Marbled Murrelet Foraging Ecology:
Spatial and Temporal Characteristics of Habitat Use in Clayoquot Sound, British Columbia

by

Kyle Andrew Muirhead
B.Sc., Brandon University, 2007

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ABSTRACT

The marbled murrelet (*Brachyramphus marmoratus*) is listed as threatened in both Canada and the United States due to logging of old-growth forest stands, their primary nesting habitat. Existing research is primarily focused on this terrestrial aspect of the species' ecology. Our understanding of their at-sea foraging ecology, however, is limited to broad-scale studies of population abundance and dynamics. In order to further understand the spatial and temporal variations of marbled murrelet at-sea foraging behaviour and habitat use, bi-weekly surveys of marbled murrelets were conducted in Clayoquot Sound, BC, between May 1 and September 1, 2007 and 2008. Data were first analysed using a Getis Ord G*i**spatial analysis to identify high-use foraging areas. Total marbled murrelet presence was consistent between years, but spatial distribution varied significantly in both years. A subsequent analysis of oceanic environmental variables found that temperature, salinity and phytoplankton densities (measured as chl *a*) were spatially ubiquitous, with no significant variation in measures across the study area. Chl *a* levels showed significant temporal variation, though similar trends in marbled murrelet abundance over time in both seasons suggest that phytoplankton levels do not directly affect murrelet presence. Marbled murrelets were also observed foraging within several metres of gray whales (*Eschrictius robustus*) feeding on epibenthic zooplankton in 2006 and 2008, a previously undocumented relationship. Join count statistics identified significant clustering of murrelets up to 300m from 39 feeding gray whales in 2006, and no association with 5 gray whales in 2008, marking a foraging association conditional on the abundance of both gray whales and their prey, but potentially significant to marbled murrelet survival and fecundity.

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Chapter 1:
Seabird Foraging in a Coastal Ecosystem: Background and Thesis Outline

Our understanding of seabird ecology is limited when compared to that of their terrestrial counterparts, and research has typically focused on two aspects of seabird ecology: 1) foraging in a large, dynamic and patchy marine landscape (Hunt *et al.* 1999, Becker & Beissinger 2003, Peery *et al.* 2009), and 2) competition and fecundity at nest sites (e.g. Ainley & Boekelheide 1990, Ballance *et al.* 1997, Serrano-Meneses & Szekely 2006). Seabird research has traditionally focused on breeding colonies and nest success, due to the inaccessibility of marine habitat where seabirds spend on average 90% of their lives (Hay 1992).

Unlike most other seabirds, the marbled murrelet (*Brachyramphus marmoratus*) has a more tangible association with terrestrial habitat because they nest in old-growth forests up to tens of kilometres inland (Ralph *et al.* 1995). Despite being a "marine species", the terrestrial component of the marbled murrelet's habitat requirements has led to a focus on terrestrial nesting habitat (e.g. Naslund 1993, Kuletz *et al.* 1995, Burger *et al.* 2000, Bradley & Cooke 2001, Marks & Kuletz 2001, Meyer & Miller 2002, Raphael *et al.* 2002, Ripple *et al.* 2003, Burger & Bahn 2004, Peery *et al.* 2004, Baker *et al.* 2006). This focus is due to substantial loss of their old-growth nesting habitat over the past century, and the relationship this has with population declines (e.g. Naslund *et al.* 1995, Bahn & Newsom 1999, Zharikov *et al.* 2007).

The marbled murrelet is listed as threatened through most of its range (Nelson 1997). In Canada, they are protected under the *Species at Risk Act* (SARA) (Rodway 1990, Hull 1999), and in British Columbia they are provincially Blue listed (status S3B, S3N) as a species of special concern (BC Conservation Data Centre 2010). In the United States, populations in

Washington, Oregon and California are federally protected under the *Northwest Forest Plan* (Thomas *et al*. 2006). Their status is attributed to population declines resulting from low reproductive rates combined with rapid deforestation of old growth forest (Rodway 1990, Hull 1999, Burger 2002). Oil spills and increased nest predation are also potential factors (Ralph *et al.* 1995).

