

AN ABSTRACT OF THE DISSERTATION OF

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Title: Towards an Integrated Decision Tool for Managing Wildlife with Visitor Restrictions in Glacier Bay National Park.

Abstract approved: _____

James T. Peterson

The National Park Service has a dual mission of providing public access to exceptional natural resources, but in a manner such that these resources are left “unimpaired for the enjoyment of future generations.” Human activities in parks undoubtedly affect wildlife, but the degree to which such activities cause impairment is often unclear and difficult to assess. It is the task of park administrators to take actions and impose restrictions to prevent impairment based on park values and the information provided through research and monitoring programs. Finding an appropriate balance between wildlife protection and visitor access is difficult because decision makers must consider numerous interrelated factors, many of which are not known with certainty. In light of these challenges, scientific approaches that allow decision makers to incorporate uncertainty and evaluate trade-offs between human access and resource protection are greatly needed. Glacier Bay National Park (the “Park” hereafter) contends with the challenge of managing visitors in an area containing many species of conservation concern. Therefore, the Park seeks a systematic and data-driven process for evaluating the tradeoffs that current and potential restrictions represent, in terms of protecting sensitive resources versus enabling full access to the public. The goal of my dissertation

was to assist administrators and biologists at the Park with the development of an integrated decision tool for the Park through a structured decision making process.

This task entailed first identifying and structuring objectives, then coordinating with subject-matter experts on the development of biological sub-models for informing the future decision tool. Park Service administrators and staff drew on fundamental purposes of the Park to define measurable attributes that characterize the Park's values and inform management decisions. This process also identified focal species whose conservation status was viewed as a priority and had motivated management actions in the past. Focal species included Steller sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina richardsi*), humpback whales (*Megaptera novaeangliae*), and several species of ground-nesting coastal waterbirds. Much of the work described here involved collaborating with subject-matter experts to develop biological models. These models served three main purposes: (1) characterize the state of focal species by incorporating available research and on-going monitoring; (2) respond interactively to changes in the value of population parameters (e.g., population size, distribution), whose influence decision makers would want to assess; and (3) generate estimates that would serve as valuable inputs in subsequent models of visitor-wildlife encounters.

Biological models provide data-driven descriptions of the state of populations. The structured decision-making process places emphasis on models that are as explicit as possible. To this end, I formulated biological sub-models in a manner that would permit estimation of actual population parameters for focal species rather than raw counts or indices. Survey data were modeled as a function of these key parameters, but also as filtered through an imperfect detection process affected by survey effort and

uncontrollable variables, such as weather conditions. The Steller sea lion sub-model estimated abundance, spatial distribution, and the proportion of time spent on land (attendance probability) using counts at terrestrial sites and sightings-at-sea. I used a similar approach to model abundance for a sub-population of harbor seals, but with modifications meant to account for the excessive number of zero counts in the data set. The sub-model describing the condition of ground-nesting coastal waterbirds estimated probabilities of survey sites being occupied, of the species being abundant at the site, and of the nesting status for nine different species across 20 key concentration sites that are surveyed in the Park. Finally, the humpback whale sub-model used sightings of whales from active surveys and observers onboard cruise ships to estimate whale abundance and, for the first time, fine-scale spatial distribution in the Park.

Structuring objectives and developing biological sub-models was a key step in an ongoing process of decision tool development. The Park is now in the position to move forward with combining biological sub-models with information on visitor usage. I describe pathways for accomplishing this task, and assess the capacity of each biological sub-model for generating the measurable attributes that decision makers care about. Although decision tool development is ongoing, the work herein is a valuable contribution to the fields of ecology and resource management for several reasons. At the level of individual studies, population parameter estimates from sub-models contribute to conservation efforts for those species, and the novel modeling techniques described are readily generalizable to other systems. The broader contribution of this body of work, however, is in illustrating the value of adopting a structured decision-making approach to resource management in parks. Specifically, this work shows that the process of

connecting fundamental objectives to monitoring information can be used identify information gaps and reveal creative ways of using available information to inform management.

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Towards an Integrated Decision Tool for Managing Wildlife with Visitor Restrictions in
Glacier Bay National Park.

by

Steven L. Whitlock

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Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Steven L. Whitlock, Author

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I would like to dedicate this dissertation to my parents Nell and Jim Whitlock, and to all of my teachers and professors that inspired me to want to learn more.

CHAPTER 1: GENERAL INTRODUCTION

The growth and spread of human populations has had an indelible impact on ecosystems throughout the world, particularly since the rise of industrialization (Ramankutty and Foley 1999; Nelson et al. 2006). In response to these changes, many governments have deemed it necessary to create parks which preserve, and hold in public trust, areas of aesthetic and ecological significance for the use and enjoyment of future generations (Groombridge 1992; Eagles and McCool 2002; Chape et al. 2005). In many cases, these areas are intended to be minimally affected by human development, but also to provide opportunities for recreation and wilderness experiences. The task of preventing anthropogenic alteration while providing access is often daunting for resource managers (Boyle and Samson 1985; Loomis 1993; Marion et al. 2016), particularly considering that knowledge of natural resources and ecological processes is always imperfect (Ascher 2001; DeFries and Nagendra 2017). In light of these challenges, scientific approaches that allow decision makers to incorporate uncertainty and evaluate trade-offs between human access and resource protection are greatly needed.

Administrators of protected areas traditionally arrive at decisions in the same manner as all natural resource managers. They examine the available scientific information, consider the social and political situation, and draw on personal experience. In essence, administrators apply their own “mental models” to the decision situation. Alternative actions have anticipated outcomes based on the decision maker’s understanding of relevant mechanisms. This approach to decision making is problematic for several reasons (Fleischman and Briske 2016). The process by which decisions are

arrived at is often convoluted and difficult to explain, which can make decisions appear arbitrary to members of the public. In addition, this practice also limits the transference of institutional knowledge, because when an administrator leaves so does the “mental model” (Conroy and Peterson 2013). There is a larger issue with this approach, however, beyond just a lack of transparency. When humans approach decisions subjectively, regardless of their experience, they tend to predictably make irrational choices (Ariely 2008; Kahneman 2011). This happens because humans are beset by a number of cognitive biases which can lead to mismanagement of natural resources (Patt and Zeckhauser 2000; Iftekhar and Pannell 2015). The best way to improve the manner in which decisions are made and avoid pitfalls is through the application of a structured and formal approach to decision making.

Over the last thirty years, frameworks and techniques have been developed to address the challenges of decision making in the field of natural resource management (Walters 1986; Conroy and Peterson 2013). The terms that commonly denote these approaches in the ecological literature are structured decision making (SDM) and adaptive resource management (ARM), and the products produced by applying these approaches can be referred to as decision models, decision support systems, or decision tools. Structured decision making is defined as a formal method for connecting decisions to objectives (Conroy and Peterson 2013). Adaptive resource management is a subcategory of SDM in which decisions are revisited and information from ongoing monitoring is used to resolve uncertainties regarding how a system operates (i.e., structural uncertainty; Nichols and Williams 2006; Williams and Brown 2014). The SDM process makes use of techniques from fields that are outside the training that most

managers and scientists receive (Sit and Taylor 1998). The process draws on the field of decision science in stressing the importance of identifying values and objectives (Keeney 1996), and makes use of techniques from the fields of operations research and computer science in integrating quantitative information and identifying optimal decisions (Schreiber et al. 2004).

The specific steps of the SDM process are to: (1) identify the decision problem; (2) structure objectives; (3) define decision alternatives; and (4) link decisions to measurable attributes through the use of models. Identification of the decision problem sets the boundaries within which actions will be considered. Structuring objectives is a process that is intended to separate the objectives that are valuable in and of themselves (e.g., persistence of a species; fulfillment of a legal mandate), from those that are thought to be necessary or useful for achieving something more fundamental (e.g., increasing habitat availability). Identifying decision alternatives and linking them to measurable attributes exposes the reasoning and assumptions within the minds of decision makers. Models are an important component because they provide explicit descriptions of how decision makers think the system functions and would respond to potential management actions and outside influences. Mathematical models are beneficial because their structure and assumptions can be clearly examined and tested, as opposed to narrative descriptions which are inherently vague (Regan et al. 2002). When all of the components have been integrated the performance of resulting decision tools are evaluated and modified through a process known as sensitivity analysis. Once this process is completed, decision makers can evaluate the trade-offs of various management alternatives and, if

warranted, use a solution algorithm to identify the optimal or satisficing set(s) of decisions (Williams and Nichols 2014).

The goal of my dissertation was to assemble components of an integrated decision tool for managing visitor restrictions in Glacier Bay National Park, and in so doing, develop novel methods for characterizing the state of focal species groups (pinnipeds, whales, ground-nesting waterbirds). These models were structured in a manner such that the Park could, in the near future, begin to quantify interactions between wildlife and visitors. In addition to providing an important sub-component to the future decision model, each chapter also stands alone as a valuable research study. Chapters 2-5 focus on developing population models for each of the target species groups. Chapter 6 provides illustrations of how the biological models will be connected to visitor usage patterns. I devote the remainder of this introduction to a description of the decision situation in Glacier Bay National Park and the initial phases of the structured decision making process.

Description of Glacier Bay National Park (GBNP)

Glacier Bay National Park is located in Southeast Alaska and encompasses approximately 1.3 million hectares of terrestrial and marine areas. Glacier Bay National Park (“Park” hereafter) encompasses of the Glacier Bay basin, the southern portion of the Fairweather Range to the west, and the shoreline stretching from the west entrance of the bay to the mouth of the Alsek River to the north. Many of the most significant landmarks in the Park are located within Glacier Bay proper, and include islands, lagoons, and tidewater glaciers. The waters of Glacier Bay are highly productive and support a diversity of waterbirds, as well as terrestrial and marine mammal species (Etherington et

al. 2007), most notably harbor seals (*Phoca vitulina richardsi*), Steller sea lions (*Eumetopias jubatus*), and humpback whales (*Megaptera novaeangliae*). The environment of the bay is also extremely dynamic because of the relatively recent glacial retreat in the area. Most of the east arm of Glacier Bay was covered by Muir Glacier less than 120 years ago and the entire bay was covered by ice during the period of the Little Ice Age (Catton 1995). Glacial retreat over the last several centuries has led to a cascade of physical and ecological processes that are ongoing. For example, isostatic rebound from glacial retreat influences the elevation and connectivity of islands which, in turn affects successional processes and the distribution of wildlife (Chapin et al. 1994).

Management practices of GBNP stand out relative to other units in the National Park System. The first major difference between GBNP and other parks is the emphasis placed on research of both the physical and ecological characteristics of the area. Allowing for research of the dynamic tidewater glacial environment is part of the foundation statement (NPS 2010), and the Park demonstrates its commitment to this purpose by issuing many research permits and providing logistical support. The Park also supports on-going monitoring and research programs either directly or in conjunction with other agencies and programs, including the “Vital Signs” program and the Southeast Alaska Network (SEAN; Fancy et al. 2009). The second distinguishing characteristic of GBNP is that, unlike most other units in the National Park system, administrators of GBNP have the authority to regulate vessels within Park waters. Vessel management consists of establishing quotas, issuing permits, and restricting the speed and access of vessels in specific areas. Having authority over Park waters is significant because visitors rely on vessels (motorized or nonmotorized) to enjoy virtually all of the

main attractions (e.g., tidewater glaciers, marine wildlife viewing) in the Park. The most strictly regulated vessels are cruise ships that are responsible for bringing more than 90% of the annual visitors to the Park (Gende 2007). Of course, Park administrators do not have absolute control over vessels and are required to uphold restrictions mandated through laws such as the Marine Mammal Protection Act (MMPA) and the Endangered Species Act (ESA), and must also grant limited commercial fishing access to several areas of Glacier Bay (Mackovjak 2010).

Structured Decision Making Process for Area Closures and Vessel Management in GLBA

Administrators and scientists associated with GBNP partnered with the Oregon Cooperative Fish and Wildlife Research Unit in 2016 with the goal of developing a decision tool for managing area closures and vessel restrictions within the Park. The following sections describe the motivation for pursuing the project and summarize the discussions and choices made during an initial planning workshop and subsequent meetings that occurred.

Motivation

Administrators and resource specialists with the Park were motivated to engage in the SDM process for several reasons. The primary reason was due to newly proposed rule changes to the coded federal regulations (CFR) for the GBNP, which greatly increased the flexibility with which the superintendent can impose and remove area closures and vessel restrictions. In the past, the superintendent's decisions had to be explicitly added to the CFR, but the new regulations allow the superintendent to impose closures and restrictions at will. The greater flexibility to manage closures and restrictions has led to an increased interest in developing a science- and values-based approach for prescribing

closures and restrictions that is both consistent and transparent. Developing a decision support tool was believed beneficial because it would provide an opportunity for managers and scientists to reexamine closures and restrictions that are presently in the CFR, but which may no longer be necessary for preventing the impairment of Park resources. In addition to ensuring that closures and restrictions are appropriate given Park values, there was also interest in engaging in the SDM process as a way to strengthen the justification for Park policies in the event of legal disputes.

Initial steps of the SDM process

A workshop was conducted in 2016 for the purpose of initiating and carrying out the first several steps of the SDM process. The goals of this workshop were to identify objectives, define the decision context concerning vessel restrictions within the park, and sketch out a framework for developing the decision tool. A large portion of the meeting involved structuring objectives, identifying decision alternatives, and linking objectives and measurable attributes to candidate decision alternatives. The meeting was attended by Park administrators including the superintendent, and chiefs of resources, concessions, and law enforcement. Also in attendance were research staff, composed of those stationed at Park headquarters as well as those affiliated with SEAN. Together the group involved in the workshop had significant knowledge and experience concerning the state of the Park's ecological resources and the experience of different user groups.

The first task of the meeting was the definition of the problem statement, the purpose of which was to ensure that group members agreed about the proposed actions and how they are intended to fulfill objectives. The mutually agreed upon problem statement for the decision situation was:

“Implement annual area closures and use restrictions only when necessary to ensure that park resources and values are unimpaired for the enjoyment of future generations, recognizing that greater levels of closures/restrictions should be associated with a greater magnitude and certainty of benefits.”

The phrase “only when necessary” implies that restrictions and closures should be chosen conservatively. Furthermore, the focus on “future generations” and “certainty of benefits” further indicated that closures and restrictions should be implemented in cases where the long-term sustainability of a Park resource is directly affected by humans.

The second task that the group performed was to define and structure objectives. During this process, attendees drew on the founding legislation of the National Park Service (i.e., The Organic Act) and on the Foundation Statement for the Park itself (NPS 2010). The group decided that the decision tool’s fundamental objective was to uphold the original mission of the National Park Service. This objective was decomposed into two competing means objectives of minimizing impairment of resources and maximizing visitor experience (Figure 1.1). The visitor experience objective was more explicitly defined using another hierarchy with daughter nodes of visitor opportunity and safety (Figure 1.2). These nodes were further subdivided into values and specific measures that characterize the limitations that would be imposed on visitors by the various decision alternatives. Similarly, the objective to minimize impairment of Park resources was decomposed into means objectives concerned with avoiding the impairment of three groups of target species: humpback whales, pinnipeds (harbor seals and Steller sea lions), and ground-nesting waterbirds. The reason for selecting these target species groups was because of their ecological importance, value in terms of enhancing visitor experiences,

and their potential to be negatively impacted by humans. The fundamental objective hierarchy for focal species was changed from its original 2016 version (

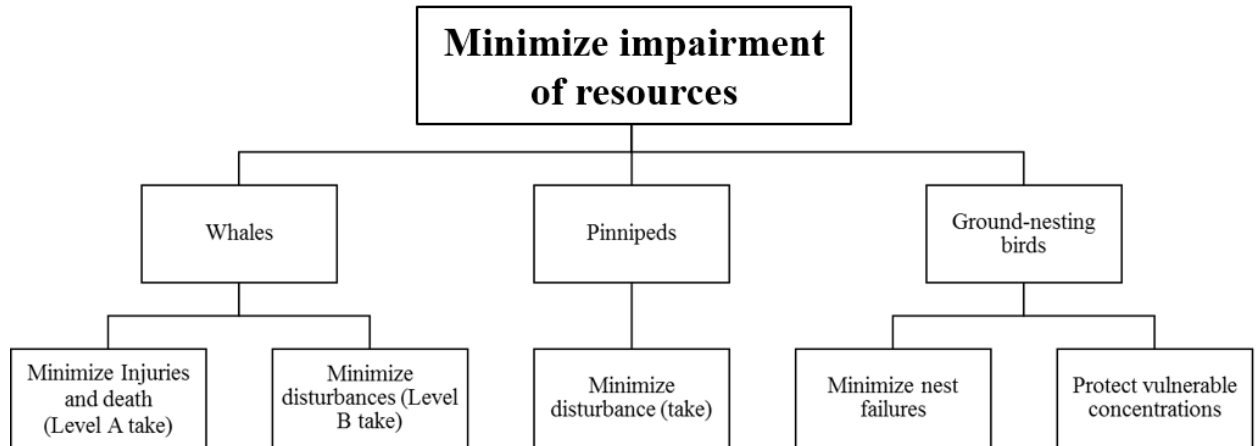


Figure 1.3). The updated hierarchy from 2018 put greater emphasis on minimizing “human-caused” disturbances and also redefined pinniped disturbances in relation disturbing pups rather than take (Figure 1.4).

After discussing components of these hierarchies the group proceeded to defining the potential management actions that should be considered within the decision tool. Some of the following information, especially regarding the spatial grain of decisions, was contributed in subsequent meetings. Potential vessel restrictions that the group decided to consider within the decision tool were speed limits and shoreline buffers. The two alternative speed limits for areas of the Park were 13 versus 20 nautical miles per hour (kn). Shoreline buffer restrictions refer to the rules that prohibit motorized vessels from traveling within 1 nautical mile (nm) of the shoreline. At present, both buffers and speed restrictions are seasonally implemented at the mouth of Glacier Bay as measures for reducing the likelihood of whale-ship collisions; these combined regulations are known as “seasonal whale waters” (Figure 1.5; Jelinski et al. 2002; Gende et al. 2011).

The spatial grain within which to consider alternative speeds was roughly defined as a manageable number (<100) zones of water of similar size and defined using recognizable landmarks and minutes of latitude and longitude. The presence or absence of buffers was also to be considered within the same water zones, but only those zones adjacent to shorelines.

Potential closure decisions were placed into two categories: water closures and land closures. The decision alternatives concerning water closures were simply whether or not to allow vessels to access Johns Hopkins Inlet, which is both a major attraction and the area of the Park with the highest concentration of harbor seals. Potential land closure decisions were to be considered for both island and shoreline areas of the Park. Five alternatives were defined for each land closure: closed to overnight camping, closed to foot traffic, and closed with a minimum approach distance from water of 50 yards, 100 yards, or 0.25 nm. Participants determined that islands should be managed as a whole, with the exception of large islands (e.g., Willoughby Island), which could be subdivided using recognizable landmarks. Discussions following the initial meeting indicated that shoreline segments should be no smaller than 1 mile in length and should be clearly definable in terms of shoreline features, but that the minimum shoreline segment length for closure would ideally be based on the probable movement patterns of the species whose presence prompted the closure (i.e., smaller for nesting waterbirds than for a bear).

There were several aspects of current vessel and area closure management that the group was uninterested in altering or examining within the decision tool. For example, the group did not wish to consider altering regulations that seasonally or permanently prevent motorized vessels from entering certain areas of the Park (e.g., Rendu Inlet). The

group was also uninterested in considering management actions that would differentially apply to user groups (e.g., prohibition of charter vessels, but not kayaks, from camping on an island). The group also decided that it was unnecessary to integrate shoreline closures into the decision tool except in areas with known concentrations of ground-nesting waterbirds. Shoreline closures were removed from consideration because these decisions are made automatically for safety reasons and do not relate to resource impairment concerns.

References

- Ariely, D. 2008. Predictably irrational: the hidden forces that shape our decisions. Harper Collins.
- Ascher, W. 2001. Coping with complexity and organizational interests in natural resource management ecosystems 4(8): 742–757. doi:10.1007/s10021-001-0043-y.
- Boyle, S.A., and Samson, F.B. 1985. Effects of nonconsumptive recreation on wildlife: a review. *Wildlife Society Bulletin (1973-2006)* 13(2): 110–116.
- Catton, T. 1995. Land reborn: a history of administration and visitor use in Glacier Bay National Park and Preserve. National Park Service.
- Chape, S., Harrison, J., Spalding, M., and Lysenko, I. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philos Trans R Soc Lond B Biol Sci* 360(1454): 443–455. doi:10.1098/rstb.2004.1592.
- Chapin, F.S., Walker, L.R., Fastie, C.L., and Sharman, L.C. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecological Monographs* 64(2): 149–175.
- Conroy, M.J., and Peterson, J.T. 2013. Decision making in natural resource management: a structured, adaptive approach. John Wiley & Sons.
- DeFries, R., and Nagendra, H. 2017. Ecosystem management as a wicked problem. *Science* 356(6335): 265–270. doi:10.1126/science.aal1950.
- Eagles, P.F.J., and McCool, S.F. 2002. *Tourism in National Parks and Protected Areas: Planning and Management*. CABI.

- Etherington, L.L., Hooge, P.N., Hooge, E.R., and Hill, D.F. 2007. Oceanography of Glacier Bay, Alaska: Implications for biological patterns in a glacial fjord estuary. *Estuaries and Coasts: J ERF* 30(6): 927–944. doi:10.1007/BF02841386.
- Fancy, S.G., Gross, J.E., and Carter, S.L. 2009. Monitoring the condition of natural resources in US national parks. *Environmental Monitoring and Assessment* 151(1–4): 161–174. doi:10.1007/s10661-008-0257-y.
- Fleischman, F., and Briske, D. 2016. Professional ecological knowledge: an unrecognized knowledge domain within natural resource management. *Ecology and Society* 21(1). Available from <http://www.ecologyandsociety.org/vol21/iss1/art32>.
- Gende, S.M. 2007. Understanding how cruise ships affect resources and visitor experiences in Glacier Bay National Park and Preserve - Google Scholar. *Alaska Park Science* 7: 22–27.
- Gende, S.M., Hendrix, A.N., Harris, K.R., Eichenlaub, B., Nielsen, J., and Pyare, S. 2011. A Bayesian approach for understanding the role of ship speed in whale–ship encounters. *Ecological Applications* 21(6): 2232–2240. doi:10.1890/10-1965.1.
- Groombridge, B. 1992. Protected Areas. In *Global Biodiversity*. Edited by B. Groombridge. Springer Netherlands. pp. 447–478. doi:10.1007/978-94-011-2282-5_29.
- Iftekhar, M.S., and Pannell, D.J. 2015. “Biases” in adaptive natural resource management. *Conservation Letters* 8(6): 388–396. doi:10.1111/conl.12189.
- Jelinski, D.E., Krueger, C.C., and Duffus, D.A. 2002. Geostatistical analyses of interactions between killer whales (*Orcinus orca*) and recreational whale-watching boats. *Applied Geography* 22(4): 393–411. doi:10.1016/S0143-6228(02)00051-6.
- Kahneman, D. 2011. *Thinking, fast and slow*. In 1 edition. Farrar, Straus and Giroux.
- Keeney, R.L. 1996. *Value-focused thinking*. Harvard University Press.
- Loomis, J.D. 1993. *Integrated Public Lands Management: Principles and Applications to National Forests, Parks, Wildlife Refuges, and BLM Lands*. Columbia University Press.
- Mackovjak, J.R. 2010. *Navigating troubled waters: a history of commercial fishing in Glacier Bay, Alaska*. National Park Service, U.S. Dept. of the Interior.
- Marion, J.L., Leung, Y.-F., Eagleston, H., and Burroughs, K. 2016, May 1. A review and synthesis of recreation ecology research findings on visitor impacts to wilderness and protected natural areas. Available from

<http://orst.library.ingentaconnect.com/content/saf/jof/2016/00000114/00000003/art00013> [accessed 9 June 2017].

- National Park Service (NPS). 2010. Glacier Bay National Park and Preserve foundation statement. National Park Service, Gustavus, Alaska.
- Nelson, G.C., Dobermann, A., Nakicenovic, N., and O'Neill, B.C. 2006. Anthropogenic drivers of ecosystem change: An overview. *Ecology and Society* 11(2). Available from <http://www.ecologyandsociety.org/vol11/iss2/art29/> [accessed 9 June 2017].
- Nichols, J.D., and Williams, B.K. 2006. Monitoring for conservation. *Trends in Ecology & Evolution* 21(12): 668–673. doi:10.1016/j.tree.2006.08.007.
- Patt, A., and Zeckhauser, R. 2000. Action bias and environmental decisions. *Journal of Risk and Uncertainty* 21(1): 45–72. doi:10.1023/A:1026517309871.
- Ramankutty, N., and Foley, J.A. 1999. Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global Biogeochem. Cycles* 13(4): 997–1027. doi:10.1029/1999GB900046.
- Regan, H.M., Colyvan, M., and Burgman, M.A. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. *ecological applications* 12(2): 618–628. doi:10.1890/1051-0761(2002)012[0618:ATATOU]2.0.CO;2.
- Schreiber, E.S.G., Bearlin, A.R., Nicol, S.J., and Todd, C.R. 2004. Adaptive management: a synthesis of current understanding and effective application. *Ecological Management & Restoration* 5(3): 177–182. doi:10.1111/j.1442-8903.2004.00206.x.
- Sit, V., and Taylor, B. 1998. Statistical methods for adaptive management studies. British Columbia, Ministry of Forests Research Program. Available from <http://static.adaptivemanagement.net/sites/default/files/Statistical%20Methods%20for%20AM%20Studies.pdf>.
- Walters, C.J. 1986. Adaptive management of renewable resources. Blackburn Press.
- Williams, B.K., and Brown, E.D. 2014. Adaptive management: from more talk to real action. *Environmental Management* 53(2): 465–479. doi:10.1007/s00267-013-0205-7.
- Williams, B.K., and Nichols, J.D. 2014. Optimization in natural resources conservation. In *Application of threshold concepts in natural resource decision making*. Edited by G.R. Guntenspergen. Springer New York. pp. 45–65. doi:10.1007/978-1-4899-8041-0_4.

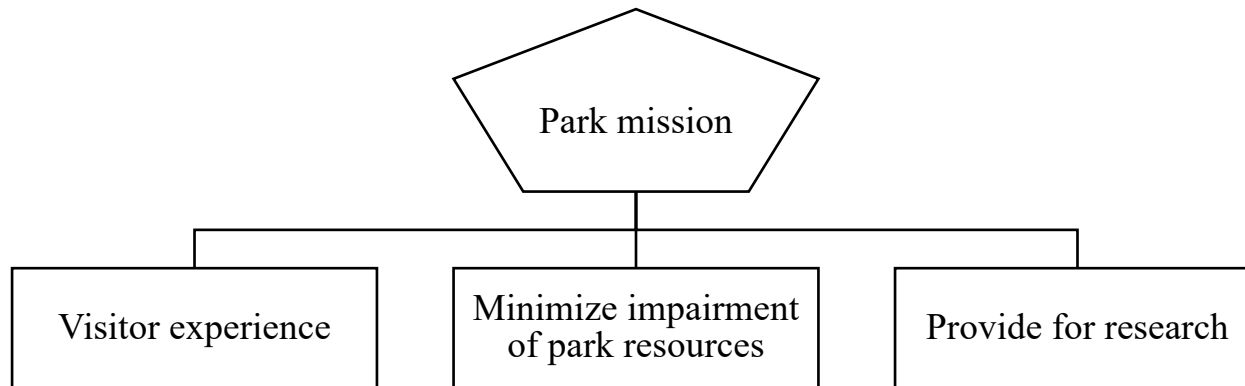
Figures

Figure 1.1. Fundamental objective hierarchy for Glacier Bay National Park. The fundamental objective (achievement of Park mission) is shown at the top of the hierarchy and mean objectives, which would indicate achievement of the fundamental objective, are shown below.

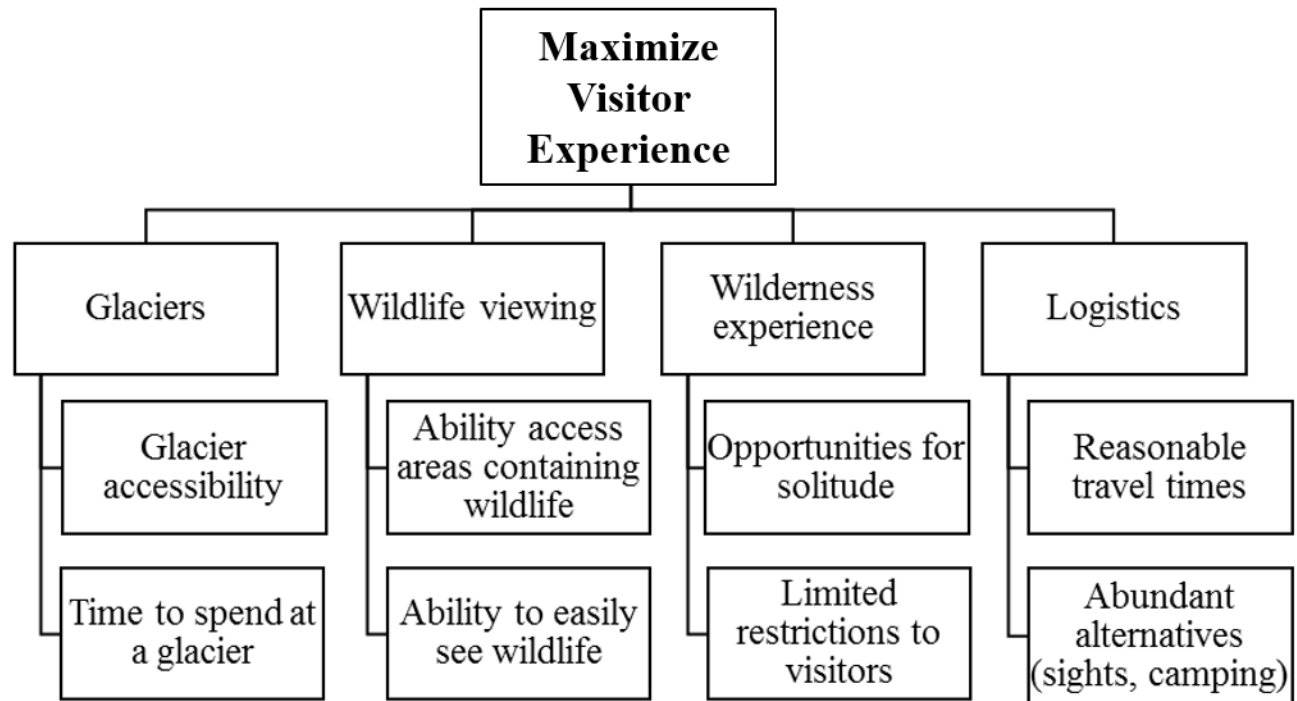


Figure 1.2. Hierarchy for the means objective of providing for safe and unimpeded visitor experiences.

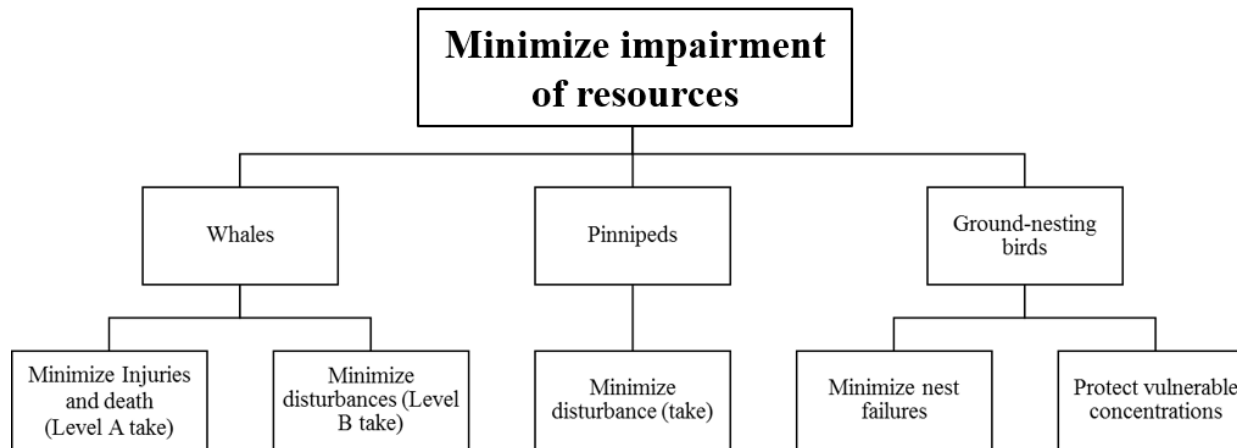


Figure 1.3. Initial means-objective hierarchy for minimizing impairment of Park resources.

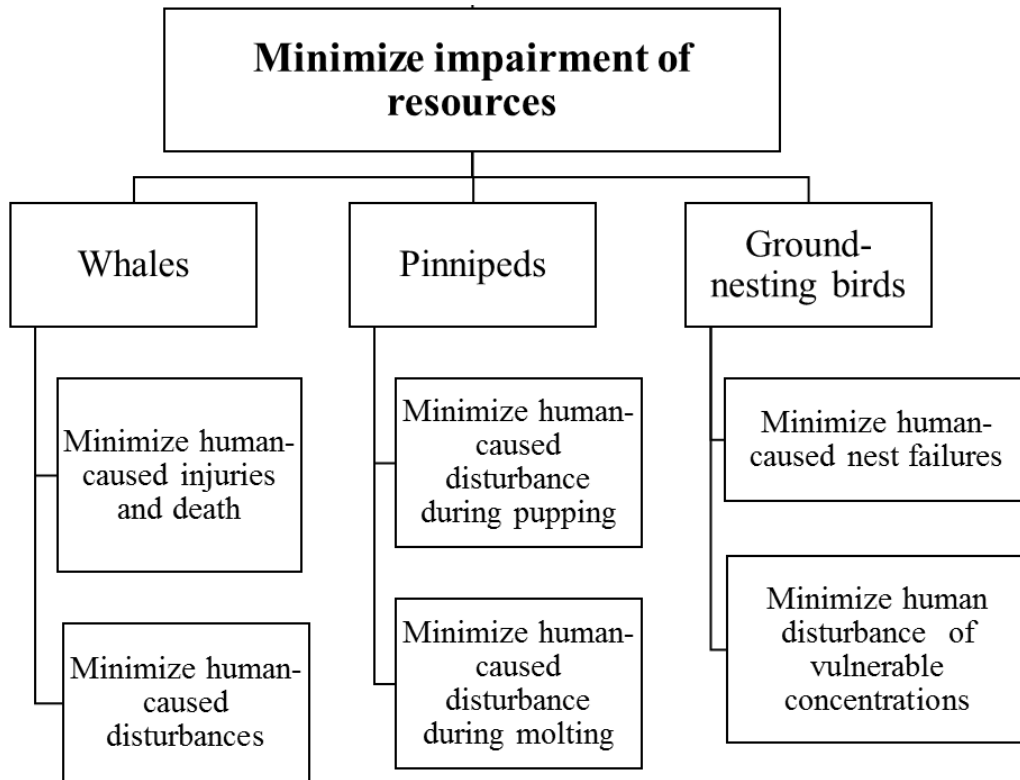


Figure 1.4. Updated means-objectives for minimizing impairment of Park resources.

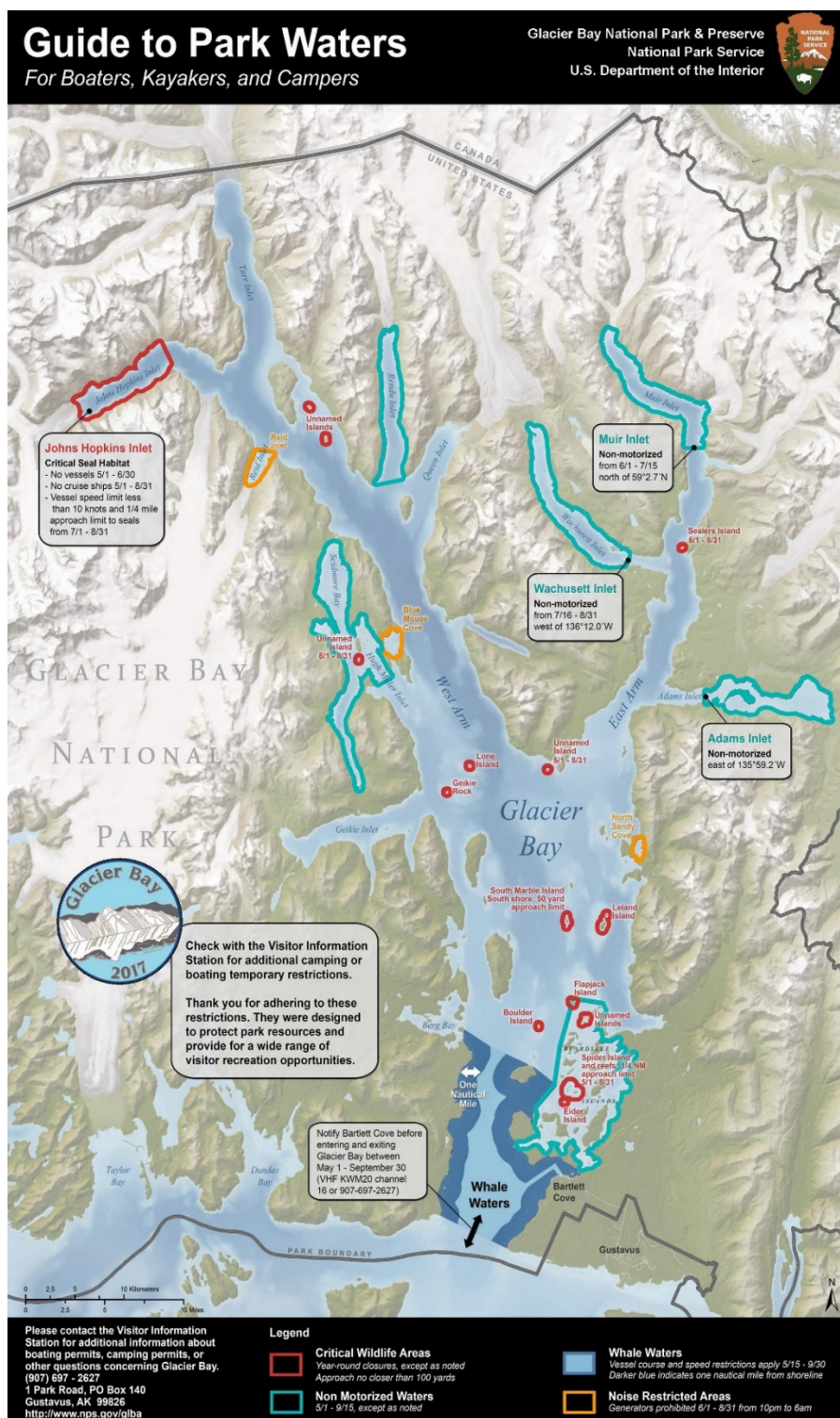


Figure 1.5. An official map of Glacier Bay National Park depicting the various seasonal and permanent vessel restrictions used to prevent the impairment of wildlife.

CHAPTER 2: MODELLING PINNIPED ABUNDANCE AND DISTRIBUTION USING COUNTS AT TERRESTRIAL SITES AND IN-WATER SIGHTINGS

(At time of submission, this chapter was under review by the journal Ecological Modelling)

Abstract

Pinnipeds are commonly monitored using aerial photographic surveys at land- or ice-based sites, where animals come ashore for resting, pupping, molting, and to avoid predators. Although these counts form the basis for monitoring population change over time, they do not provide information regarding where animals occur in the water, which is often of management and conservation interest. In this study, we developed a hierarchical model that links counts of pinnipeds at terrestrial sites to sightings-at-sea and estimates abundance, spatial distribution, and the proportion of time spent on land (attendance probability). The structure of the model also allows for the inclusion of predictors that may explain variation in ecological and observation processes. We applied the model to Steller sea lions (*Eumetopias jubatus*) in Glacier Bay, Alaska using counts of sea lions from aerial photographic surveys and opportunistic in-water sightings from vessel surveys. Glacier Bay provided an ideal test and application of the model because data are available on attendance probability based on long-term monitoring. We found that occurrence in the water was positively related to proximity to terrestrial sites, as would be expected for a species that engages in central-place foraging behavior. The proportion of sea lions in attendance at terrestrial sites and overall abundance estimates were consistent with reports from the literature and monitoring programs. The model we

describe has immediate utility for park managers who wish to better understand the overlap between pinnipeds and visitors, and the framework that we present has potential for application across a variety of study systems and taxa.

Introduction

Characterizing the abundance and spatial distribution of animal populations is a fundamental challenge in ecology (Scott et al. 2002; Krebs 2009). The task typically involves fitting a model that relates counts or detections of animals to environmental variables to make inferences about the state of a population and the location of individuals belonging to the population (Hegel et al. 2010). Unfortunately, there are common sources of sampling bias that can produce inaccurate inferences from this basic model, including nondetection of animals that are actually present in the survey area (Gu and Swihart 2004; Kellner and Swihart 2014), and temporary emigration of animals during periods of assumed geographic closure (Valente et al. 2017; Yamaura and Royle 2017). Accounting for non-detection and temporary emigration is particularly important for species that are cryptic or highly mobile within the study area (MacKenzie et al. 2002; Chandler et al. 2011).

Pinnipeds are a group of animals that typify these sampling-related challenges. These species are difficult to study because they are highly mobile and occupy the boundary between marine and terrestrial environments. Locating and enumerating animals while in the water is often considered infeasible; thus, population monitoring is generally carried out by counting animals at terrestrial or sea-ice sites where animals come ashore for resting, pupping, molting, and to avoid predators (Boyd et al. 2010).

Although counts at locations on ice platforms and on land are sufficient for monitoring broad-scale population change (Small et al. 2003; Mathews et al. 2011), they communicate no information about the distribution of animals in the water. For the cases in which in-water sighting or remote tracking data are available, they are often analyzed separately from spatially implicit count data gathered at fixed sites (Herr et al. 2009; Himes Boor and Small 2012; Vincent et al. 2017). The ability to assess factors that influence the in-water distribution of pinnipeds is especially relevant to management and conservation because of the potential for interactions between pinnipeds and fishery operations (Read 2008; Kovacs et al. 2012).

Many of the challenges associated with surveying pinnipeds and synthesizing information from different data sources can be addressed by adopting a hierarchical modelling approach (Ver Hoef and Frost 2003; Ver Hoef et al. 2014; Williams et al. 2017). Hierarchical models represent ecological processes as latent state variables and the data obtained from surveys as a function of the true state and an incomplete and potentially misleading observation process (Royle and Dorazio 2008; Kery and Schaub 2011). This approach allows parameters to be separately related to predictor variables (e.g., sampling effort, environmental attributes), and facilitates the integration of multiple sources of data into a single model (Kery and Royle 2015). Integrated models use different sources of information to inform a shared set of parameters, which can improve the precision of estimates, fill important gaps in information, and more realistically represent ecological processes (Schaub et al. 2007; Abadi et al. 2010; Cole and McCrea 2016). Previous developments in integrated modelling have focused on estimating demographic rates from survey and mark-recapture data (Buckland et al. 2004; Besbeas

et al. 2009), but there has also been recent progress in the development of models that incorporate different types of spatially explicit data (Chandler and Clark 2014; Nadeem et al. 2016).

