Foraging behavior and productivity of a non-colonial seabird, the marbled murrelet (*Brachyramphus marmoratus*), relative to prey and habitat

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ABSTRACT

For seabirds, resource limitations may be most severe during the breeding season, when birds are aggregated and energetic costs high. Nonetheless, 98 % of seabird species are colonial, which has been partly attributed to the demands of foraging in a dynamic marine environment. Little is known about behaviors and resource limitations for the few non-colonial species. I studied the foraging behavior and breeding success of the marbled murrelet (*Brachyramphus marmoratus*), a non-colonial seabird that is widely dispersed throughout the North Pacific. My study site in Prince William Sound (PWS), Alaska, is the northernmost population center for marbled murrelets, but they have declined there since the 1970s. Poor reproductive success due to lack of food was proposed as a reason for their decline, but murrelets were also hypothesized to be adapted to low prey densities. I investigated murrelets to determine if their responses to temporal and spatial changes in prey abundance were indicative of food limitation. I used telemetry to monitor foraging movements and habitat use of individuals, and at-sea surveys or land-based observations to determine prey use, foraging behavior, and reproductive success. Aerial surveys and boat-based sampling provided data on distribution and relative abundance of forage fish.

Murrelets in PWS foraged an average of 16 km from their nests and individuals showed forage site fidelity. This suggests that murrelets learned local patterns of prey availability. Murrelets selected waters < 30 m deep, although at a deep water fjord, they used sites of upwelling rather than travel far to access shallow waters. Ninety percent of their diet was Pacific herring (*Clupea pallasi*) and Pacific sand lance (*Ammodytes hexapterus*), and there were consistent site-specific patterns of prey use that coincided with the spatial distribution of fish species. When obtaining chick meals, murrelets selected larger prey (81-135 mm, 1+ age class) than when self-feeding (< 80 mm, 0+ fish), and selected fish of high caloric value, consistent with an optimum foraging strategy for central place foragers. Large, high-caloric fish were captured as meals for chicks near twilight hours by solitary adults, and their availability may be a limiting factor for murrelets. Self-feeding murrelets were more flexible; when fish were abundant, murrelets usually foraged individually or in pairs, but as fish abundance decreased, they foraged in larger groups.

During this study (1995 – 1999, at three sites), fish abundance generally increased, yet the density of juvenile murrelets at sea declined. Concurrently, the ratio of juveniles to adults was relatively stable, suggesting that the decline in adult numbers, and not breeding failure, was the cause of lower recruitment and population decline. Alternatively, the stress of raising chicks contributed to reduced annual survival of adults. In support of this scenario, average adult body mass of murrelets in summer decreased between the 1970s and 1990s. Declines in herring stocks during this period may have been a contributing factor. Productivity was more strongly linked to site than to annual fish school density. I propose that local marine characteristics that affect fish species, abundance, and availability for birds are key factors in murrelet nesting distribution in PWS. These results have implications for the monitoring of murrelet populations, as well as their management and conservation.

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INTRODUCTION

It was through observation of seabirds that Ashmole (1963) formulated his theory that population regulation occurred through density-dependent processes, when animals were aggregated and constrained. Resource limitations were presumably most severe during the breeding season, when as central place foragers feeding chicks, birds were aggregated and energetic costs were high. The temporal and spatial concentration of birds could potentially deplete prey near the colony, or lead to interference competition. There are other potential detriments to nesting colonially, including competition for nest sites, extra-pair copulations, and parasite infestations (Birkhead and Furness 1985, Wittenberger and Hunt 1985). Nonetheless, the majority of seabird species evolved as highly colonial nesters (Ricklefs 1990). The prevalence of this behavior has in large part been attributed to the demands of foraging in a dynamic marine environment while raising chicks on land. Our knowledge of seabird ecology is largely based on colonial seabirds, and little is known about life history traits, behavior, and resource limitations of non-colonial species.

I studied the foraging behavior and breeding success of the non-colonial marbled murrelet (*Brachyramphus marmoratus*) which occurs throughout the eastern North Pacific and nests primarily in old-growth trees from central California to Alaska. My study occurred in Prince William Sound (PWS), Alaska, which has the northernmost substantial population of this species (Nelson 1997), and where marbled murrelets are the most abundant breeding seabird (Agler et al. 1998). One hypothesis for the numerical dominance of marbled murrelets in portions of their range is that they appear well adapted to foraging on small, dispersed schools of fish (Carter and Sealy 1990, Ostrand et al. 1998). Presumably, this has allowed murrelets to nest solitarily, and subsequently they are less subject to density-dependent limitations associated with colonial nesting. However, marbled murrelets have declined in PWS since 1972. Because other piscivorous birds have declined (Agler et al. 1999) and there have been shifts in the food web of the Gulf of Alaska since the 1970s (Anderson and Piatt 1999), changes in prey type or abundance could be a factor.

The foraging behavior and breeding success of murrelets has not been well studied because of the difficulties in tracking individuals, particularly at their nests. In this study, I used telemetry to monitor foraging movements of individuals and habitat use, and at-sea surveys to address the hypothesis that this non-colonial bird is not limited by food. I incorporated related studies of forage fish abundance within and among years and sites. My study asked four questions: 1) Do murrelets fly farther to access sites with more abundant prey, and do they show forage site fidelity? 2) Do murrelets alter foraging behavior and prey use with respect to habitat, prey abundance or self vs. chick feeding? 3) Is it possible to determine annual or spatial differences in murrelet productivity, when researchers must rely on at-sea surveys and there are no central breeding locations? 4) Does productivity of a widely dispersed, non-colonial bird respond to temporal or spatial variation in prey abundance?

For the first question, radio telemetry was determined to be the only means to follow individual birds, because of the lack of known nest sites and unknown foraging distances. At the time these studies began

(1993-1994), little was known about the foraging behavior of murrelets, particularly the movements of individual birds. My study was designed to test the hypothesis that murrelets nesting in a resource-poor area would fly farther than birds in a resource-rich area to access more abundant prey. Birds in a resource-poor area should incur energetic costs which would be expressed in lower murrelet productivity, thus supporting the hypothesis that murrelets were food limited. In PWS, forage fish abundance tends to be lower in the deep water fjords than more exposed coastline or areas with shallow sills or underwater shelves (Brown et al. 1999, Norcross et al. 2001). I captured birds in three locations with different habitat characteristics and radio-tagged 51 murrelets with brood patches (indicative of breeding) to track their foraging locations relative to capture location or suspected nest sites.

In Chapter 2, I examined interannual and spatial differences in diet and foraging behavior of murrelets, which might indicate resource limitation. I focused on two study sites with different habitat characteristics and conducted at-sea surveys and land-based observations of murrelets. At this point, my study became a component of the Alaska Predator Ecosystem Experiment (APEX; Duffy 1998), which provided data on prey species composition, distribution, and abundance. This allowed me to examine murrelet group size, diving patterns, and prey selection for birds self-feeding and those foraging for their chicks. By conducting the observations over three years (1997 – 1999), I was able to test for temporal as well as spatial aspects of murrelet behavior.

Monitoring murrelet abundance and productivity has proven a challenge (Burger 2002, McShane et al. 2004) and remains so a decade after my project began. Chapter 3 addresses the question of whether it is possible to detect change in murrelet abundance and productivity, when there are no central breeding sites on which to focus and researchers must rely on at-sea surveys. What parameters, and what sampling scheme, will give you the best power to monitor trends? While radio telemetry may provide more concise data on a limited number of birds (Bradley et al. 2004, Peery et al. 2004), it is not likely to be used for long-term monitoring, particularly in remote areas with difficult access, such as much of Alaska (where an estimated 90 % of the world population of murrelets breed [McShane et al. 2004]). My goals in this chapter were to assist in the design of future monitoring efforts, and specifically for PWS, to know how best to use at-sea data to examine questions related to murrelet productivity. To do this, I worked with co-author Shay Howlin and used data I collected at three sites over four years (1995, 1997 – 1999). From the original data, we generated 2000 datasets and simulated the effect of variable sampling effort and sampling time frame on the detection of site and year differences for three dependent variables: adult density, juvenile density, and juvenile:adult ratios. I also used the original data to estimate power to detect changes under four different management goals, using the TRENDS program (Gerrodette 1993).

As one of the few non-colonial seabirds, and one with a broad breeding dispersal, the marbled murrelet is uniquely suited to address the question of food limitation independent of the effects of colonial nesting. In Chapter 4, I asked whether the productivity of a widely dispersed, non-colonial bird varied with respect to temporal or spatial variation in prey abundance. My study sites were fairly large (~ 50 km of shoreline) and oceanographically diverse, yet subject to the same large-scale influences of a well-defined ecosystem (Niebauer et al. 1994, Brown 2003). This allowed me to examine murrelet productivity and fish abundance at a scale relevant to murrelet ecology. At three sites I used four years of data (1995, 1997 – 1999) on murrelet productivity and prey abundance to examine annual and site-specific patterns of both independently, and their interactions. Because seabird breeding chronology is often closely linked to prey availability and seabird reproductive success (Vermeer 1980, McGowan et al. 1998, Bertram et al. 2001, Abraham and Sydeman 2004), I also examined annual and site-specific patterns in chronology, using at-sea counts of juveniles. Marbled murrelets are considered asynchronous in timing of nesting, and this has been attributed to their solitary nesting habits (Nelson 1997, Gaston and Jones 1998), but the influence of environmental factors on their chronology has not been well described.

Study of a species' foraging ecology and productivity should be interpreted within the context of population trends (Russell 1999). The murrelet has undergone drastic changes in abundance throughout its range, and is federally listed in Canada (Burger 2002) and the United States (McShane et al. 2004). Although not listed in Alaska, the marbled murrelet has declined in PWS (Lance et al. 2001). Marine birds in PWS were monitored by the U.S. Fish and Wildlife with support of the *Exxon Valdez* Trustee Council, and at-sea data from 1972 and 1989-2004 (9 survey years) were available to track population trends. These data had not been fully examined specifically for the marbled murrelet since the 1996 survey (Agler et al. 1998), in part because of annual variability in species identification between marbled and Kittlitz's murrelets (*B. brevirostris*). To address the problems in interpreting trends for marbled and Kittlitz's murrelets, I worked with biometricians Bryan Manly and Chris Nations. We applied a model-based technique that incorporated unidentified *Brachyramphus* murrelets into an evaluation of population trends for each species. This effort is included as an appendix, because of its relevance to the dissertation.

In Chapter 5, the results and conclusions of the four chapters are synthesized to address how prey, foraging, and productivity interact in the ecology of a non-colonial seabird, with a focus on the importance of spatial, as well as annual variability. I also address the implications to management and conservation efforts for a widely dispersed, solitary nesting seabird. The chapters and appendix were prepared for journals, and thus include co-authors involved in each.

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CHAPTER ONE

FORAGING RANGES AND HABITATS USED BY RADIO-TAGGED MARBLED MURRELETS IN PRINCE WILLIAM SOUND, ALASKA

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ABSTRACT

We studied foraging patterns and marine habitat use of radio-tagged marbled murrelets (*Brachyramphus marmoratus*) in Prince William Sound (PWS), Alaska. In 1993 and 1994, we tracked 56 birds and recorded 288 locations during 36 aerial searches from June through August. We used aerial relocations for 51 birds with brood patches to determine foraging distances per bird, six with potential nest sites. Mean distances from suspected nests to locations at sea were 16 km (SE = 5, max = 31) straight-line and 21 km (SE = 6, max = 40) over-water. For all birds, average straight-line distances were 10 km from capture site (likely near nesting areas) to relocations (max = 81 km each way). There was little overlap in foraging areas among birds tagged at three sites, and relocations for individuals usually clustered in a 5 km radius. We found no significant differences in foraging distances among birds from different sites, despite different oceanographic surroundings; a shallow fjord, a deep fjord, and an island surrounded by shallow water. Murrelets usually foraged near shore, in protected waters, and at two sites they selected for shallow waters. At the deep fjord, murrelets also foraged in waters > 200 m deep, but within 2 km of underwater sills or shelves. These were likely sites where upwelling concentrated prey. Our results suggest that marbled murrelets in PWS tend toward forage site fidelity, and generally do not travel great distances when breeding. Such behavior is consistent with their solitary, dispersed nesting habits and the distribution of fish in PWS.

INTRODUCTION

Seabird foraging patterns have primarily been described for colonially nesting species (Birkhead and Furness 1985, Hunt et al. 1999), and little is known about foraging patterns in relation to nest sites for non-colonial seabirds. Marbled murrelets (*Brachyramphus marmoratus*) are a non-colonial auk and may be the ultimate expression of Diamond's (1978) observation that nearshore feeders tend to have small, scattered colonies. In the eastern North Pacific, marbled murrelets are one of the most widely dispersed breeding seabirds. These murrelets nest solitarily and are distributed from central California to Alaska in habitats that differ considerably in their terrestrial, coastal, and marine characteristics (Nelson 1997). Although they are non-colonial, they are still subject to the energetic constraints of raising chicks as central place foragers, just like other seabirds. Because they are dispersed along an array of habitats, they might be expected to exhibit different foraging patterns throughout their range, or even within a region. Indeed, telemetry studies have shown considerable intraspecific variability in foraging ranges and habitats used by breeding marbled murrelets (Whitworth et al. 2000, Hull et al. 2001).

The variability in foraging distances exhibited by marbled murrelets may be partly explained by their nesting habits, since nests have been documented from < 1 km to > 60 km inland, primarily in trees (Nelson 1997). The distances from sea to inland nests of marbled murrelets are equivalent to the foraging ranges of other seabirds that nest on the coast. For example, terns and cormorants normally forage within 10 – 18 km from their colonies, whereas gulls, kittiwakes and murres may forage 60 -100 km (Coulson 2002). In Prince William Sound (PWS), Alaska, the 21 murrelet nests found to date have all been < 6 km from the sea, and the steep topography and low tree-line may restrict murrelets to relatively near shore nest sites. With the distance from nest to water relatively minimal, foraging distances in PWS might be more directly influenced by local marine habitat types.

In PWS, marbled murrelets are the most abundant seabird in summer (Agler et al. 1998). Here they nest primarily in old-growth conifers, although a small portion nest in cliff crevices or under alders (*Alnus* spp) (Kuletz et al. 1995a). Murrelets, which feed primarily on small fish, are typically associated with nearshore, relatively shallow waters (Carter and Sealy 1990, Ostrand et al. 1998, Day and Nigro 2000). In contrast, much of PWS is characterized by deep, fjord-type systems. In PWS, deep fjords tended to have fewer seabirds than other areas and were presumed to have generally lower fish availability (Irons et al. 1988). Later studies confirmed low fish abundance in deep fjords of PWS (Brown, et al. 1999), and a similar spatial pattern was found in Glacier Bay, Alaska (Robards et al. 2003). From previous work, however, we knew that activity of murrelets inland at dawn, indicative of nesting, was high in some PWS fjords (Kuletz et al. 1995a, Marks et al. 1995). Presumably, there would be energetic costs incurred by breeding birds that had to commute long distances from the fjord uplands to good forage areas.

Forage fish abundance and their availability to seabirds are influenced by oceanic and bathymetric features (Hunt et al. 1999), and Ostrand et al. (1998) showed that murrelets in PWS selected for fish schools in shallow water. We therefore hypothesized that birds nesting near a deep fjord would have to fly farther between nest and forage sites, than birds nesting near shallow water areas. In this study, we compare the foraging distances traveled and habitats used by radio-tagged murrelets that we caught in oceanographically distinct habitats - a relatively shallow water fjord, a deep water fjord, and shallow water surrounding an island. Additionally, we describe the foraging habitats used by radio-tagged murrelets in PWS. This region has high densities of marbled murrelets (Agler et al. 1998) and it represents the northernmost extension of their breeding range. Our results contribute to the sparse information on the daily foraging patterns of a non-colonial seabird.

METHODS

Our study was conducted in Prince William Sound (PWS), a fjord-type embayment in the northern Gulf of Alaska. Capture sites included Unakwik Inlet (Unakwik), Port Nellie Juan (Nellie Juan) and Naked Island (Naked) (Fig. 1). Unakwik has a maximum water depth of 308 m and a 2 m deep glacial sill mid-way up the channel, with side bays and a terminal, tidewater glacier. Nellie Juan has a tidewater glacier at its terminus, and a maximum water depth of 750 m, with depths of 200 m common near shore. Naked and nearby Storey and Peak islands are surrounded by water < 30-50 m deep within 1 km of shore and < 200 m deep out to about 5 km. During our surveys, average sea surface temperature ranged from 13.0 ^{0}C at Nellie Juan to 14.8 ^{0}C at Naked. Waters in the two fjords were less saline (13.6 ± 1.3 psu) and more opaque (Sechi depth = 6.6 ± 0.6 m) than at Naked (24.8 ± 1.0 psu and 9.7 ± 0.4 m, respectively).

The study areas differed in potential nesting habitat for murrelets. Unakwik had forested hills to 700 m elevation near the mouth, but barren slopes to 2,800 m near the head of the bay. Nellie Juan had mountains to 1700 m and few sections of forested habitat, which ended at 300 m. At the Naked group, the highest peak was 400 m and the islands were forested to their summits. Marbled murrelets were the most abundant seabird on the water around all three study sites, and inland activity at dawn indicated that murrelets were nesting near each capture site (Kuletz et al. 1995a, Marks et al. 1995).

Data collection

We caught birds using floating mist-nets (Burns et al. 1995) at (Fig. 1) Siwash Bay in Unakwik (14-17 July 1993), and East Finger Inlet in Nellie Juan, and Cabin Bay at Naked (3 June - 4 July 1994). We set nets between 1 hr before sunset (around 22:00 Alaska Standard Time [AST]) and 2 hr after sunrise (around 05:00 AST). We anesthetized captured birds with the inhalant Isoflurane, attached a transmitter with an absorbable suture through the skin between the scapula, and anchored it to the feathers with marine epoxy. Radio-transmitters were model Holohil BD-2G (Holohil Systems Ltd., Woodlawn, Ontario, Canada), with a 15.6 cm antenna, weight of ≤ 2.0 g, and battery life of 6 weeks. For details see Burns et al. (1994) and Kuletz et al. (1995b). Dive times were similar between tagged and untagged murrelets, and relative use of marine areas by tagged birds was similar to the distribution of untagged murrelets (Kuletz et al. 1995b). We therefore considered the behavior of these tagged birds to be representative of PWS murrelets.

To track murrelets, we used Telonics TR-2 and ATS receivers with directional two-element Yagi antennas. We conducted air searches on 10 days (41 hr) between 18 July and 25 August 1993 and on 26 days (122 hr) between 4 June and 28 July 1994. We used a Cessna 185 float-plane equipped with one antenna on each wing for selective monitoring. Half of the air searches began after 16:00 hr and 76% of the relocations were made between 16:00-20:00 hr; this time corresponds to when birds might be diving to provision chicks (Nelson 1997, Chapter 2). We considered our relocations to be independent, since aerial search effort was sporadic throughout the summer and resightings were usually separated by several days. Based on concurrent at-sea surveys (Kuletz and Kendall 1998, Chapter 4), we obtained telemetry data in the mid to late nestling phase in 1993, and during the incubation and early nestling phase in 1994.

Search flights began in eastern PWS and we searched en route to Unakwik, Naked, and Nellie Juan, and then spiraled out from core sites to other areas of PWS. In 1993, we also searched the coast southwest of PWS (Burns et al. 1994). Cruising altitude was 500 - 1700 m, weather-dependent. The maximum signal range detected from an altitude of 1300 m was 17 km. Nearshore waters required closer surveillance than open waters, due to the convoluted coastline and mountainous terrain.

When a signal was detected, the pilot flew a 'box formation' to pinpoint the location, which we recorded on a nautical chart along with the coordinates. We confirmed the accuracy of aerial relocations by occasionally landing the plane to confirm the bird's presence, and by ground-tracking 11 stationary signals. If a signal was on land, a ground crew searched with a hand-held antenna to within ~ 100 m of the signal. Because we did not wish to disturb nesting birds, we confirmed only one of the six potential nests. We monitored inland signals from land-based and boat-based platforms, and mapped them with a Global Positioning System. We defined incubation activity as three consecutive days of alternating (inland vs at sea) 24 hr schedules (Nelson 1997).

Mist nets were located where birds were funneled from the head of a bay with upland nesting activity toward open water, and nets were set between dusk and dawn, when murrelets visit nesting areas (Nelson 1997). Thus, for birds with brood patches, we assumed that the capture site was in the vicinity of the bird's nest.

Treatment of telemetry data

Telemetry relocations were digitized into a geographic information system (GIS; [Atlas GIS 1992]). For most analyses we used only high accuracy locations, which were those signals we circled repeatedly and mapped on-site. When examining individual site fidelity we included locations that could not be pinpointed, and we included the three birds without brood patches (which were omitted from other analyses). We used GIS to measure distance between locations and the area (km^2) encompassed by the locations. Murrelets may fly over ridges and passes during crepuscular nest visits (Nelson 1997, Burger 2001), and because relocations were separated by at least one night, we measured both straight-line distance between locations (regardless of topography) and over-water distances (the shortest route over water only). Over-water distances from nests included a straight-line segment from nest to water, which ranged from 1.5 to 6.0 km.

For each bird we determined: distance between capture site and each relocation; distance between consecutive locations ≥ 1 day apart (if a bird was found twice on the same day, we used the afternoon relocation); maximum distance between any two locations. For birds with ≥ 4 locations, we obtained a minimum area polygon. To minimize the effect of two unusually large distances, for two birds we excluded an outlier > 2 times the average maximum distance for all birds. Thus the polygons reflect a conservative estimate of total area covered by each bird, but it also minimized the potential for overestimating the foraging ranges of birds from nest areas. We think this was justified because the unusually long distances were final locations before losing the bird, suggesting they did not return to the area. For six birds with potential nest locations, we determined the distance between nest and each location at sea, and the minimum area polygon both with and without the nest location. We considered a cluster of locations within a 5 km radius an 'individual forage site' (based on frequency distribution of consecutive relocations for all birds). We used the number of individual sites, and visits per site relative to total locations for the bird, to examine forage site fidelity. Maps depicting these relocations for each bird are available in Burns et al. (1994) and Kuletz et al. (1995b).

We tested for differences among birds at the three sites using the mean distance (separately for each type of distance measure) for each bird and Kruskal-Wallis rank sum tests. For two-way comparisons we used a Wilcoxon test or paired *t*-test, as appropriate. All means are presented ± SE. For minimum area polygons, we also provide the 95% confidence interval (CI). Statistical analyses were done with SAS (SAS Inst. 1988) or S-PLUS (MathSoft, Inc. 1998). Significance was set at alpha = 0.05.

Characterization of foraging habitat.

We measured distances between each relocation and the nearest land (including islands) with GIS, and used the mean distance offshore for each bird for subsequent analyses. We determined mean water depth used by each bird by overlaying relocations on GIS bathymetric coverage (developed from National Oceanographic and Aeronautical Administration data and nautical charts). We calculated weighted average water depth in a 100 m radius around each location, using the midpoint of the following depth categories: 0-20 m, 21-40 m, 41-60 m, 61-80 m, 81-100 m, 101-120 m, 121-200 m, and $\geq$ 200 m. True depths in areas with water > 200 m deep were thus underestimated.

When birds were located, we could determine if birds were sitting on the water (as opposed to flying through) by circling the area of the signal. We assumed that birds located on the water were foraging or had foraged in that location. We defined availability (in surface km^2) of water depths in each of five geographic sub-areas. Sub-areas were defined by geographic features and distribution of 98% of bird relocations (Fig. 1). In addition to Unakwik, Nellie Juan, and Naked sub-areas, we included two sub-areas combined (Perry and Knight), because these areas were used by birds from all sites. For each sub-area, frequency of use of depth classes was determined by summing observations (assumed independent; see above) in each depth class for each bird and tallied across birds. We used Chi-square tests to compare the number of observations in each depth category vs expected distribution of birds across depth strata (using surface area in km^2 of each strata). To keep expected values (number of bird locations) per cell $\geq$ 5 (Sokal and Rohlf 1981), we combined depth categories into: 0-40 m, 41-80 m, 81-200 m and > 200 m.

RESULTS

Capture and tracking

In 1993 we caught and tagged nine marbled murrelets and in 1994 we caught 51 murrelets (37 in Nellie Juan, 14 at Naked), of which we tagged and tracked 46. No birds were captured twice. We assumed that birds with brood patches had initiated nests, although a brood patch may remain after nest failure and prior to a re-nesting attempt (McFarlane-Tranquilla et al. 2003). Three of the tagged birds lacked brood patches and these were not included in most analyses of distances (Kuletz et al. 1995b). In 1993 we located on average 67% of the murrelets each day from the air. In 1994 we located an average of 26% of the murrelets each day for 30 days, but lost contact with most birds by mid July. During the last 35 days (2

July - 7 August) we averaged five murrelets per day. On average we located each bird 9.4 ± 1.0 and 8.9 ± 7.3 days in 1993 and 1994, respectively. Time between tagging and last relocation averaged 16.3 ± 2.4 days (maximum 26 days), and 14 ± 1.3 days (maximum 32 days) in 1993 and 1994, respectively. We made 288 aerial relocations of birds, with 253 of those considered high-quality, of which 56, 157, and 40 relocations were for birds from Unakwik, Nellie Juan, and Naked, respectively.

Foraging distances

Distances from nests. Of the located probable nests, all in Nellie Juan, three were within 1 km of each other, in trees 1 km inland at the head of East Finger Inlet, the capture site. The remaining three were ground or cliff nests, 0.5, 2.3, and 5.7 km inland in treeless, steep terrain. We confirmed one cliff nest (Kuletz and Marks 1997). These six birds were caught 3.0 - 13.8 km from their nests (mean = 7.8 ± 2.1 km).

Mean straight-line distance from the potential nest to all relocations for the six birds was 16.2 ± 4.6 km (median = 11.9) and mean over-water distance was 20.9 ± 5.6 km (median = 15.0). The bird with the greatest mean forage distance from its nest averaged 31.4 km straight-line and 40.1 km over-water. All six birds foraged in the middle portion of Nellie Juan, and three were also found outside the fjord prior to relocation back in the fjord. The longer trips included one-way distances of 36 km to Perry Island, 60 km to Storey Island, 55 km to Knight Island and 28 km midway to Perry Island. The minimum area polygon for these six birds varied considerably (mean = 119 km^2, 95% CI = 15 - 223 km^2). The inland location always formed an outer point of the polygon, and omitting it decreased the minimum area polygon by 57%, to a mean of 51 km^2 (95% CI = 14 - 89 km^2).

Distances from capture sites and total area used. We found no significant differences among birds from Unakwik, Nellie Juan, and Naked in forage distances (Table 1). There were fairly distinct zones of use among birds caught in different areas (Fig. 1), because most relocations were within 17 km of the capture site (Fig. 2A). Average distance from capture site was not affected by the number of days a bird was tracked ($n = 51$ birds, $R^2 = 0.01$, $P = 0.45$) nor with total number of relocations ($n = 51$ birds, $R^2 = 0.05$, $P = 0.10$). The waters near islands mid-way between Naked and Nellie Juan were visited by three birds from Naked and seven from Nellie Juan. Four birds went to southern PWS (Fig. 1), but only one of those returned to its capture site, making the longest round-trip of 162 km. A bird that was relocated 91 km from its capture site was not subsequently relocated. For 40 birds lost before our tracking efforts ended, their final relocations were farther from the capture site than the mean of their previous relocations (paired t-test; $t = 2.4$, df = 39, $P = 0.02$). However, removing these final relocations for each bird did not significantly alter the mean distance from capture site for the population (mean = 16.0 km ± 1.8, median = 12.3 km).

Minimum area polygons for 33 birds averaged 143 ± 37 km^2 (95 % CI = 68 – 219 km^2; median = 77 km^2). The median polygon size was smaller for Naked birds (28 km^2) than for Nellie Juan (91 km^2) or

Unakwik birds (62 km^2), but variance among individuals was high, and these differences were not statistically significant.

Distances between relocations. Birds from different areas did not differ significantly in distances between consecutive relocations separated by $\geq$ 1 day (Table 1). In most cases, birds were < 10 km from their previous location (Fig. 2B), and 43% of relocations were < 5 km from the previous location. The greatest distance between consecutive daily locations was 79 km. Movement within a day was much less; for birds located on morning and afternoon flights on the same day, mean over-water distance between relocations was 4.7 $\pm$ 1.2 km (n = 8 birds; range = 0.7 - 8.8 km).

Of the 53 birds with multiple relocations, 44 made repeat visits to individual forage sites (within a 5 km radius); these visits comprised 70% of total relocations per bird, on average. In fact, most of the locations within a bird's individual forage site were within 2 km of each other (71%, range 33 - 100%; see Fig. 2), even when separated by up to 27 days or visits to other sites. Nineteen birds also made repeat visits to a second site (16 - 50% of total relocations per bird), but only one made repeat visits to a third site. The number of repeat visits to the primary individual forage site was strongly correlated to the total number of relocations (Fig. 3; $n = 44$ birds, $R^2 = 0.68$, $P < 0.01$). The correlation between repeat visits to a secondary site and total number of relocations was not as strong, but still significant ($n = 19$ birds; $R^2 = 0.48$, $P < 0.01$).

Forage habitat

Radio-tagged birds were located a mean of 0.6 $\pm$ 0.6 km offshore, and distance offshore did not differ by area or year (Kruskal-Wallis $X^2 = 0.17$, df = 2, $P = 0.92$). For all relocations, 68% were within 0.5 km of shore, 16% were 0.6 - 1.0 km offshore, and 16% were > 1 km offshore. Birds located within the Nellie Juan sub-area (regardless of origin of capture) used depth classes proportionate to their availability, but birds in other sub-areas (Naked, Unakwik, Perry-Knight) used shallow areas more than expected (Table 2). In Nellie Juan, 40% of locations were in waters > 200 m deep, whereas at other sites combined, 9% of locations were in this depth category. Average depth used by birds varied significantly among areas (Kruskal-Wallis $X^2 = 6.2$, df = 2, $P < 0.05$), and was deepest by birds from Nellie Juan (n = 26 birds, mean = 115 $\pm$ 11 m, median = 90 m), followed by Unakwik birds (n = 9 birds, mean = 61 $\pm$ 19 m, median = 52 m) and Naked birds (n = 10 birds, mean = 52 $\pm$ 10 m, median = 44 m).

At Unakwik (Fig. 4A), areas visited by the most birds included the upper inlet (six birds), Siwash Bay in the fjord (six birds) and Olsen Island near the mouth of the fjord (four birds). Birds found more than a few hundred km from shore were near shallow sills, over underwater ledges or in protected bays of < 20 m depth. At Naked (Fig. 4B), tagged birds also tended to use shallow or protected bays, and none used the equally shallow but exposed shoreline on the east side of the island. In Nellie Juan (Fig. 4C), most tagged murrelets were at some time found along the edges of the main channel or in side bays. The site visited by the most birds, however, (16, including two from Naked) was near a bend in the fjord, above an underwater shelf near Elbow Island. There were also three bands of murrelet activity that stretched across the Nellie

Juan channel; these were either about 2 km from a deep water sill, or a bend in the channel, or near the inlet's mouth (Fig. 4C). Only Nellie Juan birds were found in the bays along the mainland and northwest side of Knight Island, south of Nellie Juan. One of these bays, Main Bay (Fig. 1), is the site of a fish hatchery, and was visited by five Nellie Juan birds. Thus, birds traveling far from their capture site still tended to use nearshore areas of protected or shallow bays (Fig. 1).

DISCUSSION

Foraging distances.

Foraging distances for these PWS murrelets were similar between years and among study sites, with most trips < 20 km over-water (median = 15 km) from the nest or capture site. We had hypothesized that, because murrelets tend to associate with shallow waters (Ostrand et al. 1998, Day and Nigro 2000), birds from the deep fjord (Nellie Juan) would fly farthest to forage. However, the birds from Nellie Juan, including those with potential nests, didn't vary from other birds in their at-sea locations relative to capture site or other measures of foraging range. Murrelets appeared to use a greater range of habitats within Nellie Juan (Table 2), rather than travel farther to access shallow waters (Table 1). Individual variation was considerable, with individual mean distances for the entire tracking period ranging from 10 to 40 km; this variability could have masked local effects on foraging distances, given the small sample size at two of the three study sites.

Our results were similar to those of other studies regarding marbled murrelet foraging in terms of straight-line distance from capture to forage sites (approximately 10 km in British Columbia; R. B. and L. P., unpubl. data) and the over-water distance between consecutive locations in southeast Alaska (< 10 km; Quinlan and Hughes 1992). Distances were also similar to those found for murrelets at sea relative to a nesting area in California (10 km; Ainley et al. 1995). In contrast, however, nine murrelets radio-tagged in southeast Alaska traveled an average 78 km from suspected nest sites (Whitworth et al. 2000). Similarly, 23 radio-tagged murrelets traveled an average 39 km from nest sites in British Columbia (Hull et al. 2001). These latter studies also reported large differences among individuals, and it is apparent that at least some birds in all regions where radio-tracking has been conducted travel > 80 km between nest and forage sites. Individual variation within regions may be greater than variation among regions, but more data will be required to test this.

Despite some similarities in flight distances among studies, overall the average and median distances from nest to forage site or between forage sites, indicated that murrelets in PWS travel less than half the distances as birds do farther south. It is possible that we did not locate birds foraging outside PWS, but we did search the outer coast to the southwest without finding birds (Burns et al. 1994). Furthermore, because the last location of individuals was significantly farther from the capture site than its previous locations, it suggests that those birds had completed or abandoned their nesting attempt and were no longer tied to their breeding site. We may also have located birds closer to their capture or nest site because our aerial search effort focused on the late afternoon or evening hours, when birds might begin foraging for their chicks

(Chapter 2). As the adult switches to being a central place forager late in the day, it would be more efficient to move closer to its nest. Hull et al. (2001) noted a tendency for radio-tagged murrelets to forage closer to their nests during chick feeding periods than other periods, although they did not find a significant difference.

Several factors may influence the apparent regional differences in forage range. The local topography and availability of nesting habitat near murrelet forage areas might circumscribe the choice of nest location. For example, in California birds must fly inland from a relatively straight coastline to small pockets of remaining old growth. The PWS coastline is highly convoluted and islands are abundant, such that potential nesting habitat is often accessible from the water from many directions. At our study sites in PWS, slopes in the fjords are steep and the low elevation tree line is usually within a few km of the sea. At Naked and other large islands, maximum elevation is 400 m, and no point on Naked is greater than 6 km from the sea. In southeast Alaska (Whitworth et al. 2000) and British Columbia (Hull et al. 2001), potential nesting habitat near the coasts had been harvested, and old-growth forests were farther inland or along the edges of long, narrow inlets that extended tens of kilometers inland. Thus, access to good nesting habitat may have required greater energy expenditure by birds in these areas, compared to birds in PWS.

Site fidelity

Foraging distances for individual birds were generally less than the distances among the study sites, resulting in distinct foraging zones by birds from different sites (Fig. 1). Although murrelets varied in their foraging distances, most birds made multiple visits to specific sites (< 5 km radius), regardless of sample size or time span for a given bird. Boat-based telemetry in the study areas, which was biased for those areas and thus not used in these analyses, confirmed the consistent use of sites by individuals, and indicated individual site-use was actually smaller (< 2 km radius) (Burns et al. 1994, Kuletz et al 1995b). Other studies of marked murrelets have also shown evidence of at-sea site fidelity. In southeast Alaska, four of seven radio-tagged murrelets returned to their capture site (Quinlan and Hughes 1992). Lougheed et al. (2002) found high local survival of radio-tagged murrelets in their study area, indicating that adults tended to forage in the same inlet through early chick-rearing. Hull et al. (2001) recorded more locations for radio-tagged birds that nested near the area covered by their boat-based telemetry. Banded murrelets have also returned to the same at-sea site in successive years, indicating multi-year site fidelity (Beauchamp et al. 1999).

Forage site fidelity has been recorded for other seabird species (Hunt et al. 1999), and suggests that seabirds select foraging sites based on memory and past experience. The range of spatial scales and types of birds exhibiting site fidelity include far-ranging albatrosses (Weimerskirch et al. 1993), surface-feeding kittiwakes (Irons 1998), and deep-diving murres (Benvenuti et al. 1998). Such colonial seabirds may follow conspecifics to prey patches (Wittenberger and Hunt 1985, Hunt et al. 1999) or may benefit from an 'information halo' by watching incoming birds from just offshore of the colony (Burger 1997). Marbled murrelets lack this advantage, and their generally solitary foraging habits may necessitate greater familiarity with local conditions. During at-sea surveys in PWS, murrelets recorded as foraging were primarily singles or pairs, and were not usually associated with forage flocks (Chapter 2). The use of particular sites by up to six radio-tagged individuals, which rarely overlapped temporally, suggests attraction to certain habitat features rather than cooperative or socially facilitated foraging behavior.

Visits by five tagged birds to Main Bay, where a fish hatchery is located, indicates that murrelets can be opportunistic foragers on a resource that is temporally and spatially limited. The murrelet diet in PWS consisted primarily of sand lance and herring (Chapter 2) but murrelets occasionally feed on salmon fry (Carter and Sealy 1986, Chapter 2). Our results parallel observations made by Scheel and Hough (1997), who in May 1995 noted that murrelet numbers increased at the Main Bay fish hatchery for four days after release of smolts.

Foraging habitat.

Radio-tagged murrelets in all three study areas primarily used nearshore waters < 1 km from shore, consistent with at-sea surveys of murrelets throughout most of their range (Carter and Sealy 1990, Burger 1995, Day and Nigro 2000). The propensity of murrelets to forage in shallow water is difficult to separate from their preference for foraging near shore (Ostrand et al. 1998). However, where we found murrelets farther offshore (e.g., Perry Island, Wells Bay), the areas usually had a shallow shelf, indicating that water depth was an important feature. Foraging 'hot spots' (e.g., Siwash Bay, Olsen Island, Elbow Island, Cabin Bay) also usually had shallow shelves, often < 20 m deep.

Murrelets forage throughout the water column, but their small body size probably restricts them to the upper 25-50 m of the water column, and most observations of murrelet dives have been in waters < 30 m (Burger 1991, Jodice and Collopy 1999). In contrast, murrelets at Nellie Juan also foraged in deep waters. Although murrelets are not typically abundant in deep fjords (Irons et al. 1988, Hunt 1995), they will aggregate over sills and sites of upwelling or currents (Carter and Sealy 1990, Hunt 1995, Speckman 1996). In this study, marbled murrelets clearly associated with bathymetric features that promote upwelling and currents (Fig. 4A-C). These included underwater shelves, the mouths of side bays (e.g. Siwash and Deepwater) and channels between islands (e.g. Olsen, Fairmont, Ingot). These sites were subject to strong tidally-induced currents, which in PWS can reach 5 km hr $^{-1}$ (Royer et al. 1990).

Underwater shelves, glacial sills, channel bends, or fjord mouths create local upwelling, tidal rips, currents, and eddies (Burrell 1986). These hydrographic features may create temporally predictable concentrations of plankton and fish at a particular depth stratum or lift them into the upper water column (Hunt et al. 1990, 1999; Coyle et al. 1992). Such sites of upwelling and prey concentration may be important to murrelets nesting adjacent to the deep waters of PWS. Only 19 % of the surface water area of PWS is < 20 m deep, another 22 % is 20 – 100 m deep, and 59 % is > 100 m (based on GIS analysis of NOAA bathymetric data by G. Esslinger, USGS, Anchorage, Alaska).

The frequent use of protected bays and the lack of birds in exposed waters suggest that sea state also influences murrelet choice of foraging habitat. For example, tagged birds were often on the west side of

Naked, but were never recorded on the east site, which is generally the wind-ward side. Where birds used sites with southeastly exposure (e.g., Perry Island), water depth was shallow and protected by neighboring islands. Jodice and Collopy (1999) recorded longer dive bouts for marbled murrelets in moderate, compared to calm seas, and suggested that the birds had to increase foraging effort in rougher seas. The PWS murrelets may thus have minimized energy expenditure by foraging primarily in relatively protected waters.

Implications for Conservation

Most murrelet conservation efforts are directed toward nesting habitat, but proximity of suitable marine habitat should also be considered. For the six murrelets we tagged that were potentially nesting, the location of the nest contributed substantially to total area used by the bird, as illustrated by the larger minimum area polygons with nest locations included. In PWS, the distances from the coast for 15 confirmed nests (DeGange 1996) were all < 1 km and in this study were < 6 km. This might partly be due to lack of search effort in alpine areas, but is likely related to the low elevation of tree line. Dawn watches in PWS revealed little murrelet activity indicative of nesting in treeless areas (Kuletz et al. 1995a, Marks et al. 1995). In contrast, potential nest locations in southeast Alaska were 4 – 9 km from the sea (Whitworth et al. 2000), and in British Columbia were 4 – 15 km inland (Hull et al. 2001). In Oregon, mean distance inland for nests was 17 km, with a maximum of 40 km (Nelson 1997). Thus at all sites south of PWS, murrelets were nesting farther inland than our tagged birds, which would further increase the energetic cost of transporting prey to chicks.

Distances from nest to nearest water might have energetic implications to birds nesting far inland (Hull et al. 2001), but distance to good forage areas is also important for raising chicks. Long flights to suitable forage areas should be energetically costly, although Hull et al. (2001) did not find a correlation between breeding success and distance from nest to forage site for murrelets. Still, the regional distribution of marbled murrelets at sea generally reflects the distribution of their preferred forest habitat (Piatt and Ford 1993, Raphael et al. 2002). The murrelet's geographic range covers a variety of marine regimes (Hunt 1995, Nelson 1997), and murrelet foraging range may also vary annually depending on ocean conditions (Ainley et al. 1995). Given the variability among individuals, the relationship between murrelet foraging range and reproductive success may be best examined by contrasting at large spatial scales. Murrelet productivity tends to be higher in PWS than in California and Oregon (Kuletz and Kendall 1998, McShane et al. 2004), and one factor could be the close proximity of foraging habitats for birds nesting in PWS.

For seabirds in general, traveling long distances appears to be beneficial only if the chance of energetic reward is high (Putz et al. 1998, Weimerskirch and Cherel 1998). The murrelets in southeast Alaska that traveled up to 124 km (Whitworth et al. 2000) were foraging in the highly advective and productive waters of Icy Strait, an area that regularly attracts thousands of seabirds (Robards et al. 2003). There is nothing comparable in PWS, but we did find low-end coarse (1-10 km) and finer scale bathymetric associations with murrelets. Compared to other areas in the Gulf of Alaska, PWS has low primary productivity (Sambrotto and Lorenzen 1986), water is highly stratified and as a result, fish schools are small and widely dispersed (Ostrand et al. 1998, Piatt et al. 1999, Brown et al. 1999). Under these conditions, familiarity with local conditions may be a more optimal foraging strategy than long-distance searching (Hunt et al. 1999), particularly for a non-colonial species that is widely dispersed.

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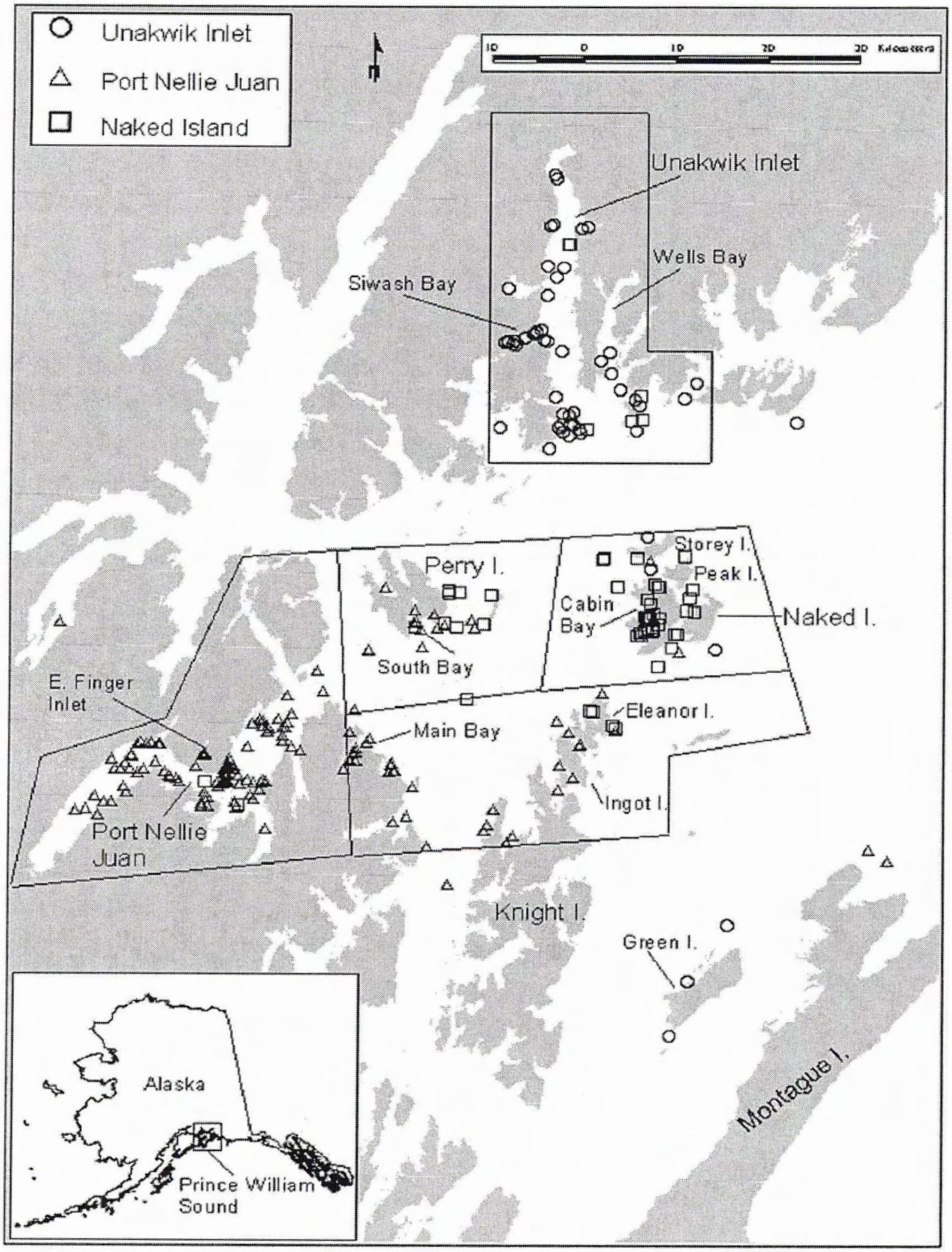

Figure 1. The study area, with capture locations at Siwash Bay, Cabin Bay, and East Finger Inlet. Sub-areas (solid lines) were used to determine availability of water depth categories from GIS bathymetric coverage. Symbols show aerial relocations of radio-tagged marbled murrelets caught at Unakwik Inlet (circles), Port Nellie Juan (triangles) and Naked Island (squares).

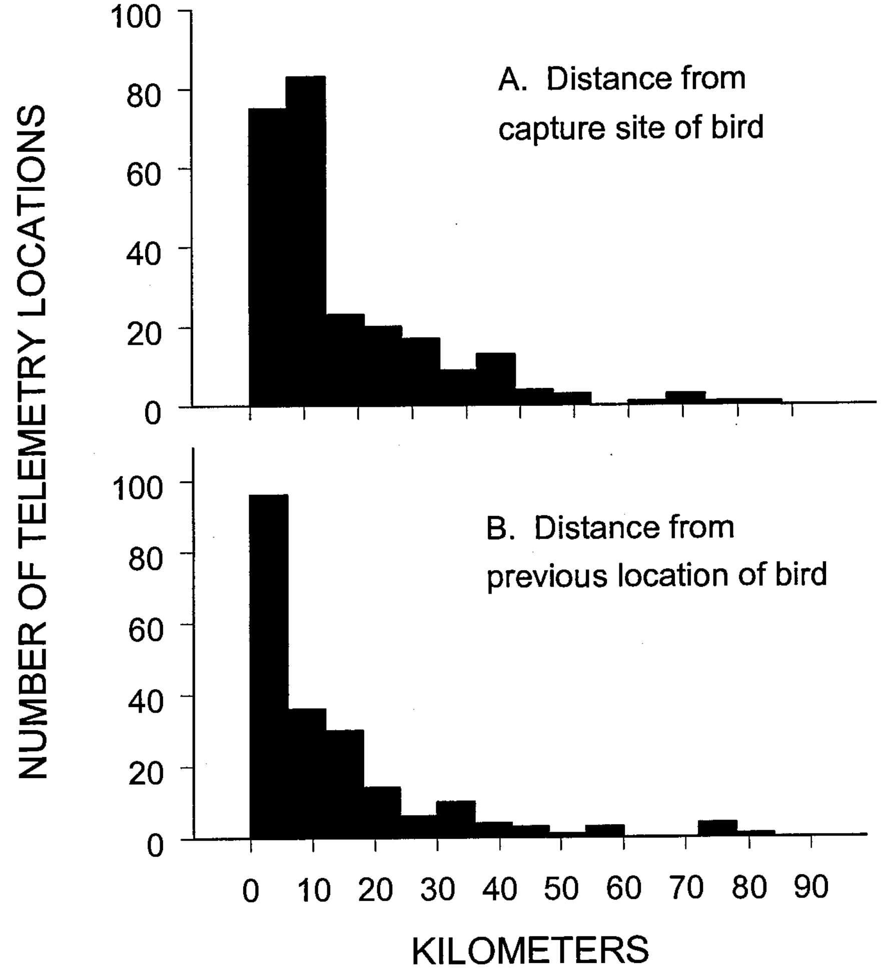

Figure 2. Frequency distributions for all aerial relocations of radio-tagged marbled murrelets in Prince William Sound in 1993 and 1994. Distances from capture site (A) were slightly greater than distances from previous location of birds (B).

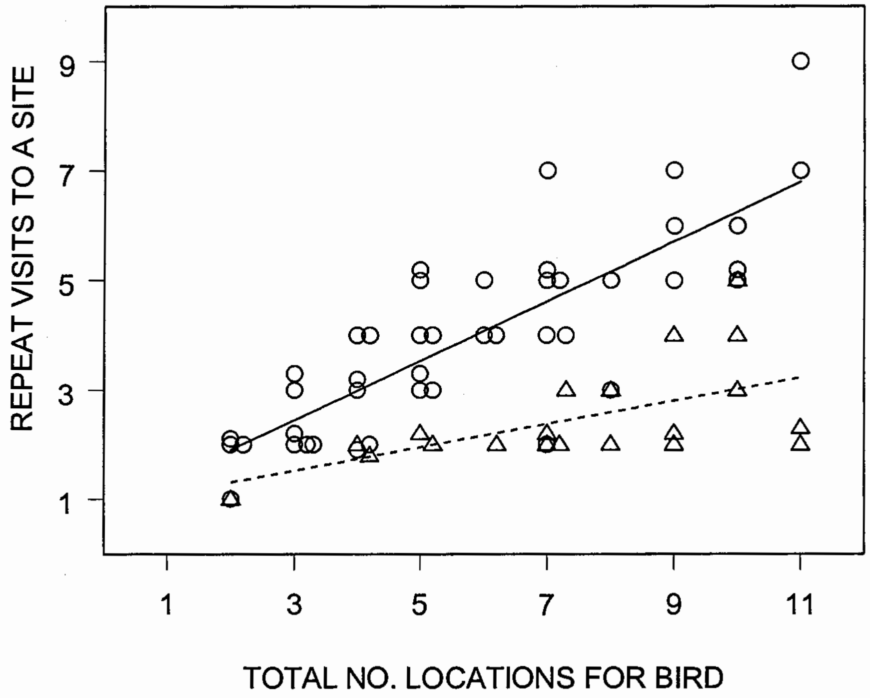

Figure 3. The number of repeat visits to the primary site (circles) increased with subsequent relocations (n = 44 birds, $R^2 = 0.68$, $P < 0.01$), as did repeat visits to a second site (triangles) (n = 19, $R^2 = 0.48$, $P < 0.01$). Individual forage sites were defined as clusters of relocations of the same bird within a 5 km radius.

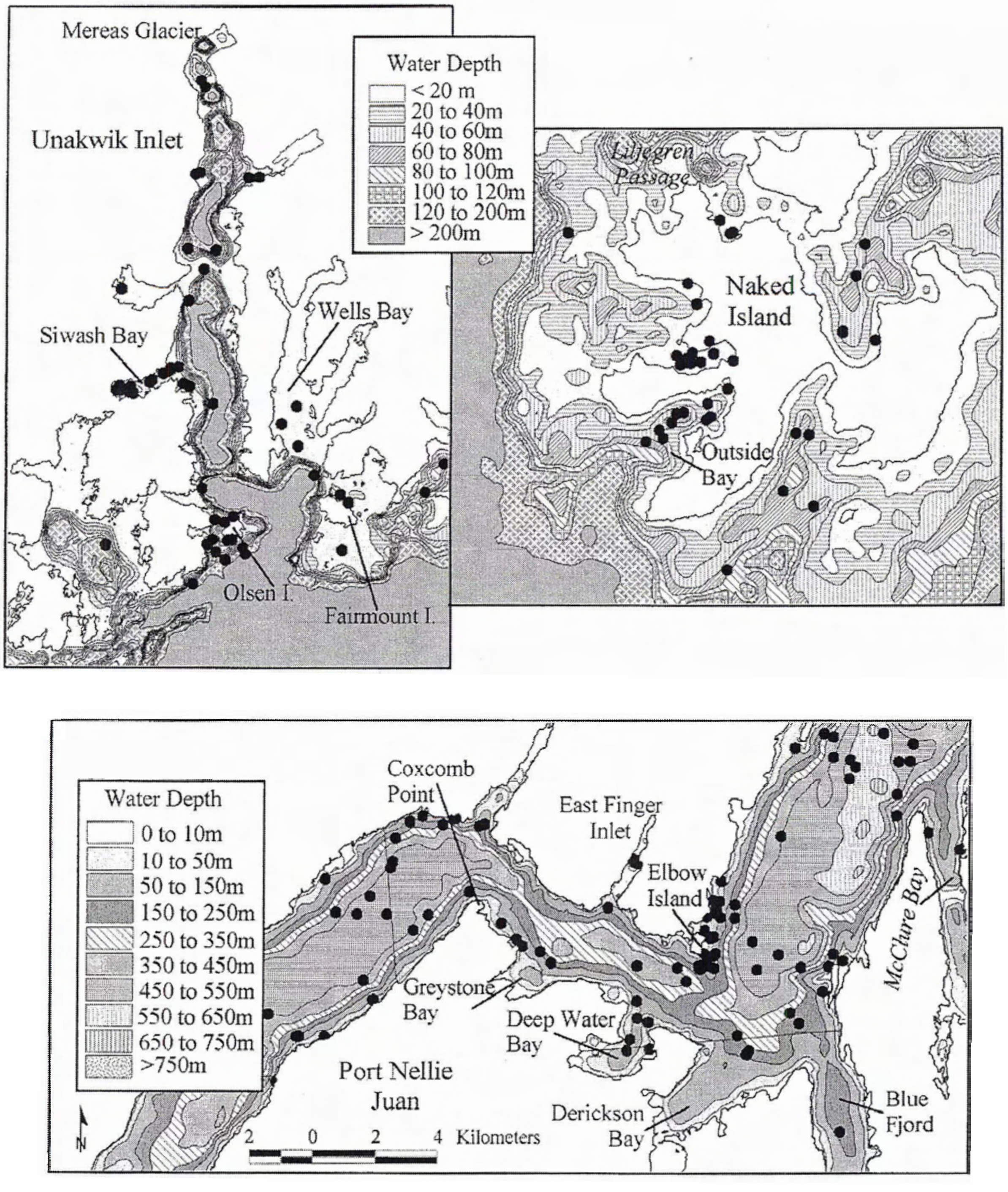

Figure 4. Aerial relocations of radio-tagged marbled murrelets in Prince William Sound, in relation to bathymetry at (A) Unakwik Inlet, (B) Naked Island, and (C) Port Nellie Juan. Bathymetry for Port Nellie Juan shows a larger scale, to illustrate locations of deep water sills and contours.

