The Abundance and Behavioral Ecology of Cape Cod Gray Seals

Under Predation Risk from White Sharks

by

Jerry Moxley

Marine Science and Conservation
Duke University

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in Marine Science and Conservation
in the Graduate School of Duke University

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ABSTRACT

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Abstract

The ultimate goal of wildlife recovery is abundance growth of a species, though it must also involve the reestablishment of the species’ ecological role within ecosystems frequently modified by humans. Reestablishment and subsequent recovery may depend on the species’ degree of adaptive behavior as well as the duration of their functional absence and the extent of ecosystem alteration. Successful reestablishment may entail adjusting foraging behavior, targeting new prey species, and encountering unfamiliar predatory or competitive regimes. Recovering species must also increasingly tolerate heightened anthropogenic presence, particularly within densely inhabited coastal zones.

In recent decades, gray seals (*Halichoerus grypus*) recovered from exploitation, depletion, and partial extirpation in the Northwest Atlantic. On Cape Cod, MA, USA, gray seals are reestablishing growing breeding colonies and seasonally interacting with migratory white sharks (*Carcharodon carcharias*). Though well studied in portions of their range due to concerns over piscivorous impacts on valuable groundfish, there are broad knowledge gaps regarding their ecological role within US marine ecosystems.

Furthermore, there are no known studies that explicitly analyze gray seal behavior under direct risk of documented shark predation.

In this dissertation, I apply a behavioral and movement ecology approach to telemetry data to understand gray seal abundance and activity patterns along the coast.
of Cape Cod. This coastal focus complements extensive research documenting and describing offshore movement and foraging behavior and allows me to address questions about movement decisions and risk allocation. Using beach counts of seals visible in satellite imagery, I estimate the total regional abundance of gray seals using correction factors from haul out behavior. Analyzing intra-annual space use patterns, I document small, concentrated home ranges utilizing nearshore habitats that rapidly expand with shifting activity budgets to target disperse offshore habitats following seasonal declines in white sharks. During the season of dense shark presence, seals conducted abbreviated nocturnal foraging trips structured temporally around divergent use of crepuscular periods. The timing of coastal behavior with different levels of twilight indicates risk allocation patterns with diel cycles of white shark activity derived empirically via acoustic telemetry. The emergence of risk allocation to explain unique behavioral and spatial patterns observed in these gray seals points to the importance of the restored predator-prey dynamic in gray seal behavior along Cape Cod.
Dedication

In honor and joy of Sandman of the Swellansea, for we are all just riding on the shells of our ancestors.

“Most of the time he was out sailing, searching for that island and a new set of sails” –

The Wreck of the Zephyr, Chris Van Allsburg
# Contents

Abstract ..................................................................................................................................................... iv

List of Tables ............................................................................................................................................... x

List of Figures ............................................................................................................................................ xi

Acknowledgements ...................................................................................................................................... xiv

1. Gray seal recolonization of US marine habitats and restoration of its ecological role ... 1
   1.1 Long-standing conflicts with recovering piscivore populations ........................................... 2
   1.2 Recovery trajectories and effects of common wildlife .......................................................... 3
   1.3 The ecological relevance of gray seal population recovery .............................................. 7
   1.4 Annual cycles of reproduction and behavior in gray seals .................................................. 8
   1.5 Dissertation overview ............................................................................................................. 10

2. Google Haul Out: digital aerial surveys in coastal wildlife management and abundance estimation ........................................................................................................ 12
   2.1 Introduction ............................................................................................................................... 12
       2.1.1 Gray seals in the Northeast United States ..................................................................... 14
   2.2 Methods ...................................................................................................................................... 17
       2.2.1 Remote Sensing Imagery ............................................................................................... 17
       2.2.2 Digital aerial survey .......................................................................................................... 17
       2.2.3 Correction factors for interspecific haul out mixing ..................................................... 18
       2.2.4 Correction factors for haul out probability ..................................................................... 19
   2.3 Results ......................................................................................................................................... 21
   2.4 Discussion ................................................................................................................................. 24
2.5 Conclusion

3. Reduced space use and rapid changes in activity budgets of Cape Cod gray seals

3.1 Introduction

3.2 Methods

3.2.1 Data collection and processing

3.2.2 Home range analysis

3.2.3 Behavioral and cluster analysis

3.3 Results

3.3.1 Tag Cohort

3.3.2 Home range analysis

3.3.3 Activity budget changes

3.3.4 Cluster analysis and variability

3.4 Discussion

4. Nocturnal foraging of gray seals and risk allocation in the presence of white sharks

4.1 Introduction

4.1.1 Predation risk and risk allocation

4.1.2 Shark-seal interactions

4.2 Methods

4.2.1 Data collection and processing

4.2.2 Foraging foray analysis in seals

4.3 Results

4.3.1 Foraging trip analysis

viii
4.3.2 Diel cycles in foraging trips ................................................................. 76
4.3.3 Ambient environmental light ............................................................... 77
4.3.4 Multi-scale risk allocation .................................................................... 78
4.4 Discussion ............................................................................................... 79

5. The recovery of Cape Cod gray seals: an opportunity for empirical tests of predation risk theory and applied understanding of complex conservation decisions .......... 93

5.1 Carnivore conservation in the modern era .............................................. 93

5.2 Abundance of Cape Cod’s gray seals: evidence for rapid growth in a pinniped prey base. ..................................................................................... 94

5.3 Reduced space use and the potential for pre-breeding growth tradeoffs for the southernmost breeding colony of gray seals ......................................................... 96

5.4 Risk allocation and predator-prey dynamics in Cape Cod shark-seal interactions ......................................................................................................................... 98

5.5 Risk-mediated decision making in behavior ......................................... 99

5.6 Complex considerations in presence of conservation success ............... 103

5.7 Role of technology in generating co-existence ...................................... 106

5.8 Cape Cod gray seals as an opportunity .................................................. 107

Biography .......................................................................................................... 136
List of Tables

Table 1: Survey details for Google Earth™ imagery with adequate ground resolution to resolve individual seals (See Figure 2 for example image) .......................................................... 47

Table 2: Total and adjusted counts, correction factors, and estimated abundance (+/- 95% CI for the three surveys conducted with Google Earth Imagery of Cape Cod, MA and the surrounding islands and shoals. Upper bounds of bootstrap correction factors overlapped with zero and were not calculated. .......................................................... 50

Table 3: Details of cohort of tagged animals active between September 2012 and March 2014. Behavioral activity budgets are calculated for all individuals with complete records, excluding incomplete records. .......................................................... 72

Table 4: Monthly home range summaries of the 95% kernel area (km2) across sexes. Slight sexual differences appear, but generally follow trends expected from Beck et al. 2003, Breed et al. 2006, and Breed et al. 2009. All further analyses will be conducted at the scale of individuals due to data richness considerations. ........................................ 72

Table 5: Seasonal foraging trip characteristics for male (n = 4) and female (n = 4) gray seals. ........................................................................................................................................ 104

Table 6: Paired comparisons of daily and nightly activity before and after the breakpoint show statistical differences consistently across individuals................................. 129

Table 7: Even just within just the small home range cluster, activity budgets still exhibit significant changes across the breakpoint demonstrating behavioral shifts disassociated from changes in area of space used............................................................................... 130
List of Figures

Figure 1: Map of the study area with persistent haul outs of seals marked in white. .... 32

Figure 2: Screenshot from Google Earth (Version 7.1.2.2041) running on Mac OS X 10.9.4. This image shows two large groupings of seals hauled out at Great Point on Nantucket Island, MA. The image was acquired on 12 March 2012 and is viewed at a virtual height of 220m (720ft) ................................................................. 33

Figure 3: The observable proportion of the seal population during low tide surveys exhibits a seasonal pattern. Here estimated monthly mean proportion is presented with 95% CI that overlap with seasonal estimates (warm months -- orange; cold months -- blue). The post-breeding period during the month of January during which animals recover from an energetically expensive fast is shown in red.................................................. 34

Figure 4: Representative maps of 8-day seasonal home range patterns. a) Summer season map shows home ranges of 5 tagged animals for the 8-days about 01 September 2015. b) Winter season shows home ranges of 5 tagged animals for the 8-days about 02 February 2014. ........................................................................................................ 59

Figure 5: Monthly summaries of 8-day home ranges show dramatic expansion of space use in cold months (November – March). Space use in warm months (June – October), conversely, show no change or slight declines................................................................. 60

Figure 6: A structural change in the space use pattern is set at the date of minimized deviance in of a linear mixed effects model testing the effect of the day of year on the area of home range observed. Here, models using a breakpoint in early November show clear parsimony between the seasonal patterns of space use........................................ 61

Figure 7: Individual home range estimates demonstrate the abrupt change in space use in late autumn. Vertical lines indicate key dates, the left hand bar indicating the structural change in the data and the right hand bar indicating the onset of breeding at terrestrial colonies.................................................................................. 61

Figure 8: Across the seasonal shift, there are associated differences in diurnal and nocturnal activity budgets of behavior. Reductions in surface behavior appear to be offset by large increases in diving (diurnal and nocturnal). The portion of time devoted to haul out behavior similarly declines, as does its variability, over both day and night periods .................................................................................................................. 63
Figure 9: Cluster groupings of home ranges demonstrate the temporal structure captured by the breakpoint identified through the structural change analysis (vertical black bar, November 5). .................................................................................................................. 64

Figure 10: (a) Clustering of kernel areas show three distinct groupings of small, moderate, and large home ranges. (b) Activity budgets associated with each cluster show distinct differences and reductions in variability for behavior at the surface and at depth (but not haul out) in clusters with large home ranges. ................................................................. 65

Figure 11: Cumulative and latitudinal distributions of white sharks in the NW Atlantic throughout the year. a) Cumulative distribution of sightings (across multiple years) through the year. Vertical bar is anchored to the date identified as a structural change gray seal space use patterns, when 98.2% of sharks have been observed for the year. (data courtesy G. Skomal); b) Cumulative distribution of acoustic detections of tagged sharks in 2013. Again, vertical bar is the date of structural change in gray seal space use patterns, when 97.6% of the acoustic-tagged sharks have been detected. (detection data courtesy G. Skomal); c) monthly latitudinal distribution of white sharks throughout the entire Northwest Atlantic (reproduced from Figure 4, Curtis et al. 2014). For reference, gray seals were tagged at 41 degrees North (red line in c) in June 2013........................................ 66

Figure 12: Typical movement patterns across two seasons. Summer (above) is characterized by overnight forays and concentrated use of nearshore habitats less than 12km from haul outs. Winter movement is characterized by long foraging trips over multiple days to offshore habitats................................................................................................................. 87

Figure 13: Rose diagrams of the time of day (24-hour clock) of coastal departures (left) and arrivals (right) for two seasons. Summer offshore foraging trips show a clear nocturnal pattern consistent across all tagged individuals. Winter behavior shows no discernable patterns. For reference, mean sunrise (yellow bar) and sunset (gray bar) for each season are shown using the average time of day for months of August and January, respectively. Mean vectors of the distribution are shown in red, with thickness scaled to the strength (i.e., concentration, or resultant length) of that vector. The circular uniformity in the winter distributions is evident in the weak mean vector....................... 88

Figure 14: Departures and arrivals of seasonal foraging trips in relation to the nearest sunrise or sunset event. The nocturnal cycle of summer foraging is apparent, while winter movements show no similar pattern. Histograms are color coded to match daylight periods (yellow = daylight, pink = twilight, or the 90 minutes before or after the crepuscular event, and black = night). ......................................................................................... 89
Figure 15: The mean difference between summer departures or arrivals and various reference points of twilight demonstrate the astronomical context most closely associated with the mean of the distribution. Summer departures are centered evenly about sunset (0°, when the sun is crossing the horizon). The distribution of summer arrivals, however, is left skewed and not centered around sunrise. Instead, the mean arrival is centered around a solar position of -18° below the horizon, commonly referred to as astronomical dawn.

Figure 16: Diel cycles of acoustic detections (2013-2014) of white sharks at inshore monitoring stations show three peaks of activity: dawn, dusk, and midnight local time (data and figure courtesy, G. Skomal). The temporal patterns of shark activity (blue line) is inferred as encounter risks for seals departing and arriving on summer foraging forays, which conforms with predictions of risk allocation (Figure 17).

Figure 17: Conceptual figure of risk allocation in seal behavior. Seasonal and diel variation in shark presence on shown on the right (courtesy Curtis et al. 2014, G. Skomal). This is used to reflect cycles of temporal variation experienced by seals during summer foraging trips. Activity of coastal departures and arrivals are shown throughout the day, with expected predation risk shown in the curve’s color (green = relatively safe; red = relatively risky). Departures are characterized by a peaked distribution coincident with maxima in shark presence. Though more temporally-disperse, arrivals are asynchronous with the morning peak in shark activity, indicating divergent allocation of risk on foraging trip legs.
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1. Gray seal recolonization of US marine habitats and restoration of its ecological role

Gray seals have recolonized the Northeast US emigrating from robust Canadian populations that have been increasing over the last 5 decades (Wood et al. 2011, Bowen et al. 2007). Across their range, gray seal populations are growing rapidly, expanding into previously extirpated habitat, and re-establishing their ecological role within marine ecosystems, many of which have been highly altered since depletion (Bowen et al. 2003, Wood et al. 2011, Harding and Harkoken 1999, Duck and Thompson 2007, Harkoken et al. 2007, Abt and Engler 2009, Brasseur et al. 2015). On Cape Cod and surrounding islands of southeastern Massachusetts, the establishment of a permanent breeding colony in the mid-1990s has been followed by rapid population growth and increasing concern over resulting impacts. This population growth has not been matched by an increase in research focus of their re-establishment in US marine ecosystem. Numerous knowledge gaps continue to limit scientific understanding of the adaptations of the seals’ generalist ecology within local systems. In this first study of the spatial and behavioral ecology of wild gray seals in the US, I mobilize high-resolution telemetry to monitor animal movement and behavior and analyze these data streams to understand crucial aspects and adaptations of their unique ecological role at the southern portion of their range around Cape Cod, MA, USA.
1.1 Long-standing conflicts with recovering piscivore populations

Exclusively native to the North Atlantic, gray seals (Halichoerus grypus) are a true phocid that have been well studied at large breeding colonies in Canada and the United Kingdom. Their facilitative life history with repeat annual visitation to terrestrial colonies has permitted the amalgamation of an in-depth understanding of their movement and foraging, diet and feeding, and social and reproductive ecology (Thompson et al. 1991, McConnell et al. 1999, Bowen et al. 2003, Breed et al. 2013, Russell et al. 2015). For multiple decades, intrinsic population growth at the species’ largest breeding colony in the world (Sable Island, Nova Scotia, Canada) has maintained maximal population growth for many decades (Bowen et al. 2003). The Canadian colony’s exponential population growth in the early 1990s was coincident with collapses in valuable cod (Gadus morhua), when stock abundance plummeted and prompted a fishing moratorium that shut down large portions of the groundfish fishing industry in eastern Canada (Frank et al. 2005, Frank et al. 2006, Frank et al. 2011). Due to a piscivorous diet and perceived competition with fisheries industries, gray seal recovery and population growth is implicated the groundfish stock collapse and subsequent depensation. As a result, scientific efforts have focused to understand gray seal ecology (Beck et al. 2003a-c, Austin et al. 2004, Austin et al. 2006, Breed et al. 2006, Harvey et al. 2008, Breed et al. 2009, Breed et al. 2013), dietary habits and their influence on natural mortality of commercial fish stocks (Bundy 2001, Beck et al. 2005, Beck et al. 2007, Tucker
et al. 2008, Bundy et al. 2009, Benoit et al. 2011, Harvey et al. 2012, Hammill et al. 2014, Lidgard et al. 2014), and respond to requests for population control and culling (Bowen and Lidgard 2012). On Cape Cod, concerns and conflicts about local recoveries of gray seal populations are similar in addition to impacts to recreational fishing, water quality, and beach tourism and coastal recreation. Conflicts have escalated to a point where 6 seals were found shot dead in 2011 (Goodnough 2011, NYT). To help increase scientific and public understanding and mitigate potential conflict (Morzillo 2014), I have organized this dissertation to include a regional estimate of seal abundance, annual trends in space use, home ranges, and activity budgets, and fine-scale analysis of foraging movements. My intention is for this dissertation to provide ecological findings that better define the natural role of this marine wildlife population in the public discourse.

1.2 Recovery trajectories and effects of common wildlife

Recovery of depleted populations is a foundational goal of conservation (Soule 1985, Estes et al. 2011). Appropriate research responses to a wildlife population’s endangerment and recovery however can depend on the context of its depletion and conservation. In spite of differential defaunation rates between terrestrial and marine species (Dirzo et al. 2014, McCauley et al. 2015), there are informative parallels in the depletion and subsequent recovery trajectories of some exploited populations in spite of separate environmental realms (Wilcove 2000). Many wildlife species are depleted
through direct drivers of overexploitation and habitat loss, in addition to interspecific interactions with alien species or extinction cascades (Diamond 1984, Gaston and Fuller 2008). Overexploitation can derive from high natural value of animal products (e.g., commercially valuable fish resources, fur-bearing mammals, etc.) or intentional removal due to perceived negative presence over human safety or consumptive concerns (e.g., wolves depredating wildlife; seals consuming commercial fish stocks). Bounty hunting programs codify this exploitative relationship and create incentives for rapid wildlife depletions by levying prizes for “proof of kill” of an individual wolf or seal (Riley et al. 2004, Lelli et al. 2009). In the state of Massachusetts and Maine, state governments paid five dollars per seal nose submitted up until the mid-20th century (Lelli et al. 2009).

