A REVIEW OF LITERATURE FOR GRAY AND HARBOR SEALS

Gabrielle Calandrino[1], Daniel Pendleton[2], and Michelle Staudinger[1,3]

[1]Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, MA

[2]Anderson Cabot Center for Ocean Life, New England Aquarium, Central Wharf, Boston MA

[3]Department of the Interior Northeast Climate Adaptation Science Center, Amherst, MA

OVERVIEW

Climate change is impacting marine species, causing shifts in occurrence, distribution, and phenology, which can ultimately effect ecosystem structure and functioning (Parmesan & Yohe 2003; Burrows et al. 2011). The study of the timing of recurring biological events throughout an organism's life is known as phenology (Parmesan & Yohe 2003). The way organisms respond to climate change through altered timing offers insight into their sensitivity and adaptability (Parmesan & Yohe 2003).

To gain an understanding of pinniped vulnerability to climate change, specifically through changes in phenology, a comprehensive literature search was conducted using several online databases (e.g., Web of Science, Google Scholar and PubMed). Combinations of relevant terms were searched in order to find studies pertaining to the life history of two regionally important pinniped species: the gray seal (*Halichoerus grypus)* and the harbor seal (*Phoca vitulina)*. Although special attention was given to studies conducted in the Northwestern Atlantic region, publications giving information on populations in other parts of the world provided important proxy information. Keyword searches were conducted in Web of Science and Google Scholar and represent the published literature through 2017 (Table 1). The remainder of the publications found were cited in the literature returned from the two searches.

This document provides an annotated bibliography organized by species (gray and harbor seals) and region, with topical sections for important attributes (e.g. foraging). The focus of this search was for the Gulf of Maine region, but other relevant information yielded by the literature search is presented in order of approximate distance from the focal area.

Table 1. Literature search key words and results.

Keywords Searched	**Papers Yielded**
North Atlantic marine mammals AND climate change	Thompson et al. (1989) Boehme et al. (2012) Lesage & Hammill (2001)
Breeding*North Atlantic AND harbor seal*	Van Parijs et al. (1996) (Baechler et al. 2002)
Pinniped AND Massachusetts	Bogomolni et al. (2010) Schneider & Payne (1983)
Harbor seals* AND temperature	Hamilton et al. (2014) Paterson et al. (2012) Hind & Gurney (1998) Hansen & Lavigne (1997a) Grellier et al. (1996)
Gray seals* AND temperature	Twiss et al. (2002) Hansen & Lavigne (1997b) Boily & Lavigne (1996)
Gray seals AND Gulf of Maine	Harris et al. (2003) Gilbert et al. (2005)

	Bowen et al. (2007)
Gray seal AND New England	Waring et al. (2006)
Gray seal AND Duck Island	Amos et al. (1995)
Gray seals AND climate	Karlsson et al. (2005)

HALICHOERUS GRYPUS (Gray seals)

Population Numbers

Sable Island

- From 1962 to 1997 there was an exponential increase in the pup production at the Sable Island colony but since that time the rate of increase has declined. Between 1997 and 2004 (when this study was conducted) the estimates of demersal fish populations on the Scotian Shelf were unusually low. Because there was no shortage of haul-out/pupping habitat, food sources were determined to be a likely regulator of gray seal numbers (Bowen et al. 2007).

Eastern Canada

- Gray seals were found to be abundant and increasing in Eastern Canadian waters, whereas there were relatively less gray seals in U.S waters (Gilbert & Guldager 1998).

Foraging

Gulf of Maine

- After the winter breeding season (February-April), seals feed in pelagic habitats. Seals haul-out for molting in May – June before dispersing and feeding prior to the next pupping season (Lesage and Hammill, 2001; Kenney & Vigness-Raposa 2010).
- Flounder, silver hake, sand lance, skates, and gadids were found in scat samples from Muskeget Island, Massachusetts (Kenney & Vigness-Raposa 2010 and references therein).
- There were no observed difference in prey preferences of adults vs. juveniles (Kenney & Vigness-Raposa 2010).

Sable Island

- Gray seals forage intensely during the summer and winter months, but the foraging trips are usually shorter in the summer due to higher predictability of prey at nearby areas, such as Middle Bank. In winter their prey is spread out along the whole continental shelf, and thus is less consistent and reliable as a food source (Breed et al. 2009).

Gulf of St. Lawrence, Canada

- The summer diet (August – September) at Anticosti consisted primarily of cod (*Gadus morhua*), herring (*Clupea haengus harengus*) and mackerel (*Scomber scombrus*) (Goulet et al. 2001 and references therein).
- In the southern part of the gulf, flatfish and other groundfish were important autumn prey. During January - March on the Scotian Shelf, grey seal diets were

focused on sand lance (A*mmodytes dubius)* (Goulet et al. 2001 and references therein).

- Females are present in the southern part of the gulf and on the Scotian Shelf from November - March. During this period females dove near or on the sea floor indicating feeding on groundfish and other demersal prey (Goulet et al. 2001).

Scotian Shelf

- The preferred diving depths (70-100 m) of two tagged gray seals strongly overlapped with regional sand lance habitat of 73-90 m (Scott 1982; Goulet et al. 2001).