The objective of this paper is to develop a hierarchical model for pinnipeds and similar species and to use this model to broadly characterize the abundance and distribution of Steller sea lions (*Eumetopias jubatus*) in Glacier Bay National Park in southeastern Alaska. Our approach integrates counts from aerial photographic surveys at terrestrial sites and in-water sightings from vessel surveys, and combines elements of N-mixture models (Royle 2004; Dail and Madsen 2011) and models that use unstructured sampling approaches (Thompson et al. 2012; Russell et al. 2012; Broekhuis and Gopalaswamy 2016). Replicated counts of sea lions at terrestrial sites inform estimates of site-level abundance and the probability that an individual is out of the water, which we term “probability of attendance”. In-water sightings and abundance parameters are then used to estimate sighting intensity and the spatial distribution of animals.

We fit the model to counts from aerial photographic surveys at a terrestrial haul-out site (Womble et al. 2005, 2009; Mathews et al. 2011), and in-water sightings gathered opportunistically during vessels surveys for humpback whales (*Megaptera novaeangliae*; Gabriele and Lewis 2012; Keller et al. 2016). We evaluated the performance of the model using a simple sensitivity analysis and by comparing model predictions of abundance and attendance to those reported by monitoring programs and from results derived using different methods (e.g., tagged animals) reported in the scientific literature. This model is intended to form part of a larger decision tool for managing wildlife and visitor restrictions within the Park.

Methods

Our model is composed of two sub-models that describe the abundance of pinnipeds at particular terrestrial sites and their distribution in the water, based on sightings from vessels. The first sub-model, which we term the “count portion” informs several key parameters: (1) overall abundance of pinnipeds in the study area and (2) the probability that an animal is out of the water, and thus available to be counted. The second sub-model, which we refer to as the “sighting portion” uses sightings of pinnipeds in the water to describe their spatial distribution while accounting for imperfect detection and non-uniform survey effort. The model assumes that pinnipeds not available to be counted at terrestrial sites during aerial surveys, are in the water. The number of individuals in the water at a given time is derived from the count model and combined with data on in-water sightings to make inferences about spatial distribution. In the following sections we outline the data sets involved in the Steller sea lion case study, then define the structure of the model and its attributes. Finally, we describe our procedures for fitting the model and evaluating its performance.

Steller sea lions in Glacier Bay National Park

Steller sea lions are distributed along the North Pacific rim from Japan to California, USA (Loughlin et al. 1987). The species exhibits central-place foraging behavior and typically aggregates at rocky sites and islands, from which they radiate and feed primarily on marine fishes and invertebrates (Womble and Sigler 2006). Sites may be occupied throughout the year or seasonally (Sease and York 2003), with seasonal movements driven by life-history events (e.g., pupping, breeding) and shifts in prey resources (Womble et al. 2005, 2009). In Alaska, Steller sea lions give birth to pups from

mid-June to early July. Steller sea lions have garnered considerable conservation attention in the last several decades due to population declines (Trites and Donnelly 2003). The species occurs in two distinct population segments: the western distinct population segment, west of 144° W, which is listed as endangered and the eastern distinct population segment, which was delisted in 2013 (National Marine Fisheries Service 2013; Allen and Angliss 2015). The Glacier Bay region represents a mixing zone between the endangered western Distinct Population Segment (wDPS) of Steller sea lions and the recently delisted eastern Distinct Population Segment (eDPS; Jemison et al. 2013; O’Corry-Crowe et al. 2014; Rehberg et al. 2018).

We confined our analysis of count data to terrestrial sites in Glacier Bay proper that were occupied consistently from May – September and where aerial photographic counts were performed regularly. This decision excluded a rookery at Graves Rocks along the outer coast of Glacier Bay and several sites that are commonly occupied during other periods of the year (Tarr Inlet, Gloomy Knob, Harbor Point, Cape Fairweather, and Point Carolus), leaving only South Marble Island (Figure 2.1). South Marble Island was initially colonized by sea lions around 1985 and was initially occupied only seasonally; however, since approximately 2001 Steller sea lions have been present at South Marble Island throughout the year (Womble et al. 2005; Womble et al. 2009, Mathews et al. 2011). From 2001 to 2004, the number of Steller sea lions at terrestrial sites in Glacier Bay were monitored during monthly aerial photographic surveys (Womble et al. 2005, Womble et al. 2009). Beginning in 2005, sea lions were only monitored during June and August in conjunction with harbor seal aerial photographic surveys (Womble et al. 2010). We assembled the aerial photographic counts data set by compiling 101 observations

made by National Park Service personnel with 5 observations from the National Marine Fisheries Service - Marine Mammal Laboratory Steller Sea Lion Count Database (2009-2013; Fritz et al. 2015). The data set included vertical aerial photographic counts of non-pups during the years 2001-2017, with the exception of 2006 (Figure 2.2).

Aerial surveys coincided with opportunistic sightings of Steller sea lions recorded during vessel surveys for humpback whales, which occur in park annually from April through October. During these surveys, a small vessel (4.9-6.7 m) actively searched for whales using prior knowledge of preferred habitat, and visual and auditory signals, from whales (e.g., breaching and spouting). There is a protocol for recording sightings of non-target marine mammal species during surveys that has remained relatively consistent through time (Gabriele and Lewis 2000, 2012; Keller et al. 2016). Observers record the location and estimated group size of marine mammals that pass within 100 m of the survey vessel and make efforts to avoid double counting. The study area for the spatial component of our analysis encompassed a 1,332 km² area, including the entirety of Glacier Bay and extending slightly into Icy Strait to the south (Figure 2.3). We compiled sighting and track point data from 610 survey days that occurred between May and September, 2006-2016. The mismatch of temporal overlap between this data set and that of the aerial counts did not pose a problem, because the in-water sighting data set still included 10 years and our specific objective was to estimate the average in-water distribution of sea lions. We omitted sightings of sea lions with >20 individuals, due to concerns about miscounting; these sightings accounted for ~0.4% of the total.

Model description

Basic structure

The abundance of sea lions during year i were assumed to be Poisson distributed with mean and variance (λ_i)

$$N_i \sim \text{Pois}(\lambda_i).$$

We modeled λ_i as a log-linear function of the annual site abundance parameters (α_i)

$$\log(\lambda_i) = \alpha_i$$

which were treated as fixed effects in the model (i.e., log abundance for each year was estimated separately). We linked counts of sea lions to abundance with a binomial distribution:

$$C_{it} \sim \text{Bin}(N_i, \gamma_{it}),$$

where γ_{it} is the probability of a sea lion being in attendance at the terrestrial site on day t of year i (Figure 2.4). By adopting this parameterization, we assumed that variation in counts at sites was driven solely by changes in attendance probability, and that the probability of detecting an individual sea lion given presence was equal to one. We believed this assumption to be reasonable because counts were determined by scrutinizing aerial photographs rather than counting from plane or water (Snyder et al. 2001; Boyd et al. 2010). We used abundance and attendance probabilities to derive the expected number of sea lions not in attendance at the terrestrial site, and therefore present in the water on a given day (W_{it}):

$$W_{it} = \lambda_i \cdot (1 - \gamma_{it}).$$

We assumed that the population of animals in the water at a given time were distributed across J non-overlapping sections, each with probability of occurrence π_j ($\sum_{j=1}^J \pi_j = 1$). We partitioned the study area into 60 non-overlapping sections, by

overlaying a 500 m grid on the study area, and then merging cells with an area less than 12.5 km² with their neighbors. Eleven of the sections were not visited by the whale survey vessel and included areas that are closed to vessels from May 1 to September 15 (Beardslee Islands, Hugh Miller Inlet, Rendu Inlet, and Adams Inlet), and areas in the East and upper West Arms of Glacier Bay. Finally, we assumed that in-water sightings of sea lions in each section were linked to the expected in-water abundance by a Poisson distribution:

$$S_{ijtr} \sim \text{Pois}(W_{it} \cdot \pi_j \cdot P_{ijtr}),$$

where S_{ijtr} is the number of sea lions sighted in year i , in section j , on day t , and during time-interval r ; P_{ijtr} is the probability of detecting an individual sea lion. We include the subscript r to signify that sections can be, and often are, visited multiple times in a day. We represented sightings as a Poisson process because they are rare events that occur with a frequency proportional to the expected number of sea lions expected to be present and that detection probability was tied to a measure of survey effort. Sea lions are highly mobile within the study area and constantly transitioning between land and water, thus modeling sightings in terms of a rate of encounter was more suitable than, for example, apportioning the in-water population at a given time across all sections using a multinomial distribution.

Incorporating predictor variables

The basic model structure provided a framework for evaluating relevant predictors of ecological and observation processes. Additional information were included by defining parameters using linear combinations of predictors and applying appropriate link functions. All linear predictors may also contain random error terms (random effects)

at different levels, however, care should be taken to ensure that chosen combinations of error terms and parameters are identifiable (Cole and McCrea 2016). We defined mean annual abundance using fixed effects via a log link function, however, many alternative parameterizations for mean abundance are also possible. For example, it would be relatively simple to represent mean abundance using a trend line or random intercept terms, as in a formal N-mixture model.

We modelled attendance probability (γ) via a logit link function, defined as.

$$\text{logit}(\eta) = \frac{1}{1 + e^{-(\eta)}}$$

where η is a linear predictor (e.g., $\beta_0 + \beta_1 X$). Hereafter we denote this transformation using the left-hand expression $\text{logit}(\eta)$. To identify an appropriate model for interpretation, we fit and evaluated six alternative linear predictors for attendance probability and used a model selection procedure to identify a top model. Candidate models included combinations linear and quadratic effects for the day of year (DOY), a linear effect for the number of hours before or after the nearest high tide ($TideHour$), as well as a null model. All linear predictor also included a daily normal random error term meant to account for extra-binomial variation (τ_t) which may be the result of behavioral heterogeneity (Dorazio et al. 2013). The global model with the full set of predictors was:

$$\text{logit}(\gamma_{it}) = \beta_0 + \beta_1 DOY_t + \beta_2 DOY_t^2 + \beta_3 TideHour_{it} + \tau_t,$$

$$\tau_t \sim \text{Norm}(0, \sigma_{attend}),$$

with β s denoting coefficients. We hypothesized that more sea lions would be attendance at lower tide (i.e., positive relationship with the number of hours to closest high tide), as this would relate to there being more space on land on which to haul out. It should be

noted that the *TideHour* is measured at a finer scale than *DOY* and known for all aerial counts and all survey intervals indexed by r , thus inclusion of this predictor would result in sub-daily predictions of in-water abundance. Attendance probability was the only parameter for which we compared alternative sets of predictors.

We related the distribution of sea lions across sections to several predictors using a multinomial logit link function (Agresti 2013; Royle and Converse 2014), where probability of occurrence for all but one of the sections ($J - 1$) is defined as:

$$\pi_j = \frac{e^{(\theta Z_j)}}{1 + \sum_{j=1}^{J-1} e^{(\theta Z_j)}}; j = \{1, 2, 3, \dots, J - 1\},$$

and π_j serves as a reference category. Section-specific probability of occurrence is defined by a linear combination with one or more coefficients (θ) and section-specific variables (Z). Similar to above, we denote this transformation using the left-hand expression $mlogit(\eta_j)$, where η_j is the section-specific linear predictor. Given that Steller sea lions are central-place foragers, we hypothesized that probability of occurrence in the study area was inversely related to the distance to sites where sea lions are known to haul-out of the water. We used distance to South Marble Island as a predictor of probability of occurrence in the water. In addition to including a site that is occupied throughout the year, we included distance to a seasonally occupied terrestrial site at Point Carolus, near the mouth of Glacier Bay (Figure 2). The function used to describe section-specific occurrence probability (π_j) was as follows:

$$mlogit(\pi_j) = \theta_1 D(\text{South Marble Island}_j) + \theta_2 D(\text{Point Carolus}_j),$$

where θ s are slope coefficients, and $D()$ is a function describes the distance, in kilometers, between the centroid of a survey cell and each of the two sites. The section nearest to Point Carolus served as the reference category in the model.

We modeled the probability of the survey vessel detecting a sea lion using a logit-linear regression with search time ($Time$) in each section as a predictor

$$\text{logit}(P_{ijtr}) = \delta_0 + \delta_1 Time_{ijtr} + \epsilon_{ijtr}, \epsilon_{ijtr} \sim \text{Norm}(0, \sigma_{detection}),$$

where δ s are coefficients and ϵ_{tr} is a random error term meant to account for additional observation error. We computed the time spent in each section by summarizing time-stamped vessel tracking data.

Model fitting

We fit the model using a likelihood-based approach, which entailed using optimization to identify the set of parameters that jointly maximize the likelihood of the observed data. A Bayesian approach could also be used to estimate parameters, as with all hierarchical models (Cressie et al. 2009). We calculated the joint likelihood for all data and parameters in the integrated model by combining the likelihood contributions of the count and in-water sighting portions of the model into a single objective function. We accomplished this by defining the objective function to be minimized as the sum of the negative log-likelihood contributions of the two portions of the model (ℓ_1 and ℓ_2):

$$\ell_{total} = \ell_1 + \ell_2,$$

where ℓ_{total} is the joint likelihood to be minimized using an optimization procedure. We carried out the analysis in the R statistical platform using the Template Model Builder (TMB) package, a tool that interprets user-defined C++ model templates and uses

automatic differentiation to efficiently compute the derivatives of a joint likelihood function while also enabling random effects to be estimated via the Laplace approximation (Kristensen et al. 2015; R Core Team 2017). For clarity, and because they are integrated out during model fitting, we ignore the random effects in the notation.

To compute the likelihood contribution of the count portion of the model we marginalized over the joint Binomial-Poisson likelihood. This process entailed summing the likelihood values over a wide range of possible abundances for each year in the manner shown below:

$$\ell_1 = -\log \left[\prod_{i=1}^I \sum_{N_i=\max(C_i)}^K \prod_{t=1}^{T_i} \text{Bin}(C_{it}|N_i, \gamma_t) \cdot \text{Pois}(N_i|\lambda_i) \right],$$

where ℓ_1 is negative log likelihood component for the count portion of the model, I is the number of years, K is the upper bound used for N , T_i is the number of replicate counts on the i th year. We examined the influence of our choice of K by comparing joint likelihood values and abundance estimates over a range of values, ultimately deciding that a value of 15,000 was suitably large (Dennis et al. 2014). We computed the negative log likelihood component for the in-water sighting portion of the model, more simply, as the product of likelihood of all sighting records assuming a Poisson distribution

$$\ell_2 = -\log \left[\prod_{i=1}^I \prod_{j=1}^J \prod_{t=1}^T \prod_{r=1}^R \text{Pois}(S_{ijtr}|W_{it} \cdot \pi_j \cdot P_{ijtr}) \right].$$

Minimization of the objective function, was performed using the base non-linear optimization function `nlnmb()`. To facilitate convergence, we normalized predictor

variables for attendance probability and detection effort and estimated σ parameters on the log scale.

Attendance Probability (γ) Model Selection

As noted above, we were interested in identifying a top model or models on which to base inferences about the sea lion population in Glacier Bay. We ranked six different candidate models using Akaike' information criterion. These models represented six alternative sets of predictors defining attendance probability; all other sets of predictors were held constant. We based our determination of a suitable top model on recommendations of Burnham and Anderson (2002), and we considered models within the 2.0 AIC of the top model as competitive.

Model Evaluation

After identifying a top model for interpretation, we evaluated its performance using a simple sensitivity analysis and by comparing model predictions of abundance and attendance probability to those reported in the literature. We were interested in examining the effect that inclusion of sighting data would have on predictions of abundance and attendance, so we compared predictions from the final model with those of a reduced version of the model, in which we omitted in-water sighting data. This comparison enabled us to examine the influence of the in-water sighting data on both the estimated relationships and the precision of estimates. We compared model estimates of abundance to indices of abundance from monitoring surveys. Past studies estimated attendance probabilities by making detailed observations at haulouts or by affixing tags to sea lions, some of which were equipped to record the time spent in the water (Merrick and Loughlin 1997; Milette 1999; Rehberg, et al. 2009; Rehberg et al. 2018). Although, many

of these studies focused on the foraging behavior primarily from postpartum or lactating females at breeding sites, we assumed that attendance estimates of this age-sex class would provide an indication of the model's realism. The estimated coefficients and associated uncertainty were also used in determining the degree to which the model reasonably reflected abundance, distribution, and sighting processes.

Results

We successfully fitted the pinniped abundance and distribution model to the Glacier Bay sea lion data set to the six different candidate models. Model selection using AIC suggested substantial support for the two models containing quadratic day-of-year effects, including the global model and a model with only a quadratic day-of-year effect (Table 2.2). We chose to interpret the model ranked second, which described only the quadratic day-of-year effect:

$$\text{logit}(\gamma_{it}) = \beta_0 + \beta_1 \text{DOY}_t + \beta_2 \text{DOY}_t^2 + \tau_t .$$

We based this decision on the recommendation of Burnham and Anderson (2002) that if two competing models differ by one parameter and difference in likelihoods is minimal, then the model with fewer parameters is preferred. This decision was further justified by the observation that the 95% confidence interval for the *TideHour* coefficient in the global model overlapped zero and was in the direction opposite that which we had hypothesized.

Our selected model produced parameter estimates that appeared to reasonably describe the population trend at terrestrial sites and in-water distribution of Steller sea lions. The model indicated that sea lion abundance at South Marble Island increased over

the study period from 2001 to 2017 (Table 2.2; Figure 2.5). The overall abundance and attendance patterns were similar for the fully integrated model compared to the reduced version that relied solely on aerial counts. Abundance estimates were more precise for the reduced version model; however, the fully integrated model was able to estimate the annual abundance for 2006, based on in-water sighting data alone. Attendance probability predictions were comparable for the models with and without in-water sighting data, although predictions from the fully integrated model were more precise (Figure 2.6). Estimated attendance probability began at 30% in May, peaked at the end of June at 73%, and then declined to 31% by the end of August (Figure 2.6). There was considerable uncertainty in these estimates, however, with the 95% confidence interval for attendance probability spanning values from 37% to 67% for the entire season (May-August). Estimates for attendance coefficients were also more precise for the combined model (Table 2.2).

Time that a survey vessel spent in the section was found to be positively related to the probability of detection of an individual sea lion (Table 2.3). The coefficient for the effect of search time indicated that odds of sighting an individual sea lion increased by 51% (32%, 73% [95% LCL, UCL]) for every 30 minutes that the survey vessel was present. The estimated effect of predictor variables on occurrence and detection probability matched our hypotheses and were consistent with central-place foraging behavior. Coefficients for the effect of distance to South Marble Island and secondary sites were both significantly less than zero, suggesting that the geographic location of the site influenced the in-water distribution of sea lions (Table 2.3). However, the effect of proximity to Point Carolus was greater and more precisely estimated than at South Marble Island. Interpretation of distribution coefficients is somewhat difficult considering that the two predictor variables are based on the distance to two different sites and are thus non-independent. The clearest possible interpretation of the coefficients comes from computing an odds ratio for the slope terms separately and expressing changes in the odds of occurrence as a percentage ($100\% \times [1 - e^\theta]$). Based on this approach, odds of a sea lion being present in a cell diminish by 3.5% and 5.6% with every kilometer traveled from South Marble Island and Point Carolus, respectively. The influence of these parameters on prediction is more easily interpretable, however, by examining a map of in-water occurrence probability (π) across the study area (Figure 2.7). This map describes the probabilities that a given sea lion in the water would be found in each cell; those not in the water are assumed to be present at South Marble Island.

The abundance and attendance probability estimates were comparable to those reported in the literature. The pattern of increasing abundance at South Marble Island was

consistent with the findings of Mathews et al. (2011) during the period when the two studies overlapped; however, there were decreases in estimated abundance in 2016 and 2017 that differed from the trend line reported by Mathews et al. (2011). Attendance probabilities reported in previous studies fell within the range estimated by our model. For example, Merrick and Loughlin (1997), Rehberg et al. (2009), and Milette (1999) reported that female Steller sea lions spent on average 47%, 52%, and 59% of their time on land, respectively. The main discrepancies between our model predictions and previous work were related to seasonal patterns in attendance. Several studies that analyzed counts of Steller sea lions at South Marble Island in the early 2000s described a bimodal pattern with peaks in the spring and fall (Womble et al. 2009; Mathews et al. 2011). In contrast, our model estimated a mid-season peak in attendance (mid-June to mid-July).

Discussion

The objective of this study was to develop a pinniped abundance and distribution model for situations in which both in-water sighting information and counts at terrestrial sites are available. We used a hierarchical modelling framework to accomplish this task, which consisted of separating ecological and sampling-related processes into separate tiers of a model and then specifying intuitive connections between data sets and a shared set of parameters (Royle and Dorazio 2008; Cressie et al. 2009). The key assumption linking these data sets was that attendance at a terrestrial site and availability to be sighted in the water were mutually exclusive states. We demonstrated the utility of this framework by applying it to Steller sea lions in Glacier Bay, Alaska. The clearest benefits

of our approach were improved precision in attendance predictions, the ability to estimate abundance for 2006 in lieu of any aerial count data, and the ability to characterize in-water density of sea lions in the bay over the course of the spring and summer.

Model predictions of abundance and attendance probabilities showed general agreement with the range of estimates reported in the literature. It bears mentioning, however, that the attendance probability estimates to which we compared our model outputs were obtained from studies that took place at different times of year, different geographic areas, and a limited sex and age range of sea lions (Merrick and Loughlin 1997; Milette 1999; Rehberg, et al. 2009). The greatest inconsistency between our findings and previous research was with respect to seasonal attendance patterns at South Marble Island (Womble et al. 2009; Mathews et al. 2011). Our model identified a convex seasonal attendance relationship for the time span from 2001 to 2017, whereas these other studies described patterns with relatively low mid-season attendance at the same location from 2001 to 2004. The inconsistency was somewhat surprising considering that all analyses shared at least some of the same aerial count data. We did not regard the difference between our model and these other studies as indicative of poor performance, considering that our model included counts from thirteen additional years. It is possible that the attendance pattern identified for the early 2000s has since shifted and that our model instead detected a prevailing pattern with a mid-season peak.

The abundance and distribution model that we describe in this paper combines elements from several modelling approaches, specifically N-mixture and spatial capture-recapture models and may be applied to other taxa. The count portion of the model broadly resembles an N-mixture model in that counts at terrestrial sites are viewed as a

binomial random variable and a function of the underlying abundance parameter. The traditional N-mixture model uses replicated counts to simultaneously estimate detection probability and abundance, assuming that nondetection is the sole explanation for the variation in observed counts. In contrast, our model assumes perfect detection and attributes variation in counts to changes in the availability of individuals to be counted by an aerial survey (i.e., temporary emigration). Availability and its complement, temporary emigration, are sometimes viewed as nuisance parameters in hierarchical models because they can be used to account for transitions of individuals into unobservable states (Kendall and Nichols 2002; Kery and Royle 2015). We thought it more appropriate to apply the term “attendance probability” for this model because transitions occur between two observable states, water and land, and the term “attendance” is commonly used in the pinniped literature to refer to occurrence at a terrestrial site (Milette and Trites 2003; Meise et al. 2014). Although this study focuses on developing a model for monitoring pinnipeds, this or a similar framework could also be applied to other species. Seabird species are one such candidate for this type of model, because they aggregate at terrestrial breeding colony sites, where they may be easily counted, but are also sightable from vessels during foraging trips at-sea.

Although our model uses only counts of unmarked (unidentifiable) individuals, the sighting portion of the model bears some resemblance to spatial capture-recapture models. Spatial capture recapture models relate observations of animals to their distance from an estimated activity center, and derive abundance estimates by summing the number of such centers in the study area (Royle et al. 2013; Royle and Converse 2014). The sighting portion of the pinniped model can be parameterized in a manner that is

conceptually similar, specifically when distance to the terrestrial site is used as a predictor of distribution in water. In this case, the location of activity centers is fixed at terrestrial sites rather than estimated, and the number of such centers is also informed by the count sub-model. Another way in which our model broadly relates to spatial capture-recapture approaches is in its reliance on unstructured spatial sampling, in which surveyors roam the study area recording animal sightings or scats (Thompson et al. 2012; Broekhuis and Gopaldaswamy 2016). Some models that rely on unstructured surveys are also defined using spatial capture-recapture terminology, even referring to grid cells as “conceptual traps” (Russell et al. 2012). Our approach does not build individual encounter histories from sightings in cells as these models do, but instead uses replicate visits and measures of effort within grid cells to provide information regarding detection and occurrence probability.

The realism and utility of the model that we describe is predicated on assumptions regarding latent ecological and data collection processes, many of which it inherits from the approaches that we discussed above. The most significant assumption of the model is that the population remains closed during each season and that variation in counts only reflects changes in attendance probability and not, for example, imperfect detection or movement of individuals among sites (Dénes et al. 2015). Violation of this assumption is likely to result in additional heterogeneity in the attendance parameter, which could obscure relevant patterns in the attendance process and lead to positive bias in abundance estimates (Barker et al. 2017; Duarte et al. 2018). Another key assumption of the model is that the spatial extent of the study area encompasses the home range within which pinnipeds travel during each season and does not overlap with the home ranges of

populations at other terrestrial sites. If the second assumption is violated, then estimates of individual detection probability will be affected as well as abundance estimates. The sighting portion of the model assumes that counts of animals in cells are independent after adjusting for covariate effects, the pinniped species is not miscounted or misidentified by surveyors, and that pinnipeds are neither avoidant of or attracted to the survey vessel. An additional assumption of unstructured sampling approaches is that survey routes are independent of the density (Thompson et al. 2012).

The data used in the Steller sea lion case study satisfied the model assumptions reasonably well, considering our objective of broadly characterizing trends in abundance and spatial distribution. There are several important aspects of sea lion ecology, however, that are not captured by the model, and some assumptions could not be assessed. We could not readily assess the geographic closure assumptions because of the paucity of detailed movement or demographic information on the South Marble Island population over the study period; however, some degree of within-season movement among nearby sites was likely, based on previous studies (Jemison et al. 2013, 2018; Rehberg et al. 2018). We also assumed that sightings of individuals were independent although Steller sea lions are known to forage and are sighted in groups (Fiscus and Baines 1966; Gende et al. 2001; Sigler et al. 2004). The greater estimated effect of proximity to Point Carolus relative to that of South Marble Island was another unexpected result from the model. This was surprising considering that substantially fewer sea lions have been observed hauled-out at Point Carolus, relative to South Marble Island. The most likely explanation is that distance to Point Carolus is correlated with a latent variable that also predicts the in-water occurrence of sea lions, most likely having to do with prey availability. Sea lions

have been observed in the vicinity Point Carolus in late summer and autumn, which coincides with the migration of Pacific salmon (*Oncorhynchus* spp.) through Cross Sound and Icy Strait from the Gulf of Alaska (Womble et al. 2009). In addition, a shallow glacial sill at the mouth of Glacier Bay promotes localized upwelling and increased productivity in the Sitkaday Narrows, an area of intense tidal currents and mixing (Etherington et al. 2007). In addition, most of the water that is entrained into Glacier Bay comes in on the west side of the mouth, producing a headland wake system that has been positively related to quality of foraging habitat for whales (Chenoweth et al. 2011), and fish schools are commonly observed near Point Carolus during aerial surveys (Jamie Womble, personal observation).

A major advantage of hierarchical models is that there are a number of extensions to the model that can be made to improve estimates and confront potential assumption violations. With respect to the sea lion case study, there are additional sources of information that could be leveraged to improve the model. For example, uncertainties regarding inter-seasonal movement among sites could be reduced by incorporating transition probability estimates obtained via telemetry (Rehberg et al. 2018) or mark-resight studies (Jemison et al., 2013). The precision of the model could also be improved by incorporating additional types of data, including counts of pups or observations gathered using more error-prone methods (e.g., counts from vessels), provided that an additional detection parameter be included in the model. The issue of non-independent sightings could be addressed by directly modeling the process that determines group size (Martin et al. 20011; Schmidt and Rattenbury 2018).

This study illustrates the value of a hierarchical modelling approach for characterizing abundance and spatial distribution when multiple data sources are available. This approach is particularly useful for pinniped monitoring programs because of the behavioral complexity of these animals and the expense and logistical challenges associated with conducting population surveys (Ver Hoef and Frost 2003; Boyd et al. 2010). The modeling framework presented in this paper, provides a method for supplementing these surveys with spatially explicit in-water sighting data and for creating model-based predictions that provide a full accounting of where populations of pinnipeds occur on land and in the water. Without the integrated model for Steller sea lion in Glacier Bay it would not have been possible abundance estimate for 2006 or to have identified a seasonal attendance pattern that will be instrumental for reconstructing in-water density patterns across all study years. Other possible management application for this type of model would be for estimating the degree of overlap between pinnipeds and commercial fishing operations, based on the location and occupancy status at terrestrial haul-out sites. Furthermore, species with similar ecology and types of monitoring data available (e.g., sea birds) may also benefit from the application of this framework.

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References

- Abadi, F., Gimenez, O., Arlettaz, R., and Schaub, M. 2010. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology* 91(1): 7–14. doi:10.1890/08-2235.1.
- Agresti, A. 2013. *Categorical Data Analysis*. John Wiley & Sons.
- Allen, B.M., and Angliss, R.P. 2015. Alaska marine mammal stock assessments, 2014. NOAA technical memorandum NMFS-AFSC: 301.
- Barker, R.J., Schofield, M.R., Link, W.A., and Sauer, J.R. 2017. On the reliability of N-mixture models for count data. *Biometrics* 74(1): 369–377. doi:10.1111/biom.12734.
- Besbeas, P., Borysiewicz, R.S., and Morgan, B.J.T. 2009. Completing the ecological jigsaw. *In* modeling demographic processes in marked populations. Springer, Boston, MA. pp. 513–539. doi:10.1007/978-0-387-78151-8_22.
- Boyd, I.L., Bowen, W.D., and Iverson, S.J. 2010. *Marine Mammal Ecology and Conservation: A Handbook of Techniques*. Oxford University Press.
- Broekhuis, F., and Gopalaswamy, A.M. 2016. Counting cats: spatially explicit population estimates of cheetah (*Acinonyx jubatus*) using unstructured sampling data. *PLOS ONE* 11(5): e0153875. doi:10.1371/journal.pone.0153875.
- Buckland, S.T., Newman, K.B., Thomas, L., and Koesters, N.B. 2004. State-space models for the dynamics of wild animal populations. *Ecol. Model.* 171(1): 157–175. doi:10.1016/j.ecolmodel.2003.08.002.
- Burnham, K.P. and Anderson, D.R. 2002. *Model selection and inference: a practical information-theoretic approach*. New York: Springer-Verlag.
- Chandler, R.B., and Clark, J.D. 2014. Spatially explicit integrated population models. *Methods Ecol. Evol.* 5(12): 1351–1360. doi:10.1111/2041-210X.12153.
- Chandler, R.B., Royle, J.A., and King, D.I. 2011. Inference about density and temporary emigration in unmarked populations. *Ecology* 92(7): 1429–1435. doi:10.1890/10-2433.1.
- Chenoweth, E.M., Gabriele, C.M., and Hill, D.F. 2011. Tidal influences on humpback whale habitat selection near headlands. *Mar. Ecol. Prog. Ser.* 423: 279–289.
- Cole, D.J., and McCrea, R.S. 2016. Parameter redundancy in discrete state-space and integrated models. *Biom. J.* 58(5): 1071–1090. doi:10.1002/bimj.201400239.
- Cressie, N., Calder, C.A., Clark, J.S., Hoef, J.M.V., and Wikle, C.K. 2009. Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. *Ecol. Appl.* 19(3): 553–570. doi:10.1890/07-0744.1.
- Dail, D., and Madsen, L. 2011. Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* 67(2): 577–587.

- Dénes, F.V., Silveira, L.F., and Beissinger, S.R. 2015. Estimating abundance of unmarked animal populations: accounting for imperfect detection and other sources of zero inflation. *Methods Ecol. Evol.* 6(5): 543–556. doi:10.1111/2041-210X.12333.
- Dennis, E.B., Morgan, B.J.T., and Ridout, M.S. 2014. Computational aspects of N-mixture models. *Biometrics* 71(1): 237–246. doi:10.1111/biom.12246.
- Dorazio, R.M., Martin, J. & Edwards, H.H. 2013. Estimating abundance while accounting for rarity, correlated behavior, and other sources of variation in counts. *Ecology*, 94, 1472-1478.
- Duarte, A., Adams, M.J., and Peterson, J.T. 2018. Fitting N-mixture models to count data with unmodeled heterogeneity: bias, diagnostics, and alternative approaches. *Ecol. Model.* 374: 51–59. doi:10.1016/j.ecolmodel.2018.02.007.
- Etherington, L.L., Hooge, P.N., Hooge, E.R., and Hill, D.F. 2007. Oceanography of Glacier Bay, Alaska: Implications for biological patterns in a glacial fjord estuary. *Estuaries Coasts* 30(6): 927–944. doi:10.1007/BF02841386.
- Fiscus, C.H., and Baines, G.A. 1966. Food and feeding behavior of Steller and California sea lions. *J. Mammal.* 47(2): 195–200. doi:10.2307/1378115.
- Fritz, L., Sweeney, K., Lynn, M., Gelatt, T., Gilpatrick, J., and Towell, R. 2015. Counts of Alaska Steller sea lion adult and juvenile (non-pup) conducted on rookeries and haul-outs in Alaska Aleutian Islands, Bering Sea, and others from 1904-01-01 to 2015-07-18 (NCEI Accession 0128190). NOAA National Centers for Environmental Information. doi:10.7289/V54F1NP1.
- Gabriele, C.M., and Lewis, T.M. 2000. Summary of opportunistic marine mammal sightings in Glacier Bay and Icy Strait 1994-1999. Glacier Bay National Park and Preserve. National Park Service, Gustavus, AK.
- Gabriele, C.M., and Lewis, T.M. 2012. Summary of opportunistic marine mammal sightings in Glacier Bay and adjacent waters 2000-2010. Progress report. Glacier Bay National Park and Preserve. National Park Service, Gustavus, AK.
- Gende, S., Womble, J., MF, W., and BH, M. 2001. Cooperative foraging by Steller Sea Lions, *Eumetopias jubatus*. *Can. Field Nat.* 115: 355–356.
- Gu, W., and Swihart, R.K. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. *Biol. Conserv.* 116(2): 195–203. doi:10.1016/S0006-3207(03)00190-3.
- Hegel, T.M., Cushman, S.A., Evans, J., and Huettmann, F. 2010. Current State of the Art for Statistical Modelling of Species Distributions. In *Spatial Complexity, Informatics, and Wildlife Conservation*. Springer, Tokyo. pp. 273–311. doi:10.1007/978-4-431-87771-4_16.
- Herr, H., Scheidat, M., Lehnert, K., and Siebert, U. 2009. Seals at sea: modelling seal distribution in the German bight based on aerial survey data. *Mar. Biol.* 156(5): 811. doi:10.1007/s00227-008-1105-x.

- Himes Boor, G.K., and Small, R.J. 2012. Steller sea lion spatial-use patterns derived from a Bayesian model of opportunistic observations. *Mar. Mammal Sci.* 28(4): E375–E403. doi:10.1111/j.1748-7692.2011.00541.x.
- Jemison, L.A., Pendleton, G.W., Fritz, L.W., Hastings, K.K., Maniscalco, J.M., Trites, A.W., and Gelatt, T.S. 2013. Inter-population movements of Steller sea lions in Alaska with implications for population separation. *PLOS ONE* 8(8): e70167. doi:10.1371/journal.pone.0070167.
- Jemison, L.A., Pendleton, G.W., Hastings, K.K., Maniscalco, J.M., and Fritz, L.W. 2018. Spatial distribution, movements, and geographic range of Steller sea lions (*Eumetopias jubatus*) in Alaska. *PLOS ONE* 13(12): e0208093. doi:10.1371/journal.pone.0208093.
- Keller, K.B., Gabriele, C.M., Pearson, H.C., Neilson, J.L., and Keller, E.K. 2016. Sighting frequency and distribution of marine mammals opportunistically recorded in Glacier Bay, Alaska and adjacent waters (2005-2014). *Prog. Rep.*: 40.
- Kellner, K.F., and Swihart, R.K. 2014. Accounting for imperfect detection in ecology: a quantitative review. *PLOS ONE* 9(10): e111436. doi:10.1371/journal.pone.0111436.
- Kendall, W.L., and Nichols, J.D. 2002. Estimating state-transition probabilities for unobservable states using capture–recapture/resighting data. *Ecology* 83(12): 3276–3284. doi:10.1890/0012-9658(2002)083[3276:ESTPFU]2.0.CO;2.
- Kery, M., and Royle, J.A. 2015. *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1*. Academic Press.
- Kery, M., and Schaub, M. 2011. *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Academic Press.
- Kovacs, K.M., Aguilar, A., Aurioles, D., Burkanov, V., Campagna, C., Gales, N., Gelatt, T., Goldsworthy, S.D., Goodman, S.J., Hofmeyr, G.J.G., Härkönen, T., Lowry, L., Lydersen, C., Schipper, J., Sipilä, T., Southwell, C., Stuart, S., Thompson, D., and Trillmich, F. 2012. Global threats to pinnipeds. *Mar. Mammal Sci.* 28(2): 414–436. doi:10.1111/j.1748-7692.2011.00479.x.
- Krebs, C.J. 2009. *Ecology: the Experimental Analysis of Distribution and Abundance*. Pearson Benjamin Cummings.
- Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., and Bell, B. 2015. TMB: automatic differentiation and Laplace approximation. *J. Stat. Softw.*
- Loughlin, T.R., Perez, M.A., and Merrick, R.L. 1987. *Eumetopias jubatus*. *Mamm. Species* (283): 1–7. doi:10.2307/3503908.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., and Langtimm, C.A. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83(8): 2248–2255. doi:10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2.

- Martin, J., Royle, J.A., MacKenzie, D.I., Edwards, H.H., Kery, M. & Gardner, B. 2011. Accounting for non-independent detection when estimating abundance of organisms with a Bayesian approach. *Methods in Ecology and Evolution*, 2, 595-601.
- Mathews, E.A., Womble, J.N., Pendleton, G.W., Jemison, L.A., Maniscalco, J.M., and Streveler, G. 2011. Population growth and colonization of Steller sea lions in the Glacier Bay region of southeastern Alaska: 1970s–2009. *Mar. Mammal Sci.* 27(4): 852–880.
- Meise, K., Piedrahita, P., Krüger, O., and Trillmich, F. 2014. Being on time: size-dependent attendance patterns affect male reproductive success. *Anim. Behav.* 93: 77–86. doi:10.1016/j.anbehav.2014.04.019.
- Merrick, R.L., and Loughlin, T.R. 1997. Foraging behavior of adult female and young-of-the-year Steller sea lions in Alaskan waters. *Can. J. Zool.* 75(5): 776–786. doi:10.1139/z97-099.
- Milette, L.L. 1999. Behaviour of lactating Steller sea lions (*Eumetopias jubatus*) during breeding season: a comparison between a declining and stable population in Alaska. PhD Thesis, University of British Columbia.
- Milette, L.L., and Trites, A.W. 2003. Maternal attendance patterns of Steller sea lions (*Eumetopias jubatus*) from stable and declining populations in Alaska. *Can. J. Zool.* 81(2): 340–348. doi:10.1139/z03-008.
- Nadeem, K., Moore, J.E., Zhang, Y., and Chipman, H. 2016. Integrating population dynamics models and distance sampling data: a spatial hierarchical state-space approach. *Ecology* 97(7): 1735–1745. doi:10.1890/15-1406.1.
- National Marine Fisheries Service. 2013. Status review of the eastern distinct population segment of Steller sea lion (*Eumetopias jubatus*). National Marine Fisheries Service, Juneau, AK.
- O’Corry-Crowe, G., Gelatt, T., Rea, L., Bonin, C., and Rehberg, M. 2014. Crossing to safety: dispersal, colonization and mate choice in evolutionarily distinct populations of Steller sea lions, *Eumetopias jubatus*. *Mol. Ecol.* 23(22): 5415–5434. doi:10.1111/mec.12944.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/>.
- Read, A.J. 2008. The Looming Crisis: Interactions between Marine Mammals and Fisheries. *J. Mammal.* 89(3): 541–548. doi:10.1644/07-MAMM-S-315R1.1.
- Rehberg, Andrews, R.D., Swain, U.G., and Calkins, D.G. 2009. Foraging behavior of adult female Steller sea lions during the breeding season in Southeast Alaska. *Mar. Mammal Sci.* 25(3): 588–604. doi:10.1111/j.1748-7692.2008.00278.x.

- Rehberg, M., Jemison, L., Womble, J.N., and O’Corry-Crowe, G. 2018. Winter movements and long-term dispersal of Steller sea lions in the Glacier Bay region of Southeast Alaska. *Endanger. Species Res.* 37: 11–24. doi:10.3354/esr00909.
- Rehberg, M.J., Andrews, R.D., Swain, U.G., and Calkins, D.G. 2009. Foraging behavior of adult female Steller sea lions during the breeding season in Southeast Alaska. *Mar. Mammal Sci.* 25(3): 588–604. doi:10.1111/j.1748-7692.2008.00278.x.
- Royle, J.A. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60(1): 108–115.
- Royle, J.A., Chandler, R.B., Sollmann, R., and Gardner, B. 2013. *Spatial capture-recapture*. Academic Press.
- Royle, J.A., and Converse, S.J. 2014. Hierarchical spatial capture–recapture models: modelling population density in stratified populations. *Methods Ecol. Evol.* 5(1): 37–43.
- Royle, J.A., and Dorazio, R.M. 2008. *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Academic Press.
- Russell, R.E., Royle, J.A., Desimone, R., Schwartz, M.K., Edwards, V.L., Pilgrim, K.P., and Mckelvey, K.S. 2012. Estimating abundance of mountain lions from unstructured spatial sampling. *J. Wildl. Manage.* 76(8): 1551–1561. doi:10.1002/jwmg.412.
- Schaub, M., Gimenez, O., Sierro, A., and Arlettaz, R. 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conserv. Biol.* 21(4): 945–955. doi:10.1111/j.1523-1739.2007.00743.x.
- Schmidt, J.H., and Rattenbury, K.L. 2018. An open-population distance sampling framework for assessing population dynamics in group-dwelling species. *Methods Ecol. Evol.* 9(4): 936–945.
- Scott, J.M., Heglund, P., and Morrison, M.L. 2002. *Predicting Species Occurrences: Issues of Accuracy and Scale*. Island Press.
- Sease, J.L., and York, A.E. 2003. Seasonal distribution of Steller’s sea lions at rookeries and haul-out sites in Alaska. *Mar. Mammal Sci.* 19(4): 745–763. doi:10.1111/j.1748-7692.2003.tb01128.x.
- Sigler, M.F., Womble, J.N., and Vollenweider, J.J. 2004. Availability to Steller sea lions (*Eumetopias jubatus*) of a seasonal prey resource: a prespawning aggregation of eulachon (*Thaleichthys pacificus*). *Can. J. Fish. Aquat. Sci.* 61(8): 1475–1484. doi:10.1139/f04-086.
- Small, R.J., Pendleton, G.W., and Pitcher, K.W. 2003. Trends in abundance of Alaska harbor seals, 1983–2001. *Mar. Mammal Sci.* 19(2): 344–362.