Extirpation, or the complete local extinction of an animal from portions of its historic range, can follow overexploitation and restrict remnant populations to remote refuges with reduced threats of further exploitation, habitat loss, and other drivers of scarcity. In the parallel cases of extirpated American gray wolf and gray seal populations, neighboring remnant populations found refuge in Canada (Mansfield 1977, Weaver 1978), where they persisted and survived. Subsequently and after both species received protective measures enacting conservation mandates within US territory (i.e., Endangered Species Act, ESA; Marine Mammal Protection Act, MMPA), Canadian populations became sources for reintroduction (in the case of wolves in Yellowstone and Idaho; Bangs and Fritts 1996, Smith et al. 2003) and recolonization (in the case of gray
seals along the Northeast US coastline; Wood et al. 2011). The degree of management involvement in facilitating recovery is a primary distinction between these comparative examples. Northern Rocky Mountain gray wolves were subject to an intentional bi-national reintroduction program (Bangs and Fritts 1996, Smith et al. 2003) while gray seals in the Northeast recovered without any direct proactive interventions. Both populations, however, have had to adapt to land- and seascapes altered and modified since their extirpation (Fogarty and Murawski 1998, Frank et al. 2005, Hebblewhite and Merrill 2008).

While adapting to ecosystems that have been altered and modified by human actions is important to wildlife recovery and persistence (DeStefano and Degraaf 2003), wildlife recovery in human-dominated landscapes can also affect human-wildlife interaction and relationships (Morzillo et al. 2014, Wiens and Hobbs 2015). The ESA regulations that accompany the presence of endangered species can engender negative landowner incentives and perceptions that jeopardize stakeholder engagement in conservation (Wilcove et al. 2004). When wildlife colonizes unexpected or surprising habitats near human developments, frequent human contact and interactions with wildlife can intensify problems of wildlife impacts (DeStefano and DeGraaf 2003), concerns over presence (Carter et al. 2012), and tolerance and acceptance of regained abundances (Gomper 2002, Morzillo et al. 2014, Bruskotter et al. 2015). Though considered extirpated in central Atlantic states by the start of the 20th century, white-
tailed deer, black bears, beavers, coyote, and wild turkeys are now increasingly common in more urbanized habitats, intensifying human-wildlife conflicts (Wilcove 2000, Gomper 2002, DeStefano and DeGraaf 2003) and impacting human relationships with and behavior towards wildlife (Morzillo et al. 2014). With deer, there are now widespread concerns of herbivory limiting forest regeneration (Stromayer and Warner 1997), while beaver activity in urban and suburban areas can result in localized flooding and storm water management issues (Deblinger et al. 2004). Proliferation of landfills and garbage has sustained growth in great black-backed and herring gull populations, which are increasingly viewed as pests. The impacts of dense flocks of Canadian geese, primarily through prolific defecation, are influential enough to affect people’s acceptance of their presence (DeStefano and DeGraaf 2003).

Gray seal population recovery on Cape Cod may be best viewed in a similar paradigm, whereby rapid growth on a human-dominated coastline has intensified human interactions, disrupted coastal activities, and impacted the social capacity of acceptable pinniped densities. Local communities are now framing increasing gray seal populations as a pest management issue, their recolonizing and recovery efforts as biological invasion, and their extraordinary protections by the MMPA as unnecessary and unduly. Such relationships and perceptions (both positive and negative) affect and potentially limit intrinsic notions of wildlife acceptance capacity that governs the maximum wildlife population level of tolerable human-wildlife cohabitation (also
termed the “cultural carrying capacity”, Decker and Purdy 1988, Carpenter et al. 2000). Scientific evaluation of perceived claims and conflicts over gray seal abundance however are limited by widespread knowledge gaps in the ecological role of these animals in the Cape Cod region. In this dissertation, I attempt to provide quantitative understanding the abundance, behavior, and ultimately ecological role of gray seals locally around Cape Cod to help accommodate understanding and acceptance.

1.3 *The ecological relevance of gray seal population recovery*

An animal’s ecological role is defined as the entire set of its interspecific interactions, often primarily consumptive relationships but also including other interactions including competition, facilitation, and disease transmission (Kiszka et al. 2015). While both trophic and non-trophic interactions are re-established during recovery, most work (particularly for marine mammals in exploited ecosystems) focus on consumptive and/or competitive effects on other valued or exploited species (Kaschner et al. 2001, Morissette et al. 2012). As piscivores, gray seal population recoveries have always been embroiled in conflict over the consumption of fishery stocks like cod and flounder and the effect of seal predation on fishery rebuilding programs (Bundy et al. 2001, Bundy et al. 2005, Bundy et al. 2009, Benoit et al. 2011, O’Boyle and Sinclair 2012, Hammill et al. 2014). Beyond a fishery-centric view, the response of ecosystems and communities to growth in gray seal abundance further emphasizes their ecological importance (Kiszka et al. 2015). Swain et al. (2015) map
landscape-scale distribution shifts in gray seal prey species (cod, hake, skate) that were not observed in non-prey species, indicating potential risk-mediated spatial shifts due to growing gray seals in the St. Lawrence. In addition to redistributions of preyfish, abundance of predatory white sharks is increasing (Curtis et al. 2014) and increasing use of nearshore habitats and coastal waters along Cape Cod is targeting seal colonies (Skomal et al. 2012). Additionally, trends of harbor seals abundance are declining in correlation with increasing gray seal populations (Johnston et al. 2015) and the most recent population surveys exhibit a potential harbor seal population decline (NMFS 2015 SAR). While the causal role of gray seals in these broader changes is unclear (Skomal et al. 2012, Johnston et al. 2015), ecosystem changes seems common around gray seal population recoveries and indicates their ecological importance in nearshore temperate ecosystems.

1.4 Annual cycles of reproduction and behavior in gray seals

Gray seal foraging and life history patterns are punctuated annually by energy-intensive periods of breeding and molting when large aggregations of animals congregate at terrestrial colonies and fast. In reference to these seasonal periods, animals experience large intra-annual changes in body condition, body mass, and energy storage due to energy costs preparing for and recovering from fasting windows (Beck et al. 2003). Energy gains necessary to fuel costs of reproduction (mate acquisition in males; lactation in females) or molting are acquired through seasonally-distinct
patterns in foraging ecology, diet shifts, and diving effort as well as energy maximization strategies (Austin et al. 2004, Breed et al. 2006, Beck et al. 2007, Breed et al. 2009, Breed et al. 2013). As benthic foragers, generalist feeding behavior involves offshore movements that target diverse patches of prey fish (Breed et al. 2006, Beck et al. 2007, Breed et al. 2009). While adults exhibit a degree of diet specialization (Beck et al. 2007), sand lance (*Ammodytes* spp.) are a seasonally-integral diet item across the animal’s range that occur in patchy concentrations at shallow, inshore habitats (McConnell et al. 1999, Breed et al. 2006, Beck et al. 2007, Ampela 2009). Winter flounder (*Pseudopleuronectes americanus*), red and white hake (*Urophycis* spp.), and Atlantic cod (*Gadus morhua*) are additionally important species in gray seal diets along the northeastern United States (Ampela 2009). Foraging effort is structured across multiple temporal scales that include dive bouts (on individual patches over the scale of hours) and offshore trips (across multiple patches over the scale of days; Beck et al. 2003), when animals depart haul outs for multiple days at a time and cover tens to thousands of kilometers while targeting offshore shallow banks and ledges (Austin et al. 2004, Austin et al. 2006, Breed et al. 2006, Breed et al. 2009).

Most research from the well-studied Sable Island colony has focused on understanding periods around reproduction when sex differences are most pronounced and individuals (though more primarily, females) are under selective pressure to recover lost energy stores. Importantly, Breed et al. (2013) developed a kernel-based
analysis to understand intraspecific competitive mechanisms between age classes in heavily-used inshore habitats around central place haul outs, particularly during summer season when diet, spatial, and movement differences are diminished between adults (Breed et al. 2006, Beck et al. 2007, Breed et al. 2009) but displacement of young-of-year juveniles is greatest (Breed et al. 2013). Throughout this work I build on that work exploring ecological explanations and potential hypothesized mechanisms that can result in a high degree of spatial overlap seasonally, intense inshore habitat use, and similar behavioral patterns between individuals expected to exhibit a high degree of variation.

1.5 Dissertation overview

To anchor baseline understanding about the ecological role of gray seals in US marine habitats, I employ quantitative methods to evaluate the abundance, movement, space use, coastal behavior, and offshore forays of animals tagged with GPS telemetry devices in Chatham, MA. Chapter 2 produces the first known regional abundance estimate of gray seals by identifying dominant seasonal patterns in haul out behavior, using these to calculate correction factors of unobservable proportions of the population, and applying these corrections innovatively to beach counts from publically-available satellite imagery. Chapter 3 assesses space use through time to quantify seasonal changes in distribution and activity budgets that demonstrate behavioral differences that may underlie an adaptive annual cycle and have hypothetical life history
implications. Chapter 4 investigates summer season’s exclusively-nocturnal foraging behavior, when tagged animal’s movement ecology and coastal behavior are bounded by crepuscular changes and interact with divergent levels of shark presence in ways indicative of risk-sensitive foraging. In all, I produce novel understandings of gray seal ecology within intact predatory relationships at the southern extreme of the breeding range and provide directions for future research.
2. Google Haul Out: digital aerial surveys in coastal wildlife management and abundance estimation

2.1 Introduction

Population monitoring is a key aspect of both wildlife species conservation and resource management. Knowledge of an organism’s abundance is essential to the ecological understanding of trophic relationships and ecosystem structure (Kiszka et al. 2015). Additionally, due to the role of abundance trends in triggering policy regulations (e.g., listing criteria), population data can dictate human relationships with wildlife, direct mitigation measures of harmful interactions, and determine attitudes and values about species conservation (Decker and Purdy 1988, Redpath et al. 2013). Population monitoring is thus a fundamental source of information both in assessing the decline of endangered and threatened species and in evaluating the recovery of re-established species (Lancia et al. 2005).

The critical nature of this data to species management has elicited the development of a diverse range of analytical methods and data sources that include targeted surveys, opportunistic sightings, biotelemetry, and harvesting records (Lancia et al. 2005). For most scientific and management purposes, abundance estimates are drawn from targeted surveys that are designed to account for sources of bias and error. The focus of these surveys are often species of conservation concern and the surveys are conducted to ensure accuracy of low-density population estimates or commercially-exploited populations to safeguard long-term viability and resource sustainability. In
cases of rapidly-increasing populations of recovering wildlife, population growth may
outpace the design of dedicated surveys targeted to track precise changes in abundance
and result in knowledge gaps. Such incomplete information limits successful
management of wildlife, exacerbates conflicts with wildlife population recoveries, and
can harm societal perceptions of conservation successes (Carpenter 2000, Redpath et al.
2013).

Difficulties enumerating marine species often dictate the specific design features
of these surveys (Lancia et al. 2005, Taylor et al. 2007). Compared to terrestrial
counterparts, many marine species are inaccessible, largely unavailable, and sometimes
cryptic. As such, at-sea surveys for mobile marine species are expensive, requiring large
amounts of ship time and extensive human labor. They are also often imprecise and
occur less frequently than necessary because of large inherent costs (Taylor et al. 2007).
For marine animals that periodically return to coastal locations (e.g., pinnipeds;
seabirds), surveys can capitalize on predictable returns to terrestrial colonies and
aggregation habitats to produce reliable and robust survey counts. In these cases, new
remote sensing approaches may produce sufficient data for abundance estimation and
reduce the need for costly aerial surveys (McMahon et al. 2014).

In particular, recent advances in remote sensing and networked geospatial data
archives represent a growing opportunity for researchers to augment traditional
population assessment programs for some marine species (Laliberte and Ripple 2003,
LaRue et al. 2011). Satellite and aerial survey data collected at extremely high-resolution for commercial purposes are becoming increasingly accessible to researchers for scientific projects (e.g., Geo-EyE1, WorldView-1, WorldView-2, QuickBird-2), including the remote assessment of populations of marine organisms that use terrestrial habitats to rest, molt or breed (Fretwell and Trathan 2009, Hughes et al. 2011, Platonov et al. 2013). For example, relatively high-resolution data archives have been used to identify, monitor and even assess a number of marine vertebrate populations in remote locations including penguins (Fretwell et al. 2012), seals (McMahon et al. 2014) and whales (Fretwell et al. 2014). These remote assessments require careful calibration and correction to produce useful estimates of abundance (McMahon et al. 2014). While abundance estimation has been accomplished for some species of penguins (Fretwell et al. 2012, Lynch and Schwaller 2014, Lynch and LaRue 2014), most marine mammal satellite-based surveys have focused on verifying simple counts (McMahon et al. 2014, Fretwell et al. 2014) and have not provided correction factors to scale counts to estimates of abundance.

2.1.1. Gray seals in the Northeast United States

Gray seals are a large phocid seal found only in the waters of the North Atlantic Ocean, from approximately N 71.3° to N 40.3°. They are gregarious animals that spend their time ashore in colonies throughout the year (Hall 2002). Gray seals were depleted in the Northwest Atlantic during the 19th and 20th centuries, through a combination of
harvests and directed bounties and were believed to have been extirpated in Canadian and US waters until the 1960s (Lelli et al. 2009, Wood et al. 2011). Since that time they have recovered across the range (Bowen et al. 2007, Wood et al. 2011), with the largest breeding colony found on Sable Island, Nova Scotia, Canada (Bowen et al. 2003). The recovery of gray seals in eastern Canada has been well studied at Sable Island (Bowen et al. 2003, Bowen et al. 2007). The population was rediscovered in the late 1960s (Mansfield 1977), and pup production increased exponentially at 12.8% per year between the 1970s and 1997 (Bowen et al. 2003) but declined to about 4% growth per year between 2007 and 2010 (Bowen et al. 2007).

The recovery of gray seals in the Gulf of Maine is also evident. Beach counts of gray seals are increasing, and the number of pups born at Muskeget Island—the largest known breeding colony of gray seals in US waters—has been rising rapidly since the first recorded observations of pupping in the US. While these indices illustrate that gray seals are recovering rapidly from exploitation in the Gulf of Maine (Wood et al. 2011), very little is known about their true present abundance, despite the importance of this information to ongoing ecological and demographic studies in addition to management efforts. In general, there are two approaches to abundance estimation in pinnipeds: 1) correction methods that adjust survey counts for various biases (e.g., correction factors; Gilbert et al. 2005, Lonergan et al. 2011); and 2) modeling methods that predict the population on the basis of biological (e.g., age- and sex-specific mortality) and
production (e.g., age of primiparity, etc.) mechanisms (e.g., pup production; Myers and Bowen 1989, Mohn and Bowen 1996, Bowen et al. 2007). Generally, pup production modeling methods are preferable given access to pups during post-weaning phases when reliable absolute counts can be made (Bowen et al. 2007). However, this method is effort- and data-intensive, requires known estimates of key life history parameters (e.g., mortality, productivity), and is less viable for unstable populations subject to immigration in addition to intrinsic growth. For the purposes of this study, the U.S. gray seal population growth is supplemented by immigration and exchange with neighboring Canadian populations at or near carrying capacity (Breed et al. 2009, Wood et al. 2011, Wood 2009) and thus a correction-based approach is most appropriate for implementation.

Here, we assess the potential of adopting opportunistic earth observation imagery data for surveying a coastal pinniped species in coastal habitats of Southeastern Massachusetts. Multiple single-day synoptic surveys across multiple years were conducted using archived imagery publicly available in Google Earth™, tallying the abundance of seals visible on coastal beaches. These raw beach counts were integrated with additional biotelemetry and observational data to estimate regional abundance of gray seals (*Halichoerus grypus*) in southeastern Massachusetts that accounts for two potential sources of error: 1) potential interspecies mixing with sympatric harbor seals (*Phoca vitulina*) at surveyed locations; and 2) the proportion of the local population not
available to the surveys. Through the application of traditional methods of seal abundance estimation to atypical opportunistic survey imagery, we identify the benefits, drawbacks, and additional considerations of utilizing new satellite-based sources of beach imagery as a population assessment tool.

2.2 Methods

2.2.1. Remote Sensing Imagery

We employed remote sensing imagery of the coastline of Southern New England available in the freely downloadable application, Google Earth™. Current and archived imagery was collected for time steps that exhibit adequate ground resolution to distinguish individual seals at known haul outs along the ocean-facing coastlines of Cape Cod, Nantucket, and Martha’s Vineyard, Massachusetts, including coastlines of nearby smaller islands and shoals (Figure 1). This resulted in synoptic beach imagery of the region for March 12, 2012, June 16, 2014, and May 24, 2015. Assessments of known tidally-dependent sandbars, water levels, and shadow directions within Chatham Harbor, Cape Cod were used to estimate the point in the tidal cycle of image capture (Table 1).

2.2.2. Digital aerial survey

The coastline of Southeastern Massachusetts from N 41.15° to N 42.12°, including the shoreline of all islands and sandbars was surveyed from a digital altitude of approximately 200-300m (Figure 1). For all images, seal haul outs and aggregations
were identified visually and all individuals counted. An example of one haul out image is presented in Figure 2. To tally individuals, screen captured images of each haul out were taken and then loaded into a specialized data collection software (Logger Pro) for counting. In Logger Pro, each seal was marked with a dot and logged. Counts were then tallied on each image to produce a total number of seals at each haul out. Initial counts of dense haul outs, where seals were tightly packed, were counted by three separate individuals and address any observer bias arising from densely packed targets on images. As multiple surveys of the same image revealed no apparent observer bias, counts were then conducted individually by trained observers.

