Effects of environmental variables on northern elephant seal thermoregulation on the Southeast Farallon Island

Cambrie S. Congdon

ABSTRACT

Climate change and subsequent global warming have conspicuous, widespread effects on ecosystems. These increasing terrestrial climate stressors restrict the ability of semi-aquatic species to respond to changes when transitioning from water to land. Northern elephant seals are adapted to living underwater, but must haul out on shore to breed and molt. Seals have different thermoregulatory adaptations to allow them to cope with changing environments and maintain their body temperature, primarily to conserve heat. However, thermoregulatory costs increase when elephant seals haul out on land. Greater thermal stress caused by global warming may cause behavioral trade-offs. For example, seals may spend more time and energy behaviorally thermoregulating than on other important behaviors such as mating. My research addresses how environmental variables affect seal thermoregulation at two different habitats on the Southeast Farallon Island. I collected weather data via a localized weather station, and seal skin surface temperature data via infrared thermography. I found solar radiation to be significant in impacting average and maximum skin surface temperatures and thermal gradients, while relative humidity and ambient temperatures had significant influence on thermal window areas. There was no significant difference in location for any seal thermoregulatory variable. Although there are many laws protecting against direct impacts on marine mammals, indirect impacts such as habitat degradation and loss should be taken into consideration for management and conservation strategies. Studies such as this are able to predict future impacts of climate change on wildlife, and give insight on how to mitigate these effects.

KEYWORDS

Marine Mammal, Skin Surface Temperature, Climate Change, Habitat Degradation, Conservation Physiology

INTRODUCTION

More extreme environmental variations due to global change are having many far-reaching effects on ecosystems. Increasing terrestrial climate stressors impair the ability of semi-aquatic species to respond to changes when moving between marine and terrestrial ecosystems. These climate stressors include habitat degradation, sea level rise, and warming temperatures. The dangerous combination of global warming and human overexploitation of resources has caused a dramatic increase in habitat loss and general degradation (Lotze et al. 2006). Human actions such as centuries of overharvesting and poor coastal disaster management have led to decreased biodiversity in coastal ecosystems causing the decline of over 90% of commercially, structurally, and functionally important species and over 65% of coastal and intertidal habitat (Adger et al. 2005, Jackson et al. 2001, Lotze et al. 2006). More conspicuously, sea level rise is a major cause of habitat loss and is accelerated by anthropogenic causes (Galbraith et al. 2002). Sea level rise exacerbates the impact of storm surges which can rapidly degrade habitats. Warming ocean surface temperatures due to climate change also increase the magnitude of storms, worsening habitat degradation (Webster et al. 2005, Emanuel et al. 2005). Although climate change has dramatically caused swift changes in the environment, many animals have adaptations that help them survive changing environments.

Northern elephant seals are semi-aquatic and are adapted to living underwater, but must haul out on shore for certain life history stages. When not hauled out on offshore islands or the coast of California, northern elephant seals are commonly found foraging deep underwater in the northern Pacific Ocean from the Pacific Northwestern to the Alaskan coasts. Northern elephant seals have different types of thermoregulatory adaptations to maintain their core body temperature in response to changing environmental conditions, most of which are used to stay warm. Seals are able to stay warm with fur and a thick layer of blubber acting as insulation from cold water (Liwanag 2008). They also modify their circulatory system to shunt blood flow away from their skin to prevent heat loss to the environment (Davis 2019). This ensures that their vital organs and core are at a constant warm temperature. However, thermoregulatory costs increase as elephant seals move from water to land due to greater air temperatures and less conductive heat loss than in the water (Noren 2002). The ability to shunt blood allows seals not only to divert blood away from the skin when diving deep in cold water, but also divert blood, the opposite direction, towards the surface of their skin creating a thermal window to offload heat when they need to cool down while hauled out. Seals and other animals are able to control the size of their thermal window in order to modulate more or less heat dissipation (Mauk et al. 2003). If seals are under greater thermal stress, they will supplement physiological adaptations with behavioral adaptations such as flipping wet sand over their bodies or moving to cooler areas with access to shade or sea spray. However, highly homogeneous habitats may not provide these opportunities. Certain body positions can also facilitate heat loss such as laying with a flipper up into the air. This helps two-fold as the flippers of phocids emit more heat than other parts of their body and raising their flipper in the air increases convective heat loss (Khamas et al. 2012). Despite the many mechanisms that seals have to regulate heat, these adaptations may not be adequate as global warming continues which will cause animals to make trade-offs based on energetic demands.