- Snyder, G.M., Pitcher, K.W., Perryman, W.L., and Lynn, M.S. 2001. Counting Steller sea lion pups in Alaska: an evaluation of mediumformat, color aerial photography. *Mar. Mammal Sci.* 17(1): 136–146. doi:10.1111/j.1748-7692.2001.tb00984.x.
- Thompson, C.M., Royle, J.A., and Garner, J.D. 2012. A framework for inference about carnivore density from unstructured spatial sampling of scat using detector dogs. *J. Wildl. Manag.* 76(4): 863–871. doi:10.1002/jwmg.317.
- Trites, A.W., and Donnelly, C.P. 2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. *Mammal Rev.* 33(1): 3–28. doi:10.1046/j.1365-2907.2003.00009.x.
- Valente, J.J., Hutchinson, R.A., and Betts, M.G. 2017. Distinguishing distribution dynamics from temporary emigration using dynamic occupancy models. *Methods Ecol. Evol.* 8(12): 1707–1716. doi:10.1111/2041-210X.12840.
- Ver Hoef, J.M., Cameron, M.F., Boveng, P.L., London, J.M., and Moreland, E.E. 2014. A spatial hierarchical model for abundance of three ice-associated seal species in the eastern Bering Sea. *Stat. Methodol.* 17: 46–66. doi:10.1016/j.stamet.2013.03.001.
- Ver Hoef, J.M., and Frost, K.J. 2003. A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska. *Environ. Ecol. Stat.* 10(2): 201–219.
- Vincent, C., Huon, M., Caurant, F., Dabin, W., Deniau, A., Dixneuf, S., Dupuis, L., Elder, J.-F., Fremau, M.-H., Hassani, S., Hemon, A., Karpouzopoulos, J., Lefeuvre, C., McConnell, B.J., Moss, S.E.W., Provost, P., Spitz, J., Turpin, Y., and Ridoux, V. 2017. Grey and harbour seals in France: Distribution at sea, connectivity and trends in abundance at haulout sites. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 141: 294–305. doi:10.1016/j.dsr2.2017.04.004.
- Williams, P.J., Hooten, M.B., Womble, J.N., Esslinger, G.G., Bower, M.R., and Hefley, T.J. 2017. An integrated data model to estimate spatiotemporal occupancy, abundance, and colonization dynamics. *Ecology* 98(2): 328–336. doi:10.1002/ecy.1643.
- Womble, J.N., and Sigler, M.F. 2006. Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. *Mar. Ecol. Prog. Ser.* 325: 281–293.
- Womble, J.N., Sigler, M.F., and Willson, M.F. 2009. Linking seasonal distribution patterns with prey availability in a central-place forager, the Steller sea lion. *J. Biogeogr.* 36(3): 439–451. doi:10.1111/j.1365-2699.2007.01873.x.
- Womble, J.N., Willson, M.F., Sigler, M.F., Kelly, B.P., and VanBlaricom, G.R. 2005. Distribution of Steller sea lions *Eumetopias jubatus* in relation to spring-spawning fish in SE Alaska. *Mar. Ecol. Prog. Ser.* 294: 271–282.

Yamaura, Y., and Royle, J.A. 2017. Community distance sampling models allowing for imperfect detection and temporary emigration. *Ecosphere* 8(12).
doi:10.1002/ecs2.2028.

Tables

Table 2.1 Ranking of integrated abundance and distribution models for Steller sea lions in the vicinity of Glacier Bay, Alaska based on AIC. The top model, interpreted in the remainder of the analysis, is shown in bold.

Model	AIC	Δ AIC	ℓ_{total}	k
$\lambda(t) \pi(Distance) \gamma(DOY^2 + TideHour) P(Time)$	9496.4	0	4721.2	27
$\lambda(t) \pi(Distance) \gamma(DOY^2) P(Time)$	9496.7	0.31	4722.3	26
$\lambda(t) \pi(Distance) \gamma(DOY + TideHour) P(Time)$	9538.2	41.85	4743.1	26
$\lambda(t) \pi(Distance) \gamma(TideHour) P(Time)$	9539.7	43.29	4744.8	25
$\lambda(t) \pi(Distance) \gamma(DOY) P(Time)$	9539.9	43.49	4744.9	25
$\lambda(t) \pi(Distance) \gamma(.) P(Time)$	9542.9	46.48	4747.4	24

Table 2.2 Abundance estimates from an integrated abundance and distribution model for Steller sea lions in the vicinity of Glacier Bay, Alaska. LCL and UCL denote the lower and upper 95% confidence limits, respectively. The asterisk in 2006 denotes the only year for which no aerial count data were available.

Year	Abundance	LCL	UCL
2001	511	465	557
2002	673	630	716
2003	861	648	1,074
2004	1,046	681	1,412
2005	908	622	1,194
2006*	345	133	557
2007	445	270	619
2008	915	806	1,024
2009	1,312	1,178	1,446
2010	2,183	2,062	2,303
2011	1,341	1,193	1,490
2012	1,284	1,079	1,489
2013	865	747	983
2014	2,527	2,273	2,781
2015	2,471	2,277	2,666
2016	1,447	1,192	1,701

Table 2.3 Selected parameter estimates from an integrated abundance and distribution model for Steller sea lions in the vicinity of Glacier Bay, Alaska. LCL and UCL denote the lower and upper 95% confidence limits, respectively.

Parameter	Description	Estimate	Standard Error	LCL	UCL
Integrated Model					
<u>Attendance (γ)</u>					
β_0	Intercept	1.04	0.17	0.71	1.38
β_1	Day of year linear effect	-0.37	0.09	-0.56	-0.19
β_2	Day of year quadratic effect	-0.70	0.10	-0.90	-0.50
σ_{attend}	Attendance standard deviation	0.88	0.06	0.76	1.00
<u>Occurrence (π)</u>					
θ_1	Distance South Marble Island	-0.035	0.010	-0.055	-0.016
θ_2	Distance to Point Carolus	-0.058	0.007	-0.072	-0.044
<u>Detection (P)</u>					
δ_0	Intercept	-10.5	0.165	-10.9	-10.2
δ_1	Time in area	0.29	0.07	0.15	0.42
$\sigma_{detection}$	Detection standard deviation	6.78	0.30	6.20	7.37
Reduced Model (Aerial counts only)					
<u>Attendance (γ)</u>					
β_0	Intercept	1.36	0.22	0.92	1.79
β_1	Day of year linear effect	-0.59	0.13	-0.85	-0.32
β_2	Day of year quadratic effect	-0.86	0.15	-1.16	-0.56
σ_{attend}	Attendance standard deviation	1.27	0.12	1.04	1.49

Figures

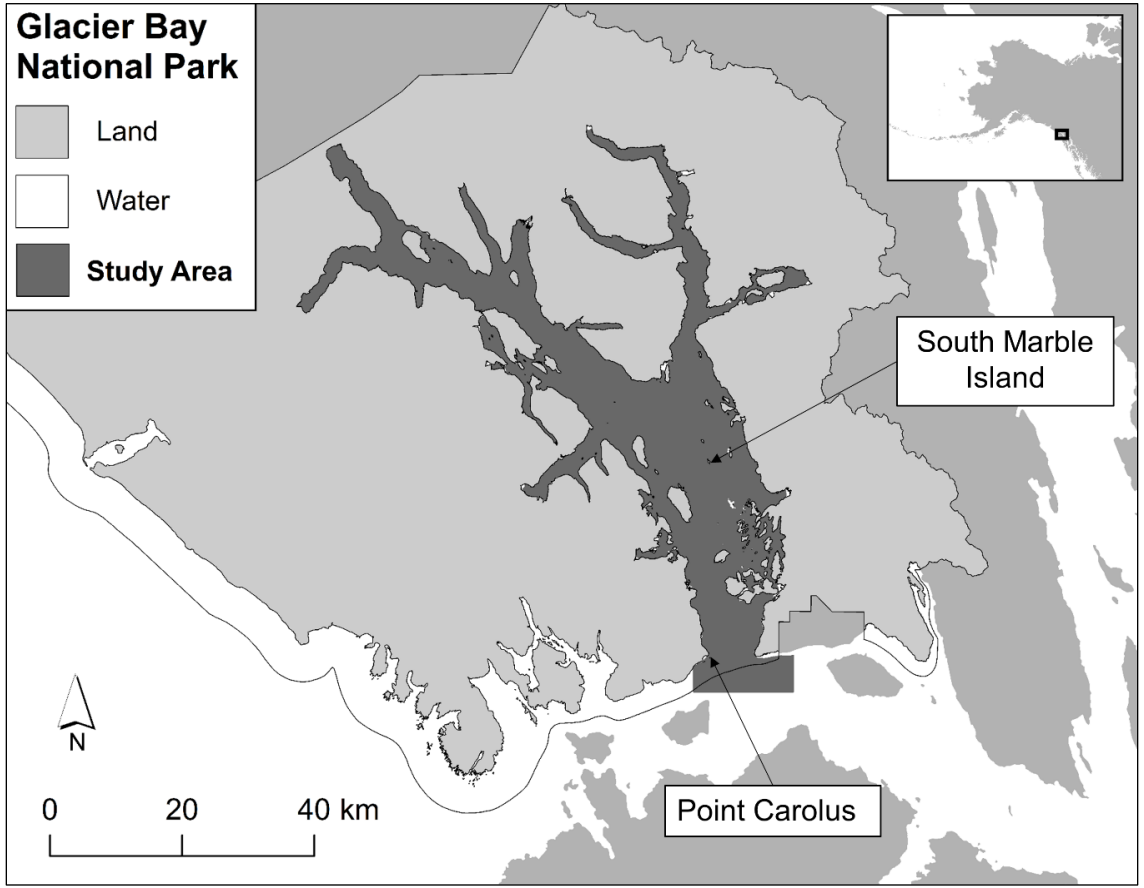


Figure 2.1. Glacier Bay National Park, Alaska, and the study area for an example application of a pinniped abundance and distribution model involving Steller sea lions.

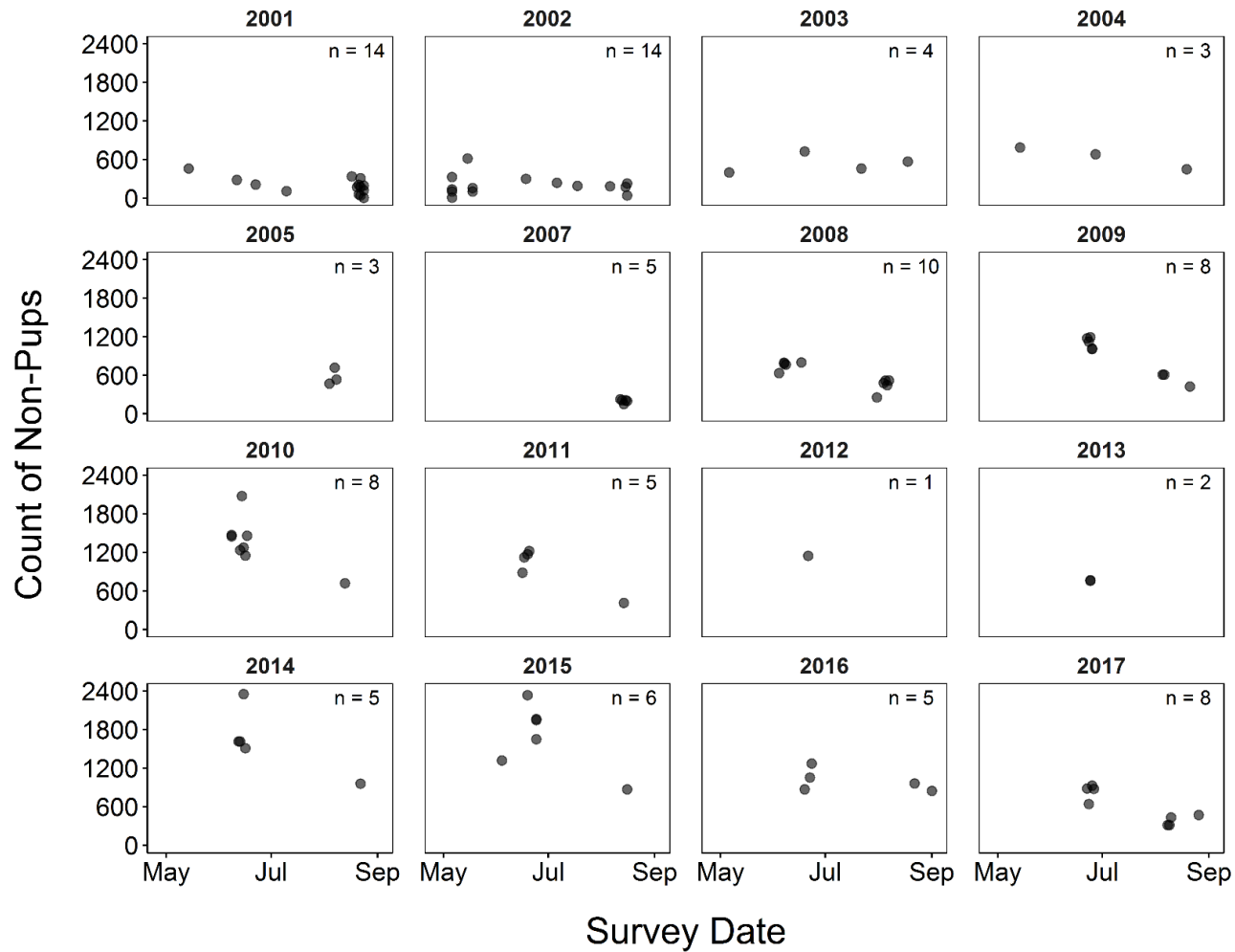


Figure 2.2. Counts of non-pup Steller sea lions at South Marble Island in Glacier Bay National Park, Alaska, from vertical aerial photographic surveys. Sample size noted in the upper right corner of each panel.

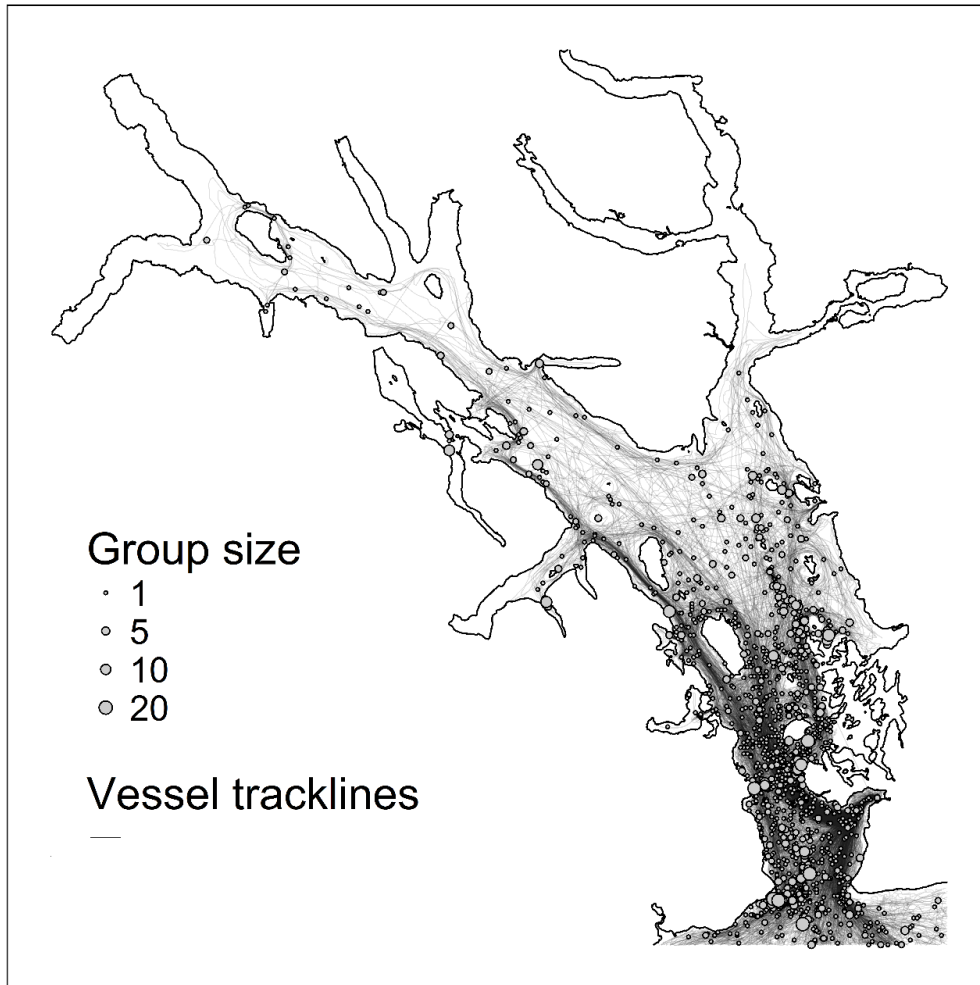


Figure 2.3. Steller sea lion sightings recorded during whale surveys in the vicinity of Glacier Bay National Park, Alaska (2007-2017).

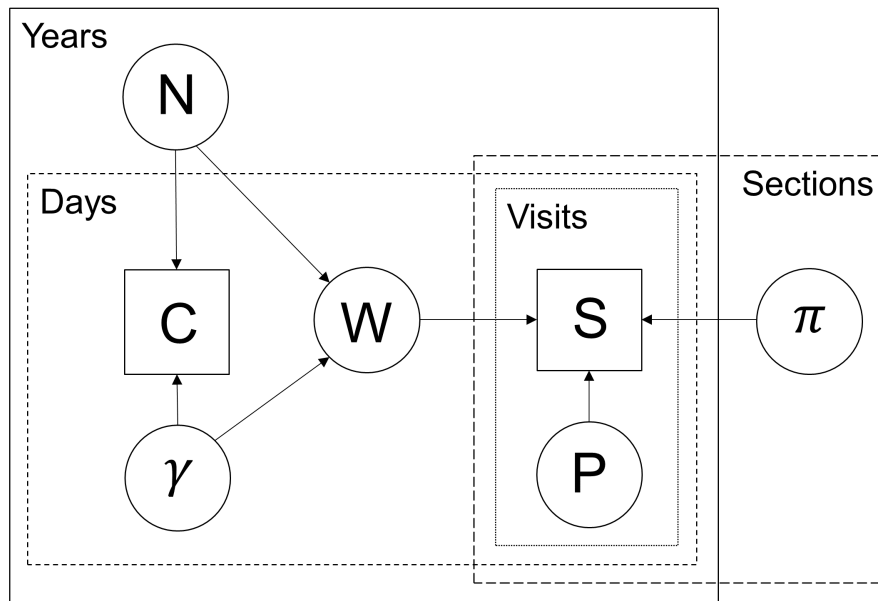


Figure 2.4. Directed acyclic graph describing relationships between parameters (circles) and data sources (boxes) in the pinniped abundance and distribution model applied to Steller sea lions in Glacier Bay National Park, Alaska. The count portion of the model is shown on the left side of the graph with abundance of pinnipeds in the study area denoted by N , the probability of attendance at a terrestrial site by γ , the number of pinnipeds counted at a terrestrial site by C , and the number of pinnipeds in the water by W . The sighting portion of the model is shown on the right side of the graph, with the probability of occurrence in each survey area denoted by π , the number of pinnipeds sighted in a section on a given day by S , and the individual probability of detection by P .

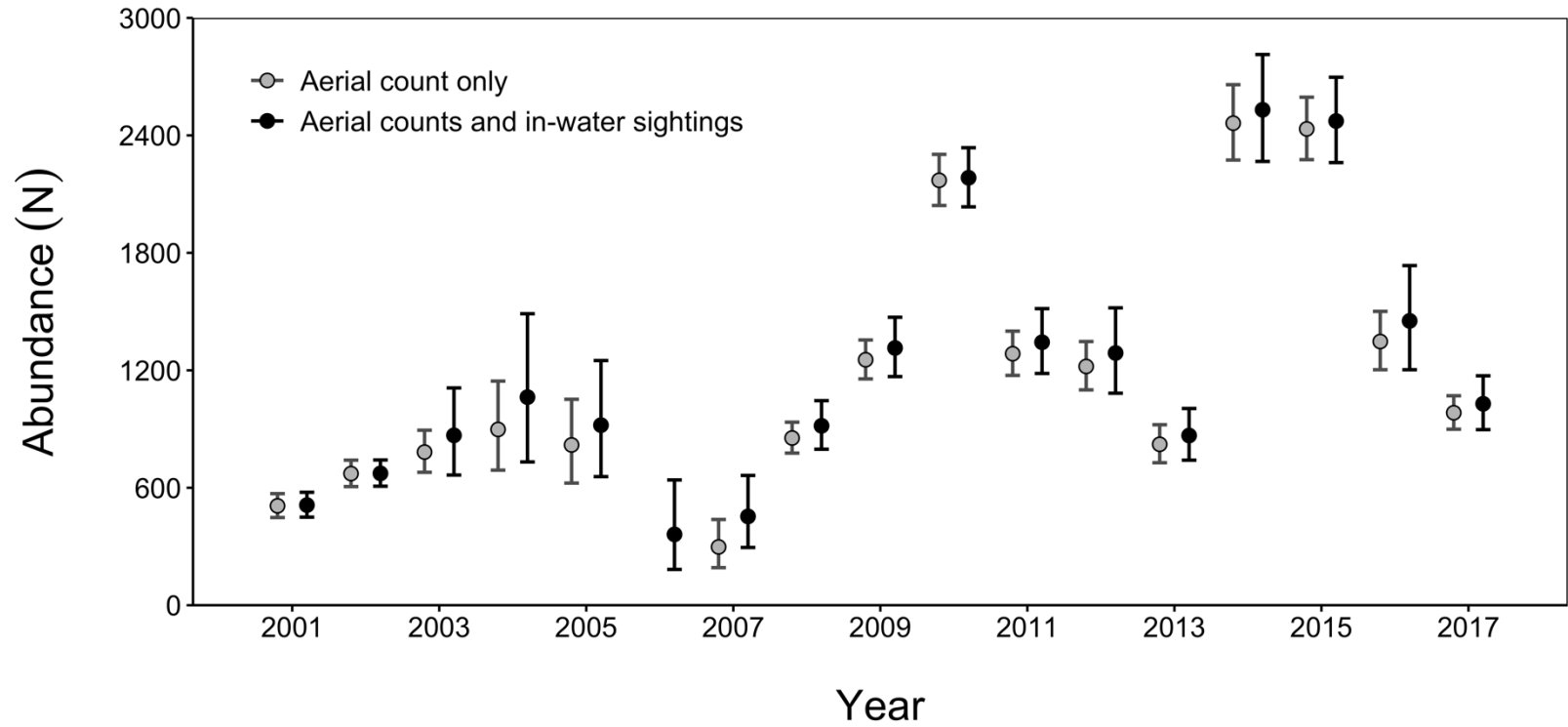


Figure 2.5. Estimates of Steller sea lion abundance at South Marble Island in Glacier Bay, Alaska, with 95% prediction intervals, based on models fitted using only an aerial count data set (gray) and both aerial counts and in-water sighting data set (black). There is no estimate for 2006 because only in-water sighting data were available that year.

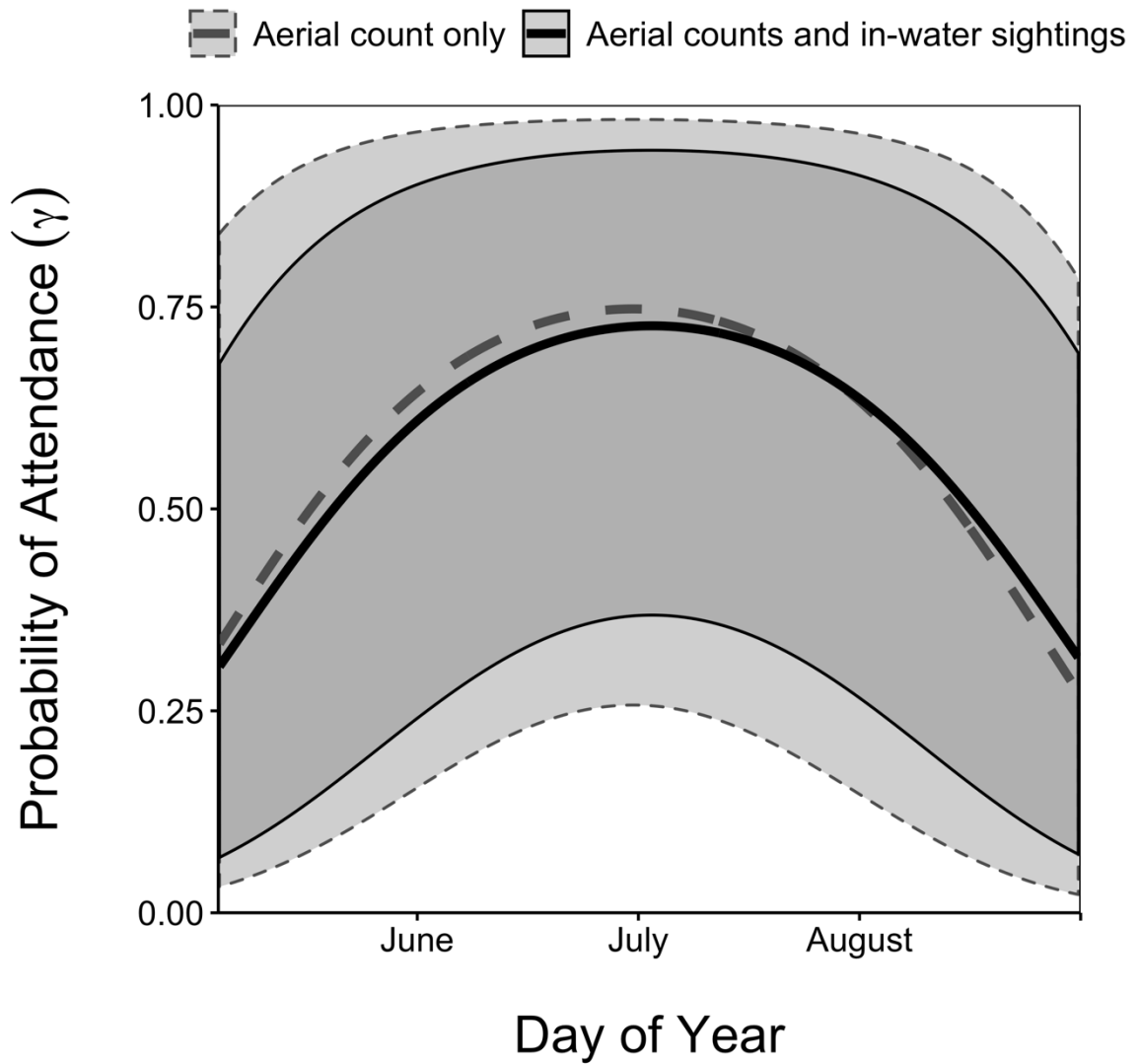


Figure 2.6. Predicted probability of attendance for Steller sea lion at South Marble Island in Glacier Bay, Alaska, with 95% prediction intervals based on models fitted using only an aerial count data set (dashed gray) and both aerial counts and an in-water sighting data set (black).

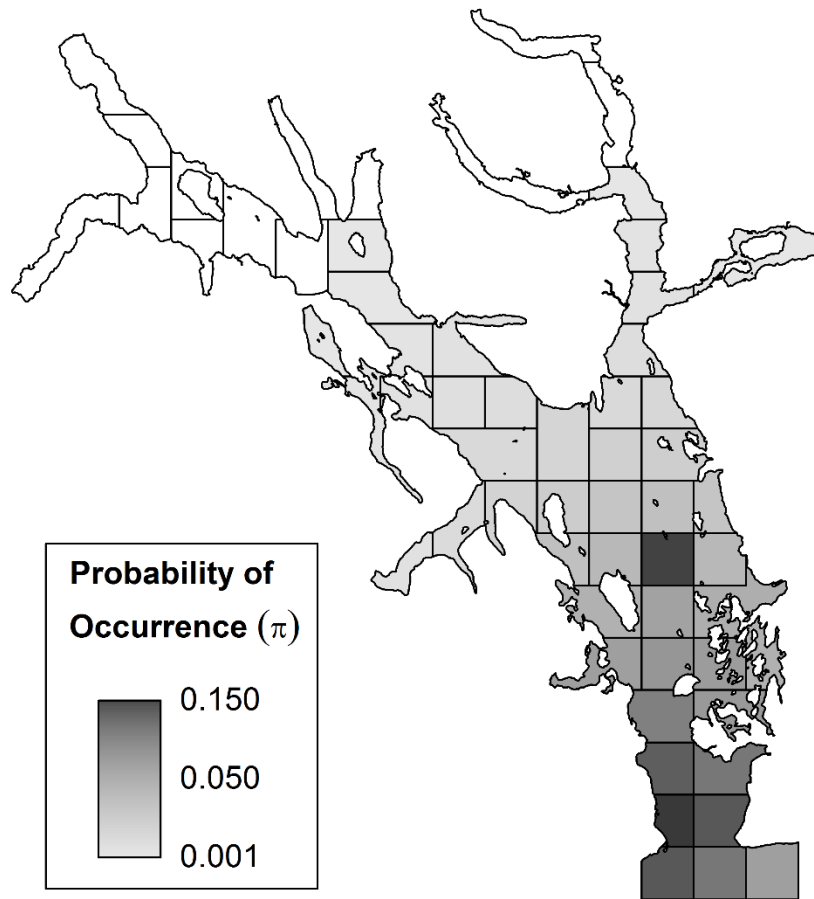


Figure 2.7. Estimated Steller sea lion occurrence probability in the vicinity of Glacier Bay National Park. Probabilities of occurrence sum to 1, and should be interpreted as the probability that a given sea lion in the water is contained within a cell; sea lions that are out of the water are assumed to be present at South Marble Island.

**CHAPTER 3: MODELING HARBOR SEAL ABUNDANCE AND ATTENDANCE
AT TERRESTRIAL SITES AND MCBRIDE INLET IN GLACIER BAY,
ALASKA**

Abstract

Harbor seals are a key resource in Glacier Bay National Park because of their conservation importance and the experiential value that they provide to visitors. The species is monitored using aerial photographic surveys conducted at land or ice-based sites using aerial photographic surveys. Raw counts at these locations have been used in the past to monitor population and distribution changes over time; however estimating actual abundance requires methodologies that properly account for the portion of the population that is in the water, and thus not available to be counted. Much of the survey attention is focused in Johns Hopkins Inlet, a glacial fjord where the majority of harbor seals in Glacier Bay rest out of the water. A recent analysis of counts at this location has been used to retroactively produce abundance estimates, however a technique for estimating abundance at other locations is needed. In this chapter, I developed a model for estimating abundance and attendance of harbor seals at nine terrestrial sites and one glacial area in the Park. The model produced estimates that were comparable to previous studies and its structure allowed for the inclusion of predictors of abundance, attendance, and excessive zero-counts. Model outputs from this study and the previous analysis in Johns Hopkins Inlet will be useful for informing a decision model for managing vessel restrictions in the Park. Furthermore, the modeling framework that I developed

contributes to an existing body of research on estimation techniques for semiaquatic animals.

Introduction

Harbor seals (*Phoca vitulina richardsi*) are an important resource within Glacier Bay National Park (the “Park” hereafter) because of their key role in the ecosystem and the added value they provide to visitor experiences. The species may be found in the waters throughout the Park, as well as out of the water (“hauled-out”) on ice platforms near calving tidewater glaciers and at terrestrial sites (Calambokidis et al. 1987, Blundell et al. 2011). Harbor seals are sensitive to the presence of humans and their ubiquity makes human-seal encounters unavoidable (Henry and Hammill 2001, Jansen et al. 2010, Young et al. 2014). The National Park Service has a dual mission of providing public access while preventing impairment of biological resources. The degree to which an encounter between a visitor and a harbor seal could be viewed as impairment varies widely (Suryan and Harvey 1999). For example, if a harbor seal encounters a vessel in the water this may only slightly alter its behavior. In the worst case, seals resting out of water flush in response to an approaching vessel, leading to energy expenditure that could affect the fitness of adults and decrease the survival rate of pups (Bowen et al. 2001, Harding et al. 2005, Jansen et al. 2010). The Park’s policies focus on limiting these events by imposing vessel restrictions to protect harbor seals that are hauled-out during sensitive periods of the year (pupping and molting; Young et al. 2014); these include mandatory approach distances and seasonal closure of Johns Hopkins Inlet to vessels (Figure 3.1).

Park administrators seek a quantitative decision tool for rigorously evaluating tradeoffs between visitor restrictions and conservation benefits to harbor seals. An intuitive way to quantify the extent to which visitors disturb this species is to estimate the frequency of encounters between vessels and the locations where seals rest out of the water. Estimating encounters requires knowledge of harbor seal abundance at these locations and attendance probability. Attendance probability is defined as the probability that a given seal is out of the water, and thus capable of being disturbed by a visitor. Fortunately, there is significant research and monitoring focused on harbor seals in the Park that can be brought to bear for this task.

Research and monitoring of harbor seals in Glacier Bay dates back to the 1970s; however, a more standardized annual survey protocol has been in place since 2006. The monitoring program consists of aerial photographic surveys at terrestrial sites and areas near tidewater glaciers where seals rest on ice platforms (Womble et al. 2010). Survey effort is concentrated in the area of Johns Hopkins Inlet, where the majority of harbor seals in the Park occur (Figure 3.1; Womble et al. 2010). Recent modeling efforts have provided estimates of abundance and attendance at Johns Hopkins Inlet and been used to retrospectively estimate abundances in this area during 1992-2017 (Womble et al. *In review*). While this work provides information necessary for informing the quantitative decision tool, estimates of abundance and attendance at other locations used by harbor seals are needed.

The goal of this chapter is to describe an approach for characterizing the abundance and attendance probability of harbor seals at locations outside of Johns Hopkins Inlet. These locations include terrestrial sites distributed throughout Glacier Bay

and also glacial areas with less significant numbers of hauled-out seals. I describe a model that produces estimates by leveraging replicated aerial photographic counts of harbor seals over more than 10 years. Specific objectives of this chapter were to (1) describe the structure of the model, and (2) evaluate its accuracy using a model checking procedure and by comparing with estimated parameter values reported in previous studies.

Methods

Data description

Aerial surveys for harbor seals involved using fixed-wing aircraft to fly above sites where harbor seals were known to occur and taking multiple photographs so that the number of individuals could be later counted. Surveys were conducted primarily during pupping and molting periods in June and August, respectively. Photographs were taken within 2 hours of low tide, when a greater proportion of the seal population is thought to be hauled-out (Womble et al. 2010). In the months following surveys, images were reviewed with the aid of ArcGIS mapping software, and the number of seals at each location was counted twice by experienced observers. Additional details on the survey and counting methods can be found in (Womble et al. 2015).

Not all locations were surveyed every year, or within the same timeframe; therefore, it was necessary to limit the analysis to periods and locations that were surveyed consistently. I confined the analysis to aerial surveys carried out between May 1 and August 31, 2004-2014. Nearly 70 unique locations were surveyed during this period, but most of these locations were surveyed infrequently or were often absent of seals. My

criteria for including locations was that they were surveyed at least once per year and appeared to represent relatively significant or stable numbers of seals. The nine locations that I included were (1) Adams Inlet, (2) Flapjack Island, (3) Geikie Rock, (4) Kidney Reef, (5) Leland Reef, (6) Lone Island, (7) Spider Island, (8) Spider Reef, and (9) McBride Inlet. All these sites met the specified criteria except Spider Island, which was not surveyed in 2004 and 2005, but was otherwise similar to the other eight sites.

McBride Inlet was unique in that counts were based on seals hauled out on ice platforms, rather than on land. As in past studies (Womble et al. 2010), I treated McBride Inlet the same as terrestrial sites, because the portion of this area that was occupied by seals was relatively small and could be completely captured in a small number of aerial photographs. Hereafter I refer to all locations as sites.

Modeling approach

The model I developed borrowed significantly from that which I developed for Steller sea lions in Chapter 2, but differed in several important respects. One significant difference between the two datasets was the much higher prevalence of zero counts in the harbor seal data, which had to be addressed by changing the structure of the model. The change in model structure further led me to change the inferential approach from frequentist (maximum likelihood estimation) to Bayesian. This transition was motivated by the differing capabilities of the available software, rather than a deliberate decision to take advantage of a particular facet of the Bayesian framework. Another significant difference between the sea lion model and the seal model was that I used only counts of harbor seals at terrestrial sites to inform the model, and not a combination of aerial photographic counts and in-water sightings.

I applied an extension of the traditional N-mixture model (Royle 2004, Dail and Madsen 2011) in which I substituted an attendance probability parameter for that of detection. A key assumption of N-mixture models is that the population is closed during the period that repeated surveys are conducted. This assumption can be relaxed in cases where the probability that an animal temporarily emigrates from the site is estimated within the model, typically with additional data (Chandler et al. 2011, Johnson et al. 2014). As in the sea lion model, I assumed that detection was perfect ($p = 1$) and that variation in counts across surveys was driven entirely by an attendance parameter (γ). This assumption was based on the fact that counts were made by scrutinizing aerial photographs, and seals are relatively easy to enumerate in photography against the background.

A challenge unique to modeling harbor seal counts was the relatively high frequency of zeroes in the dataset. Excessive zeros in count data is a common and poses a significant challenge for ecologists (Martin et al. 2005, Wenger and Freeman 2008). I dealt with this by modeling abundance using a Bernoulli-Poisson mixture distribution. A site-level Bernoulli process determined whether abundance was zero or a positive integer, and a site-year-specific process determined the abundance value. I assumed that some zeros emerged from a Bernoulli process:

$$Z_{ijt} \sim \text{Bern}(\theta_i),$$

where θ_i is the probability that the i th site will have zero seals at the time of counting and Z_{ijt} is a binary latent variable describing whether or not seals are present on day t during year j . The probability of zero count at a given site was modeled using a logit-normally distributed random effect

$$\text{logit}(\theta_{it}) = a_{it}, \quad a_{it} \sim \text{Norm}(\mu_a, \sigma_a).$$

I assumed that the abundance of harbor seals at a particular site and year (N_{ij}), followed a Poisson distribution

$$N_{ij} \sim \text{Pois}(Z_{it} \times \lambda_{ijt}),$$

where λ_{ijt} . An important aspect of this parameterization is that counting zero harbor seals at a site may come about either from a low expected mean abundance or the zero-inflation process. Mean abundance was modeled on the log scale as:

$$\log(\lambda_{ijt}) = \beta_i + b_j + c_{ijt},$$

where β s are site-level log abundances, b s are error terms describing inter-annual variability, and c s are observation-level error terms for explaining extra-Poisson variability in counts (overdispersion; Warton and Hui 2011). Both random effects in the abundance regression equation were modeled using normal distributions

$$b_j \sim \text{Norm}(0, \sigma_{[b]}) ; c_{ijt} \sim \text{Norm}(0, \sigma_{[c]}).$$

Finally, I connected latent variables to the observed counts using a binomial distribution

$$y_{ijt} \sim \text{Bin}(M_{ijt}, \gamma_{ijt}),$$

where y_{ijt} is the observed count of harbor seals and γ_{ijt} is the predicted probability of attendance at the site. Attendance probability was modeled on the logit scale with a normally distributed observation-level random effect

$$\text{logit}(\gamma_{ijt}) = \alpha + d_{ijt}, \quad d_{ijt} \sim \text{Norm}(0, \sigma_{[d]}).$$

The d error terms helped accommodated extra-binomial variability not otherwise characterized in the abundance and zero-inflation tiers of the model.

Derived estimates

After estimating all parameters in the model I derived posterior distributions for quantities related to abundance and attendance probability. I derived estimates of mean site-level abundance by simulating values for the β parameter and the two associated error terms and then exponentiating these values. I used the same approach to estimate posteriors for the total abundance across all sites for each of the 11 years. Finally, I combined abundance estimates from the nine sites in the study with those from the recent modeling in Johns Hopkins Inlet to provide a sense of the bay-wide abundance of harbor seals and the proportion of the population using each of the habitat types (Womble et al. *in review*).

I derived two posterior estimates for quantities related to attendance probability. These estimates were generated by simulating parameters describing the γ s and applying an inverse-logit transformation:

$$\text{logit}^{-1}(x) = \left(\frac{1}{[1 + e^{-x}]} \right),$$

The first derived value was a posterior for the mean attendance probability ($\bar{\gamma}$), which I computed by inverse-logit transforming simulated values of the α parameter. I then derived a predicted attendance posterior (γ^*), which combined uncertainty at both the parameter and observation level. I did this by simulating variability in the α parameter and adding additional error based on the model-estimated $\sigma_{[a]}$ parameter, producing another posterior on the logit scale with the same mean, but lower precision (α^*). I calculated the posterior for γ^* by inverse-logit transforming simulated values of α^* . The mean attendance posterior described the probable value of the attendance parameter itself, whereas the predicted attendance posterior described the distribution of attendance

probabilities that would be expected based on the variability of the data included in the model.

Model fitting and evaluation

I fit the model using Bayesian inference with non-informative prior distributions. I assigned diffuse normal priors to all log-abundance parameters, Jeffreys priors to logit-linear regression coefficients (Lunn et al. 2012), and diffuse uniform priors to all σ parameters. Posterior parameter distributions were estimated using Markov Chain Monte Carlo (MCMC) simulation within the JAGS software package (Version 4.2.0; Plummer 2003). I ran four Markov chains simultaneously and determined a suitable burn-in number of iterations using the Gelman-Rubin statistic (\hat{R}) and by examining trace plots (Gelman et al. 2014). Following model fitting, I evaluated the performance of the model using a standard posterior predictive checking procedure and computing a Bayesian P value (Gelman et al. 2014). Bayesian P value estimates between 0.05 and 0.95 are generally regarded as evidence that the model is reasonably specified (Conn et al. 2018).

Results

I succeeded in fitting a zero-inflated N-mixture model to a data set containing 701 counts of harbor seals from aerial surveys. A similar number of counts were made during the pupping ($n=324$) and molting ($n=377$) periods (Figure 3.2). The number of visits per site-year combination ranged from one to 12 with 91% surveyed three or more times. The proportion of zeros within counts ranged from 1% to 83% across the nine sites. I used traceplots to determine that a burnin of 100,000 iterations was sufficient for reaching stationarity for parameters in the model. I estimated posterior distributions of parameters

by summarizing an additional 1.9 million iterations, which I thinned by a factor of 10 to conserve memory and reduce autocorrelation. Thinned chains appeared to be well mixed and \hat{R} values for all parameters were less than 1.1. The model estimated a Bayesian P value of 0.71, indicating that it was reasonably described the data.