2.2.3. Correction factors for interspecific haul out mixing.

Gray seals and harbor seals are known to haul out in the same locations in the Cape Cod region (NMFS 2015). To correct overall pinniped beach counts for interspecific mixing, a regional mixing rate of 0.83 was estimated using direct haul out observations reported in DiGiovanni et al. (2011). Due to the conservative nature of the survey, this rate was applied to all beach counts despite observational knowledge species composition at haul outs changes seasonally and that gray seals are now dominating many haul outs. Due to this and other conservative assumptions made at all other modeling stages, the estimates presented here should be viewed as minimum estimates.
2.2.4 Correction factors for haul out probability

To estimate the abundance of gray seals in the region, beach counts must be scaled to account for animals not on land (and thus not counted) during the survey window. This likelihood is dependent upon the probability of animals exhibiting haul out behavior, where they exit the water and rest on sandy habitat above the waterline. Haul out data was collected from 8 GSM/GPRS telemetry tags (SMRU, St. Andrews, Scotland) deployed on gray seals caught in June 2013 at a local haul out near Chatham, MA (USA) and attached with quick-setting two-part epoxy (n.b. one tag was deployed opportunistically on a juvenile in September 2012). Both males (n=4) and females (n=4) were tagged, including one juvenile in each sex. For the remainder of the tag record (range: 2-9 months), the telemetry devices monitored the tagged animal’s movement, diving activity, local water temperatures, and haul out behavior and transmitted the data to servers via the GSM network. All haul out records were examined, a total of 8155.4 hours of relevant animal behavior, and aggregated to quantify haul out rates at monthly and seasonal scales. A haul out record is initiated when the tag has been continuously dry for 10 minutes, at which point the tag records the location, date, and start time. The record is completed when it senses it has been wet for 40 seconds, at which point it records the haul out record’s end time. Using these start and end times, the total number of seconds of each haul out record was calculated easily. All haul out records located at sea or away from land were removed.
Correction factors that adjust survey counts into abundance estimates by accounting for the proportion of the population surveyed are calculated following standard pinniped survey techniques (i.e., monitor beach behavior at low tide when the maximum beach, and thus haul out habitat, is exposed) and published analytical methods (Lonergan et al. 2011). Thus, beach count results were converted into population estimates by dividing raw counts (adjusted for interspecies mixing) by the estimated proportion of the population observable during the survey windows (Ries et al. 1998, Jeffries et al. 2003, Gilbert et al. 2005). This proportion is estimated from the probability of observing tagged individuals during a low tide survey (Lonergan et al. 2011), defined as the 2 hours before and after daytime low tide (Watts 1996, local low tides from NOAA tidal record, tidesandcurrents.noaa.gov, station ID 8447435).

In the case of continual behavioral telemetry monitoring (as compared to point detections with radio telemetry), the probability is calculated from the proportion of time tagged individuals exhibit haul out behavior (i.e., “observable”) to the amount of time surveyed (i.e., the 4 hours of low tide survey). This ratio is tallied daily across all active tags, then converted into a correction factor and used in an abundance estimate for each day of the telemetry study (June – March) in order to propagate the uncertainty completely. Each metric (i.e., proportion of population available, correction factor, and abundance estimates) is summarized at the monthly scale as well as across seasonal (warm months: June - October; cold months: November - March, excluding January).
during the post-breeding period) to supplement periods of low tag numbers at the ends of the data set. Further emphasizing the intentional precautionary approach and accounting for bias in low tag numbers (n = 3-8 depending on the month), probabilities for days without tagged individuals observed hauling out were neglected and instead imputed from a random normal centered on that month’s mean and standard deviation. To further account for scaling low tag sizes to population parameters, a bootstrapping procedure (5000 replicates) with individual animals as the resampling unit was used to account for unsampled individual variation from the inter-individual variability within the tag dataset.

2.3 Results

Over 4 years, Google Earth™ imagery of adequate resolution was available for surveys for 3 dates, all at least a year apart. Data from these surveys is presented in Table 1, including date of image capture, approximate time of day and tidal cycle, total seals counted, and estimated number of gray seals corrected for interspecific mixing. The synoptic beach counts for two surveys (2012 and 2015 counts of 15,331 and 20,554 total seals, respectively) matches the scale of a single-day maximum count captured in March 2011 from a traditional aerial survey and reported in stock assessments (15,756 gray seals, NMFS 2015), furthering our confidence in these two digital survey counts. June 2014 survey totals are much lower than raw beach counts in all other surveys and were deemed unreliable, likely due to inopportune tidal cycle for monitoring beach
wildlife particularly around the region’s tidal sandbars. This is further confirmed by a high degree of seals observed in shallow waters around traditional haul out sites for this survey date (J. Moxley, unpublished data). Correcting these total counts for mixing of gray and harbor seals at haul out sites, an estimated total of 12,725 and 17,060 gray seals are observed on the study area’s beaches for 2012 and 2015 surveys, respectively (Table 1). Despite known mixing at haul out colonies, this number is likely an underestimate of gray seals since 1) gray seals are known to account for increasing proportions of regional haul outs; and 2) the application of the correction factor for interspecific mixing does not account for temporal or spatial variation in haul out composition. However, the novelty of this approach and methods (described above) suggests that a conservative approach is preferable.

Estimates of the mean proportion of a daytime, low tide survey window that animals spend hauled out followed an apparent seasonal pattern. Figure 3 shows monthly rates (mean +/- 95% confidence intervals) of haul out behavior around low tides. During warm months (June - October), haul out behavior is nearly daily and occurs regularly in at least 50% of survey windows. Beginning in November, haul outs become more infrequent and the time between consecutive haul out periods lengthens. Haul out behavior is infrequent in the month of January during a post-breeding period after adult animals emerge from fasting and presumably increase foraging effort to recover body mass and energy stores lost during reproduction. Given stark differences
between months of different seasons (e.g., warm: June - October; and cold: Nov - March excluding post breeding behavior in January; ANOVA with Tukey multiple comparisons: F = 18.87, p < 0.000001), haul out behavior was also summarized in seasonal metrics (see shaded boxes, Figure 3, comprising 95% SE around the mean).

By applying the most appropriate monthly and seasonal correction factors, Table 2 lists the abundance estimates for each survey for both total seals counted and estimated gray seals that applies the interspecific mixing factor in addition to haul out correction factors. Estimates from 2012 and 2015 are considered the most reliable, and suggest a range of gray seals between 30,000 and 50,000 animals using monthly correction factors. Seasonal correction factors aggregate from more individuals over a greater period of time, and thus reflect a more variable range of possible abundance estimates. The 2012 survey counts are potentially affected by an increase in haul out behavior due to impending molt in late March and early April, when animals attend haul out sites for elongated periods while fur is molted and regenerated. However, seasonal estimates using 2015 survey counts and a warm season haul out correction factor encapsulate monthly estimates of both 2012 and 2015 abundance estimates, furthering confidence that the true mean lies within this 95% CI of this estimate. Given the range of these various estimates, it is safe to assume the minimum population size of gray seals in Cape Cod region is 30,000 animals and is likely higher due to the conservative estimation approach and data limitations.
2.4 Discussion

In this study, we demonstrate the capabilities of using digital aerial surveys to produce regional abundance estimates when integrated with biotelemetry devices that can monitor behavior and produce correction factors. Monitoring wildlife colonies through satellite-based imagery is becoming more common, though mostly as an additional source to corroborate traditional surveys or supplement counts in difficult to survey regions (Fretwell and Trathan 2009, Fretwell et al. 2012, McMahon et al. 2014). This study extends this novel remote sensing data source further by applying correction factors to estimate the regional abundance of a recolonizing, rapidly-increasing coastal predator population. As such, the utility of the present method demonstrated here introduces new considerations for management funding priorities between traditional population surveys and technologically-novel solutions. If adequate imagery can be harnessed cost-effectively, funding could be redirected towards individual-based behavioral monitoring through telemetry that dually supports a broader set of scientific and management objectives beyond abundance estimation. As a first demonstration of concept for marine mammals (see Lynch and Larue 2014), this study outlines both benefits and drawbacks that must be considered in future applications.

First, given the growing ubiquity and expansion of earth imagery, wildlife ecology should embrace new data sources that can supplant traditional methods and release dedicated resources (funding and effort) to other scientific aims (Laliberte and
Ripple 2003, Horning et al. 2010). Spatially-explicit traditional survey methods can be expensive, effort-intensive, and error-prone (Taylor et al. 2007), while undirected imagery is being collected frequently for many portions of the globe at increasingly relevant resolutions by third party commercial operators. Variable ground resolution in freely-available Google Earth impedes implementing this method for other stretches of the Western Atlantic gray seal stock (e.g., Maine, eastern Canada). Still, adequate imagery of these areas is likely available in fee-based formats from other commercial imagery providers. By taking advantage of commercial structures already in place to pay for image acquisition, scientists may be able develop survey counts in a more cost effective manner in comparison to dedicated surveys that require design, effort, and execution within already tight management budgets. Growing applications of unmanned aerial vehicle systems similarly present technological solutions to acquire the equivalent imagery at lower costs (Linchant 2015). Cost-savings in image acquisition can be applied towards data-rich telemetry approaches that produce correction factors (sensu Lonergan et al. 2011), as demonstrated here, as well as document movement, foraging, and other unique associated behaviors that produce a rich database of species ecology (Cooke et al. 2004, Hart and Hyrenbach 2009, Block et al. 2011, Kays et al. 2015, Wilmers et al. 2015). Given the ubiquity of funding constraints, methods that support a more diverse range of objectives ought to prevail over single purpose approaches (Hart and Hyrenbach 2009, McIntyre 2014).
Survey design must be able to control sources of bias and precision in order to be effective and drawbacks exhibited in this study serve to guide future applications and implementation of satellite-based methods as a substitute of tradition population assessment methods. Opportunistic imagery permits no control of season or time of day of imagery, thus affecting surveys that utilize aspects of species biology (e.g., aggregations due to behaviors such as breeding and molting) or habitat changes (e.g., maximization of survey-capable habitat at low tide or times of the year with high background contrast or low obstruction from vegetation or clouds) to improve survey counts. In response to this and other explicit assumptions to ensure conservative estimates, I purposefully executed a precautionary modeling approach at all stages of estimation. However, commercial image databases have greater sampling frequency and specific imagery can be selected that matches the most sensible time frame and time of year for population surveys (McMahon et al. 2014) or ensures surveys account for environmental factors affecting animal behavior (Simpkins et al. 2003). Opportunities to schedule commercial image capture furthers the method by allowing repeat imaging throughout the year or intensively across a few days to develop robust and precise population estimates (McMahon et al. 2014).

For surveying endangered species or other species of concern where highly-accurate abundances are paramount, a targeted approach that utilizes a scheduled remote imaging effort presents a great opportunity for an adaptive and accurate
technological solution for monitoring abundance and the trajectory of populations, particularly in remote areas difficult to survey. In cases of recovering populations or animals of less conservation concern, exact accuracy may be less important than an understanding of population growth and trends (Buckland et al. 2000). In these cases, the approach executed in this study may be initially sufficient to address questions about population size without devoting resources or effort on a targeted traditional survey.

Recovering gray seals along the Northeast US coast are an ideal case for applying this approach. Their recent recolonization and rapid growth have led to concerns and questions about their impacts and conflicts in the marine ecosystems and communities around Cape Cod (Rafferty et al. 2012, Bogomolni et al. 2010, O’Boyle and Sinclair 2012, Johnston et al. 2015). Unfortunately, the growth of the population has not been matched by increased research focus, largely due to limited funding and prioritizing species of concern (e.g., the highly-endangered right whale and Atlantic salmon, etc.) over thriving gray seal colonies. Resultant knowledge gaps about the species local ecology have therefore precluded some management actions (e.g., minimum population size, calculation of potential biological removal), despite evidence of direct and indirect interactions with commercial and recreational fishing sectors (Rafferty et al. 2012, Nichols et al. 2014, Johnston et al. 2015), societal concern over space conflicts and water quality (Bogomolni et al. 2010, Gast et al. 2012), and potential impacts on other protected
species (harbor seals, Johnston et al. 2015; white sharks, Skomal et al. 2012). This study demonstrates the initial capabilities of telemetry investments to harness data from freely-available imagery in order to produce knowledge for a key management metric—abundance estimates in a changing regional population.

Telemetry data additionally uncovered seasonal patterns in the regional haul out behavior of gray seals, characterized by an amplified occurrence and longevity of haul out behavior in the warmer months (June - Oct of tagging record) and a rapid shift to less frequent haul out activity in cold months (Nov - Mar of tagging record, Figure 3). These haul out patterns are likely driven by a combination of factors, including prey availability, predation risk, and other dynamic environmental conditions. Without a clear delineation of the molting assembly which aggregations are often targeted for monitoring surveys (G. Waring, personal communication), this seasonal pattern suggests summer surveys have access to the largest proportion of the population and can minimize estimation errors in future surveys. The opportunistic imagery available to this study exhibited variability between surveys on different dates. While we apply correction factors to all survey counts, ecological reasoning can help us narrow our confidence in the abundance estimate, eliminating estimates that are lower than total beach counts available in other surveys both before and after the low counts (e.g., 2014 survey). These larger beach counts are further validated by total beach counts reported in stock assessment reports, lending additional credibility to these estimates (NMFS
2015). The remaining range of point estimates provide an upgrade of a much-cited single beach count (NMFS 2015) to the first abundance estimates of gray seals for the Cape Cod region, while still representing a minimum abundance estimate due to purposefully conservative modeling assumptions.

As the range of our abundance estimates suggests, the gray seal population appears to have grown dramatically in abundance and are now an abundant marine predator in the waters of the Gulf of Maine. The rapid growth supports other observations that the population is experiencing both intrinsic growth and immigration from other populations (Breed et al. 2009, Wood 2009, Wood et al. 2011). Trends in pup growth from tens of individuals in the early 1990s to 2,095 in 2008 (the most recent publicly-available pup count, NMFS 2015) are fit well by exponential curves that further support growth via intrinsic and extrinsic sources (Wood 2007). Even still, single day beach counts are increasing rapidly and breeding colonies are expanding into additional sites within the region. With this dramatic growth of a visible marine predator, there is growing recognition of the impacts and role of these animals to the future of the region’s marine ecosystems. Operational interactions with fishing activities are increasing (Rafferty et al. 2012, Nichols et al. 2014, Johnston et al. 2015) and there is growing concern about consumptive impacts of a large regional seal herd. Sympatric marine predators are also responding to local growth in gray seal populations, as white sharks are observed more frequently around Cape Cod (Skomal et al. 2012) and harbor seals are
less frequently observed in traditional areas of presence (G. Waring, personal communication). Issues of environmental health and disease ecology may be affected by abundant gray seal colonies (Gast et al. 2012, Runstadler et al., in review). Rapid growth in this pinniped colony and widespread response from natural and human communities underline the ecological importance of these animals to marine ecosystems and defines priorities in understanding their ecological role, which begins with abundance estimates.

2.5 Conclusion

This dramatic growth of the Cape Cod region’s gray seal population has been remarkable, but not well monitored due to alternate funding priorities and regional research interests. We outline a technological approach that produces the first abundance estimates of a marine mammal from publically available remote sensing imagery. The generalizable approach and growing ubiquity of high quality imagery sources for earth observation suggest this method can serve an important role in monitoring and estimating abundance for a wide variety of other species not the focus of funding or devoted survey efforts. As researchers embrace new sources of imagery, cost-effective savings can be applied to other methods like telemetry that can produce correction factors for abundance estimates, monitor a range of behaviors, and supplement numerous research questions with ancillary data streams. As demonstrated by the variability in the counts and resulting estimates, this method is not a complete substitute for traditional population monitoring efforts, particularly for species of
concern where precision is a high priority. However, it does expand the opportunities for high quality abundance monitoring and population trajectories to more species than currently considered by management agencies. Furthermore, it outlines a technological solution to a common management concern (i.e., population monitoring) that is likely more cost-effective, accurate, and repeatable than traditional dedicated surveys, while preserving valuable funding for other research priorities that supplement a range of scientific questions.
Figure 1: Map of the study area with persistent haul outs of seals marked in white.

Table 1: Survey details for Google Earth™ imagery with adequate ground resolution to resolve individual seals (See Figure 2 for example image).

<table>
<thead>
<tr>
<th>Year</th>
<th>Survey Date</th>
<th>Low Tide (EST)</th>
<th>TOD</th>
<th>Tidal Cycle</th>
<th>Total Seals</th>
<th>Est. Gray Seals</th>
</tr>
</thead>
<tbody>
<tr>
<td>2012</td>
<td>3/12/2013</td>
<td>11:18</td>
<td>Late AM</td>
<td>Near Slack</td>
<td>15331</td>
<td>12725</td>
</tr>
<tr>
<td>2014</td>
<td>6/16/2014</td>
<td>10:43</td>
<td>Early AM</td>
<td>Falling</td>
<td>3816</td>
<td>3167</td>
</tr>
<tr>
<td>2015</td>
<td>5/23/2015</td>
<td>13:10</td>
<td>Late AM</td>
<td>Falling</td>
<td>20554</td>
<td>17060</td>
</tr>
</tbody>
</table>
Figure 2: Screenshot from Google Earth (Version 7.1.2.2041) running on Mac OS X 10.9.4. This image shows two large groupings of seals hauled out at Great Point on Nantucket Island, MA. The image was acquired on 12 March 2012 and is viewed at a virtual height of 220m (720ft)
Figure 3: The observable proportion of the seal population during low tide surveys exhibits a seasonal pattern. Here estimated monthly mean proportion is presented with 95% CI that overlap with seasonal estimates (warm months -- orange; cold months -- blue). The post-breeding period during the month of January during which animals recover from an energetically expensive fast is shown in red.
Table 2: Total and adjusted counts, correction factors, and estimated abundance (+/- 95% CI for the three surveys conducted with Google Earth Imagery of Cape Cod, MA and the surrounding islands and shoals. Upper bounds of bootstrap correction factors for the winter season overlapped with zero and were not calculated.
3. Reduced space use and rapid changes in activity budgets of Cape Cod gray seals.