Due to the terrestrial nature of these threats, limited research has documented marine habitat use in relation to oceanographic variability, especially short-term oceanographic variation that can rapidly redistribute prey (Hunt *et al.* 1999). The marbled murrelet spends the majority of its life at sea and breeding success depends heavily on the quality of prey (Burkett 1995). Analyses of stable-isotopes in feathers of museum specimens have shown that, since the 1950s, diet quality has been a limiting factor in murrelet population growth in the Georgia Basin (Norris *et al.* 2007). Literature on marbled murrelet interactions with the marine environment, however, is lacking, and the majority of at-sea studies are directed at population research and less at the nature of its foraging habitat.

Foraging ecology is the link between many aspects of murrelet biology and population dynamics, such as energy budgets and nesting success. However, little is known about the physical characteristics of foraging habitats, or how shifts in oceanographic variables, such as temperature or productivity, influence murrelet behaviour and distribution. Determining marine habitat use characteristics and seabird response to environmental fluctuations can better inform conservation and management policies, such as recovery strategies and marine protected area design and implementation.

Marbled Murrelet Foraging Ecology

An adult murrelet can fly up to 120 kilometres per hour and dive up to 47 metres when pursuing prey (Mathews & Burger 1998, Burger & Chatwin 2002). The shape of their wing requires an elevated platform for flight and landing, making tall trees with broad mossy limbs optimum nesting sites (Burger & Chatwin 2002). Marbled murrelets will fly up to 80 kilometres from nest sites to their near-shore coastal feeding habitat (Burger 1995).

Correlations between coastal habitat types, offshore abundance of marbled murrelets and high use inland nesting habitats (Miller *et al.* 2002, Becker & Beissinger 2003) suggest that foraging habitat selection is driven by the amount of upwelling, or influx of primary productivity, in the region. When upwelling is low, individuals tend to forage in areas with a low sea surface temperature, but when the amount of upwelling is high, individuals forage in areas that are closer to their nesting habitats. Marbled murrelets also forage farther from nesting sites during El Niño years when prey availability is low for reasons other than a lack of upwelling (Becker and Beissinger 2003).

Previous studies suggest that marbled murrelets will take a wide variety of prey items potentially impacted by seasonal, inter-annual and inter-decadal oceanographic variation, including mysid shrimp (Family *Mysidae*), krill (*Thysanoessa spinifera* and *Euphausia pacifica*), northern anchovy (*Engraulis mordax*), sand lance (*Ammodytes hexapterus*), market squid (*Loligo opalescens*), juvenile rockfishes (*Sebastes* spp.), Pacific sardine (*Sardinops sagax*), and Pacific herring (*Clupea harengus*) (Sealy 1975b, Carter *et al.* 1984, Burkett 1995). Marbled murrelets have an intermediate trophic level among alcids, primarily eating fish, and to a lesser extent zooplankton (Hobson 1990). According to Becker & Beissinger (2006) murrelets should select low- and mid-trophic level prey (invertebrate zooplankton such as krill) if their availability and ease of capture outweigh the costs of finding larger, energetically superior prey.

Marbled Murrelets in Clayoquot Sound

Clayoquot Sound is occupied by a significant population of marbled murelets, and has been included in previous studies of population dynamics (Burger *et al.* 2000, Tranquilla *et al.* 2003, Burger and Bahn 2004). Clayoquot Sound maintains expanses of intact old-growth forests for nesting marbled murrelets, as well as productive waters. Censes conducted at 10-year increments found a 40 percent decline in the Clayoquot Sound population (Beissinger 1995). Similarly, surveys repeated in 1992 and 1993, when compared to original 1982 survey data, found that in 341 contiguous 1-kilometre quadrats in fjord, channel and inshore marine habitats murrelet populations declined from 4,500 individuals in 1982 to 2,622 in 1993, constituting a 40 percent drop in the population size and coinciding with a 24.5 percent loss in old-growth forest in the region (Kelson *et al.*1995). At-sea surveys along 148 kilometres of coastline between 1996 and 2000 found that marbled murrelet distribution in this region was highly variable within-season (Mason *et al.* 2002). It was also noted that spatial distribution at-sea was consistent among transects from year to year, with consistent areas of high- and low-use, and sightings increased steadily through June and into July, and then declined in August.

