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

Julie M. Andersen[1*], Yolanda F. Wiersma[1], Garry B. Stenson[2], Mike O. Hammill[3], Aqqalu Rosing-Asvid[4] and Mette Skern-Maurizen[5]

[1]Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada
[2]Science Branch, Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, St. John's, NL A1C 5X1, Canada
[3] Science Branch, Department of Fisheries and Oceans, Institute du Maurice Lamontang, Mont Joli, Quebec, G5H 3Z4, Canada
[4]Greenland Institute of Natural Resources, 3900 Nuuk, Greenland
[5] Marine Mammal Research Department, Institute of Marine Research, 5817, Norway

Abstract:

We examined annual habitat use for 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 combined approach using First Passage Time (FPT) analysis and a generalized additive model (GAM) was applied to test for habitat selection, with a focus on environmental parameters of depth, slope, ice, sea surface temperature (SST) and chlorophyll. The models were run on adult males, adult females and juveniles separately, and the results identified SST, depth and chlorophyll as the most important factors influencing habitat selection across all categories. Furthermore, 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 patterns focusing their search effort in areas of complex seafloor relief such as Baffin Bay, Davis Strait and the Flemish cap, while females concentrated their search effort along shelf areas (e.g., the Labrador shelf). These findings support our hypothesis that hooded seals prefer areas where topography and oceanographic processes create favorable foraging conditions. Sexual segregation could reflect different energy requirements

* Corresponding author: julie.andersen@mun.ca

when preparing for and recover from important life history events such as whelping and lactation for females and competition for mates among males.

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

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 Atlantic (NW) and Northeast Atlantic (NE) 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) (See Fig 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 fall or early winter (Andersen et al. 2009).

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 and productive; demonstrating pronounced seasonal and annual variation in ocean climate (e.g. Gulland 1974, Loeng 1991). The ocean environment on the Newfoundland and Labrador Shelf is 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 characterized 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 2000 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 the 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 overwintering animals (Heide-Jørgensen and Laidre 2004).

Due to the pelagic distribution of hooded seals and our lack of knowledge regarding their prey selection at various times of the year, the extent of fish consumption is difficult to assess (Folkow et al. 1996). 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 has intensified (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 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*)).

Being a highly 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. Bajzak et al. (2009) found that although 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) support these findings by showing how male and female hooded seals forage on different benthopelagic prey. They also found a difference in diet preference between seasons and geographical areas for both sexes. Although these studies suggest that there might not be competition for prey between the sexes, there may be overlap in prey preference with other species such as harp seals, beluga (*Delphinapterus leucas*) and narwhal (*Monodon monoceros*) (Richard et al.1998, Laidre et al. 2003, 2004) in important feeding areas for hooded seals during their post moult migration.

Here, we hypothesize that hooded seals forage in areas of complex oceanographic conditions. We expect that if complex seafloor relief concentrates prey, hooded seal movement patterns and extended space use 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 pupping/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 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/or sex.

Methods

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.1).

Deployment of SRDLs

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 (1mg. 100kg-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.

Seal locations were determined by the ARGOS collection and location system (CLS/Service Argos), and 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 2m/s between successive locations which was similar to that used for grey seals (Austin et al. 2003).

Seal and habitat data:

Satellite transmitters were deployed on 65 seals over a period of four years (2004-2008), of which there were 32 adult females, 17 adult males and 16 juveniles (10 female and 6 male)

(Table 1). 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, chlorophyll (primary productivity), SST and slope. The distribution patterns of male, female and juvenile hooded seals were compared to look for differences in habitat preference by sex and age, where the year was separated into two periods: spring (April-June = post breed/pre moult period) and fall/winter (August-February = post moult/pre breed 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 data, 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 seal locations.

Daily ice cover data (25 km by 25 km resolution) were obtained from the National Snow and Ice Data Center in Colorado (http://nsidc.org/index.html). Depth, slope and the 1000 m depth contours were derived using bathymetry data from the General Bathymetry Chart of the Ocean (GEBCO; http://www.gebco.net/).

Kernel maps (Fig. 2a-f) 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 20 000 metres.

First passage Time (FPT) is defined as the time required for an animal to cross a circle of a given 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). This was done by plotting FPT against the distance travelled and the difference in sample size was taken into account by employing a bootstrap routine to extract ARS for each group. We then created a new dataset based on the average ARS scale, and related high use areas and FPT to oceanographic variables through extraction of data and GAM models.

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 General Additive Models (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 dependencies between observations within individuals, 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"), data, method="REML")

where y is the response variable and x, z, v etc are the predictive variables. A GAM can deal with simple random effects, by exploiting the link between smooths and random effects to treat 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, bs is a basis penalty smoother, and the "re" class implements simple random effects (Wood 2008). REML is a likelihood smoothing parameter, and this approach is a conventional likelihood based treatment of random effects (Wood 2008).

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 $\Delta_i < 2$ 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 (A4a, b, c)). Parameter weights were calculated based on AIC weights for all models. 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).

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

Results

The FPT analysis showed that hooded seals ARS scale is stable for juveniles and males throughout the year, but females show a smaller search radius during spring than fall/winter. The dataset yielded 4011 data locations based on the calculated search radius (Table 2).

The kernel maps were created using the modified dataset based on ARS, and we only display FPT (circles) where they spend more than 2 days (based on average FPT at ARS scale; Fig. 2a-f). Dark areas signify that the seals have spent time there, but crossed the ARS circle in less than 2 days. Our results show that females spend 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. 2a). Males do not spend much time along the Reykjanes ridge during spring (Fig. 2c) compared to females (Fig. 2a). Females and males breeding in the Gulf tend to remain there, presumably to feed, before heading over to Greenland by July (Fig. 2a and c). Following the moult, females spend extended periods of time along the Labrador shelf area (Fig. 2b) while the majority of males traveled to Baffin Bay and Davis Strait. A few animals remained along the east coast of Greenland before heading directly over to the breeding grounds (Fig. 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. 2e). In fall, they start to show a similar migration pattern to adult seals, although they seem to have a wider distribution pattern (Fig. 2f).