3.1 Introduction

The ways animals access food resources and expend energy have important consequences for foraging ecology, energy gain, and ultimately reproductive fitness. An individual’s strategy of energy gain for fueling a reproductive attempt is largely determined by a species’ life history (Stearns 1992, Stephens et al. 2009). Integrating annual life history decisions longitudinally, an individual is expected to allocate resources and expend reproductive efforts in efficient manners that maximize lifetime fitness by balancing short- and long-term costs and benefits (McNamara et al. 1991, Houston 2006). For mobile animals, resource acquisition can be observed in the spatial patterns of an individual’s movement as it interacts with its environment. Ultimately, this resource acquisition must support growth, reproduction, and survival needs (Aarts 2008, Nathan et al. 2008). Changes to space use patterns often reflect shifts in these history demands as the underlying movement tracks environmental fluxes in abiotic (e.g., temperature), biotic (e.g. nutrient blooms), or predator and prey fields (Nathan et al. 2008).

Due to different tactics of energy utilization during reproduction, capital or income breeding life histories generate different expectations about foraging behav
and space use patterns (Houston et al. 2006, Stephens et al. 2009). Whereas income breeders use energy acquired concurrently with reproduction, capital breeders must finance reproduction through energy stores acquired prior to breeding and accumulated through surplus foraging that could lead to starker space use changes (Stearns 1989, Stearns 1992, Houston et al. 2006, Stephens et al. 2009). Long-lived, iteroparous pinnipeds often adhere to one of these life history strategies in manners expected to maximize lifetime reproductive fitness (Costa 1991, Schulz and Bowen 2005). Due to the temporal separation of resource acquisition and expenditure in capital breeders (Costa 1991), pre-breeding foraging decisions must balance costs and benefits of energy gain and storage for both the current breeding opportunity and future reproductive opportunities (Williams 1966, Newton 1989, Jonnson et al. 1998). Research has focused on benefits of foraging to reaching energetic thresholds for successful reproduction and recovery (McNamara et al. 1991, Pomeroy et al. 1999, Mellish et al. 1999, Mellish et al. 2000, Crocker et al. 2001, Schulz and Bowen 2004, Crocker et al. 2011, Milner et al. 2012), a further ecological testament to the principle that food equals love. Comparatively, there is less discussion about pre-breeding costs to increased foraging and resultant mass gain necessary for achieving a reproductive state.

Fattening and energy gain in mammals is facilitated through reductions in metabolic rate (Markussen et al. 1992, Fuglei and Ortland 1999, Sparling et al. 2006,
Szafranska et al. 2013, Rosen and Trites 2014), increased energy intake through selection of higher quality or quantity of food (Beck et al. 2007), or some combination of both (Dark and Zucker 1986, Speakman and Rowland 1999). Though optimal energy gain strategies are commonly evaluated in animals preparing for migration (Totzke et al. 2000, Butler and Woakes 2001) or hibernation (Kunz et al. 1998, Carey et al. 2003), relatively little attention is given to pre-breeding fattening and costs associated with mass gain in capital breeders. Pervasive physiological tradeoffs underlie the change in reproductive state variables within annual routines that result in changes to behavior (e.g., initiation of breeding, migration, hibernation) and activity (Zera et al. 2001, Houston et al. 2006, McNamara and Houston 2008). While the benefits of energy gains to achieve successful reproductive states are well studied (Houston et al. 2006), costs of energy gain to metabolism and thermoregulation, risk of predation or injury, and effects on locomotion and maneuverability are relatively unexplored (Houston et al. 1993, Jonsson 1997, Jonsson et al. 1998). In small animals, energy gains mitigate effects of starvation and lean foraging periods, but often incur greater predation risk due to increased foraging and higher metabolism required to support a larger mass (Welton and Houston 2001). In birds, mass gain can make the individual less able to escape predators (Witter and Cuthill 1993, Gentle and Gosler 2001, Hedenstrom 2001) and increase locomotion costs of flight (Gosler 1995, Veasey et al. 1998).
Many pinnipeds exhibit large changes in body condition during their annual cycle related to breeding life histories, and can maximize energy gain through a mixture of metabolism reductions (Sparling et al. 2006) and surplus foraging (Jonsson 1997, Beck et al. 2003, Breed et al. 2006, Beck et al. 2007). The gray seal (Halichoerus grypus) is a large-bodied, long-lived (> 40 years), size-dimorphic phocid found throughout temperate coastal areas of the North Atlantic (71.3°N and 40.3°N). Male and female gray seals exhibit capital breeding strategies to fuel costs of mate acquisition or lactation and offspring provisioning (Iverson et al. 1993, Lidgard et al. 2005). Beck et al. (2003) monitored intra-annual energy storage and body condition in wild gray seals, associating non-linear mass gain with intensification of diving effort (Beck et al. 2003) and diet switching (Beck et al. 2007) while Sparling et al. (2006) noted metabolism reductions in captive seals in advance of breeding periods. Seasonal space use and movement patterns change in association with annual breeding routines, switching from reduced summer foraging effort in concentrated coastal areas to long-range forays over multiple days to offshore habitats (McConnell et al. 1999, Matthiopolous et al. 2004, Breed et al. 2006, Breed et al. 2009, Breed et al. 2013, Cronin et al. 2013). Changes in home range size and space use patterns encompass the shift in movement adjusting to counteract incipient energetic losses in winter breeding and subsequent molting (Austin et al. 2004, Austin et al. 2006, Harvey et al. 2008, Baker et al. 2015).
While most understanding of gray seal ecology comes from well-studied populations in the United Kingdom and Canada, a small and growing subpopulation of gray seals with expanding breeding colonies has recently established in southeastern Massachusetts where they are reassuming an ecological role in the region’s ecosystems (Wood et al. 2011, Wood 2009, Chapter 2). Ecological research, however, has not kept pace with rapid growth in this colony, resulting in broad knowledge gaps about the ecology and space use of these animals at the southern extreme of their range. This study presents the first known space use estimates for telemetry tracked, free-living adult US gray seals and quantifies structural change between seasonal patterns in home range size. Across this seasonal break, associated changes in activity budget and individual variation are investigated. Resulting space use and activity budget patterns are investigated from a novel context of reduced summer foraging in a capital breeder attempting to bulk up for reproduction at the warmest breeding colony in the species’ range while surviving within an active and seasonally-dense predator field.

3.2 Methods

3.2.1 Data collection and processing

In June 2013, 7 GPS/GSRM telemetry tags (Global System for Mobile Communications/General Packet 145 Radio System, SMRU Instrumentation, St. Andrews, Scotland) were deployed on adult (>3 years old, n = 6 individuals, 4 females, 3
males) gray seals during the post-molt period. Individuals were live-caught in beach seines (Jeffries et al. 1993, Waring et al. 2006) at a tidally-dependent sandbar haul out within the harbor of Chatham, MA, USA (41.67° N, 68.95° W) and sedated intramuscularly with 0.58-0.8 mg/kg of 100mg/ml tiletamine/zolazepam (Telazol®, Fort Dodge Animal Health, Fort Dodge, IA; see Baker et al. 1990). Following attachment methods of Goulet et al. 2001 and Jessop et al. 2013, the telemetry device (10 cm x 17 cm x 4 cm, 370 g in air) was affixed to the dorsal neck/head region of the animal’s fur using quick-setting epoxy-based adhesive. In addition, 1 tag was deployed opportunistically in September 2012 on a rehabilitated juvenile male released on Cape Cod, MA, USA. In total, 4 adult females, 3 adult males, and 1 sub-adult male were tagged. For the subsequent 2-9 months, tags monitored the animal’s movement, diving activity, local water temperatures, and haul out behavior and transmitted data to servers via the GSM network.

To evaluate changes in space use patterns of gray seals over the foraging and breeding season, I used a robust product kernel method (Keating and Cherry 2008) available in the adehabitat package (Calenge 2015) in the R development environment (R Core Team). This method extends traditional utilization distribution (UD) methods by allowing additional dimensions, including time in linear or circular units, to be modeled in addition to geographic units x and y. Bandwidths for x and y were set at
1000 m after initial exploration of the data. Once monthly statistics were calculated (sensu Breed et al. 2006), a temporal smoothing unit of 8 days was selected as a median value of foraging trip lengths across sexes and seasons observed in other gray seal populations (Breed et al. 2009) so that resulting UDs could encapsulate entire foraging events. All analyses were tested with adjusted smoothing parameters, including temporal windows between 3 and 30 days, to ensure consistencies in patterns observed that were not related to assumptions regarding model parameters. In spite of known autocorrelation, De Solla et al. (1999) concluded that removal of autocorrelation from animal tracks does not improve kernel home range estimates and so no adjustments were made to the time series.

### 3.2.2 Home range analysis

Using the entire temporal range of location data for all animals, a spatio-temporally smoothed UD was calculated every 8th day after the beginning of the tag record. Based on average foraging trip durations reported in Breed et al. (2009), 8-day smoothing windows should encapsulate the scale of entire foraging movements. Preliminary analyses showed no changes in the space use patterns across a wide range of temporal windows between 3 and 30 days. For each UD, the home range during that sampling period was derived from a 95% spatially-explicit isopleth with area in square kilometers. Regression modeling was then used to assess changes in space use and area
covered over time. Due to apparent structural changes in the data, a segmented regression approach with a breakpoint sensitivity analysis was used to quantify temporally observed shifts in distribution and behavior. A segmented regression was fit iteratively with breakpoints between October 1 and January 1 and monitoring the change in deviance explained. Anchoring the breakpoint at the partition that minimizes deviance, a Chow test is used to test statistical significance of this structural change (Chow 1960).

### 3.2.3 Behavioral and cluster analysis

To understand potential behavioral changes underlying shifting space use patterns, behavioral rates and individual variability were compared across the two periods identified in the home range analysis. Activity budgets in terms of time spent at depth, at the surface, or hauled out on the beach were tested with non-parametric rank sum tests. Changes in these budgets reflect shifts in time allocation to various behaviors between the two periods established via the segmented regression techniques described above. To assess individual variation, a k-medoids clustering analysis was conducted on spatial home range estimates. Medoids are a measure of centrality similar to medians used for analysis with small sample sizes. Medoids are selected to anchor the clusters to observed data and must be an observed member of the data set and not interpolated. Resulting clusters were analyzed for metrics of cluster cohesion and behavioral
variability between clusters to assess the degree to which different annual space use patterns are influenced by colony-wide forces versus individual forces.

3.3 Results

3.3.1 Tag Cohort

8 GPS/GSMR tags were deployed and remained active between 53.3 and 281 days (Table 3). Only one deployment was shorter than 190 days and was ended prematurely as the result of a shark predation in the beginning of August 2013 (Autopsy report, M. Moore, personal communication). All other tags deployed in June 2013 remained active for over 250 days, transmitting data until January 2014 (n = 1), February 2014 (n = 1), and March 2014 (n = 4). Two tags were recovered from beach haul outs in Spring 2014 with swaths of fur still attached and still collecting and transmitting data, indicating tag deployments ended due to molting rather than battery life. One tag (tag# 646) malfunctioned in July 2013 and only transmitted a single point for the remainder of its tag life (March 2014). The tag deployed in September 2012 remained active until March 2013, similar to other tags in the cohort suggesting that it also was likely shed during an annual molt. A total of 35,577 locational fixes were recorded with Fastloc® GPS technology (median residual = 7.8m, $\sigma = 0.2$), with a median of 5387.5 per individual (range 991-8972, $\sigma = 2944.9$) and median of 22.5 per individual per day (range 3.56 -
31.93, \( \sigma = 9.6 \)). For most deployments except the malfunctioning tag, animals recorded approximately one location per hour.

### 3.3.2 Home range analysis

Home range areas for the 8-day sampling periods are summarized by month in Table 4, with medians ranging between 6.93 (August) to 378.66 (January) km\(^2\). Across months, there are divergent trends apparent for an initial period with little (or slightly decreasing) changes in home range size and range between individuals during warm months (June - October) and a subsequent period of cold months (November - March) when size and inter-individual range are expanding (Figure 6). Due to small sample sizes, all further analyses focus at the scale of individuals to limit bias from any age and sex effects. Figure 5 shows typical home ranges for these two periods of divergent space use pattern.

To quantify structural change in trends in home range size, the breakpoint of the segmented regression was anchored in early November by a linear mixed model with fixed temporal effects (i.e., sampling period) and random individual effects that exhibited minimum deviance (Figure 6). Figure 6 shows the deviance for all models evaluated in the iterative sensitivity analysis of breakpoints and demonstrates the structural change in early November. Overall, there is a 4.79 fold increase in the rate of space use expansion (2.18 km\(^2\)/sampling period compared to 10.46 km\(^2\)/sampling period,
respectively) between the warmer period (June - November 5th) and colder period (November 5th - March). A Chow test statistic found this structural break in the dataset to be highly significant (Chow test, \( f = 9.43, p < 0.01 \times 10^{-5} \)). It is important to note that space use expansion during the cold period includes data from animals attending breeding colonies (50% attended Muskeget Island, a primary breeding colony), including females who fast and nurse pups resulting in a weekly home range near zero (see right hand vertical bar, Figure 7). Figure 7 shows individual trends in space use through the tagging record in reference to the identified breakpoint (left hand vertical bar) and onset of breeding (right hand vertical bar).

3.3.3 Activity budget changes

Rapid space use changes throughout the year were also accompanied by shifts in activity budgets. Figure 8 shows pairwise shifts in individual’s 4-hour activity budgets across the warmer and colder periods of space use pattern. For both day and night periods, time at depth increased between warm and cold periods in contrast to consistent declines in activity at the surface (Figure 8). Daily median values during diurnal and nocturnal periods for each individual with sufficient data showed significant differences (Mann-Whitney test) across the breakpoint for both activity at the surface (diurnal mean \( W = 12322.917 (\sigma = 4289.0931), p < 0.00001 \); nocturnal mean \( W = 12195.667 (\sigma = 4465.4176), p < 0.001 \)) and at depth (diurnal mean \( W = 2712.167 (\sigma = \ldots \)
behavior showed less consistent differences across individuals, as evident in Figure 8 and supplementary Table 6. On average, these differences result in a 55% decrease in behavior at the surface for both day (range = 16.4 - 73.3% decrease) and nighttime periods (range = 20.9 - 77.8% decrease). However, time spent at depth increased 330% in diurnal periods (range = 21.06 - 4873.3% increase) and 81% in nocturnal periods (19.9 - 481.0% increase) from warm to colder months (Figure 8).

### 3.3.4 Cluster analysis and variability

On the basis of minimized sum of dissimilarity across the number of k clusters, scaled home range areas were partitioned optimally around 3 medoids of increasing home range sizes (average silhouette width = 0.71). Cluster groupings had visible temporal structure (Figure 9): the small home range cluster (standardized cluster medoid = -0.690) accounted for 96% of samples prior to the breakpoint, 118 of a total 188 home range estimates, and no samples following breeding (when home range of reproductive individuals is expectedly near zero due to terrestrial fasting). The two larger clusters of moderate (standardized cluster medoid = 0.362) and large home ranges (standardized cluster medoid = 1.766) evenly accounted for greater portions of the period following the estimated breakpoint (41% and 31% of post-breakpoint home ranges, respectively).
Despite encapsulating a majority of home range estimates (62.7%), the cluster of small home ranges exhibited the tightest dissimilarity and smallest diameter (average dissimilarity = 0.129 in comparison to 0.220 and 0.546 for moderate and large home range groupings, respectively; diameter = 0.626 in comparison to 1.18 and 3.15 for moderate and large home range groupings, respectively). Thus, small home ranges are less variable spatially than moderate and large home ranges, which vary more greatly in area (Figure 10a). Contrary to expectation, behavioral activity at the surface and depth in these larger home ranges is less variable than small home ranges at a variety of modeling scales (Figure 10b). Overall, behavior associated with the largest home range cluster had the smallest variability and standard deviations for all behaviors. Moderately-sized home range sizes typically had lower measures of variability than the small-sized home range cluster, except for haul out behavior. Indeed, scatterplots of diving and surface activity show a greater spread for the small home range cluster, than clusters of moderate or large home ranges, which visually appear only distinct in their areal extent and not behavior. An ad hoc intracluster analysis of small home ranges revealed contrasting and significant differences in the mean activity of surface and diving behavior and a significant increase in variability across all activities (Figure 9, Table 7). Thus, the breakpoint is indeed capturing some degree of a behavioral shift,
even when that change is dissociated from significant changes in home range size
(Kruskal-Wallis, chi = 1.97, p = 0.16).

3.4 Discussion
This study provides the first insights into the space use and activity budgets of
wild caught gray seals in the northeastern United States. Gray seal movements
exhibited an abrupt shift in distribution patterns and rapid expansive changes in the
scale of space use. During warmer months of summer and early fall, tagged seals
remained exclusively coastal, concentrated movement in small, overlapping foraging
areas adjacent to local haul outs, and focused activity and behavior on nocturnal
periods. In the course of a single month (November), these patterns subsided
consistently across all individuals and gave rise to rapid expansion in home range sizes,
exploitation of alternative foraging habitats, and a balancing of activity between diurnal
and nocturnal periods. Movement, distribution, and space use during colder months
were characterized by patterns more typical of other well-studied gray seal populations:
multi-day foraging movements to offshore feeding grounds, ledges, and shallow banks
with individual variability in the foraging habitat utilized (Breed et al. 2009).

Seasonal changes in gray seal distribution have been observed in other
populations, though at larger scales than observed in this study. On Sable Island,
animals exhibit similar offshore shifts in winter foraging with animals traveling farther
and to more diffuse locations in comparison to summer and fall foraging that are characterized by intense, focused use of inshore areas near haul outs (Breed et al. 2009, Breed et al. 2013, Baker et al. 2015). In the Gulf of St. Lawrence population, animals exhibit directed movements (sometimes termed an autumn migration, Harvey et al. 2008) out of the St. Lawrence estuary and northern Gulf into areas in the southern Gulf or exiting the Gulf region entirely (Lavigeur and Hammill 1993, Goulet et al. 2001).