The probability of a zero-inflated counts (θ_i) varied considerably among the nine sites. McBride Inlet and Spider Reef were among the sites with the lowest probability of unexplained zeroes ($\leq 95\%$), whereas Spider Island and Leland Reef had the highest frequency ($\geq 73\%$; Table 3.1). Mean abundance estimates varied considerably across sites as well, from 24 seals at Lone Island to 440 seals at Spider Reef. Point-estimates of total abundance across sites ranged from a low of 916 in 2008 to a high of 1,156 in 2013. Overlap in 95% credible intervals over study period suggested that there was no clear temporal trend over the study period (Table 3.2; Figure 3.3). Random effects within abundance log-linear regression suggested that temporal variability in abundance (σ_b) was somewhat lower than the observation-level error (σ_c ; Table 3.3). Combined abundance estimates from this model and those reported in Womble et al. (*In review*) suggested that 72-80% of the harbor seals population in Glacier Bay occupy Johns Hopkins Inlet during pupping and molting periods (Figure 3.3).

Posterior distributions describing mean attendance and predicted attendance both indicated that greater than half of the harbor seals at each site were counted during surveys (Figure 3.3). Mean attendance probability ($\bar{\gamma}$) was estimated as 0.77 with a 95% credible intervals between from 0.47 to 0.94 (Figure 3.4). The posterior was somewhat skewed, as evidenced by the greater values for the median (0.79) and mode (0.84) of the distribution. The predicted attendance posterior (γ^*) was spread much more broadly

across the 0-1 scale and exhibited more significant left skew. The mean of the predicted attendance was 0.68, with a 95% credible interval from 0.07 to 0.99. However, the mean and credible intervals of this distribution alone did not fully capture the pattern in attendance that the model suggested. For example, the medians of the two attendance-related posteriors were nearly equal (0.79), but the mode of the predicted attendance was substantially greater (0.98).

Discussion

I achieved the goal of estimating harbor seal attendance probability and abundance at important terrestrial sites in Glacier Bay and at McBride inlet. be found in the waters throughout the park or removed from the water (“hailed-out”) on ice platforms near calving tidewater glaciers and at terrestrial sites Harbor seal populations are commonly monitored by counting animals at sites on land or ice where they have removed themselves from the water for resting and other behaviors (Thompson and Harwood 1990, Bengston et al. 2007, Boyd et al. 2010). This chapter contributes to an existing body of research on techniques for estimating trends in the status of semi-aquatic marine mammals (Ver Hoef and Frost 2003, Ver Hoef and Jansen 2007), specifically by describing an additional method for making inference about abundance and attendance in the presence of significant zero-inflation.

The model described abundance and attendance rates that were reasonable compared to past studies; however, comparisons were complicated by differences in methodologies. A recent report by researchers in Glacier Bay used some of the same data as this study to describe trends in mean counts at terrestrial sites, as an index of

abundance (Womble et al. 2015). Estimates from Womble et al. (2015) were not directly comparable to this study, because their analysis included additional sites and estimated adjusted mean counts as opposed to abundances. Nonetheless, total abundance estimates from my model aligned with their findings in that abundance estimates were greater than mean counts across the overlapping years. Also, the difference between estimates was not so high as to suggest severe overestimation. With regards to attendance probability, point estimates from the model appeared to align with Simpkins et al. (2003), who reported 0.82 for harbor seals in glacial fjords. Attendance probabilities for seals on ice platforms are usually considered to be higher than those at terrestrial sites (Blundell et al. 2011), suggesting that my model may have overestimated attendance. Womble et al. (*In review*) estimated abundance in Johns Hopkins Inlet by adjusting counts based on an attendance probability between 0.5 and 0.55, much lower than Simpkins et al. (2003).

The model described in this chapter had several deficiencies of varying significance, the greatest of which was the high observation-level variability in abundance and attendance processes. The relatively large error term in the abundance tier of the model was undesirable in that it obscured any meaningful temporal variation among years. The large error term for attendance ($\sigma_{[a]}$) combined with the nonlinear inverse-logit transformation to produce a posterior with probability density “piled up” mostly near the upper extreme. I suspect that excessive variability in attendance and abundance can be explained, in part, by a small number of counts that were very low compared to others of the same site-year combination, but still greater than zero. These observations occurred at Adams Inlet in 2007 and 2008, Flapjack Island in 2012, and Lone Island in 2014 (Figure 3.2). Counts of this type contributed to imprecision in

attendance and abundance because they were low outliers that could not be explained by the zero-inflation processes. Omitting these problematic points is unlikely to fully resolve the issue of large error terms because there was another pattern in the dataset mostly unexplained by the model, positive outlying counts. These outliers all occurred in 2004 at Lone Island, Geike Rock, and Flapjack Island. A possible explanation for these patterns is temporary movement of individuals from the area of John Hopkins Inlet to various terrestrial sites. Past studies have described evidence for individual movements between glacial areas and terrestrial sites in Glacier Bay (Blundell et al. 2011). Temporary movement out of Johns Hopkins Inlet may be a satisfactory explanation for positive outliers at Lone Island and Geike Rock, because these terrestrial sites are nearest the glacial area. Another limitation of this model was the omission of harbor seals counts from other survey locations throughout the Park. I mainly excluded these locations due to concerns that sparse data would destabilize estimates, and I assumed that their removal would not dramatically affect abundance predictions. To examine the validity of this assumption, I summed the maximum counts of seals across these excluded sites in each year (a proxy for minimum abundance) and compared these value to my abundance totals. On average, pooled maximum counts for excluded sites were equivalent to 12% of the total abundances estimated by my model (study sites), and 3% of the total Bay-wide abundance estimate (study sites plus Johns Hopkins Inlet). Based on this evaluation I concluded that the omitted sites did not substantially affect the abundance patterns that I described.

Although the model met the goals of the analysis, there are a number of potential refinements and decisions that could be made to increase its utility. The sizeable

observation-level error terms in attendance and abundance processes suggested that there is the potential for covariates to explain variation in counts and increase the precision of estimates. Inclusion of date, time, and environmental covariates can be used as a technique for improving precision in estimates of mean counts and abundance. I did not include covariates in my model for several reasons. I wanted to validate that a simplified (null) version of the model would perform reasonably well before adding complexity. I also assumed that the standardization built into the survey methods buffered against temporal and environmental variation. I am skeptical that problems of imprecision in the model will be eliminated only by the inclusion of explanatory variables, because a post hoc examination of the outliers described above did not reveal any obvious environmental cause for their deviations (e.g., tidal pattern).

References

- Bengston, J. L., A. V. Phillips, E. A. Mathews, and M. A. Simpkins. 2007. Comparison of survey methods for estimating abundance of harbor seals (*Phoca vitulina*) in glacial fjords. *Fishery Bulletin* 105:348–356.
- Blundell, G. M., J. N. Womble, G. W. Pendleton, S. A. Karpovich, S. M. Gende, and J. K. Herreman. 2011. Use of glacial and terrestrial habitats by harbor seals in Glacier Bay, Alaska: costs and benefits. *Marine Ecology Progress Series* 429:277–290.
- Bowen, W. D., S. J. Iverson, D. J. Boness, and O. T. Oftedal. 2001. Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Functional Ecology* 15:325–334.
- Boyd, I. L., W. D. Bowen, and S. J. Iverson. 2010. *Marine mammal ecology and conservation: A handbook of techniques*. Oxford University Press.
- Calambokidis, J., B. L. Taylor, S. D. Carter, G. H. Steiger, P. K. Dawson, and L. D. Antrim. 1987. Distribution and haul-out behavior of harbor seals in Glacier Bay, Alaska. *Canadian Journal of Zoology* 65:1391–1396.
- Chandler, R. B., J. A. Royle, and D. I. King. 2011. Inference about density and temporary emigration in unmarked populations. *Ecology* 92:1429–1435.
- Conn, P. B., D. S. Johnson, P. J. Williams, S. R. Melin, and M. B. Hooten. 2018. A guide to Bayesian model checking for ecologists. *Ecological Monographs* 88:526–542.
- Dail, D., and L. Madsen. 2011. Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics* 67:577–587.
- Gelman, A., J. B. Carlin, H. S. Stern, D. B. Dunson, A. Vehtari, and D. B. Rubin. 2014. *Bayesian data analysis*. Third edition. CRC Press, Boca Raton.
- Harding, K. C., M. Fujiwara, Y. Axberg, and T. Härkönen. 2005. Mass-dependent energetics and survival in harbour seal pups. *Functional Ecology* 19:129–135.
- Henry, E., and M. O. Hammill. 2001. Impact of small boats on the haulout activity of harbour seals (*Phoca vitulina*) in Metis Bay, Saint Lawrence Estuary, Quebec, Canada. *Aquatic Mammals* 27:140–148.
- Jansen, J. K., P. L. Boveng, S. P. Dahle, and J. L. Bengston. 2010. Reaction of harbor seals to cruise ships. *Journal of Wildlife Management* 74:1186–1194.

- Johnson, F. A., R. M. Dorazio, T. D. Castellón, J. Martin, J. O. Garcia, and J. D. Nichols. 2014. Tailoring point counts for inference about avian density: dealing with nondetection and availability. *Natural Resource Modeling* 27:163–177.
- Lunn, D., C. Jackson, N. Best, A. Thomas, and D. Spiegelhalter. 2012. *The BUGS Book: A Practical Introduction to Bayesian Analysis*. CRC Press.
- Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. P. Possingham. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. *Ecology Letters* 8:1235–1246.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 20–22 *in* Proceedings of the 3rd International Workshop on Distributed Statistical Computing. ISSN, Vienna, Austria.
- Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60:108–115.
- Simpkins, M. A., D. E. Withrow, J. C. Cesarone, and P. L. Boveng. 2003. Stability in the proportion of harbor seals hauled out under locally ideal conditions. *Marine Mammal Science* 19:791–805.
- Suryan, R. M., and J. T. Harvey. 1999. Variability in reactions of Pacific harbor seals, *Phoca vitulina richardsi*, to disturbance. *Fishery Bulletin* 97:332–339.
- Thompson, P. M., and J. Harwood. 1990. Methods for estimating the population size of common seals, *Phoca vitulina*. *Journal of Applied Ecology* 27:924–938.
- Ver Hoef, J. M., and K. J. Frost. 2003. A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound, Alaska. *Environmental and Ecological Statistics* 10:201–219.
- Ver Hoef, J. M., and J. K. Jansen. 2007. Space—time zero-inflated count models of harbor seals. *Environmetrics* 18:697–712.
- Warton, D. I., and F. K. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:3–10.
- Wenger, S. J., and M. C. Freeman. 2008. Estimating species occurrence, abundance, and detection probability using zero-inflated distributions. *Ecology* 89:2953–2959.
- Womble, J. N., G. M. Blundell, S. M. Gende, M. Horning, M. F. Sigler, and D. J. Csepp. 2014. Linking marine predator diving behavior to local prey fields in contrasting habitats in a subarctic glacial fjord. *Marine Biology* 161:1361–1374.

- Womble, J. N., G. W. Pendleton, E. A. Mathews, G. M. Blundell, N. M. Bool, and S. M. Gende. 2010. Harbor seal (*Phoca vitulina richardsi*) decline continues in the rapidly changing landscape of Glacier Bay National Park, Alaska 1992–2008. *Marine Mammal Science* 26:686–697.
- Womble, J. N., G. W. Pendleton, E. A. Mathews, and S. M. Gende. 2015. Status and trend of harbor seals (*Phoca vitulina richardsi*) at terrestrial sites in Glacier Bay National Park from 1992-2013 progress report. Glacier Bay National Park.
- Womble, J. N., Ver Hoef, J. M., Gende, S. M., and Mathews, E. A. *In review*. Calibrating and adjusting counts of harbor seals in an Alaskan glacial fjord to estimate abundance and trends from 1992-2017. Submitted to *Ecosphere*.
- Young, C., S. M. Gende, and J. T. Harvey. 2014. Effects of vessels on harbor seals in Glacier Bay National Park. *Tourism in Marine Environments* 10:5–20.

Tables

Table 3.1. Mean site-level abundance estimates and probabilities of zero counts for harbor seals in Glacier Bay, Alaska (2004-2014). Summary statistics include standard error (SE), and lower (LCL) and upper (UCL) 95% credible intervals.

Site	Estimate	SE	LCL	UCL	Estimate	SE	LCL	UCL
	Mean Abundance				Probability of Zero			
Adams Inlet	144.4	76.7	48.2	340.2	0.33	0.16	0.09	0.67
Flapjack Island	173.3	92.4	57.1	405.7	0.24	0.14	0.05	0.57
Geikie Rock	23.0	12.8	7.3	55.5	0.72	0.14	0.40	0.93
Kidney Reef	40.0	23.0	12.2	98.2	0.81	0.11	0.53	0.96
Leland Reef	27.6	15.3	8.8	66.6	0.82	0.11	0.56	0.96
Lone Island	23.5	12.7	7.6	56.1	0.37	0.16	0.10	0.71
McBride Inlet	120.0	65.1	39.1	286.1	0.06	0.08	0.00	0.28
Spider Island	63.4	36.6	19.3	156.8	0.89	0.08	0.68	0.98
Spider Reef	438.2	233.1	145.4	1034.7	0.12	0.09	0.02	0.36

Table 3.2. Total abundance estimates for harbor seals in Glacier Bay, Alaska (2004-2014). Summary statistics include standard error (SE), and lower (LCL) and upper (UCL) 95% credible intervals.

Year	Estimate	SE	LCL	UCL
2004	1092.0	293.4	654.4	1791.3
2005	1061.3	283.8	636.0	1738.3
2006	958.6	274.3	551.5	1608.4
2007	937.4	250.2	560.7	1530.0
2008	915.9	244.3	549.6	1494.1
2009	993.2	262.6	600.0	1619.9
2010	1059.2	278.9	640.4	1722.3
2011	1193.6	323.0	710.4	1964.9
2012	1111.1	294.1	671.5	1808.0
2013	1156.4	310.5	691.7	1894.8
2014	1088.8	293.0	651.5	1794.9

Table 3.3. Parameter estimates from a harbor seal count model. Columns describes the scale on which parameters were estimated (Scale), standard error (SE), and lower (LCL) and upper (UCL) 95% credible intervals.

Parameter	Description	Scale	Estimate	SE	LCL	UCL
$\mu_{[a]}$	Zero-inflation mean	Logit	0.74	0.74	-0.75	2.20
$\sigma_{[a]}$	Zero-inflation error (year-level)	Logit	2.43	0.82	1.36	4.48
$\sigma_{[b]}$	Abundance error (year-level)	Log	0.14	0.07	0.03	0.28
$\sigma_{[c]}$	Abundance error (observation-level)	Log	0.46	0.06	0.33	0.57
α	Attendance mean	Logit	1.32	0.73	0.11	2.99
α^*	Predicted attendance	Logit	1.32	2.05	-2.70	5.34
$\sigma_{[d]}$	Attendance error (observation-level)	Logit	1.92	0.39	1.33	2.83

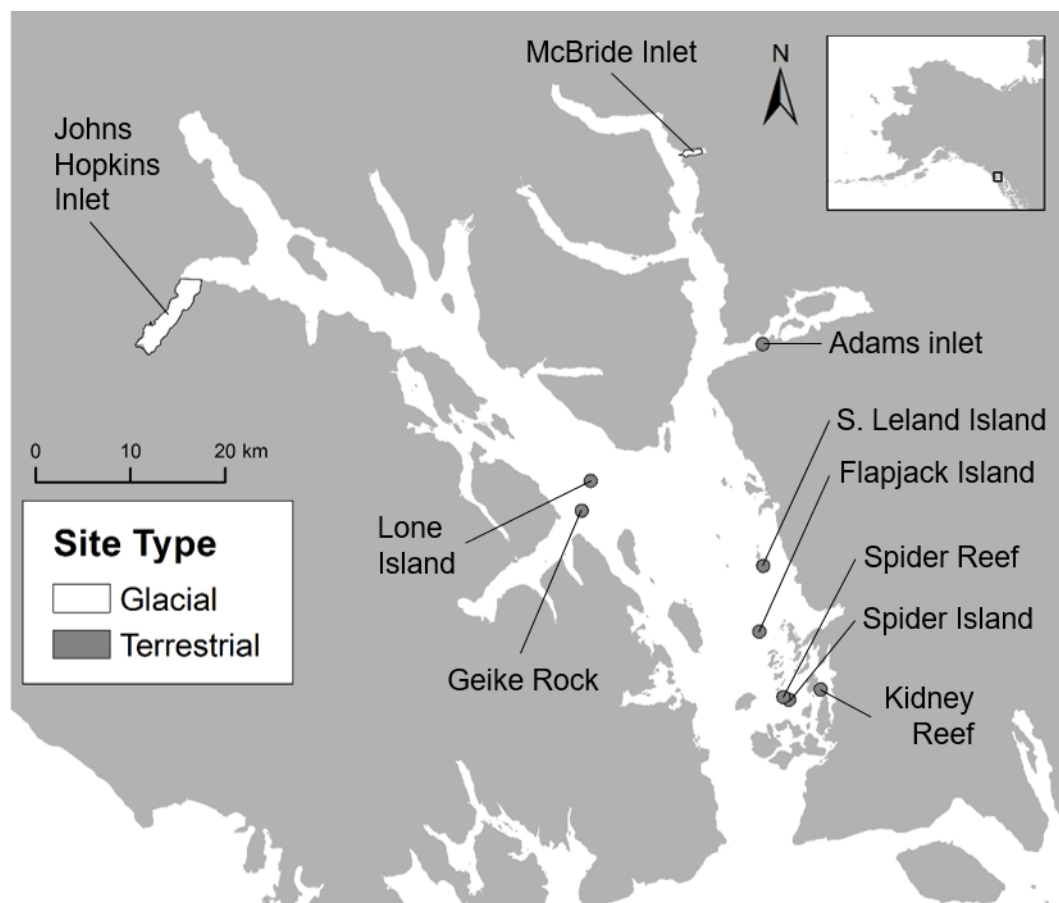
Figures

Figure 3.1. Map of prominent terrestrial sites and tidewater glacial areas where harbor seals haul-out in Glacier Bay, Alaska (2004-2014).

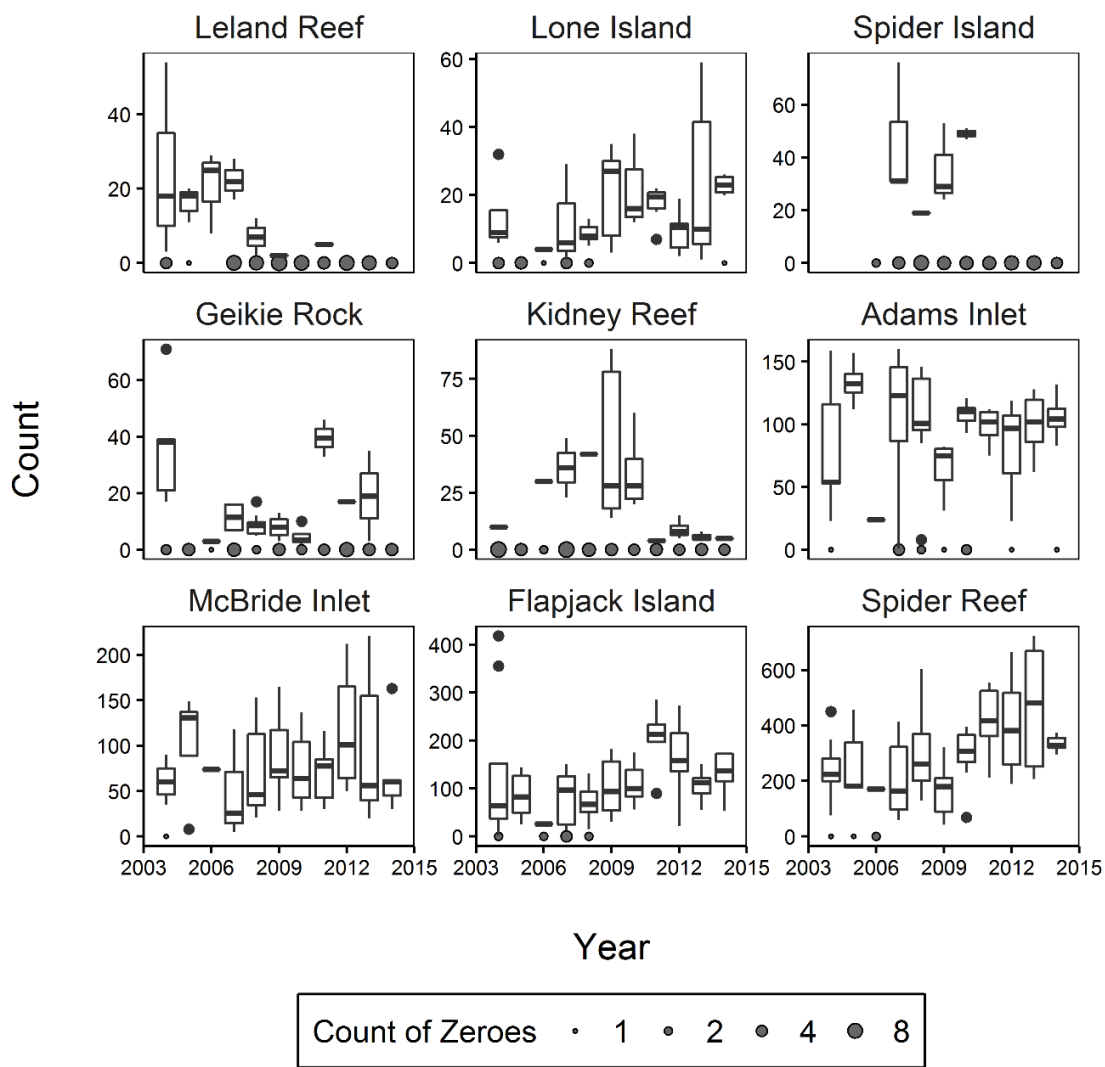


Figure 3.2. Counts from aerial photographic surveys of harbor seals hauled-out at terrestrial sites and tidewater glacial areas in Glacier Bay, Alaska (2004-2014). Boxplots described the distribution of non-zero data and the size of gray points corresponds to the number of surveys in which the count was zero. Sites are ordered by maximum counts.

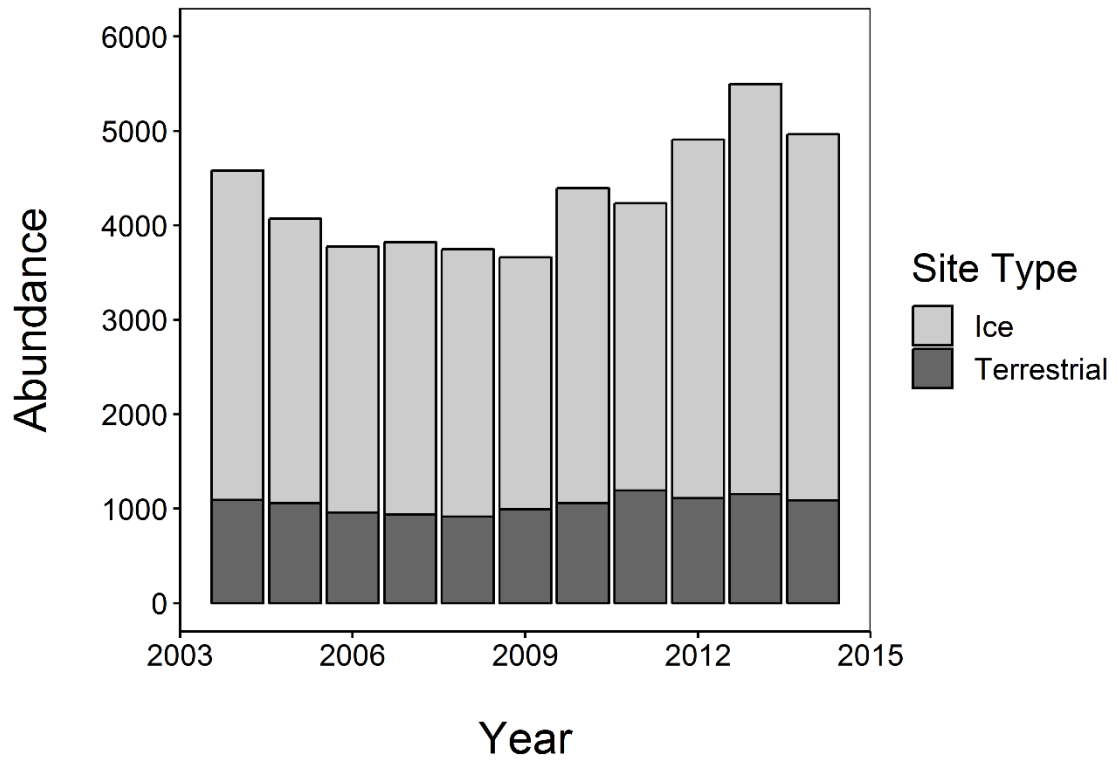


Figure 3.3. Abundance estimates for harbor seals in Glacier Bay, Alaska (2004-2014), separated by habitat association.

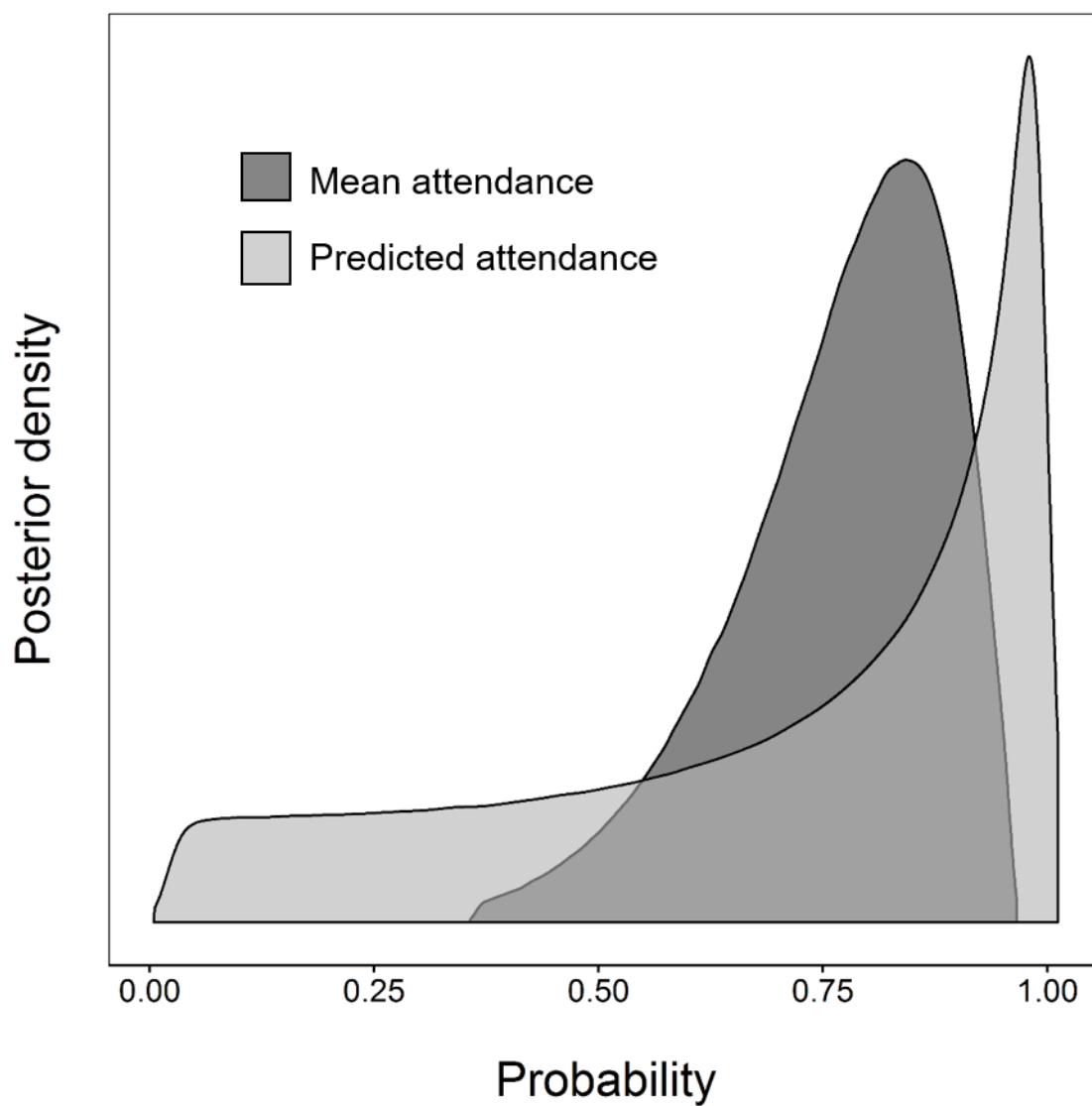


Figure 3.4. Posterior densities of mean attendance probability ($\bar{\gamma}$) and predicted attendance probability (γ^*) for harbor seals occupying nine locations in Glacier Bay, Alaska (2004-2014).

CHAPTER 4: USING A BAYESIAN MULTISTATE OCCUPANCY MODEL TO ASSESS SEABIRD AND SHOREBIRD STATUS IN GLACIER BAY, ALASKA

(At time of submission, this chapter was under review by the journal Wildlife Society Bulletin)

Abstract

The National Park Service is charged with both monitoring avian communities and evaluating the influence of visitors to National Parks on sensitive species; however, this task is challenging because sampling programs often involve multiple species, each with differing behavior, habitat requirements, and detectability. The objectives of this study were to build a model to describe the status of waterbirds in Glacier Bay National Park, Alaska and assess the effects of area closures on these species. We used a Bayesian multistate occupancy model to describe the status of multiple species and to make the best possible use of existing survey data. We modeled up to five states per species and evaluated predictors of occupancy, nesting, and abundance, as well as survey-related predictors of state-dependent detection probability. We found that occupancy probability varied across species and habitats (islands versus glacial outwashes). For most species, occupancy probability was substantially higher at sites occupied in the year previous (site persistence). We found weak evidence that area closures affected the occurrence of species in the study, but this was largely because most sites were closed for the entirety of the study period. The probability of detecting occurrence, nesting, and abundance varied across species and survey methods (ground vs. vessel). Detection parameters

provided valuable information for enhancing the efficiency of future surveys, by identifying preferred survey methods and sampling periods for specific waterbird species.

Introduction

The National Park Service is obligated to monitor species and evaluate effects of visitor activities on resources in the National Park System (National Park Service 2006). Avian communities are monitored widely within the system (Stohlgren et al. 1995, Fancy et al. 2009); however, many of these programs are ill-equipped for assessing the effects of visitors on wildlife for both ecological and sampling-related reasons (Hill et al. 1997, Nichols et al. 1998, Nisbet 2000). Designing and implementing such programs is difficult because there are often many species involved, each with different behaviors and habitat requirements (Thompson 2002, Purcell et al. 2005, Kéry and Schmid 2006). Moreover, non-detection of a particular bird species during a survey can rarely be considered as proof of absence, and detectability can vary substantially depending on the species and survey method (MacKenzie et al. 2002, Gu and Swihart 2004). Surveyors may fail to detect species that occupy but have temporarily left the site, or surveys may not coincide with the nesting season. Without a method for properly accounting for these biases, one cannot clearly ascribe causes for change in community structure or manage ecosystems effectively (Nichols and Williams 2006, McCarthy and Possingham 2007). Multispecies monitoring efforts are further encumbered by the logistics associated with surveying species in protected areas. The frequency of surveys at some sites may be limited by remoteness or wilderness protections that require reaching sites using nonmotorized modes of transport.

Many of these challenges pertain to the monitoring and management of avian communities in Glacier Bay National Park (hereafter the “Park”). The Park monitors ground-nesting waterbirds because they occupy and nest in shoreline areas that are susceptible to disturbance by visitors (Verhulst et al. 2001, Chatwin et al. 2013). Many sensitive species cluster at a relatively small number of islands and glacial outwash areas throughout the Park where they nest (Figure 4.1); thus, visitor access may be temporarily or permanently restricted in many of these areas to avoid causing nest failure or colony abandonment. Glaucous-winged gulls (*Larus glaucescens*) are especially important members of the waterbird guild in the Park because they nest colonially in the Park and their eggs are harvested for cultural and subsistence purposes (Zador et al. 2006).

Many short-term research studies have been conducted on breeding waterbirds in the Park over past decades (Patten 1974, Arimitsu et al. 2007); however, sustained monitoring of waterbird nesting concentrations only began in 2012, largely because of the resumption of gull egg harvest in the Park (Lewis et al. 2017). Surveys entail counting individuals and/or nests from land or vessel, with active nests either observed directly or inferred from parental behavior. Sites containing gull colonies are surveyed multiple times per year, whereas other sites may be surveyed only once in a year or passed over for sampling in multiple years. Park resource managers want to gain a better understanding of waterbird population dynamics and potential impacts on nesting success if visitors could access currently restricted sites.

We aimed to develop an approach for monitoring and modeling the state of waterbird breeding populations at locations throughout the Park. Specific objectives included defining and evaluating a model that could (1) provide a means to predict

patterns in occupancy, abundance, and nesting; (2) accommodate irregular sampling data; and (3) provide a basis for assessing the effect that opening sites to visitors would have on the occurrence and nesting of target waterbird species. The focal species and grouping for the analysis included arctic terns (*Sterna paradisaea*), black oystercatchers (*Haematopus bachmani*), black-legged kittiwakes (*Rissa tridactyla*), Caspian terns (*Hydroprogne caspia*), glaucous-winged gulls, mew gulls (*Larus canus*), pigeon guillemots (*Cepphus columba*), semipalmated plovers (*Charadrius semipalmatus*), and unidentified cormorants (*Phalacrocorax* spp.). Unidentified cormorants could have included double-crested cormorants (*Phalacrocorax auritus*), but were most likely pelagic cormorants (*P. pelagicus*). The two species of cormorant were not distinguished during surveys and exhibit similar behaviors and nesting habitats, so we deemed it appropriate to group them.

Methods

Study Area

Glacier Bay National Park is located in Southeast Alaska and encompasses approximately 1.3 million hectares of terrestrial and marine areas (Figure 4.1). The Park is made up of the Glacier Bay basin, the southern portion of the Fairweather Range to the west, and the shoreline stretching from the west entrance of the bay to the mouth of the Alsek River to the north. The Park contains a broad range of terrestrial and marine habitats, which support a variety of resident and migratory waterbirds species that nest in the Park, including seabirds (gulls, terns, alcids), waterfowl (ducks, geese), and

shorebirds (sandpipers, plovers, oystercatchers), as well as great blue herons (*Ardea herodias*) and bald eagles (*Haliaeetus leucocephalus*; Arimitsu et al. 2007).

Data Collection

We analyzed ground and vessel survey data collected between 1 May and 31 August during 2012-2017 (Figure 4.2). The purpose of these surveys was to count individuals, nests, and nesting adults present at each site. Surveyors classified adults as nesting if they exhibited any of the following behaviors: alarm calls, broken-wing distraction displays, dive bombing, nest-building, apparent incubation, or chick-rearing (Lewis et al. 2017). Two experienced observers conducted ground surveys by walking adjacent transects within suitable nesting and loafing habitats. Surveyors performed vessel-based surveys using both motorized and nonmotorized vessels, depending on whether sites were within wilderness areas. Surveys occurred within two hours of high tide to maximize detection of birds using the islands for nesting as opposed to non-breeders using the intertidal zone for foraging. Surveys from motorized vessels consisted of traveling parallel to shore at a relatively slow speed (<5 knots) and scanning the area from a distance of approximately 100 m from shore using binoculars. Nonmotorized vessel surveys occurred in a similar manner, only from kayaks. Observers counted birds on sections of the shoreline independently and then compared counts with each other, with multiple observers recounting in the case of significant disagreement (i.e. >10%; Lewis et al. 2017). We surveyed sites with nesting colonies of glaucous-winged gulls multiple times per year and during all years (Table 4.1). We surveyed glacial outwash areas and islands without glaucous-winged gull colonies less frequently.

Multistate Occupancy Models

Occupancy modeling is an approach for assessing the status and distribution of avian species while also accounting for detection bias during surveys (Hoeting et al. 2000, MacKenzie et al. 2002, Thompson 2002, Tyre et al. 2003). This approach uses replicated surveys to simultaneously estimate a species' probability of occurrence and probability of detection given occurrence. The tiered structure of these models can account for imperfect detection, and allows ecological and detection-related parameters to be defined as a function of predictor variables and information to be shared across sites and years. Multistate models are an extension of occupancy models, which recast counts or observations made during surveys into categories known as states (MacKenzie et al. 2009). Possible states in a multistate model can include absent, occupied, nesting, abundant, or combinations of occupied, nesting, and abundant (Royle and Nichols 2003, Nichols et al. 2007, MacKenzie et al. 2018).

Base Model Structure

To meet the objectives of our study we constructed a multistate occupancy model with a maximum of five states for a given waterbird species/group: (1) absent, (2) occupied, (3) nesting, (4) abundant, and (5) both abundant and nesting. We considered birds to be nesting if nests with eggs or chicks were sighted, or if adults exhibited behaviors associated with nesting. We classified species as abundant using thresholds defined by Park personnel, which we discuss later. We estimated the state of a given species for each location and year, and state-dependent detection probabilities by treating replicate visits within each season as primary sampling occasions. By “detection probability” we refer to the probability of observing a species in a particular state, given that the species was in that state at some time during each survey period. Our definition

differs from that of a traditional occupancy model (i.e. probability of detection given presence) in that failure to correctly characterize the status of a species at a site may be the result of their status going undetected by observers or their status being unobservable at the time of the survey (temporary dispersal or colony abandonment). For example, we assumed that nesting at a site might go undetected because surveyors visited the site before or after the nesting season, or a species may not be classified as abundant because a site was surveyed when breeding aggregations were not at their seasonal maximum.

We begin our description of the model by broadly outlining its structure, then describe the subcomponents of detection processes, the definition of state probabilities, our approach for including temporal effects (persistence), and finally our approach for selecting useful predictor variables. We denoted the observed state of a species during a survey (y) using integers 1-5, corresponding to the numbered states above. We assumed that the observed state of a species during a particular visit to a site originates from a multinomial distribution with the number of trials (n) fixed at 1. We expressed the observed states as a categorical distribution:

$$y_{i,t,k} \sim \text{Categorical}(\mathbf{p}_{z_{i,t}})$$

where $y_{i,t,k}$ is an integer referencing states 1-5 for a given species on visit k at site i , during year t , and $\mathbf{p}_{z_{i,t}}$ is a state-dependent probability vector corresponding to each state, which sums to 1. The $\mathbf{p}_{z_{i,t}}$ vector represents the probabilities of observing each of the five states conditional on the actual latent state ($Z_{i,t}$). We assumed that latent states also arise from a categorical distribution

$$Z_{i,t} \sim \text{Categorical}(\boldsymbol{\phi}_{i,t}),$$

where $Z_{i,t}$ is an integer referencing states 1-5 and $\phi_{i,t}$ is a vector of probabilities describing latent state probabilities.

The probability of a surveyor detecting a species in a particular state depends on what the true state of the species is at that site. For example, if a species is absent at a site then it is only possible to observe absence. If a species occupies a site and is nesting, then the surveyor can possibly observe: absence; occupancy but not nesting; or both occupancy and nesting (MacKenzie et al. 2009). Likewise, if a species is abundant at a site and nesting, then the surveyor may observe any of the five possible states. We parameterized the state-dependent probability vectors according to the definitions of the various states in the model. Table 4.2 outlines the state-dependent detection probabilities as a 5×5 matrix. We defined state-dependent detection probabilities (ps) for occurrence, nesting, and abundance using a conditional binomial structure, with probabilities of detecting nesting or abundance conditional on also detecting occupancy. We allowed these probabilities to vary depending on the underlying state and to be influenced by predictor variables, which we discuss later. We also assumed that observers made no false positive errors in the classification of states, meaning that observers did not misclassify absent species as present, or classify species as nesting or abundant in error.

Because occupancy is a necessary condition for exhibiting nesting or abundance, we also chose to define state probabilities using a conditional binomial structure, in which the five state probabilities were derived from three easily interpretable parameters (MacKenzie et al. 2009). These parameters include the probability that a given site is occupied ($\psi_{[Occ]}$); the probability that the species is nesting, given that the site is occupied ($\psi_{[Nest|Occ]}$); and the probability that the species is abundant $\psi_{[Abn|Occ]}$, given

that the site is occupied. We denote the latent state probabilities using the parameter ϕ , with the subscript within the square bracket corresponding to the states listed above.

Thus, the probability that site i is unoccupied by a given species at time t is defined as

$$\phi_{[\text{Absent}],i,t} = (1 - \psi_{[\text{Occ}],i,t}).$$

Only the occupancy probability is used in computing the probability of this state, because the other ψ s are conditional on occupancy. The remaining state probabilities include all three ψ parameters:

$$\phi_{[\text{Occ}],i,t} = \psi_{[\text{Occ}],i,t} (1 - \psi_{[\text{Nest}|\text{Occ}],i,t}) (1 - \psi_{[\text{Abn}|\text{Occ}],i,t}),$$

$$\phi_{[\text{Nest}],i,t} = \psi_{[\text{Occ}],i,t} \psi_{[\text{Nest}|\text{Occ}],i,t} (1 - \psi_{[\text{Abn}|\text{Occ}],i,t}),$$

$$\phi_{[\text{Abn}],i,t} = \psi_{[\text{Occ}],i,t} (1 - \psi_{[\text{Nest}|\text{Occ}],i,t}) \psi_{[\text{Abn}|\text{Occ}],i,t},$$

$$\phi_{[\text{Nest \& Abn}],i,t} = \psi_{[\text{Occ}],i,t} \psi_{[\text{Nest}|\text{Occ}],i,t} \psi_{[\text{Abn}|\text{Occ}],i,t}.$$

We defined the three ψ parameters as a function of habitat information and related the current status of species to their status in the previous year (temporal autologistic effect; MacKenzie et al. 2018). Relating the current state of species to past years enabled us to evaluate a species persistence in a given state at a site, in terms of occupancy, nesting, and abundance. These parameters also provided a means for interpolating states for years without surveys. To maximize the amount of data informing the temporal parameters, we initialized the model in the year prior to the beginning of the dataset ($t = 0$) and defined the initial states using a categorical distribution with a site-specific Dirichlet hyperprior (α_i):

$$Z_{i,0} \sim \text{Categorical}(\alpha_i).$$

We derived three separate binary indicator variables based on the latent state for each site and year for use as predictors of future states within the model. The variable F described whether a species occurred at a site in a given year

$$F_{i,t} = \left\{ \begin{array}{l} 1, \text{ if } Z_{i,t} > 1 \\ 0, \text{ if otherwise} \end{array} \right\};$$

whereas the variables R and M served as binary indicators for predicted occupancy, nesting, and abundance:

$$R_{i,t} = \left\{ \begin{array}{l} 1, \text{ if } Z_{i,t} = 3 \text{ OR } Z_{i,t} = 5 \\ 0, \text{ if otherwise} \end{array} \right\}$$

$$M_{i,t} = \left\{ \begin{array}{l} 1, \text{ if } Z_{i,t} > 3 \\ 0, \text{ if otherwise} \end{array} \right\}.$$

These variables were updated dynamically within the model-fitting algorithm.

We defined the parameters governing state probabilities using the following logit-linear regression equations:

$$\text{logit}(\psi_{[Occ] i,t}) = \mu_{[Occ]} + \eta_{1,i} + \gamma_1 \cdot F_{i,t-1},$$

$$\text{logit}(\psi_{[Nest|Occ] i,t}) = \mu_{[Nest]} + \eta_{2,i} + \gamma_2 \cdot R_{i,t-1},$$

$$\text{logit}(\psi_{[Abn|Occ] i,t}) = \mu_{[Abn]} + \eta_{3,i} + \gamma_3 \cdot M_{i,t-1};$$

where i and t index sites and years, μ denotes intercept terms, η denotes linear combinations with additive combinations of coefficients and habitat variables, and γ describes the dependency of the state probabilities on the realized state in the previous time step.

