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ECOLOGICAL IMPLICATIONS OF FORAGING AND LIFE-HISTORY IN THREE COLD-ADAPTED SPECIES

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ECOLOGICAL IMPLICATIONS OF FORAGING AND LIFE-HISTORY IN THREE COLD-ADAPTED SPECIES

By

Andrew Lee Von Duyke

A DISSERTATION

Submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

In Forest Science

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This dissertation has been approved in partial fulfillment of the requirements for the Degree of DOCTOR OF PHILOSOPHY in Forest Science.

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Preface

This dissertation is composed of four chapters. Chapter 1 provides a brief introduction to the theoretical and ecological frameworks that unify this body of work. Chapter 2 is planned for submission to the journal *Polar Biology*. Andrew Von Duyke has been the Principal Investigator (PI) for ice-seal research at the North Slope Borough - Department of Wildlife Management (NSB-DWM) since 2013, and was responsible for primary data collection, analyses, and manuscript writing. Jason Herreman was the PI at NSB-DWM from 2010-12, collected the 2011 seal data, and provided editorial reviews of the manuscript. David Douglas made significant contributions to the data management and analysis, provided numerous editorial reviews, and assisted with planning. Finally, Justin Crawford contributed editorial reviews. Chapter 3 is planned for submission to the journal *Oikos*. Andrew Von Duyke was responsible for the data analysis and writing of the manuscript, and for overseeing much of the sample analyses. Leah Vucetich managed fieldwork—overseeing sample collection and their analyses—and provided editorial reviews. Rolf Peterson collected and analyzed the moose and wolf abundance data, oversaw sample collection, and provided editorial reviews of the manuscript. John Vucetich collected and analyzed the moose and wolf abundance data, provided editorial reviews of the manuscript, and played a large role in the conceptual design of this research. Chapter 4 has been published in the peer-reviewed journal *Arctic*[1]. Andrew Von Duyke was the first author, and was responsible for the analysis, manuscript writing, and

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[1] **Von Duyke, A.L.**, R. Stimmelmayr, G. Sheffield, T. Sformo, R. Suydam, G.H. Givens, and J.C. George. 2016. Prevalence and abundance of cyamid "Whale Lice" (*Cyamus ceti*) on subsistence harvested bowhead whales (*Balaena mysticetus*). Arctic 69(4):331-340. http://dx.doi.org/10.14430/arctic4593

a data collection. Raphaela Stimmelmayr provided valuable editorial reviews and took part in the data collection, as did Gay Sheffield, Todd Sformo, and Robert Suydam. Geoff Givens provided editorial reviews and statistical guidance. Finally, John C. “Craig” George has been instrumental in the direction of bowhead whale research in Alaska, involved in data collection, and provided both guidance on this manuscript and editorial reviews.

Acknowledgements

This work would not have been possible without the support of many people. I would first like to thank my adviser John Vucetich for his patience and willingness to work with me throughout the long and convoluted path that I have travelled, both figuratively and literally, given my change of residence to Utqiaġvik, Alaska (71.3° N, 156.8° W)—over 350 miles north of the Arctic circle! I am also grateful for his efforts to find ways to help me work through several iterations of my research. I benefitted from and am grateful for the professional and personal relationships that I gained through the Isle Royale Wolf-Moose Study at Michigan Technological University, and am proud to include Leah Vucetich, Marcy Erickson, Jen Adams, Rolf and Candy Peterson as colleagues and friends, who kindly and generously gave of their time and expertise. And to my committee members: Chris Webster, Matt Seigel, Joseph Bump, and Craig George, I thank you for your roles in my professional development.

Speaking of Craig, I cannot overstate my gratitude to him for introducing me to the Arctic, an incredibly interesting and challenging part of the world that is at the forefront of ecological change. I also value his mentorship and the countless hours we have spent discussing wildlife and numerous other topics. I have been privileged during my time in the Arctic to work directly with and learn from many Iñupiat hunters, who are experts in wildlife ecology in their own right. It has also been truly a pleasure to work with such a great group of professionals at the North Slope Borough Department of Wildlife Management. In particular I would like to thank my director, Taqulik Hepa, for her interest in and support of my graduate studies. And, to the whale harvest sampling

crews, I offer my many thanks for working that much harder and losing even more sleep so that I could have the luxury of time to focus on writing.

My father, the late David Von Duyke, is an inspiration to me. He was a self-taught man who was curious about everything and had a broad set of interests and expertise. We started SCUBA diving together so long ago, which made an everlasting impression and probably was the spark that ignited my interest in all things wild.

My mother, Marilu Laubenthal showed me the value of lifelong learning and I appreciate her encouragement throughout my time in graduate school.

Finally, I am grateful for the love and support of my family. Betsy, you have shouldered more than your fair share of the load during my time as graduate student—raising our children almost singlehandedly. That they turned out so wonderfully is a tribute to you as a person. To my daughters Anna and Ellie, I am so proud of you and am constantly impressed by what incredible women you have both become.

List of abbreviations

ADF&G	Alaska Department of Fish and Game.
AEWC	Alaska Eskimo Whaling Commission.
AIC_C	Akaike's Information Criterion corrected for small sample size.
BCB	Bering-Chukchi-Beaufort Seas. A portion of the North Pacific and Arctic Oceans in the region of Beringia that is important to migratory marine mammals.
BWCA	Barrow Whaling Captains' Association.
CTD	Oceanographic instrument that measures the Conductivity, Temperature, and Depth within the water column. Often incorporated into satellite transmitting tags that are attached to marine animals.
CRAWL	Correlated RAndom WaLk movement model.
dL	Deciliter or 1/10th of a liter.
DNA	Deoxyribonucleic Acid. Large molecule that encodes genetic information.
JD (DOY)	Numeric sequence of the day of year that starts on 1-Jan (doy = 1) and ends on 31-Dec (doy = 365).
DVM	Diel Vertical Migration. Movement by prey species vertically within a water column over the course of the day, typically in response to light availability, as a means of foraging while minimizing predation risk.
ESA	Endangered Species Act.
GDD_t	Growing Degree Days in year t. A measure of cumulative temperature and phenology that is useful for characterizing the growing conditions of plant communities.
GLMM	Generalized Linear Mixed-Model.
GMT	Greenwich Mean Time. Local time in Greenwich, England (0° Long).
ISRO	Isle Royale.

kcal	Measure of energy stored in food. Equal to 1,000 calories or 1 Cal.
KR	Kill Rate or the number of prey killed per predator per unit of time.
LME	Linear Mixed-Effect model
NARW	North Atlantic Right Whale (Eubaleana glacialis)
N_t	Prey abundance (in year t).
NAO_t	North Atlantic Oscillation (in year t). An index of winter severity.
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration.
NSB-DWM	North Slope Borough – Department of Wildlife Management.
P_t	Predator abundance (in year t).
PR_t	Predation Rate (in year t). Equal to $(KR_t \times P_t) / N_t$
PSM	Plant secondary metabolites. Chemical compounds produced by plants as protection from herbivory. Examples include tannins and phenols.
r_t	Per capita population growth rate (in year t). Equal to $(N_{t+1} – N_t) / N_t$
SD	Standard Deviation.
t	Subscript used to denote a time period such as year.
UME	Unusual Mortality Event. Designated by NOAA during periods in which large die-offs of marine animals occur.
UN:C	A metric that is informative about body condition. It is the ratio of urea-nitrogen (UN) to creatinine (C). UN can indicate the level of catabolism in energetically depleted animals. C is secreted in proportion to lean muscle mass, and is used to normalize measurements of other metabolites (e.g., UN) to adjust for body-size and/or dilution.

Dissertation Abstract

This research investigates the ecology of: ringed seals (*Pusa hispida*), moose (*Alces alces*), and bowhead whales (*Balaena mysticetus*). Each of these species draws upon specialized strategies to meet the physical demands of life in their extreme environments. However, they are currently experiencing unprecedented changes in their habitats. This work adds to what is known about the behavior, physiology, and population dynamics of cold-adapted species—providing insights of value for an improved understanding of foraging and life-history theory, and informing conservation and ecosystem monitoring efforts.

Chapter 1 provides a brief introduction to the scope of work within this dissertation. Chapter 2 documents the seasonal movements of ringed seals in the Alaskan Arctic, along with their diving, foraging, and haul-out behaviors. Their behavior, including daily activity budgets and habitat use, is characterized and interpreted with respect to life-history and foraging theory. Demographic habitat partitioning is documented and is consistent with theoretical expectations. Results highlight the importance of benthic diving and suggest that reduced sea ice during critical periods may have energetic consequences for ringed seals. Chapter 3 compares the influences of top-down, bottom-up, and abiotic effects on moose body condition and per capita population growth at Isle Royale National Park. Body condition was quantified using the ratio of urea-nitrogen to creatinine (UN:C) during the late winter, when severe reductions of forage abundance and quality increase catabolic processes. Body condition responded to abiotic effects, including warm summer temperatures. Spatial heterogeneity also influenced body condition, likely due to different forest ecosystems. Per capita population growth responded most to top-down effects, but also to bottom-up effects. The

substantial influence of predation rate upon per capita population growth is discussed with respect to “masking” other potentially complex interrelationships among energetics, body condition, and population dynamics. Chapter 4 improves understanding of the relationships among factors with life-history implications that are potentially informative on the status of bowhead whales and their ecosystem. In particular, factors that influence cyamid ectoparasite prevalence and abundance are examined. Also important are observed relationships between whale age, body condition, and ancillary data that have potential to influence ecological interpretations.

1 Introduction

Questions of why animals do what they do are fundamental to the study of wildlife ecology—the answers to which refine theory and inform conservation (Skalski et al. 2005, Sutherland et al. 2013). At fine scales, energetic explanations to these questions are dominant (Gittleman and Thompson 1988) because all life-forms face numerous challenges associated with acquiring energy from the environment and transporting it down a path toward its allocation to future generations (Brown et al. 1993). While the most efficient paths in this process should be favored, many are not straightforward due to predation, competition, habitat heterogeneity, and environmental variability. Furthermore, variable body condition alters the relative importance of each step along this energetic path (Marrow et al. 1996). The need to reconcile these ecological complexities with the energetic demands for sustaining life creates selective pressures that favor diverse sets of behaviors and/or physiological processes (i.e., strategies) that are fine-tuned through natural selection to be as efficient as surrounding conditions will allow.

Together, foraging theory and life-history theory (Stearns 1976, Stephens and Krebs 1986, Dobson and Oli 2007) are complementary in their abilities to frame the understanding of the processes by which energy is both acquired and allocated; and are similar in their economic approaches, which strategically optimize costs versus benefits, while accounting for limiting constraints (Belovsky 1978). Foraging theory considers constraints that can limit the intake rate of energy (kcal), including: search and handling time (Cohen et al. 1999), predation (Barnier et al. 2014), patch depletion (Charnov 1976), and/or digestive physiology (Marsh et al. 2006, Robbins et al. 2007). Meanwhile, the central paradigm of life-history theory concerns a fundamental tradeoff in how organisms allocate their finite energetic resources between the competing demands of somatic repair/maintenance and reproduction (Kirkwood 2002, Carranza et al. 2004). Favorable solutions to this tradeoff are dependent upon the underlying ecology of a species—within a spatiotemporal context—and can have implications for: lifespan, body- and litter-size, non-linear growth patterns (e.g., compensatory growth), body condition, and costly sexual ornaments/weapons such as tusks, antlers, and showy feather displays (Clutton-Brock 1982, Promislow and Harvey 1990, Metcalfe and Monaghan 2003, Mangel and Munch 2005, Emlen 2008). These two bodies of theory are complementary. For example, life history constraints relating to sexual reproduction favorably select for sexual dimorphism. As such, each sex experiences a different set of foraging constraints relating to their respective digestive capabilities and the heterogeneous distribution of forage resources (Bowyer 2004). Beyond responding to habitat characteristics, such mechanisms also have the potential to influence the surrounding habitat at numerous scales (Brown et al. 1999, Christianson and Creel 2008, Garnick et al. 2014), thereby fitting into a broader hierarchy of ecological functions.

Addressing questions relating to foraging and life-history theory can be facilitated by studying the ecology of animals that rely upon specialized strategies to meet the physical demands of life in extreme environments. These questions are also important as environmental conditions shift in response to climate change (IPCC 2014). This dissertation investigates the behavior, physiology, and population dynamics of three cold-adapted species. Ringed seals (*Pusa hispida*) and bowhead whales (*Balaena mysticetus*) both occupy the Arctic, while moose (*Alces alces*) occupy temperate, sub-Arctic, and Arctic regions. The ecology of cold-adapted species lends itself to these questions because it has been shaped by strong selective forces that result from dealing with greater environmental variation than species in warmer environments. Predictions from foraging theory and life-history theory suggest that forces including: environmental/seasonal fluctuations, mating systems, predation risk, and competition may be important to body condition and/or population dynamics. Thus, by describing behavioral and physiological variability with respect to these factors, the resulting insights should promote a greater understanding of how animals get the most fitness value out of their hard earned calories.

Certain aspects of ringed seal physiology (Ling 1984, Routti et al. 2010) and reproduction (Smith and Hammill 1981), in conjunction with their dynamic habitat, sets the stage for a number of potential behavioral and physiological adaptations that relate to seasonal extremes and energy balance (Harrington 2008). Thus, the study of ringed seal seasonal movements, along with their diving, foraging, and haul-out behavior (chapter 2) lends itself to energetic and life-history interpretations. For example, dives associated with foraging are the dominant daily activity for ringed seals (see results - chapter 2) and appear to be consistent with an energy-maximization strategy (Schoener 1971).

Meanwhile, their seemingly counterproductive use of inferior habitat during an important intensive feeding period (see results - chapter 2) suggests a possible life-history strategy related to seasonal dynamics in their body condition. Whether and how ringed seals partition their habitat use (e.g., sex, age, and season) should also be indicative of their energetic and/or life-history tactics (Crawford et al. 2012). Finally, given the physiology of their annual pelage molt, seasonal variation in body condition, and capital breeding strategy (Boyd 2004), ringed seals likely have specific habitat requirements that could have negative energetic consequences—potentially influencing their population dynamics—if not met due to climate induced loss of sea ice.

Moose experience a wide range of body conditions annually—likely the function of seasonally reduced forage abundance and quality, mating behavior, and physiology. Understanding of how and why body condition varies over time can help to clarify questions about their population dynamics. Chapter 3 compares the influences of top-down effects, bottom-up effects, and abiotic effects (Hunter and Price 1992) on moose body condition and per capita population growth. Body condition can be quantified using urinary metabolites during the late winter, when restrictions to energy intake increase and body condition becomes more closely associated with catabolism (DelGiudice 1995). The study location, Isle Royale National Park, is notable in its spatial heterogeneity and high predation pressure from wolves (*Canis lupus*). Long-term data on moose and wolf abundance (Vucetich and Pederson 2017), environmental and habitat data, and moose body condition can address questions relating to both foraging and life-history theory. Like ringed seals, moose are capital breeders (Jönsson 1997), which links foraging performance to reproduction, thereby underscoring the importance of body condition and the factors that affect it. For example, how body condition responds to abiotic effects (i.e., temperature; Renecker and Hudson 1986, Lenarz et al. 2009) can help forecast the trajectory of moose populations at the edge of their range—information that is particularly useful considering that warming trends are expected to continue. The results described in chapter 3 demonstrate the importance of understanding the complementary nature of foraging and life-history theory. Meanwhile, the possibility that more complex interrelationships are “masked” by the substantial influence of predation rate upon per capita growth bears further consideration. Finally, characterizations of the relationship between spatial heterogeneity in habitat and body condition can help clarify specific moose habitat requirements and the potential impacts of changing environmental conditions.

The Arctic is at the forefront of environmental change, which, given the importance of sea ice loss, has led to calls for comprehensive monitoring of Arctic marine ecosystems (Moore 2008). The ability to do so relies in part on clearly understanding the mechanisms that can influence the metrics used. Bowhead whales, which occupy the Beaufort, Chukchi, and Bering Seas (Citta et al. 2015), can be useful for understanding Arctic marine ecosystems in this region, and their health status has been proposed as one metric of ecosystem assessment. As a subsistence species, hunter harvested bowhead whales have been sampled and studied in relatively high numbers for over four decades (George et al. 2017). Pettis et al. (2004) suggested that ectoparasite load is negatively associated with the health of North Atlantic Right Whales (NARW, *Eubaleana glacialis*), a close relative of the bowhead whale. This relationship, however, is not well understood in bowhead whales. Chapter 4—reprinted from a publication in the journal Arctic (Von Duyke et al. 2016)—considers factors associated with this question (See Appendix A for documentation of permission to republish this material). The results generated were unlike those found in NARWs, but appear to make sense within the context of life-history theory. For example, counterintuitive relationships among bowhead age, length, and body condition (George et al. 2016) can complicate the interpretation of events that occur over time. Consequently, failing to incorporate the “extreme” life-history strategies of bowhead whales (George et al. 1999, 2015; Givens et al. 2016) into assessments of their health can lead to incorrect conclusions about their status and/or the level of change occurring in their habitat.

Altogether, this work adds to the body of knowledge on the behavior, physical status, and population dynamics of cold-adapted species. Insights gained through this work not only serve to improve the understanding of both foraging and life-history theory, but also, in conjunction with the documented baseline data, serve to facilitate the conservation and management of species and ecosystems that are currently experiencing rapid environmental change throughout their range.

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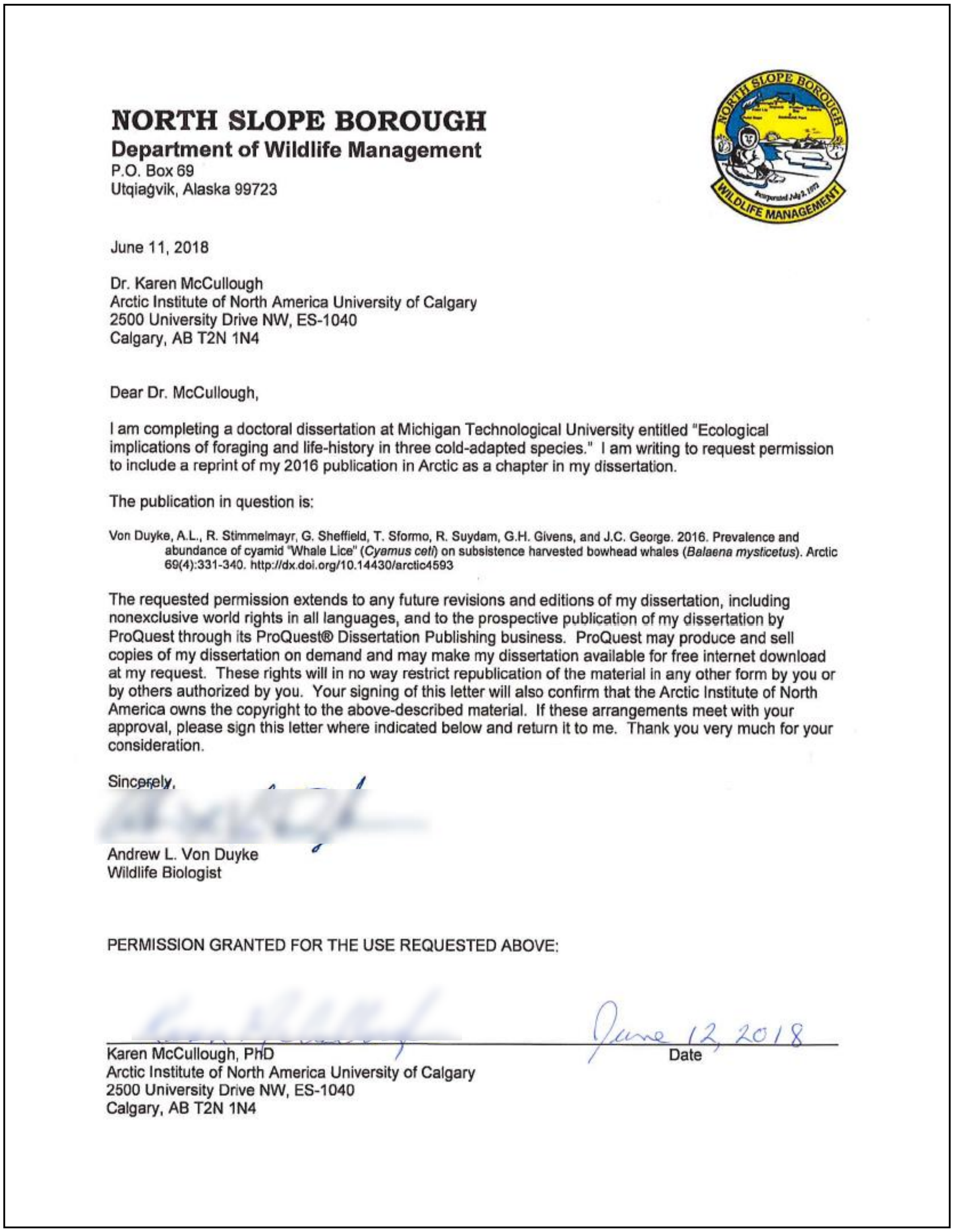
Appendix A

Letter signed by the journal *Arctic* granting permission to use a reprint of Von Duyke et al. (2016) as chapter 4 of this dissertation. Note that signatures have been redacted for privacy.



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June 11, 2018

Dr. Karen McCullough
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Dear Dr. McCullough,

I am completing a doctoral dissertation at Michigan Technological University entitled "Ecological implications of foraging and life-history in three cold-adapted species." I am writing to request permission to include a reprint of my 2016 publication in Arctic as a chapter in my dissertation.

The publication in question is:

Von Duyke, A.L., R. Stimmelmayr, G. Sheffield, T. Sformo, R. Suydam, G.H. Givens, and J.C. George. 2016. Prevalence and abundance of cyamid "Whale Lice" (*Cyamus ceti*) on subsistence harvested bowhead whales (*Balaena mysticetus*). Arctic 69(4):331-340. http://dx.doi.org/10.14430/arctic4593

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Sincerely,

[redacted]

Andrew L. Von Duyke
Wildlife Biologist

PERMISSION GRANTED FOR THE USE REQUESTED ABOVE:

[redacted] June 12, 2018

Karen McCullough, PhD
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Date

2 Ringed seal (*Pusa hispida*) seasonal movements, dives, and haulout behavior in the Beaufort, Chukchi, and Bering Seas (2011-2017)

2.1 Abstract

We used satellite transmitters to document the movements and behavior of ringed seals (*n* = 17) tagged near Utqiaġvik, AK ($\bar{x}$ duration = 248 days). Dives were classified as mixed or repetitive. Repetitive-diving was the dominant daily activity ($\bar{x}$ = 16 hrs/day) and was almost exclusively benthic when on the continental shelf—leading us to associate it with foraging. From July to October, 70% of the seals periodically ventured into the deeper Arctic Basin, spending much of their time hauled out ($\bar{x}$ duration = 12 hrs/day). They also appeared to forage at different strata of the water column (60 – 300 m). Deeper (>25 m) repetitive-diving frequency was associated with the hours of the day with highest light levels, whereas haul-out behavior showed the opposite trend. Seals moved south in the fall, dividing their winter locations evenly between the Chukchi and Bering Seas, with sea ice habitat use varying by both age and sex. Collectively, seals tagged in 2011 were smaller, in lower body condition, and showed different behaviors, including higher: movement rates, haul-out time, and sea ice concentration. This, along with morphological differences, led us to speculate that our 2011 sampling may have included seals from a different ecotype—perhaps relating to an unusual mortality event (UME). This work adds to the growing body of knowledge about ringed seal movements and behavior, improves Arctic ecosystem monitoring, and facilitates a deeper

understanding of the eco-physiological processes that are important to the conservation and management of a vulnerable species of high ecological and cultural value.

2.2 Introduction

The Arctic is warming at twice the global rate (Overland et al. 2016, AMAP 2017) with sea ice loss outpacing model predictions (Stroeve at al. 2007, Maslanik et al. 2011). Considerable ecological repercussions are likely (Grebmeier et al. 2006, Arrigo et al. 2008) given the importance of sea ice to Arctic marine ecosystems (Hoegh-Guldberg and Bruno 2010). But spatiotemporal variation in the rate and magnitude of Arctic sea ice decline (Kovacs et al. 2011) complicates understanding of its potential ecological impacts. Ringed seals (*Pusa hispida*) are an important component of the Arctic ecosystem as predators, prey, and as a valuable subsistence resource for many native people (Fall 2014). Therefore, monitoring the status of ringed seals can be an informative tool for understanding larger scale ecological trends (Moore 2008, Moore and Huntington 2008).

Ringed seals are a small, highly abundant phocid with a circumpolar distribution and a varied diet (McLaren 1958, Dehn et al. 2007). More ice-associated than other Arctic seals (Smith et al. 1991), ringed seals are adapted to over-wintering in dense sea ice (Stirling 1977), which is used for resting, pupping, and molting (Fay 1974, Smith and Stirling 1975). During the winter, ringed seals use their powerful front claws to clear and maintain breathing holes, and to excavate lairs in the snow that has drifted above breathing holes. Lairs provide both thermal cover (Smith et al. 1991) and concealment from predators, particularly polar bears (*Ursus maritimus*; Stirling and Archibald 1977; Smith 1980), and thus are linked to ringed seal reproductive success (Ferguson et al. 2005, Kelly et al. 2010a). In May and June ringed seals undergo an annual molt—shedding and replacing their epidermis and fur. At this time, sea ice is used as a haul-out platform, whereupon seals bask in the sun in order to facilitate the molting process (Feltz and Fay 1966). Although ringed seal populations number several hundred thousand in the Chukchi and Bering Seas (Conn et al. 2014, Kelly et al. 2010a), they were listed as *threatened* under the Endangered Species Act (ESA; National Marine Fisheries Service 2012) due to predicted negative trends in snow cover on sea ice (Stroeve et al. 2012, Hezel et al. 2012, IPCC 2014), which could negatively affect ringed seal reproduction. Meanwhile, further repercussions for human/wildlife interactions are possible as diminishing sea ice makes the Arctic more accessible, allowing for increasing commercial shipping and industrial development (Harsem et al. 2015, Smith and Stephenson 2013).

There were several issues that provided impetus for this study. For example, conservation efforts and mandates, such as ESA recovery plans and critical habitat designation, require the use of the best available science, the spatial extents of which are patchy for ringed seals in Alaska. Furthermore, aerial surveys for pinnipeds in the Bering and Chukchi Seas require visibility correction factors derived from seal movement and behavioral data to increase accuracy (Conn et al. 2014). Polar bear conservation can also benefit from a better understanding of relationships between polar bears and their primary prey (Durner et al. 2009, Wilson et al. 2014). Finally, mitigation planning for conflicts between humans and wildlife will be an increasing need in an ever more ice-free and accessible Arctic.

Several investigations have characterized ringed seal movements and behavior in Alaska (Harwood and Stirling 1992, Kelly et al. 2010b, Crawford et al. 2012a, Harwood et al. 2012, Harwood et al. 2015), but comprehensive range-wide documentation remains incomplete. As such, the objectives of this study were to: (1) improve the baseline understanding of ringed seal seasonal movements and habitat use in the Alaskan Arctic, and (2) quantify diving and haul-out behavior. To accomplish these objectives, we tagged ringed seals with satellite transmitters near Utqiaġvik (formerly Barrow), AK; a region that has not been well studied. This work augments previous datasets and broadens the information available for comprehensively monitoring a sentinel species of the Arctic (Moore et al. 2014).

2.3 Materials and Methods

Ringed seals were captured near Utqiaġvik, AK (71.3° N, 156.8° W) in mid-to-late summer using braided monofilament nets (25cm mesh size; 5 x 50 m). Each net had a highly visible float-line and light weight lead-line, ensuring that entangled seals could surface to breathe and that observers could readily determine when a seal was caught. Nets were deployed in the open-water among ice floes where ringed seals had been observed. Depending upon conditions, some nets were left free-floating, whereas others were anchored from the float line to an ice floe, the seabed, and/or the boat. All nets were monitored continuously while they were deployed.

Entangled seals were physically restrained during sampling and instrumentation. We recorded body mass, standard length, axillary girth, sex, and age-class (Geraci and Lownsbury 2005). Age-class was determined by the number of alternating light and dark bands on the front claws (McLaren 1958). Seals with ≥6 clawbands (McLaren 1958) or weighing ≥35 kg (Crawford et al. 2012a) were considered to be adults. All other seals were classified as juveniles. We instrumented each seal with two satellite transmitters (hereafter tags): one that was glued to the fur of their mid-dorsum or head and one mounted to a hind flipper. Most seals (n = 15) received a glue-on SPLASH tag (Wildlife Computers, Redmond, WA, USA; 7.6 x 5.6 x 3.2 cm; 125g in air), which provides location, dive, and haul-out data. Dive-depth was measured by a pressure transducer that samples depth (i.e., pressure; 0.5 m resolution, ±1%) every 10 seconds. The SPLASH tags deployed in 2014 and 2016 reported data for individual dives (start- and end-time, surface duration, and maximum dive-depth), whereas SPLASH tags deployed in 2011 reported summary dive statistics in histograms of 6-hr time blocks. All SPLASH tags used a saltwater sensor—sampling every 10 seconds—to determine whether the tag was immersed. In 2016, we also deployed Conductivity Temperature Depth (CTD) tags (Sea Mammal Research Unit, St. Andrews, Scotland; 10.5 x 7 x 4 cm; 545g in air) on two large ringed seals. The CTD tags provided location, dive and haul-out behavior, as well as oceanographic data associated with individual dives. Five-minute epoxy and/or cyanoacrylate adhesive was used to glue the SPLASH or CTD tags to the seal's fur. Glue-on tags were expected to stay attached for a maximum of ~10 months before being shed during the seal's annual molt the following spring. We also attached a SPOT tag (Wildlife Computers, Redmond, WA, USA; 5.8 x3.2 x1.8 cm; 50 g in air) to the seal's rear flipper by screwing it into a backing plate through two holes punched in the seal's interdigital webbing.

For this paper, we limited our analyses to only those seals whose tags provided data beyond December 31st of the deployment year to bolster the representation of time, space, habitat conditions, and seal physiological states. Location and dive-behavior data were obtained using the Argos System (Harris et al. 1990) and saved as a time series for each seal. Implausible locations were excluded using the Douglas Argos Filter (Douglas et al. 2012), which is based on movement rates, turning angles, and location quality. High quality locations (Argos classes 1, 2, or 3) were retained unconditionally. Auxiliary locations (Argos classes 0, A, B, and Z) within 5 km of a preceding or subsequent location were retained. Any remaining auxiliary locations were included only if the resultant movement rates were $<5.6\ \text{m}\cdot\text{s}^{-1}$ and the turning angles were not suspiciously acute (Supplemental Materials S1).