Marbled murrelets in Clayoquot Sound appear in high densities in the exposed nearshore waters off Vargas Island and Flores Island, and the sheltered waters between these islands, based on both transect and grid surveys (Sealy & Carter 1984, Kelson *et al.* 1995, Mason *et al.* 2002). These observations, from data collected over 20 years and with different methods, present evidence that marbled murrelets in Clayoquot Sound, and specifically in the coastal waters of

Flores and Vargas Islands, have high foraging site fidelity, despite diurnal and seasonal variations in at-sea locations (Mason *et al.* 2002). These habitat use characteristics have also been found in multi-year surveys from Barkley Sound (Carter & Sealy 1990), Desolation Sound (Lougheed 2000), areas along Haida Gwaii (Gaston 1996) and in Alaska (Kuletz 1996, Speckman *et al.* 2000)

This thesis is organized into 3 main chapters that assess the spatial distribution of foraging marbled murrelets in the study area, and examine the spatial and temporal relationships between murrelet habitat use and their environment. To determine how marbled murrelets distribute themselves within a known foraging area, I present in Chapter 2 the spatial and temporal distribution of marbled murrelets within the Clayoquot Sound study area, identifying areas of significantly high use through analyses of spatial autocorrelation for data in 2007 and 2008. To identify what, if any, environmental factors are influencing marbled murrelet distribution, I examine oceanographic variability in the study area measured at sampling stations during marbled murrelet survey transects in Chapter 3. Data are then examined against murrelet distribution patterns to identify if any correlation exists. In Chapter 4, I examine the potential biological influence from another common foraging species at the site, the gray whale (*Eschrichtius robustus*).

Literature Cited

Ainley, D.G. and R.J. Boekelheide. 1990. Seabirds of the Farallon Islands. Stanford University Press. 450pp.

Bahn, V. and D.N. Newsom. 1999. Marbled murrelet as target species for land management in coastal British Columbia. *Proc. Biology and Management of Species and Habitats at Risk*, Kamloops, B.C.

Baker, L.M., Peery, M.Z., Burkett, E.E., Singer, S.W., Suddjian, D.L. and S.R. Beissinger. 2006. Nesting habitat characteristics of the marbled murrelet in central California redwood forests. *Journal of Wildlife Management,* 70(4): 939-946.

Ballance, L.T., Pitman, R.L., and S.B. Reilly. 1997. Seabird community structure along a productivity gradient: Importance of competition and energetic constraint. *Ecology,* 78(5): 1502-1518.

BC Conservation Data Centre. 2010. Conservation Status Report: *Brachyramphus marmoratus*. *B.C. Ministry of Environment*. Available: http://a100.gov.bc.ca/pub/eswp/ (accessed September 29, 2010).

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

Becker, B.H. and S.R. Beissinger. 2006. Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology,* 20(2): 470-479.

Beissinger, S.B. 1995. Chapter 37: Population trends of the marbled murrelet projected from demographic analyses. In *Ecology and conservation of the Marbled Murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, CA: U.S. Forest Service. pp.385-393.

Bradley, R.W. and F. Cooke. 2001. Cliff and deciduous tree nests of marbled murrelets in southwestern British Columbia. *Norhtwestern Naturalist,* 82(2): 52-57.

Burger, A.E. 1995. Marine distribution, abundance and habitats of marbled murrelets in British Columbia. In *Ecology and conservation of the Marbled Murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, CA: U.S. Forest Service. pp.295-312.

Burger, A.E. 2002. Conservation assessment of marbled murrelets in British Columbia: a review of the biology, populations, habitat associations and conservation. *Technical Report Series No. 387,* Pacific and Yukon Region, B.C.: Canadian Wildlife Services.

Burger, A.E. and V. Bahn. 2004. Inland habitat associations of marbled murrelets on southwest Vancouver Island, British Columbia. *Journal of Field Ornithology*, 75(1): 53-66.

Burger, A. and T.A. Chatwin. 2002. Introduction and overview of the Clayoquot Sound study. In *Multi-scale studies of populations, distribution and habitat associations of marbled murrelets in Clayoquot Sound, British Columbia*, Burger, A.E. and T.A. Chatwin (eds.), Victoria, B.C.: British Columbia Ministry of Water, Air, and Land Protection.