Moray Firth, Scotland

- This area is considered to be preferred summer foraging habitat for gray seals in the northeastern Atlantic (Thompson et al. 1996), which is believed to be a larger foraging area than harbor seals typically use.

Range/Movement and Site Fidelity

Maine Coast

- In aerial surveys conducted during 1998, gray seals were only seen between Pemaquid Point and Schoodic Peninsula, Maine during the summer, and were not present in the southern region (including the Isles of Shoals), nor the northern region (including at the US/Canadian border) (Gilbert & Guldager 1998).

- It is likely that gray seals found in Maine waters in the summer come from Canadian populations (Gilbert & Guldager 1998).

Gulf of St. Lawrence

- The Gulf of St. Lawrence is believed to represent the northernmost limit of the gray seal's range in the western Atlantic due to the inefficient thermoregulatory ability of pups (Lesage & Hammill 2001).
- Tagging data shows starting in mid-October through the end of November, seals begin leaving the Anticosti Island area and slowly move into the southern Gulf of St. Lawrence and to Sable Island. Timing of departure varied among individuals over the course of a 6 weeks period, but actual southward migration was completed in 6-10 days (Goulet et al. 2001). This southward movement happens in tandem with changes in the distribution of important prey species.
- Similar to other regions, seals in the Gulf of St. Lawrence exhibited site fidelity to particular haul-out sites. In the northern Gulf, seals used a greater diversity of haul-out sites than in the Baltic Sea (Goulet et al. 2001 and references therein).
- Satellite telemetry indicated grey seals largely use coastal habitats in the Gulf during summer even when they are not pupping or molting (Hammill, unpublished data; Lesage et al. 1995).

Isle of May, Scotland

- The topography at this location is variable which could account for the higher levels of site fidelity observed here compared to Sable Island. Seals appear to prefer certain ledges likely because they provide the most ideal pupping haul-out topography (Pomeroy et al. 2000).

Amrum, Southeastern North Sea

- Unknown individual gray seals appeared in this area around mid-May, indicating an end of spring immigration to the area (Abt et al. 2002).
- Juvenile immigration from a colony in the UK to this Dutch colony was responsible for a rapid increase in numbers at the haul-out, demonstrating the Dutch North Sea population is not a closed population (Abt et al. 2002).
- At least 2/3 of identified individuals from the Amrum colony used mixed haul-out sites during spring and summer (Abt et al. 2002); an overall decrease in numbers was observed over the course of the summer.
- Records of individuals show a resident Amrum breeding stock as well as a significant number of temporary residents/seasonal immigrants (Abt et al. 2002)
- It is common for gray seals to travel long distances outside of the breeding season, usually to known haul-out sites (Abt et al. 2002).

Baltic Sea

- Grey seals are capable of embarking on movements one to multi-day trips across vast areas in search of prey or between haul-out sites (McConnell et al. 1992; Sjoberg and Ball 2000; Thompson et al. 1991), and most seals generally returned to their original haul-out between consecutive trips (McConnell et al. 1992; Sjoberg and Ball 2000). Satellite tracking showed seals (N=11) spent ≥70% of their time within 50 km of a specific haul-out (Sjoberg and Ball 2000; Karlsson et al. 2005).

- Re-sightings of gray seals from pelage patterns (i.e., photo-identification) were found to exhibit strong site fidelity during the summer (Karlsson et al. 2005).
- Re-sightings of gray seals show they return to a particular summer haul-out site for at least several years. The majority of re-sights were made within 80 km of the original identification site (Karlsson et al. 2005).

Seasonal Changes

Northern New England coastline

- Survey sightings decreased between May-June (N=100) and August (N=45) in the area (Gilbert & Guldager 1998).

Sable Island, Canada

- Seasonal changes in gray seal body mass occur when hauling-out occurs for extended periods due to fasting, which can last approximately a month for pupping and molting periods (Beck et al. 2000).

Moray Firth, Scotland

- Gray seals are absent from this area in winter and spring. Changes in abundance changes may be due to movements between breeding and foraging areas throughout the UK, indicating gray seals may have wider-scale movements than harbor seals (Thompson et al. 1996).
- Haul-out numbers peak in late summer (Thompson et al. 1996).

Amrum, Southeastern North Sea

- Gray seal numbers show a distinct peak in late March - early April, which is approximately three times higher than the period between June - January (Abt et al. 2002).
- The phenology of gray seals at Amrum reflects seasonal behavior changes that are related to the seals' biological cycle (Abt et al. 2002)

Sex-Specific Differences

New England

- Females reach sexual maturity between 4 - 5 years of age. Males are considered sexually mature at 6 years, but don't start breeding until 8 years of age and most breeding bulls are between 12 - 18 years of age (Kenney & Vigness-Raposa 2010).

Sable Island, Canada

- Males travel longer distances compared to females when foraging (Breed et al. 2009).

Southeast North Sea

- Sex-specific differences were not detected in occurrences of photographically identified individual gray seals (Abt et al. 2002).