Table 1. Distances traveled by marbled murrelets captured at three sites in Prince William Sound, Alaska. Birds were caught at Unakwik Inlet (1993), Port Nellie Juan (1994), and Naked Island (1994). Means for each bird (n) were calculated from 253 relocations obtained on 36 aerial searches. Distances were 'Straight-line' (shortest distance between points regardless of land topography), and 'Over-water'(shortest distance over water). The minimum area polygon was calculated using outer points for each bird with > 4 relocations. Means + SE and number of birds (n) are shown. There were no significant differences among birds from different sites.

	Km between capture site and at-sea location		Km between consecutive at-sea locations		Maximum km between two at-sea locations		
Capture Site	Straight	Over-water	Straight	Over-water	Straight	Over-water	Minimum Area Polygon (km^2)
Unakwik Inlet	13.2 ± 3.1 (9)	14.6 ± 3.3	11.7 ± 3.5 (9)	12.9 ±3.8	35.8 ± 10.7 (9)	38.2 ±10.8	204 ±98 (8)
Nellie Juan	17.5 ± 2.3 (32)	20.6 ± 2.5	11.8 ± 2.0 (26)	14.2 ± 2.3	24.2 ± 3.4 (26)	32.1 ± 3.9	136 ±44 (20)
Naked Island	16.3 ± 4.5 (10)	18.9 ± 4.0	9.1 ± 2.4 (8)	11.1 ± 2.6	26.4 ±12.6 (7)	29.2 ±12.2	73 ± 49 (5)

Table 2. Frequency of use of water-depth classes compared to the amount available to 53 radio-tagged marbled murrelets in Prince William Sound, Alaska, in 1993 and 1994 (n = 253 telemetry locations). 'Available' indicates the area (km^2) of the depth classes for each sub-Area (see Figure 1), as determined by GIS bathymetric coverage (shown here as proportions). 'Used' indicates the number of locations for radio-tagged birds found in each depth class for that area (shown as proportions).

	Unakwik Inlet		Port Nellie Juan		Naked Island		Perry & Knight Islands	
Water depth (m)	% Available	% Used	% Available	% Used	% Available	% Used	% Available	% Used
0-20	41	64	21	12	11	32	10	19
20-40	8	8	6	8	10	8	5	14
40-60	6	4	5	12	9	32	4	10
60-80	6	7	4	3	6	20	4	8
80-100	5	0	4	5	5	0	4	5
100-120	4	0	3	3	5	0	9	5
120-200	12	15	11	17	14	8	13	14
>200	18	2	46	40	40	0	51	25
Total n		47		93		25		88
Chi-square[a]	18.2		6.7		35.1		20.5	
P	0.0004		0.082		0.0001		0.003	

[a] Four depth categories were used for the Chi-square test (df = 3), due to cells with expected counts of < 5 (in bird use) for Naked Island and Unakwik areas. The categories tested for all sites were 0-40 m, 41-80 m, 81-200 m, and > 200 m. Test result for Port Nellie Juan using eight categories was Chi-square = 10.57, df = 7, $P = 0.16$.

CHAPTER TWO

VARIATION IN FORAGING BEHAVIOR OF MARBLED MURRELETS: THE ROLES OF PREY, HABITAT, AND SELF VS. CHICK FEEDING

K.J. Kuletz, A.E. Burger, E. D. Brown, R.G. Ford

ABSTRACT

Seabirds are central-place foragers when provisioning chicks, and adults often select larger or more energy-dense prey for their chicks than they select for themselves, consistent with optimal foraging theory. The energetic demands of chick-rearing are increased by the spatially and temporally ephemeral nature of marine prey. One hypothesis is that seabirds facilitate the location and exploitation of ephemeral prey patches by group foraging and colonial nesting, but these behaviors have not been examined for the few non-colonial seabirds. We studied foraging behavior of marbled murrelets (*Brachyramphus marmoratus*), a non-colonial diving seabird for which there is little information on chick-provisioning. We examined murrelet group size, diving patterns, and prey selection relative to prey type and abundance, habitat, and self vs. chick-feeding. Two study sites in Prince William Sound, Alaska, were 50 km apart and were monitored June - August in 1997- 1999. Prey species and abundance were determined from aerial surveys and sampling of fish schools. Murrelet diet and behavior were determined by observations from vessels and land-based watches of forage areas. Sand lance (*Ammodytes hexapterus*) and juvenile Pacific herring (*Clupea pallasi*) comprised 90 % of murrelet diet. The two sites exhibited differences in prey types available and use by murrelets that were temporally and spatially consistent over three years. Herring were numerically dominant at one site (Jackpot) and comprised 95 % of murrelet chick diet there, whereas sand lance were numerically dominant at another site (Naked), where they comprised 84 % of chick diet. Murrelets delivered larger fish (age 1+ herring and 1+ and 2+ sand lance; 81-135 mm) to their chicks than those that they fed on themselves (0+ sand lance and herring; 40-80 mm). Diving patterns did not differ between self vs. chick-feeding birds, but varied between sites with prey type and habitat. Adults foraged as solitary individuals for the larger fish during pre- and post-twilight hours, when few other birds were present. During the day, murrelets foraged as singles or pairs when prey were abundant, but group size and murrelet participation in mixed feeding flocks increased as fish abundance declined. Thus murrelets altered their typically solitary behavior in response to changes in prey abundance, and possibly to prey type.

INTRODUCTION

Seabirds must find and capture prey in a dynamic marine system where food patches are often dispersed and ephemeral. Some aspects of the marine environment such as substrate, bathymetry, and currents are relatively stable, but the distribution and abundance of zooplankton and fish on which seabirds depend also are influenced by environmental factors that fluctuate with tidal and seasonal cycles (Russell et al. 1992, Hunt et al. 1999, Shealer 2002). Presumably, seabirds can accommodate such changes in resource availability. Foraging strategies are more complex for birds raising young because as obligate central place foragers they must maximize energy delivered to their young while maintaining their own body condition (Stearns 1992, Ricklefs 2000).

Seabirds have evolved a variety of physiological and behavioral adaptations for delivering food to chicks. Some species regurgitate predigested food while others carry multiple or single whole prey in their bills. Albatrosses (Diomedeidae) and some penguins (Sphenisciformes) may leave their chick for days or weeks to forage, whereas alcids (Alcidae) and larids (Laridae) make one or more deliveries every day. Almost universally, however, adult seabirds nest in large, multi-species colonies and they feed in flocks at sea. Such group behaviors are hypothesized to be adaptations that enhance the individual's ability to find patchily-distributed food in the marine environment (Wittenberger and Hunt 1985, Davoren et al. 2003a) as well as provide protection for its young left at the nest (Birkhead and Harris 1985, Anderson and Hodum 1993).

Colonial seabirds were well suited for the study of and development of many aspects of foraging theory (Stearns 1992, Ricklefs 2000), because energetic demands on individuals were high at this critical period, and large numbers of breeding individuals were concentrated under the same environmental conditions (Birkhead and Furness 1985, Hunt et al. 1999). Very few seabird species (about 2 – 4 %) nest solitarily (Lack 1968, Coulson 2002). Because it is difficult to study them, little is known about how non-colonial seabirds adjust foraging behavior to provision chicks, or even how they forage for themselves. We studied the self-feeding and chick-feeding behavior of a non-colonial seabird, the marbled murrelet (*Brachyramphus marmoratus*). Our study sites were in PWS, where this species was the most abundant breeding seabird (Agler et al. 1998). From Canada to California, the marbled murrelet is listed as threatened (Burger 2002, McShane et al. 2004), and although most of the world population breeds in Alaska, less is known about the biology of the northern populations.

Because seabirds can feed themselves at sea, the foraging strategy they use for self-feeding is often markedly different from the one used for chick-feeding (Ydenberg 1994, Ydenberg et al. 1994). Where this has been examined in detail, adults appear to maximize energy per delivery to chicks while minimizing energy expended for self-feeding (Kacelnik and Cuthill 1990, Weimerskirch et al. 1997). Once a prey patch is located, adults can make multiple dives in one location to feed themselves on small fish, but delivering the same small fish to chicks would not be energetically profitable. Seabirds that carry whole prey to chicks in their beaks, such as terns and most alcids, often deliver larger, more nutrient-rich prey to chicks than those that they consume themselves (Harris and Hislop 1978, Bradstreet and Brown 1985, Vermeer et al. 1987, Gaston and Jones 1998, Davoren and Burger 1999).

Marbled murrelets are classic central-place foragers when provisioning chicks (Orians and Pearson 1979), because they make an average of 3 trips to the nest within a 24 h period (Nelson 1997). While murrelets use a variety of forage fish (Burkett 1995), observers have noted that fish held by adults for delivery to chicks tend to be larger than those consumed by the adults themselves (Sealy 1975, Carter and

Sealy 1987, 1990, Mahon et al. 1992). In addition, observed changes in at-sea distribution have led to speculation that such patterns are related to self vs. chick-feeding periods (Sealy 1975, Carter and Sealy 1990, Speckman et al. 2000, Hull et al. 2001, Bradley et al. 2002). If, as suggested by Ostrand et al. (2004), murrelets use different selection criteria when feeding on schools of Pacific herring (*Clupea pallasi*) vs. gadids (Gadidae spp.), they likely also alter their foraging mode under different prey or environmental conditions.

The difficulty of finding food in the marine environment is believed to be one of the main forces driving the life history of seabirds (Ashmole 1963, Lack 1968, Wittenberger and Hunt 1985, Croxall and Rothery 1991). Seabirds may minimize foraging effort by using social cues to locate prey, and by feeding in groups to keep fish concentrated and accessible (Ward and Zahavi 1973, Camphuysen and Webb 1999, Hunt et al. 1999, Davoren et al. 2002, 2003b). In contrast, marbled murrelets typically are observed as single birds or in pairs, but to various degrees, they have also been observed feeding in groups (Carter and Sealy 1990, Mahon et al. 1992, Hunt 1995a, Ostrand 1999). As non-colonial birds and being widely dispersed at sea, the foraging dynamics of murrelets are not well understood, and the interactions between foraging behavior, prey, and self vs. chick-feeding have not been closely examined or tested.

In our study, we hypothesized that murrelets provisioning their chicks would demonstrate behavior consistent with that of an optimal central-place forager, because chick-rearing entails the same high energetic demands whether a seabird nests solitarily or colonially. However, murrelets should demonstrate a wide variety of foraging behaviors when self-feeding, because they are relieved of the need to return to the nest. Thus, murrelets should respond to different prey types, levels of prey abundance, and habitat characteristics by altering behaviors such as group size, participation in mixed species flocks, and dive patterns. Finally, although murrelets are generalist feeders (Burkett 1995), the array of prey suitable for raising young may be limited, and so we examine the diet and foraging behavior of murrelets in the context of murrelet population trends in Prince William Sound (PWS), Alaska. Understanding how murrelets adjust foraging behavior to the demands of chick rearing and variation in prey species or abundance, will improve our knowledge of how changes in the marine environment affect their populations.

METHODS

Study Area

The study was conducted in Prince William Sound, a 10,000 km^2, fjord-type embayment in the northern Gulf of Alaska. The coastline is highly convoluted, with islands, passages, estuaries, shallow bays, and deep fjords, and thus highly variable coastal habitats. Study sites were Naked Island (Naked) in central PWS, and Jackpot Bay vicinity (Jackpot) on the mainland in southwest PWS (Fig. 1). At these sites, sea surface temperatures (SST) ranged from 9 - 17 ^{0}C, and sea surface salinity (SSS) ranged from 15 to 32 psu. SST and water clarity (secchi depth) was similar at Naked and Jackpot, but SSS was significantly higher at Naked (27.7 psu) than Jackpot (21.0 psu; $F_{1,38} = 204.3$, $P < 0.001$). SSS varied among years ($F_{2,38} = 4.3$, $P = 0.02$), with 1997 (23.6 psu) significantly fresher than in 1999 (25.2 psu).

Naked is surrounded by a wide shelf with water primarily < 50 m deep within 1 km of shore and < 200 m deep out to 5 km offshore. Jackpot includes Jackpot Bay, which is 100 m deep, and a passage that is 300 m deep.

Large scale features that influence physical and biological characteristics of PWS include nutrient rich saline waters entering Hinchinbrook Entrance (HE) from the Gulf of Alaska (GOA), via the Alaska Coastal Current (ACC), during late winter and early spring. A counter-clockwise cyclonic circulation pattern from HE wraps around the east and north sides of Naked Island and then moves south past the Jackpot area before leaving PWS through the southwest passages (Royer et al. 1990, Niebauer et al. 1994). Naked is at the boundary zone between northern fjord waters that tend to be colder and fresher and the ACC-influenced waters that are warmer and more saline (Wang et al. 2001). Jackpot is not in the direct path of the cyclonic current, and is heavily influenced by freshwater flow from surrounding mountains, typical of the southwestern fjords of PWS (Gay and Vaughan 2001). By summer, the relaxation of coastal downwelling near HE, together with lower wind forcing and an influx of freshwater from surrounding mountains and glaciers, results in highly stratified surface waters throughout PWS (Niebauer et al. 1994). Because of more direct influence from freshwater runoff at the heads of deep fjords (such as Jackpot), these regions become even more highly stratified (Gay and Vaughan 2001). Naked is largely ice free year-round, whereas the main basin of Jackpot Bay, surrounded by steep mountains, is ice-covered until spring (USFWS, Anchorage, AK, unpubl. data).

In this study, meso-scale refers to entire study sites (Naked or Jackpot), as covered by the at-sea surveys. Fine-scale refers to the specific bays covered by diet cruises and forage watch sites (Cabin Bay at Naked, and Jackpot Bay at Jackpot), which were monitored more intensively to provide information on foraging behavior and diet.

Background on principal forage fish of PWS

Marbled murrelets will feed on invertebrates, but in summer their main food is fish, and at least 16 species or families of fish have been identified in the diet of murrelets (Burkett 1995). The icthyofauna of PWS includes most of the fish identified as murrelet prey, and is relatively diverse (Okey and Pauly 1999). Forage fish used by seabirds in PWS are dominated by five species presented below, including Pacific herring, Pacific sand lance (*Ammodytes hexapterus*), capelin (*Mallotus villosus*), walleye pollock (*Theragra chalcogramma*), and pink salmon (*Oncorhynchus gorbuscha*). Various smelt and gadid species are also consumed (KJK, pers. obs.), but we lack species-specific information on their importance to murrelets.

Pacific herring are a dominant part of the icthyofauna of PWS (Okey and Pauly 1999, Stokesbury et al. 1999a). They spawn in mid-March to mid-April in nearshore areas, primarily in the eastern regions. In May, pelagic larvae are transported via the PWS cyclonic current north, westward and then south to inner bays, where they remain until their second year. The larvae remain in the nursery bays and feed on copepods and a variety of macrozooplankton (Stokesbury et al. 1999a, Norcross et al. 2001). In summer, the 0+ and 1+ age classes of juvenile herring (those used by murrelets and other seabirds) rarely overlap with older herring age-classes, which are in deeper waters (Stokesbury et al. 1999a).

The PWS herring population has fluctuated widely, with a peak estimated adult biomass in 1988 of about 100,000 metric tons (Mt), followed by a series of declines. The herring stock collapsed in 1993, declining from an estimated 16,082 Mt in 1993 to a low of 6,384 Mt in 2001 (Thomas and Thorne 2003). There is no agreement on the cause of the collapse, and it could have been due to a combination of the 1989 *Exxon Valdez* oil spill (Paine et al. 1996, Spies et al. 1996), over-harvest when stocks were low (Thomas and Thorne 2003), and competition with hatchery-reared salmon (Pearson et al. 1999, Purcell and Sturdevant 2001). Since 1993, other than a few trial openings between 1996 and 1998, the herring fishery has been closed (Thomas and Thorne 2003). During the approximate years of this study (1995 – 1997), estimated annual biomass of juvenile herring (0+ and 1+ age classes) was approximately 102,000 Mt (Okey and Pauly 1999). This 'ballpark' estimate was based on aerial surveys (E. Brown, University of Alaska, Fairbanks) and used the 3-year mean Mt / km^2 multiplied by the surface area of PWS.

Pacific sand lance of all age classes are consumed by most seabird species in PWS (Piatt et al. 1997, Suryan et al. 2000, Golet et al. 2000). Little is known about sand lance in PWS, and estimates of stock size are unknown. Based on the aerial surveys of 1995 – 1997, the mean estimate of sand lance biomass in PWS was approximately 5,400 Mt, with a high of 14,400 Mt in 1997 (Okey and Pauly 1999). In other areas of Alaska this species is typically found in water < 100 m deep and is associated with sandy substrate, into which it burrows when not active (Blackburn and Anderson 1997). Sand lance spawn in the fall, larvae emerge in winter (Robards et al. 1999a), and undergo a growth spurt after the spring primary production bloom (Robards et al. 1999b). Adult sand lance in some areas move offshore in late July, thus by late summer, most nearshore sand lance are usually juveniles.

Capelin are mainly consumed by birds as adults, when they enter nearshore waters of bays and fjords to spawn in June and July (Brown 2002). Although capelin had declined in the northern GOA in the 1980s and nearly disappeared from seabird diets (Anderson and Piatt 1999, Kuletz et al. 1997) they were present in the mid-1990s (Brown 2002). In PWS, capelin larvae were most prevalent in the southeastern area (Brown 2002), but occasional aggregations of adults have been observed around Naked Island (KJK, pers. obs.). The Okey and Pauly (1999) estimate of capelin biomass in PWS extrapolates to approximately 2,100 Mt, but capelin were difficult to census with aerial surveys (Brown et al. 1999) on which this estimate was based.

Juvenile gadids of several species are present in PWS (Thedinga et al. 2000) and are consumed by adult seabirds (Kuletz et al. 1997, Agler et al. 1999). The primary gadid in PWS is walleye pollock, which tends to occupy deeper waters farther offshore than other forage fish of PWS (Haldorson et al. 1999). Juvenile pink salmon are a potential prey, but only temporarily abundant in the bays. Natural pink salmon runs were historically low and have declined, but since 1977, hatchery-reared pink salmon smolts have been released in April to coincide with the spring plankton bloom. The release of hatchery salmon smolts increased throughout the 1980s, and since 1988, over 500 million have been released annually (Pearson et al. 1999, Thomas and Thorne 2003).

Data Collection for Fish Abundance

Fish abundance within the study sites was monitored via aerial surveys from a fixed-wing aircraft. Each aerial survey was conducted in a single day, with 5-12 survey days flown in a given year at each site, separated by at least 2 days ($n = 40$ days). In 1997 – 1999 aerial surveys were flown between 16 June and 10 August, but the majority of aerial surveys occurred in July, during the peak chick-rearing period for murrelets. Details on the methodology for aerial surveys are available in Brown et al. (1999). An observer in a Cessna 185 flew at approximately 204 km h^{-1}, parallel to shore, at a mean altitude of 305 m (range 274 – 366), observing a transect ~ 325 m wide. When an area of high fish school density was encountered, the pilot circled the area to allow the observer to count all schools. The number and size (length and width, estimated using a sighting tube with internal grid) of fish schools were recorded onto a continuous computer log, which entered the school's location via global positioning system (GPS) connection. Distances of the schools from shore were also determined from the air (Brown et al. 1999).

Unlike acoustic surveys, aerial surveys covered a large area quickly and measured abundance of small schools of fish, including sand lance, close to shore. The surface area of fish schools was calculated from their length and width. In preliminary analyses, there was a positive correlation between total school surface area and the number of fish schools, thus either could be used as a measure of fish abundance. In PWS, fish schools tend to be small (Brown et al. 1999, this study), and murrelets select for small schools (Ostrand et al. 1998). Therefore, we used the number of fish schools as the best indicator of foraging conditions for murrelets and the best indicator of fish abundance.

Species identification. -- Species identification from the air was based on the fish school's shape, size, and location from shore. To obtain error rates in identification, boats were directed to schools during aerial surveys and fish were sampled (primarily in 1996) with seine nets, dip nets, or underwater video (Brown et al. 1999). Discriminant function analyses from the samples vs. aerial identification determined an accuracy of 96 % for herring and 80 % for sand lance (Brown et al. 1999). Aerial surveys were not able to distinguish age classes of juvenile herring, but because of shifts in age composition in PWS over the summer, most surface schools of herring in June were 1+ and 2 years, and in July more 0+ herring were encountered. Adult herring were present, but rare near shore in June - August (Brown et al. 1999). The age-2 herring (> 130 mm), which are too large for murrelets (Burkett 1995), tend to be farther from shore and deeper in summer, and herring sampled in conjunction with aerial surveys were always 0+ and 1+ age classes. We therefore considered all fish schools of herring and sand lance identified during aerial surveys to be potential prey for murrelets. The fish samples taken for validation of aerial surveys (Fig. 2) were used to obtain size and age class of potential prey species. Where necessary, we used the length-mass regression of measured fish to estimate mass of each size class, and obtained caloric and lipid or energy values from available literature.

Effectiveness of aerial surveys. -- Aerial surveys were effective in estimating abundance of small schools of fish close to shore (Brown et al. 1999), which was the area we surveyed for murrelets. They were effective at locating schools of herring and sand lance, but less effective in detecting species which tend toward less tightly structured or scattered schools, such as capelin that are feeding, or juvenile pollock. Aerial survey observers also had difficulty detecting fish in deeper waters, or in waters with heavy sediment loads (Brown et al. 1999). Because the murrelet surveys were conducted nearshore where water tends to be shallower, and neither Naked nor Jackpot sites had direct glacial runoff, the aerial surveys were well suited to these study sites. Additionally, both Sites had similar surface water clarity as measured by secchi disk (see study sites, above), thus minimizing potential bias in spotting fish schools from the air.

The murrelet surveys were conducted within portions of the sound-wide aerial fish surveys, so we extracted site-specific data on fish schools by circumscribing a 10 km radius around the center of the murrelet transects at each site (Fig. 3), using a geographic information system (GIS; ArcView). The 10 km radius captured all surveyed shoreline and adjacent waters within each murrelet site; 10 km was also the mean straight-line distance traveled among forage sites on different days by radio-tagged murrelets in PWS (Chapter 1). Thus, for this study, number of fish schools refers only to schools observed within the 10 km radius of these study sites. The aerial fish surveys were not necessarily concurrent with the murrelet surveys, but were treated as an index of meso-scale fish abundance and availability for each site and season.

Data treatment for aerial surveys. -- Because Naked is surrounded by water, whereas the Jackpot site consists of mainland bays and a pass, the Naked site included greater water surface area (262 km^2) than did the Jackpot site (112 km^2). To standardize for the different surface area and variable flight paths, the number of fish schools observed were converted into densities. Using GIS, the locations of observed fish schools were binned into 0.25 x 0.5 nm (0.93 km) blocks (Fig. 3), and the number of schools was weighted for the distance flown in each block per survey. The daily weighted measure of fish abundance was calculated from the average school density for all blocks within the 10 km radius of the study area. Daily averages were then used to calculate annual mean fish school density (schools / km^2) for each study area. Thus, fish school density as used here refers to the relative abundance of fish schools within a given area, not the density of fish within those schools.

Fish school density was log-transformed (adding 0.001 to compensate for zero values) prior to analysis, to meet the assumptions of normality. Because 98 % of fish schools observed from the air (and validated) were either juvenile herring or sand lance, we used densities for these two species only, to test for spatial (between Sites) and temporal (inter-annual) differences in fish abundance. Similar tests were conducted on distance from shore (m) and surface area (m^2) of schools. In the field, distance to shore or surface area of schools was not always recorded, or the fish were not identified to species, so sample sizes varied slightly for different analyses.

Murrelet Diet

Adult diet. – The prey used by adult murrelets were identified opportunistically during boat-based at-sea surveys for murrelets (see below) and during land-based forage watches (see below). These observations and samples were used only to validate species used by murrelets, not as indicators of abundance. Murrelets rarely brought fish to the surface when self-feeding (KJK, pers. obs.), but when they did, we identified the fish to the nearest taxon and estimated fish size relative to bill tip-to-eye length ($\bar{x}$ = 23 mm on PWS specimens) of the murrelet (because the true bill length was difficult to discern in poor light). When murrelets were participating in feeding flocks, observers identified fish held by other birds, which were primarily glaucous-winged gulls (*Larus glaucescens*), black-legged kittiwakes (*Rissa tridactyla*), tufted puffins (*Fratercula cirrhata*), horned puffins (*F. corniculata*), and pigeon guillemots (*Cepphus columba*), all of which brought fish to, or captured fish at, the surface. We also captured fish below feeding murrelets (singles, pairs, mixed groups) using a small mesh dipnet. We bagged and froze all fish from small dipnet loads, or subsampled 10-100 fish from large loads for later confirmation of identification.

Chick diet - Marbled murrelets at sea hold fish in their bills for extended periods prior to flying inland to deliver food to chicks, usually in early morning or late evening hours (Carter and Sealy 1987). We recorded fish-holding behavior by conducting diet cruises throughout the chick-rearing period, 26 June to 30 August in 1997-1999, rotating between Jackpot Bay (Jackpot) and Cabin Bay (Naked; Fig. 1). During diet cruises, conducted in the morning (0330 - 0800) or evening (1900 - 2330), a two or three-person crew recorded murrelets holding fish. Diet cruises lasted 2 h, during which the 4 - 7.5 m vessel traveled in a slow (~3 km/h) systematic zig-zag pattern across the bay. Observers used 10x40 binoculars to identify fish held by adult murrelets to the nearest possible taxonomic category. Observers were trained to identify fish and estimate size using pictures, laboratory specimens, or captured fish. Photographs and drawings of fish and fish size relative to murrelets were on-hand for reference. We allowed up to 15 min ($\bar{x}$ = 5 min) to identify fish species and kept track of the bird's movements to avoid double counting the same bird. It was possible to follow individual birds because usually, few other birds of any species were present. For each sighting we recorded time, prey identification (or 'unknown'), and estimated fish length. Because murrelets hold the fish cross-wise in their bills, the full length of the fish is usually visible, although the tails of longer fish may be underwater. If the bird swallowed the fish it was not counted as a chick diet sample, but if a bird flew off with the fish, the sample was considered a chick food item. Because we rarely observed birds holding fish during early morning diet cruises in 1997, in subsequent years we focused efforts on the evening period, thus 88 % of the diet cruises were conducted in the evening.

Murrelet Activity Patterns and Foraging Behavior

At-Sea Surveys. – In 1997 - 1999 we conducted boat-based shoreline surveys at Naked and Jackpot, 3-6 times each during incubation period (between 31 May-16 June), and 6-10 times each during fledging period (20 July - 30 August). Each survey took one day (0700 - 1600 h) and covered approximately 58 km at Naked and 55 km at Jackpot, with some variation depending on tides. We surveyed from 7.5 m vessels traveling at a distance of 100 m from shoreline at speeds of 10-20 km h^{-1}. Transects within each survey route were defined by topographic reference points and averaged 3.9 km (range 1 – 10). Prior to each transect we measured sea surface temperature (SST) and sea surface salinity (psu) with a digital conductivity meter, and used a secchi disk to measure water clarity.

Following standard USFWS protocol for strip transects (Agler et al. 1998, Lance et al. 2001), a boat operator and 2 observers recorded all birds within 100 m on either side of and ahead of the boat. We used the strip transect to follow USFWS protocol used in other PWS surveys (Agler et al. 1998). Additionally, because we traveled 100 m off shore, we would have had to truncate distances to the same (200 m) transect width, and the high densities of murrelets in nearshore waters of PWS made strip transects more practical than distance sampling. Observations were entered directly into a computer which automatically logged time (DLOG, F.G. Ford Consulting, Inc., Portland, OR). Observers entered behavior codes for each entry indicating if the bird was forage diving (as opposed to avoidance diving, which has a different entry posture), on water, flying, or part of a foraging flock. Each record thus consisted of either a single bird, a pair (2 murrelets associated with each other, usually < 2-m apart) or a flock (recording number of birds). For each foraging flock encountered on transect, we recorded the number and type of other bird species present.

We also recorded foraging flocks during land-based forage watches (see below) and opportunistically during diet cruises, and these were examined separately to obtain the percentage of murrelets in mixed flocks during chick-feeding periods. Murrelets usually deliver meals to their chicks near dusk and dawn (Nelson 1997), thus all at-sea surveys were considered murrelet self-feeding periods, since 90 % of the transects (n = 1,019) began after 0800 h (local sunrise occurred between 0505 h and 0630 h during the July –August surveys) and even early transects often continued past 0900 h. Because the 1999 June murrelet densities were substantially lower than during five previous years of surveys since 1989 (Kuletz 1996, Kuletz and Kendall 1998), we conducted additional June surveys that year to confirm that the first surveys were not aberrations.

Forage Watches. – We conducted forage watches from land-based platforms ~ 10 m above sea level in Cabin Bay (Naked) and in Jackpot Bay (Jackpot) between 11 June and 20 August, on 41 days in 1998 and 32 days in 1999. Based on Nelson (1997) and observations of fish-holding during our diet cruises, forage watches were divided into two periods defined as 'self-feeding' (in June prior to hatching, or between 0900 h and 1700 h), and 'chick-feeding' (after 1 July and at < 0900 or > 1700 h). Although some birds could have been feeding chicks in late June, the majority likely were not. Once every other hour, the observer slowly scanned a fixed observation area with a spotting scope, beginning with a randomly selected side and alternating in subsequent hours. Observations were recorded into a tape recorder and later transcribed. Murrelet behaviors were recorded as flying, on water (resting), diving, fish-holding, or maintenance (bathing, preening, wing-flapping). Recognizing that birds underwater were missed, these counts were minimum estimates of the proportion of birds diving. Prior to each scan, the observer recorded time and sea state (Beaufort scale). Scans totaled 106 in 1998 and 120 in 1999, for an average 2.6 scans (range 1- 5) per day of observation. Most forage watches lasted 4 -5 hours, since scans were conducted only every other hour to increase independence of counts. Forage watches were distributed in nearly equal portions spatially (between Sites) and temporally (between self- vs. chick-periods, and seasonally).

Diving observations. – During alternate hours, the observer made visual records of duration of dive and pause (surface interval between dives) for murrelets, using binoculars when necessary, and a stopwatch. We recorded the duration of dives and pauses to the nearest second. Observers monitored murrelets diving singly and as pairs, but not birds in groups. Pairs were timed by marking the first bird to dive or surface and treated the dive session as a single observation; pairs were usually synchronized within 1 s of each other. Birds were usually diving at the time observation began, and the observation of a dive session was terminated when the bird remained on the surface > 2 min, began preening, flew off, or mixed with other murrelets. When the dive session was terminated, the observer moved to another quadrant of the forage watch area and selected another bird. Because of the appearance of other birds or sun glare, it was not usually possible to follow the same bird long enough to determine length of a complete forage bout or time between bouts.

Data analyses

Statistical tests . -- Analyses for meso-scale data, such as fish school density and characteristics, and bird data from the at-sea surveys, included three Years (1997 – 1999) and both Sites. Analyses for fine-scale data, such as diet cruise and forage watch observations, included two Years (1998 and 1999) and both Sites. Values were transformed if necessary to meet the assumptions of normality; counts were log-transformed and proportions were square-root transformed. Except where stated otherwise, for tests between Sites and Years, we used a two-way ANOVA, with a Tukey multiple comparison test among Years. For non-parametric multiple comparisons we used Kruskal-Wallis rank sum test. For comparison between two means, we used a Welch modified two-sample t-test for unequal variances, or a Wilcoxon rank-sum test, as appropriate. All means are presented ± SE, with significance set at $p < 0.05$. Statistical analyses were done with S-Plus-6 (Insightful 2001).

Data treatment for diet and foraging behavior

At-sea surveys. -- We compared group size of birds observed to be actively foraging or not (non-foragers), omitting birds in the air. We tested for differences in group size by Site and Year (see statistical tests, above). For both foraging and non-foraging birds, we summed the number of birds for each Site and Year into six group-size categories based on frequency distributions of bird observations (1, 2, 3-6, 7-15, 16-30, and >30 birds). We tested for differences in distribution with a two-sample Kolmogorov-Smirnov test. For these analyses, five large, loose aggregations (> 100 scattered murrelets) entered as single records were excluded because we did not obtain true group sizes in the field.

Feeding flocks. – Because the foraging behavior of murrelet pairs appears to be synchronized and qualitatively different from feeding flock activity, we defined a flock as consisting of at least three birds of any species that were actively foraging (surface plunging or diving). The frequency of forage flocks encountered on transect during at-sea surveys (number/survey), total flock size, number of murrelets, number of other birds, and percentage of murrelets were compared among Years and Sites. Similarly, flock size was compared among Years and Sites, between flocks with 100 % murrelets and mixed flocks, and among the three seasonal stages: incubation (June), early fledging (20 July – 10 August), and late fledging (11 – 31 August). We used a linear model to examine the relationship between the number of other birds and the number and proportion of murrelets in a flock, using transformed values. For this test, we only used flocks that had at least one murrelet present, but was not 100 % murrelets, to minimize potential biases resulting from differential prey selection among species.

Diet. – Estimated lengths of fish held for chicks (chick diet) were compared among Years and between Sites, and between adult and chick food items. We also examined within-season changes in fish size. We used Wilcoxon rank-sum test, Friedman chi-square, or differences in size-class distribution with a Kolmogorov-Smirnov two-sample test. We did not test for differences between fish used by murrelets and those taken in the validation seine operations, because most of the validation samples were caught in 1996.

Foraging watches. – Group size, total number, and number of murrelets in each behavioral category were summed for each hourly scan of each watch day. For each hour, we calculated the proportion of murrelets in each behavior category, including participation in feeding flocks. We tested for differences in counts or proportions between Sites and Years, using transformed values to meet assumptions of normality. Graphic presentation of behaviors relative to hour and group size used the spline graphic procedure in S-Plus-6 (Insightful 2001). The spline fits a smooth function to the data for a three-dimensional plot, using the line segments to connect points in a grid frame (Venables and Ripley 1999). This provides a visual contour of changes in proportion of total birds, or proportions in a dependent behavior category, relative to two independent variables.

Dive observations. – Before analyzing dive and pause times of foraging birds, we removed outliers by establishing a cut-off for times > 2 times the standard deviation (SD) above the means, as suggested by Jodice and Collopy (1999). This minimized the potential influence caused by missing the surfacing of a bird, or of prolonged pauses between dive bouts that were not limited by physiological effects. We then calculated the mean time for each bird per dive session, and used the birds' means to test for differences in average dive and pause times by Year, Site, self vs. chick period, and sea condition. Dive times were normally distributed but pause times were not. Sample distributions were similar between groups, and under these conditions standard t-tests are robust (Ramsey and Schafer 1997). We first tested for differences between single birds and pairs, and since these did not differ in duration of dive (two-sample t-test; $t = 0.16$, df = 132, $P = 0.87$) or pause ($t = 1.67$, df = 124, $P = 0.10$), we combined them for remaining analyses.

RESULTS

Forage Fish Abundance and Distribution

Between 1997 and 1999, 703 schools of forage fish were counted during aerial surveys within the 10 km radius of the Naked and Jackpot sites. Schools were 70 % sand lance, 28 % juvenile herring, and 2 % gadids and capelin. The two primary fish species showed distinct spatial patterns of distribution throughout PWS (Fig. 2) and between our two study sites (Fig. 3), with sand lance predominating at Naked (84 % of fish schools) and herring predominating at Jackpot (95 % of fish schools at that site; Fig. 4). Naked tended to have the highest density of total fish schools (Fig. 4). Overall, there were frequently differences in total fish school density between Sites, and marginally ($P < 0.10$) differences among Years. Within each Year, the Sites differed significantly in total fish school density only in 1999 (Table 1).

Within-Site, Naked showed a significant difference among years ($F_{2,22} = 3.87$, $P = 0.04$), with 1997 being significantly lower in fish abundance than 1999 (Tukey test). For each prey species within-Site, herring abundance at Naked showed significant differences among years (Fig. 4; $F_{2,22} = 20.5$, $P < 0.01$), with 1998 having significantly higher herring densities than the other two years at Naked (Fig. 4). However, at Jackpot, the density of fish schools in 1998 was roughly 10 times higher than in 1997 or 1999, due to abundant herring at that site in 1998 (Table 1). High variance in fish school density among survey days made it difficult to detect statistically significant results (Fig. 4).

Attributes of fish schools. – Surface areas of fish schools were generally < 80 m^2, with a median size of 24 m^2 for herring (range 1 – 670 m^2) and 27 m^2 for sand lance (range 1 – 1,191 m^2; Table 2). Three large schools > 500 m^2 were recorded within the study sites. Preliminary analyses indicated that including these unusually large schools did not alter the tests for significance, so we retained all schools for analyses, in order to provide the full range of fish school characteristics encountered. Overall, fish school size varied between Sites and among Years (Table 2), with a significant interactive effect ($F_{2,632} = 8.84$, $P < 0.001$). Among years with data from both Sites pooled, schools in 1997 were significantly smaller ($\bar{x} = 36.1 \pm 4.5$ m^2) than in 1998 or 1999 (respectively, 40.5 ± 2.5 and 54.5 ± 7.1 m^2). Within Year, fish school size was similar between Sites in 1997, but in 1998 and 1999, school size was significantly larger at Jackpot (Table 2). However, sample sizes were unbalanced, because few schools were observed at Jackpot in 1999, whereas Naked had its highest number of schools recorded that year.

Fish schools tended to be < 200 m from shore, but this varied among years (Fig. 5). Overall, there were no Site effects on distance from shore, but Years were significantly different (Fig. 5, Table 2) with significant interaction of Site and Year ($F_{2,632} = 6.1$, $P < 0.002$). In 1999, mean distance from shore of schools (113.8 ± 5.2 m) was significantly greater than in 1997 (19.3 ± 2.8) or 1998 (21.2 ± 2.4). Within Year, fish schools at Naked were significantly closer to shore than those at Jackpot in both 1997 and 1998 (Table 2).

For all years and sites combined, mean distance from shore was similar between schools of herring ($\bar{x}$ = 61.3 ± 9.1 m) and sand lance (65.0 ± 3.5 m), but maximum distance was 1000 m for herring and only 400 m for sand lance. Furthermore, within years, herring were significantly farther from shore than were sand lance in 1997 (herring $\bar{x} = 45.5 \pm 8.4$, sand lance 9.4 ± 0.6; $t = 9.6$, df = 37, $P < 0.001$) and 1998 (herring 40.2 ± 8.9, sand lance 9.9 ± 1.1; $t = 7.05$, df = 2.37, $P < 0.001$).

To summarize, fish abundance (density of fish schools) was usually higher at Naked, where both 0+ herring and sand lance were present, whereas few schools other than juvenile herring were at Jackpot. Jackpot had comparable fish school densities in 1998, due to high local abundance of juvenile herring that year. Combined abundance of fish schools was lowest (and fish schools smaller) in 1997, and highest in 1999. The size of fish schools was typically small (median 25 m^2), but larger at Jackpot than Naked. Fish schools tended to be < 200 m from shore, but in 1999 they were significantly farther offshore than the previous two years, and thus a larger proportion of fish schools were beyond the nearshore zone surveyed for murrelets. Herring were typically farther offshore than sand lance, and correspondingly, fish were farther from shore at Jackpot, because herring were prevalent there.

Diet

Adult diet. – Because 1+ herring (common at Jackpot) proved difficult to capture by dipnet, all but one sample caught below foraging birds came from Naked, and those consisted of 0+ and 1+ sand lance and 0+ herring (Tables 3 and 4). The 0+ fish were typically < 85 mm, and the 1+ and 2+ sand lance typically 110 – 132 mm. In 32 dipnet samples (> 1000 fish), 59 % of the fish were < 81mm, 28 % 81-100 mm and 13 % 101-130 mm. These fish ranged in size from 19 mm and 0.06 g (three-spine stickleback) to 130 mm and 24 g (1+ herring), with the latter coming from the Jackpot sample. In both areas, visually identified prey (n = 61) associated with or eaten by adult murrelets were comprised of 41 % herring, 52 % of sand lance, 5 % capelin, and 2 % gadids (Table 4). Of these, most of the herring (84 %) were observed at Jackpot and most of the sand lance (94 %) at Naked. We were not usually able to identify fish eaten by adults during forage watches, but of 28 observations of birds consuming fish on the surface, identified prey included 8 sand lance and 1 possible capelin at Naked, and 7 herring at Jackpot.

Chick diet. – We conducted a total of 94 diet cruises, and recorded 482 fish-holding birds at Jackpot and 129 at Naked. Of these 611 fish, 64 % were identified to species or species group (Tables 3 and 4). Murrelets at Jackpot fed their chicks primarily 1+ juvenile herring (74 – 88 % in a given year), whereas at Naked, they used primarily 1+ and 2+ adult sand lance (67 – 100 %; Table 4).

There was no significant change in chick meal size seasonally, for all observations combined, but there was a brief period of smaller prey in late June and early July (Fig. 6). Chick meal size increased slightly over time in 1999 at both Sites, but average fish size was actually larger in 1997 (Kruskal-Wallis rank sum test $\chi^2 = 10.83$, n = 609, df = 2, P = 0.004). Fish held for chicks (Fig. 7) tended to be smaller at Naked (n = 129, $\bar{x} = 77.1 \pm 1.6$ mm) than at Jackpot (n = 482, $\bar{x} = 85.4 \pm 0.9$; Wilcoxon rank-sum test, $z = 3.83$, $P < 0.001$). Overall, chick-meal fish were usually between 80-100 mm, but ranged up to about 130 mm. The lengths of the larger fish (> 90 mm) could have been underestimated, because as held by the murrelets, their tails often hung below the water's surface. Nonetheless, when compared to fish caught below feeding birds (Fig. 8), those held for chicks were larger (Friedman chi-square = 4.0, df = 1, $P < 0.05$).

At neither Site did chick diet vary among years in the proportions of herring, sand lance, and other species (Table 4; Naked $\chi^2 = 0.55$, df = 2, $P = 0.76$, Jackpot, $\chi^2 = 0.67$, df = 2, $P = 0.72$). However, in 1999, species other than herring and sand lance were observed more frequently, and comprised 17 % of (identified) chick diet at Naked and 14 % at Jackpot (Table 4). Other species included gadids and sandfish in 1997, smelt (Osmeridae) species in 1998, and capelin, gadids, smelt, and salmon in 1999 (Table 4).

Activity Patterns and Foraging Behavior

At-sea surveys

Murrelet density. -- Murrelet densities (Table 5) varied significantly among years ($F_{2,64} = 17.1$, $P < 0.001$), with 1999 having significantly lower densities than the previous two years (Tukey test). Murrelet densities were not significantly different between sites for all years combined ($F_{1,64} = 0.11$, $P = 0.74$) but they were higher at Naked in 1997 and 1998, and slightly higher at Jackpot in 1999 (Table 5). Both sites showed declines during the late fledging period in 1997 and 1998. In 1999, both sites had very low murrelet densities in June (Table 5).

Group Size. – For all surveys ($n = 70$, with 11,280 murrelets), a majority of murrelets were observed as singles (22 %) or pairs (53 %) (Fig. 9). Mean group size for murrelets (Table 6) was largest in 1997 (2.11 ± 0.07), followed by 1998 (1.96 ± 0.04), and 1999 (1.75 ± 0.03). For all years combined (Table 6), mean group size at Naked (2.00 ± 0.05) was slightly but significantly larger than mean group size at Jackpot (1.94 ± 0.05). Overall, group size varied by Site, and had a marginally significant Year effect, with significant interaction between those two factors (Table 6). Within each Site, group size was largest in 1997 and decreased in 1998 and again in 1999 (Table 6). Within Years, the only significant difference in mean group size between Sites was in 1998, when Naked had larger groups of murrelets (Table 6; $t = -3.30$, df = 1958, $P = 0.001$).

In 1997, foraging birds were in larger group sizes than those of non-foraging birds (Table 6), and foraging birds were distributed in groups larger than those observed in 1998 and 1999 (Fig. 9). Group size for foraging murrelets did not differ between Sites, but did differ among Years, with 1999 having significantly smaller group sizes than in the previous two years (Tukey test; Table 6). Pooling data from both Sites, mean group size for foraging murrelets was highest in 1997 (2.82 ± 0.35), intermediate in 1998 (2.49 ± (0.21) and lowest in 1999 (1.56 ± 0.08). In 1999, nearly all foraging birds were either single or in pairs (Fig. 9).

Feeding flocks. – The number of feeding flocks per survey varied between Sites ($\chi^2 = 9.7$, df = 1, $P < 0.01$) and among Years ($\chi^2 = 17.1$, df = 2, $P < 0.01$), with occurrence of feeding flocks always higher at Naked, and decreasing in frequency from 1997 to 1999 (Table 7). Size of mixed-species feeding flocks was generally larger at Naked than Jackpot, and decreased in size each year from 1997 to 1999 (Table 7), but the difference was not significant by Site (Kruskal-Wallis $\chi^2 = 1.8$, df =1, $P = 0.18$) or Year ($\chi^2 = 2.0$, df

= 2, $P = 0.37$). Among mixed-species feeding flocks, murrelets comprised an average of 17.3 % (± 2.1) of all flocks, but ranged from 7 to 33 %. Flock size was highest at both Sites in 1997 (Table 7). Relative to the total numbers of murrelets, only a small percentage (< 9 %) were in feeding flocks, although roughly half of murrelets recorded as foraging did so in flocks of ≥ 3 birds (Table 7). This proportion varied considerably at Jackpot, with participation in flocks for foraging birds ranging from 8 to 58 % (Table 7). Feeding flocks consisting only of murrelets were smaller ($\bar{x} = 5.6 \pm 0.5$ birds, n = 56) than mixed-species feeding flocks ($\bar{x} = 11.5 \pm 1.1$ birds, n = 219; $z = 3.79$, $P < 0.001$).

In mixed-species flocks containing murrelets, the number of murrelets was weakly, but positively related to the numbers of other birds ($R^2 = 0.12$, df = 1,62, $P = 0.004$), but the proportion of murrelets per flock had a stronger, negative correlation with the numbers of other birds (Fig. 10; $R^2 = 0.39$, df = 1,62, $P < 0.001$). Among murrelets involved in mixed-species feeding flocks, nearly 90 % occurred in flocks with < 20 birds of other species, and 50 % foraged in flocks with < 10 birds.

Of the 47 feeding flocks observed during Diet Cruises (late evening, i.e., chick-feeding period), 40 were at Naked. The composition of evening flocks was similar to those observed during daytime surveys at Naked. Evening flocks tended to be larger than those encountered during daytime, and had higher proportions of murrelets, but these differences were not significant. As with daytime flocks, the proportion of murrelets in mixed-species flocks during Diet Cruises were negatively correlated with numbers of other birds ($R^2 = 0.28$, P < 0.001).

Diet Cruises

Overall, the number of adult murrelets encountered during Diet Cruises did not differ between Jackpot Bay ($\bar{x} = 79.0 \pm 7.5$ birds) and Cabin Bay at Naked (84.7 ● 9.0), but the number and proportion of murrelets holding fish varied between Sites ($t = 4.7$, df = 51, $P < 0.001$), with Jackpot having a higher proportion of birds holding fish than at Naked ($\bar{x} = 18.3 \pm 2.9$ % and 4.8 ± 0.7 %, respectively). Neither Site showed significant annual changes in the proportion of birds holding fish, although at Jackpot the 1998 mean (21.5 ± 4.0 %) was nearly twice what it was in 1997 (12.7 ± 5.1 %). At Jackpot, there were no obvious feeding flocks and few or no other species present, but it was obviously a 'hot spot' of murrelet foraging activity in the evening, with a maximum of 44 out of 280 murrelets holding fish during a single cruise. The Sites had distinct diel patterns in occurrence of birds holding fish, and patterns were consistent in all years. At Jackpot, the number of fish-holding birds per half-hour increased rapidly beginning 2 hours prior to sunset and peaking about 0.5 hr before sunset (Fig. 11). At Naked, the number of birds holding fish remained low but steady from 4 hours to 0.5 hr prior to sunset.

Forage Watches

For both Years and Sites combined, during the 73 days of surveys and 226 scans, 11,903 murrelets were counted, of which 3.2 - 9.4 % were observed actively foraging (Table 8). As with the daytime at-sea surveys, few of the total murrelets observed were participating in feeding flocks (< 9 %), but among foraging birds, participation in flocks was more common, if variable. The highest proportion of foraging birds in flocks was at Jackpot in 1998 (72.2 %), but in 1999, none of the foraging birds at that site were in flocks (Table 8). The number of feeding flocks counted during scans was low, but in neither year was there a significant difference between self vs. chick feeding periods in the number of murrelets participating in feeding flocks (1998, n = 13, $z = 1.19$, $P = 0.23$; 1999, n = 20, $z = -9.91$, $P = 0.36$), nor was there a significant difference between Years or Sites. Murrelet group size observed during forage watches did not vary between Sites ($F_{1,5516} = 0.52$, $P = 0.47$), or Years ($F_{1,5516} = 0.34$, P = 0.56), but did vary between periods ($F_{1,5516} = 4.74$, $P = 0.03$), with smaller mean group size during chick period (2.08 ± 0.04 birds) than during self period (2.20 ± 0.04).

During forage watches, there were some Site-specific differences in numbers of birds and behaviors per hourly scan. In 1998, Naked had higher numbers of birds, but similar to the Diet Cruises, Jackpot had higher proportions of birds holding fish (Table 9). In 1999, however, the only significant differences were in the proportion of birds diving and flying, which were both higher at Naked. There were more significant differences between self and chick-feeding periods than between Sites. In both Years, the average number of birds per scan was higher during the self-feeding periods, whereas the proportion of birds holding fish was higher during the chick-feeding periods (Table 9). In both years, higher proportions of birds were diving during the self-feeding periods, but this was only significant in 1998. Maintenance (preening, bathing, etc.) also tended to be more frequent during the self-feeding period, and this was significant in 1999. Most birds, 70 – 90 % on average, were simply recorded as 'on water', which included resting, swimming or socializing. Because the scans did not focus on the behavior of individuals, it is likely that some portion of these birds were between dives, and we would have missed birds underwater, thus the number of diving and foraging birds is a minimum count.

Because differences in most behaviors did not vary by Site or Year, we pooled scans to examine murrelet activity relative to hour of day and group size (Fig. 12). For all hourly scans, most fish-holding occurred between 1700 and 2100 hrs, with a peak around 1900 hrs (Fig. 12). No fish holding was observed after 2100 hrs, although the sample size was small due to insufficient light for observers, and only 9.3 % of scans during chick-feeding period occurred after 2100 hrs. The fish holding occurred in conjunction with smaller group sizes of murrelets. There was a slight increase in fish-holding during early morning hours when more murrelets were present (Fig. 12). This contrasts with observations of birds diving, which occurred throughout the day almost entirely in the smallest group sizes. Neither fish-holding nor diving coincided with total murrelet abundance, which peaked in the morning when large groups were present. Group size dropped sharply in the afternoon hours, and by late evening the few birds present were usually in small groups or single (Fig. 12).

Diving patterns. – Differences in dive and pause durations were more pronounced between Sites than between Years or self vs chick-feeding periods (Table 10). In general, dive times were shorter at Naked, and varied significantly between Sites ($F_{1,130} = 8.23$, $P = 0.005$), but not between Years ($F_{1,130} = 1.55$, $P =$ 0.22). Pause times, also briefer at Naked, varied both by Year ($F_{1,122} = 6.26$, $P = 0.01$) and by Site ($F_{1,122} =$

15.96, $P < 0.001$). Within-Site, there were no significant differences in dive or pause times by Year or between self vs. chick-feeding periods (Table 10). In both 1998 and 1999, pause times were significantly longer at Jackpot, and dive times tended to be longer, but not significantly so, at Jackpot. Sea conditions during forage watches did not range widely (glassy to light chop and occasional whitecaps), because of the protected topography of the bays, and because we stopped observations when it became difficult to follow birds. Within these parameters, sea state had no significant effect on dive ($F_{1,122} = 1.72$, $P = 0.19$) or pause duration ($F_{1,115} = 2.78$, $P = 0.10$).

DISCUSSION

Prey Selection and Energetic Implications

Murrelets in PWS delivered large, nutrient-rich prey to their chicks, while they often consumed smaller fish themselves. This is consistent with optimal foraging theory for a central-place forager (Orians and Pearson 1979) and with patterns observed in other alcids (Gaston and Jones 1998, Davoren and Burger 1999, Jones et al. 2002). The most efficient way for a parent to increase energy delivery to its chick is to increase the size of prey (Anthony et al. 2000), which murrelets did by selecting 1+ or 2+ sand lance and 1+ herring for their chicks. Similar patterns have been observed elsewhere (Carter and Sealy 1990, Mahon et al. 1992, Strachan et al. 1995) but not examined relative to differences in prey. We show this pattern to be consistent across years, even when prey types varied spatially, suggesting that the minimum requirements for chick meals fall within a narrow range of fish size and nutrient value.

Parents will also be restricted at the larger end of chick-meal size, because chicks are limited in what they can swallow, and fish girth may be more limiting than length. For example, pigeon guillemot chicks consume sand lance and gunnels (Pholidae) that are much longer than the flatfish (Pleuronectidae) they often reject (Kuletz 1983), and red-throated loon (*Gavia stellata*) chicks often reject deep-bodied seaperch (Embiotocidae; Reimchen and Douglas 1984). In Alaska, sizes of sand lance and herring juveniles increase substantially during the summer (Robards et al. 1999b, Iverson et al. 2002), and 1+ herring > 130 mm, which are wider than sand lance, may be at the upper size limit for murrelets (Burkett 1995). We did not see a consistent seasonal trend in size of fish held for chicks, with the exception of smaller fish early in the chick-rearing period (Fig. 6). This suggests that parents are selecting small fish for newly hatched chicks, but quickly switch to larger prey. Our estimates of fish size relative to bill length may have been too crude to track seasonal size increases in prey, although there was some indication of such an increase in 1999 (Fig. 6).

