Assessing Predator Risk to Diadromous Fish Conservation in the Penobscot River Estuary

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ASSESSING PREDATOR RISK TO DIADROMOUS FISH CONSERVATION

IN THE PENOBSCOT RIVER ESTUARY

By

Lauri Leach

B.S. University of Rhode Island, 2009

A THESIS
Submitted in Partial Fulfillment of the Requirements for the Degree of Master of Science (in Marine Biology)

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Successful conservation of pinnipeds in the northwest Atlantic has led to increasing populations of harbor (Phoca vitulina) and gray seals (Halichoerus grypus) in the Gulf of Maine. Seals are often perceived as predators and competitors for fish, and as a result, come into conflict with fisheries and fish conservation. Increasing numbers of seals have become a recent concern in the Penobscot River Estuary in Maine, as habitat restoration and diadromous fish conservation have been top priorities in this region for the past decade.

To understand how pinnipeds are responding to these efforts, as well as the risks they pose to diadromous fish, we evaluated spatial and temporal overlaps in the presence of seals and diadromous fish from 2012 to 2020. Utilizing data from a survey in the estuary, counts of seals on haul-outs, as well as presence of swimming seals, were compared across seasons and years, and related to fish biomass estimates. Seal presence in the estuary peaks in the spring, and we did not detect significant differences in counts of hauled out seals in recent years. We detected a non-significant, negative relationship between seal count and fish biomass, presumably due to relative presence of each peaking in different seasons.
Seal predation of endangered Atlantic Salmon (Salmo salar) is a concern, so we assessed the risk seals pose to salmon. Salmon demographic data, including the presence of seal-induced injury, have been collected from salmon passing upriver at the southernmost dams. A comparison of seal-induced injury rate from 2012 to 2019 revealed that seal-induced injury has been declining. Rather than being most influenced by local seal populations, increasing river herring returns were strongly related to declining seal-induced injury rates, highlighting the importance of prey buffering in this system.

We used photo-identification to understand how individual seals are using the estuary. Photographs were taken of individual seals between 2019 and 2020. Overall, 27 harbor seals and 88 gray seals were identified. There were 62 harbor seal and 29 gray seal resighting events. Continued efforts could allow for eventual abundance estimates of gray seals using the lower estuary. Comparison to other photo-identification catalogs in the region would also allow a better understanding of how these animals utilize regional sites and an improved understanding of the role pinnipeds play in marine and coastal ecosystems.

It appears that seal presence in the Penobscot is based more on regional trends in seal abundance and distribution rather than local prey biomass, however, it is possible that pinnipeds may be slower to respond to restoration efforts than the fish species in this system. Better understanding pinniped response to restoration and changing predator-prey interactions in this system could help reconcile the competing objectives of marine mammal protection and fish restoration. A multi-species approach is essential to successful conservation. A healthier ecosystem can benefit both predators and prey, as improved water quality, increased access to historic habitat, and rebounding fish populations are already proving to have significant benefits to multiple species that use the river.
ACKNOWLEDGEMENTS

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CHAPTER 1

ASSESSING PINNIPED RESPONSE TO DIADROMOUS FISH RESTORATION EFFORTS IN THE PENOBSCOT RIVER ESTUARY

Abstract

Successful conservation of pinnipeds in the northwest Atlantic has led to increasing populations of harbor seals (*Phoca vitulina*) and gray seals (*Halichoerus grypus*) in the Gulf of Maine. In the Penobscot River Estuary in Maine, habitat restoration and diadromous fish conservation have been top priorities for the past decade. To understand how pinnipeds are responding to habitat restoration efforts and increasing forage fish populations, we evaluated spatial and temporal overlaps in the presence of seals and diadromous fish from 2012 to 2020. Utilizing data from a vessel-based survey in the estuary, counts of seals on four major haul-outs were compared across seasons, across years, and to fish biomass estimates. Species-specific analyses of seals were conducted using photographs to confirm sightings during 2019 and 2020. Similar trends in swimming seal presence were explored using occupancy modeling to account for low detection rates of seals in the water. In general, seal presence in the estuary peaks in the spring and declines through the summer and fall, and we did not detect significant differences in counts of hauled out seals from 2015 through 2020. Similarly, year was not a significant factor in determining swimming seal presence in the estuary. While we did not detect a significant relationship between counts of hauled out seals and fish biomass between 2012 and 2020, we did detect a positive relationship between harbor seals and fish biomass during our species-specific analysis in 2019 and 2020, suggesting that changes in harbor seal interactions with diadromous fish may be beginning to emerge. We also found evidence of increasing gray seals in the estuary, which seem to displace harbor seals to a different haul-out when they arrive. It appears
that seal presence in the Penobscot could be based more on regional trends in seal abundance and
distribution rather than local prey biomass, however, it is possible that pinnipeds may be slower
to respond to restoration and conservation efforts than the fish species in this system. Better
understanding predator-prey interactions and pinniped response to restoration in this system
could help reconcile the competing objectives of marine mammal protection and fish restoration.

Introduction

Habitat restoration and conservation efforts have led to many successful recovery stories
worldwide, however increasing populations or communities are, alone, an insufficient goal.
These success stories often result in unintended consequences, such as increasing numbers of
protected species encountering human activity, or protected predators beginning to recover and
impacting vulnerable, protected prey populations (Marshall, Stier, Samhouri, Kelly, & Ward,
2016; Yodzis, 2001). Balancing the competing needs of multiple protected species with human
use is challenging and is further complicated by a general lack of understanding of predator-prey
dynamics in recovering systems. Gaining a better understanding of how predators and prey both
respond to habitat restoration efforts could ultimately increase our ability to successfully and
adaptively manage natural resources while promoting overall ecosystem health.

Predators are important ecosystem components, in part because their presence indicates
that the system is healthy enough to support them (Hairston, Smith, & Slobodkin, 1960).
Predators also play important roles in shaping an ecosystem, through both direct and indirect
(non-consumptive) effects on lower trophic levels. Predators can increase biodiversity and
ecosystem resiliency through top-down controls and can help suppress disease by predating prey
that are ill and easier to catch (Pongsiri et al., 2009; Ritchie & Johnson, 2009).
Viewed primarily as marine predators, seals are present along the eastern coast of the United States (U.S.) from the Canadian border to the mid-Atlantic states (Hayes et al., 2017). The Gulf of Maine is home to two year-round, resident species of seal: harbor seals (*Phoca vitulina*) and gray seals (*Halichoerus grypus*). Both species exhibit seasonal movements; while some individuals have a year-round presence in the Gulf of Maine, others spend summer months in the Gulf of Maine and disperse to southern New England and the mid-Atlantic states between September and May (Hayes et al., 2017). Seasonal events such as pupping and molting also play a role in seal distribution; harbor seals move into the Gulf of Maine for their pupping season in May and June, while gray seals pup on islands off Cape Cod, Massachusetts and the coast of Maine between December and February (Gilbert, Waring, Wynne, & Guldager, 2005; Hayes et al., 2017; Pace, Josephson, Wood, Murray, & Waring, 2019; Wood, Murray, Josephson, & Gilbert, 2020). A recent study on Cape Cod found local gray seal counts peaked between mid-April and mid-May, likely coinciding with the adult gray seal molt (Pace et al., 2019).

Seals were hunted to near extinction across the North Atlantic, but have been increasing in the Gulf of Maine since federal legislation aimed at their conservation was passed in 1972 (Hayes et al., 2017; Roman et al., 2013). The most recent population assessment in 2012 estimated the harbor seal population in the Gulf of Maine to be at carrying capacity or in decline, with approximately 75,834 individuals (Waring, Digiovanni Jr, Josephson, Wood, & Gilbert, 2015). Gray seals in U.S. waters were estimated at 27,131 individuals in 2016, and this population is continuing to increase (Hayes et al., 2017; Wood et al., 2020). Seals spend a significant amount of time hauled out on land, and tend to congregate on intertidal ledges, rocky islands, and uninhabited beaches (Schneider & Payne, 1983). While gray seals and harbor seals are often found hauled out together and exhibit site fidelity to the same locations, gray seals have
also displaced harbor seals at many sites throughout New England, which could be a factor in the recent decline of harbor seal population growth rates (Pace et al., 2019; Waring et al., 2015).

Successful conservation of seals in the Gulf of Maine and elsewhere, combined with high visibility of these species, has renewed human perception of them as predators of fish species of commercial value or conservation concern, and as a result, seals have come into conflict with numerous fisheries across the world (Harwood, 1984). For example, gray seals are often blamed for the failed recovery of cod in Canada (Chouinard, Swain, Hammill, & Poirier, 2005), and pinnipeds have been lethally removed in Canada, Europe, and on the west coast of the United States where they interact with fisheries (Olsen, Galatius, & Harkonen, 2018; Schakner et al., 2017; Yodzis, 2001). These concerns have resulted in numerous studies and an improved understanding of seal diet. Harbor seals and gray seals are both opportunistic predators, typically feeding on whatever is locally abundant throughout the year (Murie & Lavigne, 1992; Pierce et al., 1991). Recent dietary studies in the northeastern U.S. tend to focus on gray seal populations on Cape Cod, Massachusetts, the epicenter of U.S. gray seal population growth, where their diet consists primarily of sand lance (Ammodytes spp.) (Hernandez et al., 2019; Lerner et al., 2018). One study of harbor seals off the coast of Maine suggested this species prefers a summer diet of silver hake (Merluccius bilinearis), Acadian redfish (Sebastes fasciatus), and Atlantic herring (Clupea harengus) (Kopec, 2009). These seals selected specific age classes of their preferred prey, despite local abundance, and their preferred prey size was between 10 and 35 centimeters (Kopec, 2009). Further studies in this region would be helpful, as seal diet is known to change throughout the year, and prior studies have relied heavily on analysis of hard parts in feces, which biases our understanding of diet (Bowen, 2000; Tverin et al., 2019). For example, “belly bites” in larger fish like salmon have been frequently observed (Kusnierz, Trial, Cox, &
Saunders, 2014), but because seals eating salmon in this way only ingest soft flesh, the prey lack detectable hard parts.

The Penobscot River Estuary in Maine, which is the largest watershed in the state, provides an opportunity to examine how these rebounding, protected predators interact with protected prey species in the face of major habitat restoration efforts. In addition to harbor and gray seals, commonly sighted predator species in the Penobscot River Estuary include double-crested cormorants (Phalacrocorax auritus), multiple species of gulls (Larus spp.), bald eagles (Haliaeetus leucocephalus), osprey (Pandion haliaetus), and harbor porpoise (Phocoena phocoena). The Penobscot River is also home to 11 species of diadromous fish, all of which have experienced significant population declines due to dam construction, pollution, and overfishing (NOAA, 2016; Saunders, Hachey, & Fay, 2006). With the goal of restoring diadromous fish runs while balancing the need for hydropower production, major restoration efforts occurred in the river, resulting in the removal of two dams (Great Works and Veazie dams) in 2012 and 2013, the installation of the river’s first fish lift (at Milford dam) in 2014, and the construction of a nature-like fish bypass at a second dam (Howland dam) in 2016 (NRCM, 2019). The Penobscot River was also listed as one of the National Oceanic and Atmospheric Administration’s (NOAA) Habitat Areas of Focus in 2014 (NOAA, 2016), and is designated as critical habitat for the endangered Atlantic Salmon (Salmo salar) and the threatened Atlantic sturgeon (Acipenser oxyrhynchus oxyrhynchus) (NOAA, 2009, 2017). The endangered shortnose sturgeon (Acipenser brevirostrum) is also found in the Penobscot River (M. E. Altenritter, Zydlewski, Kinnison, Zydlewski, & Wippelhauser, 2017).

Restoration and conservation efforts in the Penobscot River have resulted in increasing diadromous fish using the river and estuary each year (Gardner, Coghlan Jr, Zydlewski, &
Fish counts at the river’s southernmost dam reveal significant increases in blueback herring (*Alosa aestivalis*) and alewives (*Alosa pseudoharengus*), collectively known as river herring, since dam removal began in 2012 (MDMR, 2018, 2019). Similarly, fish biomass in the estuary has been increasing since 2012, with more areas of high density and larger fish appearing in later years (Stevens, 2019).

While habitat restoration and conservation efforts have focused on diadromous fish, little research to date has focused on how predator species are affecting and being affected by recovering fish populations in this system. As fish populations have increased in the Penobscot River, anecdotal reports of seals in the Penobscot River Estuary, as well as observations of seal predation on diadromous fish, primarily Atlantic Salmon, have become more frequent (Kusnierz et al., 2014). Accordingly, concern has grown regarding the impacts of these predators on fish species of conservation concern in the river. This study aims to understand how pinnipeds are responding to habitat recovery efforts and increasing forage fish populations, as well as to assess the potential risks pinnipeds pose to diadromous fish conservation. Taking a multispecies perspective, we assessed the potential ecological impact of pinnipeds in the Penobscot River by evaluating spatial and temporal overlaps in the presence of seals and diadromous fish from 2012 to 2020.

Seal abundance is commonly estimated by aerial survey, during which satellite-tagged individuals are used to calculate the percentage of the population onshore at the time of the survey (Gilbert et al., 2005; Waring et al., 2015; Yochem, Stewart, DeLong, & DeMaster, 1987). These surveys typically occur within two hours of low tide and during the pupping season, to maximize the number of animals onshore and available for counting (Brown & Mate, 1983; Watts, 1996). Traditional approaches do not include counts of swimming animals, as swimming
animals can be hard to detect and accurate counts can be difficult to obtain since an unknown number of seals could be underwater at a given time and not all individuals surface at once. In addition to analyzing counts of seals on the haul-outs, we used occupancy modeling to understand how swimming seals have been using the estuary over time. Occupancy modeling is designed to estimate species occupancy and detection rate when the probability of detection is less than 1 (MacKenzie et al., 2002). Using presence/absence data rather than counts, this approach has significant potential in marine mammal research, where swimming animals are not always reliably detected or accurately counted.

This study utilized a unique opportunity to assess trends in seal counts and distribution in a system responding to concerted conservation efforts. Our objectives were to: 1) assess whether counts, distribution, and species composition of seals in the Penobscot River Estuary have changed from 2012 to 2020; and 2) determine whether these changes are related to changes in fish biomass. Conservation efforts were evaluated based on predator-prey interactions, which could inform future management decisions on how to best reconcile the competing objectives of marine mammal protection and fish restoration. This insight could be applicable to other systems involving multiple protected species with ongoing conservation measures, e.g., improved habitat and decreased exploitation.

**Methods**

**Data Collection**

Boat-based transect surveys of the Penobscot River Estuary were conducted by NOAA from 2012 through 2020 to assess fish and predator abundance and distribution. As described in Lipsky et al. (2019), hydroacoustic surveys of the Penobscot River Estuary were conducted from April through October, as weather allowed, each year. Surveys were scheduled weekly through
mid-June, during the peaks of several diadromous fish runs, and biweekly throughout the remainder of the season. Beginning on a flood tide, surveys followed pre-determined transect lines north from Stockton Springs to Bangor (Figure 1.1). This section of the river is approximately 50km long (Lipsky, Saunders, & Stevens, 2019).

Figure 1.1: Study Area: Map of transect survey route with major seal haul-out locations labeled.
During the survey, environmental data, including temperature and salinity, were recorded every minute by a data logging multi-meter, and hydroacoustic data were gathered using mobile split beam echosounders that operate at 38kHz and 120kHz frequencies (Lipsky et al., 2019). GPS locations were recorded continuously by a laptop onboard. Throughout the survey, an observer recorded all mammal and bird sightings using Nikon 10x50 magnification binoculars. Both sides of the river, as well as the area in front of the boat were regularly scanned for sightings, and the time, species, number of animals, and behavioral data for all sightings were recorded. We acknowledge that since these surveys were not designed to assess seal abundance, these counts represent a minimum number present, not absolute abundance.

In addition to opportunistic sightings along the survey route, increased efforts were made in obtaining counts at three major seal haul-outs along the survey route, Odom’s Ledge, Fort Point Ledge, and the Eastern Shore, all near Stockton Springs (Figure 1.1). Prior to 2019, haul-outs were not approached for targeted assessment of seals; given the difficulty in identifying these animals at a distance, all analyses that include data from 2012 to 2018 therefore focus on the total number of seals (i.e., pooled data including counts of both gray and harbor seals) instead of specifying species. During 2019 and 2020, counts and identification of species present at Odom’s Ledge and Fort Point Ledge were verified by photograph, and haul-outs were approached more closely than in previous years.