Molene Archipelago, France

- 56% of males at this colony displayed seasonal site fidelity during all seasons, and had a seasonal immigration/emigration rate of 44% (Gerondeau et al. 2007).
- Males demonstrated a regular use pattern of the archipelago. 50% of individuals were present during two consecutive seasons, demonstrating high fidelity to the area (Gerondeau et al. 2007).
- Detection rates of males was 92% (Gerondeau et al. 2007).
- Females showed varying degrees of site fidelity (40%-75%) between seasons from 1998-2000 (Gerondeau et al. 2007).
- Females were detected at a rate of 100% in the archipelago area (Gerondeau et al. 2007).
- Females used the archipelago preferentially in the summer, but many breed in other areas (Gerondeau et al. 2007).
- Females show high inter-annual natal site fidelity, which could explain dispersal patterns from the archipelago prior to the breeding season (Gerondeau et al. 2007).
- 60% of females that stayed in the archipelago to breed, which was the minority of all individuals, also stayed in the same area to molt (Gerondeau et al. 2007).
- Immigration was highest between the molting season and summer, and lowest between summer and the breeding season (Gerondeau et al. 2007).

Pupping/ Breeding

Northwest Atlantic

- Gray seals primarily pup at four established colonies in U.S. waters: Muskeget and Monomoy islands in Massachusetts, and Green and Seal islands in Maine (Hayes et al. 2016, p 146-153).
- Female gray seals pup during winter, specifically from late December - January (Beck et al. 2000).

Sable Island, Canada

- Females tend to be more land-based during the pupping and weaning period compared to other times of the year (Beck et al. 2000).

Eastern Canada

- In eastern Canada there are three breeding aggregations: Sable Island, Gulf of St. Lawrence and along the coast of Nova Scotia. Animals overlap during non-breeding times from different colonies (Harvey et al. 2008; Breed et al. 2006, 2009) and are considered a single genetic population (Hayes et al. 2016).

Gulf of St. Lawrence, Canada

- Seals aggregate on two main breeding colonies from December - February on Sable Island off the east coast of Nova Scotia, and in the southern Gulf of St. Lawrence (Goulet et al. 2001 and references therein).

Western Atlantic and Baltic Sea

- Female gray seals give birth during the coldest months of the year. Peak pupping occurs in mid-January for seals in the Western Atlantic and in early March for the Baltic Sea population (Hansen & Lavigne 1997b)

Scotland

- Gray seal breeding behavior shows two modes: they may be polygynous, with males showing high dominance behaviors; however, many gray seals prefer to mate with a previous partner (Amos et al. 1995).

Isle of May, Scotland

- Breeding colony haul-out sites are densely occupied in central locations (Pomeroy et al. 2000).
- Re-sighting probabilities for females at this breeding site between 1990 and 1994 was 70% (Pomeroy et al. 2000).
- Re-sightings of tagged seals occurred within at least one year after their original sighting (Pomeroy et al. 2000).
- 97% of marked females returned to Isle of May in at least one subsequent year, while two females moved to another breeding site 90 km away (Pomeroy et al. 2000).

Global

- Females are highly concentrated resulting in polygyny, and males showing dominance by defending harems or compete for a position within breeding grounds (Twiss et al. 1994; Van Parijs et al. 1996 and references therein).

Molting

Sable Island, Canada:

- Gray seals return to this area in April to molt (Lesage & Hammill 2001).

Temperature Thresholds/Preferences

Gulf of St. Lawrence, Canada

- At 7 months of age, gray seals are better at adapting to temperatures between -7°C and 20°C (Lesage & Hammill 2001)

Canada

- During the post-weaning fast, pups have a zone of thermoneutrality in air (Mount 1979) that extends from -7°C to 23°C. Metabolic rates of adult seals do not increase until air temperatures reach a threshold of approximately -10°C. Responses to high air temperatures are unknown (Boily & Lavigne 1996 and references therein).

Island of North Rona, Scotland

- Adult female gray seals occurred in the water more than on land when air temperatures were ≥10.8°C (Twiss et al. 2002).

Global

- Global distribution is limited to surface water temperatures <20°C. It is unlikely that animals limit their distribution due to thermoregulation capabilities. Phocids are generally homeothermic up to SSTs of 30°C (Boily & Lavigne 1996 and references therein).

Captivity

- Resting metabolic rates (RMRs) showed no significant changes between –18 and 35°C; hyperthermia occurred at air temperatures >30°C. During the breeding season, air temperatures are usually within this range at -7.5 and 20°C (Boily & Lavigne 1996).

Sea Surface Temperature

Global

- Sea surface temperature and water depth appear to affect grey seal distribution (Boehme et al. 2012).

Wind Speed/Direction

Scroby Sands, UK

- Numbers of gray seals was positively correlated with wind speed, with higher counts when winds were from the north (Skeate et al. 2012).

Human Interaction

Massachusetts

- >45% of all grey seal mortality was attributed to human interactions, primarily due to entanglements in Nantucket Sound and the southern outer Cape region near one of the largest seal haul-out sites on the northeastern coast, Monomoy National Wildlife Refuge (Bogomolni et al. 2010).