Despite apparent similarities, the home ranges of Cape Cod gray seals occur at a much smaller spatial scale than Canadian populations. Mean summer home ranges estimated in this study were 10%, on average, of the mean reported in Harvey et al. 2008 (8900 km2), and even the individual maximum (2600 km2, tagID = 652, Table 3) more than 3 fold smaller than the Canadian average. Cape Cod animals exhibited median difference of 6000 km2 (range of differences: 4300 - 6877 km2) from even the lower bound of the summer home range areas in Harvey et al. (2008). Similarly in winter, home range estimates were smaller, though to lesser degree accounting for only 38% of mean Canadian kernel areas over the same months (Harvey et al. 2008). Even using more constrained spatial smoothing methods, only the most “intensely-sampled” area (delineated by a 25% isopleth) estimated collectively over twice as many Sable Island seals matched the scale of small space use reported here for US individuals (Baker et al.)
Despite similarities in the seasonal changes of gray seal distribution, US animals exhibit much more reduced home ranges, especially during summer seasons.

Apparent low foraging effort and the concentrated, overlapping coastal behavior observed in summer may stem from multiple factors, largely non-mutually exclusive. Breed et al. (2006) outlines how both high and low prey availability could result in observed summer reductions in space use and foraging behavior due to short foraging trips that meet energetic needs quickly (i.e., high prey availability) or short trips abbreviated to conserve energy due to minimal foraging success (i.e., low prey availability). Multiple studies document large portions of summertime behavior, especially for females, concentrating within 10km of the coastline (50-80% in Breed et al. 2013; 40% in McConnell et al. 1999). As before, this study documents even starker differences, with males and females respectively spending 97.1% and 99.8% of the summer (June – October) within 10 km, in comparison to only 38.4% and 68.1% in the winter (n.b.: winter rates are likely inflated due to inclusion of terrestrial breeding periods). Taken altogether, these studies explain nearshore behavior with low apparent niche separation as likely targeting of patchily-concentrated sand lance (Ammodytes spp.) that burrow in sandy gravel substrate, a spatially-predictable habitat common in the animal’s coastal home ranges (Breed et al. 2009, McConnell et al. 1999). Multiple diet studies confirm sand lance as a key diet item and predictable prey base, particularly in
summer seasons (Beck et al. 2007, Ampela 2009). Indeed, a survey of stomach contents of fishery-bycaught animals found sand lance only in the stomachs of animals caught near this study’s tagging location (Chatham harbor) during warm months (F. Wenzel, personal communication). Fitness effects of such heightened inshore concentration seasonally remain unevaluated until demographic data can be integrated with movement patterns, though only two tagged animals (tagID = 658 and 652; Table 3) attended the Muskeget breeding colony and exhibited the absence of movement expected from a reproductive fast. Another individual (tagID = 654, Table 3) likely suffered fitness consequences due to a failed migration to the vicinity of Sable Island during peak breeding season, but never arrived at the large Canadian breeding colony.

While observed patterns of reduced summer foraging and space use are potentially related to prey and patch quality, the small scale and rapid expansion observed in this study’s southerly subpopulation may present additional mechanisms related to pre-breeding costs of energy gain that would select for delayed energy storage until immediately prior to breeding. For many taxa, mass gain and energy storage are associated with decreased mobility and maneuverability, changes in thermoregulatory costs, as well as increased risk of predation (Hedenstrom 1992, Witter and Cuthill 1993, Witter et al. 1994, Gosler et al. 1995, Sinervo and DeNardo 1996, Jonsson 1997, Jonsson et al. 1998, Hedenstrom 2001, Lima 2009). Though these costs are not fully evaluated for
most phocids, the fact that the study population resides at the southern extreme of the species range suggests the possible interplay of these costs in rapid shifts in pre-breeding space use and foraging ecology (Lima 1998). Due to loss of terrestrial predators and protected haul out sites on tidal sand bars and islands, reduced terrestrial locomotion as a result of mass gain is unlikely to exert strong influence on the foraging ecology of US gray seals.

However, increased thermoregulation costs of mass gain during a hot summer season may be especially important given this is the southernmost breeding colony of gray seals in the world and animals are approaching or exceeding their thermal neutral zone (Hansen and Lavigne 1997). Observed haul out rates (Figure 8, Chapter 2) are almost double the rates observed in other gray seal studies (Breed et al. 2013, Russell et al. 2015), and there are subsequent effects for amount of time at-sea. Elevated daytime haul out behavior would exacerbate any metabolic costs due to thermoregulatory changes around energy storage. High rates of activity in surface waters prior to the breakpoint (Figure 7) may additionally manage thermoregulation during warm summer months.

Additionally, the study population strongly overlaps seasonally with the northwest Atlantic population of white sharks (*Carcharodon carcharias*), which appear to redistribute and concentrate at the latitude of Cape Cod during the summer season of
exceptionally reduced space use and nocturnal behavior observed in this study (Skomal et al. 2012, Curtis et al. 2014, Figure 11). Complex interactions between buoyancy (Beck et al. 2000, Sato et al. 2003), cost of transport during diving (Williams et al. 2000, Fahlman et al. 2008, Miller et al. 2012, Adachi et al. 2014), and risk of predation (Heithaus and Frid 2003, Frid et al. 2007) are expected to have a selective effect during the summer season of high shark presence. Given potential predation costs to transporting accumulated blubber, leaner individuals may be better able to extend bottom phases of dives, when agile seals are most able to detect and outmaneuver sharks (Martin and Hammerschlag 2012), or shorten surface intervals, when diving animals are often most vulnerable to attack (Heithaus and Frid 2003, Martin and Hammerschlag et al. 2005). Even within the tag cohort of 8 individuals, one of the smallest individuals captured (one-sample Wilcoxon test, V = 36, p < 0.06) experienced a fatal shark interaction in August 2013 (Autopsy report, M. Moore, pers. comm.). Necropsy results showed the individual was pregnant, likely with her first offspring given her age (4 years, assumed age of primiparity, Bowen et al. 2006), and field data from capture showed the individual had thicker than average levels of dorsal blubber fat (one-way Wilcoxon test, V = 0, p < 0.003) and dark fat (one-way Wilcoxon test, V = 2, p < 0.005; M. Moore unpublished data). Breed et al. (2006) and Breed et al. (2013) also suggest the potential adaptation of restricted summer foraging and concentration of reduced
coastal space use as a strategy to minimize exposure to increased numbers of migratory sharks (sensu Byers 1997), as shark predation appears highest in adult populations during summer months on Sable Island as well (Brodie and Beck 1983, Lucas and Stobo 2000). Given possible recovery of the regional white shark population (Curtis et al. 2014) and increased sightings on Cape Cod (Skomal et al. 2012), this study population becomes a fruitful system to test ecoevolutionary hypotheses and theoretical model assumptions about the intra- and interannual balance of costs and benefits of energy gain in reproductive strategies (Houston et al. 2006).

U.S. gray seals exploit resources within the some of the smallest area and spatial scale observed for the species in the literature (particularly in summer months), experience high levels of predation pressure through these months, and haul out for extended periods along beaches in the warmest stretches of their global range. Complex tradeoffs between predatory interactions, optimal thermoregulation, and behavioral decisions concerning resting, foraging, and preparation for reproduction are thus proposed to influence space use, distribution, and animal movement patterns (Heithaus et al. 2009, Wirsing et al. 2011). Rapid shifts to large, broad space use patterns—indicative of compensatory foraging and surplus feeding—occur at a time of year when air temperatures are declining and 98% of predatory sharks have been observed for the season (Figure 11). Still if animals follow the similar fetal phenologies as Canadian
animals, increased foraging activity over larger home ranges occurs over 3 months after fetal growth rate is expected to increase due to reproductive (and thus energetic) state transitions from suspended to active development (Yunker et al. 2005, McNamara and Houston 2008). Thus, tradeoffs between the future uncertainty of achieving a reproductive state through energy storage and survival and maintenance costs of energy gain appear to underlie observed reduced foraging effort and niche separation in gray seals during summer. While initially counter-intuitive that individual variability is highest in the smallest home ranges (Figure 10b), reductions in summer foraging effort would permit a more diverse allocation of behaviors. In preparation for breeding, animals may use larger home ranges to acquire resources after November but imminent energetic demands and metabolic conservation may restrict behavioral routines. The present study indicates that there may be selective advantages to delaying energy storage until immediately prior to breeding and unevaluated survival and maintenance costs associated with inopportune mass gain. Further work with increased sample sizes of both males and females will be required to determine the tradeoffs between immediate and lifetime fitness and how these tradeoffs relate to space use, foraging effort, and energy gain and storage.
Table 3: Details of cohort of tagged animals active between September 2012 and March 2014. Behavioral activity budgets are calculated for all individuals with complete records, excluding incomplete records.

<table>
<thead>
<tr>
<th>Age Class</th>
<th>Years</th>
<th>Sex</th>
<th>Status</th>
<th>Recovery</th>
<th>Tag #</th>
<th>Duration (days)</th>
<th>N</th>
<th>Daily Rate</th>
<th>Breakpoint (BP)</th>
<th>Max Depth (m)</th>
<th>Behavior</th>
<th>Home Range Area (km²)</th>
</tr>
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<tr>
<td>SA</td>
<td>NA</td>
<td>M</td>
<td>Tag off</td>
<td>N</td>
<td>12358</td>
<td>193.7</td>
<td>1483</td>
<td>7.66</td>
<td>pre-BP 78.30</td>
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</tr>
<tr>
<td>A</td>
<td>4</td>
<td>F</td>
<td>Dead</td>
<td>Y</td>
<td>12373</td>
<td>53.3</td>
<td>1184</td>
<td>22.21</td>
<td>pre-BP 64.30</td>
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<td>NA</td>
<td>NA</td>
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<td>12397</td>
<td>250.5</td>
<td>4850</td>
<td>19.36</td>
<td>pre-BP 96.10</td>
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<td>A</td>
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<td>278</td>
<td>991</td>
<td>3.36</td>
<td>pre-BP NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
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<tr>
<td>A</td>
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<td>219</td>
<td>6352</td>
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<td>12654</td>
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<td>9176</td>
<td>32.82</td>
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<td>56.93</td>
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<td>6283</td>
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<td>pre-BP 20.30</td>
<td>25.25</td>
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Table 4: Monthly home range summaries of the 95% kernel area (km2) across sexes. Slight sexual differences appear, but generally follow trends expected from et al. 2003, Breed et al. 2006, and Breed et al. 2009. All further analyses will be conducted at the scale of individuals due to data richness considerations.

<table>
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<tr>
<th>Month</th>
<th>Median Male</th>
<th>Median Female</th>
<th>SD Male</th>
<th>SD Female</th>
<th>Minimum Male</th>
<th>Minimum Female</th>
<th>Maximum Male</th>
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<td>262.60</td>
<td>234.62</td>
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<td>165.91</td>
<td>506.08</td>
<td>218.24</td>
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Figure 4: Representative maps of 8-day seasonal home range patterns. a) Summer season map shows home ranges of 5 tagged animals for the 8-days about 01 September 2015. b) Winter season shows home ranges of 5 tagged animals for the 8-days about 02 February 2014.
Figure 5: Monthly summaries of 8-day home ranges show dramatic expansion of space use in cold months (November – March). Space use in warm months (June – October), conversely, show no change or slight declines.
Figure 6: A structural change in the space use pattern is set at the date of minimized deviance in of a linear mixed effects model testing the effect of the day of year on the area of home range observed. Here, models using a breakpoint in early November show clear parsimony between the seasonal patterns of space use.
**Figure 7:** Individual home range estimates demonstrate the abrupt change in space use in late autumn. Vertical lines indicate key dates, the left hand bar indicating the structural change in the data and the right hand bar indicating the onset of breeding at terrestrial colonies.
Figure 8: Across the seasonal shift, there are associated differences in diurnal and nocturnal activity budgets of behavior. Reductions in surface behavior appear to be offset by large increases in diving (diurnal and nocturnal). The portion of time devoted to haul out behavior similarly declines, as does its variability, over both day and night periods.
Figure 9: Cluster groupings of home ranges demonstrate the temporal structure captured by the breakpoint identified through the structural change analysis (vertical black bar, November 5).
Figure 10: (a) Clustering of kernel areas show three distinct groupings of small, moderate, and large home ranges. (b) Activity budgets associated with each cluster show distinct differences and reductions in variability for behavior at the surface and at depth (but not haul out) in clusters with large home ranges.
Figure 11: Cumulative and latitudinal distributions of white sharks in the NW Atlantic throughout the year. a) Cumulative distribution of sightings (across multiple years) through the year. Vertical bar is anchored to the date identified as a structural change gray seal space use patterns, when 98.2% of sharks have been observed for the year. (data courtesy G. Skomal); b) Cumulative distribution of acoustic detections of tagged sharks in 2013. Again, vertical bar is the date of structural change in gray seal space use patterns, when 97.6% of the acoustic-tagged sharks have been detected. (detection data courtesy G. Skomal); c) monthly latitudinal distribution of white sharks throughout the entire Northwest Atlantic (reproduced from Figure 4, Curtis et al. 2014). For reference, gray seals were tagged at 41 degrees North (red line in c) in June 2013.
4. Nocturnal foraging of gray seals and risk allocation in the presence of white sharks.

4.1 Introduction

4.1.1 Predation risk and risk allocation

Foraging models describe behavioral decisions of feeding individuals in terms of energy costs and gains (i.e., currency, Charnov 1976, Stephens and Krebs 1986) and as a function of prey patch density, distribution, or clustering (Macarthur and Pianka 1966, Zollner and Lima 1999). Many animals are constrained by the need to return to a central place between foraging excursions (Orians and Pearson 1979), leading to a focus of patch characteristics such as distance and quality that influence an individual’s ability to maximize the benefits of an individual foraging foray (Olsson et al. 2008). Only recently has foraging theory explicitly incorporated risk-mediated effects into models of animal behavior and more rarely in a temporally-variable manner (Ferrari et al. 2008), in spite of early reviews on the effects of predation risk on behavior (Lima and Dill 1990, Peacor and Werner 2001). As such, the strength and ubiquity of this ecology of fear (Laundre et al. 2014) indicates any movement by away from central places, that provide refuge but limited foraging opportunities, elevates predation risk in manners that can influence resource acquisition (Peacor and Werner 2001, Creel and Christenson 2008). Furthermore, sociality at a central place results in predictably heightened densities of foragers immediately adjacent to the central place that may amplify behavioral signals of
trait-mediated effects since relative tradeoffs between foraging and antipredator behavior are reduced (Brown and Kotler 2004, Caro 2005, Olsson et al. 2008).

The recent embrace of the influence of predation risk in the foraging literature (Hebblewhite et al. 2005, Foam et al. 2005, Heithaus et al. 2006, Hebblewhite et al. 2009, Wirsing et al. 2007) incorporates important top-down forces into foraging theory (Heithaus et al. 2009). Nonconsumptive risk effects account for effects not involved in lethal consumption and exhibit pivotal roles in structuring competitive interactions (Peacor and Werner 2001), trophic cascades (Beckerman et al. 1997, Schmitz et al. 1997, Trussell et al. 2003, 2004, 2006b), and ecosystem function (Stief and Holker 2006, Trussell et al. 2006b, 2008, Schmitz et al. 2008). Given their ubiquity and pervasiveness (Creel and Christianson 2008), risk effects have been shown to outweigh the effects of direct consumption (Schmitz et al. 2004, Pressier et al. 2005, Trussell et al. 2006a) and emerge even in the absence of direct predation (Creel and Christenson 2008). Responses to predation risk vary widely (Werner & Peacor 2003, Creel 2011), can be behavioral or morphological (Tollrian and Harvell 1999, Lima 1998), and include tactics of time allocation, tenacity, and the use of apprehension or vigilance (Brown and Kotler 2004).

Reliance on a social central place as refuge creates risky areas in the immediate vicinity surrounding the location where animals must traverse to access the central place (Bakker et al. 2005, Kauffman et al. 2007). Dependable visitation to a location by prey animals reduces the spatial complexity of predator avoidance (Mitchell and Lima 2002), restricting the dimensions of antipredator response to behavioral and temporal dynamics (Caro 2005). Behaviorally, animals utilize group behavior (de Vos et al. 2015,
Childress and Lung 2003, Bednekoff and Lima 2004), vigilance (Wolff and Van Horn 2003, Fortin et al. 2004), and apprehension (Brown and Kotler 2004, de Vos et al. 2010, de Vos et al. 2013, de Vos et al. 2015) to mitigate predation risk. Additionally time allocation (i.e., the schedule of where, when, and for how long animals spend time; Brown and Kotler 2004), is a compelling mechanism for central place foragers to avoid predation risk and predatory encounters.

At its simplest, theory predicts that optimal behavior should avoid periods with high predatory encounter or attack rates (i.e., the “risky times” hypothesis; Creel et al. 2008). However, the opportunity cost of missed foraging opportunities increases when risky periods become longer or more frequent, and so the risk allocation hypothesis alternately suggests optimal allocation of foraging activity between high and low risk periods depends on the frequency and duration of predation risk pulses (Lima and Bednekoff 1999). While not mutually-exclusive, the two hypothesis explicitly incorporate the temporal variation in risk effects on behavior differently. Namely, the risky times hypothesis disregards additional information beyond absolutes of “high” and “low” risk, while the risk allocation hypothesis explicitly integrates the temporal patterns of predation risk into theoretical predictions. However, paradoxical predictions can emerge from this incorporation of the sequence and duration of high and low risk periods (Ferrari et al. 2009). Expectedly, the hypothesis predicts foraging activity to increase during low risk periods so a forager can remain inconspicuous and seek refuges in the presence of predators (Lima and Bednekoff 1999). As these low risk periods become shorter or less frequent, a forager must counter intuitively increase foraging
activity during high risk periods to compensate for lost foraging opportunities (Lima and Bednekoff 1999, Ferrari et al. 2009, Bednekoff and Lima 2011, Trussell et al. 2011, Matassa and Trussell 2011). Outbound and inbound legs of successful foray of a central place forager can traverse risky zones around central places at different points in the risk cycle, and result in divergent responses to fine-scale changes in predation.

