Patterns and Processes of Marine Habitat Selection: Foraging Ecology, Competition and Coexistence among Coastal Seabirds

by

Robert Alfredo Ronconi
B.Sc., University of Alberta, 2000

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Abstract

Changes in the marine ecosystem can affect the distribution, survival, and reproductive success of seabirds. Therefore, a better understanding of factors influencing the marine distribution and abundance of seabirds can provide insight into ecological hypotheses and have important conservation implications. Yet at-sea habitat selection by seabirds has received far less attention than have investigations of their breeding biology. I studied the patterns and processes of marine habitat selection by seabirds in nearshore waters of Pacific Rim National Park Reserve, Vancouver Island, British Columbia. The study focused on comparative analyses among five sympatric species: marbled murrelet (*Brachyramphus marmoratus*), common murre (*Uria aalge*), rhinoceros auklet (*Cerorhinca monocerata*), pigeon guillemot (*Cepphus columba*) and pelagic cormorant (*Phalacrocorax pelagicus*). I used a multi-scaled and multi-disciplined approach combining shore-based telescope observations, vessel-based surveys, and developed new techniques for mapping nearshore seabird distributions.

Patterns of habitat selection were examined through vessel-based surveys and species-habitat modeling. Vessel-based transects are fundamental to studies of seabird ecology, yet standardized protocols often fail to account for detectability biases. Distance-sampling methods were used to quantify seabird detectability along transects and showed extensive variability (20-80% of birds detected) depending on species, year, and observer. Corrected estimates of bird densities were used in habitat selection modeling, which demonstrated inter-specific and inter-annual differences in species-habitat associations. Most species showed distinct partitioning in habitats, particularly with respect to substrate and along gradients of depth and sea-surface temperature/salinity. Thus, environmental variability is a key factor structuring habitat use and coexistence in this community of piscivorous seabirds.

Processes of habitat selection were studied through observations of foraging behaviour, estimates of prey availability, and spatial-statistical analysis of seabird distributions. Marbled murrelets increased foraging effort in years and seasons with scarce prey and poor oceanographic conditions and decreased foraging effort at sites with high prey availability. Despite their flexible activity budgets, increased foraging effort was inadequate to buffer reproductive success in a poor prey year, suggesting that prey availability is a limiting factor in habitat use and population growth for murrelets. Theodolite-based mapping studies examined the fine-scale distribution patterns of murrelets and murres. Nearest neighbour spatial statistics tested for competition over foraging space and showed avoidance of murres by murrelets.

The results of these studies have implications for the management and conservation of the imperiled marbled murrelet in British Columbia and elsewhere in their range. I demonstrate a clear link between prey availability and consequences for reproductive success. Habitat selection models provide a step towards identifying critical marine habitats which must be protected under the Species at Risk Act. Murrelets show high forage site fidelity and associations with spatially fixed habitat components (beaches), suggesting that marine protected areas may have an important role to play in the conservation, management and recovery of murrelet populations.

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Acknowledgments

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Dedication

I dedicate this to my parents Lynn and Diego Ronconi who have always encouraged me in all of my undertakings. Little did you know that summer camps and bug collections would lead to a love of the wild and a life by the seas.

Epigraph

A few inches from where I stood, human history ended. The bronze age, the industrial revolution, the space age – gone. One hundred years ago, one thousand years ago, one million year ago, ten million years ago, much of the world looked like this. Sixty million years ago, the creature I was now watching, the shark slowly circling me, looked like this. Already perfected. In the beginning, all was void, and darkness was upon the waters. Ancient before Creation itself: the eternal sea.

- CARL SAFINA

Chapter 1 - Habitat selection in the marine environment: background, theory and dissertation outline

Habitat selection by animals includes the suite of behavioural processes displayed by organisms that result in non-random habitat use and maximization of survival and fitness of individuals (Hutto 1985, Block & Brennan 1993, Jones 2001). For several decades, studies of habitat and resource selection have been an important focus of biological research (Hildén 1965, Cody 1985, Block & Brennan 1993, Jones 2001, Manly *et al*. 2002). Early work on habitat and resource selection shed insight into theory on competition (Fretwell & Lucas 1970), species coexistence (Levins & Culver 1971, Rosenzweig 1981), niches, speciation and range expansion (Manly et al. 2002). More recently, resource selection studies have been important in applied ecological research for assessing resource requirements of populations, modeling species distributions, estimating population size, and predicting impacts of habitat change (Boyce & McDonald 1999, Hirzel et al. 2002, Manly et al. 2002). Studies of habitat selection offer considerable promise for both applied and theoretical ecological research for a wide range of species.

Although habitat selection studies have been widely applied to terrestrial bird species (Jones 2001), resource selection by marine birds has received far less attention. Explicit quantitative treatment of habitat selection and resource partitioning is notably lacking in recent reviews of seabird biology (Schreiber & Burger 2002). Moreover, although the terrestrial (i.e. breeding) ecology of seabirds has been extensively studied at colonies, the *marine* ecology of many seabird species remains poorly understood. The challenge is three-fold: marine and terrestrial processes operate on much different spatial and temporal scales (Steele 1991), marine birds are highly mobile and typically use larger habitat areas than terrestrial birds (Hunt & Schneider 1987), and marine habitats are highly dynamic and more difficult to quantify than terrestrial habitats. As a result, there is a need to better understand the marine habitat requirements of marine birds.

The Alcidae are one seabird family for which marine ecology has been studied extensively for some species but only marginally for others. For example, research on puffins (*Fratercula* spp.) and murres (*Uria* spp.) has sought to understand patterns of marine habitat use, processes of habitat selection, and predator-prey interactions (Erikstad et al. 1990, Piatt 1990, Wanless et al. 1990, Ostrand et al. 1998a, Fauchald et al. 2000, Swartzman & Hunt 2000, Davoren et al. 2003a,b). However, marine habitat selection in other alcids has received less attention. This represents a significant gap in our knowledge of marine top predators in North America since alcids are the dominant pursuit divers in the northern hemisphere and a major component of most temperate and polar marine avifauna. Seabirds consume vast amounts of prey globally (Brooke 2004), particularly in temperate coastal waters of the northern hemisphere where alcids are highly abundant (Karpouzi et al. 2007).

On southwest Vancouver Island, four species of Alcidae are commonly found during the summer in nearshore waters (Burger *et al*. 2008): marbled murrelet (*Brachyramphus marmoratus*), common murre (*Uria aalge*), rhinoceros auklet (*Cerorhinca monocerata*), and pigeon guillemot (*Cepphus columba*). All four species are primarily piscivores (Vermeer et al. 1987, Gaston & Jones 1998). The co-occurrence of these four species, along with other pursuit diving seabirds like cormorants (*Phalacrocorax* spp.), offers the opportunity to investigate several questions about the marine ecology of coastal seabirds. Comparisons between habitat selection of coexisting species may shed insight into competition, resource partitioning and habitat specialization among seabirds. Since habitat selection processes can also be influenced by morphological and physiological constraints (Walsberg 1985, Winkler 1985), the study of habitat selection among related species may shed insight into evolutionary processes (e.g. Day *et al*. 2003). Finally, the four alcid species in this study exhibit differences in nesting strategies, thus comparisons of these species may further reveal the significance of nesting patterns to marine habitat use and selection.

Changes in the marine ecosystem can affect the distribution (Hunt et al. 1999), survival (Croxall & Rothery 1991, Cairns 1992a) and reproductive success (Ainley & Boekelheide 1990, Gjerdrum et al. 2003) of seabirds. Therefore, a better understanding of factors influencing the marine distribution and abundance of seabirds can have important conservation and management implications, especially for the threatened marbled murrelet. Locally, within Pacific Rim National Park where this study takes place, the management of living resources is a primary mandate of Parks Canada's. This area is also at risk of catastrophic or chronic oil spills due to hundreds of oil tankers and thousands of other vessels that transit adjacent waters when entering the Juan de Fuca Strait (Ford et al. 1991, Burger 1992, Anon. 2002). Thus, local knowledge of seabird distributions and habitat use can help with the management and contingency planning for Parks and oil spill response teams. More broadly, knowledge of marine habitat requirements can improve our ability to census and monitor seabird populations and predict potential effects of changes in marine ecosystems, including changes in water temperatures and food availability associated with global climate and ocean changes. Defining and mapping "critical habitat" for marine birds may provide additional tools for seabird conservation, especially for threatened or endangered species. Defining critical habitat is a key element in the Species at Risk Act in Canada. Thus local knowledge of seabird marine habitats can help with management and contingency planning.

The **goal** of this dissertation is to examine the patterns and processes of marine habitat selection among seabirds along the southwest coast of Vancouver Island. Broad scales tend to reveal generalized ecological patterns, whereas mechanistic understandings are better determined from fine-scale studies (Wiens 1989). I take a multi-scaled and multi-disciplined approach to exploring habitat selection, limiting factors, and critical habitat of seabirds at sea. Scales of my research will investigate habitat associations at coarse spatial scales (1-100 km; Hunt & Schneider 1987), but mechanistic understandings of ecological patterns will be examined from fine-scale studies (1-100's m; Hunt & Schneider 1987). These are the scales most likely to affect the behaviour and foraging distributions of marine predators (Murphy et al. 1988, Hunt et al. 1999).

The **objectives** of this research are to: (1) expand current and develop new methodological approaches for studying marine birds at sea; (2) model marine habitat selection among coexisting species and examine the interacting effects of terrestrial habitat (i.e. nesting locations) with marine habitat; (3) examine mechanisms of habitat selection including i) the influence of prey availability on foraging activity and as a limiting factor of reproductive success and ii) the role of competition and niche partitioning in determining species coexistence; (4) identify the conservation and management implications of marine habitat selection for threatened marbled murrelets.

BACKGROUND INFORMATION

Study Site

The study was conducted along southwestern Vancouver Island, British Columbia, within the West Coast Trail unit of Pacific Rim National Park Reserve of Canada (Fig. 1.1). The Park boundary includes a strip of temperate coastal rainforest and a seaward boundary defined by the 20 m bathymetric contour. All research was conducted in nearshore (<2 km from land) in waters less than 40 m deep. Inland areas include large tracts of old-growth forest which provide nesting habitat for marbled murrelets (Burger & Bahn 2004). Other seabirds (guillemots, auklets, and cormorants) nest at Seabird Rocks (48°45'N, 125°09'W) and several cliffs and caves along the study area. The closest common murre colony is at Tatoosh Island, WA (48°23'N, 124°44'W), approximately 20 km from the nearest point in the study area.

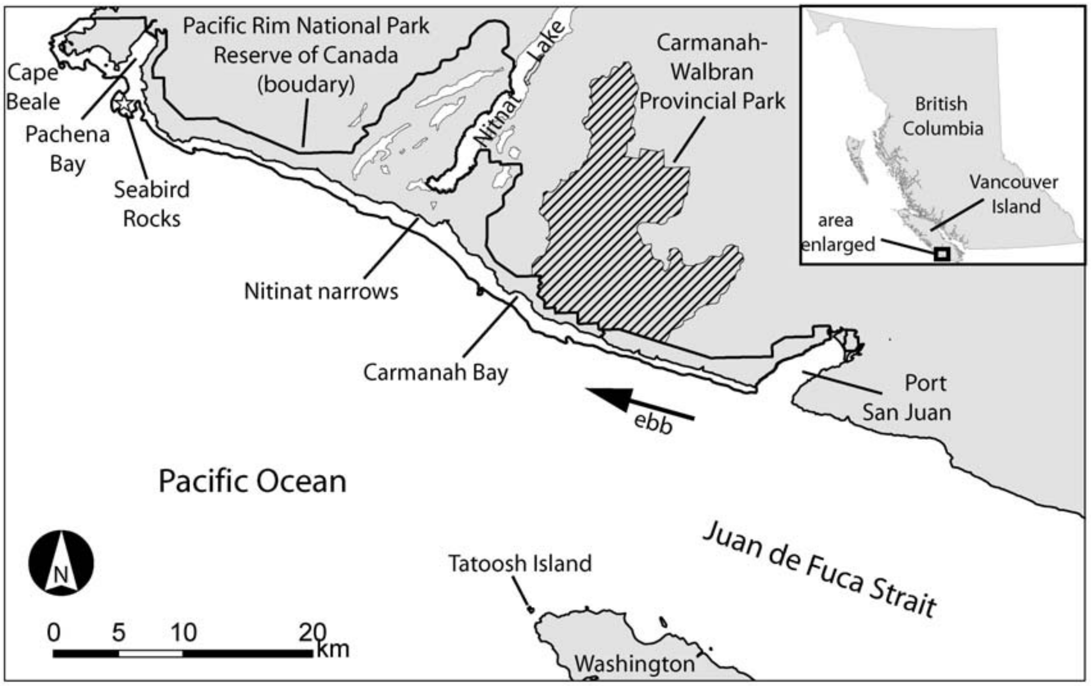


Figure 1.1 - Study area. Research took place along the West Coast Trail unit of Pacific Rim National Park between Port San Juan and Cape Beale.

This region is a relatively straight stretch of coastline at the entrance to the Juan de Fuca Strait. The coastline consists mainly of straight stretches of rocky bluffs indented by small bays, often with sandy beaches. Many of the sandy substrate areas provide habitat for Pacific sand lance (*Ammodytes hexapterus*) (Haynes et al. 2007), a primary prey item of many seabirds. Wide submarine rock platforms with narrow sand/gravel beaches make up the largest portion of the coastline (Howes et al. 1997), though these are not suitable habitat for sand lance (Haynes et al. 2007). Dominant features of this coastline include i) Port San Juan, a large bay that receives significant amounts of freshwater input from Gordon and San Juan rivers, ii) Nitinat Narrows, a narrow channel connecting Nitinat Lake to the ocean and where tidal streams create a surge of freshwater (from several rivers draining into the lake) into the ocean at low tide (Thomson 1981), and iii) Pachena Bay, a large shallow sandy bay at the north end of the study area.

The study area has predictable summer winds and dominant tidal currents which are predominantly influenced by the Juan de Fuca Strait (details in Thomson 1981, Thomson et al. 1989). The maximum tidal current (0.75 m/s) runs from the southeast to the northwest on the ebb. Predominant surface winds during the summer are from the northwest. Summer upwelling also occurs along the west coast of Vancouver Island, but this tends to be more intermittent and less well developed than upwelling along California and Oregon coasts (Thomson 1981). Upwelling, surface temperatures and a large eddy system all interact to influence the seasonal distribution and abundance of seabirds in areas 10-30 km offshore of the study site (Burger 2003).

Seabird species

This study considers four species of the family Alcidae and one species of cormorant (Pelagic cormorant, *Phalacrocorax pelagicus*). All are pursuit diving seabirds that feed at similar trophic levels (Hobson et al. 1994), on similar prey items (e.g., Vermeer et al. 1987, Burkett 1995, Lance & Thompson 2005), and which can be considered generalist species feeding on a mixed diet of fish and invertebrates (Gaston & Jones 1998). One key difference is that guillemots and cormorants feed primarily on demersal prey while murrelets, auklets and murres prefer epipelagic prey.

For several reasons, the marbled murrelet is a central focus of my dissertation. First, it is the most abundant seabird in the study area for much of the year, and this region supports some of the highest at-sea densities of marbled murrelets anywhere in British Columbia (Burger 2002, Burger et al. 2008). Studying the species in well-used marine habitat is likely to reveal key elements of their biology. Second, murrelets are an anomaly among seabirds in that they are non-colonial and nest inland, in tracts of old-growth forest (Nelson 1997). This makes them a particularly interesting species in which to examine linkages between marine and terrestrial habitat associations. Finally, research on this species has important conservation and management implications. Since marbled murrelets are listed as threatened in Canada by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (Rodway 1990, Hull 1999). In the USA, they are federally listed as a threatened species in California, Oregon and Washington, and the state of California lists them as endangered (Ralph et al. 1995).

The threatened status of marbled murrelets in Canada is based primarily on their low reproductive rate and the rapid loss of nesting habitat due to commercial logging of old-growth forests (Rodway 1990, Hull 1999, Burger 2002). This has spurred more than two decades of intensive research into the nesting ecology and terrestrial habitat requirements of murrelets (Ralph et al. 1995, Burger 2002, McShane et al. 2004, Piatt et al. 2007a). Recent studies have revealed the importance of marine conditions to the reproductive success and population trends of murrelets (Becker et al. 2007, Norris et al. 2007, Piatt et al. 2007a). Thus understanding the marine ecology of murrelets can have important ramifications for their conservation and management. Although some of the earliest studies on marbled murrelets focused on their marine ecology (Sealy 1975, Carter 1984, Carter & Sealy 1990), efforts to understand the marine habitat requirements of this species has lagged behind terrestrial research. Marine habitat requirements have been identified as an important information gap in the management and recovery of marbled murrelets in Canada (Canadian Marbled Murrelet Recovery Team; CMMRT 2003).

The marine habitat use of murrelets has been studied by radio-telemetry and vessel-based transect surveys. Telemetry work has shown that breeding murrelets use habitat up to 100 km or more from nest sites in Alaska (Whitworth 2000), but in Canada typical commuting distances are closer to 30 km (Lougheed 2000, Hull et al. 2001).

Results from vessel-based studies of marine habitat selection have shown differences among regions. In Alaska, murrelets are (i) associated with dense fish schools in shallow habitats (Ostrand et al. 1998a), (ii) avoid icy waters (Day et al. 2003), and (iii) show segregation in habitat use between juvenile and adult murrelets (Kuletz & Piatt 1999). In Washington, Oregon and California, marine habitat use has been linked to nesting habitat (Miller et al. 2002, Raphael et al. 2002, Becker & Beissinger 2003, Raphael 2006), estuaries (Miller et al. 2002), and ocean temperatures (Becker & Beissinger 2003). In British Columbia, one large scale study of marine habitat use showed links with nesting habitat, estuaries, and sandy shorelines (Yen et al. 2004a). Within the study area, murrelets have been associated with sandy shorelines (Burger 1997a), distribution of prey (Burger et al. 2008), fluctuations in abundance related to ocean temperature (Burger 2000), and there are close associations between juvenile and adult murrelets (Wong et al. in press). However, underlying mechanisms of habitat selection (i.e., behavioural responses) remain poorly understood. Murrelets may also avoid habitat used by other larger alcids (Burger et al. 2008) suggesting competitive interactions.

The marine ecology of common murres has been studied extensively in North America and Europe (e.g., Croll 1990, Wanless et al. 1990, Fauchald et al. 2000, Swartzman & Hunt 2000, Davoren et al. 2003a,b). Along the West Coast Trail rhinoceros auklets and murres frequently aggregate together, but pigeon guillemots do not aggregate with either species (Burger et al. 2008). Around Seabird Rocks, the behaviour and distribution of foraging auklets is closely tied to prey distributions (Davoren & Burger 1999, Davoren 2000). Nevertheless, the species-habitat associations of rhinoceros auklets, pigeon guillemots, pelagic cormorants and common murres are relatively unknown throughout British Columbia, and interactions among sympatric populations of these species are poorly understood throughout their range.

HABITAT SELECTION

Definitions

Habitat includes both the physical and biological environmental factors that result in the occupancy of a given organism (Morrison et al. 1992, Block & Brennan 1993). However, there is an important distinction to be made between habitat *use* and habitat *selection*. *Habitat use* is the way in which an organism uses habitats to meet its life needs such as feeding, reproduction, rearing of young (Block & Brennan 1993, Jones 2001). *Habitat selection* is the process of behavioural responses by individuals, resulting in the disproportional (i.e. non-random) use of habitats which influence their survival and fitness (Hutto 1985, Block & Brennan 1993, Jones 2001). More succinctly, habitat selection is the *process* that results in the *pattern* of habitat use (Jones 2001). The term *habitat preference* is often used synonymously with *habitat selection*.

The term *niche* is another important concept that is related to habitat selection. Defined by Hutchinson (1957), the multidimensional ecological niche is the collection of environmental elements that determine the distribution of a species. Habitat and niche are clearly interrelated and neither is mutually exclusive (Block & Brennan 1993). The distinction becomes clear when defining the *fundamental* and the *realized niche*. The *fundamental niche* is the biotic and abiotic conditions that allow a species to live in the absence of interspecific interactions, whereas the *realized niche* is the actual space occupied by a species resulting from restrictions imposed by competitors, predators, barriers or any other factors (Molles 1999). The realized niche is a more realistic interpretation of a species habitat selection, and competition has played an important role in the development of habitat selection theory.

Although two species can co-occur in the same habitat, if the two species utilize the same resources (i.e. food), then a certain amount of niche overlap will occur. Competition implies that some shared resources within a habitat are limited (Molles 1999). Therefore, competition for limited resources could exclude a species from a particular habitat, however competitive exclusion is not inevitable. Similar species often coexist (Tokeshi 1999). One mechanism which allows competing species to coexist is the partitioning of resources within a habitat. *Habitat partitioning* is defined as the subdivision of similar resources within a habitat type (Cody 1985). A classic example of habitat partitioning is found in MacArthur's (1958) work which illustrates that different warbler species utilize different positions within a tree canopy, to minimize competition for resources with coexisting species.

Theory

Block and Brennan (1993) identify the many factors that influence the habitat selection process in birds including morphological and physiological constraints, biotic factors, resource distribution, and vegetative structure and distribution, among others. These factors can be further grouped as ultimate and proximate factors (Hildén 1965, Cody 1985, Block & Brennan 1993). Ultimate factors are those that relate directly to the fitness (i.e. survival and reproduction) of individuals and species, whereas proximate factors are the species-specific stimuli of a habitat which attract individuals to settle in that habitat (Hildén 1965, Block & Brennan 1993). Proximate factors attract birds to a habitat while ultimate factors enable them to survive and/or reproduce in an area.

The distinction between ultimate and proximate factors in habitat selection led to the early categorization of habitat selection processes. First introduced by Johnson (1980), several authors have since developed and adopted a hierarchical model to explain the sequence of habitat selection processes (Hutto 1985, Orians & Wittenberger 1991, Block & Brennan 1993). The hierarchical model recognized that habitat selection occurs in four steps. *First-order selection* occurs when a species selects a physical or geographical range (i.e. the distribution of a species). *Second-order selection* occurs within that range, whereby individuals or social groups select a home range. Selection of habitat components within a home range (e.g. feeding or nest sites) is termed *third-order selection*. Finally, *fourth-order* is the selection of food items within a particular site.

The hierarchical model has played an important role in fusing various concepts of habitat selection. Block and Brennan (1993) illustrated the inter-relationship between the hierarchical concept of habitat selection and the ultimate and proximate causation of habitat selection. Proximate factors may be acting at the broadest scales (first- and second-order) indicating that a site is suitable to settle in, whereas ultimate factors may influence lower hierarchical levels when resource and nest site acquisition is essential for survival and reproduction. Most importantly, the hierarchical model also addresses important issues of temporal and spatial scale in habitat selection studies (Orians & Wittenberger 1991). Spatial scales decrease as the hierarchical processes increase from 1st to 4th order (Hutto 1985, Orians & Wittenberger 1991, Block & Brennan 1993), and temporal scales vary with hierarchical level. First-order selection may take place over longer time scales (i.e. migration period), but initial decisions to explore habitats (2nd order) are often made quickly (Orians & Wittenberger 1991). Issues of scale are critical to understanding links between organisms and their environment (Wiens 1989) and, thus, multi-scaled studies have played an important role in understanding seabird-habitat relationships (Logerwell & Hargreaves 1996, Fauchald et al. 2000, Davoren et al. 2002, Vlietstra 2005).

Application

By definition, habitat selection results in the disproportional (non-random) use of habitats which ultimately influences the survival and fitness of individuals. Although fitness is an integral part of this definition, fitness is often difficult to measure in field settings. Thus, many studies of habitat selection have instead focused on the "disproportionate use of habitats" and assumed that this non-random use is due to some relative increase in fitness. For example, Becker and Beissinger (2003) conducted a study of habitat selection by marbled murrelets. They found that habitat use by murrelets was non-random and that they selected foraging habitat by three factors (sea-surface temperatures, distance from nesting sites, and prey availability). However, fitness was not measured in this study. Instead, fitness may be inferred by understanding the behavioural and energetic contexts of their results: by foraging closer to nesting sites the energetic costs of foraging are reduced, thus enhancing fitness. Jones (2001) urges that researchers think critically about the methods used for testing habitat selection so that behavioural and fitness implications may be inferred properly.

In general, two methods have been used to test for habitat selection: comparing used habitats with either unused or available habitats (Jones 2001). However, proving that a species does not use a specific habitat is difficult. Consequently, habitat use relative to available habitat has become the cornerstone in habitat selection modeling (Johnson 1980, Manly et al. 2002). Although this approach has been widely accepted, it is contingent on a suitable definition and delineation of "available" habitats (Jones 2001). Arbitrary decisions by researchers about which resources are available can have profound effects on the results of resource selection studies (Johnson 1980). The delineation and measurement of habitat availability is difficult (Jones 2001), but careful consideration of the autecology of a species (e.g., home range size, foraging requirements) can allow for appropriate definitions and analyses of available habitats in habitat selection studies. Nevertheless, the availability of appropriate and high quality data on habitat variables may present a strong limitation to many analyses. In most studies researchers cannot include all the variables which are likely to affect the distribution of a species' because the necessary data are just not available. Consequently, many studies focus on readily available but not necessarily the most important data, sometimes leading to erroneous conclusions.

Once used and available habitats variables are defined and sampled, the next focus is on modeling species-habitat relationships. Species-habitat relationships can be modeled in many ways (Guisan & Zimmermann 2000, Scott et al. 2002, Redfern et al. 2006) and the most appropriate approach will depend on the goals of the study and the purpose of the model (e.g. descriptive, predictive or hypothesis testing). Although correlative approaches have been widely used to study species-environment relationships (e.g., Haney & Schauer 1994), there has been a recent shift in approach to species-habitat modeling focusing on *constraints* rather than correlates, thus emphasizing factors as limiting agents to species abundance or distribution (Huston 2002, O'Connor 2002). This "constraints approach" is largely based on algorithmic modeling (Breiman 2001) and is an approach rapidly gaining attention in the field of wildlife biology (Hochachka et al. 2007). While traditional modeling approaches assume that data can be fit to statistical models (e.g., linear/logistic regressions), algorithmic modeling treats the shape of the response as unknown and uses algorithms to describe data patterns (e.g., decision trees) (Breiman 2001). While data modeling has been fundamental in understanding species-habitat relationships (e.g., resource selection functions; Manly et al. 2002), algorithmic techniques are providing new perspectives on species-habitat modeling and investigations of coexistence and niche partitioning (MacLeod et al. 2007).

Dissertation framework

The definitions, theory and applications of habitat selection provide a framework within which my dissertation is developed. First, I use a multi-scaled approach that mirrors several levels in the hierarchical habitat selection model. *First-order* selection is assumed based on the species range associated with old-growth forests in coastal North America. For *second-order selection,* I examined species distributions within the study area thus assessing general patterns of habitat use. Analysis of used relative to available habitats then focuses on *third-order selection*; selection of habitat components for foraging. Finally, at the finest spatial scales (1-100's m), I examine how prey-availability and competitors may influence foraging behaviour and habitat use within particular sites (*fourth order*). This multi-scaled approach therefore helps to identify both proximate (suitable habitats for foraging) and ultimate factors (preferred habitats that increase reproductive success) which interact to define marine habitats of seabirds.

Second, the definitions of used, unused and available habitats were important to the framework of this study. Because seabirds are highly mobile, it is difficult to quantify "unused" habitats. For example, vessel surveys are an important source of data in seabird habitat studies, yet habitats along transects that are apparently unused (segments with no birds) may become occupied at a later point in time as birds and/or prey move. Therefore, habitat selection analyses in this study are based primarily on comparisons of used vs. available habitats. This requires careful delineation of available habitat which I achieved by the layout of transects within the study area. Because I was studying the habitat use of diving seabirds, maximum water depths provide an important limitation to available habitat for seabird, particularly for pigeon guillemots and pelagic cormorants that forage on benthic prey. Therefore transect layout was designed to cover the range of depths "available" to all species.

Finally, there are many analytical approaches available for examining species-habitat relationships. There has also been a recent paradigm shift from statistical modeling approaches to algorithmic modeling approaches (described above). To thoroughly address species-habitat relationships, I have therefore selected several approaches that include both statistical and algorithmic modeling. I contrast a correlative approach, which assesses habitat use, with a decision tree approach that infers habitat selection.

DISSERTATION OUTLINE

This study examined both patterns (Chapters 2 and 3) and processes (Chapters 4 and 5) of habitat selection. I examine issues of limiting factors, niche partitioning and interspecific competition as mechanism for habitat selection. Moreover, I develop and expand methodological techniques for studying marine birds at sea. The following is an outline of the remaining chapters of my dissertation.

Reliable census techniques and accurate assessments of animal densities are fundamental to wildlife research, monitoring and estimation of population size (Braun 2005). Most vessel-based transect surveys for seabirds use fixed-width strip transects to measure the distribution and abundance of birds at sea (Tasker et al. 1984), yet distance-sampling techniques have shown empirically that many animals are missed during surveys and, thus, that densities are often underestimated (Buckland et al. 2001). In **Chapter 2** I use distance-sampling (Buckland et al. 2001) to assess the detectability of seabirds along transect surveys in order to provide more accurate abundance estimates for modeling species-habitat relationships.

With accurate estimates of species abundance and distribution, **Chapter 3** models *used* and *preferred* habitats among five species of seabirds. The analysis links terrestrial (i.e. nesting habitat) and marine habitat to seabird surveys at coarse- and fine-scales (<100 km and 100’s m respectively; Hunt & Schneider 1987). Results identify species-specific patterns and inter-annual variability in habitat selection. I provide evidence that habitat selection plays a critical role in niche partitioning and the coexistence of pursuit diving seabirds in coastal environments.

Chapter 4 examines relationships between murrelet foraging behaviour, prey availability, and reproductive success. Animals use habitats primarily for feeding, breeding and shelter. Since seabirds can neither nest nor hide on the ocean, the marine habitat functions primarily as a foraging ground for seabirds. I show that seabird reproductive success is mediated by relationships between foraging effort and prey availability, thus providing a fitness context for murrelet habitat use. This suggests that resource limitation is a key mechanism driving habitat use.

Competition between murrelets and murres has been suggested as one mechanism influencing the habitat use by these species (Burger et al. 2008, Chapter 3 of this study). **Chapter 5,** thus, examines competition for foraging space as a mechanism driving the habitat use of murrelets and murres. I developed new techniques for mapping the fine-scale distribution (10's of m) of seabirds, and use spatial statistics to infer competition for foraging space.

Chapter 6 provides a synthesis of my dissertation and identifies the development of novel methodological techniques that are transferable to studies of marine habitat selection of seabirds elsewhere. It summarizes my research findings in the context of ecological theory including aspects of foraging behaviour, niche partitioning, competition, and species coexistence. Lastly, I discuss the implications of my results in the context of the conservation and management of the threatened marbled murrelet.

Chapter 2 - Estimating seabird densities from vessel transects: distance sampling and implications for strip transects

ABSTRACT

Vessel-based transects have been a mainstay of seabird research for decades, yet there has been surprisingly little effort devoted to evaluating the detectability of seabirds within strip transects. Distance-sampling methods offer an opportunity to quantify detectability and to assess the proportions of birds on the water that may be missed during strip transects. Three summers of line-transect surveys were analyzed using program DISTANCE to model detection functions of six species (marbled murrelet *Brachyramphus marmoratus*; rhinoceros auklet *Cerorhinca monocerata*; common murre *Uria aalge*; pigeon guillemot *Cepphus columba*; pelagic cormorant *Phalacrocorax pelagicus;* gulls *Larus* spp.). I tested the effects of covariates (Year, Observers, Sea State, and Cluster Size) on detection function estimation. Year and observer were the most important covariates for some but not all species. For a 300 m wide transect (150 m on either side), 20-80% of birds were detected, depending on species, year, and observer. Detectability was highest for cormorants (59-91%) and among the other species typically 40-60%. Sea state had a significant effect on encounter rate for murrelets suggesting that *g*(0), detection probability near the transect line, may be <1 when wave height increases. These data emphasize that a high proportion of birds on the water remain undetected during strip-transect surveys. It is important that surveys develop independent estimates of detection probability to account for detectability among species, years, observers, vessel types/speed, and viewing conditions. The application of distance sampling to seabird surveys can provide more accurate abundance and population estimates, which can hep to improve conservation and management efforts.

INTRODUCTION

Reliable census techniques and accurate assessments of animal densities are fundamental to wildlife research, monitoring and the estimation of population size (Braun 2005). Vessel-based transect surveys have been a part of seabird research for nearly a century (Jespersen 1924, Wynne-Edwards 1935) and a mainstay of seabird biology since the 1960's (Brown et al. 1974, Tasker et al. 1984). Transect surveys using standardized protocols (Tasker et al. 1984) have contributed substantially to understanding seabird ecology (>150 peer-reviewed publications; Web-of-Science search engine). Despite their ubiquitous use in seabird research, vessel-based transects are not without their methodological problems and biases. This is of particular interest when monitoring populations of threatened species or in conducting environmental impact studies for seabirds at sea. Of central importance are factors affecting accuracy of density and abundance estimates (Hyrenbach 2001, Spear et al. 2004).

In all such studies, some birds on the water are not detected, leading to underestimates of seabird densities. With standardized strip-transect surveys (Tasker et al. 1984), however, the basic assumption is that *all* objects within the strip are detected. Distance-sampling methodology has shown empirically that this assumption is usually violated because individuals closer to the transect line have a higher probability of detection than those further from the line (Buckland et al. 2001, 2004). Rather than counting organisms within a pre-determined transect width, distance-sampling records the distance of individuals (or clusters/flocks) from the transect line. Based on these distances, distance analysis (e.g., DISTANCE software, Thomas et al. 2006) provides estimates of the proportions of organisms missed during surveys, thus allowing more accurate density estimates.

For decades, marine mammal and sea turtle researchers have been developing and employing distance sampling protocols (Burnham et al. 1980, Laake et al. 1997, Beavers & Ramsey 1998) that have become the backbone of robust density and population estimates (Forcada et al. 2004, Slooten et al. 2004, Gomez de Segura et al. 2006). Distance sampling has been advocated to improve the reliability of bird surveys

(Rosenstock et al. 2002, Thompson 2002), yet transect surveys for marine birds have been slow to adopt this method. The one exception has been with marbled murrelets (*Brachyramphus marmoratus*) where distance sampling has been used readily (Becker et al. 1997, Evans Mack et al. 2002, Peery et al. 2004, 2006, 2007). Newer monitoring programs have been amenable to adopting distance-sampling protocols (RIC 2001, Raphael et al. 2007), but established and longer-term seabird survey programs have continued to use strip-transects and are hesitant to change protocols (Pyle 2007). Several European (Komdeur et al. 1992, Camphuysen et al. 2004) and one Canadian program (Eastern Canadian Seabirds At Sea) have adopted distance-sampling protocols for seabird surveys.

Distance sampling methodology has been thoroughly developed (Buckland et al. 2001, 2004) and evaluated across many species (Kulbicki & Sarramegna 1999, le Mar et al. 2001, Norvell et al. 2003). My goal is not to validate the technique further but, rather, to demonstrate its relevance for seabird surveys and to examine the variability in detection probabilities for a variety of species and conditions. I assessed the effects of year, observer bias, sea state, and cluster size on seabird detection functions. I compared parameter estimates showing the proportion of birds detected for fixed-width strip transects of 200 or 300 m (100 or 150 m on either side of the boat). The results and methods are relevant to other vessel-based transect surveys using distance sampling to improve the accuracy of seabird density estimates, including those based on strip transects.

METHODS

Study area and organisms

Line-transect surveys were conducted between 20 May and 8 August in three years (2004-2006). The study area was located in the West Coast Trail unit of Pacific Rim National Park on the southwestern coast of Vancouver Island, British Columbia, Canada, a 65 km stretch of coast exposed to the Pacific Ocean. All surveys were conducted within 2 km from land in waters less than 40 m deep.

Sample sizes for distance sampling analysis were sufficient to investigate six taxa: four Alcidae (marbled murrelet; rhinoceros auklet *Cerorhinca monocerata*; common murre *Uria aalge*; pigeon guillemot *Cepphus columba*), one cormorant (pelagic cormorant *Phalacrocorax pelagicus*), and gulls (glaucous-winged gull *Larus glaucescens*; and California gull *L. californicus*; pooled as *Larus* spp.). This range of species provides a representative array for distance-sampling analysis typical of the communities encountered in coastal waters of the northern hemisphere: pursuit divers (alcids/cormorants) vs. surface feeders (gulls), small (murrelets/guillemot/auklet) vs. large birds (murre/cormorant/gull), and drab (murrelet/auklet) vs. conspicuous alcids (guillemot/murre).

Survey methods

All surveys were conducted from a 5 m rigid-hull inflatable boat traveling at approximately 10 km h^{-1}. Surveys were conducted using paired observers (Evans Mack et al. 2002) at the bow, each scanning one side of the transect line from directly ahead to 90^{o} abeam. Observer height was 1.5-2 m above the water surface. Surveys followed distance-sampling protocols recording bird clusters (individual birds or groups of birds of the same species), perpendicular distance from the transect line (estimated at the time of first detection), and cluster size (Buckland et al. 2001). Although Buckland et al. (2001) recommend recording angles to birds and distance at first detection (radial distance), I estimated perpendicular distance from the transect line which, for murrelets, is as accurate as radial distances (Raphael et al. 1999). Birds were considered to be in clusters if within 2 m of each other or birds slightly further apart that foraged together or exhibited similar behavioural cues (Becker et al. 1997). Observers were trained in distance estimation by towing a line with three buoys spaced at 10, 25, and 50 m behind the boat. The buoy line was used for the first three weeks each year, until observers were competent at estimation to ±10 m, and used again periodically several days per month. There were multiple observers each year (two in 2004 and three in 2005/2006) with one observer (R. Ronconi) consistent in all years.

During each survey I collected environmental data on viewing conditions, and restricted surveys to periods of low swell (<1.5 m) and low winds (Beaufort sea state ≤3). For analysis I coded sea state into two categories as per Becker et al. (1997): excellent/very good (Beaufort 0 to 1) and good/fair (Beaufort 2 to 3).

Transects layout included two designs: zig-zags and parallel lines perpendicular to the shore. The zig-zag transect layout was systematic to cover the length of the study area and was bounded by the 5 and 20 m depth contours, the latter delineating the seaward park boundary. Depending on shoreline complexity and navigation hazards, zig-zag legs were on average 1.6 km long (range 0.9-2.9 km) and typically bisected the coastline at 45^{o} angles. Total zig-zag length was 77 km which was surveyed 5-6 times in 2005 and 2006. In some sectors of the study area, I established a series of parallel transects, spaced 500 m apart and oriented perpendicular to shore. These transects were bounded by the 5 and 40 m depth contours (approx. 1-2 km offshore). This design was used at one site in 2004 (total length 13.4 km; 7 parallel legs) and expanded to six other sites in 2005 and 2006 (avg. length 7.0 km, range 5.2-8.3 km; 3-4 parallel legs). Transect type, as a stratum with Conventional Distance Sampling (Thomas et al. 2006), had no effect on detection function (R. Ronconi, unpl. data) therefore all data were pooled for analysis.

Calculating densities from transects

I present a basic equation useful for the interpretation of results in this study (see also Buckland et al. 2001 for complete distance-sampling equations). The basic estimate of density $\hat{D}$ for objects in a study area can be calculated by the number of objects counted n divided by the area surveyed a. In the case of a strip-transect line, the area surveyed is equal to the strip width $2w$ multiplied by L, the total length of the transect. Here w represents the width on one side of the boat (e.g. 150 m) multiplied by 2 when observers are counting birds on both sides of the boat.

Eq. 2.1 $$\hat{D} = \frac{n}{2wL}$$

With line transects, however, not all of the objects within the survey area (*a*) are detected, thus, P_a, estimated with the DISTANCE software, is included to represent the proportion of birds detected within the survey area.

$$\text{Eq. 2.2} \quad \hat{D} = \frac{n}{2wL\hat{P}_a}$$

When objects *n* are groups of organisms, an estimate of mean group size *E(s)* is introduced as a multiplier in the equation.

$$\text{Eq. 2.3} \quad \hat{D} = \frac{n \cdot E(s)}{2wL\hat{P}_a}$$

Buckland et al. (2001) present several methods for unbiased estimates of *E(s)*. I used the regression estimator which estimates mean cluster size by the predicted mean cluster size on the transect line, where object detection is certain (Buckland et al. 2001).

Other multipliers may also be included in the equation to correct for discrepancies in the detection function. One important multiplier is $g(0)$, the probability of detecting a detecting a bird on or near the transect line. One critical assumption of distance sampling is that all objects on or near the transect line are detected, $g(0) = 1$, however if this assumption is not met then $g(0)$ can be introduced into the equation as:

$$\text{Eq. 2.4} \quad \hat{D} = \frac{n \cdot E(s)}{2wL\hat{P}_a} \cdot \frac{1}{g(0)}$$

Assumptions of distance sampling

For distance sampling analysis to be accurate, there are three basic assumptions that must be met (Buckland et al. 2001, Rosenstock et al. 2002). The first is that all birds on the transect line are detected: $g(0) = 1$, where $g(0)$ is the probability of detecting birds at distance zero. Few studies validate this critical assumption (Bächler & Liechti 2007). There are two reasons why seabirds may not be detected: availability bias (animals are missed because they are submerged) and perception bias (visible animals that are missed for reasons such as sea state, distance, etc.) (Laake et al. 1997). Availability bias should be minimal for seabird species that spend a high proportion of time visible on the surface. Moreover, average dive times for murrelets are only 25 s (Jodice & Collopy 1999), therefore at a speed of 10 km·h^{-1} birds that dove <70 m ahead of the boat would resurface after the boat had passed. I expect to be able to detect most birds within this distance before they dove. Average dive times for other species are similar or slightly longer, but these are larger and more conspicuous species. Using a double observer method Evans Mack et al. (2002) tested perception bias for marbled murrelets finding that $g(0)$ ranged from 0.84-0.93 depending on sea state and individual observers. However, average boat speed in their study was 20 $\text{km}\cdot\text{h}^{-1}$, twice that of this study, therefore, $g(0)$ may be closer to 1 in this study. Nevertheless, I conducted a test of potential sea state effects on $g(0)$ (see *Data analysis* section).

The second assumption is that birds are detected prior to evasive movements. I recorded perpendicular distance to the transect line at the time of first detections, therefore typically before the boat was close enough to cause evasive movements. In this study area most murrelets do not react to boats until within 40 m of an approaching vessel (Bellefleur et al. in press). Elsewhere, murrelets typically moved < 10 m before detection for distance sampling (Brennan 2000).

The final assumption is that distances were measured accurately. I maintained the accuracy of distance estimation by thorough and repeated training (details above), but because distances in the field were rounded to 10 m increments, precision is limited to this scale and therefore distances were grouped into bins for analysis (Buckland et al. 2001).

Data analysis

Data were analyzed using DISTANCE 5.0 release 2 (Thomas et al. 2006) and the multiple covariates distance sampling (MCDS) engine. I followed analysis guidelines outlined by Buckland et al. (2001) which include exploratory analysis, model selection, and final analysis and inference.

Exploratory analysis included plotting of histograms of various groupings (distance bins), truncation of data, and inspection of cluster-size bias. Histograms of various bin sizes were constructed in SPSS 15.0. The minimum bin size of 10 m indicated heaping or rounding errors, but bins of 20 m increments (Fig. 2.1) showed a broad shoulder (most detections near the transect line), no evidence of evasive movements, and evidence of outliers beyond 150 m (Buckland et al. 2001). Consequently analyses were done using distance bins of 20 m (0-20, 21-40, etc.).

Buckland et al. (2001) recommend data truncation to eliminate outliers and improve model fitting. I selected a truncation of 150 m on either side of the boat (i.e. overall a 300 m band) for two reasons. First, 150 m falls within the range of truncation from previous studies using distance sampling with murrelets (160 m, Becker et al. 1997; 120 m, Peery et al. 2006). Second, a 150 m width on both sides has been the standard for annual surveys conducted by Parks Canada in this study area since 1993 (Burger et al. 2008) and for other seabird surveys off the British Columbia coast (Burger et al. 2004a). Note that 300 m bands (typically on one side of the vessel) have been the standard protocol (Tasker et al. 1984), but this distance was selected particularly to count flying birds.

Cluster-size bias frequently occurs in survey work because larger clusters of birds are more easily detected than smaller ones (Buckland et al. 2001). Unbiased estimation of mean cluster size is essential for accurate density estimation. I tested for cluster-size bias by examining correlations between cluster size and distance from transect line, $g(x)$, for different truncation distances (300, 150, 100, 50 m) using SPSS 15.0. When cluster-size bias was detected, regression techniques were used to determine an unbiased cluster size estimate for density calculations in subsequent analyses (Buckland et al. 2001).

Program DISTANCE allows several key functions and series expansion terms for the modeling of the detection function. For each species, I tested the following models (and series expansion terms) which may be used in MCDS: Half-normal (Cosine or Hermite-polynomial) and Hazard-rate models (Cosine or Simple-polynomial). Model fit and ranking was assessed using Akaike's Information Criterion with correction for small samples sizes (AIC_c) (Burnham & Anderson 2002). For all species, except pigeon guillemot, Hazard-rate models provided the best fit to the data (lowest AICc score). For pigeon guillemots, the Half-normal model fit best though the Hazrad-rate model also fit the data well ($\Delta AICc < 2$). For gulls, cormorants and guillemots, series expansion terms were not included in the best fit model. Cosine series expansion was included in the best fit model for murrelets and simple-polynomial terms were included in the best fit models for auklets and murres. Hazard-rate models with or without appropriate series expansion terms were used for subsequent analyses. Note however that in other instances with distance sampling of marbled murreles Raphael et al. (2007) found problems with the hazard rate model.

MCDS analyses were conducted to test for effects of covariates Year, Observers, Sea State, and Cluster Size on the estimation of detection functions for each species. The year covariate was assessed at three levels for murrelets (2004/2005/2006), two levels for murres and cormorants (2005/2006), and not tested for other species due to sample size constraints. I excluded one observer (Obs 2) from guillemot, cormorant and gull models because n < 5 observations for each species. Sea state was coded at two levels for analysis: Beaufort sea states 0-1 and 2-3 (described above). When evaluating the relative importance of covariates, automatic selection of adjustment terms is not appropriate, therefore I manually limited the models to allow no adjustment terms (Thomas et al. 2006: DISTANCE User's Manual p. 119). Moreover, when covariates are included in MCDS, the shape of the detection function will change at different values of the covariate, therefore a scale parameter was used to preserve the shape of the detection function while allowing the scaling to change for each covariate (DISTANCE User's Manual p. 117).

A set of competing models were tested which included perpendicular distances (x) and all possible combinations of up to 2 additional covariates. For each species, model fit was assessed with (1) AIC_c, the small sample Akaike's information criterion, (2) ΔAIC_c, the difference in AIC_c between a fitted model and the lowest AIC_c of any model, and (3) AIC_cw, the AICc weight, which is the evidence in favour of one model being the actual "best" model from the set of candidate models that were evaluated (Burnham & Anderson 2002). The relative importance of individual covariates was determined using AIC_c weights for each covariate: sums of the AIC_cw of all models in which a unique covariate appeared (Forcada et al. 2004).

I developed estimates of P_a which are relevant to commonly used widths in fixed-width strip transects surveys of seabirds: 300 m (150 m truncation on both sides) and 200 m (100 m both sides; e.g., Agler et al. 1998). Parameter estimates of P_a were obtained for global models (all data) and individual covariate levels using post-stratification by the covariates.

Finally, I assessed the potential effects of sea state on *g*(0). Evans Mack et al. (2002) demonstrated that g(0) is indeed affected by wave height, and Becker et al. (1997) recorded lower murrelet densities with increased wave height. I compared murrelet encounter rates (*n/L* = number of clusters counted per distance traveled) for different sea state conditions (Beaufort sea state 0 to 3). Encounter rates were calculated for each sea state code (if >1 km of survey was conducted at for that sea state) on each survey day (unit of analysis). Detection of birds should remain certain or nearly certain at small distances from the line (Buckland et al. 2001), therefore I limited the assessment of encounter rates to birds detected near the line (≤60 m for murrelets and murres, ≤80 m for cormorants) which corresponds with the "shoulder" of the histograms (Fig. 2.1), akin to the distance of "perfect" detection (Kissling & Garton 2006). Analysis was conducted only for species with sufficient sample size (murrelet, murre, cormorant).

RESULTS

During three years I conducted 1,429 km of line transect surveys (2004 = 105 km; 2005 = 631 km; 2006 = 693 km). I recorded >8000 clusters of seabirds, 70% of which were marbled murrelets, and most were detected within 80 m of the transect line (Fig. 2.1). Two species, pigeon guillemots and pelagic cormorants, showed some decrease in detection for intervals closer to the transect line, suggesting that these two species may exhibit evasive behaviour from approaching boats. However, because the decrease in detections close to the line was not extreme and these are both fairly conspicuous species, I assume that most birds were detected before undertaking evasive movements.

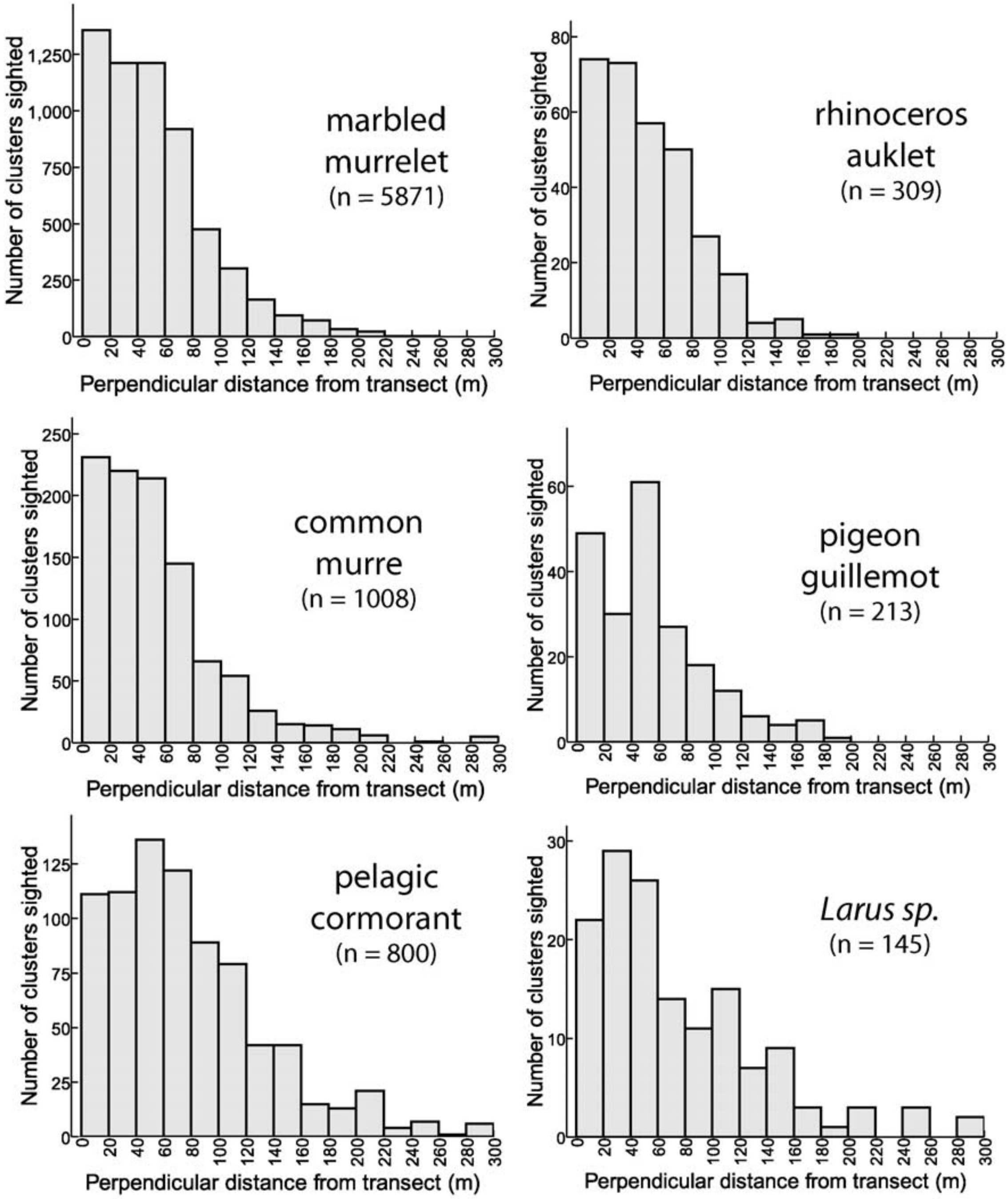


Figure 2.1 - Histograms displaying detection distance of seabird clusters (groups/flocks) sighted on the water during vessel-based transects, binned in 20 m intervals.

Cluster-size bias

Based on distance vs. cluster-size correlations, pigeon guillemots and pelagic cormorants showed no evidence of cluster-size bias, and common murres and gulls showed no bias when data were truncated at 150 m or less (Table 2.1). Marbled murrelets and rhinoceros auklets showed extensive cluster-size bias at most truncation distances. This bias was only eliminated for data less than 50 m from the boat. Moreover, Akaike weights showed cluster size as an important covariate for auklets, but less so for murrelets (Table 2.2). Therefore, density estimates for murrelets and auklets must take cluster-size bias into consideration when calculating *E(s)*.

Table 2.1 - Evaluation of cluster-size bias when sighting seabird clusters/groups from line-transect surveys. Effects of data truncation on mean cluster size (CS). Pearson's r correlations test the correlation between cluster size and cluster distance from transect line for data truncated at different distances.

	Truncation Distance			
	300m	**150m**	**100m**	**50m**
Marbled murrelet				
n	5871	5738	5369	3781
mean CS ± SE	2.09 ± 0.04	2.05 ± 0.04	1.99 ± 0.03	1.83 ± 0.04
Pearson's r	0.139*	0.103**	0.119**	0.028
Rhinoceros auklet				
n	309	307	291	204
mean CS ± SE	1.69 ± 0.09	1.66 ± 0.09	1.63 ± 0.08	1.46 ± 0.07
Pearson's r	0.251**	0.179**	0.148*	-0.022
Pigeon guillemot				
n	213	207	192	140
mean CS ± SE	1.22 ± 0.04	1.22 ± 0.04	1.22 ± 0.04	1.17 ± 0.03
Pearson's r	0.088	0.112	0.178	0.068
Common murre				
n	1008	971	917	665
mean CS ± SE	2.13 ± 0.21	1.68 ± 0.11	1.64 ± 0.11	1.51 ± 0.10
Pearson's r	0.342**	0.075	0.054	0.042
Pelagic cormorant				
n	800	733	630	359
mean CS ± SE	1.23 ± 0.03	1.20 ± 0.03	1.18 ± 0.03	1.17 ± 0.04
Pearson's r	0.074	0.002	-0.037	-0.113
***Larus* sp.**				
n	145	133	111	77
mean CS ± SE	19.88 ± 4.25	15.71 ± 3.29	16.79 ± 3.81	16.08 ± 4.06
Pearson's r	0.229*	0.032	0.111	0.1

Significance of Pearson's r with Bonferroni adjustments for multiple comparisons within species: *<0.05 and **<0.01

Model selection and covariates

Multi-covariate distance sampling (MCDS) tested the influence of potential covariates on the fit of detection functions. Akaike weights for individual covariates (Table 2.2) found observer as the most important covariate for three species (murrelets, cormorants, guillemots), sea state the most important for common murres, and cluster size the most important for rhinoceros auklets. No single covariate appeared to be important for gulls. Year was also an important covariate for murrelets and cormorants but not murres. Table 2.3 summarizes fit of models comparing models with and without covariates. For three species (murres, auklets, gulls) the best fit model contained no covariates. Observer was included as a covariate in the best fit model for all other species and year was included in the best model for murrelets and cormorants.

Parameter estimates

I developed parameter estimates of P_a, proportion of clusters detected, for each species and significant covariates identified in Tables 2.2 and 2.3. Table 2.4 provides parameter estimates for data truncation at 150 and 100 m, i.e. 300 and 200 m wide transects respectively. For 300 m wide transects, P_a estimates suggest that generally between 40 and 60% of alcid groups are detected, apparently unrelated to size or conspicuousness of the species. For the largest species, 68% of cormorants were detected but surprisingly only 44% of gulls were detected. P_a estimates varied considerably among years (murrelets, 0.393 to 0.587; cormorants, 0.605 to 0.837) and observers (murrelets, 0.228 to 0.625; cormorants, 0.578 to 0.915; guillemots, 0.336 to 0.817), but less so among sea states (murres, 0.419 to 0.449). For 200 m wide transects, P_a estimates increased by about 0.1 for most species but as much as 0.2 for cormorants and guillemots.

Table 2.2 - Comparison of Akaike weights (AIC_cw, see 'Data Analysis' for details) for individual covariates tested in multivariate detection function models with all possible combinations of detection function perpendicular distance (x) and 1 or 2 additional covariates. Model weights are given for models in which each covariate or set of covariates was tested (brackets indicate covariates in the model). Sums indicate comparative explanatory power of each covariate compared to the others for each species. All combinations of covariates were evaluated with hazard-rate models with no adjustment terms. n = number of clusters/groups evaluated.

Species	Covariate							
	Year (yr)		Observer (obs)		Sea State (ss)		Cluster Size (cs)	
Marbled murrelet	(yr)	0.000	(obs)	0.000	(ss)	0.000	(cs)	0.000
(n = 5378)	(yr, obs)	0.746	(obs, yr)	0.746	(ss, yr)	0.000	(cs, yr)	0.000
	(yr, ss)	0.000	(obs, ss)	0.000	(ss, obs)	0.000	(cs, obs)	0.254
	(yr, cs)	0.000	(obs, cs)	0.254	(ss, cs)	0.000	(cs, ss)	0.000
	Sum	0.746		1.000		0.000		0.254
Common murre	(yr)	0.016	(obs)	0.001	(ss)	0.251	(cs)	0.007
(n = 941)	(yr, obs)	0.001	(obs, yr)	0.001	(ss, yr)	0.005	(cs, yr)	0.006
	(yr, ss)	0.005	(obs, ss)	0.000	(ss, obs)	0.000	(cs, obs)	0.000
	(yr, cs)	0.002	(obs, cs)	0.000	(ss, cs)	0.002	(cs, ss)	0.002
	Sum	0.023		0.002		0.258		0.015
Pelagic cormorant	(yr)	0.000	(obs)	0.033	(ss)	0.000	(cs)	0.000
(n = 723)	(yr, obs)	0.955	(obs, yr)	0.955	(ss, yr)	0.000	(cs, yr)	0.000
	(yr, ss)	0.000	(obs, ss)	0.002	(ss, obs)	0.002	(cs, obs)	0.010
	(yr, cs)	0.000	(obs, cs)	0.010	(ss, cs)	0.000	(cs, ss)	0.000
	Sum	0.955		1.000		0.002		0.010
Rhinoceros auklet		n/a	(obs)	0.002	(ss)	0.066	(cs)	0.077
(n = 307)		n/a	(obs, ss)	0.001	(ss, obs)	0.001	(cs, obs)	0.001
		n/a	(obs, cs)	0.001	(ss, cs)	0.026	(cs, ss)	0.026
	Sum			0.003		0.093		0.104
Pigeon guillemot		n/a	(obs)	0.497	(ss)	0.000	(cs)	0.000
(n = 202)		n/a	(obs, ss)	0.199	(ss, obs)	0.199	(cs, obs)	0.304
		n/a	(obs, cs)	0.304	(ss, cs)	0.000	(cs, ss)	0.000
	Sum			1.000		0.199		0.304
Larus sp.		n/a	(obs)	0.111	(ss)	0.113	(cs)	0.113
(n = 129)		n/a	(obs, ss)	0.040	(ss, obs)	0.040	(cs, obs)	0.046
		n/a	(obs, cs)	0.046	(ss, cs)	0.039	(cs, ss)	0.039
	Sum			0.197		0.192		0.198

Table 2.3 - Summary of detection function model fits with AICc model selection (see 'Data Analysis' for descriptions of Akaike's statistics) and estimated proportion of bird clusters detected *Pa* along the transect. Hazard-rate models were used testing models with all combinations of perpendicular distance (x) and up to 2 additional covariates. Only models with $AIC_c w$ above 0.005 are shown in comparison to model with no covariates (x). K = total number of parameters in the model. yr: year; obs: observer; ss: sea state; cs: cluster size.

Species	Model	K	AIC_c	ΔAIC_c	$AIC_c w$	P_a
Marbled murrelet						
	(x, obs, yr)	9	19039.66	0.00	0.746	0.445
	(x, obs, cs)	8	19041.81	2.15	0.254	0.439
	(x)	2	19554.21	514.55	0.000	0.469
Common murre						
	(x)	2	3152.09	0.00	0.711	0.451
	(x, ss)	3	3154.17	2.08	0.251	0.445
	(x, yr)	3	3159.74	7.65	0.016	0.461
	(x, cs)	3	3161.48	9.39	0.007	0.463
	(x, cs, yr)	4	3161.53	9.45	0.006	0.461
	(x, ss, yr)	4	3161.96	9.87	0.005	0.461
Pelagic cormorant						
	(x, obs, yr)	7	2766.26	0.00	0.955	0.694
	(x, obs)	6	2773.02	6.76	0.033	0.665
	(x, obs, cs)	7	2775.31	9.04	0.010	0.669
	(x)	2	2801.72	35.45	0.000	0.677
Rhinoceros auklet						
	(x)	2	1040.71	0.00	0.828	0.425
	(x, cs)	3	1045.46	4.75	0.077	0.472
	(x, ss)	3	1045.76	5.05	0.066	0.472
	(x, ss, cs)	4	1047.60	6.89	0.026	0.473
Pigeon guillemot						
	(x, obs)	6	677.97	0.00	0.497	0.468
	(x, obs, cs)	7	678.96	0.98	0.304	0.472
	(x, obs, ss)	7	679.80	1.83	0.199	0.480
	(x)	2	709.88	31.91	0.000	0.513
Larus sp.						
	(x)	2	498.86	0.00	0.539	0.442
	(x, ss)	3	501.99	3.12	0.113	0.544
	(x, cs)	3	501.99	3.13	0.113	0.542
	(x, obs)	6	502.03	3.17	0.111	0.530
	(x, obs, cs)	7	503.79	4.93	0.046	0.530
	(x, obs, ss)	7	504.06	5.19	0.040	0.531
	(x, ss, cs)	4	504.10	5.24	0.039	0.545

Table 2.4 - Parameter estimates for detectability of seabirds surveyed using line transects. *Pa* estimates from program DISTANCE indicate the proportion of birds on the water detected for 150 and 100 m data truncation which corresponds to 300 and 200 m wide strip transects respectively. Parameter estimates are provided only for covariates which were identified as important predictors (Table 2.2) and included in best fit models (Table 2.3). Density estimates are not provided for individual observers or sea states because these values are additive for higher level stratum (year or global model). Global model parameters are calculated from the weighted means of year parameters.