Model selection: Our results for model selection are presented in Table 3 consisting of the best or most equally plausible models ($\Delta_i < 2$) per seal group and season. The best models all include SST, depth and/or chlorophyll. The ranking of the model parameters included in all the models are displayed in Table 4 and 5, and these results are presented below in more detail together with the predicted results from Figures 3-7 (a-f). The model goodness of fit is presented by the deviance explained (%) in Table 3. The plots show the estimated effects as a solid line, with 95% confidence limits shown as dashed lines (Wood 2006). The confidence of the confidence limits 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).

Chlorophyll: Chlorophyll plays an important role when it comes to habitat selection by female and juvenile hooded seals during their annual migration. The predictive graphs show that this is not an important variable on its own for males, although it is important in conjunction with other variables (Table 3, 4 and 5; Fig 3b, e). During spring, female and juvenile seals preferred to be in areas with low concentrations of 0-0.5 mg/m^3 and from medium to high concentrations of 4 mg/m^3-30 mg/m^3, respectively. In fall/winter they still show a preference in the low ranges: 0.25-0.5 mg/m^3, although, females also appear to prefer a second range around 1-1.75 mg/m^3.

Depth: The parameter weights for depth were very high across all categories during spring (females: 1; males: 0.9; juveniles: 0.9; Table 4), and for the fall/winter the scores were slightly lower for males and females (0.86 for both; juveniles: 0.99; Table 5). The predictive graphs (Fig. 4) show that this is an important variable for all three groups when it comes to annual habitat selection. In spring, juveniles prefer depths of 0-600 m, males >600 m and females the range of 200-1200 m. In fall/winter juveniles use areas with depths from 750 m while females used areas with depths from 600 m and deeper.

SST: Temperature at the surface seems to influence all seals during their annual migration except for females during the fall/winter season (Fig. 5d, Table 5). Males and females show a preferred temperature range of -2 to +2°C during the spring season, while juveniles use areas within the ranges of -2 to 0°C and +3 to +9°C.The results further indicate that the preferred temperatures vary greatly during fall/winter. Juveniles prefer temperatures in the range of -8 to +5 °C and males -2 to +3°C. As mentioned, females do not show strong trends, although the results suggest a preference towards a temperature range of -7 to+5°C which is similar to that of juveniles (Fig. 5d, f).

Ice: Ice was the least important variable to explain habitat selection for hooded seals (Table 4 and 5). Most of the seals used areas with little or no ice, and the model did not identify this as an important factor in hooded seal habitat selection (Fig.7). We did not have enough data to test juveniles for ice associations during spring.

Slope: Males and juveniles scored a much higher parameter weight for slope during fall/winter than for spring season. In contrast females scored a much higher weight in the spring season compared to fall/winter, although the ranking placed it second to last for all groups (Table 4 and 5). However, the predictive graphs do not show that juveniles have a positive relationship towards slope at any season. The graphs show that females prefer a slope from about 1-11 degrees in spring, while it does not seem to be of importance in fall/winter. They further indicate that slope does have some influence on habitat selection for males during fall/winter when they tend to prefer a slope of about 1 degree (Fig.6).

Discussion

This study supports earlier findings that, in general, hooded seals are inclined to migrate along, and use the continental shelf and areas of high topographic relief (Folkow et al. 1996, Anon 2006, Andersen et al. 2009). However, sexually dimorphic animals are often found to differ in habitat use and feeding strategies (Le Boeuf et al. 1993, Mysterud 2000, Breed et al. 2006, Bailleul et al. 2007) and our results suggest that males and females from the largest part of the NW population (Front breeders alone consist of about 90%) are separated on a horizontal scale during annual migration. Females tend to use the Labrador shelf more intensively than males especially in the fall/winter season (post moult and pre breed; Fig. 2b, d) and the Reykjanes ridge area during spring season (post breed and pre moult; Fig. 2a, c). Males use the Baffin Bay and Davis Strait areas more frequently during fall/winter (Fig. 2d), and in spring they spend time in SE Greenland as well as Davis Strait and the Gulf for those who breed there (Fig. 2c). Other sexually dimorphic seals, such as southern elephant seals (*Mirounga leonina*) (Bailleul et al. 2007) and grey seals (Breed et al. 2006), share this segregation behavior where males and females are separated on a geographic scale. In constrast, Bajzak et al. (2009) found that adult male and female hooded seals tagged in the Gulf of St. Lawrence during the pupping season overlapped geographically, but differed 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 southeast 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 NE hooded seal populations differ in their migration patterns, both on a population level and by sex. In the NE, 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. Seals of the NE 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 population embarks on a more or less synchronized annual round-trip with the basin of the Labrador Sea in centre. The differences in migration behavior between these two populations (and also between Gulf animals and the rest of the NW 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 sexual differences in the feeding behavior of grey seals where, during the post breeding period (spring), females selected fewer and higher quality prey species than males. This behavior is consistent with the nutritional-needs hypothesis (NNH) which predicts that when males are much larger than females they 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 sp.*) 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. Figure 2a and c illustrate habitat use by adult hooded seals during the spring season (post breed and pre moult) and we can see that males spend more time in the breeding areas than females, and cross over to the moulting grounds in a more direct route (Fig 2a, c). We found that females leave the breeding area immediately after mating and feed over the Reykjanes Ridge and the SE Greenland shelf, which is an area with significant redfish fisheries (ICES 2010). Our results do not show the same pattern for males, although they also appear to feed predominantly on redfish during this time (Tucker et al. 2009). This difference could simply be due to the sample size, or alternatively males may hunt their redfish prey along the shelf area in SE Greenland when building up energy reserves prior to the moult.

Figures 2b and d illustrate the habitat use by females and males during the fall/winter migration periods (post moult), respectively. The patterns indicate that males have a more specific, and northern, habitat preference than females during this period. Females display a more southern distribution and use a larger area as they feed along the Labrador shelf. 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 breed 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.