Burger, A.E., Bahn, V., and A.R.M. Tillmanns. 2000. Comparison of coastal fringe and interior forests as reserves for marbled murrelets on Vancouver Island. *The Condor*, 102: 915-920.

Burkett, E.B. 1995. Marbled Murrelet food habits and prey ecology. In *Ecology and conservation of the Marbled Murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, CA: U.S. Forest Service. pp.223-246.

Carter, H.R. and S.G. Sealy. 1984. Marbled Murrelet (*Brachyramphus marmoratus*) mortality due to gill-net fishing in Barkley Sound, British Columbia. In *Marine birds: Their feeding ecology and commercial fisheries relationships*, Nettleship, D.N., Snager, G.A. and P.F. Springer (eds.), Canadian Wildlife Service Special Publication. Ottawa: Minster of Supply and Services. pp. 212-220.

Carter, H.R. and S.G. Sealy. 1990. Daily foraging behaviour of marbled murrelets. In *Auks at sea,* Sealy, S.G. (ed.), *Studies in Avian Biology*, 14: 93-102.

Gaston, A.J. 1996. Seabird distribution in Laskeek Bay. In *Laskeek Bay Conservation Society annual scientific report, 1995,* Gaston, A.J. (ed.), Laskeek Bay Conservation Society, Queen Charlotte City, B.C.: 2-28.

Hay, R.B. 1992. The oceanic habitats of seabirds: Their zonal distribution off Vancouver Island, British Columbia, Canada. *Journal of Biogeography*, 19(1): 67-85.

Hobson, K.A. 1990. Stable isotope analysis of marbled murrelets: Evidence of freshwater feeding and determination of trophic level. *The Condor*, 92(4): 897-903.

Hull, C.L. 1999. Marbled murrelet research in Desolation Sound, British Columbia. *Proceedings of the Biology and Management of Species and Habitats at Risk, Kamloops, BC*: 751-758.

Hunt, G.L., Mehlum, F., Russell, R.W., Irons, D., Decker, M.B., and P.H. Becker. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. In *Proc. 22 Int. Ornithol. Congr.,* Adams, N.J. and R.H. Slotow (eds.), Durban: 2040-2056.

Kelson, J.D., Manley, I.A., and H.R. Carter. 1995. Decline of the marbled murrelet in Clayoquot Sound, British Columbia: 1982-1993. *Northwestern Naturalist*, 76(1): 90-98.

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

Kuletz, K.J., Marks, D.K., Naslund, N.L., Goodson, N.J. and M.B. Cody. 1995. Inland habitat suitability for the marbled murrelet in southcentral Alaska. In *Ecology and conservaton of the marbled murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, CA: U.S. Forest Service, pp. 141-150.

Lougheed, C. 2000. Breeding chronology, breeding success, distribution and movements of marbled murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. *Technical Report Series No. 352*, Canadian Wildlife Service, Pacific and Yukon Region, Delta, BC: 1-89.

Marks, D.K. and K.J. Kuletz. 2001. Use of treeless and forested habitat by marbled murrelets in south-central Alaska. *Waterbirds*, 24(2): 161-168.

Mason, A., Burger, A.E., and B. Hansen. 2002. At-sea surveys of marbled murrelets in Clayoquot Sound, 1996-2000. In *Multi-scale studies of populations, distribution and habitat associations of marbled murrelets in Clayoquot Sound, British Columbia*, Burger, A.E. and T.A. Chatwin (eds.), Victoria, B.C.: British Columbia Ministry of Water, Land and Air Protection.

Mathews, N.J.C. and A. Burger. 1998. Diving depth of a marbled murrelet. *Northwestern Naturalist*, 79(2): 70-71.

Meyer, C.B. and S.L. Miller. 2002. Use of fragmented landscapes by marbled murrelets for nesting in southern Oregon. *Conservation Biology*, 16(3): 755-766.

Miller, S.L., Meyer, C.B., and C.J. Ralph. 2002. Land and seascape patterns associated with marbled murrelet abundance offshore. *Waterbirds*, 25(1): 100-108.

Naslund, N.L. 1993. Why do marbled murrelets attend old-growth forest nesting areas year-round? *The Auk*, 110(3): 594-602.