Increased thermal stress to seals when hauled out on shore may cause seals to divert energy from important behaviors such as breeding or nursing young to thermoregulating. Additionally, a 2016 study at Point Reyes National Seashore indicated that as solar radiation increases, the probability that a mother pup pair would enter the water also increases (Codde et al. 2016). This behavior is considered dangerous and novel as the pups cannot swim. Other impacts due to climate change to hauled out seals are habitat degradation and homogeneity. A 2012 model predicted that sea level rise at Point Reyes National Seashore could inundate 50% of potential haul out habitat by 2050 and 66% by 2099 (Funayama et al. 2012). Degraded habitats due to sea level rise result in habitat loss as there is less suitable beach or shore for seals to haul out on once inundated. The Southeast Farallon Island (SEFI) within the Farallon Island National Wildlife Refuge (FINWR) includes a haul out site which used to have sand many years ago, but was washed away due to large storm events and is now mostly granite substrate. Lack of heterogeneity in the environment could also cause thermal stress. For example, limited available shade, lack of suitable substrate or access to wet sand could inhibit the ability of seals to efficiently thermoregulate and increase thermoregulatory costs beyond what is typically experienced while being on land. A lack of heterogeneity is observed at the haul out site on the SEFI, in which the lack of sand prohibits seals from flipping sand when they need to thermoregulate more efficiently. In contrast, Año Nuevo State Park's habitat has varying degrees of heterogeneity such as trees for shade and multiple coves that provide shelter to hide from the sun. Although there have been a few studies on northern elephant seal thermoregulation on the mainland, there is a gap in research observing seals on offshore islands, mainly due to the island's remote locations and logistical challenges.

My research addresses how environmental variables affect northern elephant seal thermoregulation at two different locations on SEFI. To answer this question my sub-questions include: 1) what environmental variables have the greatest effect on thermoregulation and 2) does habitat choice affect thermoregulation? I predicted that solar radiation and ambient temperature will have the greatest effect on average skin surface temperature in which average skin surface temperature is positively correlated with solar radiation and/or ambient temperature. Additionally, I expect that habitats with greater thermal refuge for seals will result in lower average skin surface temperatures and smaller thermal window area percentages than habitats with less thermal refuge. I collected environmental data via a localized weather station, and seal thermoregulatory data via infrared thermography. I conducted this study in conjunction with a long-term monitoring project on multiple sites in Northern California.

METHODS

I conducted this project in collaboration with Emily Lam, a Ph.D. candidate in the Vázquez-Medina lab at UC Berkeley and with researchers from Point Blue Conservation Science. Our larger purpose was to determine the feasibility of establishing a long-term monitoring program to assess the effects of environmental variables on elephant seal physiology and behavior at three sites in California, Año Nuevo, Point Reyes, and SEFI. For this project, Lam collected preliminary data on SEFI located 43 km off the coast of the San Francisco Bay estuary.

Study sites

To determine differences in seal thermoregulation between varying habitat types, Lam took thermographic photos of elephant seals at two locations with differing landscapes and substrates: Mirounga Beach (approximate coordinates: 37°41'51.1"N 123°00'19.5"W) and Sand Flat (approximate coordinates: 37°41'52.0"N 123°00'21.7"W) (Figure 1) on the southwestern side of the SEFI. Mirounga Beach is characterized as a sheltered cove with prominent water accessibility and a small to medium pebble substrate. In contrast, Sand Flat is greatly exposed with no direct access to water; and despite its name, the substrate consists of a flat bed of granite rather than sand.

We observed that Mirounga Beach housed a small harem of seals (1 bull, 2-6 cows, 0 - 3 pups) while Sand Flat had a larger harem (1 bull, 5-7 cows, 1-6 pups).

Study species

Northern elephant seals are large marine mammals with high breeding-site fidelity and have been hauling out at the FINWR during the winter months since their population resurgence in 1972 (Lee 2011). Lam dye-marked and assigned each seal with unique numeric identifiers to distinguish individuals before they molt within a breeding season. To distinguish individuals across seasons, Lam also gave each seal two flipper tags, one on each hind flipper.