Buck’s Ledge, in Bucksport, is the northernmost haul-out site in the estuary. The surveys typically passed Buck’s Ledge at a higher point in the tide cycle when the ledge was flooded, so seal counts were not available for that haul-out site from the transect survey. In 2019 and 2020, counts from photos taken while transiting *en route* to the start of the survey transect were used to more accurately assess number of individuals present by species. Land-based surveys were also
conducted from a point overlooking Buck’s Ledge from July 2019 through September 2020. These surveys consisted of 30 to 60-minute observations every one to two weeks. Data collected included number of seals hauled out and swimming, wind speed and direction, sea state, time of day, and time from low tide. Data from these surveys that took place between May and October during each year were combined with data collected from the boat-based survey to help characterize seal usage of Buck’s Ledge throughout the survey season.

**Spatiotemporal Analysis of Hauled Out Seals**

To understand how the number of seals in the estuary has changed over time, we first conducted an analysis of the sightings of hauled out animals, which are more reliably counted than seals in the water. These analyses were conducted for the individual haul-out locations (Fort Point, Odom’s Ledge, and Eastern Shore) as well as the pooled data of all hauled out animals counted on each survey. Site-specific factors including time from low tide, time of day, and wind have been shown to affect the number of seals hauled out at a given time (Raposa & Dapp, 2009; Schneider & Payne, 1983; Watts, 1996; Yochem et al., 1987). Our surveys typically occurred in the morning, so time of day was not a confounding factor for our analyses. The data were filtered to limit variation in the remaining environmental effects so that we could conservatively assess trends in counts over time, but we do not attempt to draw conclusions from these data regarding absolute abundance. This filtering approach was used to exclude whole surveys from the pooled analysis and individual sites for the haul-out analysis.

Times from the environmental data collected along the survey route were compared to tide data to construct “time from low tide” data. Approximate time from low tide was associated with individual sightings using the “rtide” package (v0.0.5; Thorley, Miller, & Fleishman, 2018) in RStudio and historic tide data from a station in Stockton Springs. Typically, seal surveys are
conducted within two hours on either side of low tide, as this is when the greatest number of
animals tend to be hauled out on land (Watts, 1996). The Penobscot River Estuary surveys were
targeted to begin at Fort Point around low tide and we excluded any surveys that did not begin
within two hours of low tide from the pooled analysis. Similarly, we excluded from the haul-out
analysis any data that were not collected within two hours of low tide for Fort Point and Eastern
Shore. Odom’s Ledge is surveyed later on the transect line, and we therefore excluded haul-out-
specific observations from this haul-out that were not collected within 1 to 3 hours from low tide.

Environmental variables, such as sea state and wind, were not recorded during the
surveys, so our ability to account for the effects of these environmental factors is limited.
Approximate wind speed data for each sighting were pulled from NOAA’s National Climactic
Data Center’s (NCDC) recordings from a sensor at Bangor International Airport. An average
wind speed was calculated for the southern section of each survey using the NCDC data. A plot
of wind speed versus number of seals counted showed a negative correlation and a clear drop in
seal sightings around 5.3 kilometers per hour (Figure A1), so surveys with average wind speeds
above 5.3 kilometers per hour were excluded from the pooled analysis. Wind speed was also
associated with individual haul-out sightings, and sightings that occurred at wind speeds over 5.3
kilometers per hour were similarly excluded from the haul-out analysis.

Finally, incomplete surveys were also removed from the pooled analysis if animals at
Fort Point were not included in the day’s seal count. In total, this conservative filtering approach
retained 66 out of 133 surveys for the pooled analysis, and 70 observations at Fort Point Ledge,
74 observations at Odom’s Ledge, and 68 observations at the Eastern Shore for the individual
haul-out analysis (Table 1.1). Similar filtering of the 2019 and 2020 photo-count data, which
included species-level information, retained 17 out of 24 surveys.
Table 1.1: Summary of Surveys: Number of Surveys Included in Pooled Analysis. See appendix, tables A1-A4, for sample sizes and seal counts associated with haul-out specific and 2019/2020 photo-count analyses.

<table>
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<th>Summer</th>
<th>Fall</th>
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</table>

Each survey date was associated with a standard week and season. Seasons were determined by standard week: spring (weeks 17-26; April through June), summer (weeks 27-35; July and August), and fall (weeks 36-48; September through November). Each survey date was also associated with an estimated value of fish biomass present in the estuary, calculated by Stevens (2019). These estimates were calculated using the hydroacoustic data from the estuary survey, which were collected along the survey transect line from which seal observations were also recorded (Lipsky et al., 2019; Stevens, 2019). A one-way ANOVA was used to look for
differences in seals counted on haul-outs across years, and a Kruskal Wallis test was used to analyze differences in seal counts between seasons. Significant ANOVAs were followed with a Tukey test and significant Kruskal Wallis tests were further analyzed with a Dunn’s test.

Anecdotally, seal counts in the Penobscot are highest in the spring. To determine whether the proportion of annual surveys conducted in the spring impact our ability to compare seal counts across years, we used Spearman’s correlation coefficient to describe the relationship between the average number of seals counted and the percentage of spring surveys by year.

In the pooled analysis, we wanted to see if increasing fish biomass was correlated with hauled out seal counts. We also calculated the proportion of seals sighted per survey that were swimming and used this as a metric to explore trends in swimming animals that were detected based on fish biomass, standard week, and year. Spearman’s correlations were used to assess these relationships.

A generalized linear model was constructed to assess significant predictors of the number of seals counted on the haul-outs. A negative binomial distribution was used to correct for overdispersion. Predictor variables included standard week and fish biomass. The models were ranked based on Akaike’s Information Criterion (AIC), and the top model was evaluated using a deviance goodness of fit test.

In our haul-out analysis, we used Spearman’s correlations to evaluate the relationships between seal counts at individual haul-outs, standard week, and year, with the goal of determining whether haul-outs followed an overall estuary trend or if haul-outs were utilized differently throughout the year. We also wanted to look for evidence of displacement of animals between haul-outs during the season. The Holm-Bonferroni method was used to control family-wise error rates. Since the seasonal comparison in our pooled analysis only accounted for
animals hauled out in the lower estuary, we conducted an analysis of variance with Buck’s Ledge data from 2019 and 2020 to explore seasonal differences in seal presence and compared this to trends observed in the lower estuary.

The 2019 and 2020 photo-count data were also evaluated as described above for the haul-out analysis to explore differences in haul-out usage by each species throughout the year, as well as to look for evidence of gray seals displacing harbor seals to different haul-out locations in the estuary. We also used these comparisons to explore potential species-specific relationships with fish biomass.

**Occupancy Modeling of Swimming Seals**

**Sampling Set Up.** Occupancy models assume that the population is closed (i.e., there is no movement into or out of sites) during the primary sampling period, but multi-season models allow movement between seasons, and in turn, allow us to estimate the probability of colonization (the probability that an unoccupied site will become occupied) and the probability of extinction (the probability that an occupied site will become unoccupied) between seasons (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). Based on this assumption of closure, we defined a single survey as a “season”, to allow for movement of seals between our survey days. Similar to studies that have conducted surveys along a trail or road (Hines et al., 2010; Midlane, O’Riain, Balme, Robinson, & Hunter, 2014; Thorn, Green, Bateman, Waite, & Scott, 2011), and based on a power analysis recommending more than 35 sites, the estuary survey transect line was divided up into 51 1-kilometer sites (Figure 1.2). Visit 1 was defined as the first 500m of transect line in a site and visit 2 was defined as the second 500m of transect line in a site. This resulted in an occupancy model “season” consisting of two visits to 51 sites; we did not use more sites or visits because swimming seal sightings were infrequent. With this
approach, we analyzed harbor seal data from surveys conducted from 2012 through 2020. Similarly, we analyzed gray seal data from surveys conducted from August 2018 through September 2020. The gray seal model start date was August 14, 2018 because gray seal sightings in earlier years were sparse. Swimming seal sightings were associated with a site and visit. Presence was indicated with a 1 and absence with a 0.

Figure 1.2: Occupancy modeling set-up: Sites used for occupancy modeling.
Probability of presence and probability of detection must be constant or modelized through covariates, so we have detailed the covariates to be included in this analysis in the following section. Detections in each site must also be independent, meaning the same individual is not counted twice (MacKenzie et al., 2003). This was a concern with seals, as there is no reliable method to identify a swimming animal as an individual that has already been counted. However, the greatest number of occupied sites in a single visit was 5, so repeat counts do not appear to be a concern. Pinniped swim speed is 1-3 meters per second, or 1.94-5.88 knots (Hindell & Lea, 1998; Ponganis, Kooyman, Castellini, Ponganis, & Ponganis, 1993; Watanabe et al., 2011). Harbor seals also spend 82-92% of the time submerged when they are swimming at speeds below 2.33 knots; this percentage submerged decreases with increased swimming speed, making it more likely that they will be detected (Williams, Kooyman, & Croll, 1991). In the upper parts of the river, where the zigzag of the trackline is less pronounced, the survey boat traveled at 6 knots, moving slightly faster than a seal swimming at its top sustained speed. The lower estuary is more complicated; there are 13.88km of trackline compared to 6.12km straight line distance, but this is also where the major haul-outs are located, and thus more seals. It is possible that a single individual could be sighted multiple times but given the number of animals on the rocks in these areas, and the low number of occupied sites, it is unlikely that the assumption of independence is being violated to the point of overestimating site occupancy.

**Covariates Used in Modeling.**

1.) River width was measured in kilometers at the middle of each 1-km site. Width could affect detection of seals, as it may be easier to miss an animal in a wider stretch of river.
2.) Distance from the bay was measured in river kilometers from the middle of each site to a point in the bay just south of Stockton Springs. More animals are located closer to the bay, so this covariate could affect all four model parameters: probability of detection, probability of occupancy, probability of colonization, and probability of extinction.

3.) Distance from nearest major haul-out site (Fort Point Ledge or Odom’s Ledge) was measured in river kilometers from the middle of each site. Since seals haul out on these ledges in synchrony with the tide, it is likely that proximity to haul-out sites would affect all four parameters.

4.) Year was added to the model to see if occupancy in the river has changed as a result of the Penobscot River Restoration project and increasing fish populations.

5.) Standard week was included as a covariate to look for trends from spring through fall.

6-8.) Hourly historic wind speed and direction data from the NCDC station at Bangor International Airport were associated with a site based on the time of day each site was visited. Wind direction was broken into two vectors (sin and cos), which were included together when modeled. Similarly, a combined wind effects covariate was created by multiplying wind speed by each vector, and these were also modeled together (Bramer, 2013). Missing values were filled in with the average wind speed and direction from that day. Wind, and subsequently sea state, can affect observer ability to detect animals, so this was included as a covariate for modeling detection.
9.) Temperature was collected every minute during the survey. A spatial join in ArcMap 10.7 assigned each datapoint to a visit, and the average value for each visit was calculated. Missing values were filled in by averaging the temperatures from the two nearest visits.

10.) Salinity was also collected every minute during the survey and was assigned to each visit as described for temperature.

11.) Time of day was spatially joined to each visit. The average value for each site was calculated and converted into hours from low tide. Missing values were filled in by averaging the time from tide from the two nearest visits. Seals are more likely to haul out on the rocks within two hours of low tide (Gilbert et al., 2005; Watts, 1996), so hours from low tide could potentially influence all four parameters.

12.) Total biomass of the estuary was calculated from the survey’s hydroacoustic data by Stevens (2019). Total biomass was chosen instead of site-specific biomass to account for the wide range of a seal. Biomass on a small spatial scale may not be relevant to seal presence, but overall biomass could affect all four parameters.

13.) Distance from peak biomass was calculated to see if seals are more likely to be sighted closer to areas of high biomass in the estuary. This metric is more biologically meaningful than individual site biomass, as seals can be sighted while transiting, not just while foraging. Fish biomass estimates for every 500m of survey were calculated by Stevens (2019), and these were assigned to a site using a spatial join in ArcMap 10.7. The average value for each site was then calculated, and the site with peak biomass for each survey was selected. Distance in river kilometers
from the middle of each site to the middle of the site with peak biomass was then calculated.

Surveys with biomass estimates that were incomplete, either due to equipment malfunction or weather preventing a full survey from being conducted, were removed from the analysis. Similarly, survey days that had zero data points for one of the covariates were also removed. This resulted in 99 “seasons” of data for harbor seals, 26 “seasons” of data for gray seals, 3 site covariates, 5 seasonal covariates, and 5 sample covariates.

**Statistical Modeling.** While the haul-out analysis did not allow for species-specific comparisons because haul-outs were not closely approached from 2012 to 2018, swimming animals are often sighted closer to the boat, allowing easier species identification. Changing protocols and incorporation of photographs in 2019 did not affect observer ability to identify swimming seals. For these reasons, separate models were constructed for harbor and gray seals. Harbor and gray seal sightings and covariate data were uploaded into the program PRESENCE, version 2.12.37, covariates were scaled, and AICc was used to account for a small sample size (n=51 sites). As sampling along a river can result in spatial dependence between sites, and because a site could be occupied due to a nearby haul-out or because a seal is transiting rather than suitability of the site, a simple multi-season model with no covariates was compared to a multi-season model with correlated detections. Distance from haul-outs seemed more influential than occupied neighboring sites, so this covariate also aimed to account for spatial autocorrelation. Overall, so few sites were occupied that spatial autocorrelation between sites may not be a significant issue. Similarly, a multi-season model with seasonal effects (detection probability varies by season) was run. In both cases, the simple multi-season model resulted in a lower AIC.
Detection (p) was modeled for river width, distance from the bay, distance from haul-outs, year, standard week, hours from low tide, wind speed, wind direction, combined wind effects, temperature, salinity, total estuary biomass, and distance from peak biomass. Additive models using covariates within 2ΔAIC of the top model were also conducted.

Retaining the covariates from the top model for probability of detection, probability of presence (ψ) was then modeled for distance from bay, distance from haul-outs, year, standard week, hours from low tide, total estuary biomass, and distance from peak biomass. Additive models using covariates within 2ΔAIC of the top model were also conducted.

Again, including the top model covariates for detection and presence, the probability of colonization (γ), was modeled for distance from bay, distance from haul-out, year, standard week, hours from low tide, total estuary biomass, and distance from peak biomass. Additive models using covariates within 2ΔAIC of the top model were conducted and the covariates present in the top model were retained.

Finally, while accounting for the top model covariates for detection, presence, and colonization, probability of extinction (ε) was modeled for distance from bay, distance from haul-out, year, standard week, hours from low tide, total estuary biomass, and distance from peak biomass. Goodness of fit was assessed with the MacKenzie and Bailey goodness of fit test using packages unmarked and AICcmodavg in RStudio (Fiske & Chandler, 2011; MacKenzie & Bailey, 2004; Mazerole, 2019).

**Results**

**Spatiotemporal Analysis of Hauled Out Seals**

The number of hauled out seals counted per survey varied significantly by season (Figure 1.3; Kruskal-Wallis chi-squared=33.271, df=2, p<0.001). A Dunn’s test with a Bonferroni
adjustment revealed that the average number of seals counted during spring surveys (55.6±23.1, n=28) was significantly greater than during both summer surveys (27.2±20.4, n=20, p<0.01) and fall surveys (11.2±9.53, n=18, p<0.001), but that summer and fall were not significantly different from each other (p=0.108).

Figure 1.3: Seasonal variation: Hauled out seals, fish biomass, and percentage of swimming seals in the Penobscot River Estuary by season, 2012-2020. The blue square represents the average value for each season. Spring seal counts (n=28) were significantly greater than both summer surveys (n=20, p<0.01) and fall surveys (n=18, p<0.001), but summer and fall were not significantly different from each other (p=0.108). Fish biomass was higher during summer surveys than both spring surveys (p<0.05) and fall surveys (p<0.01), but spring and fall were not significantly different from each other (p=0.414). The percentage of seals that were swimming was significantly higher in summer (p<0.001) than spring. Fall was not significantly different from spring (p=0.100) or summer (p=0.541).

As significantly higher numbers of hauled out seals are counted during spring surveys than during summer and fall surveys, the percentage of annual surveys conducted during the spring each year could impact our ability to compare average seal counts between years. There
was not a significant relationship between percentage of spring surveys and average seal counts (Spearman rs=0.594, p=0.092), which allows us to compare seal counts across years, despite different numbers of surveys conducted each year.

We did find significant differences in seal counts across years from 2012 to 2020 (Figure 1.4; one-way ANOVA F(8,57)=2.362, p<0.05). A post-hoc Tukey test revealed that seal counts in 2013 (56.8±32.7, n=12) and seal counts in 2014 (14±20.6, n=6) were significantly different from one another (p<0.05). The mean number of seals counted during 2013 and 2014 represent the highest and lowest annual means in the study period. The analysis for 2013 included 7 out of 12 total surveys that were conducted in spring, while 2014 included 6 surveys, only 1 of which was conducted in spring; while the percentage of annual spring surveys across all years was not significantly related to average seal count, it is likely that the difference between the number of spring surveys in these two years is influencing the detected difference in seals counted.