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 (<0.5) and the highest r values were between temperature and depth (A2a and A3a; 0.48 and 0.50 respectively).

The parameter weightings show that SST and depth were the most important parameters explaining male habitat selection in both seasons (Table 4 and 5). The best models in fall/winter for this group contain all the parameters (depth, SST, ice, slope and chlorophyll) and this may indicate that target prey distribution in cold areas such as Baffin Bay may be more influenced by oceanographic processes driven by topography and mixing in the water column than by water depth. Slope does not appear to be significant for males during spring (Table 4; parameter weighting = 0.24), although the lack of importance for the combination of depth and slope could suggest that they actually feed on top of the shelf or sea mounts. Tucker et al. (2009) found that redfish is the most prominent prey item in their diet during the post breed period. Even though males seem to travel fast when they are crossing the Labrador Sea (< 2 days per ARS distance), it does not necessarily mean that they are not finding food to replenish their reserves. Redfish is among the most dominant deep sea fishes in the Reykjanes ridge area and Greenland shelf (Hareide and Garnes, 2001, ICES 2010) and according to Hareide and Garnes (2001), this species occupy depths between 500-1000 m and can be found close to the top of sea mounts and coral formations. This supports our theory that male hooded seals prefer flat surfaces for foraging during this time.

Females tend to prefer deeper waters (> 600 m, Fig 5d) during the fall/winter, while being more generally distributed across various depths (200-1200 m, Fig 5a) in spring. In comparison, males do not have a particular depth preference in fall/winter (ca. 200-1000 m), but prefer somewhat deeper waters in spring (ca. 500-2000 m; Fig. 5b and e, respectively). Folkow et al. (1996) found that adult hooded seals in the NE Atlantic displayed a significant seasonal difference in dive depths and that dive depth was dependent on area, as well as time of day. However, they did not find a significant difference between male and female dive behavior.

The variation in preference to SST among the groups, reflect that males, females and juveniles appear to respond to different cues when they select a habitat. Also, 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.

Chlorophyll is an important variable for females and juveniles throughout the year (Tables 4 and 5; Fig 3 a, c, d, f), but according to the predictive graphs (Fig 3b, e), male habitat choice does not seem to be influenced by chlorophyll at either times of the year. The best models (Table 3) and the parameter weights tell a different story (Table 4; 0.459 and Table 5; 0.801) and these findings suggest that chlorophyll can be of importance when 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 ladder 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 behavior 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. 3e, f), although they exhibit a slightly different ranking of parameter weights (Table 4 and 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). This supports our findings that juvenile hooded seals prefer depths between 0-600 m during spring season (Fig 5c). Furthermore, Folkow et al. (2010) found that NE population pups seem to improve their diving abilities greatly in the first year as they use areas deeper than 600 m during fall/winter season (Fig.5f). Tucker et al. (2009) found that juvenile hooded seals target mainly 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 (fall/winter; Table 5). This positive relationship between FPT and ice covered areas during fall/winter (~ >5%; Fig. 7e) could have various explanations. For instance, the parameter weights for this category show that chlorophyll is of great importance to juveniles at all times of the year (Table 4 and 5), which could further be linked to the ice results as ice edges are known to be productive. This could also mean that young seals may 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 behavior on ice throughout the year could provide more information of 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, 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 preferred 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 combination of, 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 of 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, as well as temperature measurements collected real time vertically and horizontally by the tags, in an attempt to provide more information on habitat use within the areas identified here.

Conclusion

This study has shown that male, female and juvenile hooded seals select habitat differently, although they prefer areas with similar complex topographic properties. A geographic and/or vertical separation may indicate that they have different dietary needs and/or show competition avoidance as they may feed on similar prey. How competition with other species feeding in these same areas 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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SUPPPLEMETARY MATERIAL:

Supplementary material is available at the ICESJMS online version of the paper and includes the following:

A1: Summary table presenting tag data, including tag performance

A2: Table with Spearman correlation information on the included predictive variables; Spring season.

A3a: Table with Spearman correlation information on the included predictive variables; Fall/Winter season.

A4a-c: Full AIC table showing all models run for females, males and females per season.

