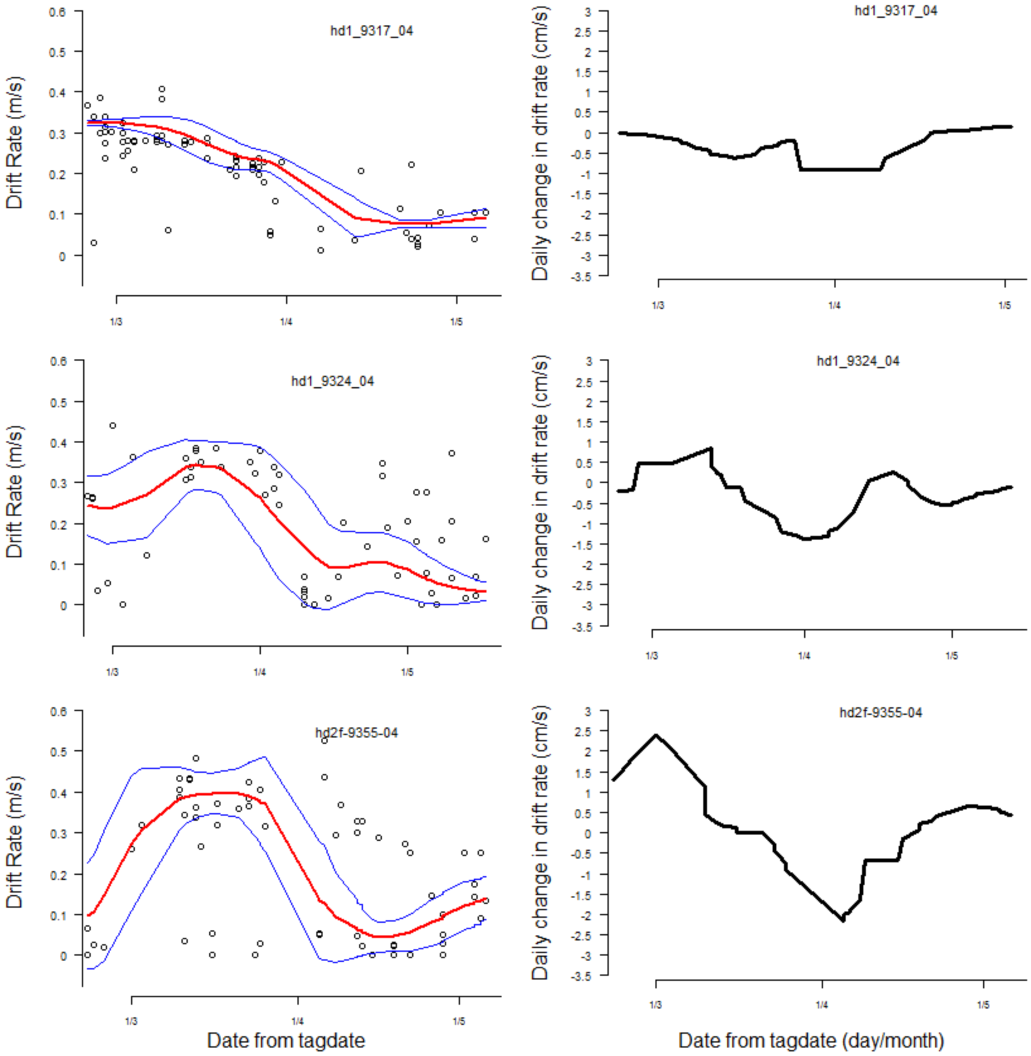