Figure 1.4: Annual variation: Hauled out seals counted by year. Seal counts varied significantly across years from 2012 to 2020 (one-way ANOVA F(8,57)=2.362, p<0.05). The blue squares represent the average number of seals counted per year.
Fish biomass varied significantly by season (Kruskal Wallis chi-squared=12.504, df=2, p<0.01), with summer surveys (102,995±68,138, n=20) having significantly higher fish biomass than both spring surveys (59,382±39,196, n=28, p<0.05) and fall surveys (46,700±23,054, n=18, p<0.01; Figure 1.3). Fish biomass in spring and fall surveys were not significantly different from each other (p=0.414). Fish biomass also exhibited a moderate positive correlation with year (Figure A2; Spearman rs=0.514, p<0.001).

Hauled out seal counts were not significantly related to fish biomass (Figure A2; Spearman rs= -0.105, p=0.412), but the percentage of total seals sighted that were swimming from each survey was positively correlated with fish biomass (Figure S2; Spearman rs=0.379, p<0.01). The percentage of seals that were swimming also increased significantly across years (Figure A2; Spearman rs=0.336, p<0.01), and was significantly higher (Figure 1.3; Kruskal-Wallis $\chi^2=14.051$, df=2, p<0.001) in summer (0.361±0.326, n=20, p<0.001) than spring (0.0931±0.112, n=28). Fall (0.243±0.278, n=18) was not significantly different from spring (p=0.100) or summer (p=0.541).

We constructed a model to predict the number of seals counted during a survey using a negative binomial distribution to correct for overdispersion and determined that the best model for predicting seal haul-out counts was:

$$\hat{Y}=\beta_0 + \beta_1(\text{Standard Week}) + \beta_2(\text{Biomass}) \text{ (Equation 1.1)}$$

Both standard week ($\beta_1 = -0.075$, standard error=0.011, p<0.001) and biomass ($\beta_2 = -1.73e-06$, standard error=1.743e-06, p=0.345) exhibited a negative relationship with total seal count ($\hat{Y}$) (Figure 1.5), however the relationship with biomass was not significant. A chi-square
deviance goodness of fit test found no evidence for lack of fit (deviance=73.534, df=60, p=0.113).

Figure 1.5: Model Predictions: Observed and Predicted values for the negative binomial generalized linear model presented in Equation 1 with 95% confidence intervals. Estimated regression parameters: $\beta_0 = 5.680$ (SE=0.344), $\beta_1 = -0.075$ (SE=0.011, p<0.001), $\beta_2 = -1.73e-06$ (SE=1.743e-06, p=0.345).

Our individual haul-out analysis revealed significant declines in numbers of seals counted at Fort Point Ledge and Odom’s Ledge throughout the year (Table 1.2). The number of seals at these haul-outs were positively related to each other. In contrast to these haul-outs, Eastern Shore seal counts significantly increased from spring through fall, and across years. Based on our vessel and land-based surveys from 2019 and 2020, Buck’s Ledge does not appear to experience significant differences in seal counts between seasons (Figure 1.6; Kruskal-Wallis $\chi^2=1.059$, df=2, p=0.589).
Table 1.2: Haul-out specific correlations: Haul-Out Data, 2012-2020. Spearman’s Correlation Coefficient, significant at p<0.05 in bold, still significant with Holm-Bonferroni adjustment has an asterisk.

<table>
<thead>
<tr>
<th></th>
<th>Standard Week</th>
<th>Year</th>
<th>Fort Point, All Seals</th>
<th>Odom’s, All Seals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fort Point, All Seals</td>
<td>-0.592*</td>
<td>-0.080</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Odom’s, All Seals</td>
<td>-0.658*</td>
<td>-0.294</td>
<td>0.463*</td>
<td>-</td>
</tr>
<tr>
<td>Eastern Shore, All Seals</td>
<td>0.465*</td>
<td>0.565*</td>
<td>-0.281</td>
<td>-0.308</td>
</tr>
</tbody>
</table>

Figure 1.6: Buck’s Ledge seasonal variation: Seals sighted at Buck’s Ledge by season, 2019-2020 (land and vessel-based data). No significant differences in the average number of seals sighted per survey was observed between spring (n=18), summer (n=23), and fall (n=19) (Kruskal-Wallis $\chi^2=1.059$, df=2, p=0.589).

Our analyses of the 2019 photo-counted data (Table 1.3) revealed that harbor seal counts significantly decreased throughout the season and that harbor seal counts increased with increasing fish biomass. Similar relationships with gray seals were not detected. Species and
haul-out specific comparisons did not reveal many significant relationships, but Eastern Shore harbor seals exhibited a significant positive relationship with overall and Fort Point gray seal counts, and Fort Point harbor seals appeared to have a strong negative relationship with gray seals at Odom’s Ledge. There were no significant differences in counts between 2019 (harbor: 41±28.5, n=9; gray: 6.78±7.85, n=9) and 2020 (harbor: 49.8±18.9, n=8; gray: 13.5±12.8, n=8) for total harbor seals (t=-0.754, df=13.986, p=0.464) or gray seals (t=-1.286, df=11.36, p=0.224).

Non-significant results presented in these sections may be due to low sample size (n<15 in many comparisons across years and n<20 in comparisons using the 2019 and 2020 photo-counted data) and low power. Higher statistical power is needed to detect small effect sizes and demonstrate more subtle changes in seal counts over time.
Table 1.3: Photo-Counted Correlations: 2019 and 2020 Photo-Counted Data: Spearman’s Correlation Coefficient, significant at p<0.05 in bold, still significant with Holm-Bonferroni adjustment has an asterisk. Buck’s Ledge correlations use vessel data only.

<table>
<thead>
<tr>
<th></th>
<th>Fish Biomass</th>
<th>Standard Week</th>
<th>All Harbor Seals</th>
</tr>
</thead>
<tbody>
<tr>
<td>All Gray Seals</td>
<td>0.088</td>
<td>0.320</td>
<td>-0.111</td>
</tr>
<tr>
<td>All Harbor Seals</td>
<td><strong>0.650</strong>*</td>
<td><strong>-0.834</strong>*</td>
<td>-</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>All Gray Seals</th>
<th>All Harbor Seals</th>
<th>Fort Point Gray Seals</th>
<th>Fort Point Harbor Seals</th>
<th>Odom’s Gray Seals</th>
<th>Odom’s Harbor Seals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eastern Shore Harbor Seals</td>
<td><strong>0.701</strong>*</td>
<td>-0.159</td>
<td><strong>0.690</strong>*</td>
<td>-0.344</td>
<td><strong>0.565</strong></td>
<td>-0.210</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>All Gray Seals</th>
<th>All Harbor Seals</th>
<th>Fish Biomass</th>
<th>Standard Week</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buck’s Ledge Harbor Seals</td>
<td>0.047</td>
<td>-0.191</td>
<td>-0.148</td>
<td>-0.022</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>All Gray Seals</th>
<th>All Harbor Seals</th>
<th>Fort Point Gray Seals</th>
<th>Fort Point Harbor Seals</th>
<th>Odom’s Gray Seals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fort Point Gray Seals</td>
<td>-</td>
<td>0.075</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Fort Point Harbor Seals</td>
<td>-0.279</td>
<td>-</td>
<td>-0.100</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Odom’s Gray Seals</td>
<td>-</td>
<td><strong>-0.533</strong></td>
<td>0.414</td>
<td><strong>-0.669</strong>*</td>
<td>-</td>
</tr>
<tr>
<td>Odom’s Harbor Seals</td>
<td>-0.216</td>
<td>-</td>
<td>-0.111</td>
<td>0.354</td>
<td>-0.421</td>
</tr>
</tbody>
</table>

**Occupancy Modeling of Swimming Seals**

Harbor seals and gray seals have both been sighted in the water throughout the Penobscot River Estuary from Stockton Springs to Bangor. Our analysis of occupancy models did not identify any models within 2 ΔAICc of the top model constructed for harbor seals (Table 1.4). Our top model showed no evidence of lack of fit ($\chi^2=408.329$, $p=0.48$), and we did not find more variation in the data than expected (c-hat=0.99). The top model for harbor seals indicated that
salinity was the main factor affecting detection (Table 1.4) and detectability increased as salinity increased (Figure 1.7).

Table 1.4: Top Occupancy Models: Harbor seal and gray seal occupancy models within 2 ΔAICc of the top model. The probability of presence (ψ), colonization (γ; that an unoccupied site will become occupied), extinction (ε; that an occupied site will become unoccupied), and detection (p) were each modeled using swimming seals counted during vessel-based surveys of the Penobscot River Estuary from 2012 to 2020. Variables in parentheses indicate those which were found to significantly affect the modeled parameter. (.) represents parameters that were better modeled as constants rather than as a function of a measured variable.

<table>
<thead>
<tr>
<th>HARBOR SEAL</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AIC weight</th>
<th>Model Parameters</th>
<th>Nagelkerke’s R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>ψ(., γ(., ε(distance from nearest haul-out), p(salinity))</td>
<td>1952.81</td>
<td>0.00</td>
<td>1.0000</td>
<td>6</td>
<td>0.82</td>
</tr>
<tr>
<td>GRAY SEAL</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ψ(., γ(., ε(distance from bay), p(salinity))</td>
<td>404.77</td>
<td>0.00</td>
<td>0.24</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>ψ(., γ(., ε(., p(salinity))</td>
<td>405.03</td>
<td>0.26</td>
<td>0.21</td>
<td>5</td>
<td>0.39</td>
</tr>
<tr>
<td>ψ(., γ(., ε(hours from low tide), p(salinity))</td>
<td>405.08</td>
<td>0.31</td>
<td>0.21</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>ψ(., γ(., ε(standard week), p(salinity))</td>
<td>405.99</td>
<td>1.22</td>
<td>0.13</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>ψ(., γ(., ε(hours from low tide), ε(., p(salinity))</td>
<td>406.26</td>
<td>1.49</td>
<td>0.22</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>ψ(., γ(., ε(total fish biomass), p(salinity))</td>
<td>406.53</td>
<td>1.76</td>
<td>0.10</td>
<td>6</td>
<td></td>
</tr>
</tbody>
</table>
Figure 1.7: Harbor seal predicted probabilities: Untransformed estimates from the top harbor seal model (Table 1.4) were converted into predictions for probability of detection (Intercept = -2.806, Slope = 0.163±0.038) and extinction (Intercept = -1.614, Slope = 0.947±0.380) using the logistic equation. The solid lines show predicted probability and the dotted lines represent standard error of the slope.
We found that probability of harbor seal presence in a site, as well as the probability of an unoccupied site becoming colonized was constant, but that the probability of an occupied site becoming “extinct” in between surveys was most dependent on the distance of a site to the nearest major haul-out. Sites close to the haul-outs were least likely to become extinct, while sites at least 2.0km away had a greater than 50% chance of being unoccupied the following survey (Figure 1.7). Occupied sites over 5km away from a major haul-out were extremely likely to be unoccupied at the next survey.

When constructing occupancy models for gray seals, we ended up with six models within 2 ΔAICc of the top model (Table 1.4). Since five of the top models were not significantly better than the model with null values for probability of presence, colonization, and extinction, we focused our analysis on the model that only modeled detection. The MacKenzie and Bailey goodness of fit test was also used to assess this model, and we did not find evidence of lack of fit ($\chi^2=70.236$, p=0.39). Similarly, the model did not have more variation than expected (c-hat = 0.93). As with our harbor seal model, the probability of detection was most dependent on salinity, with detection increasing as salinity increases (Figure 1.8).
Figure 1.8: Gray seal predicted probabilities: Untransformed estimates from the gray seal model were converted into predictions for probability of detection (Intercept = -4.890, Slope =0.385±0.077) using the logistic equation. The solid lines are showing predicted probability and the dotted lines represent standard error of the slope.

In this model, the probability of presence, colonization, and extinction were all constant. Year was not an important covariate in our top models, so we can conclude that gray seal occupancy in the estuary does not appear to have changed significantly since August 2018. Our other top models include hours from low tide as a function of the probability of colonization and distance from the bay, hours from low tide, standard week, and total biomass as a function of the probability of extinction. While these variables did not result in a model better than the null model for these parameters, these variables could become more important if more “seasons” of data were collected.
**Discussion**

The Penobscot River Estuary survey has provided a unique opportunity to study trends in seal populations in a recovering system over time. While survey protocol and conditions may not allow for traditional seal population assessments, there is power in the repeatability of the survey and knowledge to be gained by the trends that emerged over time. Given that the survey follows the same route, at relatively the same point in the tide cycle, in similar weather conditions, observed changes over time have ecological meaning.

As demonstrated by our generalized linear models, standard week is the most significant predictor of number of seals present on the haul-outs. Seal counts generally peak at the start of the season, which corresponds to harbor seal pupping season in May and June, when harbor seals tend to spend more time on the rocks (Brown & Mate, 1983). Seal counts tend to decline through the rest of the year, with the exception of some higher counts in July and August during harbor seal molting season, when they also spend more time hauled out (Brown & Mate, 1983).

While fish biomass in the estuary peaks in the summer, the spring peak in seal count does overlap with the peaks of numerous fish runs. Adult Atlantic Salmon spawning runs from the ocean into the river typically peak between May 24 and July 1, and adult river herring peak between May 15 and June 7, while American shad runs peak between June 1 and June 30 (Bruchs, Simpson, & Valliere, 2018). Downstream migration of juvenile Atlantic Salmon smolts also occurs in spring (McCormick, Hansen, Quinn, & Saunders, 1998; Saunders et al., 2006; Stich, Zydlewski, Kocik, & Zydlewski, 2015). This overlap is a potential concern, but prey buffering by increasing river herring returns appears to provide some protection to Atlantic Salmon (Kusnierz et al., 2014).
We observed no significant change in the number of seals hauling out in the estuary between 2015 and 2020, despite increasing fish populations in the river and estuary since restoration efforts were enacted (MDMR, 2018; Scherelis, Zydlewski, & Brady, 2020; Stevens, 2019). This result was unexpected, as anecdotal reports of these animals have increased. Based on various models of predator-prey dynamics that predict cycling predator and prey populations in which the predator population lags slightly behind that of the prey (Gause, 1935), one possible explanation for our results could be that more time is needed before predator populations will begin to respond, especially considering the different life histories and reproductive strategies of seals compared to river herring. Continued assessment of pinniped abundance and distribution in this system remains important to test this hypothesis.

It is also possible that seals in the Penobscot River Estuary could be spending more time on the rocks, and thus creating a false sense of population increase, if they are able to forage closer to their haul-outs due to increasing biomass (Sharples, Moss, Patterson, & Hammond, 2012). While it is difficult to know where seals are feeding without further information, for example from a tagging study, we know that seals can adapt their foraging strategy in response to prey availability (Russell et al., 2015; Sharples et al., 2012). In our study, we estimated the percentage of seals swimming per survey as the number of animals counted in the water divided by the number of total animals counted that day. It is important to note that counting swimming animals is subjective and thus this analysis is exploratory. These values do not reflect an actual percentage of the seal population in the water, and we therefore consider only relative changes in these values over time, leveraging the longevity of the survey. Our analysis showed that this percentage of swimming animals was positively correlated with year, refuting the hypothesis.
stated above that the public perception of increasing seal populations in the river may be due to animals spending more time hauled out.

If a larger proportion of seals in the river are swimming over time, while the counts on the haul outs do not significantly change, another possible explanation for our results could be that the overall number of seals in the estuary has increased, but that this change is reflected only in animals swimming, and perhaps foraging, in the estuary. There are several harbor seal haul-outs in the upper part of Penobscot Bay near the towns of Castine and Islesboro. These sites are within 10 to 25km of Fort Point, a distance easily traveled by harbor seals with foraging trips that can range from 5km to several hundred kilometers from haul-out sites (Cunningham et al., 2008; Lowry, Frost, Hoep, & Delong, 2001; Sharples et al., 2012). A satellite-tagging study across haul-out sites in Penobscot Bay and Maine’s mid-coast and downeast regions could help reveal whether the estuary has become a more desirable foraging location for seals located elsewhere in this part of the Gulf of Maine. Similarly, while we cannot know what these seals are eating without performing a diet study, it is possible that a fourth explanation for our results is that these animals, as opportunistic predators that feed on whatever is locally abundant, have simply switched their dietary preferences in response to increasing fish biomass rather than experiencing population growth (Murie & Lavigne, 1992; Pierce et al., 1991).