Naslund, N.L., Kuletz, K.J., Cody, M.B. and D.K. Marks. 1995. Tree and habitat characteristics and reproductive success at marbled murrelet tree nests in Alaska. *Northwestern Naturalist*, 76(1): 12-25.

Nelson, S.K. 1997. Marbled murrelet (*Brachyramphus marmoratus*). In *The Birds of North America No. 276*, Poole, A. and F. Gill (eds.), Washington, D.C.: The American Ornithologists' Union. 32p.

Norris, D.R., Arcese, P., Preikshot, D., Bertram, D.F. and T.K. Kyser. 2007. Diet reconstruction and historic population dynamics in a threatened seabird. *Journal of Applied Ecology*, 44(4): 875-884.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Becker, B.H., Burkett, E. and T.D. Williams. 2004. Individual and temporal variation in inland flight behaviour of marbled murrelets: Implications for population monitoring. *The Condor*, 106(2): 344-353.

Peery, M.Z., Newman, S.H., Storlazzi, C.D. and S.R. Beissinger. 2009. Meeting reproductive demands in a dynamic upwelling system: Foraging strategies of a pursuit-diving seabird, the marbled murrelet. *The Condor*, 111(1): 120-134.

Ralph, C.J., Hunt, G.L., Raphael, M.G., and J.F. Piatt. 1995. Ecology and conservation of the marbled murrelet in North America: an overview. In *Ecology and conservation of the Marbled Murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, CA: U.S. Forest Service, pp.3-22.

Raphael, M.G., Mack, D.E., and B.A. Cooper. 2002. Landscape-scale relationships between abundance of marbled murrelets and distribution of nest habitat. *The Condor*, 104: 331-342.

Ripple, W.J., Nelson, S.K. and E.M. Glenn. 2003. Forest landscape patterns around marbled murrelet nest sites in the Oregon Coast Range. *Northwestern Naturalist*, 84(2): 80-89.

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

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

Sealy, S.G. and H.R. Carter. 1984. At-sea distribution and nesting habitat of the marbled murrelet in B.C.: Problems in the conservation of a solitary nesting seabird. In *Status and conservation of the world's seabirds,* Croxall, J.P., Evans, P.G.H. and R.W. Schreiber (eds.), Cambridge, U.K.: International Council for Bird Preservation, Technical Publication No. 2. 737-756.

Serrano-Meneses, M.A. and T. Szekely. 2006. Sexual size dimorphism in seabirds: sexual selection, fecundity selection and different niche-utilisation. *Oikos*, 113: 385-394.

Speckman, S.G., Springer, A.M., Piatt, J.F., and D.L. Thomas. 2000. Temporal variability in abundance of marbled murrelets at sea in southeast Alaska. *Waterbirds*, 23: 364-377.

Thomas, J.W., Franklin, J.F., Gordon, J. and K.N. Johnson. 2006. The Northwest forest plan: Origins, components, implementation experience, and suggestions for change. Conservation *Biology*, 20(2): 277-287.

Tranquilla, L.A.M., Yen, P.P-W., Bradley, R.W., Vanderkist, B.A., Lank, D.B., Parker, N.R., Drever, M., Lougheed, L.W., Kaiser, G.W., and T.D. Williams. 2003. Do two murrelets make a pair? Breeding status and behaviour of marbled murrelet pairs captured at sea. *Wilson Bulletin*, 115(4): 374-381.

Zharikov, Y., Lank, D.B. and F. Cooke. 2007. Influence of landscape pattern on breeding distribution and success in a threatened alcid, the marbled murrelet: model transferability and management implications. *Journal of Applied Ecology*, 44: 748-759.

Chapter 2

Spatial-Temporal Analysis of Marbled Murrelet Abundance and Distribution in Clayoquot Sound, British Columbia

Introduction

Habitat selection refers to an innate and learned behavioural response in wildlife that allows them to distinguish among various components of their ecosystem, resulting in the disproportional use of certain aspects to influence survival and fitness of individuals (Krebs & Davies 1991, Block & Brennan 1993). Rosenzweig (1985) suggested that habitat selection theory was a subset of optimal foraging theory, and thus, habitat selection was driven by prey availability. Though focusing primarily on foraging, my research also looks at other behaviours (e.g. loafing). This scope requires a broader view of habitat selection, such as that provided by Block & Brennan (1993) who contend that foraging theory is actually a subset of habitat theory, since animals use habitats to meet several life history needs (e.g. breeding, loafing). Southwood (1977) theorized that habitat characteristics act as a "templet" that influence strategies used by animals to survive and reproduce, and this has become a unifying theoretical framework for habitat ecology (Block & Brennan 1993).