In addition to the energetic considerations, murrelets are subject to predation *en route* to or at the nest (Marks and Naslund 1994, Nelson 1997), so they should reduce risk by minimizing trips. During the approximately 30 day chick-rearing period (Nelson 1997, Bradley et al. 2002), each member of the nesting pair of marbled murrelets will fly from forage grounds to its inland nest 1 - 5 times daily, primarily around dawn, and less frequently at dusk (Burger 2001, Bradley et al. 2002, 2004). A murrelet is thus constrained at least two ways when provisioning chicks: First, being a single prey loader it must maximize energetic content of the meal delivery. Second, because of predation risks, it has only a few hours near twilight in which to capture and deliver chick meals, and it must maximize foraging efficiency during this crucial period.

Based on observations at nests, the combined efforts of both parents result in a mean of about 3 meal deliveries per 24 hr period, but can range up to 8 deliveries (Nelson 1997). In British Columbia (BC) male parents made, on average 1.3 times more deliveries overall and as much as 2.3 times, than did the female (Bradley et al. 2002). Thus there is considerable range in number of trips made by provisioning birds, and a male might make 5 captures and deliveries during the dusk and pre-dawn chick-feeding periods. Hull et al. (2001) speculated that the number of deliveries may be influenced by pay load size and distance of the nest inland. A more direct influence might be the energy needs of the chick relative to the energy density of available prey.

Using the mass of the chick at fledging and the duration of the nestling period, it is possible to approximate the energetic requirements of chicks (Weathers 1992). Using these two components, the peak level of daily metabolized energy (peak-DME, kJ d^{-1}) and the total amount of energy metabolized until fledging (TME, kJ) can be calculated. Visser (2002) found that both of these values were significantly higher for seabirds than birds in general, and provided modified equations for seabirds. Using Visser's equations and kJ values for different prey types (Table 11), we examined the range of potential delivery requirements for marbled murrelets. For simplification, we assumed consistent prey use at a nest and similar assimilation efficiencies among prey types. The estimates (Table 12) illustrate the range in parental foraging and delivery trips possible under different scenarios. For marbled murrelet chicks, we calculated a peak-DME of 261 - 303 kJ d^{-1} (depending on fledging mass of the chick and length of nestling period). With these energetic demands, the daily number of fish required varied considerably with type of prey, and ranged from approximately 2 herring to 9 male capelin (Table 12). These numbers correspond to observed delivery rates for marbled murrelet chicks (Nelson 1997). Over the course of the 27 – 40 day nestling period, estimated fish deliveries could range from 38 herring to 255 capelin to raise a chick. Under all scenarios, relative to the number of required 1+ herring, deliveries must be multiplied by 2.0 for 2+ sand lance, 2.6 for pollock, 3.4 for 1+ sand lance, and 4.3 for male capelin.

Murrelets selected prey for their chicks that were the most energy-dense prey available at each site. In other seabirds, high-lipid, energy-dense fish such as herring and sand lance have been shown to increase chick growth rate, fledging weight, and chicks per brood (Golet et al. 2000, Litzow et al. 2002, Romano 2000, Suryan et al. 2000). The extra cost of obtaining a large herring, which is typically farther offshore in deeper water than sand lance (Haldorson et al. 1999, this study), and may only be near the surface for limited times (Foy and Norcross 1999, Thomas and Thorne 2001), could be offset by the energetic savings of making fewer deliveries. In comparison, the 0+ herring, at an average 6 g and 32 kJ (similar to a male capelin), would necessitate quadrupling the delivery rate, which apparently makes it unsuitable for murrelet chick meals, even though per gram it is energy-dense (Table 11). For seabirds that carry multiple fish per load (whether whole or regurgitations), and deliver throughout the day, the 0+ age class fish are acceptable as chick-food. In PWS, black-legged kittiwakes (Suryan et al. 2000), tufted puffins (Piatt et al. 1997), and arctic terns (*Sterna paradisaea*) (KJK, pers. obs.), make multiple deliveries throughout the day, and typically feed their chicks 0+ herring and sand lance.

Fish species used infrequently by PWS murrelets were generally of low nutrient value. Although capelin can be energy-dense, their lipid content varies considerably by sex and breeding condition (Anthony et al. 2000), and the post-spawn schools around Naked would have been at the lower end of their energetic value (Table 11), though adequate for adult murrelets to consume for their own needs (Table 3). Additionally, capelin were not a consistent presence during this study (Tables 3, 4; Brown 2002), and even nutrient-rich prey will be ignored by seabirds if they are not regularly available in sufficient quantities (Kuletz 1983, Erickstad et al. 1990, Piatt 1990, Skov et al. 2000). During this study, walleye pollock comprised the largest fish species biomass in PWS (Haldorson et al. 1999), but they were a minor part of seabird diet during the breeding season (Tables 3 and 4; Golet et al. 2000, Suryan et al. 2002,). Gadids were rarely taken as murrelet chick food, but adult murrelets consumed gadids in PWS between 1977 and 1991 (Kuletz et al. 1997). These early diet studies were based on stomach samples, and since we relied on visual observations during the present study, we could have missed fish that were consumed below the water's surface.

Although we did not observe or catch gadids below feeding birds, hydroacoustic surveys indicated that they were present, but farther offshore, around both sites (Ostrand 1999, Haldorson et al. 1999). In these deeper, offshore waters, Ostrand et al. (2004) concluded that murrelets altered their prey selection criteria as prey availability changed. In a year when herring were abundant, murrelets selected small schools near the surface, but when gadids were abundant, murrelets selected for herring, regardless of ease of access. This suggests that adult murrelets prefer high-value herring for themselves as well as for their chicks. Besides occupying deeper waters, gadids have a low proportion of lipids (Table 11), and experimentally, tufted puffin chicks raised on gadids did poorly compared to chicks raised on high-lipid fish (Romano 2000). Other low-lipid fish such as smelts, sandfish, salmon smolt, and stickleback, were also present at both sites, as indicated by prey fed to pigeon guillemot chicks (Golet et al. 2000) or caught below adult murrelets (Table 3), but they were rarely used as murrelet chick meals.

The energetic content of prey delivered to young is critical for central place foragers (Kacelink and Cuthill 1990, Ydenberg 1994), and the importance of high-nutrient prey for seabird chick growth and fledging success has been demonstrated under experimental (Romano 2000) and field conditions (Hislop et al. 1991, Golet et al. 2000, Suryan et al. 2000). By increasing reproductive success, the adult improves its long-term fitness in lifetime productivity (Stearns 1992, Ydenberg 1994). However, there are indirect, short-term costs to the provisioning adult, such as loss of time for nest site defense, social interactions, and self-maintenance (Monaghan et al. 1994, Suryan et al. 2002, Litzow and Piatt 2003). For alcids, an additional energetic cost of reproduction for the female is production of a large egg (Monaghan and Nager 1997). Bradley et al. (2002) proposed that for murrelets, the greater chick-feeding contribution by the male allows the female to recoup the energetic costs of producing an egg equivalent to 20 % of her body weight

(Nelson 1997). Such energetic trade-offs (costs and risks of provisioning, reduced social and maintenance time, sex-biased provisioning rates) suggest that the selection of prey for chicks is important to the welfare of the individual.

Foraging Behavior

Prey location and site-specificity

Colonially nesting birds may obtain information on prey location from neighbors at or near the colony (Ward and Zahavi 1973, Wittenberger and Hunt 1985, Burger 1997). Away from the colony, birds may benefit from 'local enhancement' cues (aggregations of other birds) to find food patches (Buckley 1997, Davoren et al. 2003a). Presumably, non-colonial birds like the marbled murrelet would lack the advantage of obtaining information on prey location from neighbors while at its nest. Because murrelets may nest up to 70 km inland (Nelson 1997), they could not easily observe birds in nearshore waters to obtain local enhancement cues until they returned to sea. Additionally, murrelets in PWS were foraging for their chicks in secluded nearshore areas when few other birds were present, further reducing local enhancement cues. Murrelets holding fish might be a form of local enhancement, assuming the fish-holding adults remained for some time at the catch site, which appeared to be the case at Jackpot. For murrelets, however, particularly during crepuscular hours, familiarity with local prey and local conditions may be more reliable than social cues.

Within-site, the use of prey species by murrelets was fairly consistent across years, for both self and chick feeding, and corresponded to the relative abundance of common species at a site (Table 4, Fig. 2, 3). Other prey, such as capelin, smelt and gadids, also tended to be site-specific (Table 4). The spatial distribution of fish in PWS is highly heterogeneous and locally consistent over time, being closely linked to meso- and fine-scale habitat features (Foy and Norcross 1999, Brown and Moreland 2000, Stokesbury et al. 1999a, 1999b, 2002). Our findings were consistent with these more comprehensive studies of fish distribution (Fig. 2,3). The prey fed to murrelet chicks also mirrored the spatial differences found among pigeon guillemots at these two sites. For example, guillemots at Naked fed their chicks more sand lance, and guillemots at Jackpot fed their chicks 1+ herring (Golet et al. 2000, 2002). Pigeon guillemots are sensitive indicators of local prey availability (Litzow et al. 2000, Golet et al. 2002), and our results indicate that murrelet prey use also reflects the availability of energy-dense prey in an area.

Because murrelets often forage alone or in pairs, knowledge of specific forage areas would increase foraging efficiency. Familiarity with a habitat and local prey patterns may be an important foraging strategy for seabirds (Irons 1998, Hunt et al. 1999). Radio-tagged murrelets in PWS tended to forage within a few kilometers of their other foraging locations (Chapter 1), and studies of radio-tagged murrelets in British Columbia suggested similar fidelity to meso-, and perhaps fine-scale forage areas (Hull et al. 2001, Bradley et al. 2004). Forage site fidelity, combined with persistent (i.e., spatially predictable) populations of key fish species, would result in the spatially consistent pattern of prey use that we observed over these three years.

In addition to spatial patterns, knowing the diel activity patterns of prey would also reduce the search time involved in their capture. Juvenile herring rise towards the surface in pursuit of vertically migrating zooplankton during crepuscular hours (Foy and Norcross 1999, Thomas and Thorne 2001, 2003), making them temporally predictable. The temporal patterns and numbers of murrelets foraging for chick food in Jackpot Bay (Fig. 11) clearly indicates that it was a 'hot spot' for evening procurement of a high-value prey. In contrast, we never located a comparable site at Naked. Notably, the evening foraging activities at the two fine-scale sites (Jackpot Bay and Cabin Bay) were not indicative of murrelet breeding density or success at the meso-scale (Jackpot and Naked). Previous studies showed that Naked had inland dawn activity indicative of nesting (Kuletz et al. 1995b), and compared to Jackpot, Naked had higher adult and juvenile murrelet densities at sea (Kuletz and Kendall 1998, Chapter 4). This suggests that birds foraging at Naked in the evening were either too dispersed to quantify with the diet cruise, or most birds foraged elsewhere in the evening.

Diving and temporal patterns

Dive patterns. -- Although murrelets selected larger prey during chick-feeding periods, we found no evidence of longer, deeper dives at this time. This contrasts with rhinoceros auklets (*Cerorhinca monocerata*), which made shorter dives during the day when self-feeding on small fish, and longer dives during chick-feeding periods when they foraged for larger fish (Davoren and Burger 1999). However, it is consistent with the shorter dives made by thick-billed murres (*Uria lomvia*) during crepuscular hours compared to daytime (Jones et al. 2002). Jones et al. concluded that the shorter dives were due to reduced light levels, and possibly to feeding on vertically migrating prey near the surface. Similarly, our results suggest that habitat and prey species affected the dive patterns of murrelets more than the pursuit of a particular prey size for chicks, although these factors are not mutually exclusive.

Differences in dive duration were site-specific, with both dive and pause durations shorter at Naked. Compared to Jackpot, waters at Naked were generally shallower, and fish (i.e., sand lance) tended to be smaller. Sand lance also tend to form smaller schools closer to shore in shallower water compared to juvenile herring (Brown et al. 1999, this study). The longer dives and longer pause durations at Jackpot compared to Naked, suggest that 1+ herring were slightly more costly for murrelets to procure than sand lance. In all three years, dive duration was consistent, but pause duration was longer in 1999, when fish schools were larger and farther offshore, and presumably fish had access to deeper water for escape. Due to physiological constraints, pause duration is more variable than dive duration, and may be a better indicator of effort (Monaghan 1996, Jodice & Collopy 1999). Maximum dive depth for murrelets is estimated to be approximately 40 m (Burger 1991, Mathews and Burger 1998), but they are more often associated with shallower water (Day and Nigro 2000, Chapter 1), and in deeper water may rely upon physical oceanic features that bring prey towards the surface (Carter and Sealy 1990, Hunt 1995b, Chapter 1).

Although birds may have been diving deeper for herring at Jackpot than they did for sand lance at Naked, behavioral observations suggested that birds at Naked were taking longer to capture chick meals. In both 1998 and 1999, a larger percentage of birds were observed diving at Naked, yet a much lower percentage of birds were holding fish (Table 9). We could not track complete foraging bouts of individuals, but our results were consistent with the scenario that access to larger, energy-rich 1+ herring was energetically efficient for the adult bird despite the potentially greater diving effort.

Night foraging. – During forage watches, murrelets sharply increased fish-holding late in the evening and during diet cruises we observed more birds holding fish at dusk than at dawn. Murrelets showed similar patterns elsewhere (Sealy 1975, Carter and Sealy1990, Speckman et al. 2000). Despite the infrequent observations of murrelets at sea holding fish near dawn, most chick meal deliveries occur during this period (Kuletz et al. 1995a, Nelson 1997, Burger 2001, Bradley et al. 2002). It seems unlikely that fish caught in the evening were held for up to four hours, given that fish would desiccate during that time. Fish held in the early evening were probably delivered later as darkness increased. The temporal differences in murrelet fish-holding activity between Cabin Bay and Jackpot Bay probably reflect the greater use of herring at the latter, which had increasing numbers of murrelets holding fish as sunset neared (Fig. 11). Because most murrelets leave nearshore waters and return after sunrise, it is more likely that fish delivered before sunrise were caught offshore and delivered immediately. In PWS a variety of birds and marine mammals feed at night on herring that migrate to the surface, and this activity can occur in offshore waters (Thomas and Thorne 2001, 2003).

Murrelets in PWS foraged between sunset and sunrise, with chick meal deliveries recorded for one radio-tagged bird at 60 and 110 min after sunset and 40 min prior to sunrise (Kuletz et al. 1995a). Six radio-tagged murrelets with suspected nests also showed a peak in flying activity in and out of a fjord 1 – 2 hours before sunrise, presumably feeding chicks (Kuletz et al. 1995a). Light conditions at these hours are low, but at latitude 61^{0}N during July, there is no official 'nautical twilight' until August (U. S. Navy 2005). There is some evidence for 'night time' chick-feeding as far as 54^{0}N in British Columbia (Sealy 1975, Carter and Sealy 1990), but not farther south (Nelson and Hamer 1995, Jodice and Collopy 1999). Murrelets thus appear to adjust diel foraging patterns to latitudinal difference in hours of civil twilight, and in PWS they make maximum use of longer periods of twilight to forage. Similar latitudinal differences in foraging behavior have been observed among populations of thick-billed murres (Jones et al. 2002).

Influences on foraging group size

Participation in mixed-species feeding flocks by murrelets is highly variable, ranging from no participation to occurrence in every flock (Porter and Sealy 1981, Chilton and Sealy 1987, Mahon et al. 1992, Hunt 1995a, Ostrand 1999). These early studies did not quantify the proportion of total murrelets foraging in flocks or the prey conditions that prevailed. Our results indicate that differences in observed behaviors may result from differences in fish abundance or prey types that affect the propensity of murrelets to participate in feeding flocks. Fish schools in PWS are typically small and dispersed (Brown et al. 1999, Haldorson et al. 1999, this study), and murrelets appear to be adapted to locating and feeding at small schools (Ostrand et al. 1998). Presumably this is why murrelets were often the main initiators of feeding flocks in British Columbia and PWS (but see Porter and Sealy 1981) - they drive fish to the surface, attracting other seabird species (Mahon et al. 1992, Hunt 1995a, Maniscalco and Ostrand 1997, Ostrand 1999). However, murrelets are often displaced or suffer kleptoparasitism by larger birds (Mahon et al. 1992, Maniscalco and Ostrand 1997). Group foraging thus appears to have disadvantages for murrelets, which may explain the negative relationship we found between numbers of other birds and the proportion of murrelets in a flock. Foraging in groups is obviously a flexible behavior influenced by multiple factors, including prey abundance, prey type, and chick provisioning.

Prey abundance. -- With low prey abundance (1997), murrelets tended to form larger murrelet groups and participated in more mixed-species flocks. At intermediate prey abundance (1998), more murrelets foraged as pairs and group sizes were intermediate. When prey were abundant (1999), murrelets foraged primarily as individuals or pairs (Fig. 9). Thus, group size for murrelets, both intra- and inter-specific, declined as prey abundance increased. In contrast, Piatt (1990) found that for murres and puffins, group size and abundance of feeding flocks increased with capelin school density. For murrelets, unlike most seabirds, the preferred mode at high prey abundances may be to forage solitarily or in pairs. Nonetheless, murrelets will forage in groups when prey abundance is low, despite the potential for interference.

With fewer schools around our study sites in 1997, birds might have had more difficulty in locating prey patches, which were also smaller in surface area that year. Multi-scale studies have found that the relationship between seabird and prey distribution breaks down at fine scales (100s m), suggesting that birds are adept at finding coarse-scale forage areas, but are less successful at locating every fish school (Schneider and Piatt 1986, Mehlum et al. 1996, Davoren et al. 2002). In addition, predators may find it profitable to forage widely on dispersed patches when prey are abundant, but when abundance is low they must closely track prey patches (Hunt et al. 1999, Letcher and Rice 1997, Vlietstra 2005). In the latter case, murrelets would be less likely to find fish schools that did not already have other birds associated with them, which may be why murrelets were found in feeding flocks more frequently in 1997.

The distributional relationship between seabirds and their prey often show a threshold effect, i.e., the aggregation of birds requires a certain level of prey density (Piatt 1990, Vlietstra 2005), or its converse, birds reach a threshold where they will avoid gathering at higher densities regardless of prey abundance (Davoren et al. 2003b). Although murrelets at Naked and Jackpot made less use of feeding groups when prey were abundant, we witnessed activity elsewhere suggesting that at a higher threshold of fish abundance large groups were not avoided. In northeast PWS, where large schools of 0+ herring occurred in 1997 and 1998 and attracted thousands of birds, murrelets formed large loose aggregations, and individuals and pairs moved frequently among ephemeral 'hot spots' that emerged throughout the general area (KJK pers. obs). Similar aggregations have been noted in southeast Alaska (Speckman et al. 2003) and British Columbia (Sealy 1975, Carter and Sealy 1990, Burger 2002), but not farther south where murrelets are less abundant (Nelson 1997).

Prey type. -- Foraging strategy of a seabird is likely influenced by prey type (i.e., species or size) as well as prey abundance (Davoren 2000, Irons et al. 2000, Jones et al. 2002, Davoren et al. 2003b). Although greater annual abundance of fish corresponded to smaller group sizes and less participation in feeding flocks, spatially, Naked had generally higher fish abundance coincident with more mixed-species flocks, greater participation in flocks by murrelets, and larger murrelet groups than at Jackpot. This is contrary to the temporal (annual) relationship between murrelet group size and total fish abundance, but it is consistent with evidence that birds foraging on smaller fish may require greater cooperation among predators (Götmark et al. 1986, Irons et al. 2000). At Naked, where there were more schools of 0+ age class fish, all birds foraged in larger groups (Table 7). For murrelets, if smaller fish can be swallowed below the water's surface, there is also less risk of kleptoparasitism. Finally, the presence of more birds during daytime hours, as at Naked (Table 7), may make interspecific interactions unavoidable.

Chick provisioning. -- Murrelets demonstrated distinct changes in group foraging patterns during chick-feeding periods, with fewer murrelets near shore and more holding fish at the surface, concurrent with smaller group sizes and lower numbers of other bird species. A similar pattern was observed in rhinoceros auklets, which fed in groups during the day but during evening chick-feeding periods were solitary (Davoren and Burger 1999). The need to bring fish to the surface prior to meal delivery might necessitate procuring chick food during twilight hours, when fewer other birds were present. Small group size also coincided with larger prey size, as observed at Jackpot where larger herring were the predominate food.

Environmental Influences. -- In summary, murrelets tended to forage solitarily when provisioning chicks, but foraging group sizes, whether intra- or inter-specific, were also influenced by prey abundance and prey type. Ultimately, foraging patterns are determined by environmental factors acting on prey (Ricklefs 2000, Hamer et al. 1993, Suryan et al. 2002). Local patterns in fish distribution are overlaid on large-scale fluctuations in climate and marine conditions that affect primary productivity and finally, prey abundance and availability. Murrelets have been shown to alter their distribution at large geographic scales, such as movement offshore and to cooler waters, under anomalous warm ocean conditions (Strachan et al. 1995, Becker and Beissinger 2003, Yen et al. 2003). Within PWS, murrelets may depend on characteristically stratified waters to forage efficiently (Hunt 1995b, Ostrand et al. 1998), and this feature varies with the amount of freshwater runoff and wind-forcing (Gay and Vaughan 2001). At the meso-scale we studied, in 1997 surface waters were fresher than the following two years (see Study Area, Methods), which can intensify stratification and eventually lower productivity or result in fish moving into deeper waters (Abookire et al. 2000). We did, in fact, observer lower fish abundance at our study sites in 1997, concurrent with more murrelets foraging in relatively large groups.

Marbled murrelets have one of the largest geographic ranges among alcids, extending from central California to the Bering Sea (Nelson 1997), and thus occupy a wide variety of marine habitats, including several major ocean currents, continental shelf features, and basins (McShane et al. 2004). Given this range, murrelets would have to be flexible in diet, and consequently, should be flexible in foraging behavior (Hunt 1995a). Even within a year, murrelets in PWS must adapt to changes in prey size and distribution. At sites only 50 km apart we found prey use and foraging behaviors that were different from each other, but consistent in several aspects over time. Characteristics closely associated with meso- and fine-scale habitat features, such as prey species and age classes consumed, as well as murrelet diving patterns, remained consistent over time, whereas group size and participation in feeding flocks were more flexible, and were affected by prey abundance, prey type, and chick provisioning. In addition, there was indirect evidence that murrelet foraging behavior could be affected by the relative abundance of other seabird species.

Conservation Implications

Since the early 1970s the marbled murrelet population in PWS has declined 85 % (Appendix A). Although loss of nesting habitat has been implicated as a primary factor in murrelet population declines south of Alaska (Burger 2002, McShane et al. 2004), changes in available prey may have impacted murrelet populations in southcentral Alaska (Agler et al. 1999, Kuletz et al. 1997, Lance et al. 2001). Both herring and sand lance are important forage fish for murrelets throughout their range, although their relative use by murrelets varies geographically (Burkett 1995). At our study sites, sand lance and herring accounted for > 90 % of all murrelet diet observations of adults and chicks. In earlier PWS studies, the diet of adult murrelets changed from primarily sand lance in the 1970s, to gadids in the mid-1980s and early 1990s (Kuletz et al. 1997). It is not known whether this affected productivity of murrelets, but declining population trends suggest that either productivity or adult survival have been poor. In particular, the crash of herring stocks in PWS after 1993 (Pearson et al. 1999, Thomas and Thorne 2003) could have affected murrelets.

Alternative prey species (i.e., capelin, gadids, smelt), while part of adult murrelet diet, do not appear to be used substantially for raising chicks. Sand lance are energy rich and important to murrelets at some locations, but they are limited primarily to the central and southwest islands of PWS (Fig. 2), and have large fluctuations in availability (Golet et al. 2000). Capelin are of moderate energy-density but are limited spatially, occurring mainly in southwest PWS (Brown 2002). Salmon smolt have only a brief period of availability in the bays and nearshore waters (Willette et al. 2001) and, like pollock, are not energetically advantageous as chick food.

Herring appear to comprise the 'wasp-waist' of the PWS ecosystem, occupying a key position between lower and upper trophic levels (Thomas and Thorne 2001, 2003). Adult murrelets depend on the 0+ age group to provision themselves, and on the 1+ age group to raise their chicks. Murrelets will fly great distances to forage at sites that have consistently high fish abundance (Carter and Sealy 1990, Whitworth et al. 2000), but such sites are not typical of PWS (Ostrand 1999, Brown et al. 1999). There has been recognition of the need to protect daytime feeding areas for murrelets (Day and Nigro 2000, McShane et al. 2004, Speckman et al. 2004), but not of habitats or sites specifically valuable to birds rearing chicks. Sites such as Jackpot Bay, even if they have low numbers of murrelets during the day, could be important for procuring chick food. Identifying these sites will require a methodology specific to the behaviors and distribution of murrelets foraging for chick food.

Management of important foraging areas may be more critical when prey stocks have been depleted. If PWS herring stocks remain depressed, it could have long-range implications for the ecosystem (Thomas and Thorne 2001) and for murrelets. There could be indirect effects as well, such as the potential for greater murrelet participation in mixed-species groups when prey is scarce. With low prey abundance, murrelets might simultaneously face intra-specific interference and competition for fewer fish. The changes in seabird species composition in PWS suggest that this could in fact become a problem. In 1989, the PWS murrelet population was twice the size of the next most abundant species, black-legged kittiwakes, and roughly equal to that of all larids combined (data in Sullivan et al. 2005, Appendix D). Murrelets have since declined (Appendix A), and in 2004 they were roughly equal to the kittiwake population, and half that of total larids (data in Sullivan et al. 2005, Appendix D). Hunt (1995a) speculated that increasing numbers of larids could be detrimental to murrelets, and studies of murrelet interactions with other species substantiate this scenario (Maniscalco and Ostrand 1997, Ostrand 1999, this study).

The interactions between dietary requirements, prey availability, and foraging behaviors require that we have a better understanding of these connections to address conservation issues. Our results illustrate the importance of multi-year and multi-habitat studies when examining these relationships, to better anticipate potential problems with changes in prey stocks or seabird communities.

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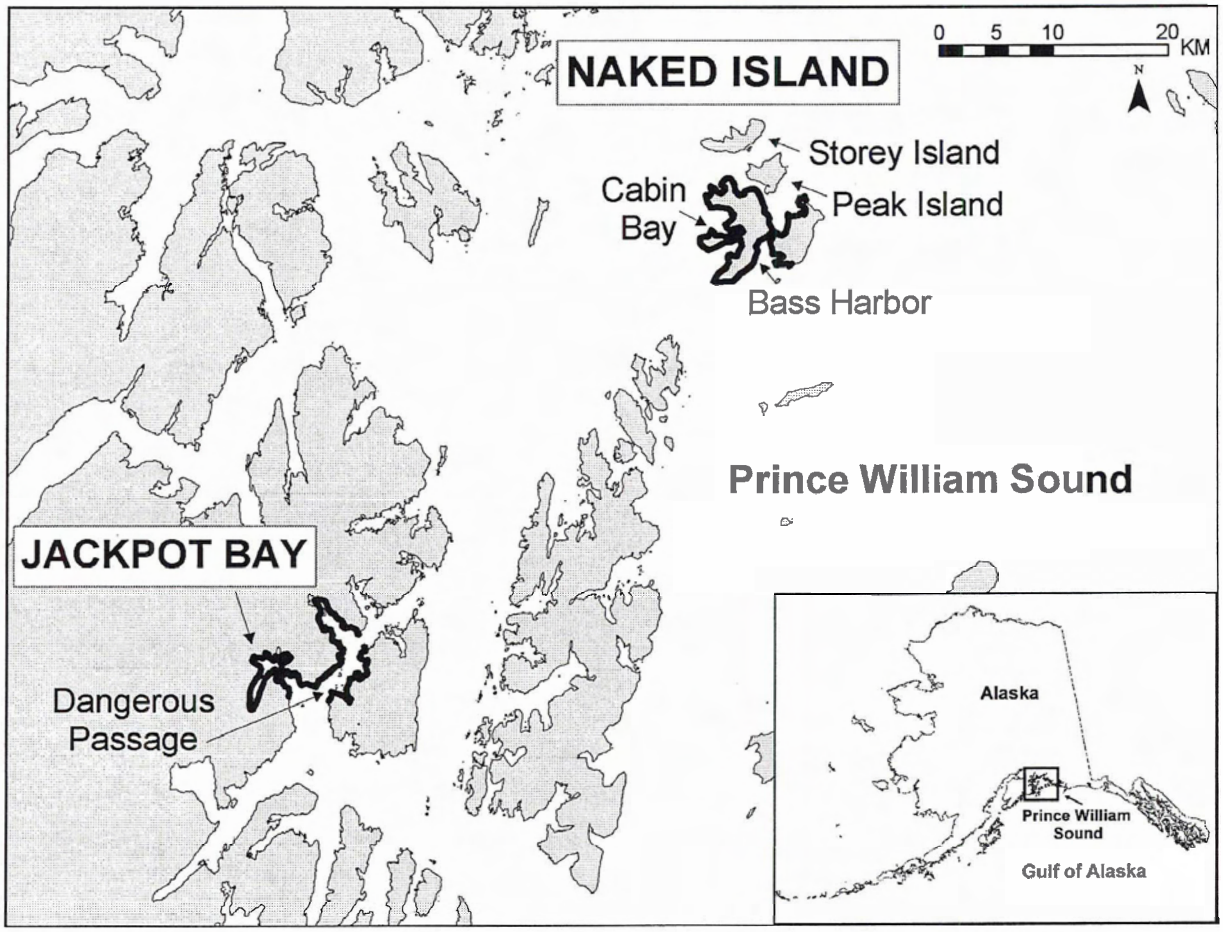

Figure 1. Study sites in Prince William Sound, Alaska for murrelet foraging studies from 1997 – 1999. Dark shoreline indicates location of transects covered during boat-based surveys. The land-based forage watch sites were in Jackpot Bay and Cabin Bay.

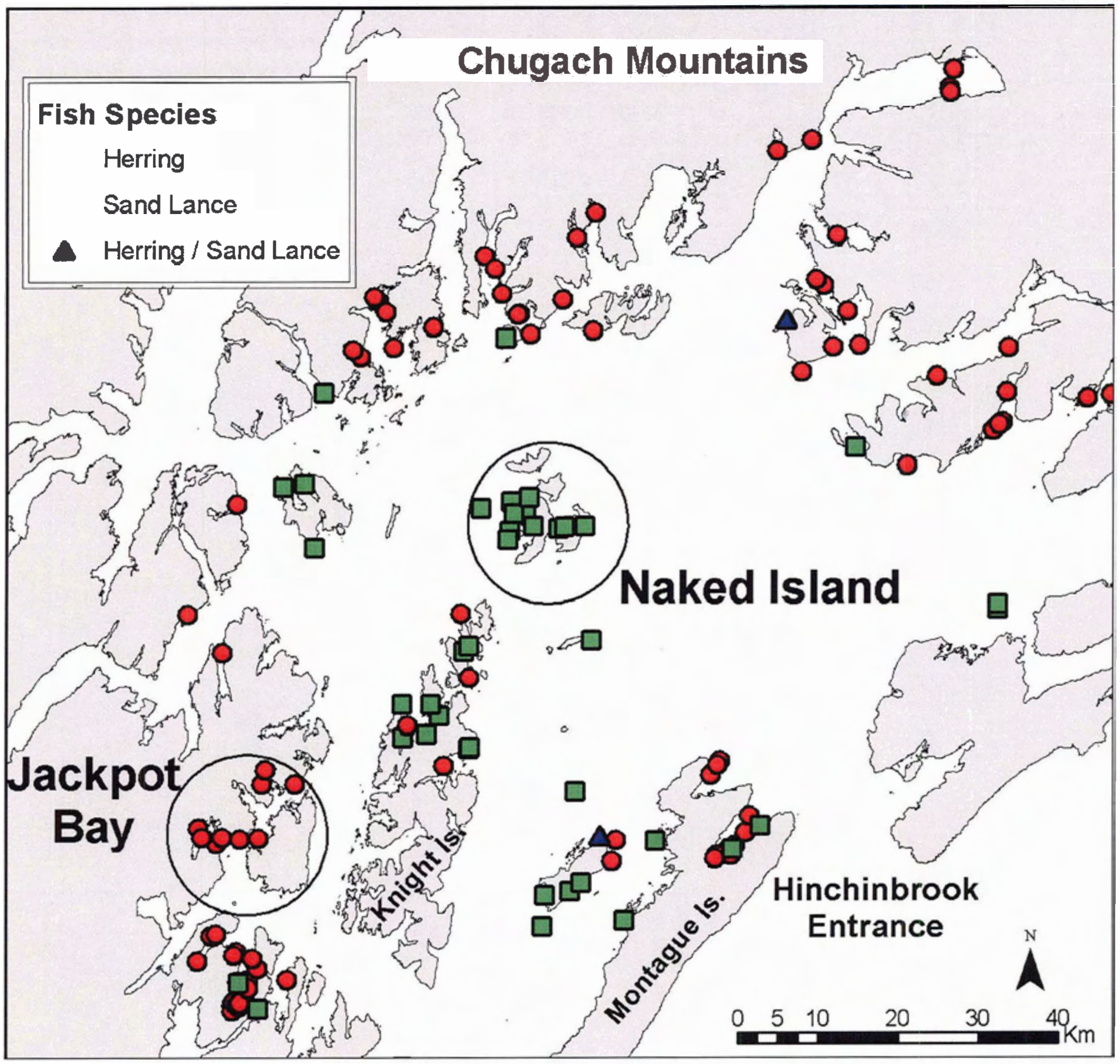

Figure 2. Location of herring and sand lance samples obtained in conjunction with fish and murrelet surveys in Prince William Sound, Alaska, from 1996 to 1999.

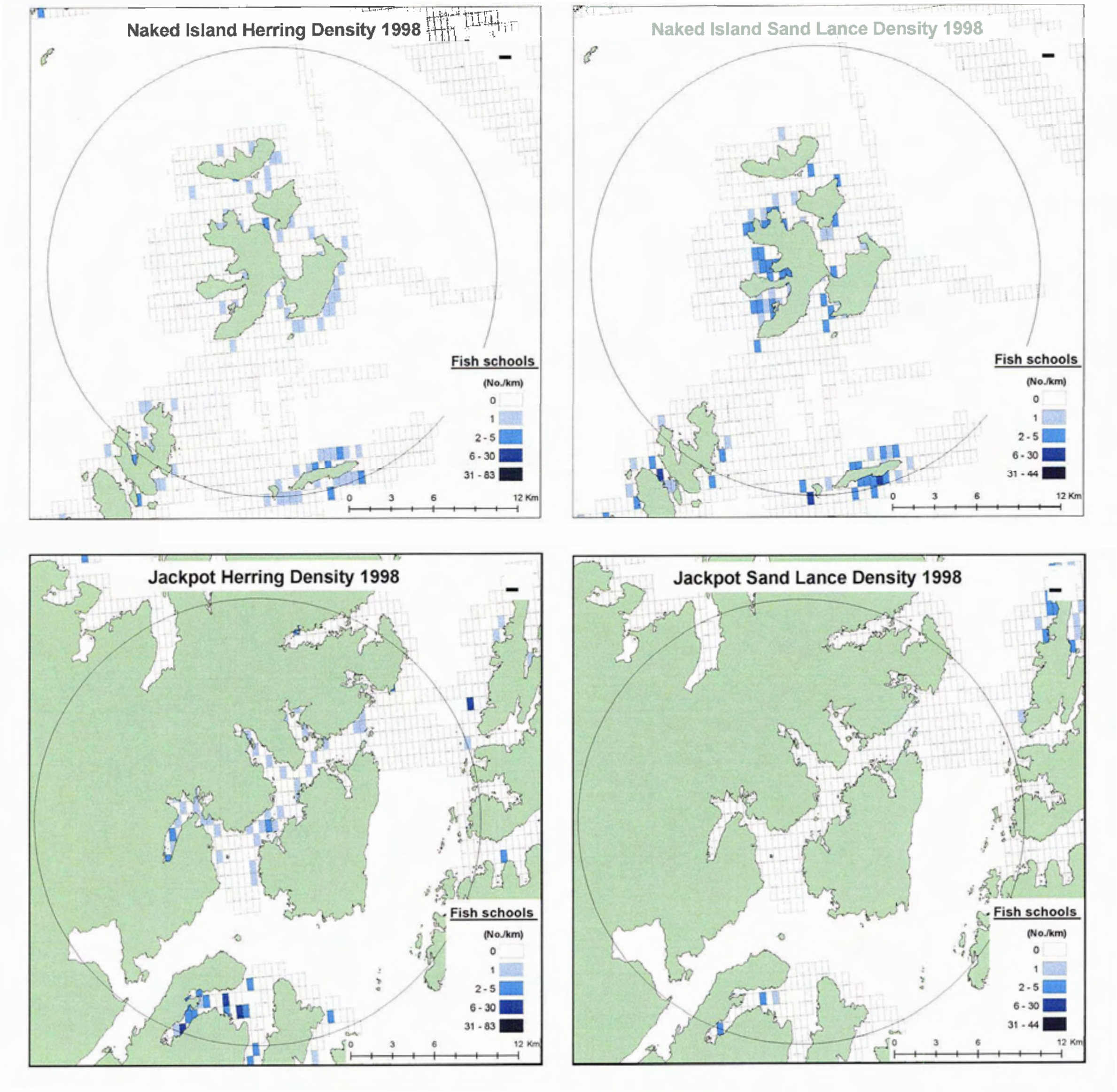

Figure 3. An example of aerial coverage and binning blocks used to calculate fish school density at murrelet study sites. Shown are maps of herring (left) and sand lance (right) fish school densities for Naked (top) and Jackpot (bottom) in 1998.

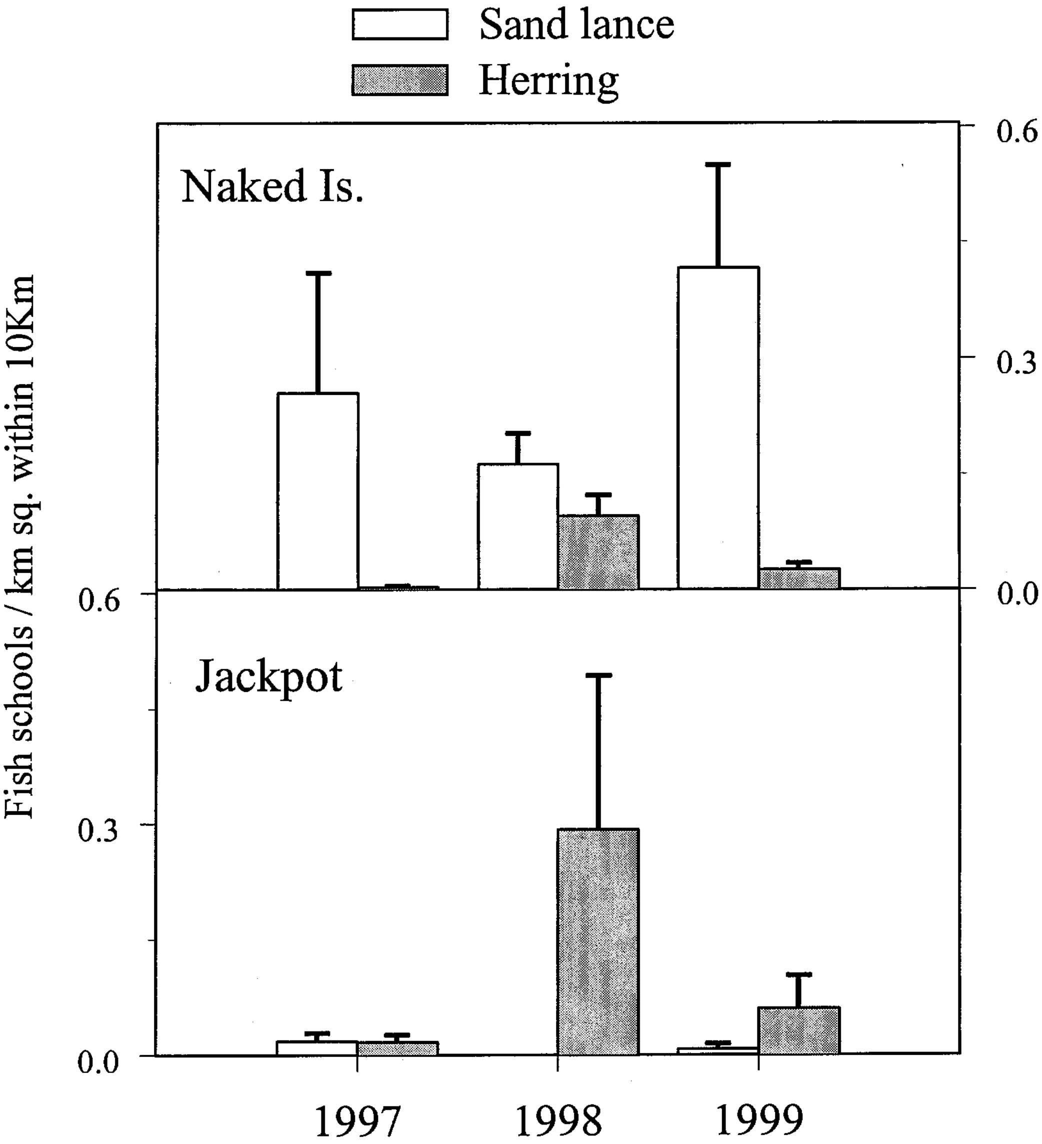

Figure 4. Density of fish schools observed during aerial surveys, within 10 km radius of Naked and Jackpot study sites in Prince William Sound, Alaska. Shown are means ± SE.

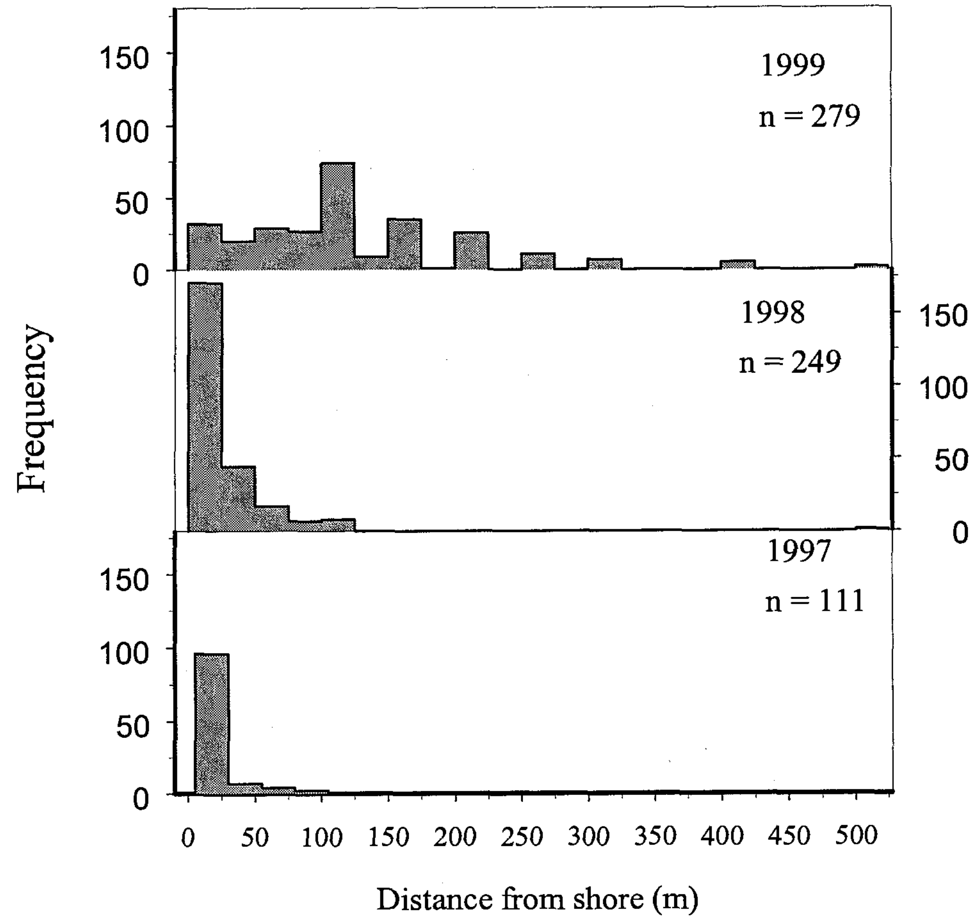

Figure 5. Frequency of fish schools relative to distance from shore recorded during aerial surveys of the Naked and Jackpot sites (10 km radius) in Prince William Sound in 1997 – 1999. Two schools > 800 m from shore were omitted for this graph (but not from the analyses). The difference in distance from shore was not significant between sites, but was among years (ANOVA; $F_{1,634} = 247$, $P < 0.00$). Years 1997 and 1998 were both significantly different from 1999 (Tukey test, $P < 0.05$).

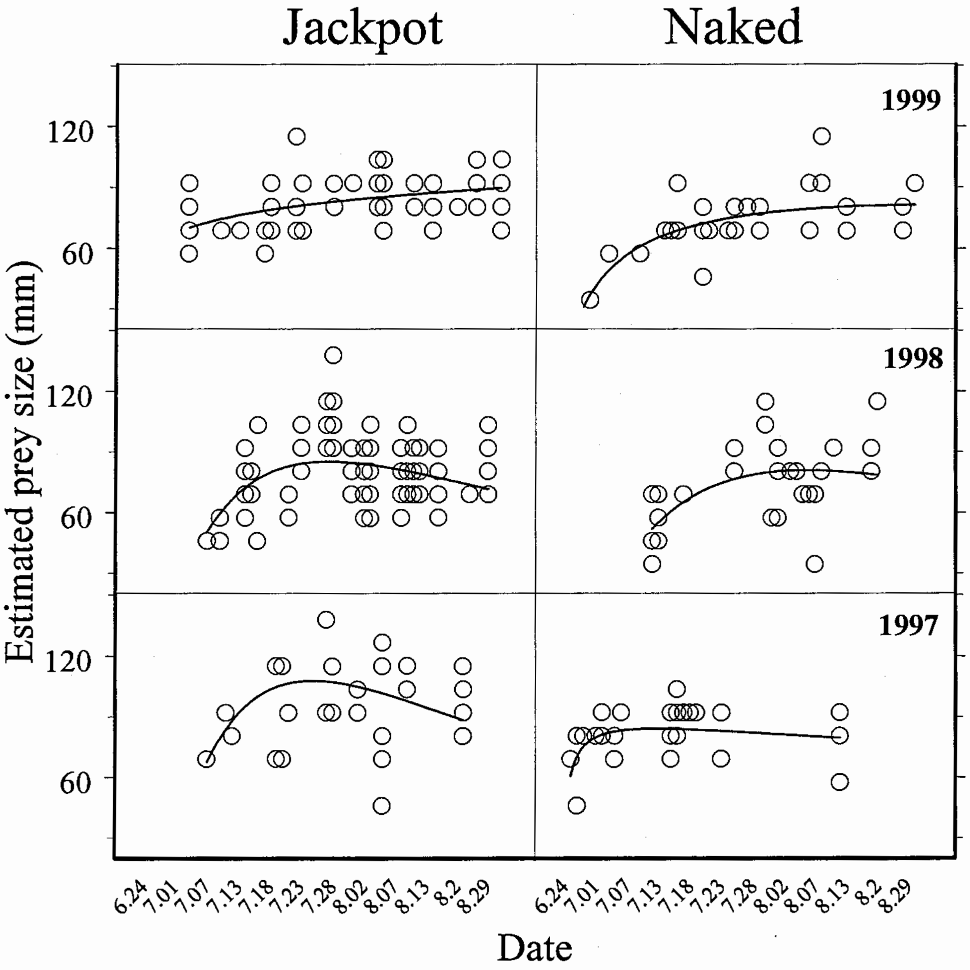

Figure 6. Estimated size of fish held by murrelets for their chicks, by date, for Naked and Jackpot sites in 1997 – 1999. Fish size was estimated from eye-to-bill tip length of the bird, during Diet Cruises (see Methods). A polynomial curve was fitted through each set of observations.

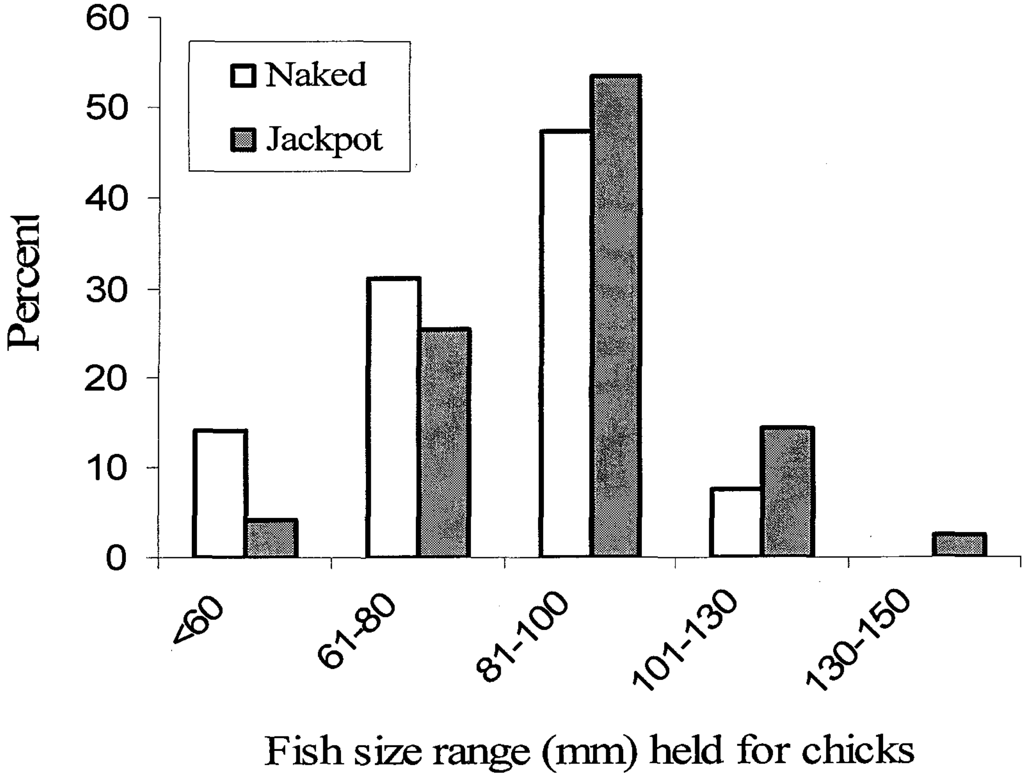

Figure 7. Between-Site comparison of sizes of fish held by adult murrelets prior to delivery to chicks (n = 467 with size estimates), shown here as percentages for each Site. Observations were made during diet cruises at Naked and Jackpot sites in Prince William Sound, Alaska, 1997 – 1999. Fish sizes were estimated relative to eye-to-bill tip of the adult bird. Jackpot fish held for chicks were significantly larger ($z = 3.83$, $P < 0.001$) and distribution of sizes differed between Sites ($KS = 0.17$, df = 1, $P = 0.02$).

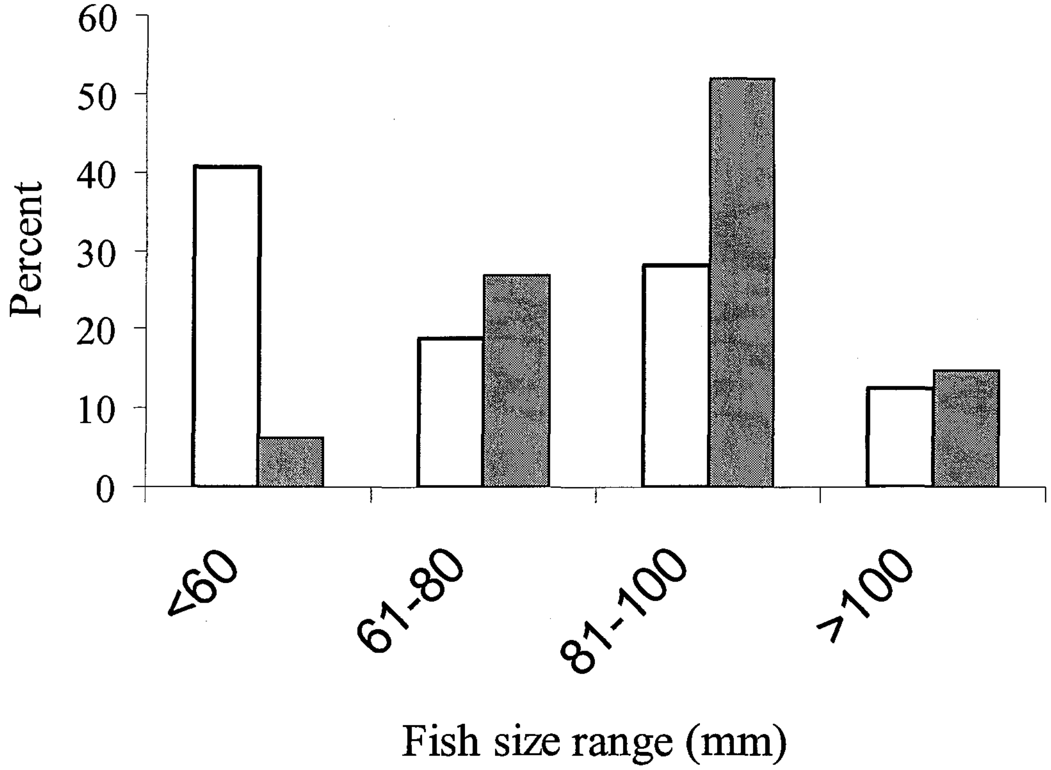

Figure 8. Comparison of fish sizes used for self-feeding and chick-feeding (shown here as percentages of each). Observations of fish held at the surface prior to delivery to chicks (gray bars) and fish caught below feeding murrelets (clear bars) were made at Naked and Jackpot, Prince William Sound, Alaska, in summer 1997 – 1999. Tests were done on 467 fish held for chicks and 32 samples (953 fish) caught by dipnet below feeding birds. Fish held for chicks were larger than those eaten by adults (Friedman chi-square = 4.0, df = 1, $P < 0.05$).