The percentage of swimming animals was lowest in spring, which we expect, as harbor seals spend more time out on the rocks during their spring pupping season (Brown & Mate, 1983). The percentage swimming was highest in summer, which supports the possibility that female harbor seals are foraging more in early summer to recover from raising a pup (Carlini, Daneri, Marquez, Soave, & Poljak, 1997). This, however, does not support the fact that harbor seals tend to spend more time hauled out during their molting season in July and August (Brown
This peak in percentage swimming in summer also coincides with the peak in estuary fish biomass (Stevens, 2019), and our analysis showed that the percentage of animals swimming does slightly increase with biomass. While a tagging study would be needed to explore foraging time, this trend is the opposite of what we would expect from reduced foraging time due to nearby prey availability, and overall, the number of seals counted on haul-outs was not significantly related to fish biomass in the estuary. In contrast, the relationship between hauled out seal count and biomass was negative, likely reflecting the differences in peak times: seal counts peak in spring while fish biomass peaks in summer. In support of the importance of this relationship, our model predicting overall seal count was better when biomass was included as a predictor variable, despite the lack of significance. Another possibility to consider is that relationships between hauled out seals and fish biomass are just beginning to change, as the photo-count data from 2019 and 2020 did reveal a strong, positive relationship between overall harbor seal count and biomass that was not detected across our full study period. More information about how seals are moving in the estuary and bay, as well as where they are foraging, are needed to further explore these relationships as fish continue to respond to restoration efforts.

The haul-out specific data reveal several trends that we would expect. Fort Point and Odom’s Ledge seals reflect the larger trend of the estuary as counts at both decrease throughout the season. Our analysis at Buck’s Ledge, however, revealed no significant differences between seasons. Anecdotally, seal counts at this ledge are highest in the spring, so it is possible that more data across a broader time period would reveal a significant difference between spring seal counts and those in other seasons.
At Buck’s Ledge, future research could focus on predator-prey interactions. Shortnose sturgeon and Atlantic sturgeon are commonly found near Buck’s Ledge each year (M. N. Altenritter, Zydlewski, Kinnison, & Wippelhauser, 2017; Fernandes, Zydlewski, Zydlewski, Wippelhauser, & Kinnison, 2010). Shortnose sturgeon have been shown to concentrate in the stretch of the river near Buck’s Ledge in late spring and early summer, with the majority of individuals shifting further upriver by mid-July (Fernandes et al., 2010). Atlantic sturgeon, on average, will enter the estuary in mid-May and depart at the end of August (M. N. Altenritter et al., 2017). During this time period, tagged Atlantic sturgeon also tend to congregate in the stretch of river that contains Buck’s Ledge, and have been shown to spend 67-84% of their time in this location (M. N. Altenritter et al., 2017). Predation of sturgeon by larger gray seals would be a concern if these species overlap in space and time. Gray seal sightings at Buck’s Ledge occurred between late September and early November in 2019, and the species was resighted in late June and August 2020. Sightings of either seal species were rare between mid-June and early August, suggesting that future research in this area should continue to monitor for changes in gray seal presence and the frequency of gray seal and sturgeon interactions, especially in mid to late August. Gray seal predation of a shortnose sturgeon was observed in a cove north of Buck’s Ledge on August 24, 2006, supporting our assessment that predation risk would be higher during the second half of August (Fernandes, 2008).

In contrast to the declining trend at Fort Point and Odom’s Ledges, Eastern Shore seal counts significantly increased throughout the survey season and are increasing across years as well. This suggests that seals could be moving from Fort Point and Odom’s ledge to Eastern Shore throughout the year. These dynamics were further explored with our photo-count data.
Overall, our 2019 and 2020 photo-count data support the idea that gray seals may displace harbor seals when they first arrive at haul-out sites in the river. At both Fort Point and Odom’s Ledge, the first sighting of gray seals on the haul-out coincided with a decline in harbor seals. Coincident with the first sighting of gray seals on Fort Point, we also observed the first sightings of harbor seals at Eastern Shore, located across the river from Fort Point Ledge, suggesting harbor seals may move to this haul-out when gray seals are present. Harbor seal counts on Fort Point increased again when the gray seals left at the end of the season. Eastern Shore harbor seal counts exhibited a significant positive relationship with the total number of hauled out gray seals, as well as gray seals hauled out specifically at Fort Point Ledge. Eastern Shore seal counts also exhibited a nonsignificant, negative relationship with the total number of hauled out harbor seals. Competitive exclusion by gray seals can result in each species hauling out at separate times, with harbor seals preferring to haul-out in the second half of the day (Russell et al., 2015). Displaced harbor seals could therefore also be resting offshore, while gray seals are present, and hauling out later in the afternoon. Surveys typically survey the haul-outs in the morning, so this dynamic would not be captured.

Across years, seal counts on Eastern Shore have typically increased throughout the year, which is opposite the overall trend in the estuary. Seal counts at Eastern Shore have also increased over time throughout the 9-year study period, suggesting that an increasing number of gray seals may be moving into the estuary each year. Seal counts at Eastern Shore were low in 2013 (n=1) and 2014 (n=2), but began increasing in 2015, suggesting that gray seals may have started increasing in the estuary around that time. Individual gray seals were documented as hauled out four times from 2012 to 2018, but as we have mentioned, species level identification in those years may not have been accurate as seals were not the subject of the survey and haul-
outs were not approached. In 2019, we observed gray seals hauled out on three major haul-outs in the survey area, with as many as 26 gray seals seen at one haul-out site in one day, 20 of which were hauled out while six were swimming nearby. The presence of multiple gray seals at the haul-out sites was first documented on our July 8, 2019 survey. While this influx of gray seals appears to be new for the Penobscot River Estuary, it reflects similar changes that have been documented throughout the Gulf of Maine (Gilbert et al., 2005; Pace et al., 2019).

Looking at the photo-counted data from 2019 and 2020, we don’t see a significant correlation between number of harbor seals and gray seals, but perhaps this will change as we collect more years of species-specific data.

Our top occupancy models for harbor and gray seals both suggest that the probability of detection is most dependent on salinity. It is important to note that salinity is correlated with both distance from the bay, distance from major haul-out sites, and seasonality in our study system. Salinity is higher in the southern part of the estuary and lower further upriver. High river discharge in spring results in lower overall salinity compared to summer and fall. These results therefore support higher detectability in the lower part of the estuary, where the seal haul-outs and highest density of seals are located. Our results also support lower detectability of swimming seals during the spring season, which corresponds to harbor seal pupping season, when we know animals spend more time out of the water. This also aligns with the increase in gray seal sightings in the estuary that occurred in late June and early July in 2019 and 2020.

Our harbor seal occupancy model also showed that the probability that an occupied site will become unoccupied is most dependent on the distance to the nearest haul-out. This finding is consistent with seal behavior; seals leave haul-outs to forage but will return to haul-outs to rest after foraging events. A seal would not remain upriver indefinitely.
Since year, standard week, total biomass, and distance to peak biomass were not significant covariates in our top models for either species, we can conclude that occupancy throughout the river does not appear to be changing significantly over time and that biomass does not appear to significantly affect it. Our models estimated that probability of presence was approximately 0.4 at all sites for both species, and that probability of detection ranged from just above 0 to approximately 0.25 for both species, with the highest probability of detection occurring at Fort Point Ledge (site 1) and the lowest at sites upriver near Bangor. In addition to these low probabilities of presence and detection, both models only had two visits per site, and most sites were unoccupied, resulting in a high likelihood that these analyses had low power.

Overall, our analyses support the idea that observed number of seals hauling out in the Penobscot River Estuary have not changed significantly over the past 9 years, despite diadromous fish restoration activities. More frequent surveys throughout the year could provide more robust analyses with improved power and ability to detect smaller effect sizes, which could reveal changes that our analyses were not able to detect. Yet, based on our analyses, it appears that seal presence in the Penobscot may be based more on regional trends in seal abundance and distribution rather than local prey biomass. Harbor seal numbers peak in the Penobscot when the population moves into the Gulf of Maine for their pupping season (Gilbert et al., 2005; Hayes et al., 2017), and gray seals tend to arrive in early summer, following peak counts in Cape Cod during their molting season (Pace et al., 2019). Furthermore, increasing gray seal abundance across the northeast U.S. (Hayes et al., 2017; Pace et al., 2019; Wood et al., 2020) are reflected in the trends we report in the Penobscot. If the regional stock of harbor seals is no longer increasing in abundance, and instead is exhibiting a slowed or potentially reversed growth rate, as suggested by the two most recent population surveys (Gilbert et al., 2005; Waring et al.,
2015), this trend is mirrored in the Penobscot as well. Despite this apparent dominance of a regional effect on pinniped abundance in the Penobscot River Estuary over the past decade, we believe continued monitoring of seal counts should remain a research priority, as pinnipeds may be slower to respond to restoration and conservation efforts than the fish species in this system.
CHAPTER 2

EXAMINING THE IMPACTS OF PINNIPEDS OF ATLANTIC SALMON: THE EFFECTS OF RIVER RESTORATION ON PREDATOR-PREY INTERACTIONS

Abstract

Seal populations in the Gulf of Maine have been recovering from historical bounty-driven declines since they received federal protection in 1972. As a result, seals in this area have become a source of conflict with fish conservation. In the Penobscot River in Maine, restoration efforts over the past decade have aimed at restoring diadromous fish runs, and seal predation on the endangered Atlantic Salmon (*Salmo salar*) has become a concern. Salmon demographic data, including the presence of seal-induced injury, have been collected from salmon passing upriver at the southernmost dams in the Penobscot River since 2012. A comparison of seal-induced injury rate with demographic data, river herring returns, estuary biomass estimates, and timing of peak estuary biomass revealed that the seal-induced injury rate declined in the Penobscot River from 2012 to 2019, correlated with increasing river herring returns. These findings suggest the importance of prey buffering in this system. The presence of multiple wounds on an individual salmon was significantly associated with the probability of a salmon having a seal-induced injury. Lamprey wounds and lacerations on salmon were commonly associated with seal-induced injury. This assessment of the risk seals pose to Atlantic Salmon illustrates how the diadromous species restoration activities in this system may alter predator-prey interactions and salmon conservation efforts. This insight could help inform future management decisions in systems where a healthier ecosystem could benefit both protected predators and endangered prey.
**Introduction**

Following severe population decline as a result of seal bounty programs in the 19th and 20th centuries (Lelli, Harris, & Aboueissa, 1962), pinniped recovery in the Gulf of Maine has been a source of controversy as these populations have continued to increase since the Marine Mammal Protection Act granted them protections in 1972 (Hayes et al., 2017; Roman et al., 2013). Successful pinniped conservation efforts have resulted in increasing numbers of harbor (Phoca vitulina) and gray (Halichoerus grypus) seals in coastal areas and the re-establishment of haul-out sites they have not occupied in decades (Gilbert et al., 2005; Pace et al., 2019; Waring et al., 2015). These protected marine mammals have gained attention, both positive and negative, as they continue to rebound. As marine predators, pinnipeds are often perceived as predators of and competitors for fish, resulting in frequent conflict with both commercial fisheries and fish conservation. These types of conflict are not limited to the Gulf of Maine; for example, the failed recovery of cod in Canada is often attributed to gray seals (Chouinard et al., 2005), and pinnipeds in Europe, Canada, and the west coast of the United States have been lethally removed in efforts to prevent fisheries interactions and predation (Harwood, 1984; Olsen et al., 2018; Schakner et al., 2017; Yodzis, 2001).

These conflicts are often assessed and addressed with a focus on a single predator species, overlooking the inherent complexity that typifies coastal ecosystems. For example, a previous study showed that an increasing harbor seal population in the Gulf of Maine from 1978 to 2010 was associated with higher seal-induced injury rates to Atlantic Salmon (Salmo salar) in the Penobscot River (Kusnierz et al., 2014). The same study showed that the risk of a salmon having a seal-induced injury was highest in the spring (Kusnierz et al., 2014), when seal counts in the Penobscot River estuary are also at their highest (Chapter 1). However, ecosystem-level
changes since 2013 warrant revisiting this issue to consider how river restoration efforts and increasing fish populations have affected these predator-prey interactions.

Major restoration efforts in this river help demonstrate why a multispecies approach is essential to successful conservation. Historically, more than 100 dams were constructed on the Penobscot River, contributing to the decline of diadromous fish populations and the closure of commercial fisheries, in addition to other economic and cultural impacts (Maine River Basin Report, 2007). In 1999, several organizations began the Penobscot River Restoration Project, with the goal of restoring ecosystem connectivity and function. As a result of this project, two dams were removed in 2012 and 2013, the first fish lift was installed in 2014 at the first dam most fish encounter as they move upriver, and a fish bypass was added to a second dam in 2016 (NRCM, 2019). The National Oceanic and Atmospheric Association’s (NOAA) Habitat Blueprint Initiative also designated the Penobscot River as a Habitat Area of Focus in 2014 (NOAA, 2016). Together, these river restoration projects aimed to restore diadromous fish populations and the riverine ecosystem.

Today, the Penobscot River is home to 11 species of diadromous fishes, which utilize both freshwater and saltwater habitats in their life cycles. Several of these species enter the Penobscot River each spring to spawn in upriver lakes and streams (Atkins & Foster, 1869; Maine Department of Inland Fisheries and Game, 1868; MDMR, 2018). The river is designated as critical habitat for the endangered Atlantic Salmon and is home to the largest, though severely depleted, Atlantic Salmon run in the United States (NOAA, 2016; Sigourney, Zydlewski, Hughes, & Cox, 2015). Significant time, effort, and resources from federal, state, and local agencies continue to support salmon conservation efforts in the Penobscot River. Current conservation efforts include the planting of eggs, and stocking of fry, parr, and smolt, increasing
habitat connectivity and improving fish passage and water quality. In part as a result of these recent efforts, Atlantic salmon returns in 2019 were the highest they have been since 2011 (MDMR, 2018, 2019).

Successful conservation efforts have also resulted in the documented increase in some populations of other diadromous fish that use the river and estuary as spawning habitat (Gardner et al., 2013; Stevens, 2019). Counts of fish passing through the river’s southernmost dam, provided by Maine’s Department of Marine Resources, show increases in blueback herring (Alosa aestivalis) and alewives (Alosa pseudoharengus), collectively referred to as river herring, returns since dam removal began in 2012 (MDMR, 2018). While dam removal appears to have contributed to these increases, annual alewife stocking efforts began in 2010 in order to help restore the population, and likely influenced subsequent river herring returns as well (MDMR & MDIFW, 2009). In the estuary, where juvenile and adult diadromous fish spend time and utilize resources, fish biomass has increased seasonally, as well as annually, since 2012 (Stevens, 2019). This increase in biomass is a result of both more areas of high density and increase in overall fish size that have appeared in the estuary post-restoration (Stevens, 2019).

As fish populations have responded to conservation activities in the Penobscot River, reports of seals in the Penobscot River Estuary have increased and observations of predation on diadromous fish, primarily Atlantic Salmon, have become more frequent (Kusnierz et al., 2014). Accordingly, concern has grown regarding the impacts these top predators may have on fish species of conservation concern in the river. Harbor and gray seals are both known to be opportunistic predators; their diets change throughout the year, based on what is locally abundant (Murie & Lavigne, 1992; Pierce et al., 1991). Seal diet can be characterized through gut or fecal DNA metabarcoding (Purcell, Mackey, LaHood, Huber, & Park, 2004), the identification of fish
otoliths and other hard parts in fecal samples (Bowen, 2000; Kopec, 2009), and stable isotope
(Hernandez et al., 2019; Lerner et al., 2018) or fatty acid analysis of vibrissae, lanugo, or tissue
samples (Tverin et al., 2019). When it is not possible to collect these types of samples, bite
analyses have been conducted to determine the impact seals have on target species and fisheries
(Kusnierz et al., 2014; Rafferty, Brazer Jr., & Reina, 2012; Sirak, 2015; Thompson & MacKay,
1999; Van Bleijswijk et al., 2014). Seal bites often present as ragged, rectangular or trapezoidal
wounds to the abdomen, with canine punctures typically present (Rafferty et al., 2012; Sirak,
2015). Seal-induced injury has also been described as paired, parallel scratches on the fish’s
body, likely caused by the seal’s canine teeth (Harmon, Thomas, McIntyre, & Paasch, 1994;
Thompson & MacKay, 1999).

In addition to the direct impacts of seals, the effects of river restoration, species
interactions, and prey buffering are all essential to understanding predator-prey interactions in
this system. It has been suggested that interspecific prey buffering by American shad (Alosa
sapidissima) and river herring could reduce the seal-induced injury rate on salmon in the
Penobscot (Kusnierz et al., 2014; Saunders et al., 2006). This idea of prey buffering, or predator
swamping, occurs when the sheer number of prey increases the chance that an individual will
survive. Interspecific prey buffering has been demonstrated with Atlantic salmon smolts
(Svenning et al., 2005), and has the potential to be more effective with generalist predators, such
as seals, that will switch prey based on abundance and the time it takes to locate, capture, and eat
prey (Werner & Hall, 1974). Other studies have shown that river restoration efforts have
significantly affected the ecology of the estuary (Stevens, 2019), and changes in fish assemblage
have also been documented as connectivity has increased in this system (Watson, Coghlan,
Zydelewski, Hayes, & Kiraly, 2018).
The Penobscot River in Maine provides us an opportunity to explore a widely reported conflict between pinnipeds and salmon. Our objectives were to: 1) evaluate the trend in seal-induced injuries to Atlantic Salmon during the period of river restoration activities between 2012 and 2019 as collected at the first dam on the river; 2) explore covariates affecting seal-induced injury rates including estuary fish biomass, river fish biomass, temperature, Salmon run timing, Salmon run duration, and relative abundance of seals; and 3) explore the effects of Atlantic Salmon demographics on seal-induced injury prevalence and location, including size, sex, sea-age, and comorbidity. This research provides an opportunity to assess the risks pinnipeds pose to Atlantic Salmon conservation. It will also allow us to understand how the recovery of this system may alter predator-prey interactions and salmon conservation efforts. This insight could inform future management decisions in systems where a healthier ecosystem could benefit both protected predators and endangered prey.