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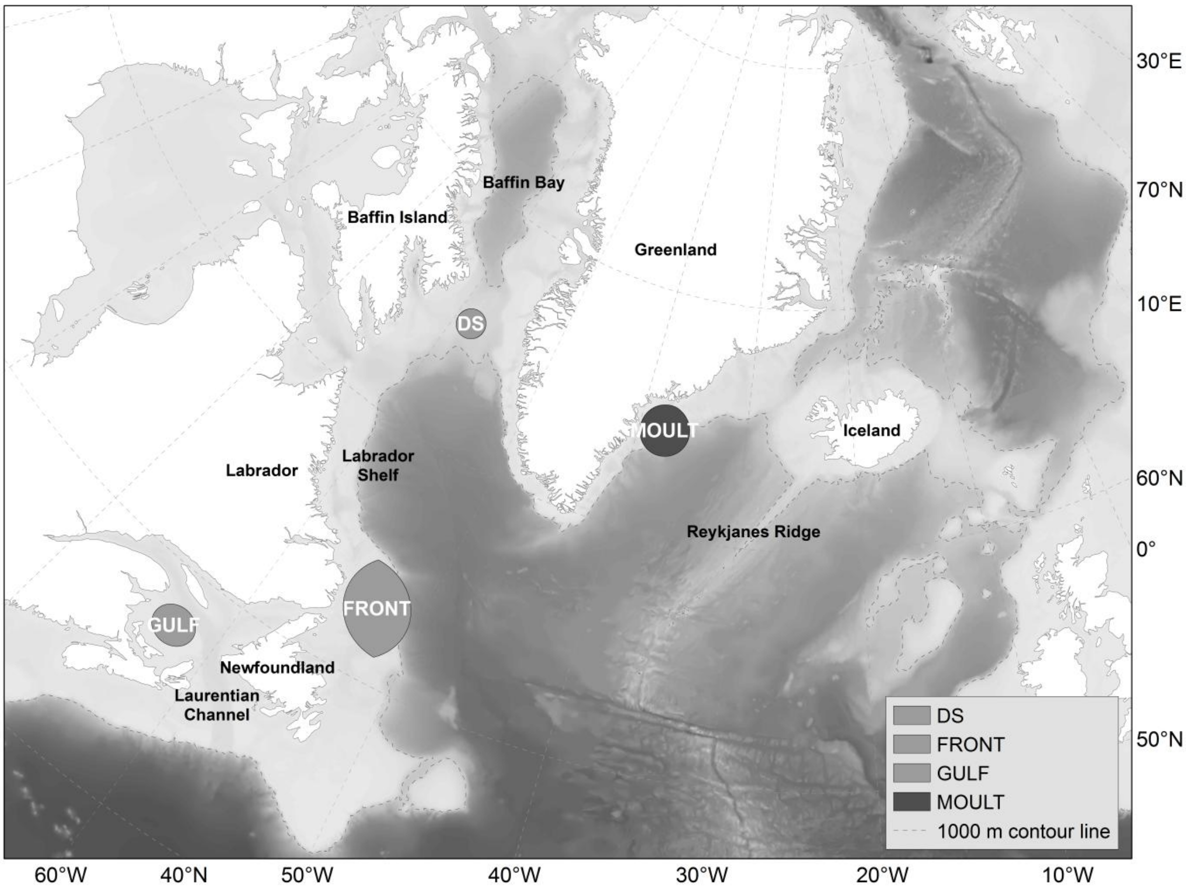
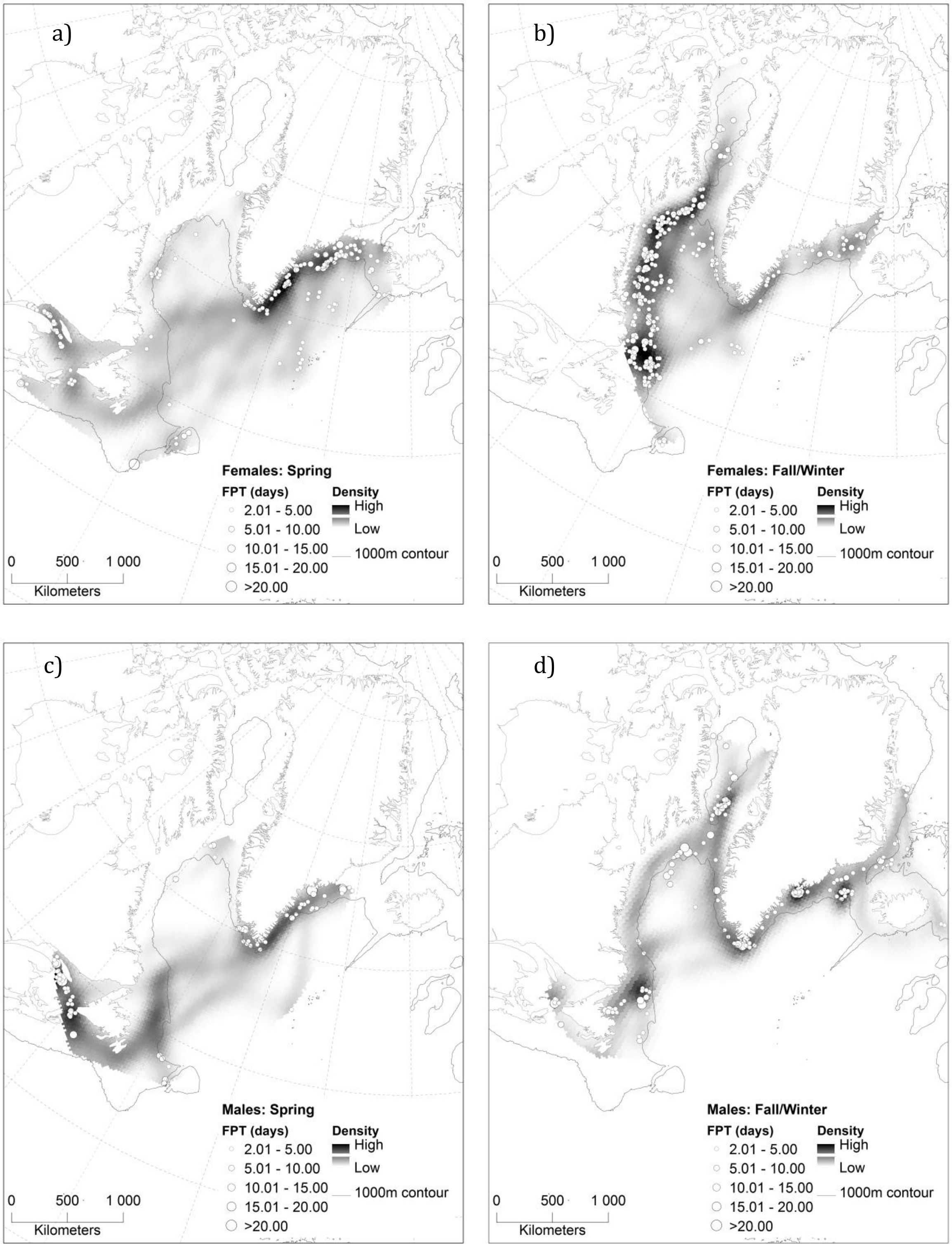


Figure 1: Andersen et al.


a)
Females: Spring
b)
Females: Fall/Winter
c)
Males: Spring
d)
Males: Fall/Winter
FPT (days)
2.01 - 5.00
5.01 - 10.00
10.01 - 15.00
15.01 - 20.00
>20.00
Density
High
Low
1000m contour
0
500
1 000
Kilometers