Variable Selection

We used a variable selection procedure to improve the predictive performance of the model and test general hypotheses regarding the occupancy dynamics and detection

process for species in the study. The parameters used to derive the state-dependent detection probabilities (p s) and latent state probabilities (ψ s) were defined using a series of logit-linear regression equations with a set of candidate predictors. We used a Bayesian indicator variable procedure to identify a preferred set of these predictors and prevent overfitting (Kuo and Mallick 1998, Royle and Dorazio 2008, Hooten and Hobbs 2015). This technique first entailed fitting a “global” model with all candidate predictor variables and coefficients multiplied by binary indicator variables, to which we assigned a vague prior [$\mathbf{w} \sim \text{Bern}(0.5)$], representing the probability of including a predictor in a given iteration of the model fitting algorithm. We then fit and interpreted a “final” version of the model without any indicator variable and containing only parameters for which the mean posterior of indicator variables exceeded 0.5.

These candidate variables for detection parameters included the type of survey (SurveyType), and linear and quadratic effects of survey date (DayOfYear). We evaluated a survey method predictor because we hypothesized that the detectability of species would be influenced by survey method, owing to differing habitat preferences and behaviors among species. We allowed for a quadratic effect of day of year to evaluate evidence for seasonal patterns in detectability, and hypothesized that occupancy, nesting, and abundance may exhibit a linear or convex pattern over the course of the season for one or more species. We defined probabilities of detecting occupancy in the global model as:

$$\begin{aligned} \text{logit}(p_{[occ],h,i,j}) = & \zeta_{[occ],h} + \theta_{1,1} \text{SurveyType}_{i,j} \cdot w_{1,1} + \theta_{1,2} \text{DayOfYear} \cdot w_{1,2} \\ & + \theta_{1,3} \text{DayOfYear}^2 \cdot w_{1,3}, \end{aligned}$$

where $p_{[Occ],h,i,j}$ is the probability of detecting species j at site i ; ζ is a state-specific intercept term; h is an index from 1:4 corresponding to the four unique detection probability intercepts (); and \mathbf{w} is a binary vector indicating whether a given θ is included in an iteration of the model fitting algorithm. We evaluated the same predictor variables for conditional probabilities of detecting nesting and abundance:

$$\begin{aligned} \text{logit}(p_{[Nest],m,i,j}) = & \zeta_{[Nest],m} + \theta_{2,1} \cdot \text{SurveyType}_{i,j} \cdot w_{2,1} + \theta_{2,2} \cdot \text{DayOfYear} \cdot w_{2,2} \\ & + \theta_{2,3} \cdot \text{DayOfYear}^2 \cdot w_{2,3}, \end{aligned}$$

$$\begin{aligned} \text{logit}(p_{[Abn],m,i,j}) = & \zeta_{[Abn],m} + \theta_{3,1} \cdot \text{SurveyType}_{i,j} \cdot w_{3,1}; + \theta_{3,2} \cdot \text{DayOfYear} \cdot w_{3,2} \\ & + \theta_{3,3} \cdot \text{DayOfYear}^2 \cdot w_{3,3}; \end{aligned}$$

where m is an index from 1:2 corresponding to the probabilities of detecting nesting or the abundant state conditional on occupancy, and both nesting and abundance.

Predictors we evaluated for latent state probabilities included an indicator variable for glacial vs. island sites (Glacial), and continuous predictors for survey area (Area), and an island site's distance to shore (Distance):

$$\eta_{1,i,t} = \beta_{1,1} \cdot \text{Glacial}_i \cdot w_{4,1} + \beta_{1,2} \cdot \text{Area}_i \cdot w_{4,2} + \beta_{1,3} \cdot (1 - \text{Glacial}_i) \cdot \text{Distance}_i \cdot w_{4,3},$$

$$\eta_{2,i,t} = \beta_{2,1} \cdot \text{Glacial}_i \cdot w_{5,1} + \beta_{2,2} \cdot \text{Area}_i \cdot w_{5,2} + \beta_{2,3} \cdot (1 - \text{Glacial}_i) \cdot \text{Distance}_i \cdot w_{5,3},$$

$$\eta_{3,i,t} = +\beta_{3,1} \cdot \text{Glacial}_i \cdot w_{6,1} + \beta_{3,2} \cdot \text{Area}_i \cdot w_{6,2} + \beta_{3,3} \cdot (1 - \text{Glacial}_i) \cdot$$

$\text{Distance}_i \cdot w_{6,3};$

where η s describes linear combinations of predictor variables used in calculating state probabilities; and w s are binary indicator variables dictating whether a given β is included in an iteration of the model fitting algorithm. We included a predictor for glacial vs. island sites to evaluate differences in habitat preferences (e.g., semipalmated plover

are known to preferentially select glacial outwash areas; Kessel 1979). We hypothesized that the area of a survey site would have a positive effect on the probability of occupancy, nesting, and abundance because larger sites are likely to include more space and habitat heterogeneity. The distance-to-shore variable was included to account for habitat preferences, but also as a proxy for a site's accessibility to terrestrial predators (Warwick-Evans et al. 2016).

Assessing Effect of Site Closures

One of the objectives of this study was to build a model capable of ascertaining the effect of area closures on the status of waterbird communities within the Park. Unfortunately, the extent to which we could address this question with this dataset was limited. The main issue was that of confounding, in that many of the survey sites were either closed or open to visitors throughout the study period (Figure 4.3). To avoid this confounding issue, we chose to evaluate the influence of closures for only sites that were both open and closed during the study period, which included N.W. Spider and S. Leland islands. We accomplished this by adding to the base logit-linear regression for occupancy:

$$\text{logit}(\psi_{[Occ]_{i,t}}) = \mu_{[Occ]_{i,m}} + \dots + \delta \text{TempClose}_{it},$$

where the TempClose_{it} indicator variable describes whether or not either of the two sites were temporarily closed during year t , and δ describes the species-specific effect of the closure. We restricted our assessment of closures to $\psi_{[Occ]}$ and not $\psi_{[Nest|Occ]}$ or $\psi_{[Abn|Occ]}$, due to the limited number of surveys and lack of recorded

nesting or abundance at the two sites with intermittent closures (Figure 4.3). We did not subject coefficients describing the effect of closures to the variable selection procedure.

Models for Specific Species

Although we have outlined the structure of a five-state model, we only used the full five state structure for two species, arctic terns and glaucous-winged gulls (Table 4.3). We had both technical and biological reasons for omitting particular states for the seven other target groups. We modeled occupancy and nesting state for black oystercatchers, Caspian terns, mew gulls, and pigeon guillemots; occupancy and abundance for cormorants; and only occupancy states for black-legged kittiwakes and semipalmated plovers. We omitted the nesting state for species never or only seldom found to be nesting during surveys. Similarly, we omitted abundance states for species whose survey counts lacked natural breaks, or which occupied relatively few sites. In addition to the ecological and data-related reasons for excluding specific states for certain species, there were also technical considerations. The threshold we used for classifying abundance was 50 estimated adults for arctic terns and cormorants, and 100 estimated adults for glaucous-winged gulls. The number of estimated adults was calculated as either the number of adults counted at the site or twice the number of nests (assuming two parents were associated with each nest), whichever quantity was greater. Park personnel defined abundance thresholds of 50 and 100 nesting birds to be used as one of several criteria in establishing visitor restrictions.

We made additional species-specific alterations to the base model to adjust for differences between black-legged kittiwake colonies and glaucous-winged gull colonies, relative to the other species. The cliff habitats that black-legged kittiwakes occupy and

nest in make them virtually undetectable from ground surveys; thus, we only allowed the model to estimate detection for vessel surveys for this species and fixed the probability of detection for ground surveys at zero. For glaucous-winged gulls, we included a site-level predictor for whether or not the area contained an established colony within the linear predictor for both $\psi_{[Nest|Occ]}$ and $\psi_{[Abn|Occ]}$, based on Lewis et al. (2017). The purpose of this alteration was to reduce the influence of intensive sampling that occurred at established glaucous-winged gull colony locations in conjunction with egg harvest. We did not subject coefficients describing the colony effects to the variable selection procedure.

Model Fitting

We estimated the parameters of our multistate model using Bayesian inference with a combination of noninformative and informative prior distributions. We assigned noninformative logit-normal Jefferys priors to all intercepts and coefficients in the model (Link and Barker 2009, Northrup and Gerber 2018). The only informative priors assigned were to parameters governing the state probabilities ($\phi_{i,0}$) in the year prior to the start of the surveys (2011). We specified a categorical prior with hyperpriors for initial states arising from a Dirichlet distribution. We deviated from the common, noninformative, approach of setting Dirichlet hyperpriors in multistate models to a vector of 1s (i.e. a flat or multivariate uniform distribution; MacKenzie et al. 2009, Kery and Schaub 2011), and instead specified site- and species-specific Dirichlet priors based on an earlier study by Arimitsu et al. (2007). We accomplished this by reviewing the findings from this work and identifying the observed state of particular species at sites in Glacier Bay during the

period between 2003 and 2005 (Supplemental Figure 4.1). We then specified corresponding Dirichlet priors to specific species and locations such that the prior probability of a species being in the previously observed state was twice that of all other states combined. Specifically, this entailed assigning a prior of $2/3$ to the previously observed state and $1/(3 + s)$ to the priors for the remaining states, where s is the number of states modeled for the species. We choose this scheme for assigning priors because it caused the previously observed state to be assigned twice as much weight as the other states, which provided a simple interpretation and was not a far departure from the typical noninformative assignment of 1 for hyperpriors(α). The purpose of including these initial state probabilities was to incorporate existing knowledge concerning the distribution of target species.

We estimated posterior distributions of parameters using Markov Chain Monte Carlo (MCMC) simulation (Kery and Schaub 2011), implemented using the JAGS software package (Version 4.2.0; Plummer 2003). We combined data for all focal species groups in a single model. All predictor variables were standardized prior to model fitting by subtracting the mean and dividing by the standard deviation to speed convergence and aid interpretation. We ran simulations using four Markov chains and determined suitable burn-in and iterations using the Gelman-Rubin statistic (\hat{R}) and by examining trace plots (Gelman et al. 2014).

Derived Variables

After estimating the parameters discussed above, we derived several additional quantities of interest to assist in describing site-level differences and to inform future

monitoring efforts. We derived estimates of the probability of persistence using the intercept (μ) and persistence parameters (γ):

$$\text{logit}(\text{Persistence}_{[Occ]}) = \mu_{[Occ],j} + \gamma_1,$$

$$\text{logit}(\text{Persistence}_{[Nest]}) = \mu_{[Nest],j} + \gamma_2$$

$$\text{logit}(\text{Persistence}_{[Abn]}) = \mu_{[Abn],j} + \gamma_3$$

We also used detection probability estimates to derive functions describing the influence of the number of within-season surveys on the probability of observing the true state of a species at a site. We estimated these functions for the two species that we modeled using all five states (arctic tern and glaucous-winged gull). We calculated the within-season probability of detecting occupancy, given an occupied latent state as:

$$D_{[Occ|Occ],i} = 1 - \left(1 - P_{[Occ|Occ]}\right)^i,$$

where i is the number of visits and $P_{[Occ|Occ],j}$ is the probability of detecting occupancy given that the species occupies the site, corresponding to row 2 and column 2 of the estimated state-dependent detection probability matrix (Table 4.2). We computed the remaining within-season detection probability estimates using rows 3:5, and estimated the expected number of visits required to observe nesting in the same manner. We found these quantities to be useful for highlighting species-specific differences in detectability, comparing survey methods, and for providing practical survey recommendations (Royle and Dorazio 2008).

We estimated the species richness of study sites by simulating states for all species and years using a categorical distribution, counting the number of species in states other than absent in each iteration, and then summarizing the sampling distribution

of the counts (Dorazio et al. 2006, Russell et al. 2009). We used the same procedure to derive estimates of the number of nesting species across sites, and to compute the proportion of sites where each species was present and nesting during the study period.

Model Validation

Following model fitting, we used a cross-validation procedure to assess the final model's performance. We partitioned the data into five roughly equal size groups by randomly subsampling site-year combinations, then fit the model five times, making predictions for out-of-sample data in each fold. We repeated this process 25 times to assess the variation in the predictive ability. We summarized the frequency of correct and incorrect predictions by estimating species-specific confusion matrices, with rows and columns corresponding to predicted and observed states, respectively (Fielding and Bell 1997, Guisan and Zimmermann 2000).

We assessed the value of our variable selection procedure and informative Dirichlet hyperpriors by comparing the predictive performance of three alternative models, using the cross-validation procedure described above. We compared the global model with all possible coefficients, and non-informative priors for initial states and no indicator variables (Full—Uniform), to a model with predictors selected by the variable selection procedure and non-informative priors for initial states (Final—Uniform), and a model with selected coefficients and informative priors (Final—Informative). We compared alternative models using two criteria: the estimated correct classification rate and a likelihood-based scoring function. We computed the correct classification rate by dividing the number of correct predictions (diagonal of the confusion matrix) by the total

number of visits in the data set ($n=170$). The scoring function was calculated using a method similar to that described in Hooten and Hobbs (2015):

$$score = -2 \sum_{v=1}^5 \left(\frac{\sum_{t=1}^T \log(\text{Categorical}[\mathbf{y}_v | \mathbf{y}_{-v}, \mathbf{p}_{Z_{i,t}}^*])}{T} \right),$$

where \mathbf{y}_v is a vector of observed states in the out-of-sample data, the likelihood of which is computed using predicted state-dependent probability vectors ($\mathbf{p}_{Z_{i,t}}^*$) estimated using the within-sample data (\mathbf{y}_{-v}), T is the total number of MCMC samples, and v is an index for a particular fold of the data set. The lower the scoring function the greater the predictive performance of the model.

Results

We succeeded in fitting a multistate occupancy model to waterbird survey data in Glacier Bay National Park. The variable selection procedure retained approximately one quarter of the candidate predictors for both the state probability (15/54) and detection tiers of the model (15/54). We excluded one detection-related coefficient (θ s) that the variable selection procedure selected, because we thought the effect was spurious. This coefficient was a quadratic term that produced an unreasonable, concave pattern in seasonal detection of glaucous-winged gulls. The final model with a selected predictors and informative priors (Final—Informative) showed superior predictive performance compared to alternative models, based on estimates of correct classification rate and model scores (Figure 4.4). The correct classification rate of all models exceeded 0.75, indicating that the models could correctly predict the majority of the out-of-sample observations. Confusion matrices indicated that the final model did not predict some of

the less commonly observed states (Supplemental Figure 4.2). For example, the final model did not predict any absent states for black oystercatchers or nesting states for pigeon guillemots, and only predicted absences for Caspian terns. The influence of the informative prior distribution varied by species (Supplemental Figures 4.3-4.6). The prior increased the frequency of predicted absences for arctic terns and mew gulls, had the opposite effect on cormorants and glaucous-winged gulls, and did not appear to effect estimates for other species.

Mean probability of occupancy and persistence varied across species and habitats, and all but two species showed clear evidence of site persistence (Table 4.4; Figure 4.5). Mew gulls and semipalmated plovers probabilities exhibited substantially higher occupancy at glacial outwashes than island sites. Site area and distance to shore were retained as predictors in the final model for several species, but coefficient estimates were relatively imprecise. Posteriors for coefficients describing the effect of area closures overlapped with zero considerably, suggesting that area closures did not substantially influence occupancy patterns at the two sites where closures were intermittent (Table 4.4). Habitat type did not substantially influence conditional probabilities of nesting and abundance (Table 4.5-4.6). The model revealed evidence of nesting persistence for glaucous-winged gulls and persistence in the abundant state for arctic terns and cormorants. The conditional probability of nesting glaucous-winged gulls was also greater at known colony sites.

The detection coefficients indicated that both survey type (ground vs. vessel) and sampling date influenced detection for multiple species (Table 4.7). The probability of detecting occupancy differed by survey method for black oystercatchers, cormorants,

glaucous-winged gulls, and semipalmated plovers (Table 4.7). The model identified seasonal detection patterns for arctic terns, black-legged kittiwakes, and mew gulls (Figure 4.6; Supplemental Figure 7). The probability of detecting occurrence of arctic terns and mew gulls was greater in the earlier half of the season, whereas the probability of detecting occurrence of black-legged kittiwakes increased over the season. We used detection probabilities to examine within-season detection probability estimates for arctic terns and glaucous-winged gulls for both survey methods and different survey periods (Figure 4.7). These estimates indicated that surveys in mid-June of sites where these species were both nesting and abundant were virtually guaranteed to detect occurrence of both species within three visits. The within-season probability of confirming nesting was significantly lower, particularly for arctic terns.

Estimates of other derived variables were relatively consistent throughout the study period and their level of precision varied across sites and species. Distinguishable year-to-year differences in species richness or the number of nesting species were only present for the more frequently sampled sites (e.g., Boulder Island, Geike Rock, and Tlingit Islet; Figure 4.8). Estimates of species richness and the number of nesting species were especially imprecise at glacial outwash sites. The species with the greatest estimated proportion of occupied sites included black oystercatchers, black-legged kittiwakes, and glaucous-winged gulls, whereas semipalmated plovers were estimated to occupy the fewest sites (Figure 4.9). Estimates for the proportion of sites occupied by Caspian terns and cormorants were relatively imprecise. Variance in the proportion of sites occupied by arctic terns, mew gulls, and semipalmated plovers increased over time, likely a result of less widespread sampling effort during the latter half of the study period.

Discussion

We generally succeeded in our objective of characterizing the dynamics of waterbird populations at survey sites in Glacier Bay National Park. The model identified patterns of occupancy, site persistence, and detection probability that corresponded with existing knowledge. For example, we detected relatively high site and nesting persistence (philopatry) among glaucous-winged gulls and mew gulls (Cramp 1993), and higher occupancy probability for semipalmated plovers and mew gulls in glacial outwash sites (Kessel 1979). Estimated detection probability was higher for cormorants encountered during vessel surveys, which was reasonable considering that these species roost and nest on cliff faces and can be more easily seen from the water (Robbins et al. 2001, Kotzerka et al. 2011). The higher early-season nesting detection probability that we documented for arctic terns and mew gulls was also consistent with previous studies in the region (Baird et al. 1983, Arimitsu et al. 2007). By relating occupancy, nesting, and abundance to prior states we were able to accommodate irregular survey effort and predict states at sites that were visited infrequently, albeit with lower precision. We were unable to detect an effect of closure to the public on species occupancy probability; however, this was likely the result of the low number of sites ($n = 2$) that transitioned between open and closed to visitors during the study period.

The Bayesian multistate occupancy approach that we adopted for this study was beneficial because it provided a means of using data of varying quality across species and incorporating prior information from an earlier study, resulting in greater overall predictive performance. The utility of Bayesian modeling for incorporating *a priori* information has been covered extensively in the ecological literature (Martin et al. 2005,

McCarthy and Masters 2005, Morris et al. 2015). In our analysis, informative priors exerted greater influence on predictions at sites visited less frequently (S3-S6) and had different effects across species. We found that weighting Dirichlet priors with information from previous surveys was an intuitive approach for influencing the model, and noted that the data tended to readily “wash out” the prior in cases where the two were discordant.

There were several ways in which the model predictions were imprecise or did not conform to expectations, which we largely attribute to the sparsity of data. Our analysis was unable to discover evidence of a convex seasonal pattern in the detection of glaucous-winged gulls despite the relatively high survey intensity at established colonies. Inability to detect a coherent seasonal nesting pattern could be attributable to the species’ relatively long breeding season or inter-annual variability in nesting chronology, which has been noted in previous studies (Zador et al. 2006, Lewis et al. 2017). Vessel-based surveys were more likely to detect occurrence and abundance for glaucous-winged gulls than land-based surveys. One possible explanation for this pattern is that the purpose of some early-season ground surveys was to determine whether nesting by glaucous-winged gulls had been initiated, and vessel surveys tended to occur later in the season when nesting colonies were more likely to have formed (Figure 4.2). This explanation suggests that the higher estimated detection probabilities for vessel surveys were due to the sampling design and that the model's findings regarding the higher detection probabilities for vessel surveys of glaucous-winged gulls should be viewed with skepticism.

There are a number of steps that could be taken to improve the utility of the model, and these fall into two main categories: (1) inclusion of additional habitat

information, (2) alteration of the survey protocol. Our variable selection procedure excluded nearly all of the survey area and distance-to-shore variables from the final model, indicating that these data were insufficient for characterizing site-to-site differences in species composition and nesting. Inclusion of additional habitat information would likely improve the precision of the model by better resolving site-to-site variation in state probabilities. For example, knowledge of the area of cliff habitat and treeless vegetated habitat across sites would be useful for predicting cormorant and gull occupancy, respectively (Baird et al. 1983). Another way to improve the realism of the model is to increase the resolution of the analysis by subdividing sites according to habitat type. Provided that the spatial dependence among sub-sites was accounted for, this alteration might improve estimates of detection, especially if there are portions of sites that are only visible from either land or water. One such location is South Marble Island, which cannot be fully surveyed from land due to the presence of Steller sea lions (*Eumetopias jubatus*), a species protected by the Endangered Species Act. Finally, simple alterations to the survey protocol could improve the model predictions. One potentially useful method is using double independent observers, where surveyors conduct independent counts and do not exchange information (Nichols et al. 2000). This technique would be advantageous for surveys in remote areas of Glacier Bay because different individual surveyors serve as replicates. This approach is likely to be ineffective for ground surveys, however, because some birds may disperse as soon as the first surveyor enters an area. Several other promising approaches include recording the time until detection of various species within the study area (Alldredge et al. 2007), or

employing newly developed dependent double-observer survey techniques (Golding et al. 2017).

One of the objectives of this study was to develop a model with the capacity to measure the responses of waterbird populations to encounters with Park visitors. While our model could be used for this purpose, the low number of closure management actions taken during the study period and the relatively limited information available on habitat prevented us from measuring such an effect. The two sites where we could evaluate changes in closure status (NW Spider and S. Leland islands) were surveyed across comparatively few years before and after the closure management action. In addition, the ability to properly assess disturbance effects can only be accomplished by including relevant site-specific habitat information. This information would not only improve the precision of estimates, but would be key for establishing evidence of disturbance independent of habitat and behavioral factors (Nisbet 2000).

One objection to assessing wildlife closures as we did in this analysis is that we assumed that decisions to open or close sites were independent, rather than prompted by observations by Park personnel during the previous year. One approach for incorporating the lag in implementing closures would be to reformulate the multi-state model in a manner that would enable managers to assess the influence of site closures or openings on the probability of local colonization or abandonment by specific species, rather than annual mean occupancy (Royle and Kéry 2007, MacKenzie et al. 2018). The most rigorous approach for assessing the effect of area closures would be to continue monitoring and randomly assign closures, although this approach may not be feasible. If Park managers choose to open more islands in the future, it may be helpful to incorporate

more detailed visitor information into analyses. Sites made open to the public receive unequal levels of visitation; thus, it would be valuable to incorporate information regarding the intensity of usage of different areas. Webber et al. (2013) used counts of human tracks as a proxy for human intrusion into snowy plover (*Charadrius nivosus*) habitats in Florida. This measure or something similar could be taken during land-based surveys. Alternatively, campsite reports or visitor surveys could also be used to quantify the relative intensity of visitation across sites, as well as the desirability of visiting presently closed areas.

Management Implications

Findings from this study suggested pathways for improving the efficiency of future surveys for waterbird concentrations in Glacier Bay National Park. Our model suggests that surveys in June are ideal for documenting nesting by arctic terns and mew gulls, and that late season vessel surveys are ideal for detecting nesting black-legged kittiwakes. We also generated estimates that can be used to determine the number of within-season visits required to confirm the absence of nests or adults with a particular degree of certainty. A higher frequency of surveys at newly opened or closed sites, additional habitat information, and a greater effort to determine whether birds detected in surveys are nesting or not would greatly enhance the capacity to assess the influence of Park visitors on the occupancy and nesting of species at important aggregation and nesting sites.

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References

- Allredge, M. W., K. H. Pollock, T. R. Simons, J. A. Collazo, and S. A. Shriner. 2007. Time-of-detection method for estimating abundance from point-count surveys. *Auk* 124:653–664.
- Arimitsu, M. L., J. F. Piatt, and M. D. Romano. 2007. Distribution of ground-nesting marine birds along shorelines in Glacier Bay, southeastern Alaska: an assessment related to potential disturbance by back-country users. U.S. Geological Survey. <<https://pubs.er.usgs.gov/publication/sir20075278>>.
- Baird, P. A., P. J. Gould, C. J. Lensink, and G. A. Sanger. 1983. The breeding biology and feeding ecology of marine birds in the Gulf of Alaska. US Fish and Wildlife Service, Anchorage, Alaska.
- Chatwin, T. A., R. Joy, and A. E. Burger. 2013. Set-back distances to protect nesting and roosting seabirds off Vancouver Island from boat disturbance. *Waterbirds* 36:43–52.
- Cramp, S., editor. 1993. Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic. Volume 3: waders to gulls. Reprinted (with corrections). Oxford Univ. Press, Oxford.
- Dorazio, R. M., J. A. Royle, B. Söderström, and A. Glimskär. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842–854.

- Fancy, S. G., J. E. Gross, and S. L. Carter. 2009. Monitoring the condition of natural resources in US national parks. *Environmental Monitoring and Assessment* 151:161–174.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental conservation* 24:38–49.
- Gelman, A., John B. Carlin, H. S. Stern, David B. Dunson, A. Vehtari, and Donald B. Rubin. 2014. *Bayesian data analysis*. Third edition. Texts in statistical science, CRC Press, Boca Raton.
- Golding, J. D., J. J. Nowak, and V. J. Dreitz. 2017. A multispecies dependent double-observer model: A new method for estimating multispecies abundance. *Ecology and Evolution* 7:3425–3435.
- Gu, W., and R. K. Swihart. 2004. Absent or undetected? Effects of non-detection of species occurrence on wildlife–habitat models. *Biological Conservation* 116:195–203.
- Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
- Hill, D., D. Hockin, D. Price, G. Tucker, R. Morris, and J. Treweek. 1997. Bird disturbance: improving the quality and utility of disturbance research. *Journal of Applied Ecology* 34:275.
- Hoeting, J. A., M. Leecaster, and D. Bowden. 2000. An improved model for spatially correlated binary responses. *Journal of Agricultural, Biological, and Environmental Statistics* 5:102–114.
- Hooten, M. B., and N. T. Hobbs. 2015. *A guide to Bayesian model selection for ecologists*. Ecological Monographs 85:3–28.
- Kery, M., and M. Schaub. 2011. *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Academic Press.
- Kéry, M., and H. Schmid. 2006. Estimating species richness: calibrating a large avian monitoring programme. *Journal of Applied Ecology* 43:101–110.
- Kessel, B. 1979. Avian habitat classification for Alaska. *Murrelet* 60:86–94.
- Kotzerka, J., S. A. Hatch, and S. Garthe. 2011. Evidence for foraging-site fidelity and individual foraging behavior of pelagic cormorants rearing chicks in the Gulf of Alaska. *Condor* 113:80–88.
- Kuo, L., and B. Mallick. 1998. Variable selection for regression models. *Sankhyā: The Indian Journal of Statistics, Series B* 65–81.

Lewis, T. M., C. Behnke, and M. B. Moss. 2017. Glaucous-winged gull *Larus glaucescens* monitoring in preparation for resuming native egg harvest in Glacier Bay National Park. *Marine Ornithology* 45:165–174.

Link, W. A., and R. J. Barker. 2009. *Bayesian inference: with ecological applications*. Academic Press.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. E. Hines. 2018. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier.

MacKenzie, D. I., J. D. Nichols, M. E. Seamans, and R. J. Gutiérrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90:823–835.

Martin, T. G., P. M. Kuhnert, K. Mengersen, and H. P. Possingham. 2005. The power of expert opinion in ecological models using Bayesian methods: impact of grazing on birds. *Ecological Applications* 15:266–280.

McCarthy, M. A., and P. Masters. 2005. Profiting from prior information in Bayesian analyses of ecological data. *Journal of Applied Ecology* 42:1012–1019.

McCarthy, M. A., and H. P. Possingham. 2007. Active adaptive management for conservation. *Conservation Biology* 21:956–963.

Morris, W. K., P. A. Vesik, M. A. McCarthy, S. Bunyavejchewin, and P. J. Baker. 2015. The neglected tool in the Bayesian ecologist's shed: a case study testing informative priors' effect on model accuracy. *Ecology and Evolution* 5:102–108.

National Park Service. 2006. *Management Policies*. U.S. Department of the Interior. <<http://www.nps.gov/policy/mp/policies.html>>.

Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998. Inference methods for spatial variation in species richness and community composition when not all species are detected. *Conservation Biology* 12:1390–1398.

Nichols, J. D., J. E. Hines, D. I. Mackenzie, M. E. Seamans, and R. J. Gutierrez. 2007. Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology* 88:1395–1400.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* 117:393–408.

- Nichols, J. D., and B. K. Williams. 2006. Monitoring for conservation. *Trends in Ecology & Evolution* 21:668–673.
- Nisbet, I. C. T. 2000. Disturbance, habituation, and management of waterbird colonies. *Waterbirds* 23:312–332.
- Northrup, J. M., and B. D. Gerber. 2018. A comment on priors for Bayesian occupancy models. *PLoS ONE* 13:e0192819.
- Patten, S. M. 1974. Breeding ecology of the glaucous-winged gull (*Larus glaucescens*) in Glacier Bay, Alaska. Masters thesis, University of Washington, Seattle, USA.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 20–22, in. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*. ISSN, Vienna, Austria.
- Purcell, K. L., S. R. Mori, and M. K. Chase. 2005. Design considerations for examining trends in avian abundance using point counts: examples from oak woodlands. *Condor* 305–320.
- Robbins, C. S., B. Bruun, Herbert Spencer Zim, and Herbert S. Zim. 2001. *Birds of North America: A guide to field identification*. Macmillan.
- Royle, J. A., and R. M. Dorazio. 2008. *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Academic Press.
- Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. *Ecology* 88:1813–1823.
- Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence–absence data or point counts. *Ecology* 84:777–790.
- Russell, R. E., J. A. Royle, V. A. Saab, J. F. Lehmkuhl, W. M. Block, and J. R. Sauer. 2009. Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. *Ecological Applications* 19:1253–1263.
- Stohlgren, T. J., J. F. Quinn, M. Ruggiero, and G. S. Waggoner. 1995. Status of biotic inventories in US national parks. *Biological Conservation* 71:97–106.
- Thompson, W. L. 2002. Towards reliable bird surveys: accounting for individuals present but not detected. *The Auk* 119:18–25.
- Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications* 13:1790–1801.

Verhulst, S., K. Oosterbeek, and B. J. Ens. 2001. Experimental evidence for effects of human disturbance on foraging and parental care in oystercatchers. *Biological Conservation* 101:375–380.

Warwick-Evans, V. C., P. W. Atkinson, L. A. Robinson, and J. A. Green. 2016. Predictive modelling to identify near-shore, fine-scale seabird distributions during the breeding season. *PLoS ONE* 11.
<<https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4816348/>>. Accessed 12 Oct 2018.

Webber, A. F., J. A. Heath, and R. A. Fischer. 2013. Human disturbance and stage-specific habitat requirements influence snowy plover site occupancy during the breeding season. *Ecology and Evolution* 3:853–863.

Zador, S. G., J. F. Piatt, and A. E. Punt. 2006. Balancing predation and egg harvest in a colonial seabird: A simulation model. *Ecological Modelling* 195:318–326.

Tables

Table 4.1. Summary of waterbird surveys in Glacier Bay National Park, Alaska (2012-2017). Asterisks denote glacial outwash sites and the remaining sites are all islands.

Site	Survey Area (km ²)	Years Surveyed	# Surveys (Ground)	# Surveys (Vessel)	Unique Species
Adams Inlet*	2.33	2	2	3	7
Boulder Island	0.06	6	14	11	7
Eider Island	0.08	3	3	2	4
Flapjack Island	0.09	6	10	0	4
Flapjack Islets	1.58	3	3	1	3
Geikie Rock	0.01	6	8	11	7
Grand Pacific Glacier*	0.29	2	2	0	3
Hugh Miller Complex	0.05	3	3	4	6
Leland Island	0.88	4	4	2	4
Lone Island	0.02	5	6	9	5
McBride Glacier*	0.06	3	4	0	4
Muir Glacier*	1.50	2	2	2	6
NW Spider Island	0.05	3	5	3	3
Reid Inlet*	0.14	2	2	1	5
Russell Islets	1.94	6	3	7	7
Sealers Island	0.06	4	3	2	7
S. Marble Island	0.17	6	4	11	6
Sturgess Island	0.11	2	1	4	1
Tlingit Islet	0.07	6	2	0	8

Table 4.2. Probability of detection assigned to the five observable states (OBSERVED) as a function of the estimated true underlying state (TRUE), where “Occ”, “Nest”, and “Abn” denote the status of the site *vis a vis* occupancy, nesting, and abundance, respectively. Indices for particular sites, species, and survey occasions are omitted to improve readability.

		OBSERVED				
		Absent	Occ	Occ + Nest	Occ + Abn	Occ + Nest + Abn
TRUE	Absent	1	–	–	–	–
	Occ	$(1 - p_{Occ,1})$	$p_{Occ,1}$	–	–	–
	Occ + Nest	$(1 - p_{Occ,2})$	$p_{Occ,2}(1 - p_{Nest,1})$	$p_{Occ,2} p_{Nest,1}$	–	–
	Occ + Abn	$(1 - p_{Occ,3})$	$p_{Occ,3}(1 - p_{Abn,1})$	–	$p_{Occ,3} p_{Abn,1}$	–
	Occ + Nest + Abn	$(1 - p_{Occ,4})$	$p_{Occ,4}(1 - p_{Nest})(1 - p_{Abn,2})$	$p_{Occ,4} p_{Nest,2} (1 - p_{Abn,2})$	$p_{Occ,4}(1 - p_{Nest,2}) p_{Abn,2}$	$p_{Occ,4} p_{Nest,2} p_{Abn,2}$

Table 4.3. Shading indicates modeled states for waterbird species at islands and glacial outwash areas in Glacier Bay National Park. Species include arctic tern (ARTE), black oystercatcher (BLOY), black-legged kittiwake (BLKI), unidentified cormorants (Cormorant), Caspian tern (CATE), glaucous-winged gull (GWGU), mew gull (MEGU), pigeon guillemot (PIGU), and semipalmated plover (SEPL).

		STATES				
		Absent	Occupied	Occupied & Nesting	Occupied & Abundant	Occupied & Nesting & Abundant
SPECIES	ARTE					
	BLKI					
	BLOY					
	CATE					
	Cormorant					
	GWGU					
	MEGU					
	PIGU					
	SEPL					

Table 4.4 Parameters affecting the probability of occupancy by arctic terns (ARTE), black oystercatchers (BLOY), black-legged kittiwakes (BLKI), Caspian terns (CATE), unidentified cormorants (Cormorant), glaucous-winged gulls (GWGU), mew gulls (MEGU), pigeon guillemots (PIGU), and semipalmated plovers (SEPL) at islands and glacial outwash areas in Glacier Bay National Park. Estimates are shown with lower (LCL) and upper (UCL) 95% credible intervals; coefficients with intervals not overlapping zero are shown in bold.

Species	Estimate	SE	LCL	UCL	Species	Estimate	SE	LCL	UCL
Intercept (μ_{occ})					Persistence (γ_1)				
ARTE	-1.13	0.93	-2.68	1.06	ARTE	2.65	1.05	0.52	4.69
BLKI	-0.31	1.19	-2.5	2.19	BLKI	1.79	1.29	-0.92	4.19
BLOY	1.76	1.11	-0.31	4.02	BLOY	3.09	1.23	0.61	5.44
CATE	-0.79	0.68	-1.92	0.83	CATE	2.11	1.08	0.15	4.37
Cormorant	-0.93	0.56	-2.02	0.2	Cormorant	2.30	0.97	0.56	4.33
GWGU	1.64	1.5	-1.11	4.47	GWGU	2.23	1.35	-0.32	4.90
MEGU	-2.15	0.52	-3.25	-1.21	MEGU	3.62	0.71	2.31	5.10
PIGU	-2.24	0.56	-3.4	-1.23	PIGU	3.90	0.73	2.54	5.39
SEPL	-3.23	0.64	-4.6	-2.08	SEPL	1.03	1.18	-1.37	3.25
Glacial ($\beta_{1,1}$)					Closure (δ)				
BLKI	-0.53	1.63	-3.72	2.65	ARTE	-0.42	1.08	-2.46	1.83
BLOY	-1.37	1.24	-3.6	1.45	BLKI	-0.66	1.73	-3.9	2.8
GWGU	-0.21	1.59	-3.09	3.07	BLOY	0.31	1.52	-2.49	3.45
MEGU	1.92	1.04	0.03	4.12	CATE	-1.16	1.42	-3.89	1.6
PIGU	-1.44	1.04	-3.48	0.58	Cormorant	-1.47	1.25	-4.1	0.87
SEPL	3.44	0.99	1.54	5.42	GWGU	-0.23	1.5	-3.01	2.9
Area ($\beta_{1,2}$)					MEGU	0.1	1.07	-1.91	2.28
BLKI	-1.66	1.24	-4.24	0.65	PIGU	-1.03	1.3	-3.7	1.42
SEPL	0.83	0.46	-0.05	1.77	SEPL	-0.47	1.42	-3.38	2.17
Distance ($\beta_{1,3}$)									
BLKI	-1.13	1.33	-3.84	1.49					

Table 4.5. Parameters affecting the probability of nesting conditional on occupancy for arctic terns (ARTE), black oystercatchers (BLOY), Caspian terns (CATE), unidentified cormorants (Cormorant), glaucous-winged gulls (GWGU), mew gulls (MEGU), and pigeon guillemots (PIGU) at islands and glacial outwash areas in Glacier Bay National Park, Alaska. Estimates are shown with standard error (SE) and lower (LCL) and upper (UCL) 95% credible intervals; coefficients with intervals not overlapping zero are shown in bold.

Species	Estimate	SE	LCL	UCL
Intercept ($\mu_{[Nest]}$)				
ARTE	0.45	1.65	-2.72	3.61
BLOY	2.37	1.02	0.57	4.52
CATE	-0.81	1.47	-3.31	2.42
GWGU	-0.45	1.04	-2.02	2.38
MEGU	0.12	0.89	-1.51	2.09
PIGU	1.27	1.07	-0.63	3.69
Glacial ($\beta_{2,1}$)				
CATE	-0.31	1.56	-3.38	2.80
GWGU	-1.73	1.46	-4.40	1.56
MEGU	-1.31	1.11	-3.44	0.93
PIGU	-0.13	1.69	-3.39	3.23
Distance ($\beta_{2,3}$)				
ARTE	-0.72	1.49	-3.50	2.54

Species	Estimate	SE	LCL	UCL
Persistence (γ_2)				
ARTE	1.35	1.44	-1.45	4.21
BLOY	1.09	1.32	-1.43	3.74
CATE	0.07	1.67	-3.19	3.32
GWGU	2.94	1.22	0.49	5.36
MEGU	1.24	1.45	-1.72	4.00
PIGU	1.58	1.35	-1.09	4.24
Colony				
GWGU	1.98	1.20	-0.35	4.42

Table 4.6. Parameters affecting the probability of abundance conditional on occupancy for arctic terns (ARTE), unidentified cormorants (Cormorant), and glaucous-winged gulls (GWGU) at sites in Glacier Bay National Park, Alaska. Estimates are shown with standard errors (SE) and lower (LCL) and upper (UCL) 95% credible intervals; coefficients with intervals not overlapping zero are shown in bold.

Species	Estimate	SE	LCL	UCL
Intercept ($\mu_{[Abn]}$)				
ARTE	-2.13	0.77	-3.59	-0.58
Cormorant	-1.61	0.64	-2.84	-0.35
GWGU	-0.34	0.69	-1.65	1.08
Glacial ($\beta_{3,1}$)				
GWGU	-0.74	1.43	-3.62	2.03
Persistence (γ_3)				
ARTE	2.97	1.05	0.93	5.10
Cormorant	2.46	0.98	0.62	4.50
GWGU	0.75	1.22	-1.49	3.31
Colony				
GWGU	3.14	1.08	1.07	5.29

Table 4.7. State-dependent probabilities of detecting occupancy for arctic terns (ARTE), black oystercatchers (BLOY), black-legged kittiwakes (BLKI), Caspian terns (CATE), unidentified cormorants (Cormorant), glaucous-winged gulls (GWGU), mew gulls (MEGU), pigeon guillemots (PIGU), and semipalmated plovers (SEPL) at islands and glacial outwash areas in the Glacier Bay National Park. Survey method is shown in parentheses for species with differing detection probabilities based on survey method. Asterisks denote species with seasonal detection effects; mid-season detection estimates are provided for these species (calculation based on mean DayOfYear). Estimates are shown with standard errors (SE) and lower (LCL) and upper (UCL) 95% credible intervals.

Parameter	Estimate	SE	LCL	UCL
ARTE*				
P[OCC]	0.45	0.19	0.13	0.81
P[OCC OCC+R]	0.36	0.25	0.03	0.88
P[OCC OCC+ABN]	0.52	0.32	0.02	0.98
P[OCC OCC+R+ABN]	0.84	0.17	0.36	0.99
BLKI*				
P[OCC]	0.39	0.10	0.21	0.59
BLOY (Ground)				
P[OCC]	0.91	0.11	0.59	1.00
P[OCC OCC+R]	0.83	0.20	0.29	1.00
BLOY (Vessel)				
P[OCC]	0.76	0.16	0.39	0.96
P[OCC OCC+R]	0.64	0.25	0.11	0.98
CATE				
P[OCC]	0.30	0.14	0.09	0.61
P[OCC OCC+R]	0.24	0.20	0.02	0.75
Cormorant (Ground)				
P[OCC]	0.25	0.14	0.06	0.58
P[OCC OCC+ABN]	0.37	0.30	0.01	0.96
Cormorant (Vessel)				
P[OCC]	0.62	0.10	0.41	0.80
P[OCC OCC+ABN]	0.63	0.29	0.06	0.99
GWGU (Ground)				
P[OCC]	0.39	0.21	0.07	0.83
P[OCC OCC+R]	0.32	0.25	0.02	0.88
P[OCC OCC+ABN]	0.47	0.32	0.01	0.98
P[OCC OCC+R+ABN]	0.80	0.21	0.24	0.99
GWGU (Vessel)				
P[OCC]	0.71	0.16	0.36	0.94
P[OCC OCC+R]	0.59	0.26	0.10	0.96
P[OCC OCC+ABN]	0.70	0.28	0.08	1.00
P[OCC OCC+R+ABN]	0.94	0.09	0.69	1.00
MEGU*				
P[OCC]	0.68	0.12	0.41	0.88
P[OCC OCC+R]	0.55	0.24	0.10	0.94
PIGU				
P[OCC]	0.64	0.19	0.24	0.93
P[OCC OCC+R]	0.53	0.27	0.06	0.96
SEPL (Ground)				
P[OCC]	0.83	0.18	0.34	0.99
SEPL (Vessel)				
P[OCC]	0.50	0.18	0.17	0.82

Table 4.8. State-dependent probabilities of detecting occupancy for arctic terns (ARTE), black oystercatchers (BLOY), Caspian terns (CATE), unidentified cormorants (Cormorant), glaucous-winged gulls (GWGU), mew gulls (MEGU), and pigeon guillemots (PIGU) at islands and glacial outwash areas in the Glacier Bay National Park. Survey method is shown in parentheses for species with differing detection based on survey method. Asterisks denote species with seasonal detection effects; mid-season detection estimates are provided for these species calculation based on mean DayOfYear). Estimates are shown with standard errors (SE) and lower (LCL) and upper (UCL) 95% credible intervals.