PHOCA VITULINA (Harbor seals)

Population

Northwest Atlantic

- The NWA population, which includes the eastern US and Canada is considered a single population (Temte et al. 1991). Genetic studies are still needed to resolve whether there is high philopatry or local sub-structure in the region (Andersen & Olsen 2010).

Foraging

Gulf of Maine

- Harbor seals feed primarily on relatively abundant small to medium sized fishes, squid and octopus, as well as crabs and shrimp (Kenney & Vigness-Raposa 2010).
- Sand lance is a primary prey off Cape Cod, Massachusetts
  - 87% of the diet at Race Point (tip of Cape Cod)
  - 85% at Monomoy Island (at the "elbow")
  - 50% at Jeremy Point (on the west side in the middle of the "forearm")
- Followed by squid (22%), gadids, herring, flounders and to a lesser extent mackerel and skate.
- At the Isles of Shoals off southern Maine gadids and rockfishes were equally important (22%), followed by flounders and herring (>10%), as well as cunner, sand lance, and skate (Kenney & Vigness-Raposa 2010).

Eastern Canada

- In 602 harbor seal stomachs, herring dominated the diet, followed by squid (*IIlex illecebrosus* and unidentified individuals), flounders (mainly *Pseudopleuronectes americanus*), alewife, and hake (Boulva & McLaren 1979).
- Prey sizes were as large as 30 cm long (herring), and approximately 3-4% of the total body weight (Boulva & McLaren 1979).
- Squid was more important in the lower Bay of Fundy (15% of diet) than at Sable Island and southeastern Cape Breton Island (7%). In the lower Bay of Fundy, flounder were common (28%), but only comprised 2% of the stomach contents from Sable Island and Cape Breton Island (Boulva & McLaren 1979).

Gulf of St. Lawrence, Canada

- Foraging was close to shore (<6.11-11.0 km) during ice free periods. Seasonal migrations to overwintering sites were as far as 266 km (range 65-520 km) (Sharples et al. 2012).

Inshore Scotland

- Foraging duration varied by region but not by sex (Sharples et al. 2012).
- Region and time of year predicted foraging behavior better than ize, sex or body condition (Sharples et al. 2012).

Moray Firth, Scotland

- January abundance and winter diet were believed to be related to clupeid abundance (Thompson et al. 1996).

Range/Movement and Site Fidelity

Gulf of Maine

- Harbor seals use southern New England as winter habitat and some move into Maine coastal waters right before pupping in late spring/early summer (Waring et al. 2006).
- Radio tags recorded long-range movements made by harbor seals, and found that the furthest distance a tagged seal traveled was 60 km (Waring et al. 2006).
- Harbor seals exhibit site fidelity by bay subunits in Maine coastal waters, however they may move between haul-out sites (Pauli and Terhune 1987; Waring et al. 2006).
- A general southward movement from the Bay of Fundy to southern New England waters occurs in autumn and early winter. A northward movement occurs prior to the pupping season from southern New England to Maine to eastern Canada during mid-May through June along the Maine Coast (Waring et al. 2006 and references therein; Hayes et al. 2016).
- Harbor seals are observed year-round in coastal Maine and Canadian waters, while they have a seasonal occurrence from September to late April-early May in southern New England (Kenney & Vigness-Raposa 2010 and refernces therein).

North Atlantic

- Tagged harbor seals were found to be relatively sedentary with movements associated with foraging and some juvenile mediated long-range dispersal events (Thompson et al. 1989; Andersen & Olsen 2010 and references therein).

Britain

- Most harbor seals used the same haul-out site (or sites close by) repeatedly, but a few traveled between regions of Britain and elsewhere in Europe (Sharples et al. 2012).

Moray Firth, Scotland

- Local movement by harbor seals (< 75 km) occurs year round (Thompson et al. 1996).
- Population is considered to be comprised of year round residents due to the presence of local foraging sites (Thompson et al. 1996).

Orkney, Scotland

- Individuals returned to a haul-out site located at the core of their home range instead of hauling-out at sites adjacent to foraging areas (Thompson et al. 1989).

Grand Island & Bristol Bay, Alaska

- Migration rates and haul out behavior vary with sex and age, consequently haul-out sites varied in demography, particularly during the mating season. Adult females return to natal sites while juveniles and adult males disperse (Thompson et al. 1989; Simpkins et al. 2003).

Seasonal Changes

Casco Bay, Maine

- Harbor seals were present on 97% of days that counts were conducted in August, but only on 20-30.8% of days in January (Harris et al. 2003).
- The mean number of harbor seals hauled-out was greatest in August and lowest in January-February (Harris et al. 2003).

Gulf of Maine/New England

- Harbor seals move between US and Canadian waters seasonally (Waring et al. 2006).
- The overall preference for ice-free waters (Baechler et al. 2002) drives harbor seals to move into southern New England waters during the winter and spring (Raposa & Dapp 2009).
- Along the Maine coast, fewer ledges had seals seen on them in August compared to earlier in the summer (Gilbert & Guldager 1998).

Sable Island, Canada

- Fewer seals were present on this haul-out from July-August during the harbor seal molting period (Boulva & McLaren 1979).