Using R statistical software v3.4.2 (R Core Team 2017) and the filtered Argos locations (Lambert's equal area projection), we applied a continuous-time correlated random walk model to generate tracks for each seal (R-package CRAWL v2.0.1; Johnson et al. 2008). The CRAWL model generated four seal location estimates daily (i.e., 6 hour intervals). Those with standard errors >25 km were excluded from further analysis. Seal locations were annotated with habitat metrics describing distance to mainland, ocean depth, distance to sea-ice edge, and sea-ice concentration (Supplemental Materials S2). Daily averages were calculated for all habitat metrics. Sea-ice concentration was based on the average within a 100 km diameter circle (excluding land) centered on the midday (12:00 h GMT) estimated seal location. Minimum distance to the sea ice edge was measured from the midday location to the nearest periphery of sea ice comprised of ≥10 contiguous pixels of ≥15% ice concentration.

We determined when seals were hauled out based on the hourly percent-dry time series that was collected by the SPLASH tags. Specifically, any hour with a mean percent-dry time ≥80% was defined as a haul-out hour. The 80% threshold was relatively insensitive because the distribution of hourly percent-dry values was strongly bimodal: 95% of all sampled haul-out hours (*n* = 62,279) were either ≥80% dry (11.5%) or ≤25% dry (83.5%). We excluded the first week of post-deployment haul-out behavior data to reduce potential biases associated with capturing seals near-shore.

Individual dive-behavior metrics from SPLASH and CTD tags deployed in 2016 tags (*n* = 10) included dive-duration, maximum dive-depth, and surface-interval between dives. We annotated the dive-behavior data with estimated location, sea ice concentrations, and bathymetry associated with the respective dive dates. Dives were classified as bottom-dives when the recorded dive-depth attained >75% of the reported ocean depth. We did not attempt to classify bottom-dives in shallow water (<10 m) where discrimination became increasingly sensitive to inaccuracies between spatial and bathymetric data.

Based on comparisons of successive dive-depths and intervening surface intervals (Supplemental Materials S3), the dive behavior data were parsed into three classes: (1) <u>Resting</u>, which includes any surface interval between two successive dives that lasted ≥10 minutes. This behavior was isolated from the dive time-series before further analysis; (2) <u>Repetitive-Diving</u>, which is any series of ≥5 sequential dives during which the maximum dive-depth was within ±15% of either of the preceding two dives. Single dives of nonconforming depth (>15% different) were allowed within a repetitive-diving episode; and (3) Mixed-diving: which consists of all remaining dives not classified as repetitive-diving.

Though most of the seal locations were on the shallow (<300 m) continental shelf (see results), 12 of the 17 seals in our analysis (71%) spent time in the deep-water Arctic Basin (>1,000 m). As such, we partitioned location, dive, and haul-out data into the two periods when seals occupied either the continental shelf or the Arctic Basin. To avoid misrepresenting the relationship between dive- and bottom-depth (caused by spatiotemporal mismatch between dive- and location-data), we excluded the small number of seal-days (*n* = 23) with locations along the steep shelf-break (300 – 1,000 m deep) from our analyses.

We calculated monthly dive summaries that included the daily average time spent diving and the proportions of repetitive- vs. mixed-diving. Daily averages were calculated by summing all daily dive durations into monthly sub-totals, extrapolating the monthly sub-totals into grand totals based on the monthly sample-size, and dividing monthly grand totals by the number of days in the respective month. Poorly represented seal-months that were sampled at <10% of possible hours per month were excluded from the analysis. We also excluded seal-months if the average distance to mainland was <5 km because near-shore seals often occupied waters where ocean depths were less than the tag's 3.5 m threshold for dive detection. We verified that daily dive behavior data were sampled randomly throughout the day (Supplemental Materials S4) to ensure that temporal sampling bias did not interact with diurnal dive-behaviors.

We constructed linear mixed-effects models (R-package 'lme4', Bates et al. 2012) or generalized linear mixed models (R-package 'glmmADMB', Fournier et al. 2012) for each of six response variables: movement rate ($\bar{x}$ km/day), distance to land ($\bar{x}$ km), haul-out time ($\bar{x}$ hrs/day), sea ice concentration ($\bar{x}$ %), distance within the pack-ice ($\bar{x}$ km), and distance outside the pack-ice ($\bar{x}$ km). All response variables were transformed (square-root or log) prior to analysis. Four factors were used as fixed-effect explanatory variables: sex, age-class (*adult*, *juvenile*), year tag was deployed (Y_{11}, $Y_{14.16}$), and season (P_{open} = Jul-Nov, P_{ice} = Dec-Jun). We included the deployment year factor (Y) to account for a disease outbreak among ice seals in 2011 (NOAA 2012). No seals tagged in 2011 were symptomatic. Season definitions targeted apparent breaks in the sea ice concentration and distance to pack ice habitat metrics (see results). All models included random intercepts for individual seals. We modeled each response variable with a univariate model for each of the four fixed-effects, and a bivariate model for each of the six possible pairwise interactions among the four factors (Supplemental Materials S5). Visual inspections of residual plots from all significant models revealed no obvious deviations from homoscedasticity. For each significant model, we used least-square means (R-package 'lsmeans', Lenth 2016) to generate model predictions (see Results). Least-square means are useful for summarizing the effects of factors when the subjects (seals) were repeatedly measured with unequal sample-sizes (Lenth 2016).

2.4 Results

The tags from 17 of the 37 ringed seals tagged since 2011 provided the minimum duration of transmissions required for this study. These 17 seals included 11 males (2 juveniles) and 6 females (3 juveniles) (Table 2.1). Adults averaged 102.5 cm long (SD = 9.3) with an average weight of 40.7 kg (SD = 11.2). Juveniles averaged 88.2 cm in length (SD = 10.0) and weighed 26.8 kg on average (SD = 8.0). The mean length ($\bar{x}$ = 92 cm, SD = 0.8) and weight ($\bar{x}$ = 28.0 kg, SD = 4.8) of adult seals tagged in 2011 were both significantly less than the mean length ($\bar{x}$ = 107.8 cm, SD = 6.4) and weight ($\bar{x}$ = 47.1 kg, SD = 6.7) of adults tagged in 2014 and 2016 (Supplemental Materials S6).

A total of 52,431 satellite locations were obtained from all tags. The median number of locations per seal was 2,778 (range = 2,146 – 6,020), the median tracking duration was 239 days (range = 178 – 331), and the median time between sequential locations was 0.52 hours (range = 0.01 – 1,157; 99th percentile = 20.3). High quality Argos locations (class = 1, 2, or 3) comprised 7,471 (7.2%) of the seal locations. Filtering excluded 3,757 Argos auxiliary locations (class = 0, A, B, or Z). After applying the CRAWL model and excluding 596 estimated locations with SEs >25 km, the final data set of CRAWL 6-hr location estimates contained 16,260 locations that represented 4,083 individual seal-tracking days (median = 237 tracking days/seal; range = 174 – 330).

Over the course of tracking, ringed seals made extensive movements (Fig. 2.1), into regions of varying ocean depth at different times. Ultimately, ringed seals spent most (96.2%) of their time occupying continental shelf waters <300 m deep. From July to mid-October ringed seals occupied waters with highly variable depths (median = 47 m, range

= 1 – 3,838 m) because 12 of the 17 seals undertook ~ weeklong forays into the Arctic Basin (Figs. 2.1 and 2.2).

All seals showed seasonal variability in distance-to-mainland while residing within the pack ice from January to May (Fig. 2.3). By early November, all seals had moved south of Utqiaġvik, with one notably early southward movement into the Bering Sea in mid-September (PH2014BW01). From mid-October to mid-December, seals occupied shallow waters in proximity to the Bering Strait (Figs. 2.2 and 2.3). Eight seals moved south through the Bering Strait from November to mid-December, while eight others remained in the Chukchi Sea into January (Fig. 2.3). In the months thereafter, seals in the Bering Sea continued to move southward with the advancing sea ice, except for one seal (PH2014BW01) that stayed in the shallow waters of Norton Sound. Three of four seals tagged in 2011 that wintered in the Bering Sea moved southwest into deeper waters south of the Gulf of Anadyr (Fig. 2.1), while the fourth 2011 seal and all four of the 2016 seals that wintered in the Bering Sea moved south into waters off of the Yukon-Kuskokwim Delta (Fig. 2.1). Six of the 10 ringed seals tagged in 2016 remained in the Chukchi Sea for the duration of their winter tracking—four along the Alaskan coast between Utqiaġvik and Cape Lisburne, one at the mouth of Kotzebue Sound, and one at Kolyuchin Inlet in northern Chukotka. One seal tagged in 2014 (PH2014BW02) also moved into the western Chukchi Sea during winter, just north of the coast of Chukotka; and one seal tagged in 2011 (PH2011BW13) was in the vicinity of the Bering Strait when its tag stopped transmitting in February 2012.

By December, ringed seals tended to occupy areas within the ice pack that had substantial sea ice cover (Fig. 2.2). Tags on five ringed seals provided data from April through May. By early April, some of the seals that wintered in the Bering Sea began making modest northward movements, but all remained south of the Bering Strait (Fig. 2.3). Starting in April, the average sea ice concentration occupied by seals began to diminish (Fig. 2.2), suggesting that ringed seals in the Bering Sea were not aggressively pursuing the retreating ice pack northward.

Ringed seal movement rates (Fig. 2.4) varied over the course of the year. During the period with tracking data for all 17 seals (Aug-Dec), the median cumulative distance traveled was 4,790 km/seal (range = 2,719 – 5,988). Thereafter, some seals continued to move throughout the winter, while others occupied specific locales for extended periods (Fig. 2.3). Daily movements (Fig. 2.4; Supplemental Materials S7) were significantly greater during the open-water season than during the ice-covered season ($P_{\text{open}} = 22.4$ km/day; $P_{\text{ice}} = 9.2$ km/day), and also varied significantly with respect to the interaction between season and year, with higher movement rates during the ice-covered season for seals tagged in 2011 ($Y_{11} = 14.5$ km/day) than for seals tagged in other years ($Y_{14.16} = 6.8$ km/day). No other significant differences in movement rates were observed based solely on sex, age-class, or year.

While ringed seals primarily occupied continental shelf waters, their distance to mainland (Fig. 2.4) varied with year, season (for females), and the interaction between year and season. Seals tagged in 2011 maintained significantly greater distances from the mainland on average than seals tagged in 2014 or 2016 ($Y_{11} = 125.8$ km; $Y_{14.16} = 49.6$ km). For females there was a significant increase in mean distance to mainland from 43.3 km during the open-water season to 86.1 km during the ice-covered season, but no significant difference for males. During the ice-covered season, seals tagged in 2011 maintained significantly greater distances from the mainland on average than seals tagged in 2014 and 2016. Neither sex, nor age class as main effects showed significant differences in distance to mainland.

Locations within the pack ice (Fig. 2.4) were farther from the ice edge for males than for females during the ice-covered season, but not during the open-water season. Ice concentration in areas occupied by ringed seals varied significantly by age-class, season, and the year tagged (Fig. 2.4). Not surprisingly, ringed seals occupied areas with higher overall ice concentration during the ice-covered season. Generally, adults occupied areas with higher average ice concentration (54%) than juveniles (34%). This was also true for adult females, which occupied areas with significantly higher concentrations than those occupied by juvenile females (40% vs 12%). During the ice-covered season, adult males occupied regions of higher mean ice concentration than juvenile males (74% vs 58%). Year of tag deployment was also significant, with seals tagged in 2011 occupying more concentrated sea ice than seals tagged in later years (Y_{11} = 68%; $Y_{14.16}$ = 40%). This was also evident among adult females, who occupied regions of more concentrated sea ice than juvenile females.

Ringed seal associations with sea ice were weakest during the relatively ice free open-water season (Jul-Nov) when seals occupied habitats characterized by the lowest sea ice concentrations and the greatest distances to the ice edge (Figs. 2.2 and 2.3). Seals frequently used off-shore habitat, often >100 km from the mainland and with distances >300 km (maximum ~ 575 km) not uncommon (Fig. 2.3). The strength of the sea ice associations increased during ice-covered season (Dec-Jun), with surrounding mean sea ice concentrations ranging from 60 – 100% at locales that were well within the ice pack

(Fig. 2.2). Male ringed seals occupied regions within the pack ice that were farthest from the sea-ice/ocean edge (Fig. 2.4).

On average, ringed seals spent most of their daily time budget diving ($\bar{x}$ = 16.5 hrs/day), most of which ($\bar{x}$ = 13.2 hrs/day) was repetitive-diving (Table 2.2). The mean proportion of daily hours spent diving remained relatively constant across July-January (69%), as was the proportion of that time associated with repetitive-diving episodes (80%). By February, the proportion of repetitive-diving dropped to 55%, at this time the sample size was very small (*n* = 2 seals).

Among all dives recorded on the continental shelf (*n* = 96,414), 65% were classified as bottom-dives. During 7,369 episodes of repetitive-diving (consisting of 67,355 dives), 78% met the criteria for bottom-dives (Fig. 2.5). Dive histogram data from seals tagged in 2011 also indicated that most dives over the continental shelf were bottom-dives (Supplemental Materials S8). Overall, when occupying continental shelf waters, most dives were bottom-dives and, therefore, dive-depth was largely predicted by the bathymetry at any given location. The dives that implausibly exceeded ocean depth (Fig. 2.5) were likely due to imprecise spatiotemporal pairing of locations and dives as well as inaccuracies in both the bathymetry and location data.

Median dive duration (Figure 2.6) was 3.9 minutes (99th percentile = 10.7 min, *n* = 81,916). Logarithmic regression of median dive duration within 10-meter intervals of dive-depth indicated an upper median dive duration asymptote of 8.4 minutes. Median surface duration between dives was 0.7 minutes (~42 sec) (99th percentile = 4.1 min, *n* = 76,964) and exhibited an exponential increase as dive-depths increased beyond 150 m. Note that while the regressions of dive time and surface time in Figure 2.6 reflect the dominant (median) relationship with dive-depth, a fairly consistent 10-12 minute maximum dive duration was observed across all dive-depth intervals.

Partitioning of dives by type and depth revealed diurnal and monthly patterns (Fig. 2.7). Histograms for repetitive-diving >25 m deep showed a midday increase in frequency, which became more narrowly focused around midday as the season progressed into fall and winter (Nov-Feb). The resting behavior histograms also showed diel and monthly patterns, similar but complementary to the repetitive-diving (>25 m) histograms. The shape and magnitude of the mixed dive histograms also resembled the resting histograms, but with less well defined diel or monthly patterns.

Daily one-hour percent dry time series data were collected for an average of 72% (SD = 8.9%) of the tracking period. After excluding the first week of data post-deployment, the median duration of uninterrupted haul-out bouts was 3 hours (range 1 – 28, *n* = 1,025 haul-outs). As expected, the least-square mean for haul-out time (Fig. 2.4) was significantly longer in the ice-covered season in comparison to the open-water season (P_{ice} = 5.9 hrs; P_{open} = 3.2 hrs/day), while the mean daily haul-out time during the ice-covered season was significantly longer for seals tagged in 2011 ($P_{\text{ice}} \sim Y_{11}$ = 7.1 hrs) compared to seals tagged in 2014 and 2016 ($P_{\text{ice}} \sim Y_{14.16}$ = 4.5 hrs/day). On days with a CRAWL location estimate, 86% of the haul-out hours were spent >10 km from the coast, indicating that most haul-outs occurred offshore on the sea ice. No seals tracked in this study were documented to have hauled out on land post-deployment. Coastal haul-out behavior was frequently observed in 2011 near Utqiaġvik, but very infrequent thereafter (North Slope Borough, *unpublished data*). The proportion of ringed seals engaged in haul-out behavior showed circadian patterns that varied on a daily and monthly scale

(Fig. 2.8). During July, 15-20% of the seals were hauled out during any given hour of the day, with little indication of a daily pattern. The proportion of seals hauled out declined from August through October, with a subtle indication of midday avoidance. From November through March, nocturnal patterns became more pronounced as seals preferentially hauled out at night. Haul-out behavior switched from nocturnal to diurnal in April and May as seals showed a strong midday preference; although the sample-size of tagged seals had markedly declined (*n* = 2) by April.

From early-July to mid-October, a majority of tagged ringed seals (12 of 17) undertook one or more multi-day forays into the deep-water Arctic Basin (Fig. 2.9; Table 2.3). These included 7 males (2 juvenile) and 5 females (1 juvenile). All of the ringed seals tagged in 2011 (*n* = 5) ventured into the Arctic Basin, contributing 9 of the 16 observed forays. The median duration of the deep-water forays was 7 days (range = 2 – 21) (Fig. 2.9). These off-shelf forays were usually associated with seemingly deliberate and sometimes far-ranging trips to the sea ice (Fig. 2.10). While in the presence of sea ice in the Arctic Basin, seals tended to haul out for extended periods of time (median duration = 11 hrs, maximum duration = 34 hrs, *n* = 42, Table 2.3)—usually returning directly thereafter to the continental shelf. Three seals made multiple off-shelf trips to the sea ice edge (Fig. 2.9), while three other forays did not encounter substantive ice cover and haul-outs were not recorded (Fig 2.10).

Seals exhibited both repetitive and mixed diving behaviors in the Arctic Basin, but given the extreme depths, no dives were to the bottom. Rather, seals dove to uniform and moderate depths within the water column (<100 m), which were occasionally punctuated by intermittent deeper dives (200 – 300 m; Supplemental materials S8). On other occasions, these deeper dives led to repetitive diving to deeper strata.

2.5 Discussion

Our results suggest that ringed seal movements, diving, and haul-out behavior vary in a manner consistent with reconciling the tradeoffs that occur where ecology and physiology intersect (Born et al. 2004, Ferguson and Higdon 2006). Ringed seals enter the spring in their poorest body condition due to the demands of reproduction and of the previous winter (Ryg et al. 1990); and therefore, must forage intensively during the open-water season to replenish their energetic reserves before winter (Ryg and Oritsland 1991, Härkönen et al. 2008, Young and Ferguson 2013). The substantial effort that ringed seals invest into foraging is indicated by the high proportion of their activity budget spent repetitive-diving (Table 2.2). Bouts of repetitive diving often lasted for hours at a time and were almost always associated with habitat where important prey species are known to aggregate—i.e., the sea floor over the continental shelf (Benoit et al. 2010) and moderately shallow strata (0 – 300 m) in the water column over the Arctic Basin (Crawford et al. 2012b, Majewski et al. 2015). But ringed seals face challenges in maximizing their foraging opportunities due to the dynamic nature of their habitat, which varies seasonally with respect to spatiotemporal relationships among sea ice, prey availability, and seal physiology. In characterizing how ringed seals address these challenges under a range of conditions, we provide interpretations below that we feel can inform seal conservation and management.

Repetitive-diving shows patterns that are consistent with a foraging strategy that maximizes the rate of energy intake. For example, the association between repetitive-dives and the benthos while over the continental shelf may reflect optimal foraging (Stephens and Krebs 1986) with respect to the behavior of Arctic cod (*Boreogadus saida*)—an important forage species for ringed seals (Holst et al. 2001). Planktivorous fish synchronize their movements to the diel vertical migration (DVM) of their prey (Stich and Lampert 1981, Hays 2003, Rabindranath et al. 2011). But as potential prey themselves, fish must also balance their own metabolic requirements with predation risk from, in this case, ringed seals (Pearre 2003). Among Arctic cod, larger and more energy-rich adults occupy the demersal zone (Benoit et al. 2010) as a means to avoid predation (Stich and Lampert 1981); and because they have the metabolic reserves that enable them to remain at greater depths longer, they are not constrained to follow the DVM of their planktonic prey into shallower, more dangerous strata in the water column. This leads to aggregations of larger cod at depth (Benoit et al. 2010) that physically displace smaller conspecifics into the shallower water layers where they are known to be more prevalent (David et al. 2016). Thus, Arctic cod are partitioned by water depth (cost to seals) and body-size (benefits to seals). Our observations of primarily benthic repetitive-diving in ringed seals suggest that they may be targeting larger, more energy rich cod (Bowen et al. 2002). This is consistent with an *energy maximization* strategy (Santini and Chelazzi 1996, Bergman et al. 2001) that invests more energy into deeper dives to achieve a higher net energetic intake rate than would be possible by foraging on more accessible but less energetically profitable prey.

Repetitive-diving also occurs in the Arctic Basin, but because bottom-diving at great depths is impossible for ringed seals (Gjertz et al. 2000), repetitive-dives tended to terminate at different strata in the water column—presumably where prey are located. Occasionally, repetitive-diving episodes were punctuated by single dives to substantially greater depths (Supplemental Materials S9). Potentially exploratory in nature (Simpkins et al. 2001), these intermittent deep dives are consistent with a strategy of investigating alternative foraging patches to minimize lost foraging opportunities (Stephens and Krebs 1986, Kohlmann and Risenhoover 1998). This strategy may be more profitable in habitats with lower prey densities, heterogeneously distributed prey, and/or when a foraging patch is nearing depletion. Our observation of seals shifting their repetitive-diving behavior into deeper strata in the water column suggests that these exploratory trips were profitable on occasion.

Temporal patterns of diving and resting behavior (Fig. 2.7) suggest that ringed seals prioritize their foraging time to coincide with maximum levels of available light. In waters >25 m deep, repetitive-diving behavior shows a diel pattern in which frequency was highest during hours centered on midday. A seasonal shift in this pattern is also apparent, with hours of highest repetitive-diving frequency becoming more narrowly focused on midday as light availability decreases into the fall and winter. This pattern suggest that ringed seals may benefit from visual foraging tactics—particularly so in deeper water where light is more attenuated. In contrast, repetitive-diving in shallower water (<25 m) showed no diel or seasonal patterns possibly due to less light attenuation.

Dive histogram data from the tags deployed in 2011 (Supplemental Materials S8) were consistent with the results from 2016 in that they suggest a prioritization of the hours with the most available light for bottom-dives. Meanwhile, both resting and mixed-diving exhibited diel patterns complementary to those of repetitive-diving. If mixed-diving was less associated with foraging behavior, then it is conceivable that ringed seals were restricting other activities (e.g., resting, travel) to times in which foraging success was lower (i.e., darkest hours). Altogether, these behavior patterns appear to prioritize and respond to seasonal changes in day length, presumably to maximize the likelihood of foraging success. A better understanding of the role of light with respect to the foraging success of visual hunting Arctic marine predators will take on increasing importance to ecosystem function as sea ice continues to decline with associated increases to light penetration into the water column (Langbehn and Varpe 2016).

Haul-out behavior in ringed seals was also consistent with the strategy of allocating hours with the most available light for foraging. For example, during the onset of the ice-covered period, the haul-out behavior appeared to favor the darkest hours of the day (Fig. 2.8), leaving those hours centered on midday available for other activities—presumably foraging. These results concur with previously observed patterns of nocturnal haulout behavior in ringed seals (Härkönen et al. 2008). In May-June during the molt, however, ringed seals shifted to a preference for midday haul-out; also concurring with previous reports (Kelly et al. 2010b). Although day length at Arctic latitudes is maximal in May and June, there is still diel variation in solar elevation. Prioritizing haul-out during the time of day that may be the most productive for foraging exemplifies how seals vary their behavior to accommodate other energetic and physiological requirements.

The metabolically demanding process of molting (Feltz and Fay 1966) in ringed seals introduces tradeoffs to the costs and benefits of foraging and hauling out. Molting is facilitated by infusing the epidermis with blood, thereby providing the nutrients, oxygen, and warmth needed for tissue regeneration (Boily 1995). But this also leads to unsustainable levels of heat loss for seals immersed in frigid Arctic waters unless they can haul out (Boily 1995). Ringed seals compensate by hauling out more and foraging less (Ashwell-Erickson et al.1986, Young and Ferguson 2013). Another reason to haul out involves a relationship between sea ice availability and molt duration. Years with less available sea ice have been linked with longer periods needed to complete the molt—lasting well into the prime open-water foraging season (McLaren 1958, Berta et al. 2015, p. 183), thereby reducing time allocated to foraging opportunities. Given the importance of the open-water season to foraging performance (Härkönen et al. 2008), behavioral choices that reduce energetic losses while also accelerating the completion of the molt should be favored.

Relationships between the timing, availability, and location of sea ice and the energetic constraints of molting may be important to decisions that ringed seals make concerning their movements and behavior, particularly during the early open-water season. Abundant sea ice over the productive continental shelf allows molting seals to efficiently forage with minimal costs associated with heat loss. But recently, sea ice has been retreating earlier and further to the north (Comiso et al. 2017), and so available sea ice haul-outs have become spatially restricted to inferior foraging habitat (i.e., the Arctic Basin). As such, ringed seals in the Alaskan Arctic appear to be faced with choosing from among the following options: (1) Forage in continental shelf waters, but with no platform on which to haul out—potentially extending molt and contending with unsustainable energy losses; (2) haul out on sea ice situated in unproductive foraging habitat, thereby decreasing molt duration but potentially reducing longer-term losses in foraging opportunities; or (3) haul out on land (Lydersen et al. 2017), which may be viable provided that predation risk is low. For healthy ringed seals, option 3 has not yet been observed in the Alaskan Arctic, but was observed among numerous “sick” seals in 2011 (discussed below).

The ringed seal haul-out behavior that was recorded in the Arctic Basin during the open-water foraging season offers several insights concerning the tradeoffs seals face concerning haul-out and habitat use. For brief periods, most of the seals in our study (70%) ventured from the shallow and highly productive continental shelf (Kingsley et al. 1985, Teilmann et al. 1999, Born et al. 2004) to the deep waters of the Arctic Basin, a region typically considered to be unproductive (Frey et al. 2016). These movements differ from ringed seal populations at Svalbard that swim long distances to access highly productive habitat (Freitas et al. 2008). Movements into the Arctic Basin were unexpected, particularly at a time when seals were in their poorest body condition, because it appears to be counterproductive to foraging efficiently. One possible explanation presumes a strong innate behavioral drive to haul out, compelled by the need to complete the molt. From an evolutionary perspective, a behavioral drive to haul out would be beneficial, provided that energetic losses are minimized and that prey are available, either in the presence of the sea ice (e.g., Arctic cod; Mecklenberg et al. 2002) or at depths accessible to diving ringed seals (Crawford et al. 2012b, Majewski et al. 2015) when hauled out over deep water. Certainly the presence of sea ice promotes more profitable foraging dives because seals can haul out between foraging bouts and minimize their time in the water. If the trend of early, rapid, and extensive summer sea ice retreat continues, then off-shelf movements to haul-out on sea ice to complete molt may become energetically unsustainable. Consider the energetic costs incurred by a ringed seal tagged in 2017, that traveled nearly 900 km north of Point Barrow (79.5° N), far into the Arctic Basin, before it reached the sea ice (ADF&G *unpublished data*).

To some extent, we found that patterns of habitat use varied demographically. Similar to Crawford et al. (2012a), we observed demographic habitat partitioning on the basis of sex and age class (Fig. 2.4). However, the age class partitioning we observed was not as discrete as that observed by Crawford et al. (2012a); possibly the result of smaller sample-size and/or the different tagging locations and years. No models with interactions between demographic factors and capture year were significant in our analysis (Supplemental Materials S5 and S7). However, the disease that was widespread among ice-seals in 2011 represented a significant ecological event. Ultimately designated as an "Unusual Mortality Event" or UME (NOAA 2013, Stimmelmayr et al. 2013), this illness or factors leading up to it may have introduced other unaccounted for variables.

The seals captured and tagged in 2011 were physically and behaviorally different from those tagged in subsequent years. They were shorter and lighter than the seals tagged in 2014/2016 (Supplementary Materials S6), exhibited higher movement rates, were more pelagic, and occupied regions of the sea ice deeper within the perimeter of the ice edge (Figs. 2.1 and 2.4). Numerous published accounts have suggested the existence of two ringed seal ecotypes: (1) a smaller, pelagic "pack-ice seal", and (2) a larger, coastal "fast-ice seal" (Freuchen 1935, McLaren 1958, Fedosyev 1975, Finley et al. 1983, Gorlova et al. 2012). Our data suggest that the seals tagged in 2011 were more similar to the pack-ice ecotype. Though it is beyond the scope of our study to draw definitive conclusions about ecotypes, the topic is relevant to ringed seal conservation. No definitive cause of the 2011 UME has been identified to date. “Sick” seals tended to show an abnormal molt, skin lesions, and lethargy—including the tendency to haul out on land (J. Herreman, *pers. comm.*). We note that the seals tagged in 2011 had poorer body condition, but no visible lesions. Perhaps it was the UME that brought “pack-ice ecotype” seals, otherwise unlikely to be captured, to terrestrial haul-outs where they dominated the sample that was captured and tagged in 2011. Assuming that the two purported ringed seal ecotypes occupy different niches, it is plausible that one ecotype may experience different ecological perturbations and/or respond differently. Further inquiry into ringed seal ecotypes and their ecology is warranted and may have conservation implications for a species experiencing rapid change throughout much of its Arctic range.

This study makes new contributions to a small but growing body of literature about ringed seal seasonal movements and behavior, particularly for those seals near Utqiaġvik, AK during the summer—a portion of their seasonal range that had not been the focus of tracking efforts before.

Benthic repetitive-diving in waters over the continental shelf was the dominant daily activity ($\bar{x}$ = 16 hours/day), occurring at somewhat higher frequencies during the daytime when dives exceeded 25 m in depth—especially in winter. This may be a strategy that exploits the behavior of Arctic cod, an important prey species, while preferentially using visual hunting tactics. Similar to previous investigations, ringed seals exhibited seasonal migratory movements and demographic habitat partitioning (Crawford et al. 2012a, Harwood et al. 2012, Harwood et al. 2015). Seals moved south in the fall, and divided their winter locations evenly between the southern Chukchi and northern Bering Seas. Movements varied by age class, while sea ice varied by sex. From July to October, 70% (12 of 17) ringed seals periodically ventured into the deeper Arctic Basin, spending much of their time hauled out ($\bar{x}$ duration = 12 hrs/day). They also appeared to forage at different strata of the water column (60 – 300 m), occasionally exploring alternative foraging patches (strata).

Observed patterns of movement and behavior highlighted the potential importance of individuals balancing energetic requirements with respect to dynamic environmental and physiological constraints. Distinctions among individuals tagged in 2011 in morphology, behavior, and seasonal distribution, were consistent with previous reports about the possibility of a pelagic “pack-ice” ecotype among ringed seals. In addition to lending insight into that year’s UME outbreak, the existence of ecotypes within the greater population of circumpolar ringed seals would have far reaching implications for further understanding their overall ecology.

Bearing in mind that change is occurring throughout the Arctic (Post et al. 2013) in habitat that is both varied and dynamic (Walsh 2008), further research should be attentive to the diversity of spatiotemporal or demographic contexts that occur throughout the breadth of the species’ circumpolar range (Bluhm and Gradinger 2008). Caution is also warranted when generalizing from observations that cover a subset of conditions experienced by ringed seals. Such efforts will facilitate a comprehensive approach to monitoring the Arctic ecosystem, generating improved recognition and understanding of the eco-physiological processes that can influence the conservation and management of a vulnerable species with high ecological and cultural value and the ecosystem in which it lives (Condon et al. 1995, Huntington et al. 2016).