My research tests the spatial and temporal heterogeneity of the study area, a concept that has a prominent role in Southwood's (1977) theoretical framework. This theory refers to the unequal ability of habitats, in both time and space, to provide resources for an individual or species to survive and reproduce. In the case of seabirds, survival and reproductive success depends on finding profitable foraging sites in a marine environment where prey density is very patchy and changes quickly in space and time (Hunt *et al.* 1998, 1999). Becker & Beissinger

(2003) found that the presence of marbled murrelets along the coast of California, at a scale of 10s to 100s of kilometres and covering habitat from 20 to 2500 metres offshore, was negatively correlated with depth, distance from nest flyways and water temperature, positively correlated with prey fish schools, and were not significantly correlated with water stratification, fronts, or the presence of other species of seabirds (common murres, *Uria aalge,* and pigeon guillemots, *Cepphus columba*). Short-term temporal variability on the scale of days and weeks elicited a rapid response in the foraging behaviour and habitat selection of marbled murrelets.

The marbled murrelet is listed as threatened through most of its range (Nelson 1997). In Canada, they are protected under the *Species at Risk Act* (SARA) (Rodway 1990, Hull 1999), and in British Columbia they are provincially Blue listed (status S3B, S3N) as a species of special concern (BC Conservation Data Centre 2010). In the United States, populations in Washington, Oregon and California are federally protected under the *Northwest Forest Plan* (Thomas *et al.* 2006). Marbled murrelet population decline is thought to be a result of a low reproductive rate combined with the rapid deforestation of old growth forest, the primary nesting habitat of murrelets (Rodway 1990, Hull 1999, Burger 2002). These threats have led to limited effort towards documenting marine habitat use in relation to short-term oceanographic processes that can rapidly redistribute foraging areas (Hunt *et al.* 1999). Murrelet breeding success depends heavily on the quality of prey it is able to acquire from nearshore marine habitat (Burkett 1995). Though literature on marbled murrelet interactions with the marine environment does exist (e.g. Becker & Beissinger 2003), the majority of at-sea studies are directed more at population research and less at ecological associations between the marbled murrelet and its foraging habitat.

In this chapter I use tests of spatial autocorrelation to analyze marbled murrelet distribution and abundance within the study area to identify areas where foraging density is higher than would be expected if foraging processes were spatially random. Previous studies of at-sea foraging habitats are focused on the biological components of habitat selection (e.g. Hunt 1995, Strachan *et al*. 1995), and few have analyzed marbled murrelet habitat use from a spatial analysis approach, which allow for large sets of data points to be analyzed to identify potential relationships not always perceived by the observer. Within- and between- season variations in spatial distribution of marbled murrelets will be examined to identify what if any change in habitat use occurs over the season, and between years. Based on these high-use areas, an analysis of environmental variables may identify the factors that drive this spatial distribution.

Methods

Study Area

Clayoquot Sound is a 90 kilometre long series of inlets and bays along the west coast of Vancouver, reaching up to 35 kilometres inland and occupying 265,000 hectares of land and 85,000 hectares of inlets. Data were collected in the region between Dagger Bay to the north and Ahous Bay to the south and out to 4-5 kilometres from shore (Figure 2.1). The study area includes shallow and exposed rock reefs, sand and mud bays, and boulder and rock beds. Water depths range from 0 to 35 metres. The marine environment in Clayoquot Sound, and particular that around Flores Island, is highly turbid with strong currents around the headlands and weaker flow in the bays (Kopach 2004).