	150 m Data Truncation				100 m Data Truncation			
Species and Covariate/Stratum	**No. of Clusters**	**P_a**	**95% CI**	**Density Estimate (birds km^{-2})**	**No. of Clusters**	**P_a**	**95% CI**	**Density Estimate (birds km^{-2})**
Marbled murrelet								
Global	5738	0.469	0.457 - 0.482	49.86	5369	0.549	0.523 - 0.577	57.12
2004	479	0.442	0.346 - 0.564	68.00	394	0.539	0.411 - 0.707	66.56
Obs 1	178	0.514	0.360 - 0.735		145	0.628	0.430 - 0.917	
Obs 2	301	0.397	0.284 - 0.555		249	0.482	0.327 - 0.710	
2005	2288	0.393	0.381 - 0.404	47.98	2270	0.548	0.527 - 0.570	50.49
Obs 1	809	0.439	0.417 - 0.461		799	0.628	0.593 - 0.665	
Obs 3	494	0.228	0.209 - 0.250		494	0.330	0.297 - 0.368	
Obs 4	985	0.417	0.417 - 0.461		977	0.616	0.588 - 0.644	
2006	2971	0.587	0.568 - 0.607	48.05	2705	0.654	0.601 - 0.711	55.47
Obs 1	1145	0.535	0.506 - 0.566		1069	0.570	0.489 - 0.666	
Obs 2	52	0.285	0.100 - 0.813		45	0.375	0.116 - 1.000	
Obs 5	754	0.603	0.568 - 0.640		685	0.810	0.757 - 0.866	
Obs 6	1020	0.625	0.591 - 0.661		906	0.714	0.624 - 0.816	
Common murre								
Global	941	0.451	0.422 - 0.483	7.37	891	0.537	0.478 - 0.604	8.54
Sea State 0-1	626	0.449	0.416 - 0.485		593	0.581	0.522 - 0.646	
Sea State 2-3	315	0.419	0.359 - 0.490		298	0.501	0.357 - 0.704	
Pelagic cormorant								
Global	723	0.677	0.630 - 0.728	3.07	621	0.879	0.826 - 0.935	3.15
2005	441	0.605	0.563 - 0.651	4.20	409	0.849	0.793 - 0.909	4.22
Obs 1	157	0.588	0.485 - 0.714		138	0.831	0.736 - 0.938	
Obs 3	105	0.578	0.501 - 0.666		99	0.817	0.696 - 0.960	
Obs 4	179	0.614	0.566 - 0.665		172	0.890	0.801 - 0.988	
2006	282	0.837	0.720 - 0.973	2.10	212	0.946	0.832 - 1.000	2.14
Obs 1	133	0.656	0.459 - 0.937		107	0.831	0.591 - 1.000	
Obs 5	55	0.736	0.438 - 1.000		40	0.857	0.695 - 1.000	
Obs 6	94	0.915	0.811 - 1.000		65	1.000	0.884 - 1.000	
Rhinoceros auklet								
Global	307	0.425	0.369 - 0.489	2.40	291	0.516	0.401 - 0.665	2.75
Pigeon guillemot								
Global	202	0.513	0.447 - 0.589	1.08	187	0.707	0.611 - 0.819	1.08
Obs 1	92	0.478	0.392 - 0.583		87	0.673	0.544 - 0.833	
Obs 3	19	0.336	0.263 - 0.430		19	0.505	0.394 - 0.646	
Obs 4	34	0.407	0.336 - 0.493		34	0.610	0.503 - 0.740	
Obs 5	13	0.411	0.138 - 1.000		11	0.592	0.306 - 1.000	
Obs 6	44	0.817	0.686 - 0.974		36	1.000	0.975 - 1.000	
Larus sp.								
Global	129	0.442	0.277 - 0.705	10.90	108	0.564	0.345 - 0.921	11.42

Sea state effects on g(0)

Comparison of cluster encounter rates of birds near the transect line can provide some indication of sea state effects on *g*(0). From 1,429 km of transects (54 days), 22% (n = 29 days), 43% (n = 44), 29% (n = 32) and 6% (n = 14) were conducted during sea states 0, 1, 2, and 3 respectively. Sea state effects were variable among species (Fig. 2.2). Encounter rates did not vary among sea states for common murres (ANOVA: $F_{3,115}$ = 0.679, p = 0.567) or pelagic cormorants ($F_{3,115}$ = 0.125, p = 0.945). Sea state did affect encounter rates for marbled murrelets ($F_{3,115}$ = 2.716, p = 0.048), with significant post-hoc tests (Tukey's HSD) showing higher encounter rates during sea state 0 (mean 3.93 ± 0.59 SE clusters km^{-1}) compared to sea state 2 (2.22 ± 0.32, p = 0.036) but not sea states 1 (2.65 ± 0.33, p = 0.132) or 3 (3.03 ± 0.70, p = 0.671). This suggests the potential of g(0) < 1 for murrelets, but not murres of cormorants, when sea state increases.

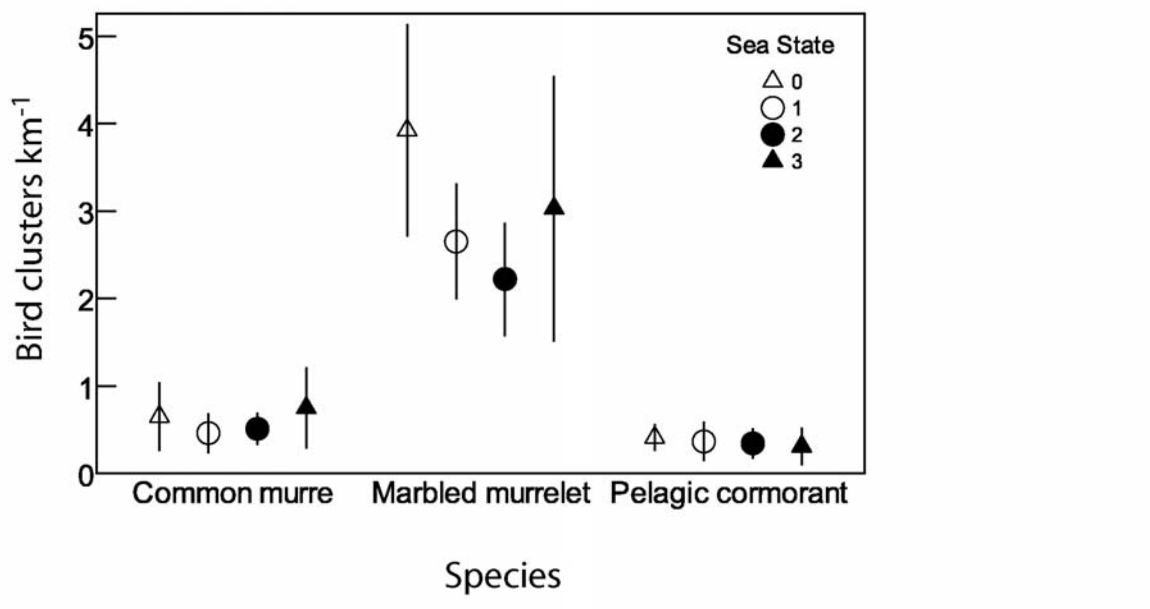


Figure 2.2 - Effects of Beaufort sea state on mean encounter rate of bird clusters along a transect line. Includes only bird clusters near the transect line (≤ 60 m for murres and murrelets; ≤ 80 m for cormorants). Bars indicate 95% CI.

DISCUSSION

Detection of seabirds

Reliable assessment of animal densities is an integral part of wildlife research (Thompson 2002, Braun 2005). Accurate density estimates allow for robust population estimations which is essential for the conservations and management of threatened marine species (Slooten et al. 2004, Gomez de Segura et al. 2006, Slooten et al. 2006). Although it has long been recognized that the detectability of seabirds decreases with distance from a transect line (Dixon 1977), few studies have tried to quantify this. Previous studies have developed methods to account for detectability of birds in flight (Spear et al. 2004, Hyrenbach et al. 2007a). This study provides a comprehensive analysis of detectability of birds on the water.

Our results suggest that even within 150 m of a boat in relatively calm conditions just 20-80% of bird groups on the water may be detected, depending on the species, year and/or observer. Marbled murrelets were the smallest species evaluated and estimates of detection probability among years ranged from 39-59% for 150 m truncation and 54-65% with 100 m truncation. Becker et al. (1997) reported 49-66 m effective strip widths from 160 m truncated data which convert to 31-41% detection. With 120 m data truncation, Peery et al. (2006) had detection probabilities ranging from 44-55% (calculated from $f(0)$ estimates in their appendix Table 2.2). (Raphael et al. 2007) had detection probabilities of 55% (175 m truncation; calculated from $f(0)$ estimates in their appendix 4). Therefore, across multiple studies, marbled murrelet detection probabilities appear to vary considerably between 40-65% partially depending on transect width.

Conspicuousness to human vision can affect the detection and counting of animals along transects (Ryan & Cooper 1989, Spear et al. 2004). Marine mammal surveys frequently incorporate correction factors for different species (Forney & Barlow 1998), but there are few published data on detection probabilities for seabirds other than marbled murrelets. Hyrenbach et al. (2001) used distance sampling to count shearwater carcasses for mortality estimates and found effective strip widths of 42-55 m which are comparable to estimates for live murrelets (Becker et al. 1997). Although several studies have recommended the use of distance sampling for seabird transects (Hyrenbach et al. 2001, Camphuysen et al. 2004, Huettmann & Diamond 2006), I found no published detection functions for other seabird species. My data demonstrate that detectability varied among species though most alcids showed similar detection functions. Pelagic cormorants were detectable over much greater distances likely owing to their size and height. Different analytical methods have also shown species-specific differences in seabird detectability for different strip-transect widths (Hyrenbach et al. 2007a).

Effects of covariates

Systematic biases in counting procedures can be an important source of error in estimating bird abundance (Thompson 2002) but inclusion of covariates can minimize the heterogeneity in detection probabilities (Marques & Buckland 2003). In this study, I assessed variability in detection functions with the inclusion several covariates: year, observer, sea state and cluster size.

Year was an important covariate for murrelets and cormorants but not murres. Likewise, other studies incorporated year effects by stratifying data among years population estimates (Becker et al. 1997, Peery et al. 2004, 2006). The significance of year as a covariate could be explained by annual changes in bird abundance and distribution in the study area. Changing distribution of prey from one year to the next can significantly alter the distribution and aggregation of seabirds (Davoren 2000). In years when seabirds are more dispersed and in smaller groups, they may be harder to detect and thus the detection functions may differ. The detectability of birds during transects may decrease as a function of decreasing bird density (Ostrand et al. 1998b). In this study, murrelet and cormorant densities varied annually (Table 2.4) which may explain the significance of year as a covariate for these species.

Differences among observers' abilities to detect birds in vessel-based seabird surveys may sometimes be large (van der Meer & Camphuysen 1996). Observer biases may result from differences in observer's visual acuity, attentiveness and experience (Ralph & Scott 1981, Laake et al. 1997). Observers may even show differences in detecting birds on the transect line, $g(0)$, where birds should be easiest to detect (Evans

Mack et al. 2002). Observer was an important covariate in other murrelet studies (Peery et al. 2006) and for several species in this study. These biases appear to be unrelated to experience in this study since *Pa* estimates for inexperienced observers (Obs 3, 4, 5) overlapped with those of experienced observers (3+ yrs experience: Obs 1, 2, 6). Rather, I suspect that observer biases may have resulted from general over- or under-estimation of distances by particular individuals (Obs 3, consistently lowest *Pa* estimates; Obs 6 consistently highest *Pa* estimates). Thus despite continual training during the field season, observer accuracy in estimating distances may vary. I encourage others to include testing as well as training to evaluate accuracy.

Winds and associated waves can affect observers' abilities to detect animals at sea. This may be particularly true for smaller cryptic species such as marine birds (Evans Mack et al. 2002, Peery et al. 2006) or turtles (Beavers & Ramsey 1998). Surprisingly sea state was not included in the best models for any species in this study. Sea state was the most important covariate for common murres (Table 2.2) but the magnitude of this effect was marginal on estimates of *Pa*: 0.449 sea state 0-1, and 0.419 sea state 2-3. The lack of significance for sea state as a covariate simply means that the proportion of birds detected vs. not detected, P_a, does not change. This suggests that even when fewer birds overall may be detected in poor viewing (e.g. 10 birds) vs. good viewing conditions (100 birds), the proportion of birds detected near the transect line vs. farther from the transect line could remain the same (9:1 during poor conditions vs. 90:10 during good viewing conditions). Thus P_a may remain unaffected by sea state, but $g(0)$ can still decrease.

This study was not designed explicitly to provide estimates of $g(0)$. Alternatively comparisons of bird densities near the transect line provides some evidence of how $g(0)$ may vary with sea state. Densities of murrelets encountered on transects decreased for sea states 2-3 compared to sea states 0-1 in California (Becker et al. 1997). Similarly, for murrelets, I observed decreased encounter rates in sea states greater than 0, though there was no statistical difference between the calmest conditions (0) and the roughest (3), potentially due to small sample sizes for observations in sea-state 3. Increased sea states may affect the behaviour of birds making them less detectable: sea state affects the diving behaviour of murrelets (Jodice & Collopy 1999), and perhaps the proportion of time spent at sea for species that frequently loaf or roost on land (cormorants, gulls, guillemots). Other factors, such as observer experience or animal group size, may also can cause *g*(0) < 1 (Laake et al. 1997, Evans Mack et al. 2002). More effort should be placed on validating this critical assumptions of *g(0)* = 1 for seabirds. In this study surveys sampled over a relatively small range of sea-states (Beaufort scale ≤3) and it is likely that sea state would greatly affect detectability in rougher seas.

Implications of parameter estimates

Estimates of P_a (Table 2.4) are potentially useful as correction factors for fixed-width strip transects. However, I do not recommend that they be used as such because these estimates varied considerably among years and observers and therefore are not directly transferable to other studies. Moreover, these surveys were conducted from a slow-moving small boat and detectability will likely vary with boat size (observer height above sea) and speed. Boat size, speed and type may also affect the extent to which birds are repelled (or attracted) and the distance at which this might happen (Hyrenbach et al. 2001, 2007a). Furthermore, correction factors are not directly applicable to all boat transect surveys because environmental factors will differ among regions and habitat types. I tested only effects of sea state, but wind direction, sun glare or water clarity are also known to affect detectability (Hyrenbach et al. 2001).

Parameter estimates for 150 m truncation (300 m strip) are also not applicable to surveys that follow Tasker et al. (1984) protocols for single-sided 300 m strip transects because birds are typically recorded only on one side of the vessel. Birds, such as alcids, that spend a considerable amount of time on the water (Tremblay et al. 2003) could be substantially underestimated with single-sided 300 m wide transects. Nevertheless, 300 m or wider single-sided strips are likely still suitable for detecting flying birds (Hyrenbach et al. 2007a).

Marine mammals researchers routinely use distance-sampling when estimating densities, abundance and population size (Forcada et al. 2004, Slooten et al. 2006). I recognize three main reasons why seabird biologists have been reluctant to incorporate distance sampling in survey protocols. First, there are many long-term seabird survey programs that have used fixed-width transects (e.g. Pyle 2007). Second, distance sampling techniques are more readily applicable to birds on the water than to birds in flight (alternative techniques may be more appropriate to assess birds in flight; Spear et al. 2004, Hyrenbach et al. 2007a). Third, distance sampling is effort intensive and seabirds are frequently encountered in high densities making recording of distances to individual birds/flocks difficult. Hyrenbach et al. (2001) commented that distance sampling “should be employed only when seabirds are sparse and non-mobile, and enough observers are available to estimate the perpendicular ranges to sightings and to monitor birds directly on the track”. Other experienced observers have claimed that true distance sampling techniques are not practical to record seabirds at sea. As a compromise, some seabird programs are using grouped (binned) distances rather than ungrouped (exact) distances for bird detections (Komdeur et al. 1992, Camphuysen et al. 2004).

While I generally agree with these sentiments, this study shows clearly that standard strip-transect methods underestimate densities of birds on the water. Although distance sampling may not be feasible in all studies, I recommend that studies at least conduct a subset of their surveys using distance-sampling methods (Pyle 2007), or assess strip-transect biases with alternative methods (see Hyrenbach et al. 2007a). Implementing distance sampling in the field still allows one to analyze the data as strip transects (of any desired width), but the opposite is not true. The probability of detecting seabirds will vary with weather, observer experience and fatigue, bird behaviour, and among species. Moreover, correction factors for these biases will vary among survey platforms depending on boat speed and observer height above sea level. Studies should develop correction factors for individual survey platforms and regions which will help increase the precision of population estimates and make survey results comparable among study areas. This is crucial for merging data sets and findings globally. Surveys that do not account for detectability issues for density estimation can be biased, which may interfere with population assessment (Norvell et al. 2003). Studies analyzing population trends or comparing the distributions of birds relative to bio-physical landscapes could, arguably, work adequately with relative abundance indices (strip transects) rather than distance-sampling density estimates. Nevertheless, the use of distance sampling to correct for detectability issues should increase the accuracy and precision of all transect-based studies of seabirds.

Chapter 3 - Coarse- and fine-scale habitat selection as a mechanism for coexistence among pursuit diving seabirds

ABSTRACT

Many pursuit diving seabirds prey on similar forage fish and overlap spatially and temporally in their at-sea distributions. It is unclear how these species coexist in competition for resources and whether they exhibit niche partitioning in areas of overlapping distribution. I studied the coarse- (<100 km) and fine-scale (100's m to 5 km habitat selection of five sympatric piscivorous seabirds in nearshore waters off southwestern Vancouver Island, British Columbia: four Alcidae - marbled murrelet (*Brachyramphus marmoratus*), rhinoceros auklet (*Cerorhinca monocerata*), common murre (*Uria aalge*), pigeon guillemot (*Cepphus columba*), and one cormorant - pelagic cormorant (*Phalacrocorax pelagicus*). Bird densities and distributions were collected in 1-minute segments (~170 to 300 m) via vessel-based transect surveys during five years in two decades (1995-1996 and 2004-2006). Bird data were linked to environmental variables that included depth, slope, seafloor substrates, shoreline substrates, sea-surface temperature and salinity, proximity to nesting habitat and prey availability. I used canonical correspondence analysis (CCA), discriminant function analysis (DFA), and classification and regression trees (CART) to model species-habitat associations. I found inter-specific and inter-annual differences in used and preferred habitats suggesting various ways that pursuit diving seabirds may be partitioning habitat in this system. Murres and auklets showed similar habitat preferences often relating to water temperature and salinity. Guillemot and cormorant habitat selection was tied to seafloor characteristics such as depth, slope, and substrates. Murrelets showed a wide range in habitat preferences that frequently included associations with substrates that likely linked forage fish to seabirds in the study area. Prey availability was not an important factor in habitat selection for seabirds but models of prey-habitat associations suggested inter-annual variability in the distribution of prey which likely reflects the high inter-annual variability in species-habitat relationships. The results support habitat-selection as a mechanism for niche partitioning among these five species. Although murrelets and murres generally differed in their habitat use, habitat-selection models (use vs. availability) and similarity in diurnal foraging activity patterns suggest a high potential for competition between these two species. Other species showed distinct spatial and temporal partitioning in habitat use particularly along gradients of depth and sea-surface temperature/salinity. Thus environmental variability is a key factor structuring habitat use and coexistence in this community of piscivorous seabirds.

INTRODUCTION

A central goal in community ecology is to explain the patterns of species distribution and abundance across the landscape (Morin 1999). At a finer scale, community ecologists seek to understand the mechanisms that maintain biological diversity and species coexistence within local communities. The competitive exclusion principle, suggests that two species with same niche should not coexist in the same community (Hardin 1960, Levin 1970). Yet nearly everywhere in nature, similar species co-occur violating this principle (Hutchinson 1961). Therefore, mechanisms must exist which promote diversity and allow species to coexist.

Hutchinson's (1961) "paradox of the plankton" pondered possible mechanisms promoting the coexistence of similar species limited by the same resources. The paradox has since been explained by disruptive influences that prevent competitive exclusion (e.g. patchiness, seasonality, predation, storms) or specialization and niche partitioning which reduces competition (Connell 1978, Hayward & McGowan 1979, Roy & Chattopadhyay 2007). Although the role of habitat selection is not new to investigations on species coexistence (MacArthur & Levins 1964, Levins & Culver 1971, Rosenzweig 1973, 1981), it remains a pervasive theme in recent studies across a wide range of terrestrial taxa (Cavender-Bares et al. 2004, Alvarez et al. 2006, Apps et al. 2006, Wasserberg et al. 2007). In marine ecosystems, much of the focus by community ecologists has been on zooplankton (Roy & Chattopadhyay 2007), benthic invertebrates and coastal systems such as inter-tidal communities and coral reef systems (Bertness et al. 2001). There is a noticeable gap in our knowledge of how habitat selection facilitates coexistence for larger marine vertebrates (but see recent examples for cetaceans: Parra 2006, MacLeod et al. 2007, Oviedo 2007).

Terrestrial and marine ecosystem processes are governed at dramatically different spatial and temporal scales: marine systems change more rapidly over comparatively larger spatial scales (Steele 1991). As a result, the habitat use and selection by large marine vertebrates can be dynamic, occurring over vast areas, and thus has been difficult to quantify. Seabirds are among the most conspicuous marine vertebrates and the co-occurrence of similar species prompted many early investigations of partitioning in marine habitats. At global scales, morphological adaptations and foraging tactics are strong determinants of marine bird assemblages (Ashmole 1971, Ainley 1977). At mega-scales (1000’s of km, Hunt & Schneider 1987) oceanic conditions create distinct species assemblages associated with particular water masses (Wahl et al. 1989, Ballance et al. 1997, Smith & Hyrenbach 2003, Hyrenbach et al. 2007). At meso-scales (100’s km) we start to see species-specific associations with marine environments (Weimerskirch et al. 1988, Hyrenbach et al. 2002). Yet at coarse- (<100 km) and fine-scales (100’s m), patterns and processes of coexistence between closely related species have been more difficult to explain. Marine birds are typically responding to physical features of the environment at larger scales, but coarse- and fine-scale patterns are more likely controlled by social interactions and foraging behaviours (Hunt & Schneider 1987). It is at these smaller scales that we are able to investigate mechanistic understandings of ecological patterns (Wiens 1989).

The Alcidae are a taxonomically diverse family of seabirds that show considerable overlap in coarse- and fine-scale habitat use. Some of the first investigations into resource partitioning by seabirds focused on alcids (Bédard 1969, Cody 1973, Bédard 1976). Cody’s (1973) basic assertion was that competing species segregated themselves via zonation of foraging distances from colonies. This simplistic view was refuted by Bédard (1976) who suggested that patterns of feeding distributions are much more complex and likely related to multiple environmental variables. Indeed, coexistence within the alcids may be facilitated by complex marine environments that create multiple niche dimensions (Haney & Schauer 1994), yet these distinctions are more readily found between, but not within, foraging guilds (piscivores vs. planktivores).

This study investigates habitat selection as a mechanism for niche partitioning within a foraging guild of coexisting seabirds. The fundamental niche refers to the resources and habitat that a population is capable of using under ideal circumstances. In reality, biological constraints, such as competition, predation, or resource availability, can force animals to use a subset of their niche space, thus resulting in a realized niche (Molles 1999). The realized niche may be a result of *habitat selection* which is defined as the behavioural responses by individuals, resulting in the disproportional (i.e. non-random) use of habitats which influences their survival and fitness (Hutto 1985, Jones 2001). Habitat *use* includes the habitat components occupied by organisms to meet life needs such as feeding, reproduction, rearing of young (Jones 2001). Jones (2001) states that “habitat-use patterns are the end result of habitat-selection processes”. Habitat selection is most often measured by comparing *used* vs. *available* habitats (Jones 2001) and is invariably referred to as *habitat preferences*. In this study I model species-habitat relationships to compare both *used* and *preferred* habitats among five sympatric seabirds to investigate niche partitioning.

Species-habitat relationships can be modeled in many ways (Guisan & Zimmermann 2000, Scott et al. 2002, Redfern et al. 2006) and the most appropriate approach will be dependent on the goals of the study and the purpose of the model (e.g. descriptive, predictive or hypothesis testing). Thus it is a dynamic and exciting time for the field of species-habitat modeling and some suggest we are entering a paradigm shift in our approach to species-habitat modeling, focusing on *constraints* rather than correlates, thus emphasizing factors as limiting agents to species abundance or distribution (Huston 2002, O'Connor 2002). This shift parallels a distinction made by Breiman (2001) regarding two modeling cultures: data modeling vs. algorithmic modeling. The first assumes that data can be fit to statistical models (e.g. linear/logistic regressions and hypothesis testing) while that latter treats the data mechanism as unknown and uses algorithmic models to describe data patterns (e.g. decision trees). The algorithmic approach is rapidly gaining attention in the field of wildlife biology (Hochachka et al. 2007) and often outperforms traditional statistical/hypothesis testing techniques (Segurado & Araujo 2004, Yen et al. 2004a). While data modeling has been fundamental towards understanding species-habitat relationships (e.g. resource selection functions, Manly et al. 2002), algorithmic techniques are providing new perspectives on species-habitat modeling towards investigations of coexistence and niche partitioning (MacLeod *et al.* 2007).

In this study I assess the habitat use and habitat preferences of five sympatric species of primarily piscivorous seabirds. The objectives are (1) to compare traditional statistical modeling approaches used by community ecologists with algorithmic modeling approaches, (2) to compare habitat use and preferences at coarse- and fine-scales, and (3) to examine the role of habitat-selection in the coexistence of pursuit diving seabirds. Where species show considerable overlap in habitat use or preference (i.e. lack of spatial partitioning), I also test the potential role of temporal partitioning (Carothers & Jaksić 1984) in habitat use by way of differential diurnal activity budgets.

METHODS

Study area and species

Five seabird species were studied along the southwestern coast of Vancouver Island, British Columbia, Canada (Fig. 3.1). The study area was located in the West Coast Trail unit of Pacific Rim National Park. This is a 65-km stretch of coast exposed to the Pacific Ocean, which supports some of the highest at-sea densities of marbled murrelets (*Brachyramphus marmoratus*) anywhere in British Columbia (Burger 2002, Burger et al. 2008). The murrelets nest in the interior old-growth coniferous forests adjacent to the study area (Burger & Bahn 2004). The park also contains several breeding colonies of other species (details below).

The five study species, ordered from smallest to largest, included marbled murrelet, pigeon guillemot (*Cepphus columba*), rhinoceros auklet (*Cerorhinca monocerata*), common murre (*Uria aalge*), and pelagic cormorant (*Phalacrocorax pelagicus*). Table 3.1 summarizes some of the main characteristics of their foraging behaviour, prey types and nesting strategies (Vermeer et al. 1987, Ewins 1993, Gaston & Dechesne 1996, Hobson 1997, Nelson 1997, Gaston & Jones 1998, Ainley et al. 2002). All species overlap in distribution along the northeastern Pacific from California to

Alaska. All are capable of diving to depths of 40 m (Burger 1991), which is the maximum depth of waters surveyed in this study, though murres are known to forage in water much deeper.

Key differences among species include one foot-propelled diver (pelagic cormorant) – the remainder are wing-propelled divers, one non-colonial nester (marbled murrelet), and a continuum of foraging assemblages from solitary foragers to mixed-species flocks (murrelets, guillemots, cormorants, auklets, murres). All five species show considerable overlap in trophic feeding level throughout the northeastern Pacific (Hobson et al. 1994), and some show considerable overlap in specific prey items (Burkett 1995, Lance & Thompson 2005). Although all species are known to take schooling fish such as sand lance (*Ammodytes hexapterus*) and juvenile herring (*Clupea harengus*), cormorants and pigeon guillemots typically feed at or near the seafloor on epibenthic fish and invertebrates (Ewins 1993, Hobson 1997). Benthic vs. epipelagic foraging tactics are likely to play a key role in species specific habitat associations.

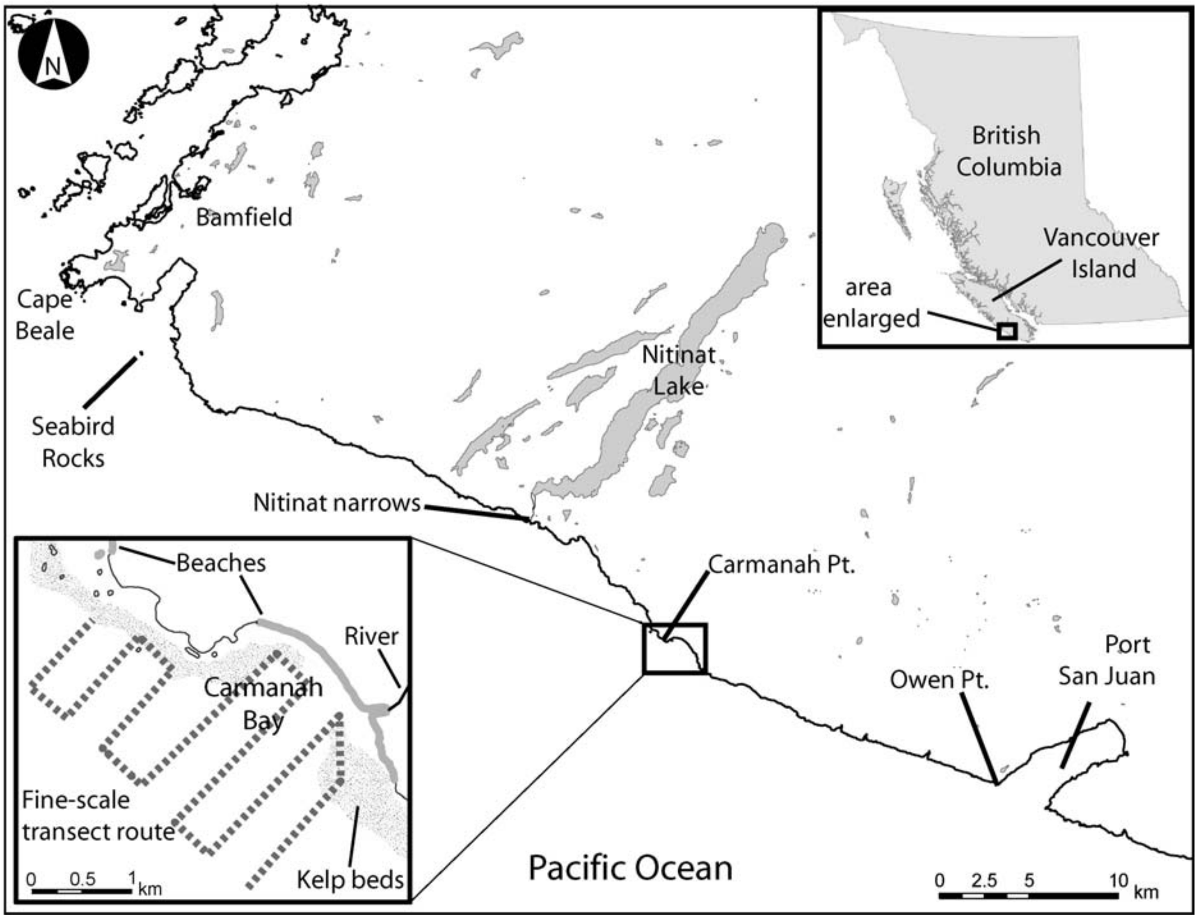


Figure 3.1 - Southwestern Vancouver Island study area. Coarse-scale transects were conducted along the length of the coastline between Cape Beale and Port San Juan. Fine-scale transects were conducted in the vicinity of Carmanah Bay (inset).

Table 3.1 - Summary of foraging methods, diet and nesting strategies for five study species.

Species	Weight (g)	Foraging method	Prey	Nesting	References
Marbled murrelet (*Brachyramphus marmoratus*)	190-270	mostly solitary or in pairs, wing-propelled diver, mid-water	opportunistic rather than specialist, schooling fish (sand lance, herring), euphasiids, others	non-colonial, old-growth forest specialist	a,b,c,d
Pigeon guillemot (*Cepphus columba*)	450-550	solitary or small groups, wing-propelled, benthic foraging	primarily epibenthic prey (gunels/sculpins), secondarily schooling fish (sand lance)	semi-colonial, small dispersed colonies, crevices in cliffs or rocky islands	a,b,e
Rhinoceros auklet (*Cerorhinca monocerata*)	500-600	flock foraging, wing-propelled, mid-water	primarily schooling fish (sand lance/herring), also euphasiids	colonial, islands	a,b,f,g,h
Common murre (*Uria aalge)*	800-1125	flock foraging, wing-propelled, mid-water	primarily schooling fish (sand lance/herring), also euphasiids	colonial, islands	a,b,h,i
Pelagic cormorant (*Phalacrocorax pelagicus*)	1500-2000	typically solitary but also joins mixed-species flocks, foot-propelled, benthic foraging	primarily epibenthic prey (fish and invertebrates), also schooling fish (sand lance)	colonial, caves and cliffs, often switch sites between years	j

a, Vermeer et al. (1987); b, Gaston & Jones (1998); c, Nelson (1997); d, Burkett (1995); e, Ewins (1993); f, Gaston & Dechesne (1996); g, Davoren & Burger (1999); h, Lance & Thompson (2005); i, Ainley et al. (2002); j, Hobson (1997)

At-sea surveys

***Coarse-scale selection*:** Boat transect surveys were conducted along the length of the study area in 1995 (N = 5), 1996 (N = 1, hereafter pooled with 1995), 2005 (N = 9) and 2006 (N = 10) between Port San Juan and Cape Beale (Fig. 3.1). In 1995/96 the vessel traveled at approximately 19 km·h^{-1} along two parallel along-shore routes at approximately 200 and 600 m from shore (details in Burger et al. 2008). These surveys were conducted between 5 June and 3 August from M.V. *Alta* and *M.V. Sea Otter* (both with eye level 2.0-3.0 m above the sea), or a large rigid-hull inflatable boat (eye level 1.5 m above the sea). Data from 1995 and 1996 was collected and provided by Alan Burger and colleagues (Burger et al. 2008). In 2005 and 2006, the vessel traveled at approximately 10 km·h^{-1} in a zig-zag pattern (Becker & Beissinger 2003). The zig-zag transect layout (total length 77 km) was systematic to cover the length of the study area and was bounded by the 5 and 20 m depth isobaths, the latter delineating the seaward park boundary. Depending on shoreline complexity and navigation hazards, zig-zag legs were on average 1.6 km long (range 0.9-2.9) and typically at 45° angles to the coastline. These surveys were conducted between 29 May and 4 August from a 5 m rigid-hull inflatable boat (eye level 1.5 m above the sea).

Surveys were conducted with paired observers at the bow, each scanning one side of the transect line from directly ahead to 90° abeam (as per Raphael et al. 2007). In 1995/96, surveys used fixed-width strip-transects (Burger et al. 2004) counting birds up to 150 m on either side of the boat. In 2005/2006, surveys followed distance-sampling protocols (Buckland *et al.* 2001) recording bird clusters (individuals or groups of birds), perpendicular distance from the transect line, and cluster size. Program Distance 5.0 (Thomas *et al.* 2006) was used to calculate seabird densities along transects correcting for species-specific, annual, and observer variability in delectability (details in Chapter 2). Detection function estimates from 2005/2006 (e.g. global P_a estimates from Table 2.4 of Chapter 2) were used to correct bird densities in 1995/96 fixed-width transects. Surveys were restricted to periods of low swell (<1.5 m) and low winds (Beaufort sea state ≤ 3).

GPS was used to record the boat position in 1-minute time intervals, which were linked to bird densities and environmental data. Due to differences in boat speed, 1-minute segments were approximately 320 m in 1995/96 and 170 m in 2005/2006. The 1-

minute line-segments became the unit of analysis for habitat selection models (below). Environmental variables (details below) included in the coarse-scale analysis were distance to beaches, estuaries, rivers and shorelines, depth, seafloor slope, seafloor substrate, sea-surface temperature/salinity anomalies and gradients, prey density and nesting habitat.

***Fine-scale selection*:** Distance-sampling survey methods were used for fine-scale surveys (N = 8/7/5 in 2004/2005/2006) in an area of consistently high seabird densities, particularly for marbled murrelets. In Carmanah Bay and waters off Carmanah Point, I established a series of parallel transects spaced 500 m apart and oriented perpendicular to shore (total length 13.4 km; Fig. 3.1). These transects were bounded by the 5 and 40 m depth contours (approx. 1-2 km offshore). The same environmental variables used in the coarse-scale analysis were included in the fine-scale analysis except the following, which were relatively constant throughout the small extent of the study area: distance to estuaries, rivers, and nesting habitat. Distance to kelp beds was introduced as a new variable in the fine-scale models.

***Prey availability and selection*:** Sonar was used to estimate prey availability concurrently with transect surveys (Piatt 1990). Relative abundance of prey (schooling fish or large zooplankton such as euphausiids) was measured with a paper-recording 200 kHz echosounder (Furuno FE-606) attached to the transom of the boat in 2004 (fine-scale transects), 2005 (fine- and coarse-scale), and one transect in 1996 (coarse-scale). Hydroacoustic surveys were not conducted in 2006 due to equipment failure. I quantified prey along transects by measuring echo-signal intensity on the paper echosounder output (Piatt 1990). Signal intensity was scored based on percentage cover (0 to 9) within blocks partitioned by time (1-min intervals) and depth (5 m intervals). Scores were squared to better estimate prey abundance (Piatt 1990) and summed within each minute to produce an abundance index (details in Chapter 4). In addition to linking prey data to bird transect surveys as an independent predictor variable, the prey data were also linked to environmental variables to model the prey-habitat associations within the study area.

Spatial autocorrelation

Spatial autocorrelation is common in seabird transect surveys (Schneider 1990) because birds often cluster in highly productive foraging areas. Failure to account for autocorrelation can result in ‘pseudo-replication’ and invalidate the use of some parametric modeling techniques thus increasing the likelihood of type I errors (Yen et al. 2004b). I assessed autocorrelation along transects as a source of information about species distribution patterns in our study area and as a tool for sub-sampling data for parametric modeling techniques used in this study (i.e., discriminant function analysis). I tested spatial autocorrelation within individual coarse-scale transect survey days (N = 25) using program Rooks Case (Sawada 1999). For each species, autocorrelation of presence/absence data was tested with join-count statistics (O'Sullivan & Unwin 2003) and statistical significance evaluated with Monte Carlo randomization tests using 1000 permutations. For marbled murrelet abundance data, autocorrelation was tested at increasing lag intervals (1-minute, 2-min., 3-min, etc. up to 10) using Moran’s I statistics (O'Sullivan & Unwin 2003) and z-values for significance testing. Given the large number of tests, I assumed significance at $P < 0.01$ (Yen et al. 2004b). Spatial autocorrelation in the residuals of the CART analysis (below) was also tested to determine how well the habitat models accounted for spatial variability in the bird densities (Cablk et al. 2002).

Environmental data

Environmental data (summarized in Table 3.2, see also Appendix I for maps of all environmental data) were collected *in situ* during transect surveys or obtained from additional sources.

***Depth and Slope*:** The bathymetry layer was interpolated from point sampled data using Inverse Distance Weighting (IDW) functions in a Geographic Information System (ArcMap 9.1, ESRI). Depth was recorded with the echosounder in 2004-2005 (see above) to the nearest 1 m at the beginning of each 1-min transect segment (n = 3499 points), and corrected to low tide (0.0 m) based on local tide tables (Canadian Hydrographic Service, station #8545; www.lau.chs-shc.gc.ca). The zig-zag orientation of transects resulted in uneven sampling throughout the study area, therefore 3259 additional points of known depth were collected from 2, 5, 10, 20, 30, and 50 m contour lines from digital marine charts (Garmin MapSource; BlueChart series). Bathymetry layers created from digitized contours can suffer from several interpolation problems, but this was overcome by adding extra points for peaks and ridges, and interpolating with a large search window using many data points (Burrough & McDonnell 1998). I used a variable search window up to 12 data points, maximum search window up to 1000 m, and a cell size of 150 m chosen to approximate the sample interval for depth sounder measurements (160-170 m). Cross-validation (comparing observed vs. predicted depth) showed a small mean error of -0.12 m (RMSE = 3.02). Using the final bathymetry model, I calculated seafloor slope with ArcGIS 9.1 using the slope tool. This measures the rate of maximal change in each 150 m bathymetry cell based on adjacent cells and calculating the inclination in degrees (range 0 to 4.5 in the study area).

***Seafloor substrate*:** Substrate was recorded using an underwater camera (Crystal Cam, Inuktun Services Ltd., Nanaimo, BC). The camera was attached to a 40 m tether and was either towed or spot-mapped along the transect route depending on bottom topography. The substrate was sampled in 2006 at ~50 m intervals for the entire fine-scale transect at Carmanah Bay and along approximately 80% of the zig-zag transect (Pachena Point to Port San Juan). In the remaining 20%, habitat was classified along the transect line based on adjacent shoreline substrates and experience in this area from snorkel surveys conducted in 2006 (Haynes et al. 2007). I was primarily interested in identifying sand/gravel substrates because, within our study area, sand lance show close associations with these substrates (Haynes et al. 2007). Image detail allowed for simple classification into i) sand/gravel, ii) rock (bedrock or rocky reefs), or iii) mix sand/gravel/rock.

***Ocean temperature and salinity*:** Sea-surface temperature (SST) and sea-surface salinity (SSS) were recorded using a temp/salinity probe (YSI Inc., Yellow Springs, OH). The probe was submerged in a small bucket with continuous water flow-through from a tube mounted to the transom. SST and SSS were logged every 10 seconds with a precision of ± 0.1 ^{o}C and p.p.t., respectively. Values were averaged for each 1-min transect interval and linked to GPS tracks. In GIS, I created continuous surface layers of SST and SSS using inverse distance weighting (IDW) interpolation with a variable search window up to 3 points (thus focusing on local measures with each 1-minute segment plus one additional point on either side of the segment), maximum search window of 500 m and cell size of 150 m. SST and SSS layers were created for individual transects in 1995/1996, thus creating real-time layers for each survey day. Due to intermittent SST/SSS coverage (computer malfunctions) in 2005/2006, I interpolated surfaces, pooling data from both years with a maximum search window up to 12 points, thus creating more generalized, “averaged” SST/SSS layers. Raster layers were created for fine- and coarse-scale transects separately in 2005/2006.

There were significant differences in SST and SSS among individual transects in 1995/1996 (ANOVA: SST, $F_{5,1500} = 332.49$, $p < 0.001$; SSS, $F_{5,1500} = 976.21$, $p < 0.001$), likely owing to the seasonal effects of warming and freshwater inputs (not tested in 2005-2006 because data were pooled in those years). I was interested in intra-survey variability in SST/SSS rather than absolute values; therefore I calculated SST and SSS anomalies (Becker & Beissinger 2003). Daily (1995/1996) and averaged (2005/2006) SST and SSS anomalies (SSTa and SSSa) were calculated as ^{o}C or ppt above or below the mean SST or SSS for the entire study area on any given day (1995/1996) or year (2005/2006). Finally, surface fronts in SST and SSS were identified from gradients of change in temperature or salinity across the water surface using GIS slope tools (Becker & Beissinger 2003). The intensity of the slope represents the strength of the gradient, thus identifying potential thermal or salinity fronts that may concentrate prey.

Kelp beds: Bull kelp (*Nereocystis leutkeana*) distribution was recorded in 1-min intervals during boat transect surveys using the depth sounder and by visual confirmation at or near the surface. However, this provided inadequate mapping of kelp throughout the study area because the boat frequently traveled parallel to kelp beds without recording them on the sonar. Thus kelp distribution was not included in coarse-scale habitat models. For kelp coverage in the fine-scale study area (Carmanah Bay), I used an electronic theodolite to map the maximum extent of kelp beds (visible at the surface at low tide) in 2004 and 2005 (Fig. 3.1 inset, details in Wong et al. in press).

Shoreline substrates**:** Shoreline maps with classified substrate types were obtained from the Physical Shore-Zone Mapping System (data accessed Jan. 2007, British Columbia Integrated Land Management Bureau, http://aardvark.gov.bc.ca/apps/metastar/home.do). These maps include physical shore-zone units, classified into 34 categories, at an effective mapping scale of 1:10,000 to 1:15,000 (Howes et al. 1997). For purposes of this study, I was interested in shore-zones consisting of sand or mixed sand/gravel which provide habitat for sand lance (Haynes et al. 2007). Of the 34 classes in the database, only sand/gravel flat (class 24), wide sand beach (27), sand flat (28) and narrow sand beach (30) were considered likely sand lance habitat based on concurrent research in the area (Haynes et al. 2007). Wide rock platforms with sand/gravel beaches (class 12) make up a large portion of the study area, but no sand lance were found in any surveys of these habitats.

Distance to estuaries: Murrelets have shown some associations with estuaries and bays (Miller et al. 2002, Yen et al. 2004a), thus I also calculated distances to nearest estuarine habitat (class 31, Physical Shore-Zone Mapping System) at five locations (Gordon River, Camper Bay, Cheewat River, 1.5 km up stream of Nitnat Narrows, and lagoons surrounding Cape Beale).

Major rivers: Distance to major rivers was also measured. Murrelets typically use rivers and associated valleys as flyways to access nesting habitat (Burger 2001). Moreover, rivers also create temperature and salinity gradients in the ocean potentially influencing foraging habitat for all seabirds. I defined major rivers as those mapped at a 1:2,000,000 scale in the BC Water Resources Atlas (www.env.gov.bc.ca/wsd/data_searches/wrbc/index.html). These included rivers known to be followed as flyways by murrelets (RAR pers. obs.) and where noticeable freshwater input was observed (measured with the SST/SSS probe during transects). Major rivers in the study area are: Pachena, Klanawa, Tsusiat, Nitinat narrows, Cheewat, Carmanah, Walbran, and Gordon.

Nesting habitat: Most species in this study nest colonially (murres, auklets, cormorants) or semi-colonially (pigeon guillemot), thus associations with nesting habitat were quantified by distance to known colony locations in the region. The closest murre colony was at Tatoosh Island, WA (48°23'N, 124°44'W), approximately 21 and 56 km from the southern and northern portions of the study area respectively. Rhinoceros auklets nest at Tatoosh and Seabird Rocks, BC (48°45'N, 125°09'W, Fig. 3.1). Pigeon guillemots nest at Seabird Rocks and several sites along the southern portion of the study area. Cormorants nest at caves and cliff sites throughout the study area (identified during boat surveys 2005/2006).

Marbled murrelets are solitary-nesting seabirds that nest inland on the limbs of old-growth conifers (Nelson 1997). Identifying and mapping murrelet nesting habitat has been the focus of extensive research for nearly two decades (Ralph et al. 1995, Burger 2002, McShane et al. 2004). Definitions of murrelet nesting habitat are based on this extensive body of work.

Availability of adjacent nesting habitat for marbled murrelets was determined from forest cover maps and satellite imagery. The following summarizes work conducted by Rick Page and Alan Burger to derive maps of suitable murrelet nesting habitat (unpublished data). The main source of data was the Vegetation Resource Inventory (VRI, British Columbia Ministry of Forests and Range [MoFR], www.for.gov.bc.ca/hts/vri/). Likely nesting habitat was classified using forest cover habitat predictors identified by the Canadian Marbled Murrelet Recovery Team (CMMRT 2003): age class 8 or higher (>140 years), height class 4 or higher (>28.5 m tall), > 0.5 km from shore, and < 900 m elevation. Gaps in these data, outside of MoFR administrative areas (i.e., parks), were filled using Ancient Forests maps of Vancouver Island produced by the Sierra Club of BC using Landsat MSS images (updated 1999, www.sierraclub.ca/bc/programs/mapping). The Sierra Club map used 60 x 60 m pixels classified into 10 simple categories, of which "Ancient Forest" was the measure of likely murrelet habitat. Finally, to remove recently clear-cut forest from the habitat map, I used an ortho-image of Vancouver Island created from 2003-2004 Landsat satellite imagery (Dr. Olaf Neimann, Dept. Geography, Univ. of Victoria). Recently logged areas were identified with a partially supervised classification using PCI Geomatica 8 (PCI Geomatics, Richmond Hill, ON). Logged areas were removed from VRI/Sierra Club maps producing the most contemporary map of likely nesting habitat for murrelets in this area. Likely nesting habitat is hereafter referred to as "old-growth".

Previous attempts to relate at-sea murrelets with old-growth habitat have focused on very large scales, typically with coastline segments > 50 km (Meyer et al. 2002, Raphael et al. 2002, Yen et al. 2004a). In my study area (< 65 km coastline), I wanted to identify potential foraging habitat within commuting range of murrelets on the water. I selected a maximum range of 30 km from the study area coastline because 1) terrestrial habitat within 25 km from shore is likely more important for murrelets (Meyer 1999, Raphael et al. 2002), 2) this is within typical commuting distances of murrelets to inland nests (Hull *et al.* 2001), 3) this encompasses most of the old-growth habitat adjacent to the study area, and 4) 30 km is used as a interior boundary for management planning of murrelet habitat in British Columbia. The 30 km radius thus included 3,101 km^2 of terrestrial habitat (excluding islands in Barkley Sound that contained no nesting habitat) within which old-growth was quantified.

The goal was to use old-growth maps to create an index of old-growth availability for adjacent marine areas. I overlaid the old-growth habitat map with as many non-overlapping evenly spaced circular plots as possible which did not overlap with the ocean and the centroid was within 30 km of the coast (Figure F in Appendix I). Circular plot radius was 2.0 km based other murrelet studies (1.6 and 3.2 km, (Meyer et al. 2002); 2.3 km, (Zharikov et al. 2006). I quantified % old-growth (%OG) within each plot (n = 181, mean 35.7 ± 25.1 SD %OG, range 0 to 96.7). Percent old-growth (%OG) was attributed to the centroid point of each circular plot (Figure G in Appendix I). Inverse Distance Weighting (IDW) was used to extrapolate %OG values to locations on the water such that %OG plots closer to the water have more influence than those farther away (Figure G in Appendix I). Thus an inland plot adjacent to the coastline would have the highest weighting (essentially weight = 1) while an inland plot at the 30 km limit would have almost no weight (weight ~ 0.01). The IDW function used no exponent (thus assuming a linear decreasing weight of plots with distance), cell size 150 m, and inclusion of all points up to a 30 km search radius. This provided a distance-weighted index of available habitat from any location on the water (hereafter %OG-index). Cross-validation, to assess IDW models, showed low prediction errors of 0.7 %OG (RMSE = 16.95). The 30 km search radius assumes that murrelets can fly in any direction to nesting habitat regardless of topographic boundaries in the landscape (ridges/valleys). In this area, elevation is typically less than 300 m and unlikely to interfere with murrelet access to adjacent habitat because murrelets regularly cross ridges 200-600 m high (Burger 2001).

Correlations among environmental variables - In ecological studies multicollinearity, correlations among two or more explanatory variables, is frequently observed. This is particularly true for environmental data collected along marine transect surveys where multiple habitat measures are recorded simultaneously (Reilly & Fiedler 1994, van Franeker et al. 2002, Becker & Beissinger 2003). Elimination of multicollinearity was not a specified criteria for any of the modeling techniques employed in this study (below). In fact, some techniques (Canonical Correspondence Analysis and Discriminant Function Analysis) actually assess correlations between predictor variables in order to build axes which represent linear combinations of environmental variables. Nonetheless, evaluation of correlations between environmental variables may improve the interpretability of the models, thus principal components analysis (PCA) was conducted to examine correlations among environmental variables.

Table 3.2 - Summary of environmental variables used in modeling species-habitat relationships for five species of pursuit diving seabirds along southwestern Vancouver Island, British Columbia.

Variable	Acronym	Summary: definitions and data source
Depth	DEPTH	Water depth (± 1 m) in 150m grid. Collected during surveys.
Slope	SLOPE	Seafloor slope (degrees incline) in 150 m grid calculated from DEPTH layer.
Seafloor substrate	SUBST	Substrates were classified in three categories (Sand, Rock, or Mixed) which were mapped by underwaer video cameras in ~ 50 m intervals in 2006.
Sea-surface Temperature and Salinity anomalies	SSTa, SSSa	SST (°C) and SSS (p.p.t.) were recorded every 10 sec during vessel surveys and averaged for 1-min intervals. SST and SSS grids (150 m resolution) were mapped in a GIS for daily surveys in 1995/96 and averaged for both years in 2005/06. SSS and SST annomalies (°C or p.p.t. above or below average) were used to look at intra-survey variability in temperature and salinity.
SST and SSS gradients	SSTg, SSSg	Daily or annual gradients (degrees incline) in SST and SST (150m resolution) were created using slope tools on SST and SSS grids. These "gradients" can represent surface fronts.
Prey abundance index	PREY	Prey availability was estimated from 200 kHz echosounder (2004 and 2005 only) during vessel surveys. Prey scored as per Piatt (1990).
Distance to kelp beds	KELP	Kelp beds were mapped by digital theodolite (Wong et al. in press) at Carmanah Bay. Distance (m) to nearest kelp bed was measured.
Distance to beaches	BEACH	Shore-zone types were derived from BC Physical Shore-Zone Mapping System (Howes et al. 1997; 1: 10,000 to 1:15,0000 scale). Distance (m) to nearest sand-gravel shoreline was measured.
Distance to estuaries	ESTU	Distance (m) to nearest estuarine habitat was measured. Data from BC Physical Shore-Zone Mapping System.
Distance to major rivers	RIVER	Distance to nearest major river was measured. Data from BC Water Resources Atlas (1:2,000,000 scale).
Distance to colonies	COLONY	Distance to nesting colonies was measured for all species except marbled murrelets. Colony locations from various sources.
% Old-growth index	%OG	Percent Old-growth index was extrapolated to marine areas based on %OG sampled within 30 km inland from the study area coastline. %OG is a measure of nesting habitat for murrelets. Data from Vegetation Resource Inventory (VRI) maps and Sierra Club Ancient Forests maps.

Modeling techniques

Three modeling techniques were deemed most applicable to this data set, and each provides a different perspective and interpretation of the data. (1) Canonical correspondence analysis (CCA) is a multivariate statistical approach looking at correlations among two groups of variables: multiple species (abundance data) and multiple habitat predictors. (2) Discriminant function analysis (DFA) utilized presence-only data to compare habitat use among species. (3) Classification and regression trees (CART) used both presence/absence and abundance data to model habitat selection. The CCA and DFA approaches examine habitat use, the components of the habitat occupied by organisms, but the CART analysis assesses habitat preferences by examining used habitats relative to the availability of habitat types, i.e. disproportionate habitat use.

Canonical correspondence analysis: Canonical correspondence analysis (CCA) falls within a class of multivariate statistics known as ordination which arranges species along habitat gradients (Jongman et al. 1995). The approach detects patterns of variation in the species data and constructs a theoretical variable from the environmental data that best explains this variation (Jongman et al. 1995). The first axis selects a linear combination of the environmental variables that maximizes dispersion of the species scores, and the second and further axes repeat this but with a combination of environmental variables that are uncorrelated with previous CCA axes (Jongman et al. 1995). The canonical axes represent habitat characteristics that show the maximum differentiation among species (Redfern et al. 2006).

CCA is a powerful tool used by community ecologists to simultaneously analyze multiple species and habitat variables. There are three main advantages of its use in this study. First, it reduces and combines the dimensions of habitat variables for easier interpretation (Reilly & Fiedler 1994, Redfern et al. 2006). Second, the method relies on nonlinear, unimodal models (i.e. Gaussian response curves), rather than unrealistic assumptions of linear relationships between species and habitat gradients (Reilly & Fiedler 1994, Guisan & Zimmermann 2000). Finally, the method is robust to datasets with many zeros, i.e. absences (Ter Braak 1985). Though several assumptions exist for CCA modeling, tests show that CCA is extremely robust against violations of these assumptions, and the only vital assumption is that the response model (species abundance data) is unimodal (Jongman et al. 1995).

Discriminant function analysis: Discriminant function analysis (DFA) is parametric multivariate technique for classification of a single categorical response variable (i.e., species) by several predictor variables. It uses a linear combination of values from independent (discriminating) variables that best separate cases into their known discrete classes of a dependent grouping variable (Tabachnick & Fidell 1996, McGarigal et al. 2000). The first function represents a linear relationship among a set of discriminating variables that best separates classes, while the second function, orthogonal to the first, is the next best separator of classes based on a different associations of discriminating variables (Karels et al. 2004).

There are several important assumptions that must be met for DFA (Tabachnick & Fidell 1996, McGarigal et al. 2000) including: 1) homogeneity of variance-covariance matrices, such that the variance within each variable and the correlation among variables is similar among the dependent classes; 2) discriminating variables have a normal distribution; 3) a discriminating variable cannot be a linear combination of other variables (e.g., varC = varA + varB); 4) samples are independent; 5) DFA is highly sensitive to outliers; and 6) relationships among discriminating variables are linear. See below for tests of assumptions. Multicollinearity among discriminating variables is not a specified assumption (McGarigal et al. 2000) but caution should be taken when interpreting results with correlated discriminating variables (Karels et al. 2004).

Classification and regression trees: Classification and regression trees (CART)(Breiman et al. 1984, De'ath & Fabricius 2000) are non-parametric algorithmic procedures which recursively partition data into two groups at optimal values of independent variables. This results in a branching tree representing a path in the ‘decisions’ taken to identify predicted abundance, or presence/absence, in an endnode, or terminal branch in the tree (Bahn & McGill 2007). CART analysis offers several advantages over parametric modeling techniques frequently used for habitat selection modeling (e.g., multiple regressions). This includes the flexibility to model different response types (categorical, numeric, rankings), ease of interpretation, and ability to handle missing values (De'ath & Fabricius 2000). Regression trees have an objective variable selection (rather than arbitrary or subjective p-values used in stepwise regression) which also model nonlinearities and interactions (Bahn & McGill 2007). As a non-parametric technique, CART is not dependent on distributional assumptions of model errors. Spatially autocorrelated data are effectively modeled with CART (Cablk et al. 2002). Classification and regression trees fall into what Breiman (2001) refers to as an “algorithmic modeling culture”. While traditional modeling practises attempt to fit data to pre-defined models (e.g., linear/logistic regression) algorithmic modeling makes no prior assumptions as to the shape of relationships between dependent and independent variables (Breiman 2001).

There is one major limitation of CART analysis when predictor variables are inter-correlated. At each split in a regression tree, the algorithm selects the *single best* predictor variable to provide a homogenous split in the dependent data. This means there is a reduced ability to consider the *combined* effects of more than one variable simultaneously. Thus there is a risk with highly correlated data that the selection criteria at each step might be erroneous – if the process selects one variable it will immediately downgrade the importance of any other closely correlated variables in future splitting. Whereas CCA deliberately seeks correlations among multiple predictor variables, CART analysis results need careful scrutiny with inter-correlated variables which may be facilitated with the Principle Components Analysis (above). Multicollinearity warrants caution in the interpretation of DFA but is not a specific assumption that needs to be addressed (McGarigal et al. 2000). These important difference between modeling techniques justifies the application of more than one method.

Statistical procedures

Canonical correspondence analysis: I used program CANOCO 4.5 for Windows (Ter Braak & Smilauer 2002) for CCA. I included all samples from fine- and coarse-scale transects in separate analyses. Abundance data (birds km^{-2}) for each species were used as the multiple response variables. Abundance data were log-transformed, to prevent a few high values from overly influencing the ordination, and I used the “downweighting for rare species” option because rare species may have an unduly large influence on the analysis (Ter Braak & Smilauer 2002). Data were analyzed separately for each year of coarse-scale transects but pooled for years among fine-scale transects because sample sizes were small for most species. Data were weighted by year for fine-scale transects so that samples from each year would have equal influence in the model such that weight-of-year-X = (total no. samples)·(no. years)$^{-1}$ / (total samples in year X). I included all environmental variables in the analysis except substrate type (because it was categorical variable), proximity to nesting colonies (because this could not be represented as a single variable for the multi-species response variable) and prey (because prey data were lacking for many transects, but see *Habitat selection by prey* below).

The analysis produced 1) four ordination axes and corresponding eigenvalues that equal the maximized dispersion of the species scores along each axis, 2) species-environment correlations which measure the associations between species and environment, and 3) amount of variance explained by each axis. Eigenvalue significance, and thus axis significance, was determined by Monte Carlo randomization tests with 1000 permutations that randomly associated environmental data sets from one case to species data sets of another case. Generally eigenvalues < 0.02 should be disregarded (Ter Braak 1985). The significance of individual environmental variables in relation to the ordination axes was assessed with Monte Carlo randomization tests and 1000 permutations for each variable. I used restricted randomizations which allowed permutations within transect survey days (Ter Braak & Smilauer 2002).

Discriminant function analysis: Data for DFA included all 1-min cases with seabird presence for each species thus including 2702 and 400 cases for coarse- and fine-scale analysis, respectively. These sample sizes were obtained after removing 1902 cases of marbled murrelets by sub-sampling every third case to ensure independence of samples due to strong spatial autocorrelation at the first two time lags (see *Results* below). All data were pooled among years for fine-scale surveys but analyzed separately for each year of coarse-scale surveys. I included all environmental variables except substrate type, proximity to colonies and prey for the same reasons described above for CCA.

Prior to analysis I tested the assumptions of DFA. Q-Q plots tested assumptions of normality and all discriminating variables were log-transformed to improve normality, except for SSTa and SSSa which had normal distributions after outliers were removed.

Outliers were identified with box-plots as those greater than 3 IQR (inter-quartile range) from the end of the box (SPSS 15.0). Outliers were deleted for each species-variable combination in each year of analysis, thus deleting 222 and 18 cases from the coarse- and fine-scale datasets respectively. Box's M-tests were used to test for equality of variance-covariance matrices among species groups (McGarigal et al. 2000). Significant differences were found, thus DFA classification was conducted using group covariance matrices of the canonical discriminant functions rather than matrices of the original variables (Tabachnick & Fidell 1996). DFA was performed using a forward stepwise procedures that maximize the Mahalanobis distance between the two closest groups with a liberal significance of $P \leq 0.15$ for variable inclusion (Costanza & Afifi 1979).

Classification and regression trees: I modeled habitat preferences using presence/absence data (classification trees) for all species and abundance data (regression trees) for marbled murrelets (other species provided insufficient abundance data to produce trees). Trees were grown for each species in each year with coarse-scale data. For fine-scale transects, low prevalence required data to be pooled across years for all species except murrelets. Rather than growing a single tree for each species-year combination, I first grew multiple trees to identify the most important independent variables for splitting. Trees were grown for each species-year combination (10 and 15 replicate trees for coarse- and fine-scale data respectively) using a random subset of the data (80% randomly selected for each replicate tree) and the remaining 20% for cross-validation to assess model fit (Seoane *et al.* 2005). More replicates were run for the fine-scale data to compensate for potentially erroneous results due to smaller sample sizes in this dataset. The importance of individual independent variables was measured using the improvement values (proportional reduction in error [PRE] analogous to r^2 in regression models) at each split, which ranked the importance of each independent variable (SPSS 1998, 2004). To facilitate comparison of variable importance across species and years, *relative* importance values were calculated such that the top ranked variable = 100% importance and each other variable importance was relative to the top ranked variable (SPSS 2004). For example, if Depth and Slope have PRE of 0.24 and 0.20 respectively, then relative importance values are Depth 100% and Slope 83.3% (0.20/0.24).

Mean PRE, from the replicate trees, was used to rank and select the four most important independent variables for each species-year. Final CART models were run using these top four predictor variables to create a single regression tree for each species to identify thresholds of species preferences. Final trees were grown using all data and simple re-substitution to evaluate model fit (% correct classification) where the original data were substituted directly into the model to determine how well the model predicted the data set used to build it.

When growing trees, the goal of each partition/split was to maximize the homogeneity in each group which was accomplished with an algorithm that minimized impurity in the groups. Splitting criteria used the following impurity measures: Gini index for presence/absence data and least squares deviation for abundance data (De'ath & Fabricius 2000). I used liberal stopping criteria for splitting: a node required at least 15 cases to allow a search for a new split, at least 5 cases had to end up in each new group after a split, and each split had to increase r^2 by at least 0.001 (Bahn & McGill 2007). Trees were pruned using the 1 standard-error rule (Breiman *et al.* 1984) to prevent overfitting (growing extremely large trees that overfit the data).