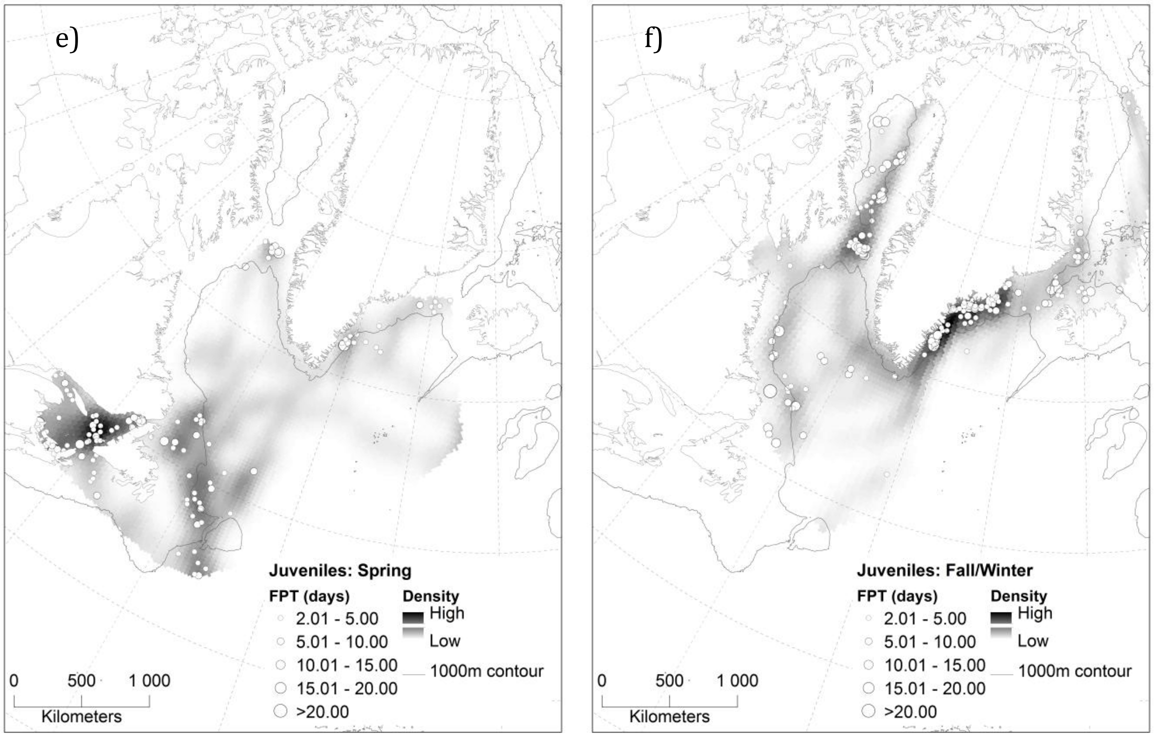


Figure 2 a-f: Andersen et al.

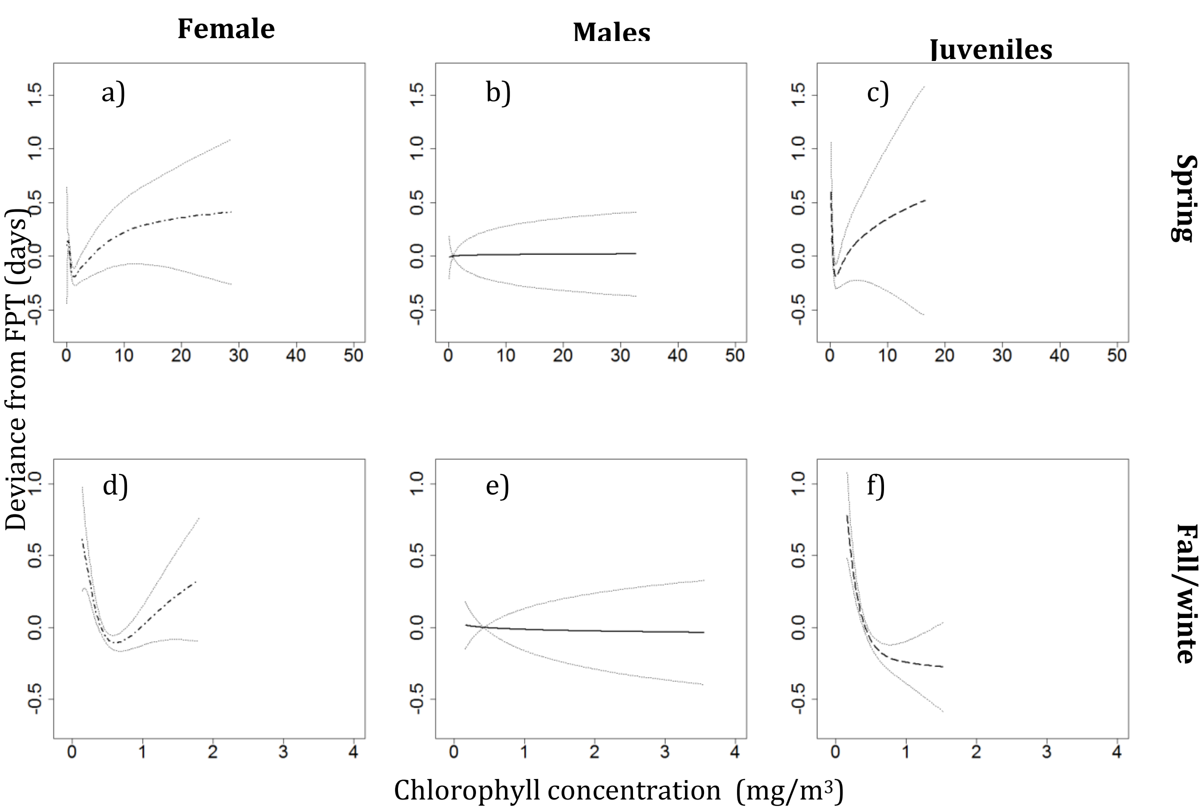
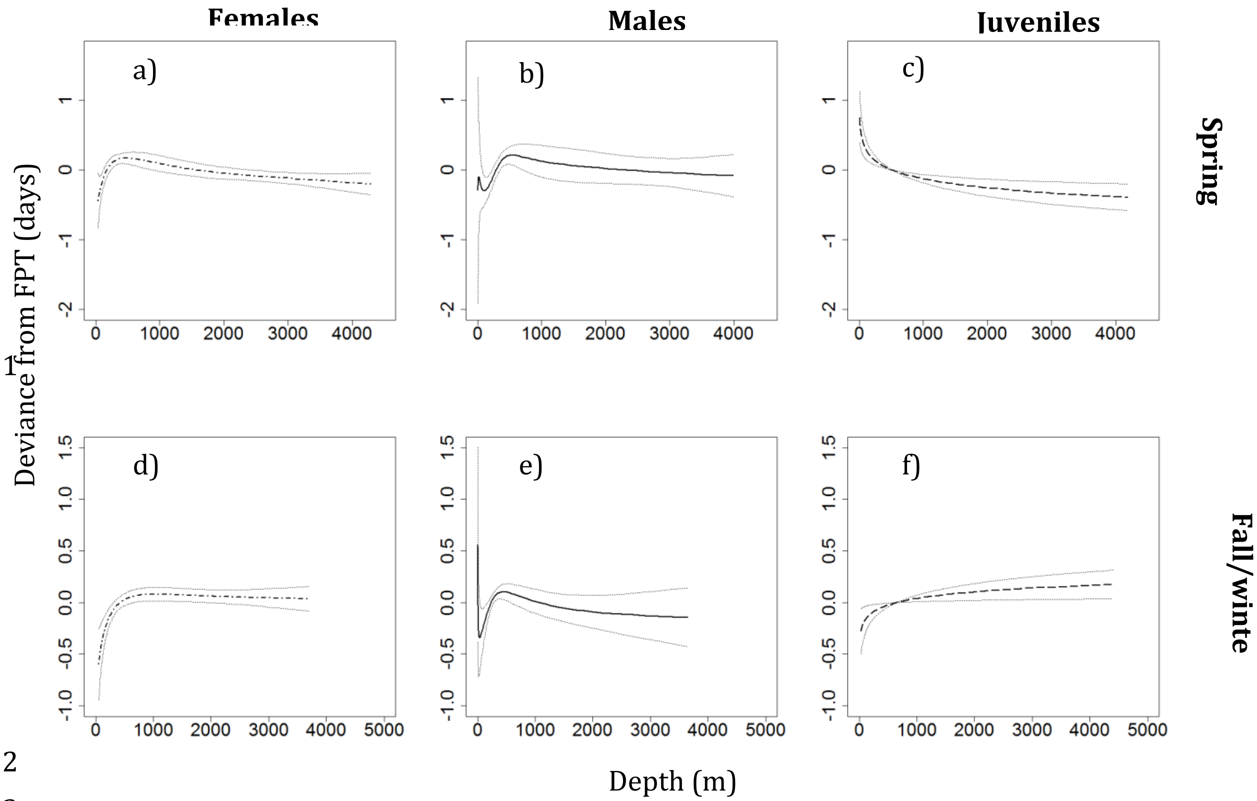