Moray Firth, Scotland

- Harbor abundance was at its highest during June, July and August compared to the rest of the year (Thompson et al. 1996).
- Individual harbor seals spend more time ashore during breeding and molting, which could explain this summer-time abundance peak (Grellier et al. 1996, Thompson et al. 1996).

- Inter-annual differences in haul-out behavior exist regionally (Thompson et al. 1996).

Southwest Ireland

- Constant numbers of harbor seals onshore were observed from April to July (Cronin et al. 2009).
- The maximum amount of time seals spent onshore occurred in October; the least amount of time ashore occurred in February (Cronin et al. 2009).

Svalbard

- Seals spent more time in the water foraging during fall than on land (Hamilton et al. 2014).

Time of Day

Gulf of Maine

- Factors influencing haul-out behavior included wind speed and direction, temperature, tidal stage, precipitation as well as time of day. The most seals hauled-out when low tide was in the afternoon on calm, sunny days (Kenney & Vigness-Raposa 2010).

Sable Island, Canada

- Diurnal haul out was observed with no seals on land at night (Boulva & McLaren 1979).

Scotland

- From May to August (encompassing both pupping and molting periods), 80% of seals were seen hauled-out midday (Cunningham et al. 2009).

Southwest Ireland

- Harbor seals demonstrated a diurnal haul-out pattern and spent more time spent on land during early to mid-afternoon (Cronin et al. 2009).

Svalbard

- The probability of seals haul-out was highest at midday (Hamilton et al. 2014).

San Miguel Island, CA

- Peak haul-out numbers occurred between 1pm and 4 pm, with numbers increasing in the morning and decreasing as sunset approached (Stewart 1984).

Age/Sex-Specific Differences

Gulf of Maine

- Females reach sexually maturity at 2-5 years of age, most at age 3 or 4, and physical maturity is attained at age 6 or 7. Males take about a year longer (Kenney & Vigness-Raposa 2010 and references therein).

Scotland

- Haul-out behavior varies by age and sex, and seals show age and sex segregation at haul-out sites (Cunningham et al. 2009).

Orkney, Scotland

- Males hauled-out most days from May to July but were observed to make short trips (< 24 hours) outside the study area, or exhibit diurnal haul-out behavior or left the study area for longer periods of time (several days) with common nighttime haul-outs. At the end of July right before the molt all males hauled-out every day diurnally (Thompson et al. 1989).
- Females hauled-out most frequently in the afternoon. During pupping females hauled-out every day and spent most of their time in the study area. There was no difference in female behavior during the pupping and molting period (Thompson et al. 1989).

Moray Firth, Scotland

- Males dispersed widely with weekly ranges of 65 to 480 km^2 in June. In early July, males markedly decreased their ranges to around 4-70 km^2 and was unrelated to time hauled out (see Thompson et al. 1994; Van Parijs et al. 1996).
- Males make wide movements during the early pupping period, but then decrease their range when females start foraging in the late lactation period (Van Parijs et al. 1996) and engaged in stereotypic diving and acoustic displays that suggest they were defending preferred areas from other males and/or attracting females (Hanggi & Schusterman 1994; Van Parijs et al. 1996).

Svalbard

- Likely due to sexual dimorphism in this population, which is uncommon elsewhere, both age and sex influenced haul-out behavior (Hamilton et al. 2014).

Breeding

Northwestern Atlantic

- Mean age of maturity was between 3 and 4 years (Boulva & McLaren 1979).
- Females mature earlier than males, and may be polygynous (see Annual Cycle and General Behavior; Boulva & McLaren 1979).

Sable Island, Canada

- Mating on Sable Island occurs between early April and late July (see Annual Cycle and General Behavior; Boulva and McLaren 1979).
- "Reproduction represents a significant energetic burden to breeding seals (Bowen et al. 1992; Walker and Bowen 1993). During gestation and lactation, the mother must meet not only her own energetic costs but also those of her pup. Lactation, which lasts for about 24 days following parturition and is energetically costly, constrains foraging by females and utilizes fat reserves (i.e., the blubber layer) (Bowen et al. 1992; Muelbert and Bowen 1993; Hind & Gurney 1998).

Molting and Pupping

Gulf of Maine

- Pupping seals stayed in the mid-coastal region from May through August, encompassing both the molt period as well as the pupping period (Waring et al. 2006).

- After pupping, annual molt occurs over 2-3 months from mid-summer through early fall (Bigg, 1981; Burns, 2002). Haul-out frequency increases during the molting period (Kenney & Vigness-Raposa 2010).

Casco Bay, Maine

- Seal abundance decreased between May and June, likely because this area is used as a molting site but not a pupping site (Harris et al. 2003).

Moray Firth, Scotland

- Presence on haul-out sites is highest during pupping and molting seasons (Grellier et al. 1996).
- There is a mid-summer peak in harbor seal haul-out presence, which corresponds to the pupping season (Grellier et al. 1996).

Alaska

- Males haul-out for extended periods of time only during molting, while females have two extended haul-out periods: during molting and pupping (Gilbert et al. 2005).
- Molting times vary by sex and timing varies annually (Gilbert et al. 2005).