Weighted CART analysis: Ecological data are often dominated by zeros which may cause regression tree splitting criteria to be ineffective (De'ath & Fabricius 2000). Our data contained many zeros ranging from 68% of transect segments for murrelets to 98% for pigeon guillemots. Most often CART analysis compares presence data (e.g. number of animal sightings) to an equal number of absence data derived from random samples within the survey area (e.g., Goetz et al. 2007). Rather than randomly sub-sampling transect segments to select an equal sample of presence and absence segments (omitting large amounts of data), I used a weighting index to normalize the influence of zeros in the CART models. The following method was used for each species in the fine-scale and coarse-scale transects separately. All segments with ≥1 bird (presence) received a weight of 1. For segments with zeros (absence), the weighting index was equal to the number-of-segments-with-birds / number-of-segments-without-birds. For example, N = 150 segments with 50 presence and 100 absence, weight = 50/100 = 0.5 which is applied to each of the 100 absence segments. In this way I modeled 150 segments as if there were equal numbers of presence segments (n = 50) and absence segments (n = 100*0.5 = 50). The weighting variable is incorporated into the model as an "influence variable" in SPSS 15.0.

Measuring niche overlap

GIS-based mapping techniques were used to compare the spatial overlap between species from observed distributions (original transect data) and expected distributions (CART-based analysis). Observed distributions represent habitat use (e.g., CCA and DFA) but expected distributions represent preferred habitat (use relative to availability).

I used kernel density functions (O'Sullivan & Unwin 2003) to map the observed distribution of birds. Kernel densities convert point data (i.e., bird counts per 1-minute transect segment), into a continuous surface grid showing relative bird densities per grid cell. Kernel densities take into account both location and density of birds at points. Kernels were calculated in ArcGIS 9.1 using Hawth tools (Beyer 2004) for each species in each year of coarse-scale data and for all years pooled at Carmanah Bay (fine-scale). The 50% volume contour was used to delineate the "core" area of used habitat. A percent volume contour represents the boundary of the area that contains x% of the volume of a probability density distribution (Beyer 2004): the 50% volume contour would contain highest probability densities and 50% of the points (the ones with the highest bird densities) used to generate the kernel density estimate.

CART models assessed habitat preferences and provide a set of 'decisions' or 'rules' which define habitat preferences based on thresholds. These thresholds were used to map preferred habitats (CART-based expected distributions) for each species-year combination. In ArcGIS 9.1 polygon layers were created using buffer tools and intersecting layers. The maximum extent of useable marine habitat was defined by a 2 km buffer from the coastline because this encapsulated all transects (coarse- and fine-scale) in the study area.

For both observed Kernel-based distributions and expected CART-based distributions, I measured polygon area for each species and area overlap between each species-pair (e.g., murrelet-murre). An index of niche overlap was measured as $\mathit{Area\ Overlap}_{(\text{species A and B})} / \mathit{Total\ Area}_{(\text{species A + B})}$. Area overlap was quantified in each year and for coarse- and fine-scale separately.

Habitat selection by prey

Studies investigating concordance between seabirds and their prey frequently show weak associations at small (<10 km) spatial scales (Logerwell & Hargreaves 1996, Fauchald et al. 2000). This is exacerbated by the limitation of hydroacoustic methods, which sample an inverted cone below the vessel and can easily miss schools of prey in shallow water adjacent to the vessel's path. Therefore, because the study area is small (<65 km) and units of analysis are very small (1-min. segments), I expected to see little, if any, habitat selection by seabirds based on prey-scores from hydroacoustic surveys. Alternatively, I modeled the habitat selection of prey using the same statistical approaches as used for seabird-habitat modeling: CCA, DFA, and CART. This approach allowed the investigation of whether prey and seabirds showed similar habitat preferences regardless of weak spatial concordance between each other. The dependent variable modeled was prey abundance scores in 1-minute transect segments (described above in *At-sea surveys*, this chapter).

A few minor differences in modeling prey-habitat associations were necessary. For CCA, prey could not be used as the dependent variable because there was only one set of prey scores and CCA requires multiple dependent variables. Instead prey scores were used as *supplementary* environmental data in the original species-environment models. This allows models to be run without using prey data but then allows prey correlations with CCA axes to be assessed post-hoc and displayed in bi-plots (Ter Braak & Smilauer 2002). Thus I can interpret the strength and direction of prey correlations with environmental data. DFA was conducted for each year of coarse- (1996 and 2005) and fine-scale (2004 and 2005) transects for which prey data were available. For classification, prey-scores were categorized into three classes: no-prey (prey-score = 0), low-prey (0.1-1), and high-prey (>1). Data were subjected to the same procedures as were used in DFA for species-habitat data (i.e., log-transformations, elimination of outliers). Finally, habitat selection by prey was assessed using CART analysis based on presence/absence of prey, following the same procedures as with bird habitat analyses.

Diurnal foraging patterns

To test temporal niche differences, diurnal foraging watches were conducted to measure foraging activity time-budgets for all species. I measured diurnal foraging activity from observations by telescopes (20 x magnifications) at 12 cliff-top vantage points along the study area during 2004, 2005, and 2006. Over three years I conducted 765 h of observation using instantaneous-scan sampling techniques to record diving behaviour of each species (Davoren & Burger 1999). A series of scans consisted of 20 one-minute scans over each hour of observation. During each one-minute interval, the scope was fixed and observers recorded the numbers of birds for each species and activity state (resting or diving) within the field of view of the scope. Rare activities such as flapping and preening were pooled with resting. This was repeated for 20 non-overlapping fields of view. The 60-sec observation interval was chosen to maximize the detection of diving birds given the average dive times of about 25 and 35 s for murrelets (Jodice & Collopy 1999) and auklets (Davoren 2000), respectively. Average dive times for other species however are longer: pigeon guillemot, 67-87s,(Thoresen 1989, Clowater & Burger 1994); common murre, 39-71s (Ainley et al. 2002, Tremblay et al. 2003); pelagic cormorants, 35-45s (Hobson 1997). other species are similar or slightly longer. Hourly surveys were conducted from dawn until dusk at three sites and the first four hours after sunrise and last three hours before sunset at other sites. All observations were made in conditions with Beaufort sea state less than three.

Proportions of birds diving were calculated for each species and each hour of observation. Proportions were sensitive to low numbers of birds observed; therefore I included only hourly scans with ≥ 5 individuals on the water. This criteria provided adequate hourly sample sizes for comparison between murrelets (n = 634 hrs) and murres (n = 310). For the other, less common species, I summed all bird sightings in two-hour bins (0500-0700, 0700-0900, etc.) to calculate proportions of birds diving.

RESULTS

Surveys yielded 110 and 33 h of coarse- and fine-scale transect surveys totalling 8664 1-minute transect segments for species-habitat modeling (Table 3.3). Overall seabird densities showed substantial variability among years (Table 3.3). In particular, murrelets, murres, and auklets were more abundant in 1995/96 than a decade later in 2005/06 (see also Appendix E in (Piatt et al. 2007). Rhinoceros auklets showed the greatest decline in abundance with a 10-fold decrease between 1995/96 and 2006. Fine-scale transects conducted in Carmanah Bay between 2004 and 2006 showed a 60-70% decrease in murrelet and murre abundance from 2004 to 2005/06. Guillemots and cormorants also showed marked fluctuations in abundance, though with no apparent trend over time. These fluctuations in abundance for all species may account for some of the inter-annual variability in habitat selection observed in this study.

Table 3.3 - Summary of seabird occurrence, densities, and sample size (no. of 1-minute transect segments) recorded during boat transect surveys along the West Coast Trail (coarse-scale) and around Carmanah Bay (fine-scale). All samples were used in subsequent species-habitat modeling, except for Discriminant Function Analysis which used only occurrence (i.e. presence) data.

	Prevalence (no. occurences in relation to no. of samples, %)			Density (birds km^{-2} ±SE)		
Coarse-scale	**1995/96**	**2005**	**2006**	**1995/96 (N = 1506)**	**2005 (N = 2053)**	**2006 (N = 3114)**
Marbled murrelet	42.8	28.0	37.8	85.7 ± 6.2	63.9 ± 3.3	63.1 ± 2.9
Common murre	13.9	12.6	6.7	18.7 ± 2.2	10.8 ± 1.2	6.2 ± 0.6
Rhinoceros auklet	16.0	6.3	1.5	10.1 ± 1.2	6.3 ± 0.8	1.2 ± 0.2
Pigeon guillemot	2.4	3.3	3.2	0.8 ± 0.1	2.2 ± 0.2	1.6 ± 0.2
Pelagic cormorant	10.0	12.3	7.2	2.8 ± 0.2	6.1 ± 0.4	2.9 ± 0.3
Fine-scale	**2004**	**2005**	**2006**	**2004 (N = 1042)**	**2005 (N = 556)**	**2006 (N = 393)**
Marbled murrelet	24.0	16.5	23.9	100.7 ± 15.4	27.9 ± 3.6	36.5 ± 5.0
Common murre	8.5	6.7	4.8	13.7 ± 1.9	4.8 ± 1	5.9 ± 2.4
Rhinoceros auklet	1.3	2.0	2.5	1.4 ± 0.4	1.8 ± 0.7	1.8 ± 0.6
Pigeon guillemot	1.0	1.1	0.5	0.8 ± 0.3	0.6 ± 0.2	0.1 ± 0.1
Pelagic cormorant	1.0	5.0	3.6	0.5 ± 0.2	2.3 ± 0.5	1.3 ± 0.4

Spatial autocorrelation

Runs tests on sequences of presence/absence data showed spatial autocorrelation to be high for murrelets but low for other species. Murrelets showed significant autocorrelation in 88% of 25 coarse-scale transects ($p < 0.01$, 1000 Monte Carlo randomizations). For other species significant autocorrelations were less frequent: murres - 28% of transects, auklets - 8%, guillemots - 12%, and cormorants - 4%.

Spatial autocorrelation in murrelet abundance (Moran's I tests) was also evident in all years (Fig. 3.2). Murrelets showed strong autocorrelation up to about 350 m (one time lag in 1995/96 and two time lags in 2005/06). Nearly all spatial autocorrelation was absent after three time lags (>960 m in 1995/96, >510 m in 2005/06). It was predicted that autocorrelation would decrease in the residuals of CART models relative to the raw abundance data (Cablk et al. 2002), however this effect was minor in 2005/06 and autocorrelation actually increased in the residuals of 1995/96 models. This suggests that CART models did not effectively model spatial variability in the murrelet abundance dataset. The failure of CART models to account for spatial variability means that much of the unexplained variance in the data, or incorrectly classified samples, may be accounted for by spatial autocorrelation. Nevertheless, because CART models are a non-parametric modeling technique, they do not require independent (uncorrelated) samples for analyses to be valid.

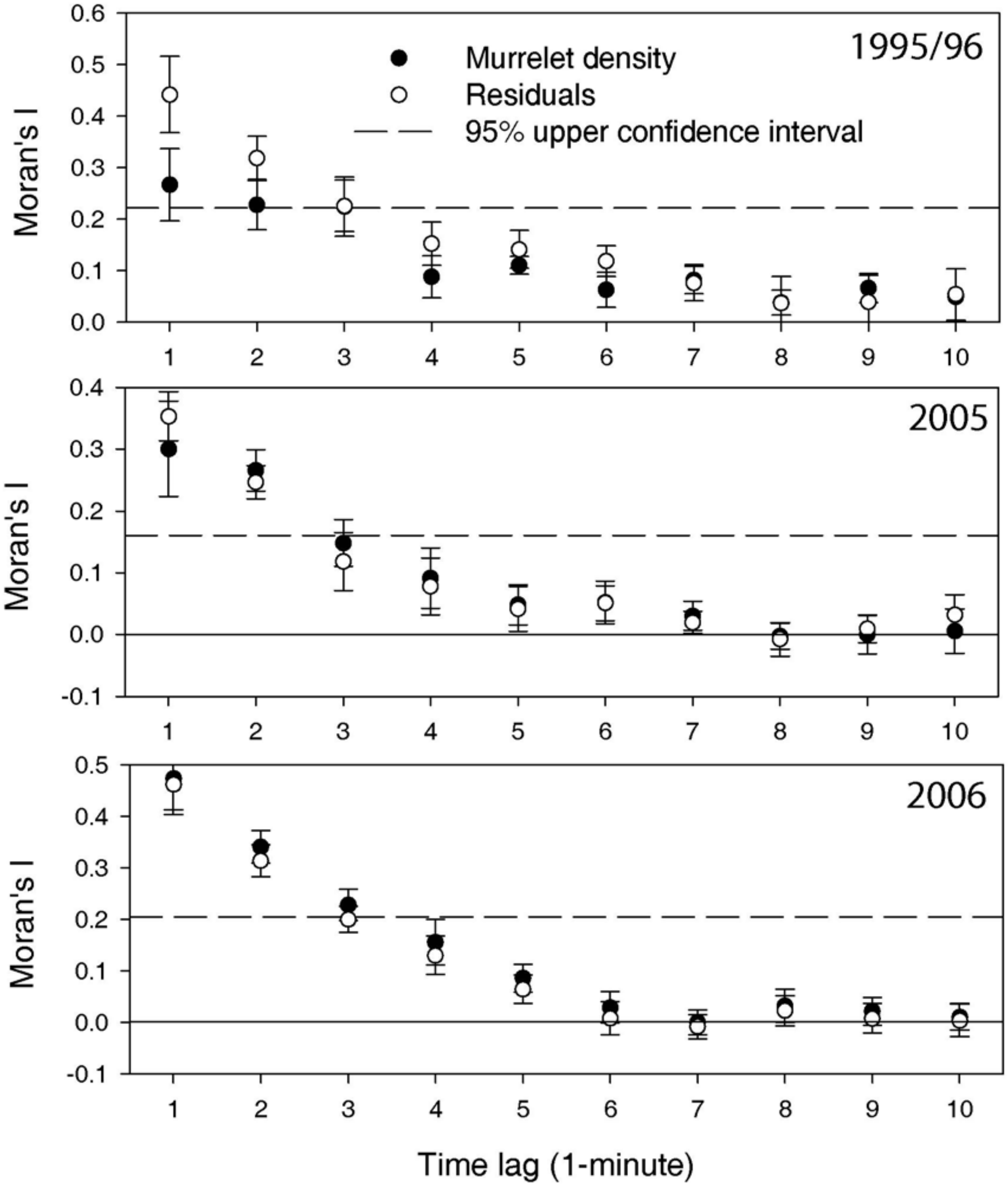


Figure 3.2 - Spatial autocorrelation of marbled murrelets along coarse-scale transect surveys. Mean Moran's I ± SE indicating average autocorrelation index for murrelet densities (●) and for residuals of the CART models (○). 1-minute time lags are approximately 320 m in 1995/96 and 170 m in 2005/06 due to differences in boat speed during transects

Correlations among environmental variables

Principal Components Analysis (PCA) results show numerous correlations among environmental variables (Table 3.4). Overall, the principal components (PC) are very similar between 2005 and 2006 both in strength and sign (+/-) of correlations, but frequently differ from 1995/96 where many of the signs (+/-) are reversed. Nevertheless, careful examinations identify similar interpretations despite sign reversals. For example, distance to river (DR) and old-growth index (OG) were correlated in all years but in 1996/96 DR had a negative sign (-) and OG (+), but in 2005/06 DR (+) and OG (-): interpretation is that old-growth index increases as distance from rivers decreases. Cumulative percent variance explained by the first two principal components (PC) was between 40.6 - 46.2 % for coarse-scale transects and 63.4 - 83.1% for fine-scale transects. The remaining PCs typically explained less than 15% of the variance.

For coarse-scale transects, the first PC was similar among years showing strong correlations among seabird colonies and distance to rivers. This reflects the proximity of many colonies to each other (or the same colonies used by multiple species, such as Seabird Rocks). Common murre colonies always had a sign opposite to that of other species' colonies reflecting the long distance to their only colony at Tatoosh Island. The second PCs illustrate correlations between oceanographic variables: increasing temperature (SST) is associated with decreasing salinity (SSS) likely owing to freshwater inputs to the study area. The third PCs showed correlations between some colonies and shoreline features (e.g. distance to beaches, estuaries or coastlines): i) cormorant colonies were close to estuaries and ii) the auklet colony (Seabird Rocks) was far from the murre colony (Tatoosh Isl.), farther from shore, but closer to beaches. Finally, the fourth PCs showed positive correlations between depth, slope and distance to shore.

In all years of the fine-scale transects, the first PCs showed strong correlations between distance to beaches, distance to shore, distance to kelp and depth. These four variables are clearly influenced by an inshore-offshore gradient reflected in the layout of transects perpendicular to the shoreline (Fig. 3.1 inset). The second PCs illustrate correlations among oceanographic variables (SST/SSS), slope of the seafloor, and prey in 2004. The coefficients suggest that decreasing slope is associated with increasing SSS gradient, decreasing SSS anomalies, and increasing SST anomalies. In 2005, a third PC suggests that prey were positively correlated with SST gradients.

PCA was not used to test for correlations between environmental variables and bird densities (e.g., Haney & Schauer 1994) because Canonical Correspondence Analysis was used for this assessment. The PCA is important to the interpretation of CART results because at each step in the analysis, CART is only able to select one variable out of many potentially correlated variables.

Table 3.4 - Principal components analysis (PCA) examining correlations between environmental variables used in habitat models. Data were analyzed separately for each year of coarse-scale (upper table) and fine-scale transects (lower table). Results show the maximum number of components extracted in each dataset and the % variance explained by each component. Values are correlation coefficients (bold **indicates highest correlations and the variables contributing most to the component). Refer to Table 3.2 for explanations of acronyms. COMU = common murre, RHAU = rhinoceros auklet, PECO = pelagic cormorant, PIGU = pigeon guillemot, n/r = data not recorded in that year.**

	1995/96				2005				2006			
Component	1	2	3	4	1	2	3	4	1	2	3	4
Dist. to Beach	-0.390	**-0.762**	-0.006	-0.196	**0.653**	0.304	**-0.534**	0.067	**0.706**	0.166	**-0.512**	0.151
Dist. to Estuary	0.128	-0.001	**0.861**	-0.189	0.060	0.355	0.116	**-0.705**	0.175	0.443	0.044	**-0.653**
Dist. to Shore	0.332	0.475	0.142	**0.529**	-0.229	0.147	**0.657**	0.430	-0.205	0.215	**0.689**	0.383
Dist. to River	**-0.719**	-0.549	0.065	-0.044	**0.829**	0.359	-0.177	0.070	**0.876**	0.213	-0.158	0.128
Depth	0.075	-0.022	-0.155	**0.599**	0.136	0.320	0.277	**0.727**	0.177	0.224	0.394	**0.714**
Slope	0.034	-0.381	-0.220	**0.522**	0.014	0.380	-0.269	0.243	0.079	0.355	-0.303	0.274
SSSa	0.437	**-0.592**	-0.082	0.124	0.063	**0.804**	0.310	0.034	0.216	**0.801**	0.254	0.072
SSSg	-0.095	0.284	-0.249	-0.302	-0.072	**-0.705**	-0.229	0.072	-0.194	**-0.708**	-0.183	0.029
SSTa	**-0.741**	**0.608**	0.050	0.062	0.420	**-0.690**	0.260	-0.099	0.260	**-0.775**	0.228	-0.145
SSTg	-0.232	0.296	-0.139	0.115	0.236	-0.303	-0.256	0.207	0.166	-0.387	-0.249	0.258
Old-growth index	**0.918**	0.221	0.063	-0.118	**-0.838**	0.260	0.210	-0.008	**-0.805**	0.348	0.175	-0.010
Dist. COMU colony	**-0.848**	0.421	0.128	0.099	**0.618**	-0.288	**0.668**	-0.131	**0.590**	-0.358	**0.633**	-0.200
Dist. RHAU colony	**0.850**	-0.171	-0.374	-0.169	**-0.699**	-0.048	**-0.596**	0.216	**-0.733**	0.024	**-0.527**	0.266
Dist. PECO colony	**0.662**	0.004	**0.568**	0.289	**-0.455**	0.436	-0.011	-0.403	**-0.338**	0.610	-0.042	-0.366
Dist. PIGU colony	**0.443**	**0.651**	-0.256	-0.356	**-0.651**	-0.442	0.212	0.037	**-0.720**	-0.370	0.214	0.011
Prey Score	-0.105	0.211	-0.272	0.289	-0.020	0.005	0.004	0.101	n/r	n/r	n/r	n/r
%Variance	**28.3**	**17.9**	**9.7**	**9.1**	**22.7**	**17.9**	**13.0**	**9.9**	**24.8**	**20.9**	**13.2**	**10.2**

	2004		2005			2006	
Component	1	2	1	2	3	1	2
Dist. to Beach	**0.954**	0.042	**0.977**	0.045	-0.023	**0.978**	0.021
Dist. to Shore	**0.962**	0.028	**0.920**	0.221	0.111	**0.925**	0.188
Depth	**0.959**	0.056	**0.968**	0.084	0.009	**0.968**	0.046
Slope	-0.515	0.115	-0.219	**-0.831**	-0.028	-0.395	**-0.775**
SSSg	n/r	n/r	-0.677	**0.476**	0.065	-0.680	**0.506**
SSSa	n/r	n/r	0.714	**-0.501**	0.035	0.670	**-0.567**
SSTg	n/r	n/r	-0.281	-0.014	**0.540**	-0.429	0.078
SSTa	n/r	n/r	-0.339	**0.452**	0.015	-0.171	**0.461**
Dist. to Kelp	**0.983**	0.014	**0.909**	0.353	0.073	**0.926**	0.316
Prey score	-0.077	**0.990**	0.017	-0.102	**0.838**	n/r	n/r
% of Variance	**66.5**	**16.6**	**47.7**	**15.7**	**10.2**	**54.3**	**17.1**

Species-habitat correlations: Canonical Correspondence Analysis

The species-environment biplots (Fig. 3.3) show the relationships between environmental variables and species. In all years of the coarse-scale transects, axis 1 separated murrelets/cormorants from auklets/murres/guillemots. The first axes were best described by distance to shore, distance to river, distance to beach, and temperature anomalies (1995/96), distance to estuary, distance to beach and depth (2005), and distance to beach, depth, and surface salinity anomalies (2006). Together these results suggest that murrelets and cormorants showed preference for shallow, nearshore habitats close to beaches. Secondary axes further separated species by habitat preferences: pigeon guillemots preferred increased sea-surface temperature anomalies (SSTa, 2005 and 2006), pelagic cormorants preferred steeper sloped seafloors (1995/96 and 2005). Axis 2 had little effect on murrelets. Murres and auklets however showed little separation in habitat preferences along either axes. Although position of species biplots relative to the first and second axes appeared to flip between 1995/96 and 2005/06, the direction of the arrows for habitat variables indicate that many of the species-environment relationships remained the same (as per changes in +/- signs in PCA, Table 3.4).

With fine-scale surveys in Carmanah Bay, biplots (Fig. 3.3) showed very similar habitat preferences between cormorants and guillemots (i.e. shallow, nearshore, closer to kelp and beaches [axis 1] and lower SSTa [axis2]). Conversely murres and auklets showed similar preferences for deeper, offshore waters further from beaches and kelp (axis 1). Murrelets showed preference for shallow, nearshore habitats, closer to kelp and beaches (axis 1) but no preference along axis 2.

Table 3.5 summarizes the results of the CCA. The first two canonical axes explained more than 80% of the variance in the species-environment relationships and eigenvalues were significant in all models ($P < 0.001$, Monte Carlo randomization tests). Eigenvalues were < 0.02 for axes 3 and 4 in all models and thus these were disregarded for interpretation of species-environment relationships (Ter Braak 1985). Axis 1 of the fine-scale (Carmanah Bay) models had the greatest eigenvalue and correlation coefficient of any model, suggesting the strongest explanatory relationship between species-environment data (>80% of the species-environment variance).

Overall in the four plots, common murres and rhinoceros auklets are always each other's closets neighbour, marbled murrelets are somewhat isolated in the two-dimensional space, and guillemots and cormorants are the most variable.

Table 3.5 - Ordination results from a canonical correspondence analysis of seabird abundance and environmental variables along southwestern Vancouver Island. Environmental variables are summarized in Table 3.2. Canonical axes 3 and 4 are omitted because eigenvalues were < 0.02 which should be disregarded (Ter Braak 1985). "Species-Env. total" is the sum of the species-environment eigenvalues (for all four axes), i.e. the species variation related to the environmental variables. "Overall total" is the total of all variation in the species encounter rate data

	Canonical axes		Species-	Overall
	1	**2**	**Env. total**	**total**
Coarse-scale 1995/96				
Eigenvalues	0.066*	0.013	0.094*	1.896
Species-environment (S-E) correlations	0.375	0.163		
% variance of S-E relation	70.1	14.0		
Coarse-scale 2005				
Eigenvalues	0.097*	0.032	0.146*	2.433
Species-environment correlations	0.388	0.232		
% variance of S-E relation	66.4	21.6		
Coarse-scale 2006				
Eigenvalues	0.063*	0.039	0.121*	2.652
Species-environment correlations	0.301	0.242		
% variance of S-E relation	52.3	32.0		
Fine-scale 2004-2006				
Eigenvalues	0.148*	0.020	0.182*	2.817
Species-environment correlations	0.427	0.165		
% variance of S-E relation	81.2	10.8		

* *P*- value < 0.001 from a Monte Carlo randomization test with 1000 permutations

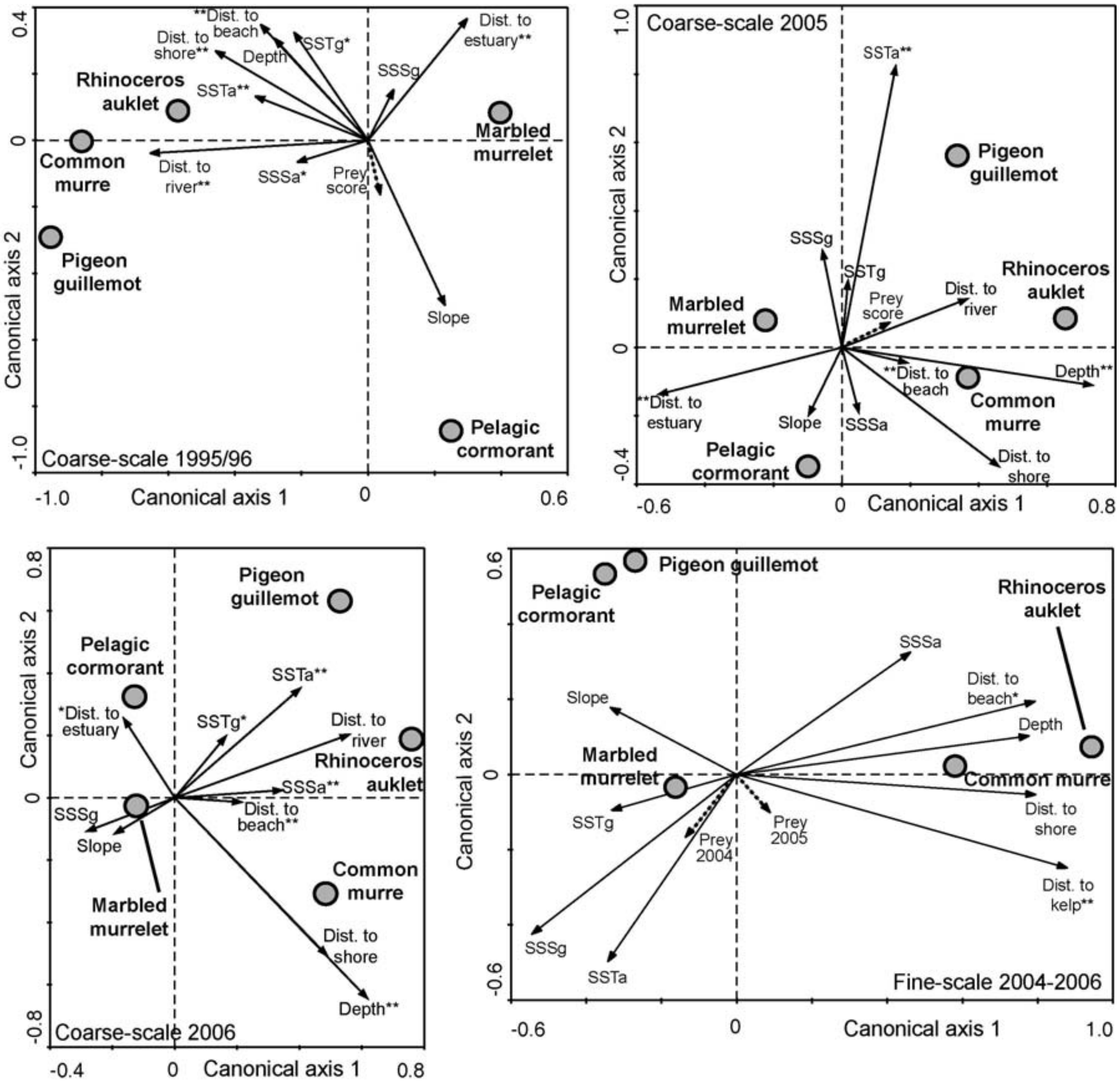


Figure 3.3 - Ordination results from canonical correspondence analysis (CCA) of seabird species and environmental/habitat variables. Arrows show the relationships of environmental variables to each other and with respect to the canonical axes (arrow length reflects strength of the correlation and arrow direction, relative to axes, reflects contribution to each axis). Biplots show seabird species relationships with environmental variables. Prey (dashed arrows) were included as 'supplementary' environmental variables, thus prey did not influence the outcome of the CCA but their relationship with environmental variables is plotted. P-values (*<0.05, **<0.01) are from Monte Carlo randomization tests with 1000 permutations for individual environmental variables.

Seabird habitat use: Discriminant Function Analysis

Comparison of habitat use among species was conducted using discriminant function analysis (DFA) to classify transect segments where species were present. In each year of the coarse-scale transects, the first and second discriminant functions accounted for most of the variation (1995/96: 79%, 2005: 84%, 2006: 96%) and significantly discriminated among species (Table 3.6). Likewise in Carmanah Bay, the first two discriminant functions accounted for most of the variance (89.9%).

Discriminating variables for species classification differed among years and between coarse- and fine-scale data (Table 3.7). The most important discriminating variables included SSTa and slope (both 1995/96 and 2006), depth and slope (2005), and distance to kelp, distance to beach and depth (fine-scale transects). Plots of the group centroids (within-group means for the first and second discriminant functions; Fig. 3.4) showed strong similarity in habitat use by murrelets and cormorants in all years along the coarse-scale transects. Overlap between murres, auklets and pigeon guillemots showed considerable inter-annual variability. In Carmanah Bay (fine-scaled analysis), cormorants and guillemots showed the greatest overlap in habitat use (Fig. 3.4). Murrelets were always separate from other alcids, although there were very minor overlaps with pigeon guillemots.

Despite the high % variance explained and the significance of the first two discriminant functions (Table 3.6), DFA showed a relatively poor ability to correctly classify species by environment variables. Post-classification tests showed only 36-42% correct classification with coarse-scale data and 25% correct classification with fine-scale data. Classification rates also differed among species (mean % of cases correctly classified: marbled murrelet, 41.1% ± 12.3 SE; common murre, 27.7% ± 8.3 SE; rhinoceros auklet, 41.9% ± 19.3 SE; pigeon guillemot, 29.2% ± 13.8 SE; and pelagic cormorant, 33.1% ± 8.8 SE). This emphasizes the high degree of overlap in habitat use among species (Fig. 3.4).

Table 3.6 - Test of discriminant functions for classification of seabird species (upper table) and for prey abundance (lower table) based on habitat variables off southwestern Vancouver Island. List of habitat variables in Table 3.2. Function four is omitted from coarse-scale results (all p > 0.05).

	Test of functions	% of variance	Wilk's lambda	X^2	df	P
Classification of seabird species by environmental predictors						
West Coast Trail (coarse-scale)						
1995/96	1	51.3	0.88	103.9	28	<0.001
	2	27.4	0.94	51.1	18	<0.001
	3	20.2	0.97	22.5	10	0.013
2005	1	56.9	0.83	147.6	24	<0.001
	2	26.9	0.92	64.8	15	<0.001
	3	14.1	0.97	24.6	8	0.002
2006	1	54.3	0.83	163.0	24	<0.001
	2	41.7	0.92	75.2	15	<0.001
	3	2.8	0.99	6.9	8	0.546
Carmanah Bay (fine-scale)						
2004-2006 (pooled)	1	72.6	0.73	120.6	16	<0.001
	2	17.3	0.91	35.3	9	<0.001
	3	8.2	0.97	13.2	4	0.010
Classification of prey scores (no-prey, low, high) by environmental predictors						
West Coast Trail (coarse-scale)						
1996	1	99.4	0.84	42.1	6	<0.001
	2	0.6	0.99	0.3	2	0.875
2005	1	100	0.99	10.5	3	0.015
	2	n/a	n/a	n/a	n/a	n/a
Carmanah Bay (fine-scale)						
2004	1	96.9	0.95	50.6	6	<0.001
	2	3.1	1.00	1.6	2	0.445
2005	1	67.5	0.96	19.3	6	0.004
	2	32.5	0.99	6.3	2	0.043

Table 3.7 - Pooled within-groups correlations between discriminating variables and standardized canonical discriminant functions coefficients describing i) species habitat use in pursuit diving seabirds (upper table) and ii) prey abundance by habitat. Variables are ordered with absolute size of correlation with Function 1 (* indicates largest absolute correlation between each variable and respective discriminant function). Discriminating variables were selected by forward stepwise procedures with a conservative minimum significance of F < 0.15. Function 4 omitted (p>0.05).

	Variables in model	**Function**		
		1	2	3
Classification of seabird species by environmental predictors				
West Coast Trail (coarse-scale)				
1995/96	SSTa	0.62*	-0.35	0.37
	Dist. to river	0.60*	0.13	-0.11
	Slope	-0.44*	-0.16	-0.33
	SSTg	0.33	0.46*	0.09
	Dist. to beach	0.17	0.27	0.30*
	SSSa	0.01	0.53	-0.34
	Dist. to shore	-0.11	0.49	0.05
2005	Depth	0.74*	0.02	0.46
	Slope	-0.26*	-0.09	0.17
	Dist. to estuary	-0.47	0.52*	0.23
	SSTa	0.48	0.47	-0.70*
	SSSa	0.06	0.35	0.53*
	Dist. to beach	0.19	-0.06	0.17
2006	SSTa	0.80*	-0.32	-0.30
	Slope	-0.39*	0.09	0.20
	Depth	0.46	0.75*	0.40
	SSSg	0.00	0.32	-0.35*
	Dist. to estuary	-0.29	-0.40	0.45
	SSTg	0.27	-0.22	0.51
Carmanah Bay (fine-scale)				
2004-2006 (pooled)	Dist. to kelp	0.93*	0.17	-0.14
	Depth	0.79*	-0.30	0.29
	Dist. to beach	0.77*	-0.39	0.00
	SSSg	-0.65	0.62*	0.19
Classification of prey scores (no-prey, low, high) by environmental predictors				
West Coast Trail (coarse-scale)				
1995	Dist. to beach	0.57*	0.36	
	Dist. to estuary	0.55*	0.45	
	Dist. to river	0.05	0.73*	
2005	SSSa	0.56*	n/a	
	SSTa	0.34*	n/a	
	SSSg	0.01	n/a	
Carmanah Bay (fine-scale)				
2004	Dist. to beach	0.72*	0.36	
	Slope	-0.71*	-0.31	
	Depth	0.53	0.61*	
2005	Slope	0.82*	0.05	
	SSSg	0.50*	-0.35	
	SSSa	-0.19	0.93*	

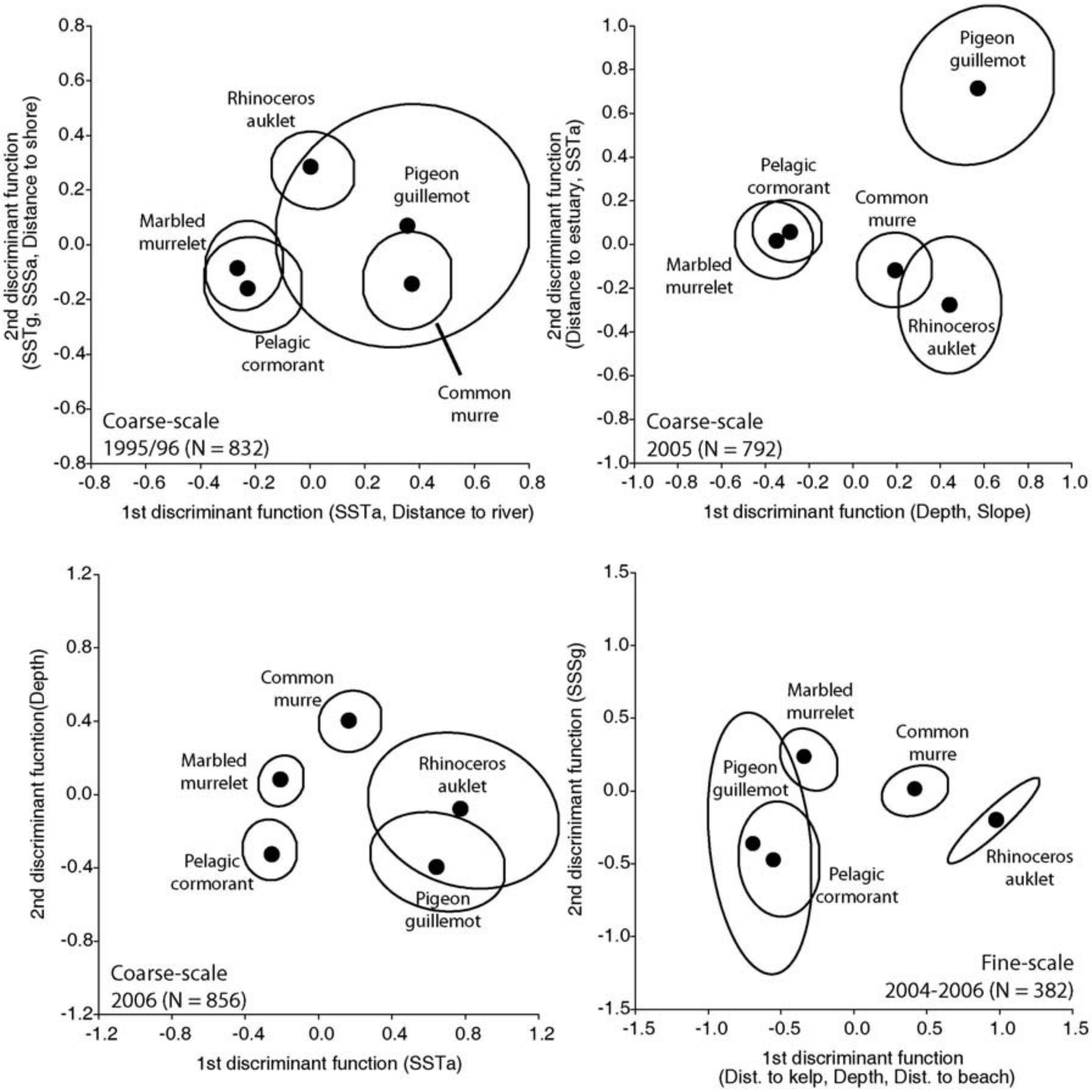


Figure 3.4 - Plots of the group centroids (within-group mean for the first and second discriminant functions) from discriminant function analysis performed on all transect segments with each species present. Ellipses represent a 95% confidence interval around the centroid. Variables in brackets for each discriminant function are those with the largest correlations with that particular function (Table 3.7).

Seabird habitat preferences: Classification and Regression Trees

CART analysis investigated habitat preferences by seabirds by comparing habitat use (presence/absence or abundance) relative to habitat availability. Multiple trees were grown for each species-year combination and averaged importance values showed distinct habitat preferences for each species (Fig. 3.5 and 3.6). Along the coarse-scale transects (Fig. 3.5), nesting habitat (% old-growth index for murrelets, distance to colony for all other species) was important in habitat selection for all species except murrelets in 1995/96 and pelagic cormorants in all years. Oceanographic variables (e.g. temperature and salinity) were most important for auklets and somewhat important for murrelets. Seafloor characteristics (e.g. depth and substrate) were important for murrelets and cormorants. Distances to shoreline features (e.g. beaches, coastline, rivers) were most important for murrelets, guillemots and cormorants. In Carmanah Bay, species differences in fine-scale habitat preferences were also obvious (Fig. 3.6).

The four most important environmental variables for each species-year combination were used to construct final CART models. This analysis found distinct habitat preferences among species and high variability among years. With coarse-scale data (Table 3.8) murrelets showed preference for proximity to beaches (<760 m), shallow water (<16 m), and proximity to nesting habitat (old-growth index >42.4% in 2005, >47.4% in 2006). Pigeon guillemots and rhinoceros auklets were closely tied to nesting habitats (preference closer to colonies). Murres and cormorants showed considerable inter-annual variability in habitat selection. Abundance data were modeled with regression trees for murrelets (Table 3.8 lower half) and showed broadly similar results as presence/absence models, even though only 5% of the variance in abundance was explained by the models.

Within Carmanah Bay (Table 3.9), fine-scaled analysis showed that murrelets preferred habitat close to beaches (<1 km) and over sandy substrates. Murres preferred higher surface temperature gradients and sandy substrate. Auklets preferred habitat more than 500 m from shore but still within 2 km of beaches. Finally, cormorants and guillemots showed nearly identical habitat preferences of shallow waters (<22 m) and closer to kelp beds (<400 m).

In the initial models, 80% of the data was used for training (building models) and 20% for testing model fit. Comparison of % correct classification between training and test data showed no significant differences for species/models ($p > 0.05$ in t-tests), except for murrelet models with fine-scale data (80.8% ± 0.7 correct *train* vs. 77.8% ± 0.7 *test*; $t_{88} = 3.05$, $p = 0.003$). Therefore testing model fit with simple resubstitution (e.g. training data) provides a good indication of model accuracy for the final models (Tables 3.8 & 3.9). In the final CART models, presence/absence data was 50 - 90% correctly classified depending on species and year. However, regression trees poorly predicted marbled murrelet abundance with percent variance explained ranging from 4.5 to 5.1% in coarse-scale models but slightly better in fine-scale models at 4.4 to 31.8%. This suggests that it is easier to predict seabird presence than abundance.

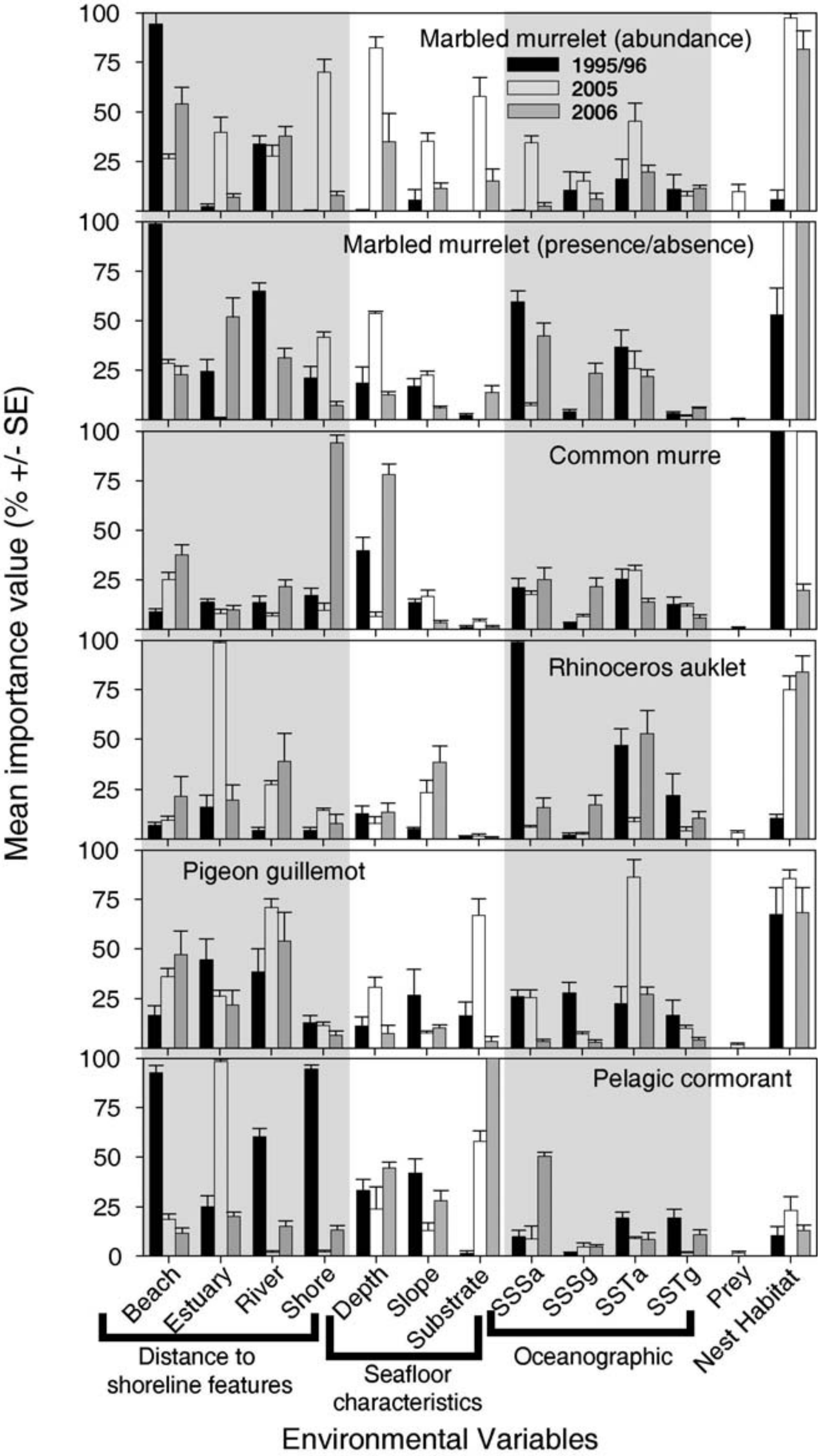


Figure 3.5 - Averaged importance values of environmental variables for CART models predicting species presence/absence or abundance along coarse-scale transects. Means are based on 10 replicate trees built for each species-year combination using a random subset of 80% of the data in each tree.

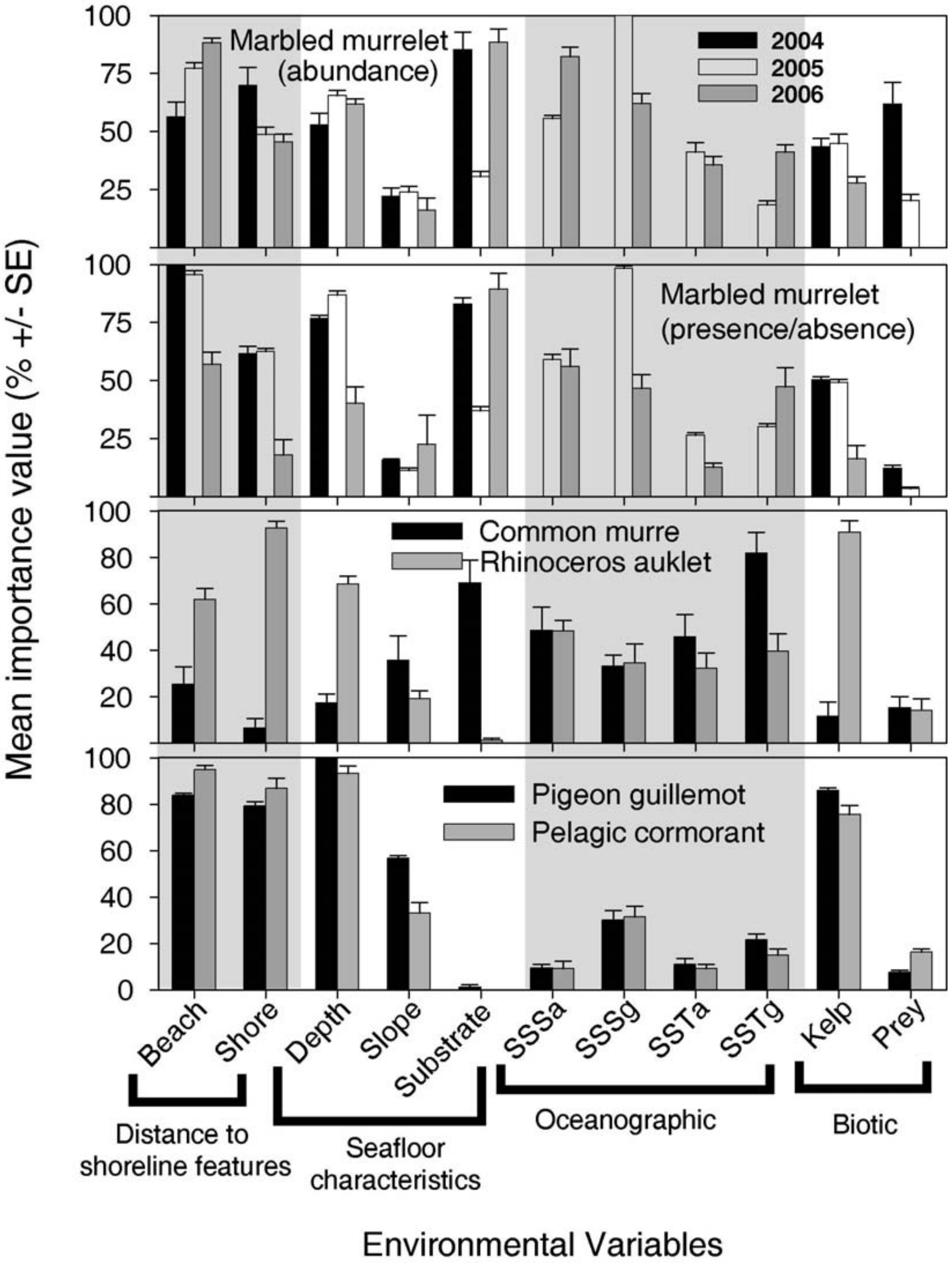


Figure 3.6 - Averaged importance values of environmental variables for CART models predicting species presence/absence or abundance in Carmanah Bay (fine-scale transects). Means are based on 15 replicate trees built for each species-year combination using a random subset of 80% of the data in each tree.

Table 3.8 - Coarse-scale habitat preferences by seabirds along southwestern Vancouver Island. Classification and Regression Trees (CART) were used to identify habitat preferences based on presence/absence (upper table) and abundance (lower table) data. Brackets indicate thresholds in preference. For example, the primary variable for murrelets in 1995/96 showed preference for regions less than 760 m from beaches. % correct classification was evaluated with simple resubstitution of data used to build the model. See Table 3.2 for acronyms.

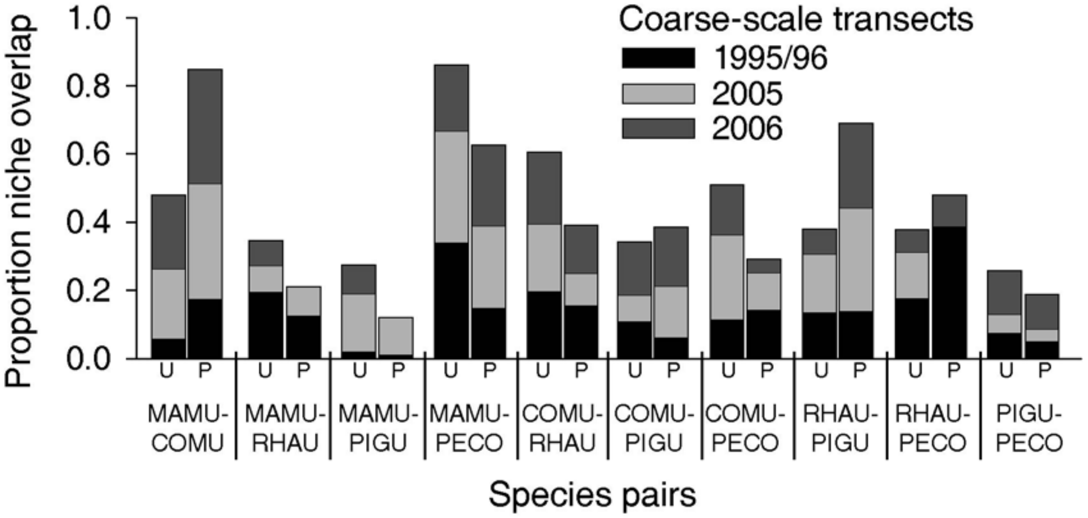
Species	Year	% Correct Classification	Primary variable	Secondary variable	Tertiary variable
Marbled murrelet					
	1995/96	61.7	Distance to beach (<= 0.76 km)		
	2005	71.2	Depth (<= 16 m)	Old-growth index (>42.4%)	Old-growth index (<54.8%)
	2006	64.3	Old-growth index (>47.4%)	Distance to estuary (<= 5.22 km)	if Dist. estuary >5.22 then SSSa (<= 0.8)
Common murre					
	1995/96	76.0	Distance to colony (>23.1 km)	Depth (<= 10 m)	SSSa (<= 0.2 p.p.t.)
	2005	54.0	Distance to colony (>24.4 km)	Distance to beach (< 6.7 km)	SSSa (> -2.2 p.p.t.)
	2006	63.5	Distance to shore (> 0.54 km)	Distance to beach (> 0.66 km)	Depth (> 10 m)
Rhinoceros auklet					
	1995/96	60.7	SSSa (>0.1 p.p.t.)		
	2005	74.1	Distance to estuary (<= 6.49 km)	Distance to colony (<= 2.6 km)	Distance to river (<= 5.3 km)
	2006	86.4	Distance to colony (<= 5.02)		
Pigeon guillemot					
	1995/96	86.3	Distance to colony (<= 1.93)	Distance to river (> 4.38 km)	
	2005	90.2	Distance to colony (<= 4.74 km)	SSTa (> 0.4 ^{o}C)	Substrate (rock/mixed > sand)
	2006	83.1	Distance to colony (<= 2.4 km)		
Pelagic cormorant					
	1995/96	50.1	Distance to shore (<= 1.06 km)	Beach (<= 5.6 km)	Slope (> 0.90)
	2005	68.8	Distance to estuary (> 6.22 km)	Distance to colony (>0.37 km)	Depth (<= 14 m)
	2006	70.4	Substrate (rock.mixed > sand)	Depth (<= 14 m)	Slope (<= 2.26)
		% Variance Explained			
Marbled murrelet (abundance data)					
	1995/96	5.1	Distance to beach (<= 0.74 km)		
	2005	4.5	Depth (<= 14 m)	Substrate (Rock > mix or sand)	Old-growth index (<= 54.3)
	2006	5.0	Old-growth index (>47.4%)	Distance to river (>3.94 km)	Distance to beach (<= 1.88 km)

Table 3. 9 - Fine-scale habitat preferences by seabirds in Carmanah Bay, southwestern Vancouver Island. Classification and Regression Trees (CART) were used to identify habitat preferences based on presence/absence (upper table) and abundance (lower table) data. Brackets indicate thresholds in preference. For example, the primary variable for pigeon guillemots showed preference for areas less than 20 m deep. % correct classification was evaluated with simple resubstitution of data used to build the model. See Table 3.2 for acronyms.

Species	Year	% Correct Classification	Primary variable	Secondary variable	Tertiary variable
Marbled murrelet					
	2004	79.6	Distance to beach (<= 0.98 km)	Substrate (sand/mixed > rock)	
	2005	85.6	Distance to beach (<= 0.98 km)	SSSg (>0.044)	
	2006	74.6	Substrate (sand > rock or mixed)	SSTg (>0.052)	
Common murre					
	2004-06	79.1	SSTg (>0.086)	Substrate (sand > mixed/rock)	
Rhinoceros auklet					
	2004-06	49.5	Distance to shore (>0.56 km)	Distance to beach (<= 2.04 km)	Distance to kelp (>0.04 km)
Pigeon guillemot					
	2004-06	76.4	Depth (<= 20 m)	Depth (> 6 m)	Distance to kelp (<=0.38 km)
Pelagic cormorant					
	2004-06	65.6	Depth (<= 22 m)	Distance to shore (> 0.26)	Distance to kelp (<=0.28 km)
		% Variance Explained			
Marbled murrelet (abundance)					
	2004	18.5	Substrate (sand or mixed > rock)	Prey Score (>0)	Distance to shore (<= 0.62 km)
	2005	31.8	SSSg (> 0.042)	SSSg (> 0.148)	if SSSg>0.148 then Dist. beach (>0.35 km)
	2006	4.4	Distance to beach (<= 0.98 km)	Substrate (sand or mixed > rock)	

Niche partitioning

Observed distributions (habitat use) and expected distributions (CART-based habitat preferences) were mapped to compare spatial overlap in area between species pairs. Overlay analysis showed a high degree of niche overlap between some species and for the most part, overlap in habitat use was similar to overlap in habitat preference for most species-pairs (Fig. 3.7). One noticeable exception was with murres that showed the greatest overlap with auklets in habitat use but the greatest overlap with murrelets in preferred habitat. This result mirrors the discrepancy between results of CCA/DFA models and those of CART models. Coarse-scale data showed the greatest overlap between the following pairs: murrelets-murres (preferred habitat), murrelets-cormorants (used and preferred habitat), murres-auklets (used habitat), and auklets-guillemots (preferred habitat). Fine-scale surveys showed the greatest niche overlap between guillemots-cormorants (preferred habitat), murrelets-guillemots (used habitat), and also murrelets-murres (both used and preferred habitats). Most of these results are generally in agreement with the three modeling techniques.



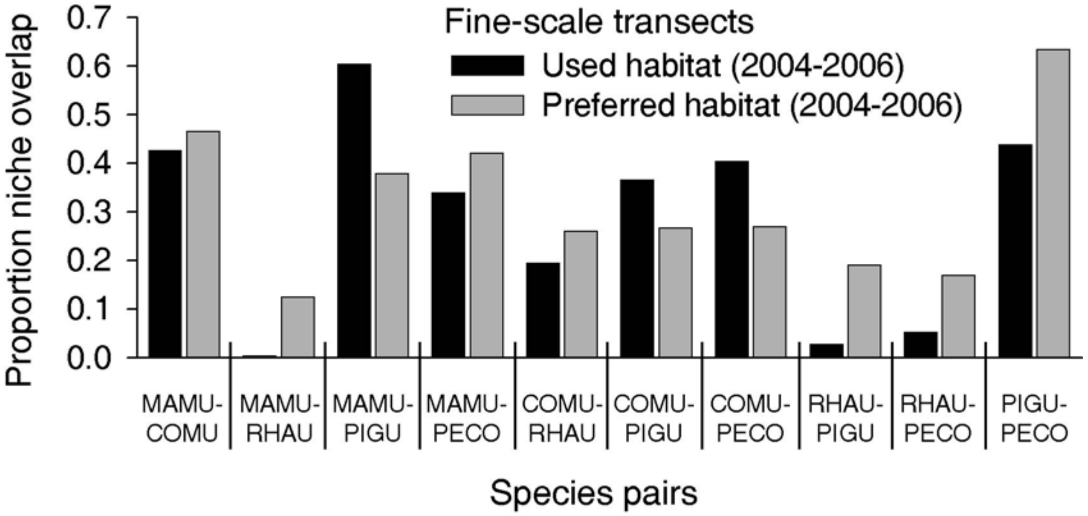


Figure 3.7 - Niche overlap between pursuit diving seabirds along the coarse-scale transects (upper figure) and in Carmanah Bay (fine-scale, lower figure). "Niche area" was mapped from "Used habitat" (U) based on kernel density analysis of original transect data, and "Preferred habitat" (P) based on preference rules derived from CART analysis (Tables 3.8 & 3.9). Proportion of niche overlap was calculated by GIS overlay analysis whereby overlap = (Area overlap between Species A & B)·(Total "niche area" for Species A & B)$^{-1}$.

Habitat selection by prey

Associations between prey and environmental variables were modeled using CCA, DFA, and CART. Prey data were only available for one transect in 1996, coarse-scale transects in 2005, and fine-scale transects in 2004 and 2005. Biplots from CCA (Fig. 3.3) show weak correlations (short arrows) between prey abundance and environmental variables, suggesting poor predictability of prey scores. DFA classified prey based on three categories (no-prey, low-prey, high-prey) showing significant classification with only the first discriminant function (Table 3.6). Coarse-scale models in 2005 failed to classify data based on the three categories but successfully classified data by prey presence/absence (Table 3.6). Plots of mean discriminant function scores (Fig. 3.8) suggest that high-prey scores occurred closer to beaches and estuaries in 1996 and prey presence was more likely with lower temperature and salinity anomalies in 2005. At Carmanah Bay, fine-scale high-prey scores were found closer to beaches, areas with low slope, and in shallower water (Fig. 3.8, 2004), and in areas with higher salinity gradients and anomalies (Fig. 3.8, 2005). DFA correctly classified between 56 and 72% of cases into the three categories. Finally, CART analysis classified prey presence/absence in relation to environmental variables (Table 3.10). Along the study area, prey were more likely to be found close to beaches (<3.2 km) in 1996 and in areas of higher temperature anomalies (> 1.2 ^{o}C) in 2005. In Carmanah Bay, prey was more likely to occur in shallow waters with moderate slopes (2004) and in areas of lower salinity and temperature anomalies and closer to beaches (2005).

Together these models suggest that the distribution and abundance of prey may be highly variable from year to year. Nevertheless, many of the variables that predicted prey (depth, beaches, SST, SSS) were also those that predicted bird distributions in any given year, thus identifying habitat as a link between predator and prey.

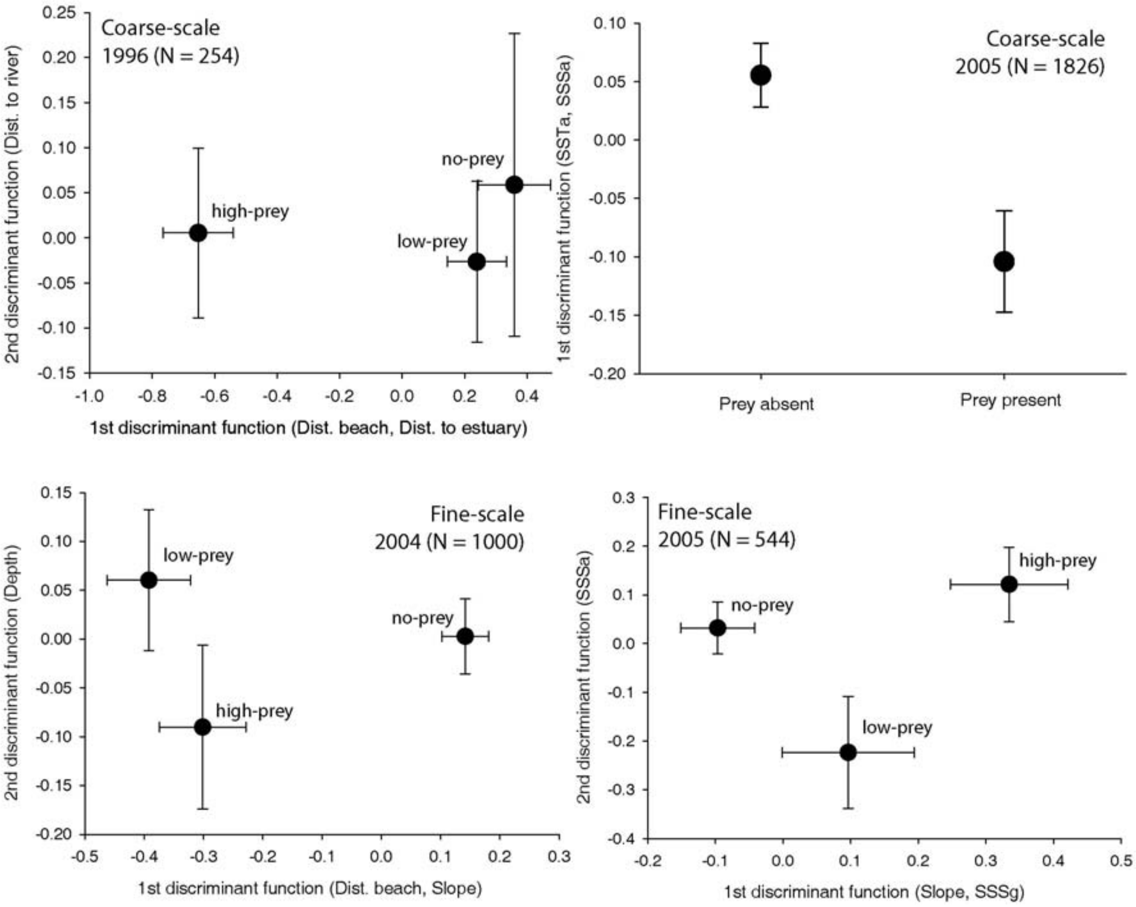


Figure 3.8 - Plots of mean ± SE discriminant function scores from DFA performed on all transect segments that recorded prey by hydroacoustic surveys. Variables in brackets for each discriminant function are those with the largest correlations with that particular function (Table 3.7). No-prey = score 0, low-prey = 0.1-1, high-prey > 1.