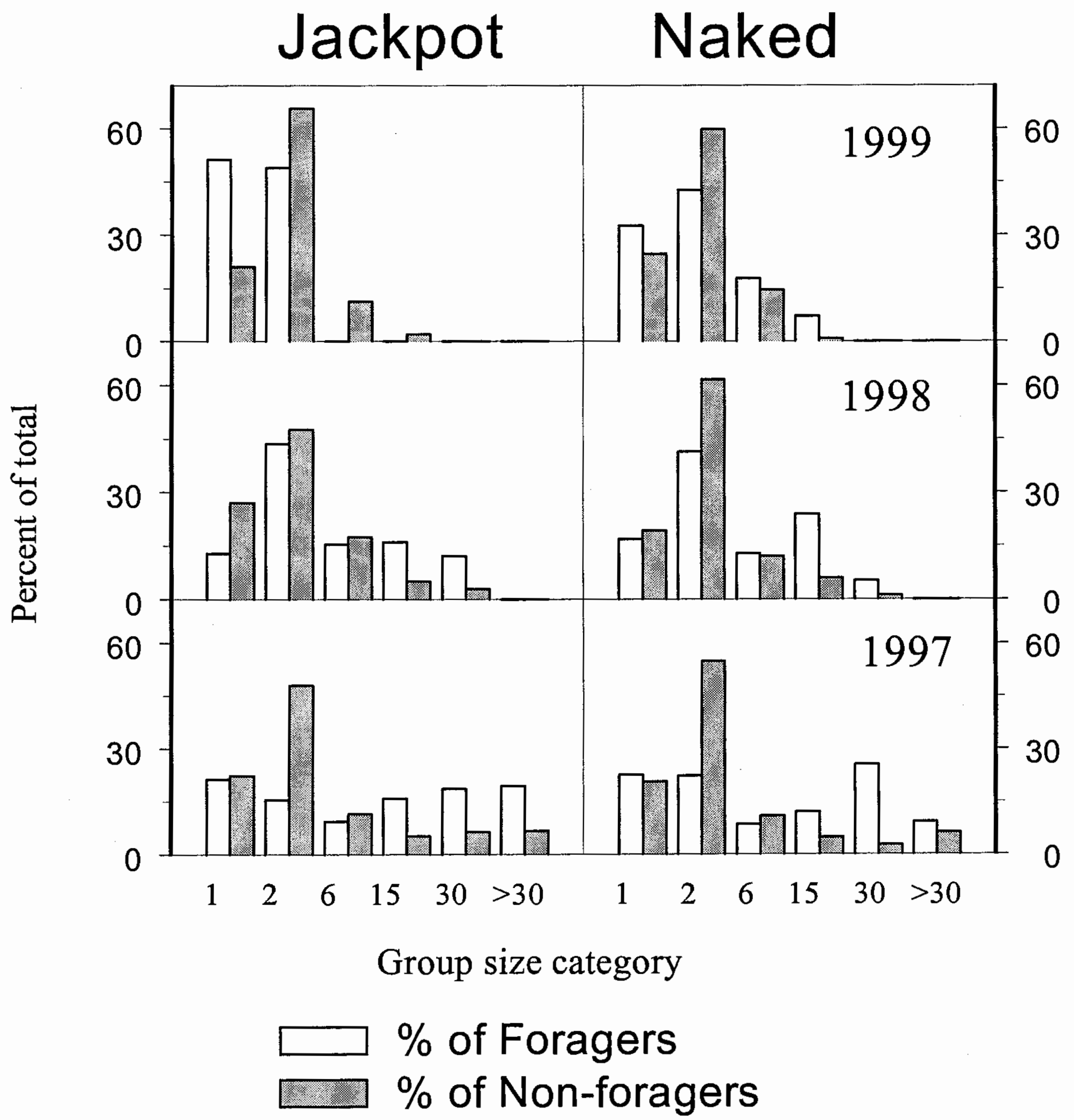

Figure 9. Distribution of group sizes for murrelets encountered during at-sea surveys at Naked and Jackpot sites in summer 1997 – 1999. The proportion of birds in each group size category is shown for foraging birds (clear bars) and birds not observed foraging (non-foragers, gray bars).

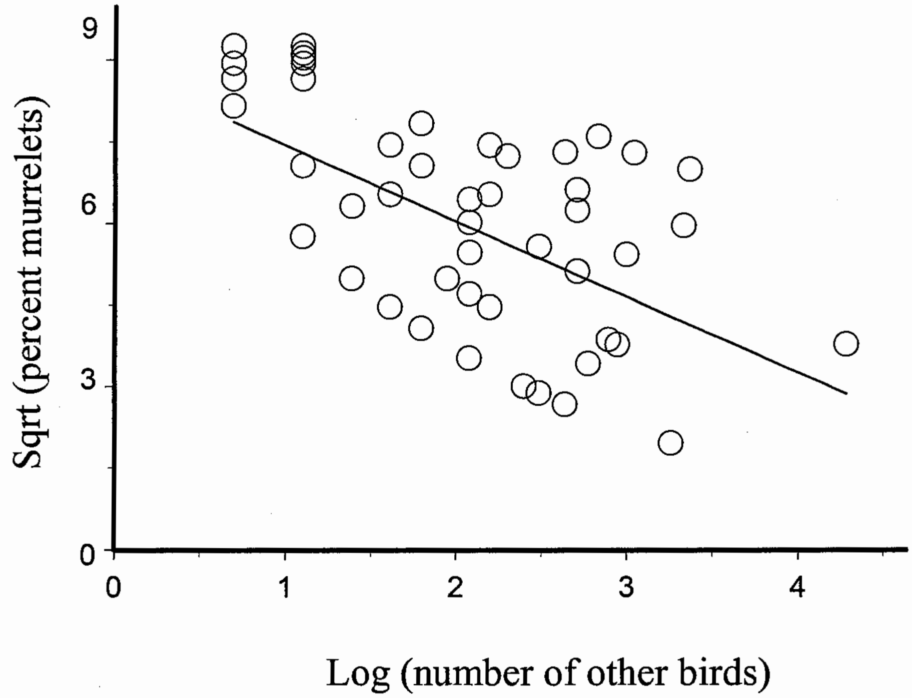

Figure 10. Relation between the percentage of murrelets and number of other birds in feeding flocks with murrelets, observed on transect during at-sea surveys at Naked and Jackpot sites, 1997-1999. The percentage of murrelets in flocks was negatively related to the number of other birds ($R^2 = 0.39$, $P < 0.001$), even though there was a weak positive relationship in numbers of murrelets and other birds ($R^2 = 0.12$, $P = 0.004$).

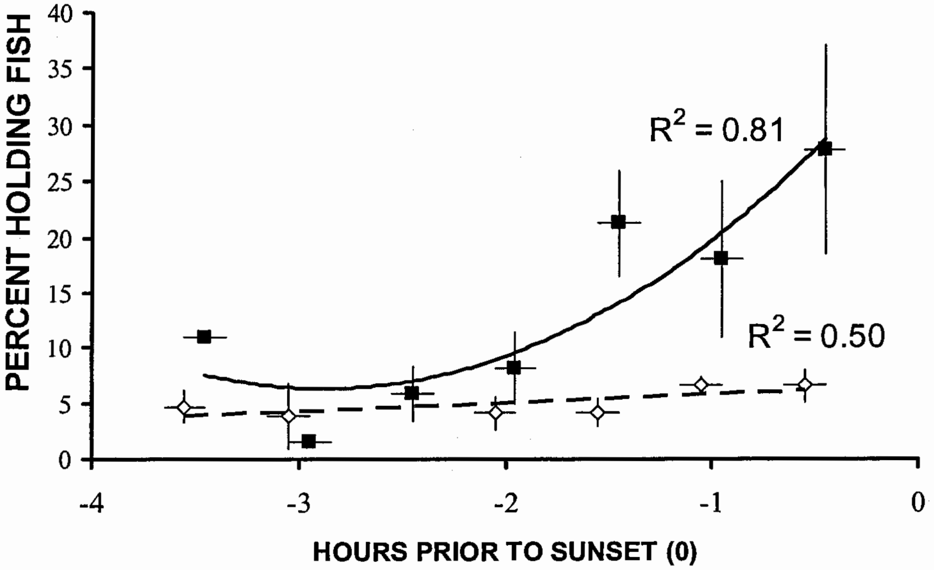

Figure 11. Percentage of murrelets holding fish for chicks, relative to hours from sunset, observed during evening diet cruises at Naked (open circles, dashed line) and Jackpot (filled squares, solid line), 1997 – 1999. Data were grouped into half-hour intervals. Actual hours ranged from approximately 1800 hrs (-4 from sunset) to 2230 hrs (sunset). The Jackpot data fit a polynomial curve, while the Naked data fit a linear curve. Symbols with horizontal lines are means, with vertical lines showing SE.

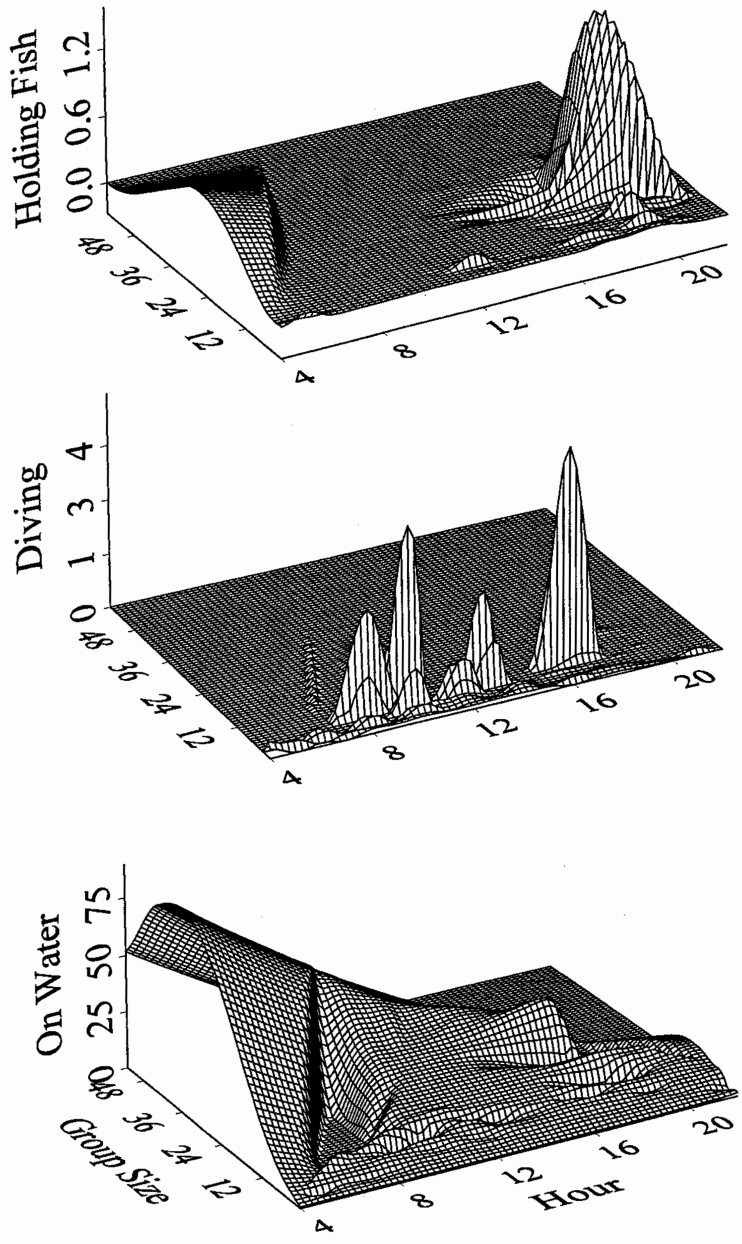

Figure 12. Marbled murrelet activity relative to hour of day and group size during forage watches at Naked and Jackpot in 1998 and 1999, all scans combined. The number of murrelets holding fish (top), diving (middle) and on the water (bottom) represent 5,516 records of > 11,000 murrelets, observed during 226 scans over 73 days. One outlier each (a large group in one record) was removed from the dive and on-water graphs. The spline graph uses line segments to connect data points in a grid frame.

Table 1. Density of fish schools observed during aerial surveys, within a 10 km radius of Naked and Jackpot study sites, 1997 - 1999. Means ± SE are raw values, with tests done on log transformed densities. Comparisons between years for ANOVAs used Tukey's multiple comparison test. There were no significant Site x Year interactions.

Year	Site	N days flown	Fish schools / km^2	Within-year Site effects			Overall Site effects			Overall Year effects		
			Mean (SE)	t	df	p	F	df	p	F	df	p
Herring and Sand Lance together												
1997	Naked	4	0.258 (0.158)	-0.47	4	0.66	20.28	1, 37	<0.001	2.58	2, 37	0.09
	Jackpot	5	0.022 (0.01)									
1998	Naked	12	0.260 (0.044)	-1.02	4	0.36						
	Jackpot	5	0.292 (0.202)									
1999	Naked	9	0.443 (0.128)	-4.63	10	<0.01						
	Jackpot	5	0.034 (0.023)									
Herring schools												
1997	Naked	4	0.003 (0.003)	0.74	7	0.49	2.39	1, 37	0.13	10.13	2, 37	<0.01
	Jackpot	5	0.013 (0.009)							1998 sig diff from 1997 & 1999		
1998	Naked	12	0.096 (0.028)	0.02	5	0.98						
	Jackpot	5	0.292 (0.202)									
1999	Naked	9	0.025 (0.009)	-1.2	14	0.25						
	Jackpot	5	0.030 (0.023)									
Sand Lance schools												
1997	Naked	3	0.255 (0.156)	-1.2	4	0.29	62.89	1, 37	<0.001	1.09	2, 37	0.35
	Jackpot	5	0.009 (0.009)									
1998	Naked	12	0.164 (0.040)	-9.05	11	<0.01				no sig diff between years		
	Jackpot	5	0									
1999	Naked	9	0.417 (0.133)	-7.94	15	<0.01						
	Jackpot	5	0.004 (0.004)									

Table 2. Surface areas (m^2) and distance offshore (m) of fish schools counted during aerial surveys for 10 km radius around Naked and Jackpot study sites, 1997 - 1999. Values were log-transformed for analysis. ANOVA were used for overall effects tests (Years and Sites), with a Tukey test for comparisons among years. Within-year site differences were done with a modified Welch t-test for unequal variances.

Year	Site	n days flown	n schools	School surface area	Within-year Site effects			Distance from shore (m)	Within-year Site effects		
				Mean (SE)	t	df	p	Mean (SE)	t	df	p
1997	Naked	4	77	37.9 (5.3)	-0.32	69	0.75	9.7 (0.6)	6.56	40	<0.01
	Jackpot	5	34	31.8 (8.6)				40.6 (7.8)			
1998	Naked	12	198	31.9 (2.3)	8.8	131	<0.01	23.2 (5.7)	4.11	80	<0.01
	Jackpot	5	51	73.9 (6.5)				32.4 (3.8)			
1999	Naked	9	269	51.9 (7.0)	2.63	10	0.02	115.0 (5.5)	-0.72	9	0.48
	Jackpot	5	10	122.9 (62.3)				150.5 (57.4)			
Overall Effects											
	Site	$F_{1,632}$		22.39				0.17			
		P		< 0.001				0.68			
	Year	$F_{2,632}$		6.65				186			
		P		< 0.001				<0.001			

Tukey test for years: 1997 schools significantly smaller than 1998 or 1999.
1999 schools significantly farther offshore than 1997 or 1998.

Table 3. Lengths of forage fish used by marbled murrelets in Prince William Sound, Alaska in summer 1997 - 1999. Samples caught by dipnet below feeding birds mid-day were considered self-feeding samples. Fish held by adults observed during Diet Cruises were considered destined for delivery to chicks. Sizes for the fish held by adults were based on the fish size relative to eye-to-bill tip of the bird. Age classes by fish length for each species are in Table 12. Sample sizes for fish caught below birds are school samples (with total number of fish in those samples in parentices). Sample sizes for fish held for chicks are individual fish held by a bird.

			Number of samples by fish length (mm)						
Year	Site	Species (n fish)	21-40	41-60	61-80	81-100	101-130	131-150	un-known
Fish caught below feeding adults sample sizes are schools									
1998	Naked	Herring (560)	1	8					
		Sand lance (165)		1	2	2			
	Jackpot	Herring (20)					1		
1999	Naked	Herring (71)		2	1				
		Sand lance (100)			3	5			
		Capelin (31)				2	3		
		Stickleback (6)	1						
Fish held for chicks sample sizes are adults with fish									
1997	Naked	Sand lance			5	26	1		1
		Other (a)			1	1			
		Unidentified		2	1	1			6
	Jackpot	Herring			1	15	17	5	3
		Sand lance			2	2			
		Other (b)					1		1
		Unidentified		1	4	7	4		5
1998	Naked	Sand lance	1	5	3	5	2		
		Unidentified	1	1	6	7	2		7
	Jackpot	Herring		8	58	107	12	2	3
		Sand lance			2	2	2		2
		Other (c)					3		
		Unidentified		5	17	11	2	2	53
1999	Naked	Herring			1	1			
		Sand lance		1	3	4			2
		Other (d)					2		
		Unidentified	1	3	13	5	1		9
	Jackpot	Herring		1	3	37	11		
		Sand lance			2	6			
		Other (e)			3	6			1
		Unidentified							14

a. Gadid (1), Sand fish (1)
b. Gadid (1) ; c. Smelt (2) ; d. Capelin (2)
e. Gadid (1), Smelt (6), Salmon (3)

Table 4. Species composition of identified prey used by marbled murrelets in Prince William Sound, Alaska, in summer, 1997 - 1999. Samples caught below feeding adults (by dipnet) during mid-day were considered self-feeding samples. Observations of fish held by adults during Diet Cruises (< 0800 or > 1800 hr) were considered distined for delivery to chicks. Unidentifed prey were not included here.

Year	Site	Identified fish samples	Percent of total (by Year and Site)							
			Herring	Sand lance	Capelin	Gadid	Smelt	Salmon	Sandfish	Stickleback
Fish caught below feeding adults										
schools (number of fish										
1998	Naked	15 (745)	66.7	33.3	0.0	0.0	0.0	0.0	0.0	0.0
	Jackpot	1	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1999	Naked	17 (208)	17.7	47.1	29.4	0.0	0.0	0.0	0.0	5.8
	Jackpot	0	nd							
Fish held for chicks										
adults with fish										
1997	Naked	34	0.0	94.1	0.0	2.9	0.0	0.0	2.9	0.0
	Jackpot	43	88.4	9.3	0.0	2.3	0.0	0.0	0.0	0.0
1998	Naked	16	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
	Jackpot	197	94.9	3.1	0.0	0.0	2.0	0.0	0.0	0.0
1999	Naked	12	16.7	66.7	16.7	0.0	0.0	0.0	0.0	0.0
	Jackpot	70	74.3	11.4	0.0	1.4	8.6	4.3	0.0	0.0

Table 5. Density of adult marbled murrelets during at-sea surveys of Naked and Jackpot sites, 1997 - 1999. Results are shown for three periods: incubation (28 May - 30 June), early fledging (20 July - 10 August), and late fledging (11 - 30 August). Between 3 - 5 surveys were conducted at each site within each period. Murrelet density for the entire season did not show a Site effect ($F_{1,64}$,= 0.11, P = 0.74) but there was a Year effect ($F_{2,64}$ = 17.10, P < 0.001), with no interaction between Site and Year. 1999 was significantly lower than 1997 and 1998 (Tukey multiple comparison).

		N	Adult Density (birds/km2) Mean ± SE			
Year	Site	surveys	Incubation	Early fledging	Late fledging	All Season
1997	Naked	10	65.5 (15.3)	29.8 (7.01)	7.3 (1.5)	33.8 (8.9)
	Jackpot	10	33.0 (1.7)	12.7 (2.7)	9.6 (1.4)	18.2 (3.5)
1998	Naked	10	28.2 (3.8)	23.9 (3.0)	5.2 (1.5)	19.6 (3.5)
	Jackpot	11	17.7 (1.9)	21.1 (6.0)	6.8 (1.3)	14.9 (2.9)
1999	Naked	14	3.2 (1.0)	13.9 (1.1)	3.6 (1.3)	6.4 (1.5)
	Jackpot	15	6.4 (1.1)	15.2 (2.8)	2.7 (0.6)	7.5 (1.5)

Table 6. Group size of murrelets during at-sea surveys at Naked and Jackpot, 1997-1999. Mean group size and ANOVA tests among Years and Sites used log-transformed values, of the number of murrelets per observation. To compare distribution of group sizes, we used six group size categories (see Fig 7), for murrelets recorded as foraging vs those not actively observed foraging, tested with a two-sample Kolmogorov-Smirnov (KS) Test.

				%	ANOVA test on effects		Distribution: Foragers	
Site	Year	Total	Group Size	Foragers	Group size		vs Non-foragers	
		Murrelets	Mean (SE)	of total	Site	Year	KS statistic	P
All murrelets								
Naked	1997	3485	2.08 (0.08)	14.4	$F_1 = 5.23$	$F_2 = 2.82$	0.83	0.03
	1998	2208	2.02 (0.05)	17.0	$P = 0.02$	$P = 0.06$	0.50	0.47
	1999	1025	1.73 (0.04)	19.7			0.50	0.47
Jackpot	1997	1649	2.17 (0.14)	18.6			1.00	<0.01
	1998	1768	1.89 (0.05)	9.7			0.67	0.14
	1999	1163	1.76 (0.03)	8.0			0.50	0.47
Foraging murrelets								
Naked	1997	439	2.73 (0.39)		$F_1 = 0.53$	$F_2 = 8.35$		
	1998	320	2.39 (0.24)		$P = 0.47$	$P < 0.01$		
	1999	169	1.71 (0.13)					
Jackpot	1997	258	3.00 (0.70)					
	1998	156	2.74 (0.40)					
	1999	86	1.34 (0.07)					
Both sites, foragers only								
	1997	697	2.82 (0.35)					
	1998	476	2.49 (0.21)					
	1999	255	1.56 (0.08)					

Table 7. Participation in forage flocks by marbled murrelets and other marine birds, as recorded on transect during the at-sea surveys conducted at Jackpot and Naked study sites, 1997-1999. Behavior of birds was recorded at the time of observation. See text for lists of other species.

				Murrelets in flocks						Mean (SE) in feeding flocks		
Year	Site	N surveys	N flocks	Total murrelets	N foragers	N in flocks	% of foragers	% of total	Flocks per survey	No. of other birds	No. of murrelets	Percent Murrelets
1997	Naked	10	81	3485	439	221	50.3	6.3	7.7 (1.3)	53.4 (13.5)	22.1 (7.8)	32.7 (7.9)
	Jackpot	10	33	1649	258	83	32.2	5.0	3.0 (0.5)	15.1 (4.1)	8.2 (2.7)	30.0 (8.3)
1998	Naked	10	46	2208	320	166	51.2	7.5	4.6 1.8)	36.5 (13.3)	16.6 (8.3)	18.2 (6.4)
	Jackpot	11	20	1768	156	90	57.7	8.8	1.8 (1.0)	8.7 (5.5)	8.2 (4.3)	22.3 (10.5)
1999	Naked	14	38	1025	169	77	45.6	7.5	2.7 (0.7)	26.4 (10.2)	5.5 (1.9)	25.3 (8.1)
	Jackpot	15	8	1163	86	7	8.1	0.6	0.5 (0.2)	2.5 (1.2)	0.3 (0.3)	6.7 (6.7)
By	1997	20	114	5134	697	304	43.6	5.9	5.4 (0.9)	34.3 (8.1)	15.2 (4.3)	31.3 (5.6)
Year	1998	21	66	3976	476	256	53.8	6.4	3.1 (1.0)	22.0 (7.5)	12.2 (4.5)	20.4 (6.1)
	1999	29	46	2188	255	84	32.9	3.8	1.6 (0.4)	14.0 (5.3)	2.8 (1.0)	15.7 (5.4)

Table 8. Participation of murrelets in foraging flocks observed during forage watches conducted at Jackpot Bay (Jackpot) and Cabin Bay (Naked), 16 June - 26 August of 1998 and 1999. Counts were summed from hourly scans. Foraging birds included birds observed diving and birds holding fish. Flocks included mixed and single species active feeding flocks.

		Sample sizes			Number of murrelets				Percentage in flocks	
Year	Site	Days	Scans	Flocks	Total	Foragers	Holding fish[a]	In Flocks	of Foragers	of Total murrelets
1998	Naked	20	54	9	5613	318	9	66	20.8	1.2
	Jackpot	21	52	4	2512	237	23	171	72.2	6.8
1999	Naked	17	63	18	2441	173	7	90	61.5	8.9
	Jackpot	15	57	2	1337	43	5	0	0	0

a. No fish-holding birds were observed participating in forage flocks.

Table 9. Mean numbers of murrelets and the proportion per hourly scan exhibiting selected behaviors during forage watches at Naked and Jackpot in summer 1998 and 1999. Self period included watches conducted in June, or between 0900 - 1700 hours in July and August. Chick period included watches conducted in July and August before 0900 hr or after 1700 hr. Tests between sites, or self vs chick periods, were done with two-sample t-test on log transformed numbers or square-root transformed proportions.

	Site or		Mean ± SE	Percentage of birds (Mean ± SE)			
Year	Period	n	Total Birds	Diving	Holding fish	Maintenance	Flying
1998	Naked	54	*33.8 (4.13)	11.58 (1.78)	*0.38 (0.17)	5.07 (1.18)	9.97 (1.24)
	Jackpot	53	20.6 (2.72)	5.96 (1.24)	2.00 (0.84)	5.21 (1.15)	7.74 (2.20)
1999	Naked	63	16.14 (2.89)	*8.96 (1.70)	0.68 (0.34)	7.62 (1.94)	*7.51 (1.45)
	Jackpot	57	11.68 (1.06)	4.52 (1.98)	1.09 (0.89)	3.42 (1.17)	4.69 (2.12)
1998	Self	68	*31.29 (3.65)	*10.27 (1.57)	*0.14 (0.10)	5.40 (0.98)	8.14 (1.71)
	Chick	39	20.23 (2.61)	6.23 (1.34)	3.00 (1.11)	4.69 (1.48)	10.12 (1.74)
1999	Self	74	*10.78 (1.25)	7.99 (1.85)	*0.21 (0.21)	*6.76 (1.71)	6.93 (1.84)
	Chick	46	19.24 (3.57)	4.75 (1.62)	1.94 (1.13)	3.79 (1.33)	4.96 (1.45)

* = $P < 0.05$

Table 10. Mean dive times for adult marbled murrelets observed in Prince William Sound, Alaska, in summer 1998 and 1999. Birds likely to be self-feeding (0900-1700 hr) or foraging for chicks (<0900 h or > 1700 hr) were compared with two-sample t-tests. A grand mean duration of dive and pause was calculated from the mean for each bird (n) observed.

Year	Murrelet	n	Dive Time (sec)	Pause Time (sec)	Dive		Pause	
(Total dives)	group	Birds	Mean (±SE)	Mean (±SE)	t	P	t	P
1998	Naked birds	46	31.2 (1.0)	13.4 (1.0)	2.00	0.05	2.40	0.02
(332)					df (62)		(56)	
	Jackpot birds	19	37.0 (3.9)	19.4 (3.0)				
	Self-feeding	42	32.3 (1.7)	15.7 (1.4)	0.46	0.65	-0.79	0.43
					df (62)		(56)	
	Chick-feeding	23	33.6 (2.3)	13.8 (2.1)				
1999	Naked birds	52	33.3 (1.6)	17.0 (1.5)	1.76	0.09	3.11	0.01
(345)					df (68)		(66)	
	Jackpot birds	19	40.9 (4.0)	27.0 (2.8)				
	Self-feeding	55	36.4 (1.8)	20.4 (1.6)	-1.1	0.27	-1.11	0.29
					df (68)		(66)	
	Chick-feeding	16	32.0 (3.8)	16.6 (3.1)				

Table 11. Size and nutrient value of prey taken by marbled murrelets for self- and chick-feeding in Prince William Sound. Nutrient data on fish were taken from identified sources.

Species	Age class	length (mm)	weight (g) mean (range)	dry mass lipid content (%)	wet mass energy density (kJ/g)	Source
Pacific sand lance	0	82 (80 - 85)	2 (1 - 2)	17.3	3.18	Van Pelt et al. 1997
Ammodytes hexapterus	1+	122 (110 - 132)	6 (4 - 8)	23.4	4.95	
	2+	165 (147 - 191)	16 (12 - 24)	24.25	5.67	
Pacific herring	0	80 (50 - 100)	6 (2 - 11)	10.5	5.4	Foy & Norcross 1999
Clupea harengus pallasi	1+	100 - 130	23.5	26.8	5.84	Paul & Paul 1999
						Anthony et al. 2000
Pink salmon	0	< 100	7	7.28	3.41	Anthony et al. 2000
Oncorhynchus gorbuscha	1	>100	15	6.35	3.73	
Walleye pollock	0+	75 (54 - 87)	3 (1 - 5)	8.99	2.73	Van Pelt et al. 1997
Theragra chalcogramma	1	154 (117 - 179)	29 (16 - 47)	6.7	3.24	Anthony et al. 2000
Pacific Tomcod /Saffron cod	0/1	< 100	3	5.59	3.04	Anthony et al. 2000
Microgadus proximus						
Smelt species	1	>100	15	16.5	4.39	Anthony et al. 2000
Hypomesus, Spirinchus						
Capelin	0	< 50	1			Brown 2002
Mallotus villosus	1	86 (50 - 90)	2 (2 - 3)	17.25	4.84	Van Pelt et al. 1997
	2 - 3	114 (100 - 130)	9 (5 - 17)	14.4 - 21.9	3.54 - 4.67*	Van Pelt et al. 1997
Threespine stickleback	?	24 (19-29)	0.13 (0.06-0.26)	na	na	this study (estimated)
Gasterosteus aculeatus						
Pacific sandfish	?	89 (80 - 95)	6 (3 - 9)	11	3.36	Van Pelt et al. 1997
Trichodon trichodon						

* Female capelin have higher lipid content and energy density

Table 12. Estimated number of fish required for marbled murrelet chicks, daily and for the duration of nestling period. Estimates are based on 1) published accounts of days to fledging and chick fledging mass (references in Nelson 1997), kJ g-1 and mean mass of fish (Table 11), and 3) energetic requirements as calculated from equations for seabird chicks in Visser (2002; p.454). Scenarios for energetic requirements include 'low' (lowest recorded fledging mass and shortest fledging period), 'moderate' (mean of recorded chick masses and mean fledging period), and 'high' (mean fledging mass and longest recorded fledging period).

Fledge mass (g)	Days to fledge	DME* kJ d^{-1}	TME** kJ	No. fish required each day				No. fish required to fledging			
				1+ Herr[a]	2+ Sand[b]	1+ Sand[c]	Cape[d]	1+ Herr[a]	2+ Sand[b]	1+ Sand[c]	Cape[d]
118	27	261	5147	1.9	3.8	6.5	8.2	38	76	129	161
147	30	303	6590	2.2	4.5	7.6	9.5	48	97	165	206
147	40	274	8169	2.0	4.0	6.9	8.6	60	120	204	255

[a] Uses 23g herring for total 137 kJ per fish

[b] Uses 12g sand lance for total 68 kJ per fish

[c] Uses 8g sand lance for total 49 kJ per fish

[d] Uses 9g capelin for total 32 kJ per fish (male capelin values in Table 11)

* DME = peak daily metabolized energy of the chick. The predictive equation is peak-DME = $14.06\ A^{0.848} \cdot t^{-0.341}$. Mass (g) at fledging was used in place of A (asymptotic mass), as A is unknown for marbled murrelets. t = days to fledging.

** TME = total energy metabolized until fledging. The predictive equation is TME = $11.09\ A^{0.771} \cdot t^{0.747}$. Mass at fledging was used in place of asymptotic mass. t = days to fledging.

CHAPTER THREE

POWER TO DETECT INTER-ANNUAL AND AMONG-SITE DIFFERENCES IN DENSITIES OF ADULT AND JUVENILE MARBLED MURRELETS AT SEA

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ABSTRACT

Managers must often rely on at-sea surveys to monitor population trends and breeding success of non-colonial marbled murrelets (*Brachyramphus marmoratus*). There is little information, however, on how to allocate survey effort, or the power to detect differences in abundance. We used 65 surveys from 1995, 1997, 1998, and 1999 at three sites in Prince William Sound, Alaska, to estimate the power to detect differences in adult densities, juvenile densities, and juvenile:adult ratios (ratios). From the original data, we generated 2000 datasets and tested for difference in means among sites or years with ANOVAs, with the proportion of significant differences (at alpha 0.05) an estimate of power. Sites with more murrelets had the highest power to detect differences, and power was higher for spatial comparisons than temporal (inter-annual) comparisons. Increasing the number of surveys (up to 6) provided better power, but 2-4 surveys were adequate at sites with high murrelet density, or when comparing juvenile densities among sites. Power to detect differences in adult densities increased when visits were concentrated early in the fledging period (late July to early August in PWS). Power to detect temporal differences in juvenile densities was low, but improved if 6 visits were conducted throughout the entire fledging period (late July to late August). Within sites, power to detect temporal changes improved to 90% (with differences < 20 %) in adult densities and juvenile ratios. Sites with high murrelet productivity could be identified with little effort, and detecting temporal trends at these sites is also possible. Areas with low, or variable murrelet densities will require alternative methods. At sites with high to moderate adult murrelet density, changes of < 20 % can be identified within five years with 90 % probability, and changes of < 10 % in 10 years. Juvenile ratios, though problematic, were the most stable parameter for monitoring long-term trends, and may be particularly useful when tracking productivity at the same site.

INTRODUCTION

The primary objective of most monitoring programs is to detect inter-annual changes in abundance or productivity and follow long-term trends in a population. To achieve this objective, managers must take into account within-season measurement error as well as normal seasonal and inter-annual variability. Most seabird monitoring programs, which typically depend on counts of birds at their colonies, usually factor in daily and seasonal variation in colony attendance (Hamer et al. 2002, Hatch 2003). Environmental factors can also alter prey distribution or timing, and can thus indirectly affect seabird nesting chronology or foraging patterns (Bertram et al. 2001, Becker and Beissinger 2003). For the few non-colonial seabird species, monitoring trends in populations and productivity presents unique problems for resource managers.

One such species is the marbled murrelet (*Brachyramphus marmoratus*), which is listed as threatened from British Columbia (Burger 2002) to California (McShane et al. 2004). Most of the marbled murrelet world population breeds in Alaska (Nelson 1997), where it is a species of management concern for the U.S. Fish and Wildlife Service (DeGange 1996).

In addition to being non-colonial, marbled murrelet nests are hard to find, which precludes counting adults at nest sites or tracking individual breeding pairs to determine reproductive success over successive seasons. Radar surveys of murrelets flying inland to their nesting areas have been found to be the most sensitive means of detecting changes in abundance, but this method provides no index of breeding success (Burger 2001, Cooper et al. 2001). Counting murrelets at sea has the advantage of providing indices of productivity, such as abundance of recently fledged juveniles or the ratio of juveniles to adults (juvenile ratios) (Beissinger 1995, Becker et al. 1997, Kuletz and Kendall 1998, Lougheed et al. 2002a, Mack et al. 2002). In this paper, we provide power and trend analyses that can be applied to such at-sea surveys.

As with other seabirds, the abundance of adult murrelets at sea can vary seasonally with different phases of their breeding cycle (Carter and Sealy 1990, Kuletz and Kendall 1998, Speckman et al. 2000). Post-breeding migration patterns might also vary in response to environmental conditions (Ainley et al. 1995, Strachan et al. 1995), and adults often exhibit different dispersal patterns than fledglings (Beissinger 1995, Kuletz and Kendall 1998, Lougheed et al. 2002a). Finally, error in measurements can occur due to weather and sea state affecting detectability of the birds (Becker et al. 1997, Mack et al. 2002).

Recently, the activity patterns of radio-tagged adults were used to identify failed and successful breeders (Hebert et al. 2003, Bradley et al. 2004, Peery et al. 2004). Lougheed et al. (2002a) integrated the movement patterns of radio-tagged juveniles to improve interpretation of at-sea surveys. Though effective, methods that rely on radio-telemetry are limited in the number of individuals that can be followed, and they are expensive and labor intensive (Bradley et al. 2004), making long-term monitoring programs difficult to maintain. Because of these limitations, at-sea surveys remain the most common method for tracking long-term changes in murrelet productivity.

Although at-sea surveys are practical for long-term monitoring of murrelet populations and productivity, expenses and time requirements can still be substantial, especially in remote areas such as coastal Alaska. The ability to detect changes in at-sea abundance of adult or juvenile murrelets, either among years (temporal differences) or among sites (spatial differences), will depend on the amount of measurement error and normal fluctuations in numbers of birds, as well as temporal or spatial distribution of survey effort. Our study investigated methods to maximize survey efficiency by addressing the following questions: 1) To monitor murrelet productivity, should surveys be concentrated within a small time frame (e.g., 2 weeks), or spread out over a longer time frame (e.g., 4 weeks)? 2) What is the optimum and minimum survey effort recommended for a desired confidence level? 3) How do temporal and spatial patterns in murrelet abundance affect the ability to detect trends over time? 4) What level of population change can we expect to track with statistical reliability at acceptable levels of cost and effort.

Adult murrelets may exhibit less variation in at-sea abundance during the incubation period compared to the fledging period (Kuletz and Kendall 1998), but we wanted to also measure murrelet productivity. Therefore, we focused on the fledging period. We used data from four years of at-sea surveys conducted at three sites in Prince William Sound (PWS), Alaska. A previous study in PWS provided a framework for establishing survey protocol and a preliminary estimate of power to detect changes in murrelets (Kuletz and Kendall 1998). This study examines the effect of variability among study sites, and provides a longer time frame to gauge the effect of temporal variability. Murrelet densities in PWS are among the highest throughout their range, with summer densities of adults averaging 12.6 birds/km^2 (Agler et al. 1998), and mean juvenile densities ranging among study sites from 0.21 to 2.12 juveniles/ km^2 (Kuletz and Kendall 1998). Using computer-intensive sampling from real data, we evaluated the power to detect differences among years and among study sites for adult densities, juvenile densities, and juvenile ratios. We also estimated the number of years required to detect trends in abundance using various objectives. While based on data from PWS, these findings may be applicable to marbled murrelets in other regions.

METHODS

Study Sites

The three study sites were located in Prince William Sound (PWS), Alaska, a 10,000 km^2 embayment along the north coast of the Gulf of Alaska. The sites, each with approximately 50 km of shoreline, included Naked Island (Naked), Jackpot Bay / Dangerous Passage (Jackpot), and Valdez Arm /Galena Bay (Galena) (Fig. 1). The sites varied considerably in marine habitats. Naked, in the center of PWS, has four large bays and is surrounded by ocean generally < 50 m deep within 1 km of shore and < 200 m deep up to 5 km offshore. Jackpot, on the southwestern mainland, includes three large bays with several shallow lagoons, and Dangerous Passage, which has a maximum depth of 300 m. Galena, in the northeastern mainland, includes the protected waters of two bays, sections of shallow narrows 10 m deep, and the steep, exposed fjord-type coastline of Valdez Arm, up to 350 m deep. In July and August sea surface temperatures at these sites averaged 14.5 ^{0}C and sea surface salinity averaged 23.7 psu.

Collection of at-sea survey data

We minimized measurement error by using the same protocol, vessel, study sites, and survey conditions (i.e., sea state and wind), and one or more of the same observers each year. We used a standard protocol (Agler et al. 1998), with minor modification, to conduct boat-based shoreline surveys at the 3 study sites 6-10 times during the fledging period in late July through August (Kuletz and Kendall 1998). Naked and Jackpot were surveyed in all four years (1995, 1997, 1998, 1999) and Galena was surveyed for three years (1995, 1997, 1998). Our modified protocol allowed us to reduce speed or go 'off-transect' temporarily to confirm age-class. We typically surveyed each site on 2 days/week, with the crew rotating among sites. Each survey took < 1 day (0700 - 1600 h) to cover the approximately 50 km of shoreline. We surveyed from 7.5 m vessels traveling 100 m from the shoreline at ~10 km/hr. To minimize the effects of sea-surface waves on murrelet detectability, we did not conduct surveys in seas > 0.6 m, and seas were typically ≤ 0.3 m.

A boat operator and 2 observers recorded all birds within 100 m on either side of and ahead of the boat. We recorded each observation into a laptop computer using DLOG (ECI, Inc., Portland OR). Birds were recorded as "on water" or "flying", and because most birds in flight (about 5 % of all murrelet observations) appeared to have recently taken off from the water, we included flying birds in our density calculations. Based on physical and behavioral characteristics described in Kuletz and Kendall (1998), murrelets were categorized as "adults" (which includes after-hatch-year birds, indistinguishable from breeding adults) or "juveniles" (recently fledged hatch-year-birds). In PWS, juveniles remain near the shore late in the summer, while adults leave the breeding area prior to molting, which makes it unlikely that molting or basic-plumaged adults will be misidentified as juveniles during surveys (Kuletz and Kendall 1998).

Murrelet abundance was expressed as birds/km^2 (adult and juvenile densities). The ratio of juveniles:adults (juvenile ratios) was calculated for each July and August survey (i.e., concurrent surveys). Kuletz and Kendall (1998) found a closer correlation between a mean June count of adults at a site and the mean juvenile count at that site during the core fledging period (sequential surveys). However, we used only concurrent surveys for these analyses. We made this choice because most monitoring programs can not accommodate the greater effort of June plus July-August surveys, and sequential ratios do not provide sufficient data to capture variability among sites or seasonal changes in murrelet abundance.

Over the four years of study, the 85 surveys conducted during the fledging period occurred from 18 July – 31 August. A preliminary examination of the data showed high frequencies of zero counts of juveniles early in the season and absent adults late in the season. To minimize the influence of these zeros and low adult numbers on the analysis, and to capture the primary fledging period, we selected surveys conducted between 27 July and 24 August (n = 65). During this period, the number of surveys varied among sites and among years, and ranged from 5 to7 surveys/site/year (Table 1). The original data were log transformed and tested for differences in abundance measures using ANOVA; all means are presented as raw values and expressed ± SE.

Power analysis

We resampled the at-sea survey data to simulate the effect of variable sample effort and sampling time frame on the detection of site and year differences in three dependent variables (adult density, juvenile density, juvenile ratio). For this computer simulation, we varied the number of surveys (visits) from 2 to 6; the maximum number of visits was set at 6 / survey period / year, because 6 visits were logistically feasible and represented the median number of visits in the original data. The visits were bracketed into three survey periods, based on the breeding chronology of murrelets in PWS (Kuletz and Kendall 1998, Chapter 4): "early" fledging (2 weeks, 27 Jul - 10 August), "main" fledging (3 weeks, 27 July - 17 August), and "entire" fledging (4 weeks, 27 July - 24 August).

All sites and years. -- From the original data (n = 65 surveys) we generated 2000 datasets by randomly selecting from the survey records, with replacement. For each dependent variable, the simulated data were used to test for a difference in means among the three sites or among the four years. ANOVAs were run for each comparison (2000 tests), and the proportion of significant differences (set at $P < 0.05$) was calculated as an estimate of power. We then used the Wilcoxon rank-sum test (with alpha = 0.05) to test for differences in mean power between site and year for each dependent variable.

Results of the ANOVA power tests were graphed using the spline procedure in S-Plus-6 (Insightful 2001). The spline fits a smooth function (applying cubic polynomials) to the data for a three-dimensional plot, using the line segments to connect points in a grid frame (Venables and Ripley 1999). These graphs present the power to detect differences under the given range of survey period and number of visits for each dependent variable (adult density, juvenile density, juvenile ratios). The result is a three-dimensional visual contour of changes in power relative to the number of visits and the survey period.

Within-site. – We examined site-specific power to detect temporal trends by estimating the power to detect a change of 10-50 % of the site mean per year over a three (Galena) or four year (Naked and Jackpot) survey period. We used the optimum survey effort as determined in the power tests on all visits and survey periods (above); thus, estimates were calculated for each site using 6 visits a year and for adult densities and juvenile ratios we used the early survey period, whereas for juvenile densities we used the entire survey period (see Results). With these criteria, we resampled data from the original dataset 2000 times and power was calculated as the proportion of tests for which the null hypothesis of 'no slope' was rejected.

Long-term trends. – We used the TRENDS program (Gerrodette 1987, 1993) to estimate power to detect changes in population from 10 – 90 %, at 5, 10, and 15 year time frames, using three representative coefficient of variation (CV) calculated from the annual means of the survey data. This program assumes a linear trend over time, and we used the constant CV option and alpha of 0.05, as recommended by Hatch (2003) for seabirds. In addition, we used TRENDS to determine the number of years, given the CVs we obtained, that would be required to detect significant changes in adult densities, juvenile densities, and juvenile ratios under four criteria. These criteria were defined by the following programs: 1) North American Waterbird Conservation Plan (NAWCP; Internet: http://www.nacwcp.org): detect a 50 % decline in population over 50 years, or -1.4% per year at $P < 0.05$; 2) The North American Breeding Bird Survey (BBS; Peterjohn et al. 1995): detect a 50 % decline in 25 years, or -2.7 % per year at $P < 0.05$; 3) Alaska Seabird Management Plan (USFWS 1992): detect a 20 % change per year at $P < 0.1$); 4) An intermediate goal defined by Hatch (2003), to accommodate the inherent variability in seabird counts and the need to identify trends of concern to managers: detect a 50 % decline over 10 years, or -6.7 % per year, at $P < 0.05$.

RESULTS

The original data (Table 1) shows a high density of adults, with site-specific means ranging from 8.93 to 22.01 / km^2. The relative abundance of adults among the three sites was not the same every year, for example, Jackpot had the highest adult densities in 1995 (15.42 / km^2 ± 4.23), but Galena was highest in 1997 (22.01 / km^2 ± 8.67). However, adult densities were not significantly different among years (ANOVA; $F_{1,61} = 0.42$, P = 0.52) or sites ($F_{2,61} = 0.56$, P = 0.94). In contrast, juvenile densities and juvenile ratios were always highest at Naked (Table 1). Both juvenile density and juvenile ratios varied significantly among the three sites (respectively, $F_{2,61} = 27.42$, $P < 0.01$; $F_{2,61} = 14.33$, $P < 0.01$), but only juvenile density varied significantly among years ($F_{1,61} = 7.43$, $P < 0.01$; Table 1).

Detecting differences among sites and years using resampled data

Using the simulated data set, overall, power to detect differences was low for temporal or spatial comparisons of adult densities, and low for juvenile density or juvenile ratios when making temporal comparisons, but high when making spatial comparisons of juvenile densities or ratios (Fig. 2).

Adult Densities. -- There was little difference between temporal or spatial comparisons in power to detect changes in adult densities (Exact Wilcoxon rank sum test; n = 15, $W = 235$, $P < 0.94$). Power to detect temporal differences averaged 0.45 ± 0.06, with a maximum power of 0.92 when 5 – 6 visits were clustered during the early period (Fig. 3A). If the survey period extended late into the season, a minimum of 6 visits was required to maintain reasonable power, and less than 4 visits reduced power regardless of survey period. Similarly, power to detect spatial differences in adult densities was low overall (Fig. 3B; $\bar{x} = 0.48 \pm 0.07$), but was high (> 0.8) when ≥ 5 visits were concentrated in the early period. Power remained low (~ 0.45) even with 4 visits during the early period, and approached zero if ≤ 4 visits were conducted late in the season.

Juvenile Densities. -- For juvenile densities, average power to detect differences among years approached zero ($\bar{x} = 0.09 \pm 0.03$), which was significantly lower (Wilcoxon rank-sum test, $z = 4.71$, $P < 0.01$) than it was among sites ($\bar{x} = 0.96 \pm 0.02$). Power to detect inter-annual differences was marginally improved (to 0.38) by conducting 5-6 visits throughout the entire fledging period (Fig. 4A). In contrast, power to detect differences in juvenile density among sites was exceptional (> 0.95) even with < 4 visits if they were conducted during the early period, or for longer survey periods when 4 – 6 visits were made.

Juvenile Ratios. -- The power to detect differences in juvenile ratios was low to moderate, with power to detect inter-annual differences ($\bar{x} = 0.10 \pm .03$) significantly lower than the power to detect differences among sites ($\bar{x} = 0.79 \pm 0.6$; Wilcoxon rank-sum test; $z = 4.71$, $P < 0.01$). For inter-annual differences, power was marginally improved to ~ 0.30 if 6 visits were conducted only during the early period (Fig. 5A). Power to detect spatial differences in juvenile ratios (Fig. 5B) was uniformly high (> 0.85) with ≥ 4 visits, but declined substantially with fewer visits.

Within-Site changes

When sites were examined individually, power to detect temporal changes in the dependent variables greatly improved, particularly at Naked and Jackpot. These two sites had relatively stable murrelet densities of both age classes (Table 1). Within sites, power to detect differences of < 20 % in adult densities and juvenile ratios approached 90 % (Figure 6). At Naked and Jackpot, changes in juvenile densities of, respectively, 25 – 37 % could be detected with 90 % probability, or changes of 19 -34 % with 80 % probability. At Galena, power to detect changes of < 50 % of the annual means did not go beyond 50 % probability for any dependent variable.

Long-term trends

As derived from the mean of annual means, CVs for all dependent variables ranged widely, from 0.14 to 0.72 (Table 2). Using representative CVs, power to detect changes as low as 10 – 20 % was high when CV = 0.14 or 0.27, except under the 5-year scheme for the latter (Figure 7). The lowest CV (0.14) is representative of what we calculated for juvenile density and juvenile ratios at one or two sites each (Table 2). The intermediate CV (0.27) was obtained for adult densities two sites, and for juvenile ratios at two sites. Higher CV ranges (> 0.60) were obtained for adult density at one site and juvenile density at two sites; these resulted in little power to detect changes of < 50 % except over a time span of 15 years (Fig. 7).

Based on the annual variation we found for murrelets at sea, the USFWS objectives were in most cases obtainable in 4 – 9 years, whereas the intermediate objectives proposed by Hatch (2003) of -6.7 % per year should be achievable in < 10 years. In both cases, the exception was the low-density site of Galena. The higher sensitivity required to meet more stringent objectives will require 12-31 years (BBS) or 20-50 years (NSWCP) (Table 3).

DISCUSSION

Adult Abundance

In general, increasing the number of visits improved power, as might be expected, but the spread of survey effort was also influential, and the optimum design depended on whether the goal was to monitor adults or juveniles. Power to detect differences in adult densities improved if visits were concentrated in the early part of the fledging period (in PWS, 27 July – 10 August). Variability in numbers increased later in the fledging period, when adults start to disperse (Kuletz and Kendall 1998, Chapter 4).

Increased variability late in the breeding season can have multiple sources. Prey availability can affect the length of the chick-rearing period for alcids, because their chicks can respond to periods of low feeding rates with delayed growth (Birkhead and Harris 1985, Barrett and Rikardsen 1992, Romano 2000), and for marbled murrelets, fledging can take from 27 and 40 days (Nelson 1997). Late in the summer, seabirds not provisioning chicks are less likely to remain near breeding sites unless food is abundant (Hamer et al. 2002, Schreiber 2002). Because they do not defend nest sites as do colonial birds, murrelets may be even less tied to breeding areas if conditions are poor, which may partly explain large inter-annual variation in their at-sea abundance. In Auke Bay in Southeast Alaska, murrelet abundance was much lower in 1992, a summer preceded by a cooler spring than in 1993, which Speckman et al. (2000) suggested may have affected prey availability. In California, murrelets were widely dispersed from nesting areas in years with low spring upwelling, which were also years when other seabird species failed to reproduce (Becker and Beissinger 2003). All of these factors could alter the timing or degree of post-breeding dispersal of adults.

It is typical of seabirds to show greater fluctuations in counts in years when they have lower overall abundance. One hypothesis is that this pattern is due to unfavorable environmental conditions that cause birds to forage over greater distances (Hatch and Hatch 1989, Becker and Beissinger 2003, Hatch 2003). We found greater variability in adult density at the site with typically low densities (Galena), and with lower numbers and greater variances, the ability to detect changes in populations is reduced (Taylor and Gerrodette 1993). For this reason, it will be intrinsically difficult to detect significant trends at low-density sites such as Galena. Such sites can have occasional spikes in abundance, however; in 1997, Galena had the highest average murrelet density for any site or year. In that year, the area around Galena had an unusually high abundance of forage fish, and a variety of piscivorous birds were abundant in the area (Brown et al. 1999, Suryan et al. 2002).

For marbled murrelets, within-site annual fluctuations in late-season abundance that result from environmental conditions may be confounded by their relatively asynchronous breeding (De Santo and Nelson 1995). More obviously, abundance patterns of murrelets also vary among sites in the same region in the same year, perhaps because of differences in local chronology (Kuletz and Kendall 1998; Lougheed et al. 2002b; Chapter 4). Such spatial variability in post-breeding migration patterns may explain why power to detect annual differences in adult density improved with more visits, but detecting differences among sites was sharply reduced as the survey period extended late into the season (Fig 3).

Productivity Indices

Juvenile densities. -- In contrast to adults, detecting differences in juvenile abundance was usually most effective when visits continued throughout the entire fledging period (here defined as 27 July – 24 August). Over these four years, the consistent ranking in juvenile densities among sites (Naked > Jackpot ≥ Galena; Table 1), resulted in significant power to detect differences among them over all years (Fig. 4B). This suggests that it would be relatively easy to identify sites that are regionally important, and also optimum for monitoring productivity.

In PWS, juveniles appear on the water in mid or late July and their numbers usually increase through mid or late August, although there is some variation among sites (Kuletz and Kendall 1998; Chapter 4). Thus, later surveys often capture the greatest number of juveniles and are most representative of reproductive success or of the attractiveness of the site for juveniles from nearby areas. Differences in the attractiveness of a site for juveniles would more likely influence our ability to detect changes among sites than among years at the same site. For inter-annual comparisons at the same site, juvenile movement would only affect survey results if the migration rate varied among years. The relatively stable annual juvenile ratios within sites did not indicate that this was occurring. Nonetheless, juvenile movement out of a study site, and by implication the size of the defined study site, is an important consideration. For example, in Desolation Sound, British Columbia, Lougheed et al. (2002a) found that juveniles left their study site in < 24 h, whereas in PWS, there was no indication of such rapid turnover (Kuletz and Kendall 1998; Kuletz and Marks 1997). However, the Desolation Sound study site was less than half the size of any of the PWS sites, and the larger scale used in PWS probably minimized the effect of post-fledging movements.

Because differences in juvenile density among sites were robust, juvenile movement would have to be substantial to affect between-site comparisons. In PWS, juveniles rarely fly, and the open water distance between any two study sites (~ 50 – 100 km), plus the lack of observations of juveniles in open water between sites (Kuletz and Kendall 1998, KJK, pers. obs.), suggests that site-specific juvenile densities were representative of the surveyed site and immediately adjacent areas. Juveniles might, however, be attracted to a site from surrounding areas. In Kachemak Bay in Cook Inlet, Alaska, juvenile murrelets were aggregated where nutrient rich waters from the Alaska Coastal Current entered the bay (Kuletz and Piatt 1999). Kelp beds and well-mixed waters may have attracted juveniles to this location, creating a 'nursery' defined by favorable habitat features. We did not find a comparable nursery at our PWS sites, and kelp beds were not present at any site except along the east side of Naked, which is subject to heavy seas. However, the nearshore waters of the rest of Naked Island, semi-protected and near the central PWS current (Chapter 2), might have attracted juveniles from nearby Storey and Peak islands. In general, the lack of an obvious nursery area in PWS may be indicative of the typically stratified waters found throughout PWS in summer, the dispersed nature of prey in this region, and absence of kelp beds except in more exposed outer coasts. In regions with murrelet nursery areas, differences in juvenile density among study sites should be more pronounced than we found in PWS, provided the correct scale is used to define each site.