Data Collection

Survey transects were oriented to incorporate a range of environmental characteristics, and to capture both exposed offshore and sheltered inlet habitats, both of which were identified as marbled murrelet foraging habitat during a previous pilot study and initial assessment of the area. A total of 15 survey transects (Figure 2.1) were used for bi-weekly surveys conducted between May 23 and August 13, 2007 and May 23 and August 31, 2008. Fixed-width surveys as outlined by Bibby *et al.* (2000) were conducted. Birds were recorded up to 300 metres from the vessel in any direction. Attribute data included the behaviour of the murrelet(s), latitude and longitude of the research vessel, bearing (degrees) to the observed murrelet(s) and the distance of the murrelet(s) from the vessel in 50 metre intervals (Buckland *et al.* 2001). The outer boundary of the study area was defined at the 30 metre isobath to incorporate average foraging depth (Strachan *et al.* 1995). A 6.5 metre aluminum vessel was used to conduct the surveys and collect samples.

Observations were taken from a height of approximately 1.5m above the surface of the water. Data were collected by a minimum of 3 observers at an approximate speed of 4.5 knots. Surveys were conducted in sea conditions that did not exceed 2m (swell + wind wave) and conditions < 3 on the Beaufort scale. One survey set included 15 transects, completed within a seven day period, and sets were conducted at 7 day intervals.