Figure 3: Andersen et al.



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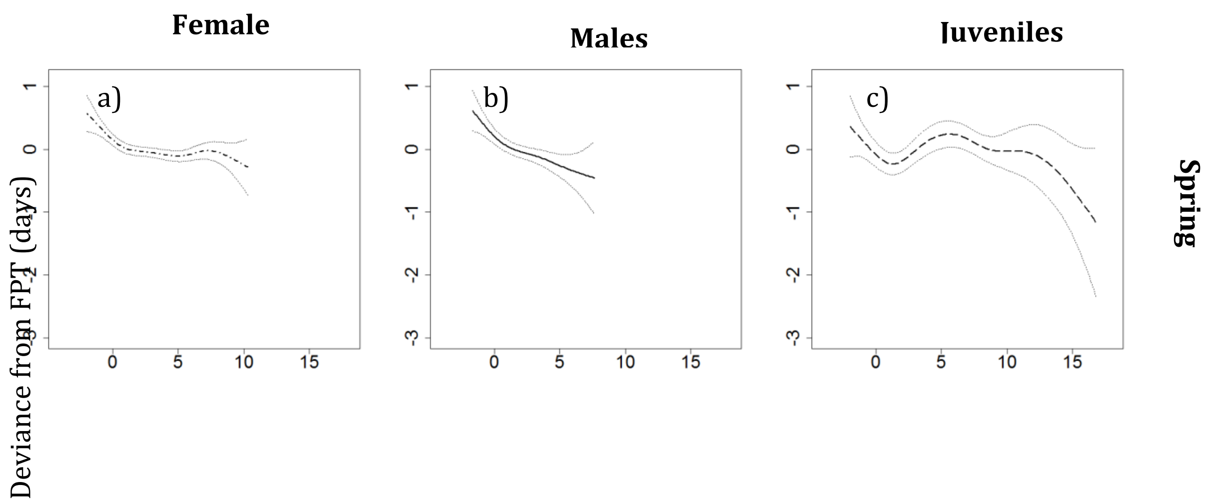