Environmental variables

To collect ambient temperature, relative humidity and solar radiation data, we constructed a weather station comprised of a smart sensor (temperature accuracy ± 0.21ºC, relative humidity accuracy ± 2.5%; Onset Computer Corporation, Bourne, MA, USA) and Onset Silicon Pyranometer (accuracy ± 10W m^{-2}). To collect wind speed and gust speed, we used an Onset wind speed sensor (accuracy ± 1.1m/s). All sensors were attached to a HOBO Micro Station data logger (37°41'53.0"N 123°00'12.1"W) that Lam and researchers from Point Blue set up at the research station about 183 meters from Mirounga Beach and 274 meters from Sand Flat (Figure 1). We set the sensors to take measurements every five minutes, 24 hours per day. When taking infrared thermographs, Lam noted whether the seal's location was at either of the two sites. To organize the data, I matched the infrared thermographs to the weather data by timestamps on the photos within the five-minute interval.

Figure 1: Map of study sites. Sand Flat and Mirounga Beach in relation to the weather station.

Seal thermoregulatory variables

To obtain thermographic photos, Lam used a FLIR One Pro infrared thermography camera attachment for iOS (accuracy ± 3ºC; Wilsonville, OR, USA). She took the photos either along a bluff above the harem or on the beach a few meters away from the seals when able to due to high densities of seals at some locations. Additionally, Lam maintained a distance of 3-5 meters and as perpendicular of an angle to the seal as was possible. To derive surface temperatures, I used the R package Thermimage, to convert the pixel data of the image into temperature data. Lam set the camera's measurement parameters to be 0.98 emissivity, 20ºC reflected temperature and distance at 3 meters. I considered these parameters when deriving surface temperatures in R. To analyze infrared thermographs, I used FIJI (or Image J) and calculated mean and maximum skin surface temperatures and thermal windows for each image. I defined thermal windows as localized areas greater than one standard deviation above the mean surface temperature of the individual in the thermograph (Norris et al. 2010). Therefore, to determine thermal windows, I created a region of interest, a polygon within the area of the seal, that included values at least one standard deviation greater than the mean surface temperature of the seal. Lastly, I considered average skin surface temperature, max skin surface temperature, thermal window area percentage, and thermal gradient (average skin surface temperature - ambient temperature) for my statistical analyses (Codde et al. 2016).

Statistical Analyses

To derive weather trends, I performed summary statistics in R version 1.2.5033. Additionally, to evaluate what environmental variables had the greatest influence on seal thermoregulation, I used a linear mixed effects model. The model included the environmental variables and habitat type on average and maximum skin surface temperature, thermal window percentage, and thermal gradient with a random effect of each individual seal. I omitted gust speed from the model due to being highly correlated with wind speed (a correlation of 1.00) and would otherwise violate the assumption of no multicollinearity present in linear mixed models. Other studies incorporated wind speed in their analyses, which is why I chose it over gust speed to analyze in my model (Codde et al. 2016, Norris et al. 2010). I also used these models to derive R^2 values. To determine the differences in variance, I performed an ANOVA in R to retrieve F-stat values.

RESULTS

Environmental variables

I analyzed weather data at the timestamp closest to the time when the thermogram was taken. Ambient temperature ranged from a minimum of 8.64ºC and a maximum of 12.75ºC with a mean of 10.91ºC. Solar radiation ranged from a minimum of 0.6 W m^{-2} to a maximum of 509.4 W m^{-2} with a mean of 154.8 W m^{-2}. Relative humidity ranged from a minimum of 78.8% to a maximum of 95.2% with a mean of 85.34%. Wind speed ranged from a minimum of 0.56 mph to a maximum of 26.49 mph with a mean of 10.46 mph. Lastly, gust speed ranged from a minimum of 2.26 mph to a maximum of 34.92 mph with a mean of 15.45 (Table 1). Two days during data collection were considered hotter than average days, defined as plus one standard deviation above the mean ambient temperature.

Table 1. Data summary of environmental variables. Ambient temperature, solar radiation, relative humidity, wind speed, and gust speed.