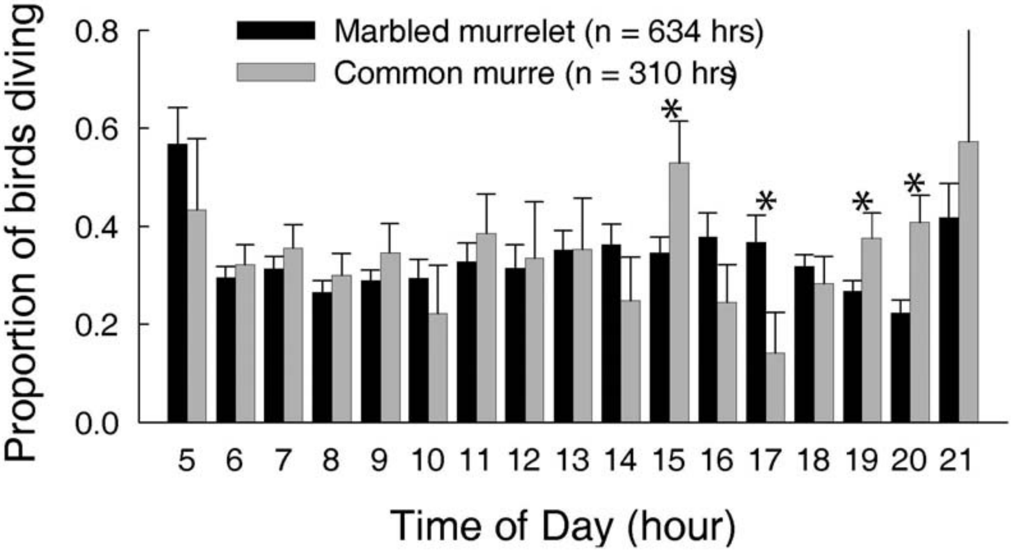
Table 3.10 - Habitat preferences by "prey" measured with hydroacoustic surveys along the West Coast Trail (coarse-scale) and around Carmanah Bay (fine-scale). Classification and Regression Trees (CART) modeled habitat preferences for the presence/absence of prey. Brackets indicate thresholds of habitat preference. For example, the primary variable for 1996 showed preference for areas less than 3.24 km from a beach. Note SST/SSS variables not included in 2004 models because they were not measured in that year. See Table 3.2 for acronyms.

Scale	Year	% Correct Classification	Primary variable	Secondary variable	Tertiary variable
Coarse-scale					
	1996	72.4	Distance to beach (<= 3.24 km)	SSSa (<= 0.1 p.p.t.)	if SSSa>0.1, then Dist to River (>2.82 km)
	2005	85.6	SSTa (> 1.2 ^{o}C)		
Fine-scale					
	2004	58.5	Depth (<= 32 m)	Slope (> 0.46)	Slope (<= 1.36)
	2005	66.0	SSSa (<= 0.8 p.p.t.)	SSTa (<= 0.0 ^{o}C)	Distance to Beach (<= 1.86 km)

Diurnal partitioning in diving activity

There was considerable inter-specific variability in diurnal diving activity for most species (Fig. 3.9). Pelagic cormorants showed the highest and most continuous diving effort throughout the day with 60 to 70% of individuals diving from dawn until dusk. Pigeon guillemots showed slightly lower diving effort (~50%) with a slight peak in the mid afternoon and no birds observed between 0500-0700 hrs. Rhinoceros auklets exhibited the lowest diving effort and a continual decline in diving activity throughout the day from ~30% near dawn to less than 10% near dusk.

Common murres and marbled murrelets showed very little divergence in diel diving activity. The pattern suggests the greatest effort near dawn and dusk with a slight increase mid-day between 1200 to 1600 hrs. Between species, only four out of 17 hours of the day showed significant differences in mean proportion of birds diving (hr 15: $t_{30} = -2.502$, $p = 0.018$; hr 17: $t_{27} = 2.253$, $p = 0.033$; hr 19: $t_{84} = -2.289$, $p = 0.025$; hr 20: $t_{86} = -3.450$, $p < 0.001$).



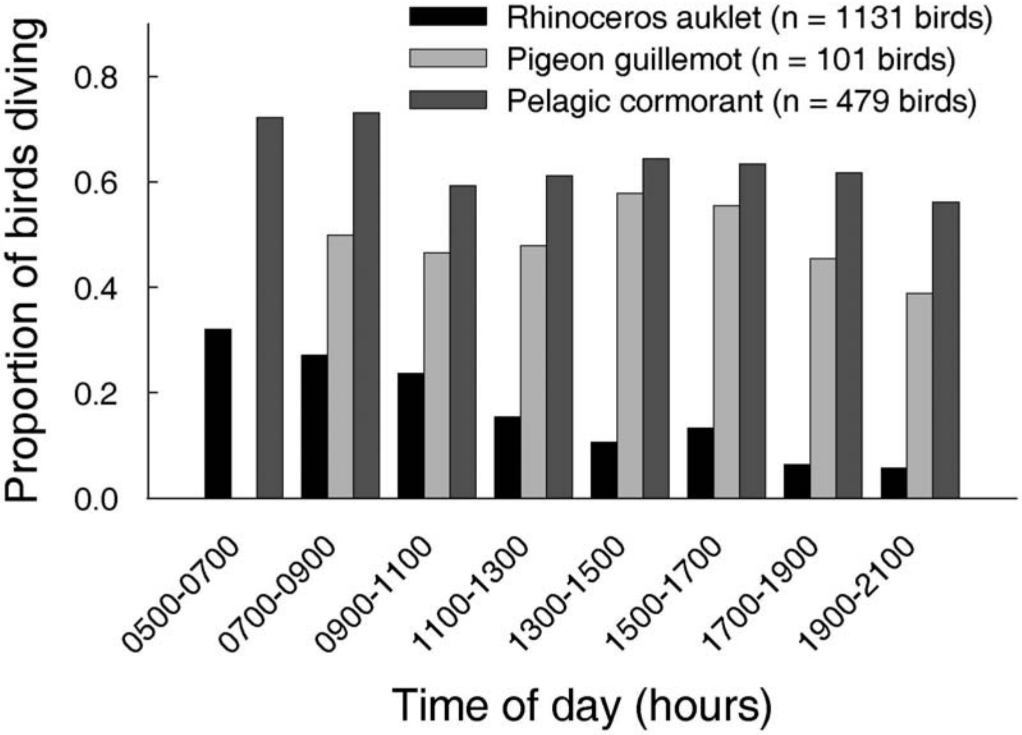


Figure 3.9 - Diurnal foraging patterns of five species of pursuit diving seabirds along southwest Vancouver Island. For murres and murrelets, mean ± SE proportion of birds diving using hours with ≥ 5 individuals. For other species (bottom figure), all observations are pooled into 2-hr bins because too few individuals were observed to calculate means per hour. * $p < 0.05$ for t-tests comparing murres and murrelets.

DISCUSSION

Model performance

In this paper, three different analytical techniques were used to model species-habitat relationships. These were chosen specifically for their ability to handle inter-correlated predictor variables (CCA and DFA), suitability for datasets with many zeros and spatial autocorrelation (CCA and CART), and have been previously used in species-habitat modeling studies (all).

Model performance varied among techniques. CCA found moderately high species-environment correlations: 0.43 to 0.30 for the first canonical axes and 0.16 to 0.23 for the second axes. However, the variance extracted by the canonical correspondence analysis (Specie-Env. total; Table 3.5) accounted for only about 5% of the total encounter rate variance (Overall total). Nevertheless, this low level of explanatory power is consistent with other ecological abundance data used in CCA (Ter Braak 1986). Reilly and Fiedler (1994) considered 15% explanatory power to be fairly good in a CCA analysis of dolphin-habitat associations because dolphins, like seabirds, are very mobile and patchily distributed animals. DFA showed a relatively poor ability to correctly classify species by environment variables: only 36-42% and 25% correct classification for coarse- and fine-scale data respectively. In contrast, CART analysis had the highest prediction accuracy with presence/absence data (typically > 60% correct classification for all species in all years), but explained very little of the variance in seabird densities (~5%, CART analysis of murrelet abundance). Algorithmic modeling techniques (e.g. CART) are thought to be more powerful and flexible than statistical modeling techniques (Hochachka et al. 2007) and are good at making predictions (Breiman 2001). Non-parametric models (CART) often preformed better (fewer false negatives, type II errors) than parametric models (Segurado & Araujo 2004), though Karels et al. (2004) saw nearly identical performance between DFA and CART models. In this study CART models performed best in the analysis of presence/absence data whereas both CART and CCA explained similar, low amounts of variance in seabirds densities. Thus it was easier to predict presence/absence and harder to predict density. This is not surprising given the wide range in density and the mobile nature of the birds.

Species specific difference may have influenced model performance as well. DFA had the highest predictability for murrelets and auklets (~40%) but CART analysis had the highest predictability for guillemots (~80-90%; coarse-scale) and murrelets (~75-85% fine-scale presence/absence). With presence/absence data, non-parametric models perform better than parametric models for species that are widespread, occupy a niche position similar to mean habitat conditions within the study area, and have a wide niche breadth (Segurado & Araujo 2004); i.e., generalists. With abundance data, species-habitat modeling had better predictability for species with high environmental specialization and higher maximum densities (Seoane et al. 2005). This suggests that generalist species are better modeled with presence/absence data while specialist species may be better predicted with abundance data. All seabirds in this study are thought to be generalists (Gaston & Jones 1998), which may explain why presence only models (DFA) and presence/absence models (CART) performed better than abundance models.

There were also some contradictory results between the three modeling techniques, particularly between DFA/CCA models and CART models. The CCA and DFA showed strong associations between murres and auklets with both of these differing from marbled murrelets. Cormorants and guillemots were quite variable in habitat associations and generally not consistently associated with other species. However, the CART models, and their derived distribution maps, produced quite different results showing high overlap between murres and murrelets. There are two main reasons why these differences may have occurred. First, CART analyses were the only models that included nesting habitat. Nesting habitat was important for most species in CART models often as the primary selection variable. Second, overlay analysis of observed distributions (Kernel-based habitat *use*) were more similar to CCA/DFA results than the expected distributions (CART-based habitat *preference*). Therefore discrepancy between CCA/DFA and CART models may reflect a difference in habitat use vs. habitat preference. For example, murrelet habitat use was most strongly predicted by depth and distance to shore (longest arrows in CCA, Fig. 3.3), but habitat preferences was often predicted by distance to beaches (Tables 3.8 & 3.9). This reinforces the importance of clearly distinguishing between habitat use and preference (Jones 2001) which have different biological interpretations and implications. Therefore, although the models show some inconsistencies, they are providing different information about how seabirds select their habitats.

Habitat use and preference

CCA and DFA models assessed patterns of habitat use and showed strong agreement at both coarse- and fine-scales. CART analysis identified many of the same environmental variables as important. Here I summarize patterns of habitat use and selection for each species and compare this with previous studies.

Marbled murrelet habitat use differed from other alcids mostly along the first canonical axis and the first discriminant function. At coarse- and fine-scales, they showed preference for shallow, nearshore waters, often closer to beaches, and close to kelp beds. In some years they also showed preference for cooler sea-surface temperatures (SST). CART analysis showed similar preferences in proximity to beaches and shallow water, though proximity to old-growth nesting habitat (i.e. higher old-growth index) was also evident in later years (2005 and 2006). At fine-scales CART analysis identified sandy substrates and SSS gradients as important.

Murrelet affinities for shallow (<30 m), nearshore (<1 km) waters have been widely reported throughout their range (Ralph et al. 1995, Burger 2002, and references therein). Murrelet associations with substrate have shown mixed results including affiliations with glacial sills (Carter 1984), tidal flats (Miller et al. 2002), and sandy shorelines in British Columbia (Burger 1997, Yen et al. 2004a), thought not in Alaska or California (Miller et al. 2002, Day et al. 2003). Even murrelet nesting areas have been associated with proximity to sandy beaches (Meyer et al. 2002). The importance of substrate/beaches suggests a strong link between murrelets and their primary prey, sand lance, which are found along sand/gravel beaches of the study area (Haynes et al. 2007). The importance of cooler SST mirrors the habitat selection of murrelets in California (Becker & Beissinger 2003) and agrees with previous work in our study area where murrelet abundance was higher in years with cooler ocean temperatures (Burger 2000). Pacific sand lance are also more abundant in colder, more saline habitats (Abookire & Piatt 2005). Along the West Coast Trail, variability in SST was associated mainly with warm river outflow (rather than upwelling conditions as in California; Becker &

Beissinger 2003), thus preference for cooler SST likely reflects a preference for habitat not influence by river outflow (though see murrelet preference for > SSS gradients in 2005 fine-scale, this chapter, when prey was scarce in Carmanah Bay, Chapter 4). Finally, because I investigated habitat use during the breeding season, it was not surprising that proximity to nesting habitat influenced marine habitat selection. At very broad scales (100's km), at-sea abundance and distribution of murrelets has been correlated with inland nesting habitat (Raphael et al. 2002, Yen et al. 2004a, Raphael 2006) and nesting habitat may even be more important than marine habitat at predicting offshore abundance (Miller et al. 2002). At coarse-scales (<100 km) proximity to nesting habitat is also important in marine habitat selection (this study, Becker & Beissinger 2003). The lack of nesting habitat association in 1995/96 in this study could either reflect a mismatch in habitat data for that year (inland habitat data was based on satellite imagery from 2003-2004) or the higher abundance of murrelets in 1995/96 which forced birds to disperse along the study area regardless of nesting habitat distribution.

Common murres and rhinoceros auklets showed broad similarities in habitat use based on CCA and DFA. Similar distributions for these two species were found in the same area by Burger et al. (2008). At coarse-scales, compared to murrelets, they were in deeper waters, farther from beaches, farther from rivers, and in warmer (>SSTa) habitats. Coarse-scale CART analysis showed slightly different habitat preferences with auklets typically in close proximity to colonies, estuaries and rivers, as well as more saline habitat (>SSSa) and murres preferring areas farther from colonies, shallow and less saline water (1995/96) or deeper more saline water (2005/06). At fine-scales, both species showed preferences for deeper waters and substrate associations (auklets closer to beaches and murres preference for sandy substrate).

Because heavier alcids can dive for longer periods of time (Watanuki & Burger 1999) the preference of deeper waters by murres and auklets is not surprising. Auklets are epipelagic foragers attacking prey in mid-water or from below (Burger et al. 1993, Kuroki et al. 2003), a behaviour which may be easier in deeper waters. They typically are found over the continental shelf but in waters >15 m deep (Burger et al. 1993, Gaston & Dechesne 1996), and colonies are often situated in cooler more saline waters (Kaiser & Forbes 1992). Likewise, at meso-scales murres show affinities for the continental shelf

(Yen et al. 2004b) and cooler waters (Haney & Schauer 1994, Huettmann & Diamond 2001). Auklet and murre associations with SST and SSS anomalies in this study suggest that birds may be cueing in on patterns of water circulation. The greatest influence on SSS and SST in the study area is from freshwater inputs either from rivers or tidal flux at the Nitinat Narrows. Both species have been associated with tidal currents elsewhere (Haney & Schauer 1994, Decker & Hunt 1996, Gaston & Dechesne 1996, Holm & Burger 2002, Zamon 2003). CART models showed colony proximity to be an important factor in habitat selection. Around Tatoosh Island, the nearest murre breeding colony to our study area, both auklets and murres forage near the colony (Parrish et al. 1998), but along the West Coast Trail murrelets showed preference for areas farther from Tatoosh. Bird densities are not always proportional to distance from breeding colonies (Haney & Schauer 1994, Burger et al. 2008) and habitat preferences and attraction of prey schools may outweigh the effects of proximity to colony at this spatial scale. Differences of 10-40 km from the colony are likely to be insignificant for predators like common murres that commute up to 100 km to foraging grounds (Davoren et al. 2003b).

Pigeon guillemots and pelagic cormorants displayed different habitat use at coarse-scales but nearly identical habitat use at fine-scales. Moreover, there was extensive inter-annual variability in habitat preferences. Overall, they selected factors associated with seafloor characteristics (e.g. depth, slope, substrate types). A major difference between the two was the close association to colonies for guillemots but not for cormorants. There is very little information on pigeon guillemot or pelagic cormorant marine habitat use. Others have noted that guillemots are found close to colonies (<7 km) during the breeding season (Ewins 1993 and references therein). The high energetic demands of rearing more than one young (Mehlum et al. 1993) make near-colony foraging an important strategy for many *Cepphus* species. Both guillemots and cormorants show preference for shallow waters and rocky substrates (Ainley et al. 1981, Haney 1991, Ewins 1993, Hobson 1997) owing to the importance of benthic prey items in their diets. Guillemots prefer waters 15-20 m deep which match their most frequent diving depths (Clowater & Burger 1994). Pelagic cormorants have also been observed foraging on the fringes of kelp beds in California (Foster & Schiel 1985). Other cormorant species are associated with shallow waters, substrates and shoreline types

(Hebshi 1998, Stapanian & Bur 2002, Heithaus 2005). Tidal currents can also play an important role in habitat use for both pigeon guillemots and pelagic cormorants (Haney & Schauer 1994, Holm & Burger 2002). Inter-annual variability in habitat use/selection may reflect the mixed diet of these birds (demersal and epipelagic fish); other cormorants readily switch habitat use from year to year depending on availability of prey types (Watanuki *et al.* 2004).

Seabird associations with prey

The distribution and abundance of prey is fundamental to our understanding of foraging strategies and habitat use by marine birds (Safina & Burger 1985, Piatt 1990, Davoren et al. 2003a). Yet seabird-prey associations are largely scale-dependent and rarely observed at small (<10 km) spatial scales (Logerwell & Hargreaves 1996, Fauchald et al. 2000, Davoren et al. 2002). In offshore areas near the study site, murres and auklets showed fine-scale associations with prey at patch radii of 2-5 km (Burger et al. 2004); similar to patch radius of seabird aggregations within the study site (1-8 km; Burger et al. 2008). The present study found very little association between seabirds and prey which was not surprising given the small study area (<70 km) and sample units (1-min. time intervals). Fine-scale predator-prey associations may be more apparent when prey is scarce and regional prey abundance is low (Vlietstra 2005). Yet Davoren (2000) suggested that in years when prey are more dispersed, it is difficult for seabirds to maintain contact with prey and thus seabird-prey associations occur at larger spatial scales. Seabirds show a threshold response to prey densities (Piatt 1990) suggesting that large patches are needed for foraging (Davoren 2000), but when prey are more abundant than predators, birds might not need to find every school and hence you can get low predator-prey correlations in transects (Woodby 1984). This highlights the variability and wide range of conditions that affect predator-prey associations with transect surveys. Nevertheless, it is important to recognize the limitations of hydroacoustic sampling along transects which typically focus only on a narrow beam of detection below the vessel: many prey may be missed adjacent to the vessel which birds might have located.

Most studies assessing seabird-prey associations have looked only at prey effects and ignored the concomitant influences of habitat which may influence the distribution of both prey and birds. The lack of prey effect in our study simply reflects the stronger link between seabirds and habitat than seabirds and prey. Seabirds may use memory to locate predictable foraging areas (Davoren et al. 2003b). Beaches or substrate played an important role in habitat selection for all species in our study, likely owing to sand lance associations with sand and gravel substrates (Robards et al. 1999, Ostrand et al. 2005, Haynes et al. 2007). In 1996 and 2004, prey abundance was higher in areas closer to beaches, but in 2005 SST and SSS was a better predictor of prey distribution. Thus inter-annual changes in prey-habitat associations may be largely responsible for inter-annual variability in seabird-habitat associations particularly for generalist species. For example, in Carmanah Bay when prey were restricted to shallow waters in 2004, murrelets selected habitat by proximity to beaches, but in 2005 both murrelets and prey were associated with SSS and SST variables. Generalist species may readily switch between demersal and epipelagic prey (Tremblay & Cherel 2000, Litzow et al. 2002) which may depend on inter-annual changes in prey availability (Watanuki et al. 2004) or prey quality (Litzow et al. 2004). Marbled murrelets also show prey switching depending on regional oceanographic conditions (Becker et al. 2007). Therefore consistent inter-annual habitat correlations may not exist because of the opportunistic nature of all the birds in this study - they will sometimes be foraging on alternative prey or habitats as prey availability changes daily, seasonally or annually.

Temporal niche partitioning

After habitat and food, activity budgets have been considered an important dimension of niche partitioning (MacArthur & Levins 1967, Schoener 1974, Carothers & Jaksić 1984) though not widely recognized as a mechanism for coexistence (Kronfeld-Schor & Dayan 2003). Diurnal temporal partitioning facilitates the shared use of common resources for many animals (Adams & Thibault 2006, Valeix et al. 2007). I investigated diurnal patterns in diving activity as a mechanism for temporal niche partitioning among seabirds.

There was some evidence to suggest temporal niche partitioning among species in this study. Timing of entrapments of murres and auklets in gillnets suggested coexistence facilitated by auklets foraging in the morning and murres more frequently in the afternoon (Lance & Thompson 2005). In this study rhinoceros auklets concentrated foraging effort early in the day with a continual decline towards dusk, potentially minimizing interactions with other species. Diurnal decline in auklet foraging may also be linked to their diel movements since observations of auklets near their nesting colony at Seabird Rocks showed increased foraging effort towards the later part of the day (Davoren & Burger 1999). This discrepancy may reflect auklets that venture farther from the colony in the morning to feed themselves but return to areas near the colony when foraging to provision chicks before sunset (Davoren & Burger 1999). With this strategy, auklets may minimize both temporal and spatial overlap in habitat use with other species.

Diurnal partitioning in diving effort offers little evidence of temporal niche partitioning for the four other species in this study. I expected marked variation in diurnal activity budgets because murres, guillemots, and cormorants deliver food to young during all daylight hours (with some diel fluctuations) whereas auklets visit colonies shortly after sunset (Davoren & Burger 1999) and murrelets predominantly early in the morning or late in the evening (Burger 2001). These differences in timing of breeders' visits to nest sites may instead have manifested in diel differences in habitat use (foraging closer to nest sites before prey delivery), which were not examined.

Diel patterns in diving activity for murrelets, murres, and rhinoceros auklets indicate crepuscular foraging (Fig. 3.9) but may also suggest nocturnal activity during periods when diving could not be monitored in this study. Elsewhere, auklets and murres have been recorded foraging at night (Croll et al. 1992, Kuroki et al. 2003), but based on VHF telemetry work there is no evidence of nocturnal foraging by murrelets (Jodice & Callopy 1999, Henkel et al. 2003, M. Z. Peery pers. comm., P. N. Hébert pers. comm.). Thus propensity for nocturnal foraging may be an additional temporal dimension in which niche partitioning occurs.

Alternatively, temporal resource partitioning may occur on longer time-scales. Partitioning and overlap of shared resources may vary with daily variability in food abundance. The superabundance of food facilitates shared resources among seabirds but food shortages promote niche differentiation (González-Solis et al. 1997). Temporal partitioning in habitat use may also be seasonal (Jones et al. 2001, Friberg et al. 2008) which may explain the post-breeding exodus of murrelets from the study area at the same time that murre densities were increasing (Burger et al. 2008). Murrelets, and other seabirds, also show seasonally variable foraging effort to accommodate the high energetic demands of chick-rearing (Chapter 4). I did not examine daily or seasonal variability in habitat use, which may additionally expand on the niche partitioning of coexisting seabirds.

Competition

Both exploitative competition (depletion of shared resources) and interference competition (aggression or fighting over resources) are ways that individuals or populations may compete for shared resources (Gotelli 2001). Exploitation competition has been difficult to demonstrate in marine systems (Birt et al. 1987), but interference competition suggests that larger species may exclude smaller species from optimal foraging habitat (Piatt 1990, Ballance et al. 1997, Burger et al. 2008). Both habitat selection and diving activity patterns suggest that murres and murrelets exhibit the highest degree of overlap in our study area and thus are most likely to be at odds for competition. Murrelets are considerably smaller than murres and therefore likely to be the subdominant species in any competitive interactions. In the Atlantic, the aggressive behaviour of murres towards smaller Atlantic puffins (*Fratercula arctica*) has been observed and may demonstrate the potential for interference competition between the two (Piatt 1987, Piatt 1990). Nevertheless, I saw no evidence of direct aggressive interactions between murrelets and murres in our study. Interference competition may also result in temporal partitioning in resource exploitation (Carothers & Jaksić 1984) whereby larger species dictate the temporal activity patterns of smaller competitors (Valeix et al. 2007).

The ecological conditions of the region may also determine the degree to which species compete. When food is scarce, animals my need to forage at the same time, but when food is abundant, temporal partitioning can occur resulting in the dominant consumer foraging first (Richards 2002). This may explain why in some situations murrelets initiate flock formation with mixed-species feeding flocks (Mahon et al. 1992, Ostrand 1999) yet in other situations murres may disrupt the feeding of smaller alcids (Chilton & Sealy 1987). Alternatively competing species may avoid each other altogether (Burger et al. 2008). Even intra-specific competition may cause foraging ranges of adjacent colonies to contract to minimize competition among neighbours (Ainley et al. 2004). Indeed differences in foraging ranges of sympatric species from nearby colonies have been viewed as a primary mechanism for habitat partitioning for some seabirds (Weimerskirch et al. 1988). Finally, there are also large seasonal changes in the relative abundance of murrelets and murres in our study area which might minimize competition. Murrelets are most abundant through the summer but decline rapidly in late July (Wong et al. in press) when murres and auklets are increasing (Burger et al. 2008). The effects of competitors are likely to be density dependent whereby competition is stronger when competitors are at higher densities (Gurevitch et al. 1992).

Habitat partitioning and coexistence

Closely related seabird species frequently show a high degree of dietary overlap (Vermeer et al. 1987, Forero et al. 2004), therefore niche differentiation among seabirds has always been somewhat of a mystery. Studies of diet (Bryant & Jones 1999), morphology (Birkhead & Nettleship 1987a), and breeding ecology (Birkhead & Nettleship 1987b) have failed to identify partitioning between closely related coexisting alcids such as *Uria* spp. Niche differences between piscivorous seabirds may not be obvious and coexistence may be facilitated by subtle differences in foraging strategies (Vermeer et al. 1987) or prey densities (Piatt 1990, Ostrand et al. 1998). Instead, habitat complexity and environmental variability has been proposed as a better mechanism to explain coexistence within alcids (Bédard 1976, Haney & Schauer 1994). Results of this study support this view by showing that habitat use and habitat selection can identify niche partitioning between coexisting seabirds at coarse- and fine-scales.

The five sympatric species in this study may be divided into two ecologically similar groups that one would expect high niche overlap. One group, marbled murrelets, common murres and rhinoceros auklets, are epipelagic foragers taking primarily small schooling fish and show high dietary overlap (Carter 1984, Hobson et al. 1994, Burkett 1995, Davoren & Burger 1999, Lance & Thompson 2005). The second group, pelagic cormorants and pigeon guillemots, are primarily benthic foragers also with similar diets (Hobson et al. 1994). Closer examination within and among these groups provides evidence of habitat partitioning which may facilitate coexistence.

Cormorants and guillemots exhibited very little overlap in habitat preferences at coarse-scales. Instead, guillemots showed greater overlap with auklets, and cormorants overlapped with murrelets. Since both auklets and guillemots nested in a mixed colony at Seabird Rocks, auklet-guillemot overlap was likely due to preferences of foraging near colonies. Without a colony effect, there was less spatial overlap between guillemots and other alcids in our study area (Burger et al. 2008, this study). Overlap between cormorants and murrelets was mainly due to preferences for shallow waters. When species do overlap in habitat preferences, differences in functional traits may create niche specializations and facilitate coexistence (Cavender-Bares et al. 2004). For example, murrelets and cormorants exhibit striking differences in morphology (smallest vs. largest species in this study), plumage, diving behaviour (wing vs. foot propulsion), and foraging tactics (epipelagic vs. benthic foragers). Moreover, species that overlap in their primary habitat may also coexist if they use different secondary habitats (Wasserberg et al. 2007). At fine-scales, habitat-partitioning was more evident between cormorants and murrelets and between guillemots and auklets.

Among the epipelagic alcids, habitat partitioning was less clear. CCA and DFA classified similarities in habitat use between murres and auklets which segregated from murrelets; this parallels observations in the same area by Burger et al. (2008). However, mapping of preferred habitats (CART-based models) showed considerable overlap between habitats of murrelets and murres (Fig. 3.7). Reasons for the discrepancy between DFA/CCA and CART results are discussed above. There are three reasons I believe this discrepancy exists between my results and those of Burger et al. (2008). First, the studies use distinct methodological approaches whereby Burger et al. examined numerical correspondence between species, but this study looked at species-habitat relationships. Thus while species may broadly overlap or segregate numerically, this may differ from their preferred habitats. Second, the murre-murrelet association was much stronger in 2005/06 (~0.20 and 0.34 proportion overlap in used and preferred habitats) than in 1995/96 (0.06, used; 0.17, preferred) when the Burger et al. study was conducted. This suggests that habitat preferences and bird distributions may have shifted over the past decade and murrelet-murre habitat preferences are more similar now. Lastly, in the 1990's both murres and auklets were much more abundant than they currently are (Table 3.3, this study). Effects of competitors are felt more strongly when competitors are at higher densities (Gurevitch et al. 1992), therefore, if competitive interactions segregated murrelets from murres/auklets in the 1990's (Burger et al. 2008), the now comparatively low densities of murres and auklets may have eliminated this segregating response.

Despite this apparent overlap in mapped preferred habitats, the actual environmental variables selected by murres and murrelets still differed suggesting some degree of habitat specialization within overlapping habitats. Moreover, at coarse-scales all species pairs showed less than 40% overlapped in mapped habitat (mean overlap 14.2 % ± 1.6 of used habitat and 14.8% ± 1.8 of preferred habitat). Since all of these species are somewhat generalist and all are highly mobile, it is not too surprising that there is some continuing habitat overlap despite their preferences. They are living in a fluid environment and feeding on mobile prey, so tight habitat correlations might never be achieved. Key differences among species in this study appear to be linkages with depth and substrates for benthic foragers, reliance on oceanographic factors (surface temperature and salinity) for murres and auklets, and variable associations with depth, oceanographic variables, and substrates for murrelets.

Together, these results suggest that habitat specializations offer a plausible mechanism to explain the coexistence of seabirds at coarse- and fine-spatial scales. Thus the competitive exclusion principle has little bearing on community structure at this scale. When the possibilities for complete spatial segregation are limited, natural selection is likely to favour traits of competitors in the same direction, suggesting that competing species should coexist (Ghilarov 1984). In the Pacific where many alcids have coevolved, environmental variability is likely a key factor structuring habitat use and coexistence in this community of piscivorous seabirds.

Chapter 4 - Limited foraging flexibility: increased foraging effort by a marine predator does not buffer against scarce prey

ABSTRACT

Flexibility in activity time budgets allows animals to cope with heterogeneous and changing environments. Many marine predators, such as seabirds, exhibit flexibility in their foraging behaviour to buffer reproductive success against periods of low prey availability. Over three years, 2004 to 2006, I studied the foraging behaviour of a threatened seabird, the marbled murrelet (*Brachyramphus marmoratus*) in southwestern Vancouver Island, British Columbia. An information-theoretic approach was used to compare among factors (temporal, spatial, environmental, and competitors) that may influence diving activity. I also quantified local prey availability by hydroacoustic surveys and regional oceanographic conditions (chlorophyll *a* concentrations and upwelling indices) to investigate relationships between diving activity, food supply and environmental conditions. Prey indices varied spatially, seasonally and annually, showing reduced prey availability during incubation and chick-rearing of 2005. Upwelling indices and chlorophyll *a* concentrations, as an index of primary productivity, were delayed in 2005. Year and breeding phase had the greatest impact on diving activity, with additional variation among sites. Murrelets increased diving activity in years and seasons with scarce prey and poor oceanographic conditions (incubation and chick-rearing 2005) and decreased diving activity at sites with high prey availability. There was a linear relationship between diving activity and food availability, suggesting no clear thresholds in response to decreases in prey. Despite their flexible activity budgets, increased foraging effort by murrelets in 2005 was inadequate to ensure average levels of reproductive success. Thus, flexible foraging behaviour by murrelets may be ineffective to buffer reproductive success when environmental conditions are extremely poor.

INTRODUCTION

The ability of animals to adjust activity budgets affords several advantages to their survival and reproduction. In the marine environment, where food resources are often patchy and ephemeral, flexible activity budgets can allow predators to cope with fluctuations in prey availability (Mori & Boyd 2004, Weimerskirch et al. 2005). Spatial and temporal environmental variability are thought to be important factors driving the evolution of life histories (Stearns 1992). Although some life-history traits, such as number of offspring, may be relatively unchangeable in the face of short-term environmental perturbations, others, like foraging behaviour, appear comparatively flexible. This is particularly true for many seabirds that have several fixed life-history traits (e.g. clutch sizes, delayed age of maturity; Gaston 2004) but flexible foraging behaviours that are adaptable to variable environmental conditions (Waugh & Weimerskirch 2003).

Flexibility in foraging has been demonstrated widely in seabirds (Monaghan et al. 1996), and in particular piscivorous alcids (Alcidae), that adjust their activity budgets in years when foraging conditions are poor (Burger & Piatt 1990, Monaghan et al. 1994, Davoren 2000, Litzow & Piatt 2003). Behavioural responses to prey may be observed much earlier than physiological or reproductive responses (Piatt et al. 2007b), and foraging behaviour, more than other parameters (e.g. diet, population numbers, reproductive success), can be a useful index of the status of prey populations (Monaghan 1996). Nevertheless, despite the apparent flexibility of activity budgets for many seabirds, thresholds may exist whereby foraging flexibility can no longer effectively buffer against very low food availability (Dall & Boyd 2002). Seabird response to changes in prey availability may be non-linear (Cairns 1987), so that parents work hardest when food is most scarce, and therefore suggesting prey thresholds (Harding et al. 2007, Piatt et al. 2007b).

Marbled murrelets (*Brachyramphus marmoratus*) are non-colonial seabirds with cryptic nests on limbs of old-growth conifers (Nelson 1997). They have been afforded threatened or endangered status throughout much of their range due to loss of inland nesting habitat (Burger 2002, McShane et al. 2004), and recent findings have suggested that variability and changes in marine habitat are also influencing their decline and recovery. Their reproductive success has been linked to the availability of prey (Peery et al. 2004, Becker et al. 2007) and long-term dietary shifts (Becker & Beissinger 2006, Norris et al. 2007). Adult survival is dependent on large scale oceanographic conditions (Peery et al. 2006). I studied the foraging behaviour of marbled murrelets in southwestern British Columbia during three years, 2004 to 2006, with contrasting prey availability. In 2005, coastal regions of the northeastern Pacific experienced highly anomalous conditions with the onset of upwelling delayed by two to three months (Schwing et al. 2006), which resulted in widespread ecosystem changes affecting many organisms including seabirds (Sydeman et al. 2006). The role of behavioural flexibility by marbled murrelets to buffer variations in foraging conditions is unknown, but is likely to be important in understanding the long-term responses of this species, and marine predators in general, to changing oceans.

I used an information-theoretic approach (Burnham & Anderson 2002) to decipher between different factors that may be influencing foraging activity budgets of marbled murrelets. I compared models with (1) temporal predictors (time of day, breeding phenology, year), (2) spatial predictors (multiple sites), (3) environmental predictors (tide, sea state, cloud cover), and (4) inter- and intra-specific interactions (densities of murrelets and competitors). I quantified local prey availability and regional oceanographic conditions (chlorophyll *a* concentrations and upwelling indices) to investigate relationships between foraging effort and food supply, and tested the shape of this relationship to examine threshold effects predicted by Cairns (1987). Finally, I examined indices of reproductive success to determine if foraging flexibility enabled murrelets to safeguard reproductive success against periods of poor prey availability.

METHODS

From 2004 to 2006 I studied the foraging behaviour of marbled murrelets during the breeding season (mid May to early August) along the West Coast Trail unit of Pacific Rim National Park Reserve on Vancouver Island, British Columbia (Fig. 4.1). This 65 km stretch of coast is exposed to the Pacific Ocean with adjacent inland areas that include large tracts of old-growth forest which are nesting habitat for marbled murrelets. Boat-based prey measurements and land-based foraging behaviour observations were made from 12 sites along this area. During the breeding season, murrelets are effectively studied by land-based observations because they typically forage in shallow water within 2 km from shore (Burger 2002) on small schooling fish such as sand lance (*Ammodytes hexapterus*) and herring (*Clupea harengus*).

Sampling design simultaneously considered the interactions between murrelet diving activity (as a proxy for foraging effort), prey availability, regional oceanographic conditions and the resultant effects on murrelet reproductive success. Collection of prey data were limited due to equipment failure, but those data that were collected measured prey at Carmanah Bay in two years (allowing for interannual and seasonal comparison) and prey was measured at multiple sites in 2005 (allowing for spatial comparison). Limitations of this sampling design are discussed below.

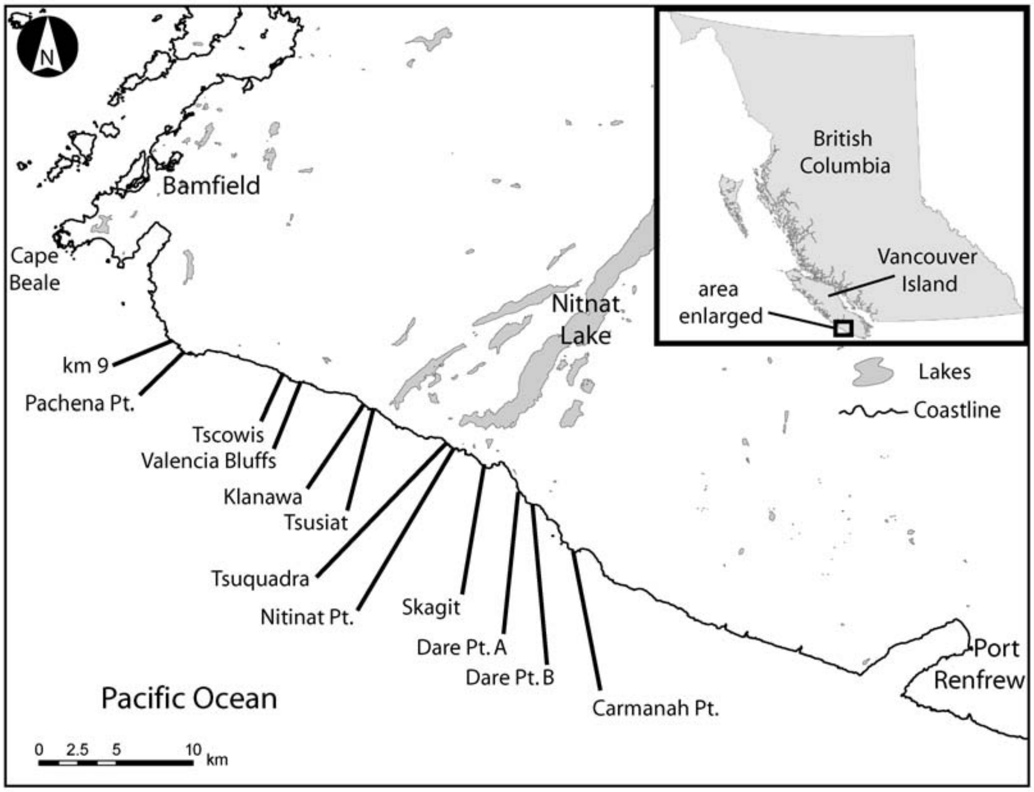


Figure 4.1 - Study area located along the southwest coast of Vancouver Island, British Columbia. Land-based telescope observations and boat-based hydroacoustic surveys were conducted at each of the 12 observation sites.

Behavioural Observations

Observations of murrelet diving activity were made from 12 cliff-top observations sites (Fig. 4.1) using 20 x magnification telescopes. Observer was between ~10 to 30 m from the waters edge depending on the site. Each site was surveyed two to five times in 2004. In 2005 and 2006, one site (Carmanah Bay) was surveyed five to eight days each year while other sites were surveyed one or two days each year. This uneven sampling design means that observations at Carmanah contribute to the bulk of the dataset; however this is controlled for by inclusion of site as a random variable in the analysis.

Instantaneous scan sampling techniques (Davoren & Burger 1999) were used to record murrelet behaviours. A series of scans consisted of 20 one-minute scans over each hour of observation. During each one-minute interval, the scope was fixed and I recorded the numbers of birds (murrelets and other seabird species), group sizes, and activity state of individuals on the water (resting or diving) within the field of view of the scope. This was repeated for 20 non-overlapping fields of view. The 60-sec observation interval was chosen to document all diving individuals given the average dive (~25 sec) and surface (~20 sec) times for murrelets (Jodice & Collopy 1999). Proportion of birds diving is used as a proxy for foraging effort (details below). Hourly surveys were conducted from dawn until dusk at three sites (Carmanah, Pachena, Tsusiat) and the first four hours after sunrise and last three hours before sunset at other sites. All observations were made in conditions with Beaufort sea state less than three.

I recorded murrelet age-class in all scans. Newly-fledged murrelets (hatch-year; HY) can easily be distinguished from after-hatch year (AHY) birds based on plumage differences, and ratios of HY to AHY birds may be used as indices of murrelet reproductive success (Kuletz & Kendall 1998). I compared HY and AHY densities and HY:AHY ratios to examine intra- and inter-annual variation in murrelet demographics. Ratios of HY:AHY were calculated for chick rearing and post fledging periods. However, because AHY numbers decline in our study areas as HY numbers increase (Wong et al. in press) an overall HY:AHY ratio calculated by comparing peak HY densities to peak AHY densities (Kuletz & Kendall 1998) in each year. Also, because observations were made before August 9th each year, this was a period when most adults would still be in breeding plumage and, thus, not mistaken for juvenile birds.

All observations were categorized by into three breeding phases: incubation, chick-rearing and post-fledging periods. Based on average known laying dates for Vancouver Island (McFarlane Tranquilla et al. 2005) and known incubation and fledging duration (Nelson 1997), I categorized peaks in nesting chronology as incubation (15 May - 7 June), chick-rearing (8 June - 15 July), and post-fledging (16 July - 8 August).

Indices of Prey, Primary Productivity, and Upwelling

To assess relative abundance of prey (schooling fish or euphausiids) among years, seasons and sites, hydroacoustic surveys were conducted by boat transects in waters visible from the shore-based observation points. A paper-recording 200 kHz echosounder (Furuno FE-606) was used from a 5 m rigid-hull inflatable boat traveling at 10 km h^{-1} to measure relative prey abundance (Piatt 1990). Transect lines 500 m apart were perpendicular to shore from the 5 m to 30 m depth contours, approximately 100 m to 1.5 km from shore. At Carmanah Bay, 13.4 linear km of transects were surveyed in 2004 ($N = 8$ surveys) and 2005 ($N = 6$ surveys). The other 11 sites had 2 to 7 km of transects surveyed three to four times each in 2005. Hydroacoustic surveys were not conducted in 2006 due to equipment failure.

I quantified prey along transects by measuring echo-signal intensity on the paper echosounder output (Piatt 1990). Signal intensity was scored based on percentage cover (0 to 9) within blocks partitioned by time (1-min intervals; approx. 160 m of travel) and depth (5 m intervals). Scores were squared to better estimate prey abundance (Piatt 1990). Three indices of prey were quantified to describe prey availability for each survey at each site: (1) abundance index (sum of scores in each depth block for each minute; averaged for each survey), (2) prey concentration index (mean score of non-zero blocks; averaged for each survey) to indicate different prey concentrations despite similar abundance estimates, and (3) Green's index (GI) of dispersion (Ludwig & Reynolds 1988) calculated by $(s^2/\bar{x})$-1/n-1 where $\bar{x}$ = mean abundance, s^2 = variance of abundance, and n = number of 1-minute segments. Abundance indicates the quantity of prey, concentration indicates the density of prey where it occurs, and GI indicates the distribution of prey throughout the survey area.

To test the shape of the relationship between prey availability on diving activity, I plotted the mean proportion of birds diving (for each of 10 survey days at Carmanah) with respect to the most recent prey estimate (usually from a hydroacoustic survey made within 1 day, mean 2.0 days ± 0.4SE, range 1 to 4). Five hydroacoustic surveys at Carmanah were omitted from this test because the most recent observations of diving activity were greater than six days apart. To examine relationships among sites, I calculated the mean proportion of birds diving for each site in 2005. These means were paired with mean prey abundance, concentration, and GI for each site.

I assessed regional indices of primary productivity (chlorophyll *a*) and upwelling. Weekly composite chlorophyll *a* data were downloaded from SeaWiFs satellite images (http://oceancolor.gsfc.nasa.gov/) for the period of study in each year. Images were obtained as compressed Hierarchical Data Format (.hdf) files which were un-zipped and the .hdf extension was added to each file. Files were opened using HDF Viewer 2.3 (The HDF Group, Champaign, IL, http://hdf.ncsa.uiuc.edu/) and values were extracted from the region surrounding the study area and pasted in a spreadsheet for further analysis. SeaWiFs images provide chlorophyll *a* concentrations in $mg \cdot m^{-3}$ at a resolution of 9 x 9 km pixels. For each week, I determined a mean regional chlorophyll concentration by averaging pixel values along the study area coastline up to two pixels (18 km) from shore (total $N = 828$ pixels; 26 pixels per week less those obscured by cloud cover, average 1 pixel excluded due to cloud cover, maximum 15 pixels excluded). The overall mean chlorophyll level was 4.13 $mg \cdot m^{-3}$ ± 0.26 SE. ANOVA compared chlorophyll levels among years within each breeding phase using individual pixels as the unit of analysis. Accuracy of SeaWiFs images are most greatly affected cloud cover. Images on any give day are likely to show high proportions of cloud cover, however, by using weekly composite images nearly all images were free of cloud cover since at least one day in any given week was clear enough for high image accuracy.

Upwelling indices (http://www.pfeg.noaa.gov/products/PFEL/modeled/indices/) were obtained from the location nearest to our study area (48°N, 125°W; ~ 68km away). I included daily upwelling indices (cubic-meter·second^{-1}·100-meters-of-coastline^{-1}) which overlapped temporally with chlorophyll images ($N = 88$ days each year; 16 May to 11 August). I averaged daily upwelling indices for each week (overall mean upwelling index was 21.6 ± 2.7 SE). ANOVA compared upwelling among years within each breeding phase using individual days as the unit of analysis.

Data Selection, Observer Reliability, and Temporal Autocorrelation

Proportions of birds diving (relative to the total number of birds observed on the water) were calculated for each hour of observation. Proportions may be sensitive to low numbers of birds observed (e.g. one individual diving means 100% diving), therefore I included only hourly scans with ≥ 5 individuals on the water. Mean number of murrelets observed per hour was 39.1 ± 1.6 SE. There were 41 hours with no murrelets observed and of the remaining 90 hours with <5 birds, the mean proportion diving was 0.36 ± 0.37SD. For hours with more ≥ 5 birds, mean proportion diving was 0.31 ± 0.19SD.

This suggests that hours with < 5 birds showed nearly twice as much variability (2x SD) in estimates of diving activity, thus, justifying the removal of these data.

During three years, six observers conducted spotting scope observations with one observer (RAR) observing in all years. I compared inter-observer reliability by testing differences among observers (Mann-Whitney U and Kruskal-Wallis tests dependent on the number of observers in each year) in measures of proportion diving and bird densities (birds per one-minute scan). Observer comparisons were grouped by three time blocks (incubation, chick-rearing, and post-fledging) in each year. There were no significant inter-observer differences in bird density estimates during any time block of any year. Estimates of percent diving showed significant inter-observer differences in only two of nine time blocks (chick-rearing 2006, $P = 0.047$; post-fledging 2005, $P = 0.031$). Thus there was no observer bias in the numbers of birds observed, and occasional, though not systemic, reliability issues for proportion diving estimates. I retained all data to maximize sample size.

Data were collected in consecutive hours, therefore proportions of birds diving may be autocorrelated between adjacent hours. Traditional autocorrelation analyses could not be applied because data were collected in short (3 to 4 hour) non-consecutive time blocks. I used a modified autocorrelation analysis which lagged hours by sequentially shifting time series by 1, 2, 3 hours, etc. (max. 14hrs), and calculating Pearson's correlation coefficients for each shift. Significance of correlations was determined at $p < 0.05$.

Foraging Behaviour Analysis and Modeling

Proportion of birds diving in each hour was the dependent variable in all analyses. Hourly observations were categorized by tide phase, time of day, breeding phase (described above), bird densities, year, and site. Time of day was discriminated by chick- vs. self-feeding periods (dawn/dusk vs. other daytime hours). Murrelets feed their chicks at all times of the day though the majority of feedings occur near dawn and dusk; up to 60 minutes after sunrise, and after 90 minutes before sunset (Burger 1997). I was only able to conduct observations during daylight hours, therefore I considered primary chick-feeding periods as the first hour after sunrise and the last two hours before sunset. To test whether the presence/absence of conspecifics and other seabird species influenced the diving activity of murrelets, I calculated densities (number of birds divided by number of 1-min scans) of murrelets and common murres (*Uria aalge*), the two most common diving piscivores and possible competitors (Burger et al. 2008), for each observation hour.

I modeled the response variable (proportion of birds diving) using Generalized Linear Models (McCullagh & Nelder 1989) in SPSS 15.0. Proportional data were modeled with a binomial distribution and logit link function. Overdispersion, which is common with proportional data in binomial models and can lead to underestimates of standard error, was corrected with the addition of a dispersion parameter (ø) that is equal to Pearson X^2/DF estimated from the global model (Vieira et al. 2000). In our global model, Pearson $X^2/DF = 4.346$, suggesting overdispersed data, therefore 4.346 was used as an estimate of ø in all models and ĉ for QAICc calculations (below).

An information-theoretic approach with Akaike's Information Criterion (AIC) scores was used to rank alternative candidate models, including a global model (all possible parameters) and a null model (intercept only) to assess model fit (Burnham & Anderson 2002). I used quasi-likelihood adjustments and corrections for small sample size (QAICc) to rank candidate models, with $\hat{c} = 4.346$ as the variance inflation factor, to account for overdispersion (Burnham & Anderson 2002). The parameter count (k) for each model included all estimable parameters: +1k for an intercept, +1k for the dispersion parameter, +1k for each covariate, and +(N-1)k for each categorical variable, where N = number of categories. A parameter count of k = 1 was given to the categorical variable *Site* which was treated as a random effect variable.

I modeled the effect of several covariates and fixed factors on the response variable. Covariates included marbled murrelet density (MM_dens), common murre density (CM_dens), and percent cloud cover in 10^{ths} (CC). The following categorical predictor variables were included in models: Year (2004, 2005, 2006), Phase (incubation, chick-rearing, post-fledging), Time-of-Day (dawn, daytime, dusk), Site, Tide phase (high ± 1.5 hr, ebb, low ± 1.5 hr, flood), and Beaufort sea-state (0, 1, 2, 3). Candidate models were selected *a priori* from combinations of potential factors, and included biologically plausible interactions. Candidate models were developed in four categories (with candidate variables in parentheses): (1) Temporal (Year, Phase, Time of Day), (2) Spatial (Site); (3) Inter- and Intra-specific interactions (murrelet density index, common murre density index); and (4) Environmental (Tide phase, Sea State, Cloud Cover). Candidate models were ranked across model categories using QAICc scores and multi-model averaging was used to determine parameter likelihoods to test the weight of individual parameters. Finally, to assess interaction between models in the four categories, I then added each factor independently to a model containing the parameters with the highest parameter likelihoods (i.e. best model + other parameters).

RESULTS

Prey, Primary Productivity, Upwelling

Hydroacoustic measures of prey abundance, concentration and dispersion varied both annually and seasonally (Table 4.1). In Carmanah Bay there was a trend towards higher prey concentrations in 2004 than in 2005 ($t_{12} = 1.765$, $p = 0.103$). Seasonally, prey concentrations varied significantly in both 2004 ($t_6 = 2.407$, $p = 0.053$) and 2005 (ANOVA: $F_{2,40} = 3.867$, $p = 0.029$). Prey concentrations were higher during chick-rearing than post-fledging in 2004, but were higher during post-fledging than during incubation or chick-rearing in 2005 (Table 4.1). Similar seasonal and annual trends in prey abundance and dispersal (Green's index) were apparent; prey was more abundant and clumped early in 2004 but later in 2005. In summary I saw higher prey availability for murrelets early in the 2004 season but late in 2005.

Regionally, there were strong differences in primary productivity and upwelling indices among years within each of the three nesting phases (Fig. 4.2). During the incubation period, chlorophyll concentrations were significantly lower in 2005 (ANOVA $F_{2,229} = 11.238$, $p < 0.001$; Tukey's post-hoc 2005 < 2004, $p < 0.001$, 2005 < 2006, $p = 0.009$) and upwelling indices were lower in 2005 than in 2004 ($F_{2,69} = 2.998$, $p = 0.056$).

During chick-rearing, chlorophyll concentrations were lower in 2005 than 2004 ($F_{2,284}$ = 3.710, p = 0.026) and upwelling was lower in 2005 than 2006 ($F_{2,93}$ = 7.278, p = 0.001). During post-fledging periods the pattern was reversed and 2005 showed higher chlorophyll concentrations ($F_{2,306}$ = 4.603, p = 0.011; 2005 > 2004, p = 0.015, 2005 > 2006 p = 0.045) and upwelling indices ($F_{2,93}$ = 5.942, p = 0.004; 2005 > 2004, p = 0.009, 2006 > 2004, p = 0.012). Overall this illustrates a pattern of delayed upwelling and primary productivity in our study area in 2005.

Table 4.1 - Annual and seasonal variation in prey indices (mean ± SE) measured by hydroacoustic surveys along southwest Vancouver Island.

Category	No. of Transects	Abundance Index[†]	Concentration Index[†]	Green's Index of Dispersion[‡]
Year (Carmanah only)				
2004	8	1.13 ± 0.26	1.94 ± 0.24*	0.07 ± 0.01
2005	6	1.03 ± 0.34	1.36 ± 0.21*	0.09 ± 0.03
Season				
2004				
Incubation	0	n/a	n/a	n/a
Chick Rearing	6	1.32 ± 0.29	2.20 ± 0.21**	0.08 ± 0.01
Post Fledging	2	0.57 ± 0.38	1.18 ± 0.37**	0.05 ± 0.04
2005				
Incubation	13	0.70 ± 0.19	1.11 ± 0.14**	0.14 ± 0.07
Chick Rearing	20	0.89 ± 0.22	1.31 ± 0.33**	0.21 ± 0.05
Post Fledging	10	1.23 ± 0.49	2.62 ± 0.79**	0.19 ± 0.04

[†] Indices of prey and have no units because they are based on relative prey scores after Piatt (1990). Abundance index suggests quantity of prey while Concentration index indicates the average intensity of prey scores (e.g. several small fish schools vs. one large school). [‡] Green's index of dispersion quantifies the distribution of prey within the survey area (1 = maximum clumping, 0 = randomness, < 0 towards uniformity). T-test for two categories and ANOVA for three categories: * $P < 0.1$, ** $P < 0.05$

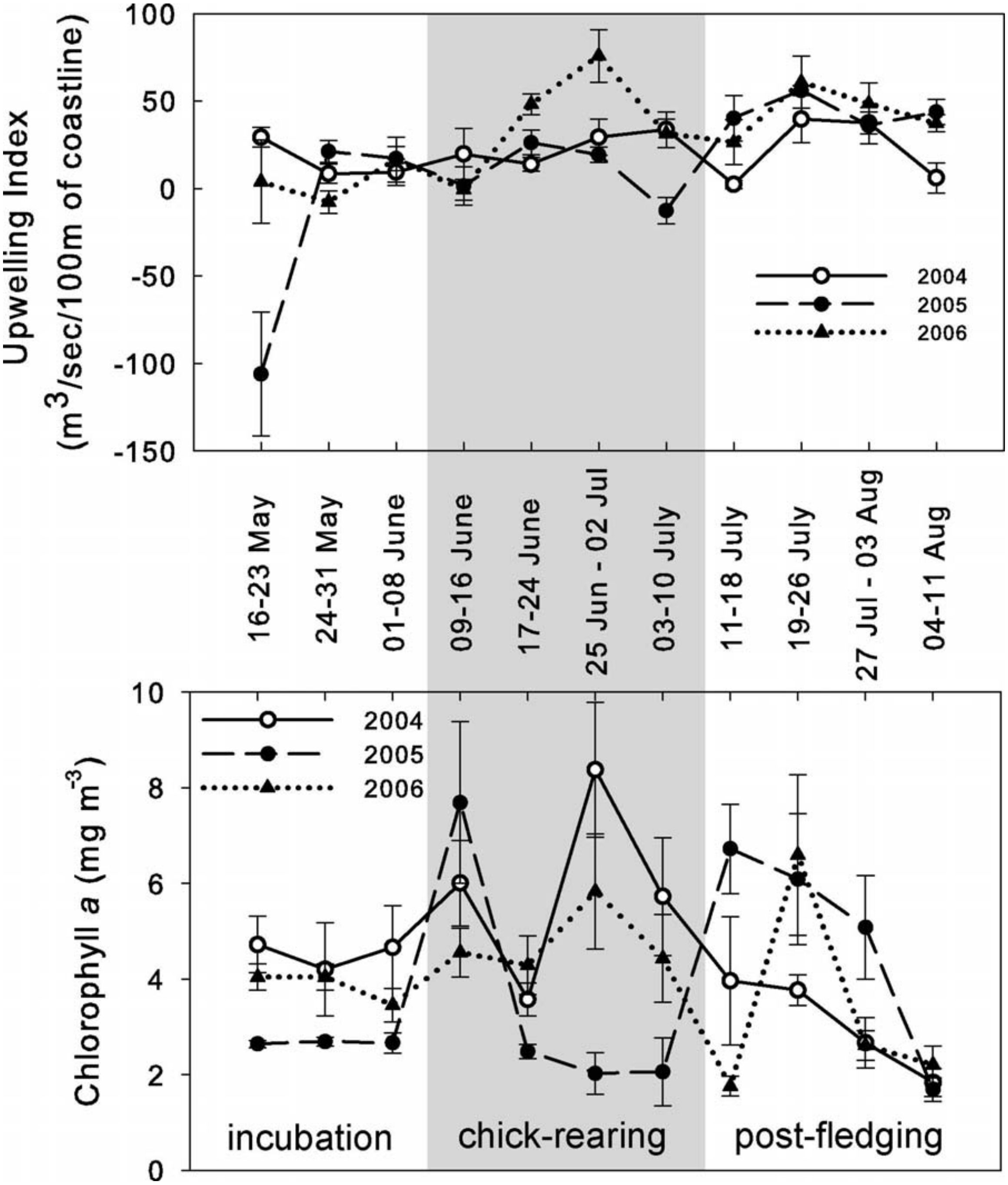


Figure 4.2 - Regional weekly indices (mean ± SE) of upwelling and chlorophyll *a* concentrations during the study period. Chlorophyll concentrations were obtained from SeaWiFs satellite images within 18 km of the study area. Upwelling indices were obtained from NOAA on-line data derived for location 48°N, 125°W.

Murrelet Foraging Behaviour

Over three years I recorded observations on 25,391 sightings of individual murrelets during 765 hours of observations. Data were insufficient (< 5 birds) for proportion diving to be calculated in 131 hours. General patterns in diel diving activity showed increased foraging near dawn and dusk (Fig. 4.3), supporting categorization of time-of-day variable (see methods) for the main models. Temporal autocorrelation in murrelet diving activity was apparent but was not consistent across years or breeding phases. Proportions of birds diving were correlated at 1- and 2-hour time lags in 2005 (incubation and chick-rearing), a 1-hour lag during chick-rearing in 2004, and not at all in 2006. To remove autocorrelation, I sub-sampled hourly observations from periods containing autocorrelation by systematically removing alternate hours (periods with 1-hour lagged correlations) and two out of three consecutive hours (periods with 2-hour lags), thus removing 153 hours of observation. The remaining 481 independent hours of observation were used in Generalized Linear Models.

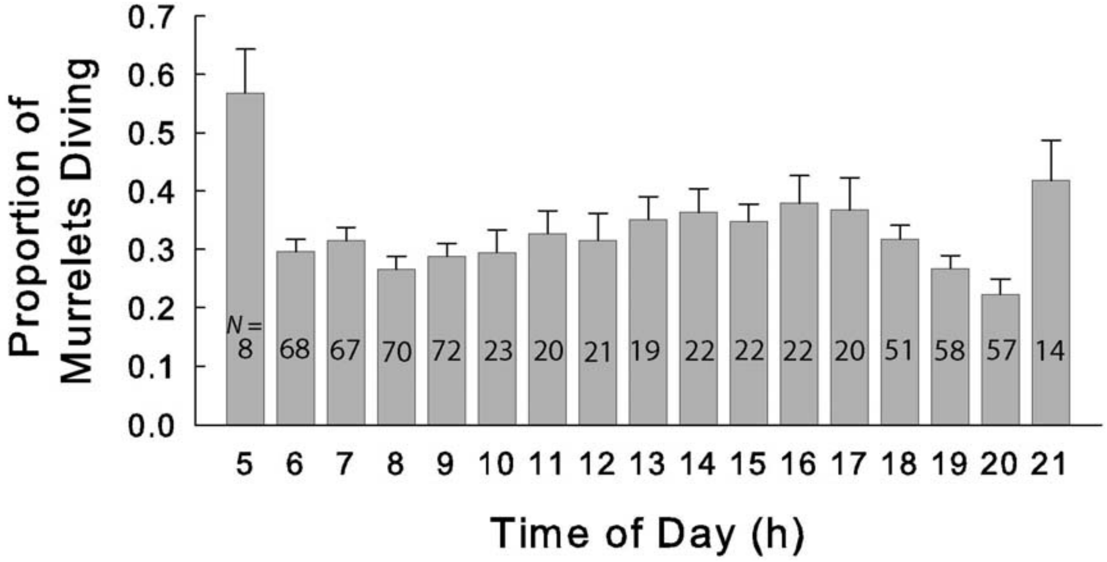


Figure 4.3 - Diel patterns in marbled murrelet (*Brachyramphus marmoratus*) foraging activity. Mean ± SE proportions of murrelets diving are given for each hour (sample size in bars). Data include all years and sites combined.

I tested models across four broad categories including Temporal, Spatial, Environmental, and Inter- & Intra-specific Interactions. Model ranking showed substantial support (ΔQAICc ≤ 2) for two temporal models (Year and Year*Phase), less support for other temporal models and the spatial model, and essentially no support (ΔQAICc > 10) for the null model, most of the environmental models, and the inter-/intra-specifics models (Table 4.2). Parameter likelihoods (sum of w_i for each parameter from alternative models; Burnham & Anderson 2002) suggests that Year (0.56) and Year*Phase (0.28) were the parameters with the most support. Site had a parameter likelihood of 0.05 and several other temporal parameters had likelihoods of about 0.10 (Phase, TimeDay, Year*TimeDay). Evidence ratios suggest potential model uncertainty between the top two models: the Year model ($w_i = 0.40$) was only twice as likely as the Year*Phase model ($w_j = 0.20$) to be the best model (evidence ratio $w_i/w_j = 2$). Thus, both Year and the Year*Phase interaction appear to be the strongest parameters predicting murrelet diving effort.