The strong influence of site on indices of productivity suggests that local environmental influences consistently either affected local murrelet breeding success, or juvenile retention and attraction to the site. In addition, because of localized differences in chronology, surveys concentrated early in the season may capture the peak of juvenile abundance at one site, but the beginning of fledging at another. For example, among PWS sites (the three in this study and three additional sites) differences of up to 20 days were noted in timing of first juvenile appearance or in peak fledging numbers (Kuletz and Kendall 1998, Chapter 4). For this reason, the longer survey period would be desirable when monitoring multiple sites, as indicated by the increased power to detect changes using the longer four week survey period. For a specific site, however, prior knowledge of typical chronology will dictate the best survey window to use.

Juvenile Ratios. -- Because of the unpredictability of adult presence late in the season, and its affect on juvenile ratios, there is general recognition that ratios must be used with caution (Beissinger 1995, Kuletz and Kendall 1998, Lougheed et al. 2002a). We found much greater power to detect differences in juvenile ratios among sites than among years with pooled data from all sites, but within-site, detecting temporal changes was relatively robust. In contrast to juvenile densities, the number of visits appears to be more influential on juvenile ratios than length of survey period. This is likely related to the need for a high number of visits to detect differences in adult densities (Fig. 3). Extending visits late into the season will not improve power, because of the decline in adult numbers and the concurrent influence on juvenile ratios. With high juvenile densities, however (e.g., Naked), obtaining juvenile ratios late into the season did not lower power.

With fewer visits (< 4), the power to detect spatial differences in juvenile ratios was slightly lower than it was for juvenile densities. This may partly be due to inherent difficulties when using ratios (see above). However, another aspect of juvenile ratios is that it standardizes sites for differences in overall murrelet abundance. Sites with relatively small breeding populations might have breeding success equivalent to sites with larger breeding populations. Among sites in the same region (i.e., PWS), differences in juvenile ratios might differ less than absolute juvenile abundance and would be difficult to detect with few visits, particularly if chronology varied among sites.

Long-term monitoring and management implications

Site, as well as the type of dependent variable being monitored, affected the estimated time frame required to derive statistically significant results. In general, at sites with high to moderate murrelet densities that were also relatively consistent from year to year, ability to monitor trends was more powerful for adult densities or juvenile ratios than for juvenile densities. An exception was the site with consistently high juvenile densities (Naked) which had the maximum ability to detect trends under any program for both juvenile density and juvenile ratio. For a site such as Galena, with small or erratic densities and ratios, many more years of effort would be required, under any program, to detect significant change in the population. Under these circumstances, at-sea monitoring will unlikely detect changes of < 3 % per year for adults or productivity indices. This rate of decline in adult abundance can be particularly detrimental to small populations (Taylor and Gerrodette 1993, Reed and Blaustein 1997) or to species with low recruitment and high adult survival like marbled murrelets (Beissinger 1995, Cam et al. 2003). A precautionary approach would be to relax power to ~ 0.8, and accept an alpha of 0.1. Still, the number of years (up to 50) required to detect changes in murrelets at low-density sites with high variance, means that at-sea surveys may not be practical for management needs in those situations.

For the relatively large marbled murrelet population of PWS, at-sea surveys will be useful for detecting < 3 % decline per year. Focusing on a group of consistently high-density sites will greatly improve the ability to track population size and productivity trends. At such sites, change of less than 20 % can be identified within five years, and less than 10 % change in 10 years. Given the normal variance encountered in seabirds (Schreiber 2002, Hatch 2003), these are reasonable and useful goals for monitoring this species.

For monitoring juvenile densities, even a few visits can identify sites that are important for a breeding population, and thereby focus management and conservation efforts. This approach would be especially useful in large remote regions with high numbers of murrelets, such as Southeast Alaska, PWS, or Cook Inlet (Agler et al. 1998). It may not be possible to monitor temporal trends in productivity at low-density sites, such as Galena. However, the value in monitoring sites that are possible ‘sinks’, is that they may be the first to show signs of change, or the spatial distribution of the birds may change (Buckland et al. 2004, p. 106). To integrate these peripheral sites into a monitoring plan for a large region, other methods need to be explored, perhaps using a simple presence/absence or adaptive sampling survey design. The latter allows for inclusion of low-density areas, but provides a protocol that increases survey effort in grids adjacent to where the target animal is found (Thompson and Seber 1996). With this method, areas where murrelets are patchy or unpredictable could be monitored as part of a large-scale program while minimizing effort at such sites.

Two methods for tracking population declines, demographic (models based on life history parameters) and survey (analysis of field counts) were compared by Taylor and Gerrodette (1993). They showed that for large populations, the survey method was more robust, because power to detect trends increases with greater population size. Small populations are subject to stochastic effects for both methods, however, mark-recapture methods used to estimate demographic parameters were more powerful with small populations than was the survey method. Additionally, it was the density of animals, not the size of study area, that determined the optimum method. For marbled murrelets, mark-recapture methods of defining demographic parameters have very low power to determine the health of the population, despite extensive effort (Cam et al. 2003). Thus several studies suggest that, for marbled murrelets, regions with very small populations or very low densities will be difficult to monitor with demographic or at-sea survey methods, and may require radar counts (Burger 2001, 2002) or other approaches that enable precise counts targeting specific breeding populations.

For long-term monitoring of murrelet productivity, the trend analyses indicate that juvenile ratios, with all their inherent problems, may still be the best method, as indicated by their generally lower time frame to detect change, compared to bird densities (Table 3). Over these four years, juvenile ratios proved the most stable characteristic, particularly among sites. At sea surveys thus provide reliable measures of productivity while providing reasonable measures of local population trends.

The overriding impact of site on indices of murrelet productivity corroborates other studies (Becker and Beissinger 2003, Cam et al. 2003) showing that strong spatial, thus habitat features, circumscribe murrelet productivity. By habitat features, we refer not just to nesting habitat, but also to local marine characteristics that determine prey availability. In California, Peery et al. (2004) concluded that marbled murrelet productivity was limited in some years by local food availability, while predation was important in other years. Within PWS, fish species and abundance patterns are highly heterogenous and defined by very localized marine habitat features, and these patterns are consistent over time (Foy and Norcross 1999, Stokesbury et al. 1999, Brown and Moreland 2000). We found evidence that murrelet prey use reflected these spatial patterns (Chapter 2), and these patterns thus will ultimately influence our ability, or appropriate methodology used, to monitor the population. This study provides a basis for detecting significant changes in a population, but it will be important to determine the biological significance of these levels of change to the local and meta-population.

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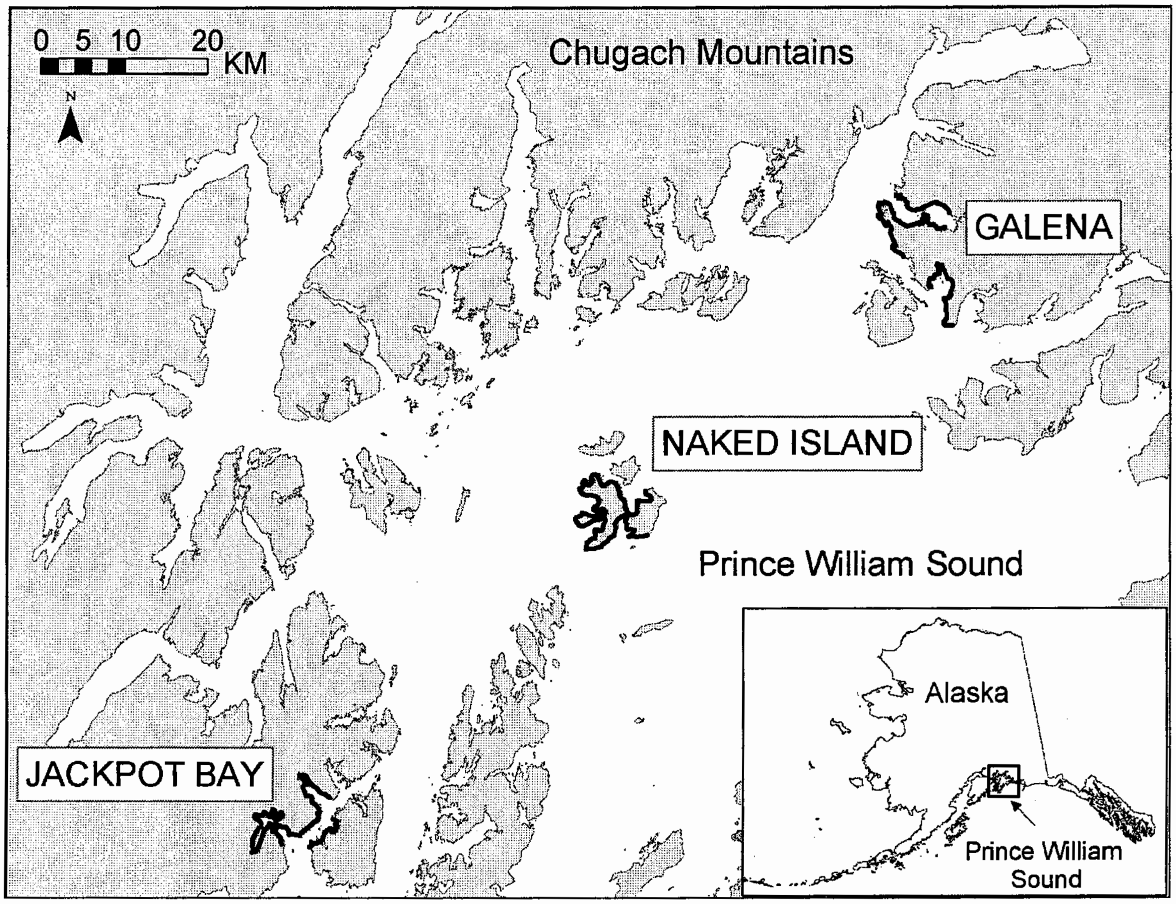


Figure 1. The three study sites (shoreline in bold) surveyed during summers of 1995, 1997, 1998, and 1999, to track adult and juvenile abundance of marbled murrelets in Prince William Sound, Alaska.

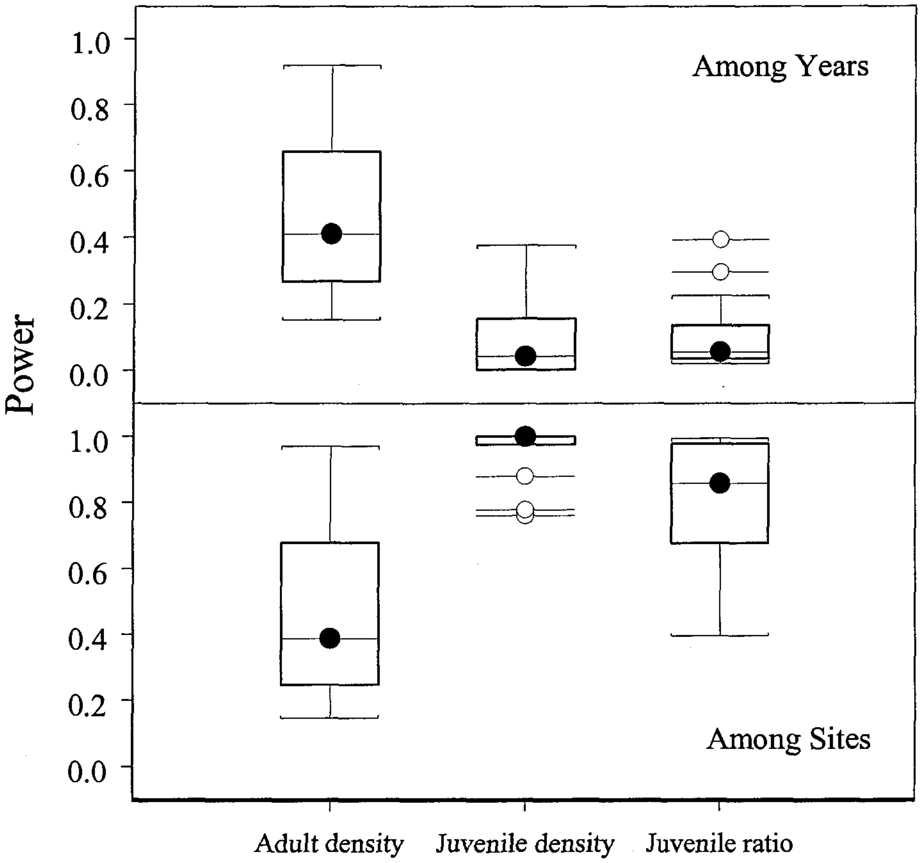
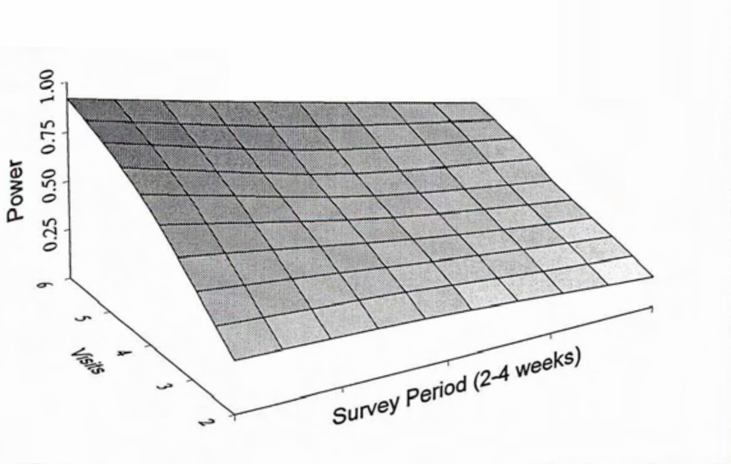


Figure 2. The power to detect differences among years (top) and among sites (bottom), for adult density, juvenile density, and juvenile ratios (juveniles:adults) for marbled murrelets. Results were computer generated using data from 65 surveys conducted in Prince William Sound, Alaska at 3 sites over 4 years (Table 1). The box-plots show mean (solid circles), upper and lower quartiles (boxes), and range (whiskers) without the outliers (open circles), with the latter defined as 1.5 x the interquartile range.

A. Adult density among Years



B. Adult density among Sites

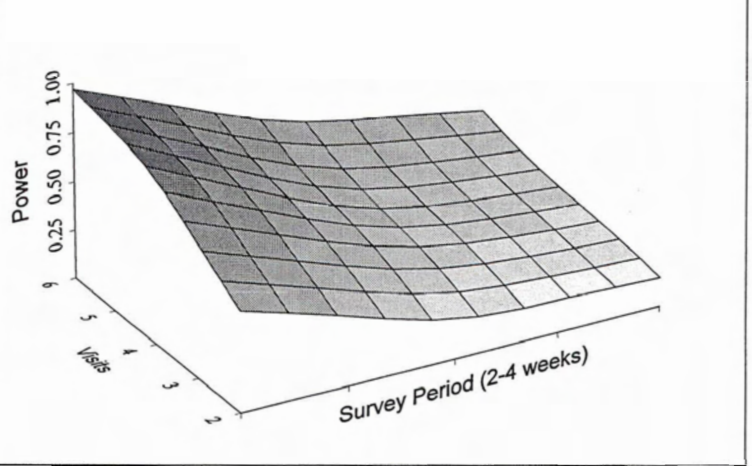


Figure 3. The power to detect differences in adult marbled murrelet density among years (A), and among sites (B), as a function of the number of visits (surveys) and the length of survey period (see text; categories were 2 – 4 weeks, shown interpolated in this spline graph). Darker shades indicate higher power to detect differences. Data were generated from actual surveys conducted at 3 sites in Prince William Sound, Alaska, in 1995, 1997, 1998, and 1999.

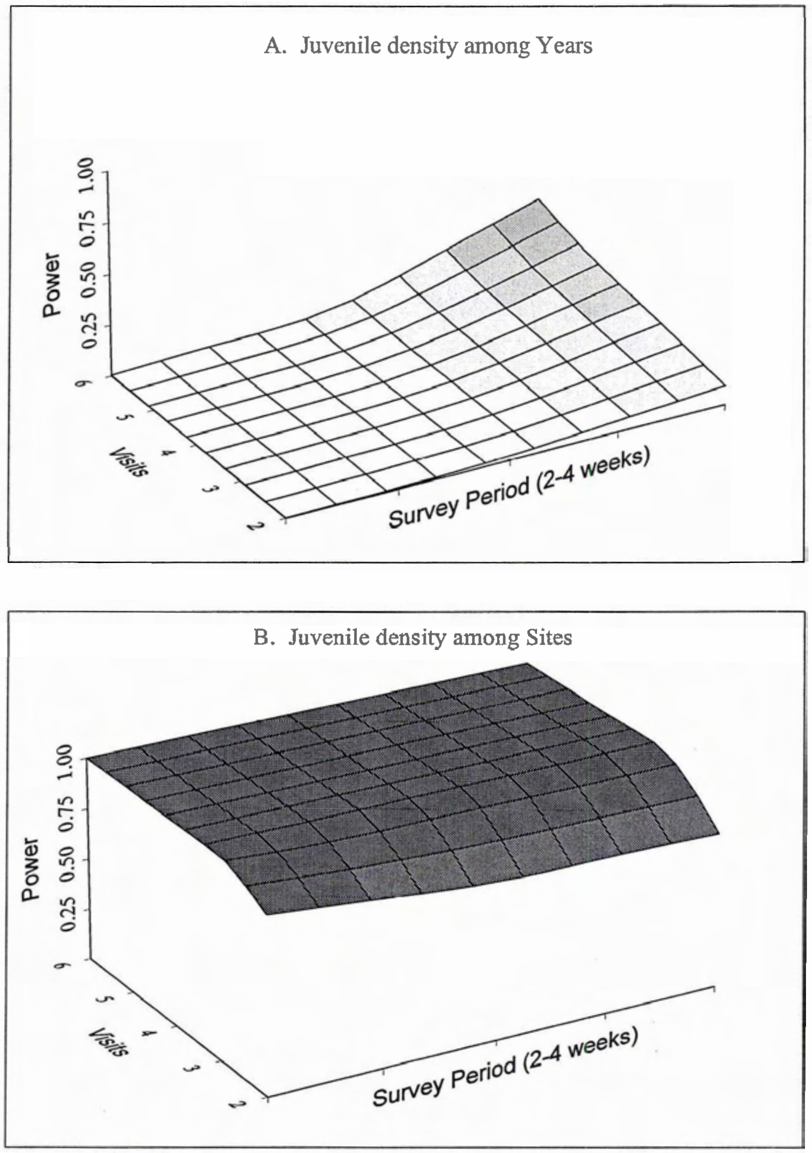
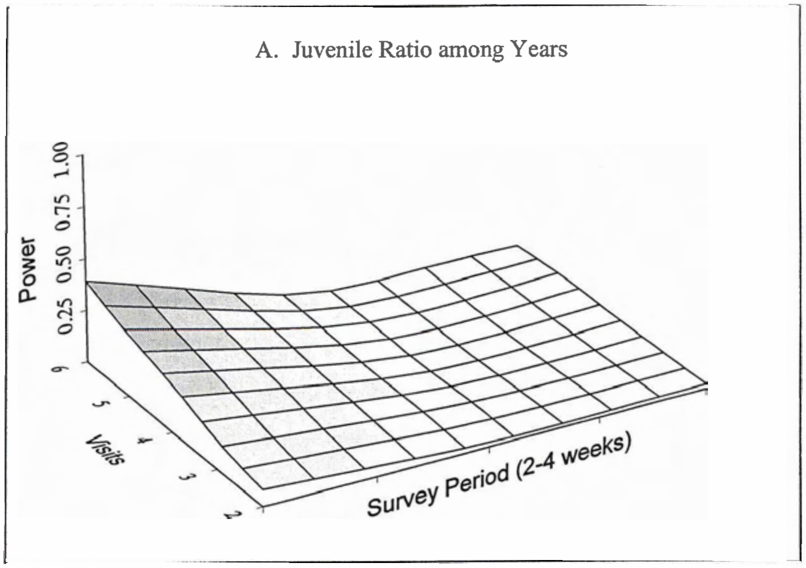
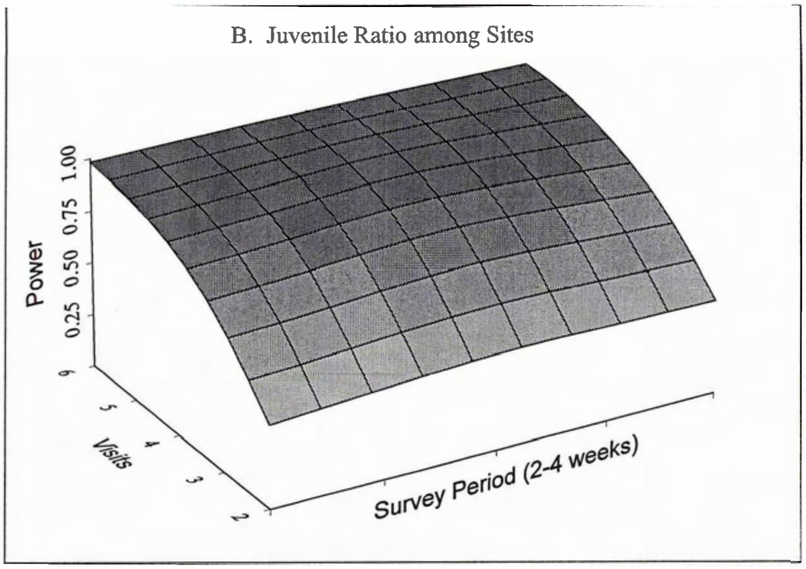


Figure 4. The power to detect differences in juvenile marbled murrelet density among years (A), and among sites (B), as a function of the number of visits (surveys) and the length of survey period (categories were 2-4 weeks, shown interpolated in this spline graph). Darker shades indicate higher power to detect differences.



A. Juvenile Ratio among Years



B. Juvenile Ratio among Sites

Figure 5. The power to detect differences in juvenile murrelet ratios among years (A), and among sites (B), as a function of the number of visits (surveys) and the length of survey period (see text; categories were 2 – 4 weeks, shown interpolated in this spline graph). Darker shades indicate higher power to detect differences

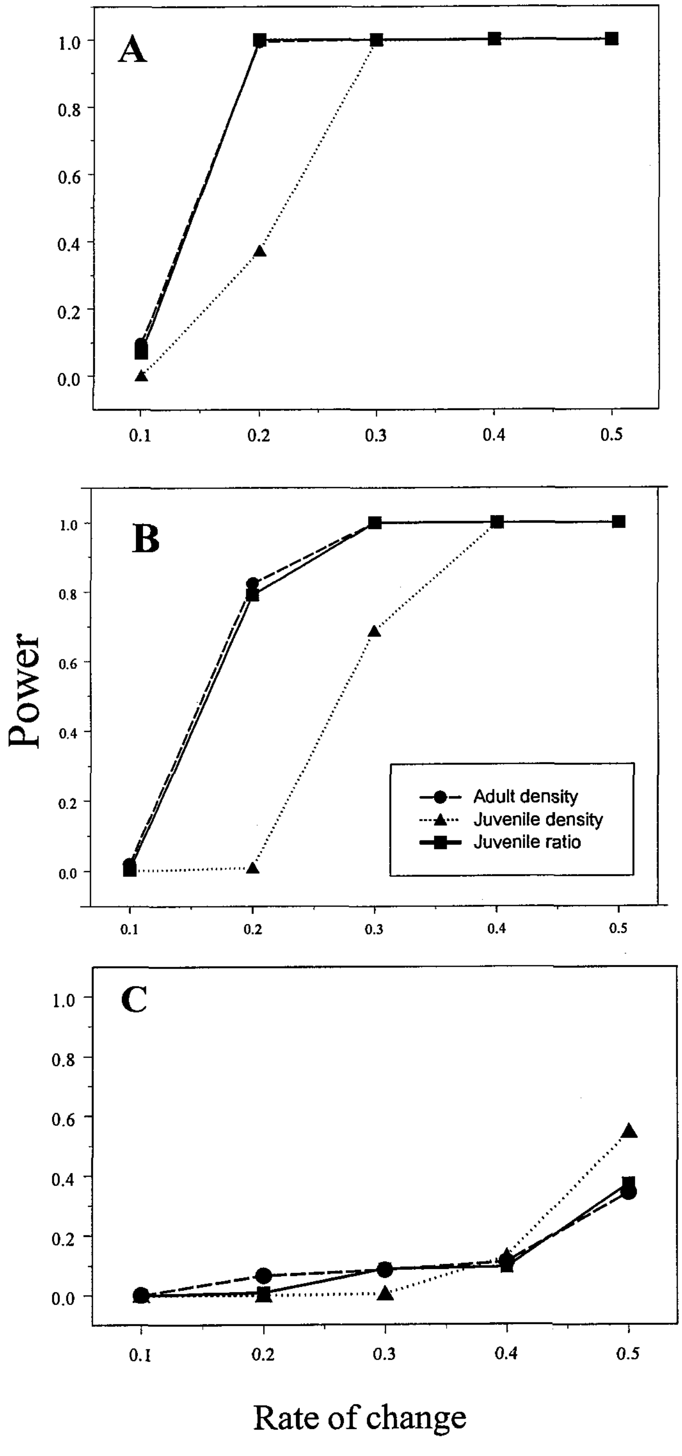


Figure 6. Power to detect changes of 10 to 50 % over four years, for adult densities (circles, dashed line), juvenile densities (triangle, dotted line), and juvenile ratios (square, solid line) at sites with juvenile densities typically high (A; from Naked data), moderate (B; from Jackpot data), and low (C; from Galena data; note lower Y-scale). Based on optimum sampling schemes (see text), these power tests assumed six visits per survey period, and used only the early survey period for adult densities and juvenile ratios, and the entire survey period for juvenile densities.

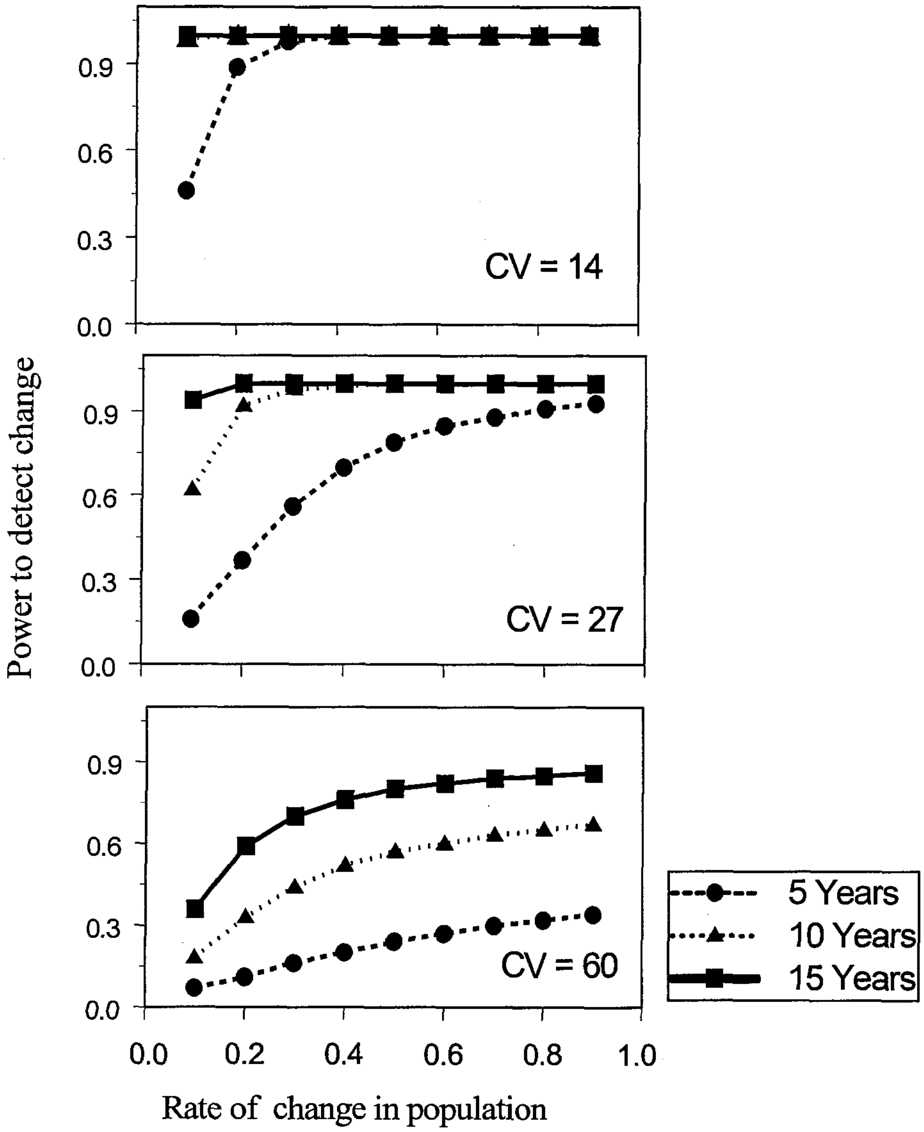


Figure 7. Power to detect changes in population size over time spans of 5, 10, and 15 years of survey effort, given coefficient of variation (CV) at three levels. The representative CVs were derived from murrelet surveys in PWS conducted over four years, and used SD of the mean of annual means for each site and dependent variable (see Table 2). Power was calculated using the TRENDS program (Gerrodette 1993), assuming constant CV and a linear function.

Table 1. Summary of original data on marbled murrelet abundance and productivity, based on surveys conducted at three sites in Prince William Sound, Alaska, in 1995, 1997, 1998, 1999. Means (± SE) are shown for adult density (birds / km^2), juvenile density (birds / km^2), and ratios (number of juveniles:adults), using only surveys conducted between 27 July and 24 August of each year. Differences among sites and years were tested with ANOVA, with df = 2, 61. There was no significant interaction between Site and Year for any variable. Juvenile density and juvenile ratios were significantly higher at Naked compared to Galena or Jackpot (Tukey pair-wise comparisons).

Year	Site	N surveys	Adult Density	Juvenile Density	Juvenile:Adult Ratio
1995	Naked	6	13.82 (2.79)	1.47 (0.28)	0.13 (0.04)
	Jackpot	5	15.42 (4.23)	1.02 (0.17)	0.11 (0.04)
	Galena	5	8.93 (1.82)	0.23 (0.07)	0.03 (0.01)
1997	Naked	6	17.60 (6.30)	1.38 (0.14)	0.13 (0.04)
	Jackpot	6	10.40 (1.64)	0.58 (0.18)	0.07 (0.02)
	Galena	6	22.01 (8.67)	0.64 (0.08)	0.06 (0.02)
1998	Naked	6	13.39 (3.89)	1.23 (0.30)	0.13 (0.03)
	Jackpot	7	15.26 (4.25)	0.26 (0.06)	0.03 (0.01)
	Galena	5	8.07 (1.96)	0.19 (0.07)	0.02 (0.01)
1999	Naked	6	9.67 (2.31)	1.07 (0.25)	0.12 (0.02)
	Jackpot	7	10.10 (2.82)	0.39 (0.09)	0.06 (0.01)
	Galena	0	nd	nd	nd
Difference among Sites			ns	< 0.001	< 0.001
Difference among Years			ns	< 0.01	ns

Table 2. Mean abundance estimates (birds km^{-2}) for murrelets at three sites in Prince William Sound, Alaska. The Coefficient of variations (CV) were used to estimate power to detect differences in the three variables (adult density, juvenile density, juvenile ratios) over time. The survey periods used (early or entire) were selected based on power analyses conducted on the total surveys (n = 65) conducted over the four years.

		Adult density (early period)		Juvenile density (entire period)		Juvenile ratio (early period)	
Site	N Years	Mean	CV	Mean	CV	Mean	CV
Naked	4	20.69	0.27	1.29	0.14	0.09	0.13
Jackpot	4	17.14	0.30	0.56	0.59	0.04	0.31
Galena	3	16.44	0.72	0.35	0.71	0.04	0.29

Table 3. Results of TRENDS analysis, with number of years required to obtain a power of 0.9 to detect differences in murrelet abundance or ratios, under the criteria established or recommended by four programs. CVs were obtained from murrelet surveys conducted in Prince William Sound, Alaska, in 1995, 1997, 1998, and 1999, and represent the mean of all annual means for a given site and survey period.

			Number of years to detect change at given criteria			
Variable	Site	CV	USFWS [a]	Hatch [b]	BBS [c]	NAWCP [d]
Adult density	Naked	0.27	8	10	18	29
(early period)	Jackpot	0.30	8	10	20	31
	Galena	0.72	23	16	31	50
Juvenile density	Naked	0.14	4	7	13	20
(entire period)	Jackpot	0.59	18	14	28	45
	Galena	0.71	23	16	31	50
Juvenile ratio	Naked	0.13	4	6	12	19
(early period)	Jackpot	0.31	9	10	20	32
	Galena	0.29	8	10	19	31

[a] 20 % change per year, alpha = 0.1; objective of Alaska Maritime National Wildlife Refuge, U.S. Fish and Wildlife Service.

[b] 50 % change in 10 years (-6.7 % per year), alpha = 0.05; suggested for colonial seabirds by Hatch (2003).

[c] 50 % in 25 years (-2.7 % per year), alpha = 0.05; objective of Breeding Bird Survey and Partners in Flight.

[d] 50 % change in 50 years (-1.4 % per year), alpha = 0.05; objective of North American Waterbird Conservation Plan (primarily for waterfowl).

CHAPTER FOUR

PRODUCTIVITY OF MARBLED MURRELETS IN RELATION TO PREY VARIABILITY IN A HETEROGENEOUS ENVIRONMENT

ABSTRACT

For the 2- 4 % of seabird species that do not nest in colonies, it may be possible to examine productivity relative to food availability without the influence of colony-related stressors. I studied the non-colonial marbled murrelet (*Brachyramphus marmoratus*) in Prince William Sound, Alaska, to determine if murrelet productivity was affected by variability in prey abundance, and thereby a source of population decline. At three sites (separated by 40 - 90 km) I measured total murrelet productivity by juveniles at sea (juveniles / km^2), and obtained an index of breeding success per pair by using juvenile:adult concurrent ratios. Vessel-based surveys were conducted from June through August in 1995 and 1997-1999. Fish school densities (schools / km^2) were measured with aerial surveys during the same periods. Evidence of site-specific differences in breeding chronology suggested that murrelets were responding to environmental cues that influenced the timing of fledging or nest initiation. Murrelet productivity was also site-specific, and was consistently highest at the site (Naked) with characteristics that would enhance fish availability, even though fish school density was not highest there. The annual density of juveniles at sea generally declined during this study, despite an increase in fish school abundance, which suggests that prey was not limiting murrelet productivity. However, within each site, murrelet productivity was highest in the year that local fish school abundance was highest. There may be a threshold of fish abundance necessary before it is possible to detect differences in murrelet productivity. During these four years, concurrent ratios indicated that reproductive success per pair did not decline. Adult murrelet abundance declined, and because it was correlated with juvenile abundance, I propose that declining numbers of adults, and not low breeding success, was responsible for the decline in juvenile density. There has been a decline in body mass of murrelets in PWS between 1977 and 1998, suggesting adult stress during the breeding season. Alternatively, adult mortality is occurring at other times of the year when birds disperse from PWS breeding sites. The factors causing of loss of adult murrelets warrants further investigation.

INTRODUCTION

Many aspects of seabird breeding success and chick-rearing behavior have been linked to changes in prey (Cairns 1987, Baird 1990, Burger and Piatt 1990, Regehr and Montevecchi 1993, Golet et al. 2000, Suryan et al. 2002, review in Coulson 2002). Because most seabirds nest in colonies, questions regarding the regulation of seabird populations are often approached as density-dependent factors, such as competition for nesting space and food (Ashmole 1963, Croxall and Rothery 1991, Ricklefs 2000). Empirical support, however, for the connection between prey, coloniality, and population regulation, has been harder to clarify (Croxall and Rothery 1991). Colonial nesting occurs in 13 – 30 % of all avian species but in 96 – 98 % of all seabirds (Lack 1968, Rolland et al. 1998, Coulson 2002). Such nesting behavior may predominate in seabirds because of a need for increased safety from predators, information exchange on location of food, or centralized social activity that promotes synchronous breeding (Ward and Zahavi 1973, Wittenberger and Hunt 1985, Coulson 2002). The main arguments for density-dependent population regulation revolve around the potentially negative effects of colonial nesting. Seabirds are densely concentrated at a time when their energetic demands are highest and they become obligate central-place foragers to feed their chicks, thereby creating the potential for competition and food depletion near the colony (Ashmole 1963). The size of colonies has been positively linked to foraging range, foraging trip duration, and size of the forage grounds (Furness and Birkhead 1984, Cairns 1989, Danchin and Wagner 1997), or proximity to other colonies (Furness and Birkhead 1984, Ainley et al. 2003). All of these indirectly support the theory that density-dependent factors, acting through food limitation, regulate seabird populations.

In keeping with the theory of local prey depletion or ‘hinterlands’ (Cairns 1989), non-colonial seabird species should not be subject to competition resulting from food depletion near the nest site. This makes it possible to examine productivity and population change relative to food availability with less influence from colony-related activities. There are inherent logistic problems, however, in determining nesting success and chick diet for non-colonial birds, and thus the study of food limitation has been largely neglected for the few non-colonial seabirds. Such has been the case for the marbled murrelet (*Brachyramphus marmoratus*), which has one of the largest geographic ranges of any alcid (family Alcidae), and numbers in the hundreds of thousands throughout the eastern North Pacific (Nelson 1997, McShane et al. 2004). Despite the marbled murrelet’s wide distribution and numerical dominance in some northern portions of its range (Agler et al. 1998), little is known about how the marine environment, particularly the prey base, affects its abundance or productivity. Because of its distribution and solitary nesting habits, some have suggested that marbled murrelets are not dependent on large aggregations of prey (Carter and Sealy 1990, Ostrand et al. 1998), and thus their productivity would be less subject to fluctuations in prey abundance or aggregation than their colonial cousins. In this study, I investigated the hypothesis that productivity of a non-colonial seabird has high tolerance to fluctuations in fish abundance, with the goal of understanding the conditions that limit marbled murrelet populations. Secondarily, I investigated the relationship between chronology and site-specific characteristics for this widely-dispersed seabird.

Throughout its range, populations of marbled murrelets (hereafter, murrelets) appear to have declined, but identifying the primary causes has been elusive. The murrelet almost certainly has been impacted by the loss of up to 80 % of its nesting habitat from British Columbia to California, due to the harvest of old-growth forests (Burger 2002, McShane et al. 2004), and most research has focused on that aspect of their biology. More recently, studies have examined their marine habitat requirements (Day and Nigro 2000, Yen et al. 2003 Ostrand et al. 2004), which may also impact murrelets. Because an estimated 90 % of the murrelets in the eastern Pacific breed in Alaska (McShane et al. 2004), it is an important region for tracking changes in the population relative to changes in the marine environment. I studied murrelet productivity in Prince William Sound (PWS), Alaska, which is the northernmost substantial breeding population of marbled murrelets. In PWS, marbled murrelets are the most abundant breeding seabird (Agler et al. 1998), but they have declined 85 % since 1972 (Appendix). Because of this, I considered the opposing hypothesis that food has been limiting the productivity of murrelets. I examined this by testing whether murrelet productivity correlated with spatial and temporal differences in prey abundance. Because a component of being non-colonial is purported to be asynchronous nesting (Gaston and Jones 1998), and murrelets are less synchronous than other alcids (Lougheed et al. 2002a), I investigated the relationships between prey, breeding chronology, and productivity of murrelets.

Seabirds can be sensitive indicators of changes in the marine ecosystem (Furness and Nettleship 1991, Abraham and Sydeman 2004), but this is not always evident in their reproductive success. In response to changes in food availability, seabirds may alter nest attendance patterns (Burger and Piatt 1990, Monaghan et al. 1994, Litzow and Piatt 2003), foraging distances (Suryan et al. 2002), or food delivery rates to chicks (Baird 1990, Suryan et al. 2002). Because of the difficulties in locating and monitoring nest sites, studies of these behaviors are usually not possible, or are extremely limited for murrelets (Bradley et al. 2004). Marbled murrelets nest up to 75 km inland (Nelson 1997) and nests are difficult to find, making observation of multiple nests prohibitive. Radio telemetry has been used to track individual murrelets to obtain foraging ranges (Chapter 1, Whitworth et al. 2000, Hull et al. 2001), frequency of inland chick-feeding trips (Bradley et al. 2002), and breeding success (Bradley et al. 2004). Such effort, however, is expensive and can not be maintained for long-term studies or over large spatial scales.

Several studies have suggested that low prey availability (sometimes linked to El Niño conditions) may be responsible for low murrelet breeding success (Becker and Beissinger 2003, Peery et al. 2004) or low attendance in nesting habitat (Burger 2002). These studies did not simultaneously measure prey abundance. In this study, I used aerial surveys to obtain an index of fish abundance in each study site and for all of PWS. At-sea surveys were used to assess patterns of adult and juvenile abundance (and provided an index of chronology) within and among four years and three sites. I used indices of fledging success to monitor total productivity of each site (juvenile density at sea) and as an index of reproductive success of local birds (juvenile:adult ratios). This approach was possible because of the concurrent fish studies (Brown et al. 1999), and because of the relatively high density of murrelets in PWS. The study sites encompassed different marine habitats and were widely dispersed, allowing comparisons among fairly large (50 km shoreline) and oceanographically diverse sites within a well-defined ecosystem. Previous studies of murrelet foraging range in PWS (Chapter 1) and the murrelet productivity index in Alaska (Kuletz and Kendall 1998, Kuletz and Piatt 1999) provided a framework for establishing study sites and sampling design. I incorporated results from power analyses (Chapter 3) to select the best productivity indices, and incorporated associated studies of murrelet foraging behavior and diet (Chapter 2).

Furthermore, a long-term monitoring program provided documentation of regional murrelet population trends (Appendix).

METHODS

Study Area

The study sites were in Prince William Sound (PWS), Alaska, a 10,000 km^2 embayment along the north coast of the Gulf of Alaska. The three sites surveyed for murrelets, each approximately 50 km of shoreline, were in the northeast, central, and southwest portions of PWS (Fig.1). I conducted surveys at Galena Bay/Tatitlek Narrows (Galena), Naked Island (Naked), and Jackpot Bay / Dangerous Passage (Jackpot) (Fig. 1) in 1995, 1997, 1998, and in 1999. In 1999 Galena was not surveyed. At Galena, study site boundaries were shifted south after 1995 to better match fish survey coverage. The central part of this site remained Galena Bay, and because habitats were similar and preliminary analyses showed no difference in murrelet abundance, I treated 1995 and 1997-98 boundaries as the same site.

The aerial fish surveys, conducted by E. Brown (University of Alaska Fairbanks), encompassed most of the shoreline of PWS, but focused efforts on the eastern, central and southwest regions (Fig. 2). The murrelet surveys were conducted within portions of the sound-wide fish surveys, so I extracted site-specific data on fish schools (G. Ford, ECI, Inc., Portland Oregon). In Chapter 2 my study sites were defined by circumscribing a 10 km radius circle around the center of the murrelet transects at each site, because I wanted to compare adult behavior and abundance within nearshore waters of the sites. To compare murrelet productivity with fish abundance, however, in this study I defined the site as a 16 km radius from the center (Fig. 1), because this is the zone most likely used by a bird foraging for its chicks (Chapter 1). I used a geographic information system (GIS; ArcView) to define the 16 km radius, which was the mean straight-line distance traveled from suspected nest sites to forage sites by six radio-tagged murrelets in PWS. It was also greater than the mean 11 km traveled by 51 radio-tagged murrelets from capture site to subsequent forage sites (Chapter 1).

Background on murrelet diet

Murrelets in PWS depend on many of the same forage fish as other North Pacific piscivorous seabirds (Chapter 2), in particular juvenile and adult sand lance (*Ammodytes hexapterus*), juvenile and adult capelin (*Mallotus villosus*), juvenile Pacific herring (*Clupea pallasi*), and juvenile gadids (Gadidae), with the most abundant gadid being walleye pollock (*Theragra chalcogramma*) (Chapter 2). They may also take juvenile salmonids (*Oncorhynchus* spp.), smelts (Osmeridae), and Pacific sandfish (*Trichodon trichodon*). In Chapter 2, I showed that 90 % of the fish observed being used by adults and held by adults for delivery to chicks consisted of juvenile herring (0+ and 1+ age classes, < 66 and 66 – 130 mm in length, respectively) and juvenile (0+, < 60 mm) and adult (1+ - 3+ age class, 60 -130 mm) sand lance. Thus for this study we considered only the abundance of juvenile herring and sand lance < 130 mm in length. In Chapter 2, I reviewed the biology of key prey species, and the basic oceanography of.

Data Collection

Fish surveys. – I used aerial surveys of fish school abundance because they were most appropriate for comparison with the murrelet surveys. Hydroacoustic surveys were also conducted during our study, but proved less useful for several reasons. Hydroacoustics were conducted > 1 km off shore, beyond where most forage fish and seabirds occur in PWS (Norcross et al. 2001, Brown et al. 1999). Boats could not effectively deploy hydroacoustic gear close to shore, and boat avoidance behavior by the fish interfered with data collection (Haldorson et al. 1999). Acoustic surveys could not usually detect sand lance, which were known to be a key prey species used by murrelets in PWS (Chapter 2). Finally, hydroacoustic surveys were conducted at each murrelet site only for a few days each year, yielding a single biomass estimate, and thus did not provide data on temporal changes in local abundance within years, and potentially made their single estimate affected by seasonal changes in fish distribution. In contrast, aerial surveys were able to measure abundance of small schools of fish, including sand lance, close to shore. Aerial surveys allowed greater coverage of PWS and multiple visits to each site throughout the chick-rearing season. Each aerial survey was conducted in a single day, with 5-14 survey days flown at each site in a given year between late June and early August. The number of aerial overflights per site is higher than noted in Chapter 2 because of the greater area used for each site in this study. Otherwise, the methods and protocol for aerial surveys, and treatment of the data, are presented in Chapter 2

The surface area of fish schools was calculated from length and width measured from the air, but I present fish abundance using only the number of fish schools. In preliminary analyses, I found no statistical differences in the abundance of fish (by site, year, or season) as measured by school surface area as opposed to number of schools. Additionally, the number of fish schools was significantly correlated with total surface area of schools for all surveys combined. Forage fish in PWS are characterized by small (< 80 m^2) schools (Brown et al. 1999, Chapter 2), and murrelets usually select for small schools in PWS (Ostrand et al. 1998), thus I consider the number of fish schools, rather than the size of schools, to be the most appropriate for comparisons with murrelet abundance. In deeper water and in years when gadid abundance is much higher than that of herring, murrelets will select for herring as prey species rather than overall school size of fish (Ostrand et al. 2004). However, in the nearshore waters we surveyed, herring and sand lance were 90 % of the murrelet prey used (Chapter 2), thus we assumed that school size remains the primary selection criteria for murrelets. This approach also assumed that murrelets do not control fish abundance or distribution.

To obtain seasonal information on fish abundance, each season was divided into six 10-day blocks (periods) and average fish abundance within each period was obtained from the surveys within that time period. The aerial fish surveys were not necessarily concurrent with the murrelet surveys, but were treated as an index of meso-scale (i.e., spatially 10s -100s km and temporally weeks-months; Hunt and Schneider 1987) fish abundance and availability for each site, season, and period. In this study, meso-scale refers to the study sites (Galena, Naked, Jackpot), as covered by the at-sea murrelet surveys, and regional scale refers to all of PWS.

Murrelet surveys. -- I used boat-based surveys to measure abundance of adult and juvenile marbled murrelets. Included in the 'adult' category are after-hatch-year immature birds (likely 1 – 3 years old; Nelson 1997) which can not be visually distinguished from breeding birds. Juveniles refer to hatch-year birds, fledged between July and August of each year. In each year, two sets of surveys were conducted. The first occurred during pre-laying and incubation (28 May – 16 June), and the second set occurred during the fledging period (18 July - 30 August. Each survey took a full day (0700 - 1600 h). I surveyed from 7.5 m vessels traveling 100 m from shoreline. A boat operator and 2 observers recorded all birds and marine mammals 100 m either side of and ahead of the boat. All observations were entered into a computer, along with behavior (on water, in air, foraging), plumage characteristics, and group size. When I encountered potential juvenile murrelets (black-and-white plumage) I paused to identify the age class using standard criteria (Ralph and Long 1995, Kuletz and Kendall 1998). In PWS most adults leave the area throughout August before molting into non-breeding black-and-white plumage, which reduces the chances of misidentification of age classes during this period (Kuletz and Kendall 1998).

Murrelet counts from each survey day were considered independent, since surveys were separated by several days. I assumed that most juveniles observed at a site originated there or nearby, and thus reflected local breeding success of murrelets. In PWS the assumption is reasonable at least until late August (Kuletz and Marks 1997, Kuletz and Kendall 1998, KJK unpublished data on 6 radio-tagged juveniles). Net juvenile movement out of the study sites would mean that our estimates of productivity were minimums, while a continual or net movement into a study site would overestimate local fecundity. Lougheed et al. (2002a) report an average residence time of about 5 days for juveniles at Desolation Sound in British Columbia (BC), which depressed the estimate of juvenile:adult ratios. Based on their results, Lougheed et al. (2002a) recommend applying a correction factor to account for low survival of juveniles (interpreted as turnover) in their survey area. However, the area traveled by the radio-tagged juveniles tracked by Lougheed et al. (2002a) was roughly one-third the size of any of our study sites, and thus well within the spatial scale of our study. Although some level of juvenile movement (immigration, emigration, or both) likely occurred, it was more likely to involve adjoining areas, since our sites were separated by > 40 km. In the absence of data on turnover rates for this study, I assumed that there was no bias in turnover rate of juveniles by site or year.

Data Analysis

Murrelet chronology

Indices for murrelet chronology were obtained by observations of juveniles on the water during boat-based surveys. For each site, I determined date of first juvenile appearance, highest juvenile count, and cumulative percentage of juveniles at 50 and 75 % of annual site total (50th percentile and 75th percentile, respectively). To compare chronology without bias from site-specific juvenile abundance, I standardized indices by calculating the average day of each index by site and year (using May 25 as day 1), and then calculated deviations as:

$$\text{anomaly} = (d_i - d_m)/d_m$$

where d_i is average day for that site and year, and d_m is the overall average (n = 11 site-years). I tested for differences in the anomalies among years and among sites with non-parametric Kruskal-Wallis rank sum test.

Murrelet productivity

Murrelet productivity was based on two basic types of measures, juvenile density (birds / km^2) and the ratio of juveniles to adults. Juvenile density was considered an index of total productivity at a given site, being the product of local adult densities, breeding success of pairs, and early juvenile survival to the time of survey. The juvenile:adult ratio was considered an index of the productivity per breeding pair, being the product of juvenile density weighted for adult abundance in an area. To examine total murrelet productivity (by site and year) I used juvenile density. To examine breeding success (analogous to fledglings per breeding pair) of the local population, I used ratios.

Based on previous analyses (Chapter 3) and murrelet chronology in PWS (Kuletz and Kendall 1998, this study), I used different sets of survey dates for different indices. Early surveys often had no or few juveniles, which greatly increased variance in an area's annual sample (Kuletz and Kendall 1998, Chapter 3), whereas measures of adult abundance, which affected ratios, were compromised by post-breeding migration from the area after early or mid-August. Power analyses indicated that the ability to detect differences in juvenile abundance increased when surveys were extended late into the fledging period (Chapter 3). I wanted the index of productivity to more closely estimate local fledging success before it was heavily affected by juvenile mortality, therefore, I omitted the last week of August. In late August, some sites showed declines in juveniles that could have indicated juvenile movement or mortality that would affect productivity indices. Thus, 'entire fledging period' was defined as 27 July - 24 August, which encompassed the beginning of fledging at all sites and the approximate date when all sites reached at least 75th percentile of juvenile observations (see Results). A refinement of juvenile density, the 'core density' used the average of the five highest juvenile counts at a given site and year (Kuletz and Kendall 1998). This ensured that each site had equivalent numbers of their highest juvenile counts to derive an index of local productivity.

I examined two types of ratios, 'concurrent ratios' and 'sequential ratios'. Concurrent ratios were derived from the number of juveniles divided by the number of adults on the same survey, using surveys from 18 July – 10 August. The early fledging period was used because the post-breeding dispersal of adults later in August affected ratios, and power to detect differences in concurrent ratios was optimized by focusing surveys on the early period (Chapter 3). Additionally, the 10 August is the approximate date that each site reached at least the 50th percentile in juvenile abundance (see Results). The advantage to using concurrent ratios was a larger sample size and error estimates for each site, and power analyses found them to be the most stable and thus optimum measurement for detecting differences in murrelet productivity (Chapter 3).

Sequential ratios were derived by dividing the average core juvenile density by the average June adult density. Sequential ratios provide only one sample per site-year, but earlier studies suggested that it would be less subject to fluctuations in adult numbers that occurs later in the breeding season, and June counts should be representative of the local breeding population (Kuletz and Kendall 1998).

Statistical tests. - Normality of fish and bird indices were tested using the Anderson-Darling test (Snedecor and Cochran 1989) and visual inspection of the normal probability plots. Where appropriate (Anderson-Darling p-value < 0.01), abundance indices were log-transformed prior to analysis. Two-way analysis of variance (ANOVA) was used to test for differences between sampling site and year. P-values for main effects in the two-way ANOVA are reported from partial sums of squares adjusted for the other main effect. After testing of main effects I entered the interaction term adjusted for both main effects. For murrelet indices, I specified a Type-IV test (SAS 1996), because of the missing cell in 1999 (when Galena was not surveyed). I used the Tukey adjustment to control the error rate on p-values when comparing least squares means. Residual plots were examined to assess model fit. For within-year comparison among sites, I used a Kruskal-Wallis rank sum test.

I used simple linear regression to examine within-season (by 10-day block period) and annual trends in murrelet abundance or productivity indices (juvenile density or ratios) relative to fish school density. I used linear regressions to test average juvenile density at the site over the entire fledging period (27 July – 24 August) as a function of average adult density at each site during the early fledging period (18 July – 10 August) or average adult density in June. A 3-dimensional regression plane was used to visually examine the relationship between year, fish school density, and juvenile density or ratio, using site and year samples from the three sites ($n = 11$). Tests were considered significant at $P < 0.05$. I used SAS (SAS 1996) and SPLUS software for analysis, and SPLUS for graphic presentations (Insightful 2001).

RESULTS

Fish School Abundance

During these four years, a total 115 survey days were flown, with 11,473 km flown within the three study sites (Fig. 1) and 1,502 schools of herring or sand lance were counted from the air (Table 1). PWS regional school abundance (for 6 sites and herring and sand lance schools combined; schools / km^2) increased each year from 1995 to 1999 (Fig. 4). A single outlier (included in the analyses) in 1995 came from the Jackpot site, where 33 and 44 herring schools were observed on two separate days. At the three murrelet study sites combined, total (herring and sand lance) fish school density was slightly higher in 1995 than 1997, and then increased in 1998 and again in 1999 (Fig. 5). The higher value for 1995 for these three sites (compared to all 6 sites used to index PWS fish abundance), came from the large number of herring schools at Jackpot that year. As noted in Methods, the number of fish schools correlated with total surface area of fish schools by survey and year, and because murrelets selected for small schools (Ostrand et al. 1998), fish school density is considered the best measure of fish abundance for this study. Thus, for the three study sites, overall school abundance was lowest in 1997 and highest in 1999.