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2.8 Tables

Table 2.1. Attributes and tracking duration for 17 ringed seals marked with satellite transmitters during the summer near Utqiaġvik, AK. These seals reported location data until at least January 1st of the year following tag deployment. Duration between the first and last location is shown as *elapsed days*, while *CRAWL days* denote the number of elapsed days in which the CRAWL movement model estimated the seal's location with a standard error of <25 km. We did not include data from PH2014BW01 in the dive behavior analysis because, unlike the 2016 SPLASH tags that used a pressure threshold to define dive start- and end-times, the 2014 SPLASH tag used a saltwater sensor, which was prone to incorrectly pool sequential dives when intervening surface events were not detected. **Juvenile*

seal ID	sex	weight (kg)	length (cm)	ax. girth (cm)	claw bands	first loc	last loc	elapsed days	CRAWL days
PH2011BW03 [a]	M*	24.8	95	84	4+	07/16/11	06/09/12	330	330
PH2011BW10 [a]	F	26.6	92	72	8+	07/21/11	05/01/12	286	276
PH2011BW11 [a]	F	23.2	93	76	7+	07/22/11	06/04/12	319	307
PH2011BW12 [a]	M	27.2	92	81	8+	07/22/11	05/04/12	288	288
PH2011BW13 [a]	M	34.8	91	84	8+	07/22/11	01/11/12	174	174
PH2014BW01 [b,c]	M	53.6	100	95	6	07/23/14	05/19/15	301	301
PH2014BW02 [a]	M*	18.3	74	70	--	07/23/14	02/02/15	195	195
PH2016BW01 [b]	M	50.9	110	101	6+	07/03/16	04/04/17	276	276
PH2016BW03 [b]	F*	24.8	86	81	1+	07/03/16	01/26/17	208	195
PH2016BW04 [b]	M	49.1	114	101	6+	07/03/16	03/22/17	263	263
PH2016BW06 [b]	F*	25.9	86	84	1	07/03/16	01/21/17	203	203
PH2016BW09 [b]	F	46.7	113	101	5+	07/04/16	02/23/17	235	205
PH2016BW10 [b]	F*	40.0	100	92	4	07/04/16	02/09/17	221	217
PH2016BW11 [b]	M	36.6	98	92	5+	07/04/16	02/25/17	237	237
PH2016BW12 [b]	M	36.8	103	93	6+	07/04/16	01/06/17	187	180
PH16BRW-120350 [d]	M	51.6	112	124	8+	07/03/16	04/06/17	278	258
PH16BRW-120353 [d]	M	51.6	112	105	7+	07/03/16	01/31/17	213	178

[a] SPLASH tag without dive-behavior time series

[b] SPLASH tag with dive-behavior time series

[c] did not record 24x1 hr % dry (haul-out) data

[d] CTD tag with dive-behavior time series

Table 2.2. Monthly estimates of the mean hours per day spent diving, and the fraction (%) of those hours spent engaged in episodes of repetitive-diving. Sample (%) is the fraction of the month for which we obtained dive-behavior time series data for any given seal-month. For each month, at least a 10% sample of the dive-behavior time series data was required for a seal to be included in the respective monthly estimate. Analysis used the 8 SPLASH tags deployed in 2016. Seal-months with an average distance from the coast of <5 km were excluded (*n* = 4 months).

		Diving (h)		Repetitive (%)		Sample (%)	
month	*n*	mean	sd	mean	sd	mean	sd
Jul	8	14.7	2.0	80.0	15.5	19.2	7.2
Aug	7	17.1	2.0	80.2	4.0	34.1	10.8
Sep	7	17.3	3.3	81.1	10.0	24.8	10.8
Oct	7	17.4	5.1	81.8	9.3	32.2	14.6
Nov	6	16.4	2.3	81.3	12.9	29.0	11.5
Dec	6	16.5	3.0	82.5	8.8	30.7	12.3
Jan	5	16.2	3.9	80.1	9.3	18.4	3.5
Feb	2	16.3	0.5	54.6	16.4	15.8	3.1
Pooled	*48*	*16.5*	*3.1*	*79.9*	*11.4*	*26.5*	*11.6*

Table 2.3. Details of the forays by ringed seals into the Arctic Basin. Most forays included days when seals hauled out on sea ice (Figs. 2.9 and 2.10), as deduced by hourly summaries of saltwater sensor data indicating that the tag was dry for ≥80% of a given hour. Mean hours per day hauled out are shown for just those days during a foray that the seal hauled out for ≥1 hour. The letter in the first column references the corresponding map in Figure 2.10.

				number of days			hours/day hauled-out				
map	seal ID	start	end	total	sensor data	haul-out ≥1 hr	$\bar{x}$	sd	min	max	*n*
a	PH2011BW13	8/2/11	8/11/11	10	10	5	9.6	4.7	3	15	5
b	PH2011BW10	8/13/11	8/21/11	9	8	2	16	9.9	9	23	2
c	PH2011BW13	8/12/11	8/22/11	11	11	2	14	2.8	12	16	2
d	PH2011BW12	8/16/11	8/22/11	7	6	2	15	4.2	12	18	2
e	PH2011BW11	8/22/11	8/28/11	7	7	3	10	6.2	3	15	3
e	PH2011BW03	8/22/11	8/27/11	6	6	3	14.7	6.1	8	20	3
f	PH2011BW03	9/18/11	9/27/11	10	9	0	--	--	--	--	--
g	PH2011BW12	10/5/11	10/15/11	11	10	5	18.4	4.7	11	24	5
h	PH2011BW13	10/7/11	10/14/11	8	8	0	--	--	--	--	--
i	PH2014BW02	8/8/14	8/11/14	4	3	2	9.5	3.5	7	12	2
j	PH2016BW06	7/4/16	7/18/16	15	13	13	10.4	6.5	1	21	13
j	PH2016BW09	7/9/16	7/13/16	5	5	5	15.8	6.9	7	23	5
j	PH2016BW10	7/9/16	7/18/16	10	8	6	14	6.2	7	22	6
k	PH2016BW01	8/8/16	8/9/16	2	2	0	--	--	--	--	--
l	PH2016BW12	8/9/16	8/14/16	6	5	3	11.3	6.1	6	18	3
na	PH2014BW01	8/14/14	8/17/14	4	--	--	--	--	--	--	--
na	PH2016BW03	8/6/16	8/7/16	2	2	1	1	--	1	1	1

2.9 Figures

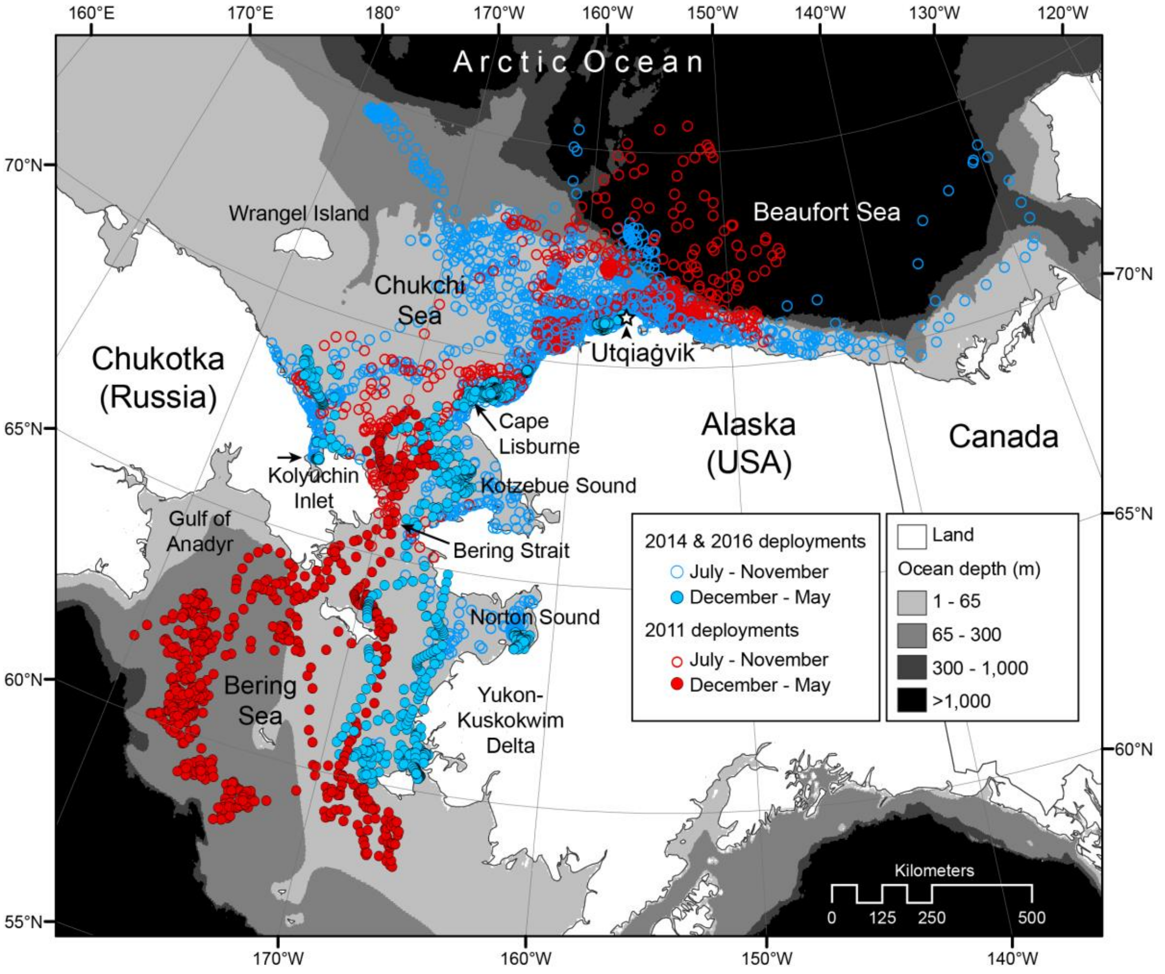


Figure 2.1. Daily CRAWL location estimates (n = 4,083) of 17 ringed seals instrumented with satellite tracking tags during summer near Utqiaġvik, Alaska. Colors distinguish seals tagged in 2011 (red, n = 5) from those tagged in 2014 and 2016 (blue, n = 2 and 10, respectively). Symbols distinguish July-November locations (open) from December-May locations (filled).

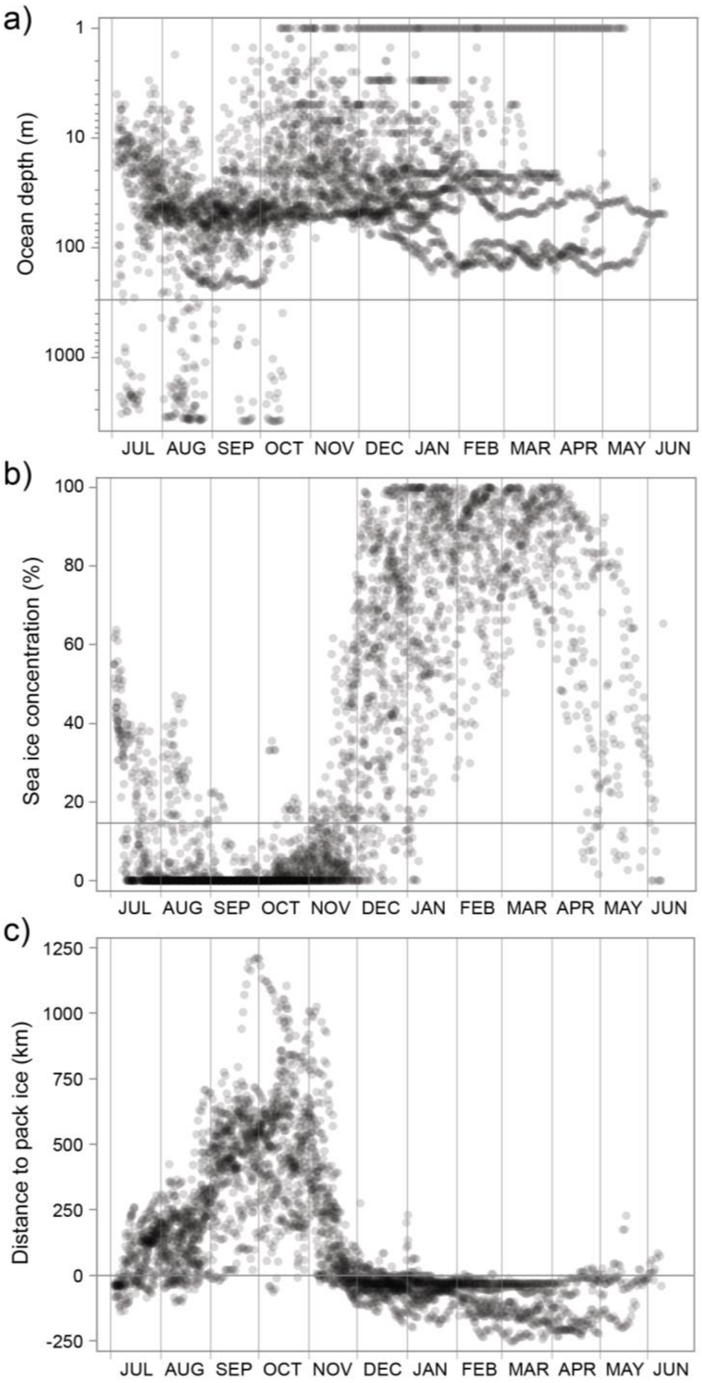


Figure 2.2. Seasonal time series of daily ringed seal location attributes. (a) Ocean depth is shown on a log scale with a horizontal line at the shelf-break (300 m depth). (b) Mean sea ice concentration (within a 50 km radius) is divided into open-water versus ice covered (above or below the horizontal reference line at 15% concentration respectively). (c) Distance to the edge of the pack ice is divided by the horizontal reference line at the zero distance, with negative values showing distances within the pack ice and positive values showing distances outside.

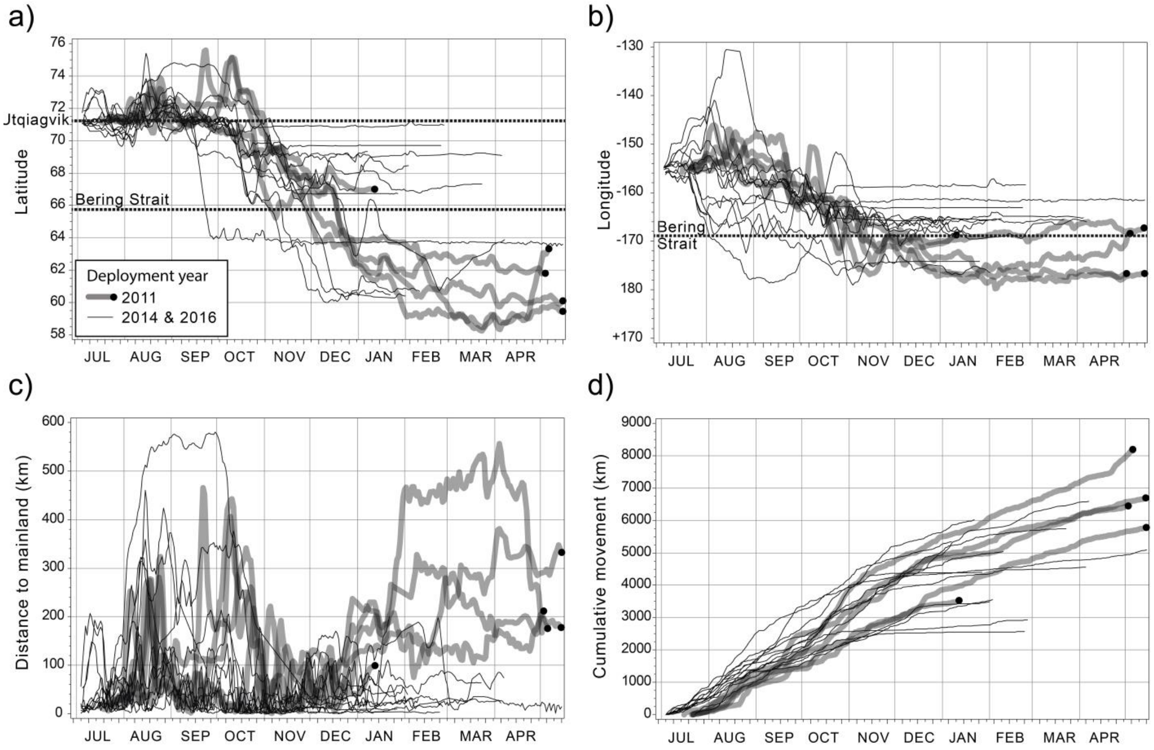


Figure 2.3. Seasonal movements of 17 ringed seals. Figure panels indicate: (a) latitude, (b) longitude, (c) distance to mainland (islands excluded), and (d) cumulative daily tracking distance. Thin black lines are seals tagged in 2014 and 2016. Thick gray lines with black terminal dots are seals tagged in 2011. Distances were calculated on the basis of daily CRAWL location estimates.

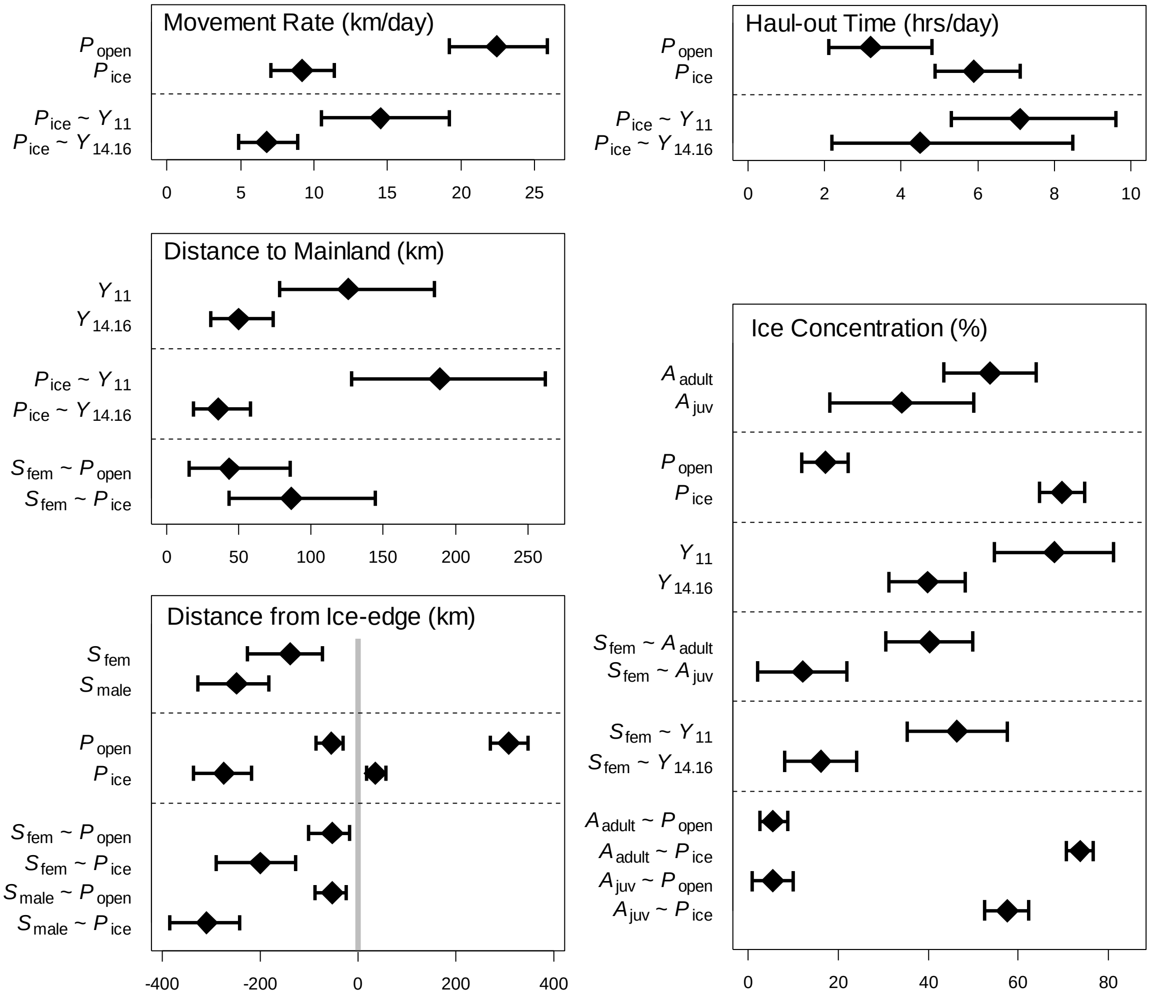


Figure 2.4. Least-square mean estimates of ringed seal movements and habitat use. LS-means values were generated from significant models only (Supplemental Material S5). Open-water and ice-covered periods are designated P_{open} and P_{ice} respectively. 2011 tag deployments are designated as Y_{11}, while 2014 and 2016 are designated $Y_{14.16}$. Adults and juveniles are designated A_{adult} and A_{juv} respectively. Each sex is designated S_{fem} and S_{male} respectively. Interactions are denoted with a tilde (~). Negative values of distance from the ice-edge refer to locations inside the pack-ice, while positive values refer to locations outside the pack-ice (Supplemental Materials S7).

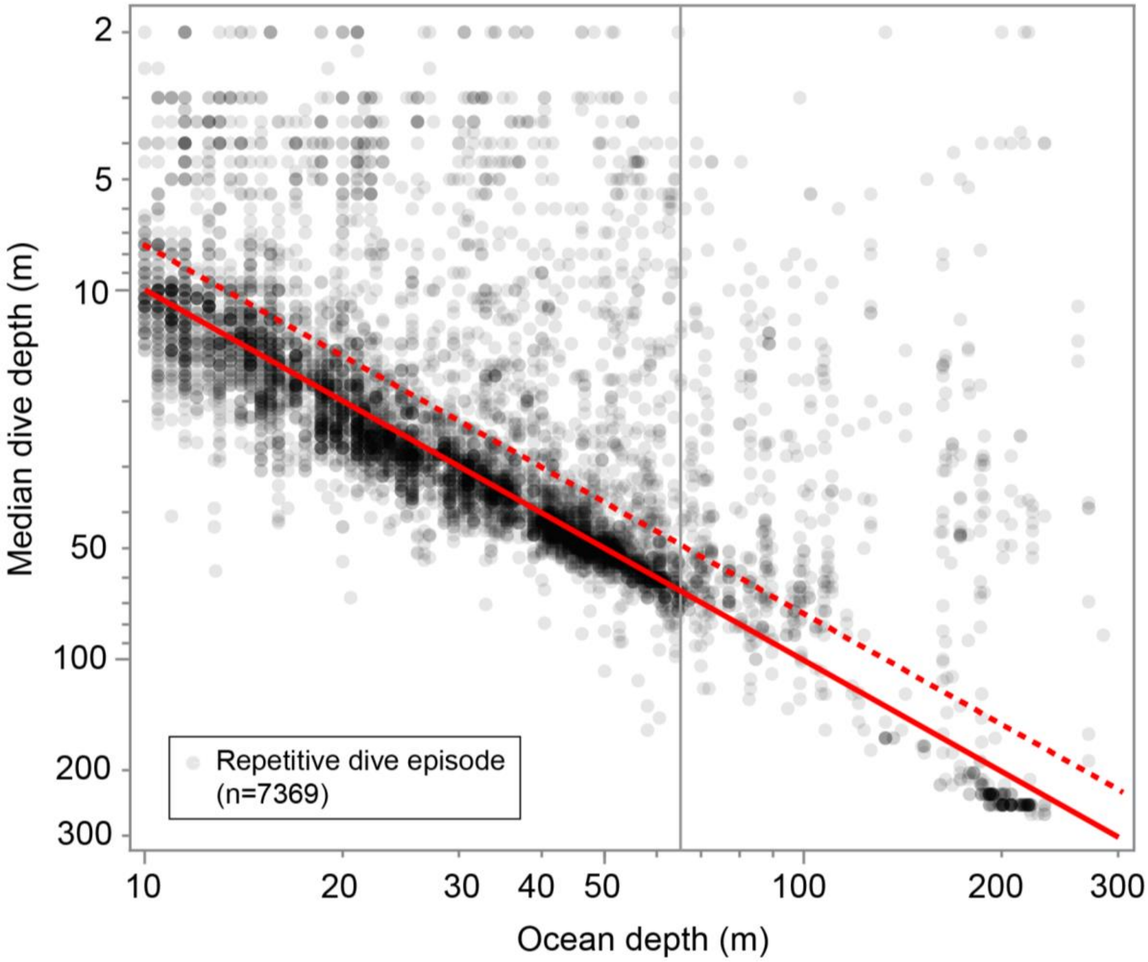


Figure 2.5. Median dive-depth recorded during repetitive-diving episodes in relation to the mean ocean depth underlying seal locations. Analysis was restricted to days when seals were located in water 10-300 m deep. The solid red line references a 1:1 dive-depth to ocean depth relationship and the dotted red line references the dive-depth threshold (75% of documented depth) for classification as a bottom-dive. The gray vertical line references 65 m ocean depth as mapped in Figure 2.1. Note log scales on both axes. See Supplemental Materials S8 for a summary of dive behavior based on the dive histogram data received from tags deployed in 2011.

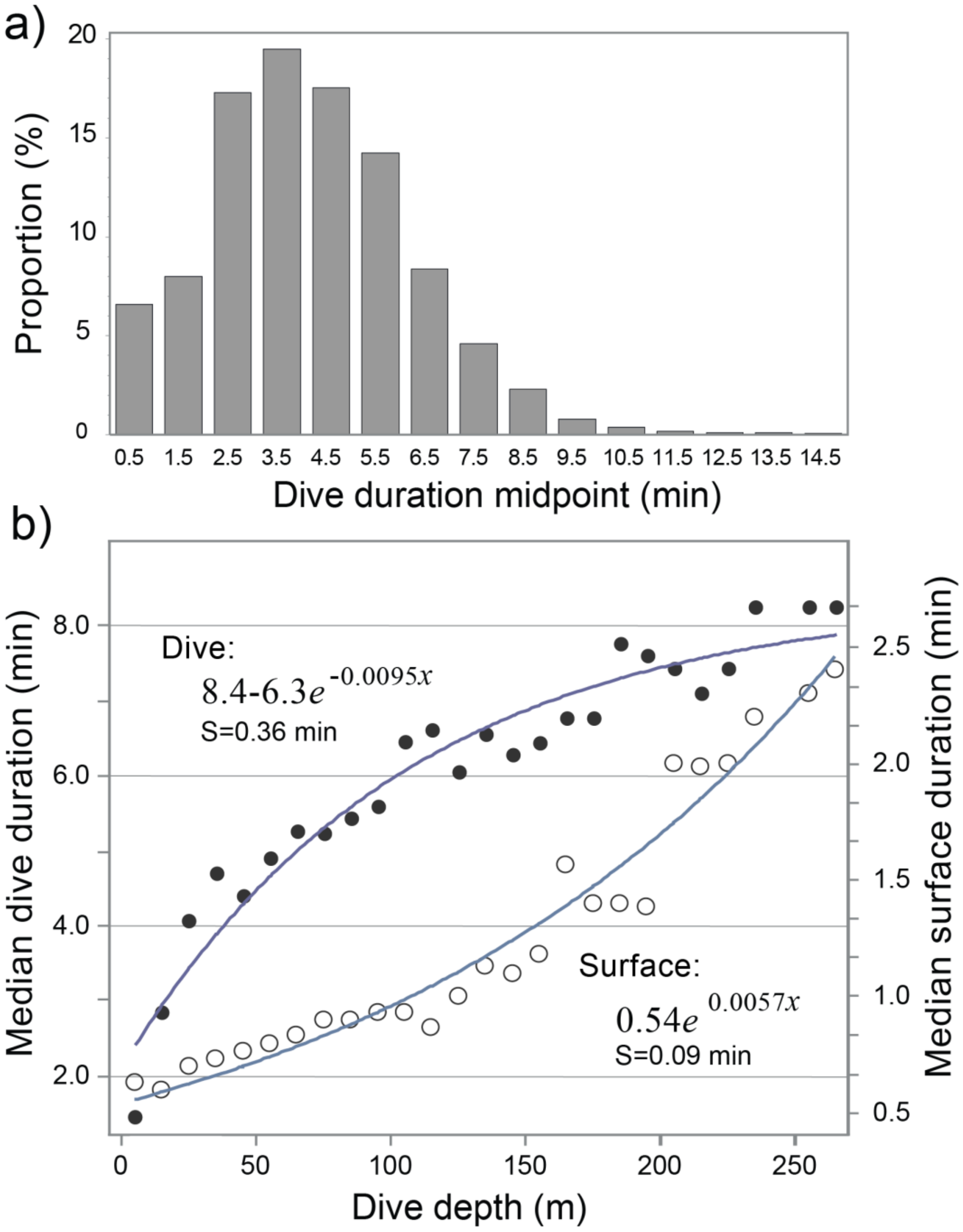


Figure 2.6. Ringed seal dive duration and surface intervals. (a) Dive duration frequency distribution across 1-minute duration bins. (b) Logarithmic regressions fitting median dive duration (solid circles) and median surface duration (open circles) as a function of dive-depth in 10-m depth intervals. For intervals with $n \geq 10$ the standard error of the regression (S) represents the average distance (minutes) that the medians fall from the regression line. Data originated from the dive-behavior time series collected by both SPLASH and CTD tags deployed in 2016 (n = 10) and for dives ≤15 minutes in duration (n = 81,916).