Captivity

- The amount of time spent hauled-out peaks after pupping and during molting (Paterson et al. 2012).
- Relative humidity and air temperature were considered significant positive influences on haul-out time (Paterson et al. 2012).

Temperature Thresholds/Preferences

Southeastern Massachusetts

- Numbers of hauled-out harbor seals had a negative relation to air temperature, with a peak in haul-out abundance during the coldest months of the year (Schneider & Payne 1983).

Narragasset Bay, Rhode Island

- Harbor seals do not appear to decrease their haul-out occurrence even when air temperatures drop to -12°C (Raposa & Dapp 2009).

Gulf of Maine

- Haul-out decreases with temperatures (Kenney & Vigness-Raposa 2010).

Sable Island

- Harbor seals spend more time in water than on land when air temperature approaches -15°C (Boulva & McLaren 1979).
- Seals use more offshore waters when temperatures are extremely cold (Boulva & McLaren 1979).

New Brunswick, Canada

- Hauled out seals at Saint Croix Island appeared to be related to warmer air temperatures (e.g. solar radiation) and air-water temperature differences (Pauli & Terhune 1987).

Svalbard

- The probability that all age-classes of seal would haul-out decreases as temperature increased (Hamilton et al. 2014).

Eastern Pacific

- The 2006 decline in pup numbers in the San Francisco Bay area was hypothesized to be related to an unusual upwelling event, which caused warmer waters (Manna et al. 2006).

Captivity

- Metabolic rates increased in seals hauled-out in air temperatures ≥12.9°C (Hansen & Lavigne 1997a).
- The upper critical temperature limit of harbor seals is between 28.6 and 35 °C (Hansen & Lavigne 1997a).
- Between 23°C and 30°C, metabolic rates increased three-fold, and respiration rates also increased (Hansen & Lavigne 1997a).
- The upper critical temperature was 25.1°C, and high ambient temperatures effected internal temperatures of hauled-out seals. Seals exposed to ambient temperatures of 30°C had an average internal body temperature of 37.5°C, and when the ambient temperature was increased to 35°C, the seal's body temperature increased to an average of 39.3°C (Hansen & Lavigne 1997a).
- During peak molting, body surface temperatures reached 25-30°C (Paterson et al. 2012).
- Weaned seals exhibit a thermal neutral (or optimal) zone of -7.1° C +/- 0.7 and 23.0 +/- 0.4°C (Hansen & Lavigne 1997a).

Tidal stage/height

Maine coast

- Harbor haul-out behavior reflects the tidal cycle, and seals begin to return to ledges at falling tides (Gilbert & Guldager 1998).

Southeastern Massachusetts

- Seals hauled out less before and after low tide and increasing wave intensity (Schneider & Payne 1983).

Sable Island, Canada

- Harbor haul-out behavior was not dependent on tides, but seals did haul-out more when there was high wave intensity (Boulva & McLaren 1979).

Nova Scotia, Canada

- In this region, more seals hauled-out at low tides compared to high tides. This contrast to Sable Island haul-out behavior indicates a potential regional pattern in haul-out behavior (Boulva & McLaren 1979).

New Brunswick, Canada

- Tide height was negatively related to haul-out numbers and found to be the most important variable affecting haul-out behavior (Pauli & Terhune 1987).

Orkney, Scotland

- Harbor haul-out behavior was positively correlated with tidal cycle (Thompson et al. 1989).

Southwest Ireland

- Tidal level had a significant effect on harbor haul-out behavior (Cronin et al. 2009).

Svalbard

- During the months harbor seals in this region haul-out on land instead of ice, the probability of haul-out increased near low tide, decreasing thereafter (Hamilton et al. 2014).

San Miguel Island, California

- A greater number of harbor seals hauled-out during afternoon low tides compared to afternoon high tides (Stewart 1984).
- Tide height influenced the number of seals observed during peak afternoon haul-out times during autumn (Yochem et al. 1987).

Wind Speed/Direction

Narragasset Bay, Rhode Island

- Wind speed was negatively associated with the number of seals hauled-out, especially when wind speeds were >9 mph (Raposa & Dapp 2009).

Scroby Sands, UK

- Haul-out numbers were significantly influenced by both wind speed and direction (Skeate et al. 2012).
- Higher numbers of seals hauled-out when wind came from the SE, followed by the N and then NW (Skeate et al. 2012).
- Numbers were positively influenced by wind speed (Skeate et al. 2012).

Captivity

- Wind speed and water temperature were found to have a significant impact on variation in seal body surface temperature (Paterson et al. 2012).

Precipitation

Rhode Island

- The number of harbor seals on land was lower on days with precipitation (Raposa & Dapp 2009), indicating they may avoid hauling-out in stormy conditions.

Human Interaction

Northwest Atlantic

- Fishery-related mortality and injury is ≥10% (Hayes et al. 2016, p 137-145).

ACKNOWLEDGEMENTS

This work was conducted as part of a senior honors thesis project at the University of Massachusetts Amherst and an internship with the Anderson Cabot Center for Ocean Life, New England Aquarium as part of the project "How and why is the timing and occurrence of seasonal migrants in the Gulf of Maine changing due to climate?" funded by the Department of the Interior Northeast Climate Adaptation Science Center, managed by the USGS National Climate Adaptation Science Center (G16AC00237).