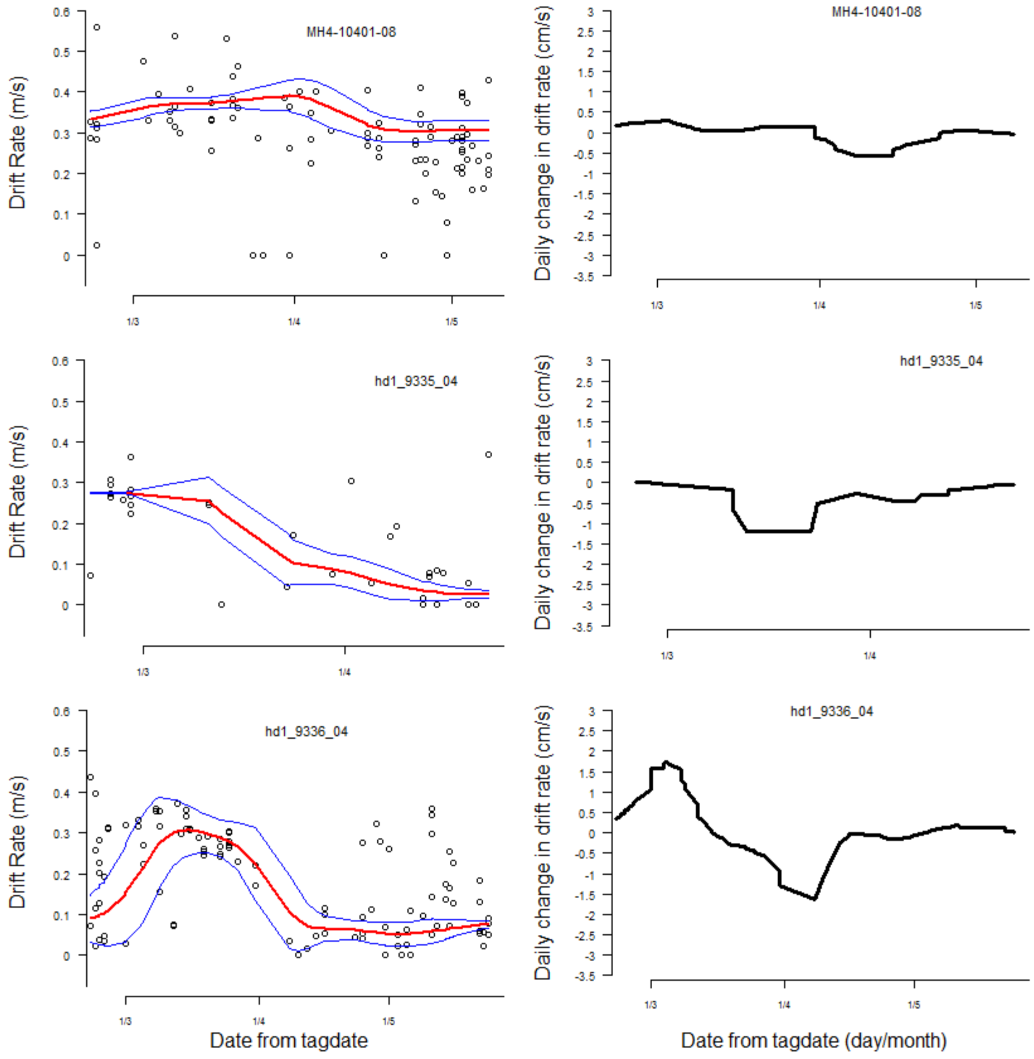