Parameter	Estimate	SE	LCL	UCL
ARTE*				
P[R OCC+R]	0.07	0.07	0.00	0.27
P[R OCC+R+ABN]	0.24	0.19	0.02	0.72
P[ABN OCC+ABN]	0.33	0.24	0.01	0.84
P[ABN OCC+R+ABN]	0.60	0.26	0.08	0.96
BLOY (Ground)				
P[R OCC+R]	0.37	0.11	0.12	0.56
BLOY (Vessel)				
P[R OCC+R]	0.28	0.13	0.05	0.52
CATE				
P[R OCC+R]	0.09	0.10	0.00	0.38
Cormorant (Ground)				
P[ABN OCC+ABN]	0.26	0.22	0.01	0.73
Cormorant (Vessel)				
P[ABN OCC+ABN]	0.44	0.22	0.04	0.80
GWGU (Ground)				
P[R OCC+R]	0.10	0.10	0.00	0.36
P[R OCC+R+ABN]	0.34	0.21	0.04	0.78
P[ABN OCC+ABN]	0.26	0.25	0.00	0.86
P[ABN OCC+R+ABN]	0.50	0.30	0.02	0.96
GWGU (Vessel)				
P[R OCC+R]	0.19	0.12	0.02	0.46
P[R OCC+R+ABN]	0.40	0.22	0.06	0.83
P[ABN OCC+ABN]	0.40	0.24	0.03	0.86
P[ABN OCC+R+ABN]	0.62	0.27	0.08	0.97
MEGU*				
P[R OCC+R]	0.33	0.17	0.06	0.67
PIGU				
P[R OCC+R]	0.17	0.10	0.02	0.39

Figures

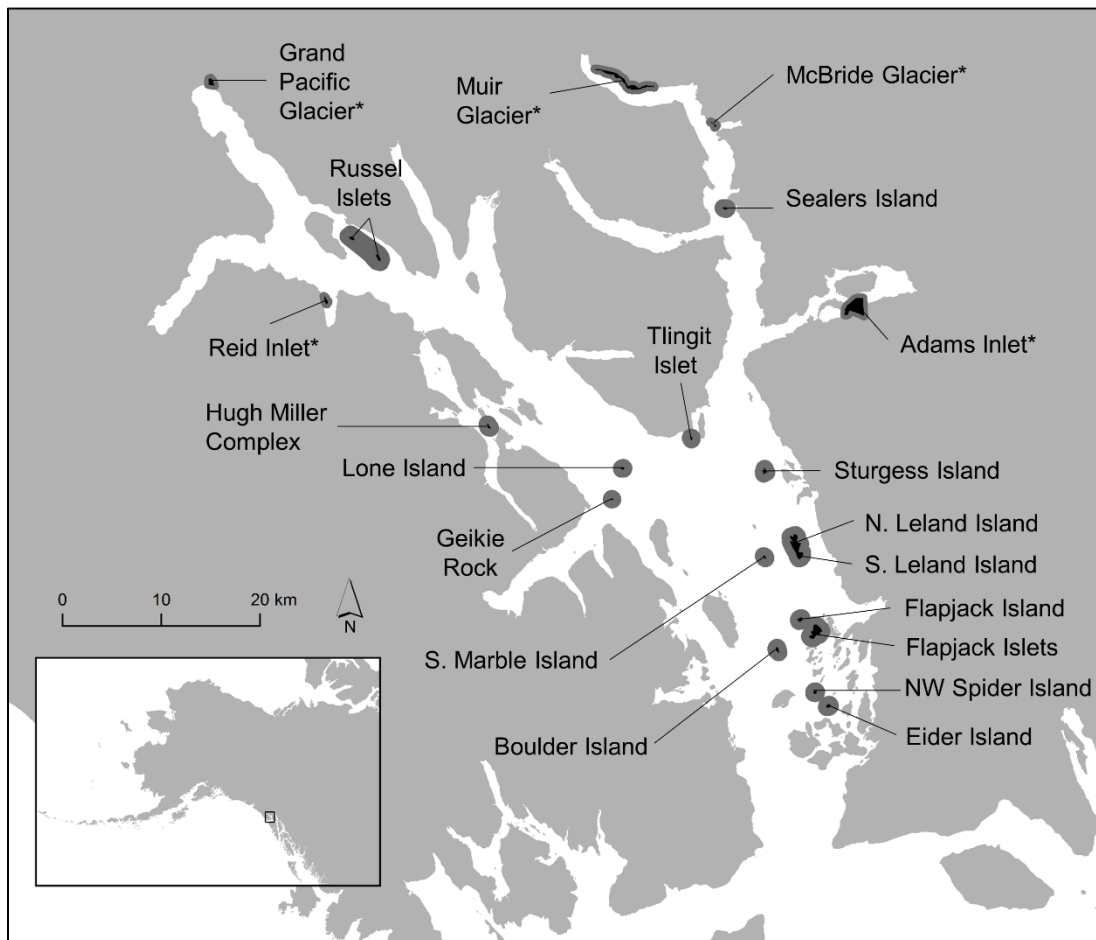


Figure 4.1. Waterbird survey sites in Glacier Bay National Park, Alaska. Asterisks denote glacial outwash areas.

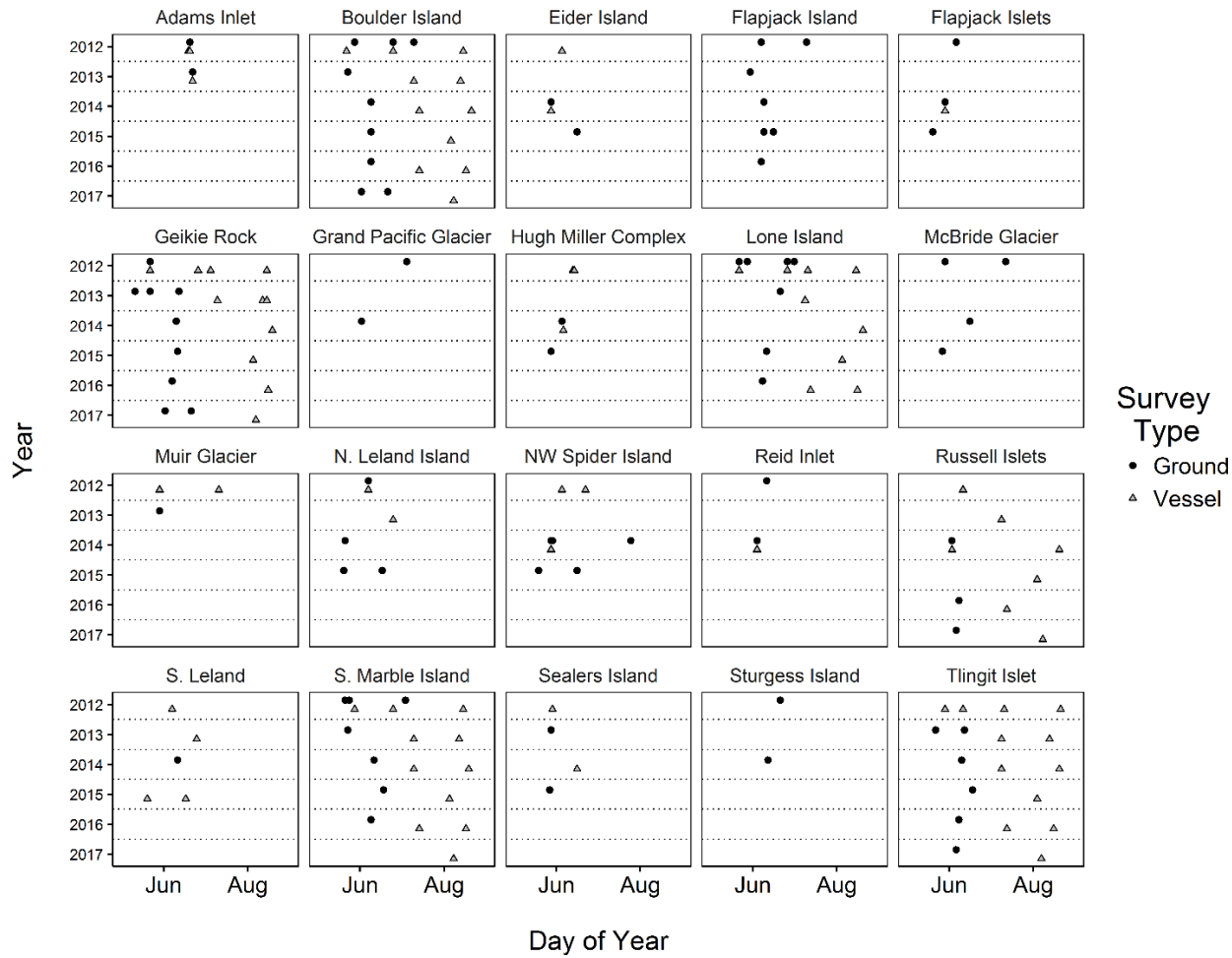


Figure 4.2. Temporal distribution of ground and vessel surveys for waterbirds at islands and glacial outwash areas in Glacier Bay National Park, Alaska.

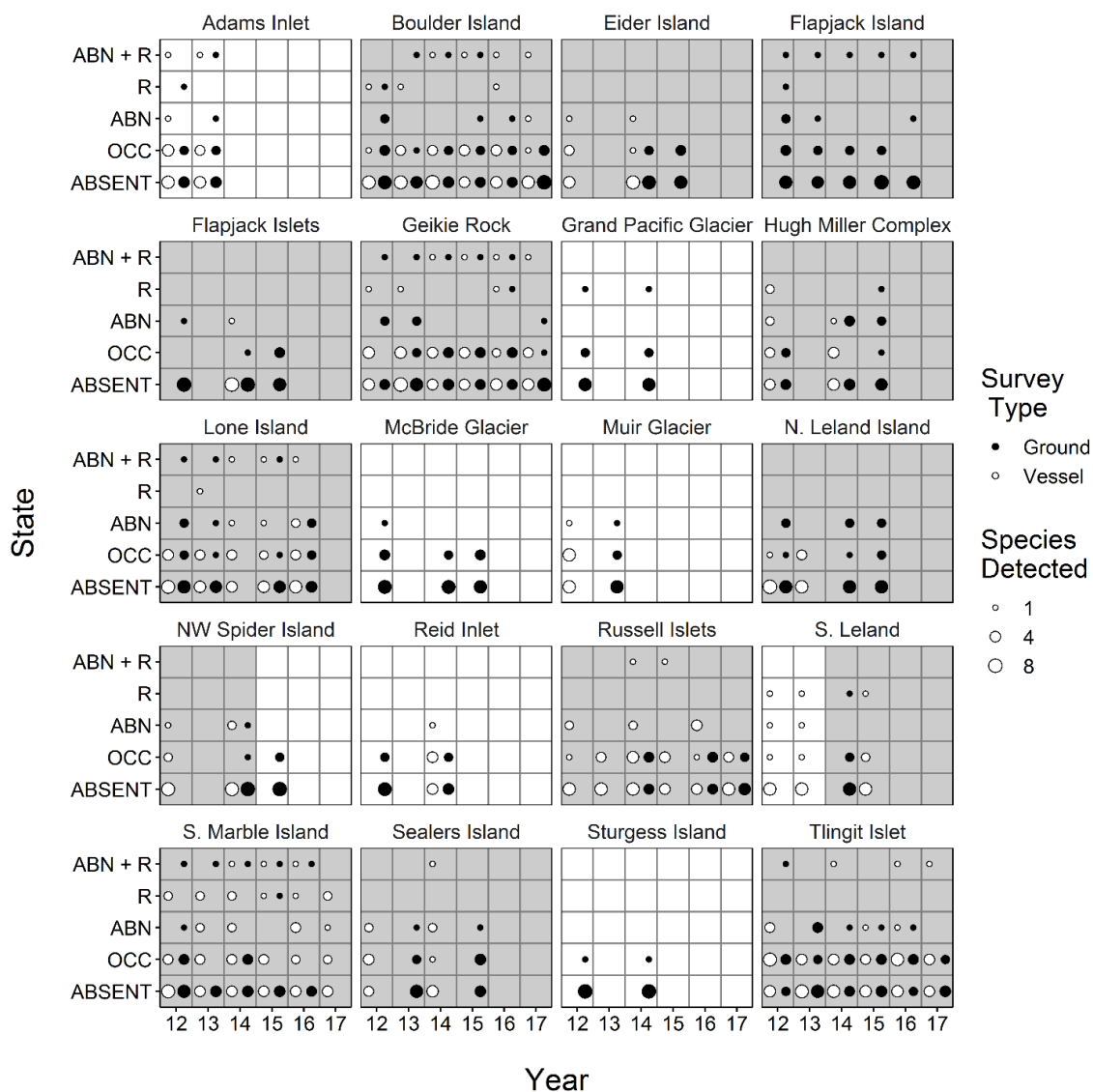


Figure 4.3. Detections of waterbird species in various states (OCC = occupied; ABN = abundant; R = nesting) in Glacier Bay National Park, Alaska. Gray shading in the background denotes years when sites were closed to Park visitors.

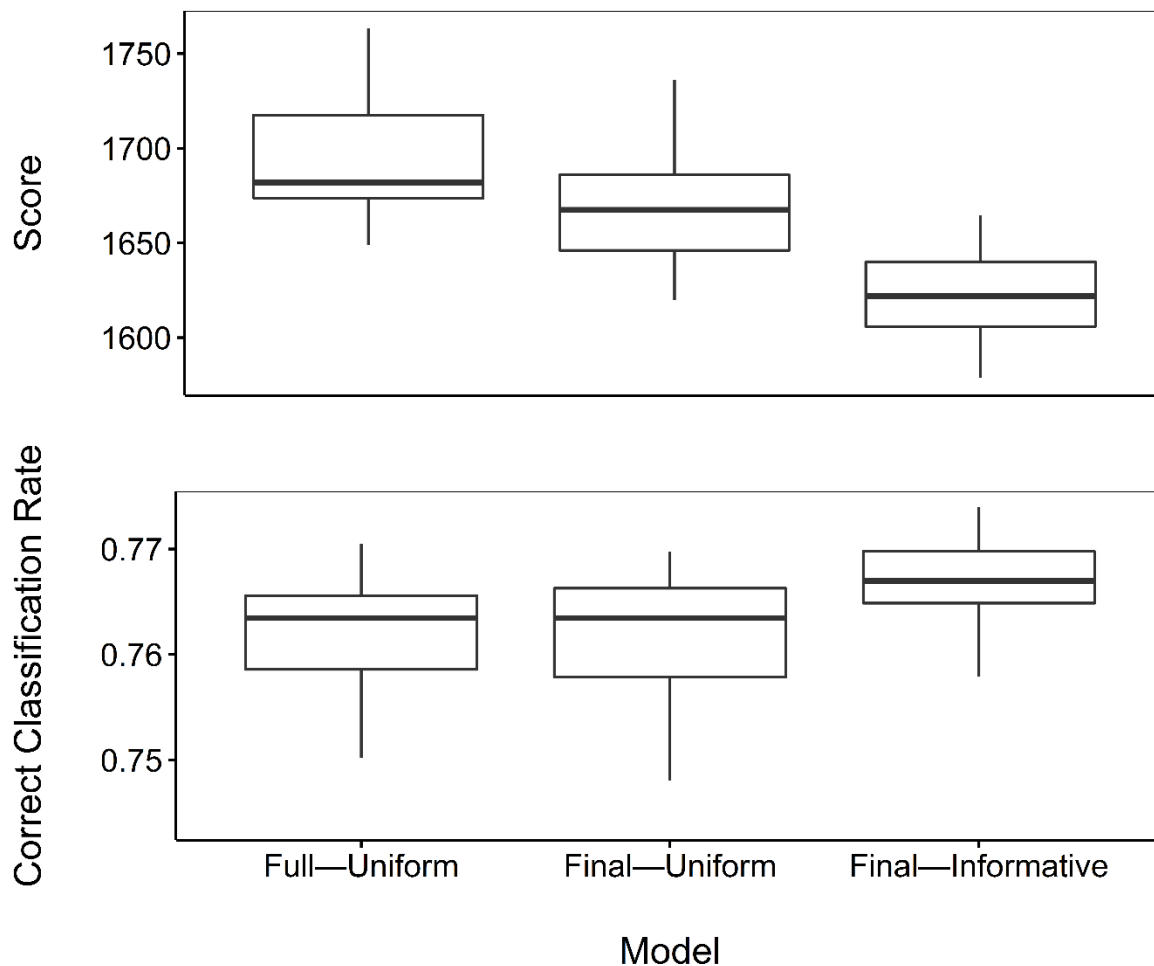


Figure 4.4. Measures of predictive performance for three Bayesian multistate occupancy models based on a five-fold cross-validation procedure. The Full—Uniform model included all possible predictor variables and uniform Dirichlet hyperpriors, whereas Final—Uniform and Final—Informative models contained a subset of predictors and uniform and informative hyperpriors, respectively. Score is computed by summing the log likelihood of out-of-sample data across folds (lower is better), and Correct Classification Rate is the estimated proportion of out-of-sample observations correctly predicted by the model (higher is better).

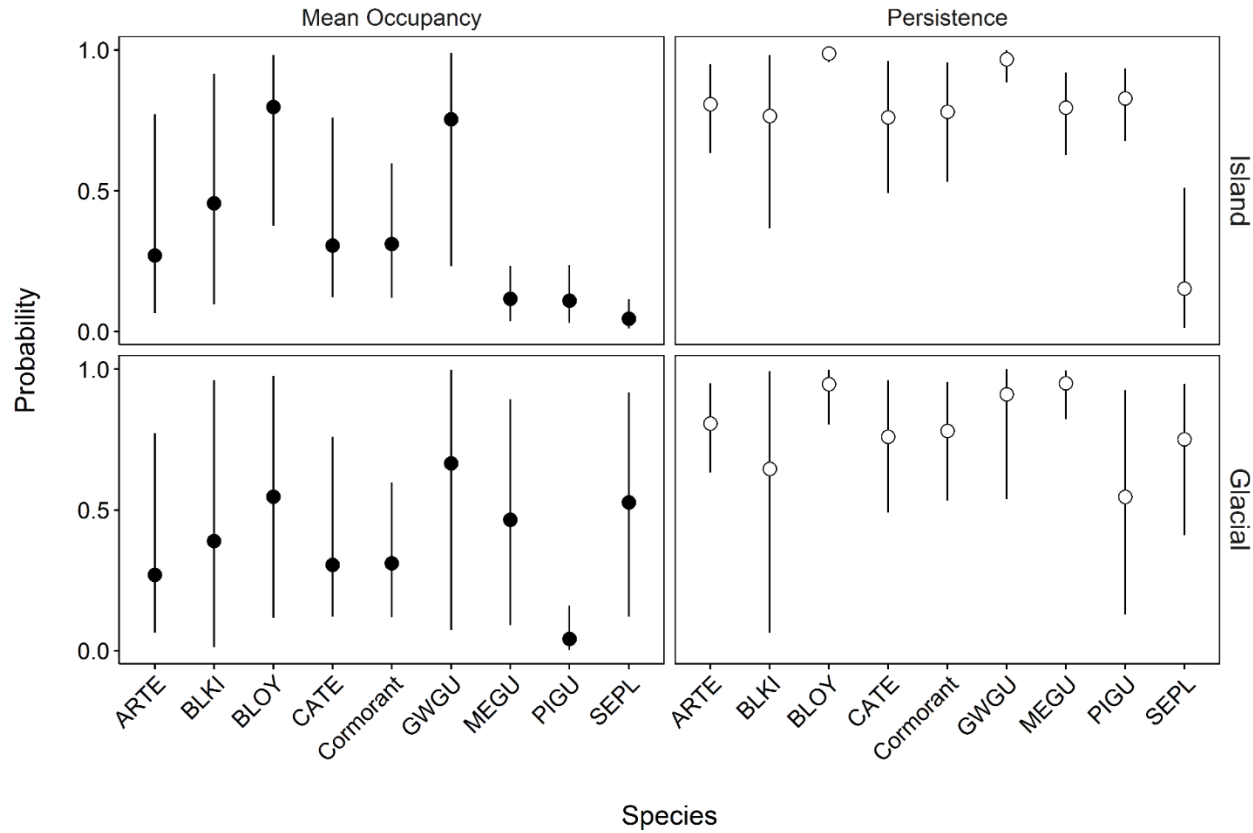


Figure 4.5. Estimated probability of occupancy and persistence for arctic terns (ARTE), black oystercatchers (BLOY), black-legged kittiwakes (BLKI), glaucous-winged gulls (GWGU), unidentified cormorants (Cormorant), mew gulls (MEGU), pigeon guillemots (PIGU), and semipalmated plovers (SEPL) across two habitat types (island and glacial outwash) in Glacier Bay National Park, Alaska. Estimates are shown with 95% credible intervals. Estimates for glaucous-winged gulls are for non-colony sites.

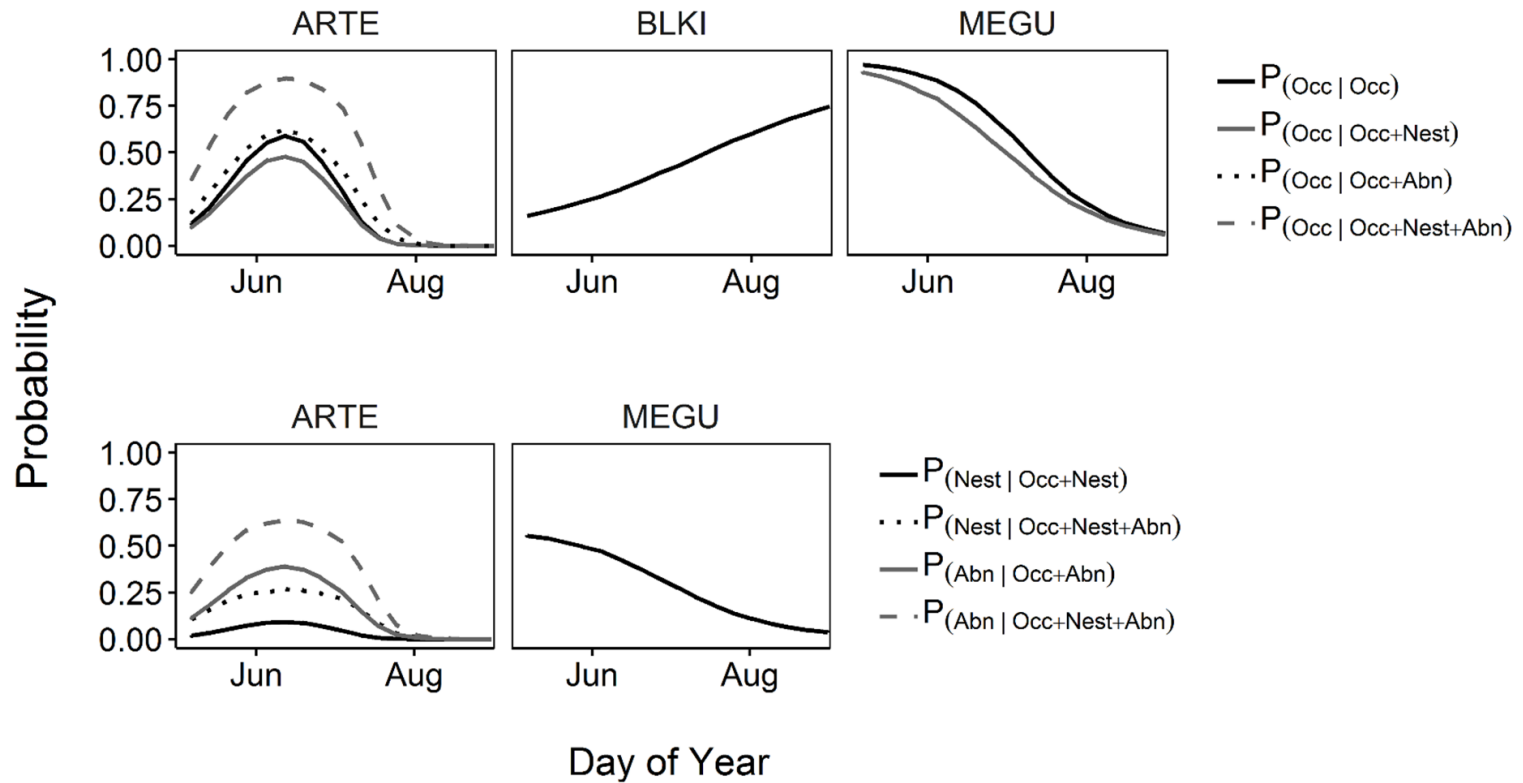


Figure 4.6. Seasonal patterns in probabilities of detecting occupancy (top) and nesting or the state of abundance (bottom) of waterbird species in Glacier Bay National Park, Alaska, conditional on the true underlying state. Species include: arctic tern (ARTE), black-legged kittiwake (BLKI), and mew gull (MEGU). Estimates shown represent detection probabilities averaged over the two survey methods (ground- and vessel-based).

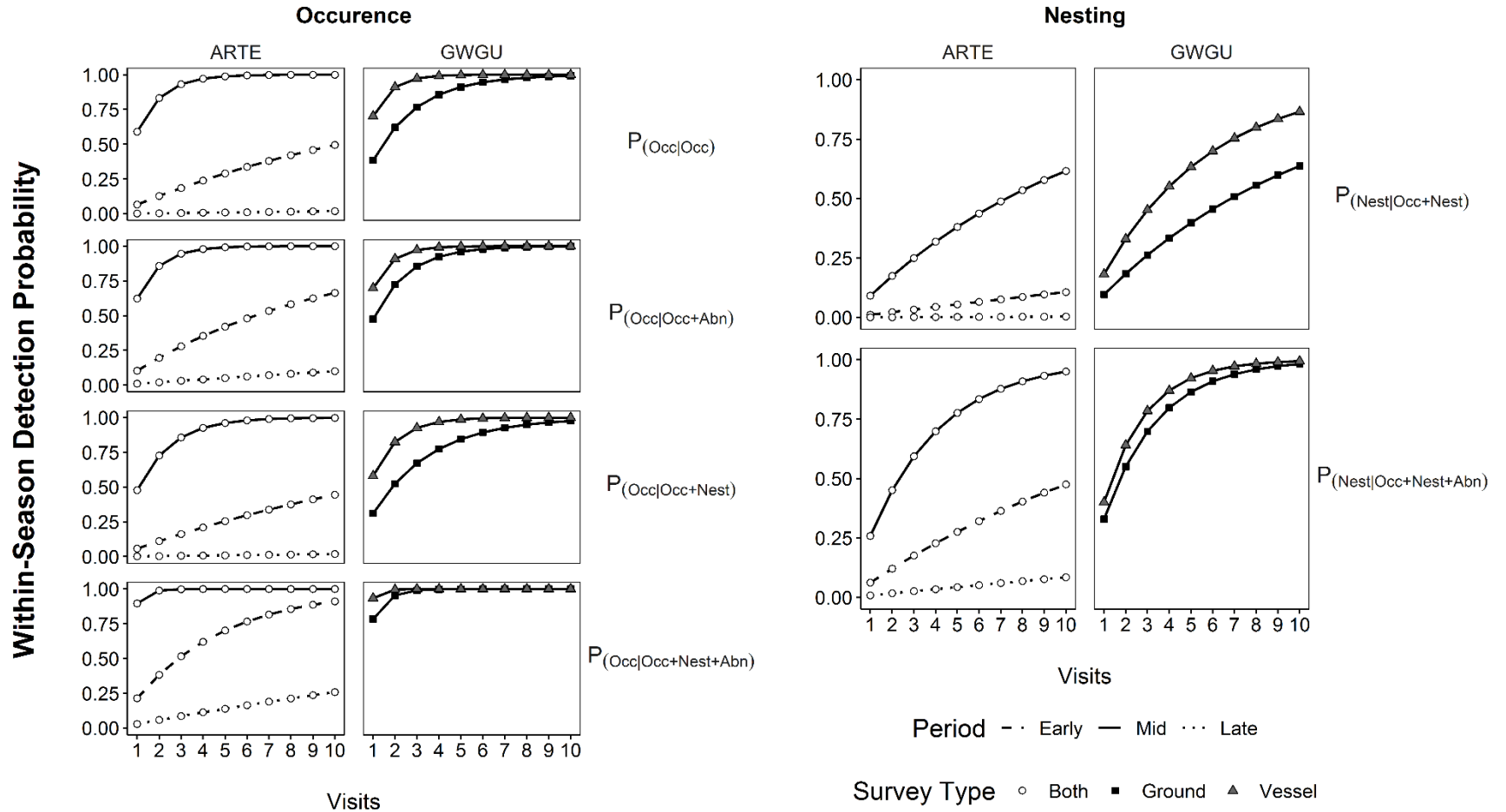


Figure 4.7. Probability of detecting the occurrence (left) or nesting (right) of arctic terns (ARTE) and glaucous-winged gulls (GWGU) at a given site in Glacier Bay National Park, Alaska as a function of the number of repeated visits within a season, survey type, and survey period. The three survey periods included: early (May 1), mid (June 15), and late (August 1). Only the mid survey period is shown for glaucous-winged gulls because the final model did not include a seasonal detection effect for this species.

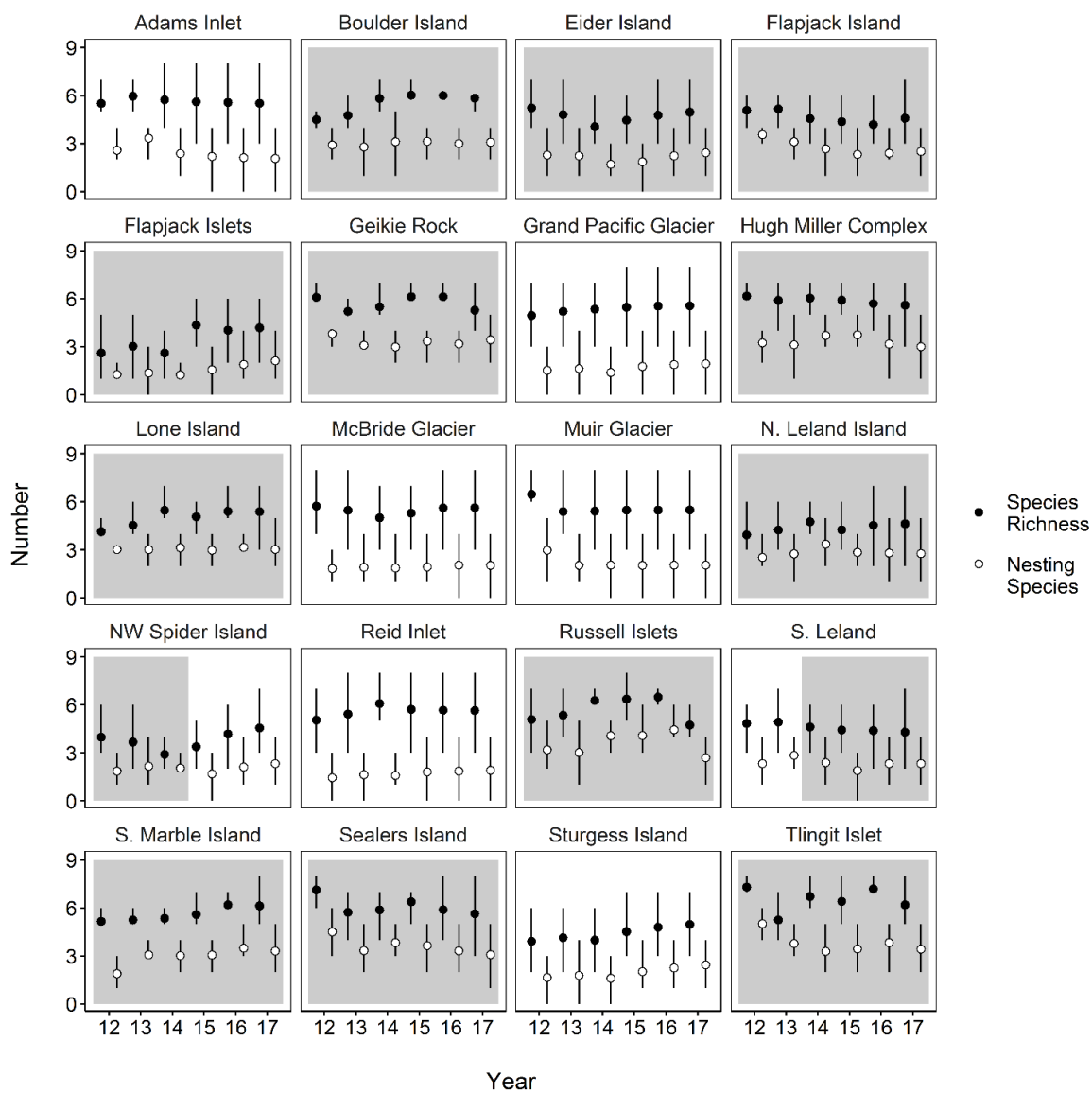


Figure 4.8. Predicted species richness and number of nesting species of waterbirds at islands and glacial outwash sites in Glacier Bay National Park, Alaska. Error bars describe 95% credible intervals and background shading denotes years when sites were closed to visitors.

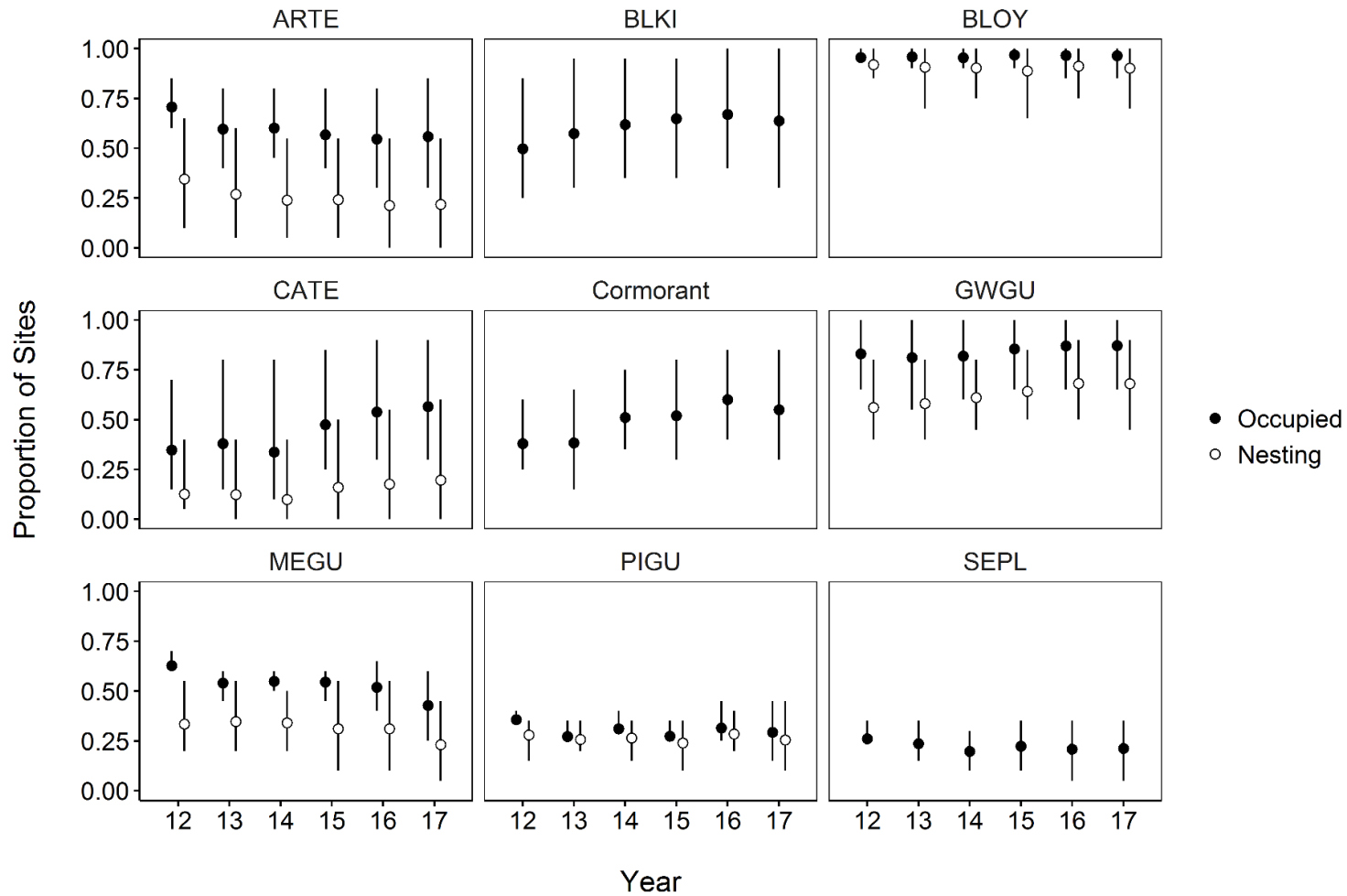


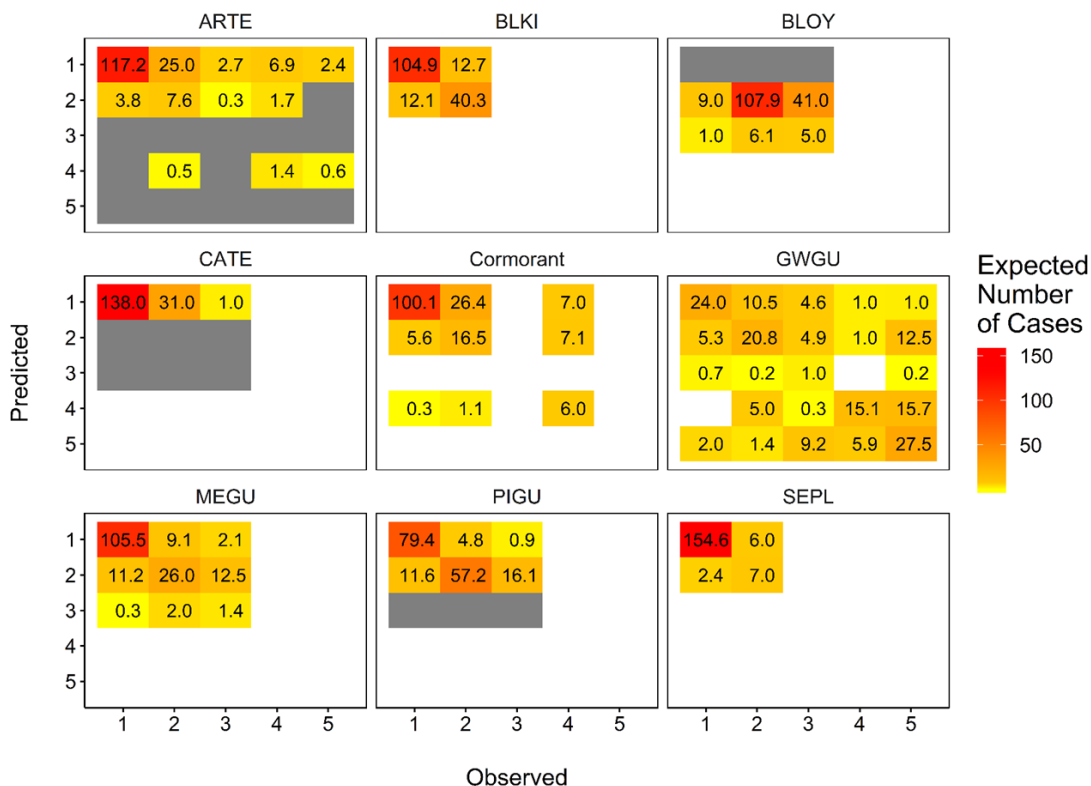
Figure 4.9. Estimated proportion of sites in Glacier Bay National Park, Alaska, occupied by arctic terns (ARTE), black oystercatchers (BLOY), black-legged kittiwakes (BLKI), Caspian terns (CATE), unidentified cormorants (Cormorant), glaucous-winged gulls (GWGU), mew gulls (MEGU), pigeon guillemots (PIGU), and semipalmated plovers (SEPL) are denoted by closed circles. Open circles denote sites where species were both present and nesting and error bars denote 95% credible intervals.

Supplemental Figures

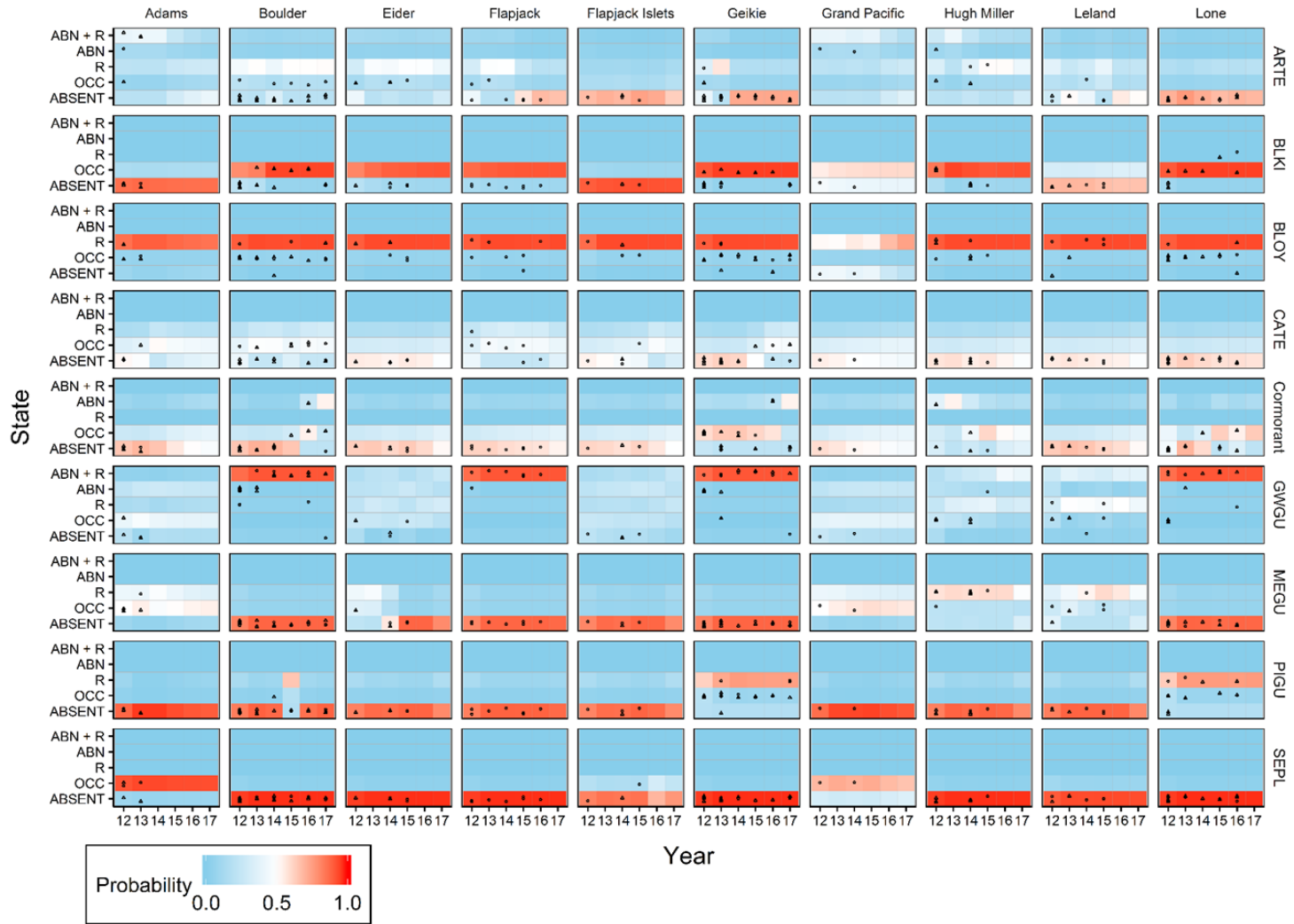
Supplemental Figure 4.1. Table of initial states for focal species groups at the 20 sites in the study based on previous vessel based surveys described in Arimitsu et al. (2007). Numbers 1-5 correspond to the five states in the model: (1) absent, (2) occupied, (3) nesting, (4) abundant, and (5) both abundant and nesting. Focal species groups include arctic tern (ARTE), black oystercatcher (BLOY), black-legged kittiwake (BLKI), Caspian tern (CATE), unidentified cormorant (Cormorant), glaucous-winged gull (GWGU), mew gull (MEGU), pigeon guillemot (PIGU), and semipalmated plover (SEPL). We assigned site- and species-specific Dirichlet hyperpriors based on these initial states, specifying a value of $2/3$ for initial state and $1/(3 + s)$ for the remaining states, where s is the number of states modeled for the species.