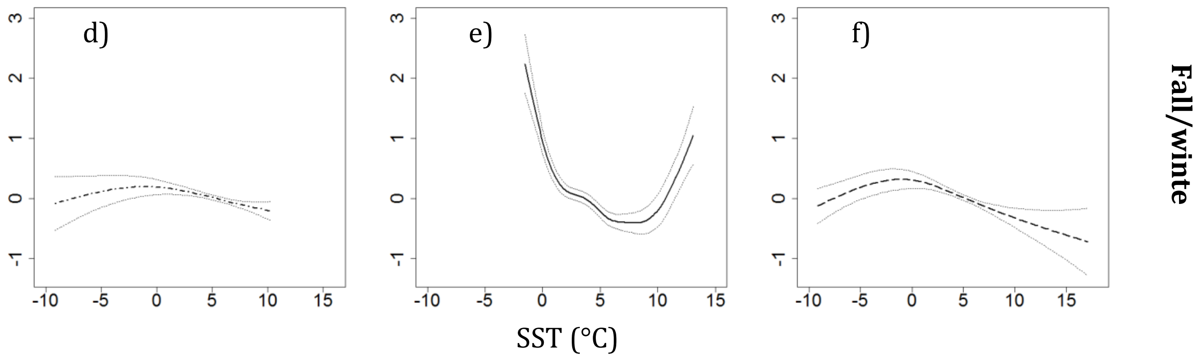

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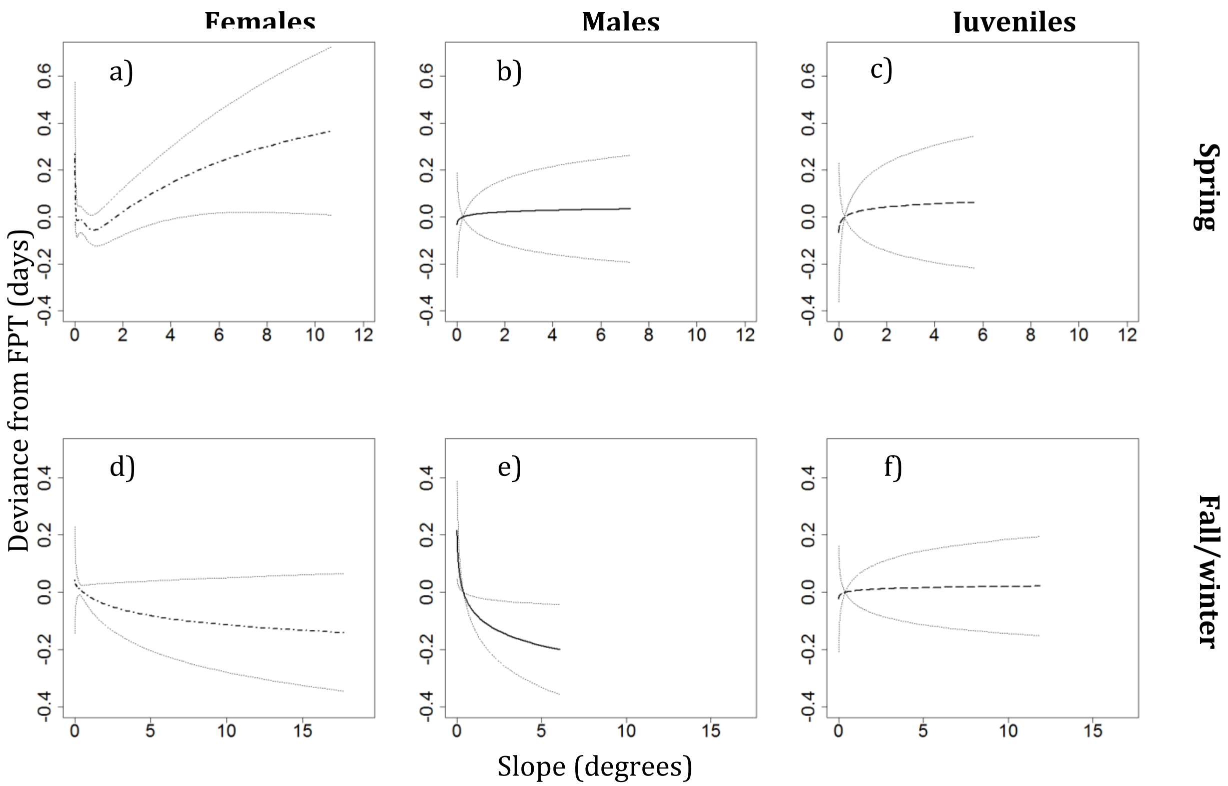

Figure 6: Andersen et al.

Females **Males** **Juveniles**

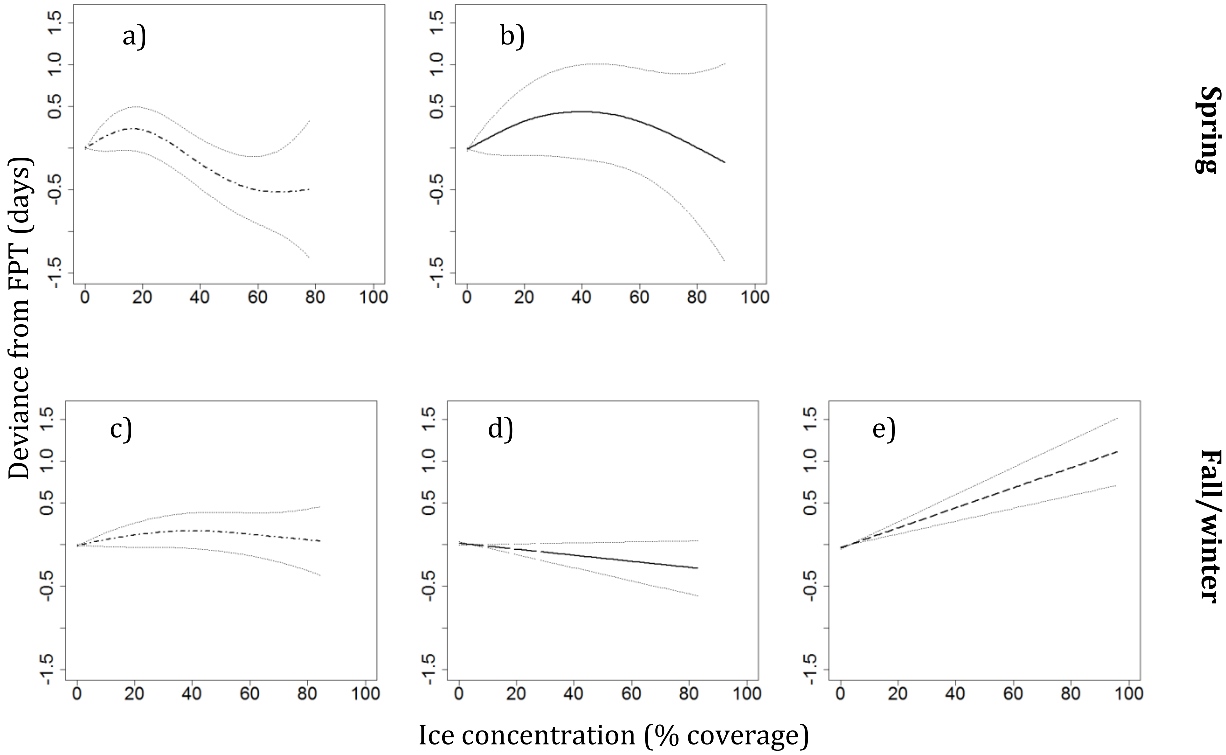

Figure 7: Andersen et al.