Environmental Variable	**Min**	**Max**	**Mean ± SD**
Ambient temperature (ºC)	8.64	12.75	10.91±1.18
Solar radiation (W m^{-2})	0.6	509.4	154.8±182.44
Relative humidity (%)	78.8	95.2	85.34±3.96
Wind speed (mph)	0.56	26.49	10.46±6.38
Guest speed (mph)	2.26	34.92	15.45±8.28

Seal thermoregulatory variables

Mean skin surface temperature was 15.17ºC (n=117 from 11 individuals), with a range of minimum and maximum skin surface temperatures being -1.051ºC and 35.77ºC (Table 2). Solar radiation had the strongest influence on skin surface temperatures, while relative humidity and ambient temperature had little to no influence on skin surface temperatures (Table 3 and Figure 2A). Maximum skin surface temperatures were found to be a mean of 25.73ºC with a minimum and maximum of 3.32ºC and 40.50ºC. Solar radiation and wind speed had significant impacts on maximum surface temperatures with wind speed having the greatest influence on variance (Table 3 and Figure 2B).

I found thermal gradients ranged from a minimum difference in skin surface temperature from ambient temperature of -9.69ºC to a maximum of 23.02ºC with a mean difference of 4.26ºC (Table 2). Solar radiation had the strongest influence on creating large thermal gradients, while location and relative humidity had little to no influence on thermal gradients (Table 3 and Figure 2D).

Mean thermal window areas encompassed 13.87% of the total area of the seal, and the minimum and maximum areas were 2.23% and 28.77% respectively (Table 2). Skin surface temperatures within thermal window areas ranged from a minimum of 0.49ºC to a maximum of 39.74ºC with a mean of 20.29ºC (Table 2). Relative humidity and ambient temperature had the strongest influence on thermal window area, while wind speed had little to no influence on thermal window area (Table 3 and Figure 2C).

Table 2. Data summary of seal thermoregulatory variables. Average skin surface temperatures, max skin surface temperatures, thermal window area percentage (thermal window area/total body area), and thermal gradients (ambient temperature - average skin surface temperature).

Seal Thermoregulatory Variable	Min	Max	Mean± SD
Average skin surface temperature (ºC)	-1.051	35.77	15.17±7.41
Max skin surface temperature (ºC)	3.318	40.50	25.73±7.07
Thermal window area percentage (%)	2.23	28.77	13.87±4.78
Thermal window area surface temperatures (ºC)	0.49	39.74	20.29±7.93
Thermal gradient (ºC)	-9.69	23.02	4.26±6.81