Within years, total fish abundance varied among sites in all years but 1997 (Table 2). There was no consistent pattern of relative abundance among sites, except that Naked did not have the highest fish school abundance in any year (Table 2). Among the three sites, Galena had the highest fish school abundance in 1997 and 1999, and Jackpot was highest in 1995 and 1998. At Galena and Naked, the year with highest fish school abundance was 1999, whereas Jackpot had more fish schools in 1995 and 1998 (Fig. 5). Total fish school abundance varied by site and by year, but year effects were stronger and there was a significant interaction between the main effects (two-way ANOVA; Table 2). Overall, 1999 was significantly higher in fish school abundance than 1995 or 1997, and Galena was significantly higher in fish abundance than Jackpot (Tukey comparisons tests; Table 2).

Species-specific fish abundance. – Species identification for aerial surveys was not well developed in 1995, so herring and sand lance was only examined for each species separately in 1997 – 1999. Overall, herring school abundance increased each year between 1997 and 1999, but as a main effect, the difference among years was not significant (Table 3). The main effect of site was significant for herring, with school abundance at Galena significantly greater than at the other two sites (Table 3). However, there were interactive effects between site and year, which may be why within years, sites differed in herring school abundance only in 1999, when Galena had the highest recorded herring school density of all years or sites. Herring school abundance was highest at Jackpot in 1998 and highest at Galena and Naked in 1999 (Table 3).

Sand lance school abundance increased slightly between 1997 and 1998, and increased dramatically in 1999 at all three sites. As main effects both site and year were significant, and there were no interactive effects (Table 3). Jackpot had significantly lower sand lance school abundance than the other two sites and Naked always had the highest school abundance of sand lance, although Galena was nearly equivalent in 1999. Sand lance school abundance in 1997 was significantly lower than in 1999. Within years, sand lance school abundance varied among sites in 1998 and 1999, but not in 1997 (Table 3).

In summary, there was a general increase in fish school abundance from 1995 to 1999. There were significant differences among sites, both in the type of fish that predominated and in their annual abundances. Naked always had more sand lance schools and Jackpot or Galena had the most herring schools. Jackpot differed from the other two sites by having more fish schools in 1995 than in 1997, and in having high densities of herring schools in 1998.

Seasonal patterns in fish abundance. – Fish school density varied seasonally among sites and between herring and sand lance (Fig. 6). Herring didn't vary among years, and though sand lance did, site was the stronger main effect, so to examine seasonal trends I combined four years of data (10-day blocks) for each site. In general, fish school abundance increased from June to July, with a fairly broad peak in school abundance during July and early August. Herring tended to be early at Galena and Jackpot, peaking first at Galena during the first 10 days of July, and peaking later in July at Jackpot. Herring appeared relatively late at Naked, starting in late July, but continued into mid August. Sand lance occurred at Galena and Jackpot mainly in 1999, and arrived late relative to herring. Sand lance peaked first at Galena, but tapered off quickly after mid July, and appeared at Jackpot only near late July. Naked had sand lance present throughout the season (and every year), particularly from mid July through early August (Fig. 6).

Murrelet Chronology, Abundance, and Productivity

Seasonal patterns indicative of chronology. -- Across all sites and years, adult abundance was highest in mid to late July, and declined sharply throughout August, which roughly paralleled the general patterns of fish abundance (Fig. 7), although the decline in fish preceded that of murrelets. The seasonal patterns of adult abundance were relatively consistent among sites, although murrelet abundance at the beginning of July surveys varied by site and year (Fig. 8). In all cases there was a general decline in adult numbers throughout the fledging period. In 1997, adult densities were particularly high in late July, at the beginning of the fledging period (Fig. 8).

Juvenile occurrence from late July through August varied among sites both in abundance and seasonal patterns (Fig 8). With the exception of 1998, Naked showed evidence of a second, smaller peak in abundance, separated from the first peak by 19, 15, and 23 days in 1995, 1997, and 1999, respectively (Fig. 8). As a way to gauge the seasonal patterns of juvenile appearance at sea, I used the percentage of a site's annual number of juveniles counted in each survey. In general, juveniles increased in late July and reached peak daily proportions from early to mid-August (Fig. 9). This means that fledglings arrived on the water at least 10 days after the peak in fish school abundance.

In 8 of 11 first surveys (and in all years at Naked) at least one juvenile was present (Table 4), thus I did not usually capture the beginning of fledging. The longest span between date of first juvenile observation was 8 – 13 days in 1995, between Naked and Galena (with uncertainty because of survey schedules). Date of highest juvenile count was the most variable index (Fig. 10) and ranged from 31 July to 23 August (Table 4). Date of the 50th percentile for juvenile observations ranged among sites between 6 – 11 August (Table 4), with a maximum difference of 10 days, between Naked and Jackpot in 1997. The 75th percentile was reached between 10 – 23 August (Table 4), with the greatest difference between Naked and Galena (12 days), when the relatively few juveniles at Galena peaked early in 1995. Naked reached the 75th percentile 4 – 7 days earlier than Jackpot each year between 1997 and 1999 (Table 4).

For the 11 site-years, only the 50th percentile index varied significantly overall, among sites (Kruskal-Wallis rank sum $X^2 = 6.69$, df = 2, P = 0.04). No index varied significantly among years, but highest juvenile counts occurred early in 1995 and 1999, and late in 1997 and 1998 (Fig. 10). The date of the 50th percentile was used to compare chronology among sites, because it was less variable than the highest juvenile count, and appeared to reduce the variability caused by second 'peaks' (the latter of which may result from re-nesting by pairs with failed first attempts; McFarlane-Tranquilla et al. 2003a,b). The date when juveniles reached the 50th percentile showed site-specific patterns, with Galena and Naked typically earlier than the overall mean date, and Jackpot always later than the mean (Fig. 11).

Adult murrelet abundance. – Adult murrelet densities in June were highest in 1997, but declined overall at all sites between 1995 and 1999 (Table 5). Adult density in June varied between years and sites.

Across all years of the study, Galena had lower adult densities than both Jackpot and Naked in June. The significant difference for year was primarily from a lower level of adult densities in 1999 than the previous years (Table 5).

During the early fledging period (18 July – 10 August), for the no interaction model, there was a significant difference by site but not by year (Table 5). Galena had significantly lower adult densities than Naked but was not lower than Jackpot. There was, however, a significant interaction between site and year for adults in July and August (Table 5). Galena had lower mean adult densities than Naked in 1995 and 1998, but the two sites had comparable levels in 1997. Overall, during early fledging, abundance of adults at Naked was significantly higher than at the other two sites.

Juvenile murrelet abundance. – Juvenile density, whether for the entire fledging period or the selected core surveys, varied significantly among sites and years (Table 5). Across all years of study, Naked had higher juvenile densities than Jackpot and Galena. The significant effect of year was accounted for in a decrease in juvenile densities between 1997 and 1998. However, these trends should be interpreted with caution as the site by year interaction was significant when added to the model ($P = 0.02$). Mean densities show that Naked consistently had higher juvenile densities than the other two sites. At Naked, the decrease in juvenile density between 1995 and 1999 was significant ($R^2 = 0.97$, $n = 4$, $P = 0.01$). Juvenile density at Jackpot also declined from 1995 to 1998, but the decline for the four years of this study was not significant (Table 5). In 1995 and 1998 Jackpot had higher juvenile densities than Galena, but in 1997 juvenile densities were similar between the two sites (Table 5). Overall, juvenile densities were significantly lower in 1998 than in other years. In all analyses, there were no differences in results for tests using Core surveys or the entire fledging period (Table 5), therefore I refer only to the juvenile densities during the entire fledging period.

Concurrent ratios during the early fledging period varied significantly among sites, but not among years (Table 5). Across all years of the study Galena had lower concurrent ratios (Least Squares mean = 0.012) than Naked (Least Squares mean = 0.046, $P = 0.03$), and ratios at Naked were also higher than at Jackpot, although the difference across years was not significant (Table 5). Sequential ratios (which used average June adult density at a site) did not vary significantly among sites or years, although the difference among years approached significance (Kruskal-Wallis Chi-Square = 6.97, $df = 3$, $P = 0.073$). The sequential ratio was highest at Naked except in 1997 (Table 5). In 1999, the sequential ratio was affected by the extremely low density of adults nearshore in June (Table 5), particularly at Naked, which resulted in an unusually high ratio of 0.45.

Juvenile densities and concurrent ratios were highly correlated during these 11 site-years ($R^2 = 0.65$, $df = 1,9$, $P = 0.003$), which would be expected since juvenile densities are incorporated into the ratios. While they both showed significant site effect, the year effect was only significant when using juvenile densites (Table 5). For both concurrent ratio and juvenile density, the site effect was primarily because of the much higher productivity at Naked compared to Galena. Only juvenile density indicated the significantly lower productivity in 1998, because while Galena and Jackpot showed a much lower concurrent ratio in 1998, Naked showed little change (Table 5).

By site and year, mean juvenile densities (entire fledging period) were positively correlated with mean adult densities during the early fledging period (before most adults leave the area) (Fig. 12; $R^2 = 0.42$, df = 1,9, $P = 0.03$). There was no significant correlation between juvenile densities during the entire fledging period and adult density in June (Fig. 12; $R^2 = 0.11$, df = 1,9, $P = 0.33$).

Fish abundance relative to murrelets

On an annual basis, there was no significant linear relationship between fish school density and adult murrelet density in June or during the early fledging period. However, when adult murrelet density and fish school density were averaged for each 10-day block of each site, there was a weakly positive, but significant linear relationship ($R^2 = 0.28$, df = 1,12, $P = 0.05$). This was likely related to the fact that both adult murrelets and fish peaked in mid to late July and declined after mid August (Fig. 7).

Across all sites and years ($n = 11$), neither juvenile density nor concurrent ratios had a significant linear relationship to fish school density. Because murrelet productivity was consistently so much higher at Naked, and spatial relationships between seabirds and prey can be stronger when prey are less abundant (Vlietstra 2005), I examined the relationship between fish school density and murrelet productivity separately for the two low-productivity sites (Galena and Jackpot) and the high-productivity site (Naked) (Fig. 13). Although there were positive trends of higher fish school densities corresponding to higher juvenile densities at Jackpot and Galena, and with concurrent ratios at Naked, the regressions were not significant (all Ps > 0.20). Because fish school density at Naked increased each year, while juvenile density at Naked decreased each year, juvenile density at Naked was significantly, but negatively correlated with fish school density ($R^2 = 0.97$, df = 1,2, $P = 0.01$). The decline in juvenile density at Naked was equivalent to a 9.8 % per annum decline.

For Naked and Jackpot, both juvenile ratios (Table 5) and fish school density (Table 2) were highest in 1999, but for the three years when all three sites were surveyed for murrelets, the increase in fish school abundance between 1995 and 1998 was not reflected in significantly greater juvenile ratios. When juvenile density or concurrent ratio were graphed as a function of fish school density and year in a 3-dimensional regression (Fig. 14), the regression plane shows a trend of higher murrelet productivity with higher fish school density. For juvenile densities, the graph also shows the decline from 1995 to 1999, while concurrent ratios appear stable or show a slight increase over time. Although the sample size was small ($n = 11$), and statistical tests not significant, the slopes of the regression planes in these two graphs suggest that other site effects may have masked a subtle positive influence of fish school abundance on murrelet productivity.

DISCUSSION

Murrelet productivity and fish abundance

The density of juveniles at sea generally declined during this study, despite an increase in fish school abundance, which suggests that prey was not limiting the productivity of murrelets during these years. However, within sites, high murrelet productivity occurred when local school abundance was highest, and there may be a non-linear threshold of fish school abundance (in this case, of approximately 0.4 fish schools/ km^2) before it is possible to measure differences in murrelet productivity (Fig. 13). My sample size was small (11 site-years), but the absence of a strong relationship nonetheless suggests that murrelets were responding to factors other than simple fish school abundance within the 16 km radius study site. Because adult numbers declined over these four years (Table 5), and adult abundance (by site and year) was correlated with juvenile abundance (Fig. 12), declining numbers of adults, and not low breeding success, was most likely responsible for the decline in juvenile density. Indeed, the concurrent ratios suggest that reproductive success per breeding pair remained relatively stable or even increased slightly in the late 1990s (Figs. 13).

An assumption I made during this study was that murrelets would forage close to their nest site when possible, because of the energetic costs of travel and delivery of large prey to their chicks (Chapter 2; Hull et al. 2001). This is a basic prediction of optimal foraging theory for central place foragers (Orians and Pearson 1979, Ydenberg et al. 1994), and in PWS it was supported by observations of radio-tagged murrelets, which tended to forage within 16 km of their nests and 10 km from their capture sites, regardless of local habitat types (Chapter 1). On a larger scale, murrelets in California were found to forage closer to nesting habitat when upwelling created favorable foraging conditions (Becker and Beissinger 2003).

Marbled murrelets can travel much farther than I found in PWS (averaging 78 km in one study; Whitworth et al. 2000). Based on maximum ranges that have been recorded (Whitworth et al. 2000, Hull et al. 2001), they could hypothetically cover most of PWS. However, if they travel far for food, murrelets should incur greater energetic costs, which in other seabird species has corresponded to lower reproductive success (Suryan et al. 2002). Thus, murrelet productivity should be low when there is insufficient food near the nest and they must travel far, or if there is simply not enough food within foraging range. Murrelet productivity should be highest when food is available near the nest. In support of this hypothesis, at two of the sites (Jackpot in 1995 and Galena in 1997), the year when juvenile density was highest (Table 5) was also the year that fish school abundance was higher than other years at the site (Table 2). At all three sites (including Naked in 1999), the concurrent ratio was highest during the year when fish school abundance was highest for that site (Table 5). These 'high productivity/high fish' years, with a threshold effect, may explain the tendency for murrelet productivity to increase with fish school abundance (Fig. 14), despite the lack of a statistically significant relationship.

Another assumption I made was that murrelets did not exert 'top-down' control on forage fish, such as that exerted by fish on zooplankton in some marine systems (Cury et al. 2000). As an indicator of the relative impact murrelets might have on herring (the forage fish with the best biomass estimates), I estimated the proportion of juvenile herring biomass consumed by murrelets. In the Okey and Pauly (1999) model for PWS (for years 1994 – 1996), murrelets were estimated to consume 341.2 kg · km^{-2} · $year^{-1}$, or 0.3412 t · km^{-2} · year $^{-1}$. Based on a juvenile herring biomass of 11.307 t · km $^{-2}$ (Okey and Pauly 1999), this equates to roughly 3 % of the juvenile (0+ and 1+) herring biomass annually. The biomass estimates were based on many caveats, but nonetheless, the relatively small proportion of biomass consumed, even if murrelets fed only on herring, would not support the scenario of murrelet control of forage fish abundance.

Changes in seabird productivity are not always evident, because within a certain threshold of prey abundance, adults can alter their behavior to 'buffer' chicks against short-term fluctuations in prey (Cairns 1987). Additionally, many seabird chicks are resilient to fluctuations in meal delivery rates or energy content, and will fledge despite periods of food stress (review in Visser 2002). Under these conditions, more sensitive indicators of food stress include adult time budgets (Burger and Piatt 1990, Regehr and Montevecchi 1997. Zador and Piatt 1999), chick-feeding rates (Uttley et al. 1994, Hamer and Thompson 1997), or foraging distances of adults provisioning their young (Suryan et al. 2002). During the years of this study, there was no indication from several colonial seabird species in PWS that prey was ever low enough to cause a drastic reduction in their productivity, although there were some changes in the indicators mentioned above. These studies included surface-foraging black-legged kittiwakes (*Rissa tridactyla*; Suryan et al. 2002), nearshore diving pigeon guillemots (*Cepphus columba*; Goelet et al. 2000), and deep diving tufted puffins (*Fratercula cirrhata*; Piatt et al. 1997). In the absence of a strong signal indicating lack of prey for other seabirds, it would be less likely that I could detect a difference in productivity for a widespread, non-colonial bird.

Chronology

Sites differed in appearance of first juvenile, and dates of 50th and 75th percentile by 1 – 2 weeks, with Galena and Naked early and Jackpot always late. The variability among sites was generally consistent across years, indicating that breeding patterns were more synchronous for birds within sites than for birds at sites 45 – 90 km apart. Since these are not colonial nesters, it suggests the murrelets were responding to environmental cues or conditions that influenced the timing of fledging or nest initiation. The appearance of fledglings could be an indication of timing of nest initiation, but it is not a precise measure of hatch date, because murrelet chicks can take between 27 and 40 days to fledge (Nelson 1997). Presumably, as with other seabirds, this range in the length of the nestling phase results from the chick's ability to adapt to periods of low food availability by altering growth patterns (reviews in Birkhead and Harris 1985, Visser 2002). Thus, a possible scenario is that the early appearance of fledglings (as in 1995 and 1999; Fig. 10) was indicative of abundant food, which promoted faster chick growth and earlier fledging. A shorter chick phase could itself contribute to higher breeding success, because nest predation (of adults, eggs, and chicks) can be high for murrelets (Nelson 1997, McShane et al. 2004).

The second, smaller peak in juveniles at Naked could reflect successful re-nesting. Second peaks in juveniles at sea have been observed in murrelets farther south (Nelson 1997), and there is evidence from radio-tagged birds (Hebert et al. 2003) and physiological markers (McFarlane-Tranquilla et al. 2003a) that murrelets can re-nest after a failed attempt. At least one nest found on Naked Island was believed to be a re-nesting attempt (Naslund et al. 1995). Production of a second replacement egg is likely to require about two weeks for alcids (Vanderkist et al. 2000), the approximate time between the peaks in juveniles at Naked (Fig. 8). McFarlane-Tranquilla et al. (2003a) suggested that because of the time necessary for re-nesting, the tendency to re-nest declined later in the season. Because the Alaska breeding season for murrelets is 12 – 64 days shorter than for populations farther south (increasing from British Columbia to California; Hamer and Nelson 1995), there is very limited time for re-nesting in PWS. There was little or no evidence of second peaks at the other PWS sites, which is further indication that conditions are optimum and last longer at Naked then at the low-productivity sites (Jackpot and Galena). Notably, the year without a second peak at Naked, 1998, was also the latest year for chronological markers at that site, (Table 4), and the year with the lowest mean concurrent ratio for all sites combined (Table 5). Although there was no comprehensive pattern of fledging date anomalies relative to fish school abundance, there was a non-significant trend at Naked of an earlier date of juvenile 75th percentile each year, as school abundance increased (Table 4).

Re-nesting may contribute to the apparent asynchrony in murrelet chronology (McFarlane-Tranquilla et al. 2003a) which is otherwise attributed to the murrelet's solitary nesting habits (Hamer and Nelson 1995, Gaston and Jones 1998). Because of the extended range in nesting and fledging dates, it has proven difficult to detect interannual changes in chronology of murrelets (Lougheed et al. 2002b, McFarlane-Tranquilla et al. 2003b). The site-specific patterns of chronology found in this study suggest that meso-scale environmental cues may be as influential as large-scale environmental cues.

Interannual differences in murrelet chronology are more likely influenced by large-scale environmental conditions (Bertram et al. 2001, Abraham and Sydeman 2004), although ultimately, they will affect the local (site-specific) systems (Mackas and Galbraith 1992, Bertram et al. 2001). Fish school abundance was measured during the chick-rearing season, but oceanographic processes affecting fish abundance began months earlier (Brown 2003). As an example, satellite imagery of the Gulf of Alaska (GOA) (SeaWIFFS 2004) shows that in PWS, the spring of 1998 was relatively poor in chlorophyll-a (ranging ~ 1.0 – 2.0 mg/m^3), whereas the spring of 1999 was relatively high (ranging ~ 2.5-4.0 mg/m^3). High primary productivity in 1999 was followed by high fish abundance that summer (Figs 4 and 5), a year which also had high concurrent ratios for murrelets (Table 5). In PWS, the zooplankton community (consumed by the forage fish) is also periodically subsidized by deep water exchange from the GOA, possibly during summer relaxation of downwelling (Kline 2001). The influx from the GOA may strongly influence productivity within PWS, but the magnitude varies annually, and the forces driving these influxes are not well understood (Kline 2001).

Chronology and seasonal patterns of fish. -- Based on the appearance of fledglings (Table 4), and assuming an average 58 days from egg laying to fledging (Hamer and Nelson 1995), I estimate that the earliest hatching occurred from 22 June to 4 July, with the majority of chicks hatched by 12 July. Thus, peak chick-rearing coincided with peak fish abundance (11 – 30 July; Fig. 7), at least as measured by density of fish schools in surface waters. Fledging occurred as fish abundance generally declined in August (Figures 7 and 9), although there were more fish present during August at Naked than at the other sites (Fig. 6). This means that in most areas of PWS, newly-fledged birds spend their first weeks under deteriorating prey conditions. Alternatively, birds were accessing prey that were not evident from aerial surveys (i.e., small dark coves or kelp beds; Kuletz and Piatt 1999, KJK pers. obs.). Murrelets fledge at 58 - 71 % of adult weight, are not fed by parents after fledging (Nelson 1997), and appear to be weak divers (KJK, unpubl. data). Parker et al. (2003) estimated from radio-tagged juveniles a survival rate of 0.8621 for the first 80 days after capture at sea, but they acknowledged that initial survival could be lower, since the juveniles they caught could have been on the water several weeks since leaving the nest. The immediate conditions that a juvenile encounters upon fledging (i.e., within the first week) could be critical. A site like Naked, with protected, shallow waters (Table 6) and fish present later into the season (Fig. 6) might enhance survival.

Additional factors.

There were two complicating factors when examining the site-specific fish-murrelet relationship. First, I assumed that the density of fish schools counted during aerial surveys represented all prey needs of murrelets, but that may not be valid. Adult murrelets use a variety of prey species and age classes (Burkett 1995, Ostrand et al. 1998, 2004) but to raise chicks they require larger (80-130 mm) energy-dense fish, which are obtained during late evening or pre-dawn hours (Chapter 2). The 1+ age class herring may only be near the surface during evening hours, when they move up in the water column to feed (Foy and Norcross 1999, Thomas and Thorne 2001), and thus may not be documented in the daytime aerial surveys. An example was the apparent mismatch at Jackpot, where chick-rearing continued later than at the other two sites, when aerial surveys indicated fish had left the area (Fig. 6). However, our late-evening diet cruises found that Jackpot Bay was a 'hot-spot' for murrelets catching 1+ herring for their chicks (Chapter 2). This highlights the need to distinguish between prey necessary for adults vs. chicks, when investigating the influence of prey abundance on productivity.

The age-class composition of fish important to murrelets (0+ and 1+ age classes) varies spatially and interannually (Brown 2003). For example, hydroacoustic surveys near the Jackpot area found above-average biomass of 1+ herring in 1995 (when juvenile murrelet density was high), but below-average biomass of that age class in 1997 (Haldorson et al. 1999). In northeast PWS (near Galena), prey delivered to black-legged kittiwake chicks indicated that 1+ herring prevailed in 1998, but only 0+ herring were available in 1999 (Suryan et al. 2002). Thus, even when food was abundant for adult murrelets, food adequate for raising chicks may not have been equally abundant.

The second complicating factor was that fish abundance does not necessarily mean that fish are available to the birds (Montevecchi 1993, Hunt et al. 1999). To forage efficiently, birds often use oceanographic features that concentrate prey near the surface, such as hydrographically enhanced tidal flows, eddies, small fronts, or underwater sills (reviews in Schneider 1990, Hunt et al. 1999). When murrelets foraged in deep fjords, they concentrated over underwater shelves, sills, or near headlands that would most likely be sites of upwelling (Chapter 1). Murrelets are more limited in maximum diving depth than larger alcids (Piatt and Nettleship 1985, Burger 1991), and in PWS as elsewhere, murrelets appear to prefer waters 20 - 30 m deep (Day and Nigro 2000, Chapter 1). The site-specific associations found in this study could have been due to marine habitat characteristics that affected prey availability, as much as prey abundance. Associated with the issue of prey availability vs. abundance is that the aerial surveys were limited in their ability to detect fish in deeper waters. Fish deeper in the water column may not have been detected, but could have moved towards the surface or into shallower waters at other times.

Methodological considerations. -- Although the relative values for sequential ratios were generally consistent with the trends shown by concurrent ratios (Table 5), the unusual value at Naked in 1999 illustrates their sensitivity to changes in adult density. Using June adult densities (pre-laying and early incubation phase) should be the best period to capture the size of the local breeding population (Kuletz and Kendall 1998, Lougheed et al. 2002b). The Kuletz and Kendall (1998) study included data for 1994 and 1995, but the longer data set in the current study indicates that adult presence in June was more variable in 1995 - 1999. Despite the extremely low numbers of adults in June 1999, productivity indices indicated that birds were breeding and successfully raising young. In 1999, adults may have been foraging beyond the near shore zone that we surveyed, since fish schools were farther offshore that year (Chapter 2; Fig. 5). Despite the inherent problems in using ratios (Lougheed et al. 2002b), they serve as a gauge of reproductive success independent of local murrelet abundance. As shown by this study, total productivity as measured by juvenile density could be misleading, particularly without concurrent data on regional population trends.

Importance of location

Murrelet productivity was strongly linked to site, and in PWS, location determines species, abundance, and seasonal presence of fish (Stokesbury et al. 1999, Brown and Moreland 2000, Norcross et al. 2001). The marine habitat in PWS is highly heterogeneous, and this is reflected in the consistent spatial and temporal distribution of herring and sand lance among the study sites (Chapter 2). Indirectly, the effect of prey abundance and availability on murrelet productivity may be mediated through location. Because the primary interest in this study was to investigate food as a limiting factor for murrelets, I assumed that breeding habitat was not a limiting factor. I based this assumption on the fact that murrelets breed throughout PWS in a variety of upland habitats (Kuletz et al. 1995, Marks et al. 1995), and a relatively small proportion of the forest (5 – 10 %; U.S. Forest Service, Chugach National Forest, Anchorage, Alaska) has been harvested compared to regions farther south. In effect, I am assuming an ideal-free distribution (Fretwell and Lucas 1970) of murrelets in PWS that is based on both the terrestrial and marine habitats. Under ideal-free distribution, murrelets would be distributed according to habitat quality, such that optimal habitat would be saturated, and to corresponding lesser degrees, birds would nest in (terrestrial) and near (marine) lower quality habitats. If they are like most other alcids (reviews in Birkhead and Harris 1985, Coulson 2002), murrelets are likely to be philopatric (Nelson 1997). A 'behavioral tradition' of occupation should perpetuate the use of an area for nesting, particularly if it is in close proximity to good foraging habitat (Hull et al. 2001, Yen et al. 2003).

A body of literature has been devoted to the establishment and maintenance of seabird colonies, and there is growing evidence that colonies with a history of breeding success retain or attract breeding birds, while breeding failure leads to eventual abandonment of a site (Danchin et al. 1998, Brown and Brown 2002, Ainley et al. 2003). This process can result in geographic structure of colony distribution and colony sizes within a regional population (Danchin and Wagner 1997, Ainley et al. 2003). Similarly, murrelets could exhibit geographic structure in accordance with habitat quality. The differences observed among the three sites in this study beg the question of why they varied so consistently in murrelet productivity.

A qualitative summary of site characteristics (Table 6) suggests that a combination of habitat (upland and marine) and species interactions (other seabirds and humans) could potentially influence murrelet abundance. These site-specific attributes warrant further investigation. For example, Galena (low murrelet productivity) is characterized by fair amounts of shallow (< 60 m) waters and large areas of forested uplands. However, it has relatively fresh water due to glacial and mountain runoff (Gay and Vaughan 2001), and is the farthest (~ 30 km) from the main counter-clockwise current of PWS. Fish present were typically 0+ herring and lower amounts of 0+ sand lance. It has high disturbance factors, including vessel traffic, large numbers of larids, and past timber harvest southeast of the site boundaries. Jackpot (low to intermediate murrelet productivity) has the smallest area of shallow water, but is closer (~ 5 – 20 km) to the southern reaches of the main PWS current. Age 1+ herring were present, and in some years (1995 and 1998) abundance of 0+ and 1+ herring was high. The area of forested habitat is large, and disturbance factors at Jackpot are low. Naked (high murrelet productivity) has more saline waters, and is in the path of the central PWS current (derived from the Alaska Coastal Current south of PWS, and source of nutrient-rich, saline waters; Royer et al. 1990, Niebauer et al. 1994). Sand lance of all age groups were present, as were 0+ herring and occasional shoaling of post-spawning capelin (Brown 2002, KJK pers obs.). Although there is little total area of forest compared to the other sites, a large proportion of it is high quality nesting habitat. Human disturbance factors are low at Naked, and colonies with 4 species of alcids and smaller numbers of two species of larids nest there.

At Naked, large areas of relatively shallow water, large protected bays, and a dynamic boundary zone of water may make more species of fish available for murrelets, and for a longer period throughout the summer. These characteristics could compensate for the relatively moderate fish biomass in the central (Naked) region of PWS (Haldorson et al. 1999). The presence of alternative prey species, in particular, can improve seabird productivity. Murres (*Uria aalge*) in the Barents Sea were able to reproduce successfully where they had three types of prey available, despite declines in key species in some years (Barrett 2002). In PWS, kittiwakes at a colony near an area with herring, sand lance, and capelin, were able to access alternate prey when herring were low, whereas birds at a colony with access only to herring experienced lower success in some years (Suryan et al. 2002). The oceanographic conditions of PWS do not favor high biomass or huge concentrations of fish compared to outer GOA regions (Sambrotto and Lorenzen 1986, Brown 2003). However, sites with reliable fish availability are generally favored by birds over sites with sporadic prey (Erikstad et al. 1990, Piatt 1990, Skov et al. 2000). While Galena and Jackpot alternately had the highest abundance of fish (Table 2), Naked was intermediate in three of four years, and consistently had the highest sand lance abundance (Table 3).

Population changes in PWS

This study occurred in the midst of a long-term and continuing population decline. The 1989 *Exxon Valdez* oil spill may have exacerbated the decline in the murrelet population, but there was also evidence that changes began prior to the spill (Kuletz 1996) and continued afterward (Lance et al. 2001, Appendix). Since 1989, the murrelet population has declined 5 % per annum (Appendix). During the approximate time of my study, three sound-wide surveys conducted between 1996 and 2000 showed a decline of 8.5 % per annum (data in Appendix, Table 1). This rate of decline approximates the decline observed between 1995 and 1999 for adults at my three study sites, and the 9.8 % per annum decline in juvenile densities at Naked (Table 5, Fig. 13). Since concurrent ratios did not decline, it suggests that lower survival of adults, juveniles or immature birds, reduced recruitment of birds to the breeding population. Alternatively, birds could be emigrating from PWS, but we have no data to determine if birds are leaving the area or have higher mortality than they did prior to the population decline. Most demographic models of long-lived birds, including murrelets, conclude that low adult survival is the most detrimental to the population, followed by low juvenile survival and lastly, low annual productivity (Beissinger and Nur 1997, Cam et al. 2003, McShane et al. 2004). The results from PWS are consistent with the predictions of these demographic models.

Because many of the piscivorous birds, harbor seals, and wild salmon stocks in PWS have also declined (Peterson et al. 2003), it suggests that changes in the marine food web were affecting top level predators (Agler et al. 1999, Piatt and Anderson 1996). Even if they are able to raise chicks, adult seabirds can be compromised by the stress of high energetic demands when prey availability is low (Kitaysky et al. 1999, Golet et al. 2004), which could affect over-winter or long-term survival (Saether et al. 1993, Golet et al. 1998). Data on adult murrelet body mass suggests that body condition of marbled murrelets has deteriorated in PWS since the 1970s (Fig. 15). Between 1977 and 1998, murrelet body mass during the summer did not vary significantly by month ($P = 0.08$), and showed a significant decline by year ($R^2 = 0.20$, $df = 2, 118$, $P < 0.001$). This is consistent with the hypothesis that lower adult survival is affecting the PWS population.

One potential source of food stress for murrelets could be reduced abundance of herring. Herring availability could influence murrelet energy expenditure, since foraging for other types of prey hypothetically increases adult effort (Chapter 2). It is also possible for forage fish of the same species to decline in size (Davoren and Montevecchi 2003) or caloric density (Wanless et al. 2005), with subsequent impacts on seabird reproductive success. Wanless et al. (2005) found that fish used by common murres in the North Sea in 2004 were < 25 % of their previous caloric values, and murres experienced very low breeding success despite normal delivery rates of prey to chicks. Wanless et al. cited reduced levels of zooplankton in a changed ecosystem, as one possibility for the reduced quality of prey.

If murrelets in PWS are being impacted by increased effort to raise chicks, it may be possible to test this hypothesis by monitoring fluctuations in stress hormones during the breeding season (Kitaysky et al. 1999). Herring comprised up to half of the food for murrelet adults and juveniles (Chapter 2), and a large decline in their abundance could affect murrelet adult body condition, chick growth or fledging success and juvenile survival during their first weeks at sea. Herring generally decreased in biomass from about 100,000 metric tons (Mt) in 1988 to 6,384 Mt in 2001, with the biggest decline in 1993 (Thomas and Thorne 2003). Undoubtedly, these declines had a negative effect on the biomass of juvenile herring. Herring are the 'wasp-waist' (Cury et al. 2000) of the PWS ecosystem. Changes in herring abundance have the potential to impact the zooplankton on which they feed, as well as the fish, seabirds, and marine mammals that feed on the herring (Thomas and Thorne 2003). The parallel decline in herring stocks and the murrelet population in PWS may be linked, and conservations efforts for murrelets need to consider management of forage fish such as juvenile herring as well as sand lance.

Although there was evidence that fish school density influenced murrelet productivity, it was not a dominant factor. This is consistent with the concept that murrelets can be numerically dominant in regions with relatively low fish biomass, because they are adaptable to heterogeneous marine habitats where small schools of fish predominate (Carter and Sealy 1990, Ostrand et al. 1998, 2004). The dispersal of murrelets among all marine areas of PWS (Appendix, Fig. 2b) illustrates their ability to use a diversity of marine habitats, even though some areas may be better for raising young. Although not conclusive, the results suggested that there may be a threshold of fish abundance (in terms of fish schools per area) whereby murrelet productivity is enhanced, and this could be a very localized phenomena. The recognition that certain areas are consistently more productive for murrelets suggests that managers could establish management priorities based on adult abundance at sea, specific marine features, and a detailed knowledge of fish distribution in nearshore waters.

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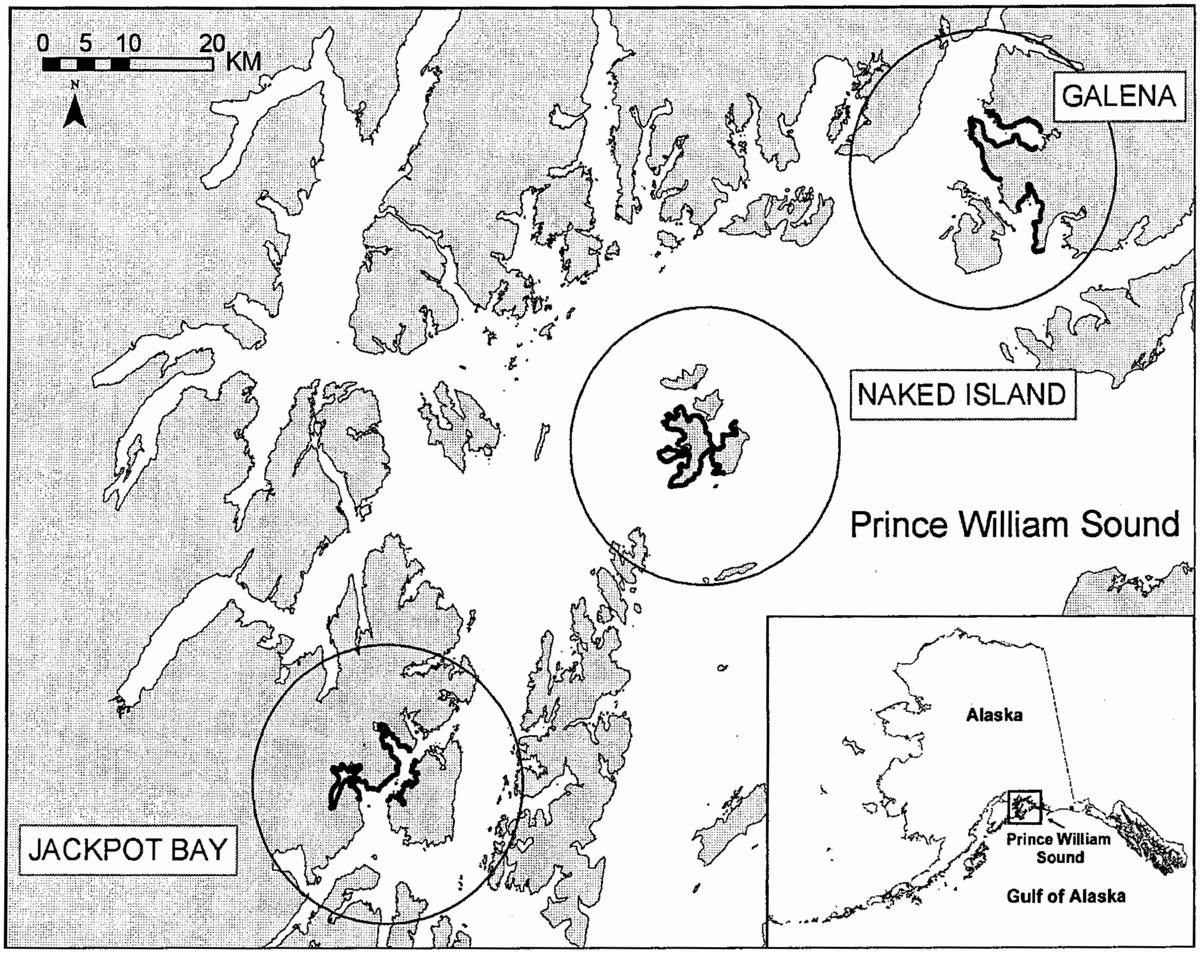

Figure 1. Study sites for murrelet surveys in Prince William Sound, Alaska. The darkened shoreline indicates location of boat-based surveys at each site. The circles represent a 16 km radius from the center of each study site, designating the area used to obtain density of fish schools from aerial surveys. Land area within each circle designates lands included in upland habitat categorization.

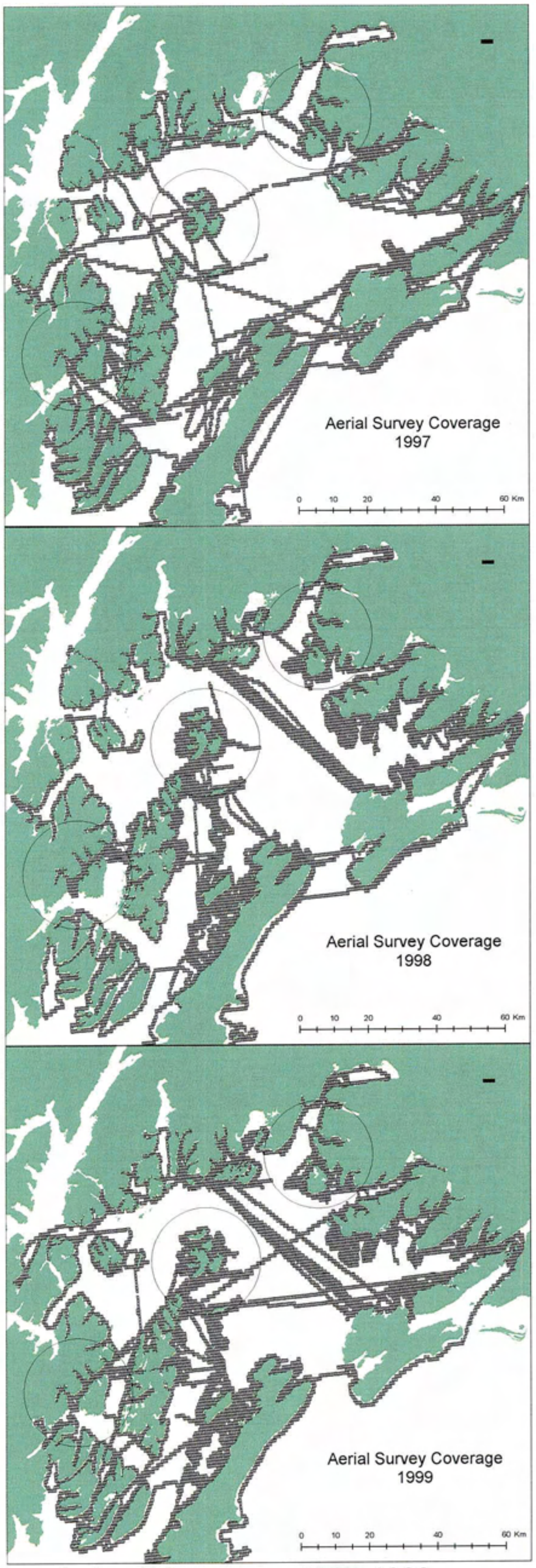

Figure 2. Aerial coverage during fish surveys, 1997-1999.

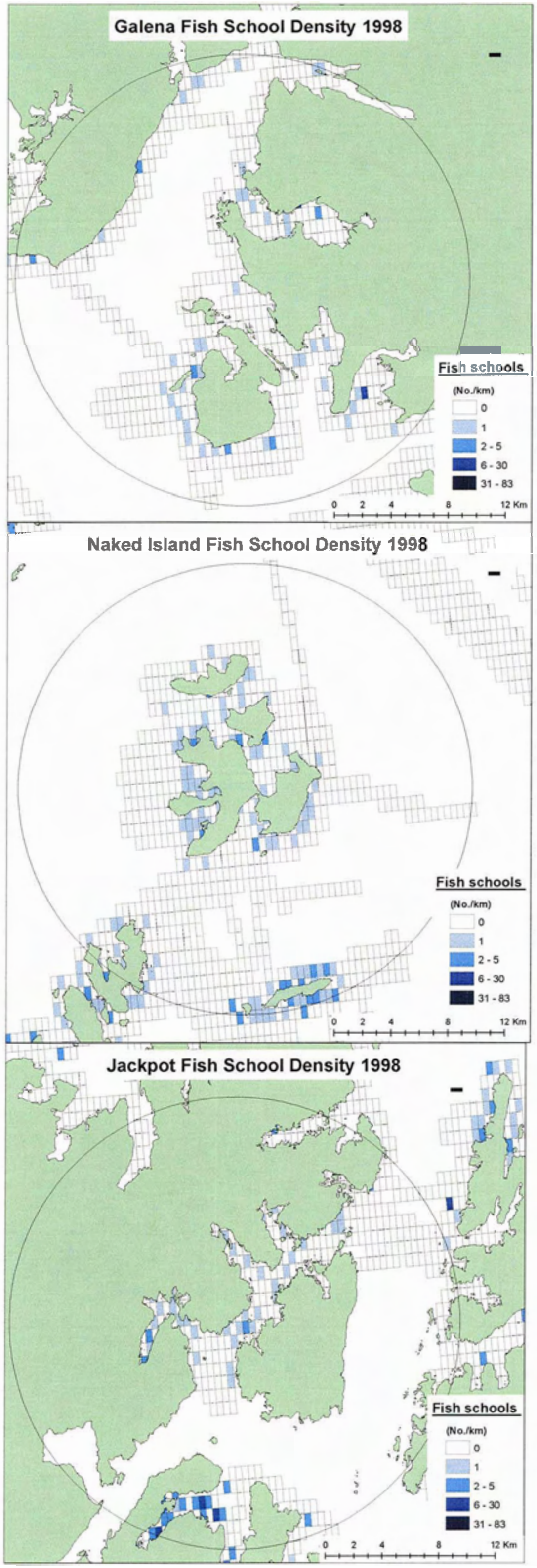

Figure 3. Examples of the grid system for calculating density of fish schools from aerial surveys.

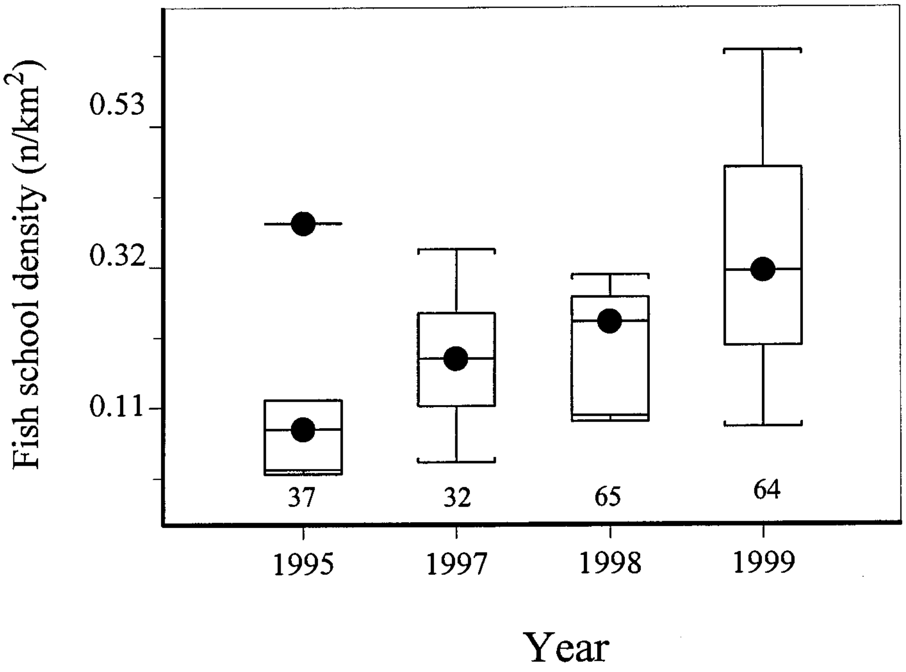

Figure 4. Density of fish schools (herring and sand lance) in Prince William Sound for each survey year. Data used the mean of each of six regions to derive the annual values (n = 24 site-years, 198 survey days). Number of survey days for each year are below each box. Box plots show the median (filled circle), quartiles (box), 1.5x quartile range (whiskers) and an outlier in 1995 (filled circle with bar).

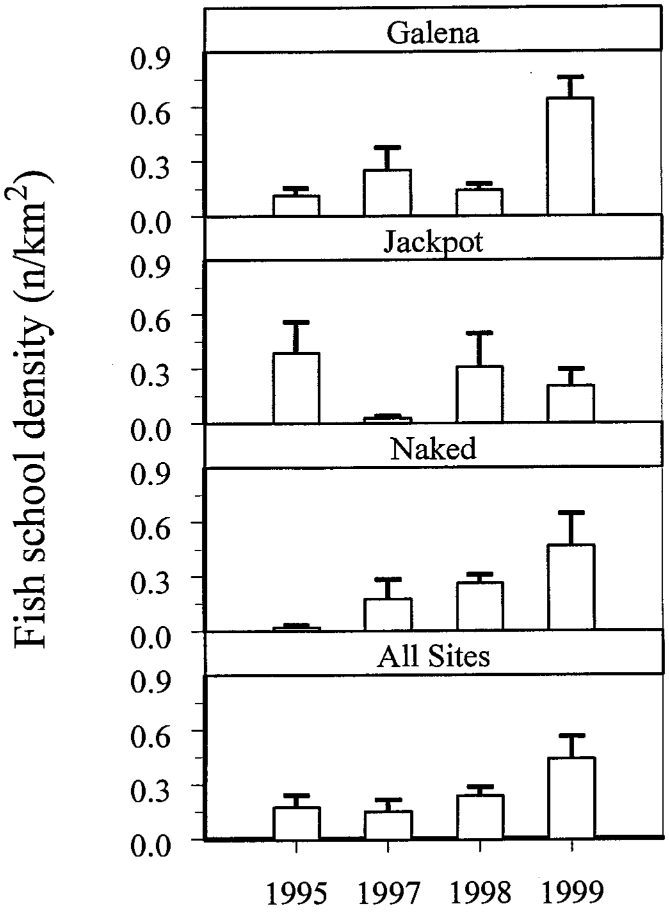

Figure 5. Total fish school density (n / km^2) for three sites in Prince William Sound, Alaska, over four years. For sample sizes, see Table 2.

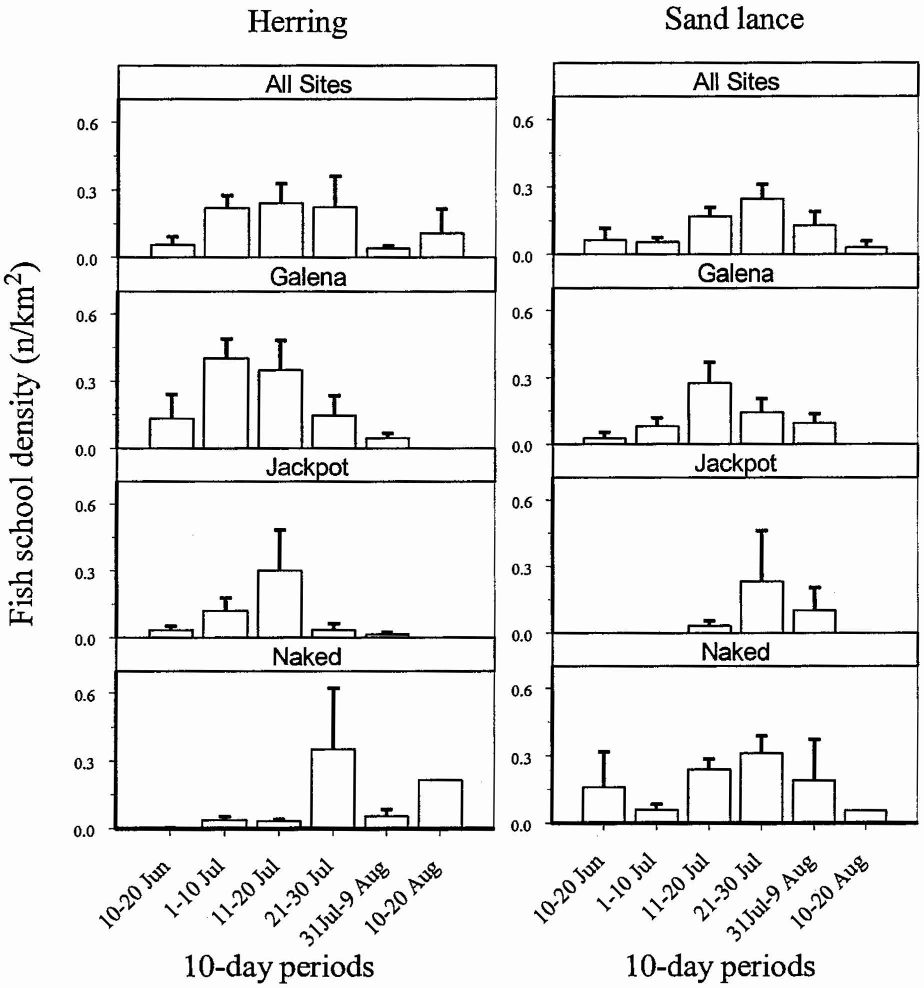

Figure 6. Herring and sand lance school density (n / km^2) by Site (each a 16 km radius), and for all sites combined (top), averaged for 10-day periods over four summers. Error bars are standard errors. Total sample size for all sites was 125 survey-days. For Galena and Jackpot, most of the sand lance occurred only in 1999.

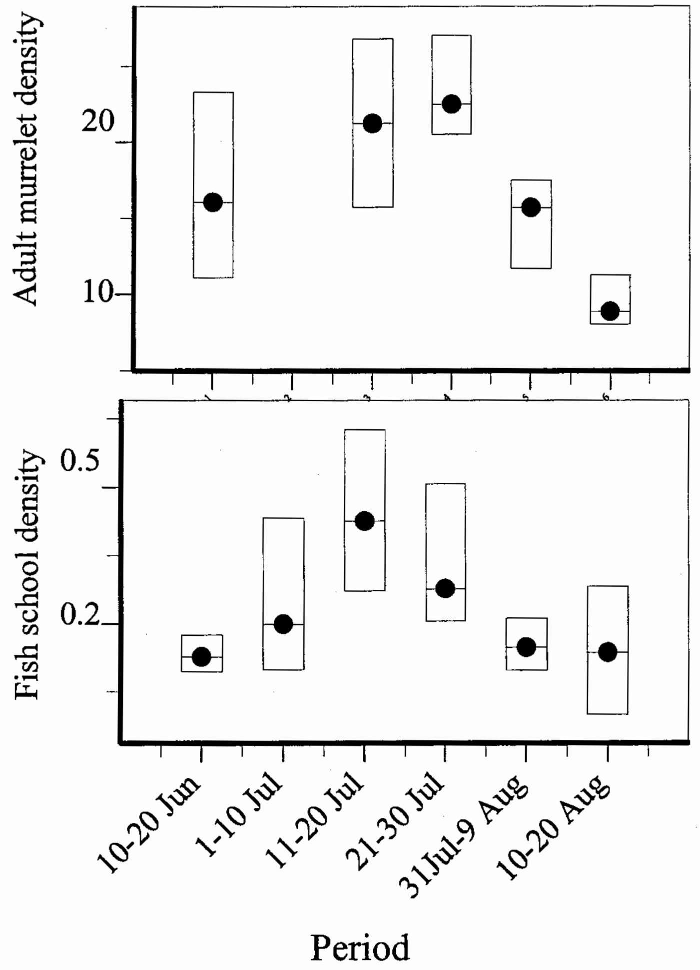

Figure 7. Adult murrelet density (birds/km^2 ; top) and fish school density (n/km^2; bottom) by 10-day survey periods. Data were summed by Site and Year for three sites over four years. The box plots show mean (solid circle) and quartiles (box). There were no outliers.