4.1.2 Shark-seal interactions

Like many pinnipeds, gray seals (Halichoerus grypus) are social central place foragers that utilize gregarious haul out sites for rest and socializing (among other behaviors) in between forays. Foraging trips depart haul outs, traverse to near- and offshore benthic habitats in the Northwest Atlantic, and target a diverse set of demersal fish. Rapid recolonization of southeastern Massachussetts (USA, Wood et al. 2011) and dramatic increases in abundance (Chapter 2) has been followed by increased sightings of and interactions with white sharks (Carcharodon carcharias). Apparent growth in the white shark stock in the region has been recently documented and associated with changes in gray seal abundance (Skomal et al. 2012, Curtis et al. 2014). Studies of other hotspots of shark-seal interactions have helped describe the predatory behavior of a seal-hunting white shark (Klimley 1994, Klimley et al. 1996, Klimley et al. 2001, Martin and Hammerschlag et al. 2005, Hammerschlag et al. 2006, Martin et al. 2009, LaRoche et al. 2008, Martin and Hammarschlag 2012). Though slight differences exist between sites, all hotspots exhibit seasonal aggregations of white sharks that concentrate activity near entry/exit points to the pinniped colonies (Compagno 2001). Attack frequency and success rate is greatest on juvenile animals in relatively shallow water (5-50m) close to
shore (<400m, Fallows et al. 2012). Using powerful jaws to subdue and capture prey (Tricas and McCosker 1984, Tricas 1985), these sharks exhibit an ambush-style attack that relies visually on backlighting prey (Martin and Hammerschlag 2012). While attacks at California sites occur uniformly through the day (Klimley et al. 2001), low-light dawn and dusk periods are associated with increased successful attacks due to optimal backlighting, scotopic conditions, and predator concealment in the more widely observed South African system (Martin and Hammerschlag 2012). Others have experimentally shown preferential approach from the direction of sun to supplement concealment with glare (Huveneers et al. 2015), again highlighting the importance of light level and direction to successful predatory attempts (Martin and Hammerschlag 2012). This preferred approach direction was observed to change along the east-west axis from morning to afternoon and was not detected on overcast days (Huveneers et al. 2015).

Given the growth in both gray seals and white shark sightings on Cape Cod, MA, USA, shark-seal interactions appear to be rising and risk-mediated responses in foraging and movement behavior are thus expected. In this study, I test how GPS-tagged gray seals allocate offshore activity, trip patterns, and foraging behavior to periods of variable risk at multiple temporal scales. Seasonally, white shark distributions exhibit an acute range contraction to the latitudes of Cape Cod during warm summer months (Figure 11), where activity of acoustically tagged individuals is tracked at inshore monitoring sites near seal colonies and beach haul outs. Circular analyses of coastal behavior elucidates patterns in the decisions about the initiation and
termination of foraging trips (termed departures and arrivals, respectively). In addition to foraging trip patterns and diel cycles of arrivals and departures, coastal movement behavior is analyzed in reference to changes in ambient environmental light.

4.2 Methods

4.2.1 Data collection and processing

On Cape Cod, USA in 2012-2013, 8 GPS/GSRM telemetry tags (Global System for Mobile Communications/General Packet 145 Radio System, SMRU Instrumentation, St. Andrews, Scotland) were deployed on adult and subadult gray seals. 7 of the tagged seals were live-caught in beach seines (Jeffries et al. 1993, Waring et al. 2006) at a tidally-dependent sandbar haul out within the harbor of Chatham, MA, USA (41.67° N, 68.95° W) and sedated intramuscularly with 0.58-0.8 mg/kg of 100mg/ml tiletamine/zolazepam (Telazol®, Fort Dodge Animal Health, Fort Dodge, IA). One animal was outfitted with a telemetry tag subsequent to rehabilitation and release efforts. Following attachment methods of Jessop et al. 2013, the telemetry device (10 cm x 17 cm x 4 cm, 370 g in air) was affixed to the dorsal neck/head region of the animal’s fur using quick-setting epoxy-based adhesive. In total, subadult and adult males (n = 4, 3-7 years of age) and adult females (n = 4, 4 - 11 years of age) were both tagged. For the subsequent 2-9 months, tags monitored the animal’s movement, diving activity, local water temperatures, and haul out behavior and transmitted data to servers via the GSM network. A total of 35,577 locational fixes were recorded with Fastloc® GPS technology (median residual = 7.8m, sd = 0.2), with a median of 5387.5 per individual (range 991-8972, σ = 2944.9) and median of 22.5 per individual per day (range 3.56 - 31.93, σ = 9.6).
Most animals recorded approximately one location per hour, though one tag malfunctioned shortly into deployment and only recorded a single point per day for the remainder of the study.

To analyze the fine-scale movement ecology of the animals, locational data recovered from the tags was fit with a continuous-time correlated random walk and movement steps standardized evenly every 30 minutes (Calenge et al. 2006, Johnson et al. 2008). As typical in pinniped tracking studies (McConnell et al. 1999, Breed et al. 2006, Breed et al. 2009), foraging trips are identified as consecutive locations more than 2 kilometers from the coastline. The focus on coastal behavior, however, required a modification to this approach that anchors the initiation and termination of foray events to actual departures and arrivals at the haul out site rather than an offshore arena 2 km from shore. Therefore, each foray was extended to include all locations up to 3 hours into the foray that were not within a harbor, backwater, or land-based haul out with the endpoints of the foray anchored at the location with the shortest distance to shore.

4.2.2 Foraging foray analysis in seals

Trip statistics (n = 412 trips) were calculated for each foraging trip and summarized across sexes by season (as defined in Chapter 3), in order to be comparable with published foraging trip statistics (see Table 2, Breed et al. 2009). Departure and arrivals at the coastline (analogous to inlet crossings when animals use an inlet to access inshore haul outs) are defined as the first and last point of each foraging trip identified, as described in the section above. For temporal variables like time of day of an arrival or departure, circular statistics of angles (radians) was used to describe distributions and
test statistical differences (Pewsey et al. 2013). Using the Rayleigh test to confirm departures from circular uniformity, mean direction ($\theta$) is analogous to the moment of centrality and mean resultant length ($\vec{R}$) is the most common measure of the concentration of a circular distribution (Pewsey et al. 2013). The complement of rho (i.e., $1 - \vec{R}$) is the sample’s circular variance, thus values of $\vec{R}$ approaching 1 indicate data are closely clustered around the mean direction. The Wallraff nonparametric test for circular homoscedascity was used to test if departures and arrivals in different seasons were drawn from distributions with a common concentration.

To better understand additional factors capable of influencing foraging forays, ancillary data was aggregated from multiple sources. Data on predatory white shark activity was collected from multiple sources including local acoustic telemetry arrays (overlapping with seal tagging efforts, G. Skomal), local field surveys (contemporaneous with seal tagging efforts, G. Skomal), and a comprehensive long-term occurrence database aggregating information from landings data, commercial fishery observer programs, recreational tournament information, scientific research surveys, commercial and recreational fishermen, collaborating scientists, newspaper articles, personal communications, and the scientific literature (Curtis et al. 2014). Changes in ambient environmental light were assumed to be analogous to different formal definitions of dawn and dusk (e.g., astronomical, nautical, and civil Twilight when the sun is $-18^\circ$, $-12^\circ$, or $-6^\circ$ below the horizon), which were calculated using algorithms provided by the National Oceanic & Atmospheric Administration (NOAA) within an R statistical framework (Bivand and Lewin-Koh 2015).
4.3 Results

4.3.1 Foraging trip analysis

Foraging trips exhibited striking sex (Table 5) as well as seasonal (Figure 12, summer: June - Oct, winter: Nov - Mar, Chapter 3) differences, as with other patterns of space use and behavioral changes (Chapter 2-3). For all trip metrics (distance traveled, max distance offshore, and duration), there was no significant sex difference during summer season foraging trips (Tukey HSD, distance: p = 0.999; max distance offshore: p = 0.999; duration: p = 0.989), though it is unclear if this is an artifact of the study’s small sample size and low power (see Breed et al. 2009). Other seasonal and sex effects showed significant differences in foraging trip parameters. In particular, females do not shift as far offshore in the winter in comparison to males, confirming other studies that have linked sex differences in energy storage patterns (Beck et al. 2003), diet composition (Beck et al. 2007), and foraging ecology (Breed et al. 2009) in advance of breeding and molting.

Seasonally, males expanded the distance traveled in a single foraging trip by an average of 12.1 times (Wilcoxon test, W = 1410, p < 0.000001) and the maximum distance offshore by an average 9 times (Wilcoxon test, W = 1666, p < 0.00000001). Foraging trips in the winter also lasted 4.3 +/- 1.6 days in the winter, in comparison to 0.44 +/- 0.08 days in summer (Wilcoxon test, W = 941, p < 0.00000001).

Females, on the other hand, expanded the distance traveled in a single foraging trip by an average of 5.3 times (Wilcoxon test, W = 812, p < 0.00000001). However they did not significantly shift foraging trips to habitats much further offshore. Trip
durations, however, do show significant differences, with females spending 5.5 times longer at sea on average than in summer (Wilcoxon test, W = 541.5, p < 2.2e-16).

4.3.2 Diel cycles in foraging trips

Departures and arrivals at beach haul out colonies show clear seasonal patterns in their timing (Figure 13). Summer foraging trips (Figure 13a-b) exhibit a clear nocturnal cycle, whereas winter behavior exhibits no discernible pattern (Figure 13c-d). For both seasons, circular distributions of departures were distinguished from uniformity (Rayleigh test; summer: Z = 0.8035, p < 0.0000001; winter: Z = 0.1838, p < 0.003). During summer months, the initiation of foraging trips clustered strongly (mean resultant length, $\bar{R} = 0.8301 \pm 0.0561$, $p < 0.0000001$) around a mean departure between 19:00 and 19:30 local time (mean $\bar{\theta} \pm 95\%$ CI = $-1.21 \pm 0.06$ radians, $\sigma = 0.66$). Winter trip departures distributed more uniformly throughout the day (Figure 13c), with a weak mean vector (mean resultant length, $\bar{R} = 0.1757 \pm 0.1044$, $p < 0.003$; mean $\bar{\theta} \pm 95\%$ CI = $-1.46 \pm 0.58$ radians) with a large standard deviation ($\sigma = 18.4$).

After completing an offshore foraging trip, patterns of arrivals throughout the day similarly show a dissipation of nocturnal cycles from summer to winter seasons (Figure 13b,d). The summer circular distribution was strongly unimodal (Rayleigh’s test, Z = 0.782, p < 0.0000001), while the winter distribution was much more uniform (Rayleigh’s test, Z = 0.0734, p < 0.4085). In the summer, trip termination clustered strongly (mean resultant vector length, $\bar{R} = 0.7814 \pm 0.0517$, $p < 0.0000001$) around a mean arrival between 03:00 and 03:30 local time (mean $\bar{\theta} \pm 95\%$ CI = 0.84 $\pm$ 0.77 radians, $\sigma = 0.70$). Winter arrivals were distributed uniformly
throughout the day (Figure 13d), with a weak mean vector (mean resultant length
\( \bar{R} = 0.1757 \pm 0.1044, p < 0.003; \) mean \( \bar{\theta} \pm 95\% CI = 2.40 \pm 1.46 \) and, again,
comparatively large standard deviation (\( \sigma = 2.29 \)). For both arrivals and departures,
seasonal changes exhibit significant changes in heteroscedascity (Wallraff’s
nonparametric test for common concentration; departures: \( \chi^2 = 54.92, p < 0.0000001; \)
arrivals: \( \chi^2 = 110.69, p < 0.000000001 \)). In spite of slight overlap in the confidence
intervals, there is slightly more variability in the distribution of arrivals (\( \bar{R} = 0.7819 \))
than the distribution of departures (\( \bar{R} = 0.8034 \)).

4.3.3 Ambient environmental light

The strong nocturnal cycles of summer foraging trips also showed preference, in
comparison to winter trips, for dark and crepuscular periods over daylight periods.
Figure 14 shows each trip’s temporal difference (in minutes) between the trip’s endpoint
and the nearest crepuscular event. Given the nocturnal patterns already observed,
summer departures were overwhelmingly associated with sunset events (92.5% of 265
trips). Conversely, arrivals were similarly highly associated with sunrise events (87.9%
of 265 trips), while winter trips were more evenly associated in temporal proximity to
either sunrise or sunset (59.9% of winter departures occurred in closer proximity to
sunset; 51.8% of winter arrivals occurred in closer proximity to sunrise). The
distribution of summer departures exhibited very peaked patterns centered around
sunset (e.g., solar position = 0°, Figure 15). Fitting a probability density function to the
distribution, 42% of the density distributes equivalently on either side of a given sunset,
with nearly half of that density (20% overall) occurring during twilight periods of
waning light following sundown. Summer arrivals were primarily phase shifted to periods prior to sunrise (Figure 14c). In this case, 50% of the density is concentrated within the 4 hours prior to a given sunrise, while only 26% is situated during the same period of time following sunrise. In the dark or low light periods prior to sunrise, 32% of the total density (and almost 2/3 of all night movements) occurs in the complete absence of solar illumination, while 18% of the total density (1/3 of night movements) occur during dawn twilight when the sky is brightening in advance of sunrise. Finding the solar position (in reference to the horizon, i.e., $0^\circ$) that these distributions are centered upon illustrates the average ambient light level movements are closely associated with. Not surprisingly given the close temporal association around sunset, the mean of departures is coincident with a solar position of $0^\circ$, the exact moment the sun is crossing the horizon (i.e., sunset, Figure 15). Given the left hand skew of the arrival’s distribution prior to sunrise, the mean of the distribution is compared to 3 alternate definitions of dawn, including solar position at civilian dawn ($-6^\circ$), nautical dawn ($-12^\circ$), and astronomical dawn ($-18^\circ$). As seen in Figure 15, the mean summer arrival is directly coincident with astronomical dawn, when the sun is still below the horizon, resulting in heavy use of dark and low light periods prior to sunrise.

4.3.4 Multi-scale risk allocation

Predation risk from white sharks exhibited distinct patterns at the two spatiotemporal scales explored, latitudinal distribution at the seasonal scale and inshore visitation at the diel scale. Seasonal changes in white shark distribution have previously been shown to correlate strongly with space use and behavioral changes in gray seals
Comparing the parameters of fine-scale movement ecology analyzed above show similar trends and differences between summer and winter seasons (Figure 13, Figure 14). In this case, seals utilize the offshore environment more extensively during low risk seasons when encounters with white sharks in the latitudes around Cape Cod are infrequent.

During the summer when shark presence around Cape Cod is high (Figure 11, Chapter 3), coastal activity of sharks and seals show more interesting interactions. Detection of sharks at inshore monitoring stations distinct exhibit diel cycles, with three peaks around sundown, midnight, and sunrise (Figure 16). The cyclic pulses of inshore visitation by sharks create temporal variation in the risk encountered during the coastal behavior of nocturnal foraging (Figure 16, Figure 17). Overlaying the mean departure vector (mean $\tilde{\theta} \pm 95\% \text{ CI} = -1.21 \pm 0.06$ radians; i.e. 19:00-19:30 local, Figure 13) with diel cycles in inshore shark visitation, tagged gray seals allocate the diurnal maximum amount of encounter risk in observed departures for nocturnal foraging. However after foraging for the night, returning animals allocate the nocturnal minimum amount of encounter risk in their observed arrivals (mean $\tilde{\theta} \pm 95\% \text{ CI} = 0.84 \pm 0.77$ radians; i.e. 03:00 - 03:30 local, Figure 13).

### 4.4 Discussion

The movement ecology and offshore foraging trips of telemetry tracked gray seals on Cape Cod exhibit clear, seasonally-distinct patterns. Summer movement behavior is characterized by brief, nocturnal trips to nearshore habitats ($<$ 12km from shore). Winter movement is more typical to movement observed in other gray seal
studies (McConnell et al. 1999, Breed et al. 2006, Breed et al. 2009), specifically the targeting of offshore habitats with long, multi-day trips that exhibit apparent individual and sex differences. Similar to observations in Breed et al. (2009), males traveled further and stayed at sea longer during the winter (Table 5), though females exhibited more trips overall (Table 5) perhaps to compensate for additional energetic demands in the magnitude of their reproductive costs (Beck et al. 2003). As documented in other well-studied populations (Breed et al. 2009, Breed et al. 2013), seasonal diet shifts to higher quality prey with greater energetic content (Beck et al. 2007, Ampela 2009) are expected to underlie changing movement ecologies and spatial patch targeting. Reduced summer foraging and a high degree of overlapping ranges are also reported in other populations (Breed et al. 2013), but not usually at such an high proportion, small spatial scale, or exclusively nocturnal as observed in this study.