**Methods**

**Data Collection**

From 2012 to 2019, data were collected from Atlantic Salmon at the Veazie, Orono, and Milford dams on the Penobscot River between May and October of each year (Figure 2.1). When Atlantic Salmon arrived at the dams on their way upriver, they were counted and moved into a handling facility for assessment before continuing upriver or being transported to a hatchery. Salmon exhibit higher handling stress with increasing water temperature, so when river temperatures were above a critical threshold of 24 degrees Celsius, fish were passed directly out into the river without being handled. The Maine Department of Marine Resources (DMR) collected data from Atlantic Salmon at the Veazie dam in 2012 and 2013 and at the

Figure 2.1: Study area: Map of the southern-most dams in the Penobscot River. Salmon wound data were collected at the Veazie Dam in 2012-2013 and at the Milford and Orono Dams from 2014-2019. The dam locations are represented by the black box on the State of Maine map, while the blue box depicts the Penobscot River Estuary.
When fish were handled, data collected included date, fork length (length from the head to the notch in the caudal fin), sex, and a scale sample used to determine sea age (the number of winters spent at sea) and origin (hatchery or wild). Any injuries were also noted, including type and location. Sex was determined based on head shape. The majority of grilse in the Penobscot are male (Baum, 1997), so all grilse were assumed to be male unless they were later confirmed as female by hatchery staff. Scales and tissue samples, typically from adipose or caudal fins, for genetic analysis, were collected. When scales were not collected, sea age was estimated based on size of the fish (12.9% of handled fish), and origin was estimated based on fin condition and the known annual proportion of hatchery and wild fish (12.0% of handled fish) (J. Valliere, DMR, personal communication, September 9, 2019). Unhandled individuals were not included in our analyses.

Injury classifications included abrasion, bite without canine punctures, bruise, laceration, lamprey wound, scale loss, seal bite, and scar. Injuries were classified as putatively seal-induced when visible canine punctures (Figure 2.2a) or “golden arches” were observed. “Golden arches” refer to two parallel, curved scratch marks along the side of the fish’s body, presumably caused by the seal’s canine teeth (Figure 2.2b; Harmon, et al. 1994). While widely accepted as being seal-induced, it is important to note that neither mark is definitive evidence of a seal predation attempt and may be caused by other types of interaction, including predation attempts by other animals.
Figure 2.2: Common seal-induced injuries: a) A wound with visible canine punctures (circled in red) and b) “golden arches”: paired, parallel scratch marks, presumably caused by seal canine teeth. Photos courtesy of Mitch Simpson, Maine Department of Marine Resources.

Water temperature was collected for each day the salmon trap was operated. River herring counts were collected at the Veazie, Milford, and Orono dams and provided by the Maine DMR. Estuary fish biomass was calculated using hydroacoustic backscatter in Nautical Area Scattering Coefficient that were collected along a 50km trackline during estuary surveys between 2012 and 2019 (Stevens, 2019). These surveys were conducted weekly to biweekly, typically from April through October of each year (Lipsky et al., 2019). Spring fish biomass
estimates were measured during standard weeks 17 through 26, which encompass mid-April through late June.

**Golden Arch Replication**

An immature harbor seal skull from Maine’s zooarchaeology lab (provided by Sky Heller) with removable upper canines and disconnected mandibles was used to try to recreate “golden arches”, a marking commonly seen on salmon and attributed to seals. The canines were used as a size comparison in the creation of “false canines” out of crayons. The false canines were then inserted into the upper jaw. Since the crayons were straight, not curved, the angle of the teeth was inaccurate, but the spacing and length was similar to a real canine. A foam cone used to represent a fish was wrapped in paper. While the cone was moved from right to left to mimic a swimming fish, the skull was manipulated to imitate a biting motion from below. The cone also passed through the seal jaws while the jaws closed. Fifteen of these trials were conducted.

**Analysis**

Seal-induced injury rates, representing the proportion of handled Atlantic Salmon with a seal-induced injury, were calculated by dividing the number of Atlantic Salmon with a seal-induced injury by the number of total salmon handled for each month of the study. The trend in monthly injury rates across years were compared to annual injury rates, and the annual seal-induced injury rates were summarized by age class, sex, and hatchery versus wild origin.

Logistic regression was used to explore how detection of seal-induced injury varies throughout the year. We also evaluated the within-year effects of water temperature (first day and proportion of days exceeding 24°C) and timing of the salmon run (first day of the run and
proportion of the run counted by the first day exceeding 24°C) on the annual rate of seal-induced injury using Spearman’s correlation coefficient with a Holm-Bonferroni adjustment.

A comparison of monthly seal-induced injury rates allowed us to assess rates and trends over time during shorter time periods that reflect cooler temperatures and the start of the run (May), warming temperatures (June), and the arrival of temperatures that prohibit handling (July). A Kruskal-Wallis test was used to assess differences between the monthly bite rates, and a Dunn’s test was used to detect significant comparisons. A one-way analysis of covariance between seal bite rate and year was used to compare trends over time in the monthly and annual seal bite rates.

Spearman’s correlations with Holm-Bonferroni adjustments to correct for family-wise error rates were used to assess the relationships between annual seal-induced injury rates and the number of river herring counted each year, average estuary fish biomass for the year, average spring biomass in the estuary, and the timing of peak estuary biomass in spring.

We used a chi-square test to compare the location of seal bites to other injury types, which were categorized as head, caudal, dorsal, side, ventral, operculum, or fin. Similarly, we compared the frequencies of other wounds found on fish with seal-induced injuries to the overall frequency of injury types and we compared the average number of injuries per fish with seal bites to fish with other injury types.

Logistic regression was used to further explore any relationship between the likelihood of an individual salmon having a seal-induced injury and characteristics including fork length, origin, and presence of multiple wounds. Sea age and sex were not included due to a strong correlation with fork length. Year, average magnitude and timing of peak spring biomass, and the proportion of days with water temperatures over 24°C were included as predictor variables.
Total salmon counted was strongly correlated with year, and thus excluded from the model. Due to the strong correlation between year and river herring returns, we assessed two model sets with one accounting for year and one accounting for river herring returns. Top models in both sets were ranked using small-sample corrected Akaike’s Information Criterion (AICc) and a likelihood ratio test was used to determine the best model. The best model from each set were then compared using AICc.

**Results**

**Golden Arch Replication**

The results of our preliminary trial support the use of golden arches as an indicator of seal-induced injury. Multiple markings similar to golden arches were observed during the golden arch replication trials. Double curve lines were created in most trials when the jaws were closed around a moving “fish” (Figure 2.3a). A simulated lunging/biting action produced markings that resembled more of an “M” shape than parallel curves (Figure 2.3b). The skull used in this trial was from an immature harbor seal, and the distance between the canines was approximately 1.5cm. The distance between the canines of a gray seal skull in the lab was 5cm, indicating that the spacing between these markings when observed in the field can vary significantly based on age and species.
Figure 2.3: Golden arch replication trial results. a.) Simulation of jaws closing around a moving fish and b.) simulated lunging/biting action created by inserting crayons into the upper canine tooth sockets of a juvenile harbor seal skull. The jaw was manipulated to create biting motions while a cone moved right to left to imitate a swimming fish.

**Analysis**

During the study period from 2012 to 2019, 5,322 Atlantic Salmon were counted passing through the dams, and 4,861 (91.34%) salmon were handled. Of the handled fish, there were 4,524 documented injuries to 2,557 individuals (Table 2.1). Common injury types included
abrasion, scale loss, laceration, and lamprey wound, and 106 injuries found on 90 individuals were classified as seal-induced.

Table 2.1: Annual summaries of Penobscot Atlantic Salmon: Number of handled fish, handled fish with seal bites, and handled fish with injuries by year. The percentage of injured fish and percentage of fish with seal bites are calculated based on handled fish, not total fish counted.

<table>
<thead>
<tr>
<th>Year</th>
<th>Total Salmon Counted</th>
<th>Total Salmon Handled</th>
<th>Percentage of Salmon Handled</th>
<th>Injured Individuals (Handled)</th>
<th>Percentage of Handled Salmon that were Injured</th>
<th>Individuals with Seal Bite (Handled)</th>
<th>Percentage of Handled Salmon with Seal Bites</th>
</tr>
</thead>
<tbody>
<tr>
<td>2012</td>
<td>624</td>
<td>624</td>
<td>100.00</td>
<td>311</td>
<td>49.84</td>
<td>22</td>
<td>3.53</td>
</tr>
<tr>
<td>2013</td>
<td>382</td>
<td>372</td>
<td>97.91</td>
<td>123</td>
<td>33.07</td>
<td>8</td>
<td>2.15</td>
</tr>
<tr>
<td>2014</td>
<td>261</td>
<td>259</td>
<td>99.23</td>
<td>68</td>
<td>26.26</td>
<td>8</td>
<td>3.09</td>
</tr>
<tr>
<td>2015</td>
<td>731</td>
<td>709</td>
<td>96.99</td>
<td>255</td>
<td>35.97</td>
<td>16</td>
<td>2.26</td>
</tr>
<tr>
<td>2016</td>
<td>507</td>
<td>494</td>
<td>98.03</td>
<td>190</td>
<td>38.46</td>
<td>7</td>
<td>1.42</td>
</tr>
<tr>
<td>2017</td>
<td>849</td>
<td>772</td>
<td>91.17</td>
<td>445</td>
<td>57.64</td>
<td>14</td>
<td>1.81</td>
</tr>
<tr>
<td>2018</td>
<td>772</td>
<td>614</td>
<td>79.79</td>
<td>363</td>
<td>59.12</td>
<td>4</td>
<td>0.65</td>
</tr>
<tr>
<td>2019</td>
<td>1196</td>
<td>1017</td>
<td>85.03</td>
<td>802</td>
<td>78.86</td>
<td>11</td>
<td>1.08</td>
</tr>
<tr>
<td>Total</td>
<td>5322</td>
<td>4861</td>
<td>91.34</td>
<td>2557</td>
<td>52.60</td>
<td>90</td>
<td>1.85</td>
</tr>
</tbody>
</table>

The salmon run follows a seasonal pattern, with differences in peak movement between age classes but not sex (Figure 2.4). Most grilse in the Penobscot are male (Baum, 1997), so the breakdown by sex only includes multi-sea-winter fish. Sea age ($\chi^2=5.353$, df=2, p=0.069) does not appear to predispose individual fish to seal-induced injury, however significantly more two-sea-winter ($\chi^2=63.661$, df=2, p<0.01) fish were found injured than were present in the handled portion of the population (Table 2.2).

The frequency of seal-induced injuries also shows a seasonal trend, with the highest frequency observed early in the season (Figure 2.5). The probability of a salmon having a seal-induced injury is highest prior to standard day 150, which falls at the end of May (Figure 2.5). Between 2012 and 2019, water temperatures typically did not exceed the handling threshold of
24 degrees Celsius until early July, by which point approximately 85% of the run had passed through the dam.

Figure 2.4: Timing of the salmon run: Proportion of the total fish run by day of year, all years combined (2012-2019), broken down by sea age and sex. Most grilse in the Penobscot are males, so the difference in timing of the run based on sex only includes multi-sea-winter fish.
Figure 2.5: Probability of having a seal-induced injury: Logistic regression was used to assess the probability of a salmon having a seal-induced injury throughout the year. Day 150 falls on May 29-30 and day 200 falls on July 18-19.

Table 2.2: Atlantic Salmon demographics: Summary of individuals with seal-induced injury, all injury types, and overall salmon count by sex (male versus female), average length, origin (hatchery versus wild), sea age (1, 2, or 3 sea-winter), and the number of individuals with multiple wounds. Grilse are assumed to be male.

<table>
<thead>
<tr>
<th></th>
<th>Male</th>
<th>Female</th>
<th>Average Fork Length</th>
<th>Standard Error</th>
<th>Hatchery</th>
<th>Wild</th>
<th>1SW</th>
<th>2SW</th>
<th>3SW</th>
<th>Multiple Wounds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seal Bites (n=90)</td>
<td>47</td>
<td>43</td>
<td>70.367</td>
<td>0.904</td>
<td>84</td>
<td>6</td>
<td>16</td>
<td>72</td>
<td>2</td>
<td>59</td>
</tr>
<tr>
<td>All Injuries (n=2557)</td>
<td>1257</td>
<td>1300</td>
<td>70.604</td>
<td>0.160</td>
<td>2249</td>
<td>308</td>
<td>428</td>
<td>2110</td>
<td>19</td>
<td>1264</td>
</tr>
<tr>
<td>Total Fish (n=4861)</td>
<td>2602</td>
<td>2259</td>
<td>69.431</td>
<td>0.129</td>
<td>4290</td>
<td>571</td>
<td>1138</td>
<td>3692</td>
<td>31</td>
<td>1264</td>
</tr>
</tbody>
</table>
The within-year effects of temperature on handling and timing of the run likely vary between years (Jensen, Heggberget, & Johnsen, 1986), possibly affecting our ability to compare seal bite rates across years. The proportion of days each year where the temperature exceeds 24°C are significantly different from each other (8 sample test for equality of proportions, \(\chi^2=90.632, \text{df}=7, p<0.01\)). While not statistically significant, it appears that warmer years are associated with a larger proportion of the run passing through the dam before the temperature threshold is reached and the subsequent closure of the handling facility (Tables 2.3, 2.4). This is supported by a strong relationship between the proportion of fish handled and the proportion of days warmer than 24°C. We also saw a tendency for more fish to be handled in years with an earlier arrival of warm temperatures. The start of the salmon run also exhibited a moderate positive relationship with the arrival of warmer temperatures.

Table 2.3: Within-year effects: Exploring effects of temperature and timing of the salmon run, 2012-2019.

<table>
<thead>
<tr>
<th>Year</th>
<th>Proportion of Salmon that were Handled</th>
<th>Proportion of Days Warmer than 24°C</th>
<th>Day of 1st Fish</th>
<th>1st Day of the Season Warmer than 24°C</th>
<th>Proportion of Run Passed at 1st day &gt;24°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>2012</td>
<td>1.000</td>
<td>0.333</td>
<td>May 2</td>
<td>July 7</td>
<td>0.962</td>
</tr>
<tr>
<td>2013</td>
<td>0.979</td>
<td>0.085</td>
<td>May 2</td>
<td>July 6</td>
<td>0.932</td>
</tr>
<tr>
<td>2014</td>
<td>0.992</td>
<td>0.173</td>
<td>May 19</td>
<td>July 2</td>
<td>0.759</td>
</tr>
<tr>
<td>2015</td>
<td>0.970</td>
<td>0.202</td>
<td>May 6</td>
<td>July 8</td>
<td>0.927</td>
</tr>
<tr>
<td>2016</td>
<td>0.980</td>
<td>0.171</td>
<td>May 19</td>
<td>June 26</td>
<td>0.769</td>
</tr>
<tr>
<td>2017</td>
<td>0.912</td>
<td>0.059</td>
<td>May 17</td>
<td>July 10</td>
<td>0.905</td>
</tr>
<tr>
<td>2018</td>
<td>0.798</td>
<td>0.048</td>
<td>May 10</td>
<td>July 2</td>
<td>0.763</td>
</tr>
<tr>
<td>2019</td>
<td>0.850</td>
<td>0.129</td>
<td>May 15</td>
<td>July 11</td>
<td>0.885</td>
</tr>
</tbody>
</table>
Table 2.4: Within-Year Correlations: Exploring effects of temperature and timing of the salmon run, 2012-2019: Spearman’s Correlation Coefficient, significant at \( p<0.05 \) in bold. None of the correlations were still significant with Holm-Bonferroni adjustment.