Figure A5.6: All individual females tagged in March (n=20). Left hand panels show the fluctuation in drift rate (m/s), fitted with a smooth line. Blue lines represent 1 standard error from the smooth. The right hand panels show the daily change in drift rate (cm/s) over the same period. The title of each plot is the individual seal id.


hd1_9317_04
Drift Rate (m/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
1/3
1/4
1/5
hd1_9317_04
Daily change in drift rate (cm/s)
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/3
1/4
1/5
hd1_9324_04
Drift Rate (m/s)
1/3
1/4
1/5
hd1_9324_04
Daily change in drift rate (cm/s)
1/3
1/4
1/5
hd2f-9355-04
Drift Rate (m/s)
1/3
1/4
1/5
Date from tagdate
hd2f-9355-04
Daily change in drift rate (cm/s)
1/3
1/4
1/5
Date from tagdate (day/month)


MH4-10401-08
hd1_9335_04
hd1_9336_04
Drift Rate (m/s)
Daily change in drift rate (cm/s)
0.6
0.5
0.4
0.3
0.2
0.1
0
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-3
-3.5
1/3
1/4
1/5
Date from tagdate
Date from tagdate (day/month)

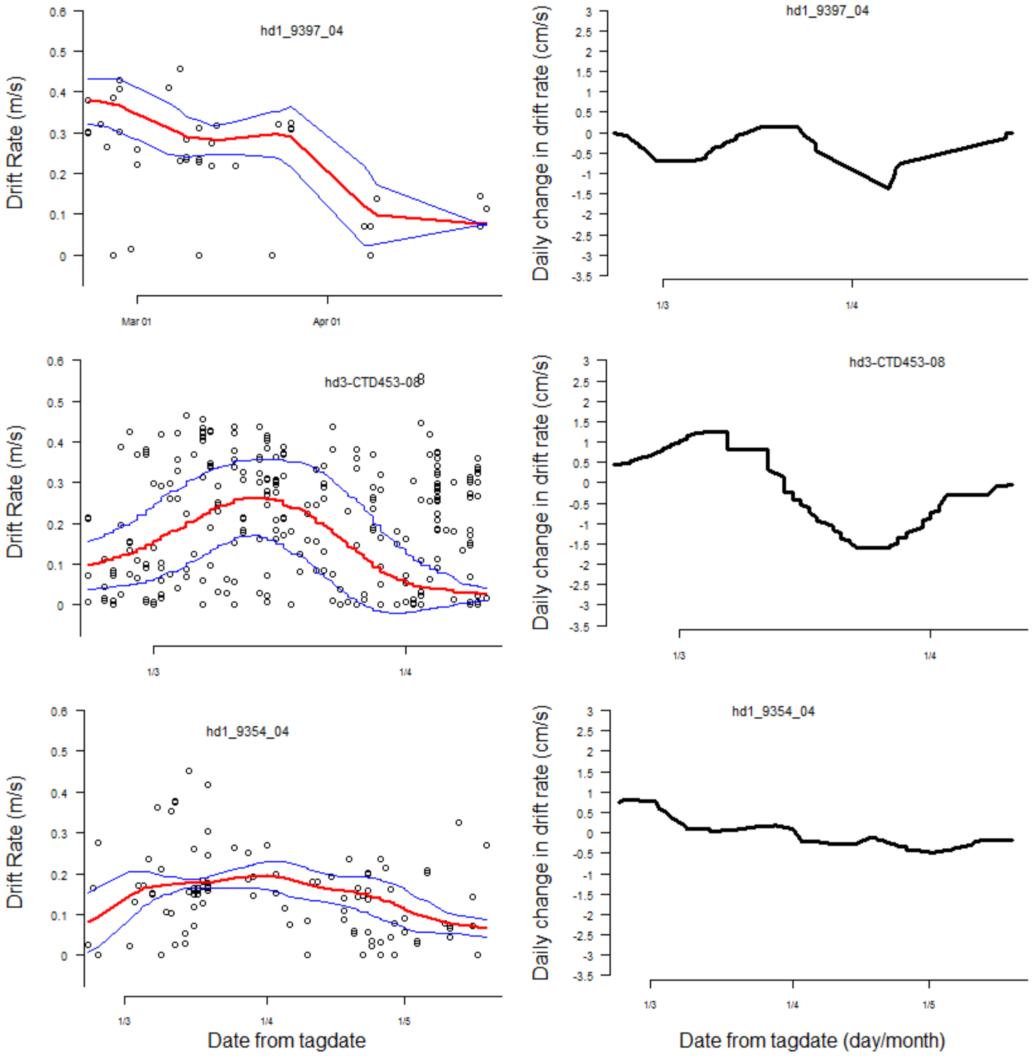


Figure A5.7: All individual males tagged in March (n = 9). Left hand panels show the fluctuation in drift rate (m/s), fitted with a smooth line. Blue lines represent 1 standard error from the smooth. The right hand panels show the daily change in drift rate (cm/s) over the same period. The title of each plot is the individual seal id.