Given that non-temporal variables may interact with the temporal models, I tested the improvement in model fit by adding independent variables to the best temporal model (Table 4.3). I considered the best temporal model to be that with Year and Year*Phase because these were the most likely parameters (above). The best temporal model was improved only with the addition of the Site variable with little evidence of competing models ($w_i = 0.84$). Thus there is strong evidence that variation in murrelet diving activity is determined primarily by temporal patterns (Year, Year*Phase; Fig. 4.4 upper) and secondarily by spatial patterns (Site effects; Fig. 4.4 lower). Overall I observed higher diving activity in 2005, particularly during incubation and chick rearing.

Table 4.2 - Candidate models of temporal, spatial, environmental, and inter- & intra-specific factors affecting marbled murrelet (*Brachyramphus marmoratus*) foraging activity. Factors included Year, Phenology (Phen), Time of Day (TimeDay), Site, Marbled Murrelet density (MMdens), Common Murre density (CMdens), Tide phase (Tide), Sea State (SS), and Cloud Cover (CC). * denotes interaction terms. *N* = 481 for all models.

Model Type	Factors Included in Model	Log-likelihood	K	Δ QAICc	QAICc weight (w_i)
Temporal	Year	-436.92	4	0.00	0.40
Temporal	Year*Phen	-431.02	6	1.38	0.20
Temporal	Year*TimeDay	-435.26	6	3.33	0.08
Temporal	Year + Phen	-435.98	6	3.66	0.06
Temporal	Time + Year	-436.82	6	4.05	0.05
Spatial	Site (as a random effect)	-450.28	3	4.11	0.05
Temporal	Year*Phen + TimeDay	-430.75	8	5.38	0.03
Temporal	Year + Year*Phen	-431.02	8	5.51	0.03
Temporal	Phen + Year*Phen	-431.02	8	5.51	0.03
Temporal	Phen*TimeDay + Year	-433.85	8	6.81	0.01
Temporal	Year*TimeDay + Phen*TimeDay	-434.37	8	7.05	0.01
Temporal	Year + Year*TimeDay	-435.26	8	7.46	0.01
Temporal	TimeDay + Year*TimeDay	-435.26	8	7.46	0.01
Temporal	Year + Phen + TimeDay	-435.83	8	7.72	0.01
Environmental	CloudCover	-458.13	3	7.73	0.01
Temporal	Year*Phen + Phen*TimeDay	-428.60	10	8.55	0.01
Temporal	Year*Phen + Year*TimeDay	-429.56	10	9.00	0.00
Environmental	Tide + CloudCover	-449.26	6	9.77	0.00
Null	intercept only	-467.63	2	10.08	0.00
Global	all factors and interactions	-402.31	35	51.65	0.00
List of Candidate Models with Δ QAICc > 10					
Temporal	[Year*TimeDay + Phen*TimeDay], [Phen], [TimeDay], [Phen*TimeDay], [TimeDay + Phen], [Phen + Phen*TimeDay], [TimeDay + Phen*TimeDay], [Year*Phen + Phen*TimeDay + Year*TimeDay]				
Inter- and intraspecifics	[CM_dens], [MM_dens], [CM_dens + MM_dens], [MM_dens*CM_dens]				
Environmental	[Tide], [SeaState + CloudCover], [SeaState], [Tide + SeaState + CloudCover], [Tide + SeaState]				

Table 4.3 - Interactions between temporal factors and other factors affecting marbled murrelet (*Brachyramphus marmoratus*) foraging activity. The temporal factors were selected from Table 4.2 and based on the parameters with the highest parameter likelihoods (Year, sum w_i = 0.56 and Year*Phen, sum w_i = 0.28). The temporal model (Year + Year*Phen) was improved with the addition of the spatial (Site) parameter.

Factors included in model	Log-likelihood	K	Δ QAICc	AIC weight (w_i)
Year + Year*Phen + Site	-413.77	9	0.00	0.84
Year + Year*Phen	-431.02	8	5.86	0.04
Year + Year*Phen + CC	-426.69	9	5.94	0.04
Year + Year*Phen + CM_dens	-428.96	9	6.99	0.03
Year + Year*Phen + MMdens*CMdens	-430.32	9	7.62	0.02
Year + Year*Phen + MM_dens	-430.90	9	7.88	0.02
Null (intercept only)	-467.63	2	10.43	0.00
Year + Year*Phen + Tide	-423.71	12	10.86	0.00
Year + Year*Phen + SS	-429.10	12	13.34	0.00

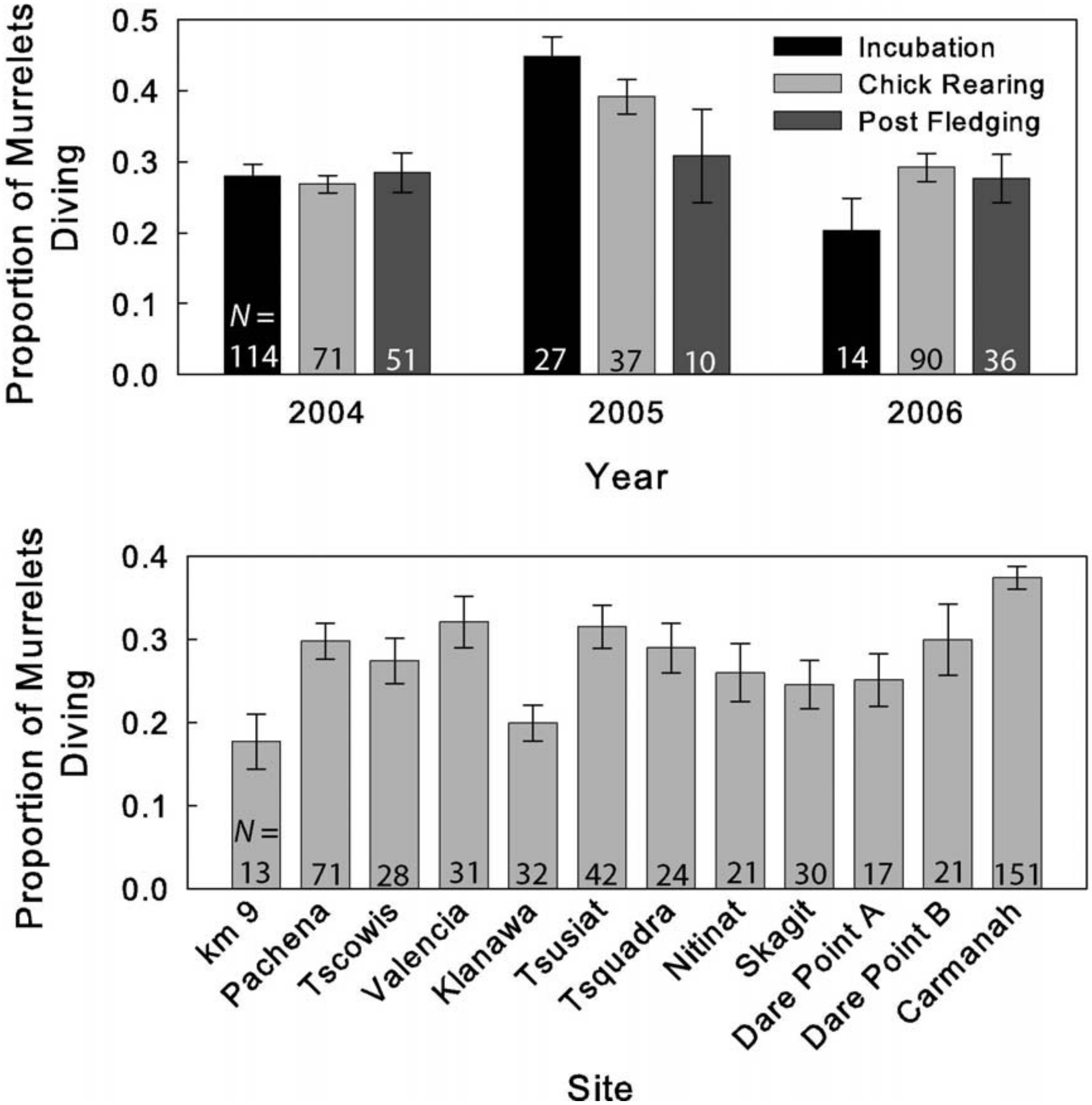


Figure 4.4 - Proportions of marbled murrelets (*Brachyramphus marmoratus*) diving (means ± SE, sample size in bars) across years and breeding phases (upper graph) and among 12 sites (lower graph). Sites are ordered along the coast from the north-west to the south-east.

Predator-Prey Associations

Correlations between prey indices and murrelet activity levels suggest that murrelet diving activity was affected by prey availability (Fig. 4.5). Within one study site (Carmanah Bay) that was surveyed multiple times in 2004 and 2005, diving activity showed no correlation with prey abundance index ($r^2 = 0.007$, $N = 10$, $p = 0.821$; Fig. 4.5a) or Green's index of dispersion ($r^2 = 0.045$, $N = 10$, $p = 0.556$; Fig. 4.5c) but showed a weak trend towards decreasing activity with increasing prey concentration index ($r^2 = 0.244$, $N = 10$, $p = 0.147$; Fig. 4.5b). Lack of fit may have resulted due to a mismatch in timing of prey surveys with timing of foraging behaviour observations (six prey surveys were ± 1 day before/after foraging estimate, two surveys ± 3 days, and two surveys ± 4 days). Among 12 sites surveyed in 2005, the proportion of murrelets diving was negatively correlated with prey abundance ($r^2 = 0.494$, $N = 12$, $p = 0.011$; Fig 4.5d), prey concentration ($r^2 = 0.418$, $N = 12$, $p = 0.023$; Fig 4.5e), and Green's index of dispersion ($r^2 = 0.627$, $N = 12$, $p = 0.002$; Fig 4.5f). In all regressions, linear models showed a better fit than logarithmic or quadratic functions.

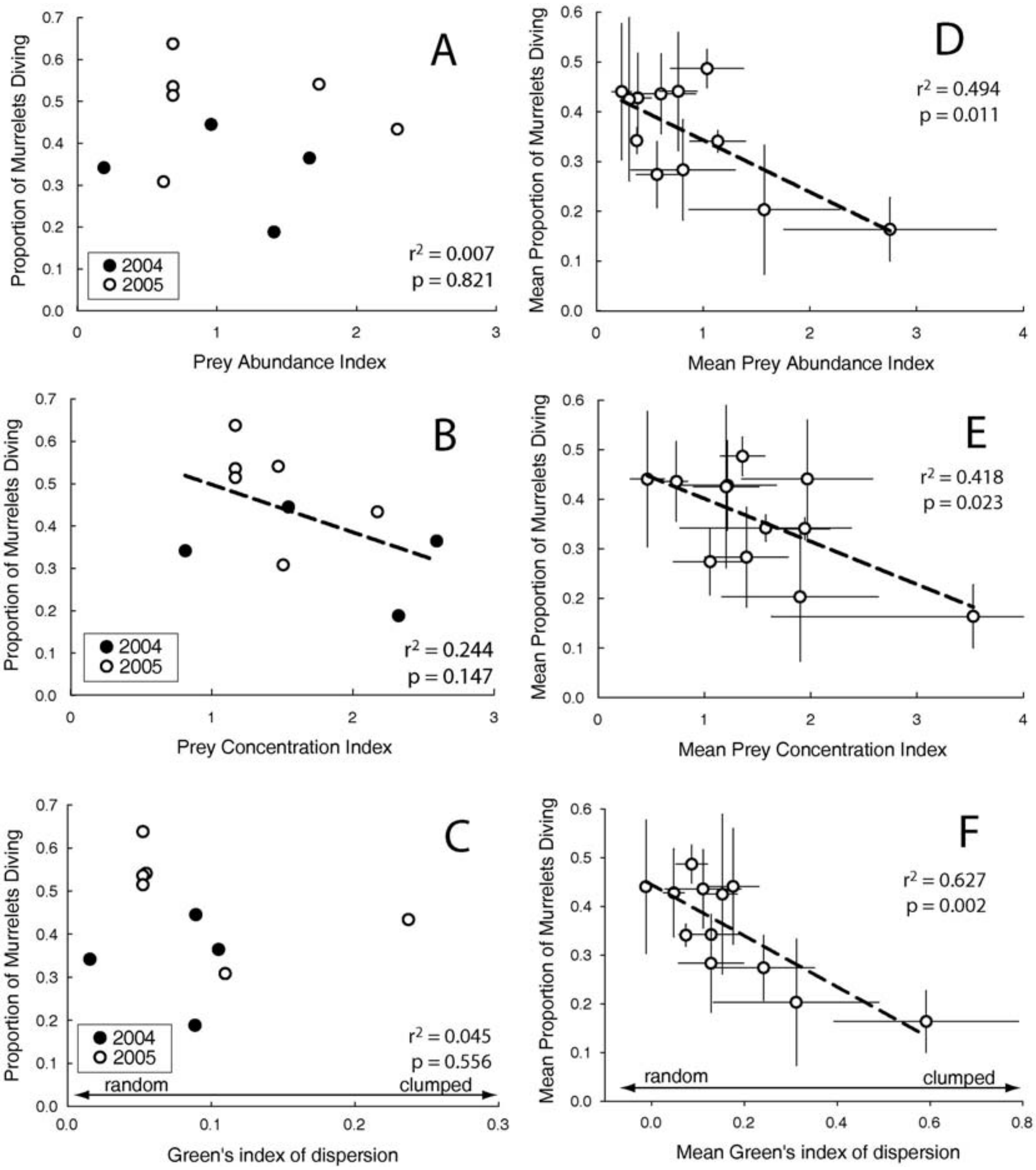


Figure 4.5 - Relationships between marbled murrelet (*Brachyramphus marmoratus*) foraging effort and prey availability. Plots A, B, and C show variation among survey dates within one site (10 surveys at Carmanah Bay). Plots D, E, and F show variation among sites within years (12 sites surveyed in 2005). Symbols in D, E, and F represent averaged prey and diving activity estimates for each site (mean ± SE). See Table 4.1 for definitions of indices.

Indices of Annual Reproductive Success

Comparing densities of murrelets in adult plumage (after-hatch-year birds; AHY) and juveniles (hatch-year birds; HY), there were striking differences among years (Fig. 4.6a&b). AHY birds were more abundant in 2004 than other years. HY birds were most abundant in 2004 and 2006. HY density and HY:AHY ratios provide indices of murrelet reproductive success (Kuletz & Kendall 1998) which both suggest that 2006 was the best year for raising chicks, 2004 was nearly as good, but 2005 was extremely poor (Fig. 4.6c). There are two important assumptions that may influence the accuracy HY:AHY ratios (Peery et al. 2007). First, these ratios assume similar at-sea distributions of HY and AHY birds, which is generally true in my study area (Wong et al. in press). Second, seasonal emigration and immigration of HY or AHY birds may bias the productivity index. In my study area, Wong et al. (in press) showed seasonally decreasing numbers of AHY birds, likely due to post-fledging dispersal, but a peak juvenile densities in late July. This suggests that emigration by adults could bias HY:AHY ratios, thus, the *overall* HY:AHY ratio (Fig. 4.6) likely provides the most accurate estimate of annual productivity. These results, along with those above, suggest that although murrelets increased their foraging effort (Fig. 4.4) to buffer against low prey availability in early 2005, they were still unable to successfully raise chicks.

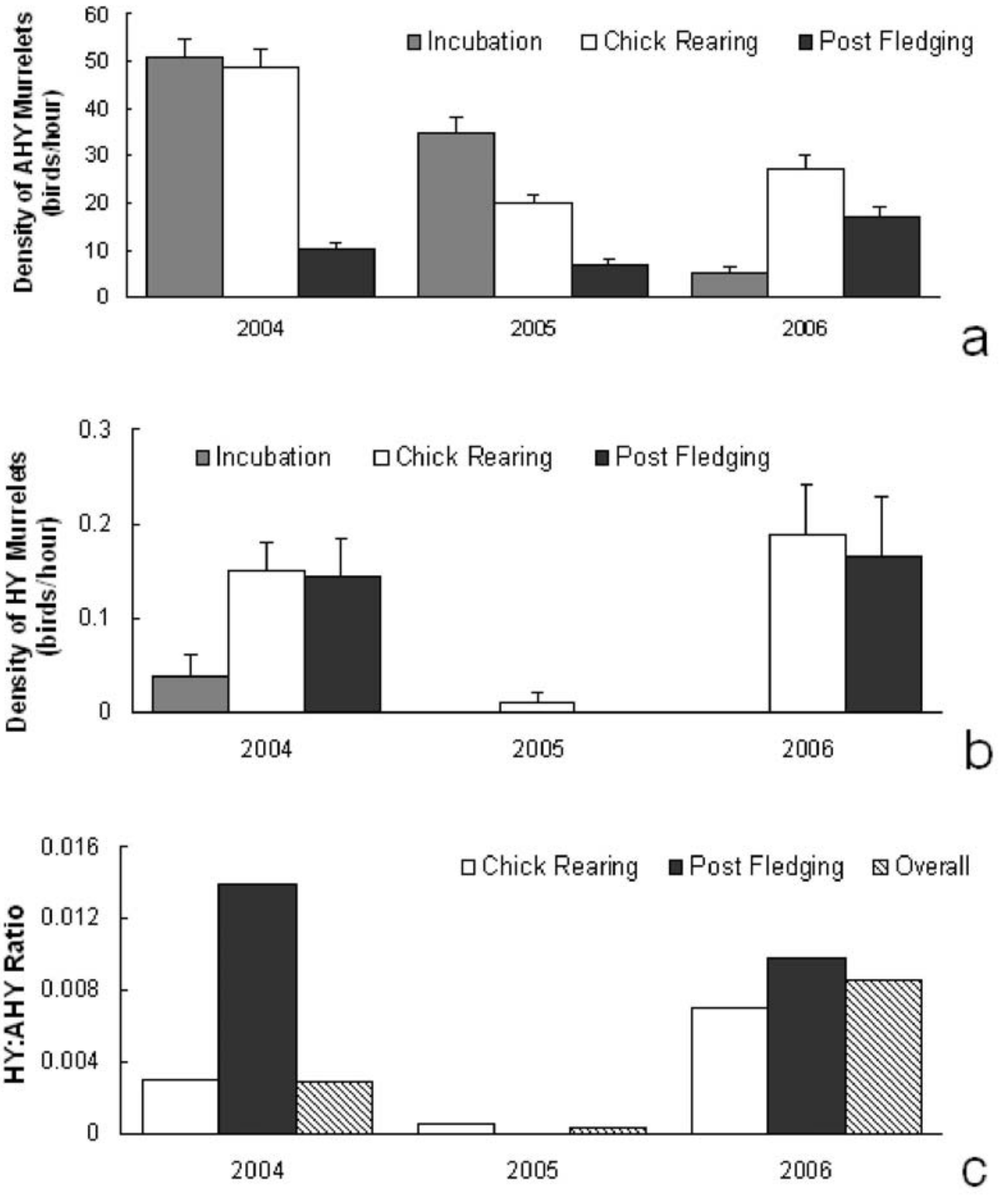


Figure 4.6 - Indices of marbled murrelet (*Brachyramphus marmoratus*) breeding effort, observed by telescope. Parts A & B: densities of after-hatch-year (AHY) and hatch-year (HY) birds. Part C: productivity indices (HY:AHY ratio) calculated for chick rearing and post fledging periods and also an overall HY:AHY ratio calculated by comparing peak HY densities to peak AHY densities (Kuletz & Kendall 1998) in each year. Indices are means ± SE and samples sizes are as follows: incubation (2004, *N* = 131 hours; 2005, 62; 2006, 35), chick-rearing (2004, 207; 2005, 90; 2006, 100) and post-fledging (2004, 76; 2005, 15; 2006, 48). Note y-axis scale differs in each figure.

DISCUSSION

Proportions of Birds Diving

I show that murrelets are flexible in their activity budgets whereby the average proportion of birds foraging may range from approximately 0.15 to over 0.5 depending on location, time of day, breeding phase, year and prey availability. This range is comparable to the time murrelets spent foraging in other studies: 23.4% in Oregon (Henkel et al. 2004), 9 to 12% in California (Peery et al. 2004), and greater than 40% in Alaska (Day & Nigro 2000). Likewise, other alcids show comparable ranges in foraging time (Davoren & Burger 1999, Litzow & Piatt 2003).

This study is based on the assumption that the ratio of birds diving/not-diving is a valid proxy for foraging effort. However, foraging effort may be measured in several other ways including shifts in foraging location with an associated increase in flight costs, changes in dive parameters (longer and/or deeper dives), or increases in active feeding period (similar frequency of dives but over a longer period of the day). With murrelets, such parameters are more readily measured by tracking individual birds (Jodice & Collopy 1999, Henkel et al. 2004, Peery et al. 2004) rather than population level assessment (this study, Day & Nigro 2000). Previous studies have also used proportion of birds diving as a proxy of foraging effort (Day & Nigro 2000) and one tracking study suggested that proportion of time diving was a measure sensitive to food availability (Peery et al. 2004).

Foraging trip duration and discrepancy time at the colony are important individual-level parameters for monitoring predator-prey relationships (Zador & Piatt 1999, Piatt et al. 2007). Our study was limited to population-level assessment of foraging effort, thus I acknowledge that other individual-level proxies of foraging effort may have provided additional insight into murrelet-prey relationships. Nevertheless, because murrelets are difficult to capture and nest-based monitoring is not practical, individual-level parameters are typically difficult and expensive to monitor. Thus the population-level approach used in this study provides an easily implemented and cost-effective approach for monitoring and management purposes.

Factors Influencing Diving Activity

Factors influencing diving activity were assessed by comparing competing models in four categories: Temporal, Spatial, Environmental, and Inter- & Intra-specific competitors. Overall, temporal and spatial factors had the greatest influence on activity budgets while environmental factors and possible competitors (i.e., murres) had little or no effects.

Breeding phase influenced foraging effort as an interaction term with year; foraging effort increased during incubation and chick-rearing, but only in 2005. Both incubation and chick-rearing are considered energetically expensive periods for birds (Whittow 2002), thus increased foraging effort during these periods should be expected, especially in 2005 when food supply was low. In other years when prey was abundant early (2004) on and when primary productivity was elevated (2004/2006), murrelets showed no increase in diving activity to compensate for energetic demands of incubation or chick-rearing. Time-of-day was a temporal factor which showed only moderate support in the models tested (Table 4.2). However, the resolution of this temporal factor was poor (divided into three broad time-of-day categories), and investigations of hourly diel activity patterns showed minor variability throughout the day (Fig. 4.3) but strong increases in diving activity near dawn and dusk. This suggests that murrelets work hardest in these hours to capture prey for delivery to young. However, the sample sizes were low near dawn and dusk (few hours with > 5 murrelets observed) and future surveys should invest more effort into investigating the importance of this crepuscular foraging period. Overall, complex interactions between all temporal factors (time-of-day, phase, and year) may combine to influence murrelet activity patterns.

Site was also an important predictor of diving activity when modeled with temporal variables and sites with higher prey availability showed decreased foraging activity (Fig. 4.5d-f). For murres, prey variability among sites influenced colony attendance and chick feeding rates (Harding et al. 2007). In Alaska, the percent of murrelets diving differed among habitat types (Day & Nigro 2000) but this was not linked to prey availability. The significance of a site effect on diving activity in this study was most likely due to differences in habitat types which may in turn influence prey availability. Visual surveys of fish schools within the study area in 2006 showed that sand lance, a key murrelet prey item, were only found in habitats with sandy/gravel substrates (Haynes et al. 2007). In our study, substrates varied among the 12 survey sites, thus habitat type may have had a confounding effect on the availability of prey among sites. Future research may seek to quantify murrelet foraging behaviour in relation to specific habitat types.

Environmental variables (tides, sea state, cloud cover) had little effect on the foraging activity of murrelets. In Alaska, tides showed no effect on murrelet feeding activity (Day & Nigro 2000), yet the foraging ecology of other alcids can be influenced by tides (Holm & Burger 2002). The lack of tidal effects in our study was perhaps because tidal amplitudes are moderate in this region and the study area included open coast with no undersea ridges or narrow passages where tidal effects might be more evident. Murrelets may increase their dive bout duration with increased wave action (Jodice & Collopy 1999), but sea-state effects were not observed in my study likely because most observations were made in relatively calm conditions. Surprisingly, there was a lack of apparent influence on diving behaviour by the presence of intra- and inter-specific competitors. Often seabirds use cues of other foraging birds to find suitable foraging locations (Wittenberger & Hunt 1985). Although typically solitary or in pairs (Nelson 1997), murrelets also partake in mixed-species feeding flocks. Alternatively, larger alcids may act as competitors for smaller alcids (Piatt 1990, Burger et al. 2008). I saw neither negative nor positive correlations between foraging activity and densities of other murrelets or murres, which might be due to murrelets in this area avoiding close proximity to murres (Burger et al. 2008). Thus murrelets may forage effectively regardless of local enhancement or potential competitors.

Threshold and Timing Effects of Prey

Seabirds typically adjust activity budgets with respect to prey availability (Burger & Piatt 1990, Uttley et al. 1994, Zador & Piatt 1999), and our study provides evidence that marbled murrelets do so as well. Murrelets foraged most intensively early in the 2005 season when prey was least abundant and more dispersed. Murrelets also foraged less intensively at sites with more food. Studies of murrelet foraging behaviour in Oregon and California speculated that changes in percentage of time diving was associated with poor prey years (Jodice & Collopy 1999, Peery et al. 2004), though prey was not quantified.

There was a was little to no relationship between diving activity and prey availability at one site (Carmanah Bay), yet among sites there was a negative correlation between diving effort and prey availability (Fig. 4.5). This discrepancy may be explained by the slightly wider range of food availabilities among sites than within Carmanah Bay. Alternatively, this may indicate a hierarchical structure in diving response to prey; murrelets may select among sites to find sites of high prey availability to minimize foraging effort, but within sites changes in prey have little effect on diving effort. Moreover, the only prey index that showed any relationship with diving activity in Carmanah was prey concentration; thus, within sites, prey densities may be more important than overall prey abundance or dispersion. Density thresholds are an important parameter in predator-prey relationships for other seabirds (Piatt 1990). Additionally, hydroacoustic measures provide only an index of potential prey, yet the types of prey items remain unknown and hydroacoustic sounders can easily miss fish schools that are not directly below the boat. These limitations of hydroacoustic sampling may also have obscured predator-prey relationships in this study.

Organisms may show non-linear responses to changes in prey densities (Holling 1965), suggesting that thresholds in prey densities exist. Marine predators frequently show numerical aggregative responses when prey reach certain density thresholds (Piatt 1990, Piatt & Methven 1992), but may also respond to prey thresholds with behavioural changes (Hines et al. 1997, Piatt et al. 2007). Cairns (1987) predicted a non-linear relationship between prey availability and predator activity budgets with high foraging effort over low to moderate food supply, but a rapid decline in foraging time with higher food supply. However, linear relationships between murrelet foraging effort and prey, suggest no obvious threshold response. Common murres also exhibit linear relationships between foraging trip duration and prey abundance (Piatt et al. 2007). The slope of the response and the presence or absence of a response threshold will likely depend on the range of prey availability observed in any particular study. The linear response observed with murrelets may possibly reflect a limited range in food availabilities during this study. The inclusion of years and/or sites with higher food ranges may yet identify a threshold response between murrelets and their prey. Nevertheless, responses of marine predators to prey may be complex with both non-linear and linear responses (Reid et al. 2005).

In addition to thresholds, a mismatch in timing between breeding activities and availability of prey, can negatively influence seabird reproductive success (Bertram et al. 2001, Suryan et al. 2006). In 2005, delayed coastal upwelling throughout the northeastern Pacific caused a strong mismatch in timing for some seabirds (Sydeman et al. 2006). In my study area, I also saw delayed prey abundance, upwelling indices and primary productivity, similar to patterns further south (Schwing et al. 2006). Moreover the timing of first fledglings observed in our study area was later in 2005 (12 July) than in 2004 (28 June) or 2006 (26 June). I suspect that the delay in upwelling, associated low primary productivity, and timing of prey availability to murrelets in 2005 had a strong influence on the low reproductive success observed that year.

Buffering Ability

Life-history theory suggests that long-lived organisms, such as seabirds, invest heavily in rearing few young (Stearns 1992). Many seabirds rear only one or two chicks per year, thus parental investment tends to be high for most species (Gaston 2004). Adjustment of foraging effort is one way seabirds can successfully rear chicks under variable environmental conditions (Cairns 1987).

If murrelets adjust foraging effort for chick rearing, then reproductive success could be buffered against years of low prey availability. This was not observed in this study when, in 2005, murrelets increased their foraging effort but failed to maintain normal levels of reproductive success. Prey availability is thought to be paramount in factors influencing the reproductive success of seabirds (Cairns 1987, Croxall & Rothery 1991), and murrelet reproductive success has been correlated with prey availability in other regions (Becker et al. 2007). Adjustable time budgets should allow birds to mitigate the effects of scarce prey (Uttley et al. 1994), though some species are simply unable to adjust foraging effort in poor food years (Hennicke & Culik 2005).

Although murrelets appeared to increase foraging effort when food availability was low, there are several reasons why this may not have been able to maintain reproductive success. First, some alcids readily adjust chick provisioning rates in response to chick needs (Hipfner et al. 2006) but marbled murrelets may be less able or willing to do so because of adult predation risks associated with nest attendance during daylight (Nelson 1997). Second, prey quality can contribute substantially to the reproductive success or failure of seabirds (Wanless et al. 2005), thus prey quality effects, not measured in this study, may also have contributed to low reproductive rates in 2005. Long-term changes in diet quality have been associated with declining murrelet populations and reproductive rates in British Columbia (Norris et al. 2007). An important limitation of this study was the lack of knowledge of prey species, but other sources of data provide evidence that schooling fish were abundant in 2006. Compared to 2004 and 2005, 2006 was a fairly strong year-class for small herring around Vancouver Island (J. Schweigert, Dept. of Fisheries and Oceans, pers. comm.). Sand lance were also abundant near beaches in the study area in 2006 (Haynes et al. 2007) though no comparable data are available in other years. Both are important prey species during murrelet nestling and fledgling phases (Burger 2002).

Finally, intensive parental investment can also jeopardize the well-being of the parent (Johnsen et al. 1994) and adults may have been energetically stressed in 2005 when conditions were poor. As such, murrelet life-history strategy likely follows the ‘fixed investment hypothesis’ (Ricklefs 1987), whereby adults compromise reproductive investment to ensure their own survival when forage conditions are precariously low or not synchronized with breeding activities. Thus changes in marine prey availability may be a limiting factor to the lifetime reproductive output of this solitary, inland nesting seabird.

Chapter 5 - Interspecific competition between marbled murrelets and common murres: fine-scale foraging space as a limited resource

ABSTRACT

Seabirds frequently forage together in groups of either single- or mixed-species flocks. Though flocking behaviour is thought to enhance the effectiveness of seabirds to find prey in a patchy marine environment, birds may also compete for resources that are spatially or temporally scarce. I tested for competition of foraging space between two coexisting pursuit-diving seabirds, the marbled murrelet (*Brachyramphus marmoratus*) and common murre (*Uria aalge*), along the southwest coast of Vancouver Island, British Columbia. New techniques based on observations with a digital theodolite were developed to map the fine-scale (± 2 m) distributions of seabirds on the water. Distance from shore measurements and nearest-neighbour spatial statistics were used to quantify the spatial overlap and segregation of the two species. Murrelets were distributed primarily in nearshore (200-800 m) waters, while murres foraged further from shore (400-1500 m). Nearest neighbour statistics showed murrelets foraging further from murres than from other murrelets, but murre groups foraged similar distances from murrelets and other murres. This suggests that murrelets may avoid feeding in close proximity to murres, whereas murre foraging distributions may be determined by both inter- and intra-specific competition. I discuss mechanisms that might allow these two species to coexist in nearshore waters, including differences in fine-scale habitat selection, preferences for schooling fish distribution and density, and behavioural differences in activity budgets.

INTRODUCTION

Flocking is widespread among foraging seabirds. Group foraging may increase foraging efficiency and allow seabirds to effectively exploit spatially and temporally patchy prey in the marine environment (Davoren 2000, Grunbaum & Veit 2003, Speckman et al. 2003). Group foraging may also be profitable to individuals when prey is abundant or highly aggregated (Götmark et al. 1986, Ostrand et al. 1998a). By cueing in on other foraging seabirds, individuals can readily find and exploit schools of fish that may only be near the sea surface for a brief period of time (Harrison et al. 1991, Haney et al. 1992, Camphuysen & Webb 1999, Davoren et al. 2003b, Silverman et al. 2004). Seabirds may also identify foraging areas from information transfer by seabirds near colonies or arriving to colonies from foraging areas (Wittenberger & Hunt 1985, Buckley 1997, Burger 1997c, Barta & Giraldeau 2001). Thus many seabirds appear to be adapted to group foraging behaviours to exploit prey in marine environments.

Group foraging is common among conspecifics but is also frequently observed in mixed-species groups. Mixed-species flocking behaviour may occur in stages whereby certain species initiate flocks, others join in to benefit, and some species may even disperse flocks (Chilton & Sealy 1987, Harrison et al. 1991, Mills 1998, Camphuysen & Webb 1999, Silverman & Veit 2001). The Alcidae in particular are thought to play an important role in flock formation by driving prey to the surface (Chilton & Sealy 1987, Mahon et al. 1992, Camphuysen & Webb 1999, Ostrand 1999). Presumably flocking seabirds are exploiting similar prey items. The principle of competitive exclusion, however, suggests that competitors may not coexist without some differentiation of their resource use (Hardin 1960, Armstrong & McGehee 1976, 1980). Thus while prey are generally shared in mixed-species flocks, some species likely partition resources in such a way as to allow coexistence or they must compete and exclude others from the resources.

Competition for resources may take several forms including exploitation, interference, and pre-emptive competition (Gotelli 2001). Exploitation competition involves the direct depletion of a shared resource, which may be a mechanism in seabird population regulation (Ashmole 1963) though this has rarely been reported with seabirds because prey depletion is not easily measured (Birt et al. 1987). Interference competition, whereby groups of birds may reduce the exploitation efficiency of other birds, is much more common among seabirds where large flocks or large species may exclude or inhibit other seabirds from prey patches (Safina 1990, Shealer & Burger 1993, Ballance et al. 1997, Maniscalco et al. 2001, Shealer 2002). Alternatively, birds may compete for space as a limiting resource (pre-emptive competition, Gotelli 2001). Unlike exploitation and interference competition which directly inhibit the capture of food, in pre-emptive competition the resource (space) is renewable and becomes available again once the competitor leaves. Though seabirds regularly compete for space (or territories) at breeding colonies, competition for foraging space at sea has not been demonstrated. As a result of these various mechanisms of competition, seabirds may avoid competitors altogether (Diamond 1978, Maniscalco et al. 2001).

The coexistence and similar prey habits of many Alcids present an interesting framework in which to test theories of interspecific competition or fine-scale niche partitioning among seabirds (Haney & Schauer 1994). It has been suggested that larger seabirds may compete with smaller birds when foraging (Piatt 1990, Maniscalco et al. 2001). Marbled murrelets (*Brachyramphus marmoratus*) and common murres (*Uria aalge*) are two species of pursuit-diving alcids that often coexist in the coastal waters of western North America from California to Alaska. Within my study area they show a high degree of overlap in coarse-scale habitat selection (Chapter 3) but mechanisms facilitating their coexistence remain unexplained. The marbled murrelet is a threatened species in Canada and the U.S. (Nelson 1997), yet we know little about factors in the marine environment that may be limiting the persistence and population growth of this species. The potential for interspecific competition with murres has never been tested and may have conservation implications in areas were murrelet and murre populations overlap (Burger et al. 2008).

I developed new methodologies for studying the fine-scale (10’s to 100’s of meters) distributions of seabirds in nearshore waters. Spatial statistical analyses were applied to quantify the spatial relationships between groups of foraging seabirds within 2 km of shore. I examined the seasonal, annual, and site-specific variation in distribution patterns to investigate aspects of competition for foraging space between marbled murrelets and common murres.

METHODS

Study Site

The study took place along the West Coast Trail (WCT) unit of Pacific Rim National Park Reserve on southwest Vancouver Island, British Columbia, between Cape Beale (N 48°47', W 125°14') and Port San Juan (N 48°32', W 124°29'). Along this 70 km stretch of coast, observations were made at seven locations. In 2004, sites were located at Pachena and Carmanah light stations. In 2005, I resurveyed both light stations and added five additional survey sites accessed by hiking along the trail. At each of the five additional sites, surveys were conducted from two vantage points, however, these data were pooled for each site due to limited sample sizes and proximity of sites (typically less than 500 m apart). Surveys took place between 14 May and 09 August in 2004, and 24 May and 03 August 2005.

Fine-scale mapping of seabird distributions

A digital theodolite (Nikon Total Station Model NPL-332 Pulse Laser) was used to map fine-scale distributions of seabirds on the water (Ronconi & St Clair 2002). This technique has a calculated accuracy within 1.7 m up to 2 km from shore (Denardo et al. 2001). The theodolite is a surveyor's equipment used to measure angles, distances and locations with high precision. Theodolites have been used to map the locations and movements of marine mammals (Denardo et al. 2001, Cox et al. 2004, Bailey & Thompson 2006) and fine-scale habitat variables such as kelp beds (Wong et al. in press) and tidal currents (Johnston & Read 2007). The theodolite has a built in scope (26x optical) to locate birds on the water, line up the bird in the cross hairs of the eyepiece, and measure angles to the birds. When positioned on a cliff-top, the instrument measures vertical angles down (90^{o} from the horizontal plane) and horizontal angles across (360^{o} relative to north) to each object. Using these two angles and the height of the observer above sea level, I calculated northing and eastings of the birds relative to the observer using basic trigonometric functions (Ronconi & St Clair 2002). These relative northing and eastings were then converted to true geographical positions (UTM, Zone 10, NAD83) based on the GPS position of the observer, and were mapped in a Geographical Information System (GIS) database for further analysis. The theodolite also has modes that enabled observers to measure their height above sea level. To account for changing tide heights, observer height was measured prior to each round of mapping or measured over a complete tidal sequence and used in conjunction with local tide tables to correct for tide height during each round of mapping. At Carmanah and Pachena the theodolite was used from the top of the lighthouse tower (~ 45 m above sea level) while the other sites were mapped from cliff-tops (~ 20 to 25 m above sea level).

Seabird distributions were mapped systematically by searching for birds within the theodolite field of view in non-overlapping vertical sweeps (horizon to shoreline). Each scan consisted of a series of vertical sweeps to the left or right, the direction of which was determined by the direction of drift by birds on the surface: scans were made against the drift to avoid double counting birds. During scans, the observer recorded the position of bird groups (individuals within 3 m of each other) using the theodolite's built-in data storage and called out the species and group size to a second data recorder. Groups of birds were mapped rather than individual birds due to the slow speed of data recording by the instrument, and because individuals in groups were thought to be closer to each other than the potential instrument precision. Each complete scan of the entire study area was a replicate (Fig. 5.1) for analysis. Each replicate scan was completed in approximately 20 minutes to one hour depending on the size of the study site and number of birds. Although birds may have moved during this time, this should make little difference in the analysis because I was primarily interested in nearest neighbours (below) which take only a few seconds to map. Samples were spread out seasonally as much as possible in 2004 and at Carmanah in 2005, however difficulty of site access meant that replicates at other sites in 2005 were sampled over a 2 day period for each site, and many sites were sampled in different weeks. All mapping was conducted under good visibility (no precipitation or fog) and low sea-state conditions (typically Beaufort sea-state ≤ 2, always sea-state ≤ 3). Shorelines were also mapped using the theodolite.

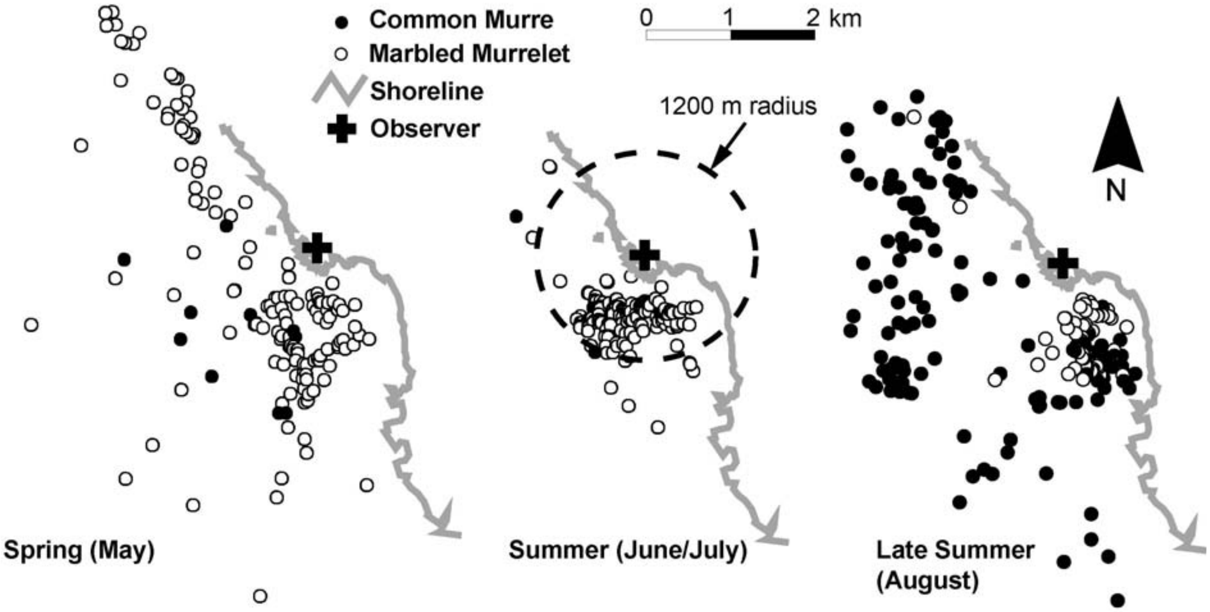


Figure 5.1 - Distributions of marbled murrelets and common murres mapped by theodolite at Carmanah Bay, southwest Vancouver Island, in 2004. Each map shows an example of a single scan (birds mapped in a single sweep) representative of seabird distributions in each of three time periods. The shoreline was also mapped at high tide using the theodolite. The 1200 m radius is the limit of reliable detection for both species and the cut-off distance for nearest-neighbour analysis (see methods for details).

All birds were mapped up to as far as they could be detected (max. approx 4 km). However, the detectability of animals invariably declines with distance from the observer with any survey method (Buckland et al. 2001) and detectability may vary among species (Chapter 2). When theodolites are used in marine mammal studies, animals are likely detectable over distances of 2 to 4 km (Denardo et al. 2001, Williams et al. 2002, Ribeiro et al. 2007). However, there is no information on the detectability of seabirds by theodolite. I used distance-sampling methodology for point transects (Buckland et al. 2001, Marques et al. 2007) to model the detectability of seabirds as a function of distance from the theodolite. I modeled both off-shore and along-shore detectability. Results of this analysis (Appendix II) were used to delineate boundaries for nearest neighbour analyses (below) which require that both species are equally detectable. Boundaries were set at 1200 m distance from the theodolite station for surveys at Carmanah and Pachena, and at 1000 m for surveys at other sites. Nearest neighbour analysis was conducted only on groups within the boundary. This artificial boundary may introduce bias near the boundary edge since birds close to the boundary might have a nearest neighbour that is outside the boundary and not considered. However, I felt that this data truncation was more important than the bias introduced by not truncating, i.e. reduced detectability of marbled murrelets (smaller species) beyond the boundary (Appendix II).

Calculations of Spatial Statistics

Seabird locations were mapped in the GIS (ArcGIS 9.0) database and spatial analysis tools (Beyer 2004) were used to calculate spatial statistics. First, the distance of each group to the nearest shore was calculated. These data were used for descriptive analyses of seabird locations relative to the coast. Second, I *calculated nearest neighbour distances* (Perry et al. 2002, O'Sullivan & Unwin 2003) between the following contrast groups for each replicate scan: murrelet to murrelet (i.e. distance of each murrelet group to nearest neighbour murrelet group; MM-MM), murrelet to nearest murre (MM-CM), murre to nearest murre (CM-CM), and murre to nearest murrelet (CM-MM). Nearest neighbour distances were averaged for each replicate scan thus creating an index of spatial distribution/clustering and the unit of statistical analysis (below). The contrast groups may be interpreted such that MM-MM and CM-CM indices represent normal distances at which birds are distributed with respect to their own species. Whereas MM-CM and CM-MM distances indicate how one species distributes itself with respect to the other species. The hypothesis then is to test for avoidance behaviour by contrasting these groups: for example, MM-MM = MM-CM indicates no avoidance (murrelets forage just as close to murres as they do to other murrelets), while MM-MM < MM-CM indicates avoidance (murrelets forage further from murres than they do to other murrelets).

Data Considerations

Nearest neighbour statistics were calculated for scans with at least two groups mapped. Average nearest neighbour (NN) measures may be sensitive to numbers of birds present. For example, if only 2 or 3 individuals are mapped, and these individuals by chance are situated far from each other, then average NN statistics will be very large and thus provide outliers in the dataset. Therefore, it was necessarily to identify and remove outliers from the data set before performing statistical analyses. Boxplots were used to identify extreme values (values greater than 1.5 times the interquartile range (Benjamini 1988). This identified 28 NN statistics as outliers (12 MM-MM, 3 CM-CM, 6 MM-CM, and 7 CM-MM), most of which had fewer than 5 points mapped for one of the two species. Thus statistical analyses were conducted on the remaining 246 NN measures (81 MM-MM, 58 CM-CM, 54 MM-CM, 53 CM-MM).

When calculating NN distances from one species to another (CM-MM, MM-CM), the NN statistic might also be sensitive to unequal proportions of the two species (i.e., many murrelets with few murres). As the proportion of murrelets increased, MM-CM nearest neighbour statistics were unaffected (linear regression, $R^2 < 0.001$, df = 54, p = 0.890) but CM-MM nearest neighbour decreased ($R^2 = 0.085$, df = 52, p = 0.034). Thus for CM-MM statistics, I removed cases where NN statistics were more extreme than ± 1 standard deviation of the mean NN for CM-MM data. This removed 4 cases and when these data were omitted, the linear correlation between NN statistics and species proportions were no longer significant ($R^2 = 0.054$, df = 48, p = 0.108).

Statistical Analyses

To investigate the factors influencing nearest neighbours I used Generalized Linear Models (GLM, multi-way ANOVA with factors and covariates; SPSS 15.0) and an information theoretic approach (Burnham & Anderson 2002) for model selection based on Akaike's Information Criteria for small sample sizes (AICc). Nearest neighbours were the dependent variables tested against the four NN contrast groups (MM-MM, CM-CM, MM-CM, CM-MM) as the main-effect factor in the model. Contrast groups were the main independent variable of interest in the analysis, however several other independent variables may have influenced the relationship between NNs of the contrast groups. To maintain contrast groups as the main-effects factor, secondary factors (year, month, site) were included in the model as interaction terms with contrast groups. To explore the effects of secondary variables on each of the contrast groups (e.g., how did MM-MM nearest neighbours vary among years, months, and sites), GLMs were conducted for each of the four contrast groups. Year by Month was the only interaction included in these secondary models because not all sites were surveyed in both years (Year by Site interaction) and many sites in 2005 were only surveyed in one month (Month by Site interaction). With the most likely model (lowest AICc value) of each data set, post-hoc analysis compared estimated marginal means testing pairwise differences between factors (e.g., 2004 vs. 2005) with Bonferroni adjustments for multiple comparisons (SPSS 15.0). Estimated marginal means are predicted means of the dependent variables (nearest neighbour), with covariates or factors held at their mean value as determined by the model. This allows for comparison of means within specified factors (e.g., year) while controlling for effects of other factors (e.g., site) in the model.

Finally, nearest neighbour statistics may also be influenced by bird abundance in the study area: when more birds are present they are likely to be closer together. To assess the effects of murrelet and murre abundance (# of groups mapped) on the models, I compared the most likely model (lowest AICc value) to models with and without abundance included as a covariate. Moreover, I used linear regressions to test the correlation and direction (positive or negative) of associations between abundance and nearest neighbour statistics.

Randomization tests

An alternative method to test the statistical significance of spatial data includes randomization tests (Fortin & Jacquez 2000). As mentioned above, the spatial patterns observed may simply be a function of bird abundance in the study area rather than a true pattern. The CM-MM and MM-CM nearest neighbour statistics are sensitive to the proportions of each species in the study area, thus randomization tests were conducted to test weather these statistics represent a distinct spatial pattern or simply an artefact of bird numbers. Permutation tests were conducted which randomly swap the identity of murrelets (MM) and murres (CM) locations within each replicate scan, while maintaining the same number of MM and CM in each scan. For each scan, 1000 permutations were conducted and the statistical significance (random vs. non-random distribution) was determined by comparing the observed nearest-neighbour statistic with respect to the 1000 randomized nearest-neighbour statistics. With 1000 permutations, a distribution was considered non-random if the value of the observed statistic was less than the values of the lowest 50 randomized statistics ($\alpha = 0.05$). Randomization tests were conducted for all scans with more than 1 individual of each species.

RESULTS

Seabird distributions were mapped at seven sites over two years. The number of scans for each year were 45 in 2004 (Carmanah Bay, 20; Pachena Point, 25) and 50 in 2005 (Carmanah Bay, 23; Pachena Point, 4; Dare Point, 5; Skagit Bluffs, 6; Valencia Bluffs, 4; Tsusiat Bluffs, 6; Tsuquadra Point, 3). Coverage was most extensive seasonally and annually at Carmanah Bay. Examples of seasonal variation in bird distributions at Carmanah are shown in three replicate scans in 2004 (Fig. 5.1).

Distance from shore and numbers of birds

Patterns in seabird distributions relative to the shoreline indicate that murrelets and murres generally occupied distinctive areas with the greatest overlap occurring between waters 400 to 1000 m from shore (Fig. 5.2). This pattern appeared to be consistent among years though murrelets foraged closer to shore in 2005 than 2004. Moreover, the patterns were fairly consistent seasonally (Fig. 5.3), though more murrelets foraged slightly further from shore in May and about 5% more murres foraged nearshore (300-600 m) in August.

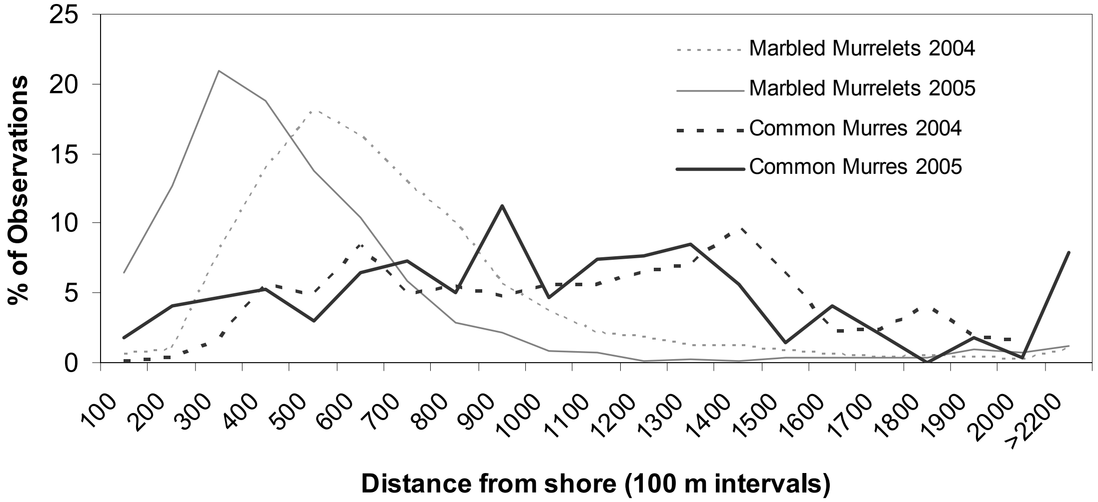


Figure 5.2 - Annual variation in marbled murrelet and common murre distributions relative to shore along the West Coast Trail, southwest Vancouver Island.

Overall, murrelets were more abundant than murres in both years and most months (Table 5.1). Between 72 and 87% of all murrelets observed were within 200 to 800 m from shore, therefore to investigate potential competitive interactions between species, I tabulated abundance statistics for each species within this distance class: percentage of each species in that zone and ratios of murrelets to murres (Table 5.1). In both years murrelets were numerically dominant over murres, with ratios ranging from 5 to 13 murrelets for every common murre. Seasonally, however, murre numbers increased towards the end of the summer as murrelet numbers decreased so that the ratio approached 1:1 ratio in August.

Table 5.1 - Summary statistics of marbled murrelets (MM) and common murres (CM) numbers recorded by theodolite mapping along the West Coast Trail, Southwest Vancouver Island. The 200-800 m zone is the area of highest overlap between murrelets and murres.

	All data			Observations within 200-800m		
	Total no. individuals		Ratio	Total no. individuals		Ratio
	Murrelets	Murres	MM:CM	Murrelets	Murres	MM:CM
May	4559	462	9.9	3310	211	15.7
June	4518	368	12.3	3606	145	24.9
July	2653	2808	0.9	2119	687	3.1
August	524	1048	0.5	456	415	1.1
2004 (all months)	9362	4189	2.2	7394	1301	5.7
2005 (all months)	2892	497	5.8	2098	157	13.4

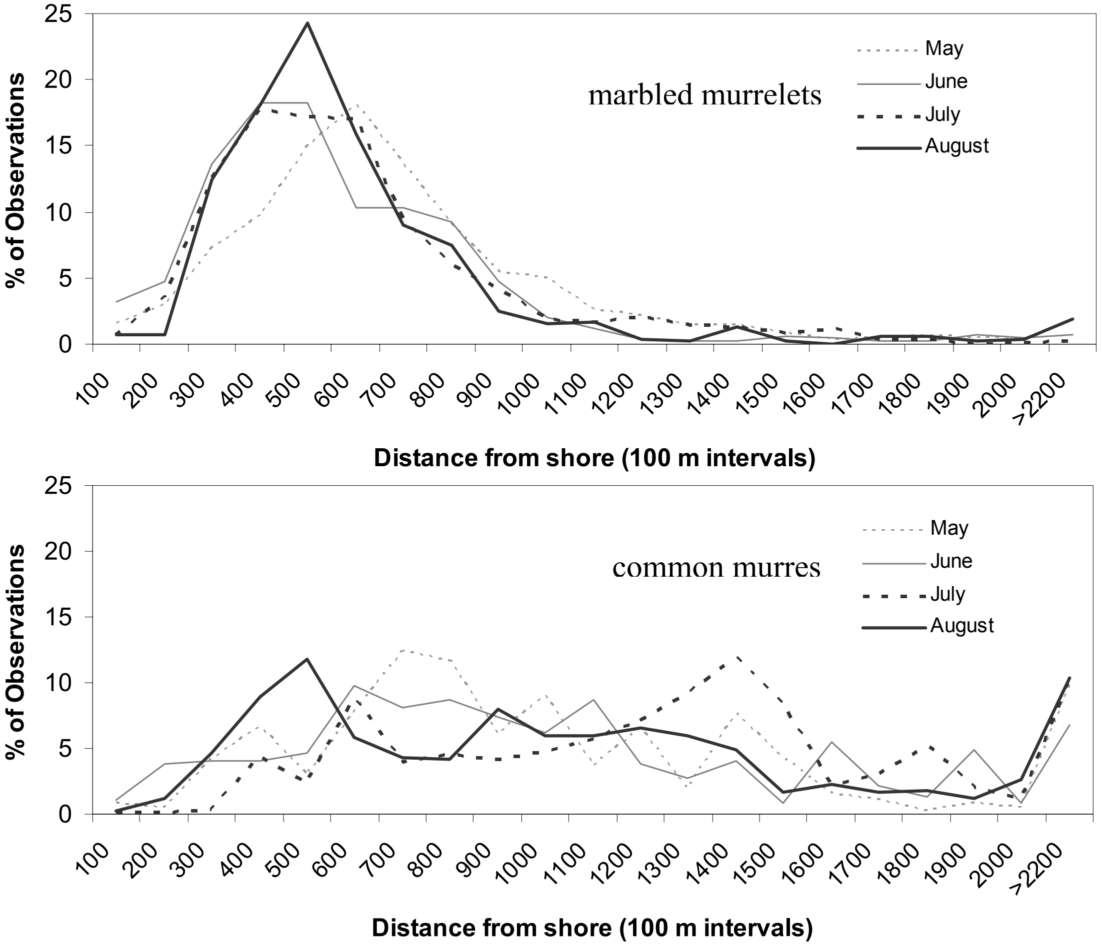


Figure 5.3 - Seasonal variation in marbled murrelet and common murre distributions relative to shore along the West Coast Trail, southwest Vancouver Island. Data pooled from two years (2004 and 2005).

Nearest neighbour distributions

Table 5.2 summarizes the effects of factors influencing nearest neighbour distances. In the main effects model, the largest differences were among contrast groups (best model, lowest AICc) with some evidence of site and year effects (second best model). With years and sites combined, murrelet groups foraged on average within 74 m (± 12 m SE) of other murrelet groups (Fig. 5.4). Common murres (CM-CM) were significantly more dispersed than murrelets ($p < 0.001$) with average nearest neighbours at 283 m (± 13 m SE). The distance at which common murres were located from nearest marbled murrelets (CM-MM contrast) was 138 m (± 14 m SE) which was significantly closer than common murre groups to other common murre groups (CM-CM; $p < 0.001$) suggesting that murres may be attracted to murrelet aggregations. Marbled murrelets, however, were significantly further from murres (MM-CM contrast; 273 ± 14 m SE) than they were to other murrelets suggesting avoidance behaviour.

The main effects models (Table 5.2) included year and site as factors in the second best model which had substantial support (ΔAICc = 2.76) as an alternative model. To investigate the year, month and site influences on nearest neighbour relationships further, I modeled these factors for each contrast group separately (Table 5.2). MM-MM nearest neighbours were influenced by site and year showing marginally closer associations in 2004 than 2005 ($p = 0.059$) and significantly closer associations at Pachena than at Carmanah ($p = 0.015$) but not other sites ($p = 0.065$). CM-CM nearest neighbour statistics showed no significant differences ($p > 0.1$) among years, sites, or months. With MM-CM contrasts, murrelets foraged closer to murres in 2004 than in 2005 ($p = 0.003$) and at other sites than at Carmanah ($p = 0.047$) or Pachena ($p = 0.008$). CM-MM contrasts were most strongly affected by month (murres were farther from murrelets in August; $p < 0.05$) and year (2005>2004; $p = 0.027$). Together these results suggest that spatial distribution and associations between these species were influenced primarily by annual variability (MM-MM, MM-CM, CM-MM) as well as some variation among sites (MM-MM, MM-CM) and months (CM-MM). CM-CM associations showed no little variability.

Introducing murrelet and murre abundance as covariates to the models improved the model fit as these variables were often included in the most likely models (Table 5.3, lowest AICc). This suggests that nearest neighbour statistics may often be influenced by bird abundance (i.e. more birds = foraging closer together). Yet some of the best models still included the main factors (e.g. contrast group in main effects model and year/site in MM-CM models) or included year/site/month factors in second best models with considerable support (ΔAICc < 2; Burnham & Anderson 2002). Linear regression was used to examine the direction and strength of correlations between NN-statistics and bird abundance (Table 5.4). Not surprisingly, these analyses suggested intra- and inter-specific crowding as bird abundance increased: when more birds were in the study area they were closer together. One unexpected result was a positive correlation between common murre abundance and MM-MM nearest neighbour distances, potentially suggesting that murrelets dispersed more as common murres crowded the study area. However, this correlation may be confounded by decreasing murrelet densities in the later part of the summer when common murre abundance increased.

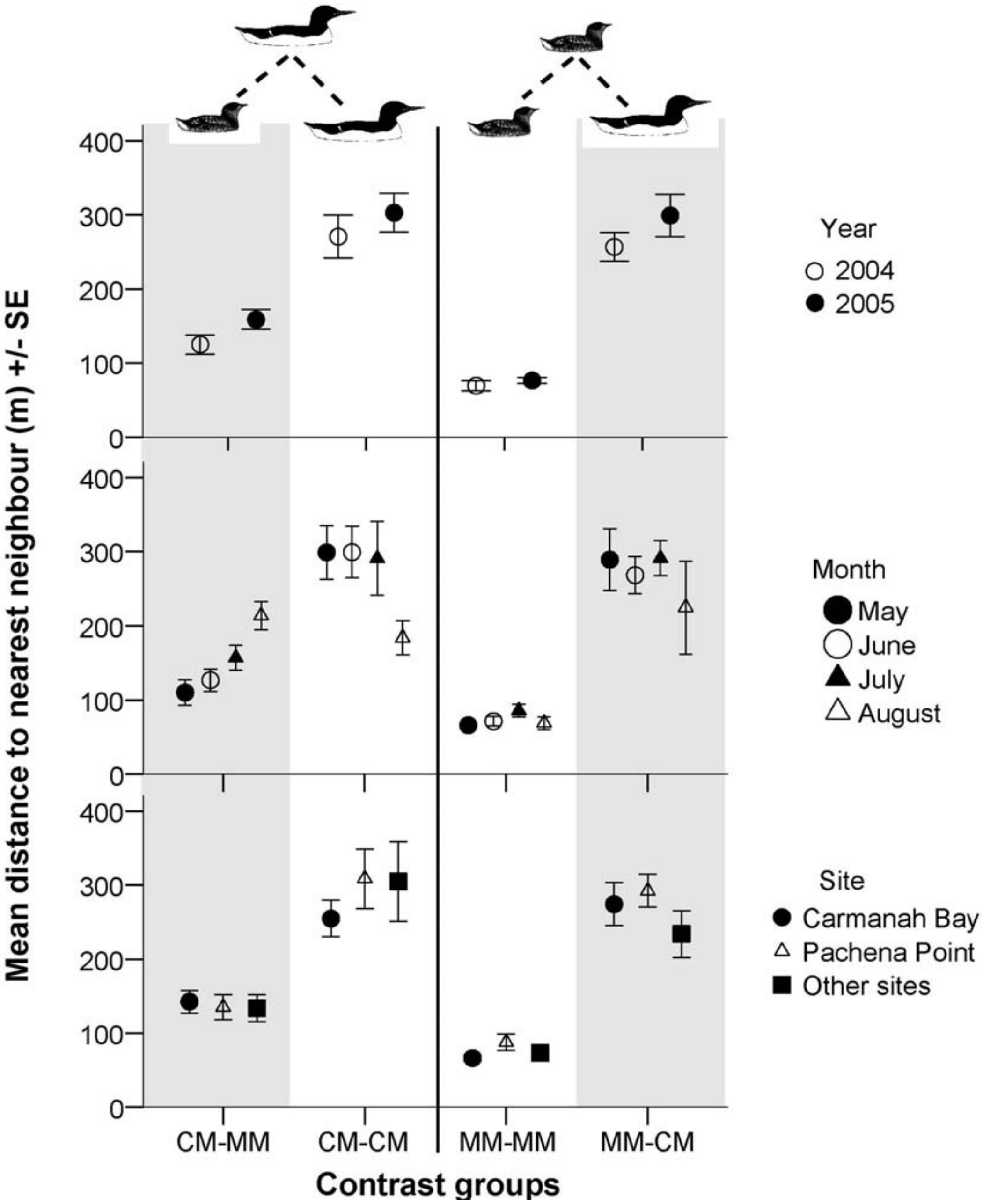


Figure 5.4 - Mean Nearest Neighbour Distances measuring spatial distributions of marbled murrelets (MM) and common murres (CM) at seven sites along the West Coast Trail in 2004 and 2005. Contrast groups compare the average distances between each pair (e.g. CM-MM = avg. distance between murres and the nearest murrelet).