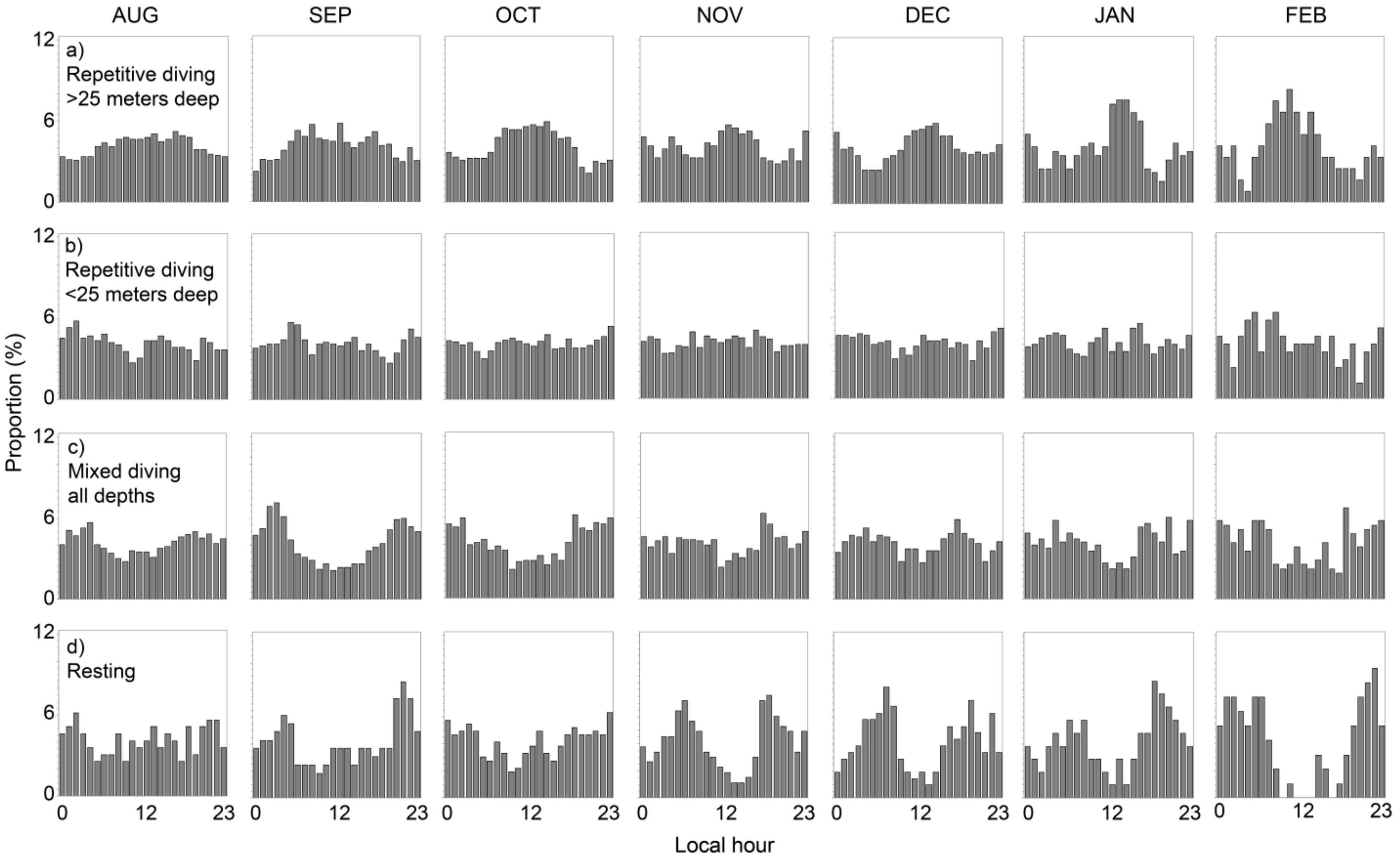


Figure 2.7. Proportion of dive-behavior classifications that occurred in each hour of the day (local, UTC-10 h) in each of seven months. Episodes of repetitive-diving (see Methods) during which median dive-depth was (a) >25 m, (b) ≤25 m deep, (c) episodes of diving to mixed depths, and (d) periods of resting at the surface for >10 minutes (but unassociated with haul-out). Data from the dive-behavior time series collected from SPLASH tags deployed in 2016 (*n* = 8 seals).

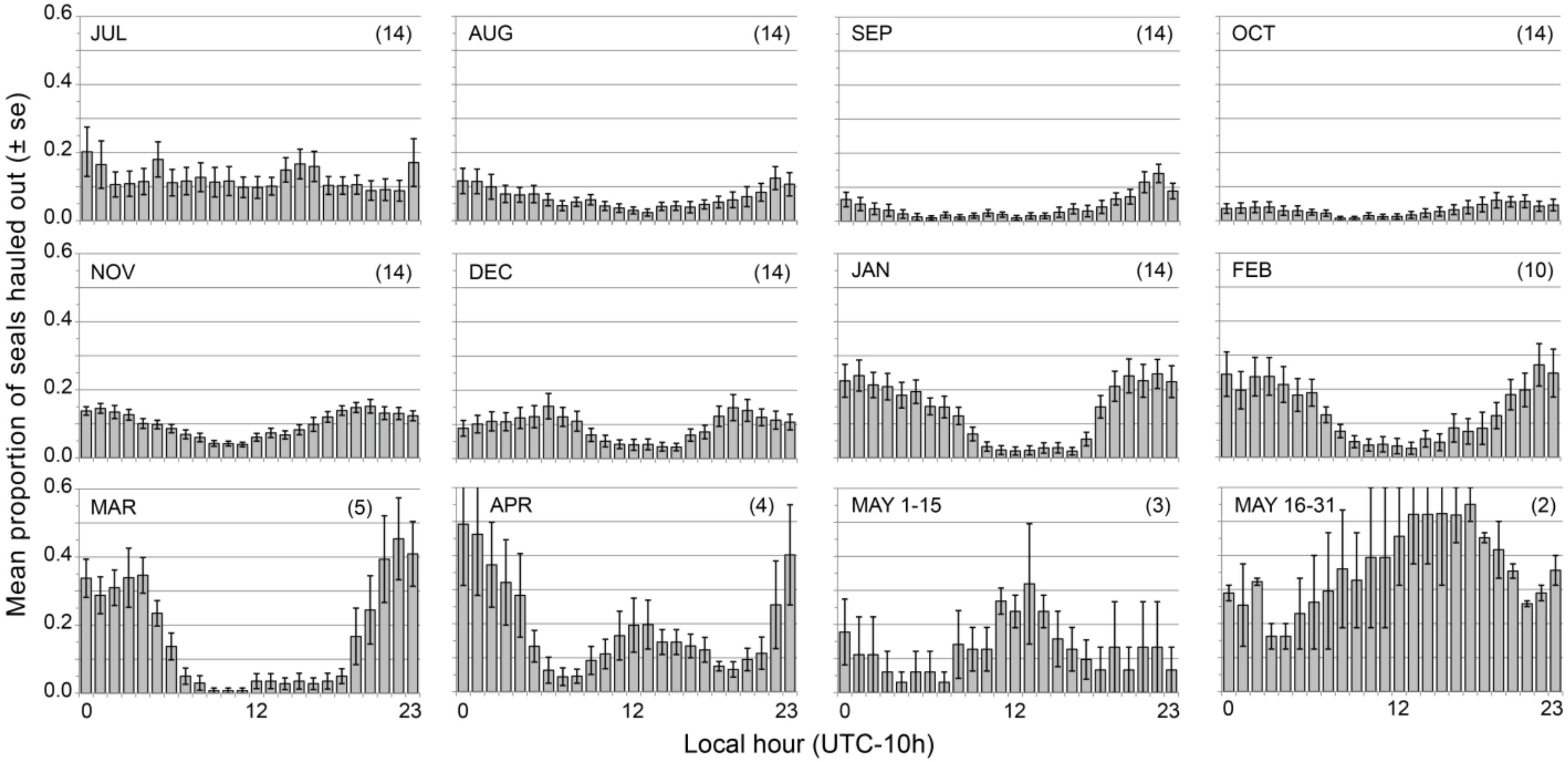


Figure 2.8. Monthly diurnal haul-out behavior shown as the mean proportion (± se) of ringed seals hauled out during each local hour (UTC-10h). Monthly sample-size (*n* seals) is shown in parentheses. May is split into 2 periods. Haul-outs during forays into the deep-water Arctic Basin are excluded.

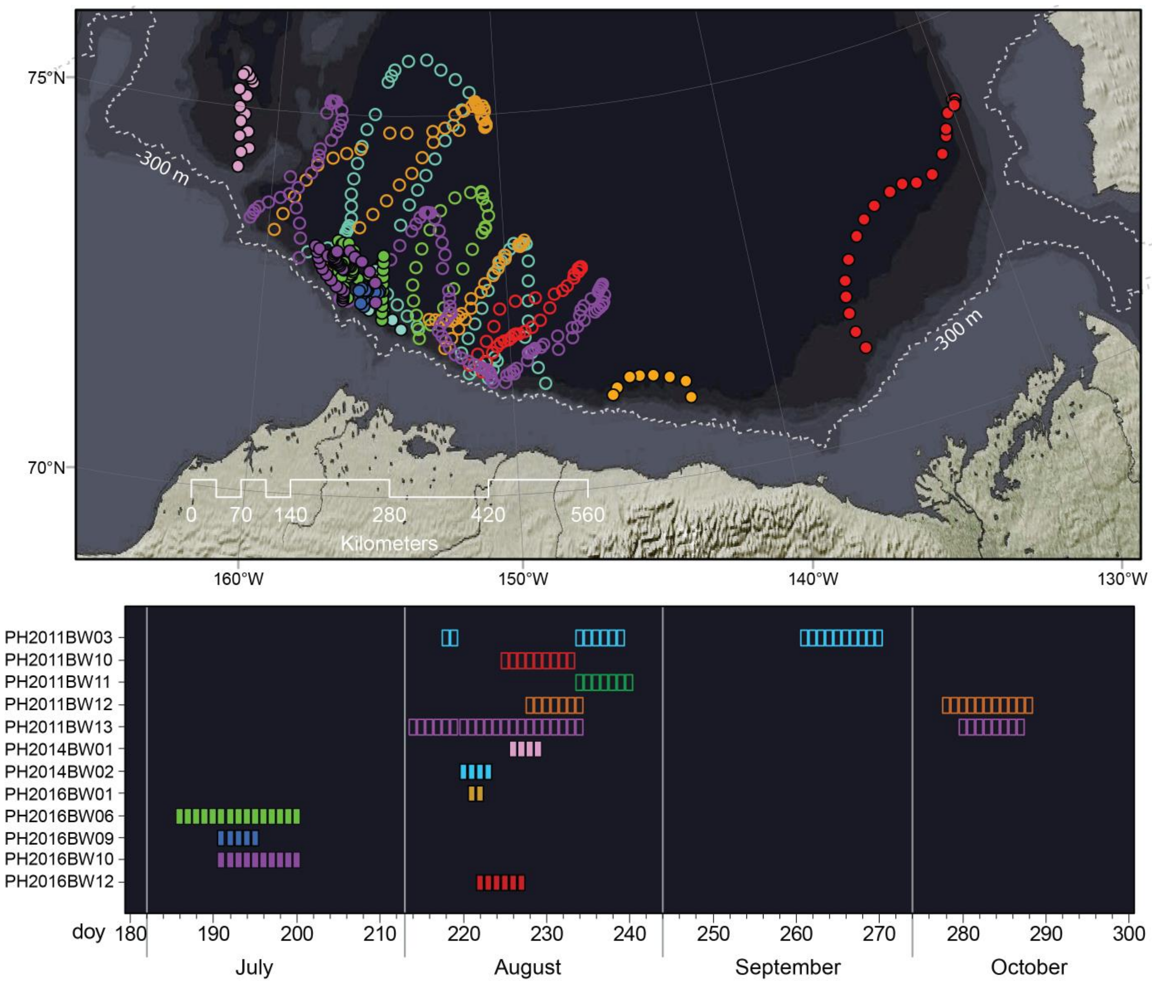


Figure 2.9. Ringed seal locations (4 per day) when they occupied the Arctic Basin. Individual seal colors in the map (top) correspond to the dates for that individual in the table (bottom). Seals instrumented in 2011 are distinguished by open symbols, and those in 2014 and 2016 by solid symbols.

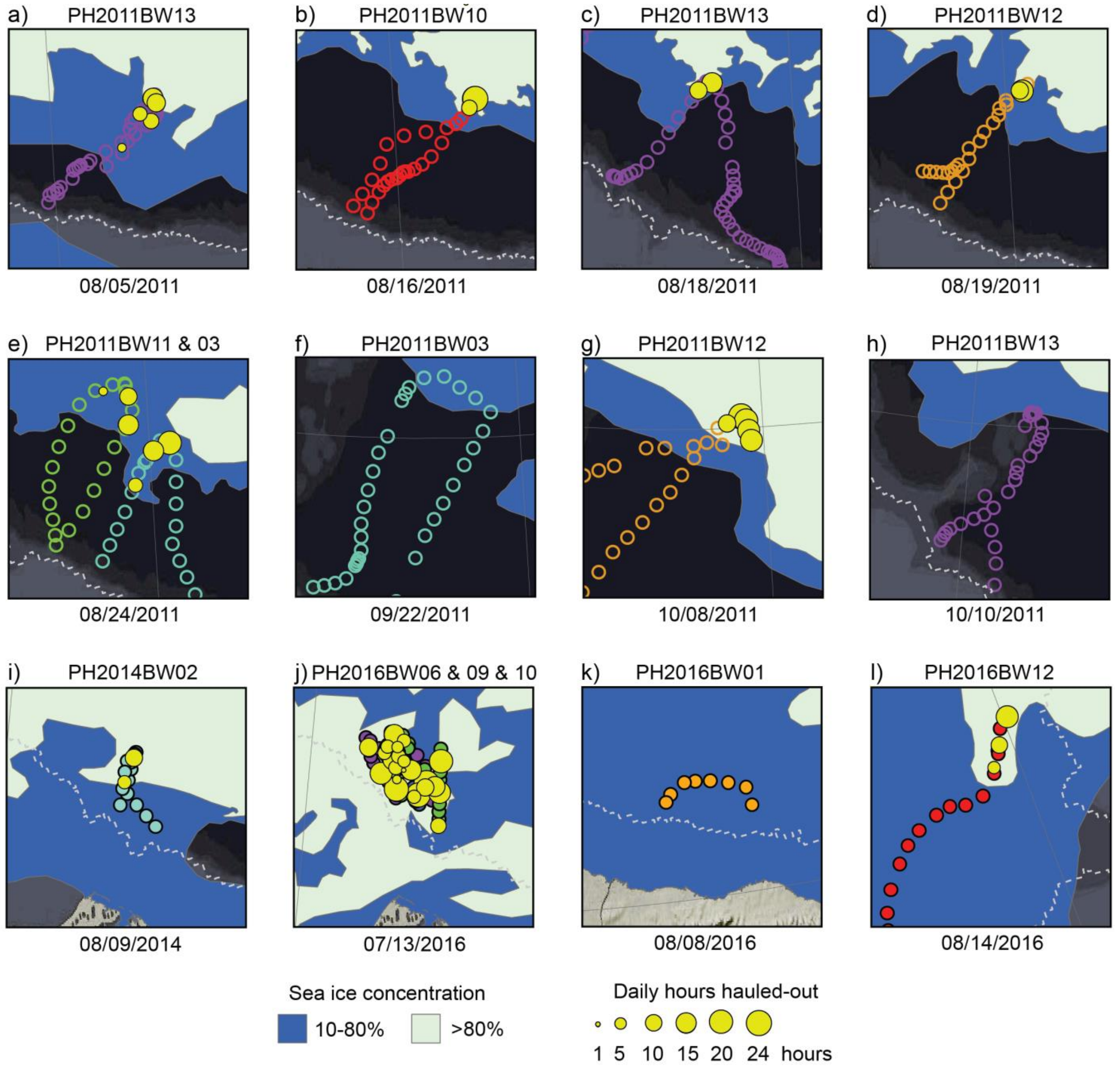


Figure 2.10. Distribution of sea ice and haul-out behavior during forays into the Arctic Basin (*n* = 11). Locations are 6-hr CRAWL estimates, as seen in Figure 2.1. Days with ≥1 haul-out hour recorded are overlaid as yellow dots scaled in size by the total hours hauled out that day. Sea ice conditions on the date shown below each panel correspond temporally with the more northerly locations and show two classes of ice concentration: marginal (blue, 10-80%) and contiguous (light blue, >80%).

2.10 Supplemental Materials

S1. Parameters used in the Douglas Argos Filter.

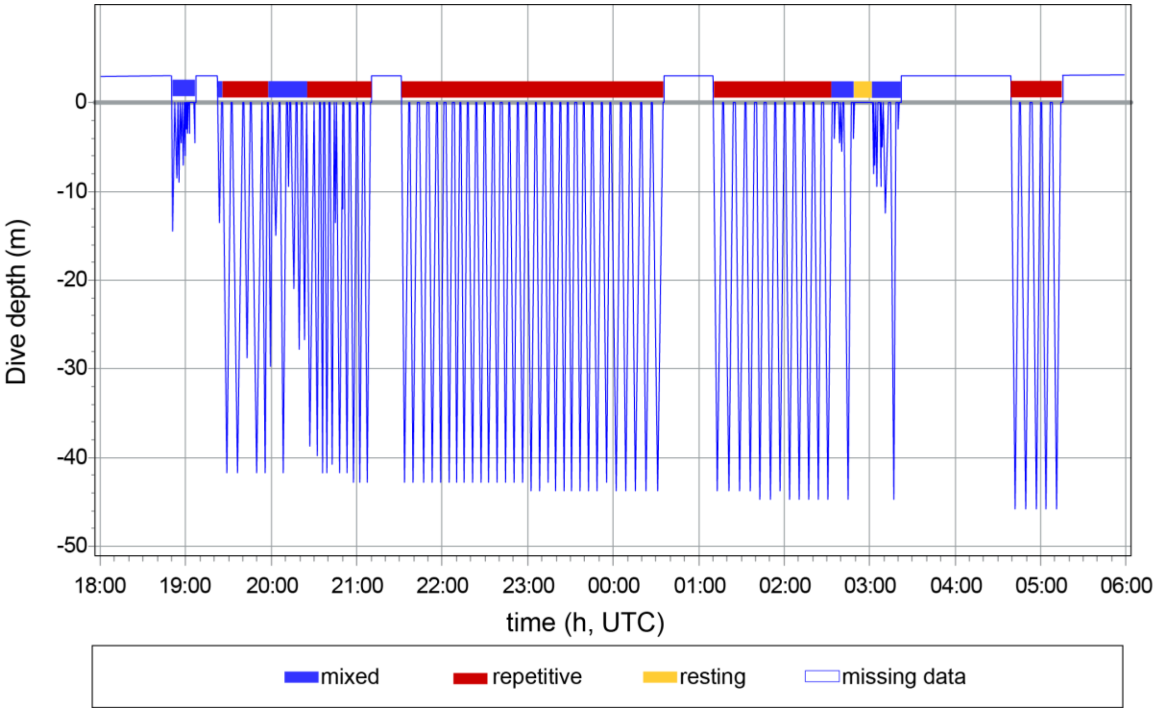
Implausible Argos locations were excluded using the Douglas Argos Filter (Douglas et al. 2012), which judges movement rates, distances, turning angles, and location quality. High quality locations (Argos classes 1, 2, or 3) were retained unconditionally. Auxiliary locations (Argos classes 0, A, B, and Z) within 5 km of a preceding or subsequent location were retained by virtue of spatial redundancy. Any remaining auxiliary locations were included only if the resultant movement rates were $<5.6 \text{ m}\cdot\text{s}^{-1}$ and the internal angles (α, in degrees) formed by preceding and subsequent vectors (of lengths d_1 and d_2 km) were not suspiciously acute ($\alpha > -25 + \beta \times \ln[\text{minimum } (d_1, d_2)]$, where $\beta = 25$). We assigned $\beta = 25$ because it performed well for our specific tracking data across seasons and regions.

S2. Data sets used to quantify habitat metrics.

Description of metric	**Data source**	**Reference**
Minimum distance between mainland Alaska or Russia (excluding barrier islands) and each seal's daily CRAWL location estimate (12:00 h GMT)	Global Self-consistent, Hierarchical, High-resolution Shoreline database.	Wessel et al. 1996
Ocean depth at each seal's CRAWL estimated location	ETOPO2 2-minute Gridded Global Relief Data, v2.	National Geophysical Data Center 2006
Distance from the sea ice edge (>15% ice concentration), and sea ice concentration.	Special Sensor Microwave Imager (SSM/I) daily sea ice concentration grid. [25 x 25 km pixel resolution]	Cavalieri et al. 1996 *and* Maslanik and Stroeve 1999

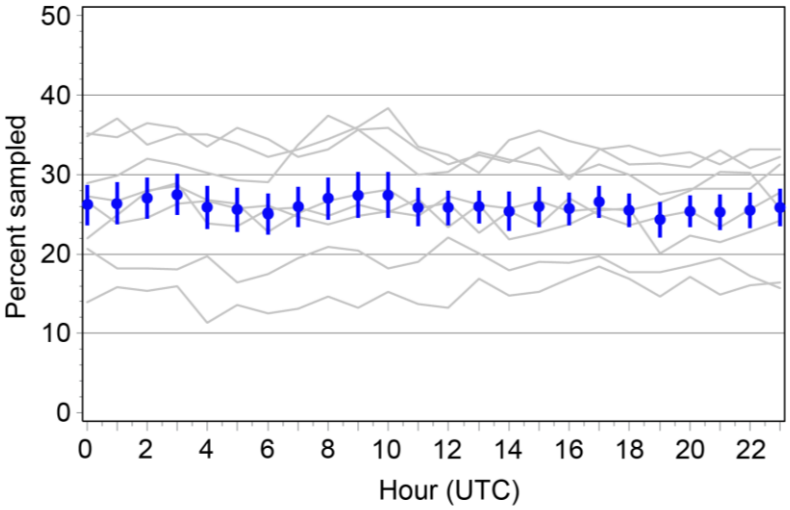
S3. Dive patterns used to classify ringed seal diving behavior.

Example of dive-behavior time series data for one ringed seal during a 14-hour period spanning December 29 – 30, 2016 (UTC). Episodes of three behavioral classes are shown with color bars across the top of the time series: repetitive-diving (similar depths, red), mixed-diving (dissimilar depths, blue), and resting at surface (durations ≥ 10 minutes, yellow). Locations of this seal on December 29 and 30 occurred where ocean depths were 35 m and 40 m based on the ETOPO2 global topographic data set, suggesting that most repetitive-dives were bottom-dives. Missing data were common within the dive-behavior time series due to bandwidth constraints of the Argos System, intermittent satellite visibility, and pre-defined transmission limits imposed to conserve battery life.



S4. Uniform distribution of dive-behavior data acquisition.

This methodology for estimating daily time budgets among *repetitive-diving, mixed-diving,* and *resting* behaviors, based on the dive-behavior time series, assumes that data acquisition was uniformly distributed across all hours of the day to ensure that diurnal patterns in dive-behavior would not introduce biased estimates by interacting with a non-uniform temporal distribution of samples. Blue points show mean (±1 SE, *n* = 8) percentage of dive-behavior data acquired within each hour of the day. Gray lines show the hourly mean percent sampled for each of the 8 individual SPLASH tags deployed in 2016. Dive-behavior data acquired from the 8 SPLASH tags deployed in 2016 achieved reasonably uniform sampling (~25%) across all hours of the day. The uniform spread was achieved, in part, by provisioning the SPLASH tag's "Transmission Control" option to "Transmit data collected over these last days" to a value of 4 days. By transmitting data drawn from a 4-day cue, short-term (within day) temporal biases of relaying data through the Argos System (due to diel patterns in satellite coverage) were overcome.



S5. Models of ringed seal movements and habitat use.

Columns are the response variables and rows are the predictors. For univariate models, significance was assessed using a likelihood-ratio test to compare models with and without the fixed-effect in question. For interaction models, a likelihood-ratio test compared the two-way interaction to a two-way additive model containing the same variables. To characterize the ice type when it is being utilized, the explanatory variable for the models of sea ice concentration included non-zero values only. Distances inside and outside the sea ice edge are related to the sea ice and open water seasons respectively. Statistically significant models are shown in bold text.

model	Movement Rate[1] ($\bar{x}$ km/day)	Dist. to Mainland[1] ($\bar{x}$ km)	Haul-out Time[2] ($\bar{x}$ hrs/day)	Sea Ice Conc.[1,3] ($\bar{x}$ %)	Dist. Inside Ice[3] ($\bar{x}$ km)	Dist. Outside Ice[3] ($\bar{x}$ km)
SEX + (1 | animal ID)	0.667	0.510	0.307	0.319	**0.045**	0.237
AGE + (1 | animal ID)	0.268	0.671	0.527	**0.040**	0.125	0.463
PER + (1 | animal ID)	**<0.001**	0.060	**<0.001**	**<0.001**	**<0.001**	**<0.001**
YR + (1 | animal ID)	0.236	**0.006**	0.517	**0.001**	0.714	0.493
SEX : AGE + (1 | animal ID)	0.381	0.567	0.671	**0.002**	0.070	0.852
SEX : PER + (1 | animal ID)	0.819	**<0.001**	0.396	**<0.001**	**<0.001**	0.129
SEX : YR + (1 | animal ID)	0.592	0.936	0.396	**0.022**	0.234	0.933
AGE : PER + (1 | animal ID)	0.084	0.740	0.752	**<0.001**	**<0.001**	0.183
AGE : YR + (1 | animal ID)	0.267	0.811	0.572	0.242	0.152	0.169
PER : YR + (1 | animal ID)	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.271	0.321

[1] Linear mixed effects models
[2] Generalized linear mixed models
[3] Based on SSM/I sea ice data

S6. Comparing body-size and -condition of 2011 seals to all others.

Seal ID#	Season	Diseased?	Weight (kg)	Girth-axial (cm)	Length-straight (cm)
PH2011BW02	2011	not recorded	30.36	85	95
PH2011BW08	2011	not recorded	21.7	74	90
PH2011BW10	2011	not recorded	26.61	72	92
PH2011BW11	2011	likely	23.21	76	93
PH2011BW12	2011	not recorded	27.19	81	92
PH2011BW13	2011	not recorded	34.82	84	91
PH2011BW14	2011	not recorded	21.34	75	92
PH2011BW15	2011	yes	34.2	85	116
PH2011BW18	2011	yes	29.78	81	109
PH2011BW19	2011	yes	27.9	83	94
PH2011BW20	2011	yes	23.75	69	91
PH2011BW45	2011	yes	34.38	90	100
PH2013BW01	2013	no	35.71	*	*
PH2013BW02	2013	no	35.71	*	*
PH2014BW01	2014	no	53.57	95	100
PH16BRW-120350	2016	no	51.56	124	112
PH16BRW-120353	2016	no	51.56	105	112
PH2016BW01	2016	no	50.89	101	110
PH2016BW04	2016	no	49.11	101	114
PH2016BW05	2016	no	41.29	102	104
PH2016BW08	2016	no	45.98	100	90
PH2016BW09	2016	no	46.65	101	113
PH2016BW11	2016	no	36.61	92	98
PH2016BW12	2016	no	36.83	93	103

* Not measured

Analysis includes ALL adult ringed seals included in this manuscript ($n = 12$) as well as those that were omitted ($n = 7$) due to the premature termination of satellite tag transmissions (i.e., prior to January 1st of the year following tag deployment).

Ringed seals captured in 2011 were smaller overall and lighter than those captured in 2013-14, and 2016. The body condition of the 2011 was lower, based on the ratio of girth to body-length and the residuals from a linear regression model that predicts the weight of the seal based on its length.

$$\text{weight} = 0.7717\cdot(\text{length}_{\text{straight}}) - 41.2199$$

$p < 0.001$ $R^2 = 0.42$

Season	n	$\bar{x}$ length (cm)	$\bar{x}$ girth (cm)	$\bar{x}$ weight (kg)	$\bar{x}$ weight predicted* (kg)	$\bar{x}$ body-condition (girth/length)	$\bar{x}$ body-condition (residuals)*
2011	12	96.3	79.6	27.9	33.1	0.829	-5.12
2013	2	105.6	101.4	44.6	40.3	0.963	6.14
2014	2						
2016	8						
T-test		$t = -2.7$ df = 19.5 $p = 0.01$	$t = -6.5$ df = 15.7 $p = 10^{-6}$	$t = -6.8$ df = 19.7 $p = 10^{-6}$	$t = -2.7$ df = 19.5 $p = 0.01$	$t = -4.1$ df = 17.2 $p = 10^{-4}$	$t = -4.3$ df = 17.2 $p = 10^{-4}$

*Based on the linear regression model

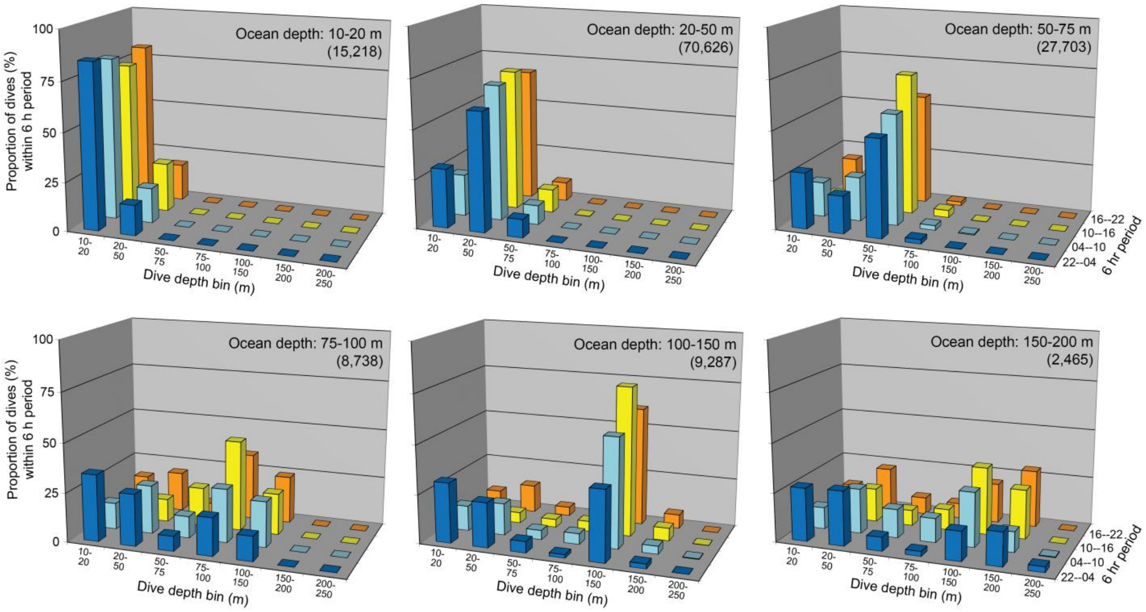
S7. Least-square Means of movements and habitat use.

Least-square mean estimates ($\bar{x}_{[95\%\ \mathrm{CI}]}$) shown in this table came from statistically significant ($\alpha = 0.05$) models (Supplemental Materials S5) and have been back-transformed. The factor *P* refers to the open-water (Jul-Nov) and ice-covered (Dec-Jun) seasons. The factor *Y* distinguishes those tags deployed during the year 2011 from tags deployed during the years 2014 and 2016. The response variable Distance to Land was subsampled every 7th day to minimize spatial autocorrelation. Distances inside and outside the ice refer to the shortest distance between seal locations and the sea ice edge.

factor	Rate (km/day)	Distance to Mainland (km)	Haul-out Time (hrs)	Concentration of Sea Ice (%)	Distance Inside Ice Edge (km)	Distance Outside Ice Edge (km)
S_{fem}					138.7 [73.3; 224.9]	
S_{male}					248.5 [181.2; 326.4]	
A_{adult}				53.8 [43.5; 64.1]		
A_{juv}				34.1 [18.0; 50.2]		
P_{open}	22.4 [19.2; 25.9]		3.2 [2.1; 4.8]	17.7 [12.0; 22.2]	53.9 [29.8; 85.2]	306.7 [270.2; 345.6]
P_{ice}	9.2 [7.1; 11.4]		5.9 [4.9; 7.1]	69.7 [64.7; 74.7]	273.2 [217.7; 335.0]	35.1 [18.2; 57.5]
Y_{11}		125.8 [77.8; 185.2]		68.0 [54.8; 81.3]		
$Y_{14.16}$		49.6 [30.1; 73.9]		39.8 [31.2; 48.3]		
$P_{ice} \sim Y_{11}$	14.5 [10.5; 19.2]	189.0 [127.7; 262.3]	7.1 [5.3; 9.6]			
$P_{ice} \sim Y_{14.16}$	6.8 [4.9; 8.9]	35.4 [18.5; 57.7]	4.5 [2.2; 8.8]			
$S_{fem} \sim P_{open}$		43.3 [15.4; 85.5]			52.3 [18.0; 104.4]	
$S_{fem} \sim P_{ice}$		86.1 [42.7; 144.7]			199.5 [126.7; 288.7]	
$S_{male} \sim P_{open}$					52.1 [25.1; 88.8]	
$S_{male} \sim P_{ice}$					308.4 [241.2; 383.8]	
$S_{fem} \sim A_{adult}$				40.3 [30.6; 50.0]		
$S_{fem} \sim A_{juv}$				12.1 [2.2; 21.9]		
$S_{fem} \sim Y_{11}$				46.4 [35.3; 57.5]		
$S_{fem} \sim Y_{14.16}$				16.1 [8.0; 24.1]		
$A_{adult} \sim P_{open}$				5.5 [2.5; 8.4]		
$A_{adult} \sim P_{ice}$				73.7[70.7; 76.8]		
$A_{juv} \sim P_{open}$				5.5 [0.9; 10.1]		
$A_{juv} \sim P_{ice}$				57.5 [52.6; 62.3]		

S8. Bottom-diving behavior of ringed seals tagged in 2011.