Table 1: Number of hooded seals tagged with satellite relay data loggers (SRDLs), 2004-2008 for which data were available for the spring (post breed – pre moult) and fall/winter (post moult – pre breed) period (Season). A total of 65 individuals were tagged. Sex/Age represent seal group, and Number is the number of seals represented in each season (Details of the individuals are provided in the supplemtary material (A1)).

ex/Age	**eason**	**umber**
emales	pring	8
emales	all/winter	1
Iales	pring	2
Iales	all/winter	
uveniles	pring	0
uveniles	all/winter	1

Table 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.

roup	eason	RS (km)
emales	pring (April-June)	7.5
Iales	pring (April-June)	7.5
uveniles	pring (April-June)	5
emales	all/winter (August-February)	7.5
Iales	all/winter (August-February)	7.5
uveniles	all/winter (August-February)	5

Table 3. AIC table showing the best models for each group (F: females, M: males, J: juveniles) per season. The best models are based on having a □$_i$ < 2. Loglik is the loglikelihood. K is the number of parameters in the model. AIC$_i$ is AIC for model *i*. and □$_i$ is the difference between the AIC of the best fitting model and that of model *i*. Exp(-0.5□$_□$) represent the relative likelihoods and the w_i is the Akiake weights. The percent deviance explained 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.

/M/J	**eason**	**est models per**	**oglik**	**(**	**IC$_i$**	**]$_i$**	**xp(-**	**/$_i$**	**eviance**

		category and season				0.5□□)		explained (%)
'	pring	ST, ice, chlorophyll, slope and depth	2729.231	470.46			.990	2.9
'	all	ST, chlorophyll and depth	591.46	390.92			.332	.15
'	all	ST, chlorophyll, slope and depth	590.97	391.94	.01	.60	.200	.35
'	all	Chlorophyll	594.35	392.70	.77	.41	.137	.99
M	pring	ST and depth	342.88	691.76			.541	5.6
M	pring	ST, chlorophyll and depth	342.80	693.59	.83	.40	.216	5.6
M	all	ST, chlorophyll, slope and depth	455.14	14.27			.582	1.3
M	all	ST, ice, chlorophyll, slope and depth	455.01	16.03	.75	.417	.243	1.3
	pring	ST, chlorophyll and depth	512.1848	032.37			.682	2.9
	pring	ST, chlorophyll, slope and depth	512.0175	034.04	.67	.435	.296	3.0
	all	ST, ice,	410.3775	32.76			.843	8.1

chlorophyll,
slope and
depth

Table 4. Parameter weightings for each seal group (females, males and juveniles) per habitat variable for spring season (Apr-Jun). Weights are calculated based on the model weights from all the models.

emales:		**Iales:**		**ıveniles:**	
ariable	**Veight**	**ariable**	**Veight**	**ariable**	**Veight**
epth		ST	.999	epth	.999
hlorophyll		epth	.999	ST	.999
ST		hlorophyll	.459	hlorophyll	.978
lope	.999	lope	.243	lope	.296
e coverage	.989	e coverage	.151		

Table 5. Parameter weightings for each seal group (females, males and juveniles) per variable for fall/winter season (Aug- Feb). Weights are calculated based on the model weights from all the models.

emales:		**Iales:**		**ıveniles:**	
ariable	**Veight**	**ariable**	**Veight**	**ariable**	**Veight**
hlorophyll	.880	ST		hlorophyll	.999
epth	.860	epth	.867	epth	.991
ST	.751	hlorophyll	.818	ST	.988
lope	.299	lope	.801	lope	.881
e coverage	.099	e coverage	.224	e coverage	.843

Supplementary material:

A1: 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

A2a: 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.

		SPRING				
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

A2b: P-values explaining the significant degree of the Spearman correlation test (reported in Table A2a) between the predictor variables in the spring (April-June dataset). "Group" represents the seal group: "J"= Juveniles. "M" = Males. "F" = Females.

		SPRING P-value				
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	

A3a: 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.

		FALL				
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

A3b: P-values explaining the significant degree of the Spearman correlation test (reported in Table A3a) between the predictor variables in the fall (Aug – Feb dataset). “Group” represents the seal group: “J”= Juveniles. “M” = Males. “F” = Females.

		FALL P-value				
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	

A4a: Full AIC table including all GAM model results for females: Loglik is the loglikelihood. K is the number of parameters in the model. AIC_i is AIC for model *i*. and Δ_i 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.

Sex/ Age	Season	Best models per category and season	loglik	K	AIC_i	Δ_i	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

A4b: Full AIC table including all GAM model results for males: Loglik is the loglikelihood. K is the number of parameters in the model. AIC_i is AIC for model *i*. and Δ_i 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.

Sex/ Age	**Season**	**Best models per category and season**	**loglik**	**K**	**AIC_i**	Δ_i	**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

A4c: Full AIC table including all GAM model results for juveniles: Loglik is the loglikelihood. K is the number of parameters in the model. AIC_i is AIC for model *i*. and Δ_i 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.

Sex/ Age	Season	Best models per category and season	loglik	K	AIC_i	Δ_i	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