Table 5.2 - Comparisons of candidate models examining marbled murrelet (MM) and common murre (CM) spatial distributions. Models tested factors affecting mean Nearest Neighbour distances between four contrast groups (MM to nearest MM, CM to CM, MM to CM, and CM to MM). Contrast Groups were compared to each other in the main effects model, then effects of Year, Month, and Site were tested within each contrast group separately. Factor covariates included: Year (2004/2005), Site (Carmanah, Pachena, Other), and Month (May, June, July, August). K = number of parameters in the model. Lowest ∆ AICc (Akaike's Information Criteria for small sample sizes) is the best fit model.

Model	Variables included in model	K	Log-likelihood	AICc	∆ AICc
Main effects	Contrast Group (CG)	4	-1460.91	2932.07	0.00
(n = 242)	CG, CG*Site, CG*Year	7	-1449.05	2934.82	2.76
	CG, CG*Year	5	-1458.37	2935.52	3.45
	CG, CG*Site	6	-1457.47	2942.54	10.47
	CG, CG*Month	7	-1453.21	2943.16	11.09
	CG, CG*Year, CG*Month	8	-1450.59	2947.38	15.31
	CG, CG*Year, CG*Site, CG*Month	10	-1442.72	2951.65	19.59
	CG, CG*Site, CG*Month	9	-1450.89	2957.80	25.73
	Null (intercept only)		-1534.83	3073.70	141.64
MM to MM	Year, Site	4	-394.84	800.47	0.00
(n = 81)	Site	3	-396.58	801.68	1.21
	Null (intercept only)	1	-399.26	802.67	2.20
	Month, Year, Site	7	-392.74	803.48	3.01
	Year	2	-398.81	803.93	3.46
	Month, Site	6	-394.43	804.40	3.93
	Month	4	-397.22	805.24	4.76
	Month, Year, Site, Year by Month	10	-391.14	805.42	4.95
	Month, Year	5	-397.12	807.38	6.91
CM to CM	Null (intercept only)	1	-375.01	754.24	0.00
(n = 58)	Year	2	-374.72	755.88	1.63
	Site	3	-374.17	757.10	2.85
	Month	4	-373.34	757.83	3.58
	Year, Site	4	-373.63	758.42	4.18
	Month, Year	5	-373.12	759.89	5.65
	Month, Site	6	-373.00	762.24	7.99
	Month, Year, Site	7	-372.54	764.01	9.77
	Month, Year, Site, Year by Month	10	-372.34	772.42	18.18
MM to CM	Year, Site	4	-329.81	670.87	0.00
(n = 54)	Null (intercept only)	1	-334.84	673.91	3.04
	Year	2	-334.01	674.50	3.64
	Site	3	-334.03	676.87	6.00
	Month, Year, Site	7	-329.12	677.45	6.58
	Month	4	-333.95	679.15	8.29
	Month, Year	5	-333.06	679.91	9.04
	Month, Year, Site, Year by Month	10	-327.00	682.29	11.43
	Month, Site	6	-333.10	682.63	11.76
CM to MM	Month, Year	5	-267.63	549.26	0.00
(n = 49)	Month	4	-269.97	551.34	2.08
	Month, Year, Site	7	-265.92	551.45	2.19
	Year	2	-274.05	554.64	5.39
	Null (intercept only)	1	-275.56	555.38	6.13
	Year, Site	4	-272.40	556.20	6.95
	Month, Site	6	-269.97	556.67	7.41
	Month, Year, Site, Year by Month	10	-263.99	557.12	7.86
	Site	3	-275.47	559.86	10.60

Table 5.3 - Comparisons of candidate models examining the effects of bird abundance on marbled murrelet (MM) and common murre (CC) spatial distributions. Models tested factors affecting mean Nearest Neighbour distances between four contrast groups (as per Table 2) and included CM and MM abundance as covariates in the models. Table compares the best models (lowest AICc values) from Table 2 to models with and without CM/MM abundance as covariates. See Table 5.2 for definitions of factor covariates, K, and Δ AICc.

Model	Variables included in model	K	Log-likelihood	AICc	Δ AICc
Main effects	CG, CM aundance	5	-1450.08	2912.51	0.00
(n = 242)	CG, MM aundance	5	-1454.01	2920.39	7.88
	Contrast Group (CG)	4	-1460.91	2932.07	19.55
	MM abundance	2	-1528.73	3063.56	151.05
	CM abundance	2	-1533.68	3073.46	160.95
MM to MM	MM abundance	2	-384.56	775.43	0.00
(n = 81)	Year, Site, MM abundance	5	-382.68	778.49	3.06
	Year, Site, CM abundance	5	-390.62	794.38	18.95
	Year, Site	4	-394.84	800.47	25.04
	CM abundance	2	-397.39	801.09	25.66
CM to CM	CM abundance	2	-365.77	737.98	0.00
(n = 58)	Year, CM abundance	3	-365.49	739.74	1.76
	MM abundance	2	-373.80	754.05	16.07
	Null (intercept only)	1	-375.01	754.24	16.26
	Year	2	-374.72	755.88	17.90
	Year, MM abundance	3	-373.74	756.23	18.24
MM to CM	Year, Site, CM abundance	5	-323.49	660.77	0.00
(n = 54)	CM abundance	2	-328.97	664.43	3.66
	Year, Site	4	-329.81	670.87	10.09
	Year, Site, MM abundance	5	-329.80	673.38	12.61
	MM abundance	2	-334.00	674.48	13.71
CM to MM	MM abudance	2	-269.28	545.09	0.00
(n = 49)	Month, Year, MM abundance	6	-265.11	546.95	1.86
	Month, Year, CM abundance	6	-267.38	551.50	6.41
	Month, Year	5	-267.63	549.26	4.17
	CM abundance	2	-275.54	557.62	12.54

Table 5.4 - Effects of bird abundance on marbled murrelet (MM) and common murre (CM) spatial distributions. Linear regression was used to examine correlations between bird abundance and changes in nearest neighbour statistics.

Nearest neighbour (NN) statistic	Effect	R_2	df	F	P	interpretation
Effects of marbled murrelet abundance on nearest neighbour statistics						
MM to MM	↑ abund. = ↓NN	0.304	80	34.57	<0.001	intra-specific crowding: murrelets are forced close together
CM to CM	no effect	0.041	57	2.39	0.128	
MM to CM	no effect	0.030	53	1.63	0.204	
CM to MM	↑ abund. = ↓NN	0.226	48	13.74	0.001	inter-specific crowding: murres are forced close murrelets
Effects of common murre abundance on nearest neighbour statistics						
MM to MM	↑ abund. = ↑NN *	0.045	80	3.73	0.057	dispersal: increase murre abundance causes murrelets to disperse
CM to CM	↑ abund. = ↓NN	0.273	57	21.03	<0.001	intra-specific crowding: murres are forced close together
MM to CM	↑ abund. = ↓NN	0.195	53	12.60	0.001	inter-specific crowding: murrelets are forced close murres
CM to MM	no effect	0.001	48	0.03	0.859	

*note effect is marginal (see p-value)

Randomization tests

Randomization tests assessed the significance of CM-MM and MM-CM statistics which are sensitive to the proportions of each species mapped in each scan. From 60 scans with > 1 individual of each species, MM-CM and CM-MM nearest neighbour statistics were non-random during 30% and 40% of the replicates respectively. This suggests that during most of the trials, the spatial patterns between murres (CM) and murrelets (MM) were random, however, in at least 1/3 of the trials the spatial patterns were non-random. Figure 5.5 shows how the random and non-random trials contrast with MM-MM and CM-CM nearest neighbour statistics. The 24 non-random trials for CM-MM statistics show that CM-MM distances are equal to CM-CM distances. Thus, murres are evenly distributed among murrelets and other murres and the previous interpretation of attraction (above) is no longer valid. In contrast, the 20 non-random trials of MM-CM statistics show that MM-CM distances are much greater than MM-MM distances. Therefore this provides stronger support for the murrelet avoidance hypothesis whereby murrelets forage farther from murres than they to from other murrelets and this is not due solely by random distributions of murrelets and murres.

Comparison of trials between random and non-random MM-CM distributions may reveal conditions that support avoidance behaviour. T-tests showed significantly more murrelet groups (mean 63.3 ± 11.4 SE) in the non-random trials than in the random trials (mean 34.3 ± 4.5 SE; $t = 2.83$, $df = 58$, $p < 0.001$). Number of common murre groups did not differ between random and non-random trials (rand 6.6 ± 0.9, non-rand 6.8 ± 1.4; $t = 0.12$, $df = 58$, $p = 0.733$). This suggests that murrelets can more effectively avoid murres when murrelets are more abundant.

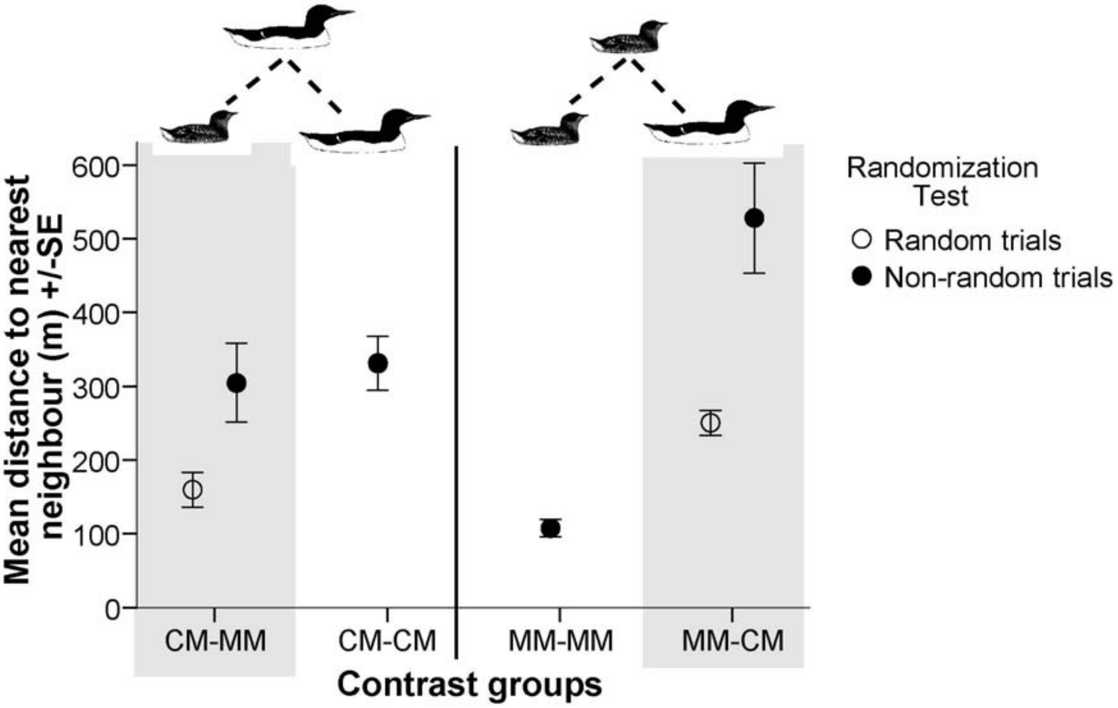


Figure 5.5 – Randomization tests and the mean Nearest Neighbour Distances measuring spatial distributions of marbled murrelets (MM) and common murres (CM). Contrast groups compare the average distances between each pair (e.g. CM-MM = avg. distance between murres and the nearest murrelet). Randomization tests were used to test the significance of the spatial patterns between CM-MM and MM-CM. Random trials are those where CM and MM locations are interchangeable, whereas the non-random trials are those where the spatial distributions between CM and MM do not occur by chance.

DISCUSSION

Numbers of murres and murrelets

Across many biological studies there are density dependent effects of competitors whereby the effects of competition are stronger when an animal's neighbours (competitors) are at higher densities (Gurevitch et al. 1992). Murrelets were numerically dominant in both years, however seasonal changes in species abundance showed lower ratio of murrelets to murres in July and an even ratio in August (Table 5.1, Fig. 5.1). Moreover, this is the same period when higher proportions of murres were occupying nearshore waters (Fig. 5.3). Thus, one might expect any competitive interaction to be strongest (greater avoidance behaviour) in July and August when murres were most abundant. The nearest neighbour results did not support these predictions, but showed that murre distances from murrelets actually increased in August (Fig. 5.4) and thus foraged further from murrelets when murrelets were least abundant. There was no significant seasonal change in MM-CM distances.

The lack of evidence for density-dependent competition and avoidance effects may simply be a function of the mathematical properties of nearest neighbour calculations. When few murrelets were present, murres by chance may have been on average further from murrelets. I attempted to control for unequal proportions of the two species (see methods above), but, randomization tests provided an alternative method for testing the statistical significance of nearest neighbour spatial distributions (Fortin & Jacquez 2000). Randomization tests showed that spatial patterns between MM-CM were non-random 30% of the time and suggest that murrelets do avoid murres during these periods. Non-random distributions (avoidance of murres by murrelets) occurred when murrelet densities were higher, thus, the ability of segregate from murres may be dependent on minimum densities of murrelets. Because murrelet densities decrease seasonally, the number of trials showing significant avoidance behaviour by murrelets (non-random trials) apparently also decreases: May = 40% of trials, June = 38%, July = 35% and August = 0%. This coincides with a trend in increasing common murre abundance suggesting that avoidance behaviour becomes more difficult of murrelets later in the summer. The August distribution of murres in nearshore waters (Fig. 5.1) suggests that high inshore murre densities may have been sufficient to exclude murrelets from habitat consistently used earlier in the summer. Low densities of murres in May, June and July, did not appear to displace murrelets.

Spatial segregation

At larger spatial scales (10's km) and within 1-minute transect segments (~280 m), Burger et al. (2008) observed spatial segregation between murres and murrelets recorded along boat transects along the same coastline between 1993 and 1996. Yet during vessel-based surveys in 2004-2006 I often saw murrelets and murres together and even foraging next to each other. Chapter 2 showed differences in habitat use between murres and murrelets, yet they showed considerable overlap in habitat selection (preferred habitat) at both regional scales (along the West Coast Trail, < 65 km) and site scales (within Carmanah Bay, < 10 km). The theodolite data, however, offer the chance to examine very fine-scale (10's or 100's m) partitioning in habitat not otherwise possible with boat-based transects.

I observed general differences in spatial distributions between marbled murrelets and common murres. Murrelets preferred nearshore waters and murres were more evenly distributed over distances up to 1500 m from shore (Burger et al. 2008, this study). Burger et al. (2008) suggested that these distributions may be related to water depth which changes rapidly with distance from shore in this region. Dive duration and dive depths of alcids are generally related to body mass (Burger 1991, Watanuki & Burger 1999). Murres (~ 800-1100 g) have more than four times the mass of marbled murrelets (~ 200-250 g) and could almost certainly exploit prey from deeper waters than murrelets. Common murres are known to regularly dive to depths exceeding 150 m (Piatt & Nettleship 1985, Burger 1991) whereas marbled murrelets are unlikely to exceed 40 m (Mathews & Burger 1998). Estimated maximum dive durations for murres and murrelets are 1.8-3.0 min. and 1.0 min, respectively (Watanuki & Burger 1999). However, typical dive durations for murrelets are only about 25 sec. and frequently occurred in waters less than 10 m deep (Jodice & Collopy 1999). This suggests potential partitioning of habitat between the two species, though murres would not be restricted to deep waters and could exploit shallow waters given the opportunity. Within the waters that I sampled (to ~1000 m offshore) depths were generally <30 m (Burger et al. 2008) within the diving range of both species. Therefore partitioning habitat by diving depth was unlikely in these nearshore areas.

Interspecific and intraspecific competition

A meta-analysis of aquatic and terrestrial organisms showed that carnivores experience similar effects from both interspecific and intraspecific competition

(Gurevitch et al. 1992). Both murrelets and murres are piscivorous species that exhibit considerable dietary overlap (Carter 1984, Hobson et al. 1994, Lance & Thompson 2005) suggesting that they may compete for food resources and may be susceptible to both inter- and intraspecific competition. In this study I observed no direct aggressive interactions between murres or murrelets. After consideration of randomization tests, nearest neighbour analyses showed that murre groups foraged at similar distances to murrelets as they did from other murre groups. This suggests that murres show no direct avoidance of murrelets but also that murres may require some minimum spacing between groups of conspecifics for efficient foraging (approximately 250 to 500 m between groups). Thus, murres may be experiencing fine-scale intra- and interspecific competition.

The relatively large distances between murre groups (approximately 300 m) suggest that murres may experience intraspecific competition, an observation that has been made in other studies of murres. Intraspecific competition may constrain chick provisioning rates by common murres (Davoren & Montevecchi 2003). Post-fledging adult/chick pairs of thick-billed murres (*Uria lomvia*) moved away from areas adjacent to the colony presumably to benefit from reduced competition while raising young (Falk et al. 2001). In areas of low prey densities off Newfoundland, murres are also found at lower densities, suggesting that intraspecific interference competition may play an important role in prey capture (Davoren et al. 2003a). Prey densities, which were not measured in this study, can play an important role in the strength of competition observed between intraspecifics foraging on shared resources (Triplet et al. 1999). The closer proximity of murre groups to murrelets than to other murres suggests that intraspecific competition may be greater than interspecific competition for common murres, and neighouring murrelet groups pose little threat of competition.

Marbled murrelets, on the other hand, foraged in much closer proximity to each other (< 100 m) and avoided foraging near murres (typically >250 m). Thus murrelets appeared to segregate themselves from murres suggesting stronger interspecific than intraspecific competition. Group foraging (typically pairs) is thought to be beneficial for murrelets (Strachan et al. 1995) but has disadvantages when groups become too large (Kuletz 2005). Possible effects of interspecific competition have not been investigated with murrelets but have been suggested with a variety of other species. Interspecific competition may explain why black guillemots (*Cepphus grylle*) do not exploit dense concentrations of pelagic prey in deep water, even though they are capable of this (Cairns 1992b). Piatt (1990) suggested that common murres may compete with Atlantic puffins (*Fratercula arctica*) for capelin (*Mallotus villosus*) and Piatt (1987) observed aggressive behavior by murres directed at puffins in areas of overlap. Dietary changes in the herring gull (*Larus argentatus*) have been attributed to interspecific competition from larger great black-backed gulls (*L. marinus*) (Rome & Ellis 2004). Alternatively, superabundant food resources may alleviate competition and facilitate a high degree of dietary/niche overlap (Gonzalez-Solis et al. 1997). Mixed-species flocking may not be beneficial for all individuals or species and therefore murrelets avoid interactions with murres when possible. In the absence of such competitors (other pursuit diving seabirds), marbled murrelets forage in mixed-species flocks with gulls (Mahon *et al*. 1992).

Although I suggest that competition is occurring, I have still not identified the proximate mechanism supporting this interaction. Although direct competitive interactions do occur between feeding seabirds (Hoffman et al. 1981), I did not observe any aggressive interactions between murres and murrelets, therefore I suggest that murrelets are either responding to passive interference competition (e.g. indirect disruption of prey by murres) or the perception of competition risk. There is evidence to support the hypothesis of indirect competition. Frequently in marine communities, the behaviour of one predator may affect the behaviour of their prey, thus indirectly affecting a competing predator that is also dependent on that prey (Dill et al. 2003). This phenomenon has been observed in seabirds where disturbance of fish schools can cause birds to travel further in search of prey (Lewis et al. 2001). Alternatively, just as the risk, or perceived risk, of predation can cause behavioural changes in prey to avoid predators (Brown et al. 1999, Heithaus & Dill 2006), the potential risk of competition (either perceived or real) could influence the foraging behaviours of competing predators. Even when aggressive interactions are few, some predators show changes in foraging behaviours when there is a risk of competition from conspecifics (Nilsson et al. 2000). Thus the perceived risk of competition with murres may be the mechanism causing avoidance of murre groups by murrelets even when murres may be attracted to murrelet groups for foraging opportunities.

Coexistence

This study provides evidence of interspecific competition (nearest neighbour distances) which may be promoting coexistence between murres and murrelets at fine spatial scales. Although murrelets are numerically dominant throughout most of the summer, the fewer but larger murres seem to influence the foraging distributions of murrelet groups. As a result this alters the patterns of murrelet habitat use and creates fine-scale segregation between competing species within foraging sites. Yet in addition to this fine-scale segregation there are several other mechanism that may also be segregating these species in space and time, thus allowing for coexistence.

Coarse-scale habitat partitioning (10-100 km) between and within species may allow for species (or high densities of the same species) to coexist within home ranges of overlapping populations. Seabirds from neighbouring colonies use different foraging sites potentially to reduce intraspecific competition through spatial partitioning (Flint & Golovkin 2002, Ainley et al. 2004). Limited overlap in foraging ranges reduces interspecific and intersexual competition among two sympatric species of giant petrels (*Macronectes* spp.) and two sympatric species of albatross (*Thalassarche* spp.) by spatial partitioning of foraging areas (Gonzalez-Solis et al. 2000, Phillips et al. 2004). Marbled murrelets show considerable ecological overlap in foraging ecology with the Kittlitz's murrelet (*Brachyramphus brevirostris*), suggesting potential for interspecific competition in the Alaskan waters where they overlap (Day & Nigro 2000), but subtle differences in habitat preferences facilitate the ecological partitioning between these two coexisting species (Day et al. 2003). I found some evidence of spatial partitioning with respect to distance from shore for murres and murrelets, and coarse-scale habitat selection suggested an additional mechanism of spatial segregation (Chapter 3).

Although murrelets and murres feed on similar prey items, they may differentiate in prey choices by other less obvious factors of fish school characteristics such as school size, location, depth, and density. Off Newfoundland, foraging on lower capelin densities may allow Atlantic puffins to coexist with common murres that require higher daily caloric intake of food because of their larger body size, and thus have higher prey density thresholds (Piatt 1990). Prey depth can also be important to seabird foraging, particularly for surface feeding birds like gulls or terns (Safina & Burger 1985). Other studies have inferred that murrelets are more adaptable to foraging on small, widely dispersed schools of fish than other alcids (Ostrand et al. 1998a, Kuletz 2005). Therefore, fine-scale investigation of murre and murrelet associations with fish school characteristics may reveal important mechanisms of resource partitioning that facilitate coexistence on shared resources. Moreover some birds may disrupt prey schools thus making them less available to other seabirds (Lewis et al. 2001). If murres somehow disrupt prey schools making capture more difficult for murrelets, this could explain why murres inhibit the presence of murrelets at mixed-species flocks (Chilton & Sealy 1987) and why murrelets distance themselves from groups of murres (this study).

Conclusions

I observed indications of interspecific competition between murres and murrelets whereby murrelets showed avoidance behaviour of murres in both years, throughout the breeding season, and across several sites. Randomization tests support this finding and this competitive effect may have been strongest in July and August when murres increased in numbers. Murrelets appear to be generally reluctant to participate in mixed-species feeding flocks especially with larger birds (Porter & Sealy 1981, Chilton & Sealy 1987, Kuletz 2005, but see also Mahon et al. 1992). In parts of Alaska where murrelet numbers have declined in relation to populations of larids that kelptoparasitize murrelets, some have speculated that increasing larid numbers could be detrimental to the recovery of murrelet populations (Hunt 1995, Kuletz 2005). Although murrelets outnumber murres throughout most of their range, recovery of very small populations of murrelets in California may be more at risk to detrimental effects of interspecific competitors.

Coexistence of similar-sized and potentially competitive species of Alcidae may be facilitated by the complexity of marine environments which create broad niches for species to exploit (Haney & Schauer 1994). For some apparently competitive species, closer investigations have revealed that fine-scale niche partitioning, rather than interspecific competition, can facilitate coexistence (Garthe et al. 1999). For marbled murrelets and common murres, these niches might also include differences in fine-scale habitat use, selection of fish-school characteristics, and diel timing of foraging activities. In this study I show that fine-scale spatial segregation between murres and murrelets (avoidance of murres by murrelets) may enable these species to coexist and exploit shared resources in nearshore waters.

Chapter 6 - Synthesis: Methodological Developments, Ecological Theory, and Implications for the Management and Conservation of Marbled Murrelets.

Using data from over 150 hours of vessel-based surveys, more than 750 hours of telescope observations, and nearly 100 replicates of fine-scale mapping by theodolite, my dissertation established both patterns of habitat selection and potential mechanisms that facilitate this. I have (1) developed new methodological techniques relevant to marine bird studies elsewhere; (2) advanced ecological theory relating to seabird population regulation, foraging ecology, competition and coexistence; and (3) produced information relevant to the conservation and management of the threatened marbled murrelet. In this chapter I provide a synthesis regarding the contribution of my thesis to these three areas.

New methodological developments

Distance sampling for seabirds

Chapter 2 was devoted entirely to examining the detectability of seabirds along vessel-based transect surveys. Issues of detectability are fundamental to obtaining accurate and reliable density and abundance estimates which area essential to wildlife ecology research (Braun 2005). Distance-sampling has been widely used by marine mammal researchers to quantify detectability (Laake et al. 1997) and develop robust abundance and population estimates (Forcada et al. 2004, Slooten et al. 2006). Chapter 2 extends the application of distance-sampling techniques (Buckland et al. 2001) to birds on the water recorded during vessel transects. Strip-transect are historically and currently the most widely used method for censusing birds at sea (Pyle 2007). Because strip-transects often underestimate animal abundance (Buckland et al. 2001), my analysis of detectability offers an important look at methods for improving the accuracy, and potentially precision, of at sea density, abundance and population estimates for seabirds.

I illustrate a high degree of inter-specific and inter-annual variability as well as observer bias in bird detectability. Along a 300 m wide transect (150 m on either side of the boat) detectability ranged from 20-80% depending on species, year and observer. Detectability of marbled murrelets in this study was similar to that of murrelets elsewhere (Becker et al. 1997, Evans Mack et al. 2002, Peery et al. 2006, Raphael et al. 2007) suggesting that murrelet detectability along vessel transects is a widespread issue for murrelet population assessment. I provide the first estimates of detectability for other alcids (murres, auklets and guillemots) as well as one species of cormorant. Correcting for detectability difference between species provides a much more accurate data set for analyses comparing habitat selection among species (Chapter 3). This study also has important ramifications for vessel-based seabird research world-wide. The application of distance sampling to seabird surveys provides more accurate abundance and population estimates, which will improve conservation and management efforts. Moreover, distance sampling can improve the precision of density estimates because seabird detectability will vary with weather, observer experience and fatigue, bird behaviour, and among species – factors that are rarely accounted for when calculating densities from strip-transects.

Fine-scale distribution mapping by theodolite

In Chapter 5, I investigated the fine-scale competition between common murres and marbled murrelets for foraging space. This required a technique to map seabird distribution at a finer spatial resolution than possible from vessel surveys. I further developed a technique for fine-scale mapping by electronic theodolite which I previously used to study interactions between seabirds and boats (Ronconi & St Clair 2002). This approach allows for the mapping of individuals or flocks of birds at very high resolution (~2 m up to 2 km from land, Denardo et al. 2001). Marine mammal researchers have used theodolites in studies of animal movements (Bejder & Dawson 2001, Gailey et al. 2007), habitat use (Bejder & Dawson 2001, Ribeiro et al. 2007) and conservation (Johnston 2002, Cox et al. 2004). Chapter 5 highlights the potential to use of this technique in studies of marine birds in coastal environments when they can be viewed from cliff tops. Moreover, there is the potential to use this instrument for fine-scale habitat mapping such as kelp beds (Chapter 3, Wong et al. in press) or tidal currents (Johnston & Read 2007).

There are many advantages to this technique over traditional distribution mapping from boats. First it allows for intensive, rapid and repeated sampling over a reasonably sized study area (~2 km^2), and it allows for the integration of spatial and temporal mapping (e.g., sequential hourly or daily maps of bird distributions). The technique also offers an innovative way to study the movement patterns of individual birds such as tracking of focal animals through dive sequences. Importantly, it eliminates the possible interference caused from research activities; all other methods to study the spatial distribution of birds at sea (vessel or aircraft surveys, telemetry studies, etc.) have some effect on the birds' behaviour. Finally, it is a relatively low cost technique ($1000/month for rented equipment) compared to the costs associated with owning, operating and maintaining boats. There are some clear limitations to theodolite mapping, such as use only in nearshore waters and during daylight hours, and there are also detectability issues for small inconspicuous species (Appendix II). Nevertheless, I hope that more researchers of marine and aquatic birds will use this technique for innovative work.

Linking terrestrial and marine habitats for murrelets

The marine distribution of marbled murrelets is frequently linked to terrestrial nesting habitat over large (100's of km) spatial scales (Miller et al. 2002, Raphael et al. 2002, Yen et al. 2004a, Raphael 2006). I sought to investigate linkages between terrestrial and marine habitats for murrelets in Chapter 3, however, the small scale of my study area (<65 km) required me to develop a new approach to measure habitat adjacency. At coarse-scales, murrelets select habitat closer to nesting habitat flyways (Becker & Beissinger 2003), potentially to reduce the energetic costs of nesting further inland (Hull et al. 2001). Assuming that murrelets prefer nesting habitat that is closer to foraging locations, I used a GIS-based approach with inverse distance weighting (IDW) to extrapolate values of nesting habitat into adjacent areas on the coast (details in Chapter 3 and Appendix I). This created an index of nesting habitat within 30 km of every location on the water. This index proved to be one of the most important factors driving the marine habitat selection of murrelets in my study area.

This technique could be applied elsewhere as a tool used to identify critical marine habitats for murrelets based on adjacent nesting habitat over bigger spatial scales. Large-scale associations between offshore murrelet abundance and inland terrestrial habitat have used rather arbitrary segmentation of terrestrial habitat sectors: 50 to 80 km bins (Miller et al. 2002, Raphael et al. 2002) or larger (Raphael 2006). This approach may create boundaries that are biolgically irrelevant since murrelets can travel 30 to 100 km from marine areas to nest sites (Whitworth et al. 2000, Hull et al. 2001). The method I developed offers a means to quantify accessible inland habitat at specific marine locations. This higher level of detail allows us to identify thresholds in associations between at-sea counts and inland habitat (Chapter 3) rather than correlations (Miller et al. 2002, Raphael et al. 2002, Yen et al. 2004a, Raphael 2006). The techniqe could also be modified for other studies linking murrelet counts to terrestrial habitats. For example, radar counts have become standard practise in murrelet population assessment (Burger et al. 2004b), but when linking radar data to inland habitats they suffer the same problem of defining habitat adjacency. Traditionally, radar stations are linked to terrestrial habitat via watershed boundaries (Burger 2001). This assumes that all areas within a watershed are equally accessible to murrelets counted at the radar station, but in reality nesting habitat closer to the ocean (and radar station) may be more important. The IDW approach could be used to relate habitat within or among watersheds to individual radar stations which may improve our ability to link radar counts to changes in old-growth forests at watershed scales.

Advancement of ecological theory

The design and analysis of studies in my dissertation was based on habitat selection theory. This framework assumes that habitat selection results in non-random patterns of habitat use that increase the survival or fitness of individuals. Moreover, habitat selection theory recognizes both proximate and ultimate factors in habitat selection that function at various scales. Proximate factors are those that attract individuals to settle in that habitat and ultimate factors relate directly to the fitness (survival and reproduction) of individuals and species (Block & Brennan 1993). By investigating the habitat selection of marine birds at multiple scales, my dissertation investigated both proximate and ultimate causes. In doing so, my dissertation has provided several advancements in ecological theory relevant to seabirds including population regulation, foraging ecology, and competition.

Population regulation in seabirds

The regulation of animal populations implies the maintenance of an average population size which may be dependent on population densities or other limiting factors such as habitat, climate, food supply, disease or social factors (Gill 1995). Seabird populations, however, are generally regulated by food supply, particularly during the breeding season (Ashmole 1963, Lack 1968, Cairns 1987, Cairns 1992a). Cairns (1987) hypothesized that food density would affect, in a hierarchical way, seabird survivorship, breeding success, chick growth and activity budgets. Most of Cairn's predictions hold true during field trials (Harding et al. 2007, Piatt et al. 2007b) and many studies have suggested that seabirds can frequently compensate for low prey by adjusting foraging effort (e.g., Harding et al. 2007). However, Chapter 4 shows that this is not the case for murrelets. Species with specialized feeding habits, energetically expensive food searching methods and small body size may be more vulnerable to food shortages (Harding et al. 2007). Species able to deliver prey to young during all daylight hours (e.g., common murre) are more flexible in their foraging behaviour and thus better able to buffer reproductive success against food shortages. Because of predation risk at breeding sites, many smaller alcids typically provision young only at dusk or night (e.g., murrelets, auklets), thus if prey is not found late in the day, flexible foraging may provide little buffering to rear young in poor prey years. Under this scenario, scarce prey is most likely to regulate seabird populations through decreased reproductive success rather than adult survival (Cairns 1987).

Overall, carrying capacity for murrelet populations may be limited by amount of suitable nesting habitat, but annual recruitment is more affected by at-sea conditions. Long-term changes in prey were correlated with long-term declines of murrelet populations in British Columbia (Norris et al. 2007), and my dissertation provides a clear mechanistic link between predators and prey in this correlation: murrelets experience high levels of reproductive failure when foraging conditions are poor. In Alaska, climate-driven regime shifts have altered the marine food web over periods coinciding with murrelet population declines (Piatt et al. 2007a and references therein) suggesting that persistent and long-term changes in the marine environment may be detrimental to the recovery of murrelet populations. In British Columbia, warming periods associated with El Nino Southern Oscillation (ENSO) events, had negative effects on murrelet abundance at several sites (Burger 2000). It is likely that these trends are associated with changes in the prey base upon which murrelets depend because some of their key prey are negatively affected by warm waters (Piatt et al. 2007a and references therein). Given the current warming trends of our oceans (Levitus et al. 2000, Walther et al. 2002) and the increasing frequency of periodic events (King 2005), it seems inevitable that long-term ecosystem changes may hinder the recovery of murrelet populations.

Foraging ecology

Three key concepts in foraging theory are prevalent in the seabird literature: central place foraging theory, search strategies, and scale-dependent predator-prey interactions. My dissertation provides insight into each of these concepts.

Optimal foraging theory predicts that animal balance trade-offs between costs (time and energy loss) and benefits (energy gain) when making foraging decisions so that the benefits outweigh the costs (Krebs & Davies 1981). Central place foraging (CPF), animals that repeatedly return to fixed points to forage or deliver prey, is an important dimension of optimal foraging theory (Orians & Pearson 1979). With CPF, animals' costs include travel time to patches, foraging time at patches and return time. Central place foragers should therefore choose food patches that minimize total time (Kramer & Nowell 1980) which can be achieved by traveling short distance to patches where prey might be scarce and difficult to capture or traveling long distances to patches where prey capture is quick. This trade-off is relevant to seabirds because they are central place foragers when incubating or rearing nestlings. Species-habitat models (Chapter 3) highlight the importance of CPF to marine habitat selection. When prey are scarce, seabirds may adjust travel time, foraging costs, or both. Of the three colonial alcids, thresholds in foraging distributions relative to possible nesting colonies increased with body size: pigeon guillemots (ranges 1.9 to 4.7 km from colonies), rhinoceros auklets (2.6 to 5.0 km) and common murre (preference for habitat > 23 km from colony). However, this was unrelated to prey availability and these differences of travel costs (5-10 km) may be trivial given that flights speeds average over 70 km/h (Burger 1997b). In 2005 when prey was less abundant (Chapter 4), murrelets adjusted both foraging effort (Chapter 4) and travel costs (changes in thresholds of attraction to old-growth habitat, Chapter 3). This provides evidence that CPF seabirds adjust both commuting costs and foraging effort in order to maximize prey acquisition.

Within thresholds of central place foraging, birds must still be able to locate prey. Two common search strategies used by seabirds to locate prey include cues from conspecifics, known as local enhancement (Wittenberger & Hunt 1985), and memory of predictable foraging locations (Davoren et al. 2003b). Birds will likely use a combination of both, since the latter brings birds to foraging sites and the former allows them to quickly find individual prey patches if there are already other birds foraging there. In Chapter 4 there was no evidence of conspecifics influencing the foraging behaviour of murrelets, suggesting that local enhancement plays little role in their search strategies. In Chapter 3, prey availability had no influence on habitat use or preference by any species. Thus, I suggest that, at the scales of my research (<70 km), seabirds are using environmental cues and memory of foraging habitats. Instead of tracking prey *per se*, birds are targeting habitats likely to have predictable prey. This approach to search strategies has been reported elsewhere where seabirds use memory to travel directly to regions of predictable prey (Davoren et al. 2003b).

Scale-dependent predator-prey associations are widely reported in studies of seabirds (Logerwell & Hargreaves 1996, Fauchald et al. 2000, Davoren et al. 2002). Seabirds typically show the strongest concordance with prey at scales > 10 km, although sometimes smaller scale seabird-prey associations are detectable (Burger et al. 2004a). Fauchald et al. (2000) explained these scale-dependent predator-prey associations as a result of a search patterns that reflect a hierarchical spatial distributions by both seabirds and prey. This hierarchy helps minimize the area to be searched (optimal foraging theory) between scales of 50 to 500 km, however, at the smallest level (~3 km) the hierarchy falls apart (no overlap between predator and prey patches; Fauchald et al. 2000). Therefore it remains unclear how birds acquire prey within these smallest scales. Hunt & Schneider (1987) suggested that at coarse- and fine-scales (100 km to 100's m) foraging behaviour and social interactions were the processes controlling the distribution patterns of both predators and prey. Prey cannot easily be detected by birds at the surface without sampling (diving) which is time and energy consuming. Therefore, habitat preferences coupled with social cues (local enhancement such as mixed-species flocking; Chilton & Sealy 1987, Porter & Sealy 1981) are the likely mechanisms whereby the birds put themselves in places where they are most likely to encounter prey. In Chapter 3, I demonstrate that seabirds do select habitat rather than prey patches, and Chapter 5 provides some insight into social cues that may be interacting within selected habitat. In this case the social cues may be attraction of murres to murrelets for foraging opportunities (local enhancement) and avoidance of murres by murrelets without direct competitive interactions (perception of competition by murrelets).

Competition

Competition and the competitive exclusion principle is a fundamental component of many ecological theories including aspects of niche partitioning and species coexistence. Competition may occur in several ways (Gotelli 2001). First, exploitative competition occurs when one species depletes the resources of another, though this has been difficult to demonstrate with seabirds (Birt et al. 1987, Shealer 2002). Interference competition may be either active (aggression) or passive (disruption of prey schools) and there is evidence for both in seabird communities (Piatt 1990, Safina 1990, Shealer & Burger 1993, Ballance et al. 1997, Lewis et al. 2001, Ainley et al. 2003). Burger et al. (2008) suggested that murrelets may simply avoid areas frequented by larger alcids within my study area, which is suggestive of interference competition. Chapter 3 identifies the potential for competition between murres and murrelets since the two have similar fundamental niches at coarse- and fine-scales. This niche space is then modified by competition so that murrelets segregate from murres at even finer spatial scales (Chapter 5) possibly at the level of individual prey patches. Between 1993 and 1996, when murre densities were quite high, Burger et al. (2008) suggested that murres may exclude murrelets from certain areas over broad scales. Yet in 2004-2006, when murres were less abundant, these species overlapped in habitat use and showed competitive interactions only at fine spatial scales. Together these results suggest that competitive exclusion between seabirds can be scale- and density-dependent.

Management and conservation of marbled murrelets in marine habitats

For the past 20 years, the thrust of marbled murrelet research has largely been focused on the conservation and management of terrestrial nesting habitat (Ralph et al. 1995, Burger 2002, McShane et al. 2004). Yet murrelets are marine birds that spend more than 90% of their lives on the ocean. Therefore, there are certainly important issues in the marine environment that may influence the management and recovery of murrelet populations. My thesis work, which focused on marine habitat, addresses several questions with important implications for murrelet management and conservation.

In addition to the studies within this dissertation, I also participated in several ancillary studies that relate directly to the findings of my dissertation. I summarize them briefly here because they are relevant to murrelet conservation and management and provide context to much of this section. In 2005 I used a GIS-based mapping approach to examine the spatial overlap in distributions between juvenile and adult murrelets (Wong et al. in press). The study showed that both adults and juveniles are using similar habitats in this study area and therefore the identification and protection of critical habitats for adult murrelets will likely enhance the conservation and survival of juveniles. Also in 2005 I mentored an honours project (Hentze 2006) and collaborated on a paper (Bellefleur et al. in press), both of which assessed the impacts of boat disturbance on marbled murrelets within Pacific Rim National Park. We showed that murrelets are flushed when boats approach closely, corroborating evidence of boat disturbance effects from studies in Alaska (Kuletz 1996). Finally, in 2006 we conducted a study of habitat selection by Pacific sand lance (Haynes et al. 2007). This study was especially important to the results of seabird-habitat selection analyses (Chapter 3) by providing a link between seabirds, habitat, and their prey.

Development of accurate abundance estimates

In the USA, distance-sampling is routinely used during transect surveys to develop abundance and population estimates of marbled murrelets (Evans Mack et al. 2002, Peery et al. 2006, Raphael et al. 2007). Although survey protocols for marbled murrelet inventory in British Columbia call for distance-sampling (RIC 2001), I am not aware of any studies that actually use distance-sampling for marbled murrelet assessment in Canada. Results in Chapter 2 provide the first density estimates of murrelets in Canada that have been calculated with distance sampling. Using fixed-width transect sampling Burger et al. (2008) estimated mean murrelet densities in the study area to be about 45 birds/km^2 between 1993 and 1996. Estimates using distance sampling over the same study area in 2005 and 2006 were about 40% higher at ~63 birds/km^2 (Chapter 3, coarse-scale surveys). Application of detection functions to 1995/96 data suggest that densities in those years may have been as high as 85 birds/km^2. The discrepancy between density estimates in this and previous studies (Burger et al. 2008) suggests that fixed-width transects may be underestimating murrelet densities and abundance. All current evidence, much of which was obtained by vessel surveys using strip transects, suggests that murrelet populations are declining along the West Coast Trail and in British Columbia as a whole (Appendix E from Piatt et al. 2007a). Surveys that use distance sampling can easily be converted to standard strip-transect counts, but not vice versa. Use of distance sampling in future surveys can contribute to long-term tracking of changes in murrelet populations using at-sea surveys (strip transects), as well as providing more accurate abundance and population estimates.

Factors affecting reproductive success and population growth

Murrelet populations are declining throughout much, if not all, of their range (McShane et al. 2004, Piatt et al. 2007a). Population models (McShane et al. 2004), derived from estimates of adult survival (Cam et al. 2003) and fecundity (Bradley et al. 2004), predict that populations will decline at rates of 3 to 5% per year for 20 years. In Desolation Sound, BC, survival estimates are quite high (range 0.83 to 0.93) and predict a potentially stationary population growth rate (lambda 0.985 but confidence interval includes 1; Cam et al. 2003). Thus low fecundity rates (0.16 to 0.23 female offspring/female adult/year; Burger 2002, Bradley et al. 2004) are more likely contributors to population declines. Therefore understanding factors affecting reproductive success are crucial to identifying causes and solutions to population declines.

There is strong evidence that terrestrial factors of nesting habitat and predation are affecting reproductive success and population declines. Both local populations (Burger 2001, Burger et al. 2004b, Raphael et al. 2001) and regional populations (Raphael 2006) are strongly correlated with availability of nesting habitat. Large-scale harvests of old-growth forests undoubtedly decrease available nesting habitat and therefore limit the opportunities for reproduction if suitable nesting platforms can not be found. In addition to overall habitat loss, forest fragmentation may have additional negative effects on occupation of murrelets in nesting habitats (Meyer & Miller 2002, Meyer et al. 2002, but see also Zharikov et al. 2007). Yet even when murrelets are able to find nest sites, nest predation seems to be a major factor affecting reproductive success (Nelson & Hamer 1995, Peery et al. 2004), and the effects of nest predation may be exacerbated by artificial forest edges from clearcuts (Malt & Lank 2007). Also concerning is the apparent increase in abundance of many murrelet predators in Alaska and BC (Piatt et al. 2007a).

Terrestrial conditions are evidently affecting murrelet population trends but there is growing evidence that marine conditions may also be influencing reproductive rates and population growth. In California, local oceanographic conditions and prey availability have been linked to murrelet reproductive success (Peery et al. 2004, Becker et al. 2007). Moreover, the collapse of Pacific sardine (*Sardinops sadax*) fisheries in the late 1940's and recent declines of similar fisheries appear to be partly responsible for current low reproductive rates of murrelets that are forced to fish further down on the food web (Becker & Beissinger 2006). In British Columbia, diet quality has been linked to long-term population declines over the past 40 years, likely mediated through effects of diet on reproductive success (Norris et al. 2007). Chapter 4 also provides strong evidence of reproductive success being influenced by prey availability. Even though murrelets foraged harder in low prey years, they were unable to fledge young. Food availability during the breeding season is thought to be one of the dominant factors regulating populations of seabirds (Cairns 1992a).

This study and that of Norris et al. (2007) suggest that efforts to enhance the recovery of murrelets in British Columbia may require the protection or restoration of marine habitats to ensure the abundance of high quality prey. Availability of rockfish was positively correlated with murrelet productivity in California (Becker et al. 2007). Although rockfish are not a primary prey for murrelets in Canada, newly created rockfish conservation areas throughout BC (Anon. 2006) may provide additional prey items in years when primary prey are limited. Chapter 3 identified sandy substrates as important marine habitat for murrelets, potentially due to the availability of sand lance as a prey item. Sand lance are an energetically rich prey item for top predators (Robards et al. 1999, Anthony et al. 2000) and their availability can influence the reproductive success of many seabirds (Willson et al. 1999). Yet relatively little is known about their habitat use (Ostrand et al. 2005, Haynes et al. 2007) or the factors that influence their distribution and abundance in British Columbia. More efforts should be put into understanding the distribution and population dynamics of this keystone prey species in British Columbia.

Competition with other seabirds

Although many endangered and threatened species may be threatened by competition from introduced species, there is less evidence of competition between indigenous species affecting population recovery. The range expansion of barred owls (*Strix varia*) in North America is one example where competitive interactions with the critically endangered spotted owl (*S. occidentalis*) is causing concern for population recovery (Gutierrez et al. 2007). Burger (2002) suggested that competition with other sympatric seabirds may be an additional threat to murrelets in the marine environment. Sometimes larger alcids may disrupt the feeding of smaller alcids (Chilton & Sealy 1987, Piatt 1990). In Chapter 3 I identify the high potential for overlap in fundamental niche between murres and murrelets suggesting the potential for competition between the two. Moreover, in Chapter 5 I identify the potential for fine-scale competition of foraging space. This suggests that in areas where populations of murres and murrelets overlap, competition for resources may be a threat to the marbled murrelet. However, because most of the large colonies of murres are located offshore and away from large murrelet concentrations, the likelihood of wide-spread competition may be minimal in British Columbia (Burger 2002). Nevertheless, in other parts of their range where murres outnumber murrelets, competition may be a more serious threat. In Alaska, others have speculated that gulls, which kleptoparasitize murrelets, may be detrimental to the recovery of murrelet populations (Hunt 1995, Kuletz 2005). The potential for competition with other large alcids may also exist in areas where populations overlap (e.g., Haida Gwai). The threat of a competing species is likely to increase as the dominant species increases in abundance (Kelly et al. 2003). As a result, the monitoring of murrelet populations should also consider the monitoring of other competing species.

Identification of critical marine habitats

Marbled murrelets are listed as threatened under schedule 1 of the Species at Risk Act (SARA 2002) which mandates that "no person shall destroy any part of the critical habitat of any listed endangered species or of any listed threatened species" (p.30). The Act defines *habitat* for wildlife species as "the area or type of site where an individual or wildlife species naturally occurs or depends on directly or indirectly in order to carry out its life processes" (p.5) and *critical habitat* as "the habitat that is necessary for the survival and recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy" (p.4).

Currently a Recovery Strategy has been drafted and is under review for approval (www.speciesatrisk.gc.ca, search marbled murrelet), therefore critical habitat is not yet protected under the act. Existing advisory documents (CMMRT 2003) and the provincial Identified Wildlife Management Strategy (IWMS 2004) are focused solely on recommendations for the conservation and management of nesting habitat. However, the pending Recovery Strategy deals with both marine and terrestrial habitat including critical habitat in both ecosystems. Therefore the defining and management of critical marine habitats will have an important role in the recovery of marbled murrelets. Moreover, the identification of critical marine habitats is necessary because the Species at Risk Act includes the protection of critical habitat in the entire exclusive economic zone of Canada's oceans.

Habitat selection theory suggests that animals exhibit non-random habitat use (habitat selection) in order to maximize the survival and fitness of individuals (Hutto 1985, Block & Brennan 1993, Jones 2001). Therefore, the identification of selected or preferred habitats is likely to be a good indication of critical habitats for murrelets in the ocean. In addition to adjacent nesting habitat, Chapter 3 identified the proximity of estuaries and sandy beaches as habitats preferred by murrelets. Likewise, province-wide habitat selection models identified estuaries and sandy substrates as important habitats predicting murrelet abundance and distribution (Yen et al. 2004a). Because shoreline substrate data (including estuaries) are readily available for British Columbia (Howes et al. 1997), this may serve as a valuable tool for predicting and mapping critical marine habitats of murrelets throughout the province. Mapping of critical marine habitats should also be done in conjunction with assessment of terrestrial nesting habitat since both are clearly important during the breeding season (Yen et al. 2004a, Chapter 3). Habitat preference models (Table 3.8) suggest hierarchical processes in habitat selection involving both terrestrial and marine habitats. For example, in 2006 the primary selection variable was old-growth index >47% followed by preference of habitat within 5.2 km of estuaries. These types of selection "rules" can be used to make predictions of murrelet hotspots in other regions, and testing such predictions would be the next logical step towards identifying priority areas for conservation and critical habitat designation.

Although my dissertation takes an important first step towards identifying critical habitats for murrelets during the breeding season, we still know almost nothing about the distribution, habitat needs and prey important to murrelets during the winter. Over-winter conditions can affect seabird populations through effects on the recruitment of immature birds to breeding colonies (Crespin et al. 2006), lagged effects on hatching and fledging success (Thompson & Ollason 2001), and especially survival of adults (Golet et al. 1998, Croxall et al. 2002, Votier et al. 2005). The identification and protection of critical winter habitat may also be important to population recovery.

Protection in marine habitats

If we can effectively identify critical habitats, the next logical step is to develop measures that protect critical habitats from pending threats. In the terrestrial realm, critical habitats for murrelets are nest sites in old-growth forest that need protection from logging. Currently in British Columbia, the CMMRT (2003) recommends the establishment of habitat areas in old-growth forest to prevent further declines in murrelet populations. On provincial land, the Identified Wildlife Management Strategy (IWMS 2004) mandates the creation of Wildlife Habitat Areas that prevent logging and protect nesting habitat. There are currently no regulations in place for protecting critical marine habitats for murrelets, but this will be addressed in the upcoming Recovery Strategy.

Marine reserves and marine protected areas (MPAs) are rapidly becoming an important tool for marine conservation and management (Lubchenco et al. 2003). Scientific consensus is that marine reserves are effective at reducing the probability of extinction and increasing the abundance, diversity and productivity of marine organisms (Lubchenco et al. 2003). Yet approaches to the design of marine reserves are diverse, debated and still developing (Botsford et al. 2003, Gerber et al. 2003, Roberts et al. 2003).

Because few marine reserves have been established to protect marine birds (Hooker & Gerber 2004), there is no consensus on the design or priorities of MPAs for seabirds. Sydeman et al. (2006, p. 249) emphasized that "ecological justification for the establishment of protected areas must be made." Approaches may include single-species management for highly imperiled birds (Louzao et al. 2006) or diversity-based designation that identifies areas of high seabird abundance (Skov et al. 2007). Often, priority conservation areas for seabirds also focus on the identification of "hotspots" (Hyrenbach et al. 2000, Hooker & Gerber 2004, O'Hara et al. 2006, Piatt et al. 2006, Yen et al. 2006, Davoren 2007) which are sites that provide critical ecosystem linkages between trophic levels (Sydeman et al. 2006). In a review of the role of marine reserves for the conservation of marine mammals and birds, Hooker and Gerber (2004) concluded that size and placement of reserves should give important consideration to i) the threats being mitigated by reserves, and ii) the distribution and life-history of the organisms. With respect to both, marbled murrelets appear to be a good candidate species for protection by the establishment of marine protected areas.

Threats to murrelets in the marine environment include changes in prey stocks, entrapment in gillnets, commercial fisheries, oil spills, and boat disturbance (Burger

2002, Piatt et al. 2007a, Bellefleur et al. in press). The establishment of marine protected areas can likely address all of these threats except for threats of oil pollution. Well enforced marine reserves could limit or exclude boats, aquaculture and fishing activities, particularly during vulnerable periods such as the breeding season. Norris et al. (2007) suggested that restoration of marine habitat quality may be important to the recovery of murrelet populations. Marine reserves, and in particular no-take zones for fisheries, are known to enhance the abundance of marine organisms (Lubchenco et al. 2003, Le Quesne et al. 2007), thus the establishment of marine reserves could contribute to replenishing murrelet prey stocks and enhancing murrelet reproductive success.

Many characteristics of murrelet distributions and life-history make them suitable species for protection under MPAs. These characteristics include:

- foraging site fidelity and "hotspots" in their distributions (Burger et al. 2008, Wong et al. in press)
- associations with spatially fixed features (depth, sandy bottoms and estuaries; Yen et al. 2004a, Chapter 3 this study)
- dietary preferences for spatially restricted prey (sand lance; Haynes et al. 2007)
- distributions restricted to nearshore habitat which is easier to protect and monitor

Marine reserves will provide fewer benefits for species with greater rates of adult movement (Gerber et al. 2003). Although murrelets are highly mobile, they are restricted during the breeding season when foraging locations are closely tied to nesting habitats (Miller et al. 2002, Raphael et al. 2002, Yen et al. 2004a, Raphael 2006, Chapter 3 this study). Therefore murrelets may warrant the application of spatially defined MPAs during the breeding season.

Conservation and management recommendations

Based on the applicability of MPAs and results of my dissertation, there are several specific conservation and management recommendations that can be made both within Pacific Rim National Park and elsewhere in the species range.

Within the West Coast Trail (WCT) unit of Pacific Rim National Park, there is strong evidence that murrelets consistently use identifiable areas which should become the focus of long-term management. In Chapter 3 kernel density methods were used to map *used habitat* and CART analysis provided rules for mapping *preferred habitat* (Fig. 6.1). Although some discrepancies are apparent between mapping approaches and among years, these techniques illustrate some predictable hotspots of murrelet occurrence (central portions of the WCT) which was also in agreement with other studies (Burger et al. 2008, Wong et al. in press). In addition to regular annual population surveys for the entire WCT, I recommend that the following specific sites be considered for focus of long-term management in the park: Carmanah Bay, Dare Point/Beach, and regions between Clo-oose Bay and Klanawa River. Within these sites I recommend the following specific monitoring and protection strategies:

1) Identification, protection, and monitoring of important prey and prey habitat. This should include seasonal and annual surveys of forage fish abundance (as per Haynes et al. 2007)
2) Seasonal (i.e., breeding season) exclusion of anthropogenic threats which may include fisheries and vessels (Bellefleur et al. in press)
3) Monitoring of murrelet foraging behaviour as an index of prey availability (Chapter 4) and changes in other environmental stressors.
4) Monitoring of reproductive success and examination of fine-scale habitat use by juvenile murrelets within these sites.

In addition to implementing these activities within these specific sites, I also recommend the selection of “control” sites which are not consistently used by murrelets. Control sites will be valuable benchmarks against which to compare trends in forage fish abundance, non-exclusion of fisheries/boats, foraging activity, reproductive success and juvenile murrelets.

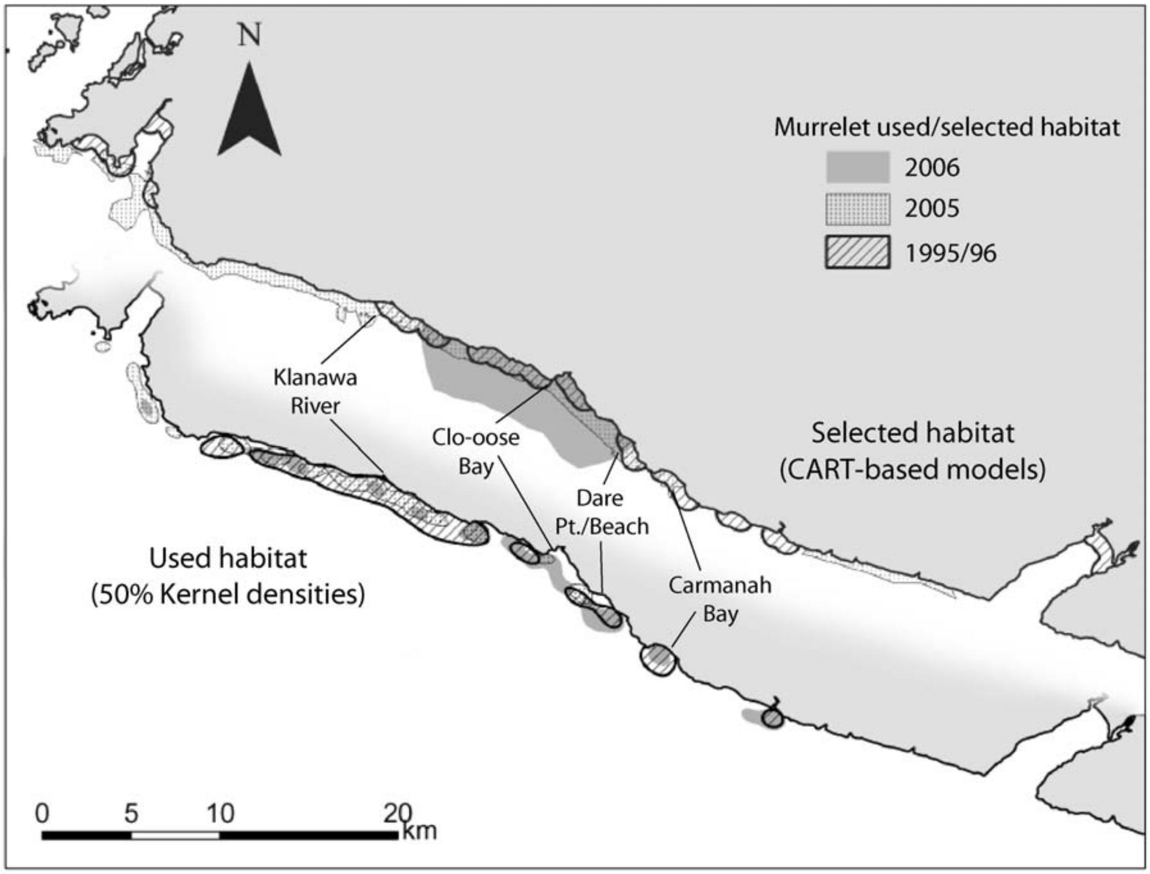


Figure 6.1 – Used and preferred habitats of marbled murrelets in three years along the West Coast Trail unit of Pacific Rim National Park. Used habitats were mapped with kernel density analysis and preferred habitats were mapped by criteria from Classification and Regression Tree (CART) models (see Chapter 3 for details).

In the upcoming years, Pacific Rim National Park and other regions of British Columbia are uniquely positioned to quantify the impacts of new marine reserves on marbled murrelets and other seabirds. In 2006 the Department of Fisheries and Oceans implemented a network of no-take marine zones (Rockfish Conservation Areas, RCAs) to bolster the recovery of rockfish populations (Anon. 2006). Although juvenile rockfish are not a primary prey item of murrelets in BC, they are important to the reproductive success of murrelets in other regions (Becker et al. 2007). Some RCAs also encompass sand/gravel beaches and substrates important to sandlance, therefore the establishment of RCAs could have spill-over effects enhancing the productivity and abundance of other murrelet prey. Pacific Rim National Park has one of the longest, continuous records (>12 years) of at-sea murrelet counts from surveys in the Broken Group Islands and the West Coast Trail. Three RCAs were established in areas where these surveys take place. This is a great opportunity for Parks Canada to assess the impacts of RCAs on murrelets. Parks should closely monitoring changes in murrelet abundance and distribution in relation to RCAs. There is also an opportunity to design experiments around the boundaries of the conservation areas to quantify changes in fish abundance or study the foraging habits (Chapter 4) of murrelets within and around these areas.

MPAs may also be useful conservation tools in other parts of the murrelet's range. The key, however, will be the identification of predictable foraging hotspots (Hyrenbach et al. 2000, Davoren 2007) that will afford the greatest protection for murrelets. Elsewhere in their range, murrelets show habitat specializations (Becker & Beissinger 2003, Day et al. 2003) and areas of predictable aggregation (Speckman et al. 2000, Kuletz 2005, Piatt et al. 2007a). Habitat selection models provide a valuable tool for identifying individual habitat components within these areas that should be protected. Although I identified substrates and beaches as features for habitat protection in my study area, substrates seem to be less important in other parts of their range (Miller et al. 2002, Day et al. 2003). Murrelets often show habitat associations with ocean temperatures (Becker & Beissinger 2003, Yen et al. 2004a) but this is not a feature that can be protected or managed. Instead the designation of MPAs should focus on spatially-fixed habitat feathers such as substrates (Yen et al. 2004a, this study), glacially influenced habitats (Day et al. 2003) or estuaries (Miller et al. 2002, Yen et al. 2004a). This means that other regions seeking to establish MPAs for murrelets will need to consider habitat needs specific to local murrelet populations.

Alternatively, fixed MPAs may not be the only solution to the marine conservation of murrelets. Seasonally and spatially variable fisheries closures in areas where birds and fisheries overlap could minimize the risk seabird entanglements in gillnets (Davoren 2007). The same applies for seasonal and moveable exclusions to eliminate effects of boat disturbance that might be most detrimental during the breeding season when capturing prey for young (Speckman et al. 2004). However, demarcated MPAs may be less useful over broader scales because murrelet prey are influenced by very large scale marine processes (Piatt et al. 2007a). Measures to reduce the impacts of long-term regime changes may be insurmountable and more research is needed to understand the potentially cascading effects of long-term and broad-scale environmental changes.

The ultimate goal of the Species at Risk Act is to prevent wildlife extinctions and recover threatened populations. Given that threats to murrelets exist in both terrestrial and marine systems, there must be some balance between these realms to maximize recovery in the short- and long-term. In the long-term, the protection of old-growth forest is absolutely essential to reduce and stop population declines. Yet the conservation of terrestrial habitat is unlikely to promote population recovery in the short-term since effective restoration of nesting habitat would take centuries to complete. This is highlighted by recommendations of the Canadian Marbled Murrelet Recovery Team (CMMRT 2003) which seek the conservation of old-growth forest to prevent a decline exceeding 30% of current murrelet populations over the next 30 years; hence no recovery. On the other hand, because marine systems have direct effects on reproductive success, efforts focused on marine conservation may offer better short-term gain towards the recovery of marbled murrelet populations.

Bibliography

Abookire, A.A. & J.F. Piatt (2005) Oceanographic conditions structure forage fishes into lipid-rich and lipid-poor communities in lower Cook Inlet, Alaska, USA. *Marine Ecology Progress Series*, 287: 229-240.

Adams, R.A. & K.M. Thibault (2006) Temporal resource partitioning by bats at water holes. *Journal of Zoology*, 270: 466-472.

Agler, B.A., S.J. Kendall & D.B. Irons (1998) Abundance and distribution of marbled and Kittlitz's murrelets in southcentral and southeast Alaska. *Condor*, 100: 254-265.