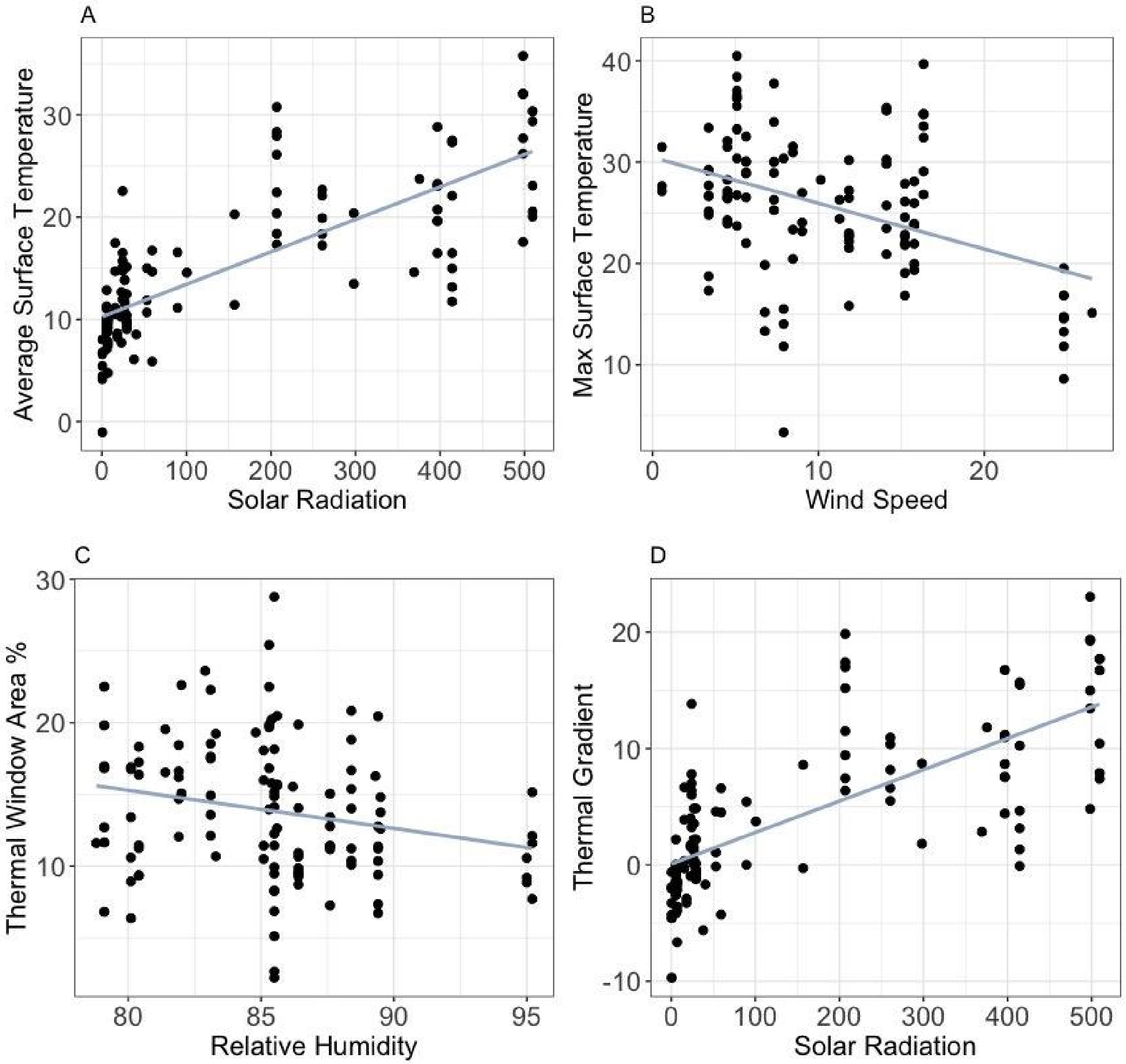

Figure 2. Linear mixed effect model results of seal thermoregulatory variables and environmental variables with greatest R^2 value. A) Average skin surface temperature (ºC) and solar radiation (W m^{-2}), B) Max surface temperature (ºC) and wind speed (mph), C) Thermal window area percentage (%) and relative humidity (%), and D) Thermal gradient (ºC) and solar radiation (ºC). Solid line indicates trends in the data.

Habitat choice

I found that there was no significance in specific locations, Sand Flat or Mirounga Beach. Habitat choice did not significantly affect any of the seal thermoregulatory variables I analyzed:

average and max skin surface temperature, thermal window percentage and thermal gradients (Table 3).

Table 3. Linear mixed model results. Influences of environmental variables on mean skin surface temperature, maximum skin surface temperature, thermal window area, and thermal gradient.

Environmental Variable	**Average Skin Surface Temperature**		**Max Skin Surface Temperature**		**Thermal Window Percentage**		**Thermal Gradient**	
	F	R^2	F	R^2	F	R^2	F	R^2
Ambient temperature	0.12	0.001	1.86	0.016	4.25*	0.04	0.96	0.008
Solar radiation	39.92***	0.26	6.11*	0.05	1.09	0.009	39.92***	0.26
Relative humidity	0.89	0	0.41	0.004	9.81**	0.08	0.02	0
Wind speed	0.12	0.021	16.96***	0.13	0.20	0.002	2.47	0.021
Location	0.92	0	0.97	0	0.82	0.0085	0.92	0

*p-value<0.5

**p-value<0.01

***p-value<0.001

DISCUSSION

Marine mammals have developed a broad range of physiological and behavioral adaptations to regulate their body temperatures to a fluctuating environment. Northern elephant seals maintain their core body temperature through evaporative cooling and conductive heat loss. They will also supplement with physiological responses, such as shunting blood, and through behaviors, such as seeking thermal refuge within their haul out site. Multiple environmental variables can affect these responses including weather conditions, the degree of habitat heterogeneity, and environmental extremes. Studies like this project that analyze these responses aim to predict how animals will respond to climate change and global warming to better mitigate these effects through management strategies.