REFERENCING THIS REPORT

Calandrino G., D. Pendleton, and M. D. Staudinger. 2018. A review of literature for gray and harbor seals. DOI Northeast Climate Adaptation Science Center Report. Amherst, MA.

LITERATURE CITED

Abt KF, Hoyer N, Koch L, Adelung D (2002) The dynamics of grey seals (*Halichoerus grypus*) off Amrum in the south-eastern North Sea—evidence of an open population. J Sea Res 47:55–67

Amos B, Twiss S, Pomeroy P, Anderson S (1995) Evidence for Mate Fidelity in the Gray Seal. Science 268:1897–1899

Andersen L, Olsen MT (2010) Distribution and population structure of North Atlantic harbour seals (Phoca vitulina). NAMMCO Sci Publ 8:15–35

Baechler J, Beck CA, Bowen WD (2002) Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbour seals (*Phoca vitulina*). Can J Zool 80:1569–1577

Beck CA, Bowen WD, Iverson SJ (2000) Seasonal changes in buoyancy and diving behaviour of adult grey seals. J Exp Biol 203:2323–2330

Boehme L, Thompson D, Fedak M, Bowen D, Hammill MO, Stenson GB (2012) How Many Seals Were There? The Global Shelf Loss during the Last Glacial Maximum and Its Effect on the Size and Distribution of Grey Seal Populations (SJ Bograd, Ed.). PLoS ONE 7:e53000

Bogomolni A, Pugliares K, Sharp S, Patchett K, Harry C, LaRocque J, Touhey K, Moore M (2010) Mortality trends of stranded marine mammals on Cape Cod and southeastern Massachusetts, USA, 2000 to 2006. Dis Aquat Organ 88:143–155

Boily P, Lavigne DM (1996) Thermoregulation of juvenile grey seals, *Halichoerus grypus*, in air. Can J Zool 74:201–208

Boulva J, McLaren IA (1979) Biology of the harbor seal, Phoca vitulina, in eastern Canada.

Bowen WD, McMillan JI, Blanchard W (2007) Reduced population growth of gray seals at Sable Island: Evidence from pup production and age of primiparity. Mar Mammal Sci 23:48–64

Breed GA, Bowen WD, McMillan JI, Leonard ML (2006) Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. Proceedings of the Royal Society B 273:2319–2326

Breed GA, Jonsen ID, Myers RA, Bowen WD, Leonard ML (2009) Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state–space analysis. Ecology 90:3209–3221

Burrows MT, Schoeman DS, Buckley LB, Moore P, Poloczanska ES, Brander KM, Brown C, Bruno JF, Duarte CM, Halpern BS, Holding J, Kappel CV, Kiessling W, O'Connor MI, Pandolfi JM, Parmesan C, Schwing FB, Sydeman WJ, Richardson AJ (2011) The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. Science 334:652–655

Cronin M, Zuur A, Rogan E, McConnell B (2009) Using mobile phone telemetry to investigate the haul-out behaviour of harbour seals Phoca vitulina vitulina. Endanger Species Res 10:255–267

Cunningham L, Baxter JM, Boyd IL, Duck CD, Lonergan M, Moss SE, McConnell B (2009) Harbour seal movements and haul-out patterns: implications for monitoring and management. Aquat Conserv Mar Freshw Ecosyst 19:398–407

Gerondeau M, Barbraud C, Ridoux V, Vincent C (2007) Abundance estimate and seasonal patterns of grey seal (*Halichoerus grypus*) occurrence in Brittany, France, as assessed by photo-identification and capture–mark–recapture. J Mar Biol Assoc UK 87:365

Gilbert JR, Guldager N (1998) Status of harbor and gray seal populations in northern New England. Final Rep NMFSNER Coop Agreem:14–16

Gilbert JR, Waring GT, Wynne KM, Guldager N (2005) Changes in abundance of harbor seals in Maine, 1981–2001. Mar Mammal Sci 21:519–535

Goulet A-M, Hammill M, Barrette C (2001) Movements and diving of grey seal females (*Halichoerus grypus*) in the Gulf of St. Lawrence, Canada. Polar Biol 24:432–439

Grellier K, Thompson PM, Corpe HM (1996) The effect of weather conditions on harbour seal (Phoca vitulina) haulout behaviour in the Moray Firth, northeast Scotland. Can J Zool 74:1806–1811

Hamilton CD, Lydersen C, Ims RA, Kovacs KM (2014) Haul-Out Behaviour of the World's Northernmost Population of Harbour Seals (Phoca vitulina) throughout the Year (D Russo, Ed.). PLoS ONE 9:e86055

Hansen S, Lavigne DM (1997a) Ontogeny of the thermal limits in the harbor seal (Phoca vitulina). Physiol Zool 70:85–92

Hansen S, Lavigne DM (1997b) Temperature Effects on the Breeding Distribution of Grey Seals (*Halichoerus grypus*). Physiol Zool 70:436–443

Harris DE, Lelli B, Gupta S (2003) Long-Term Observations of a Harbor Seal Haul-out Site in a Protected Cove in Casco Bay, Gulf of Maine. Northeast Nat 10:141

Hayes SA, Josephson E, Maze-Foley K, Rosel PE, Eds. (2016) US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments - 2016 -- NOAA Tech Memo NMFS-NE-241; Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026, or online at http://www.nefsc.noaa.gov/publications.