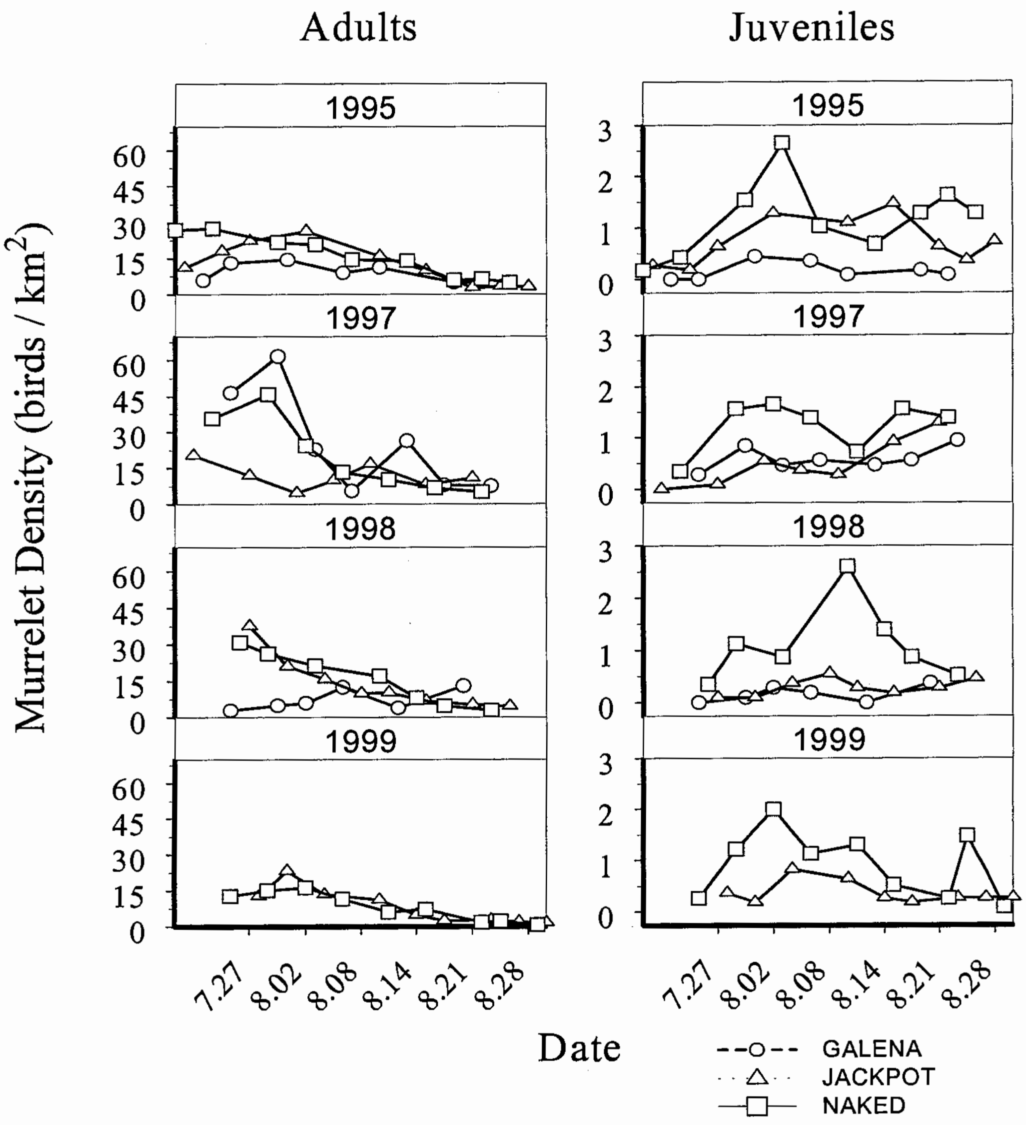

Figure 8. Seasonal changes in density (birds / km^2) of marbled murrelet adults and juveniles at three study sites over four years in Prince William Sound, Alaska. Each sample is based on a total count during a full day survey of a given Site.

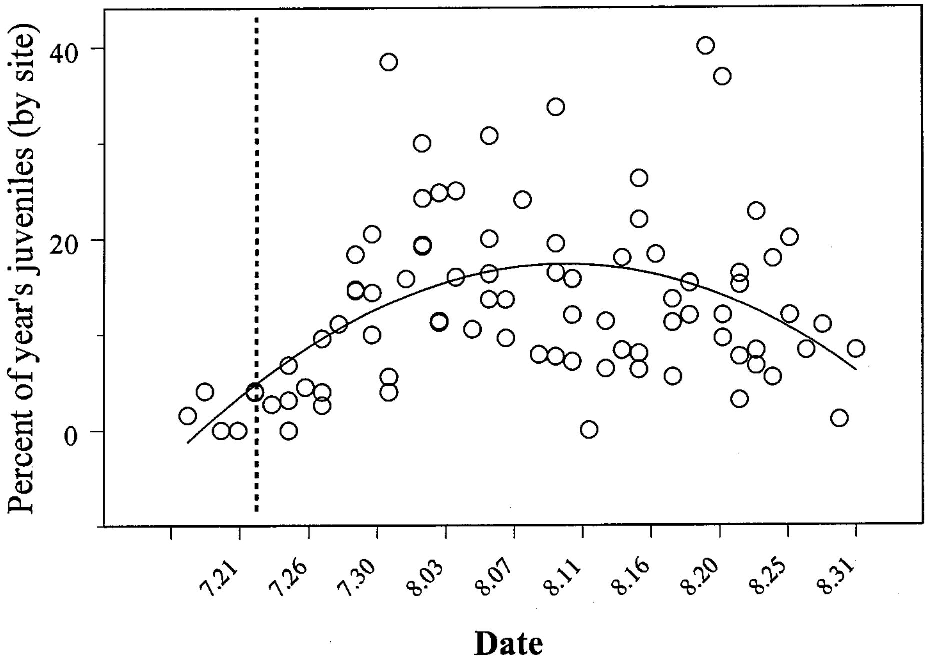

Figure 9. Juvenile appearance at sea during the summer in Prince William Sound, as the percent of each site's annual number of juveniles counted in each survey. The data came from surveys conducted at Galena, Naked and Jackpot sites in 1995 and 1997 – 1999. The vertical dashed line indicates the approximate peak of fish school density at these sites (see Fig. 7).

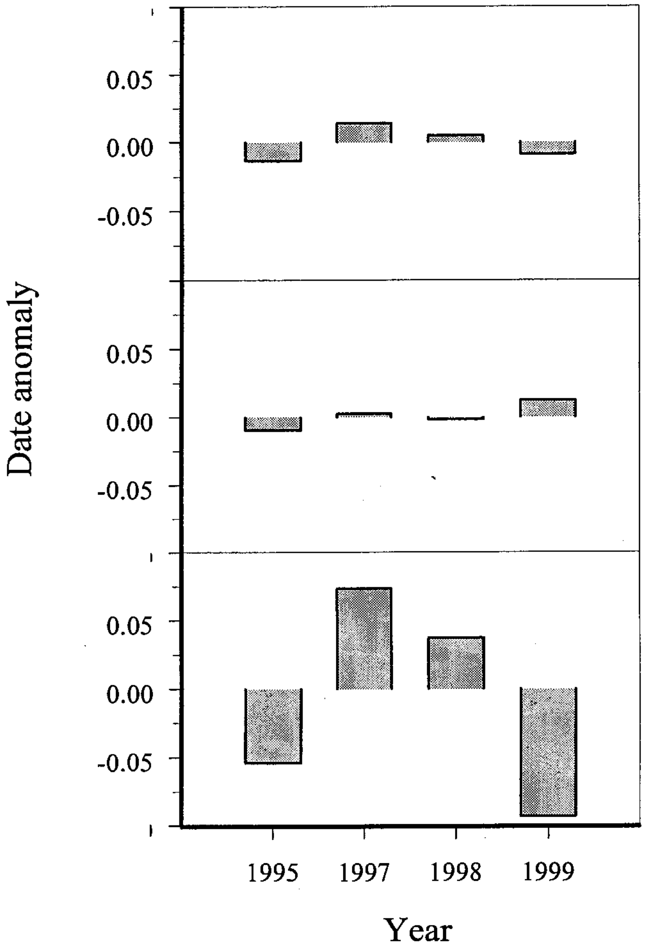

Figure 10. Date anomalies for juvenile occurrence at all three sites (Galena, Naked, Jackpot) pooled over four years in Prince William Sound, Alaska. Anomalies were calculated from mean dates of all sites and years, for the date when juveniles at a site reached the 50th percentile (top), 75th percentile (center) and had the highest juvenile count of a given year (bottom). Values below zero were earlier than the overall mean, and values above zero were later than the overall mean.

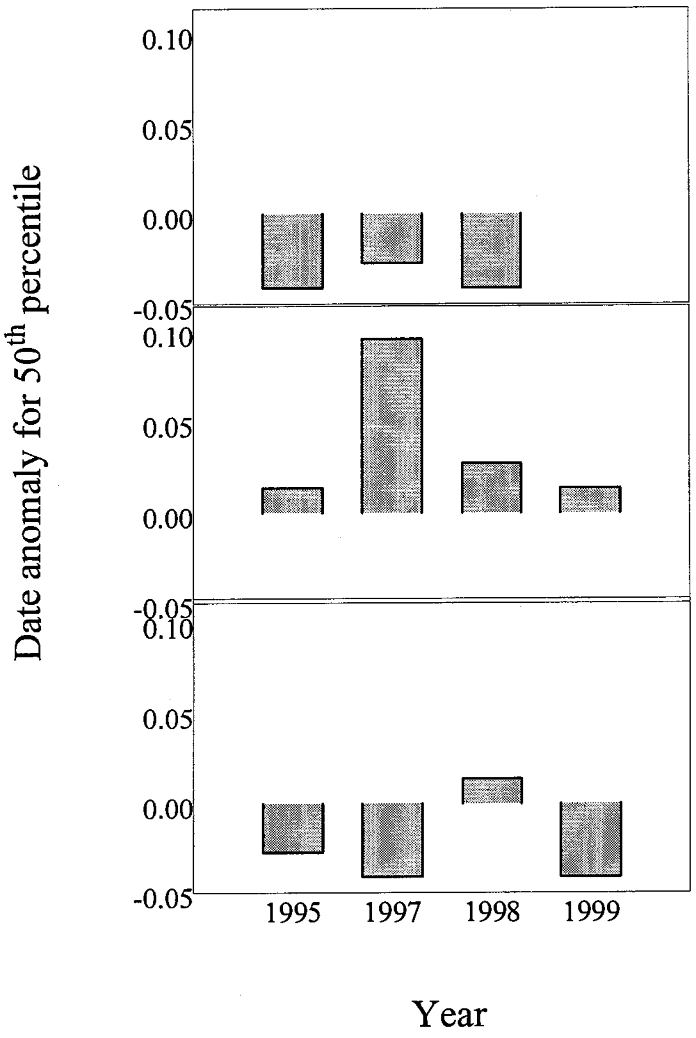

Figure 11. Date anomalies for juvenile occurrence at three sites over four years in Prince William Sound, Alaska. Anomalies were calculated from mean dates of all sites and years for the date when juveniles at a site reached the 50th percentile at Galena (top), Jackpot (center) and Naked (bottom). Values below zero were earlier than the overall mean, and values above zero were later than the overall mean.

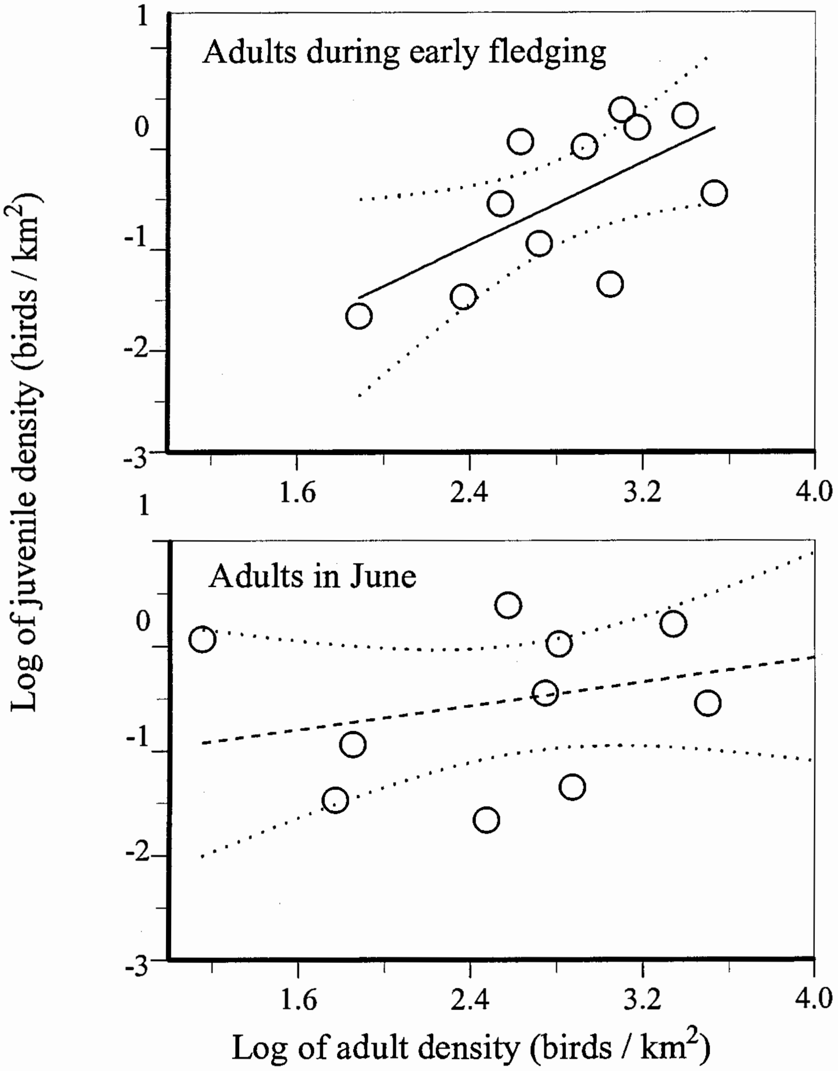

Figure 12. Regression of logged densities (birds / km^2) of juvenile and adult murrelets, showing the slope (solid or dashed lines) and 95% confidence boundaries (dotted lines). Juvenile densities were derived from the mean density at a Site and Year during the entire fledging period (27 July – 24 August). For each Site and Year, adult densities were averaged early in the fledging period (top) or during the June incubation period (bottom). Data are from three study sites surveyed over four years (with only two sites surveyed in 1999). The regression using adult densities early in the fledging period (top) was significant ($r^2 = 0.42$, df = 1,9, $P = 0.03$), but the one using June adult densities (bottom) was not ($r^2 = 0.11$, df = 1,9, $P = 0.33$).

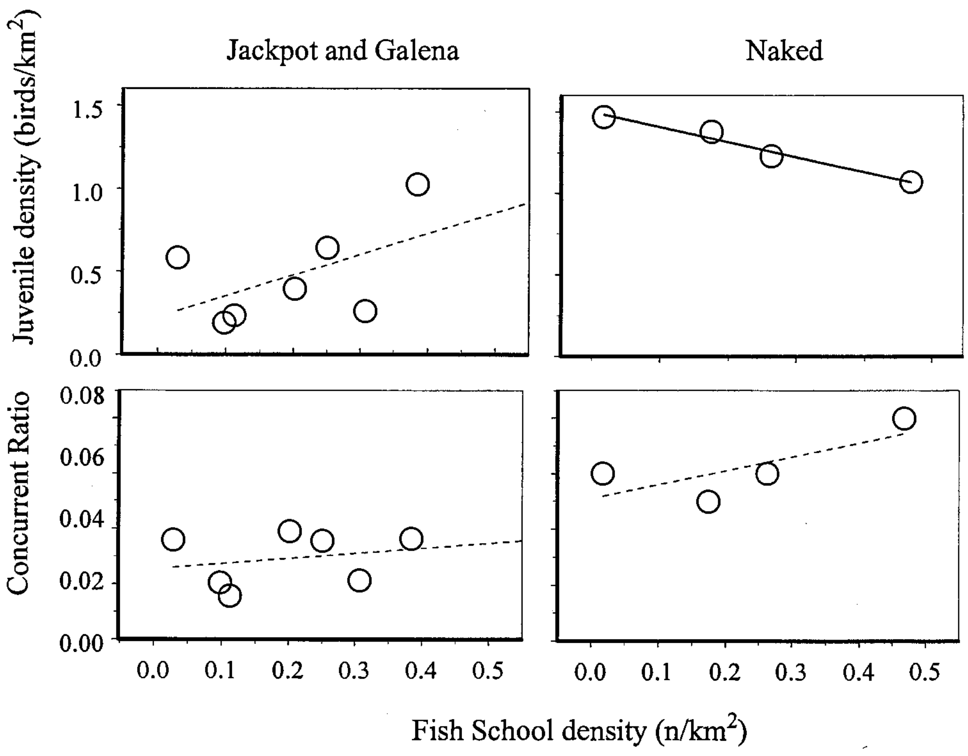

Figure 13. Annual murrelet productivity at Jackpot and Galena (left) and Naked (right) relative to mean fish school density (n / km^2) at each site. Juvenile density (birds / km2) (top) and concurrent ratio (juvenile:adults) (bottom) are means for each year and site. The only significant regression was for juvenile density at Naked ($r^2 = 0.97$, df = 1,2, $P = 0.01$). For other regressions, $P > 0.20$.

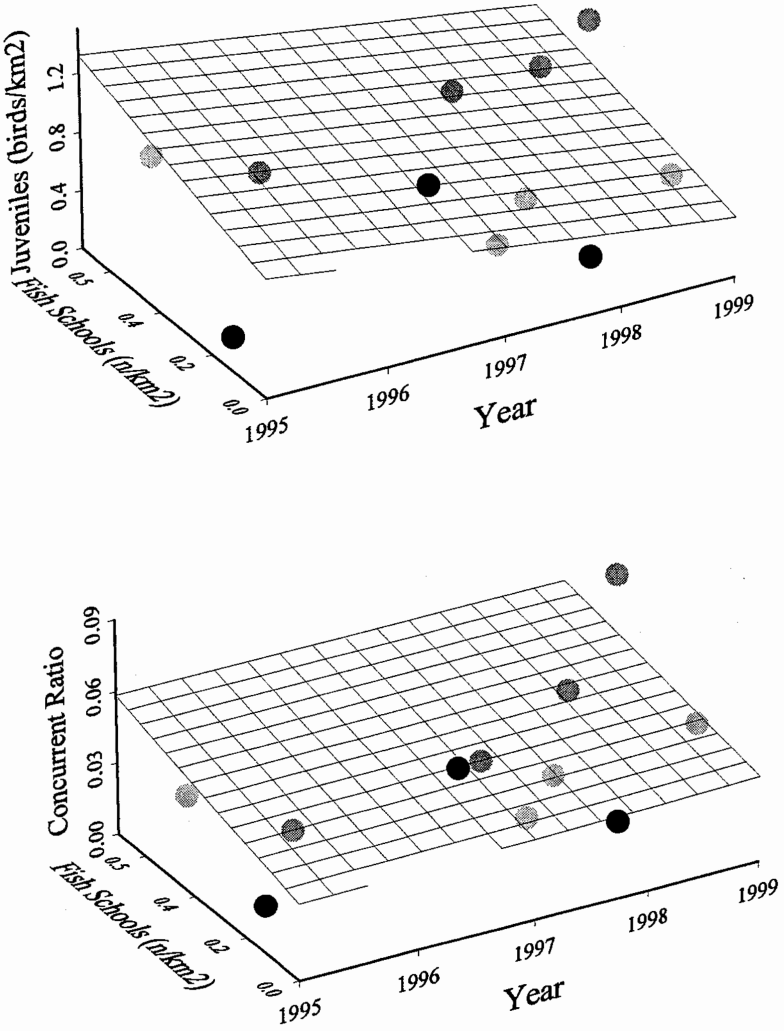

Figure 14. Mean juvenile density (birds / km^2; top) or concurrent ratios (bottom) as functions of fish school density (n / km^2) and year, using a regression plane to connect the points in a three-dimensional space. Each point represents means from a site and year for three sites surveyed over four years.

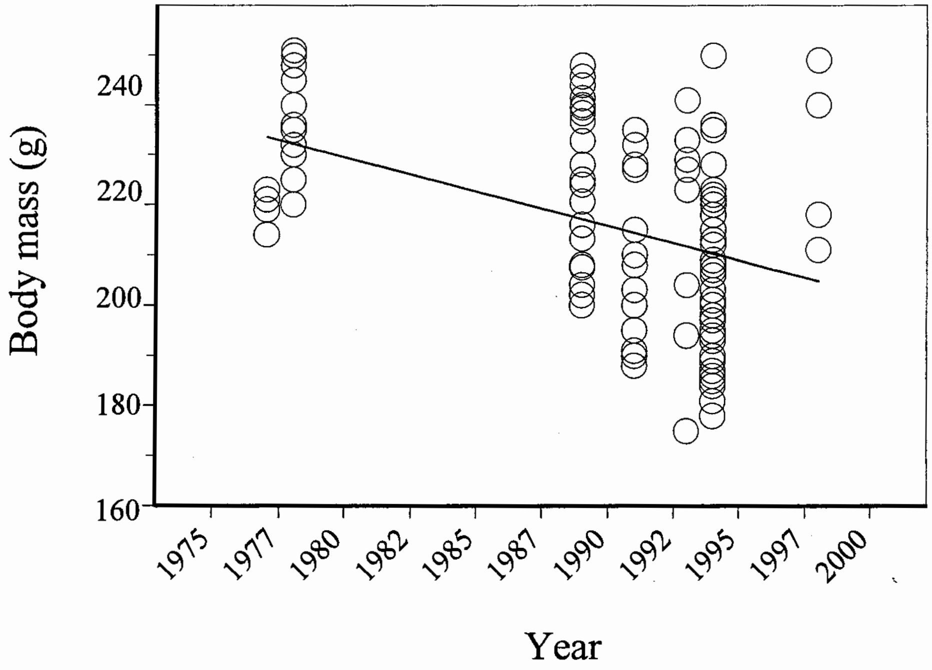

Figure 15. Body mass (g) of 121 adult marbled murrelets shot or captured (by dipnet or mist nets) in Prince William Sound, Alaska, between June and August of 1977 – 1999. The regression was significant ($r^2 = 0.20$, df = 1,118, $P < 0.001$). Month was not a significant effect. Data are unpublished from G. Sanger (1977), K. Kuletz (1978-1998), and J. Piatt (1991).

Table 1. Summary of survey effort and fish schools counted during aerial surveys, and survey effort and murrelets counted during boat-based surveys in Prince William Sound, Alaska, 1995-1999.

		Aerial fish surveys			Boat-based murrelet surveys				
Year	Site	Days flown (n)	Transect length flown (km)	No. schools (n)	June survey days (n)	Adults in June (n)	Jul-Aug survey days (n)	Adults in Jul-Aug (n)	Juveniles (n)
1995	Galena	7	614	34	3	263	5	501	13
	Naked	8	386	8	4	612	5	843	56
	Jackpot	8	586	105	4	725	6	970	103
1997	Galena	5	631	106	3	485	6	1407	41
	Naked	6	546	98	3	2264	6	1198	94
	Jackpot	7	754	15	3	1084	6	682	38
1998	Galena	14	1759	108	3	379	5	430	10
	Naked	12	1938	222	3	418	6	925	85
	Jackpot	11	635	102	3	579	7	1168	20
1999	Galena	13	1410	388	0		0		
	Naked	14	1593	293	5	182	6	668	74
	Jackpot	10	616	23	6	418	7	773	30

Table 2. Density (schools / km^2) of fish schools (herring and sand lance combined) observed during aerial surveys, within 16 km radius of Galena, Naked, and Jackpot study sites, 1995, 1997 - 1999. Two-way ANOVAs used log transformed densities, and pair-wise comparisons used Tukey's multiple comparison test. Differences among sites in the same year were tested with Kruskal-Wallis Rank Sum test.

Year	Site	N days flown	Fish Schools / km^2 Mean (SE)	Within-year Site effects Chi-Sq	df	P
1995*	Galena	7	0.113 (0.041)	5.984	2	0.05
	Naked	8	0.018 (0.015)			
	Jackpot	8	0.385 (0.175)			
1997	Galena	5	0.251 (0.124)	0.908	2	0.635
	Naked	6	0.175 (0.110)			
	Jackpot	7	0.029 (0.012)			
1998	Galena	14	0.140 (0.035)	8.088	2	0.018
	Naked	12	0.263 (0.046)			
	Jackpot	11	0.307 (0.187)			
1999	Galena	13	0.642 (0.114)	8.216	2	0.016
	Naked	14	0.468 (0.179)			
	Jackpot	10	0.202 (0.095)			
Overall Site effects*		F	3.72	Galena > Jackpot		
		P	0.027			
Overall Year effects*		F	13.86	1999 > 1995, 1997		
		P	<0.001			
Site x Year interactions*		F	4.57			
		P	0.012			

* all df = 2, 109

Table 3. Density (schools / km^2) of herring and sand lance observed during aerial surveys, within 16 km radius of Galena, Naked, and Jackpot study sites, 1995, 1997 - 1999. Two-way ANOVA tests were done on log transformed densities, and pair-wise comparisons used Tukey's multiple comparison test. Differences among sites in the same year were tested with Kruskal-Wallis Rank Sum test.

			Herring				Sand lance			
Year	Site	N days flown	Herring / km2 Mean (SE)	Within-year Site effects Chi-Sq	df	P	Sand Lance / km2 Mean (SE)	Within-year Site effects Chi-Sq	df	P
1997	Galena	5	0.206 (0.112)	2.57	2	0.276	0.045 (0.028)	1.45	2	0.484
	Naked	6	0.010 (0.008)				0.165 (0.111)			
	Jackpot	7	0.024 (0.012)				0.005 (0.005)			
1998	Galena	14	0.100 (0.035)	1.28	2	0.526	0.042 (0.013)	13.52	2	0.001
	Naked	12	0.110 (0.028)				0.153 (0.038)			
	Jackpot	11	0.284 (0.168)				0.024 (0.022)			
1999	Galena	13	0.373 (0.091)	14	2	0.001	0.269 (0.060)	5.30	2	0.071
	Naked	14	0.198 (0.178)				0.270 (0.088)			
	Jackpot	10	0.056 (0.028)				0.146 (0.100)			
				Pair-wise comparisons				Pair-wise comparisons		
Overall Site effects*		F	7.15	Galena > Jackpot, Naked			12.2	Jackpot < Galena, Naked		
		P	0.001				<0.001			
Overall Year effects*		F	2.45				5.16	1997 < 1999		
		P	0.092				0.008			
Site x Year interactions*		F	3.22				ns			
		P	0.017							

* all df = 4, 83

Table 4. Dates of juvenile marbled murrelet observations at three sites in Prince William Sound, Alaska, during four years of surveys. The 50th and 75th percentiles were the dates at which cumulative juvenile observations were more than 50 % and 75 %, respectively.

		Date of observation					
Year	Site	1st survey	1st juvenile	Highest juvenile	50th percentile	75th percentile	Total juveniles
1995	Galena	21-Jul	31-Jul	31-Jul	6-Aug	10-Aug	13
	Naked	18-Jul	18-Jul	3-Aug	7-Aug	22-Aug	125
	Jackpot	19-Jul	19-Jul	16-Aug	10-Aug	21-Aug	73
1997	Galena	25-Jul	25-Jul	23-Aug	7-Aug	18-Aug	44
	Naked	22-Jul	22-Jul	2-Aug	6-Aug	17-Aug	98
	Jackpot	20-Jul	27-Jul	21-Aug	16-Aug	21-Aug	38
1998	Galena	25-Jul	30-Jul	20-Aug	6-Aug	20-Aug	10
	Naked	26-Jul	26-Jul	10-Aug	10-Aug	14-Aug	89
	Jackpot	27-Jul	27-Jul	8-Aug	11-Aug	21-Aug	25
1999	Naked	25-Jul	25-Jul	2-Aug	6-Aug	16-Aug	95
	Jackpot	28-Jul	28-Jul	4-Aug	10-Aug	23-Aug	36

Table 5. Marbled murrelet abundance and productivity at three sites in Prince William Sound, Alaska. Mean + (SE) are shown for adult densities (n/km^2) in June (incubation phase) and 18 July - 10 August (early fledging period). Juvenile densities are shown for 27 July - 24 August (when sites have reached 75th percentiles) and for the Core surveys (5 highest juvenile counts). Concurrent ratios used the early fledging period to minimize the effect of post-breeding adult dispersal. Sequential ratios used the mean core juvenile density divided by the mean June adult density, providing one value per year, which was tested with a Kuskal-Wallis Rank Sum test. All other effects were tested with two-way ANOVA and Tukey pair-wise comparisons.

		June Surveys		18Jul-10Aug			27Jul-24Aug		Core Juvenile	Sequential
Year	Site	N	Adult Density	N	Adult Density	Concurrent Ratio	N	Juvenile Density	Density (n = 5)	Ratios
1995	Galena	3	5.87 (1.53)	5	10.69 (1.55)	0.02 (0.01)	5	0.23 (0.07)	0.23 (0.07)	0.04
	Naked	4	13.10 (3.63)	5	22.26 (2.37)	0.06 (0.02)	6	1.47 (0.28)	1.67 (0.25)	0.13
	Jackpot	4	16.58 (1.31)	5	18.71 (2.62)	0.04 (0.01)	5	1.02 (0.17)	1.04 (0.16)	0.06
1997	Galena	3	15.55 (7.60)	4	34.12 (12.42)	0.04 (0.02)	6	0.64 (0.08)	0.68 (0.09)	0.04
	Naked	3	65.5 (15.32)	4	29.83 (7.02)	0.05 (0.02)	6	1.38 (0.14)	1.51 (0.05)	0.02
	Jackpot	3	33.05 (1.69)	5	12.71 (2.73)	0.04 (0.02)	6	0.58 (0.18)	0.68 (0.19)	0.02
1998	Galena	3	11.86 (2.92)	4	6.59 (2.09)	0.02 (0.01)	5	0.19 (0.07)	0.19 (0.07)	0.02
	Naked	3	28.19 (3.84)	4	23.90 (3.02)	0.06 (0.03)	6	1.23 (0.30)	1.37 (0.32)	0.05
	Jackpot	3	17.65 (1.88)	4	21.1 (5.95)	0.02 (0.01)	7	0.26 (0.06)	0.38 (0.05)	0.02
1999	Naked	5	3.16 (1.04)	4	13.93 (1.08)	0.08 (0.02)	6	1.07 (0.25)	1.42 (0.15)	0.45
	Jackpot	6	6.37 (1.12)	4	15.16 (2.76)	0.04 (0.01)	7	0.39 (0.09)	0.48 (0.11)	0.07
Difference among Sites			< 0.001		0.007	0.017		< 0.001	< 0.001	0.416
Difference among Years			< 0.001		0.216	0.747		0.002	0.005	0.073
Site x Year Interaction			0.07		0.007	0.679		0.018	0.017	
Pair-wise : Sites			G < N, J		G < N > J	G < N		N > G, J	N > J > G	
Pair-wise : Years			99<95<97,98		99 < 95, 97	ns		98 < 95, 99	98 < 97, 99	

G = Galena; N = Naked; J = Jackpot
95 = 1995; 97 = 1997; 98 = 1998; 99 = 1999

Table 6. Habitat features for three study sites (16 km radius from center) in Prince William Sound, Alaska. Marine surface area and water depths were obtained from GIS coverage. Average water depth was weighted for the surface area covering each of eight depth contours. Upland measurements were obtained from GIS coverage which incorporated satellite photo interpretations of forested and land habitats, and a model that defined 'high-quality nesting habitat' for murrelets (HQN) (DeVelice 1998).

	Site		
Habitat feature	Galena	Naked	Jackpot
Marine			
Surface water area (km^2)	287	652	201
Weighted ave depth (m)	119.6	149.9	121.7
Water area < 60 m deep (km^2)	80.9	100.1	34.5
Mean SST ^{0}C (+ SE)[a]	14.9 (0.3)	13.8 (0.2)	14.0 (0.2)
Mean SSS ^{psu} (+ SE)[b]	19.7 (0.7)	26.1 (0.2)	20.0 (0.3)
Glacial & freshwater input	high	low	moderate
Distance from main PWS current	~ 30 km	0 km	~ 10 km
Primary fish present	0+ herring, some 0+ sand lance	0+ herring, 0-3+ sand lance, some capelin	1+ herring, occasional 0+ herring
Uplands			
Total land area (ha)	34,055	6,254	39,945
Forested area (ha)	12,695	4,545	10,601
High-quality nest habitat (ha)	6,746	3,546	6,398
% HQN habitat (of forested)	53.1	78	60.4
% HQN habitat (of all lands)	19.8	56.7	16.0
Other species & impacts			
Other seabird species	Largest kittiwake colony in PWS, high gull population	4 spp. Alcids, 2 spp larids nesting, other species present	pigeon guillemots, few small kittiwake colonies in vicinity
Vessel traffic	high	low	low
Logged areas in vicinity (not on site)	yes	no	no

a. Sea Surface Temperature, mean of survey averages, taken on each transect.

b. Sea Surface Salinity (Practical Salinity Units), mean of survey averages, taken by

SYNTHESIS OF THE DISSERTATION

In the previous chapters, I examined the foraging and productivity of marbled murrelets (*Brachyramphus marmoratus*) to determine if their responses to temporal and spatial patterns of prey abundance were indicative of food limitations. I did this first by using telemetry to look at foraging patterns and habitat use of individual birds in oceanographically distinct habitat types (Chapter 1). Next I examined prey use and foraging behaviors of murrelets within two meso-scale study sites, to determine if foraging differed with respect to prey or self vs. chick-feeding (Chapter 2). Finally, I tested a methodology specific to monitoring murrelets at sea (Chapter 3), and then examined the response of murrelet abundance and productivity to spatial and temporal differences in prey abundance (Chapter 4). To provide a context by which to interpret my results, I used regional population data available for Prince William Sound to determine long-term trends in the larger population (Appendix). In this section, I integrate information from these chapters in order to examine several key aspects of marbled murrelets, including: a) how flexible is murrelet foraging behavior and how do murrelets respond to different conditions; b) is murrelet productivity sensitive to fluctuations in prey, and could that be a cause of their population decline; and c) how can managers monitor and assist in the conservation of a non-colonial seabird that is widely dispersed?

Flexible foraging behavior

Although they are not colonial, individual murrelets are still central-place foragers when raising chicks, and in this study, the murrelet foraging behaviors were consistent with an optimal foraging theory (Ydenberg et al. 1994, Gaston and Jones 1998). When self-feeding, birds fed on a range of prey sizes and are known to also feed on both high and low-nutrient fish (Kuletz et al. 1997, Ostrand et al. 1998, 2004, Chapter 2). When foraging for their chick, murrelets selected larger, high-nutrient fish almost exclusively. Prey quality may be more important than quantity for chick growth in seabirds (Kitaysky et al. 1999, Wanless et al. 2005), and for murrelets an additional benefit could be reduced predation risk, because delivery of larger fish requires fewer inland flights (Chapter 2, Table 12).

Chick rearing is energetically the most expensive part of the year for birds (Drent and Daan 1980), and the constraints of this activity can circumscribe resource use and subsequent breeding success (Trivelpiece et al. 1980, Cairns 1987, Golet et al. 2000). The energetic benefits of different prey have not been determined specifically for murrelets, and could be a valuable avenue for future research, particularly if prey type affects the duration of the nestling phase (27 – 40 days; Nelson 1997), and thereby fledging success. Size and energy content of fish can vary within species by sex and age class (Robards et al. 1999a, Anthony et al. 2000), but have also been shown to vary seasonally, annually (Iverson et al. 2002), and over decades (Wanless et al. 2005). Within-species prey value also can vary spatially (Paul and Paul 1999, Robards et al. 1999b), which could be another link between location (site) and murrelet productivity.

The primary foraging mode for murrelets remained as solitary birds or pairs, but they also foraged in larger intra- and inter-specific flocks when prey abundance was low or was comprised of smaller size classes (Chapter 2). This behavioral flexibility suggests there was a benefit to foraging in larger groups under some conditions, despite the potential for detrimental effects (Mahon et al. 1992, Maniscalco and Ostrand 1997, Chapter 2). Birds that breed solitarily at widely dispersed nest sites would be expected to be more widely dispersed at sea than colonial birds (Dukas and Edelstein-Keshet 1998). Nevertheless, dispersed birds are still likely to locate prey via 'behavioral cascades' (Russell et al. 1992) that operate at progressively smaller spatial scales. Learning the patterns of prey in specific locations would reduce search effort. Many seabirds have shown fidelity to specific foraging areas (review in Hunt et al. 1999) or to temporally predictable events that make prey available (Irons 1998, Davoren 2003).

In PWS most of the radio-tagged murrelets tended towards forage site fidelity, despite occupying very different types of habitats (Chapter 1). The repeated use of a forage site was observed in birds foraging near their capture site, as well as by birds that traveled farther from their capture sites. It is possible that forage site fidelity occurs even where birds travel extreme distances. Murrelets in southeast Alaska flew an average of 78 km to forage in the highly advective and productive waters of Icy Strait (Whitworth et al. 2000). The stratified waters of PWS tend to have low productivity (Sambrotto and Lorenzen 1986, Brown et al. 1999), and subsequently low-density fish schools that are widely dispersed (Ostrand et al. 1998, Brown et al. 1999). Thus, for murrelets in PWS, the energetic cost of traveling long distances to feed may be greater than the potential energetic gain.

Spatial and temporal associations with prey

Marine birds and mammals often aggregate at oceanic features that concentrate prey, such as eddies off of major currents, and broad upwelling fronts (Hunt and Schneider 1987, Hunt et al. 1999). Smaller scale events (1- 10, or 10 - 100s km) also attract feeding aggregations of birds (Hunt et al. 1999, Davoren et al. 2003, Vlietstra 2005). An example is the disturbance of water flow around an island or 'island wake effect', which can result in local upwelling or concentration of prey, and can be important sources of biological productivity and subsequent feeding activity (Aristegui et al. 1997). Such a feature may be part of the hydrography of the Naked Island site in PWS, which had all of the primary forage fish species, high numbers of birds, and high murrelet productivity. Although total fish school density at Naked was not high relative to the other sites (Chapter 4), several features may have enhanced fish availability, including the currents, island wake effect, shallow bays, and adjacent shelf edge.

At the meso-scale used in these studies, site effects swamped annual variability, which indicates that local habitat features affecting prey availability to the birds were important. The foraging patterns of individually marked birds (Chapter 1), prey species and sizes, murrelet diving patterns, and even group associations (Chapter 2) were each site-specific. Finally, murrelet productivity and fecundity varied consistently by site (Chapter 4). It is unknown if this site-specific effect exists in other populations of murrelets, and may be a regional phenomenon, reflecting the highly heterogeneous marine habitat of PWS. The spatial distribution of fish in PWS is linked to meso- and fine-scale habitat features (Foy and Norcross

1999, Brown and Moreland 2000), and the diet of murrelets, both for self and chick feeding, consistently reflected the prey found by our sampling at all sites.

Fish availability can also change through the day, as was evident at the evening 'hot spot' at Jackpot, where 1+ herring were consistently available during all years of the study (Chapter 2), even when daytime aerial surveys indicated very low fish abundance. Predictability of a resource can be as influential as prey abundance to marine predators (Skov et al. 2000, Davoren 2003), and knowledge of local spatial and temporal patterns of prey availability might increase foraging and breeding success, which in turn would reinforce the benefits of natal philopatry and nest-site fidelity (Birkhead 1985, Danchin et al. 1998).

My results suggest that murrelet breeding chronology is also affected by site-specific environmental conditions and not just regional seasonal cues. The marbled murrelet is considered the least synchronous of alcids (Gaston and Jones 1998), but they showed evidence of semi-synchronous nesting by site (Chapter 4). Coloniality may be a by-product of the need to synchronize reproduction with prey availability, or it might have evolved in part to meet the need for synchronicity (Wittenberger and Hunt 1985), but it has been well established that successful recruitment depends on synchronization of breeding with availability of suitable prey (Bertram et al. 2001, Abraham and Sydeman 2004). Because nesting early in the season is typically associated with higher breeding success in seabirds (Croxall and Rothery 1991), the timing of prey availability could affect local recruitment to the colony by the return of successful breeders (Danchin et al. 1998, Ainley et al. 2003). Even at larger scales, spatial variation often drives marine productivity and animal distributions as much as, or more than, interannual fluctuations. For example, in lower Cook Inlet, abundance and species composition of plankton, fish, and seabirds responded more to spatial, than inter-annual parameters (Speckman et al. 2005). In the northern Gulf of Alaska (GOA), seabird abundance fluctuates seasonally, but is always higher over the continental shelf than the basin (Hunt et al. 2005), which corresponds to primary productivity and zooplankton stocks (Sambrotto and Lorenzen 1986).

Although murrelet productivity was site-specific at the meso-scale, the total population of murrelets in PWS has occasionally shown inter-annual fluctuations that suggest large-scale shifts in distribution, such as the large numbers that appeared in PWS in 1993 (Appendix). The extent of movement by murrelets throughout the GOA is unknown, as is the proportion of non-breeding birds (that would be less attached to specific sites). The scale and duration of such shifts, and the oceanographic processes that drive them, will require further investigation to better understand the range-wide changes in murrelet populations.

Population regulation in a non-colonial seabird

Seabirds are found throughout the world in a variety of marine habitats, yet they are generally uniform in life histories, being long-lived, with delayed breeding, low fecundity, and highly colonial when breeding (Ricklefs 1990, Croxall and Rothery 1991). The costs of nesting in large aggregations (competition for nest sites, mates, and food depletion) are potentially high (Dukas and Edelstein-Keshet 1998), which would make seabirds susceptible to density-dependent population regulation (Ashmole 1963). However, density-independent limiting factors may be particularly strong in marine environments (Cairns 1992, Croxall

1992), which may be why few studies have actually shown a relationship between breeding success, coloniality, and prey availability to birds (Croxall and Rothery 1991, but see Ainley et al. 2003). Alternatively, seabird populations may be regulated by events that occur during winter, when prey are less available (Lack 1968).

Food availability is overwhelmingly linked to changes in populations of marine birds and mammals (Croxall and Rothery 1991, Cairns 1992, Hayward 1997). At some level of prey abundance, even non-colonial seabirds should be affected by fluctuations in prey. I found some evidence of a positive threshold in murrelets, because fish abundance at the highest level (in fish schools per area) was associated with higher murrelet productivity at a given site (Chapter 4). Overall, prey abundance increased during the years of my study, but the site with the highest productivity did not have the highest annual density of fish schools. This suggests that murrelets were responding to factors other than simple prey abundance.

In PWS, Ostrand et al. (1998) concluded that marbled murrelets selected fish schools by habitat (i.e., shallow waters), whereas tufted puffins selected fish schools near their colonies. However, Ostrand et al. could not determine whether the murrelets they encountered were in fact near their nest sites. Given the foraging patterns of individual birds (Chapter 1), it is likely that nest site location partly defines foraging location, at least during the chick-rearing stage. At large scales, in British Columbia (Yen et al. 2003) and California (Becker and Beissinger 2003), both marine and terrestrial features influenced murrelet distribution. Ballance et al. (1997) points out that although birds may be limited in the area they can exploit from the colony, the locations of colonies were ultimately determined by the distribution of seabird prey. The distribution of a nearshore-feeding, non-colonial bird should reflect prey distribution as well, although for murrelets, the drastic loss of nesting habitat in the southern part of its range (Burger 2002, McShane et al. 2004) might mask such a pattern. Where nesting habitat is more intact, such as PWS, it is possible to make finer-scale links between murrelets and prey distribution.

For Alaska in general, there is a spatial correspondence between distribution of murrelets at sea and distribution of forested coastlines (Piatt and Ford 1993). This suggests that nesting sites are limiting the distribution of murrelets, but it may not be limiting population size. In PWS, murrelets use a variety of old-growth forest types and even some ground nests (Kuletz et al. 1995) and the productivity of murrelets at my study sites did not correspond to the amount of potential nesting habitat (Chapter 4, Table 6). I propose that in PWS, local marine habitat features that enhance fish availability determine the density of murrelets breeding in different locations. Murrelets may be numerically dominant in regions such as PWS and southeast Alaska (Agler et al. 1998) because, with their dispersed nesting, they can exploit low densities of prey that are widely dispersed (Ostrand et al. 1998). Concurrently, that type of prey distribution might not support equivalent numbers of birds concentrated at a colony. The abundance of murrelets is determined by the juxtaposition of upland and marine habitat features, and I propose that in PWS their nesting dispersal follows an 'ideal free distribution' (Fretwell and Lucas 1970). At least since the 1970s, with the population in decline, it is likely that forage fish abundance has been more limiting than nesting habitat. Therefore, marine habitat features (that define fish abundance and accessibility) have become the primary factor in the distribution and abundance of murrelets in PWS.

There is insufficient information on the historical abundance of forage fish in PWS to determine if they have decreased, overall, in tandem with the murrelet population. Although my study identified prey species and habitats important to murrelet breeding success, what remains unknown is the threshold of fish biomass necessary to assist recovery of the murrelet population. Certainly the crash of the adult herring stocks in PWS, which parallels the decline in murrelets, lends credence to the hypothesis that changes in prey abundance have impacted the murrelet population, despite a fairly consistent ratio of juveniles to adults during the four years of this study.

This study suggests that lower numbers of adults, and not lower reproductive success, is the main reason for the decline in juvenile abundance at sea (Chapter 4). This does not necessarily contradict the argument that prey abundance during the breeding season has impacted population size. It will require new investigations to identify the factors causing lower numbers of adults. The decline in body mass since the 1970s (Chapter 4, Fig. 15) could be indicative of a decrease in adult body condition, with a subsequent decrease in adult survival. Difficult breeding conditions can reduce adult survival over time (Saether et al. 1993, Golet et al. 2004). Although there is no information on adult murrelet survival rates for PWS, there is sufficient evidence of a population decline (Appendix), indicating that murrelets have either been emigrating, or productivity is not replacing adults. Analyses of limited demographic data for murrelets in southern regions indicates that fecundity is too low to replace adults, but as with other long-lived species (Saether and Bakke 2000, Schmidt et al. 2005), their populations are most sensitive to changes in adult survival (Beissinger and Nur 1997, Cam et al. 2003, McShane et al. 2004, Peery et al. 2004).

It might be possible to determine if adults (and post-hatch year birds) are experiencing stress by testing birds for differences in body condition or stress hormone levels (Kitaysky et al. 1999). Because it would be difficult to re-catch individual birds on the water or at the nest, it will be necessary to compare birds from different regions. Birds from a population in decline such as PWS (Appendix), could be compared to those from a stable or increasing population, such as the Kenai Fjords (Van Pelt and Piatt 2003).

The second most important factor in demographic models for long-lived animals (including murrelets) is juvenile survival. Fledging mass of birds has long been used as an indicator of breeding success (Croxall and Rothery 1991), and it is presumed that larger chicks have better survival and greater probability of recruiting to the breeding population. Testing this hypothesis has been difficult or inconclusive (Harris et al. 1992), and has only been demonstrated for the ancient murrelet (*Synthliboramphus antiquus*) (Gaston 2003). Because ancient murrelet chicks are raised at sea after a few days at the colony, it is difficult to establish a relationship between breeding location, foraging habitat or conditions, and recruitment success. Few marbled murrelet nests have been monitored, but newly fledged chicks were only 51 – 78 % of adult weight (Nelson 1997), and the lowest recorded fledging mass was in PWS (Kuletz and Marks 1997). Food availability is likely critical during a juvenile's first days at sea. The decline in nearshore densities of fish schools in late summer may be a normal seasonal pattern, but if juvenile fish abundance (especially herring) has declined dramatically, fish densities may be below the threshold necessary for efficient foraging by juvenile birds. Juvenile murrelet behavior, habitat requirements, and survival should be investigated as a source of lower recruitment.

For individual breeding birds, summer may be the most energetically demanding season, but total marine bird consumption of prey in the GOA is actually higher during winter months (Hunt et al. 2005). Much of the increase in prey consumption in the GOA resulted from an influx of birds that breed in other areas of Alaska. Additionally, a large portion of the total seabird population on the wintering grounds is comprised of non-breeders and immatures (Birkhead 1985, Croxall and Rothery 1991), which may be 3 – 5 times the number of breeding pairs (Brooke 2004). The increased demand for prey may be one reason many seabirds, including murrelets, forage lower on the food chain in winter (review in Shealer 2002), consuming more zooplankton and small crustacea (Nelson 1997). At least in northern GOA, competition for food during winter may be greater than previously considered (Hunt et al. 2005). This would be consistent with Lack's (1968) hypothesis that food limitation during winter regulates most seabird populations. Under this scenario, population regulation would be decoupled from colonial or solitary nesting behavior. It is not known to what degree murrelets overlap spatially with other birds overwintering in the GOA. Other than the Kittlitz's murrelet (*Brachyramphus brevirostris*; Appendix), few other seabird species in PWS have shown steep rates of population decline (Lance et al. 2001), although many piscivorous species have declined to some degree (Agler et al. 1999). Thus, it seems unlikely that the loss of adults is due solely to winter mortality, unless that mortality is linked to summer breeding conditions. Important breeding conditions include prey type and abudance, but may also involve anthropogenic impacts such as fishing, pollution, and nearshore disturbance.

Implications to conservation

Although large relative to other regions, the murrelet population in PWS has declined from an estimated 300,000 birds in the early 1970s to approximately 36,000 today (Appendix). Following the 1972 survey, the population was not monitored until after the 1989 *Exxon Valdez* oil spill, the largest single mortality event for marbled murrelets (Carter and Kuletz 1995). The population may have already been in decline at the time of the spill (Appendix), had not recovered to pre-spill levels as of 1998 (Lance et al. 2001), and has continued a decline that by 2004 was not sustainable (Appendix). The trajectory of the PWS population is not unique (McShane et al. 2004), and thus conservation issues for murrelets in PWS may be applicable throughout its range.

As with many marine species in decline (Ralls and Taylor 2000), conservation efforts for murrelets are hampered by the lack of easily monitored nest sites, limited knowledge of demographics or diet, and their wide dispersal at sea. Valuable information has been obtained by using telemetry (Hull et al. 2001, Bradley et al. 2004, Peery et al. 2004) and radar monitoring of inland flights (Burger 2001). However, telemetry studies can not provide population estimates and are too expensive for long-term monitoring of reproductive success, and radar counts can not provide estimates of productivity. The best option for monitoring long-term population trends in combination with productivity indices is through boat-based surveys. These have problems as well, including issues of detectability (Becker et al. 1997), and differential habitat use and migration patterns that affect juvenile:adult ratios (Kuletz and Kendall 1998, Lougheed et al. 2002, Chapters 3 and 4). Nonetheless, at-sea surveys form the basis for most monitoring efforts. The analysis of at-sea surveys (Chapter 3), provided a unique test of data spanning multiple years and sites, and suggests long-term monitoring schemes. The relatively small sample size ($n = 11$ site-years) limited my ability to detect significant links between murrelet productivity and fish school density, but juvenile surveys should have reasonable power to detect trends in productivity, particularly among sites or among years within the same site (Chapter 3).

Most research on murrelets has focused on the impact of loss of nesting habitat, but changes have occurred in the marine environment throughout its range as well (Becker and Beissinger 2003). In the North Pacific, sea temperatures have increased, fish communities have changed due to natural and anthropogenic impacts (Anderson and Piatt 1999, McGowan et al. 1998) and mortality from commercial fisheries and oil spills continues (Carter et al. 1995, Carter and Kuletz 1995). Mortality from gillnets and oil spills are two documented sources of adult mortality that have potential to impact regional populations (McShane et al. 2004). For PWS, this study identifies several other, less direct, potential impacts.

First, murrelets required a specific size and age class of fish for their chicks, which differed from the main adult diet (Chapter 2). This has implications to murrelet conservation, particularly in light of the crash of the PWS herring stocks (review in Chapter 2). Age classes of both sand lance (Robards et al. 1999b) and herring (Brown and Moreland 2000, Brown 2003) use different types of habitats and are not evenly distributed among bays. Brown (2003) found that 0+ and 1+ age classes of herring have opposing responses to environmental conditions that affected their foraging and survival, such that regional physical conditions favorable to one cohort are detrimental to the other. Brown proposed that because of this, diversity of age classes must be maintained to insure recovery and stability of the herring population, which means establishing spatial diversity of habitat reserves. Murrelets would benefit from a reserve or management system that improved survival of both 0+ and 1+ age herring, because both are necessary for murrelet reproductive success (Chapter 2).

Murrelet consumption of herring in PWS may be minimal compared to the total herring biomass (Chapter 4), but the distribution and accessibility of specific age classes could still be a limitation to the murrelet population. When juveniles of a commercially fished species are important to upper trophic levels, managers should consider this aspect as part of an ecosystem based fisheries management plan (Witherell et al. 2000, Pikitch et al. 2004). Herring are critical to many species in PWS, including fish, marine mammals, and birds (Thomas and Thorne 2003, Peterson et al. 2003). Several independent analyses of fisheries data indicate that fisheries have resulted in trophic cascades, as higher trophic level fish are replaced by planktivorous fish (Hayward 1997, Pauly et al. 1998, Steneck 1998). Authors agree that, although climate change or natural fluctuations may have contributed to some marine ecosystem changes, there are likely multiplicative effects that include anthropogenic activities. This appears to be the case for herring in PWS (Pearson et al. 1999, Peterson et al. 2003, Thomas and Thorne 2003). On a global scale, total seabird consumption of fish is equivalent to that taken by humans, which suggests the possibility for competition over a limited resource (Brooke 2004). In addition to fisheries, herring and other forage species in PWS may still be experiencing perturbations from the 1989 *Exxon Valdez* oil spill (Peterson et al. 2003). Species that depend on nearshore, low-energy beaches, such as sand lance, might have been particularly impacted by the spill.

Sand lance were an important prey at the Naked site (Chapter 2), and it could have been a key factor in the high densities of juvenile murrelets observed there. The temporal patterns of sand lance abundance suggest that this prey species could be important for survival of juvenile murrelets in late summer (Chapter 4). Although locally important, its limited distribution may reduce its importance to the PWS population. As with all forage fish in Alaska, sand lance are protected from commercial fisheries (Witherell et al. 2000). Forage fish such as sand lance may benefit from the prohibition, but this rule does not protect the nearshore habitat on which they depend. Improved information on location of important spawning and nursery areas for this species might limit damage from future development or boat traffic that affects nearshore waters.

The second potential impact is the changing composition of the seabird community in PWS. As the population of murrelets in PWS has declined, those of larids (kittiwakes and other gulls) have generally remained stable (Lance et al. 2001). If the foraging efficiency of murrelets is negatively affected by the presence of larids, but murrelets feed in groups when prey abundance is low (Chapter 2), the combination of reduced prey and increased interference competition from larids could erode the ability of murrelets to recover. Further work is necessary to determine how important this interaction is to murrelets, but the aggregation of larids near human communities could be cause for concern.

Third, it is clear that some marine sites are more productive for murrelets than others, and that these sites are relatively easy to identify (Chapter 3). Conservation efforts should locate these sites, or habitat types, with the goal of protecting them from anthropogenic impacts. Defining the types of marine habitats important to adults and juveniles will assist managers in predicting the effects of climate change. Protecting sites for murrelets would benefit nearshore fish populations, because there is likely an overlap between sites that are good for murrelets and good for nearshore forage fish. Areas of special attention should include fine-scale sites used by adults foraging for themselves and for their chicks, as well as meso-scale areas with high murrelet productivity or murrelet nurseries. Marbled murrelets could thus serve as an indicator species and a management tool for nearshore ecosystems of northeast Pacific coastal waters.

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APPENDIX

DECLINES IN KITTLITZ'S AND MARBLED MURRELETS IN PRINCE WILLIAM SOUND, ALASKA: DEALING WITH UNCERTAINTY.