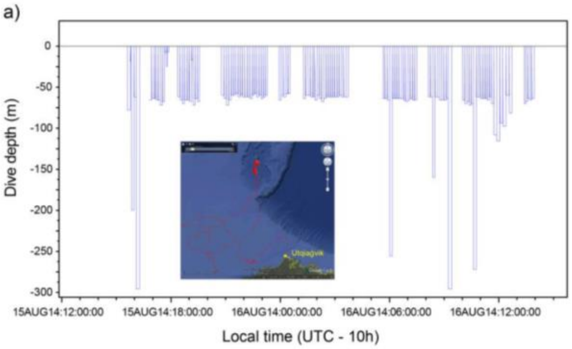
SPLASH tags deployed on ringed seals in 2011 (*n* = 5) provided summarized histogram data containing the number of dives during four 6-hr periods (local time, UTC-10h). We partitioned dive data into days when seals were located where the ocean depths were congruent with the six most commonly visited dive-depth bins, and charted the relative proportion of dives in each depth bin, for each 6-hr period. Numbers in parentheses are the number of dives summarized in the respective chart. Results corroborated that most dives attained depths near the ocean bottom (Fig. 2.5), and that deeper diving was more common during the midday (10:00-16:00) hours (Fig. 2.7).



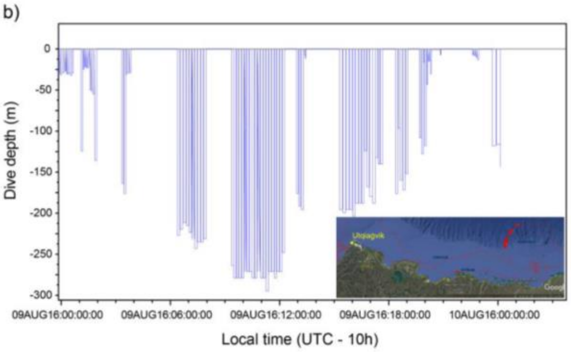
S9. Repetitive-diving examples.

Within the deep-water Arctic Basin, bottom-dives are not possible for ringed seals. However, ringed seals occupying this habitat exhibited long bouts of repetitive-diving behavior (a). The repetitive-diving episodes that appear to be separated by data gaps, may in fact be portions of a single very long repetitive-diving episode. Note the occasional exploratory dives (150 – 300 m deep). Repetitive dives to deeper strata (b) suggest foraging within a new patch were prey have been detected. Map insets show Argos locations (red dots) obtained during the respective period of plotted dive-behavior data. The scatter plot (c) summarizes all repetitive diving episodes recorded during the period when ringed seals occupied the Arctic Basin.

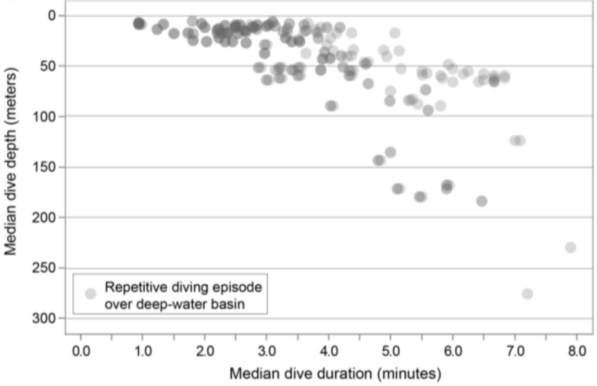
a)



b)



c)



3 A synthesis of top-down, bottom-up, and abiotic effects as they relate to the nutritional status and population dynamics of Isle Royale moose (*Alces alces*)

3.1 Abstract

The influences of nutrition and predation on population dynamics are widely appreciated; yet few studies have simultaneously assessed their joint effect on per capita population growth. We assessed these combined influences on moose in Isle Royale National Park, U.S.A. over a 24 year period (1988-2011). Midwinter nutritional condition, based on urinary urea:creatinine ratios (UN:C), tended to be lower during winters with deeper snows and following warmer summers. These predictors explained 80% of the variation in UN:C. Those climatic variables also interacted such that years with deeper snow, which were also preceded by a warmer summer, resulted in especially poor nutritional condition. Moose in the western region of Isle Royale also showed considerably better nutritional condition than moose in the eastern region. The reasons for this difference remain poorly understood but may relate to spatial variation in the chemical composition of forage. This spatial heterogeneity is notable given the relatively small population size and because it can have an important influence on population stability. Population growth rate was most sensitive to predation rate, but was also influenced by the number of growing-degree-days that had accumulated by Julian day 166 (an index for spring forage abundance). Collectively, these predictors explained 82% of the variation in population growth rate. The influence of climate on nutritional condition differed considerably from its impact on population dynamics. Also, long-term

trends in those various aspects of climate have been inconsistent. Finally, in this moose population, the influence of climate has been quite dynamic, with some aspects being important during some periods but not others. These conditions make it difficult to understand how past climate has affected this population and give reason to prepare for surprises related to the influence of future climate change on ecological systems, despite concerted efforts to anticipate its effects.

3.2 Introduction

Numerous studies characterize population dynamics in terms of top-down, bottom-up, and abiotic influences (e.g., Vucetich and Peterson 2004a, Pierce et al. 2012, Proffitt et al. 2014). Because these forces work in concert, many investigations seek integrated analytical approaches that simultaneously quantify their relative strengths and patterns (Leibold 1989, Hunter and Price 1992, Matson and Hunter 1992, Menge 1992). Due to complex interactions, these analyses are difficult and vulnerable to misinterpretation. For example, predation (top-down) exerts a sizable effect upon ungulate prey populations, occurs at varying scales, and operates both directly and indirectly (Mech et al. 1987, Ferguson et al. 1988, Gasaway et al. 1992, Messier 1995, Kotler et al. 1994). Because prey face tradeoffs between nutrition and safety (Brown et al. 1999, Kie 1999, Brown and Kotler 2004, Hamel and Côté 2007), antipredator behavior, such as modified habitat selection, may come at a nutritional cost (Edwards 1983, Barnier et al. 2014). Previous research indicates that predation risk can impose nutritional costs (Christianson and Creel 2010). This can have implications for population dynamics (Cameron et al. 1993) because ungulate life-history and nutritional status are tightly linked (Cook et al. 2004, Testa 2004, Parker et al. 2009). For example, the reduced nutritional status of prey due to non-consumptive predator effects (i.e. ‘fear’) can negatively influence pregnancy and recruitment rates (Festa-Bianchet et al. 1998); which, in turn, may be misinterpreted as bottom-up regulation (Banks et al. 1999, Creel and Christianson 2008). In systems with high predation (e.g. low neonatal survival), top-down effects can alleviate the energetic burden of lactation, thereby facilitating an increase in the rate of fat accretion and the probability of pregnancy (Cook et al. 2004). Therefore, pregnancy rates may be elevated, not as a result of greater forage abundance and/or quality (bottom-up), but, paradoxically, from top-down forces; which facilitate the elevated nutritional status that results from reduced maternal investment. Alternatively, the abundance and quality of vegetation (bottom-up) can directly influence herbivore populations as a source of nutrition, or through indirect effects which temper the influence of predation by providing cover (Gratton and Denno 2003). Moreover, spatio-temporal variation of plant phenology, abundance, and quality (Fryxell 1991) can have population level consequences if they influence productivity and/or predation risk. In this case, bottom-up effects, insomuch as they provide nutritional benefits, may be incorrectly interpreted as regulating factors when, in fact, predation (top-down) is being mitigated.

The complexities among these interactions all have a nutritional component in common, and, although it is clearly understood that nutritional processes influence population dynamics (Oedekoven and Joern 2000, Hopcraft et al. 2010, McArt et al. 2009), the nature of these relationships is not often straightforward (Crête and Courtois 1997, Peckarsky et al. 2008). It has been recognized that a better understanding of the nutritional status of a population may be useful for correctly interpreting potentially counterintuitive observations from predator-prey interactions (Brown 2007). Moreover, the prospect of climate change creates considerable interest in furthering our understanding of the connections among climate, nutrition, and population dynamics, especially for heat-sensitive species like moose (*Alces alces*). In particular, there would be value in discerning whether nutrition is more influenced by top-down factors, such as risk-sensitive foraging in response to predation risk; bottom-up factors, such as density dependent food limitation; or by abiotic factors, such as drought and winter severity.

When possible, the influence of spatial heterogeneity should also be considered (Hunter and Price 1992, Hopcraft et al. 2010) as this can alter the costs of foraging and predator-prey encounter rates (Skogland 1991), thereby shifting the importance of relevant factors. A comparison of these findings with the simultaneous assessment of factors that are important to population growth will facilitate a more nuanced understanding of population ecology which can disentangle misinterpretations that may result from unaccounted-for nutritionally mediated effects.

To address these questions, we quantified the nutritional status of a free ranging moose population via the analysis of their urinary metabolites. The relative proportions of these metabolites, particularly urea and creatinine, can be used to deduce the nutritional status of many herbivores living in northern temperate and boreal environments (DelGiudice et al. 2001). For urine samples collected throughout the early winter, low and declining ratios of urea and creatinine (UN:C) correspond to the onset of progressive malnutrition, as individuals physiologically recycle nitrogen (Robbins et al. 1974, Barboza and Parker 2006). As the winter progresses, UN:C ratios eventually stop declining and subsequently increase as the rate of net protein catabolism climbs relative to the rate of nitrogen recycling (Moen and DelGiudice 1997). In this case, higher values of UN:C measured during midwinter reflect the reduced nutritional status and increased physical deterioration of a population. As such, monitoring the urinary metabolites of a population during the winter period when UN:C ratios tend not to decline would provide a useful index of a population's nutritional status.

We rely upon a 27-year time series (1988-2014) of UN:C observations from moose living in Isle Royale National Park to assess how interannual fluctuations in UN:C are influenced by top-down, bottom-up, and abiotic factors. Given the importance of habitat quality to the fitness of ungulates (Searle et al. 2010) and the spatially heterogeneous landscape of Isle Royale (see *Study System*), we also assess how the nutritional status of this population varies over a relatively small spatial scale. Finally, we assess how interannual variability in the per capita growth rate (r_t) of this population is influenced by the same set of top-down, bottom-up, and abiotic factors, along with their nutritional status.

3.3 Methods

Study System

Our investigation occurred within Isle Royale National Park (544 km^2), an island located in northwestern Lake Superior (47°55'N, 89°W; Fig. 3.1) that is inhabited by a population of moose whose dynamics are believed to be primarily influenced by wolf predation, forage availability, and climate (Vucetich and Peterson 2004a). No hunting or logging is permitted on Isle Royale. During the study period, moose population density fluctuated between 0.7 and 4.4 moose/km^2 (interquartile range = [1.29, 2.37]), and predation rates fluctuated between 0.02 and 0.24 (interquartile range = [0.05, 0.12]). Isle Royale's forest communities are characterized by considerable spatial heterogeneity, which varies along an east-west gradient. The eastern region is dominated by balsam fir (*Abies balsamifera*) and white spruce (*Picea glauca*). The western region is characterized by a more diverse forest community, including balsam fir, white spruce, white cedar (*Thuja occidentalis*), yellow birch (*Betula alleghaniensis*), quaking aspen (*Populus tremuloides*) and sugar maple (*Acer saccharum*). Separating these two forests is a large region – approximately one fourth of the island's area – that burned during a severe fire in 1936 and which is dominated by tall mature stands of white birch (*Betula papyrifera*) and white spruce (*Picea glauca*) (Fig. 3.1). The foraging ecology of Isle Royale moose is also characterized by considerable spatial heterogeneity. In particular, balsam fir, which is the dominant winter forage for Isle Royale moose, is characterized by higher stem densities and larger bite sizes on the east end of the island (Brandner et al. 1990). Cedar, which has fewer kcal/g and is lower in nitrogen concentration (Risenhoover 1987), is more common in the diet of moose from western Isle Royale (Fig. 3.2). Aquatic vegetation, which is relatively high quality forage (Tischler 2004), is less abundant in the western region of Isle Royale. Finally, moose population density in an average year throughout the study period was approximately 65% greater in the eastern region (Vucetich and Peterson 2004b).

Basic Statistical Approach

We built and assessed several sets of regression models to assess the relative influence that top-down, bottom-up, and abiotic covariates have upon the interannual variability of moose nutritional status and per capita population growth rate. The first set of models was built to evaluate the relative influence of top-down, bottom-up, and abiotic factors on nutritional status at a population level scale. This set of models took its response variable to be annual estimates of the median value of UN:C (hereafter UNC_t). The median value for UN:C was selected because, although severe malnutrition during mid-winter is characterized by UN:C ≥ 3.5, it is not uncommon for UN:C to be an order of magnitude greater in highly nutritionally stressed animals (DelGiudice et al. 1991). The use of the median UN:C prevented samples with extremely high values from having undue influence. The second set of models had a similar aim, but also considered the influence of spatial heterogeneity, and so took its response variable to be spatially explicit annual estimates of median UN:C (hereafter $UNC_{t.reg}$). The third set of regression models aimed to evaluate the relative influence that top-down, bottom-up, and abiotic covariates have upon the interannual variability of moose population growth. This set of models took its response variable to be annual per capita population growth rate [$r_t = (N_{t+1} - N_t)/N_t$, where N_t is moose abundance].

We used the ‘step’ function (stepwise regression) in R Statistical Software (R Core Team 2016) to build models assessing main effects. We also considered several models that included interaction terms. Model performance was judged on the basis of R^2, p-values, and AIC_C (Burnham and Anderson 2002). Because automated procedures can sometimes fail to build models representing hypotheses that ought to be inspected, we evaluated several models that were not identified by the stepwise procedure.

Data Collection and Preparation

To document the annual nutritional status of Isle Royale moose throughout the 27-year study period (1988-2014), we annually collected, on average, 74 samples (interquartile range = [50, 92]) of moose urine deposited in snow. Samples were collected from mid-January to late February. Snowfall records indicate that most samples were collected within two days of deposition. We collected samples from two areas (‘east’ and ‘west’, see Fig. 3.1), each about 60 km^2 in size. Together these areas represent approximately 20% of Isle Royale’s total area, where approximately 40% of the island’s moose population lives (Vucetich ad Peterson 2004b).

We located samples by following moose tracks in the snow. To minimize the frequency of re-sampling the same moose multiple times, we abandoned trails after collecting a sample and searched for a new set of tracks to follow. When present, we collected fecal pellets that were deposited in the same tracks from which we had collected the urine samples. DNA analyses (13 microsatellite loci and sex chromosomes) of fecal samples that were paired with urine samples between 2004 and 2010 suggest that we typically collected urine samples from between 40 and 60 different moose each year (Table 3.1).

Each urine sample consisted of about 100 cm^3 of urine-soaked snow. Samples were stored frozen in one gallon plastic zip-seal bags until they could be prepared for long-term storage. Within a few days of collection, the snow in each bag was thawed, thoroughly mixed, and dispensed into 50-mL centrifuge tubes. These samples were kept frozen at -20°C until they could be analyzed by spectrophotometry to measure the concentrations of urea nitrogen (mg/dL) and creatinine (mg/dL). Samples for years 1988-2001 were analyzed at the Minnesota Department of Natural Resources laboratory (Grand Rapids, MN) and for years 2002-2014 at Wolff Laboratories, Inc. (Bloomington, MN). All analyses were conducted using an ABA-100 bichromatic autoanalyzer or an Abbott VP autoanalyzer, followed standardized commercial protocols, and used reagents prepared according to recommendations from the manufacturer (Abbott Laboratories, South Pasadena, CA). See DelGiudice (1995) for additional details. We culled samples with less than 3 mg/dL of urea or less than 0.1 mg/dL of creatinine prior to analysis because reliable laboratory measurements of UN:C depend on sufficient urine concentrations (G. DelGiudice, *pers. comm.*). Samples collected during the same year tended not to decline in UN:C with Julian day (Fig. 3.3), thereby indicating that they were collected late enough into the winter season for UN:C to be a useful index of nutritional restriction (see *Introduction*).

Moose abundance (N_t) was estimated from 1988 to 1996 by a method of cohort analysis similar to that described by Solberg et al. (1999). From 1997 to 2014, moose abundance was estimated by aerial survey, utilizing a stratified design that involves counting moose within 91 plots (1 km^2) from a fixed-wing aircraft (for details, see Peterson and Page 1988). Moose abundance was considered as a predictor because increased density has been shown to be associated with decreased nutritional condition (Stewart et al. 2005).

Two metrics of predation risk were considered as model predictors. Annual wolf abundance (P_t) was documented by means of a fixed-wing aerial census (Peterson and Page 1988). We also considered predation rate [$PR_t = (KR_t \times P_t)/N_t$] where KR (kill rate) is a measure of prey killed per predator per time unit, and P is wolf abundance (For details, see Vucetich et al. 2011). This metric represents the supply of food available to predators.

Mean daily temperatures during the hottest months (Jul – Sep; ST_t) and coldest months of the year (Jan – Feb; WT_t) were obtained from a weather station located in northeastern Minnesota (Western Regional Climate Center, 2014) located about 40 km from the western end of Isle Royale. From that same station, we also obtained estimates of precipitation during the growing season (May – Aug, SP_t).

We obtained station-based measurements of the North Atlantic Oscillation (NAO_t) index from the National Center for Atmospheric Research (Hurrell 1995). NAO is a useful index of winter severity for many ungulate populations including Isle Royale moose (Ottersen et al. 2001, Vucetich & Peterson 2004a).

Mean snow-depth (Jan – Feb; SD_t) was measured on Isle Royale. We considered snow-depth as a predictor because of its relationship with foraging costs (Telfer and Kelsall 1984), wolf predation risk (Peterson 1977), and winter foraging habitat preferences (Montgomery et al. 2013).

We also calculated the cumulative number of growing degree days reached by mid-May (Julian day 166; hereafter GDD_t). This metric relates temperature, habitat quality, and plant developmental phenology. As such, GDD corresponds to the timing of spring “green-up” (Daughtry et al. 1984), the subsequent abundance of high quality spring forage, and may be important to moose nutrition and population dynamics (Herfindal et al. 2006). Growing degree days were calculated for each Julian day by subtracting a base temperature (40°F) from the mean of the daily maximum and minimum temperatures (°F). Maximum temperatures exceeding 86°F were recorded as 86°F and minimum temperatures less than 40°F were recorded as 40°F (McMaster and Wilhelm 1997). Daily maximum and minimum temperature data were obtained from a weather station in Thunder Bay, Ontario, Canada, located about 60 km from the west end of Isle Royale (National Climate Data Center 2015).

3.4 Results

Population-wide Nutrition Models

Of the models produced by the step function, the most parsimonious model explained 80% of the variation in UN:C and included snow depth (SD_t), summer temperature (ST_{t-1}), and summer precipitation (SP_{t-1}) as significant predictors, and winter temperature (WT_t), which was not significant (Model a1 in Table 3.2). Dropping WT_t from model a1 resulted in model a2 (Table 3.2), which was comparable in terms of AIC_C and R^2.

Next, we constructed three models (Table 3.2, models a3, a4, and a5), each of which included the three fixed-effects of model a2 and one interaction term (models a3, a4, and a5 in Table 3.2). Of these models, the most parsimonious model explained slightly more variation in UN:C ($R^2 = 0.82$) and included a significant ($p < 0.01$) interaction between SD_t and SP_{t-1} (Table 3.2, model a4). That model may however be over-parameterized because it also included a non-significant coefficient for $ST_{t\text{-}1}$ (p = 0.29).

We also assessed models with a more specific kind of interaction. It is plausible that the influence of a variable (i.e., slope) is mediated by the value of another variable. This kind of interaction is represented by models with the structure $Y = \beta_1 + \beta_2 \cdot X_1 + \beta_3 \cdot X_1 \cdot X_2$, where the slope for X_1 is a function of X_2 (i.e., $\beta_2 + \beta_3 \cdot X_2$). To assess this kind of interaction, we modified models a3, a4, and a5 to create two different variants for each. One variant dropped the first fixed-effect in the interaction term. The other variant kept the first, but dropped the second fixed-effect in the interaction term. This procedure resulted in six models (models a6 through a11 in Table 3.2). One of these models (Table 3.2, model a7) had a relatively high R^2 (0.80), all significant coefficients, and was the most parsimonious of all the population-wide nutritional status models ($\Delta AIC_C = 0$). This model indicates that the amount of summer precipitation is inversely related to moose nutritional status. It also has an interaction between snow-depth and the mean temperature from the previous summer which suggests that snow-depth is negatively related to moose nutritional status following summers with a mean summer temperature that exceeds about 13° C (Fig. 3.4). Otherwise, snow-depth is associated with decreased UN:C which relates to improved nutritional status.

Finally, in addition to the automated methods employed, we were also interested in a model in which several hypotheses relating to top-down, bottom-up, and abiotic effects were explored. In particular, we constructed a model that included several covariates hypothesized to be important to the nutritional status of ungulates (see Introduction). These predictors included predation rate (PR_t, top-down), moose abundance & growing degree days (N_t & GDD_{t-1}, bottom-up), and snow-depth & mean summer temperature (SD_t & ST_{t-1}, abiotic). Model a12 (Table 3.2, $\Delta AIC_C = 16.57$) had the lowest ranking of all the population-wide nutrition models, and only the abiotic coefficients were statistically significant.

Spatially-explicit Nutrition Models

The population-wide nutritional status models (Table 3.2) analyzed all data regardless of the location from where the samples were collected. However, Isle Royale's forests vary spatially in their community composition and the relative density of forage species (see *Introduction*). To account for the influence of spatial heterogeneity, we modeled nutritional status using a spatially explicit data set. Prior to this analysis, we partitioned the population-wide UN:C data into subsets based on the region from which each sample was collected (see Fig. 3.1). Although this doubled the sample size from 27 to 54 (i.e., $n_{east} = 27 + n_{west} = 27$), each point in the response variable ($UNC_{t.reg}$) was based on approximately half as many UN:C measurements as the population-wide models. We used the previously described predictors along with a spatial indicator variable (*REG*, where 'east' = 0 and 'west' = 1) to characterize the influence that top-down, bottom-up, and abiotic factors have on nutritional status within a spatial context.

As with the population-wide models, we began by using the 'step' function in R to perform a stepwise regression using the full set of candidate variables, along with a regional indicator variable, and all possible interactions with the regional indicator variable. This procedure yielded a model with four significant main effects (WT_t, ST_{t-1}, SD_t, and GDD_{t-1}), a non-significant regional slope term ($REG \cdot GDD_{t-1}$), and a non-significant regional intercept term (*REG*) (Table 3.3, model b1). We assessed three variants of this model in which we retained the main variables from model b1 and systematically dropped the regional slope term, the regional intercept term, and both terms (Table 3.3, models b2-b4). The highest performing of these three models (Table 3.3, model b3) included the interaction between region and growing-degree days. To assess the role of other interaction terms, we started with model b3 and systematically added one interaction to the base model until all six possible interactions (from the original four fixed-effect terms in b3) were included in a separate model (Table 3.3, models b5 through b10). Of the first ten models, model b7 performed the best (and ultimately was the most parsimonious model overall), explaining 64% of the variation in UN:C. We modified this model by replacing the regional interaction term with a regional indicator term (Table 3.3, model b11). We constructed one more model (Table 3.3, model b12) that was identical in form to model a12 (Table 3.1) but used the spatially indexed data. We modified model b12 so that it included a regional indicator variable (Table 3.3, model b13), or a regional interaction with growing degree days (Table 3.3, models b14). As fixed-effects variables, only abiotic variables were significant in any of the spatially indexed nutritional models. The variable for growing degree days, when interacting with the regional indicator variable, was significant and part of the most parsimonious model (Table 3.3, model b7). Models containing top-down or bottom-up effects were among the lowest ranked ($\Delta \mathrm{AIC}_C \geq 14.81$).

Population Models

Prior to our analysis of population growth, we became aware of the presence of three possible statistical outliers in the response variable r_t (Fig. 3.5). One of these (r_{1996} = –0.63) was an extreme ecological event involving the coincidence of the highest ever observed moose density (4.4 moose/km), the most severe winter recorded in the past century, depleted forage, and an epizootic of winter ticks (*Dermacentor albipictus*). The other observations (r_{2007} = 0.69, r_{2011} = 0.45) represent population growth rates of which moose are physiologically incapable and had been identified as estimation errors at the time of observation due to exceptionally poor conditions for conducting aerial surveys of moose (Vucetich and Peterson 2008, 2011). The Generalized Extreme Studentized Deviate test was used to evaluate the presence of multiple outliers (Rosner 1983) and indicated that all three observations were outliers at a significance level of $\alpha = 0.05$ (Table 3.4). Based on this assessment, we culled three years of data (1996, 2007, and 2011) from the data set prior to further analyses of population growth—which improved the distribution of the model residuals (Fig. 3.6).

Because per capita population growth rate [$r_t = (N_{t+1} - N_t)/N_t$] is a function of a population's abundance at two different time periods (N_t and N_{t+1}), it is plausible that a predictor may have relatively more influence in a year associated with N_t or with N_{t+1}. We examined the extent of these differences by comparing the performance of two forms of each variable (subscripts 'a' and 'b', corresponding to N_t and N_{t+1}) in univariate population models (Table 3.5). We found that, in terms of $\mathrm{AIC_C}$, predation rate ($t+1$), summer precipitation (t), and North Atlantic oscillation (t) were better predictors of r_t

than their alternate form. There was no difference in performance of the remaining covariates.

The population analysis characterized which factors are important to per capita growth rate by constructing a series of regression models (Table 3.6) that used the same predictors that were used for the nutritional models (Table 3.3). Altogether, our population models incorporated the culled data set and included both forms of each covariate (each associated with N_t and N_{t+1}) as candidate predictors for all but the final two models of our analyses.

As described for the nutritional status models, our population analysis began with a stepwise regression that included the full set of covariates as candidate predictors. This procedure produced a model (Table 3.6, model c1) that included predation rate (PR_{t+1}) and two time-steps for growing-degree days (GDD_t and GDD_{t-1}) as significant predictors; along with snow depth (SD_{t+1}) and North Atlantic Oscillation (NAO_t) as non-significant predictors. We modified model c1 by dropping the two non-significant variables (Table 3.6, model c2); the resulting model including PR_{t+1}, and two time steps for growing degree days (GDD_t, and GDD_{t-1}). We next built two models that contained PR_{t+1} and one of the two forms of *GDD* (Table 3.6, models c3 and c4). Of these first four models, model c3 performed the best and was ultimately the most parsimonious population model. This model suggests that r_t tends to decline as predation rate increases, and that the rate of decline is offset during years when early season forage quality and abundance (as measured by growing degree days) was greater. Models c1 and c2 (Table 3.6) also were comparable in performance ($\Delta AIC_C < 2$) to model c3. Using the same procedure described above for the *nutritional status* models, we modified model c3 by introducing interaction terms (Table 3.6, models c5 – c7). This process generated a model with all significant coefficients (Table 3.6, model c7), but no models with interaction terms outperformed model c3. Finally, we constructed two additional models (Table 3.6, models c8 and c9) that included the best predictors of r_t (Table 3.5) from within each of four categories: nutritional status (UNC_t and UNC_{t+1}), top-down effects (PR_{t+1}), bottom-up effects (SP_t), and abiotic effects (NAO_t). The predictor for nutritional status at time-step t (UNC_t) was included in model c8 and at time-step $t+1$ in model c9 (Table 3.6) because pairwise comparisons of both time-steps indicated that they were comparable ($\Delta AIC_C < 2$) in their relative influence on r_t (Table 3.5, models $d01_a$ and $d01_b$). Conversely, the remaining three predictors showed clear differences in their relative influence on r_t (Table 3.5, models $d02_b$, $d03_b$, and $d07_a$). Neither model c8 nor c9 outperformed the top population growth models ($\Delta AIC_C = 11.19$, $R^2 = 0.78$).

3.5 Discussion

The nutritional status of moose on Isle Royale is negatively influenced by abiotic and bottom-up effects. Spatial heterogeneity is also a significant predictor, with eastern region moose experiencing comparatively lower nutritional status than moose in the west. In contrast, there is a very strong negative influence of predation – a top-down effect – on the per capita population growth rate, and a small but significant positive influence of growing degree days – a bottom-up effect.

The influence of abiotic predictors may be related to their influence on net energy intake. On a population-wide scale, winters with deeper snows and/or hotter summers were negatively related to nutritional status (Fig. 3.7). And like the population-wide models, abiotic effects (winter temperature, summer temperature, and snow-depth) are important predictors of nutritional status in the spatially indexed nutritional models. Deep snows increase mobility costs (Thompson and Stewart 1997) and may impose indirect metabolic costs due to more predation risk (Post et al. 1999). The mean temperature of the preceding summer interacted with snow-depth such that, when ST_{t-1} > 13°C, increasing snow-depths have a negative influence on nutritional status. When SD_{t-1} < 13°C, the influence of increasing snow-depths was positively associated with nutritional status. It has been observed that summer heat tends to shift the basis of moose habitat selection from meeting nutritional demands to thermoregulation (Schwab and Pit 1991). Moreover, thermoregulatory behavior, such as panting to dissipate heat, is energetically costly and detracts from foraging time (Renecker and Hudson 1986). It seems reasonable that reduced ability to store fat reserves due to summer heat would interact negatively with the increased mobility costs and predation risk associated with deeper snows. Why deeper snows would be positively related to nutritional status following cooler summers seems less obvious. One consideration is that winter temperature is inversely related to nutritional status, and deeper snows may be associated with cooler winter temperatures. This may appear to be counterintuitive, but is consistent with previous research indicating that cold winters are typically not problematic for moose due to their extremely low critical temperature (Renecker and Hudson 1986). Conversely, warm winter temperatures are a problem if they exceed 8° C – the upper critical temperature of moose (Schwab and Pitt 1991), because under such conditions energy must be used to thermoregulate.

There was also a tendency for nutritional status to decline following wetter growing seasons. Plants normally thrive under such conditions, but in doing so, allocate more of their resources to carbon rich structural carbohydrates in order to accommodate rapid growth and competition for sunlight. As such, forage quality should decline as carbon:nitrogen ratios increase. Although documented in grazing systems (Hopcraft et al. 2010), the influence of precipitation on browse quality within forested systems is not well known. What is known is that excessive rainfall can leach soil nitrogen (Kirschbaum et al. 2008) potentially leading to reductions in forage quality.