Nocturnal foraging is less well reported in gray seal literature, suggesting the behavior is relatively rare or underexplored. Russell et al. (2015) reports activity budgets coarsely across quarters of the day, but shows relatively little change in the probability diving, foraging, or traveling states throughout the day (Appendix 3, Russell et. al 2015). Gray seals are visual predators that depend on the sense of sight, as well as tactile (Hanke et al. 2013), auditory (Stansbury et al. 2014), and potentially other sensory cues, in targeting of demersal prey items. There are no studies that evaluate feeding efficiency and prey detection or capture of gray seals at night or in low-light/dark experimental conditions. However, there are known nocturnal behavioral shifts in sand lance (*Ammodytes* spp.), a dominant diet item of gray seals (Beck et al. 2007, Ampela
2009). Nocturnal shifts from schooling to burrowing behavior would make sand lance more accessible to a grasping consumer like a gray seal. Indeed sand lance comprised the predominant stomach contents of fishery-bycaught animals feeding in summer months near our tagging location in Chatham, MA (F. Wenzel, personal communication). Though habitat maps were coarse in comparison to the coastal behavior of the tagged animals, benthic habitats within the summer foraging range are primarily sand and gravel types preferred by burrowing sand lance. As with other studies, overlapping coastal behavior in gray seals appears associated with targeting of sand lance (McConnell et al. 1999, Breed et al. 2009, Breed et al. 2013). Others have suggested such foraging behavior could produce scramble competition from high consumer densities in small foraging arenas (Breed et al. 2006, Breed et al. 2013), though have only focused on intraspecific competition and not predation risk contexts.

The tagged seals in this study are under risk of predation from white sharks seasonally (Figure 11, Chapter 3), that are observed inshore along Cape Cod regularly (Skomal et al. 2012) and interacting with gray seals frequently. One tagged individual in this study suffered a fatal interaction and was found dead on the beach with a large wound from a shark bite in its hide flippers (necropsy report, M. Moore, personal communication). On its final foray, the animal utilized an inlet to access an inshore haul out an hour after sunrise, during a high risk period for visual predation (J. Moxley, unpublished data). Heavy utilization of dark and low-light twilight periods, as observed here (Figure 14), is an optimal strategy for avoidance of an ambush predator using silhouetting for prey detection. Further work, particularly exploring the interactive
effect of nocturnal illumination and cloud conditions as well as behavioral observations of predator-prey interactions in the crepuscular, has great potential for testing the role of illumination in predator avoidance by foraging gray seals.

Foragers that experience acute predation pressure near their central place must allocate risk twice per foray, on both outbound and inbound legs. As observed at other shark-seal hotspots (de Vos et al. 2015, de Vos et al. 2015), risk-mediated effects and antipredator behavior of these two trip legs can differ, likely due to inherent differences of goal motivation (e.g., feed vs. rest), energy level (e.g., rested vs. tired), onset of digestion (e.g., unlikely vs. likely), group formation and coordination (e.g., facile vs. difficult), navigation targets (e.g., multiple patches vs. restricted entry points of haul out), alignment of eyesight (e.g., toward deeper depths vs. shallower depths), direction of sun glare (e.g., from west vs. from east), and associated implications for vigilance, predator detection, and/or likelihood of escape (Figure 17). Some combination of these effects may underlie the counterintuitive decision to initiate foraging forays at the diurnal maximum of shark presence inshore (Figure 17), conforming with paradoxical behavior predicted by the risk allocation hypothesis (Lima and Bednekoff 1999, Bednekoff and Lima 2011). Upon return, coastal arrivals align with minima in shark activity, suggesting a reversal of risk-mediated effects may influence seals to reduce encounter probabilities and shift dawn periods conform closer to the temporal avoidance predicted by the risky times hypothesis (Creel et al. 2008). The risk allocation theory outlines the role of attack rate in affecting risk-mediated effects, so further observation of predator-prey interactions at dawn and dusk is expected to reveal divergent rates of shark-seal
direct interactions that explain risk-mediated differences in departures and arrival patterns (Figure 13-Figure 15). Behavior modulates the likelihood of attack, and animals often use group formation, vigilance, and apprehension to avoid predation (Brown and Kotler 2004, Caro 2005, Heithaus et al. 2009). While available data limited investigating group formation amongst tagged animals, initial analyses show a high degree of temporal concurrence between foraging departures (at least, within the half-hour temporal resolution of the movement model; J. Moxley, *unpublished data*). Vigilance on departures is also aided by the direction of the sun’s glare (over land in the west) and the alignment of the seal’s visual direction with deeper waters preferred by white sharks. These factors are reversed for inbound seals at dawn, likely affecting metrics of predatory sequence including attack frequency, predatory success rate, and ultimately the predation risk perceived by seals.

Predation risk is demonstrated to be an important force in behavioral ecology (Laundre et al. 2014), with risk allocation emerging as the primary theoretical foundation for how animals manage and mitigate temporal variation in risk while foraging (Lima and Bednekoff 1999, Higginson et al 2012). In a recent review, the hypothesis received partial experimental support, likely due to differences in experimental design and violation of key assumptions like foragers are food-stressed (Ferrari et al. 2009, Higginson et al. 2012). Still optimal patch use under predation pressure predicts patch departure when the expected benefits and reward rate of the patch are exceeded by the total costs of metabolic expenditure, predation risk, and missed opportunity costs of foraging (Brown 1992, Brown and Kotler 2004). Central
place foragers additionally must factor travel time back to a central place (Olsson et al. 2008) as well as potentially anticipate risk cycles at the central place when they arrive (Raby and Clayton 2009). In this study, the nocturnal foraging of gray seals conforms with this expectation, whereby animals depart at periods of high encounter risk to feed on patchily-concentrated prey items (e.g., sand lance) until they leave patches in order to arrive back at the beach before sunrise (Figure 14). This mean arrival time is centered upon astronomical dawn, the point at which the night sky is no longer completely dark and an instant of presumed importance to antipredator behavior against a predator silhouetting prey. Summer is a lean season for gray seals (Beck et al. 2003) and often features reduced time at-sea and foraging effort (Breed et al. 2009, Breed et al. 2013), so the missed opportunity cost of foraging during the daytime may be reduced. Metabolic costs of extremely short foraging movements are also likely small since gray seals typically conduct long trips to sea over multiple days (Breed et al. 2009, Russell et al. 2015). However, the catastrophic losses of a lethal shark interaction may be too great if the seal is able to subsist until sharks depart the nearshore environment closer to winter. If large groups and selfish herds are used to mitigate high predatory encounters upon departure, scramble competition (as suggested for other populations) would increase and thus lessen opportunity costs with increasing number of individuals foraging on a given night. Thus, costs associated with predation risk are expected to drive, at least partially, the observed movement patterns of gray seals off Chatham, MA and possibly elsewhere. Risk-mediated behavioral decisions in these seals, however, is complex and requires anticipation of cycles in predation risk that include travel costs and behavioral
switches in prey. The combination of these factors lends new insights to empirical
dynamics of risk allocation in free-ranging consumers exploiting fluctuating
environments while encountering ambush predators.
**Table 5**: Seasonal foraging trip characteristics for male (n = 4) and female (n = 4) gray seals.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Season</th>
<th># of Trips</th>
<th>Distance Traveled (km)</th>
<th>Max. Distance Offshore (km)</th>
<th>Trip Duration (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Mean ± 95% CI</td>
<td>SD</td>
<td>Mean ± 95% CI</td>
</tr>
<tr>
<td>F</td>
<td>summer</td>
<td>97</td>
<td>15.43 ± 1.56</td>
<td>7.84</td>
<td>5.06 ± 0.51</td>
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<td>102.42</td>
<td>16.49 ± 2.84</td>
</tr>
<tr>
<td>M</td>
<td>summer</td>
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<td>18.94 ± 2.88</td>
<td>17.90</td>
<td>6.07 ± 0.52</td>
</tr>
<tr>
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<td>winter</td>
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<td>191.32 ± 67.43</td>
<td>278.48</td>
<td>43.35 ± 15.07</td>
</tr>
</tbody>
</table>
Figure 12: Typical movement patterns across two seasons. Summer (above) is characterized by overnight forays and concentrated use of nearshore habitats less than 12km from haul outs. Winter movement is characterized by long foraging trips over multiple days to offshore habitats.
Figure 13: Rose diagrams of the time of day (24-hour clock) of coastal departures (left) and arrivals (right) for two seasons. Summer offshore foraging trips show a clear nocturnal pattern consistent across all tagged individuals. Winter behavior shows no discernable patterns. For reference, mean sunrise (yellow bar) and sunset (gray bar) for each season are shown using the average time of day for months of August and January, respectively. Mean vectors of the distribution are shown in red, with thickness scaled to the strength (i.e., concentration, or resultant length) of that vector. The circular uniformity in the winter distributions is evident in the weak mean vector.
Figure 14: Departures and arrivals of seasonal foraging trips in relation to the nearest sunrise or sunset event. The nocturnal cycle of summer foraging is apparent, while winter movements show no similar pattern. Histograms are color coded to match daylight periods (yellow = daylight, pink = twilight, or the 90 minutes before or after the crepuscular event, and black = night).
Figure 15: The mean difference between summer departures or arrivals and various reference points of twilight demonstrate the astronomical context most closely associated with the mean of the distribution. Summer departures are centered evenly about sunset (0°, when the sun is crossing the horizon). The distribution of summer arrivals, however, is left skewed and not centered around sunrise. Instead, the mean arrival is centered around a solar position of -18° below the horizon, commonly referred to as astronomical dawn.
Figure 16: Diel cycles of acoustic detections (2013-2014) of white sharks at inshore monitoring stations show three peaks of activity: dawn, dusk, and midnight local time (data and figure courtesy, G. Skomal). The temporal patterns of shark activity (blue line) is inferred as encounter risks for seals departing and arriving on summer foraging forays, which conforms with predictions of risk allocation (Figure 17).
Figure 17: Conceptual figure of risk allocation in seal behavior. Seasonal and diel variation in shark presence on shown on the right (courtesy Curtis et al. 2014, G. Skomal). This is used to reflect cycles of temporal variation experienced by seals during summer foraging trips. Activity of coastal departures and arrivals are shown throughout the day, with expected predation risk shown in the curve’s color (green = relatively safe; red = relatively risky). Departures are characterized by a peaked distribution coincident with maxima in shark presence. Though more temporarily-disperse, arrivals are asynchronous with the morning peak in shark activity, indicating divergent allocation of risk on foraging trip legs.
5. The recovery of Cape Cod gray seals: an opportunity for empirical tests of predation risk theory and applied understanding of complex conservation decisions

5.1 Carnivore conservation in the modern era

The recovery of depleted wildlife populations can affect trophic and non-trophic relationships in ecosystems in manners similarly insightful as ecological perturbations (Terborgh and Estes 2010). Across nature, ecological perturbations are often valuable for revealing complex interspecific interactions and ecosystem structure and function (Estes et al. 1998, Estes et al. 2011, Callan et al. 2013, Ford and Goheen 2015, Marshall et al. 2015). On Cape Cod as well as elsewhere in their global range, gray seals have recovered without major direct interventions (e.g., reintroduction, directed population recovery efforts, etc.) and are reestablishing their ecological role in altered marine ecosystems along human-dominated coastlines (Boehme et al. 2012). While a conservation success, a growing coastal carnivore population requires adaptation and response from marine and human communities. Concerns on Cape Cod focus on the effects of gray seal abundance on commercial and recreational fishing harvests, human safety concerns over seals and sharks, water quality and environmental changes, wildlife disease and parasite transmission, and space use conflicts over beach habitat and recreational activities (Bogomolni et al. 2010, Bass et al. 2016). More broadly, facets of the Cape Cod gray seal recovery illustrate new developments in theoretical expectations in risk-sensitive foraging behavior (Ferrari et al. 2009, Bednekoff and Lima...
complex considerations in the conservation of predators and carnivores (Ripple et al. 2014, Chapron et al. 2014, Marshall et al. 2015, Ferretti et al. 2015), and the role of technology in delivering novel insights of wildlife modernizing into human-dominated land and seascapes (Wilmers et al. 2015, Kays et al. 2015, Wilson et al. 2015).

In this dissertation, I developed an analytical framework to address current knowledge gaps—including abundance (Chapter 2), space use (Chapter 3), and risk-mediated behavioral ecology (Chapter 4)—in the adaptation of gray seal ecology to Cape Cod environments and restored interspecific relationships within US marine communities. In spite of a wealth of literature describing gray seal ecology and life history at population strongholds in Atlantic Canada and the United Kingdom, tagged individuals in this southern subpopulation exhibited novel or under-described behaviors seasonally, such as elevated haul out rates, consistently small and compact home ranges, and high degrees of nocturnal foraging. Seasonal overlaps with migratory white sharks and direct observations of regular shark-seal interactions introduce novel perspectives on gray seal ecology as an intermediate predator and permits exploring results within a predation risk framework.

5.2 Abundance of Cape Cod’s gray seals: evidence for rapid growth in a pinniped prey base.

Dramatic growth in US gray seal colonies since initial establishment of breeding sites in 1991 has resulted in beach aggregations of seals in southeastern Massachusetts
that are visible by satellite. Though numerically rare to absent on Cape Cod for much of the 20th century (and likely functionally absent for longer; Wood et al. 2011), I estimate a minimum at least 30,000 gray seals within the Cape Cod region currently by employing a novel satellite-based digital aerial survey. The novelty of this approach in addition its drawbacks warranted implementing a precautionary analytical approach that can be improved through better understanding of haulout patterns and correction factor parameters. Improvements to this method will be better positioned to capitalize upon continual advances in satellite observation (e.g., sampling frequency and ground resolution) that strengthen this tool for monitoring rapid changes in coastal wildlife populations. Survey design can be optimized and made more proactive through partnerships with commercial operators collecting and selling high-resolution earth observation imagery. Expanding telemetry efforts can increase parameter certainty as well as support additional scientific studies (Hart and Hyrenbach 2009, MacIntyre 2014, Wilmers et al. 2015). Cost savings could offset increased telemetry costs as the method improves to become a better substitute for already-budgeted traditional monitoring efforts.

Now with first comprehensive abundance estimate for US stronghold of gray seals, evidence indicates a dramatic resurgence of a prey base of pinnipeds in less than two generations (Graves et al. 2009, Skomal et al. 2012). Elsewhere, successful recoveries of marine mammal stocks have resulted recently in growing observations of predation-
related mortalities, including sea otters (Estes 1998, Tinker et al. 2015) and humpback whales (Pitman et al. 2015) for example. In these cases, population recovery of marine mammals may bolster the feeding ecology of sympatric predators while revealing new insights into the natural role of predation in marine mammal ecology (Kiszka et al. 2015). Intraguild recovery of predator communities and subsequent restored ecological relationships demonstrate the ecological importance of intermediate top predators (Kiszka et al. 2015) including pinnipeds whom appear particularly responsive to policy protections (Roman et al. 2013, Roman et al. 2015).

5.3 Reduced space use and the potential for pre-breeding growth tradeoffs for the southernmost breeding colony of gray seals.

To maximize lifetime fitness, a long-lived iteroparous animal must adopt annual behavioral routines that meet life history and energetic demands (McNamara and Houston 2008). Energy maximization in preparation for gray seal capital breeding include both metabolic reductions (Sparling et al. 2006) and surplus and compensatory foraging (Beck et al. 2003, Breed et al. 2006, Breed et al. 2009, Beck et al. 2007), all of which are usually evident in space use patterns (McNab 1963, McNab 1986, Tucker et al. 2014). Large differences in home range area between US and Canadian gray seals (Chapter 3, Harvey et al. 2008, Baker et al. 2015) suggest potentially unique set of life history tradeoffs, particularly during the pre-breeding season when differences are largest. Metabolic costs of inopportune mass gain (Gillooly et al. 2001) may be amplified
for capital breeders in warmer portions of their range. Extensive and frequent haul out behavior in the pre-breeding season (Chapter 2) would further modulate any thermoregulatory and metabolic effects. Mass gain can also affect predation risk (e.g., effects on buoyancy, locomotory, or diving effects), in manners that would favor small, compact home ranges during seasonal increases in predation risk. Across the entire cohort, expansion in space use, home range size, and at-sea activity occur when air and water temperatures are consistently cooler and inshore shark encounters less probable (< 2%).

Reduced summer foraging is observed in many gray seal studies as animals concentrate at-sea distributions coastally, often targeting sand lance in spatially-predictable habitats (i.e, coarse gravel and sand). Breed et al. (2006) outlines mutually exclusive hypotheses of how contrasting levels of summer prey availability can produce localized coastal foraging effort in gray seals. Non-mutually exclusive, they also invoke the “ghosts of predators past” hypothesis (sensu Byers 1997) to suggest reduced summer foraging as part of an annual energy routine adapted for historic periods of higher shark abundance. Understanding function and mechanisms in animal behavior is inherently complex (Tinbergen 1963, Levin 1992, Levin 2003, Monaghan 2014), so exploring unique ecological and environmental contexts can be fruitful to elucidating a species’ behavioral tradeoffs within well-studied annual physiological routines (Zera and Harshman 2001, McNamara and Houston 2008, Blumstein et al. 2010, Bateson and Laplan 2013). In this
case, there may be physiological, demographic, or life history effects of the smaller than expected space use, concentrated and overlapping movements, and unusual behaviors of this study population.

5.4 Risk allocation and predator-prey dynamics in Cape Cod shark-seal interactions

Commonly, forage and refuge are not spatially correlated and thus decisions about where, when, and how to feed must also manage inherent increases in predation risk (i.e., what the literature labels as the “hazardous duty pay” of foraging, Brown and Kotler 2004; also Wirsing et al. 2009). Given concurrent increases in white shark activity with gray seal population growth (Skomal et al. 2012), patch use decisions in gray seals are expected to incorporate heightened predation risk (Brown 1992). In risky coastal areas, outbound and inbound travel on foraging forays interacted with different phases of diel cycles in shark activity. By incorporating temporal variation of predation risk, the risk allocation hypothesis accommodates paradoxical decisions about foraging during periods of high risk (Lima and Bednekoff 1999, Ferrari et al. 2009, Bednekoff and Lima 2011, Higginson et al. 2012). In the case of tagged gray seals around Chatham harbor, food-motivated individuals departed colonies around sundown coincident with the maxima of diel shark activity. After feeding throughout the night, individuals were more likely return to the beach at minima in shark activity around or before early dawn. Synchronized departures in large groups could serve to dampen predation risk by using selfish herds to reduce per-capita risk. Potential tradeoffs (a la Wirsing et al. 2007) of
foraging opportunities for the safety of arriving at haulouts before sunrise remains unevaluated until more is known about prey patch (namely, sand lance) dynamics. Still, tagged animals exhibited fine-scale allocation of risk and divergent responses of risk tolerance on two phases of a central place foraging foray. The structure of each foray provides a natural experiment to contrast inherent differences between trip legs (e.g., motivational state, group formation, etc.) on the forager’s observed risk allocation, but is relatively under-utilized in the predation risk literature (Ferrari et al. 2009, Beauchamp and Ruxton 2011, but see de Vos 2015 a,b).