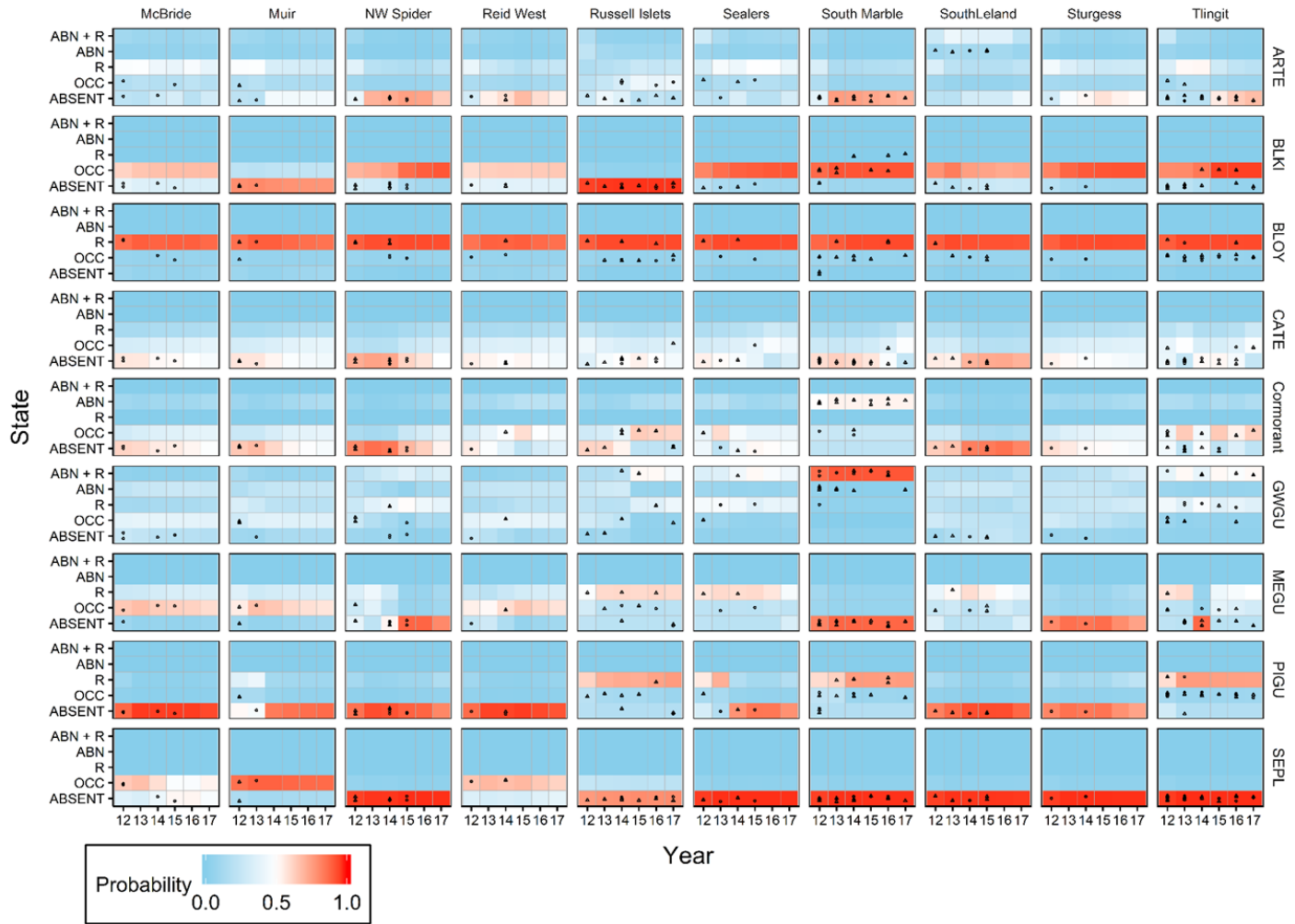
Site	Species								
	ARTE	BLKI	BLOY	CATE	Cormorant	GWGU	MEGU	PIGU	SEPL
Adams Inlet	5	1	3	1	1	1	3	1	2
Boulder Island	2	1	3	1	1	5	1	1	1
Eider Island	1	1	3	1	1	1	2	1	1
Flapjack Island	1	2	3	1	1	5	1	1	1
Flapjack Islets	1	1	2	1	1	1	1	1	1
Geikie Rock	1	2	3	1	2	5	1	2	1
Grand Pacific Glacier	5	1	1	1	1	1	3	1	2
Hugh Miller Complex	3	1	3	1	1	1	3	1	1
N. Leland Island	3	1	3	1	1	4	1	1	1
Lone Island	1	2	3	1	2	5	1	2	1
McBride Glacier	3	1	3	1	1	1	2	1	2
Muir Glacier	3	1	3	1	1	3	3	1	2
NW Spider Island	3	1	3	1	1	2	1	1	1
Reid Inlet	3	1	3	1	1	1	2	1	2
Russell Islets	5	1	3	2	1	2	2	2	1
Sealers Island	5	1	3	1	1	3	3	1	1
S. Marble Island	2	2	3	1	4	5	1	2	1
S. Leland	3	1	3	1	1	2	1	1	1
Sturgess Island	3	1	3	1	1	2	1	1	1
Tlingit Islet	5	1	3	1	1	3	3	1	1

Supplementary Figure 4.2. Confusion matrices describing estimated frequency of correctly and incorrectly predicted states. Focal species groups include arctic tern (ARTE), black oystercatcher (BLOY), black-legged kittiwake (BLKI), Caspian tern (CATE), unidentified cormorant (Cormorant), glaucous-winged gull (GWGU), mew gull (MEGU), pigeon guillemot (PIGU), and semipalmated plover (SEPL). Expected frequencies were estimated by averaging over out-of-sample predictions made from replicated five-fold cross-validation. Predicted states were based on the maximum value in the state-probability vector, any ties were assigned at random. Values in each matrix sum to 170, corresponding to the total number of site visits in the data set. Column sums describe the sample sizes of observed states in the data set.



Supplementary Figure 4.3-4.4. Plots of state probabilities predicted by the final multistate model (background color) versus detections obtained during ground (points) and vessel (triangles) surveys. Focal species groups include arctic tern (ARTE), black oystercatcher (BLOY), black-legged kittiwake (BLKI), Caspian tern (CATE), unidentified cormorant (Cormorant), glaucous-winged gull (GWGU), mew gull (MEGU), pigeon guillemot (PIGU), and semipalmated plover (SEPL). The 20 sites in the dataset are divided into two separate figures.



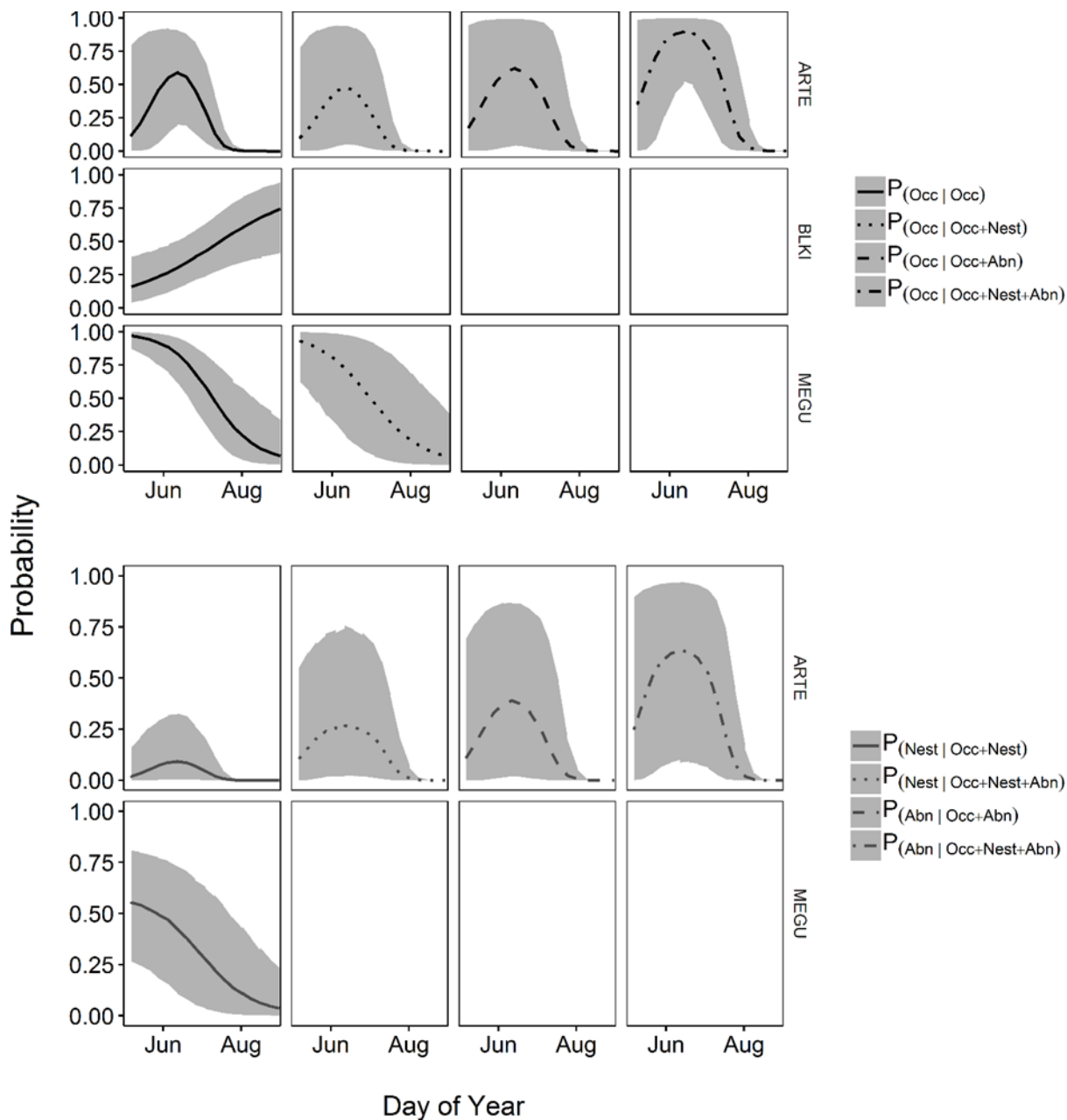


Supplementary Figure 4.5-4.6. Plots of the difference in state probabilities predicted by the final multistate model and a model with the same predictor variables but a noninformative prior (background color). Focal species groups include arctic tern (ARTE), black oystercatcher (BLOY), black-legged kittiwake (BLKI), Caspian tern (CATE), unidentified cormorant (Cormorant), glaucous-winged gull (GWGU), mew gull (MEGU), pigeon guillemot (PIGU), and semipalmated plover (SEPL). The 20 sites in the dataset are divided into two separate figures.





Supplementary Figure 4.7. Seasonal patterns in probabilities of detecting occupancy (top) and nesting or the state of abundance (bottom) of waterbird species in Glacier Bay National Park, Alaska, conditional on the true underlying state. Species include: arctic tern (ARTE), black-legged kittiwake (BLKI), and mew gull (MEGU). Estimates shown represent detection probabilities averaged over the two survey methods (ground and vessel).



CHAPTER 5: AN INTEGRATED DISTRIBUTION AND ABUNDANCE MODEL FOR HUMPBACK WHALES IN GLACIER BAY, ALASKA

Abstract

The waters of Glacier Bay National Park provide valuable summer foraging habitat for humpback whales. Most visitors experience the park by traveling aboard motorized vessels, which have the potential to strike whales, possibly resulting in injuries and death. Park administrators seek to minimize these negative encounters by imposing vessel restrictions and have shown recent interest in better quantifying the tradeoffs that these restrictions represent. A crucial step towards this goal lies in developing a technique for estimating the density of whales in the Park, so that the frequency of encounters between vessels and whales may be enumerated. In this chapter, I developed an integrated model for estimating whale density based on sightings recorded during active whale surveys and by observers aboard cruise ships. The model generally succeeded in producing annual abundance estimates and describing density dynamics at the finest spatial scale to date. The trend in abundance estimates was comparable to an annual abundance index currently in use; however there was an indication of negative bias in abundance estimates. I identified several pathways for improving the performance of the model, particularly with regard to more appropriately incorporating data from shipboard observer surveys. Beyond the main objective of the study, techniques developed in this chapter contributed to the broader literature on modeling whale densities, by providing a framework for consolidating information from multiple survey programs.

Introduction

Characterizing the spatial distribution of whale populations is a significant challenge because many species have global distributions and engage in long-distance seasonal migrations (Jaquet 1996, Edwards et al. 2015). Even during non-migratory periods, however, whale distribution can be difficult to estimate because species move in response to dynamic shifts in prey availability (Friedlaender et al. 2006, Cotté et al. 2009, Hazen et al. 2009). Despite these difficulties, estimating densities at fine scales is important for reducing negative interactions between whales and humans. Whales are indirectly affected by activities that generate underwater noise such as motorized vessel traffic and industrial activities (Erbe 2012, Todd et al. 2015), and risk injury or death from vessel-whale collisions and entanglement in fishing gear (Laist et al. 2001, Robbins and Mattila 2004, Brown et al. 2019).

Understanding the density and distribution of whales is especially important in Glacier Bay National Park (the “Park” hereafter; Figure 5.1), a marine protected area that overlaps an important summer feeding ground for humpback whales (*Megaptera novaeangliae*; Etherington et al. 2007). Glacier Bay is considered a “hot spot” for vessel-whale collisions in Southeast Alaska (Neilson et al. 2012), and the Park implements vessel speed restrictions as a tool for decreasing collision risk in areas with elevated whale density and vessel traffic. The National Park Service mission dictates that administrators take actions to prevent “impairment” of Park resources; however, the precise standard on which to base regulations is poorly defined (Gende et al. 2018). Administrators seek a systematic and data-driven approach for evaluating tradeoffs that

potential restrictions represent, in terms of reducing collision risk versus allowing visitors full access to the Park. Characterizing the density of whales is a critical step towards quantifying the degree of interaction among whales and vessels (McClellan et al. 2014). Fortunately, there are two whale monitoring programs in the Park on which to draw for this task.

Park personnel monitored humpback whales using two long-term survey programs designed to locate humpback whales in the bay: (1) a whale survey program in which a vessel actively searched for whales while traversing the vicinity of the bay (1985-2019); and (2) a shipboard observer program (2006-2018) in which surveyors, situated on the bow of cruise ships, recorded whale sightings from a distance. In this chapter, I present an integrated model for estimating the density of humpback whales in Glacier Bay, which draws on both survey programs. Specific objectives of this study were to (1) describe the construction of the model, (2) interpret parameter estimates and predictor relationships, and (3) evaluate the model's accuracy using statistical procedures and by comparing abundance estimates to counts and metrics from earlier studies.

Methods

The whale density model was constructed to inform the Glacier Bay quantitative decision tool, and therefore needed to produce specific outputs for use by other sub-models. Model predictions also needed to be responsive to changes in the value of specific parameters that decision makers might be interested in manipulating to help guide their decisions. The requirements of the model included the ability to: (1) predict actual whale densities (not a density index) and (2) generate spatially explicit predictions

as a direct function of abundance and distribution. The first of these requirements was necessary because the whale density model supplies critical input to another sub-model of the decision tool, a future vessel-whale encounter model. This encounter model will generate vessel-whale encounters as a function of whale density, vessel traffic, and the speed of vessels. An index of density, such as “whales-sighted-per-unit-effort” would not be meaningful input to the encounter model. The second requirement was important because administrators seek to examine how the tradeoffs surrounding speed restriction decisions are influenced by underlying population parameters, such as whale abundance and space use. The model needed to allow administrators to consider hypothetical situations, such as a doubling or halving of abundance or a shift in whale distribution.

To meet these requirements and effectively integrate the two data sources, I applied a hierarchical modeling approach as described by Royle and Dorazio (2009). The definition of a hierarchical model given by these authors is more specific than what is used in the statistical literature and implies that models have a particular conditional structure. Hierarchical models define population parameters (e.g., abundance, survival probability) as latent variables on which observations in the data set are conditional. Observed data are a function of the “true” ecological state filtered through an observation process that is imperfect and affected by sampling effort and uncontrollable factors (e.g., weather conditions). These models facilitate the integration of multiple information sources by enabling different data sets to inform a shared set of parameters, provided that the detection processes are properly represented.

Integrating information from the active whale survey and shipboard observer programs was possible because these programs surveyed the same population

concurrently and advantageous because they were complimentary in terms of the spatial distribution of survey effort. The lower bay was visited more frequently during active surveys, because observers typically did not board cruise ships until they had reached the waters immediately west of Bartlett Cove (Figure 5.2). In contrast, shipboard observers more frequently surveyed the west arm of Glacier Bay because virtually all cruise ships travel through this area to view the Park's scenic tidewater glaciers in Johns Hopkins and Tarr inlets.

In the following sections, I provide an overview of my approach for combining the two data sets into a cohesive modeling framework. I first summarize methods of the two survey programs. I then describe my framework for partitioning sighting data across space and time and the process for estimating survey effort and detection-related predictors. Finally, I describe the construction of the model as well as the process for validating the model using a model checking procedure and by making comparisons to past metrics.

Survey Programs

Active Whale Surveys

Vessel surveys for humpback whales were conducted annually from April through October in Glacier Bay and adjacent Icy Strait. The objectives of the program were to monitor whale demography and index annual abundance (Gabriele et al. 2017).

Demographic information was obtained by identifying individual humpback whales from photographs and tracking them over time, whereas abundance was indexed by taking the number of unique whales observed and standardizing by a measure of survey effort (Neilson et al. 2018). During surveys, a small, motorized vessel (4.9-6.7 m) actively

searched for whales by traveling at a moderate speed and pausing periodically to watch and listen for indicators of whale presence (e.g., breaching and spouting). Surveyors recorded GPS tracklines of the vessel location each day and noted time intervals in which they were actively searching for whales (“on-effort” time). When an individual or group of whales was sighted, surveyors carefully approached individuals to take photographs of distinguishing marks, and sometimes collect tissue samples. The monitoring program focused on identifying as many unique individuals as possible, while spreading search effort across all portions of Glacier Bay and Icy Strait. To this end, surveyors typically alternated survey effort between six regions in the vicinity of the Park, including the west arm, east arm, east and west sides of the middle bay, the lower bay, and east and west portions of Icy strait (Saracco et al. 2013). Surveyors sometimes delayed visiting a region or revisited a region consecutively. Deviations from the survey rotation were made because surveyors needed to assess evidence of a persistent aggregation in a high traffic area or investigate a credible report of whales in an atypical location. Additional details on the survey program can be found in Gabriele et al. (2017).

Shipboard Observer Surveys

The shipboard observer program differed from the active whale survey program in several important respects. The program was passive in the sense that paths of travel were independent of whale density. In addition, sightings were made at a distance with no attention given to capturing individualized markings. Observers boarded cruise ships in the lower bay or at the previous port of call. Once aboard, observers set-up a tripod at the bow of the ship from which they surveyed a 180° arc in the direction of travel. Cruise ships travel a similar path each day from the lower bay to the west arm, where ships

pause for several hours in the vicinity of tidewater glaciers near Johns Hopkins and Tarr inlets. When sightings occurred, surveyors marked the location of the ship using a GPS unit and measured the position of the target relative to the ship using a compass and rangefinder. When possible, observers made multiple distance measurements of targets (individual or groups of whales), tracking the diving and resurfacing behaviors until whales passed outside of the survey arc. Details on this survey protocol can be found in Gende et al. (2011) and Williams et al. (2016).

Data Compilation

The two data sources obtained for the analysis were spatially referenced point layers of whale sighting locations and GPS trackpoints, which marked the time and location of surveyors from both programs. Point layers included information about the counts of whales associated with each sighting, time of the sighting, and information on whether the observation was independent or part of a series for the same target. For cases in which multiple locations were recorded for the same target, I used only the sighting record for the whale location nearest to the ship (known as the “closest point of approach”). I only included sightings information for surveys for which there was a corresponding and apparently complete set of trackpoints. I further subdivided the dataset spatially and temporally, to ensure that the model would appropriately address objectives. Only surveys conducted from June 1 through August 31, 2007-2015 were included. These seasonal boundaries included the majority of the surveys and spanned the period in which nearly all humpback whales arrive in the area (Saracco et al. 2013), prior to their winter migration to southern latitudes (Baker et al. 1985, Dahlheim et al. 2009). To remain focused on the area affected by the decision tool, I included only sightings and

trackline segments within the waters of Glacier Bay proper (1255 km² area). The southern boundary line for the study was drawn between Point Carolous and Point Gustavus (Figure 5.2).

My procedure for estimating humpback whale density relied upon obtaining replicate counts of whales sighted within discrete spatial units. To this end, I subdivided Glacier Bay into sections systematically by overlaying a grid of hexagons with a side-to-side diameter of 7000 m onto a map of the study area. After laying down the grid, I clipped the areas of the map where land was present and consolidated fragments with an area less than 1/3 of that of a full hexagon with neighboring cells. This resulted in a map with a total of 43 polygons, ranging in area from 11 to 54 km². Subject-matter experts selected the size of the hexagons size in an effort to obtain the highest possible spatial resolution, while not making polygons so small or numerous as to create numerical issues (e.g., zero-inflation) or a significant computational burden. Biological considerations also went into the selection of the cell size. The range of polygons sizes represented the area that whales could conceivable occupy for a multi-day period.

Track-line data was central to estimating the spatial and temporal distribution of survey effort. I used times-tamped GPS track-points from both survey programs to generate a spatially referenced line feature layers. I then estimated vessel speed within segments as a means to identify and discard points with poor GPS fixes. Track-points for both methods were recorded at different frequencies. Active survey points were gathered on average every 30 seconds and shipboard observer points every 5 seconds. I thinned the track-lines for the observer data by a factor of 10 to conserve computer memory. After omitting poor fixes, I estimated the time interval that vessels spent in each section for

each survey by intersecting track-point segments with sections. I split segments that crossed section boundaries, and partitioned the time increment associated with the original segment in proportion to the degree of overlap. For the active surveys, I used estimated vessel speeds to identify periods in which the vessel traveling at relatively low velocities (< 2 kts) and confined to the same area 0.5 km^2 area. I considered these events to be “pauses” and was interested in estimating their frequency and location as a way to inform detection process in the model.

I created the final dataset by identifying intervals in which vessels were present in a given section and then summing the time spent within the area and the number of whales sighted. Each row of the data set represented a continuous interval of time in which the vessel was present in a section. The model treated repeat visits to the same section in a day as replicates. I only summed whale sighting counts that occurred within the same section in which the survey vessel was present. Due to the nature of the active survey method, the vessel was always present in the same section as the sighting for the active surveys; however, this was not the case for sightings made by cruise shipboard observers. I omitted approximately $1/3$ of the whale sightings from the cruise ship survey program because the closest point of approach was outside of the section where the vessel was present. Prior to fitting the model, I queried both aggregated data sets and omitted intervals that were suspect. I removed several extended time intervals (>2 hours) that took place when the cruise ship was in the vicinity of tidewater glaciers in the upper west arm of the bay, based on my suspicion that the observer was not actively surveying during that period.

Model Construction

Thus far, I have provided only a conceptual description of the hierarchical modeling approach and will now provide a more technical description of the model's construction. Hierarchical models are linked generalized linear models that define rate and probability parameters using regression equations (Kery and Royle 2015). These models are fitted by constructing a joint likelihood function and estimating parameters via maximum likelihood estimation or Bayesian inference (Cressie et al. 2009).

Abundance and distribution

I parameterized the humpback whale abundance and distribution model in a manner similar to both the harbor seal and sea lion models (see Chapters 2 and 3). The annual abundance of whales N_i were assumed to be Poisson distributed with mean and variance (λ_i)

$$N_i \sim Pois(\lambda_i),$$

where i is an index for the year.

In an effort to improve precision and borrow information across years, the mean annual abundance parameters were modeled as random effects (Royle and Link 2002). I assumed that the log of the annual abundance parameters were normally distributed,

$$\log(\lambda_i) \sim Norm(\mu_{[Abn]}, \sigma_{[Abn]}),$$

with the natural log of annual abundances distributed normally according to a grand mean ($\mu_{[Abn]}$) and standard deviation ($\sigma_{[Abn]}$). I assumed that the population of whales at a given time was distributed across sections of the bay according to a vector of occurrence probabilities ($\boldsymbol{\pi}$), which summed to one (Figure 5.3). Known abundance and occurrence

probability combined to produce the expected whale intensity in the j th section and i th year ($n_{i,j}$):

$$n_{i,j} = \lambda_i \cdot \pi_{i,j}.$$

The separability of abundance and occurrence inherent in this parameterization was desirable because it enables me to easily and intuitively manipulate parameters to produce spatially explicit density estimates with desired properties.

I modeled occurrence probabilities as a function of predictor variables and error terms using a multinomial logit link function (Agresti 2013, Royle and Converse 2014), with probability of occurrence for all but one of the sections ($J - 1$) defined as:

$$\pi_{i,j} = \frac{e^{\zeta_{i,j}}}{1 + \sum_{j=1}^{J-1} e^{\zeta_{i,j}}}; j = \{1, 2, 3, \dots, J - 1\},$$

where $\zeta_{i,j}$ is a linear combination of predictors and error terms. The last section indexed in each year ($\pi_{i,J}$) served as a reference category and was computed by subtraction ($\pi_{i,J} = 1 - \sum_{j=1}^{J-1} \pi_{i,j}$). The regression equation defining section-specific probability of occurrence was as follows:

$$\begin{aligned} \zeta_{i,j} &= \theta_1 \cdot D(\text{Entrance}_j) + \theta_2 \cdot \text{Area}_j + \tau_{[\text{Section}],j} + \tau_{[\text{Section:Year}]i,j}; j \\ &= \{1, 2, 3, \dots, J - 1\}, \end{aligned}$$

where θ s are coefficients describing the effect of section-level predictor variables and τ s are random error terms. Section-specific predictors of occurrence included the distance between the centroid of each section to the Park entrance (as defined by the $D()$ function), and the area of the section (km^2).

I included predictors in the occurrence regression model, primarily to improve the precision of estimates. I hypothesized that distance to the park entrance would be negatively related to whale occurrence probability, based on the long-established pattern of more frequent whale sightings in the lower bay versus the east and west arms of the bay (Gabriele et al. 2017). I included area as a predictor because I hypothesized that there would be a positive relationship between the size of the section and the number of whales that could be supported by prey there. I included error terms in the equation to glean information about the degree of spatiotemporal variation in occurrence probability and to compensate for sections with observed occurrences that were incongruent with relationships described by predictor variables. The two error terms in the regression described unexplained section-specific variation, $\tau_{[sec],j}$, and unexplained variation at the scale of both section and year ($\tau_{[Section:Year]i,j}$). Error terms were modeled as normal random effects with means of zero and corresponding standard deviations $\sigma_{[Section]}$ and $\sigma_{[Section:Year]}$.

Detection processes

The event of detecting a whale within a survey interval is conditional on at least one whale being present in the section, regardless of survey method. Furthermore, I expected the probability of detecting whales to increase with whale abundance in a section. I defined the probability of detecting presence of an individual whale in a section for an active surveyor and a shipboard observer as $p_{[Surv]}$ and $p_{[Obs]}$, respectively. Assuming that sightings of individual whales are independent, the expected count of whales detected in a section was the product of the expected density and an interval-

specific detection probability. Based on this reasoning, I assumed that the total sightings made by active surveyor (y) and a shipboard observer (z) could be approximated by a Poisson distribution:

$$y_{i,j,t,r} \sim \text{Pois}(n_{ijt} \cdot p_{[Surv],i,j,t}),$$

$$z_{i,j,t,r} \sim \text{Pois}(n_{ijt} \cdot p_{[Obs],i,j,t}),$$

where p_s are the probability of detecting an individual whale in year i , in section j , and during interval t . The Poisson distribution serves as an approximation of the binomial distribution in this case. The use of replicated counts across space and time as a means for estimating abundance placed the model in the category of so-called N-mixture models (Royle 2004, Kery and Royle 2015).

The individual detection probability in a given interval depended on survey effort plus additional factors that influence the sampling process. Interval-specific detection probability was estimated using separate regression equations for the two survey programs via a logit link function. The logit link function is a transformation, recognizable from logistic regression models, that maps values from the real number line to a scale from 0 to 1 (Hosmer et al. 2013) as:

$$\text{logit}(x) = \frac{1}{1+e^{-x}}.$$

I endeavored to define detection functions that accounted for differences in the sampling processes.

I modeled the detection probability for active whale surveys on time spent in section and two other predictors connected with putative pauses. Active survey detection probability was estimated using the following linear model:

$$\text{logit}(p_{[Surv]i,j,t}) = \beta_0 + \beta_1 \text{Time}_{i,j,t} + \beta_2 \text{PauseInSec}_{i,j,t} + \\ \beta_3 \text{PauseInLastSec}_{i,j,t} + \epsilon_{[Surv]i,j,t},$$

where β s are coefficients describing the effect predictors, and $\epsilon_{[Surv]i,j,t}$ denotes a random error term. Predictor variables included the total time that the survey vessel remained in the section (Time), and binary variables describing whether the survey vessel paused in the current section (PauseInSec) or if the vessel had paused in the section surveyed most recently (PauseInLastSec). Error terms were meant to account for unexplained observation error and were assumed to be normally distributed with mean zero and standard deviation $\sigma_{[Surv]}$. I included the PauseInSec and PauseInLastSec predictors because I hypothesized that whales would be more likely to be detected in sections where surveyors paused and in sections visited immediately after a pause occurred in another section. I based these hypotheses on the knowledge that during some pauses, surveyors turn off the boat engine to look and listen for whales, potentially extending their survey range.

I modeled the probability of the survey vessel detecting an individual whale based on the time that the vessel spent in each section as well as predictors related to visibility conditions. The detection probability function was as follows:

$$\text{logit}(p_{[Obs]i,j,t}) = \alpha_0 + \alpha_1 \text{Time}_{i,j,t} + \alpha_2 \text{VisExcellent}_{i,t} + \alpha_3 \text{VisGood}_{i,t} \\ + \alpha_4 \text{VisPoor}_{i,t} + \alpha_5 \text{VisFog}_{i,t} + \epsilon_{[Obs]i,j,t},$$

where α_0 is an intercept term, α_1 is a coefficient describing the effect of time-in-section, and $\alpha_{2:5}$ describes the effect of three different visibility conditions, with good/unknown visibility serving as a baseline. Visibility categories were assigned at a daily time scale,

based on the reported visibility at the time of whale sightings. The baseline category of good/unknown was assigned as unknown for days in which no whales were sighted.

I fitted the humpback whale density model using Bayesian inference with non-informative prior distributions. Coefficients for the occurrence linear combination were assigned diffuse normal priors, logit-linear regression were assigned Jeffreys priors (Lunn et al. 2012), and σ parameters for error terms were assigned diffuse uniform priors. Posterior parameter distributions were approximated using Markov Chain Monte Carlo (MCMC) simulation (Kery and Schaub 2011). I performed the simulation using the JAGS software package (Version 4.2.0; Plummer 2003) within the R statistical platform (R Core Team 2017). Prior to model fitting, I standardized all continuous predictor variables by subtracting the mean and dividing by the standard deviation to speed convergence and aid interpretation. I ran seven Markov chains simultaneously and determined a suitable burn-in number of iterations using the Gelman-Rubin statistic (\hat{R}) and by examining trace plots (Gelman et al. 2014).

Model Evaluation

I evaluated the performance of the model using a posterior predictive checking procedure, which is recommended for Bayesian analyses (Conn et al. 2018). Posterior predictive checking most commonly measures the frequency at which the model under- and over-estimates the data to which it was fitted (Gelman et al. 2014). I estimated the frequency of underestimation, known as a “Bayesian P value”, for the two data sets in the model separately. Bayesian P value estimates below 0.05 or above 0.95 are generally considered as evidence of a poorly specified model.

I further evaluated the performance of the model by comparing abundance estimates to values reported in previous work. Several recent studies have estimated whale abundances in the vicinity of Glacier Bay. Hendrix et al. (2012) modeled whale abundance and movement rates in multiple locations in Southeast Alaska and Saracco et al. (2013) estimated abundance and site fidelity of whales in the Glacier Bay and Icy Straits region. Unfortunately, these studies reported only the abundance of whales in both Icy Bay and Glacier Bay combined and were not directly comparable to the more limited spatial scale of my model. Instead, I compared abundance estimates from the model to counts of uniquely identified individuals, which the active survey program reports annually (Neilson et al. 2018). Although the counts of unique whales are not a substitute for measures of abundance, I nonetheless found this comparison useful for evaluating the model, because the count of unique individuals describes the lower bound for abundance of whales. I also compared trends in the estimated abundance of whales to that of the annual whale abundance index, which is also reported by the active survey program. The whale abundance index was calculated as the number of unique whales identified per year in Glacier Bay divided by the total number of “on-effort” hours that active surveyors spent searching that area. I made this comparison to determine if the temporal pattern in abundance depicted by my model departed substantially from that of the index.

Results

The humpback whale density model incorporated 455 active survey days and 481 shipboard observer surveys. In some cases, multiple cruise shipboard observer surveys were conducted on the same day by multiple observers, but only two cruise ships per day

are permitted to entire Glacier Bay. Despite the comparable number of surveys for the two survey methods, there were more than three times as many rows for shipboard observers (n=16,439) compared to active surveys (n=4,596) because cruise ships traversed more sections each a day. The density model converged and generated stable estimates for all parameters. Stationarity appeared to be reached within the first 5,000 iterations of the MCMC simulation, and posteriors distributions were estimated based on the subsequent 30,000 iterations. There was good mixing among chains and \hat{R} values for parameters were less than 1.1.

Abundance estimates per year ranged from 62 to 156 whales and were relatively precise, with coefficients of variation less than 13% in all cases (Table 5.1). Estimates from the distribution portion of the model provided insights about the relative importance of predictors and components of variance in the whale distribution process. The distance to the entrance of the bay emerged as valuable predictors of occurrence as hypothesized. The section area predictor did not appear to explain a significant portion of variability in occurrence based on the posterior distribution's considerable overlap with zero. The strength of the distance-to-entrance predictor was apparent in the estimates of section-specific occurrence, which were lower than 4% of the total estimated abundance in all sections of both the east and west arms of the bay (Figure 5.4).

The random effects associated with the occurrence model showed clear evidence of spatiotemporal variation in occurrence that was unexplained by the two predictors and allowed for the patchiness of the occurrence pattern in some portions of the study area. For example, random effects were responsible for the lower estimated occurrence probability in the section containing Bartlett Cove (Id: 2; Figure 5.4) and the section with

the highest probability of occurrence, Beartrack Cove (Id:10; Figure 5.4). The Beartrack Cove section was one of several sections with relatively high occurrence probability but which received relatively low survey effort (Figure 5.2); others included the section containing Berg Bay (Id:5; Figure 5.4) and immediately North of Geike Inlet (Id:19; Figure 5.4). Although point estimates for the mean expected abundance were relatively high in these sections, so too was the estimated error of the estimates (Figure 5.5). These sections contrasted with lower bay sections (Ids: 1, 3, 4, 6-8), which had moderate, but more precisely estimated mean expected abundances.

The importance of detection predictors was variable for both survey methods (Table 5.2). Time-in-section was positively related to detection probability for both data sets. Neither of the predictors related to pauses made by the active survey vessel were clearly supported by the model. There was evidence that surveys with excellent visibility had substantially higher detection than the baseline good/unknown category. Somewhat surprisingly, the parameter estimates for poor and foggy visibility conditions were not substantially lower than the baseline, and the estimate for the foggy visibility was positive. Random error terms were substantially greater than zero for both detection functions; however, the shipboard observer error term was much greater than that of the active surveys.

Posterior predictive checking indicated the model reasonably fit the data (Bayesian P values: 0.05-0.95), although there was some indication that patterns in shipboard observer data were not as well characterized by the model. The weighted average Bayesian P value for both datasets was 0.082, suggesting that the model sufficiently described the data to which it was fit. However, the Bayesian P value

associated with the shipboard observer data was 0.047, slightly below the acceptable threshold. This value indicated that the model systematically underestimated shipboard observer sightings. The Bayesian P value for just the active program was 0.205 and well within the accepted range.

Comparison of abundance estimates to previously reported values yielded mixed impressions of the model's performance. While the abundance pattern in the model appeared to align with the trend in the abundance index (Figure 5.6A), many of the estimates were below the minimum number of whales known to be in the population. The number of unique whales exceeded model estimates in all but two years (2012 and 2015), and exceeded the upper 95% credible interval for the model estimates in all but three years (2012, 2013, and 2015). The low value for abundance estimates relative to the number of uniquely identified whales may suggest that the model generated negatively biased estimates. Alternatively, the lower point-estimates for abundance could stem from the fact that whales in Glacier Bay take forays into Icy Strait to forage. If this is the case then seemingly low abundance estimate may reflect the average population size at a given time and not the season-wide total. The best evidence for the similarity in the temporal trend between abundance estimates and the abundance index was the fact that when the index was scaled to match the initial abundance estimate (a factor of 1:142), the transformed index value fell within the credible intervals of the abundance predictors for seven out of nine years (Figure 5.6.B)

Discussion

The integrated whale density model generally succeeds in the objective of characterizing the numbers and distribution patterns of humpback whales in Glacier Bay. The model identified several valuable predictors of occurrence probabilities and estimated spatial and temporal variability in whale occurrence, which were both essential for informing the quantitative decision tool. Annual abundance estimates reflected a similar temporal trend as the active survey's index but showed possible evidence of negative bias. Beyond the main study objectives, this analysis also contributed to the existing literature on whale distribution modeling by demonstrating a technique for integrating multiple whale sighting data sets into the estimation of abundance and occurrence.

Shortcomings of the density model were made apparent in some parameter estimates and the unfavorable model-checking diagnostic for the shipboard observer data, and potential negative bias in estimated abundance. Although time-in-section was a key predictor of detection probability for both surveys, additional variables were not well supported by the model. There was no clear evidence that pause-related predictors influenced detection in active surveys. The model also suggested that detection probability for shipboard observers was similar across most visibility conditions. This was surprising considering these visibility categories were a key predictor in detection-distance functions estimated for these surveys in the past (Williams et al. 2016). The shipboard observer data set was not well characterized by the model based on the low Bayesian P value and the relatively large standard deviation for the random error term in the detection function ($\sigma_{[Obs]}$). As for the potential underestimation of abundance, this discovery was fortunate in the sense that it was only possible to detect negative bias with

the type of comparison performed (i.e., there was no equally definitive way of detecting positive bias). Negatively biased abundance estimates were somewhat peculiar as well, because the N-mixture modeling approach that I employed is generally regarded as susceptible to overestimation of abundance (Dénes et al. 2015, Duarte et al. 2018). Potential underestimation of abundance poses a concern, but is not a hindrance to the functioning of quantitative decision tool, considering that decision makers will have the ability to examine the degree to which underestimation might otherwise influence management decisions.

I suspect that the issues of possibly underestimated abundance and poor characterization of shipboard observer data share a common cause, having mostly to do with data compilation decisions. The model included only sightings that occurred within the same section in which the vessel was present. This decision could have introduced unforeseen negative bias in estimates because of so-called “edge effects.” Edge effects may arise when analysts attempt to make inferences about spatial point processes by imposing random or arbitrarily defined survey boundaries on continuous state spaces (Baddeley 1999). The model assumed that the same number of whales were distributed across all cells, meaning that concentration of whales in a section leads to a corresponding decrease elsewhere. By not crediting sightings to neighboring sections, the model was unable to account for the fact that fewer sightable whales would be present in remaining sections, instead suggesting that the density of whales was generally lower. Based on this reasoning, the Bayesian P value for the shipboard observer dataset was produced because the observed number of whales was incongruent with the underestimated abundance. A potential remedy for this issue would be to develop a

scheme for incorporating sightings of whales made outside of just the section through which vessels passed. This would consist of adding additional rows to the shipboard observer data set corresponding to the number of sightings in sections adjacent to those occupied by the survey vessel. The detection range of shipboard observers is well studied (Harris et al. 2012, Williams et al. 2016, Gende et al. 2019), and findings from previous work could guide the definition of a ruleset for dictating which neighboring sections should be classified as surveyed and to what degree. For example, the model would not need to include neighboring sections beyond a distance threshold or positioned behind the vessel.