<table>
<thead>
<tr>
<th></th>
<th>Proportion Handled</th>
<th>Proportion of Run Passed at 1st day &gt;24°C</th>
<th>Day of 1st Fish</th>
<th>1st Day of Water Temp &gt;24°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Proportion of Days with Water Temps &gt;24°C</td>
<td><strong>0.762</strong></td>
<td>0.333</td>
<td>-0.095</td>
<td>0.024</td>
</tr>
<tr>
<td>1st Day of Water Temp &gt;24°C</td>
<td>-0.313</td>
<td>0.494</td>
<td>0.313</td>
<td>-</td>
</tr>
<tr>
<td>Day of 1st Fish</td>
<td>0</td>
<td><strong>-0.762</strong></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Proportion of Run Passed at 1st day &gt;24°C</td>
<td>0.262</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

We compared the annual seal bite rates to similarly calculated monthly seal bite rates that were also calculated for each year (Figure 2.6). The monthly rates were designed to capture smaller temperature windows and help reduce within-year variation in ability to detect seal-induced injury. May (standard day: 121-151) is characterized by cooler temperatures and the start of the run; the first salmon were detected between standard day 122 to 140 during our study period. June (standard day: 152-181) experiences warming temperatures, though water temperatures over 24°C typically do not occur until July (standard day: 182-212); the first days with water temperatures over 24°C occurred on day 178 through 192 during our study period. We observed a significant difference in seal bite rates between months (Kruskal-Wallis \( \chi^2=9.624, \text{df}=2, p<0.01 \)), with the highest bite rates observed in May (0.054±0.037) and the lowest bite rates observed in July (0.015±0.021). A one-way analysis of covariance revealed that despite the
There was no significant difference between the means of these groups, there was no significant difference between the slope of the monthly or annual linear regression lines ($F(1,28)=0.034, p=0.856$). We did not see a significant difference in the rate of change over time, so annual seal bite rates were used for the remainder of our analyses to represent this decreasing trend.

![Graph of seal-induced injury rates](image)

Figure 2.6: Seal-induced injury rates: Seal bite rate calculated based on number of fish handled by month and by year. All seal bite rates appear to have declined between 2012 and 2019. A one-way ANCOVA determined that the slopes ($F(1,28)=0.034, p=0.856$) of all four regression lines are not significantly different from each other.

We found that seal bite rate declined between 2012 and 2019 ($\text{Spearman’s rho} = -0.881, p<0.01$, Figure 2.7). River herring returns increased during this time period, and had a
significant negative correlation with seal-induced injury rate (Spearman’s rho = -0.905, p<0.01, Figure 2.7). The magnitude of spring fish biomass in the estuary, as well as the timing of peak spring biomass, were not significantly related to seal-induced injury rate, but also exhibited a moderate negative relationship (Figure 2.7; Table 2.5).
Figure 2.7: Covariate effects on seal-induced injury rate: River herring returns have significantly increased between 2012 and 2019 ($F(1,6)=77.72$, $p<0.001$). Seal-induced injury rate significantly declines between 2012 and 2019 ($F(1,6)=19.88$, $p<0.01$, $R^2=0.768$). Counts of returning river herring at the Veazie (2012-2013) and Milford and Orono (2014-2019) dams has a significant negative relationship with seal-induced injury rate ($F(1,6)=27.49$, $p<0.01$, $R^2=0.821$). Week of peak spring biomass ($F(1,6)=0.078$, $p=0.789$, $R^2=0.013$) and magnitude of
spring biomass (F(1, 6)=0.414, p=0.544, R²=0.065) did not have a significant linear relationship with seal-induced injury rate.

Table 2.5: Covariate Correlations: Seal-Induced Injury Rate Comparisons 2012-2019:
Spearman’s Correlation Coefficient, significant at p<0.05 in bold, still significant with Holm-Bonferroni adjustment has an asterisk.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Seal-Induced Injury Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>-0.881</td>
</tr>
<tr>
<td>River Herring Counts</td>
<td>-0.905*</td>
</tr>
<tr>
<td>Annual Average Fish Biomass in Estuary</td>
<td>-0.357</td>
</tr>
<tr>
<td>Average Spring Fish Biomass in Estuary</td>
<td>-0.381</td>
</tr>
<tr>
<td>Week of Peak Spring Biomass in Estuary</td>
<td>-0.325</td>
</tr>
<tr>
<td>Total Fish Counted</td>
<td>-0.571</td>
</tr>
<tr>
<td>Proportion of Days Trap was Open &gt;24°C</td>
<td>0.786</td>
</tr>
<tr>
<td>First Day of Water Temperature &gt;24°C</td>
<td>0.048</td>
</tr>
<tr>
<td>Day of First Fish</td>
<td>-0.286</td>
</tr>
<tr>
<td>Proportion of Run Passed at 1st day &gt;24°C</td>
<td>0.452</td>
</tr>
</tbody>
</table>

In our assessment of factors contributing to the probability of a salmon having a seal-induced injury, we assessed two model sets with one accounting for year and one accounting for river herring returns. We found 11 models within 2 ΔAICc of our top model when year was included (Table 2.6), and 6 models within 2 ΔAICc of our top model when river herring counts were included instead of year. In both model sets, all predictor variables were present in at least one of the models, suggesting that all factors contribute to the likelihood of a salmon having a seal-induced injury (Figure 2.8), however, the fit of the models appears to be primarily driven by the presence of multiple wounds and year or river herring counts. Likelihood ratio tests between the top model and most parsimonious model within 2 ΔAICc of the top model for the model set containing year (χ²(2)=5.451, p=0.066) and the model set containing river herring counts.
(χ²(1)=2.859, p=0.091) supported the simpler models in both cases. An AICc comparison between models revealed that probability of a salmon having a seal bite (p) is best predicted by:

\[
\log \frac{p(x)}{1-p(x)} = \beta_0 + \beta_1(\text{Presence of Multiple Wounds}) + \beta_2(\text{River Herring Returns}) \quad (\text{Equation 2.1})
\]

Presence of a seal-induced injury is significantly more likely when multiple wounds are present on a fish and the probability of seal-induced injuries significantly decreases as river herring returns increase (Table 2.7).

Table 2.6: Probability of seal-induced injury: Top models: Top models within 2ΔAICc of top model for two model sets: one contains year as a predictor variable and the other contains river herring counts. These variables were not included in the same model due to high correlation between the two. Predictor variable 1=Week of peak spring biomass, 2=Fork Length, 3=Presence of Multiple Wounds, 4=Origin (hatchery or wild), 5=Proportion of days over 24°C, 6= Average Spring Biomass, 7=Year, 8=River Herring Returns

<table>
<thead>
<tr>
<th>Predictor Variables</th>
<th>df</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>Predictor Variables</th>
<th>df</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>3,4,6,7</td>
<td>5</td>
<td>794.47</td>
<td>0</td>
<td>3,4,8</td>
<td>4</td>
<td>790.69</td>
<td>0</td>
</tr>
<tr>
<td>3,4,7</td>
<td>4</td>
<td>794.95</td>
<td>0.47</td>
<td>3,8</td>
<td>3</td>
<td>791.54</td>
<td>0.86</td>
</tr>
<tr>
<td>1,3,4,7</td>
<td>5</td>
<td>795.08</td>
<td>0.61</td>
<td>3,4,6,8</td>
<td>5</td>
<td>792.00</td>
<td>1.32</td>
</tr>
<tr>
<td>3,6,7</td>
<td>4</td>
<td>795.29</td>
<td>0.82</td>
<td>2,3,4,8</td>
<td>5</td>
<td>792.11</td>
<td>1.43</td>
</tr>
<tr>
<td>2,3,4,6,7</td>
<td>6</td>
<td>795.56</td>
<td>1.09</td>
<td>1,3,4,8</td>
<td>5</td>
<td>792.46</td>
<td>1.78</td>
</tr>
<tr>
<td>3,7</td>
<td>3</td>
<td>795.92</td>
<td>1.44</td>
<td>3,4,5,8</td>
<td>5</td>
<td>792.69</td>
<td>2.00</td>
</tr>
<tr>
<td>1,3,7</td>
<td>4</td>
<td>795.98</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1,3,4,6,7</td>
<td>6</td>
<td>795.99</td>
<td>1.52</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3,4,5,6,7</td>
<td>6</td>
<td>796.07</td>
<td>1.59</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
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<td>2,3,6,7</td>
<td>5</td>
<td>796.31</td>
<td>1.84</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2,3,4,7</td>
<td>5</td>
<td>796.40</td>
<td>1.93</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.8: Predictor variable effects on probability of seal-induced injury: Graphical representation of how each predictor variable affects the probability that a salmon will have a seal-induced injury when the other predictors are held constant. The shaded area represents 95% confidence intervals.
confidence intervals and the black bars along the x-axis represent the values present in the data.

**Effects plot for combined river herring returns is from the model that did not include a variable for year.**

Table 2.7: Top model parameters: The presence of multiple wound and river herring returns are significant predictors of seal-induced injury. Model coefficients from Equation 2.1 are presented. McFadden’s $R^2=0.124$

|                     | Estimate     | Standard Error | z-value | Pr(>|z|) |
|---------------------|--------------|----------------|---------|----------|
| (Intercept)         | -4.061       | 0.194          | -20.979 | <2e-16   |
| Multiple Wounds     | 2.204        | 0.235          | 9.389   | <2e-16   |
| (Present)           |              |                |         |          |
| River Herring       | -8.866e-07   | 1.322e-07      | -6.707  | 1.98e-11 |
|                     |              |                |         |          |

Of the 90 fish with seal-induced injuries, 59 (65.6%) fish had multiple wounds and 14 (15.6%) fish had multiple seal-induced injuries. Out of all 4861 handled salmon, only 1264 (26.0%) had multiple wounds present. The average number of wounds per fish with seal bites (1.978±1.131, n=90) was not significantly higher than the average number of wounds per fish with other injury types (1.753±0.958, n=2466; two sample t-test, t=1.86, df=93.711, p=0.066). Out of 106 seal-induced injuries, 46 (43.4%) occurred on the ventral part of the fish (Figure 2.9). During this study period, only two ventral bite wounds were not attributed to a seal. The locations of seal bites were not representative of the location of injury in general ($\chi^2=341.28$, df=7, $p<0.01$), with ventral wounds being more commonly associated with seal bites and head wounds more common among other wound types.
Figure 2.9: Wound location comparison: Locations of seal bites (left, n=106) compared to locations of all wounds (right, n=4524) are significantly different from each other ($\chi^2=341.28$, df=7, p<0.01). Seal-induced injuries are most commonly found on the ventral part of the fish and were not found on the head in this study.

Common types of other wounds documented on salmon include abrasions, scale loss, lacerations, and lamprey wounds. Salmon with seal-induced injuries have lacerations, lamprey wounds, and scars more frequently than those injuries are found in general, while scale loss and
abrasions are less frequently found in salmon with seal-induced injury ($\chi^2=30.734$, df=7, p<0.01; Figure 2.10).

![Figure 2.10: Wound Type Comparison: Other Wounds on Salmon with Seal Bites (left, n=73) and wounds on all handled salmon (right, n=4524). The frequencies of injury types associated with seal bites are significantly different from the frequencies of those injury types found in the overall population ($\chi^2=30.734$, df=7, p<0.01).](image)

Discussion

This study aimed to assess the risks seals pose to Atlantic Salmon in the Penobscot River by analyzing the seal-induced injury rate to salmon handled at the dams between 2012 and 2019. By analyzing temporal trends in this rate, we were able to examine the potential effects of local restoration efforts on predator-prey interactions. When considering how to best support Atlantic
Salmon conservation in the presence of protected predators, it is important to consider other species in the ecosystem.

Seal-induced injury rates to Atlantic Salmon were previously found to have a significant positive correlation with aerial counts of harbor seals along the coast of Maine and in Penobscot Bay (Kusnierz et al., 2014). The most recent regional harbor seal abundance estimates are from 2012, and suggest that while harbor seals in the Gulf of Maine were increasing until 2001, their growth rate has either slowed or reversed since (Waring et al., 2015). Gray seals, however, are continuing to increase throughout the Gulf of Maine (Gilbert et al., 2005; Pace et al., 2019). A study in the Penobscot River Estuary revealed no significant trends in the number of seals using the haul-out sites in the estuary between 2012 and 2020, but did detect an increasing number of gray seals moving into the area (Chapter 1). The proportion of counted seals in the water also increased during this time period, suggesting that seals from nearby haul-outs elsewhere in Penobscot Bay could be coming into the estuary to forage (Chapter 1).

Despite this potential influx of foraging and larger gray seals in the estuary, the seal-induced injury rate to Atlantic Salmon declined from 2012 to 2019. According to our study, river herring returns, which have increased in recent years following restoration efforts that included alewife stocking and dam removal (Scherelis et al., 2020), rather than local presence of seals, appear to have the most influence over seal-induced injury rate to Atlantic Salmon. Most salmon pass through the southernmost dams in the Penobscot between May and June, which corresponds with peak times for the river herring and American shad runs (Bruchs et al., 2018). In our analysis, river herring returns, as well as the magnitude and timing of peak spring biomass in the estuary, all exhibited a negative relationship with seal-induced injury rate to Atlantic Salmon. These findings suggest, as others have previously (Kusnierz et al., 2014; Saunders et
al., 2006), that prey buffering from increasing forage fish may provide protection to salmon against seal predation. River herring returns exhibited the strongest and only significant relationship with seal-induced injury, which is consistent with their earlier run time and our observation of a higher probability of seal-induced injuries to salmon early in the season. However, since fish utilize resources in the estuary, and do not just pass through during migration, increasing fish biomass in the estuary may also result in prey buffering outside of peak run times (Stevens, 2019).

It is possible that foraging preferences of seals, not just the increasing number of river herring, also contribute to the declining seal-induced injury rate. Until river herring returns began to increase, it is possible that the lack of available prey in the river resulted in seals targeting salmon more frequently (MDMR, 2018; MDMR, unpublished data). Optimal foraging theory predicts that at low prey densities, prey will be eaten as they are encountered, despite size (Werner & Hall, 1974). As smaller diadromous fish began to increase in the river, there was more opportunity for seals to target fish in their preferred size range of 10 to 35 centimeters (Kopec, 2009) rather than salmon, which ranged from 44 to 94 centimeters in our dataset. Optimal foraging theory also predicts that generalist predators will switch prey based on the costs of foraging, so more abundant, smaller prey that reduce search time and handling time are again more likely to be targeted (Werner & Hall, 1974).

Prey switching in generalist predators is often studied as a function of prey abundance, but it is also worth considering shifts in energy demands for predators. Higher rates of seal-induced injury to salmon were observed in the spring, which overlaps with harbor seal pupping season in May and June. Pregnancy and lactation are energetically costly, and as a smaller seal species, harbor seals must forage during lactation to support lactation and their own metabolism.
(Boness, Bowen, & Oftedall, 1994; Bowen, Iverson, Boness, & Oftedal, 2001; Schwarz et al., 2018). While they may preferentially target higher fat content prey items during this energetically demanding period, prior research reports approximately equal lipid content between river herring (Crawford, Cusack, & Parlee, 1986) and salmon (Hamilton et al., 2005), which does not support that high seal-induced injury rates in the spring are the result of selection by pregnant and lactating females.

Historically, smaller diadromous fish in the Penobscot served as alternative food sources for piscine, avian, and mammalian predators, creating a prey buffering effect for salmon at all life stages (Hall, Jordaan, & Frisk, 2011; Saunders et al., 2006). They were sources of prey for both adult and juvenile salmon and played a key role in enriching freshwater and terrestrial food webs with marine nutrients (Durbin, Nixon, & Oviatt, 1979; Hall et al., 2011; Saunders et al., 2006; Schindler et al., 2003). The construction of dams and subsequent decline of diadromous fish not only left the remaining salmon unprotected, but affected the connectivity, species richness and diversity, nutrient flow, and productivity of the entire ecosystem (Flecker et al., 2010; Gardner et al., 2013; Hall et al., 2011; Trinko Lake, Ravana, & Saunders, 2012). River herring returns in 2019 were lower than those in 2018, suggesting they may be plateauing at a new normal in this system (MDMR, 2019). Yet, while alewives are quick to respond to restoration efforts, responses of fish and predators with longer life cycles will take more time (Hall et al., 2011; Lichter et al., 2006; Stevens, 2019; Watson et al., 2018). If alewives have reached a new carrying capacity in this altered system, it remains to be seen whether the seal-induced injury rate will also stabilize, or if further habitat restoration and fish passage improvements, as well as the continued recovery of other species, will continue to drive the rate even lower.
There are several caveats to consider in our interpretation of seal-induced injury rates. Multiple confounding effects, including water temperature, observer variability, and the number of fish processed each day, may affect the detection rate of seal-induced injuries. As river temperatures increase above 21°C, salmon generally become less cooperative and more easily stressed, and stress levels must be balanced with the time spent processing the fish and collecting data (J. Valliere, DMR, personal communication, August 21, 2019). Water temperature can also affect the rate at which wounds heal (Anderson & Roberts, 1975; Kusnierz et al., 2014), and if wounds heal faster in warm water, it is possible that salmon are more likely to survive failed predation attempts and make it to the dam at higher water temperatures. Bite rates in warmer years may therefore be underestimated as a result of handling limitations, however, bite rates in cooler years are potentially also higher than our calculated values, as a smaller proportion of the run were handled during these cooler seasons. Our assessment of within-year effects of river temperatures revealed that the proportion of days over 24°C was not equal between years, but we observed no significant relationship between the seal-induced injury rate and the proportion of days over 24°C.