The influence of spatial heterogeneity was expressed through an interaction with growing degree days. The nature of the relationship suggests that spring forage availability is more important to moose nutritional status in the western region. Furthermore, the nutritional status of moose inhabiting Isle Royale's eastern region tends to be lower (Fig. 3.8; also see DelGiudice et al. 1991a). This spatial effect was unexpected because balsam fir, the dominant winter forage for Isle Royale moose (McLaren and Peterson 1995), is much more abundant in the eastern region (see *Study System*). In terms of caloric density (kcal/g), balsam fir is superior to all other available forage species on Isle Royale (Risenhoover 1987). Higher quality soils within Isle Royale's western region (USDA 2012) may be at least partially responsible for this spatial variation in nutritional status. For example, the nitrogen concentration of balsam fir is greater in the western portion of Isle Royale (J.A. Vucetich, *pers. comm.*).

Another important consideration is the relative concentration and types of plant secondary metabolites (PSM) present in an herbivore's diet. For example, moose consume a more diverse diet in the western region that includes a larger proportion of deciduous species (Fig. 3.2). As a result, moose in the western region may ingest a greater variety of PSMs but in lower relative quantities. This is important because it has been suggested that a dietary constraint in herbivores involves balancing their rate of forage intake with the rate at which they detoxify their food (Robbins et al. 1987, Iason and Villalba 2006). Herbivores should benefit by optimally consuming a diverse diet that can be detoxified via multiple metabolic pathways (Marsh et al. 2006). This strategy is more effective in maximizing caloric intake because it eliminates the forager's need to reduce dietary intake until its liver has sufficiently detoxified its most recent meal (Robbins et al. 2007). Spatio-temporal variation in regional nutrition was also observed. The low correlation in UN:C measurements between the two regions (Fig. 3.9) suggests that different ecological processes are simultaneously operating at opposite ends of Isle Royale. Given the small spatial scale and very high moose density (~ 1.8 moose/km^2 on average), this variability is important with respect to the potential population stabilizing influences of spatial heterogeneity (Roff 1974, Steele 1974, Stenseth 1980). Further inquiry into the role of PSMs, dietary diversity, and spatio-temporal variation on Isle Royale would further enhance the understanding of foraging constraints (Stephens and Krebs 1986) and energetics, and would inform a more nuanced interpretation of vital rates as they pertain to population dynamics.

Per capita population growth rate, unlike nutritional status, is not influenced by abiotic effects. Though it is positively influenced to a small but significant degree by growing degree days (bottom-up), predation rate (top-down) is the primary driver and exerts a negative effect on per capita growth. There is reason to hypothesize that the substantial influence of predation rate upon per capita growth (82.9% of the total explained variance; see Fig. 3.10) can overshadow the influence of other factors, and therefore deserves further attention.

For example, nutrition is known to influence components of population growth rate, such as overwinter survival and birth weight (Cameron et al. 1993, Parker et al. 2009). If predation disproportionately removes malnourished individuals from the population (Husseman et al. 2003), then this should result in an increase to that population’s overall nutritional condition. In other words, the influence of abiotic factors on population growth (via nutritionally mediated effects) may appear to be moderated or absent altogether in the presence of high predation pressure. Furthermore, if predation rate is associated with the nutritional status of a prey population, then the population level consequences of nutrition may be mitigated by the tendency for predation to be additive within populations on a high nutritional plane, and compensatory when they are not (see also Garrott et al. 2009). Similarly, the numerical reduction of a prey population via predation should reduce intraspecific competition, thereby explaining, in part, the absence of density dependent effects (e.g. moose abundance) from our population models.

The small positive influence of growing degree days on per capita population growth rate is likely related to plant phenology, the timing of forage availability, and the importance of early season, high quality forage to post-parturient cow moose that have gestated over the course of a harsh, protracted winter. Already in a very low nutritional state, these cows must meet the even more energetically demanding costs of lactation (Clutton-Brock et al. 1989). Given these energetic demands, delays in the availability of spring forage can lead to lower calf weights and/or growth rates to the detriment of calf survival and recruitment (Cameron et al. 1993, Brown 2011).

Our results differ from previous analyses of Isle Royale moose in two ways. First, population growth rate was previously found to be unrelated to NAO during the period 1959-1980 and positively related to NAO during 1980-1998 (Wilmers et al. 2006). By contrast, we failed to detect an influence of NAO in the most parsimonious per capita population growth models for the period 1988-2014. Second, an earlier analysis indicated that the population growth rate between 1958 and 1998 had a weak tendency to be greater during years with cooler springs (April and May; Vucetich et al. 2004a). Yet, in the present study we found moose population growth rate to be positively related to growing degree days for the period 1988-2014, even though spring temperature and GDD are well correlated ($r = 0.91$, $p = 10^{-11}$). As previously noted, growing degree days were not an important predictor of moose nutritional status in the eastern portion of Isle Royale. Whether this has implications for spatial variation in moose reproduction is not known because our population data did not distinguish between the regions on Isle Royale. Spatially referenced documentation of moose productivity will help to address these questions.

A potentially important cause of these differences likely involves the distinct time periods covered by each analysis. In particular, the overlap in time between this analysis and the second half of the Wilmers et al. (2006) analysis is only about 50%. Temporal variation in the strength of various processes may be a general feature of ecological systems; it certainly seems to characterize the Isle Royale ecosystem (Wilmers et al. 2006, Bump et al. 2009). These differences may also be attributed to the statistical significance of a predictor variable being influenced by the presence or absence of other predictors in a model. In this study, predation was represented by predation rate (PR), which by itself accounted for ~83% of the explained variation in population growth ($R^2 = 0.82$; see Fig. 3.10). However, in previous analyses of this system predation had been represented by wolf abundance (P) and accounted for less than 11% of the explained variation in population growth (Vucetich and Peterson 2004a, Wilmers et al. 2006). Given that predation rate exerts a great deal of influence upon per capita growth rate, it is plausible that predictors associated with climate and/or nutrition would fail to appear in the most parsimonious population models if their influence on per capita growth rate is primarily manifested through predation (i.e., prey in low nutritional condition are more vulnerable to predation). The observed switch from top-down to bottom-up regulation of moose following a disease outbreak in wolves on Isle Royale (Wilmers at al. 2006) lends support to this statement. Careful documentation of ecological change on Isle Royale in response to the near extinction of wolves (Vucetich and Peterson 2014) will further refine understanding in this area, as will documentation of the effect of introduced wolves should this become necessary.

An analysis of moose living in nearby Minnesota found that an index of heat stress in spring was not associated with annual survival during a six-year period, 2002-2008 (Lenarz et al. 2009). The same analysis also found that annual survival is inversely associated with an index of heat stress in January. Our results were similar in the inverse relationship between winter temperature and nutritional condition, but differed insomuch as we detected a positive effect of growing degree days on population growth rate (Table 3.3a). Several explanations may account for these differences. First, climate effects could be mediated by biotic conditions that differ between the two sites (Forcada et al. 2006). Our spatially indexed nutrition models clearly indicate that there are differences on a small scale (i.e., Isle Royale) that have implications for nutritional status. On a larger scale (i.e., NE Minnesota), Minnesota moose experience lower rates of predation than Isle Royale moose and, unlike Isle Royale moose, are also exposed to parasites associated with white-tailed deer (*Odocoileus virginianus*) (Murray et al. 2006). Second, the influence of a process can be related to the duration of the observation period (Vucetich et al. 2010) and time period of the analysis (Wilmers et al. 2006). Third, climate may affect survival differently than it does population growth rate, particularly given that Isle Royale's climate is affected by the moderating influences of Lake Superior and the climate in NE Minnesota is not. For example, if spring temperatures on Isle Royale are cooler than in Minnesota, then, according to our nutritional models, less spring forage should be available to Isle Royale moose. Such variation in spring forage availability, through its influence on cows with neonates, would likely have population consequences. Further complexity is revealed by observing that growing degree days are positively related to population growth, but summer temperatures are not. Years with more growing degree days and warmer spring temperatures have not been associated with warmer summers on Isle Royale ($p = 0.12$ for growing degree days and $p = 0.55$ for spring temperatures). Finally, while winter temperatures and growing degree days on Isle Royale have been increasing throughout the past five decades (p's < 0.04), spring and summer temperatures have not (p's > 0.44). These considerations highlight some of the challenges to understanding the relationship between climate and population dynamics.

Nutrition integrates ecological, physiological, and evolutionary constraints (Stephens and Krebs 1986, Parker et al. 2009, Raubenheimer et al. 2009), and can have profound population consequences. Adult survival and long-term population viability in moose depends upon winter fat reserves (Lenarz et al. 2010). Summer foraging performance is vital to the timing of estrus in capital breeders (Flueck 1994, Jönsson 1997, Cook et al. 2004) such as moose. Nutritionally mediated maternal effects can delay parturition, reduce birth-weight, lower twinning-rates (Keech et al. 2000), and can incur cohort effects with long-term demographic consequences (Forchhammer et al. 2001, Solberg et al. 2007). This should not be a surprise, because of the linkages between the timing of a critical nutritional need (early spring) and a demographic segment that is essential to population growth (cows with calves).

Given the importance of abiotic factors to nutritional status, our investigation has implications for managing moose and other heat sensitive species in a time of climate warming. By the year 2039 mean summer and winter temperatures are expected to increase by more than 3° C in the southernmost extent of moose range (Galatowitsch et al. 2009). As such, moose will experience temperatures in excess of their upper critical threshold more often, and the nutritional consequences may feed back into population dynamics. Such disruptions may also cause the southern range limit of moose to drift north (Humphries et al. 2004). Recent population declines in northern Minnesota moose (Murray et al. 2006, Lenarz et al. 2010) suggest that this process may already be occurring (Parmesan and Yohe 2003). Preparing for unpredictability in ecological systems due to climate warming is one of many challenges faced by managers tasked with conserving declining populations of heat sensitive species. Part of this preparation will require a careful synthesis of climate, nutrition, and population dynamics as the basis for understanding the population level implications of climate change.

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3.8 Tables

Table 3.1. Number of UN:C samples collected from unique moose (2004-2010). The number of unique individuals was determined via the analysis of fecal DNA at 13 microsatellite loci and markers on the sex chromosomes. This determination was possible because most snow urine samples collected between 2004 and 2010 were also paired with fecal pellets that had been deposited alongside in the same snow tracks where the urine had been sampled. The average ratio among years is 0.68. That ratio is an indicator of the number of unique individuals that one can expect to have sampled, given the number of UN:C samples collected during a year for which DNA analysis had not been possible. Though urine samples were collected from 1988-2014, during 2005-06 logistical limitations restricted our ability to uniquely identify the individual moose associated with each sample collected during these two periods of time. The most recent year for which DNA has been analyzed is 2010.

Year	UN:C samples (n_a)	Unique individuals (n_b)	Ratio (n_a:n_b)
2004	N	15	– 16.35
2007	N_t	7	– 42.66
2008	N_t	13	– 16.88
2009	$\boldsymbol{N_t}$	**11**	**– 20.35**
2010	N_t	19	– 15.90

Table 3.2. Nutritional status models (population-wide). The response variable is the median ratio of urea-nitrogen and creatinine (UNC_t). Models were run using a non-spatial data set (n = 27) that did not consider the geographic location on Isle Royale where each sample was collected. As such, the models represent factors that are important to the entire population of moose on Isle Royale. Models are presented in the order in which they were created and as described in the Methods section. Stacked variables indicate interaction terms. The most parsimonious model is shown in bold. Models a9, a8, and a4 ($\Delta AIC_C \leq 1.83$) are comparable in performance to model a7. However, all three of these models also contained coefficients that were not statistically significant.

					Estimated Coefficient									
ID	AIC_C	ΔAIC_C	R^2	Y-int.	SD_t	ST_{t-1}	SP_{t-1}	WT_t	GDD_{t-1}	N_t	PR_t	SD_t ST_{t-1}	SD_t SP_{t-1}	ST_{t-1} SP_{t-1}
a1	9.88	4.46	0.80	− 4.44	0.015*	0.310*	0.021*	– 0.036	--	--	--	--	--	--
a2	10.19	4.78	0.77	– 4.18	0.018*	0.304*	0.024*	--	--	--	--	--	--	--
a3	8.40	2.99	0.81	2.52	– 0.144†	– 0.108	0.023*	--	--	--	--	0.010*	--	--
a4	7.25	1.83	0.82	– 1.95	0.034	0.291*	– 0.028	--	--	--	--	--	0.001*	--
a5	12.95	7.54	0.77	1.05	0.018*	– 0.163	– 0.111	--	--	--	--	--	--	0.008
a6	9.18	3.77	0.78	– 3.43	--	0.258*	0.024*	--	--	--	--	0.001*	--	--
a7	**5.41**	**0.00**	**0.80**	**0.76**	**– 0.105***	--	**0.024***	--	**--**	--	**--**	**0.008***	--	--
a8	6.71	1.30	0.80	– 3.42	--	0.301*	0.006	--	--	--	--	--	0.0005*	--
a9	5.72	0.30	0.80	– 3.15	– 0.008	0.298*	--	--	--	--	--	--	0.0007*	--
a10	9.61	4.20	0.77	0.78	0.018*	--	– 0.104*	--	--	--	--	--	--	0.008*
a11	10.00	4.59	0.77	– 3.24	0.018*	0.246*	--	--	--	--	--	--	--	0.002*
a12	21.99	16.57	0.72	– 3.00	0.020*	0.266*	--	--	$6.3e^{-4}$	-6.5^{-5}	– 1.989†	--	--	--

Significance codes: * ≤ 0.05 † ≤ 0.10

Table 3.3. Nutritional status models (spatial). The response variable is the spatially indexed median ratio of urea-nitrogen and creatinine ($UNC_{t.reg}$). Models were run using a spatially indexed data set (n = 54) that considered the geographic location on Isle Royale where each sample was collected. Models with *REG* as a fixed-effect or in an interaction suggest that spatial heterogeneity is an influential factor for the nutritional status of moose on Isle Royale. Models are presented in the order in which they were created and as described in the Methods section. Stacked variables indicate interaction terms. The most parsimonious model is shown in bold. Model b11 (ΔAIC_C = 0.21) is comparable in performance to model b7. These two models, while somewhat different in form, include the same covariates and suggest the important influence that abiotic effects and spatial heterogeneity have on UN:C.

					Estimated Coefficient														
ID	AIC_C	ΔAIC_C	R^2	Y-int.	WT_t	ST_{t-1}	SD_t	GDD_{t-1}	N_t	PR_t	*REG*	*REG* GDD_{t-1}	WT_t ST_{t-1}	WT_t SD_t	WT_{t-1} GDD_{t-1}	ST_{t-1} SD_t	ST_{t-1} GDD_{t-1}	SD_t GDD_{t-1}
b1	88.73	6.09	0.59	– 3.77	– 0.074*	0.243*	0.014*	0.001*	--	--	– 0.170	– 0.001	--	--	--	--	--	--
b2	86.47	3.83	0.59	– 3.49	– 0.073*	0.238*	0.014*	0.001*	--	--	– 0.672*	--	--	--	--	--	--	--
b3	86.02	3.38	0.59	– 3.87	– 0.074*	0.245*	0.014*	0.001*	--	--	--	– 0.001*	--	--	--	--	--	--
b4	108.65	26.01	0.35	– 4.11	– 0.069*	0.269*	0.014*	0.001	--	--	--	--	--	--	--	--	--	--
b5	87.63	4.99	0.60	3.29	0.465	– 0.194	0.013*	0.001*	--	--	--	– 0.001*	– 0.033	--	--	--	--	--
b6	87.80	5.16	0.60	– 5.10	– 0.145†	0.271*	0.034	0.001*	--	--	--	– 0.001*	--	0.001	--	--	--	--
b7	**82.64**	**0.00**	**0.64**	**0.23**	**0.258†**	**0.292***	**0.013***	**– 0.005†**	**--**	**--**	**--**	**– 0.001***	**--**	**--**	**– 1.8e^{-4}***	**--**	**--**	**--**
b8	87.68	5.04	0.60	0.73	– 0.070*	– 0.037	– 0.097	0.001*	--	--	--	– 0.001*	--	--	--	0.007	--	--
b9	88.74	6.10	0.59	– 6.18	– 0.074*	0.387	0.014*	0.004	--	--	--	– 0.001*	--	--	--	--	– 1.8e^{-4}*	--
b10	87.09	4.45	0.61	– 2.56	– 0.085*	0.276*	– 0.023	– 9.3e^{-4}	--	--	--	– 7.8e^{-4}*	--	--	--	--	--	4.4e^{-5}
b11	82.86	0.21	0.64	0.71	0.267†	0.286*	0.014*	– 0.005†	--	--	– 0.682*	--	--	--	– 4.4e^{-4}*	--	--	--
b12	114.11	31.47	0.28	– 2.81	--	0.290*	0.017*	--	– 3.5e^{-5}	– 1.270	--	--	--	--	--	--	--	--
b13	97.45	14.81	0.50	– 2.67	--	0.290*	0.017*	--	5.9e^{-5}	– 0.271	– 0.645*	--	--	--	--	--	--	--
b14	99.73	17.08	0.48	– 3.02	--	0.311*	0.016*	--	7.0e^{-5}	– 0.233	--	– 7.0e^{-4}*	--	--	--	--	--	--

Significance codes: * ≤ 0.05 † ≤ 0.10

Table 3.4. Generalized Extreme Studentized Deviate Test results for multiple outliers in the bivariate model $r_t = f\,(PR_t + GDD_{t-1})$. At $\alpha = 0.05$, the results from the Generalized Extreme Studentized Deviate test for multiple outliers (Rosner 1983) provided further evidence that the three suspicious observations (1996, 2007, and 2011) are statistical outliers. Wilmers et al. (2006) recognized that 1996 represented an extreme ecological event and opted to omit this observation from their analyses.

Year	Test statistic	Critical value
2007*	2.814522	2.801551
1996*	3.353898	2.780277
2011*	3.096119	2.757735
2010	2.459152	2.733780
2002	1.632164	2.708246

Table 3.5. Comparison of univariate population growth models over two time spans. Given that $r_t = (N_{t+1} – N_t)/N_t$, the rate of per capita population growth is a function of population size (N) at times t and $t+1$. Pairwise comparisons of univariate model performance for both forms of each variable (model subscripts 'a' and 'b', associated with N_t and N_{t+1}, respectively) identified three variables (bold text) that are better predictors of r_t (i.e. $\Delta AIC_C > 2$). The remaining variables (plain text) are comparable in performance ($\Delta AIC_C < 2$).

							Estimated Coefficient							
ID	Time Step	rank	AIC_C	ΔAIC_C	R^2	Y-int.	UNC_t UNC_{t+1}	PR_t PR_{t+1}	SP_{t-1} SP_t	GDD_{t-1} GDD_t	SD_t SD_{t+1}	WT_t WT_{t+1}	NAO_t NAO_{t+1}	ST_{t-1} ST_t
d1$_a$	N_t	15	– 16.35	37.21	0.03	– 0.100	0.054	--	--	--	--	--	--	--
d1$_b^{i}$	N_{t+1}	14	– 16.50	37.06	0.03	– 0.115	0.061	--	--	--	--	--	--	--
d2$_a$	N_t	7	– 42.66	10.90	0.68	0.207	--	– 2.035*	--	--	--	--	--	--
d2$_b^{ii}$	**N_{t+1}**	6	– 49.89	3.67	**0.76**	**0.206**	--	**– 1.956***	--	--	--	--	--	--
d3$_a$	N_t	13	– 16.88	36.68	0.05	– 0.147	--	--	0.005	--	--	--	--	--
d3$_b^{iii}$	**N_{t+1}**	**10**	**– 24.70**	**28.86**	**0.31**	**– 0.451**	--	--	**0.013***	--	--	--	--	--
d4$_a$	N_t	16	– 16.33	37.23	0.03	0.185	--	--	--	– 1.8e^{-4}	--	--	--	--
d4$_b$	N_{t+1}	21	– 15.82	37.74	0.01	– 0.033	--	--	--	7.8e^{-5}	--	--	--	--
d5$_a$	N_t	17	– 16.06	37.50	0.02	– 0.023	--	--	--	--	0.001	--	--	--
d5$_b$	N_{t+1}	23	– 15.77	37.79	0.01	0.006	--	--	--	--	5.5e^{-4}	--	--	--
d6$_a$	N_t	22	– 15.80	37.76	0.01	– 0.018	--	--	--	--	--	– 0.004	--	--
d6$_b$	N_{t+1}	12	– 17.32	36.24	0.07	– 0.133	--	--	--	--	--	– 0.012	--	--
d7$_a^{iv}$	**N_t**	**11**	**– 20.35**	**33.21**	**0.18**	**0.002**	--	--	--	--	--	--	**0.025***	--
d7$_b$	N_{t+1}	18	– 16.02	37.54	0.02	0.026	--	--	--	--	--	--	0.007	--
d8$_a$	N_t	19	– 15.90	37.66	0.01	0.328	--	--	--	--	--	--	--	– 0.018
d8$_b$	N_{t+1}	20	– 15.89	37.67	0.01	0.339	--	--	--	--	--	--	--	– 0.019

Significance codes: * ≤ 0.05 † ≤ 0.10

[i] best nutritional status univariate model
[ii] best top-down univariate model
[iii] best bottom-up univariate model
[iv] best abiotic univariate model

Table 3.6. Population growth models. The response variable is the per capita rate of population growth (r_t). Population data were not spatially referenced. As such, models represent population growth on a population-wide scale. Stacked variables indicate interaction terms. The most parsimonious model is shown in bold. Model c1 (ΔAIC_C = 0.20) was similar to model c3 (ΔAIC_C = 0), but also included covariates relating to winter severity.

					Estimated Coefficient								
ID	AIC_C	ΔAIC_C	R^2	Y-int.	UNC_t	UNC_{t+1}	PR_{t+1}	SP_t	GDD_t	GDD_{t-1}	SD_{t+1}	NAO_t	PR_{t+1} GDD_t
c1	– 53.36	0.20	0.88	0.05	--	--	– 1.897*	--	$3.2e^{-4}$*	– $2.2e^{-4}$*	0.001†	0.010†	--
c2	– 52.70	0.86	0.83	0.14	--	--	– 2.039*	--	$2.4e^{-4}$*	– $1.5e^{-4}$	--	--	--
c3	**– 53.56**	**0.00**	**0.82**	**0.03**	--	--	**– 2.052***	--	**$2.3e^{-4}$***	--	--	--	--
c4	– 48.43	5.13	0.77	0.31	--	--	– 1.941*	--	--	– $1.3e^{-4}$	--	--	--
c5	– 50.33	3.23	0.82	0.025	--	--	– 2.054	--	$2.3e^{-4}$	--	--	--	$1.8e^{-6}$
c6	– 51.28	2.28	0.80	0.203	--	--	– 3.402*	--	--	--	--	--	0.002†
c7	– 50.29	3.27	0.79	– 1.151	--	--	--	--	$4.5e^{-4}$*	--	--	--	– 0.003*
c8	– 42.37	11.19	0.78	0.031	0.009	--	– 1.688*	0.003	--	--	--	0.006	--
c9	– 42.30	11.26	0.78	0.057	--	– $8.4e^{-5}$	– 1.702*	0.003	--	--	--	0.006	--

Significance codes: * ≤ 0.05 † ≤ 0.10

3.9 Figures

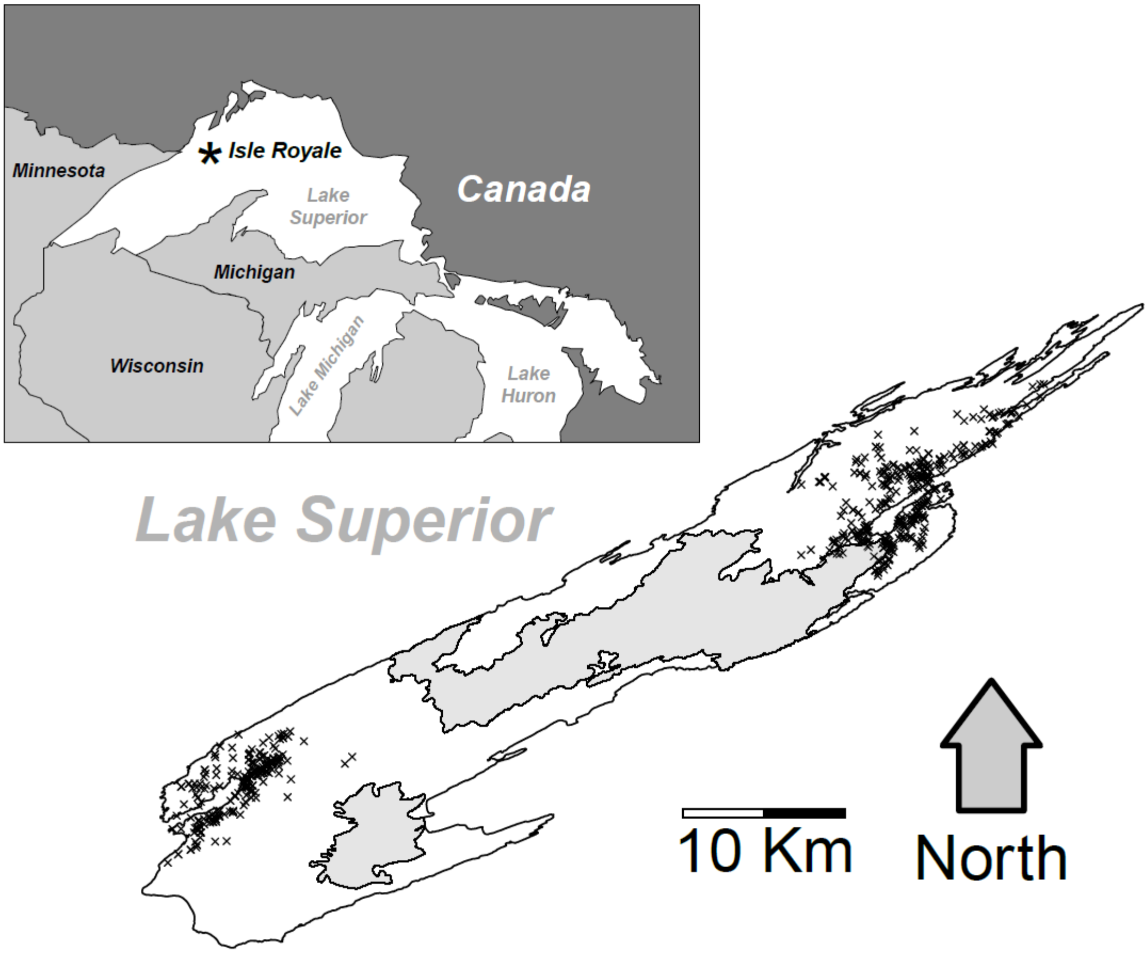

Figure 3.1. Snow-urine sampling locations (2009-14). Snow-urine sampling locations are designated by an 'x' (*n* = 597). An additional 1,374 samples were collected in 1988-2008. Those earlier samples were collected from the same two regions and the region (east or west) was recorded, but not the precise location. The shaded areas indicate the extent of a large forest fire that occurred in 1936 and now separates the eastern from the western regions of Isle Royale. These two regions are characterized by different forest community types (see Study System).

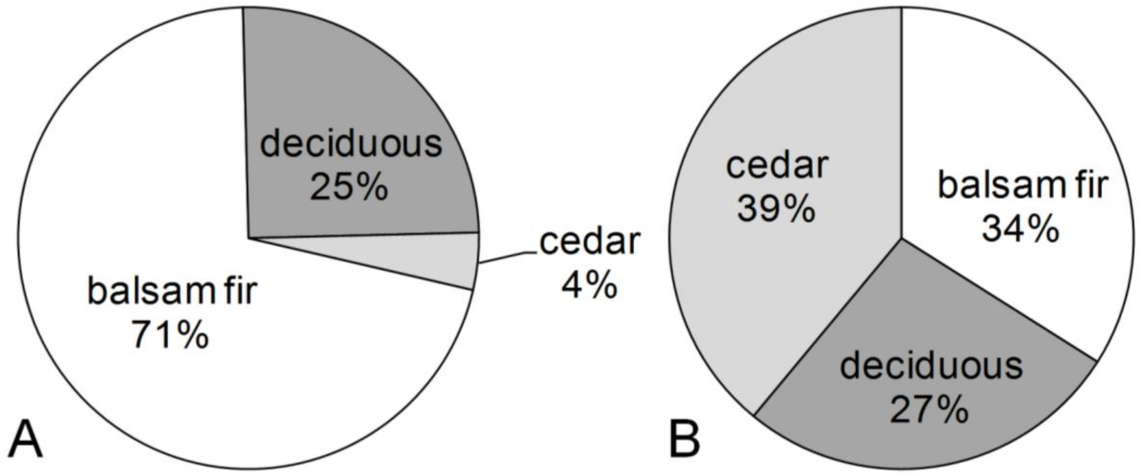

Figure 3.2. Regional differences in moose forage intake. To assess differences in diet for moose living on the eastern and western regions of Isle Royale, we used fecal microhistological analysis (Holechek and Gross 1982). Each year between 2004 and 2007, we collected five pellets from each of three pellet piles at ten different sites (five from each region of Isle Royale). That sampling effort results in 30 samples each year. Samples were collected dried and then prepared according to methods described in Sparks and Malechek (1968). One hundred fragments from each of the 30 samples were identified using a light microscope (100x magnification). Identification was based on the presence or absence of stomata and their morphological appearance. Our accuracy in making such identification for each category was >90%, and that accuracy rate was based on testing ourselves with a reference collection of known samples. These observations demonstrated that winter diet composition of eastern region moose (A) is significantly different ($X^2 = 1827.367$, df = 3, p-value $< 10^{-16}$) than the winter diet of western region moose (B).