Ainley, D.G. (1977) Feeding methods of seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. Pp. 669-686 in *Adaptations within Antarctic ecosystems* (G.A. Llano,ed. Gulf Publishing Company, Houston, TX.

Ainley, D.G., D.W. Anderson & P.R. Kelly (1981) Feeding ecology of marine cormorants in southwestern North America. *Condor*, 83: 120-131.

Ainley, D.G. & R.J. Boekelheide (eds.) (1990) Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-system Community. Stanford University Press, Stanford, CA.

Ainley, D.G., R.G. Ford, E.D. Brown, R.M. Suryan & D.B. Irons (2003) Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. *Ecology*, 84: 709-723.

Ainley, D.G., D.N. Nettleship, H.R. Carter & A.E. Storey (2002) Common murre (*Uria aalge*). Pp. in *The Birds of North America, No. 666* (A. Poole & F. Gill eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Ainley, D.G., C.A. Ribic, G. Ballard, S. Heath, I. Gaffney, B.J. Karl, K.J. Barton, P.R. Wilson & S. Webb (2004) Geographic structure of Adelie Penguin populations: Overlap in colony-specific foraging areas. *Ecological Monographs*, 74: 159-178.

Alvarez, N., L. Mercier, M. Hossaert-McKey, J. Contreras-Garduno, G. Kunstler, A. Aebi & B. Benrey (2006) Ecological distribution and niche segregation of sibling species: the case of bean beetles, *Acanthoscelides obtectus* Say and *A. obvelatus* Bridwell. *Ecological Entomology*, 31: 582-590.

Anon. (2002) *West Coast Offshore Vessel Traffic Risk Management Project*. Final project report and recommendations. Pacific States-British Columbia Oil Spill Task Force, Neskowin, OR. http://www.oilspilltaskforce.org/wcovtrm_report.htm

Anon. (2006) *Rockfish Conservation Areas: protecting British Columbia's rockfish.* Fisheries and Oceans Canada, Pacific Region. Available on-line: www.pac.dfo-mpo.gc.ca/recfish/Restricted_Areas/RCAs/booklet/default_e.htm.

Anthony, J.A., D.D. Roby & K.R. Turco (2000) Lipid content and energy density of forage fishes from the northern Gulf of Alaska. *Journal of Experimental Marine Biology and Ecology*, 248: 53-78.

Apps, C.D., B.N. McLellan & J.G. Woods (2006) Landscape partitioning and spatial inferences of competition between black and grizzly bears. *Ecography*, 29: 561-572.

Armstrong, R.A. & R. McGehee (1976) Coexistence of two competitors on one resource. *Journal of Theoretical Biology*, 56: 499-502.

Armstrong, R.A. & R. McGehee (1980) Competitive exclusion. *American Naturalist*, 115: 151-170.

Ashmole, N.P. (1963) The regulation of numbers of tropical oceanic birds. *Ibis*, 103: 458-473.

Ashmole, N.P. (1971) Seabird ecology and the marine environment. Pp. 669-686 in *Avian Biology, Vol. 1* (D.S. Farner, J.S. King & K.C. Parkes eds.). Academic Press, New York.

Bächler, E. & F. Liechti (2007) On the importance of g(0) for estimating bird population densities with standard distance-sampling: implications from a telemetry study and a literature review. *Ibis*, 149: 693–700.

Bahn, V. & B.J. McGill (2007) Can niche-based distribution models outperform spatial interpolation? *Global Ecology and Biogeography*, 16: 733-742.

Bailey, H. & P. Thompson (2006) Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. *Journal of Animal Ecology*, 75: 456-465.

Ballance, L.T., R.L. Pitman & S.B. Reilly (1997) Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology*, 78: 1502-1518.

Barta, Z. & L.A. Giraldeau (2001) Breeding colonies as information centers: a reappraisal of information-based hypotheses using the producer-scrounger game. *Behavioral Ecology*, 12: 121-127.

Beavers, S.C. & F.L. Ramsey (1998) Detectability analysis in transect surveys. *Journal of Wildlife Management*, 62: 948-957.

Becker, B.H. & S.R. Beissinger (2003) Scale-dependent habitat selection by a nearshore seabird, the marbled murrelet, in a highly dynamic upwelling system. *Marine Ecology Progress Series*, 256: 243-255.

Becker, B.H. & S.R. Beissinger (2006) Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology*, 20: 470-479.

Becker, B.H., S.R. Beissinger & H.R. Carter (1997) At-sea density monitoring of marbled murrelets in central California: methodological considerations. *Condor*, 99: 743-755.

Becker, B.H., M.Z. Peery & S.R. Beissinger (2007) Ocean climate and prey availability affect the trophic level and reproductive success of the marbled murrelet, an endangered seabird. *Marine Ecology Progress Series*, 329: 267-279.

Bédard, J. (1969) Adaptive radiation in the Alcidae. *Ibis*, 111: 189-198.

Bédard, J. (1976) Coexistence, coevolution and convergent evolution in seabird communities: a comment. *Ecology*, 57: 177-184.

Bejder, L. & S. Dawson (2001) Abundance, residency, and habitat utilisation of Hector's dolphins (*Cephalorhynchus hectori*) in Porpoise Bay, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 35: 277-287.

Bellefleur, D., P. Lee & R.A. Ronconi (in press) The impact of recreational boat traffic on Marbled Murrelets (*Brachyramphus marmoratus*). *Journal of Environmental Management*.

Benjamini, Y. (1988) Opening the box of a boxplot. *American Statistician*, 42: 257-262.

Bertram, D.F., D.L. Mackas & S.M. McKinnell (2001) The seasonal cycle revisited: interannual variation and ecosystem consequences. *Progress in Oceanography*, 49: 283-307.

Bertness, M.D., S.D. Gaines & M.E. Hay, eds. (2001) *Marine Community Ecology* Sinauer Associates, Sunderland, MA.

Beyer, H.L. (2004) Hawth's Analysis Tools for ArcGIS. Available at http://www.spatialecology.com/htools.

Birkhead, T.R. & D.N. Nettleship (1987a) Ecological relationships between common murres, *Uria aalge*, and thick-billed murres, *Uria lomvia*, at the Gannet Islands, Labrador. 1. Morphometrics and timing of breeding. *Canadian Journal of Zoology*, 65: 1621-1629.

Birkhead, T.R. & D.N. Nettleship (1987b) Ecological relationships between common murres, *Uria aalge*, and thick-billed murres, *Uria lomvia*, at the Gannet Islands, Labrador. 2. Breeding success and site characteristics. *Canadian Journal of Zoology*, 65: 1630-1637.

Birt, V.L., T.P. Birt, D. Goulet, D.K. Cairns & W.A. Montevecchi (1987) Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series*, 40: 205-208.

Block, W.M. & L.A. Brennan (1993) The habitat concept in ornithology: theory and applications. *Current Ornithology*, 11: 35-91.

Botsford, L.W., F. Micheli & A. Hastings (2003) Principles for the design of marine reserves. *Ecological Applications*, 13: S25-S31.

Boyce, M.S. & L.L. McDonald (1999) Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14: 268-272.

Bradley, R.W., F. Cooke, L.W. Lougheed & W.S. Boyd (2004) Inferring breeding success through radiotelemetry in the marbled murrelet. *Journal of Wildlife Management*, 68: 318-331.

Braun, C.E., ed. (2005) *Techniques for Wildlife Investigations and Management. Sixth edition.* The Wildlife Society, Bethesda, Maryland, USA.

Breiman, L. (2001) Statistical modeling: the two cultures. *Statistical Sciences*, 16: 199-231.

Breiman, L., J.H. Friedman, R.A. Olshen & C.J. Stone (1984) *Classification and regression trees.* Wadsworth International Group, Belmont, CA.

Brennan, K. (2000) *Testing assumptions of line transect methodology for marbled murrelets at sea using an independent observer*. M.Sc. thesis, University of Washington, Seattle, WA.

Brooke, M.deL. (2004) The food consumption of the world's seabirds. *Proceedings of the Royal Society of London B (Suppl.)*, **271**, S246-S248.

Brown, J.S., J.W. Laundre & M. Gurung (1999) The ecology of fear: Optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy*, 80: 385-399.

Brown, R.G.B., D.N. Nettleship, P. Germain, C.E. Tull & T. Davis (1974) *Atlas of Eastern Canadian Seabirds.* Canadian Wildlife Service.

Bryant, R. & I.L. Jones (1999) Food resource use and diet overlap of common and thick-billed murres at the Gannet Islands, Labrador. *Waterbirds*, 22: 392-400.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas (2001) *Introduction to Distance Sampling: Estimating Abundance of Biological Populations.* Oxford University Press, Oxford.

Buckland, S.T., D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers & L. Thomas (2004) *Advanced Distance Sampling.* Oxford University Press, Oxford.

Buckley, N.J. (1997) Spatial-concentration effects and the importance of local enhancement in the evolution of colonial breeding in seabirds. *American Naturalist*, 149: 1091-1112.

Burger, A.E. (1991) Maximum diving depths and underwater foraging in alcids and penguins. Pp. 9-15 in *Canadian Wildlife Service Occasional Paper No. 68*.

Burger, A.E. (1992) The effects of oil pollution on seabirds off the west coast of Vancouver Island. Pp. 120-128 in (K. Vermeer, R.W. Butler & K.H. Morgan, eds.) The ecology, status and conservation of marine and shoreline birds of the west coast of Vancouver Island. Canadian Wildlife Service Occasional Paper 75.

Burger, A.E. (1997a) Distribution and abundance of Marbled Murrelets and other seabirds off the West Coast Trail, Pacific Rim National Park in 1996. Unpublished report. In, Pacific Rim National Park, Ucluelet, BC.

Burger, A.E. (1997b) Behavior and numbers of marbled murrelets measured with radar. *Journal of Field Ornithology*, 68: 208-223.

Burger, A.E. (1997c) Arrival and departure behavior of Common Murres at colonies: Evidence for an information halo? *Colonial Waterbirds*, 20: 55-65.

Burger, A.E. (2000) Bird in hot water: responses by marbled murrelets to variable ocean temperatures off southwestern Vancouver Island. Pp. 723-732 in *Conference on the biology and management of species and habitats at risk, Kamloops, BC, 15-19 Feb. 1999* (L.M. Darling ed), Vol. 2. BC Ministry of Environment, Lands and Parks, Victoria, BC, and University College of the Cariboo, Kamloops, BC.

Burger, A.E. (2001) Using radar to estimate populations and assess habitat associations of marbled murrelets. *Journal of Wildlife Management*, 65: 696-715.

Burger, A.E. (2002) Conservation assessment of marbled murrelets in British Columbia: a review of the biology, populations, habitat associations and conservation. *Technical Report Series Number 387*. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

Burger, A.E. (2003) Effects of the Juan de Fuca Eddy and upwelling on densities and distributions of seabirds off southwest Vancouver Island, British Columbia. Marine Ornithology 31: 113-122.

Burger, A.E. & V. Bahn (2004) Inland habitat associations of Marbled Murrelets on southwest Vancouver Island, British Columbia. *Journal of Field Ornithology*, 75: 53-66.

Burger, A.E., T.A. Chatwin, S.A. Cullen, N.P. Holmes, I.A. Manley, M.H. Mather, B.K. Schroeder, J.D. Steventon, J.E. Duncan, P. Arcese & E. Selak (2004b) Application of radar surveys in the management of nesting habitat of Marbled Murrelets *Brachyramphus marmoratus*. *Marine Ornithology*, 32: 1-11.

Burger, A.E., C.L. Hitchcock & G.K. Davoren (2004a) Spatial aggregations of seabirds and their prey on the continental shelf off SW Vancouver Island. *Marine Ecology Progress Series*, 283: 279-292.

Burger, A.E., C.L. Hitchcock, E.A. Stewart & G.K. Davoren (2008) Coexistence and spatial distributions of marbled murrelets (*Brachyramphus marmoratus*) and other Alcids off Southwest Vancouver Island, British Columbia. *Auk*, 125: 192-204.

Burger, A.E. & J.F. Piatt (1990) Flexible time budgets in breeding common murres: buffers against variable prey abundance. *Studies in Avian Biology*, 14: 71-83.

Burger, A.E., R.P. Wilson, D. Garnier & M.P.T. Wilson (1993) Diving depths, diet and underwater foraging of rhinoceros auklets in British Columbia. *Canadian Journal of Zoology*, 71: 2528-2540.

Burkett, E. (1995) Marbled murrelet food habits and prey ecology. Pp. 223-246 in *Ecology and Conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152* (C.J. Ralph, G.L. Hunt, M.G. Raphael & J.F. Piatt eds.). Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.

Burnham, K.P. & D.R. Anderson (2002) *Model Selection and Multimodel Inference: a practical information-theoretic approach.* 2nd edn. Springer-Verlag, New York.

Burnham, K.P., D.R. Anderson & J.L. Laake (1980) Estimation of density from line transect sampling of biological populations. *Wildlife Monographs*, 72: 1-202.

Burrough, P.A. & R.A. McDonnell (1998) *Principles of Geographical Information Systems.* Oxford University Press, Oxford.

Cablk, M., D. White & A.R. Kiester (2002) Assessment of spatial autocorrelation in empirical models in ecology. Pp. 429-440 in *Predicting species occurrences: issues of accuracy and scale* (J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall & F.B. Samson eds.). Island Press, Washington, DC.

Camphuysen, C.J., A.D. Fox, M.F. Leopold & I.K. Petersen (2004) Towards standardised seabirds at sea census techniques in connection with environmental impact assessments for offshore wind farms in the U.K. In. Royal Netherlands Institute for Sea Research, Texel.

Camphuysen, K. & A. Webb (1999) Multi-species feeding associations in North Sea seabirds: Jointly exploiting a patchy environment. *Ardea*, 87: 177-198.

Cairns, D.K. (1987) Seabirds as indicators of marine food supplies. *Biological Oceanography*, 5: 261-272.

Cairns, D.K. (1992a) Population regulation of seabird colonies. *Current Ornithology*, 9: 37-61.

Cairns, D.K. (1992b) Diving Behavior of Black Guillemots in Northeastern Hudson-Bay. *Colonial Waterbirds*, 15: 245-248.

Cam, E., L. Lougheed, R. Bradley & F. Cooke (2003) Demographic assessment of a Marbled Murrelet population from capture-recapture data. *Conservation Biology*, 17: 1118-1126.

Carothers, J.H. & F.M. Jaksić (1984) Time as a niche difference: the role of interference competition. *Oikos*, 42: 403-406.

Carter, H.R. (1984) *At-sea biology of the marbled murrelet (Brachyramphus marmoratus) in Barkley Sound, British Columbia*, University of Manitoba, Winnipeg.

Carter, H.R. and P.G. Sealy (1990) Daily foraging behavior of marbled murrelets. Studies in Avian Biology 14: 93-102.

Cavender-Bares, J., K. Kitajima & F.A. Bazzaz (2004) Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs*, 74: 635-662.

Chilton, G. & S.G. Sealy (1987) Species roles in mixed-species feeding flocks of seabirds. *Journal of Field Ornithology*, 58: 456-463.

Clowater, J.S. & A.E. Burger (1994) The diving behavior of pigeon guillemots (*Cepphus columba*) off southern Vancouver Island. *Canadian Journal of Zoology*, 72: 863-872.

CMMRT (2003) Marbled Murrelet Conservation Assessment 2003, Part B: Marbled Murrelet Recovery Team advisory document on conservation and management. In. Canadian Marbled Murrelet Recovery Team Working Document No. 1. Available at: http://www.sfu.ca/biology/wildberg/bertram/mamurt/links.htm

Cody, M.L. (1973) Coexistence, coevolution and convergent evolution in seabird communities. *Ecology*, 54: 31-44.

Cody, M.L. (1985) *Habitat Selection in Birds.* Academic Press, Inc., San Diego.

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, 199: 1304-1310.

Costanza, M.C. & A.A. Afifi (1979) Comparison of stopping rules in forward stepwise discriminant analysis. *Journal of the American Statistical Association*, 74: 777-785.

Cox, T.M., A.J. Read, D. Swanner, K. Urian & D. Waples (2004) Behavioral responses of bottlenose dolphins, *Tursiops truncatus*, to gillnets and acoustic alarms. *Biological Conservation*, 115: 203-212.

Crespin, L., M.P. Harris, J.D. Lebreton, M. Frederiksen & S. Wanless (2006) Recruitment to a seabird population depends on environmental factors and on population size. *Journal of Animal Ecology*, 75: 228-238.

Croll, D.A. (1990) Physical and biological determinants of abundance, distribution, and diet of the common murre in Monterey Bay, California. *Studies in Avian Biology* 14: 139-148.

Croll, D.A., J.A. Gaston, A.E. Burger & D. Konnoff (1992) Foraging behavior and physiological adaptation for diving in thick-billed murres. *Ecology*, 73: 344–356.

Croxall, J.P. & P. Rothery (1991) Population regulation of seabirds: implications of their demography for conservation. Pp. 272-296 in *Bird population studies: relevance to conservation and management* (C.M. Perrins, J.D. Lebreton & G.M. Hirons eds.). Oxford University Press, Oxford.

Croxall, J.P., P.N. Trathan & E.J. Murphy (2002) Environmental change and Antarctic seabird populations. *Science*, 297: 1510-1514.

Dall, S.R.X. & I.L. Boyd (2002) Provisioning under the risk of starvation. *Evolutionary Ecology Research*, 4: 883-896.

Davoren, G.K. (2000) Variability in foraging in response to changing prey distributions in rhinoceros auklets. *Marine Ecology Progress Series*, 198: 283-291.

Davoren, G.K. (2007) Effects of gill-net fishing on marine birds in a biological hotspot in the northwest Atlantic. *Conservation Biology*, 21: 1032-1045.

Davoren, G.K. & A.E. Burger (1999) Differences in prey selection and behaviour during self-feeding and chick provisioning in rhinoceros auklets. *Animal Behaviour*, 58: 853-863.

Davoren, G.K. & W.A. Montevecchi (2003) Consequences of foraging trip duration on provisioning behaviour and fledging condition of common murres *Uria aalge*. *Journal of Avian Biology*, 34: 44-53.

Davoren, G.K., W.A. Montevecchi & J.T. Anderson (2002) Scale-dependent associations of predators and prey: constraints imposed by flightlessness of common murres. *Marine Ecology Progress Series*, 245: 259-272.

Davoren, G.K., W.A. Montevecchi & J.T. Anderson (2003a) Distributional patterns of a marine bird and its prey: habitat selection based on prey conspecific behaviour. *Marine Ecology Progress Series*: 229-242.

Davoren, G.K., W.A. Montevecchi & J.T. Anderson (2003b) Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecological Monographs*, 73: 463-481.

Day, R.H. & D.A. Nigro (2000) Feeding ecology of Kittlitz's and Marbled Murrelets in Prince William Sound, Alaska. *Waterbirds*, 23: 1-14.

Day, R.H., A.K. Prichard & D.A. Nigro (2003) Ecological specialization and overlap of Brachyramphus murrelets in Prince William Sound, Alaska. *Auk*, 120: 680-699.

De'ath, G. & K.E. Fabricius (2000) Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology*, 81: 3178-3192.

Decker, M.B. & G.L.J. Hunt (1996) Foraging by murres (*Uria* spp.) at tidal fronts surrounding the Pribilof Islands, Alaska, USA. *Marine Ecology Progress Series*, 139: 1-10.

Denardo, C., M. Dougherty, G. Hastie, R. Leaper, B. Wilson & P.M. Thompson (2001) A new technique to measure spatial relationships within groups of free-ranging coastal cetaceans. *Journal of Applied Ecology*, 38: 888-895.

Diamond, A.W. (1978) Feeding strategies and population size in tropical seabirds. *American Naturalist*, 112: 215-223.

Dill, L.M., M.R. Heithaus & C.J. Walters (2003) Behaviorally mediated indirect interactions in marine communities and their conservation implications. *Ecology*, 84: 1151-1157.

Dixon, T.J. (1977) Distance at which sitting birds can be seen at sea. *Ibis*, 119: 372-375.

Drent, R.H. & S. Daan (1980) The prudent parent: energetic adjustments in avian breeding. *Ardea*, 68: 225-252.

Erikstad, K.E., T. Moum & W. Vader (1990) Correlations between pelagic distribution of Common and Brünnich's Guillemots and their prey in the Barents Sea. *Polar Research* 8: 77-87.

Evans Mack, D., M.G. Raphael & J.L. Laake (2002) Probability of detecting marbled murrelets at sea: Effects of single versus paired observers. *Journal of Wildlife Management*, 66: 865-873.

Ewins, P.J. (1993) Pigeon Guillemot (*Cepphus columba*). Pp. in *The Birds of North America, No. 49* (A. Poole & F. Gill eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Falk, K., L. Dall'Antonia & S. Benvenutti (2001) Mapping pre- and post-fledging foraging locations of thick billed murres in the North Water polynya. *Ecography*, 24: 625-632.

Fauchald, P., K.E. Erikstad & H. Skarsfjord (2000) Scale-dependent predator-prey interactions: the hierarchical spatial distribution of seabirds and prey. *Ecology*, 81: 773-783.

Flint, M.V. & A.N. Golovkin (2002) How do planktivorous least auklets (*Aethia pusilla*) use foraging habitats around breeding colonies? Adaptation to mesoscale distribution of zooplankton. *Oceanology*, 42: S114-S121.

Forcada, J., M. Gazo, A. Aguilar, J. Gonzalvo & M. Fernandez-Contreras (2004) Bottlenose dolphin abundance in the NW Mediterranean: addressing heterogeneity in distribution. *Marine Ecology Progress Series*, 275: 275-287.

Forero, M.G., G.R. Bortolotti, K.A. Hobson, J.A. Donazar, M. Bertelloti & G. Blanco (2004) High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. *Journal of Animal Ecology*, 73: 789-801.

Forney, K.A. & J. Barlow (1998) Seasonal patterns in the abundance and distribution of California cetaceans, 1991-1992. *Marine Mammal Science*, 14: 460-489.

Fortin, M.-J. & G.M. Jacquez (2000) Randomization tests and spatially autocorrelated data. *Bulletin of the Ecological Society of America*, July: 201-205.

Ford, R.G., J.L. Casey, C.H. Hewitt, D.B. Lewis, D.H. Varoujean, D.R. Warrick & W.A. Williams (1991) Seabird mortality resulting from the Nestucca oil spill incident, winter 1988–89. Report of the Washington Department of Wildlife. Ecological Consulting, Portland, OR

Foster, M.S. & D.R. Schiel (1985) The ecology of giant kelp forests in California: a community profile. In. U.S. Fish Wildl. Serv. Biol. Rep. 85.

Fretwell, S.D. & H.L. Lucas (1970) On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16-36.

Friberg, M., M. Bergman, J. Kullberg, N. Wahlberg & C. Wiklund (2008) Niche separation in space and time between two sympatric sister species: a case of ecological pleiotropy. *Evolutionary Ecology*, 22: 1-18.

Gailey, G., B. Wursig & T.L. McDonald (2007) Abundance, behavior, and movement patterns of western gray whales in relation to a 3-D seismic survey, Northeast Sakhalin Island, Russia. *Environmental Monitoring and Assessment*, 134: 75-91.

Garthe, S., T. Freyer, O. Huppop & D. Wolke (1999) Breeding Lesser Black-Backed Gulls *Larus graellsii* and Herring Gulls *Larus argentatus*: Coexistence or competition? *Ardea*, 87: 227-236.

Gaston, A.J. (2004) *Seabirds: a Natural History.* T & A D Poyser, London.

Gaston, A.J. & S.B.C. Dechesne (1996) Rhinoceros auklet (*Cerorhinca monocerata*). Pp. in *The Birds of North America, No. 212* (A. Poole & F. Gill eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Gaston, A.J. & I.L. Jones (1998) *The Auks.* Oxford University Press, New York.

Gerber, L.R., L.W. Botsford, A. Hastings, H.P. Possingham, S.D. Gaines, S.R. Palumbi & S. Andelman (2003) Population models for marine reserve design: A retrospective and prospective synthesis. *Ecological Applications*, 13: S47-S64.

Ghilarov, A.M. (1984) The paradox of the plankton reconsidered; or, why do species coexist? *Oikos*, 43: 46-52.

Gill, F.B. (1995) *Ornithology, 2nd edition.* W.H. Freeman and Company, New York, NY.

Gjerdrum, C., A.M.J. Vallée, C.C. St. Clair, D.F. Bertram, J.L. Ryder, & G.S. Blackburn (2003) Tufted puffin reproduction reveals ocean climate variability. *Proceedings of the National Academy of Science* 100: 9377-9382.

Goetz, K.T., D.J. Rugh, A.J. Read & R.C. Hobbs (2007) Habitat use in a marine ecosystem: Beluga whales *Delphinapterus leucas* in Cook Inlet, Alaska. *Marine Ecology Progress Series*, 330: 247-256.

Golet, G.H., D.B. Irons & J.A. Estes (1998) Survival costs of chick rearing in black-legged kittiwakes. *Journal of Animal Ecology*, 67: 827-841.

Gomez de Segura, A., J. Tomas, S.N. Pedraza, E.A. Crespo & J.A. Raga (2006) Abundance and distribution of the endangered loggerhead turtle in Spanish Mediterranean waters and the conservation implications. *Animal Conservation*, 9: 199-206.

Gonzalez-Solis, J., J.P. Croxall & A.G. Wood (2000) Foraging partitioning between giant petrels *Macronectes spp*. and its relationship with breeding population changes at Bird Island, South Georgia. *Marine Ecology Progress Series*, 204: 279-288.

González-Solis, J., D. Oro, L. Jover, X. Ruiz & V. Pedrocchi (1997) Trophic niche width and overlap of two sympatric gulls in the southwestern Mediterranean. *Oecologia*, 112: 75-80.

Gotelli, N.J. (2001) *A primer of ecology, 3rd edition.* Sinauer Associates, Sunderland, MA.

Götmark, F., D.W. Winkler & M. Andersson (1986) Flock-feeding on fish schools increases individual success in gulls. *Nature*, 319: 589-591.

Grunbaum, D. & R.R. Veit (2003) Black-browed albatrosses foraging on Antarctic krill: density-dependence through local enhancement? *Ecology*, 84: 3265-3275.

Guisan, A. & N.E. Zimmermann (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, 135: 147-186.

Gurevitch, J., L.L. Morrow, A. Wallace & J.S. Walsh (1992) A meta-analysis of competition in field experiments. *American Naturalist*, 140: 539-572.

Gutierrez, R.J., M. Cody, S. Courtney & A.B. Franklin (2007) The invasion of barred owls and its potential effect on the spotted owl: a conservation conundrum. *Biological Invasions*, 9: 181-196.

Haney, J.C. (1991) Influence of pycnocline topography and water-column structure on marine distributions of alcids (Aves, Alcidae) in Anadyr Strait, Northern Bering Sea, Alaska. *Marine Biology*, 110: 419-435.

Haney, J.C., K.M. Fristrup & D.S. Lee (1992) Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scandinavica*, 23: 49-62.

Haney, J.C. & A.E.S. Schauer (1994) Environmental variability facilitates coexistence within an Alcid community at sea. *Marine Ecology-Progress Series*, 103: 221-237.

Hardin, G. (1960) The competitive exclusion principle. *Science*, 131: 1292-1298.

Harding, A.M.A., J.F. Piatt, J.A. Schmutz, M.T. Shultz, T.I. Van Pelt, A.B. Kettle & S.G. Speckman (2007) Prey density and the behavioral flexibility of a marine predator: the common murre (*Uria aalge*). *Ecology*, 88: 2024-2033.

Harrison, N.M., M.J. Whitehouse, D. Heinemann, P.A. Prince, G.L. Hunt & R.R. Veit (1991) Observations of multispecies seabird flocks around South Georgia. *Auk*, 108: 801-810.

Haynes, T.B., R.A. Ronconi & A.E. Burger (2007) Habitat use and behaviour of the Pacific Sand Lance (*Ammodytes hexapterus*) in the shallow subtidal region of southwestern Vancouver Island. *Northwestern Naturalist*, 88: 155-167.

Hayward, T.L. & J.A. McGowan (1979) Pattern and structure in an oceanic zooplankton community. *American Zoologist*, 19: 1045-1055.

Hebshi, A. (1998) Foraging site preferences of Brandt's Cormorants off the Santa Cruz, California, coast. *Colonial Waterbirds*, 21: 245-250.

Heithaus, M.R. (2005) Habitat use and group size of pied cormorants (*Phalacrocorax varius*) in a seagrass ecosystem: possible effects of food abundance and predation risk. *Marine Biology*, 147: 27-35.

Heithaus, M.R. & L.M. Dill (2006) Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? *Oikos*, 114: 257-264.

Henkel, L.A., E.E. Burkett & J.Y. Takekawa (2004) At-sea activity and diving behaviour of a radio-tagged marbled murrelet in central California. *Waterbirds*, 27: 9-12.

Hennicke, J.C. & B.M. Culik (2005) Foraging performance and reproductive success of Humboldt penguins in relation to prey availability. *Marine Ecology Progress Series*, 296: 173-181.

Hentze, N.T. (2006) *The effects of boat disturbance on seabirds off southwestern Vancouver Island, British Columbia*. Honours Thesis, University of Victoria, Victoria, BC.

Hildén, O. (1965) Habitat selection in birds: a review. *Annales Zoologici Fennici* 2: 53-75.

Hines, A.H., R.B. Whitlatch, S.F. Thrush, J.E. Hewitt, V.J. Cummings, P.K. Dayton & P. Legendre (1997) Nonlinear foraging response of a large marine predator to benthic prey: eagle ray pits and bivalves in a New Zealand sandflat. *Journal of Experimental Marine Biology and Ecology*, 216: 191-210.

Hipfner, J.M., A.J. Gaston & B.D. Smith (2006) Regulation of provisioning rate in the Thick-billed Murre (*Uria lomvia*). *Canadian Journal of Zoology*, 84: 931-938.

Hirzel, A.H., J. Hausser, D. Chessel, & N. Perrin (2002) Ecological-niche factor analysis: how to compute habitat suitability maps without absence data? *Ecology* 83: 2027-2036.

Hobson, K.A. (1997) Pelagic cormorant (*Phalacrocorax pelagicus*). Pp. in *The Birds of North America, No. 282* (A. Poole & F. Gill eds.). The Academy of Natural Sciences, Philadelphia, PA, and The American Ornithologists' Union, Washington, DC.

Hobson, K.A., J.F. Piatt & J. Pitocchelli (1994) Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology*, 63: 786-798.

Hochachka, W.M., R. Caruana, D. Fink, A. Munson, M. Riedewald, D. Sorokina & S. Kelling (2007) Data-mining discovery of pattern and process in ecological systems. *Journal of Wildlife Management*, 71: 2427-2437.

Hoffman, W., D. Heinemann & J.A. Wiens (1981) The ecology of seabird feeding flocks in Alaska. *Auk*, 98: 437-456.

Holling, C.S. (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, 45: 1-60.

Holm, H.J. & A.E. Burger (2002) Foraging behavior and resource partitioning by diving birds during winter in areas of strong tidal currents. *Waterbirds*, 25: 312-325.

Hooker, S.K. & L.R. Gerber (2004) Marine reserves as a tool for ecosystem-based management: The potential importance of megafauna. *Bioscience*, 54: 27-39.

Howes, D., J. Harper & E. Owens (1997) Physical shore-zone mapping system for British Columbia. In, Vol. 2007. Resources Inventory Committee, Victoria, BC.

Huettmann, F. & A.W. Diamond (2001) Seabird colony locations and environmental determination of seabird distribution: a spatially explicit breeding seabird model for the Northwest Atlantic. *Ecological Modelling*, 141: 261-298.

Huettmann, F. & A.W. Diamond (2006) Large-scale effects on the spatial distribution of seabirds in the Northwest Atlantic. *Landscape Ecology*, 21: 1089-1108.

Hull, C. L. (1999) COSEWIC Status Report Update on Marbled Murrelet *Brachyramphus marmoratus* (Gmelin). Report to Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Centre for Wildlife Ecology, Department Biological Sciences, Simon Fraser University, Burnaby, BC.

Hull, C.L., G.W. Kaiser, C. Lougheed, L. Lougheed, S. Boyd & F. Cooke (2001) Intra-specific variation in commuting distance of Marbled Murrelets (*Brachyramphus marmoratus*): ecological and energetic consequences of nesting further inland. *Auk*, 118: 1036-1046.

Hunt, G.L. (1995) Monospecific and mixed species foraging associtions of marbled murrelets. Pp. 255-256 in *Ecology and Conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152* (C.J. Ralph, G.L. Hunt, M.G. Raphael & J.F. Piatt eds.). Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.

Hunt, G.L. & D.C. Schneider (1987) Scale-dependent processes in the physical and biological environment of marine birds. Pp. 7-41 in *Seabirds: feeding ecology and role in marine ecosystems* (J.P. Croxall,ed. Cambridge University Press, Cambridge.

Hunt, G.L., F. Mehlum, R.W. Russell, D. Irons, M.B. Decker & P.H. Becker (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. Pp. 2040-2056 in *Proceedings of the 22 International Ornithological Congress, Durban* (N.J. Adams & R.H. Slotow, eds.). Birdlife South Africa, Johannesburg.

Huston, M.A. (2002) Critical issues for improving predictions. Pp. 7-21 in *Predicting species occurrences: issues of accuracy and scale* (J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall & F.B. Samson eds.). Island Press, Washington, DC.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology* 22: 415-427.

Hutchinson, G.E. (1961) The paradox of plankton. *American Naturalist*, 95: 137-145.

Hutto, R.L. (1985) Habitat selection by nonbreeding, migratory land birds. Pp. 455-476 in *Habitat Selection in Birds* (M.L. Cody ed.) Academic Press, New York, NY.

Hyrenbach, K.D. (2001) Albatross response to survey vessels: implications for studies of the distribution, abundance, and prey consumption of seabird populations. *Marine Ecology Progress Series*, 212: 283-295.

Hyrenbach, K.D., C.L. Baduini & G.L. Hunt Jr (2001) Line transect estimates of short-tailed shearwater *Puffinus tenuirostris* mortality in the south-eastern Bering Sea, 1997-1999. *Marine Ornithology*, 29: 11-18.

Hyrenbach, K.D., P. Fernandez & D.J. Anderson (2002) Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series*, 233: 283-301.

Hyrenbach, K.D., K.A. Forney & P.K. Dayton (2000) Marine protected areas and ocean basin management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 10: 437-458.

Hyrenbach, K.D., M.F. Henry, K.H. Morgan, D.W. Welch & W.J. Sydeman (2007a) Optimizing the width of strip transects for seabird surveys from vessels of opportunity. *Marine Ornithology*, 35: 29-37.

Hyrenbach, K.D., R.R. Veit, H. Weimerskirch, N. Metzl & G.L. Hunt (2007b) Community structure across a large-scale ocean productivity gradient: Marine bird assemblages of the Southern Indian Ocean. *Deep-Sea Research Part I-Oceanographic Research Papers*, 54: 1129-1145.

IWMS (2004) Identified Wildlife Management Strategy. Accounts and Measures for Managing Identified Wildlife: Marbled Murrelet *Brachyramphus marmoratus*. Ministry of Water, Land and Air Protection, Biodiversity Branch, Victoria, BC. Available at: http://www.env.gov.bc.ca/wld/frpa/iwms/accounts.html

Jespersen, P. (1924) The frequency of birds over the high Atlantic Ocean. *Nature*, 114: 281-283.

Jodice, P.G.R. & M.W. Collopy (1999) Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): testing predictions from optimal-breathing models. *Canadian Journal of Zoology*, 77: 1409-1418.

Johnsen, I., K.E. Erikstad & B.E. Saether (1994) Regulation of parental investment in a long-lived seabird, the puffin *Fratercula arctica*: an experiment. *Oikos*, 71: 273-278.

Johnson, D.H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61: 65-71.

Johnston, D.W. (2002) The effect of acoustic harassment devices on harbour porpoises (*Phocoena phocoena*) in the Bay of Fundy, Canada. *Biological Conservation*, 108: 113-118.

Johnston, D.W. & A.J. Read (2007) Flow-field observations of a tidally driven island wake used by marine mammals in the Bay of Fundy, Canada. *Fisheries Oceanography*, 16: 422-435.

Jones, J. (2001) Habitat selection studies in avian ecology: a critical review. *Auk*, 118: 557-562.

Jones, M., Y. Mandelik & T. Dayan (2001) Coexistence of temporally partitioned spiny mice: Roles of habitat structure and foraging behavior. *Ecology*, 82: 2164-2176.

Jongman, R.H.G., C.J.F. ter Braak & O.F.R. van Tongeren, eds. (1995) *Data analysis in community and landscape ecology* Cambridge University Press, Cambridge.

Kaiser, G.W. & L.S. Forbes (1992) Climatic and oceanographic influences on island use in four burrow nesting alcids. *Ornis Scandinavica*, 23: 1-6.

Karels, T.J., A.A. Bryant & D.S. Hik (2004) Comparison of discriminant function and classification tree analyses for age classification of marmots. *Oikos*, 105: 575-587.

Karpouzi, V.S., R. Watson & D. Pauly (2007) Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. *Marine Ecology Progress Series*, 343: 87-99.

Kelly, E.G., E.D. Forsman & R.G. Anthony (2003) Are Barred Owls displacing Spotted Owls? *Condor*, 105: 45-53.

King, J.R. (2005) *Report of the study group on fisheries and ecosystem responses to recent regime shifts*. PICES Scientific Report 28, 162 p.

Kissling, M.L. & E.O. Garton (2006) Estimating detection probability and density from point-count surveys: A combination of distance and double-observer sampling. *Auk*, 123: 735-752.

Komdeur, J., J. Bertelsen & G. Cracknell (1992) *Manual for Aeroplane and Ship Surveys of Waterfowl and Seabirds.* IWRB Special Publ. No. 19, National Environmental Research Institute Kalø.

Kramer, D.L. & W. Nowell (1980) Central place foraging in the eastern chipmunk, *Tamias stiatus*. *Animal Behaviour*, 28: 772-778.

Krebs, J.R. & N.B. Davies (1981) *An introduction to behavioural ecology.* Blackwell Scientific Publications, Oxford, UK.

Kronfeld-Schor, N. & T. Dayan (2003) Partitioning of time as an ecological resource. *Annual Review of Ecology Evolution and Systematics*, 34: 153-181.

Kulbicki, M. & S. Sarramegna (1999) Comparison of density estimates derived from strip transect and distance sampling for underwater visual censuses: a case study of Chaetodontidae and Pomacanthidae. *Aquatic Living Resources*, 12: 315-325.

Kuletz, K.J. (1996) Marbled Murrelet abundance and breeding activity at Naked Island, Prince William Sound, and Kachemak Bay, Alaska, before and after the Exxon Valdez oil spill. Pp. 770-784 in *American Fisheries Society Symposium 18*.

Kuletz, K.J. (2005) *Foraging behavior and productivity of a non-colonial seabird, the Marbled Murrelet (Brachyramphus marmoratus), relative to prey and habitat.* PhD dissertation, University of Victoria., Victoria, BC, Canada.

Kuletz, K.J. & S.J. Kendall (1998) A productivity index for marbled murrelets in Alaska based on surveys at sea. *Journal of Wildlife Management*, 62: 446-460.

Kuletz, K.J. & J.F. Piatt (1999) Juvenile Marbled Murrelet nurseries and the productivity index. *Wilson Bulletin* 111: 257-61.

Kuroki, M., A. Kato, Y. Watanuki, Y. Niizuma, A. Takahashi & Y. Naito (2003) Diving behavior of an epipelagically feeding alcid, the Rhinoceros Auklet (*Cerorhinca monocerata*). *Canadian Journal of Zoology*, 81: 1249-1256.

Laake, J.L., J. Calambokidis, S.D. Osmek & D.J. Rugh (1997) Probability of detecting harbor porpoise from aerial surveys: Estimating g(0). *Journal of Wildlife Management*, 61: 63-75.

Lack, D. (1968) *Ecological Adaptations for Breeding in Birds.* Methuen, London.

Lance, M.M. & C.W. Thompson (2005) Overlap in diets and foraging of common murres (*Uria aalge*) and Rhinoceros Auklets (*Cerorhinca monocerata*) after the breeding season. *Auk*, 122: 887-901.

Le Mar, K., C. Southwell & C. McArthur (2001) Evaluation of line-transect sampling to estimate nocturnal densities of macropods in open and closed habitats. *Wildlife Research*, 28: 9-16.

Le Quesne, W.J.F., S.J. Hawkins & J.G. Shepherd (2007) A comparison of no-take zones and traditional fishery management tools for managing site-attached species with a mixed larval pool. *Fish and Fisheries*, 8: 181-195.

Levin, S.A. (1970) Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist*, 157.

Levins, R. & D. Culver (1971) Regional coexistence of species and competition between rare species. *Proceedings from the National Academy of Science*, 68: 1246-1248.

Levitus, S., J.I. Antonov, T.P. Boyer & C. Stephens (2000) Warming of the world ocean. *Science*, 287: 2225-2229.

Lewis, K.P. (2004) How important is the statistical approach for analyzing categorical data? A critique using artificial nests. *Oikos*, 104: 305-315.

Lewis, S., T.N. Sherratt, K.C. Hamer & S. Wanless (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, 412: 816-819.

Litzow, M.A. & J.F. Piatt (2003) Variance in prey abundance influences time budgets of breeding seabirds: evidence from pigeon guillemots *Cepphus columba*. *Journal of Avian Biology*, 34: 54-64.

Litzow, M.A., J.F. Piatt, A.A. Abookire & M.D. Robards (2004) Energy density and variability in abundance of pigeon guillemot prey: support for the quality-variability trade-off hypothesis. *Journal of Animal Ecology*, 73: 1149-1156.

Litzow, M.A., J.F. Piatt, A.K. Prichard & D.D. Roby (2002) Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. *Oecologia*, 132: 286-295.

Logerwell, E.A. & N.B. Hargreaves (1996) The distribution of sea birds relative to their fish prey off Vancouver Island: Opposing results at large and small spatial scales. *Fisheries Oceanography*, 5: 163-175.

Lougheed, C. (2000) Breeding chronology, breeding success, distribution and movements of Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. Technical Report Series No. 352. In. Canadian Wildlife Service, Pacific & Yukon Region, Delta, BC.

Louzao, M., K.D. Hyrenbach, J.M. Arcos, P. Abello, L.G. De Sola & D. Oro (2006) Oceanographic habitat of an endangered Mediterranean procellariiform: Implications for marine protected areas. *Ecological Applications*, 16: 1683-1695.

Lubchenco, J., S.R. Palumbi, S.D. Gaines & S. Andelman (2003) Plugging a hole in the ocean: The emerging science of marine reserves. *Ecological Applications*, 13: S3-S7.

MacArthur, R.H. (1958) Population ecology of some warblers of northeastern coniferous forests. *Ecology* 39: 599-619.

MacArthur, R. & R. Levins (1964) Competition, habitat selection, and character displacement in a patchy environment. *Proceedings from the National Academy of Science*, 51: 1207-1210.

MacArthur, R. & R. Levins (1967) The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist*, 101: 337-385.

MacLeod, C.D., C.R. Weir, C. Pierpoint & E.J. Harland (2007) The habitat preferences of marine mammals west of Scotland (UK). *Journal of the Marine Biological Association of the United Kingdom*, 87: 157-164.

Mahon, T.E., G.W. Kaiser & A.E. Burger (1992) The role of marbled murrelets in mixed-species feeding flocks in British Columbia. *Wilson Bulletin*, 104: 738-743.

Malt, J. & D.B. Lank (2007) Temporal dynamics of edge effects on nest predation risk for the marbled murrelet. *Biological Conservation*, 140: 160-173.

Maniscalco, J.M., W.D. Ostrand & K.O. Coyle (1998) Selection of fish schools by flocking seabirds in Prince William Sound, Alaska. *Colonial Waterbirds*, 21: 314-322.

Maniscalco, J.M., W.D. Ostrand, R.M. Suryan & D.B. Irons (2001) Passive interference competition by Glaucous-winged Gulls on Black-legged Kittiwakes: A cost of feeding in flocks. *Condor*, 103: 616-619.

Manly, B.F.J., L.L. McDonald, D.L. Thomas, T.L. McDonald & W.P. Erickson (2002) *Resource Selection by Animals: statistical design and analysis for field studies (2nd edition).* Kluwer Academic Publishers, Dordrecht.

Marques, F.F.C. & S.T. Buckland (2003) Incorporating covariates into standard line transect analyses. *Biometrics*, 59: 924-935.

Marques, T.A., L. Thomas, S. Fancy & S.T. Buckland (2007) Improving estimates of bird density using multiple-covariate distance sampling. *Auk*, 124: 1229-1243.

Mathews, N.J.C. & A.E. Burger (1998) Diving depth of a marbled murrelet. *Northwestern Naturalist*, 79: 70-71.

McCullagh, P. & J.A. Nelder (1989) *Generalized linear models.* Chapman and Hall, New York.

McFarlane Tranquilla, L., N.R. Parker, R.W. Bradley, D.B. Lank, E.A. Krebs, L. Lougheed & C. Lougheed (2005) Breeding chronology of Marbled Murrelets varies between coastal and inshore sites in southern British Columbia. *Journal of Field Ornithology*, 76: 357-367.

McFarlane Tranquilla, L.A., P.P.W. Yen, R.W. Bradley, B.A. Vanderkist, D.B. Lank, N.R. Parker, M. Drever, L.W. Lougheed, G.W. Kaiser & T.D. Williams (2003) Do two murrelets make a pair? Breeding status and behavior of marbled murrelet pairs captured at sea. *Wilson Bulletin*, 115: 374-381.

McGarigal, K., S. Cushman & S. Stafford (2000) *Multivariate statistics for wildlife and ecology research.* Springer-Verlag, New York, NY.

McShane, C., T. Hamer, H. Carter, G. Swartzman, V. Friesen, D. Ainley, R. Tressler, K. Nelson, A. Burger, L. Spear, T. Mohagen, R. Martin, L. Henkel, K. Prindle, C. Strong & J. Keany (2004) *Evaluation report for the 5-year status review of the Marbled Murrelet in Washington, Oregon, and California*. Unpublished report, prepared for U.S. Fish & Wildlife Service. Portland, OR.

Mehlum, F., G.W. Gabrielsen & K.A. Nagy (1993) Energy expenditure by black guillemots (*Cepphus grylle*) during chick-rearing. *Colonial Waterbirds*, 16: 45–52.

Meyer, C.B. (1999) *Marbled murrelet use of landscapes and seascapes during the breeding season in California and Southern Oregon*, University of Wyoming, Laramie, WY.

Meyer, C.B. & S.L. Miller (2002) Use of fragmented landscapes by marbled murrelets for nesting in southern Oregon. *Conservation Biology*, 16: 755-766.

Meyer, C.B., S.L. Miller & C.J. Ralph (2002) Multi-scale landscape and seascape patterns associated with marbled murrelet nesting areas on the US west coast. *Landscape Ecology*, 17: 95-115.

Miller, S.L., C.B. Meyer & C.J. Ralph (2002) Land and seascape patterns associated with Marbled Murrelet abundance offshore. *Waterbirds*, 25: 100-108.

Mills, K.L. (1998) Multispecies seabird feeding flocks in the Galapagos Islands. *Condor*, 100: 277-285.

Molles, M.C. (1999) *Ecology: concepts and applications*. McGraw-Hill, Boston.

Monaghan, P. (1996) Relevance of the behaviour of seabirds to the conservation of marine environments. *Oikos*, 77: 227-237.

Monaghan, P., P. Walton, S. Wanless, J.D. Uttley & M.D. Burns (1994) Effects of prey abundance on the foraging behavior, diving efficiency and time allocation of breeding guillemots *Uria aalge*. *Ibis*, 136: 214-222.

Monaghan, P., P.J. Wright, M.C. Bailley, J.D. Uttley, P. Walton & M.D. Burns (1996) The influence of changes in food abundance on diving and surface-feeding seabirds. *Occasional Paper of the Canadian Wildlife Service*, 91: 10-19.

Mori, Y. & I.L. Boyd (2004) The behavioral basis for nonlinear functional responses and optimal foraging in Antarctic fur seals. *Ecology*, 85: 398-410.

Morin, P.J. (1999) *Community Ecology.* Blackwell Science, Malden, MA.

Morrison, M.L., C.L. Ralph, & R.W. Mannan (1992) *Wildlife-habitat relationships: concepts and applications*. University of Wisconsin Press, Madison.

Murphy, E.J., D.J. Morris, J.L. Watkins & J. Priddle (1988) Scales of interaction between Antarctic krill and the environment. Pp. 120-130 in *Antarctic Ocean and Resources Variability* (D. Sahrhage, ed.) Springer-Verlag, Berlin, Germany.

Nelson, S.K. (1997) Marbled Murrelet (*Brachyramphus marmoratus*). *The Birds of North America, No. 276* (A. Poole & F. Gill eds.). The Academy of Natural Sciences, Philadelphia, PA, and the American Ornithologists' Union, Washington, DC.

Nelson, S.K. & T.E. Hamer (1995) Nest success and the effects of predation on marbled murrelets. Pp. 89-98 in *Ecology and Conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152* (C.J. Ralph, G.L. Hunt, M.G. Raphael & J.F. Piatt eds.). Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.

Nilsson, P.A., K. Nilsson & P. Nystrom (2000) Does risk of intraspecific interactions induce shifts in prey-size preference in aquatic: predators? *Behavioral Ecology and Sociobiology*, 48: 268-275.

Norris, D.R., P. Arcese, D. Preikshot, D.F. Bertram & T.K. Kyser (2007) Diet reconstruction and historic population dynamics in a threatened seabird. *Journal of Applied Ecology*, 44: 875-884.

Norvell, R.E., F.P. Howe & J.R. Parrish (2003) A seven-year comparison of relative-abundance and distance-sampling methods. *Auk*, 120: 1013-1028.

O'Connor, R.J. (2002) The conceptual basis of species distribution modeling: time for a paradigm shift? Pp. 25-33 in *Predicting species occurrences: issues of accuracy and scale* (J.M. Scott, P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall & F.B. Samson eds.). Island Press, Washington, DC.

O'Hara, P.D., K.H. Morgan & W.J. Sydeman (2006) Primary producer and seabird associations with AVHRR-derived sea surface temperatures and gradients in the southeastern Gulf of Alaska. *Deep-Sea Research Part II - Topical Studies in Oceanography*, 53: 359-369.

Orians, G.H. & N.E. Pearson (1979) On the theory of central place foraging. Pp. 154-177 in *Analyses of Ecological Systems* (D.J. Horn, R.D. Mitchell & G.R. Stairs eds.). Ohio State University Press, Columbus, OH.

Orians, G.H. & J.F. Wittenberger (1991) Spatial and temporal scales in habitat selection. American Naturalist 137(Supplement): 29-49.

Ostrand, W.D. (1999) Marbled Murrelets as initiators of feeding flocks in Prince William Sound, Alaska. *Waterbirds*, 22: 314-318.

Ostrand, W.D., K.O. Coyle, G.S. Drew, J.M. Maniscalco & D.B. Irons (1998a) Selection of forage-fish schools by murrelets and tufted puffins in Prince William Sound, Alaska. *Condor*, 100: 286-297.

Ostrand, W.D., G.S. Drew, R.M. Suryan & L.L. McDonald (1998b) Evaluation of radio-tracking and strip transect methods for determining foraging ranges of Black-legged Kittiwakes. *Condor*, 100: 709-718.

Ostrand, W.D., T.A. Gotthardt, S. Howlin & M.D. Robards (2005) Habitat selection models for Pacific sand lance (*Ammodytes hexapterus*) in Prince William Sound, Alaska. *Northwestern Naturalist*, 86: 131-143.

O'Sullivan, D. & D.J. Unwin (2003) *Geographic Information Analysis.* John Wiley & Sons, Inc., Hoboken, NJ.

Oviedo, L. (2007) Dolphin sympatric ecology in a tropical fiord: habitat bathymetry and topography as a strategy to coexist. *Journal of the Marine Biological Association of the United Kingdom*, 87: 1327-1335.

Paisley, S. & D.L. Garshelis (2006) Activity patterns and time budgets of Andean bears (*Tremarctos ornatus*) in the Apolobamba Range of Bolivia. *Journal of Zoology*, 268: 25-34.

Parra, G.J. (2006) Resource partitioning in sympatric delphinids: Space use and habitat preferences of Australian snubfin and Indo-Pacific humpback dolphins. *Journal of Animal Ecology*, 75: 862-874.

Parrish, J.K., N. Lemberg & L. South-Oryshchyn (1998) Effects of colony location and nekton abundance on the at-sea distribution of four seabird species. *Fisheries Oceanography*, 7: 126-135.

Peery, M.Z., B.H. Becker & S.R. Beissinger (2006) Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. *Ecological Applications*, 16: 1516-1528.

Peery, M.Z., B.H. Becker & S.R. Beissinger (2007) Age ratios as estimators of productivity: Testing assumptions on a threatened seabird, the Marbled Murrelet (*Brachyramphus marmoratus*). *Auk*, 124: 224-240.

Peery, M.Z., S.R. Beissinger, S.H. Newman, E.B. Burkett & T.D. Williams (2004) Applying the declining population paradigm: Diagnosing causes of poor reproduction in the marbled murrelet. *Conservation Biology*, 18: 1088-1098.

Perry, J.N., A.M. Liebhold, M.S. Rosenberg, J. Dungan, M. Miriti, A. Jakomulska & S. Citron-Pousty (2002) Illustrations and guidelines for selecting statistical methods for quantifying spatial pattern in ecological data. *Ecography*, 25: 578-600.

Phillips, R.A., J.R.D. Silk, B. Phalan, P. Catry & J.P. Croxall (2004) Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271: 1283-1291.

Piatt, J.F. (1987) *Behavioural ecology of Common Murre and Atlantic Puffin predation on capelin: implications for population biology*. Ph.D. thesis, Memorial University of Newfoundland, St. John’s, NFLD.

Piatt, J.F. (1990) The aggregative response of common murres and Atlantic puffins to schools of capelin. *Studies in Avian Biology*, 14: 36-51.

Piatt, J.F., K.J. Kuletz, A.E. Burger, S.A. Hatch, V.L. Friesen, T.P. Birt, M.L. Arimitsu, G.S. Drew, A.M.A. Harding & K.S. Bixler (2007a) Status review of the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia. U.S. Geological Survey Open-File Report 2006-1387, 258 p.

Piatt, J.F., A.M.A. Harding, M. Shultz, S.G. Speckman, T.I. van Pelt, G.S. Drew & A.B. Kettle (2007b) Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series*, 352: 221-234.

Piatt, J.F. & D.A. Methven (1992) Threshold foraging behavior of baleen whales. *Marine Ecology Progress Series*, 84: 205-210.

Piatt, J.F., J. Wetzel, K. Bell, A.R. DeGange, G.R. Balogh, G.S. Drew, T. Geernaert, C. Ladd & G.V. Byrd (2006) Predictable hotspots and foraging habitat of the endangered short-tailed albatross (*Phoebastria albatrus*) in the North Pacific: Implications for conservation. *Deep-Sea Research Part II -Topical Studies in Oceanography*, 53: 387-398.

Piatt, J.F. & D.N. Nettleship (1985) Diving depths of four alcids. *Auk*, 102: 293-297.

Porter, J.M. & S.G. Sealy (1981) Dynamics of seabird multispecies feeding flocks: chronology of flocking in Barkley Sound, British Columbia, in 1979. *Colonial Waterbirds*, 4: 104-113.

Pyle, P. (2007) Standardizing at-sea monitoring programs for West-Coast National Marine Sanctuaries. In. Gulf of the Farallones National Marine Sanctuary, San Francisco, CA.

Ralph, C.J. & J.M. Scott (1981) Estimating numbers of terrestrial birds. *Studies in Avian Biology*, 6.

Ralph, C.J., J. G. L. Hunt, M.G. Raphael & J.F. Piatt, eds. (1995) *Ecology and conservation of the Marbled Murrelet.* General Technical Report PSW-GTR-152. Pacific Southwest Research Station, Forest, U.S. Department of Agriculture, Albany, CA.

Raphael, M.G. (2006) Conservation of the marbled murrelet under the northwest forest plan. *Conservation Biology*, 20: 297-305.

Raphael, M.G., J. Baldwin, G.A. Falxa, M.H. Huff, M. Lance, S.L. Miller, S.F. Pearson, C.J. Ralph, C. Strong & C. Thompson (2007) Regional population monitoring of the marbled murrelet: field and analytical methods. Gen. Tech. Rep. PNW-GTR-716. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Raphael, M.G., D. Evans Mack & R.J. Wilk (1999) Sampling marbled murrelets at sea: tests of survey methods and designs. http://www.reo.gov/monitoring/murrelet/pdf/pnw_atsea.pdf.

Raphael, M.G., D. Evans Mack, J.M. Marzluff & J.M. Luginbuhl (2002) Effects of forest fragmentation on populations of the marbled murrelet. *Studies in Avian Biology*, 25: 221-235.

Redfern, J.V., M.C. Ferguson, E.A. Becker, K.D. Hyrenbach, C. Good, J. Barlow, K. Kaschner, M.F. Baumgartner, K.A. Forney, L.T. Ballance, P. Fauchald, P. Halpin, T. Hamazaki, A.J. Pershing, S.S. Qian, A. Read, S.B. Reilly, L. Torres & F. Werner (2006) Techniques for cetacean-habitat modeling. *Marine Ecology Progress Series*, 310: 271-295.

Reid, K., J.P. Croxall, D.R. Briggs & E.J. Murphy (2005) Antarctic ecosystem monitoring: quantifying the response of ecosystem indicators to variability in Antarctic krill. *ICES Journal of Marine Science*, 62: 366-373.

Reilly, S.B. & P.C. Fiedler (1994) Interannual variability of dolphin habitats in the eastern tropical Pacific. I: Research vessel surveys, 1986-1990. *FIshery Bulletin*, 92: 434-450.

Ribeiro, S., F.A. Viddi, J.K. Cordeiro & T.R.O. Freitas (2007) Fine-scale habitat selection of Chilean dolphins (*Cephalorhynchus eutropia*): interactions with aquaculture activities in southern Chiloe Island, Chile. *Journal of the Marine Biological Association of the United Kingdom*, 87: 119-128.

RIC (2001) *Inventory for marbled murrelets in marine and terrestrial habitats, Version 2.0. Standards for components of British Columbia's biodiversity, No. 10.* Ministry of Environment, Lands and Parks, Resources Inventory Committee, Victoria, BC.

Richards, S.A. (2002) Temporal partitioning and aggression among foragers: modeling the effects of stochasticity and individual state. *Behavioral Ecology*, 13: 427-438.

Ricklefs, R.A. (1987) Response of adult Leach's storm-petrels to increased food demand at the nest. *Auk* 104: 750-756.

Robards, M.D., J.A. Anthony, G.A. Rose & J.F. Piatt (1999) Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) from Kachemak Bay, Alaska relative to maturity and season. *Journal of Experimental Marine Biology and Ecology*, 242: 245-258.

Robards, M.D., M.F. Willson, R.H. Armstrong & J.F. Piatt, eds. (1999) *Sand lance: a review of biology and predator relations and annotated bibliography* Research Paper PNW-RP-521. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Rodway, M.S. (1990) Status report on the marbled murrelet *Brachyramphus marmoratus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa.

Rome, M.S. & J.C. Ellis (2004) Foraging ecology and interactions between herring gulls and great black-backed gulls in New England. *Waterbirds*, 27: 200-210.

Ronconi, R.A. & C.C. St Clair (2002) Management options to reduce boat disturbance on foraging black guillemots (*Cepphus grylle*) in the Bay of Fundy. *Biological Conservation*, 108: 265-271.

Rosenzweig, M.L. (1973) Habitat selection experiments with a pair of coexisting rodent species. *Ecology*, 62: 327-335.

Rosenzweig, M.L. (1981) A theory of habitat selection. *Ecology*, 62: 327-335.

Rosenstock, S.S., D.R. Anderson, K.M. Giesen, T. Leukering & M.F. Carter (2002) Landbird counting techniques: current practices and an alternative. *Auk*, 119: 46-53.

Roy, S. & J. Chattopadhyay (2007) Towards a resolution of 'the paradox of the plankton': A brief overview of the proposed mechanisms. *Ecological Complexity*, 4: 26-33.

Ryan, P.G. & J. Cooper (1989) Observer precision and bird conspicuousness during counts of birds at sea. *South African Journal of Marine Science*, 8: 271-276.

Safina, C. (1990) Bluefish mediation of foraging competition between Roseate and Common Terns. *Ecology*, 71: 1804-1809.

Safina, C. & J. Burger (1985) Common tern foraging: seasonal trends in prey fish densities and competition with bluefish. *Ecology*, 66: 1457-1463.

SARA (2002) Species At Risk Act. *Canada Gazette, Part III*, 25 (3): Chapter 29.

Sawada, M. (1999) Rookcase: an Excel 97/2000 Visual Basic (VB) add-in for exploring global and local spatial autocorrelation. *Bulletin of the Ecological Society of America*, 80: 231-234.

Schneider, D.C. (1990) Spatial autocorrelation in marine birds. *Polar Research*, 8: 89-97.

Schoener, T.W. (1974) Resource partitioning in ecological communities. *Science*, 185: 27-39.

Schreiber, E. A. & J. Burger (eds.) (2002) *Biology of Marine Birds.* CRC Press, Boca Raton, FL.

Schwing, F.B., N.A. Bond, S.J. Bograd, T. Mitchell, M.A. Alexander & N. Mantua (2006) Delayed coastal upwelling along the US West Coast in 2005: A historical perspective. *Geophysical Research Letters*, 33: L22S01.

Scott, J.M., P.J. Heglund, M.L. Morrison, J.B. Haufler, M.G. Raphael, W.A. Wall & F.B. Samson, eds. (2002) *Predicting species occurrences: issues of accuracy and scale* Island Press, Washington, D.C.

Sealy, S. G. (1975) The feeding ecology of ancient and marbled murrelets near Langara Island, B.C. *Canadian Journal of Zoology* 53: 418-433.

Segurado, P. & M.B. Araujo (2004) An evaluation of methods for modelling species distributions. *Journal of Biogeography*, 31: 1555-1568.

Seoane, J., L.M. Carrascal, C.L. Alonso & D. Palomino (2005) Species-specific traits associated to prediction errors in bird habitat suitability modelling. *Ecological Modelling*, 185: 299-308.

Shealer, D.A. (2002) Foraging behavior and food of seabirds. Pp. 137-177 in *Biology of Marine Birds* (E.A. Schreiber & J. Burger eds.). CRC Press, Boca Raton.

Shealer, D.A. & J. Burger (1993) Effects of interference competition on the foraging activity of tropical Roseate Terns. *Condor*, 95: 322-329.

Silverman, E.D. & R.R. Veit (2001) Associations among Antarctic seabirds in mixed species feeding flocks. *Ibis*, 143: 51-62.

Silverman, E.D., R.R. Veit & G.A. Nevitt (2004) Nearest neighbors as foraging cues: information transfer in a patchy environment. *Marine Ecology Progress Series*, 277: 25-35.

Sims, D.W. (1999) Threshold foraging behaviour of basking sharks on zooplankton: life on an energetic knife-edge? *Proceedings of the Royal Society of London Series B*, 266: 1437-1443.

Skov, H., J. Durinck, M.F. Leopold & M.L. Tasker (2007) A quantitative method for evaluating the importance of marine areas for conservation of birds. *Biological Conservation*, 136: 362-371.

Slooten, E., S. Dawson, W. Rayment & S. Childerhouse (2006) A new abundance estimate for Maui's dolphin: What does it mean for managing this critically endangered species? *Biological Conservation*, 128: 576-581.

Slooten, E., S.M. Dawson & W.J. Rayment (2004) Aerial surveys for coastal dolphins: Abundance of Hector's dolphins off the South Island west coast, New Zealand. *Marine Mammal Science*, 20: 477-490.