Despite these caveats in how we interpret our results, the consistency in the salmon assessment protocol throughout the study period provides a long-term dataset that we can use to study change over time in a system with targeted recovery efforts. Determining that an injury is seal-induced is subjective; our study defined a seal-induced injury as “golden arches” or a large wound with canine punctures in it (Figure 2.2), however a similar study in the Penobscot between 2006 and 2010 used an expanded wound assessment protocol and also included multiple parallel scratches, deep wounds and gashes, and an unidentifiable category in their calculation of seal-induced injury rate (Kusnierz et al., 2014). These differences in definition prevent us from
being able to directly compare absolute estimates of seal-induced injury rates between the study periods. However, given the consistency of methods within time periods, we can compare trends in injury rate over time, recognizing that the trend seen in 2006 to 2010 may have been driven by a wound type not included in our study. Kusnierz et al. (2014) reported an increase in seal-induced injury rates between 2006 and 2010, while we found a decrease over time between 2012 and 2019 (Figure 2.11). The timing of this change in trends coincides with increased stocking of alewives and the Penobscot River Restoration Project, supporting our hypothesis that restoration efforts affected predator-prey interactions in this system.

Figure 2.11: Multi-study seal-induced injury comparison: Trends in seal-induced injury rates are significantly different between 2006-2010 and 2012-2019 (one-way ANOVA, F(1,6)=7.564, p<0.05). Seal-induced injury rates increased between 2006 and 2010 (F(1,3)=2.491, p=0.213, R²=0.454, Kusnierz et al. 2014), and decreased significantly during our study period from 2012 to 2019 (F(1,6)=22.61, p<0.01, R²=0.790).
In addition to differences in trends, we also observed a difference in the importance of salmon sea age for seal-induced injury between this and other studies. This may indicate a change in how seals are targeting salmon. In previous studies, sea age was a significant predictor of seal-induced injury in salmon, with larger, two-sea-winter salmon being more susceptible to seal-induced injury (Fryer, 2011; Kusnierz et al., 2014; Naughton et al., 2011). Since almost 100% of the females in our study were two-sea-winter fish, and only 60% of the males were two-sea-winter fish (Table 2.2), age or size-based selection of prey may result in females being disproportionately affected. Surprisingly, fork length, and therefore sea age, were not significant predictors of seal-induced injury in our study. Seals have been shown to select for a preferred age class of their primary prey (Kopec, 2009), but this was not the case here. Perhaps this seemingly random selection of salmon means that seals are not specifically targeting older salmon and are instead targeting individuals opportunistically.

The presence of multiple wounds was a significant predictor of the probability that a salmon would have a seal-induced injury, however, it is important to note that there is no way of knowing if the seal-induced injury preceded or occurred subsequent to the additional injuries. In our analysis of wound type, salmon with seal bites had scars, lacerations, and lamprey wounds more often than these wounds were found in the general population. Based on these findings, it is possible that salmon weakened by lamprey parasitism or by more serious injuries like lacerations, compared to an abrasion, bruise, or scale loss, may be more easily targeted by seals. This possibility is supported by optimal foraging theory, which predicts that prey selection is dependent on handling time (Werner & Hall, 1974), so a weak animal that is easier to catch could become a target. It is also possible that salmon spending more time in the river are more susceptible to both seal-induced injury as well as other wound types. Wound types such as
bruises and scrapes likely do not happen in the open ocean, and studies have shown that fish experience significant delays at the southernmost dam in the river (Izzo, Maynard, & Zydlewski, 2016). Delays in passage not only result in increased mortality and risk of predation, but can result in more difficult passage at dams further upriver, decreased energy reserves, and reduced spawning success (Geist, Abernethy, Blanton, & Cullinan, 2000; Gorsky, 2005; Izzo et al., 2016; Stansell, 2004).

Thoughtful interpretation of these data and data from similar studies is important, especially when considering management recommendations. A seal telemetry study would be helpful in confirming the foraging areas of seals that haul-out both in the Penobscot River and estuary and in nearby locations elsewhere in Penobscot Bay. If seals are foraging in the estuary, future diet studies could help determine how failed predation attempts compare to the number of salmon that seals are actually eating, and could also help determine the importance of prey buffering in this system by revealing whether river herring are an important prey item for seals in this area. Observing trends in the number of seals spending time at the dam, and likely taking advantage of an attractive and easily accessible food source, could provide further insight as to the level of risk seals pose to Atlantic Salmon in the Penobscot. Without a diet study, we cannot know how failed predation relates to actual predation, but based on our study, prey buffering seems to provide protection to Atlantic Salmon against predation by seals. To mitigate risks of pinniped predation on Atlantic Salmon in the Penobscot River, we therefore argue that efforts may be best spent focused on overall ecosystem health and restoration, as improved water quality, increased access to historic habitat, and increasing fish populations are already proving to have significant benefits to multiple species that use the river.
CHAPTER 3
ASSESSING PHOTO-IDENTIFICATION AS A TOOL TO STUDY PENOBSCOT RIVER PINNIPEDS

Abstract

After protections were granted through the Marine Mammal Protection Act in 1972, harbor (*Phoca vitulina*) and gray seals (*Halichoerus grypus*) in the northeast U.S. have been rebounding. Increasing numbers of seals have become a recent concern in the Penobscot River Estuary in Maine, as numerous diadromous fish species of conservation concern are also found in the river. Traditionally, photo-identification has been used as a method of studying pinniped abundance, site fidelity, survival, and large-scale movement. To assess potential applications of this tool in the Penobscot, photographs were taken of individual seals at three major haul-outs in the estuary between 2019 and 2020. Overall, 27 harbor seals and 88 gray seals were identified. There were 62 harbor seal resighting events and 29 gray seal resighting events. The majority of harbor seal resighting events occurred at Buck’s Ledge and the majority of gray seal resighting events occurred at Fort Point Ledge. Only two individual gray seals were observed at multiple haul-outs. In addition, photos were used to validate observer counts in the field, showing that observers regularly underestimate the total number of seals present and that seal species identification from a distance is not always reliable. Continued photo-identification efforts in the estuary could allow for eventual abundance estimates of gray seals using the estuary and would allow for ongoing assessment of pinniped health in this area. Comparison to other photo-identification catalogs in the region would also allow widespread tracking of individuals over time, a better understanding of how these animals utilize regional sites throughout the year, and an improved understanding of the role pinnipeds play in marine and coastal ecosystems.
Introduction

Seal bounties during the 19\textsuperscript{th} and 20\textsuperscript{th} centuries resulted in severely depleted seal populations throughout the Gulf of Maine (Lelli, Harris, & Aboueissa, 2009). Both harbor seals \textit{(Phoca vitulina)} and gray seals \textit{(Halichoerus grypus)} have been making a comeback in the northeast United States (U.S.) since the U.S. Marine Mammal Protection Act was passed in 1972 (Roman et al., 2013). Harbor seals in this area increased until 2001, after which their population growth rate has slowed or reversed (Gilbert et al., 2005; Waring et al., 2015), while the gray seal population continues to increase (Pace et al., 2019).

Seals in the Penobscot River Estuary in Maine have become a recent research interest and potential concern. Some diadromous fish populations in the river have been increasing in recent years (Gardner et al., 2013; Stevens, 2019), but anecdotal reports of seals in the river, preying upon fish species of conservation concern, have also increased during this time. The Penobscot River is designated critical habitat for the endangered Atlantic Salmon \textit{(Salmo salar)} (NOAA, 2009). The lower estuary is designated critical habitat for threatened Atlantic sturgeon \textit{(Acipenser oxyrhynchus oxyrhynchus)} (NOAA, 2017) and there are potential spawning grounds for endangered shortnose sturgeon \textit{(Acipenser brevirostrum)} in the lower river (M. E. Altenritter et al., 2017). The Penobscot River has been the target of significant river restoration and diadromous fish conservation efforts throughout the past decade (NOAA, 2016; NRCM, 2019). Atlantic Salmon in the Penobscot River are regularly observed with injuries that have been attributed to seals (Kusnierz, Trial, Cox, & Saunders, 2014, Chapter 2), and operculum damage in Atlantic sturgeon and shortnose sturgeon has also been attributed to seals (C. Ames, personal communication, February 15, 2019). Gray seal predation of a shortnose sturgeon was also witnessed in the Penobscot River in 2006 (Fernandes, 2008).
Since 2012, bird and mammal sightings were documented using binoculars from predetermined tracklines during hydroacoustic surveys of the Penobscot River Estuary (Lipsky et al., 2019; Stevens, 2019, Chapter 1). These vessel surveys recorded seal counts on three of the four major seal haul-outs in the estuary and have not documented significant changes in the number of seals hauling out in the estuary between 2012 and 2020 (Chapter 1). The potential increase in gray seals using the estuary was recently revealed in a targeted seal assessment (Chapter 1).

Typically, seal abundance is assessed by aerial survey during pupping season and utilizes mark-recapture techniques on satellite-tagged animals to calculate the percentage of the population that is available onshore for counting (Gilbert et al., 2005; Waring et al., 2015; Yochem et al., 1987). Photo-identification has been used in pinnipeds and other species as a non-invasive and cheaper method of mark-recapture. By resighting identifiable individuals over time and determining how many identifiable animals are available for observation at a given time, mark-recapture analyses using photo-identification data have been used to calculate pinniped abundance (Cordes & Thompson, 2015; Hiby et al., 2007). In addition, mark-recapture models based on photo-identification have been used to estimate pinniped survival between years, in general as well as by age class and by sex (Hastings, Small, & Pendleton, 2012; Hiby et al., 2007; Mackey, Durban, Middlemas, & Thompson, 2008). These types of studies can also help monitor rates of entanglement in fishing gear and subsequent mortality (Allen, Jarvis, Sayer, & Mills, 2012).

Pinniped behavior and habitat use can also be studied using photo-identification. Pinniped photo-identification studies have demonstrated high rates of individual site fidelity to haul-out sites (Cordes & Thompson, 2015) and have also revealed patterns in reproduction, birth
rates, and lactation duration (Cordes & Thompson, 2015). One study in northeast Scotland used photo-identification to explore seasonal trends in harbor seal abundance. This approach helped determine that harbor seals hauled out more frequently during the breeding season, but that the same number of animals were present and utilizing resources in that area throughout the year (Cordes & Thompson, 2015). Photo-identification, in combination with flipper tags, has also been used as a conservation tool in endangered Hawaiian monk seals, allowing long-term monitoring of survival, reproductive rate, and inter-island movement at the individual level (Antonelis, Baker, Johanos, Braun, & Harting, 2006). In addition to local monitoring and movement, photo-identification can also help us learn about movements at a larger scale. Gray seal movement at a regional scale was described in a photo-identification study in Europe, and the connectivity of widespread haul-out sites that was revealed in this study later informed the conservation and management of this species (Sayer et al., 2019).

While photo-identification can be a useful research technique, it is also subject to numerous limitations. Photo-identification techniques in gray seals and harbor seals rely on natural markings, scars, and the stability of pelage patterns over time. In gray seals, pelage patterns darken with age (Vincent, Meynier, & Ridoux, 2001). Gray seals are sexually dimorphic, so this darkening enhances female pelage pattern, while obscuring the pelage pattern in males, resulting in easier identification of females.

Successfully resighting an individual relies on photographing the same body part twice. This may not be possible, based on how an animal is positioned on a haul-out, and failure to recognize an identifiable individual can falsely inflate the number of animals in a photo-identification catalog. To avoid false inflation of identifiable individuals, some studies focus primarily on left or right head patterns (Cordes & Thompson, 2015; Hiby et al., 2007; Mackey et
al., 2008). Similarly, matching pelage patterns is subject to human error, resulting in both false positives and negatives in individual sighting histories. To minimize human error and processing time, many studies utilize artificial intelligence software to identify potential matches, which are later confirmed by eye (Beaumont & Goold, 2007; Hastings et al., 2012; Hiby et al., 2007; Paterson et al., 2013).

This research aims to assess the feasibility of using photo-identification in the Penobscot River Estuary to study patterns of individual distribution, site fidelity, and seasonal use of gray and harbor seals. These efforts aim to facilitate tracking of individuals throughout the year and to provide a better understanding of how seals are using and moving between sites in the river and elsewhere in the Gulf of Maine. Photo-identification efforts were conducted from vessel and land-based platforms. Collecting photos can also help inform other ongoing seal research efforts, such as hydroacoustic transect surveys, through validation and calibration of naked eye observer counts in the field. Since photo-identification work includes data collection on aspects of seal health including body condition, age class, entanglements, wounds, and scars, successful photo-identification in the Penobscot could also reveal local trends in pinniped health and human interaction.

**Methods**

Photo-identification efforts began in May 2019. Using a Canon 7D Mark I camera and a 100-400mm Canon lens, and operating under NOAA’s Letter of Authorization Document #2016-22582, identifying photos were taken of individual seals observed during vessel-based hydroacoustic transect surveys of the Penobscot River Estuary from May through October of 2019 and 2020 (Figure 1). Any visible pelage pattern on a gray seal was photographed, while ventral views of harbor seals were prioritized, as ventral pelage patterns tend to be more
pronounced and easier for a human eye to detect (Small et al., 2001). Data collected on photographed individuals included sex, age, body condition (thin, emaciated, or robust), and presence of wounds (e.g. shark bites), scars, or entanglements. Sex was determined using ventral photos of harbor seals and by pelage pattern coloration in gray seals. Relative age was determined based on the relative size of each individual. In addition, data were also recorded detailing the number and species of individuals present, number of animals that were swimming versus hauled out, number of photographed individuals, and number of animals that flushed from the rocks into the water as a result of our presence.

Additional field activities supplemental to the ongoing transect surveys and dedicated to pinniped photo-identification began in July 2019, operating under NEFSC permit 21719-01. Fort Point Ledge (Figure 3.1) was circled during each vessel-based survey to obtain a more accurate count of individuals, and to get higher resolution images for identification purposes. Land-based surveys were also conducted every one to two weeks. These surveys consisted of a 30 to 60-minute observation, within two hours of low tide, from a point of land on the eastern shore of the Penobscot River adjacent to Buck’s Ledge (Figure 3.2). During these observations, all seal sightings were documented, and data and photographs were taken according to the vessel-based photo-identification protocols. Land-based surveys occurred year-round starting in July 2019, through September 2020, with a gap from the end of March through mid-May of 2020 due to the global COVID-19 pandemic. Surveys were also not conducted from early December through mid-January due to weather and site access difficulties.
Figure 3.1: Study area: Penobscot River estuary survey transect line with major seal haul-out locations labeled. The majority of photo-identification efforts occurred at Buck’s Ledge and Fort Point Ledge. Odom’s Ledge was not approached close enough to allow for dedicated photo-identification efforts, but photographs were opportunistically collected at this location.
Figure 3.2: Buck’s Ledge field site: Buck’s Ledge, Penobscot River kilometer 21 - during land-based surveys in spring, summer, fall, and winter, surveyed from July 2019 through September 2020. Seals were primarily seen on the left side of the ledge, as well as on submerged rocks to the left of the haul-out.

Based on the vessel-based survey season running between May and October during 2019 and 2020, we also compared the abilities of the vessel and land-based surveys to detect seals at Buck’s Ledge during that timeframe. The average number of seals counted per survey were
compared between platforms, as were the average number of swimming seals and average number of hauled out seals.

Counts from photos were also used to validate seal counts recorded by observers while on the vessel-based hydroacoustic transect surveys. In 2020, the number and species of individuals determined by observers in the field were compared to the counts of seals by photographs analyzed in the lab. These counts were compared using paired t-tests and generalized linear regression models to assess the difference between observer counts and the photo counts, which represent the actual number of each species present. Counts taken when Fort Point was circled for photo-identification efforts were not included in these comparisons due to deviation from standard survey protocols.