Seal thermoregulatory variables

Average skin surface temperatures were greatly influenced by solar radiation. Solar radiation is positively correlated with average skin surface temperatures. Seals absorb heat from their environment through conduction and radiation from the sun. Seals will increase the rate of absorption of solar radiation by laying either out directly in the sun or without access to wet sand resulting in high radiative surface temperatures. Solar radiation was also significant in influencing max surface temperature, but wind speed contributed to decreasing the variance the most. Wind speed had the strongest influence on reducing max surface temperatures aiding the seals in cooling off. Environmental conditions such as high wind speeds, cloud cover, or access to shade could aid in decreasing radiation surface temperatures and provide thermal refuge (Campagna and Le Bouef 1988). Although solar radiation and wind speed was found to be the strongest influence on average and max skin surface temperatures, previous studies analyzing northern elephant seal thermoregulation have found that ambient temperatures, wind speed, and vapor pressure have significant impacts on average skin surface temperatures, and ambient temperatures on max surface temperatures (Codde et al. 2016, Norris et al. 2010). Ambient temperatures during this data collection period were not particularly extreme. Therefore, average skin surface temperatures could be lower than expected with a weaker than usual relationship between radiative surface temperatures and solar radiation or other environmental variables such as ambient temperatures.

Seals are able to control the areas of heat dissipation using thermal windows that allow conductive heat loss, but more efficiently through evaporative heat loss when their pelage, or fur, is wet. Relative humidity had a significant influence on thermal window area percentage with a negative relationship. Thermal hotspots have been shown to occur at specific locations of the body such as the flippers, which are more emissive than other body parts in phocids, or the trunk when seals are hauled out (Khamas et al. 2012, Mauk et al. 2003). Hotspots will also more likely occur on wet spots to facilitate more efficient heat loss through evaporation (Mauk et al. 2003). Although seals use moisture on their fur for more efficient evaporative cooling, moisture in the air is not equivalent. Evaporation is not expected and is inhibited when the air is highly water saturated (Girard et al. 2008). Most of our samples of seals had dry, clean pelages, thus relative humidity may be inhibiting the seals' ability to control their thermal window, but further analysis is required to fully support this claim. I found that relative humidity had a significant influence on thermal window area percentage, but similar studies did not find any significance in relative humidity affecting thermal window areas (Codde et al 2016, Norris et al. 2010). This lack of support could be due to my study's small sample size or differing environmental conditions during the previous studies' data collection period.

Evaporative heat loss is one of the main forms of thermoregulation northern elephant seals exhibit while on land, and thermal gradients may give insight on the degree of thermal stress an animal is experiencing. For example, a seal may be under greater thermal stress if the difference between average skin surface temperature and air temperatures is large in which they are dumping large amounts of heat into the air, but further research is required. I found that solar radiation and thermal gradients were positively correlated. One study examining heat exchange in terrestrial animals indicated that a 1.5ºC thermal gradient is required to dissipate significant amounts of heat (Phillips and Heath 1995). I found mean thermal gradients to be about three times this amount with a 4.26ºC gradient. This discrepancy in minimum thermal gradient to dissipate heat and the mean thermal gradient I analyzed may indicate that seals are going through greater thermal stress than what they would normally respond to. In contrast, studies researching northern elephant seal thermoregulation under similar methods have shown that ambient temperature significantly affects thermal gradients, while relative humidity does not (Norris et al. 2010, Codde et al. 2016). This significance in ambient temperature may be conspicuous as thermal gradients are a function of ambient temperatures. Additionally, although broad thermal gradients and large thermal window areas could be biomarkers of thermal stress in an animal it is necessary to analyze cellular markers for stress and inflammation to confirm this notion. For example, measuring heat shock proteins, cortisol, c-reactive protein, and lipid and/or protein oxidation in conjunction to radiative surface temperature analysis could predict the onset of cellular stress in elephant seals. Such methods could also assess the ability of seals to effectively transfer heat using their thermal window.