Hind AT, Gurney WSC (1998) Are there thermoregulatory constraints on the timing of pupping for harbour seals? Can J Zool 76:2245–2254

Karlsson O, Hiby L, Lundberg T, Jüssi M, Jüssi I, Helander B (2005) Photo-identification, Site Fidelity, and Movement of Female Gray Seals (*Halichoerus grypus*) Between Haul-outs in the Baltic Sea. AMBIO J Hum Environ 34:628–634

Kenney RD, Vigness-Raposa K (2010) Marine Mammals and Sea Turtles of Narragansett Bay, Block Island Sound, Rhode Island Sound, and Nearby Waters: An Analysis of Existing Data for the Rhode Island Ocean Special Area Management Plan.

Lesage V, Hammill MO (2001) The Status of the Grey Seal, *Halichoerus grypus*, in the Northwest Atlantic. Can Field-Nat 115:653–662

Lesage V, Hammill MO, Kovacs KM (1995) Harbor seal (Phoca vitulina) and grey seal (*Halichoerus grypus*) abundance in the St Lawrence Estuary.

Manna J, Roberts D, Press D, Allen S (2006) Harbor Seal Monitoring San Francisco Bay Area. Point Reyes Stn CA USDI Point Reyes Natl Seashore

McConnell BJ, Chambers C, Nicholas KS, Fedak MA (1992) Satellite tracking of grey seals (*Halichoerus grypus). J Zool Lond 226:271-282*

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37

Paterson W, Sparling CE, Thompson D, Pomeroy PP, Currie JI, McCafferty DJ (2012) Seals like it hot: Changes in surface temperature of harbour seals (Phoca vitulina) from late pregnancy to moult. J Therm Biol 37:454–461

Pauli BD, Terhune JM (1987) Meteorological influences on harbour seal haul-out. Aquat Mamm 13:114–118

Pomeroy PP, Twiss SD, Duck CD (2000) Expansion of a grey seal (*Halichoerus grypus*) breeding colony: changes in pupping site use at the Isle of May, Scotland. J Zool 250:1–12

Raposa KB, Dapp RM (2009) A Protocol for Long-term Monitoring of Harbor Seals (Phoca vitulina concolor) in Narragansett Bay, Rhode Island. Narragansett Bay National Estuarine Research Reserve

Schneider DC, Payne PM (1983) Factors Affecting Haul-Out of Harbor Seals at a Site in Southeastern Massachusetts. J Mammal 64:518–520

Sharples RJ, Moss SE, Patterson TA, Hammond PS (2012) Spatial Variation in Foraging Behaviour of a Marine Top Predator (Phoca vitulina) Determined by a Large-Scale Satellite Tagging Program (A Fahlman, Ed.). PLoS ONE 7:e37216

Simpkins MA, Withrow DE, Cesarone JC, Boveng PL (2003) Stability in the proportion of harbor seals hauled out under locally ideal conditions. Mar Mammal Sci 19:791–805

Skeate ER, Perrow MR, Gilroy JJ (2012) Likely effects of construction of Scroby Sands offshore wind farm on a mixed population of harbour Phoca vitulina and grey *Halichoerus grypus* seals. Mar Pollut Bull 64:872–881

Sjoberg M, Ball JP (2000) Grey seal, *Halichoerus grypus*, habitat selection around haulout sites in the Baltic Sea: bathymetry or central-place foraging? Can J Zool 78: 1661-1667

Stewart BS (1984) Diurnal Hauling Patterns of Harbor Seals at San Miguel Island, California. J Wildl Manag 48:1459

Thompson PM, Fedak MA, McConnell BJ, Nicholas KS (1989) Seasonal and Sex-Related Variation in the Activity Patterns of Common Seals (Phoca vitulina). J Appl Ecol 26:521

Thompson PM, Mcconnell BJ, Tollit DJ, Mackay A, Hunter C, Racey PA (1996) Comparative Distribution, Movements and Diet of Harbour and Grey Seals from Moray Firth, N. E. Scotland. J Appl Ecol 33:1572

Twiss SD, Wright NC, Dunstone N, Redman P, Moss S, Pomeroy PP (2002) Behavioral evidence of thermal stress from overheating in UK breeding gray seals. Mar Mammal Sci 18:455–468

Van Parijs S, Thompson PM, Tollit DJ, Mackay A (1996) Distribution and activity of male harbour seals during the mating season. Anim Behav 54:35–43

Waring GT, Gilbert JR, Loftin J, Cabana N (2006) Short-term movements of radio-tagged harbor seals in New England. Northeast Nat 13:1–14

Yochem PK, Stewart BS, DeLong RL, DeMaster DP (1987) Diel haul-out patterns and site fidelity of harbor seals (*Phoca vitulina richardsi*) on san miguel island, California, in autumn. Mar Mammal Sci 3:323–332