A photo-identification catalog for Penobscot River seals was created in ACDSee Photo Studio Standard 2019, and high quality photos that clearly captured a unique pelage pattern or other natural marking were entered into that catalog. Each individual in the catalog was assigned an identification number, and each photograph was coded for various attributes including photo quality, species, sex, body condition, body parts visible, geographic location, and percentage of spots in the pelage pattern (Figure 3.3). New photographs were manually compared to all other photographs in the catalog of the appropriate species to determine whether the individual was new to the catalog or whether it had been previously sighted (Figure 3.4, 3.5). All photos were put through this matching process twice to reduce matching errors. Sightings of individuals were tracked over time to determine if individuals utilized single or multiple haul-outs and to document when certain individuals were present and whether they returned in multiple years.
Figure 3.3: Photo-identification catalog: A photo-identification catalog has been created to help organize individual photos and to track sightings of individual seals over time. There are 88 gray seals and 27 harbor seals in the catalog.
Figure 3.4: Harbor seal photo-identification: Pelage pattern, scars, and other natural markings were used to identify individual harbor seals on the Penobscot River at Buck’s Ledge from May 2019 through September 2020. Our catalog focused on ventral pelage patterns, but we also used patterns on the side of the head and backs of individual seals. We were able to re-sight 13 harbor seals. Research activities in these images were conducted and photos were taken in accordance with the Letter of Authorization issued to the NMFS Northeast Fisheries Science Center (Document #2016-22582) and NOAA NEFSC permit #21719-01.
Figure 3.5: Gray seal photo-identification: Pelage pattern, scars, and other natural markings are used to identify individual gray seals. We were able to re-sight 14 gray seals from May 2019 through September 2020 on the Penobscot River. Research activities in these images were conducted and photos were taken in accordance with the Letter of Authorization issued to the NMFS Northeast Fisheries Science Center (Document #2016-22582) and NOAA NEFSC permit #21719-01.

**Results**

After 18 months of photo-identification efforts, the seal identification catalog has 27 identifiable harbor seals and 88 identifiable gray seals. In addition to the catalogued seals, we also have photographs of 10 “unassigned” harbor seals for which we have matchable photographs of part of their bodies, but failed to get the required ventral view for entry into the catalog. Only one scar from a shark interaction was documented during our study period, and only three seals had potential entanglement scars. No active entanglements were observed, and no emaciated individuals were recorded.
Our harbor seal catalog includes 10 individuals and 10 “unassigned” seals photographed at Buck’s Ledge, 14 individuals photographed at Odom’s Ledge, and 3 individuals photographed at Fort Point Ledge (Table 3.1). All resighting events occurred at the same haul-out site as the initial sighting, and all but one of the resighted animals were located at Buck’s Ledge. Seal sightings at Buck’s Ledge were rare in summer, so to capture the return of individuals after a summer absence from the area, our study period was broken up into three “years”: May through June 2019, July 2019 through June 2020, and July 2020 through October 2020 (Figure 3.6). There were 61 resighting events of 10 individuals and three “unassigned” seals during our study period, with 8 individuals sighted in at least two different “years” and 1 individual sighted in all three “years”. The most frequently sighted individual was seen 13 times.

Table 3.1: Photo-identification efforts by haul-out: Breakdown of photo-identification efforts by haul-out, showing the minimum and maximum number of each species sighted on one survey, the number of individuals of each species that were photographed, and the number of resighting events by species. *Two of the individual gray seals photographed at Fort Point Ledge were initially photographed at Odom’s Ledge.

<table>
<thead>
<tr>
<th></th>
<th>Buck's Ledge</th>
<th>Odom's Ledge</th>
<th>Fort Point Ledge</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Range of Gray Seals Observed</strong></td>
<td>0-2</td>
<td>0-15</td>
<td>0-26</td>
</tr>
<tr>
<td><strong>Range of Harbor Seals Observed</strong></td>
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<td>0-65</td>
<td>0-48</td>
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<td><strong>Photographed Gray Seals</strong></td>
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<td>19</td>
<td>69*</td>
</tr>
<tr>
<td><strong>Gray Seal Resighting Events</strong></td>
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<td>4</td>
<td>19</td>
</tr>
<tr>
<td><strong>Photographed Harbor Seals</strong></td>
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<td>3</td>
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<tr>
<td><strong>Harbor Seal Resighting Events</strong></td>
<td>61</td>
<td>1</td>
<td>0</td>
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</tbody>
</table>
Figure 3.6: Buck’s Ledge seal sightings: Number of seals sighted at Buck’s Ledge by standard week. Year 1 represents 05/2019-06/2019, Year 2 represents 07/2019-06/2020, and Year 3 represents 07/2020-10/2020. The solid lines at the top represent weeks of data collection for each year.

Our gray seal catalog includes 2 individuals photographed at Buck’s Ledge, 19 individuals initially photographed at Odom’s Ledge, and 67 individuals initially photographed at Fort Point Ledge. Based on a winter absence from the area, our study period for gray seals was broken up into two years: 2019 and 2020. There were 29 resighting events of 14 individuals, with 13 individuals being seen in both years. One gray seal was seen seven times at Buck’s Ledge, three gray seals were resighted at Odom’s Ledge, eight gray seals were resighted at Fort Point Ledge, and two seals were initially seen at Odom’s Ledge and later resighted at Fort Point. Of the 88 gray seals in our catalog, 52 were female, 4 were male, and 32 were of undetermined sex.
Our comparison between vessel and land-based survey methods revealed no significant difference between the average number of seals detected by either platform during the survey season (t-test, t= -0.140, df=53.949, p=0.889). When broken down by whether individuals were hauled out or swimming, there were again no differences between counts of hauled out animals (t-test, t=0.735, df=54.702, p=0.466), but the land-based survey was significantly more likely to detect swimming seals in the area (t-test, t= -2.332, df=56.737, p<0.05). Of the 51 resighting events at Buck’s Ledge during the same May through October time period, 8 of those were of swimming animals (4 harbor seal resightings and 8 gray seal resightings), and all occurred during a land-based survey. There were 36 resighting events during 36 surveys from land, and 15 resighting events during 24 surveys from the vessel.

Our assessment of observer seal counts in the field versus seal counts by photograph analyzed in the lab revealed significant differences between the two counts (paired t-test, t= -4.974, df=17, p<0.001). We would expect a linear regression between observer and camera counts to have a significant positive relationship, as both counts should increase as the actual number of seals increase. As expected, the relationship between these counts was significant (Figure 8; $\beta_0= 0.947$, $\beta_1=1.236$, p<0.001, $R^2=0.902$). The slope of the regression was 1.236, indicating that observers were underestimating the total number of seals present. To better characterize how observer counts vary from actual counts of seals on the haul-outs, we used our linear model to calculate the predicted values of actual seal counts based on observer counts obtained in the field (Table 3.2). We can see an increasing discrepancy between counts when more seals are present (Figure 3.7).
Figure 3.7: Count comparison: observer versus camera: Linear regression model ($\beta_0 = 0.947$, $\beta_1 = 1.236$, $p<0.001$, $R^2=0.902$) showing the relationship between observer and camera seal counts. The shaded area represents 95% confidence intervals.
Table 3.2: Predicted Count Quick Reference: Predicted counts of the actual number of seals present on haul-out based on the linear regression model depicted in Figure 3.7 ($\beta_0=0.947$, $\beta_1=1.236$, $p<0.001$, $R^2=0.902$).

<table>
<thead>
<tr>
<th>Observer Count</th>
<th>Predicted Count</th>
<th>Lower Confidence Interval</th>
<th>Upper Confidence Interval</th>
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<tr>
<td>5</td>
<td>7.13</td>
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<td>13.3</td>
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<td>25.7</td>
<td>23.6</td>
<td>27.7</td>
</tr>
<tr>
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<td>29.1</td>
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</tr>
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<td>55.0</td>
<td>70.5</td>
</tr>
</tbody>
</table>

In addition to analyzing total seal counts, we also analyzed observer ability to identify gray seals in the field. Due to their similar size, these species can be difficult to differentiate from a distance, and we wanted to explore the accuracy of species determination from the survey tracklines. We did not find a significant linear relationship between observer and camera counts of gray seals (Figure 3.8; negative binomial generalized linear regression: $\beta_0=0.077$, $\beta_1=0.291$, $p=0.206$). Similarly, the number of gray seals (paired t-test, $t=1.761$, df=17, $p=0.096$) and the proportion of total seals that were gray seals (paired t-test, $t=-0.648$, df=17, $p=0.526$) were not significantly different between counts.
Figure 3.8: Gray seal count comparison: observer versus camera: Generalized linear regression model with a negative binomial distribution ($\beta_0=0.077$, $\beta_1=0.291$, $p=0.206$, AIC=61.947) showing the relationship between the number of gray seals counted by an observer versus gray seals counted in photographs. The shaded area represents 95% confidence intervals.

**Discussion**

This research was designed as a feasibility assessment to determine whether photo-identification of seals can be used in the Penobscot River Estuary throughout the year. Photo-identification efforts occurred at three of the four major haul-outs in the estuary, and we have evaluated each one separately. The Eastern Shore haul-out was not approached closely enough to obtain photographs. We had photo-identification successes at all three haul-outs included in our study. At Buck’s Ledge, photo-identification proved to be a useful tool for understanding seal dynamics. Based on the number of catalogued individuals, we documented a minimum of
10 individual harbor seals using Buck’s Ledge at least once between May 2019 and October 2020. We documented two separate gray seals during this same time period, one of whom was seen in the area 7 times throughout the study period.

The photo-identification data from 2019 and 2020 vessel surveys, as well as land-based survey count data, confirmed our expectation of site fidelity (Cordes & Thompson, 2015; Pomeroy, Twiss, & Redman, 2000) at Buck’s Ledge. We were able to identify 8 individuals in at least two years, and 1 individual in all three years of the study. This not only suggests that these animals are returning to this location in multiple years, but that a small group of seals in the estuary consistently utilize this ledge.

Our photo-identification effort of harbor seals at Fort Point Ledge was less successful. Very few harbor seals were added to the catalog from this location, largely due to the low numbers of harbor seals on this haul-out when we were able to approach close enough to obtain high quality photos. We did not circle this ledge in May and June to avoid disturbing the seals during harbor seal pupping season, which coincided with peak numbers of harbor seals. Gray seals arrived in large numbers at this haul-out in early July of both years, coinciding with the subsequent decline of harbor seals (Chapter 1). This reduction in harbor seals available for photo-identification once we were able to begin these efforts negatively affected our probability of success.

Obtaining high quality photographs of gray seals at Fort Point Ledge, however, was successful. Of the 69 individuals photographed at Fort Point Ledge, we successfully resighted nine of them at this haul-out. Eight of those resighted seals were seen in both 2019 and 2020. The infrequency of matches could either be because there are a lot of gray seals in the area, or because of errors in the assignment of new individuals to the catalog. Unlike harbor seals for
which we targeted ventral views, we used any body part with distinct markings to document gray seals. This poses a problem if one side of the head is photographed during one survey, and the ventral part of the animal is photographed during the next survey; this single animal would be documented as two individuals in the catalog. To better estimate the number of unique individuals in our catalog, we looked at the number of left and right head photographs in the catalog (Cordes & Thompson, 2015; Hiby et al., 2007; Mackey et al., 2008). The catalog contains 33 individuals with left head photographs, 41 individuals with right head photographs, and only 15 individuals where both sides of the head were documented. This suggests that a minimum of 41 individual gray seals used the Penobscot River Estuary during our two-year study period.

Of the 14 individual gray seals that we were able to resight at least once, 7 had right head photographs in the catalog and 5 had both sides of the head documented. Despite this, ventral and chest pelage patterns were used to confirm matches for half of these individuals. Even though failure to assign different body parts to the same individual may falsely inflate the number of individuals that we think are present (Mackey et al., 2008), our utilization of these alternate views of the seals supports the importance of these body parts in successfully tracking these animals over time. Similarly, the ventral side of a harbor seal isn’t always visible, and pelage patterns on the side of the head significantly aided our ability to match individuals. The six harbor seals with the most resighting events at Buck’s Ledge all had documented head pelage patterns or a significant dorsal marking, in addition to a distinct ventral pelage pattern, that assisted in our ability to identify them. While adding to the complexity and time involved in matching individuals, photographing multiple body parts significantly increased the success of our photo-identification efforts.
Odom’s Ledge was a difficult site for photo-identification work. In the spring and early summer, the seals on this ledge were always on alert and were quick to flush into the water, making it difficult to approach close enough for high-quality photos. Their behavior changed slightly in mid-July, coinciding with the more regular presence of gray seals on the ledge, as well as with warmer weather and perhaps increased boat traffic in the area. There may be an as-of-yet unknown quality of this site that makes the animals particularly attuned to vessel presence. Despite the difficulty at this location, we were still able to resight three gray seals and one harbor seal. We also documented the initial sighting of two gray seals at Odom’s Ledge, and later resighted this individual at Fort Point. These were our only instances of resighting an individual at multiple haul-out sites.

Our lack of success at Odom’s Ledge may also be attributed to the number of harbor seals present at this location and the limitation of focusing on ventral photos. In the spring, we documented as many as 65 harbor seals on the ledge at one time. Despite this, we only added 14 individual harbor seals from this haul-out to the catalog. Few seals were positioned in a way to allow for ventral photographs, again supporting the necessity of utilizing multiple body parts. With so many seals in the area, our chances of resighting one of 14 individuals among a minimum of 65 was slim. Our chances of resighting an individual at Buck’s Ledge were much higher because there was a significantly smaller pool of individuals in that part of the river. As a result, we had much better success at that location.

**Future Work**

Our data suggest that while gray seals may be misidentified at a distance and under-represented in cases when zero gray seals are detected in the field, the overall difference in gray seals detected versus present is not statistically significant. In this analysis, only 4 of 18 counts
detected gray seals in the field, while 8 counts had gray seals present in photos; perhaps with more data, a clearer trend would emerge. At a minimum, future work should continue to validate species identification by photograph to more accurately document the number of gray seals present on haul-outs over time. Similarly, future analyses of the numbers of seals utilizing the estuary should account for increasing discrepancies between observer counts and actual counts as the number of seals present increases.

Future work could also include continued vessel-based surveys in the southern part of the estuary dedicated to photo-identification efforts. If more individuals are more thoroughly photographed and able to be identified each survey, we could gain a better understanding of how many gray seals regularly use haul-out sites in the Penobscot River Estuary. With more reliable resightings, we could also track the number of new additions to the catalog each year to get a sense of how the number of gray seals using the estuary is changing over time. This could be compared to changes in fish biomass and counts of harbor seals to assess how gray seals are affecting and being affected by other ecosystem components. A minimum of three years of photo-identification data with Jolly Seber models for open populations could be used as a method of mark-recapture to estimate the number of gray seals using the estuary (Koivuniemi, Kurkilahti, Niemi, Auttila, & Kunnasranta, 2019).

This type of analysis would not be useful at Buck’s Ledge with such a low number of individuals. If photo-identification efforts were to continue at this location, however, it appears that efforts would be better spent on land-based surveys, as these are more likely to detect swimming individuals, leading to more resighting events and better tracking of individuals over time. The longer, 30-minute observations of the ledge also contributed to our ability to
photograph more body parts of an individual compared to the few minutes spent passing by the ledge on the boat, also contributing to a higher rate of resighting events from land.

Continued photo-identification work and an expanding Penobscot photo-identification catalog will cause the matching of new photographs to existing individuals to become more and more time intensive. A collaboration between seal scientists in the northeast U.S. and a company that creates wildlife matching software using facial recognition technology is currently working to create an automated gray seal matching program. When this becomes available, future work could compare Penobscot River Estuary gray seals to those in catalogs elsewhere in the Gulf of Maine and the northwest Atlantic. This would allow for a better understanding of how individuals utilize regional sites throughout the year and could increase our ability to detect trends in pinniped health and human interaction at a larger scale. Pinnipeds are part of the coastal ecosystem and incorporating pinniped population dynamics and their use of sites throughout the Gulf of Maine into our understanding of ecosystem health and function is essential.
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APPENDIX: CHAPTER 1 SUPPLEMENTAL MATERIAL

Figure A1: Seals Counted versus Wind Speed: Used to determine threshold for exclusion from analysis

Table A1: Fort Point Ledge Surveys: Fort Point Ledge Observations Included in Haul-out Assessment

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Table A2: Odom’s Ledge Surveys: Odom’s Ledge Observations Included in Haul-out Assessment

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Table A3: Eastern Shore Surveys: Eastern Shore Observations Included in Haul-Out Assessment

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Table A4: 2019 and 2020 Photo-Count Surveys: Breakdown by Species and Haul-Out; Surveys Used in Analysis

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Figure A2: Effects of biomass and year: Hauled out seal counts were not significantly related to fish biomass (Spearman $rs=-0.105$, $p=0.412$), but the percentage of total seals sighted that were swimming from each survey was positively correlated with fish biomass (Spearman $rs=0.379$, $p<0.01$). The percentage of seals that were swimming also increased significantly across years (Spearman $rs=0.336$, $p<0.01$).
BIOGRAPHY OF THE AUTHOR

Lauri Leach was born and raised in Westborough, Massachusetts, graduating from Westborough High School in 2005. She attended the University of Rhode Island and graduated in 2009 with a Bachelor’s degree in Biological Sciences. She worked for several years as a veterinary technician, wildlife rehabilitator, and marine mammal biologist before entering the Marine Biology graduate program at the University of Maine in the spring of 2019. After receiving her degree, Lauri will be working as a Knauss Fellow at the Marine Mammal Commission. Lauri is a candidate for the Master of Science degree in Marine Biology from the University of Maine in December 2020.