Habitat Choice

Terrestrial animals seek thermal refuge in their habitats when experiencing thermal stress. It is important for animals to choose suitable habitat types with available thermal refuges. The thermal environment, habitat topography and substrate, and thermoregulatory requirements have been shown to greatly influence social behavior and the distribution of animals among rookeries of southern sea lions (Campagna and Le Bouef 1998). Additionally, my findings showed no evidence of influencing distribution as habitat choice between Mirounga Beach and Sand Flat did not have significance on any of the seal thermoregulatory variables I analyzed. Although I found no significance in location affecting seal thermoregulation, behavioral responses to the environment are driven by energetic demands relative to solar radiation exposure (Norris and Kunz 2012). My data collection period did not have particularly high ambient temperatures or solar radiation levels. Therefore, seals may not have given much consideration to access to water or wet sand to aid in reducing energy costs of thermoregulatory responses because their energetic demands to thermoregulate may not have been particularly high (Terrien et al. 2011). These differences may be resolved when comparing elephant seal populations at different haul out sites that may be experiencing either differential rates of warming or differing degrees of habitat heterogeneity.

Limitations and Future Directions

Study limitations could have also impacted my results. I was only able to analyze a very small sample across only seven days out of the breeding season which may not have been representative of the population's responses throughout the entire breeding season. A larger sample size across more individuals and a longer study duration within the breeding season may yield more accurate and generalizable results. Additionally, my study design in which Lam had access to only one weather station which was placed relatively far from either site may have impacted results. Although localized weather data across both sites may have given differing results, the sites tested also may not be significantly different, thus future research involving very distinct sites with varying landscapes could give greater significance between habitat choices.

There are many other methods in which to measure how animals respond to a changing environment. Methods such as long-term monitoring, examining other types of habitats that seals utilize, analyzing physiological and behavioral responses in conjunction to radiative surface temperature analysis would all give greater insight to how the environment affects seal thermoregulation. This pilot project is intended to give insight towards a long-term monitoring study at three distinct haul out sites, Año Nuevo State Park, Point Reyes National Seashore, and

FINWR by Lam to analyze thermoregulation and behavior of northern elephant seals while also assessing biomarkers for cellular stress.

Broader Implications

There are currently extensive laws protecting marine mammals such as the Marine Mammal Protection Act and the Convention on International Trade of Endangered Species, but these only address the direct impacts that humans have on marine mammals. Indirect causes such as habitat degradation and climate change should also be taken into consideration for management and conservation strategies. Studies like mine are able to predict future impacts of climate change on wildlife and can give insight into how to mitigate the indirect effects of climate change and habitat loss. A feasible implementation following predicted impacts would be to increase habitat restoration along the edges of bluffs and wetlands of haul out sites to create and restore more available thermal refuges. Although I found no significance in location affecting seal thermoregulatory variables, which is likely due to study limitations, habitat loss and degradation are major emerging threats to marine mammals who haul out on shores and should be mitigated before even greater environmental extremes begin to occur.

ACKNOWLEDGEMENTS

Thank you to all who have helped on this project. Thank you to those involved in ESPM 175 for guiding me through this process, specifically towards the professors, Patina Mendez and Sam Evans, the graduate student instructors, Leslie McGinnis, Jessica Heiges, and Roxy Cruz, and, of course, all of my peers in the class. Additionally, thank you to the Vazquez-Medina lab for welcoming me, specifically the primary investigator, Jose Pablo Vazquez-Medina, my mentor, Emily Lam, and post-doctoral fellow, David Ensminger. Thank you to the National Park Service at Point Reyes National Seashore for the support and insight on seal monitoring, specifically Sarah Allen, Sarah Codde and Marjorie Cox. Thank you to Point Blue Conservation Science for collaborating with Lam on the Southeast Farallon Island, specifically towards Garrett Duncan and Peter Warzybok and interns, Paul, Abby and Danielle. Lastly, thank you to all of my friends and family for the love and support throughout this whole process. Any opinions and conclusions I

have expressed in this project are of my own and do not reflect that of any lab, organization, or agency that has been involved.

REFERENCES

Adger, W. N., T. P. Hughes, C. Folke, S. R. Carpenter, J. Rockstrom. 2005. Social-Ecological Resilience to Coastal Disasters. Science 309: 1036-1039

Campagna, C., and B.J. Le Boeuf. 1998. Thermoregulatory behavior of southern sea lions and its effect on mating strategies. Behavior 107: 72-90.