Smith, J.L. & K.D. Hyrenbach (2003) Galpágos Islands to British Columbia: seabird communities alsong a 9000 km transect from the tropical to the subarctic eastern pacific ocean. *Marine Ornithology*, 31: 155-166.

Spear, L.B., D.G. Ainley, B. Denise Hardesty, S.N.G. Howell & S.W. Webb (2004) Reducing biases affecting at-sea surveys of seabirds: use of multiple observer teams. *Marine Ornithology*, 32: 147-157.

Speckman, S.G., A.M. Springer, J.F. Piatt & D.L. Thomas (2000) Temporal variability in abundance of Marbled Murrelets at sea in Southeast Alaska. *Waterbirds*, 23: 364-377.

Speckman, S.G., J.F. Piatt & A.M. Springer (2003) Deciphering the social structure of Marbled Murrelets from behavioral observations at sea. *Waterbirds*, 26: 266-274.

Speckman, S.G., J.F. Piatt & A.M. Springer (2004) Small boats disturb fishholding Marbled Murrelets. *Northwestern Naturalist*, 85: 32-34.

SPSS (1998) *Systat 8.0 for Windows.* SPSS Inc., Chicago, IL.

SPSS (2004) *SPSS Classification Trees 13.0.* SPSS Inc., Chicago, IL.

Stapanian, M.A. & M.T. Bur (2002) Overlap in offshore habitat use by double-crested cormorants and boaters in western Lake Erie. *Journal of Great Lakes Research*, 28: 172-181.

Stearns, S.C. (1992) *The Evolution of Life Histories.* Oxford University Press, Oxford.

Steele, J.H. (1991) Can ecological theory cross the land-sea boundary? *Journal of Theoretical Biology*, 153: 425-436.

Strachan, G., M. McAllister & C.J. Ralph (1995) Marbled murrelet at-sea and foraging behavior. Pp. 247-253 in *Ecology and Conservation of the Marbled Murrelet. General Technical Report PSW-GTR-152* (C.J. Ralph, G.L. Hunt, M.G. Raphael & J.F. Piatt eds.). Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA.

Suryan, R.M., D.B. Irons, E.D. Brown, P.G.R. Jodice & D.D. Roby (2006) Site-specific effects on productivity of an upper trophic-level marine predator: Bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. *Progress in Oceanography*, 68: 303-328.

Swartzman, G. & G. Hunt (2000) Spatial associations between murres (*Uria* spp.), puffins (*Fratercula* spp.) and fish shoals near Pribilof Islands, Alaska. *Marine Ecology Progress Series,* 206: 297-309.

Sydeman, W.J., R.W. Bradley, P. Warzybok, C.L. Abraham, J. Jahncke, K.D. Hyrenbach, V. Kousky, J.M. Hipfner & M.D. Ohman (2006) Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? *Geophysical Research Letters*, 33: L22S09.

Sydeman, W.J., R.D. Brodeur, C.B. Grimes, A.S. Bychkov & S. McKinnell (2006) Marine habitat "hotspots" and their use by migratory species and top predators in the North Pacific Ocean: Introduction. *Deep-Sea Research Part Ii-Topical Studies in Oceanography*, 53: 247-249.

Tabachnick, B.G. & L.A. Fidell (1996) *Using multivariate statistics.* Harper Collins, New York, NY.

Tasker, M.L., P.H. Jones, T. Dixon & B.F. Blake (1984) Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk*, 101: 567-577.

Ter Braak, C.J.F. (1985) Correspondence analysis of incidence and abundance data: properties in terms of a unimodal response model. *Biometrics*, 41: 859-873.

Ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, 67: 1167-1179.

Ter Braak, C.J.F. & P. Smilauer (2002) *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5).* Microcomputer Power, Ithaca, NY.

Thomas, L., J.L. Laake, S. Strindberg, F.F.C. Marques, S.T. Buckland, D.L. Borchers, D.R. Anderson, K.P. Burnham, S.L. Hedley, J.H. Pollard, J.R.B. Bishop & T.A. Marques (2006) *Distance 5.0. Release 2*. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance/.

Thompson, W.L. (2002) Towards reliable bird surveys: accounting for individuals present but not detected. *Auk*, 119: 18-25.

Thompson, P.M. & J.C. Ollason (2001) Lagged effects of ocean climate change on fulmar population dynamics. *Nature*, 413: 417-420.

Thomson, R.E. (1981) *Oceanography of the British Columbia Coast*. Canadian Special Publication of Fisheries and Aquatic Sciences 56. Dept. of Fisheries and Oceans, Ottawa.

Thomson, R.E., B.M. Hickey & P.H. LeBlond (1989) The Vancouver Island coastal current: fisheries barrier and conduit. Pp. 265-296. in *Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models* (R. J. Beamish & G. A. McFarlane, eds.). Canadian Special Publication of Fisheries and Aquatic Sciences No. 108, Ottawa.

Thoresen, A.C. (1989) Diving times and behavior of Pigeon Guillmots and Marbled Murrelets off Rosario Head, Washington. *Western Birds*, 20: 33-37.

Tokeshi, M. (1999) *Species Coexistence: ecological and evolutionary perspectives*. Blackwell Science Ltd., Oxford.

Tremblay, Y. & Y. Cherel (2000) Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. *Marine Ecology Progress Series*, 204: 257-267.

Tremblay, Y., Y. Cherel, M. Oremus, T. Tveraa & O. Chastel (2003) Unconventional ventral attachment of time-depth recorders as a new method for investigating time budget and diving behaviour of seabirds. *Journal of Experimental Biology*, 206: 1929-1940.

Triplet, P., R.A. Stillman & J.D. Goss-Custard (1999) Prey abundance and the strenght of interference in a foraging shorebird. *Journal of Animal Ecology*, 68: 254-265.

Uttley, J.D., P. Walton, P. Monaghan & G. Austin (1994) The effects of food abundance on breeding performance and adult time budgets of Guillemots *Uria aalge*. *Ibis*, 136: 205-213.

Valeix, M., S. Chamaille-Jammes & H. Fritz (2007) Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia*, 153: 739-748.

van der Meer, J. & C.J. Camphuysen (1996) Effect of observer differences on abundance estimates of seabirds from ship-based strip transect surveys. *Ibis*, 138: 433-437.

van Franeker, J.A., N.W. van den Brink, U.V. Bathmann, R.T. Pollard, H.J.W. de Barr & W.J. Wolff (2002) Responses of seabirds, in particular prions (*Pachyptila* sp.), to small-scale processes in the Antarctic Polar Front. *Deep-Sea Research Part II -Topical Studies in Oceanography*, 49: 3931-3950.

Vermeer, K., S.G. Sealy & G.A. Sanger (1987) Feeding ecology of Alcidae in the eastern North Pacific Ocean. Pp. 189-227 in *Seabirds, feeding biology and role in marine ecosystems* (J.P. Croxall,ed. Cambridge University Press, Cambridge, UK.

Vieira, A.M.C., J.P. Hinde & C.G.B. Demetrio (2000) Zero-inflated proportion data models applied to a biological control assay. *Journal of Applied Statistics*, 27: 373-389.

Vlietstra, L.S. (2005) Spatial associations between seabirds and prey: effects of large-scale prey abundance on smallscale seabird distribution. *Marine Ecology-Progress Series*, 291: 275-287.

Votier, S.C., B.J. Hatchwell, A. Beckerman, R.H. McCleery, F.M. Hunter, J. Pellatt, M. Trinder & T.R. Birkhead (2005) Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecology Letters*, 8: 1157-1164.

Wahl, T.R., D.G. Ainley, A.H. Benedict & A.R. Degange (1989) Associations between seabirds and water masses in the northern Pacific Ocean in summer. *Marine Biology*, 103: 1-11.

Walsberg, G.E. (1985) Physiological consequences of microhabitat selection. Pp. 389-413 in *Habitat Selection in Birds* (M.L. Cody, ed.) Academic Press, New York.

Walther, G.R., E. Post, P. Convey, A. Menzel, C. Parmesan, T.J.C. Beebee, J.M. Fromentin, O. Hoegh-Guldberg & F. Bairlein (2002) Ecological responses to recent climate change. *Nature*, 416: 389-395.

Wanless, S., M.P. Harris & J.A. Morris (1990) A comparison of feeding areas used by individual common murres (*Uria aalge*), razorbills (*Alca torda*) and Atlantic puffins (*Fratercula arctica*) during the breeding season. *Colonial Waterbirds* 13: 16-24.

Wanless, S., M.P. Harris, P. Redman & J.R. Speakman (2005) Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series*, 294: 1-8.

Wasserberg, G., B.P. Kotler, D.W. Morris & Z. Abramsky (2007) A field test of the centrifugal community organization model using psammophilic gerbils in Israel's southern coastal plain. *Evolutionary Ecology Research*, 9: 299-311.

Watanuki, Y. & A.E. Burger (1999) Body mass and dive duration in alcids and penguins. *Canadian Journal of Zoology*, 77: 1838-1842.

Watanuki, Y., K. Ishikawa, A. Takahashi & A. Kato (2004) Foraging behavior of a generalist marine top predator, Japanese cormorants (*Phalacrocorax filamentosus*), in years of demersal versus epipelagic prey. *Marine Biology*, 145: 427-434.

Waugh, S.M. & H. Weimerskirch (2003) Environmental heterogeneity and the evolution of foraging behaviour in long ranging greater albatrosses. *Oikos*, 103: 374-384.

Weimerskirch, H., J.A. Bartle, P. Jouventin & J.C. Stahl (1988) Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor*, 90: 214-219.

Weimerskirch, H., M. Le Corre, S. Jaquemet & F. Marsac (2005) Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. *Marine Ecology Progress Series*, 288: 251-261.

Whittow, G.C. (2002) Seabird reproductive physiology and energetics. Pp. 409-437 in *Biology of Marine Birds* (E.A. Schreiber & J. Burger eds.). CRC Press, Boca Raton, FL.

Whitworth, D.L., S.K. Nelson, S.H. Newman, G.B. Van Vliet & W.P. Smith (2000) Foraging distances of radio-marked Marbled Murrelets from inland areas in southeast Alaska. *Condor*, 102: 452-456.

Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, 3: 385-397.

Williams, R., A.W. Trites & D.E. Bain (2002) Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. *Journal of Zoology*, 256: 255-270.

Willson, M.F., R.H. Armstrong, M.D. Robards & J.F. Piatt (1999) Sand lance as cornerstone prey for predator populations. Pp. 17-44 in *Sand lance: a review of biology and predator relations and annotated bibliography* (M.D. Robards, M.F. Willson, R.H. Armstrong & J.F. Piatt eds.). Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

Winkler, H. (1985) Morphological aspects of habitat selection in birds. Pp. 415-434 in *Habitat Selection in Birds* (M.L. Cody, ed.), Academic Press, New York.

Wittenberger, J.F. & G.L. Hunt (1985) The adaptive significance of coloniality in birds. Pp. 1-77 in *Avain biology, Vol 8.* (D.S. Farner, J.R. King & K.C. Parkes eds.). Academic Press, Toronto.

Wong, S.N.P., R.A. Ronconi, A.E. Burger & B. Hanson (in press) Marine distribution and behavior of juvenile and adult Marbled Murrelets off southwest Vancouver Island, British Columbia: applications for monitoring. *Condor*.

Woodby, D.A. (1984) The April distribution of murres and prey patches in the southeastern Berring Sea. *Limnology and Oceanography*, 29: 181-188.

Wynne-Edwards, V.C. (1935) On habits and distribution of birds on the North Atlantic. *Proceedings of the Boston Society of Natural History*, 40: 233-346.

Yen, P.P.W., F. Huettmann & F. Cooke (2004a) A large-scale model for the at-sea distribution and abundance of Marbled Murrelets (*Brachyramphus marmoratus*) during the breeding season in coastal British Columbia, Canada. *Ecological Modelling*, 171: 395-413.

Yen, P.P.W., W.J. Sydeman & K.D. Hyrenbach (2004b) Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *Journal of Marine Systems*, 50: 79-99.

Zador, S.G. & J.F. Piatt (1999) Time-budgets of Common Murres at a declining and increasing colony in Alaska. *Condor*, 101: 149-152.

Zamon, J.E. (2003) Mixed species aggregations feeding upon herring and sandlance schools in a nearshore archipelago depend on flooding tidal currents. *Marine Ecology Progress Series*, 261: 243-255.

Zharikov, Y., D.B. Lank, F. Huettmann, R.W. Bradley, N. Parker, P.P.W. Yen, L.A. McFarlane-Tranquilla & F. Cooke (2006) Habitat selection and breeding success in a forest-nesting Alcid, the marbled murrelet, in two landscapes with different degrees of forest fragmentation. *Landscape Ecology*, 21: 107-120.

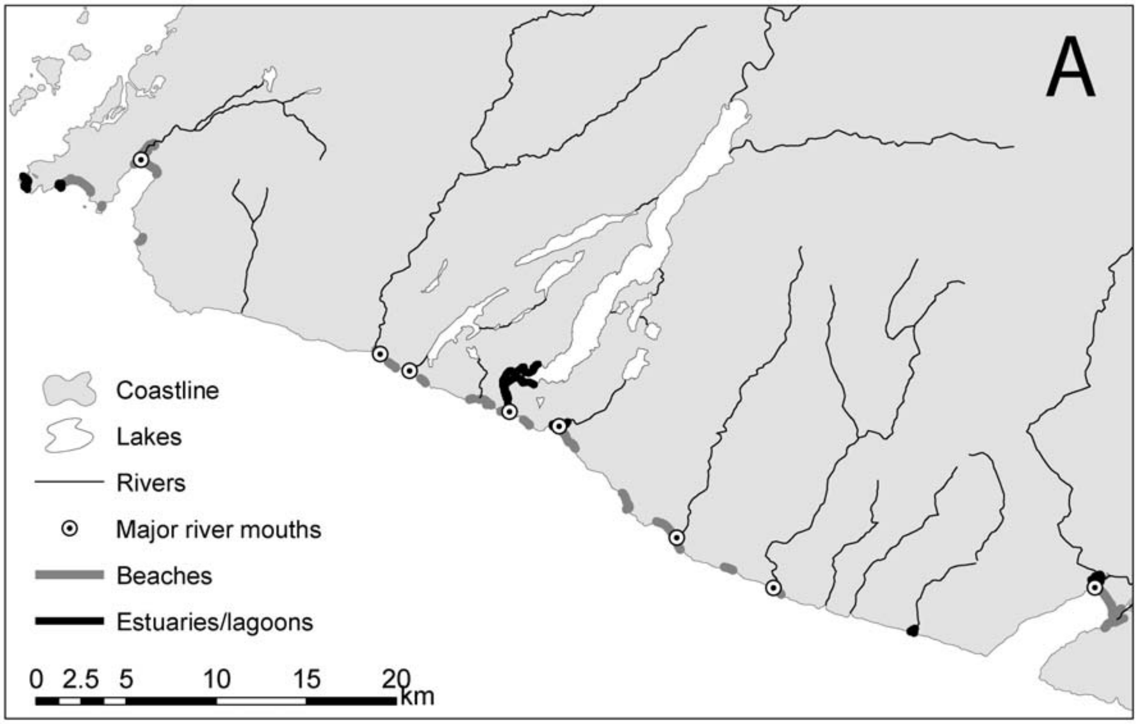
Zharikov, Y., D.B. Lank & F. Cooke (2007) Influences of landscape pattern on breeding distribution and success in a threatened Alcid, the marbled murrelet: model transferability and management implications. *Journal of Applied Ecology*, 44: 748-759.

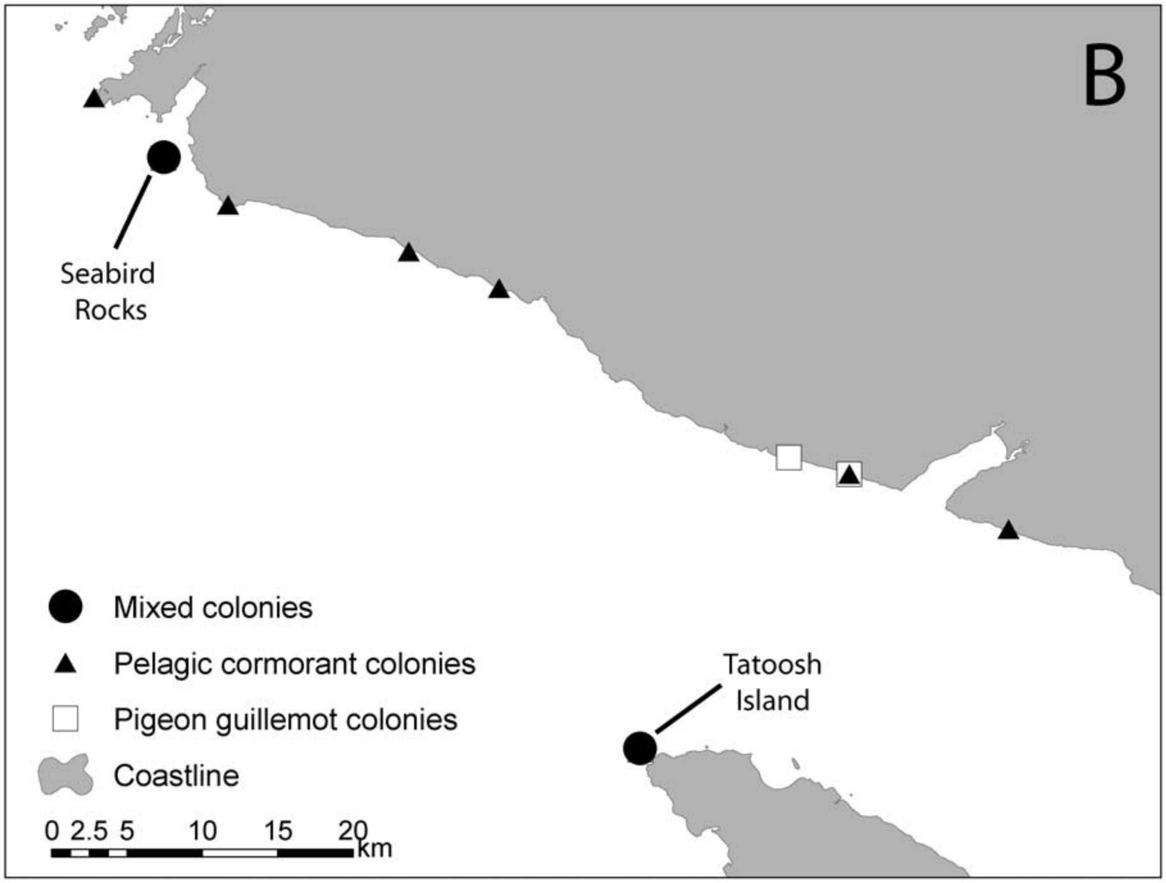
Appendix

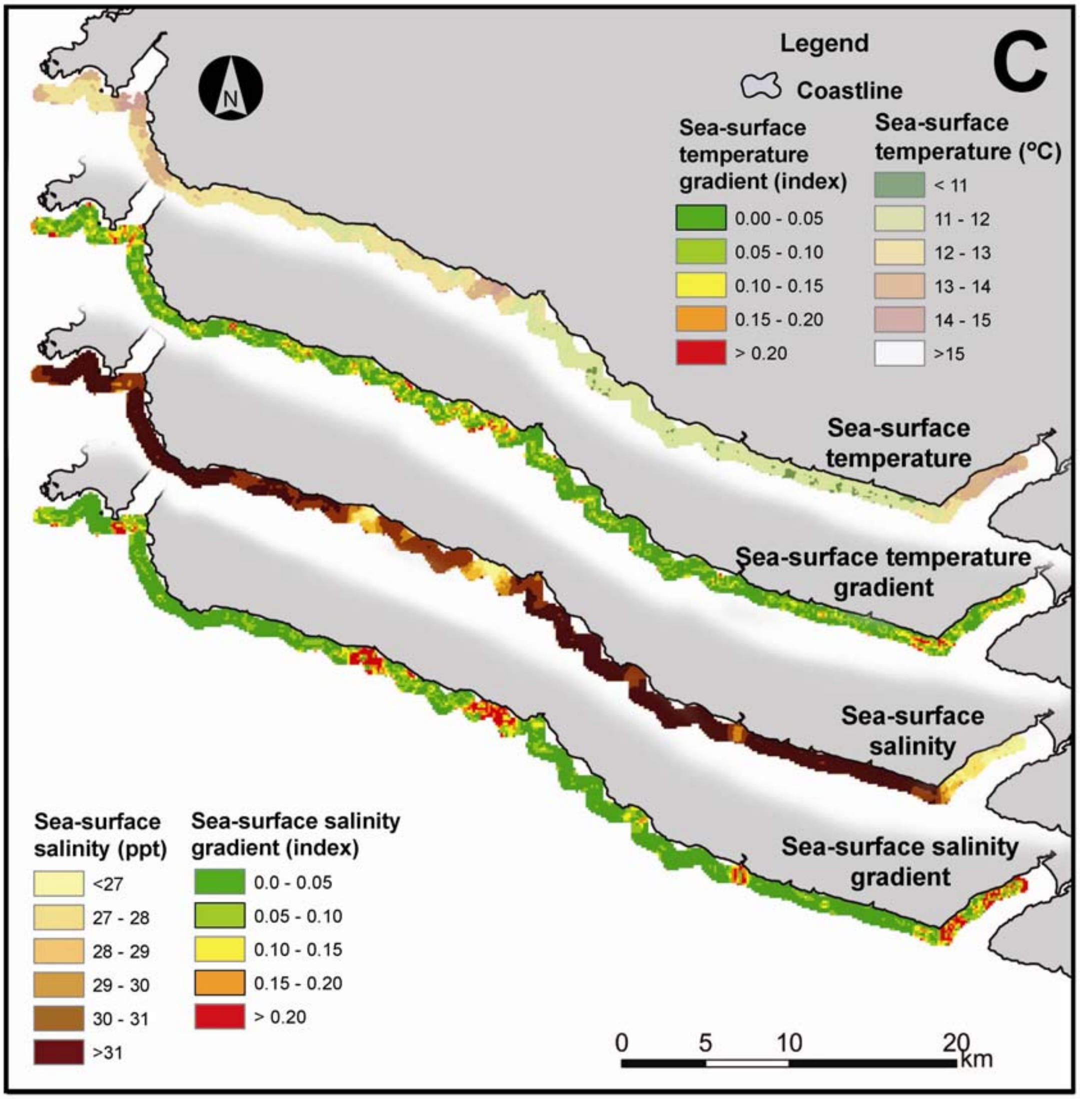
Appendix I – Maps of environmental variables used in species-habitat models for Chapter 3.

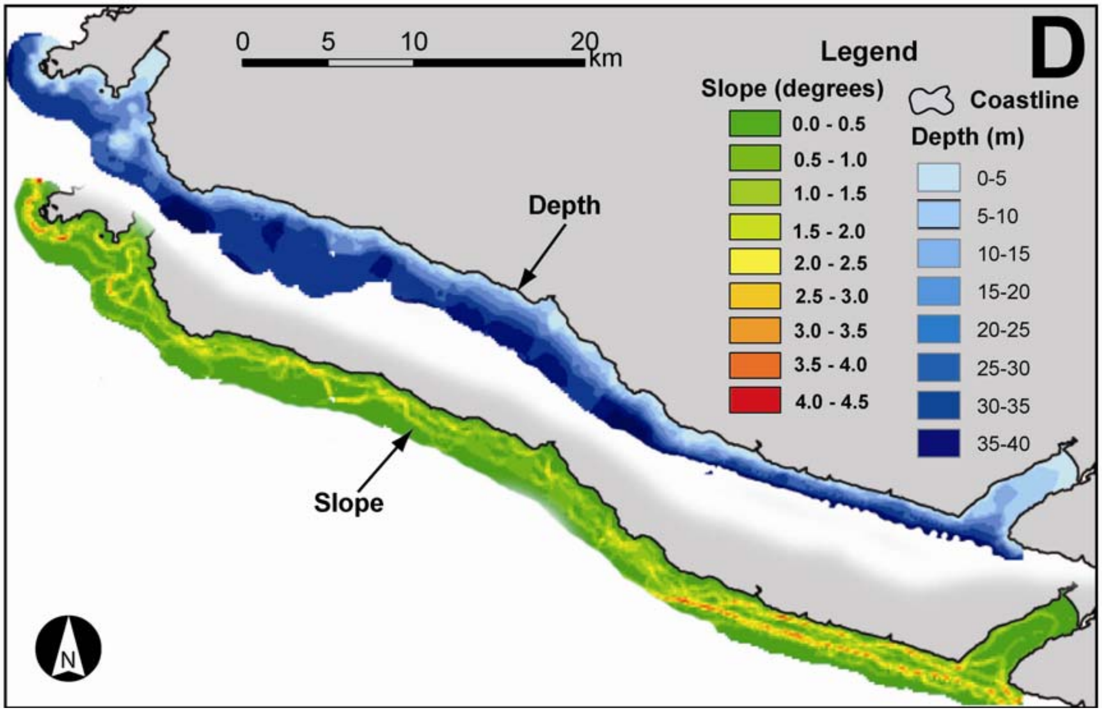
Figure A.1 – Maps of environmental variables for species-habitat modeling

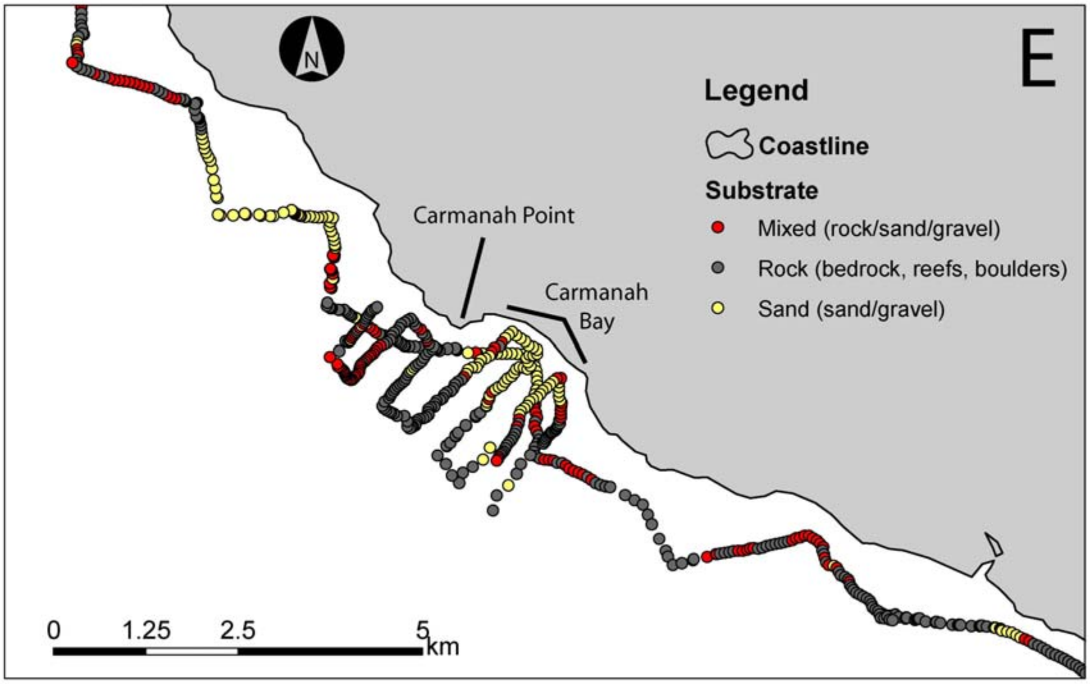
Maps include A) rivers, beaches, and estuaries; B) colony locations; C) sea-surface temperature (SST), sea-surface salinity (SSS) recorded in 2005/06, and their gradients; D) bathymetry and slope; E) sea floor substrate at Carmanah Bay and surroundings; F) marbled murrelet nesting habitat and mapping procedure; and G) measurement of % old-growth at inland plots used to calculate % old-growth index on the coast.

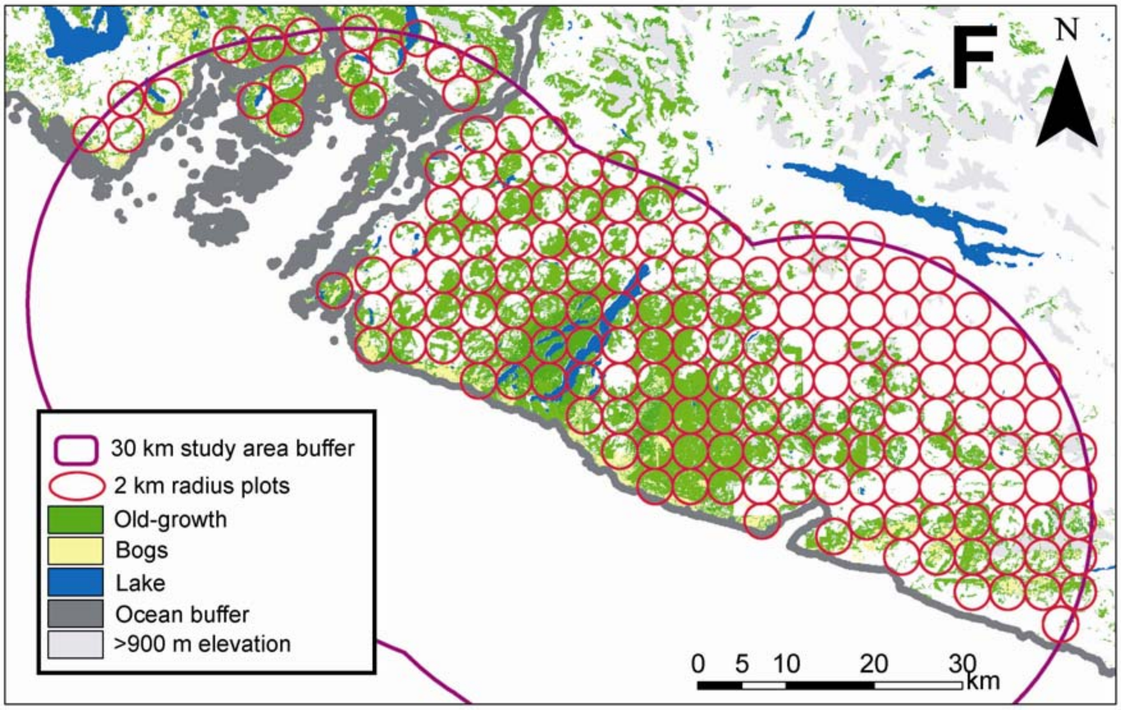


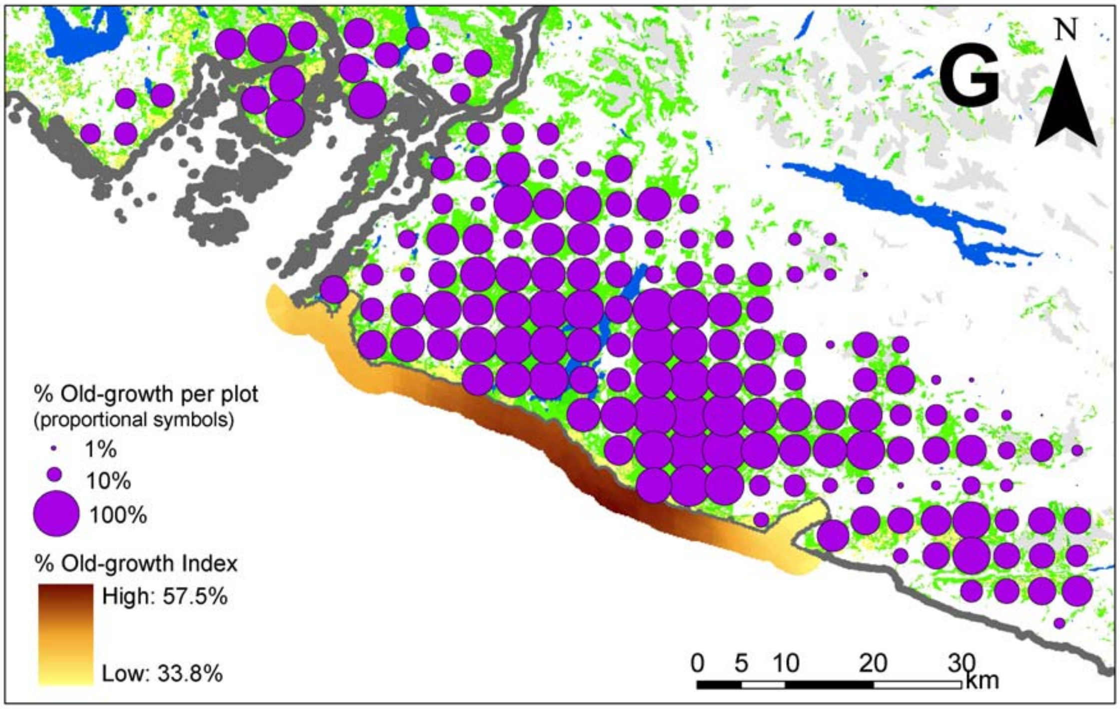

B
Seabird Rocks
Tatoosh Island
Mixed colonies
Pelagic cormorant colonies
Pigeon guillemot colonies
Coastline
0 2.5 5 10 15 20 km


C
Legend
Coastline
Sea-surface temperature gradient (index)
0.00 - 0.05
0.05 - 0.10
0.10 - 0.15
0.15 - 0.20
> 0.20
Sea-surface temperature (ºC)
< 11
11 - 12
12 - 13
13 - 14
14 - 15
>15
Sea-surface temperature
Sea-surface temperature gradient
Sea-surface salinity
Sea-surface salinity gradient
Sea-surface salinity (ppt)
<27
27 - 28
28 - 29
29 - 30
30 - 31
>31
Sea-surface salinity gradient (index)
0.0 - 0.05
0.05 - 0.10
0.10 - 0.15
0.15 - 0.20
> 0.20
N
0
5
10
20
km


D
0
5
10
20
km
Legend
Slope (degrees)
0.0 - 0.5
0.5 - 1.0
1.0 - 1.5
1.5 - 2.0
2.0 - 2.5
2.5 - 3.0
3.0 - 3.5
3.5 - 4.0
4.0 - 4.5
Coastline
Depth (m)
0-5
5-10
10-15
15-20
20-25
25-30
30-35
35-40
Depth
Slope
N


E
N
Legend
Coastline
Substrate
Mixed (rock/sand/gravel)
Rock (bedrock, reefs, boulders)
Sand (sand/gravel)
Carmanah Point
Carmanah Bay
0
1.25
2.5
5
km


F
N
30 km study area buffer
2 km radius plots
Old-growth
Bogs
Lake
Ocean buffer
>900 m elevation
0 5 10 20 30 km


G
N
% Old-growth per plot
(proportional symbols)
1%
10%
100%
% Old-growth Index
High: 57.5%
Low: 33.8%
0 5 10 20 30 km

Appendix II - Methods for determining detectability of marbled murrelets and common murres mapped by theodolite

In Chapter 5, an electronic theodolite was used to map the fine-scale distribution of seabirds at several sites. Although the precision of theodolites has been tested for mapping animals on the water (Denardo et al. 2001), there is no useful information on the distances of detectability for animals using this technique. The detectability of animals invariably declines with distance from the observer (Buckland et al. 2001) and is likely to vary among species as a function of body size and coloration (Chapter 2). Theodolites have been widely used to track the movements of marine mammals which are quite large and detectable over distances of 2 to 4 km (Denardo et al. 2001, Williams et al. 2002, Ribeiro et al. 2007). However, there is no information on the detectability of seabirds by theodolite. I used distance-sampling methodology for point transects (Buckland et al. 2001, Marques et al. 2007) to model the detectability of seabirds as a function of distance from the theodolite. I modeled both off-shore and along-shore detectability (i.e., perpendicular to and parallel with the shore, respectively).

METHODS

In 2004 and 2005 murrelets and murres were mapped at multiple sites using electronic theodolite (see Chapter 5 for details). This resulted in 95 independent maps. Each location on the map represents a group of birds of one species. Group-size was recorded for each group. During each scan Beaufort sea-state and % cloud cover were recorded as these are likely environmental variables to affect detectability. Within 2 km of shore, murres appear to distribute themselves relatively evenly but murrelets were typically found closer to shore (Chapter 5). Because most murrelets utilize waters close to shore (77% were < 550 m from shore, all within 2 km; Burger et al. in press), there is a confounding habitat effect which may influence bird detectability, i.e. few birds detected far from shore simply because few birds utilize habitats farther from shore. Thus I calculated the distance of each bird group from shore (using ArcGIS 9.0) and included distance-from-shore as an additional covariate in the models assessing off-shore detectability. Detection functions (see below) could then be modeled with the distance-from-shore covariate and without any covariates (null model testing simple decline in detectability), and model selection criteria (i.e. information theoretic approach, Burnham & Anderson 2002) would identify the best fit model. If the null model was the most likely model (lowest AIC value), then this would mean that bird detectability decreased as a function of distance from the observer. If the model with the distance-from-shore covariate was the most likely model, this would mean that detectability decreased as a function of bird distance from shore. I also examined the influence of sea-state, cloud cover, species, year and group-size on detection probability by including these variables as additional covariates. Year and species were included as factor covariates and all other variables were included as continuous variables. For all analyses I used program DISTANCE 5.0 (Thomas et al. 2006).

I used pooled data to test key functions and series expansion terms that are commonly used in distance sampling (Buckland et al. 2001). I tested two key functions (half-normal and hazard-rate) and three series expansion terms (cosine, simple-polynomial, and hermite), and used Akaie's Information Criterion (AIC) to select the best-fit model (Burnham & Anderson 2002). Hazard-rate key function with a simple-polynomial expansion term was the best fit model (lowest AIC) with no competing models (ΔAIC < 10 for all other models), therefore this detection function was used in all subsequent modeling.

Data truncation is important to eliminate spurious results which can cause detection functions to fit poorly (Buckland et al. 2001). I used left truncation to eliminate all observations within 300 m of the theodolite because this was the approximate distance to which the rocky shelf ledge protruded from land and omitted bird from being mapped. Right truncation used a rule of thumb to eliminate the largest 5% of all observations (Buckland et al. 2001). Left and right truncation thus represent the minimum and maximum distances respectively, used for fitting a detection function.

I used multiple-covariate distance sampling (MCDS) to test the effects of several variables that may affect the detectability of birds from land: Beaufort sea-state (0 to 3), % cloud-cover (because glare from sun may decrease detectability), species (larger common murre [~1kg, black and white plumage] vs. smaller marbled murrelet[~220g, brown plumage]), year (2004 and 2005), group-size (larger groups may be detected at further distances), and distance-from-shore. I used MCDS and AIC selection criteria to select among candidate models which included a null model (no covariates), models with each individual covariate, and models with each combination of up to two covariates. I tested all models in each of three datasets for surveys at Carmanah Bay, Pachena Point, and other sites (all remaining sites pooled).

With respect to this analysis, the most important parameter calculated from the models was Effective Detection Radius (EDR), which may be defined as the distance at which the number of birds detected beyond this point equals the number missed within this point (Buckland et al. 2001). In this analysis, because detectability dropped off rapidly, EDR was useful in identifying the distance at which bird detectability decreases dramatically (Fig A.2 shows an example of the relationship between probability of detection and the EDR). In the original MCDS models, EDR suggested the distance at which detectability decreases *off-shore*. I used the distance from these models to create a maximum off-shore distance where bird detectability was reliable. To examine *along-shore* detectabiliy I then reran MCDS models only on data in near shore waters (<1000 m) and excluded the distance-from-shore covariate. This analysis will thus identify the maximum extent of detectability in either direction along-shore from the theodolite station.

Finally, I calculated EDR for each species in individual scans (n = 95) within the nearshore waters (<1000 m). These EDR from individual scans allowed for investigations of individual covariate effects on bird detectability. EDR was calculated only for scans with 5 or more points (i.e. bird groups), since fewer points prohibited reliable calculation of detection probability and thus invalid EDR.

RESULTS and DISCUSSION

Off-shore detectability – Table A.1 summarizes the top five models for each site and presents estimates of effective detection radius (EDR). In each site, there was one best model (lowest AIC value) with essentially no support for other competing models (ΔAIC > 10, Burnham & Anderson 2002). At Carmanah and Pachena, there was no support for the null model (ΔAIC extremely large) and distance-from-shore appeared as a covariate in each of the top five models suggesting that naturally decreasing abundance of birds with distance from shore was the primary reason for decreasing detectability.

Species was an important covariate for Carmanah and cloud cover for Pachena. No covariates were included in the most likely model for other sites (null model had the lowest AIC), though sea state was the most common covariate in the five remaining models. EDR was approximately 1200 m at Carmanah, 1300 m at Pachena and 750 m at other sites. This identifies the limits within which detectability has no marked effect.

***Along-shore detectability* –** Given the off-shore limits of detectability I selected conservative distances at which to truncate data to examine along-shore detectability in more detail. Data were truncated at 1000 m from shore for Carmanah and Pachena and 800 m from shore for other sites. Table A.2 summarizes the top five models for each site. At Carmanah the most likely model included cloud cover (CC) and species as covariates and estimated EDR at ~1200m. Figure A.3 shows the effects of species and cloud cover on detection probability. Detection probability was lower for murrelets relative to murres and was lower with decreased cloud cover (Fig. A.3 compares 30% and 90% cloud cover for illustrative purposes). The significance of cloud cover was likely due to increased glare on sunny days. At Pachena point, the most likely model included year and species (Fig. A.4). Again, detectability was lower for murrelets in each year and detectability was lower in 2005 than 2004, likely owing to lower overall bird abundance in 2005 (Chapter 2). Finally, at other sites there were no covariates in the most likely model (null model) though there was marginal support for other candidate models (ΔAIC < 7). Fig. A.5 however shows that differences in detectability between species was marginal (EDR ~ 700 m for both species), giving support to the null model (detectability declined with distance from observer).

***Variability in effective detection radius (EDR)* –** To further examine the effects of individual covariates on effective detection radius (EDR), I calculated EDR for each species in each of 95 scans. This was limited to birds within 1000 m from shore to control for naturally decreasing abundance of birds with distance to shore. I considered EDR calculations to be unreliable with few bird detections, therefore I analyzed scans where $n \geq 5$ groups in each scan. There were 42 scans with ≥ 5 groups of both murrelets and murres; paired t-tests on EDR showed significantly greater detection distances ($t_{41} =$

6.24, $p < 0.001$) for common murres (mean 1466 m ± 51 SE) than for murrelets (1167 ± 46 SE).

Unpaired data allowed the investigation of other factors influencing EDR based on 86 scans for marbled murrelets and 46 scans for common murres. Unpaired t-tests showed significant differences between species ($t_{130} = 7.35$, $p < 0.001$) with murrelets detectable up to 999 m ± 41 SE and murres detectable to 1485 ± 49. Pooling data for both species, there was a significant site and year effect. EDR was greater at Pachena (mean 1321 m ± 56 SE) and Carmanah (1231 m ± 43) sites than for other sites (677 m ± 88; ANOVA, $F_{2,129} = 24.23$, $p < 0.001$). This large discrepancy between sites was likely due to elevation of the theodolite: at Carmanah and Pachena the theodolite was used from the top of the lighthouse tower (~ 45 m above sea level) while the other sites were mapped from cliff-tops (~ 20 to 25 m above sea level). For comparisons among years at Carmanah and Pachena (other sites surveyed in 2005 only), EDR differed between years ($t_{108} = 5.14$, $p < 0.001$) with greater detectability in 2004 (1384 m ± 38) than 2005 (1052 m ± 54).

I compared detectability among Beaufort sea states (0 to 3) for murres and murrelets separately (Fig. A.6). Sea state had marginal effects on detectability for common murres ($F_{3,42} = 2.70$, $p = 0.058$) showing decreased detectability between sea-states 0 and 3 ($p = 0.057$). For marbled murrelets, sea-state effects were significant ($F_{3,82} = 15.94$, $p < 0.001$) with the following differences: sea-states $0 = 1 > 2 = 3$ ($p < 0.01$).

Cloud cover effects were examined by categorizing cloud cover into four classes: 0-25%, 25-50, 50-75, 75-100. Within species, pooling among sites, there were no significant differences in EDR for murrelets ($F_{3,82} = 0.30$, $p = 0.823$) or murres ($F_{3,42} = 0.39$, $p = 0.763$). Within sites, pooling among species, there were no significant differences in EDR at Carmanah ($F_{3,63} = 1.53$, $p = 0.216$), Pachena ($F_{2,40} = 0.34$, $p = 0.714$) or other sites ($F_{2,19} = 0.85$, $p = 0.442$). Thus there is little evidence of cloud cover influencing detectability across the sites and species sampled.

Implications for analysis – At the two main study sites, Carmanah and Pachena, overall detectability was similar between sites. Murrelet appear to be reliably detectable up to about 1000 to 1200 m, and common murres up to about 1500 m both off-shore and along-shore. Overall detectability functions modeled with both species are about 1200 m for these sites (Tables A.1 and A.2) and this should be used as a boundary examining interactions between species. At other sites, where the theodolite height above sea level was much lower, detectability was in the range of ~650 to 750 m for both species. I am interested primarily in interactions between species, and because both species show identical detection probability at these sites (Fig. A.5) I suggest increasing the boundary to 1000 m to maximize sample size. If the goal was to assess patterns of habitat use or selection, knowledge to true absence would be more important and boundaries should be limited to 750 m.

In summary, for analysis in Chapter 5 I recommend an outer limit for analysis of 1200 m at Caramanah and Pachena, and 1000 m at all other sites. Although sea-state was shown to affect murrelet detectability (Fig. A.6), sea-state was not important in the most likely models for MCDS analysis (Table A.1 & A.2), therefore I did not reduce the outer limit for sea-state effects in order to maximize sample size. Only 14% of the scans were conducted in sea-state 3 which had the greatest effect on detectability.

Table A.1 – Off-shore detectability of seabirds mapped by theodolite.

Results from fitting different models using MCDS. I modeled the detectability of birds as a function of distance from the theodolite station. Three datasets were evaluated including Carmanah Bay, Pachena Point and all other sites pooled. Covariates included in the model were: species (murrelets vs. murres), distance from shore (Dist-shore), sea-state (SS 0 to 3), % cloud cover (CC), and cluster-size (number of birds in each group). Table shows only the top five models and the null model (no covariates). Best model is one with lowest ΔAIC value (Akaike's Information Criteria). EDR = effective detection radius.

Covariates in the model	Number of samples	Number of paramaters	Δ AIC	EDR (m)	lower CI	upper CI
Carmanah Bay						
Species + Dist-shore	4206	4	0.00	1193	1176	1211
SS + Dist-shore	4206	4	39.80	1203	1186	1221
CC + Dist-shore	4206	4	64.40	1210	1192	1227
Year + Dist-shore	4206	4	119.99	1172	1155	1189
Cluster-size + Dist-shore	4206	4	122.80	1181	1164	1198
None (null model)	4206	2	1109.86	1218	1192	1244
Pachena Point						
CC + Dist-shore	1861	4	0.00	1330	1297	1364
Year + Dist-shore	1861	4	9.70	1284	1247	1321
Dist-shore	1861	3	21.14	1383	1349	1417
Species + Dist-shore	1861	4	90.33	1370	1336	1404
SS + Dist-shore	1861	4	146.38	1529	1497	1563
None (null model)	1863	2	1698.94	1598	1552	1646
Other sites						
None (null model)	859	2	0.00	741	706	777
SS + Species	859	4	10.74	772	747	797
SS	859	3	11.31	771	746	796
SS + CC	859	4	12.05	768	743	793
SS + Dist-shore	859	4	12.42	772	747	797
Species	859	3	12.49	777	752	802

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Table A.2 – Along-shore detectability of seabirds mapped by theodolite.

Results from fitting different models using MCDS. I modeled the detectability of birds as a function of distance from the theodolite station. Data were limited to nearshore waters (<1000 or 800 m from shore) and three datasets were evaluated: Carmanah Bay, Pachena Point and all other sites pooled. Covariates included in the model were: species (murrelets vs. murres), sea-state (SS 0 to 3), % cloud cover (CC), and cluster-size (number of birds in each group). Table shows only the top five models and the null model (no covariates). Best model is one with lowest ΔAIC value (Akaike's Information Criteria). EDR = effective detection radius.

Covariates in the model	Number of samples	Number of paramaters	Δ AIC	EDR (m)	lower CI	upper CI
Carmanah Bay (within 1000m from shore)						
CC + Species	3824	4	0.00	1177	1161	1194
SS + Species	3824	4	9.18	1171	1155	1188
Species + Year	3824	4	60.92	1162	1146	1179
Cluster-size + Specie	3824	4	66.92	1181	1165	1198
Species	3824	3	110.74	1184	1168	1201
None (null model)	3824	2	331.56	1182	1159	1206
Pachena Point (within 1000m from shore)						
Species + Year	1296	4	0.00	1271	1244	1299
CC + Year	1296	4	11.21	1213	1179	1249
SS + Year	1296	4	12.48	1212	1177	1247
Cluster-size + Year	1296	4	33.30	1247	1215	1280
Year	1296	3	52.35	1240	1213	1268
None (null model)	1296	2	154.47	1310	1270	1352
Other sites (within 800m from shore)						
None (null model)	703	2	0.00	678	638	720
Cluster-size	703	3	5.10	654	634	676
CC	703	3	6.42	652	632	673
Species	703	3	6.57	651	630	672
SS	703	3	6.59	652	631	673

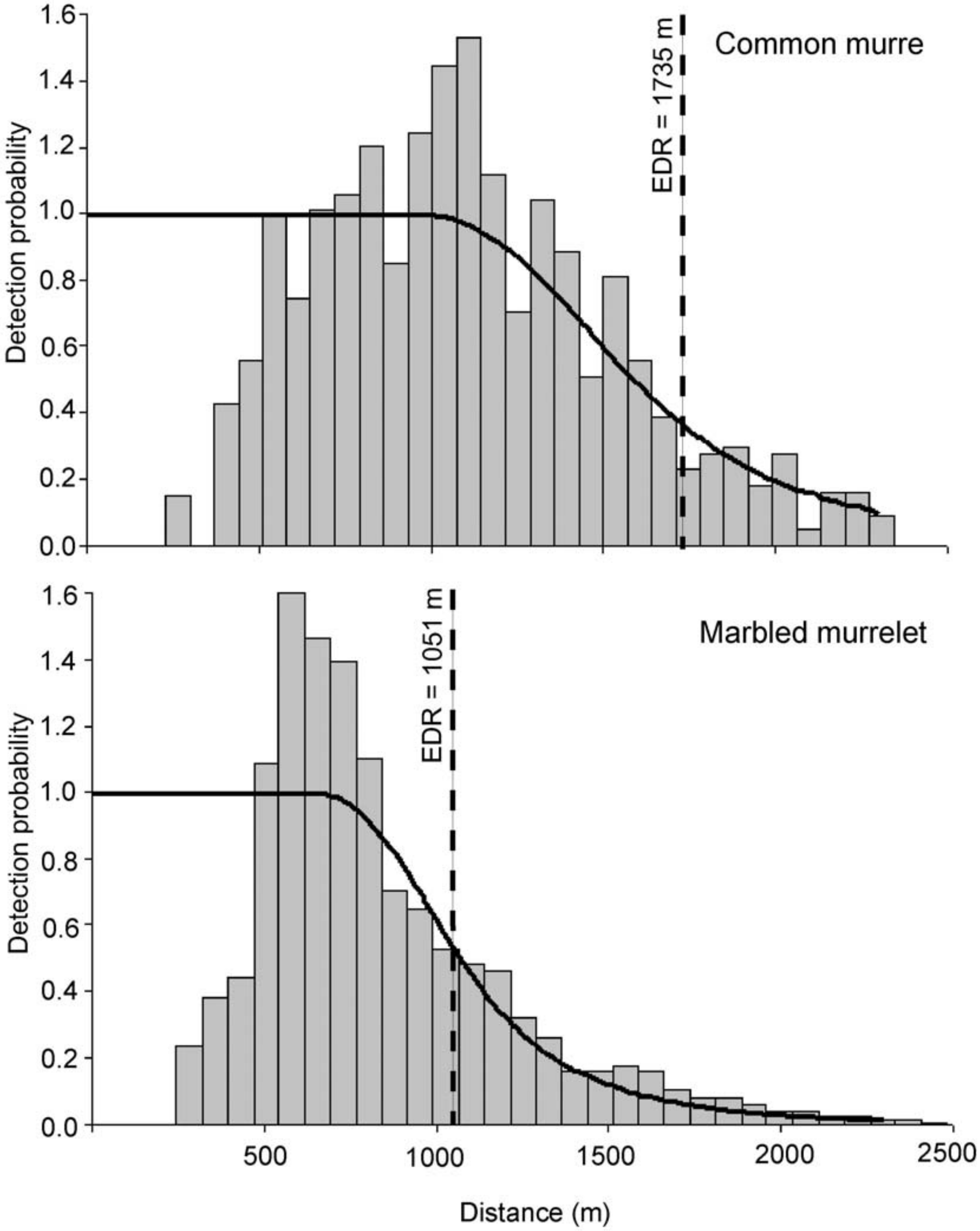

Figure A.2 - The estimated MCDS detection function for marbled murrelets and common murres mapped with digital theodolite in Carmanah Bay 2004 and 2005.
Figures based on the best models (lowest AIC value) and averaged over the observed covariate values for cloud cover. The detection function is superimposed over the histogram of observed distances, which have been scaled to adjust for increasing area surveyed at increasing distances from the survey point. EDR = effective detection radius.

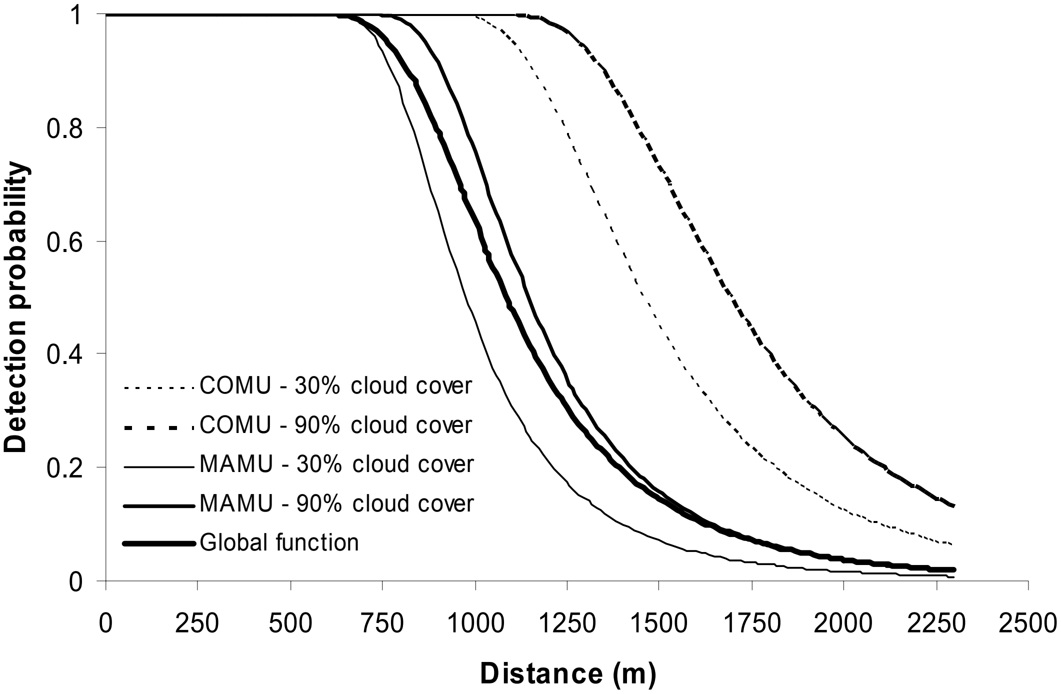

Figure A.3 - Estimated MCDS detection functions at Carmanah Bay for marbled murrelets (MAMU) and common murres (COMU) with % cloud-cover as a covariate.

Functions based on the best model (lowest AIC value) from along-shore detection functions.

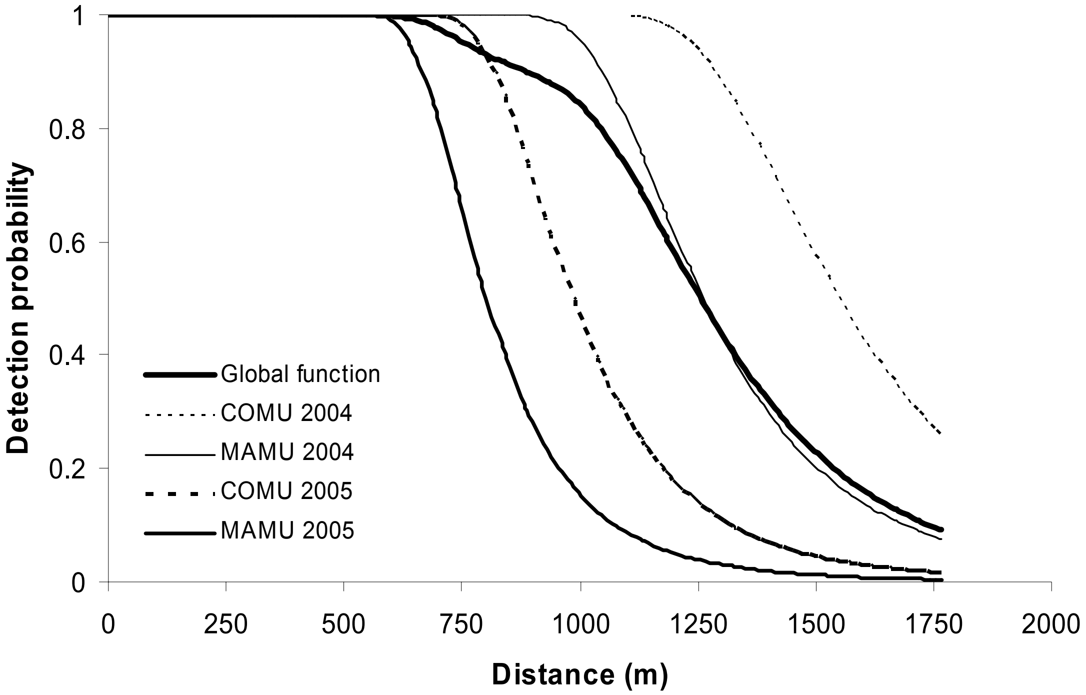

Figure A.4 - Estimated MCDS detection functions at Pachena Point for marbled murrelets (MAMU) and common murres (COMU) with year as a covariate.

Functions based on the best model (lowest AIC value) from along-shore detection functions.

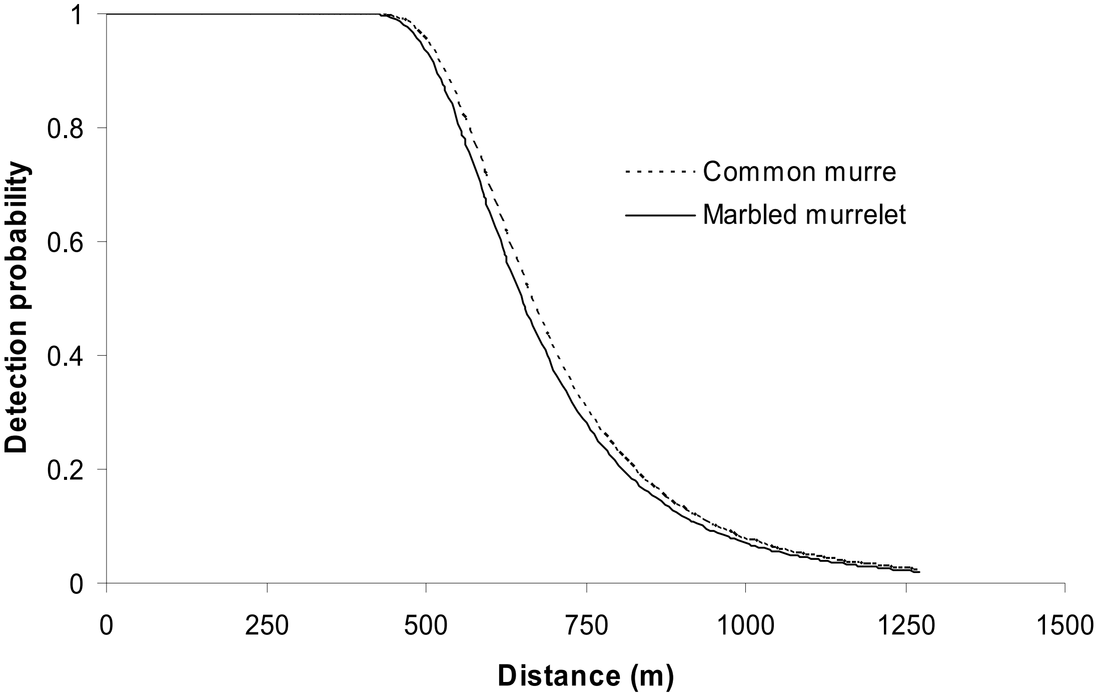

Figure A.5 - Estimated MCDS detection functions at other sites (other than Carmanah and Pachena) for marbled murrelets and common murres as covariates.

Note the lack of species effect because the null model (no covariates) was the best model (lowest AIC value) from along-shore detection functions.

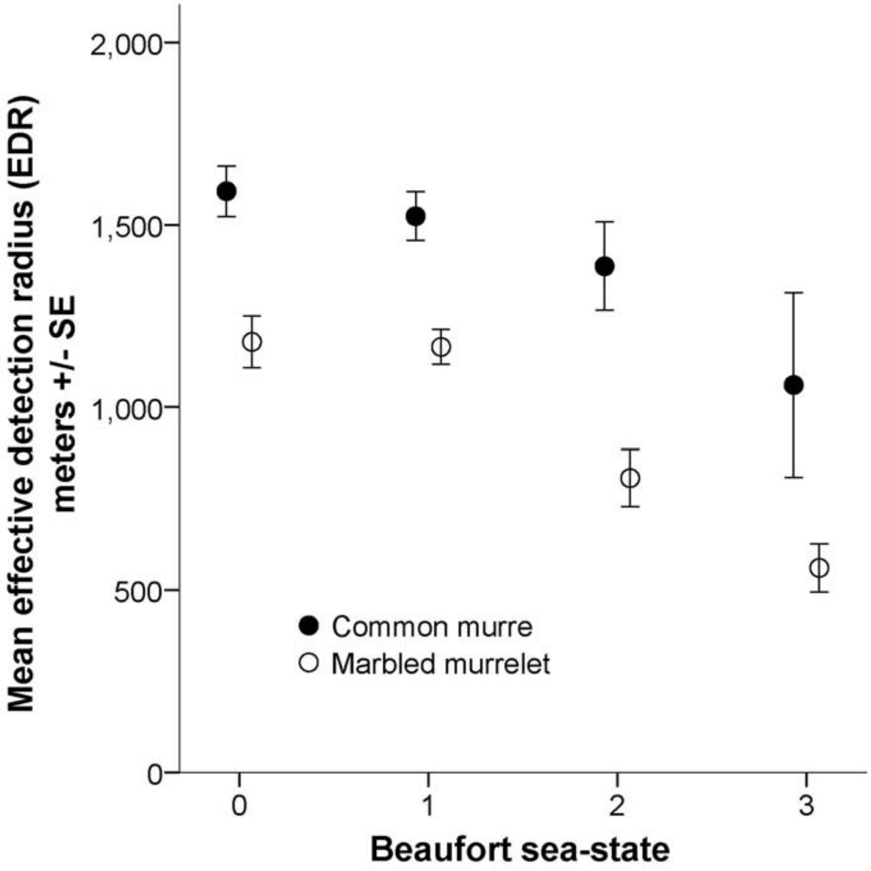

Figure A.6 - Effects of Beaufort sea-state on the detectability of murrelets and murres mapped by theodolite.