By Kathy Kuletz, Bryan Manly, Chris Nations, David Irons

ABSTRACT

Monitoring population trends of rare species can be difficult if the species are not easily separated from closely related, abundant species. We faced this problem in Prince William Sound (PWS), Alaska for two seabirds, the marbled murrelet (*Brachyramphus marmoratus*) and the Kittlitz's murrelet (*B. brevirostris*), both of which are surveyed at sea because they are non-colonial. As a group, *Brachyramphus* murrelets showed declines, but marbled murrelets (2004 population = 35,657 ± 7809 birds; 95 % CI) greatly outnumbered Kittlitz's (2004 population = 778 ± 516), and murrelets were not always identified to species in the field. Using data from 9 summer surveys (1972 and 1989-2004) we developed models that incorporated unidentified murrelets and predicted trends for each species. Model predictions reasonably fit field survey estimates, and substantiated observed trends of identified birds. Based on July (mid-breeding season) surveys, the marbled murrelet population declined at a rate of about 5% per annum, a total of 85 % since 1972, or 63 % since 1989; predicted quasi-extirpation (< 100 birds) is in year 2120. Kittlitz's have declined 17.7 % per annum since 1972 (a total of 99 %), or by 30.8 % per annum since 1989 (a total of 88 %); predicted quasi-extirpation is year 2006, although the 2004 field estimate was ~ 700 birds. The decline in July estimates in both species is of concern, but the Kittlitz's is at greater risk because of its low numbers and faster rate of decline. For Kittlitz's, the decline may be exacerbated by dependence on foraging habitat that is undergoing rapid change due to glacial recession. For both species, the ability to identify species-specific trends will be important in forming policy decisions and conservation efforts.

INTRODUCTION

Identifying and interpreting trends in populations is a critical aspect of conservation and management, and the task is complicated by uncertainties in survey data (Harwood and Stokes 2003). For rare species, detection of statistically significant trends is difficult, due to large errors in population estimates, often exacerbated by an insufficient number of years of data (Taylor and Gerrodette 1993). Inaction due to inconclusive or compromised results hampers status designations and thus management and conservation by affecting legal and policy making decisions (Reed and Blaustein 1997, Ralls and Taylor 2000, Harwood and Stokes 2003). For closely related species that are difficult to distinguish, another source of uncertainty is species identification (Hey et al. 2003). Incomplete species-specific data can result in trends of rare species being masked by trends in the more abundant species (Ludwig et al. 1993, Roberts and Hawkins 1999, Dulvy et al. 2000). We faced these problems in attempts to determine the population status of two seabirds, the rare Kittlitz's murrelet (*Brachyramphus brevirostris*) and the relatively abundant marbled murrelet (*B. marmoratus*). These closely related and phenotypically similar murrelets are sympatric in Prince William Sound (PWS), Alaska, with the Kittlitz's murrelet almost exclusively found in fjords with tidewater glaciers (Kendall and Agler 1998, Day et al. 2003, Kuletz et al. 2003), and the marbled murrelet occurring throughout coastal areas and outnumbering other seabird species in summer (Agler et al. 1998). The combined population of *Brachyramphus* murrelets was declining in PWS at least since 1989, and probably since 1972 (Lance et al. 2001). However, inconsistencies in species identification reduced confidence in interpretation of possible trends. The goal of this study was to substantiate and distinguish the trends of the two murrelet species.

Brachyramphus murrelets are small, diving, fish-eating seabirds (family Alcidae) found only in the North Pacific. Most of the world population of Kittlitz's murrelets breed along Alaska's coastlines, but some occur off eastern Russia (Day et al. 1999). In 2004, Kittlitz's murrelet became a candidate for listing under the Endangered Species Act (Federal Register 2004, USFWS 2004). Concerns about possible declines in the Kittlitz's murrelet spurred us to examine the best available data on their population trends, to insure that timely management actions could be implemented for this uniquely Alaskan species. Marbled murrelets breed from the Aleutian Archipelago in Alaska to central California (Nelson 1997) and are listed as threatened from British Columbia (Burger 2002) to California (McShane et al. 2004). Most of the world population of marbled murrelets breed in Alaska (McShane et al. 2004), and PWS has a relatively large population (Agler et al. 1998). Recently the U. S. Fish and Wildlife Service (USFWS) has proposed to eliminate the 'Distinct Population Segment' status of marbled murrelets in California, Oregon, and Washington (News Release, USFWS Pacific Regional Office, Portland, OR, September 1, 2004), which by inclusion with the Alaska population could lead to delisting. Thus, knowing the current status and trends of marbled murrelets in Alaska is important for determining the future legal status of this species. Because PWS is one of the few regions in Alaska with long-term data, it provides a valuable record of trends in the northern portion of the marbled murrelet's range.

To evaluate the status of both murrelet species and assist future management decisions, we used at-sea survey data for PWS, which has data for the longest time span (nine years within the period, 1972 – 2004) for any region in Alaska. This level of coverage was unique for marine birds at sea in Alaska, but trends analysis was complicated by wide confidence intervals in the estimates for Kittlitz's murrelets, variable proportions of unidentified murrelets among years, and unusual spikes in the estimates in two years. To address these issues, we used the PWS population estimates in a modeling technique that incorporated unidentified birds, to estimate the size and trend of populations of each species.

METHODS

Study Site. -- Our study site was PWS, a ca. 10,000 km^2 protected body of water in the northern Gulf of Alaska (GOA). Most of the shoreline is highly convoluted and includes deep fjords, shallow bays, deltas, large and small islands. There are several large icefields with over 20 tidewater glaciers entering coastal waters (Molnia 2001). The high freshwater input from rain and snow or glacial melt influences the strong cyclonic circulation that generally runs east to west (Neibauer et al. 1994). Surface waters from the GOA pulse into PWS primarily during winter months, via the Alaska Coastal Current, and in summer PWS waters become warmer and stratified (Niebauer et al. 1994).

Data Collection – Between 1989 and 2004, surveys were conducted in nine years (1989-91, 1993, 1996, 1998, 2000, 2004) during July, which is mid-breeding season (chick-rearing) for *Brachyramphus* murrelets in PWS (Kuletz and Kendall 1998, Day et al. 1999). The USFWS surveys were designed for collecting data on all marine birds and mammals using randomly selected strip transects, (n= 325-350 per year, including 187-212 shoreline and 138 offshore) of varying length and 200 m wide, including shoreline, coastal pelagic, and pelagic. Crews on three 7.7 m fiberglass boats operated daily and simultaneously to complete the survey over a three-week period. The USFWS conducted similar surveys, with different transects and slightly different design, in July 1972 (reanalyzed in Klosiewski and Laing 1994). The 1972 survey used vessels and transect widths similar to the later surveys, but the randomly selected transects of the 1972 survey used a different grid system and included a 'bay' stratum along with shoreline and pelagic strata.

For surveys since 1989, 187 shoreline transects were randomly selected in 1989, with an additional 25 transects randomly selected in 1990. Shoreline transects were defined by geographical features, and ranged from 1 to 30 km and averaged 5.6 km in length (Fig. 1; details in Agler et al. 1998, Irons et al. 2000, Lance et al. 2001); these were surveyed by piloting the boat parallel to and 100 m from shore. For offshore areas, a grid with 5-minute latitude-longitude blocks was overlaid on a nautical chart, and 69 blocks were randomly selected. Blocks that intersected the shoreline were categorized as 'coastal-pelagic' (n = 44), and those that did not touch land were 'pelagic' (n = 25). Within each block, two parallel lines running north-south were surveyed, for a total of 138 pelagic transects. For each block, bird density (birds/km^2) was averaged from the two lines, and this density was assumed to apply to the entire block, with the block density used to extrapolate to total area within its strata. Except for the lower number of shoreline transects in 1989, the same transects in all strata were surveyed every year. The surveyed area amounted to 4.6 % of the surface area of PWS waters (Agler et al. 1998).

All birds and marine mammals were recorded continuously within 100 m either side of and 100 m ahead of the boat, with two observers and a driver. Observers identified all birds to the highest possible taxon, using 10x binoculars for species identification where necessary. Because the two murrelet species were difficult to distinguish at sea, a portion of them were recorded as 'unidentified *Brachyramphus*'. More problematic, among years there was unequal emphasis on distinguishing between these two species, and the proportion of unidentified murrelets varied from 2 to 89 %.

Data Analysis - The study design used for these surveys was well-suited to abundant and widely-dispersed species such as marbled murrelets, but not for the rare and patchily-distributed Kittlitz's murrelet. For the latter species, population estimates had wide confidence intervals. Analysis of long-term trends was also complicated by the fact that the population estimates in 1972 and 1993 for both murrelet species were considerably higher than in other years. In summary, the analysis of trend data was complicated by large error in the estimates for the Kittlitz's murrelet, variable proportions of unidentified murrelets, and large population estimates in 1972 and 1993. Consequently, we analyzed three subsets of the data from PWS in July (Table 2): (1) including all years; (2) excluding 1972; and, (3) excluding both 1972 and 1993.

The original population estimates (hereafter, 'field estimates') and variances were calculated using a ratio estimator (Cochran 1977) on the densities for each stratum (shoreline, coastal-pelagic, and pelagic; see Stephensen et al. 2001 for details). The total field estimates were derived from the summed estimates and variances of each stratum. Data used for the analyses reported here were field estimates of population size and their standard errors (Table 2). Standard errors (SE) were obtained from the 95% confidence intervals (CI) originally calculated from the survey data, using SE = CI/1.96. The rate of change for population estimates of identified birds was calculated with linear regression analyses of log-transformed values. We then compared rates of change over time between the two species with a homogeneity of slopes test (Freud and Littell 1981) using linear models.

Using the field estimates and variances for marbled, Kittlitz's, and unidentified *Brachyramphus* murrelets, we developed a population model that accounts for the unidentified birds, and provides 'model predictions' of population sizes. The model assumes that the probability of being identified is the same for both species but may differ from year to year. Identifications are assumed implicitly to be correct – e.g., a bird identified as a Kittlitz's murrelet is not a marbled murrelet. The model also assumes that Kittlitz's and marbled murrelets have independent but constant trends over time. Let $N_{K,0}$ and $N_{M,0}$ represent the unknown numbers of Kittlitz's and marbled, respectively, in the starting year, t_0. The symbols K_t, M_t, and U_t are the field estimates of Kittlitz's, marbled, and unidentified birds, respectively, in year t. Let θ_K and θ_M represent the annual population growth rate for Kittlitz's and marbled, respectively, let γ_t be the probability that a bird will be identified in year t, and let E_{K_t}, E_{M_t}, and E_{U_t} represent error terms (including discrepancies between predictions of the fitted model and the observations, but also assuming measurement error in the field). The model is then

$$K_t = N_{K,0}\theta_K^{t-t_0}\gamma_t + E_{K_t}$$

$$M_t = N_{M,0}\theta_M^{t-t_0}\gamma_t + E_{M_t} \qquad \text{Eq. 1}$$

and

$$U_t = \left(N_{K,0}\theta_K^{t-t_0} + N_{M,0}\theta_M^{t-t_0}\right)(1-\gamma_t) + E_{U_t}$$

Note that model predictions for K_t, M_t, and U_t are predicted numbers seen in surveys, not predicted population sizes. To make the distinction clear, we henceforth refer to K_t, M_t, and U_t, whether from field observations or model predictions, using the term *survey size.* We estimated the unknown parameters (N_K, N_M, θ_K, θ_M, γ_t) in the model above through a weighted least squares nonlinear regression. Least squares chose the parameter values that minimized the criterion Q,

$$Q = \sum_i \sum_t \frac{\left(Y_{i,t} - \hat{Y}_{i,t}\right)^2}{V_{i,t}} \qquad \text{Eq. 2}$$

where $Y_{i,t}$ was the observed survey size for the i^{th} group of birds at time t (i.e., either K_t, M_t, or U_t), $\hat{Y}_{i,t}$ was the corresponding predicted value, and $V_{i,t}$ was the corresponding variance (the standard error squared from Table 1). For the nonlinear minimization, we used "reasonable" initial guesses based on available information. Initial values for N_K and N_M were taken from field estimates in year t_0 (Table 1). In all analyses, initial values were $\theta_K = \theta_M = 1$, representing stable populations, and $\gamma_t = (K_t + M_t)/(K_t + M_t + U_t)$, the observed proportions of identified birds.

We obtained variance for our estimators by simulation. We assumed that field observations for all three groups of birds (Kittlitz's, marbled, and unidentified) were log normally distributed with means and variances determined by the field estimates (Table 1). Random survey sizes were generated 5000 times, based on this assumption in place of the field estimates, and parameters were re-estimated from the simulated data sets using nonlinear regression. Empirical variances were then estimated from the simulated parameter estimates using

$$V\left(\hat{\phi}\right) = \frac{\sum_{i=1}^{n}\left(\hat{\phi}_i - \overline{\hat{\phi}}\right)^2}{n-1}$$

where n was the number of successful optimizations, $\hat{\phi}_i$ was the i^{th} parameter estimate, and $\overline{\hat{\phi}}$ was the mean of the n estimates. While each simulation entailed 5000 iterations, the nonlinear optimization routine failed to converge occasionally (generally < 5% of the time).

Projections of population size (rather than survey size) were generated using a simple exponential growth model implied by Eq. 1. Projected numbers of Kittlitz's murrelet, $N_{K,t}$, and marbled murrelet, $N_{M,t}$ were calculated as

$$N_{K,t} = \hat{N}_{K,0}\hat{\theta}_K^{t-t_0}$$

and Eq. 3

$$N_{M,t} = \hat{N}_{M,0}\hat{\theta}_M^{t-t_0}$$

where all parameter estimates on the right hand side of the equations were obtained from the fitted nonlinear regression. We also modeled the predicted population size to quasi-extinction (< 100 birds) for total *Brachyramphus* murrelets. All analyses were conducted in Matlab 6.5.

RESULTS

Population Estimates and Trends

Surveys. - - Between 1972 and 2004 the field survey population estimates for identified birds (Table 1) showed a decline of 19.9 % per annum for Kittlitz's murrelet and 2.3% for marbled murrelets. The slope for Kittlitz's population estimates was significant ($P = 0.04$) while that for marbled murrelets was not ($P = 0.69$), with the latter influenced by large numbers of unidentified birds in some years (Table 1). The rate of decline between species was significantly different (Homogeneity of slopes test; $F_{1,8} = 6.2$, $P = 0.03$). In July, Kittlitz's murrelets were primarily found in the upper fjords, and in 2004 their distribution was much more restricted than in 1989, with most birds found in the northwest area of PWS (Fig. 2a). Marbled murrelets were found throughout nearshore areas in all years (Fig. 2b).

Model Estimates -- The parameter estimates show that both marbled and Kittlitz's murrelets are declining ($\theta < 1.0$; Table 2). The estimated rate of decline is greater for Kittlitz's than for marbled murrelets, and θ_M is larger than θ_K in all scenarios (with 1972 or 1993, or without) even considering the estimated variances in those parameters (Table 2). Using all July data from PWS (Table 1), the estimate of θ_K is 0.8226 (a decline of 17.74 % per year). Excluding data from 1972 or both 1972 and 1993 results in even lower estimates of θ_K, 0.6908 and 0.6825, respectively (declines of 30.82 % and 31.75 % per year). The estimates of θ_M and γ_t (for those years in common) are strikingly similar in all three cases (θ_M is approximately 0.94 in each case). The model estimates indicate a rate of decline of about 5 % per annum, with a total 85 % decline since 1972 or 63 % decline since 1989. The parameter estimates for both Kittlitz's ($N_{K,0}$) and marbled murrelets ($N_{M,0}$) differ substantially, depending on the starting year (note that 1972 had much higher field estimates than 1989; Table 1).

Comparison of model and field estimates. – In most cases, the models appear to fit the field estimates reasonably well, although Kittlitz's tended to show more divergence between model and field estimates than did marbled or unidentified murrelets (Fig 3, 4). Model predictions show a pronounced decline in numbers of Kittlitz's murrelets irrespective of whether data from 1972 are included (Fig. 3a) or not (Fig. 4a). Pattern in predicted numbers of marbled murrelets is less clear particularly when data from 1972 are excluded (Fig. 3b, 4b). The sharp decline in unidentified murrelets after 1993 (Figs. 3c, 4c) reflects both greater success in species identification and decline in total *Brachyramphus* murrelets (Fig. 5). Model predictions of survey sizes for Kittlitz's change when data from problematic years (either 1972 alone, or both 1972 and 1993) are excluded (Fig. 3a, 4a). Omitting the problematic years, in both scenarios, led to smaller residuals (differences between field estimates and model predictions) in 1989 and 1990, but larger residuals in 2000 and 2004. However, whether only 1972 or both 1972 and 1993 (figure not shown) are excluded makes little difference in predicted survey size for the years in common. In contrast to the situation with Kittlitz's, results for marbled murrelets and unidentified birds (most of which would have been marbled murrelets) are little affected by exclusion of the 1972 data.

Projected trends. – Parameter estimates from the fitted model were used to project population sizes (Table 3) and trends of Kittlitz's and marbled murrelets (Fig. 6). Assuming Kittlitz's had an initial (1972) population of $N_{K,0} = 70{,}119$ (Table 2, including all years), the model estimate of θ_K leads to a predicted population of 294 in 2000, and less than 100 (treated as a quasi-extinction threshold) by 2006. Starting with the 1989 model estimate of 9,008 and $\theta_K = 0.6825$ (Table 2, excluding 1972 and 1993) yields a predicted population of only 149 in 2000. Within one year, i.e., by 2001, the predicted population is less than 100, thus, the latter set of estimates leads to a much more rapid decline (Fig. 6).

The projections for marbled murrelets are very similar whether or not model estimates include 1972 and 1993 July data. Using data from all years, where the initial population is 232,710 and $\theta_M = 0.9487$ (Table 2), the projected population in 2000 is 53,105. Because of the modest reduction and larger initial population, the predicted population does not drop below 100 until the year 2120.

DISCUSSION

Both the original population field estimates and the model estimates indicate declining populations of total *Brachyramphus* murrelets in PWS, and a more drastic decline in the Kittlitz's murrelet than the marbled murrelet. Of course, any prediction of extirpation or quasi-extinction must be qualified by the possibly unrealistic assumption of a constant rate of change in population size, and by the uncertainty in the model estimates of population growth rate. This is evident in the model estimates for Kittlitz's, which predicted less than 100 birds by 2001 (based on estimated growth rate from data since 1989) or by 2006 (using estimated growth rate from data since 1972), whereas the actual field estimates were ~ 1000 birds in 2000 and ~700 birds in 2004 (Table 1). Nonetheless, the rate of decline for field estimates of identified birds indicates that the general conclusions of the model are consistent with trends observed for identified birds. The model estimates were much closer to field estimates for marbled murrelets (e.g., the model predicted ~ 53,000 birds in 2000, and the field estimate for that year was ~ 52,000), which at the current rate of decline indicate extirpation of marbled murrelets in ~100 years. The inclusion of the 1972 data did not affect the predicted trends of marbled murrelets, and actually reduced the estimated decline of Kittlitz's murrelets when included. Although the 1972 field estimates were obtained with a different set of transects, we included them because they were a valid sampling method. They suggest that declines in both species began at least between 1972 and 1989, although for Kittlitz's, the rate of decline may have accelerated in the last 15 years.

The decline of two closely related species suggests a regional and long-term alteration in their environment may be responsible. For marbled murrelets, loss of old-growth forests where they nest has been implicated in murrelet declines farther south (Burger 2002, McShane et al. 2004). In PWS, roughly 10,000 acres of forest have been harvested since the 1940s, which is approximately 5 % of the total forested acreage today, or between 5 – 10 % of 'harvestable' timber (of commercial quality in harvestable areas) (U.S. Forest Service, Chugach National Forest, unpublished data). Thus, although timber harvests could have impacted marbled murrelets in PWS, the loss of potential nesting habitat there has been low, relative to the 80 % loss of nesting habitat from British Columbia to California (Burger 2002, McShane et al. 2004). Kittlitz's murrelets nest in remote alpine areas (Day et al. 1999) with little human impact, and alteration of nesting habitat is not documented. It is more likely that the PWS declines in *Brachyramphus* murrelets are primarily related to changes in the marine environment, either in their breeding or wintering grounds.

Both murrelet species face similar documented threats at sea. First, they are susceptible to mortality in gillnet fisheries (Carter et al. 1995, Day et al. 1999), and a 1990-1991 study in PWS estimated that between 450 and 1470 murrelets were killed in drift gillnets per year (extracted from data in Wynne et al. 1991, 1992). The proportion of Kittlitz's killed in nets was higher than for marbled murrelets, relative to their abundance in PWS, suggesting greater susceptibility to or overlap with PWS gillnet fisheries (Day et al. 1999). Second, oil spills were and continue to be a threat in PWS. In 1989, the largest spill in North America, the *Exxon Valdez* oil spill, caused direct mortality of an estimated minimum of 8,400 *Brachyramphus* murrelets (Kuletz 1996). Although most were likely marbled murrelets (Carter and Kuletz 1995), Kittlitz's lost a greater proportion of its population in the spill zone (Day et al. 1999). Small spills occur from tour and fishing vessel accidents (Kuletz 2001, USFWS 2004), primarily during the summer, when murrelets occupy inshore waters. Third, since the 1980s tourism has increased in PWS (Murphy et al. 2004), and related vessel traffic is heaviest in the fjords with tidewater glaciers, where Kittlitz's forage (Day et al. 2003, Kuletz et al. 2003). Finally, in the Gulf of Alaska (GOA), prey species composition and abundance has changed since the 1970s (Piatt and Anderson 1996, Anderson and Piatt 1999), and in PWS these changes appear to correspond to population declines in piscivorous birds in particular (Ager et al. 1999). All of these factors could have impacted the survival or productivity of murrelets in PWS. In addition, two large scale anthropogenic factors of unknown impact include fishery impacts to the ecosystem (Pearson et al. 1999) and possible long-term damage from the Exxon Valdez Oil Spill (Peterson et al. 2003).

Differences between species

Population declines of the magnitude we show for murrelets in PWS would be a concern for any long-lived species. *Brachyramphus* murrelets exhibit life-history traits that make them sensitive to loss of adults and adversity (Stearns 1992, Croxall and Rothery 1995). As with many seabirds, they are long-lived, with an estimated lifespan of 10 – 11 years (Burger 2002, McShane et al. 2004). They have delayed breeding, with age at first breeding estimated to be 2 -3 years (Burger 2002, Cam et al. 2003) and low fecundity (1 egg/year). The declines were not equal for these two species, however, and the proportion of Kittlitz's murrelet in the field counts of *Brachyramphus* murrelets went from 21 % in 1972 to less than 2 % since 1996. The faster trajectory of Kittlitz's toward extirpation suggests greater sensitivity to the same, or additional, environmental pressures. The different rates of decline for these two species could be a result of different dietary and habitat needs, and warrant further investigation.

Changes in food availability have often been linked to changes in seabird populations (review in Croxall and Rothery 1995). Both murrelet species are generalist feeders, consuming small, planktivorous fish in addition to invertebrates, but Kittlitz's murrelets appear to take a larger portion of macro-zooplankton (Nelson 1997, Day et al. 1999). There is evidence that warming trends in northern waters affects birds that feed on macro-zooplankton more than primarily piscivorous birds, because these plankton often require cooler water (Kitaysky and Golubova 2000, Crick 2004). Since the 1970s, PWS sea surface temperatures (SST) have generally increased (National Center for Atmospheric Research, data from http://www.ncar.ucar.edu).

Kittlitz's murrelets are also more specialized than marbled murrelets in their selection of foraging habitat (Day et al. 2003). In PWS, Kittlitz's are closely association with glacially influenced, turbid waters in the upper fjords (Day et al. 2003, Kuletz et al. 2003), as was evident in our surveys (Fig. 2). Kittlitz's may also be impacted by changes in these habitats arising from glacial recession, as suggested by their present day concentration in the few remaining fjords with stable or advancing glaciers (Kuletz et al. 2003). Across all taxa, species with more northerly distribution, and those more specialized, are experiencing greater declines in response to climate changes (Root et al. 2003, Julliard et al. 2004). Our results are consistent with this scenario, since Kittlitz's are both more northerly in distribution and more specialized in foraging habitat than marbled murrelets.

The causes of declines in marbled murrelets in PWS could include several factors already mentioned (timber harvest, oil spills, gillnet mortality) or extended periods of low recruitment to the population due to reproductive failure. However, unlike populations in California (Peery et al. 2004), there was no evidence of the latter. In PWS, juvenile marbled murrelet densities have been relatively high compared to populations farther south (Kuletz and Kendall 1998), and although juvenile densities declined from 1995 to 1999, the juvenile:adult ratios did not decline significantly (Chapter 4). This suggests that loss or emigration of adults is the main factor in the decline of the PWS population.

Notably, in PWS the decline in the murrelet population parallels the 88 % decline in stocks of Pacific herring (*Clupea pallasi*) between 1989 and 2000 (Thomas and Thorne 2003). The PWS herring crash could have been a consequence of the 1989 oil spill, disease, over-harvest in the early 1990s, environmental conditions, or a combination of those factors (Pearson et al. 1993, Brown et al. 1996, Petersen et al. 2003, Thomas and Thorne 2003), but the net effect on murrelets was drastic reduction of an important prey base. Juvenile herring are a key prey for marbled murrelets in PWS, both for adults (which eat age classes 0 and 1+ herring; Ostrand et al. 2004; Chapter 2) and as chick food (which require age class 1+; Chapter 2). Although 'forage fish' are protected from commercial fisheries in Alaska (Witherell et al. 2000), abundance of juveniles of commercial species, such as herring, could be indirectly impacted (Pikitch et al. 2004).

The trends in *Brachyramphus* murrelets was complicated by the unusual spike in their numbers in 1993. Although our surveys covered a large geographic area, the extent of movement between PWS and the GOA by murrelets is unknown, and it is possible that large-scale movements result in fluctuations in the size of the population within PWS. The unusually high numbers of murrelets present in July of 1993 coincided with a year of anomalously warm waters in the GOA that year, while PWS remained relatively cool (Piatt and Van Pelt 1997, Pearson et al. 1999). Marbled murrelets appear to alter their distribution at sea and their inland breeding activity in response to oceanographic conditions (Becker and Beissinger 2003, Burger 2000). In California, marbled murrelets foraged farther from nesting areas in a year with warmer SST, and they selected areas with cooler SST in a year when prey abundance was low (Becker and

Beissinger 2003). Together with our results, these studies highlight the necessity of maintaining long-term monitoring programs. Managers must also acknowledge the potential for large-scale movements when tracking murrelet population trends.

Management Implications

Marbled murrelets. -- The size of the Alaska population of marbled murrelets relative to populations farther south (McShane et al. 2004) might lead to the conclusion that the meta-population is healthy. However, the published Alaska population estimates were based on surveys conducted from 1993 to 1996 (Agler et al. 1998), and given the rapid changes evident in PWS, those estimates may not represent current populations in Alaska. In addition to PWS, recent declines in *Brachyramphus* murrelets have been documented at Glacier Bay in southeast Alaska (Robards et al. 2003), the Malaspina Forelands near Yakutat (Kissling et al. 2005), and Kachemak Bay in Cook Inlet (Speckman et al. 2005). An exception was the Kenai Fjords, where a relatively small population (~ 9,500 birds) of marbled murrelets declined between 1976 and 1986 and then increased between 1986 and 2003 (Van Pelt and Piatt 2003). Because four of five Alaska sites with trend data show evidence of declines, we suggest that the status of marbled murrelet populations warrant closer examination. In particular, current data are lacking for southeast Alaska, which was last surveyed entirely in 1994 (Agler et al. 1998) and may support > 70 % of the world population of marbled murrelets (McShane et al. 2004).

Kittlitz's murrelet. -- The rate of decline we found for the PWS population of Kittlitz's murrelet is rare for any long-lived species, and to our knowledge has not been documented in another seabird species, with the exception of intense hunting or bycatch mortality of some albatrosses. Because Kittlitz's were a small portion of *Brachyramphus* murrelets, their population trend could have been increasing or decreasing without necessarily affecting the trend for the genus. Similar situations have been found in fisheries, where the aggregate (lumped species) trend was stable, but some species within the group declined or went extinct before managers could act (Ludwig et al. 1993, Dulvy et al. 2000, 2003, Harwood and Stokes 2003). The problem of masked trends and crypto-extinctions, while documented and discussed for invertebrates and fishes, has not been widely recognized for marine birds. Yet, marine birds, especially if they are not conspicuous when nesting, have many of the same attributes that contribute to crypto-extinctions in fish; they are widely dispersed in uninhabited areas most of the year, difficult to encounter and enumerate, and may change distribution in response to a dynamic and structurally complex habitat (Croxall and Rothery 1995).

Monitoring. -- While multi-species monitoring programs such as the one in PWS are not always ideal, when protocols are consistent and continue over long time frames, they can be useful even for rare, patchily-distributed species such as the Kittlitz's murrelet. The model presented here demonstrates a way to make optimum use of population estimates for rare species that coexist with abundant ones, or when species identification is a source of error. The problem of variable proportions of unidentified *Brachyramphus* murrelets occurs in other regions of Alaska, and this model could be used to re-examine murrelet trends wherever these two species co-exist. Similar modeling could benefit trends analysis for other species groups as well. For example, during marine surveys in Alaska, cormorants (4 spp), murres (2 spp), mergansers (3 spp), and loons (5 spp) were not always identified to species (North Pacific Pelagic Seabird Database, USFWS, Anchorage, Alaska).

Compared to many species listed under the Endangered Species Act, marbled, and even Kittlitz's murrelets, still have relatively high numbers of individuals. Nonetheless, as population size is reduced, fluctuations in population size increase the probability of extinction, particularly for vertebrate populations numbering in the low thousands (Reed and Hobbs 2004). Furthermore, rapid population decline is recognized as a cause for listing species and triggering recovery actions regardless of population size (IUCN 2001, USFWS 2004). The trends observed in PWS for marbled and Kittlitz's murrelets over the last 30 years, and especially in the past decade, suggest that both *Brachyramphus* species should be conservation priorities.

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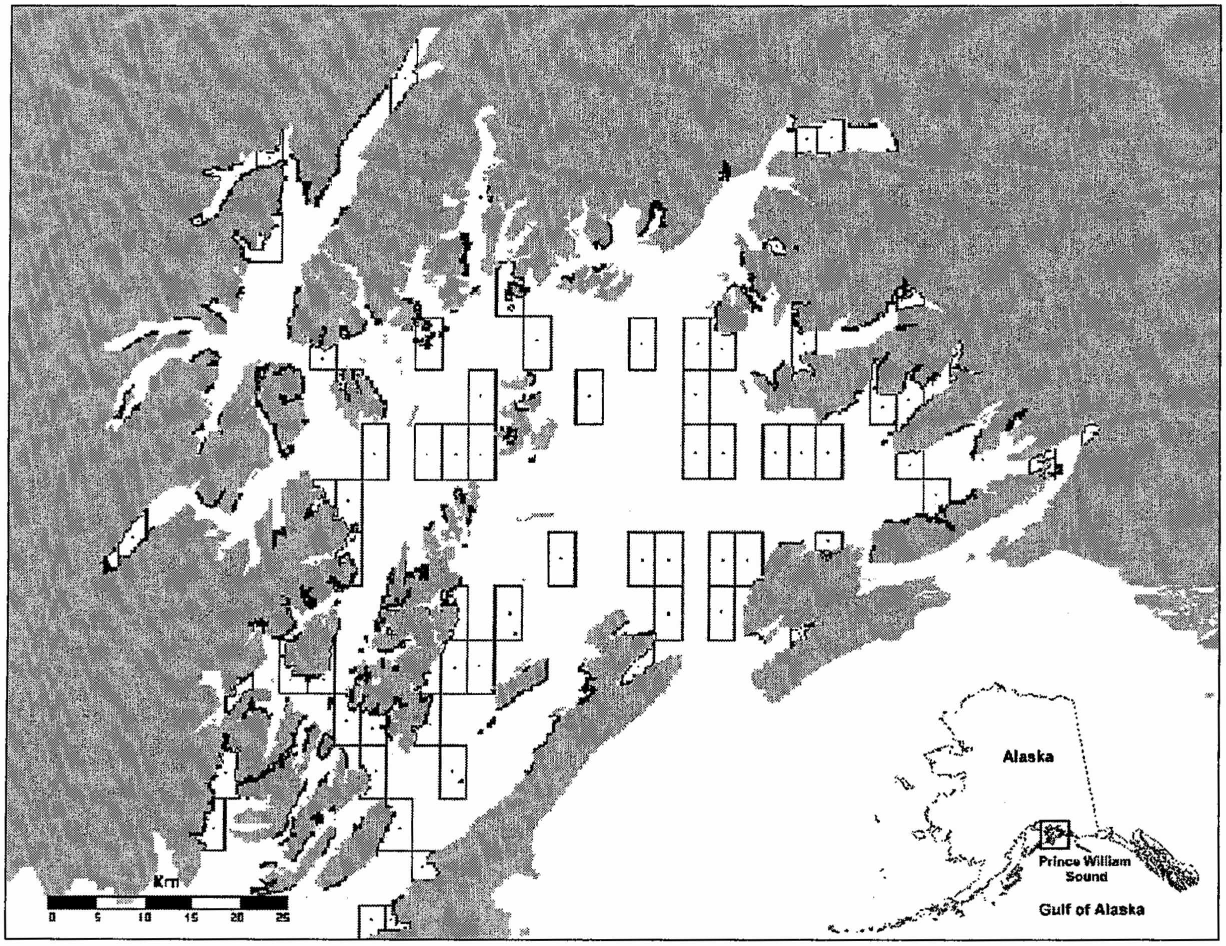

Figure 1. Prince William Sound, Alaska, showing locations of the shoreline transects (in heavy black) and blocks used for pelagic transects for marine surveys from 1989-2004. Two parallel transects running north-south were averaged for every pelagic block to obtain bird density.

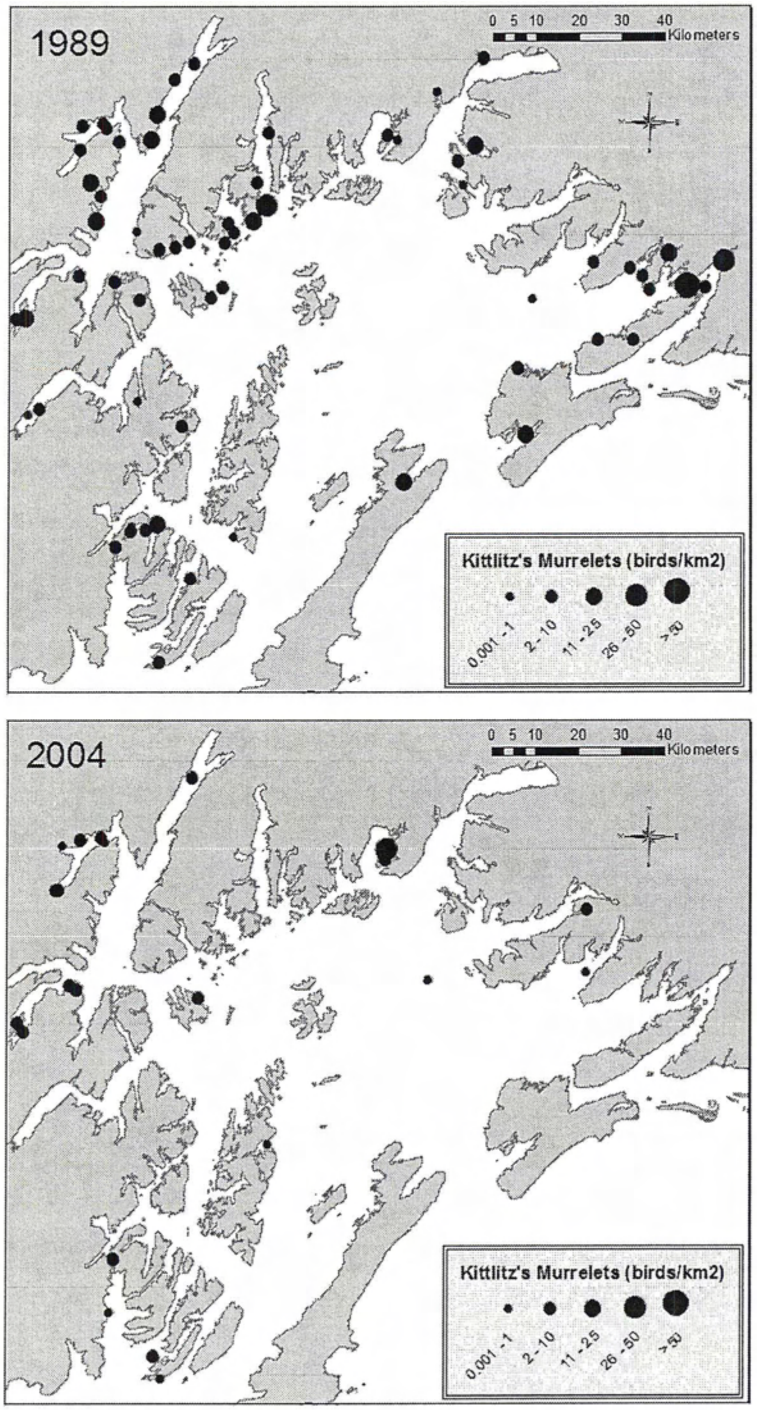

Figure. 2a. Distribution of Kittlitz's murrelets in Prince William Sound, Alaska, in July 1989 (top) and 2004 (bottom).

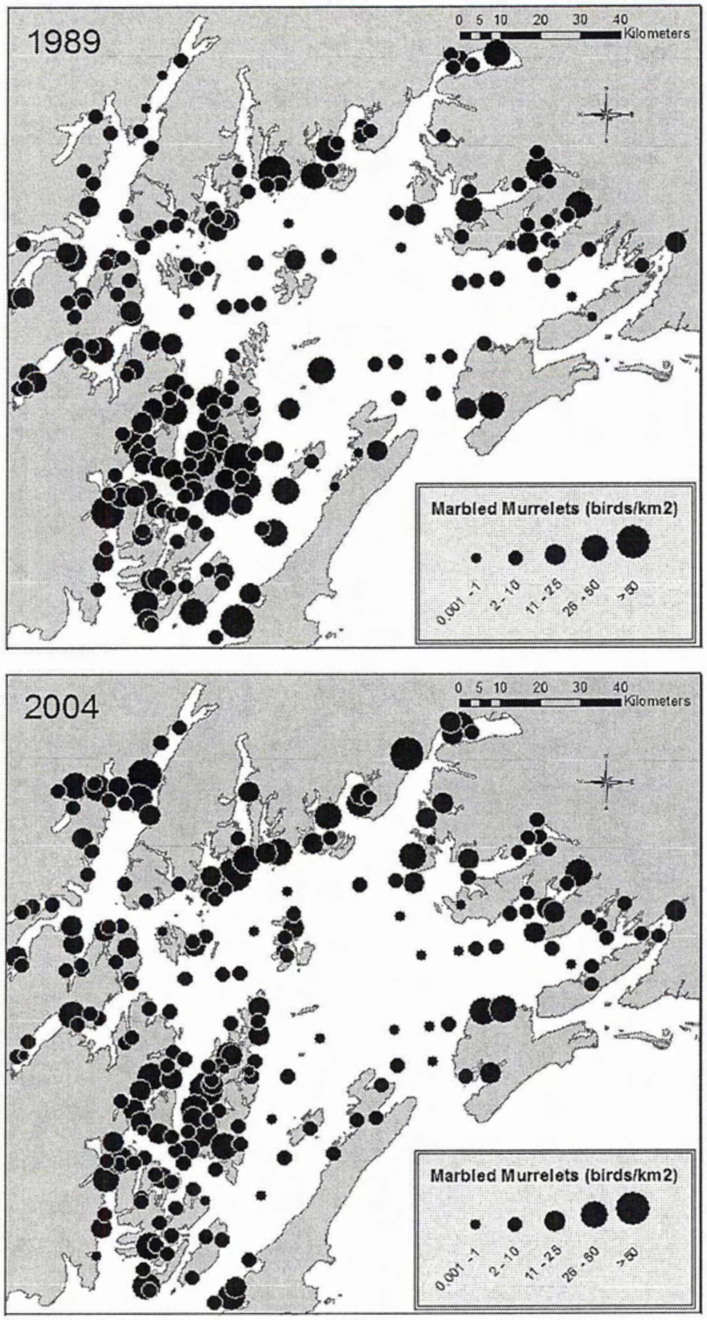

Figure. 2b. Distribution of marbled murrelets in Prince William Sound, Alaska, in July 1989 (top) and 2004 (bottom).

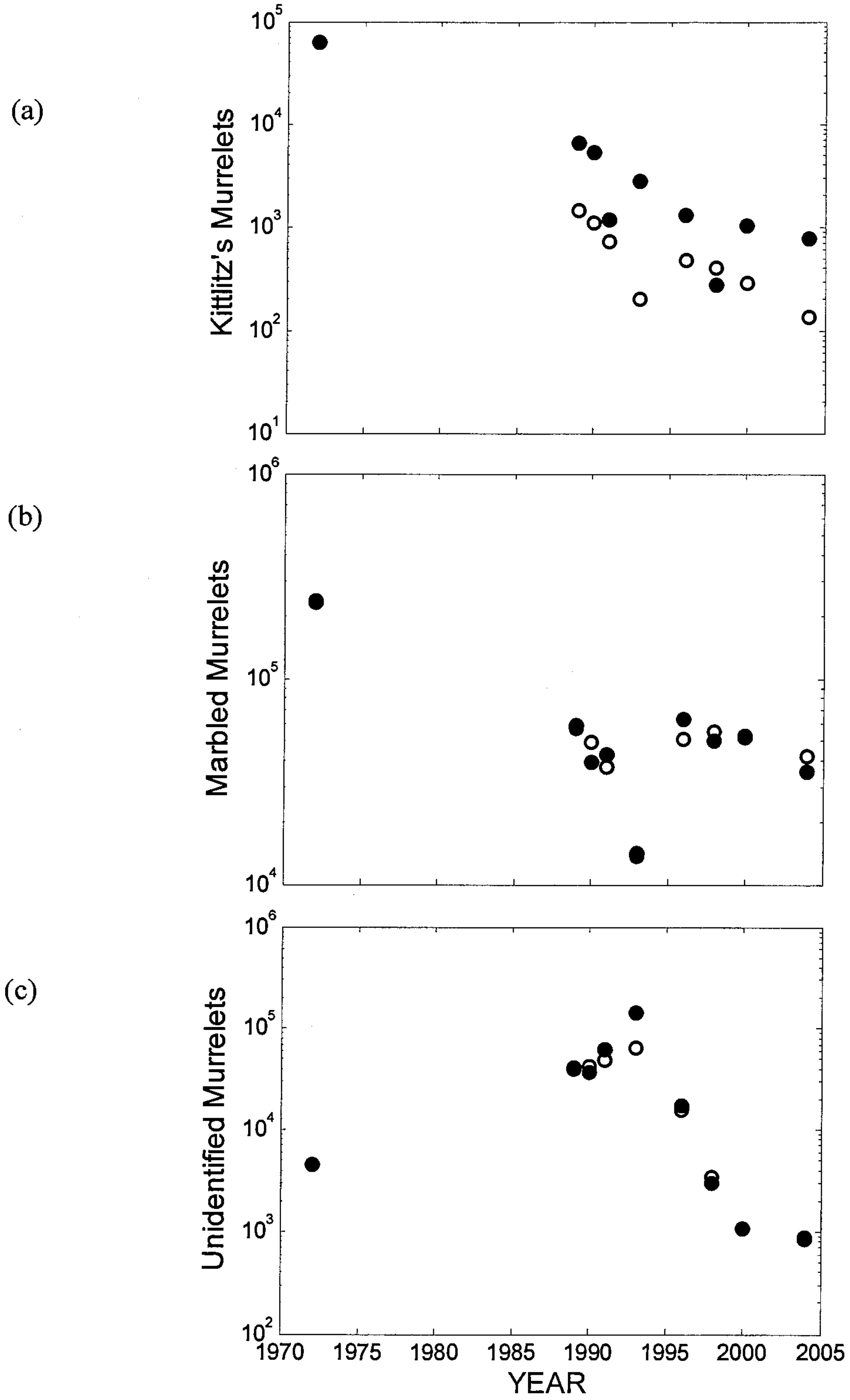

Figure 3. Estimated and predicted July survey sizes including all years.

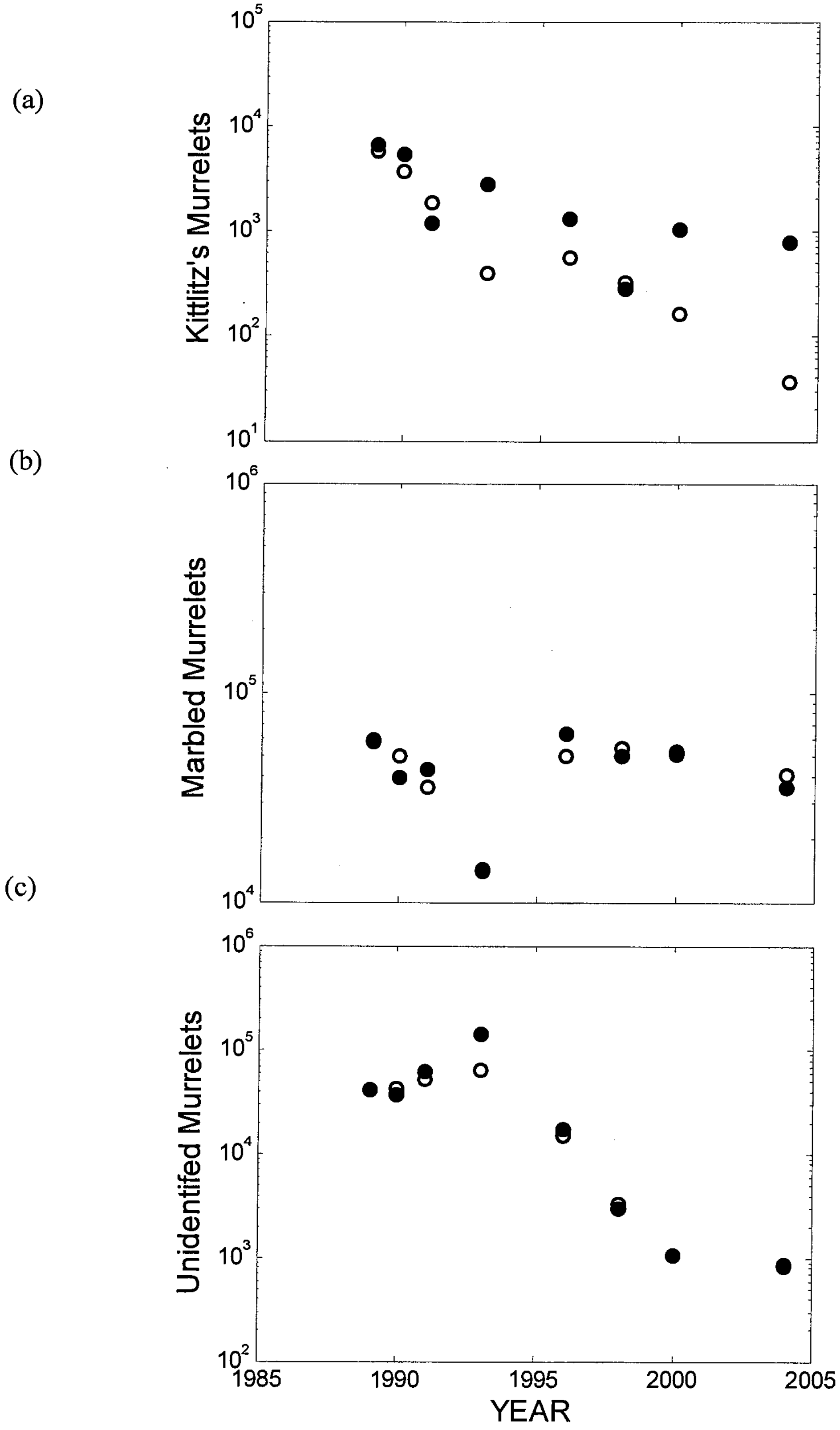

Figure 4. Estimated and predicted July survey sizes, excluding 1972.

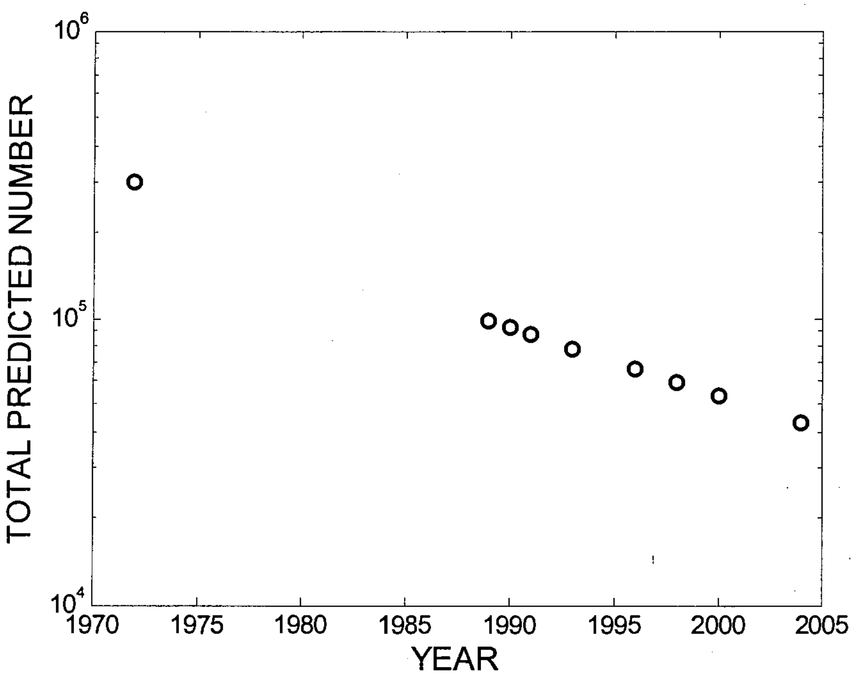

Figure 5. Total predicted survey size for July survey, including all years.

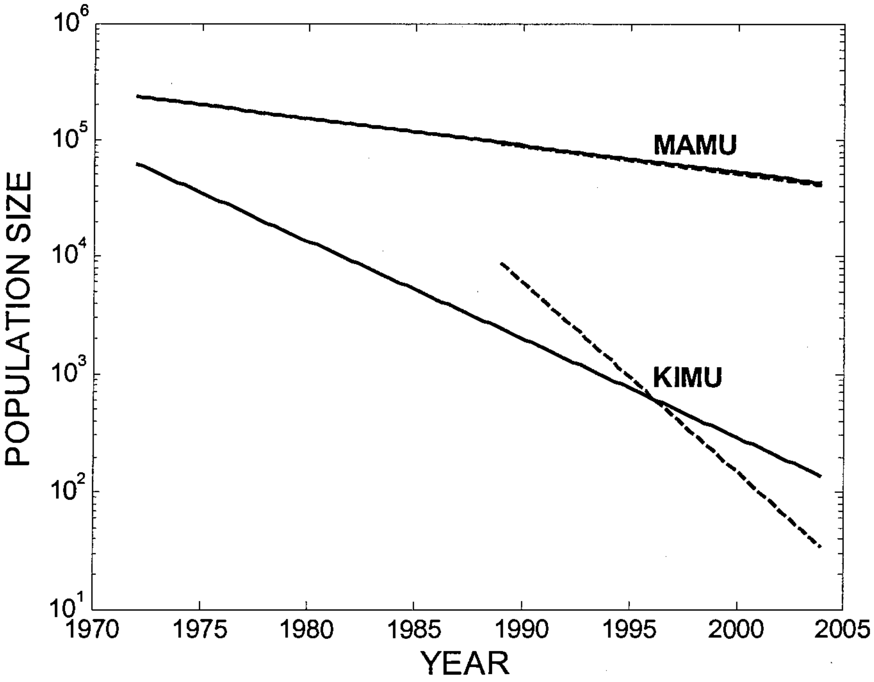

Figure 6. Population projections (Eq. 3) based on model estimates of initial numbers and growth rates.

Table 1. Original field population estimates and standard errors (SE) for Brachyramphus murrelets in July in Prince William Sound.

	Kittlitz's Murrelets		Marbled murrelets		Unidentified Birds	
Year	Estimate	SE	Estimate	SE	Estimate	SE
1972	63229	40879	236633	26391	4570	4018
1989	6436	1608	59284	6033	41634	4194
1990	5231	4315	39486	5095	36624	4036
1991	1184	572	42477	4669	62816	7149
1993	2710	685	14177	2295	142546	21365
1996	1280	696	63455	8185	17429	3056
1998	279	98	49879	4818	3036	1089
2000	1033	683	52377	7383	1077	519
2004	778	516	35658	7809	840	370

Table 2. Model parameter estimates from July survey data.

	All Years[1]		Exclude 1972[2]		Exclude 1972 & 1993[3]	
Parameter	Mean	SE	Mean	SE	Mean	SE
$N_{K,0}$	70119	21403	9403	2294	9008	2428
$N_{M,0}$	232710	9447	94981	4716	93517	4779
θ_K	0.8226	0.0098	0.6908	0.0351	0.6825	0.0561
θ_M	0.9487	0.0024	0.9468	0.0074	0.9467	0.0078
γ_{1972}	0.9853	0.0129	--	--	--	--
γ_{1989}	0.5944	0.0361	0.6105	0.0334	0.6091	0.0340
γ_{1990}	0.5415	0.0344	0.5568	0.0345	0.5546	0.0343
γ_{1991}	0.4331	0.0443	0.4171	0.0451	0.4212	0.0462
γ_{1993}	0.1776	0.0303	0.1834	0.0310	--	--
γ_{1996}	0.7673	0.0424	0.7650	0.0443	0.7641	0.0437
γ_{1998}	0.9425	0.0176	0.9430	0.0185	0.9438	0.0178
γ_{2000}	0.9798	0.0098	0.9795	0.0098	0.9792	0.0099
γ_{2004}	0.9803	0.0086	0.9797	0.0089	0.9793	0.0089

[1] Optimization successful in 4790 of 5000 iterations (95.8%).

[2] Optimization successful in 5000 of 5000 iterations (100%).

[3] Optimization successful in 4967 of 5000 iterations (99.3%).

Table 3. Population projections for murrelets in Prince William Sound in July, with estimates based on data from all years (Table 1), excluding 1972, and excluding 1972 and 1993. The projections incorporated unidentified *Brachyramphus* murrelets (see Methods).

	Kittlitz's murrelet			Marbled murrelet		
Year	All Years	Omit 1972	Omit 1972 and 1993	All Years	Omit 1972	Omit 1972 and 1993
1972	63209			236598		
1989	2425	9269	8843	95510	95210	93669
1990	2002	6420	6100	90547	90112	88667
1991	1653	4446	4209	85842	85288	83932
1993	1126	2133	2003	77153	76400	75207
1996	633	709	658	65740	64774	63791
1998	432	340	313	59086	58024	57159
2000	294	163	149	53105	51977	51218
2004	137	38	34	42898	41709	41123