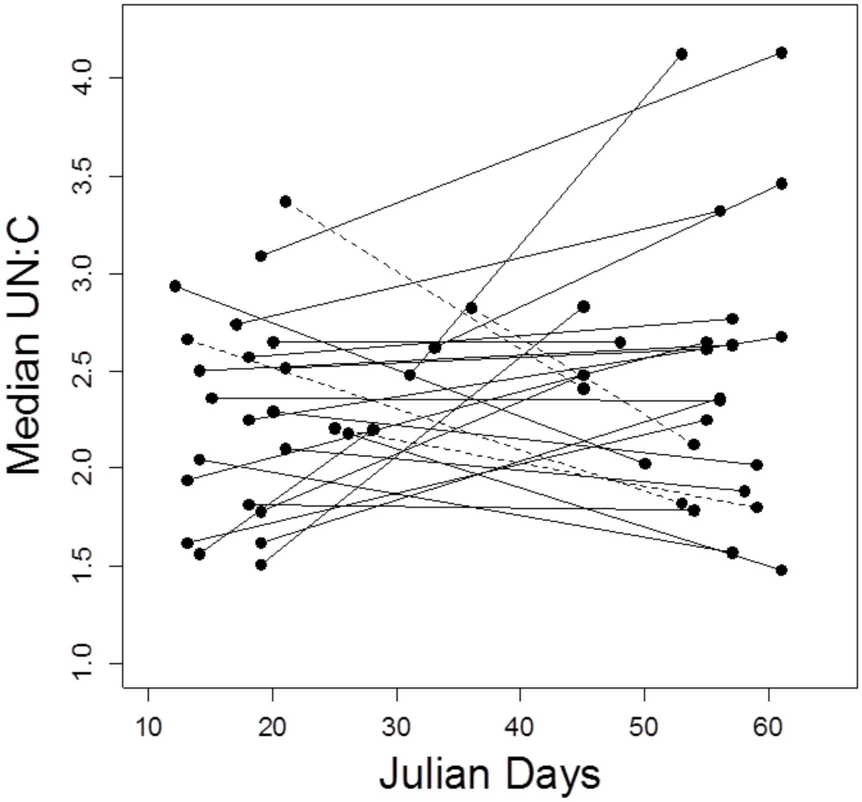

Figure 3.3. Expected relationship between Julian day and winter nutritional status for Isle Royale moose (1988-2014). Each line is the median regression (Cade and Noon 2003) representing a different year. Each regression is supported by an average of 74 UN:C samples (interquartile range = [50, 92]). Note that the line for 1989 [(JD_1 = 27, $mUNC_1$ = 7.755), (JD_2 = 60, $mUNC_2$ = 6.27), p = 0.18) has been omitted for clarity. Dashed lines indicate the four out of 27 years that had significant declining trends in UN:C. This suggests that the timing of sample collection coincided with the period when UN:C tends not to decrease, and supports the idea that increased UN:C at this time relates to a decline in nutritional status (see Introduction).

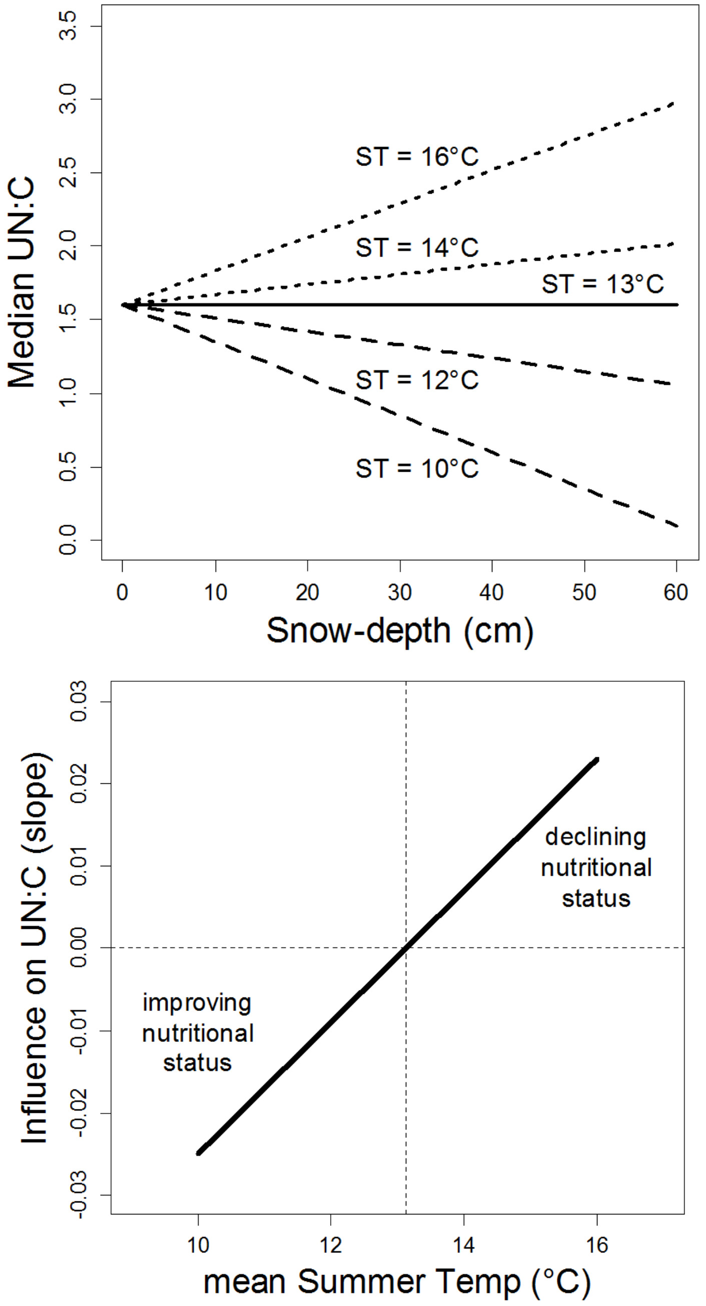

Figure 3.4. Influence of the interaction between snow-depth (SD_t) and mean summer temperature (ST_{t-1}) on *UN:C*. The most parsimonious population-wide nutritional model (Table 3.1, model a7) includes an interaction between snow-depth (SD_t) and the mean temperature of the previous summer (ST_{t-1}). At temperatures above ~13° C (top, dotted lines), the influence of snow-depth is associated with declining nutritional status (i.e., increasing UN:C), whereas at temperatures below ~13° C (top, dashed lines) it is not. The nature of this interaction suggests that, across a range of temperatures, the influence of snow-depth on nutritional status changes (bottom).

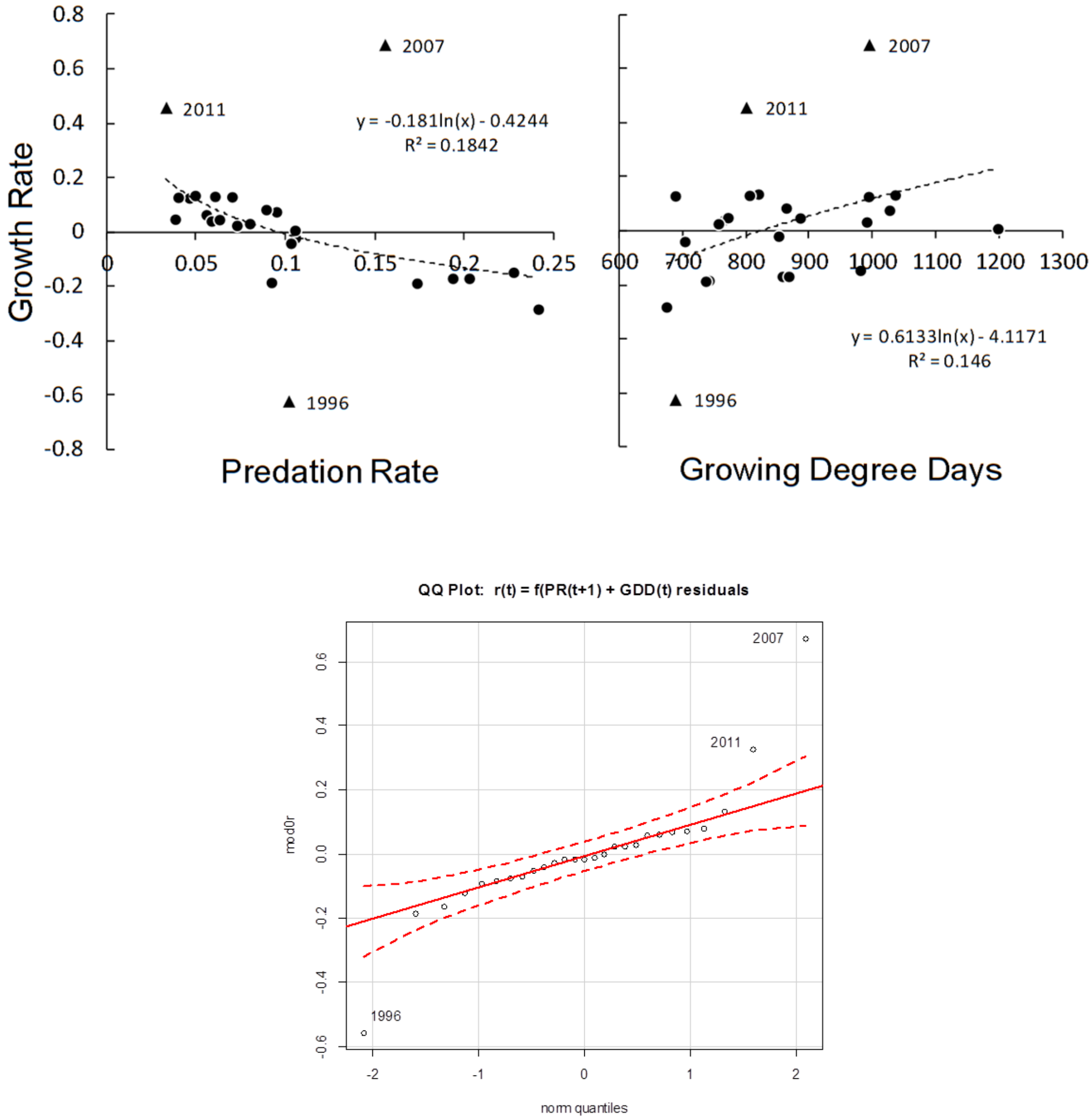

Figure 3.5. Outlier analysis. Graphical assessment (Zuur et al. 2009) of the bivariate population model $r_t = f\ (PR_{t+1} + GDD_t)$ suggested the presence of three outliers (top, left and right). The proportion of variance explained by PR_{t+1} as about twice that explained by GDD_t (0.22 and 0.10 respectively). Residual analysis (lower) further suggests the presence of suspicious points.

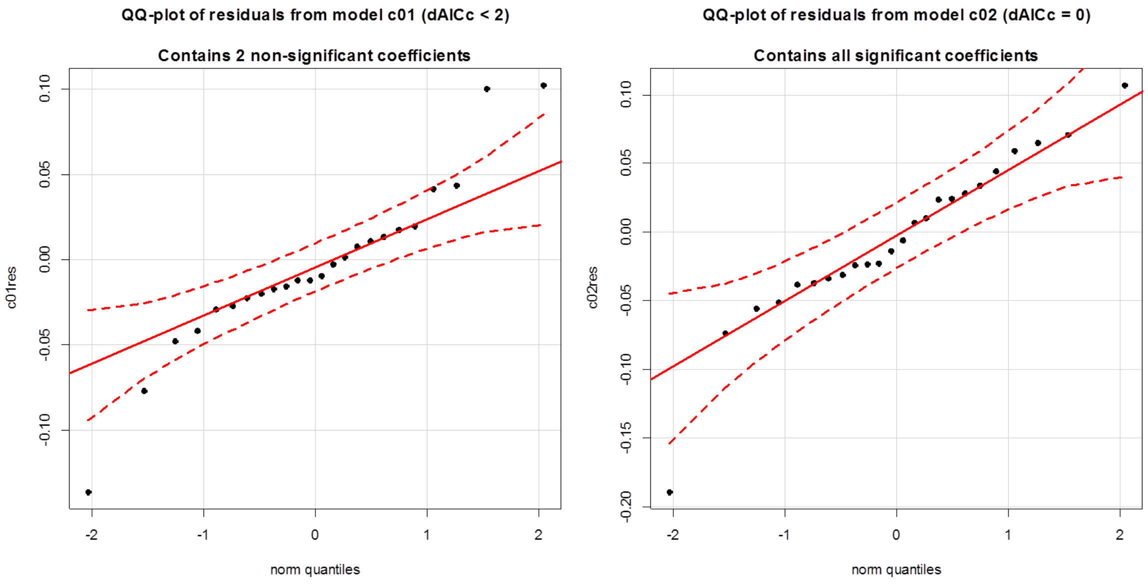

Figure 3.6. Comparison of residuals in models c1 and c2. Though comparable in terms of AIC_C and R^2, c2 (right) is better than the next best model, c1 (left), with respect to the distribution of its residuals.

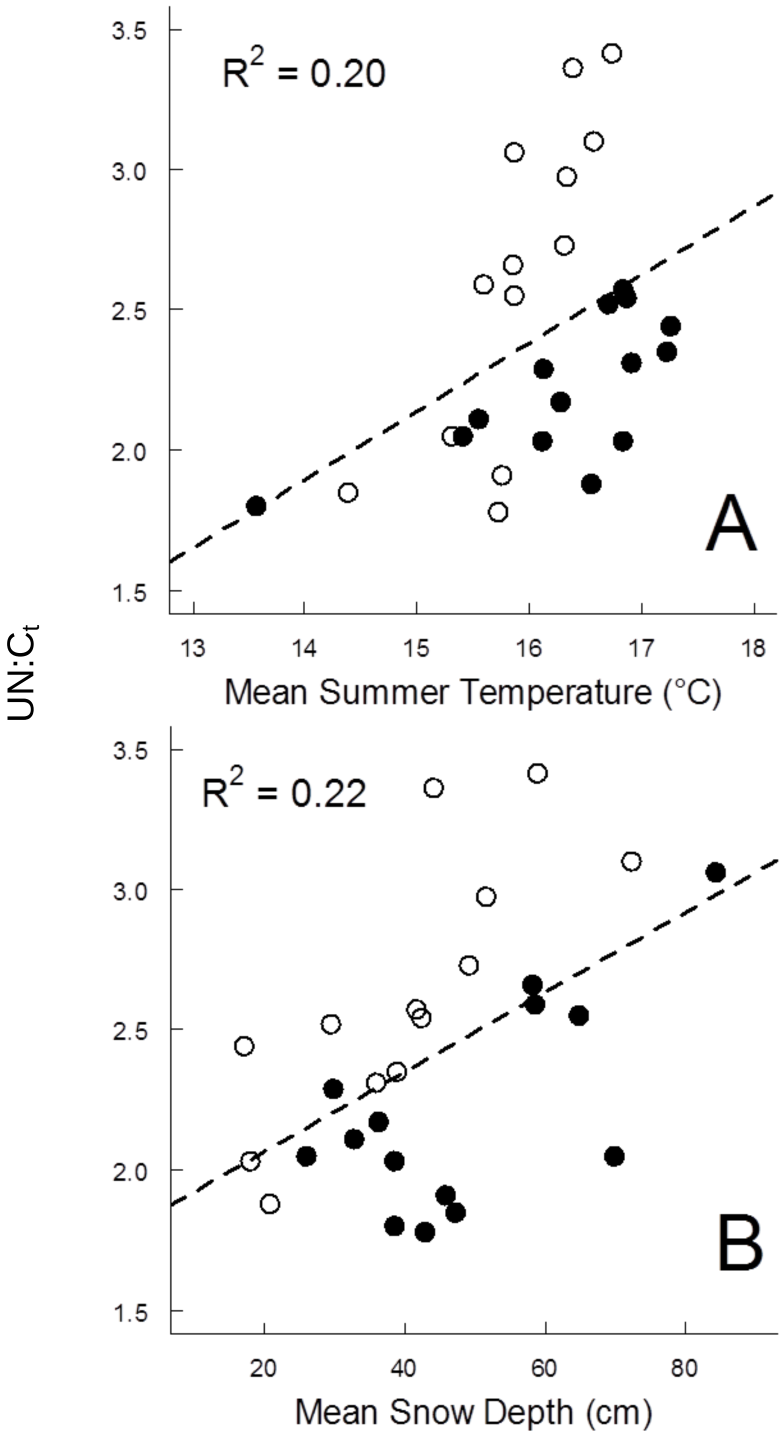

Figure 3.7. Influence of summer temperature and snow-depth on median UN:C. Each observation represents a different year (1988-2014). Open and filled symbols in (A) represent years of high and low snow depth, respectively. Open and filled symbols in (B) represent years of high and low summer temperature, respectively. Low UN:C values represent better body condition. These relationships are reflected in the most parsimonious population-wide nutritional model (Table 3.1, model a7).

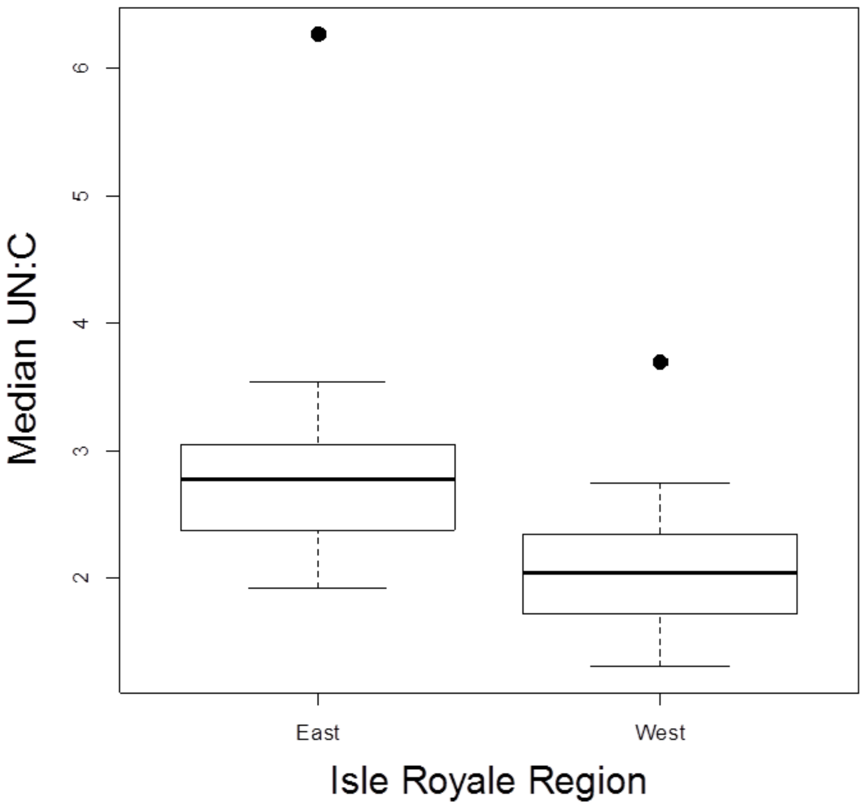

Figure 3.8. Median UN:C by region on Isle Royale (1988-2014). UN:C tends to be higher on the eastern portion of Isle Royale ($p = 10^{-6}$, paired t-test). Analysis of variance indicates that 30% of the variation in median UN:C is attributed to differences in region.

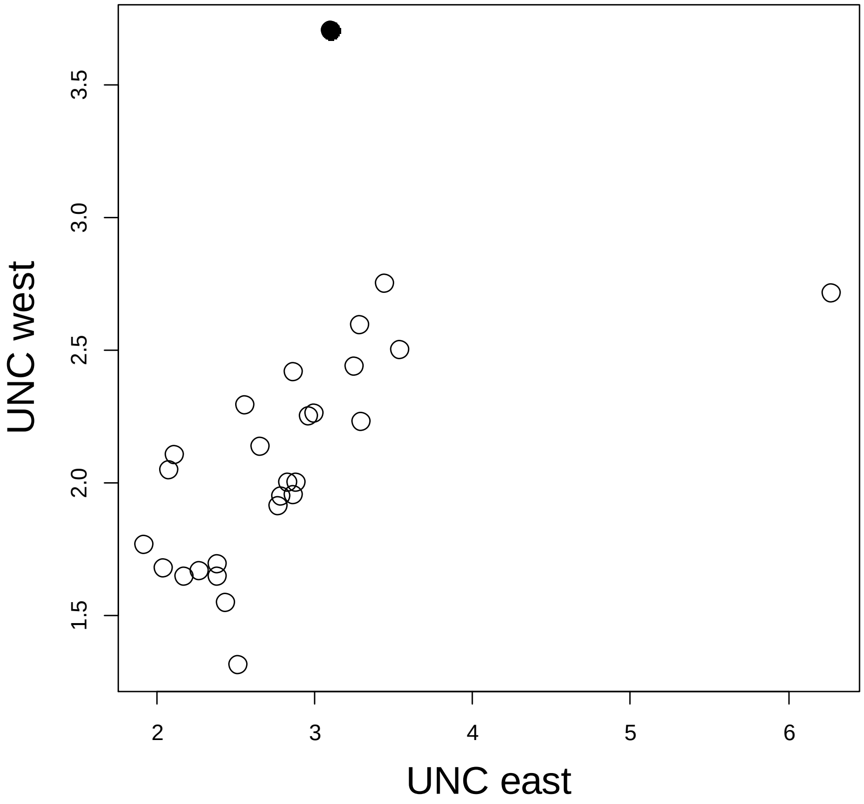

Figure 3.9. Covariation in median UN:C by region on Isle Royale (1988-2014).

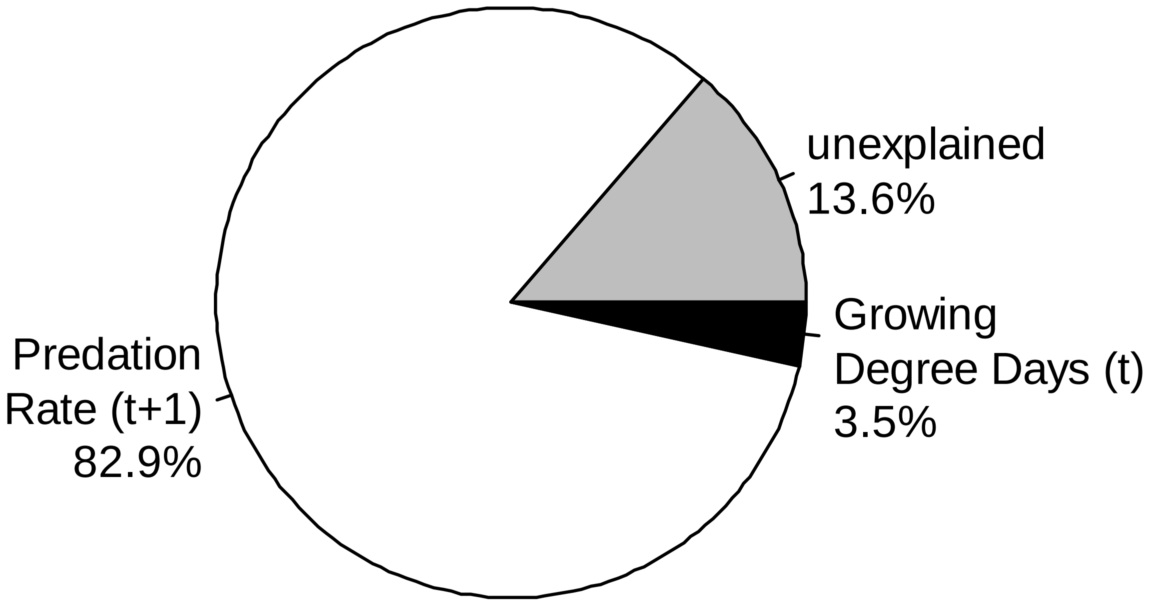

Figure 3.10. Percentage of explained variance of model c3 that is attributable to each variable. Model c3 (Table 3.3) has an $R^2 = 0.82$. The proportion of the explained variation in per capita growth (r_t) that is attributable to each predictor is calculated by multiplying each variable's standardized multiple regression coefficient by its correlation coefficient with the response variable (Schumacker & Lomax 1996). The nutritional models are not shown because they feature interaction terms and it is not possible to decompose the explained variance of models with interactions.

4 Prevalence and abundance of cyamid “whale lice” (*Cyamus ceti*) on subsistence harvested bowhead whales (*Balaena mysticetus*)

4.1 Abstract

We present findings on the prevalence and abundance of cyamid ectoparasites (*Cyamus ceti*) or “whale lice” on bowhead whales (*Balaena mysticetus*) harvested for subsistence in the Bering, Chukchi, and Beaufort Seas from 1973 to 2015. Cyamids were present on 20% of the 673 whales that were examined for cyamid ectoparasites. Logistic regression was used to determine factors associated with cyamid prevalence. The probability of cyamid presence increased with age, length, and improving body condition, but decreased over the past 35 years. Cyamid presence was also more probable on whales harvested in the spring than on those harvested in the fall. When present, cyamid abundance was typically low (< 10 per whale). Case histories provide ancillary information about the relationships between abundance of cyamids and their bowhead hosts. Environmental change and increasing anthropogenic disturbances are expected to occur in the Arctic regions inhabited by bowheads. We recommend continued monitoring of subsistence harvested whales for cyamids, as well as further investigations into the roles of environmental and anthropogenic variables in cyamid prevalence and abundance, as part of a comprehensive program of Arctic ecosystem assessment.

4.2 Introduction

Cyamids (Crustacea, Amphipoda), also known as “whale lice”, are ectoparasites that feed on the epidermis of whales (Rowntree, 1983 & 1996; Schell et al., 2000). They are able to stay attached to the surface of their cetacean hosts through several adaptions, including sharp grasping claws and a flattened shape (Fig. 4.1). Although they are common to many cetacean species, some cyamid species are host specific. For instance, *Cyamus ovalis*, *C. gracilis*, and *C. erraticus* can be found only on right whales (*Eubaleana spp.*) (Kaliszewska et al., 2005). The bowhead whale (*Balaena mysticetus*), another member of the family Balaenidae, is closely related to the right whale, and similarly, has a closely associated cyamid ectoparasite (*Cyamus ceti*, Fig. 4.1).

Long-term visual health assessments of North Atlantic right whales (NARW; *Eubaleana glacialis*) suggest a relationship among the spatial distribution and relative abundance of cyamids and the health status of their host (Pettis et al., 2004). For example, orange cyamids (*C. erraticus*) occur on all healthy adult NARWs in relatively low numbers (R. Rolland, *pers. comm.* 2015; J. Seger, *pers. comm.* 2016) where their spatial distribution is largely confined to genital and mammary folds. But the occurrence of these cyamids in large numbers on the host’s dorsal surface, particularly around the blowholes, has been associated with poor health (Schick et al., 2013; J. Seger, *pers. comm.* 2016). Such infestations have been observed in “last-sighting” photos, after which the whales were presumed dead (Pettis et al. 2004). Another example is of a NARW entangled by a line around its rostrum that prevented feeding and which became almost entirely covered with cyamids before its eventual death from starvation (R. Rolland, *pers.*

comm. 2015, M. Moore, *pers. comm.* 2015; Moore et al., 2006). Presumably, the reduced swimming speed of physically compromised whales allows cyamids to proliferate by occupying more "environments" that are hydrodynamically favorable (Rowntree, 1996).

Although the Bering-Chukchi-Beaufort Seas (BCB) population of bowheads is currently large and increasing (Givens et al., 2016), their remote Arctic home range means that they are a difficult species to monitor, and little is known about their cyamid ectoparasites. Bowheads are legally hunted by Native Alaskans and postmortem examinations of subsistence harvested bowhead whales have been conducted for over 40 years in cooperation with the Alaska Eskimo Whaling Commission (AEWC) and village Whaling Captains' Associations. This investigation reviews the harvest records collected by the National Marine Fisheries Service (NMFS) in the 1970s and the North Slope Borough Department of Wildlife Management (NSB-DWM) from the early 1980s to present. Our fundamental goal was to better understand the factors associated with cyamid prevalence and abundance on BCB bowhead whales, and this work presents, to our knowledge, the first such long-term investigation.

Our specific objectives were to characterize cyamid prevalence and abundance with respect to demographic, morphological, seasonal, and body condition variables of bowhead whales. A further objective was to improve the basic understanding of cyamid ecology. To do so, we compiled and analyzed data from all harvest records of bowheads that were visually inspected for cyamids.

4.3 Methods

In cooperation with the Alaska Eskimo Whaling Commission (AEWC) and village Whaling Captains' Associations, post-mortem examinations of subsistence harvested bowhead whales were conducted by the National Marine Fisheries Service (NMFS) in the 1970s and by the North Slope Borough Department of Wildlife Management (NSB-DWM) from the early 1980s to present. Whenever possible, the exposed skin of the whale (including the gape of the mouth, eyelids, blowholes, genital slit, and peduncle, as well as any skin depressions, scars, cracks, and wounds) was examined immediately upon landing. Upon inspection, the presence, location, and relative abundance of cyamids was noted, as were other biometric and demographic data. Detailed descriptions of the methods used to collect whale biometric and demographic data can be found in George (2009).

Because harvested bowheads typically had fewer than 10 cyamids present, and the count distribution was highly skewed (e.g., the median count was 2, but the highest three cyamid totals were recorded as 201, 200 and 100; see Fig. 4.2), absolute cyamid abundance was not formally analyzed. Instead, our analyses focused on cyamid presence.

We fit logistic regression models to predict the probability of cyamid presence. The response variable for all models was an indicator variable for cyamid presence (present = 1, absent = 0). Sex (*SEX*, female = 1 and male = 0) was determined by external visual examination. The presence of scars (*SCAR*, present = 1, absent = 0) was ascertained from the observer comments recorded in the harvest records for each whale. Whales with wounds, gouges, and/or cracks, as well as killer whale (*Orcinus orca*) bites, line entanglements, and/or ship strikes were scored as a having scars present. Total body length (*LEN*) was measured as the straight line distance from the end of the rostrum to the inside of the fluke notch. Whale age (*AGE*) was estimated via several methods including aspartic acid racemization of eye lens tissue (George et al., 1999), stable isotope analysis of the baleen (Lubetkin et al., 2008), and/or corpora counts in the ovaries (George et al., 2011). We also considered the whale's body condition (*COND*) as an explanatory variable. We defined *COND* as the residuals from a "body condition model" that predicts the whale's girth as a function of its length. Because we ran two families of logistic regression models based on two different data sets (see Tables 4.1 and 4.2) we generated residuals from two separate body condition models:

<u>BODY CONDITION MODEL 1</u> (Table 4.1)

$$GIRTH_{ax} = 124.5 + 0.56 \cdot LEN_{cm} \quad (R^2 = 0.88,\ F_{1,\,124} = 935.8,\ p = 2.2e^{-16})$$

<u>BODY CONDITION MODEL 2</u> (Table 4.2)

$$GIRTH_{ax} = 166.0 + 0.52 \cdot LEN_{cm} \quad (R^2 = 0.79,\ F_{1,\,495} = 1890,\ p = 2.2e^{-16})$$

where

$GIRTH_{ax}$ = Axillary girth of the whale. This is measured as one half of the whale's circumference (cm) taken from the dorsal center-line to the ventral center-line, and adjacent to the posterior insertion of the pectoral flippers.

and

LEN_{cm} = Total length of the whale. This is measured as the straight line distance (cm) from the end of the whale's rostrum to the inside of the fluke notch.

The sign and magnitude of the residuals from these models indicate whether a whale is fatter or thinner than predicted for its length, and thereby acts as an index that characterizes body condition (*COND*). To assess temporal relationships, we included a variable for the season (*SEAS*, where spring = 0 and fall = 1) and the year (*YEAR*) in which each whale was harvested.

Our first set of models (Table 4.1, models 1-5) considered the following six explanatory variables: *AGE*, *SEX*, *SCAR*, *COND*, *SEAS*, and *YEAR*. We did not include *AGE* and *LEN* in the same models because of collinearity (Pearson's product-moment correlation, $r = 0.77$, $p < 2.2\mathrm{e}^{-16}$). Rather, using the same data set, we replaced *AGE* with *LEN* and re-ran our models using the same procedures (Table 4.1, models 6-10). The sample size for all models in the first analysis ($n = 126$) was substantially less than the number of examined whales because relatively few whales in our harvest records had an age estimate to associate with their length and girth measurements. However, by considering whales with length and girth measurements, regardless of the presence of an age estimate, it was possible to model cyamid presence with a sample size that was approximately four times greater ($n = 497$). This set of models (Table 4.2) considered the variables *LEN*, *COND*, *SEX*, *SCAR*, *SEAS*, and *YEAR*. These models were generated using the same modeling procedures used for the models in Table 4.1.