5.5 Risk-mediated decision making in behavior

In the development of a general predictive theory of predator risk effects (Heithaus et al. 2009, Creel 2011, Higginson et al. 2012), predation risk is decomposed into two components that encapsulate 1) the probability of prey encountering a predator; and 2) the condition probability of consumption (or injury) given an encounter (Lima 1992, Hugie and Dill 1994). The risk allocation hypothesis (Lima and Bednekoff 1999, Bednekoff and Lima 2011) has emerged as a leading theory for optimal decisions levels of foraging activity throughout different phases in temporal patterns of predation risk (i.e., how often and for how long to feed in high and low risk phases, Ferrari et al. 2009). Mixed experimental support (Ferrari et al. 2009, Higginson et al. 2012) highlights the importance of two critical assumptions: 1) prey are energy limited or nutritionally-stressed; 2) prey have experience with the risk regime and can perceive or anticipate
high and low risk periods or places (Ferrari et al. 2009). While gray seals are capable of long fasts during portions of the year, the summer is a lean season and further work (including studies of stable isotopes, stress hormones, body condition, and feeding ecology) is required to understand the food stress and energetic states experienced seasonally by animals on Cape Cod. Nocturnal targeting of behavioral switches in sand lance by gray seals, however, confirms theoretical predictions that risk allocation is most pronounced when environmental conditions change quickly and resource conditions fluctuate (Higginson et al. 2012). Thus, risk allocation theory may provide a powerful theoretical foundation for understanding how the intact predatory relationship occurring between sharks and seals on Cape Cod structures spatiotemporal patterns in gray seal movement and consumption. Subsequently, additional indirect effects could affect any fishing and human interactions (e.g., bycatch, depredation), as well as expected ecological indirect effects. Given widespread interest in the interactions of marine mammals and fisheries (Morissette et al. 2012), intact predatory relationships could have an important role in structuring the interactions between extractive fisheries and growing marine mammal populations (Varjupuro et al. 2011, Roman et al. 2015).

Cape Cod gray seals seasonally overlap with white sharks (Curtis et al. 2014) and regular shark utilization of inshore habitats (Skomal et al. 2012, G. Skomal, personal communication) establishes a coastal arena for predator-prey interactions. Detection and anticipation of predation danger is governed by various modalities of risk perception
that integrates information from both social (e.g., signaling, social cues) and personal sources (e.g., sensory information, experience) employed in decision-making processes about appropriate behavioral responses (Dall et al. 2005, King and Cowlishaw 2007, Stephens 2008, Raby and Clayton 2009). Sensory systems of pinnipeds are multi-faceted (Wartzok and Ketten 1999, but little is known about predator detection and the influence of personal experiences on an individual’s umwelt (Von Uexkull 1934). Visually, seal behavior shows sensitivity to changes in ambient environmental light, perhaps as a response to reduced visual acuity in the shark’s silhouetting strategy. However, the alignment of a carnivore’s binocular vision with the deeper water habitat preferred by its predators may lead to higher risk tolerance on a foraging trip’s outbound leg from Cape Cod. While olfactory detections through chemical cues is common in aquatic risk assessment (Wisenden 2000), it is unclear how much this sense is utilized beyond chemical scents released during direct shark-seal interactions or if it is more beneficial in predator detection or prey targeting. While the acoustic biology of pinnipeds is some of the least studied of marine mammals, new evidence demonstrates seals can hear acoustic telemetry tags (outwards to 200m in harbor seals, Bowles et al. 2010) and associate their signal with ecological information (Stansbury et al. 2014). With ample experience around acoustically-tagged white sharks, gray seals may be able to use acoustic information in assessing immediate sources of risk. Additionally, social information can aid in antipredator defense, especially in facilitating group formation
and selfish herds dispersing per capita risk. In other shark-seal systems, groups of seals departing haulouts are significantly larger than groups returning from sea (de Vos et al. 2015). Local enhancement are common sources of information in central place systems (Haney et al. 1992, Silverman et al. 2004, Weimerskirch 2007, Wakefield et al. 2009), though the degree of its use in predatory risk assessment is unexplored.

No prey can have perfect information of predation risk and subsequent danger, and so many adopt morphological changes or behavioral patterns that reduce the probability of deadly interactions. These adaptations can include changes to habitat use, vigilance, foraging, aggregation, movement patterns, and sensitivity to environmental condition (Creel et Christianson 2008). The nearshore subtidal environment of Cape Cod lacks visibly complex structure that might provide microhabitat refuge (a la Heithaus et al. 2009, Wcisel et al. 2015). Instead, inlets and other shallow barriers like shoals constrain movements and concentrate prey, which may also facilitate group formation. The relative role of this movement barrier in coupling predation rates to predator density (and follow on implications for indirect predator effects; Heithaus et al. 2009) is not known but presents an interesting tradeoff given availability of haul outs not constrained by inlets.

Additionally, further work must evaluate the effect of illumination (solar and lunar, as well as dynamic interactions with local meteorological conditions) on predation rates and risk allocation in prey animals. Behavioral and physiological
studies that utilize spatiotemporal variation in shark interactions can reveal mechanisms of behavioral response, risk allocation, and relative advantages of risk-tolerant or risk-averse strategies. Comparative approaches across capital (e.g., gray seals, elephant seals) and income breeders (e.g., fur seals) at other shark-seal hotspots can further ecoevolutionary hypotheses about interactions between predation risk and life history. Furthermore, Cape Cod’s shallow and sloping sandy nearshore exhibits a distinct benthic environment for shark-seal interactions in comparison to deep-water, hard-bottom habitats present at other sites (e.g., South Africa, Farallon Islands, California). The understanding of optimal risk allocation in diving prey can be developed further through comparative behavioral studies of movement and diving across interactions with alternate predatory styles (e.g., terrestrial pressure from canids; coursing behavior by killer whales) to the ambush strategy common in white shark behavior (Frid et al. 2009, Higginson et al. 2012).

5.6 Complex considerations in presence of conservation success

Large carnivore conservation is often a conservation priority, a direct goal of protective policies, and important to ecosystem preservation due to strong regulatory effects (Sergio et al. 2008, Schmitz et al. 2010, Estes et al. 2011, Ripple et al. 2014). However, considerations of consequences beyond recovery success are often overlooked. Meanwhile, recovery outside of protected areas and acclimation to human-modified landscapes challenges intrinsic public notions of a wildlife separation model
(Packer et al. 2013, Chapron et al. 2014). In addition to challenges of sharing space, carnivore conservation outside of designated reserves can affect perceptions of ecosystem health (e.g., biological invasion verses recolonization) and exacerbate differences in values of ecosystem services (e.g., resource provisioning verses species preservation). With no indications of decelerating trends in environmental modification, modern conservation is challenged to understand, develop, and communicate tolerant coexistence models that navigate conflicting policy mandates (Marshall et al. 2015), feedback interactions between multiple species (Treves and Karanth 2003, Marshall et al. 2015), and ultimately embrace human-wildlife interactions within modernized landscapes (Chapron et al. 2014). The recovery of gray seals and subsequent responses of white sharks on Cape Cod, amidst extensive coastal development and sociopolitical focus on coastal recreation and fishery interests, presents a compelling system for understanding new challenges of coastal predator conservation in the modern era (Treves and Karanth 2003).

Globally, range expansions and recolonization of gray seals demonstrate the adeptness of their adaptive and generalist strategy in modern coastal ecosystems (Duck and Thompson 2007, Haukussen 2007, Mikkelsen 2007, Harkoken et al. 2013, Cronin et al. 2011, Oigard et al. 2012, Boehme et al. 2012, Gladilina et al. 2013). On Cape Cod as elsewhere, population growth of gray seals has prompted concerns over negative effects of their abundance. In addition to long-standing perceived competition with fisheries
(Matthiopolous et al. 2008), unique concerns arise around increasing gray seal populations on Cape Cod. The area’s focus on beach and coastal recreation is relatively novel in comparison to more remote areas around gray seal strongholds in Canada. The response of shark populations to abundance increases in pinniped populations prompts human safety concerns. Given possible effects of safety concerns on recreational sectors of coastal economies (Skomal et al. 2012, Ferretti et al. 2015), communities will need to evaluate lethal and non-lethal approaches to shark management (Neff 2012, Curtis et al. 2012, Neff and Yang 2013). The role of gray seals as disease reservoirs also arouses human health as well as epizootic concerns (Runstadler et al. 2013, Runstadler et al. in review). The single-species focus of many policy regulations are challenged if they are unable to account for complexity in species interactions with sympatric populations of harbor seals, white sharks, or finfish stocks (Johnston et al. 2015, Marshall et al. 2015). While Swain et al. (2015) indicates interdecadal distributional shifts in prey fish to avoidance of areas of seal movement (and presumably, consumption), pursuant indirect effects of risk-mediated seal foraging on fish communities is not understood in spite of the theoretical context (Heithaus et al. 2009). Risk-mediated seal behavior has further potential to drive spatiotemporal patterns of bycatch, the proportion of direct interactions between commercial and recreational sectors (Rafferty et al. 2012), and other interactive effects between predation risk and human activities (Madin et al. 2016). In order to conserve coastal carnivores and safeguard broader ecosystem effects of intact
predatory guilds, conservation actions must promote tolerant coexistence models between coastal activity, industry, and wildlife in manners that directly address sociopolitical landscapes framing the context of recovery (Treves and Karanth 2003, Redpath et al. 2013).

5.7 Role of technology in generating co-existence

Much of this work’s novelty relies on recent advances in earth observation that promote more regional understandings and telemetry technology that reveal intimate views into the lives of individual animals (Wilson et al. 2008). Most gray seal movement studies neglect behavior within 2 kilometers of the shore due to issues of locational accuracy, which excludes a majority of risk-mediated behavior in shark-seal interactions. Further, unique behavioral insights from telemetry work can directly address perceptions and concerns regarding wildlife interactions, while generating familiarity with wildlife biology and perhaps healthier human-wildlife relationships. There appears to shifts towards mature relationships regarding white sharks locally (G. Skomal, personal communication), perhaps due to outreach and communication efforts about shark research activity in the region (e.g., OCEARCH). Long-term telemetry tagging projects of gray seals could adopt similar efforts to provide information and understanding about the movements of gray seals.

As scientists, providing accurate and timely information about wildlife behavior can inform perceptions and develop understanding. While research methods should
always adopt the least invasive methods necessary, important research priorities for
gray seals necessitate animal capture and handling that is inherently dangerous. While
handling procedures and experience can be difficult to build initially, developing this
suite of specialized techniques and skills supports scientific goals and is crucial to the
ability to address wildlife concerns and questions as they arise. Difficult access to wild,
adult animals has limited the ability to describe rapid changes in gray seals and build
scientific knowledge to fill information voids that permit misperceptions. Deploying
technology can rapidly assemble and disseminate a foundation of knowledge so long as
there is funding support and dependable animal access. To test the hypotheses and
results I outline in this dissertation, it is imperative to build a team with handling skills
and experience in order to sustain a research program.

5.8 Cape Cod gray seals as an opportunity

The underlying context of Cape Cod gray seals subject to predation presents
opportunities to place well-studied gray seal foraging ecology within its natural trophic
context as an third level consumer and intermediate carnivore subject to predation. This
initial quantitative assessment of gray seal behavior in US marine habitats has produced
understandings of how gray seals are adapting their generalist approach to local
environments. However, I also utilize the restored predator-prey dynamic to raise
hypotheses about the general development of risk-mediated foraging theory.

Distinguished relatively static resources targeted by herbivorous and granivorous prey
common in other risk-sensitive mammal foraging research, gray seals target a dynamic prey source (e.g., fish) that extends empirical risk allocation to accommodate temporal variation and fluctuation in both resource and predation risk levels (Higginson et al. 2012). Still, patch characteristics of burrowing sand lance (e.g., shallow, spatially-predictable, etc.) naturally extends itself to the powerful theoretical framework of giving up densities (Brown et al. 1988, Brown and Kotler 2004). With ample resources to sample sand lance patch dynamics, any food-safety tradeoffs in gray seal foraging can quantified. This extends understandings of the importance of intact predatory relationships to ecosystem function in a highly-altered region that has seen extensive shifts in the finfish community (Heithaus et al. 2012). Dive studies can begin to understand how gray seals structure foraging effort in risk-mediated settings as well as how it might be employed in antipredator behavior. Further telemetry work must deploy tags at a broader scale to understand behavioral variability and regional variation in how gray seals are managing risk effects. At longer time scales, any behavioral tradeoffs might manifest into growth-survival tradeoffs that could provide insight into selective advantages of capital breeding over other life history strategies. Here on Cape Cod, the restored predator-prey dynamic and well-studied ecology of gray seals can investigate directly prior indications of the “ghosts of predators past” (Breed et al. 2006, but see Byers 1997). The context of multiple predator recovery and human-wildlife relationships on densely-inhabited Cape Cod additionally exemplifies
complexities in modern conservation that deepens the system’s value to both theoretical and applied fields.
Appendix A

Table 6: Paired comparisons of daily and nightly activity before and after the breakpoint show statistical differences consistently across individuals.

<table>
<thead>
<tr>
<th>Animal</th>
<th>Daytime</th>
<th>Activity</th>
<th>U</th>
<th>p</th>
<th>Significance</th>
</tr>
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<td>40898.5</td>
<td>1.87E-06</td>
<td>*</td>
</tr>
<tr>
<td>397</td>
<td>day</td>
<td>at surface</td>
<td>99691.5</td>
<td>8.95E-30</td>
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<td>day</td>
<td>at surface</td>
<td>78539</td>
<td>6.11E-44</td>
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</tr>
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<tr>
<td>709</td>
<td>day</td>
<td>at depth</td>
<td>32957.5</td>
<td>2.67E-46</td>
<td>*</td>
</tr>
<tr>
<td>358</td>
<td>night</td>
<td>at depth</td>
<td>27041.5</td>
<td>0.0009689</td>
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<tr>
<td>397</td>
<td>night</td>
<td>at depth</td>
<td>32967</td>
<td>3.15E-32</td>
<td>*</td>
</tr>
<tr>
<td>652</td>
<td>night</td>
<td>at depth</td>
<td>35241.5</td>
<td>4.38E-07</td>
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<tr>
<td>654</td>
<td>night</td>
<td>at depth</td>
<td>37479.5</td>
<td>4.47E-45</td>
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<td>658</td>
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<td>at depth</td>
<td>66392.5</td>
<td>0.00018191</td>
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<tr>
<td>709</td>
<td>night</td>
<td>at depth</td>
<td>32654</td>
<td>3.37E-47</td>
<td>*</td>
</tr>
</tbody>
</table>
Table 7: Even just within just the small home range cluster, activity budgets still exhibit significant changes across the breakpoint demonstrating behavioral shifts disassociated from changes in area of space used.

<table>
<thead>
<tr>
<th>Activity</th>
<th>Day/Night</th>
<th>ΔMean</th>
<th>ΔMedian</th>
<th>ΔSD</th>
<th>χ</th>
<th>p-value</th>
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</thead>
<tbody>
<tr>
<td>Day</td>
<td>-1.0502347</td>
<td>-1.1702843</td>
<td>0.22889018</td>
<td>25.547027</td>
<td>4.32E-07</td>
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<tr>
<td>Night</td>
<td>-1.1157359</td>
<td>-1.1924618</td>
<td>0.17733232</td>
<td>29.3994011</td>
<td>5.89E-08</td>
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</tr>
<tr>
<td>Day</td>
<td>0.04572794</td>
<td>-0.2675883</td>
<td>0.78135034</td>
<td>0.85125506</td>
<td>0.35619753</td>
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</tr>
<tr>
<td>Night</td>
<td>0.40343244</td>
<td>0.25886266</td>
<td>0.85853991</td>
<td>0.14270933</td>
<td>0.70560229</td>
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<tr>
<td>Day</td>
<td>0.85823244</td>
<td>1.145824</td>
<td>0.45240833</td>
<td>13.9427323</td>
<td>0.00018846</td>
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<td>Night</td>
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<td>0.79504919</td>
<td>0.34307147</td>
<td>11.5806764</td>
<td>0.00066641</td>
<td></td>
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</table>
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128


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Biography

I was born on March 18, 1986 in Richmond, Virginia (USA). I received my Eagle Scout rank while in high school at Douglas Southall Freeman high school, from which I graduated as salutatorian in 2004. In 2008, I graduated from Princeton University with honors with a Bachelor of Arts in Ecology and Evolutionary Biology. My thesis research, *Searching for moving targets: How antbirds find army ants in a rainforest*, received the department’s top honor for original undergraduate research, the Charles M Canon Thesis Award, as well as a top prize in the university-wide undergraduate research symposium. The research revealed intriguing concentric, always counter-clockwise, movement patterns in spotted antbirds on Barro Colorado Island, Panama. The movement patterns matched theoretical expectations from animal search theory and were functional in finding resource-rich ant swarms in a complex environment. Upon graduation, I received the High Meadows Fellowship at the Environmental Defense Fund, conducting research on fisheries management reform and marine ecosystem resilience. Following this fellowship, I began my PhD at Duke University, soon after initiating dissertation research into marine vertebrate movement and the gray seals of Cape Cod.