In addition to the alteration described above, there are additional changes to the model's data compilation procedure and structure that could improve estimates. The simplest change would be to maintain the same model structure and test additional predictor variables in the abundance, occurrence, and detection portions of the model. The difference among variance components in the occurrence sub-model suggested that more of the unexplained variability in occurrence was due to unmodeled spatial patterns, rather than patterns that vary in both space and time. This suggests that the precision of estimates would likely be improved by incorporating additional section-specific variables (e.g., bathymetry, productivity metrics). Another potentially beneficial alteration to the model would be to broaden the study area to include Icy Strait. Although the quantitative decision tool does not apply to this area, its inclusion could improve estimates in Glacier Bay by providing additional observations with which to inform occurrence and detection coefficients. At present, the model does not account for within-season movements of whales between Glacier Bay and Icy Strait. Expanding the spatial extent would likely

improve estimates of abundance for the entire study area, because the model would better satisfy the spatial closure assumption. In addition, the inclusion of Icy Strait would be helpful in that it would facilitate a direct comparison of estimated abundance to past studies (Hendrix et al. 2012, Saracco et al. 2013). Although these refinements are possible, including additional data will come at a cost in terms of computation. The runtime of the model in its current form is nearly 70 hours using a modern CPU and parallel processing. However, it may be possible that an extended version of the current model would be more tenable if the model were fitted using software that employs an alternative estimation approach (e.g., maximum likelihood estimation, Hamiltonian Monte Carlo).

Monitoring programs are designed to address specific objectives. Inevitably, however, new and important questions arise which cannot be easily answered with the information at hand. This often occurs because individual data sets may provide an incomplete picture of quantities or processes of interest. Hierarchical models provide a flexible framework with which to integrate multiple data sets and make inferences that may otherwise be impossible (Abadi et al. 2010).

In this study, I combined data from two humpback whale survey programs that differed in their purposes and survey methods and was able to generate density estimates in a manner not previously conceived. The model that I developed was not without deficiencies; however, I have identified pathways for its improvement in the future. The possible problem of negative bias in abundance estimates does not preclude the use of the model estimates in the quantitative decision-support tool, provided that decision makers are aware of this property. The model described here will fill a key role in the

quantitative decision tool by informing a function that will accept user-specified inputs of abundance and occurrence probabilities and generate spatially explicit whale density predictions, which may serve as inputs to additional sub-models.

References

- Abadi, F., O. Gimenez, R. Arlettaz, and M. Schaub. 2010. An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology* 91:7–14.
- Agresti, A. 2013. *Categorical data analysis*. John Wiley & Sons.
- Baddeley, A. J. 1999. Spatial sampling and censoring. *Stochastic geometry: likelihood and computation* 2:37–78.
- Baker, C. S., L. M. Herman, A. Perry, W. S. Lawton, J. M. Straley, and J. H. Straley. 1985. Population characteristics and migration of summer and late-season humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. *Marine Mammal Science* 1:304–323.
- Brown, D. M., P. L. Sieswerda, and E. C. M. Parsons. 2019. Potential encounters between humpback whales (*Megaptera novaeangliae*) and vessels in the New York Bight apex, USA. *Marine Policy* 106:103527.
- Conn, P. B., D. S. Johnson, P. J. Williams, S. R. Melin, and M. B. Hooten. 2018. A guide to Bayesian model checking for ecologists. *Ecological Monographs* 88:526–542.
- Cotté, C., C. Guinet, I. Taupier-Letage, B. Mate, and E. Petiau. 2009. Scale-dependent habitat use by a large free-ranging predator, the Mediterranean fin whale. *Deep Sea Research Part I: Oceanographic Research Papers* 56:801–811.
- Cressie, N., C. A. Calder, J. S. Clark, J. M. V. Hoef, and C. K. Wikle. 2009. Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. *Ecological Applications* 19:553–570.
- Dahlheim, M. E., P. A. White, and J. M. Waite. 2009. Cetaceans of Southeast Alaska: distribution and seasonal occurrence. *Journal of Biogeography* 36:410–426.
- Dénes, F. V., L. F. Silveira, and S. R. Beissinger. 2015. Estimating abundance of unmarked animal populations: accounting for imperfect detection and other sources of zero inflation. *Methods in Ecology and Evolution* 6:543–556.
- Duarte, A., M. J. Adams, and J. T. Peterson. 2018. Fitting N-mixture models to count data with unmodeled heterogeneity: bias, diagnostics, and alternative approaches. *Ecological Modelling* 374:51–59.
- Edwards, E. F., C. Hall, T. J. Moore, C. Sheredy, and J. V. Redfern. 2015. Global distribution of fin whales *Balaenoptera physalus* in the post-whaling era (1980–2012). *Mammal Review* 45:197–214.

- Erbe, C. 2012. Effects of underwater noise on marine mammals. Pages 17–22 in A. N. Popper and A. Hawkins, editors. *The effects of noise on aquatic life*. Springer New York.
- Etherington, L. L., P. N. Hooge, E. R. Hooge, and D. F. Hill. 2007. Oceanography of Glacier Bay, Alaska: Implications for biological patterns in a glacial fjord estuary. *Estuaries and Coasts* 30:927–944.
- Friedlaender, A. S., P. N. Halpin, S. S. Qian, G. L. Lawson, P. H. Wiebe, D. Thiele, and A. J. Read. 2006. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Marine Ecology Progress Series* 317:297–310.
- Gabriele, C. M., J. L. Neilson, J. M. Straley, C. S. Baker, J. A. Cedarleaf, and J. F. Saracco. 2017. Natural history, population dynamics, and habitat use of humpback whales over 30 years on an Alaska feeding ground. *Ecosphere* 8:n/a-n/a.
- Gelman, A., John B. Carlin, H. S. Stern, David B. Dunson, A. Vehtari, and Donald B. Rubin. 2014. *Bayesian data analysis*. Third edition. CRC Press, Boca Raton.
- Gende, S., A. N. Hendrix, and J. Schmidt. 2018. Somewhere between acceptable and sustainable: When do impacts to resources become too large in protected areas? *Biological Conservation* 223:138–146.
- Gende, S. M., L. Vose, J. Baken, C. M. Gabriele, R. Preston, and A. N. Hendrix. 2019. Active whale avoidance by large ships: Components and constraints of a complementary approach to reducing ship strike risk. *Frontiers in Marine Science*. <https://doi.org/10.3389/fmars.2019.00592>.
- Harris, K., S. M. Gende, M. G. Logsdon, and T. Klinger. 2012. Spatial pattern analysis of cruise ship–humpback whale interactions in and near Glacier Bay National Park, Alaska. *Environmental Management* 49:44–54.
- Hazen, E. L., A. S. Friedlaender, M. A. Thompson, C. R. Ware, M. T. Weinrich, P. N. Halpin, and D. N. Wiley. 2009. Fine-scale prey aggregations and foraging ecology of humpback whales *Megaptera novaeangliae*. *Marine Ecology Progress Series* 395:75–89.
- Hendrix, A. N., J. Straley, C. M. Gabriele, and S. M. Gende. 2012. Bayesian estimation of humpback whale (*Megaptera novaeangliae*) population abundance and movement patterns in southeastern Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 69:1783–1797.
- Hosmer, D. W., S. Lemeshow, and R. X. Sturdivant. 2013. *Applied logistic regression*. John Wiley & Sons.

- Jaquet, N. 1996. How spatial and temporal scales influence understanding of sperm whale distribution: a review. *Mammal Review* 26:51–65.
- Kery, M., and J. A. Royle. 2015. *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1*. Academic Press.
- Kery, M., and M. Schaub. 2011. *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Academic Press.
- Laist, D. W., A. R. Knowlton, J. G. Mead, A. S. Collet, and M. Podesta. 2001. Collisions between ships and whales. *Marine Mammal Science* 17:35–75.
- Lunn, D., C. Jackson, N. Best, A. Thomas, and D. Spiegelhalter. 2012. *The BUGS Book: A Practical Introduction to Bayesian Analysis*. CRC Press.
- McClellan, C. M., T. Brereton, F. Dell’Amico, D. G. Johns, A.-C. Cucknell, S. C. Patrick, R. Penrose, V. Ridoux, J.-L. Solandt, E. Stephan, S. C. Votier, R. Williams, and B. J. Godley. 2014. Understanding the distribution of marine megafauna in the English Channel region: Identifying key habitats for conservation within the busiest seaway on Earth. *PLOS ONE* 9:e89720.
- Neilson, J. L., C. M. Gabriele, A. S. Jensen, K. Jackson, and J. M. Straley. 2012. Summary of reported whale-vessel collisions in Alaskan waters. Research article. <https://www.hindawi.com/journals/jmb/2012/106282/>.
- Neilson, J. L., C. M. Gabriele, and L. F. Taylor-Thomas. 2018. Humpback whale monitoring in Glacier Bay and adjacent waters 2017. *Annual Progress Report*:56.
- Plummer, M. 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Pages 20–22, *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*. ISSN, Vienna, Austria.
- R Core Team. 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Robbins, J., and D. K. Mattila. 2004. Estimating humpback whale (*Megaptera novaeangliae*) entanglement rates on the basis of scar evidence. Final report. Northeast Fisheries Science Center, Woods Hole, Massachusetts.
- Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. *Biometrics* 60:108–115.
- Royle, J. A., and S. J. Converse. 2014. Hierarchical spatial capture–recapture models: modelling population density in stratified populations. *Methods in Ecology and Evolution* 5:37–43.

- Royle, J. A., and W. A. Link. 2002. Random effects and shrinkage estimation in capture-recapture models. *Journal of Applied Statistics* 29:329–351.
- Saracco, J. F., C. M. Gabriele, and J. L. Neilson. 2013. Population dynamics and demography of humpback whales in Glacier Bay and Icy Strait, Alaska. *Northwestern Naturalist* 94:187–197.
- Todd, V. L. G., I. B. Todd, J. C. Gardiner, E. C. N. Morrin, N. A. MacPherson, N. A. DiMarzio, and F. Thomsen. 2015. A review of impacts of marine dredging activities on marine mammals. *ICES Journal of Marine Science* 72:328–340.
- Williams, S. H., S. M. Gende, P. M. Lukacs, and K. Webb. 2016. Factors affecting whale detection from large ships in Alaska with implications for whale avoidance. *Endangered Species Research* 30:209–223.

Tables

Table 5.1. Annual abundance estimates of humpback whales summering in Glacier Bay, Alaska (2007-2015) based on an integrated density model. Summary statistics include standard error (SE), coefficient of variation (CV), and lower and upper 95% credible intervals (LCL and UCL).

Year	Estimate	SE	CV (%)	LCL	UCL
2007	63.3	6.0	9.5	52	76
2008	62.5	7.0	11.1	51	77
2009	77.8	8.8	11.3	63	98
2010	89.2	11.2	12.6	70	114
2011	115.9	10.8	9.3	97	139
2012	129.6	13.7	10.6	106	160
2013	156.2	16.3	10.4	129	192
2014	77.5	8.2	10.6	63	96
2015	130.7	10.9	8.3	112	155

Table 5.2. Parameter estimates from an integrated humpback whale density model for Glacier Bay, Alaska. The LCL and UCL columns denote lower and upper 95% credible intervals. Bold text denotes coefficients with parameter estimates that do not overlap with zero.

Parameter	Description	Estimate	SE	LCL	UCL
Abundance					
$\mu_{[Abn]}$	Mean log(Abundance)	4.55	0.16	4.21	4.85
$\sigma_{[Abn]}$	SD log(Abundance)	0.40	0.15	0.21	0.78
Distribution					
θ_1	Distance to bay entrance	-1.47	0.14	-1.78	-1.21
θ_2	Section area	-0.01	0.14	-0.29	0.30
$\sigma_{[Section]}$	Section-specific error	0.81	0.14	0.58	0.89
$\sigma_{[Year:Section]}$	Section-year- specific error	0.40	0.04	0.33	0.47
Detection (Shipboard observer)					
α_0	Intercept	-4.78	0.13	-5.03	-4.53
α_1	Time effect	2.66	0.17	2.34	3.00
α_2	Visibility (Excellent)	0.46	0.10	0.26	0.65
α_3	Visibility (Poor)	-0.07	0.17	-0.40	0.25
α_4	Visibility (Fog)	0.26	0.41	-0.58	1.06
$\sigma_{[Obs]}$	Detection error	2.31	0.09	2.13	2.49
Detection (Active survey)					
β_0	Intercept	-2.47	0.08	-2.61	-2.32
β_1	Time effect	1.72	0.06	1.61	1.84
β_2	Pause in section	-0.02	0.01	-0.04	0.01
β_3	Pause in last section	0.02	0.06	-0.10	0.15
$\sigma_{[Surv]}$	Detection error	0.30	0.07	0.20	0.44

Figures

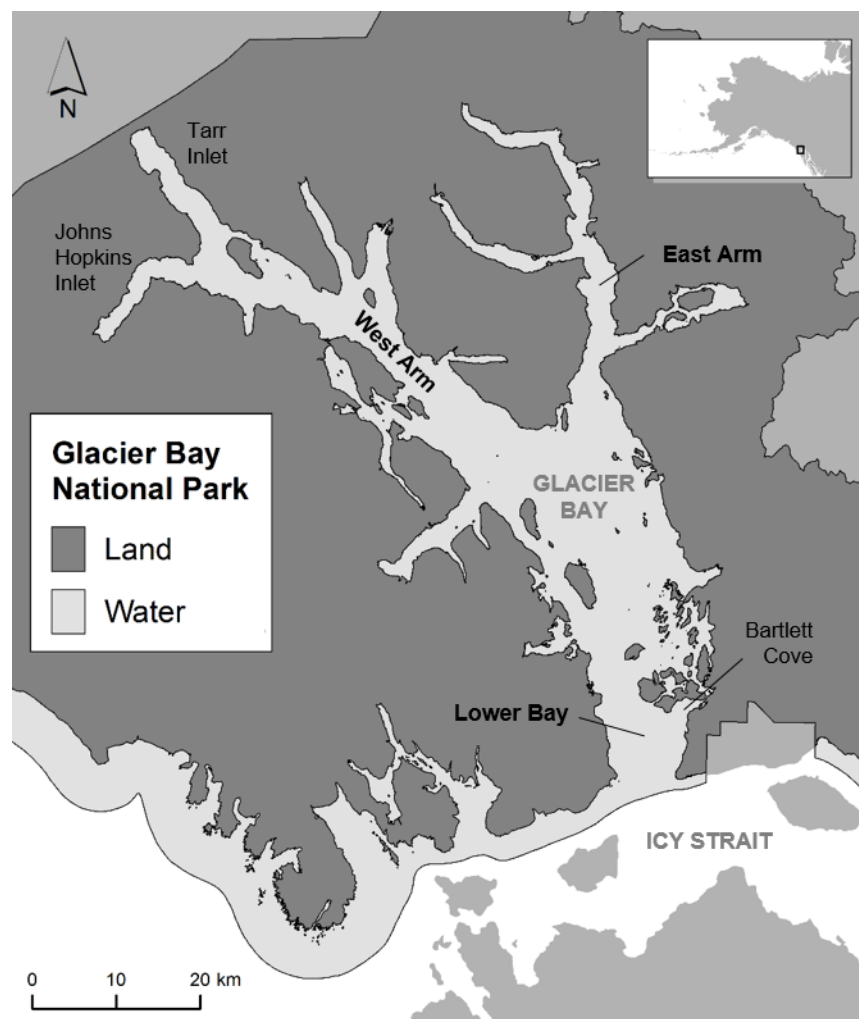


Figure 5.1. Map of the vicinity of Glacier Bay, Alaska, including boundaries of Glacier Bay National Park and labels of major zones of the bay.

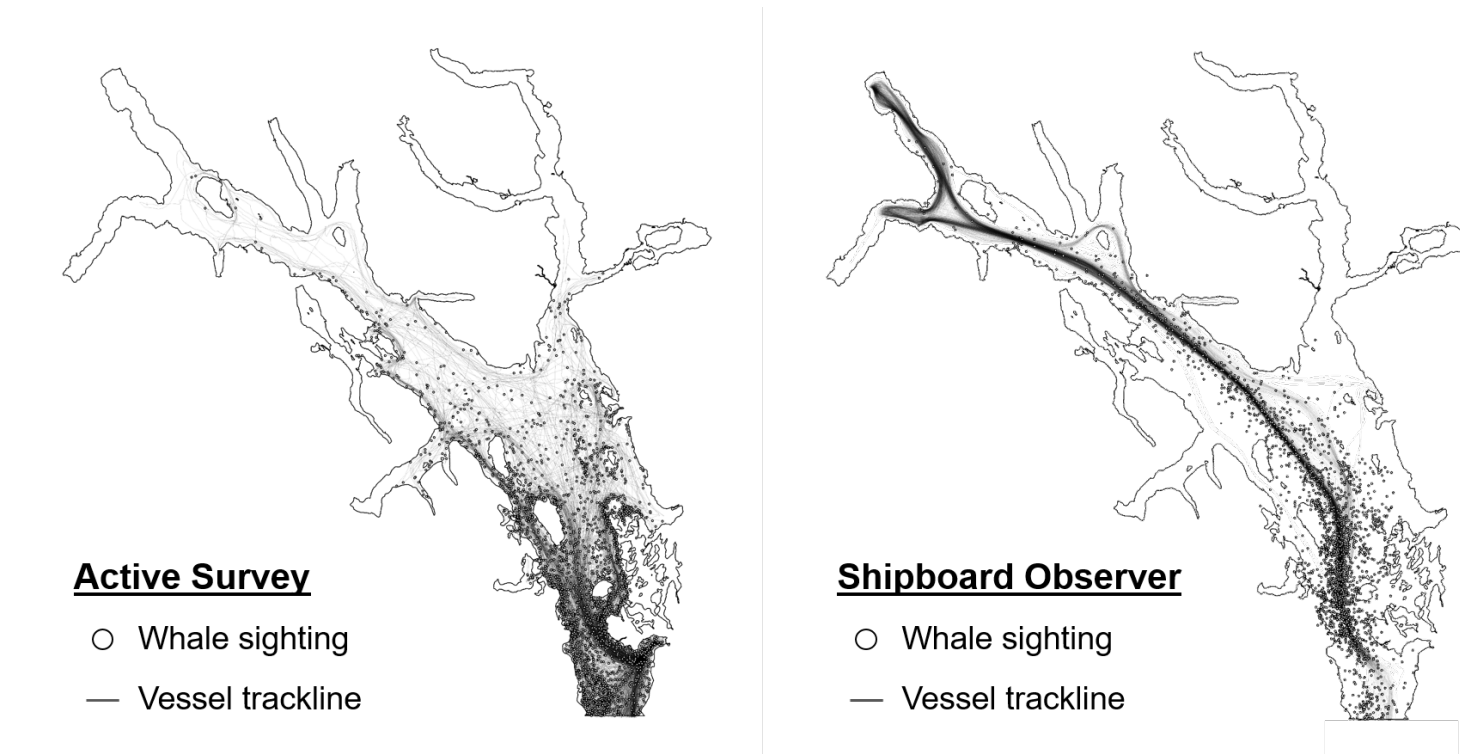


Figure 5.2. Vessel track-lines and whale sighting locations from the active whale survey and the cruise shipboard observer programs in Glacier Bay National Park, Alaska, recorded from June 1 through August 31, 2007-2015.

Years

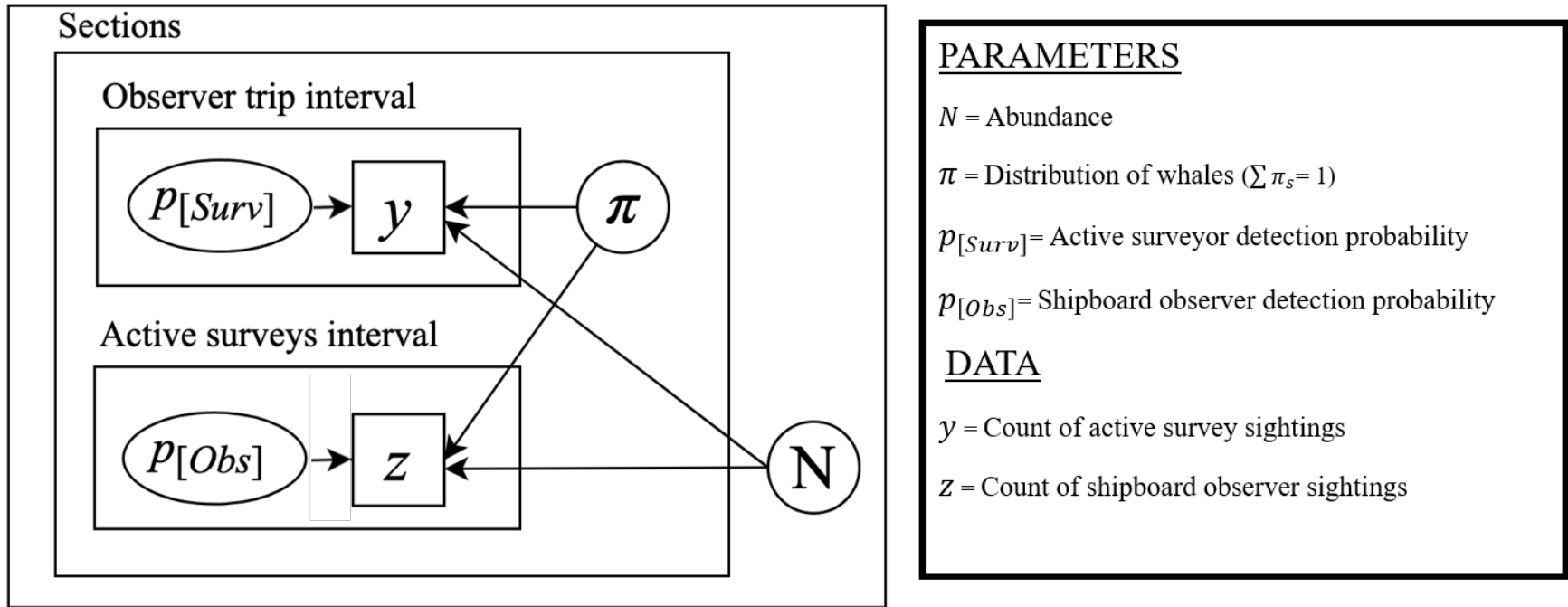


Figure 5.3. Directed acyclic graph describing an integrated humpback whale density model in Glacier Bay, Alaska.

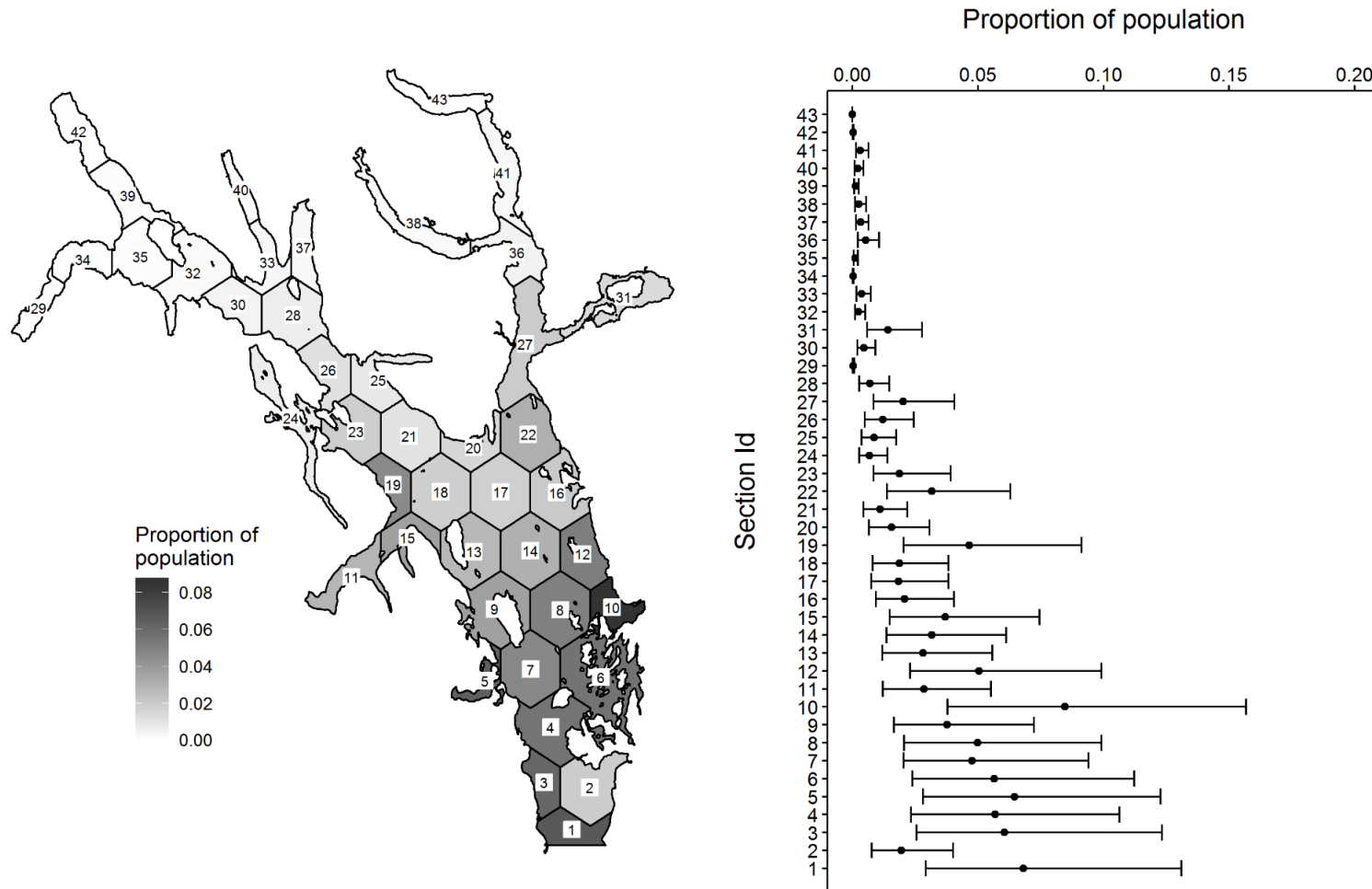


Figure 5.4. Mean population distribution of humpback whales in Glacier Bay, Alaska based on an integrated density model. Map shading indicates the expected proportion of the population found in each of the 43 sections (values for all sections sum to 1). The plot to the right also depicts estimated proportion of whales in the population found in each cell, along with 95% credible intervals.

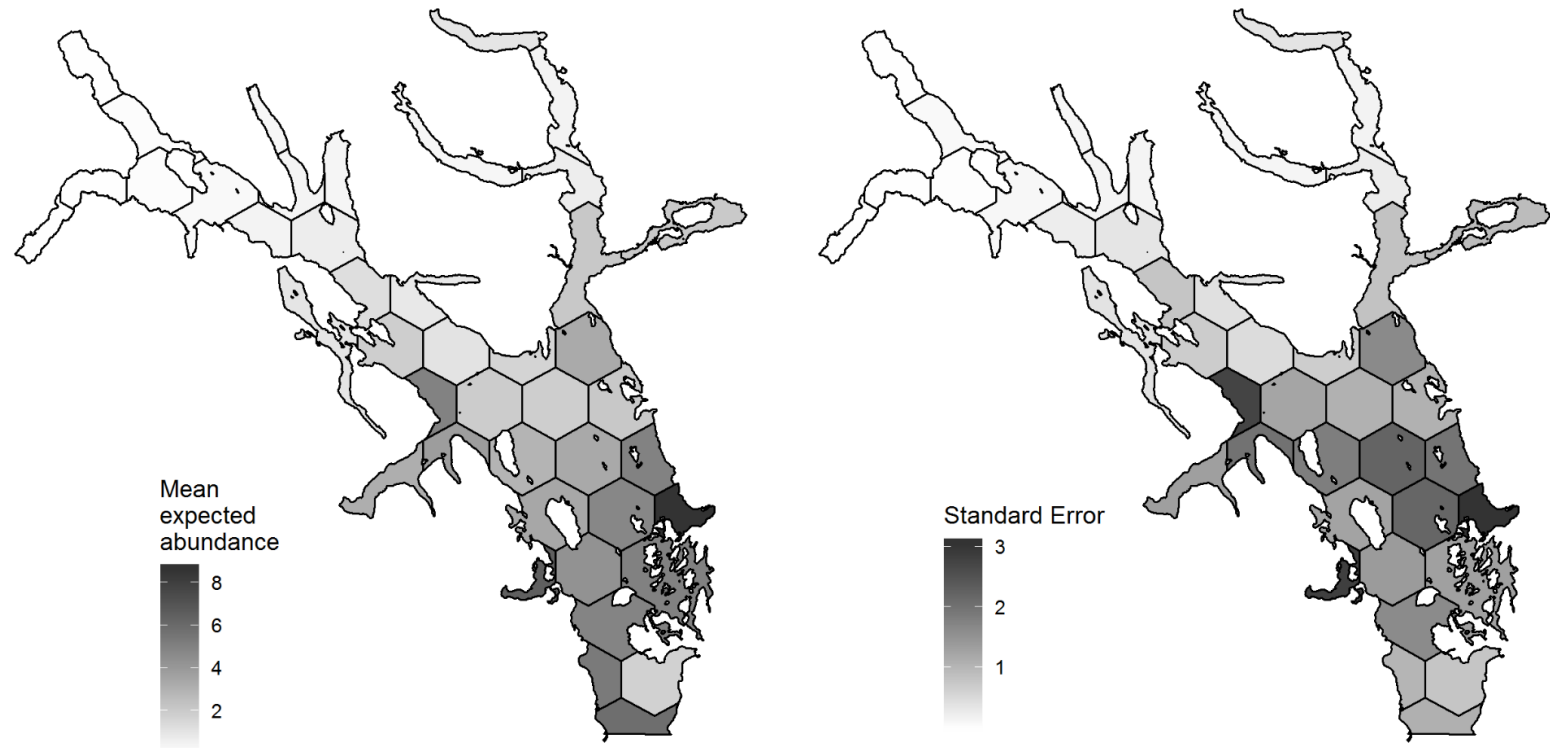


Figure 5.5. Maps of overall estimated mean density (left) and standard errors in estimated density (right) for humpback whales in Glacier Bay, Alaska, during (2007-2015).

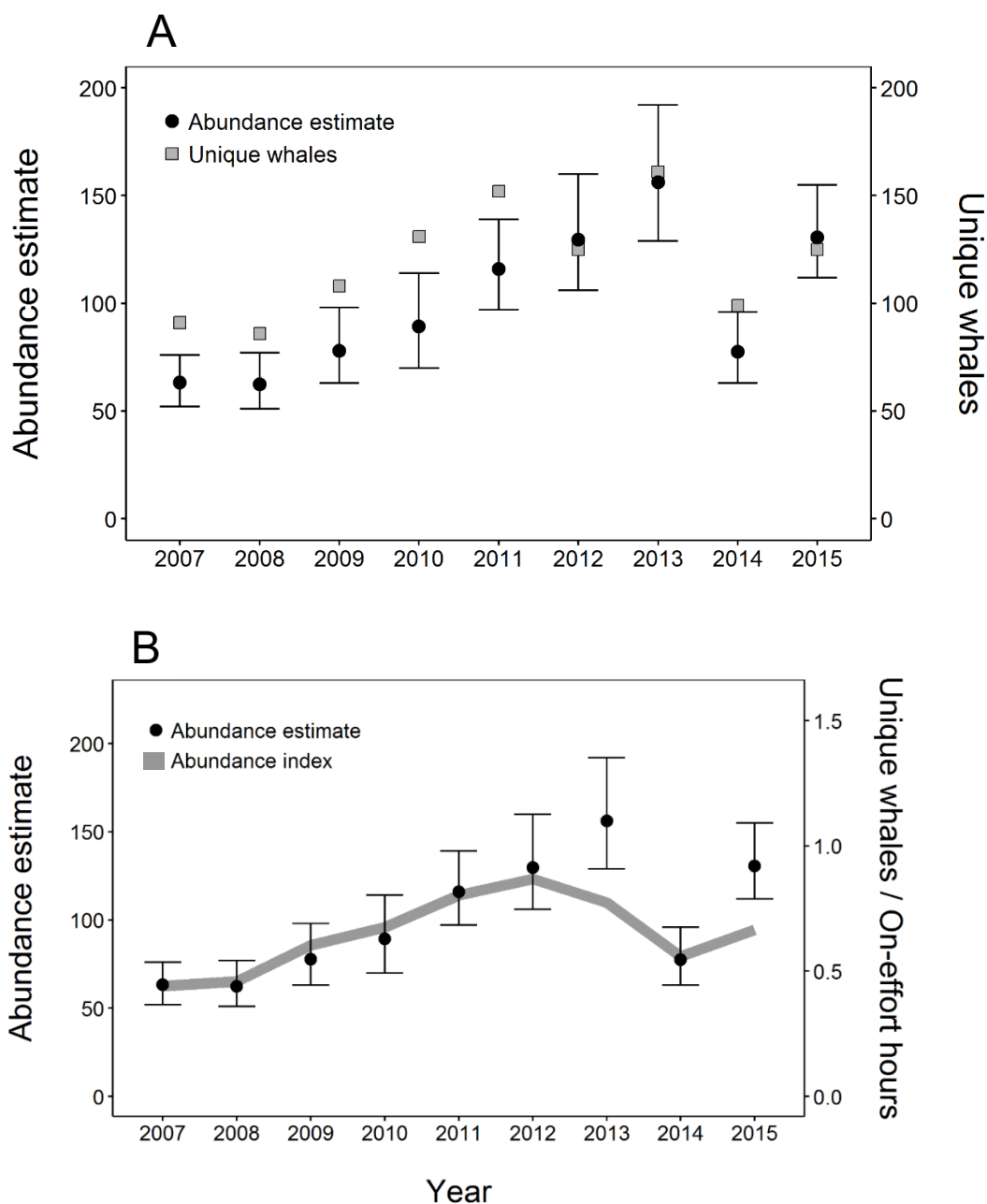


Figure 5.6. Plots of estimated humpback whale abundance in Glacier Bay, Alaska (2007-2015) versus the number of unique whales identified in active surveys (A) and an annual index of humpback whale abundance (B). The brackets surrounding solid points denote upper and lower 95% credible intervals. In the B plot, the secondary y-axis is scaled by a factor of 142, such that the that of the abundance estimate and whale abundance index were at the same vertical position at the start of the time series (2007).

CHAPTER 6: THE FUTURE OF THE GLACIER BAY NATIONAL PARK DECISION TOOL

The purpose of this final chapter is to discuss the role that biological sub-models for pinnipeds, ground-nesting waterbirds, and humpback whales will play in informing the decision tool as the structured decision making (SDM) process in Glacier Bay National Park continues to develop. Completion of biological sub-models marks an important stage in the process, one in which participants must now confront discrepancies between what they would like to know to manage resources effectively, and what available research and monitoring is capable of providing. This is also a stage in which connections among various sub-models and decision alternatives must be made explicit, if the process is to continue.

The model development process offered an opportunity to appraise the extent to which existing monitoring could be used to assess measurable attributes. Measurable attributes are quantities that decision makers use to describe how well fundamental and means-objectives are being met (Conroy and Peterson 2013). These measures made up the lower tiers of the objective hierarchies described in Chapter 1 (Figures 1.2-1.4). All measurable attributes focused on impacts and disturbances caused by visitors. As of yet, Park-wide visitor activity patterns have not been comprehensively described. Therefore, I assumed that visitor activity patterns were precisely determined when carrying out the evaluation of biological sub-models below.

In this chapter, I examine the utility of each of the four sub-models in terms of its ability to meet the needs of the decision tool, as described in the initial phase of the

project. Specifically, I evaluate whether outputs from these models map onto the measurable attributes initially defined by decision makers and resource specialists (Chapter 1). This evaluation also provides an explanation for why specific modeling decisions were made. For example, I frequently parameterized models in a manner such that population size could be easily manipulated, because decision makers were interested in examining how changes to the abundance and distribution of animals would influence outputs. I also insisted on explicitly estimating attendance probabilities for the two pinniped species, because these values are essential for estimating the number of seals or sea lions expected to be disturbed by a vessel that approaches a haul-out location.

Discrepancies between measurable attributes and outputs from biological sub-models should not be viewed as insurmountable or signs that the tool development process has failed. Rather they are impediments that can be overcome in several ways. Participants in the process may choose to eliminate or redefine some attributes to better match the available information. Alternatively, the current set of attributes can be maintained, and knowledge gaps temporally filled by judgments made by resource specialists or through a formalized expert elicitation process (O'Hagan et al. 2006). While substituting judgements for data may seem like “papering over” the issues to some, it is important to consider that the influence of all variables can be rigorously examined in the sensitivity analysis stage of the SDM process (Starfield et al. 1995, Clemen and Reilly 2013, Conroy and Peterson 2013). An awareness that all components of the model will be subject to this process can curb hesitation in taking the steps toward a fully interconnected decision tool.

Linking Biological Sub-Models to Measurable Attributes

Pinnipeds

Sea lion and harbor seal models (Chapters 2 and 3) provided a valuable means for tracking the status of the populations and estimating attendance probabilities. At the beginning of the project, measurable attributes for pinnipeds were broadly defined as “minimizing take” according to the Marine Mammal Protection Act definition (Figure 1.3). Attributes later changed to minimizing human-caused disturbances during pupping and molting periods (Figure 1.4). Estimates produced by both pinniped models mostly align with measurable attributes. A minor concern is that abundances during pupping and molting periods were held constant in both models, due to the sparsity of the data. Another minor issue is that attendance probabilities described by both models only correspond to timeframes in which aerial surveys were conducted (i.e. within 2 hours of low tide). If attendance probabilities are to be used for estimating the frequency of disturbances between vessels and pinnipeds, it may be appropriate to add additional uncertainty or otherwise shift these parameters.

Ground-nesting waterbirds

Measurable attributes for ground-nesting waterbirds remained consistent throughout the model development process and included minimizing human-caused disturbances to vulnerable concentrations of coastal breeding waterbirds and causing nest failures. Preparation for the analysis in Chapter 4 revealed that coastal waterbirds were the most poorly suited focal species group identified for inclusion in the tool. The reason for this was that quantifying measurable attributes for this species group were more

demanding than those for whales or pinnipeds, because quantifying nest failures stemming from a particular cause would require intensive sampling effort. The available monitoring data was insufficient for providing information at that resolution, owing to the sparsity of surveys across space and time. Weaknesses in the data set were not indicative of ineffectiveness on the part of surveyors or researchers, but rather a reflection of resource limitations as well as the intrinsic uncertainty in the detectability of nesting for most species. The mismatch between the data available and the ability of the data to address the questions being asked is frequently encountered in SDM. When identified, these mismatches provide an opportunity to revise decision makers objectives to match the data limitations or refine data collection efforts so the resulting data can be used to better inform decision making.

The sparseness and variability of survey data led to my decision to coarsen the model's resolution. Rather than using counts of individuals or nests, I simplified the status of waterbird species at each location into one of up to five states. This decision eliminated the possibility of estimating the number of nest failures, much less the number of nests that failed due to humans. I was compelled to exclude the "nesting" state for both black-legged kittiwakes and cormorants due to data sparsity and issues with how observations of these species were recorded. I was further compelled to remove other species and sites from the analysis because there were too few observations with which to generate reasonable estimates. In many ways, the deficiencies of the data and monitoring program for informing measurable attributes were apparent before the multistate analysis began. The fitted model was hampered by low detection probabilities and unable to identify habitat relationships beyond the general categories of "island" versus "glacial

outwash.” I still attempted to assess the effect of humans on occurrence and nesting by comparing species persistence and probabilities of nesting across sites that were both closed and open to the public. Unsurprisingly, the model did not provide evidence of human-caused decreases in occupancy or site-level nesting probability.

Another reason why current coastal waterbird monitoring is insufficient for addressing the measurable attributes was related to a broader concern that regularly monitored locations are not necessarily reflective of the status of a given species throughout the bay. It is reasonable to consider that species with a more confined nesting distribution may be more deserving of the protection provided by an island closure (e.g., arctic tern), as opposed to species with a broader distribution (black oystercatchers). Knowledge of the bay-wide distribution of coastal waterbirds is somewhat outdated, with the last bay-wide assessment conducted in the early 2000s (Arimitsu et al. 2007). These surveys were exhaustive and completed over a three year period, which would be infeasible to repeat. Furthermore, they are likely to have underestimated the nesting distribution, given my findings regarding site-level nesting detection probabilities.

Despite the problems related to coastal waterbird monitoring, I believe that it is possible for the Park to meaningfully include this focal species group in the decision tool if the participants in the SDM process perform two actions: (1) redefine the coastal waterbird measurable attributes from “minimizing human-caused nest failures” to a measure that could be more realistically estimated, that of minimizing “disturbance to nesting habitats” (2) reconfigure the waterbird monitoring program to allow for an annual bay-wide assessment of nesting distribution. The Park need not invest in exhaustive survey of the bay, but instead estimate nest occurrence by implementing a multi-season

occupancy modelling framework (MacKenzie et al. 2018), focused on tracking the nesting distribution of coastal waterbirds. The Park could create a robust and efficient sampling design by drawing information from the analysis in Chapter 4 as well as the comprehensive spatially explicit information from Arimitsu et al. (2007).

Humpback Whales

Measurable attributes associated with humpback whale protection included minimizing human-caused injuries, deaths, and disturbances more broadly. The humpback whale sub-model (Chapter 5) produced density predictions that may, in conjunction with a vessel activity data, estimate the degree of overlap between vessels and whales. The ability to quantify overlapping distributions is essential for linking the sub-model output to both measurable attributes, because overlap is an obvious requirement for all types of encounters (e.g., minor disturbances, fatalities). Quantifying rates of whale injuries and deaths is a daunting task considering that these are rare events (Gende et al. 2018). A better course of action may instead be to estimate the rate of “close encounters” between vessels and whales, defined as instances in which whales are positioned in the path of a moving vessel. These events are an appropriate proxy, in that they are a necessary condition for a collision to occur, but not so rare as to create numerical issues or be difficult to comprehend at an annual timescale.

Next Steps

The development of the quantitative decision tool for managing wildlife and visitors in Glacier Bay National Park is an ongoing process and there is much work that remains to be done in terms of specific analyses, but also careful deliberation on the part of

participants. In the near term, work will be directed towards characterizing the activities of motorized and nonmotorized vessels in the Park, so that visitor-wildlife encounters can be estimated and incorporated into the tool. Work has already begun on modeling the rate of “close-encounters” between vessels and whales as a function of whale density, vessel traffic, and vessel speed.

References

- Arimitsu, M. L., J. F. Piatt, and M. D. Romano. 2007. Distribution of ground-nesting marine birds along shorelines in Glacier Bay, southeastern Alaska: an assessment related to potential disturbance by back-country users. U.S. Geological Survey. <https://pubs.er.usgs.gov/publication/sir20075278>.
- Clemen, R. T., and T. Reilly. 2013. Making hard decisions with DecisionTools. Cengage Learning.
- Conroy, M. J., and J. T. Peterson. 2013. Decision making in natural resource management: a structured, adaptive approach. John Wiley & Sons.
- Gende, S., A. N. Hendrix, and J. Schmidt. 2018. Somewhere between acceptable and sustainable: When do impacts to resources become too large in protected areas? *Biological Conservation* 223:138–146.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. Bailey, and J. E. Hines. 2018. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier.
- O’Hagan, A., C. E. Buck, A. Daneshkhah, J. R. Eiser, P. H. Garthwaite, D. J. Jenkinson, J. E. Oakley, and T. Rakow. 2006. Uncertain judgements: eliciting experts’ probabilities. John Wiley & Sons.
- Starfield, A. M., J. D. Roth, and K. Ralls. 1995. “Mobbing” in Hawaiian Monk Seals (*Monachus schauinslandi*): The Value of Simulation Modeling in the Absence of Apparently Crucial Data. *Conservation Biology* 9:166–174.