All analyses were conducted using R Statistical Software (R Core Team, 2014). Our modeling procedure began by constructing all possible univariate models. We next constructed a “full” model. For the first analysis (Table 4.1), because *LEN* and *AGE* are highly correlated, it was necessary to construct two variants of the “full” model, each including five explanatory variables in common (*SEX*, *SCAR*, *COND*, *SEAS*, *YEAR*) and differing only in the inclusion of *LEN* or *AGE*. For the second analysis (Table 4.2) the "full" model included *LEN*, *COND*, *SEX*, *SCAR*, *SEAS*, and *YEAR*. Starting with each "full" model, we used backward elimination to sequentially drop variables based on the highest non-significant *p*-value until all remaining variables were significant at $\alpha = 0.05$. Finally, for the highest performing additive effect models we considered the influence of interaction terms. Model performance was then compared and ranked based on $\mathrm{AIC_C}$. We considered the best models to be those with $\Delta\mathrm{AIC_C}$ scores < 2 when compared to the highest ranking model (Burnham and Anderson, 2002). Among these, it is reasonable to prefer the most parsimonious model that retains all statistically significant effects.

We also ran chi-squared tests to assess whether cyamid presence was associated with sex, the village where each whale was harvested, and the harvest season (i.e. spring or fall). To consider the relationship between body condition and age, we compared the mean age of whales with body condition scores above the 80th percentile to that of whales with body condition scores below the 20th percentile. The mean length and age of whales harvested in the spring vs. fall were compared using t-tests. And, annual patterns in the percentage of harvested whales with cyamids, as well as the mean annual length of harvested whales were assessed for temporal autocorrelation using the 'acf' function in R.

To evaluate the conditions that may be related to cyamid abundance on harvested bowheads, we also qualitatively assessed the written observations from the harvest records in our database. A selection of case studies is provided in Table 4.3.

4.4 Results

We compiled records from 673 harvested bowheads which had been visually examined for ectoparasites from 1973 to 2015. This sample included 341 males (51%) and 332 females (49%). Cyamids were present on a total of 137 (20%) of examined whales. Of the whales with cyamids, 67% had 1-5 cyamids present (Fig. 4.2, Class 1), whereas the remaining 33% had 6 or more cyamids (Fig. 4.2, Classes 2 & 3). There was no significant difference in the proportion of bowheads with cyamids presence based on sex (Fig. 4.2; $\chi^2 = 0.43$, *d.f.* = 1, $p = 0.51$; $n = 666$). Although some villages (e.g., Barrow) harvest far more bowheads than others (Fig. 4.3), there was no significant difference by village in the proportion of examined whales with cyamids present ($\chi^2 = 6.5$, *d.f.* = 5, $p = 0.26$, $n = 673$).

Season was significantly related to the proportion of harvested bowheads with cyamids ($\chi^2 = 4.75$, *d.f.* = 2, $p = 0.03$, $n = 730$), with more spring whales having cyamids present. The mean age of whales with a body condition index (i.e. residuals from the ‘body condition model’ described above in the methods) above the 80th percentile was 32 years and the mean age of whales whose body condition index was below the 20th percentile was 22.8 years. However, a t-test showed no significant difference ($t = 0.93$, df = 44, p-value = 0.18). A comparison of the mean length and age of harvested bowheads by season shows that spring whales are significantly longer ($t = -2.28$, *d.f.* = 660, $p = 0.02$) and older ($t = -2.78$, *d.f.* = 149.9, $p = 0.006$) than fall whales. We also observed a pattern that might suggest periodicity in the percentage of whales with cyamids over time and in the mean annual length of harvested bowheads (Fig. 4.4). These patterns were significantly related ($R^2 = 0.27$, $F_{1,34} = 12.7$, $p = 0.001$). A temporal autocorrelation analysis also showed a significant relationship to the 3-year time lag in mean annual length of harvested bowheads, but no significant autocorrelation in the proportion of whales with cyamids.

The models in Table 4.1 were based on a subset of data in which an age estimate was associated with each examined whale ($n = 126$). Two sets of models are shown in Table 4.1: models 1-5 included *AGE* and excluded *LEN*, whereas models 6-10 did the opposite. Model 1 was the highest ranked model in the entire set of models in Table 4.1, and suggests that older whales have a higher probability of cyamid presence than younger whales. Model 1 also included a significant interaction between *AGE* and *YEAR*. Models 2-5 all had $\Delta\text{AIC}_\text{C}$ scores < 2, and are therefore comparable in performance to model 1. These top five models all included the variables *AGE*, *YEAR*, and/or their interaction. Model 4 was an exception in that it also included the variable *SCAR*. Models 6-10 in Table 4.1 utilized *LEN* as a surrogate for age. While *LEN* is statistically significant in models where it replaced *AGE*, altogether, these models have a poorer fit. The effect of *SCAR* and *COND* were not found to be important in the highest ranked models, and when present, were not significant. Although the performance of models 6-10 was substantially lower (e.g. model 6 had the lowest $\Delta\text{AIC}_\text{C} = 7.20$), their structure was similar to the higher ranking models in their inclusion of an age proxy (*LEN*), *YEAR*, and/or their interaction.

The models in Table 4.2 were based on data from examined whales regardless of whether they had an associated age estimate ($n = 497$). The top ranked model (model 1) was also the only model with a $\Delta\text{AIC}_\text{C}$ score < 2. This model suggests that a whale's length (*LEN*) is significantly related to the probability of cyamid presence, but the effect of this variable is complicated by an interaction with the season of harvest (*SEAS*). An analysis of deviance confirms that the model terms for *LEN* and *LEN:SEAS* together significantly affect the probability of cyamid presence ($p = 0.005$). Body condition (*COND*) was also significant and was positively associated with the probability that cyamids are present. Despite their lower performance, models 2-6 (Table 4.2) were very consistent with model 1 in the use of *LEN*, *COND*, and *SEAS*.

A review of selected case histories provides ancillary information concerning the *abundance* of cyamids and their complex relationships with bowhead whales. A very old and large bowhead had high cyamid abundance (Table 4.3, whale 95B09, aged 172). So too did smaller and/or younger whales (Table 4.3, whales 14B04, 04B03) as well as four other sexually immature whales (i.e., < 13.9 meters long; see Nerini et al., 1984). Severely physically compromised whales also had high cyamid abundance. Examples include whale 15KK01 (Table 4.3) which had "about 100" cyamids present; and whale 08G01, which had an apparent chronic injury to its lower spine. This whale was described as having "numerous" cyamids present, "large patches of cyamids on the middle lower portion of the body as well as in the genital slit, etc.", and with a drawing indicating "lots of bugs" posterior to the genital slit. Its skin was reported as "thin," and the skin-blubber boundary was described as "hard." In contrast, whale 99B14, despite a severe line entanglement and poor physical condition, did not have cyamids present. Finally, scarring and skin damage (e.g. 15B20, 15KK01, 92B11, 82WW01, and 76B20) were associated with cyamid presence in 21% ($n = 29$) of examined whales with cyamids.

4.5 Discussion

Although cyamids were detected on 20% of harvested bowhead whales, cyamid abundance tended to be very low. For example, 95% of the bowheads examined for cyamids had fewer than 10 present (Fig. 4.2). Because cyamids have no free-swimming aquatic life-stage (Rowntree, 1983 and 1996), parasite transmission among bowheads likely occurs via direct contact. But for cyamid proliferation to take place, not only must direct contact between whales occur, but also successful attachment to the host. Unlike right whales, bowheads have no callosities upon which cyamids can grip. Thus, the presence of damaged skin, which is more likely to occur in older whales, increases the chances that whale to whale parasite transmission is successful. Given the low cyamid prevalence, very low absolute numbers of cyamids, and the absence of callosities, the transmission of cyamids from host to host may be dependent upon the frequency of whale to whale interactions and the accumulation of skin damage. Whereas the rate of parasite transmission may be low, the very long lifespan of bowheads (George et al. 1999) makes it plausible that older whales have had more opportunities for the direct transfer of cyamids from another host through increased intraspecific interactions. Moreover, the accumulation of skin damage over time may increase the likelihood of successful parasite transmission by providing the structure to which cyamids can grip. This is supported by the preferred models of cyamid presence (Table 4.1, model 1 and Table 4.2, model 1), each of which included *AGE* or *LEN* (a surrogate for age) as a variable that was positively related to the probability of cyamid presence. The same patterns can be seen in lower performing models wherein *AGE* and *LEN* are often significant predictors. These findings are consistent with written comments from our database (Table 4.3) that relate the spatial use of cyamids to whale epidermal cracks, dents, scars, and injuries; all of which tend to accrue with age.

The positive association of body condition to cyamid presence (Table 4.2; model 1) was a surprising trend. Presumably, whales in poor body condition swim more slowly, thereby increasing the chances that cyamids can stay attached and proliferate; whereas whales in good condition swim faster, therefore making it more difficult for cyamids to stay attached. The relationship between body condition and age may explain this relationship. The positive association between bowhead age and body condition may be the result of lower foraging efficiency in young post-wean individuals with underdeveloped baleen racks. Later in life, when their baleen rack is fully formed, the body condition of mature adults tends to increase (George 2009, George et al. 2015). Additionally, if bowhead longevity is a function of body condition, then older whales (i.e. those demonstrated to be more likely to have cyamids) should have higher body condition scores. Our data suggest a weak relationship between age and body condition ($p = 0.18$), with the mean age of the whales in the best condition (body condition index ≥ 80th percentile) about a decade older than those in poor condition (body condition index ≤ 20th percentile). Given the growth dynamics of bowheads throughout their maturation process, it seems likely that the association between body condition and cyamid presence may be at least partially associated with the metric that we used to score body condition.

In addition to *AGE,* the most parsimonious model in Table 4.1 also included *YEAR* as a variable, which was negatively associated with cyamid presence (Table 4.1, model 1). The negative slope of *YEAR* indicates that, with the passage of time, the probability of cyamid presence on harvested bowheads is decreasing. Given evidence that older bowheads tend to have cyamids present, we speculated that inter-annual variation in the demographic composition of harvested bowheads may be influential. Indeed, since 1981, there has been a pronounced downward trend in the size of bowheads harvested in the fall ($R^2 = 0.56$, $p = 5.6e^{-7}$, $n = 33$), but not in the spring ($R^2 = 0.02$, $p = 0.39$, $n = 35$). A mechanistic explanation for these trends likely involves many factors. One consideration is that the current growth rate of the BCB bowhead population (Givens et al. 2016) makes it plausible that their age distribution is shifting toward greater numbers of younger whales over time. Another possibility concerns the implications of a Barrow Whaling Captains' Association (BWCA) decision to open the fall whaling season later in the year when air temperatures are cooler and smaller migrating bowheads are more abundant; thereby decreasing the chance of harvesting large bowheads (C. George, *pers. comm.*). Inter-seasonal variation (*SEAS*) was significant and included as part of the most parsimonious model in Table 4.2. The negative relationship between *SEAS* and cyamid presence indicates that, as the indicator variable increases from 0 (spring) to 1 (fall), there is a decreasing probability of cyamid presence. Because whales caught during the spring hunts are, on average, longer and older, we surmised that the demography of harvested bowheads was also important at the inter-seasonal time scale. This inter-seasonal variability is also likely related to many factors, but Iñupiat hunting practices, which differ between the spring and fall, may play a major role. Although some villages tend to harvest larger whales, Barrow, which accounts for a major proportion of our data, tends to harvest smaller bowheads. Given the complexities within this system, including: ice dynamics, hunter selectivity, population dynamics, and many other factors, caution should be taken with interpreting the temporal trends in cyamid presence and whale size until a more detailed analysis can be undertaken.

Ancillary data from our harvest records suggested no apparent trends relating to the abundance of cyamids. Our records did document high cyamid abundance in a bowhead with a spinal abnormality; similar to incidents in which humpback whales (*Megaptera novaeangliae*) with severe spinal abnormalities and very poor body condition became heavily infested (Osmond and Kaufman, 1998; Félix et al. 2007). However, few other harvest records indicated elevated abundance of cyamids on bowheads in poor body condition. Moreover, contradicting reports of young, healthy, and/or small whales with higher cyamid abundance also existed in our records. Other than associations with skin depressions and deep wounds, meaningful patterns associated with cyamid abundance were not apparent from our harvest reports. Typically, most harvested bowheads had few or no cyamids present and were generally in very good condition (Philo et al., 1993; Willetto et al. 2002; Stimmelmayr, 2015). Another consideration is that, given the overall good health of this population, low cyamid abundance per whale, and low cyamid prevalence, successful parasite transmission from host to host may simply be a rare event. Finally, other cyamid species have been shown to have varying levels of cold tolerance (Best, 1979). Perhaps because bowheads are the only mysticete that consistently winters in arctic waters, this species (*C. ceti*) may be close to its physiological limit and at the edge of its ecological niche.

Because they are difficult to observe and document on free-ranging whales (Rowntree 1983), few systematic studies of cyamids exist. This investigation suggests that most BCB bowheads do not carry cyamid parasites; and those that do, tend to have low cyamid abundance. Our models also indicate that demographic variables (e.g., age and size), body condition, and temporal variables (e.g., year and season of harvest) are significant predictors of cyamid presence. Further investigations are needed in order to disentangle the complexities of ice dynamics, population ecology, and hunting selectivity from the basic ecology of bowheads and their cyamid parasites. For example, sub-adult (post-weaning) bowhead body condition has been shown to improve as sea ice cover declines (George et al. 2015). Thus, bowhead productivity may increase in response, thereby increasing the chances of cyamid transmission from host to host through density dependent effects. Further complicating matters are the effects of environmental change within Arctic marine ecosystems, which are anticipated to continue into the future (Moore et al, 2014; Moore and Laidre 2006). Maritime traffic and industrial development are anticipated to increase in response to declining sea ice cover (Reeves et al., 2012) and will likely lead to higher anthropogenic disturbance levels.

Whether, how, and to what extent bowheads will respond to these and other changing environmental stressors remains to be seen. There is reason to believe that, given their longevity and evolutionary strategy of “weathering” environmental variability (Burns, 1993; George et al., 1999), bowhead response(s) to environmental perturbations may not be readily detectable. Cyamid prevalence and/or abundance appear to be associated with demographic, physiological, and/or anthropogenic factors, which are also subject to change with the environment. Visual examinations for cyamids are relatively easy to perform on harvested bowheads. As such, we recommend that similar assessments of cyamid prevalence and abundance be conducted on harvested bowheads and other large whale species in Arctic regions to further develop a basic ecological understanding of these species as part of comprehensive Arctic ecosystem assessment programs (Moore et al., 2014).

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4.8 Tables

Table 4.1. Ranked logistic regression models estimating the probability of cyamid presence (n = 126). No models include variables for both *AGE* and *LEN* because of collinearity. Models 1-5 are the five highest ranked models to include the variable *AGE*. Models 6-10 are the five highest ranked models to include the variable *LEN*. Explanatory variables are shown in the column headers. Colons indicate interactions. Model 1 (bold) is the highest performing model.

†Age estimates from stable isotope analyses, corpora counts, and/or aspartic acid racemization

‡Body length is used as a proxy for age.

			Estimated Coefficient								
ID	AIC_C	$\Delta\text{AIC}_\text{C}$	*AGE†*	*LEN‡*	*COND*	*SEX*	*SCAR*	*SEAS*	*YEAR*	*AGE:YEAR*	*LEN:YEAR*
1	**111.93**	**0.00**	**4.157***	--	--	--	--	--	--	**-0.002***	--
2	112.73	0.81	0.024**	--	--	--	--	--	-0.082*	--	--
3	112.75	0.83	--	--	--	--	--	--	-0.083**	1.2e^{-5**}	--
4	113.42	1.49	0.030**	--	--	--	-1.013	--	-0.065	--	--
5	113.69	1.77	2.912	--	--	--	--	--	-0.036	-0.001	--
6	119.13	7.20	--	13.057*	--	--	--	--	--	--	0.037*
7	119.46	6.72	--	0.181*	--	--	--	--	-0.080*	--	--
8	119.47	7.54	--	--	--	--	--	--	-0.081*		9.1e^{-5*}
9	121.19	9.26	--	0.177*	0.002	--	--	--	-0.078*	--	--
10	121.26	9.33	--	14.668	--	--	--	--	0.011	--	-0.007

Significance Codes $^{***} \leq 0.001$ $^{**} \leq 0.01$ $^{*} \leq 0.05$

Table 4.2. Ranked logistic regression models estimating the probability of cyamid presence (*n* = 497). These models consider LEN only as an analog for age. Explanatory variables are shown in the column headers. Colons indicate interactions. Model 1 (bold) is the highest performing model.

†Body length is used as a proxy for age.

			Estimated Coefficient							
ID	AIC_C	ΔAIC_C	*LEN†*	*COND*	*SEX*	*SCAR*	*SEAS*	*YEAR*	*LEN:SEAS*	*COND:SEAS*
1	**456.58**	**0.00**	**0.002**	**0.003^{*}**	--	--	**-3.143^{**}**	--	**0.212^{*}**	--
2	459.93	3.35	0.104^{*}	0.004^{*}	--	--	-0.840^{***}	--	--	--
3	460.98	4.40	0.095^{*}	0.004^{*}	--	--	-0.808^{***}	-0.014	--	--
4	461.97	5.39	0.010^{*}	0.004	--	--	-0.084^{***}	--	--	$8.5e^{-5}$
5	462.78	6.20	0.104^{*}	0.004^{*}	--	-0.192	-0.831^{***}	-0.013	--	--
6	464.84	8.26	0.104^{*}	0.004^{*}	-0.011	-0.193	-0.831^{***}	-0.013	--	--
7	466.36	9.78	--	--	--	--	-0.774^{***}	--	--	--
8	472.25	15.67	0.102^{*}	--	--	--	--	--	--	--
9	473.13	16.55	--	0.004^{*}	--	--	--	--	--	--
10	473.72	17.14	--	--	--	--	--	-0.026	--	--
11	476.83	20.25	--	--	--	0.223	--	--	--	--
12	477.06	20.48	--	--	0.096	--	--	--	--	--

Significance Codes $^{***} \leq 0.001$ $^{**} \leq 0.01$ $^{*} \leq 0.05$

Table 4.3. Selected case studies of bowhead whales that were harvested for subsistence in Alaskan waters. Whales are listed in chronological order beginning with the most recent.

ID	Year	Sex	Length (m)	Age (years)	Cyamid abundance	Comments
15B20	2015	♀	11.9	no age estimate	~ 30	Barrow: In a scar and immediately behind the blowhole. Few on mandible.
15KK01	2015	♂	12.8	no age estimate	~ 100	Kaktovik: Old bomb recovered from lower back contained in a large abscess capsule. Dozens of cyamids present in “indented” surface area located over abscess capsule. Harpooner said that the whale “dove differently” - likely compromised by chronic injury. Several chronic internal lesions not directly associated with old wound indicated general poor health.
14B04	2014	♂	9.0	no age estimate	> normal	Barrow: Recovered dead in the spring lead at Barrow, this whale was struck and lost near Wainwright (~ 190 km southwest of Barrow) and drifted north over a period of about four days. Many cyamids (0.5 cm to 2.0 cm) were seen scattered over the head, body, peduncle, and flukes. Four days is likely insufficient time for the cyamids to have proliferated. However, they may have dispersed across a larger area of the whale’s body because of the reduced flow rate of water.
08G01	2008	♂	14.3	no age estimate	heavily infested	Gambell: The attending AEWC Commissioner related the following observations to G. Sheffield: *Numerous large patches of cyamids on skin of lower body and genital slit. Black skin [epidermis] was reported as thin and the mangtak* tough. Large patches of cyamids on the middle lower portion of the body and genital slit. The hunters noted that the whale had two 5 cm diameter circular “swollen” scars on dorsal region ~ 25-30 cm and 3 - 4 meters anterior to peduncle. When first spotted, the whale was “oblivious to the approach” of the whaling crew, did not swim, and repeatedly dove and surfaced in one place. The whale dove normally when it was struck, taking down two floats. But it “swam at a slow pace.”* Based on this description, this bowhead was physically compromised and behaved abnormally.
04B03	2004	♀	9.1	~ 1.0	~ 100	Barrow: Whale lice, near the eye and along the mouth ~100 in 2 groups (at least).
99B14	1999	♂	14.2	64.0	none reported	Barrow: Severely entangled in crab lines through the mouth and around the peduncle. Considered to be in poor condition, with severe lacerations and gray skin. The examiners did not report cyamids on this animal. We reexamined all photographs of 99B14 and did not see cyamids.
95B09	1995	♂	17.5	172.0	*lots of lice*	Barrow: Whale 95B9 was the largest male measured at Barrow in our database and also among the oldest whales recorded. It was described as having “lots of lice”. Described as having areas of the vertebral column that had spondylosis. This has not been described in other BCB bowheads (Paul Nader, *pers. comm.*)
92B11	1992	♂	15.0	no age estimate	20-30	Barrow: Many (20-30) cyamids in old, healed, depressed lesion.
82WW01	1982	♀	17.7	64.9	45-50	Wainwright: 15-20 cyamids on eroded area on chin. About 30 larger cyamids in scar.
76B20	1976	♀	14.3	39.5	*hundreds*	Barrow: 100s of cyamids covering soft scarred area on back and around genital area.

**mangtak* = the epidermis and outer blubber layer of the whale that is consumed for food (Yupik)

4.9 Figures

Figure 4.1. Numerous cyamid “whale lice” (*Cyamus ceti*) on the surface of a 9m long female bowhead whale (*Baleana mysticetus*) harvested in Barrow in 2004 (ID 04B03). Note the depth to which cyamids embed their claw-like appendages (inset) into the whale’s epidermis. Also note the presence of distinct age classes. (Large photo: North Slope Borough - Department of Wildlife Management. Inset photo: Taken by Todd Sformo at the Advanced Instrumentation Laboratory (AIL), University of Alaska Fairbanks)

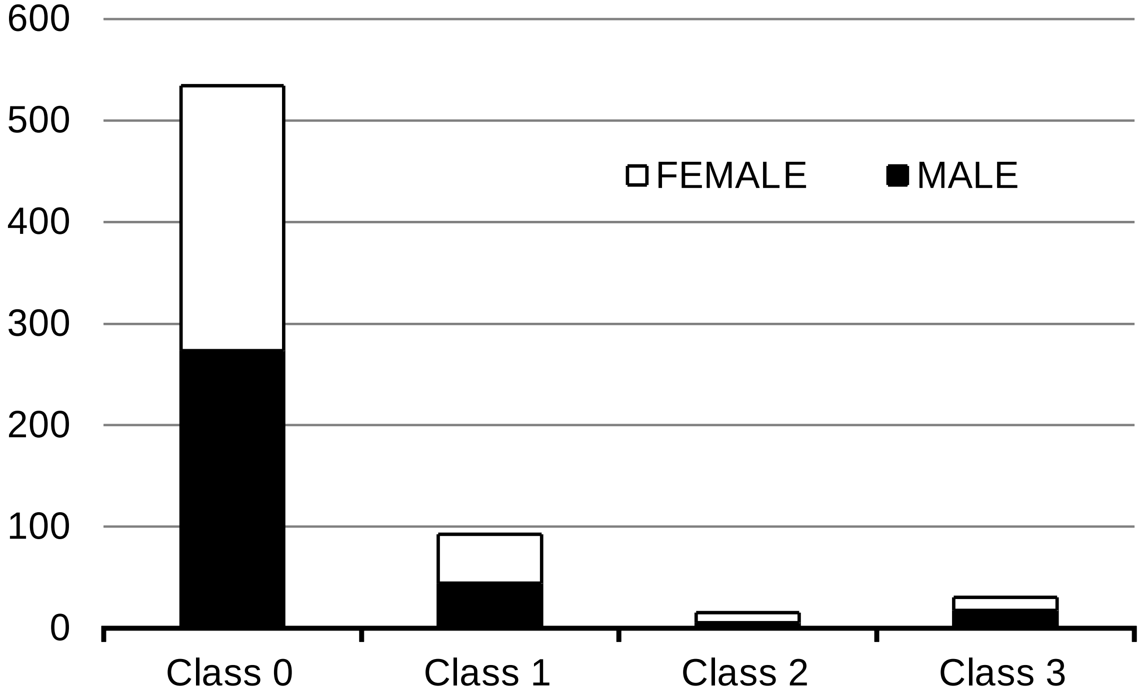
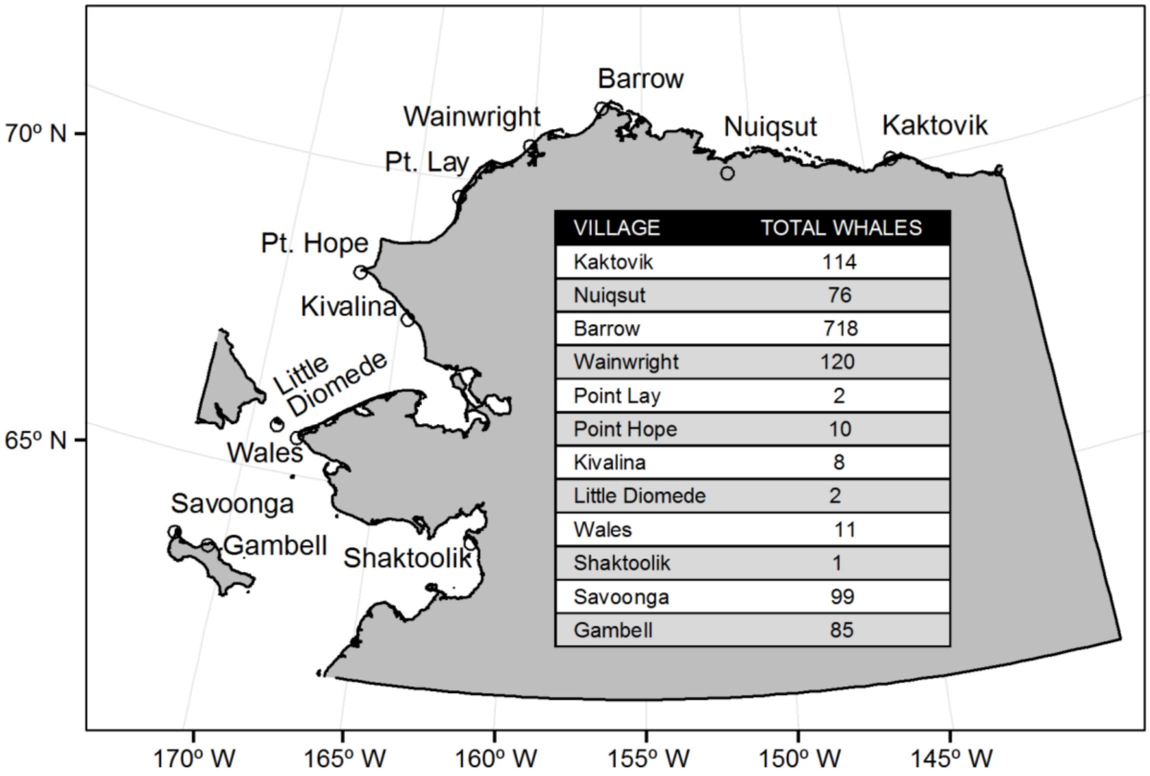


Figure 4.2. Bar chart of bowhead whales examined for cyamids (*n* = 673*). Classes indicate the number of cyamids detected on harvested whales during gross examination immediately upon landing. Class 0: none detected. Class 1: 1-5 cyamids detected. Class 2: 6-10 cyamids detected. Class 3: more than 10 cyamids detected. Categorical data were scored from observer comments on the bowhead whale harvest data forms. *Two whales without sex determination were excluded from this figure.



VILLAGE	TOTAL WHALES
Kaktovik	114
Nuiqsut	76
Barrow	718
Wainwright	120
Point Lay	2
Point Hope	10
Kivalina	8
Little Diomede	2
Wales	11
Shaktoolik	1
Savoonga	99
Gambell	85

Figure 4.3. Map of coastal villages in northern and western Alaska where bowhead whales were examined for the presence of cyamids. Inset table indicates the total number of examined whales by village (1973 to 2015).

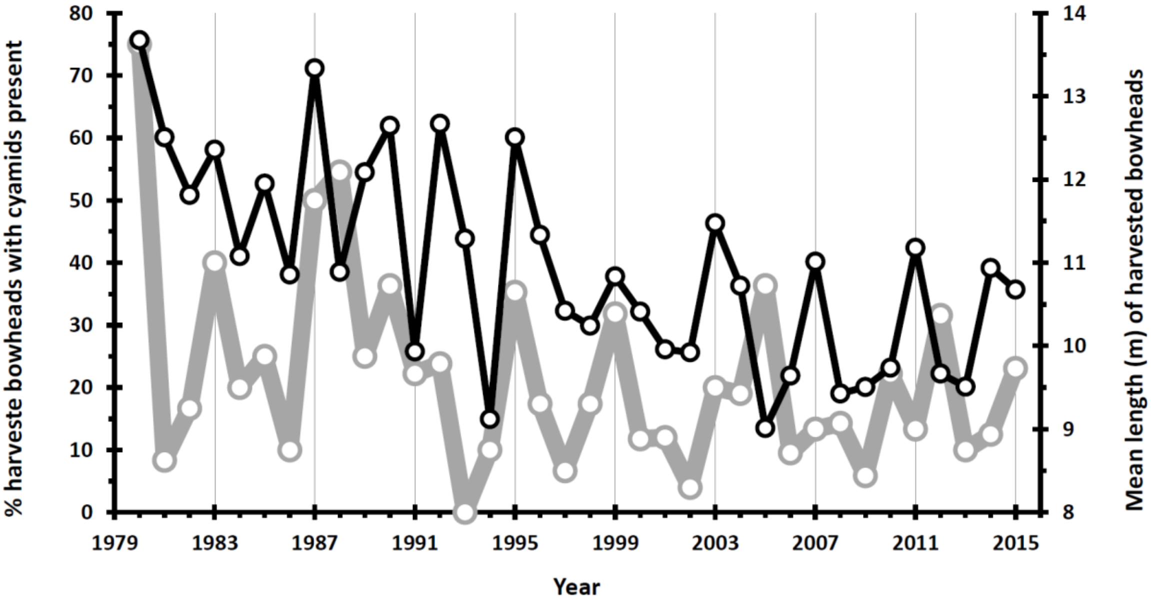


Figure 4.4. Comparison of mean lengths of harvested bowheads to the percent with cyamids present. The gray line indicates the percentage of harvested whales with cyamids present by year. The black line indicates the mean length (m) of bowheads harvested annually. There was a statistically significant temporal autocorrelation of the mean lengths at the three year time lag, but no significant autocorrelation in the percentage of whales with cyamids. Mean length and the percentage of whales with cyamids were significantly related ($R^2 = 0.27$, $F_{1,34} = 12.7$, $p = 0.001$).