Codde, S. A., S. G. Allen, D. S. Houser, and D. E. Crocker. 2016. Effects of environmental variables on surface temperature of breeding adult female northern elephant seals, Mirounga angustirostris, and pups. Journal of Thermal Biology 61: https://doi.org/10.1016/j.jtherbio.2016.09.001.

Davis, R. W. 2019. Metabolism and Thermoregulation. Pages 57-87 *in* R. W. Davis, editor. Marine Mammals. Springer, New York, New York, USA.

Emanuel K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436: 686-688.

FitzGerald, D. M., M. S. Fenster, B. A. Argow, and I. V. Buynevich. 2008. Coastal Impacts Due to Sea-Level Rise. Annual Review of Earth and Planetary Sciences 36: 601–647. https://doi.org/10.1146/annurev.earth.35.031306.140139.

Funayama, K., E. Hines, J. Davis, and S. Allen. 2013. Effects of sea-level rise on northern elephant seal breeding habitat at Point Reyes Peninsula, California. Aquatic Conservation: Marine and Freshwater Ecosystems 23: 233–245. https://doi.org/10.1002/aqc.2318.

Galbraith H., R. Jones, R. Park, J. Clough, and S. Herrod-Julius. 2002. Global Climate Change and Sea Level Rise: Potential Losses of Intertidal Habitat for Shorebirds. BioOne Complete 25: https://doi.org/10.1675/1524

Girard, F., M. Antoni, S. Faure, S., and A. Steinchen. 2008. Influence of heating temperature and relative humidity in the evaporation of pinned droplets. Colloids and Surfaces A: Physicochemical and Engineering Aspects 323: 36–49. https://doi.org/10.1016/j.colsurfa.2007.12.022.

Jackson, J. B., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, … R. R. Warner. 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science 293: 629-637.

Khamas, W. A., H. Smodlaka, J. Leach-Robinson, and L. Palmer, L 2012. Skin histology and its role in heat dissipation in three pinniped species. Acta Veterinaria Scandinavica, 54: 1-10.

Lee, Derek E. 2011. Effects of Environmental Variability and Breeding Experience on Northern Elephant Seal Demography. Journal of Mammalogy 92: 517–26. https://doi.org/10.1644/10-MAMM-A-042.1.

Liwanag, H. E. 2008. Fur versus blubber: a comparative look at marine mammal insulation and its metabolic and behavioral consequences. Dissertation. University of California, Santa Cruz, California, USA.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, … J. B. Jackson. 2006. Depletion, Degradation, and Recovery Potential of Estuaries and Coastal Seas. Science 312: 1806-1809.

Mauck, B., K. Bilgmann, D. D. Jones, U. Eysel, and G. Dehnhardt. 2003. Thermal windows on the trunk of hauled-out seals: Hot spots for thermoregulatory evaporation? Journal of Experimental Biology 206: 1727–1738. https://doi.org/10.1242/jeb.00348.

Noren, D. P. 2002. Thermoregulation of Weaned Northern Elephant Seal (Mirounga angustirostris) Pups in Air and Water. Physiological and Biochemical Zoology 75: 513-523.

Norris, A. L., D. S. Houser, and D. E. Crocker. 2010. Environment and activity affect skin temperature in breeding adult male elephant seals (Mirounga angustirostris). Journal of Experimental Biology 213: https://doi.org/10.1242/jeb.042135.

Norris, A. L., and T. H. Kunz, 2012. Effects of Solar Radiation on Animal Thermoregulation. Pages 195-215 *in* E. B. Babatunde, editor. Solar Radiation. InTech, Rijeka, Croatia.

Phillips, P. K., & J. E. Heath. 1995. Dependency of surface temperature regulation on body size in terrestrial mammals. Journal of Thermal Biology 20: 281-289.

Terrien, J., M. Perret, and F. Aujard. 2011. Behavioral thermoregulation in mammals: A review. Frontiers in Bioscience 16: 1428–1444. https://doi.org/10.2741/3797.

Webster, P. J., G. J. Holland, J. A. Curry, H-R. Chang. 2005. Changes in tropical cyclone number,
number, and intensity in a warming environment. Science 309: 1855-1846.