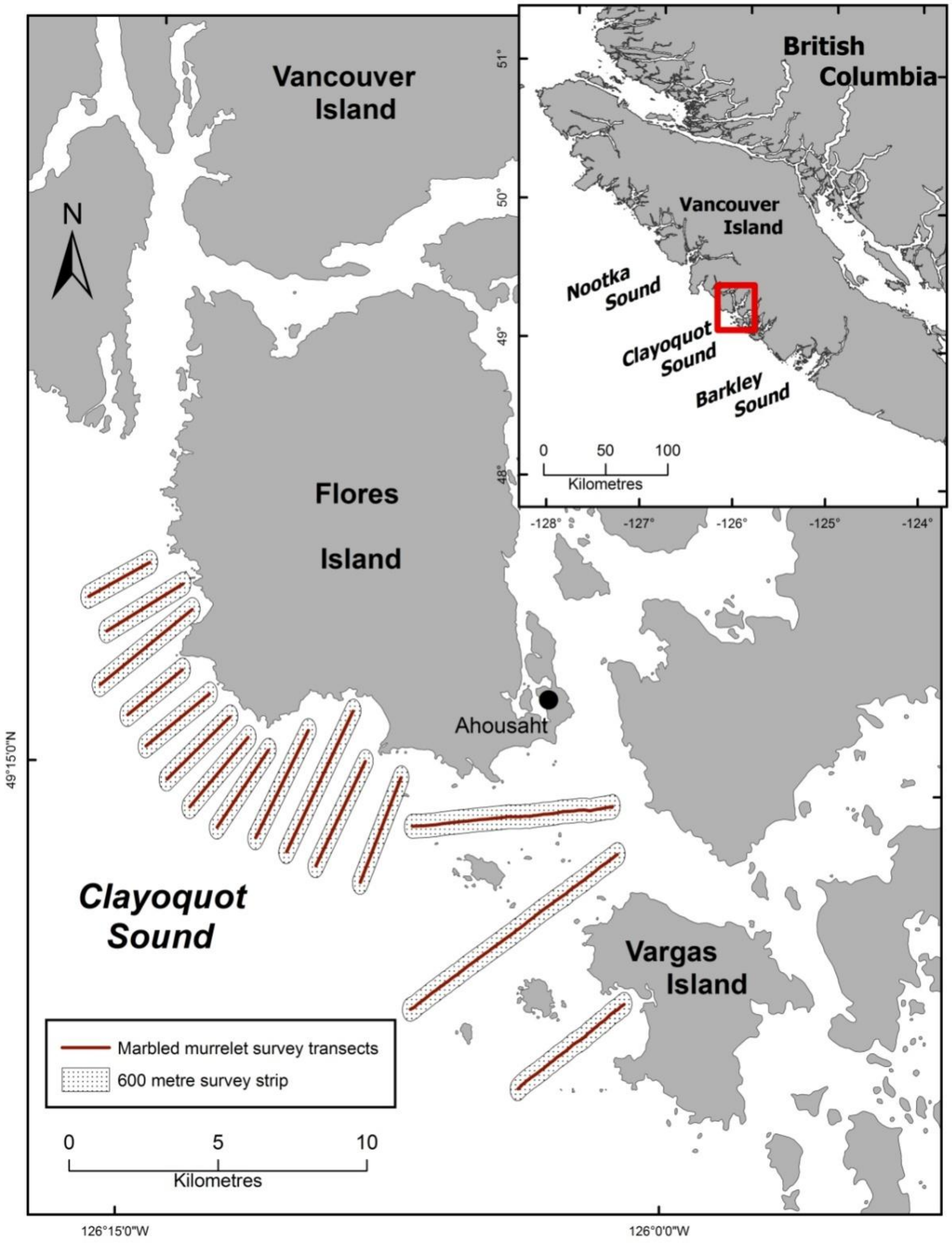


Figure 2.1: Study area along the west coast of Vancouver Island, depicting the 15 survey transects.

Data Analysis

The data set compiled during the surveys consists of a series of spatially defined data points delineated by date and transect number. Data were pooled into 3 temporal categories: incubation, chick-rearing, and fledged, based on observations collected during the surveys. Incubation refers to all data collected before hatching, when adults are foraging strictly for subsistence and are not carrying food in their bills. Chick-rearing includes all data collected between the time that juveniles are born and the time they are fledged, when adults are provisioning. The beginning of this stage was determined when adults began carrying prey at the surface for transport to the nest, bringing 1 to 2 whole fish to the nest to provision their single chick (Nelson & Hamer 1995). Fledged includes all data collected after juveniles start appearing in the study area, identified by their black and white colour characteristic of wintering plumage, and adults are once again foraging for subsistence.

A global Moran's I spatial statistic was calculated prior to fine-scale analysis of local spatial autocorrelation to identify any broader-scale spatial clustering (Nelson and Boots 2008). Significant global spatial autocorrelation increases the likelihood of falsely identifying significant local spatial autocorrelation. The absence of significant global spatial autocorrelation signifies that autocorrelation identified at the local scale is not influenced by global factors (Ord and Getis 2001, Nelson and Boots 2008).

At a local scale, a hot spot analysis was used to identify the spatial extent of significant habitat use in the study area in each breeding stage. Hot spots are considered regions of clustering, where observed density is greater than what would be expected by random chance (Azzalini & Torelli 2007). A Getis-Ord Gi* statistic was used to identify hotspots, based on the equation:

$$Gi^* = \frac{\sum_{j=1}^{n} w_{i,j} x_j - \bar{X} \sum_{j=1}^{n} w_{i,j}}{S \sqrt{\frac{\left[n \sum_{j=1}^{n} w_{i,j}{}^2 - \left(\sum_{j=1}^{n} w_{i,j}\right)^2\right]}{n-1}}}$$

Where x_j is the attribute value for feature j, $w_{i,j}$ is the spatial weight, calculated from an N x k spatial weights matrix based on 4 nearest neighbour (k) distances, between feature i and j, and n is equal to the total number of features.

A degree of clustering is inherent in data collected along strip transects, and the Gi* hotspot statistic identifies spatial autocorrelation in values relative to the mean amount of clustering present in the data set (Nelson & Boots 2008) by comparing neighbourhoods to a global average and identifying local regions of strong autocorrelation. This compensates for the overrepresentation of significant clustering that may result from other measures of local spatial autocorrelation when using a data set with inherent clustering.

Spatial representation of the data set and subsequent analysis was created using a kernel density estimation, with data points weighted by the number of murrelets in each recording. A 300 metre search threshold was implemented in density estimation, corresponding with the search radius implemented during surveys, and a 50 metre kernel was used based on the accuracy with which distance estimations were taken. Hotspots were classified based on coastal features (headlands), distance from shore and level of exposure to open ocean forces (Figure 2.2). Habitat was first divided by headlands (Dagger Bay, Grassy Knoll, Cow Bay, Fitzpatrick's). The Cow Bay area was then divided into near (3) and offshore (4) zones, due to a perceived division in marbled murrelet use during a pilot study in 2006 and the lengthened survey transects in this area. Distribution patterns between shoreline and exposed open water can be quite different, and the presence of islands and reefs can result in further variation (Burger 1995). The south-eastern study area was classified based on exposure, with an open and exposed offshore zone (6), and an inner sheltered zone (7).

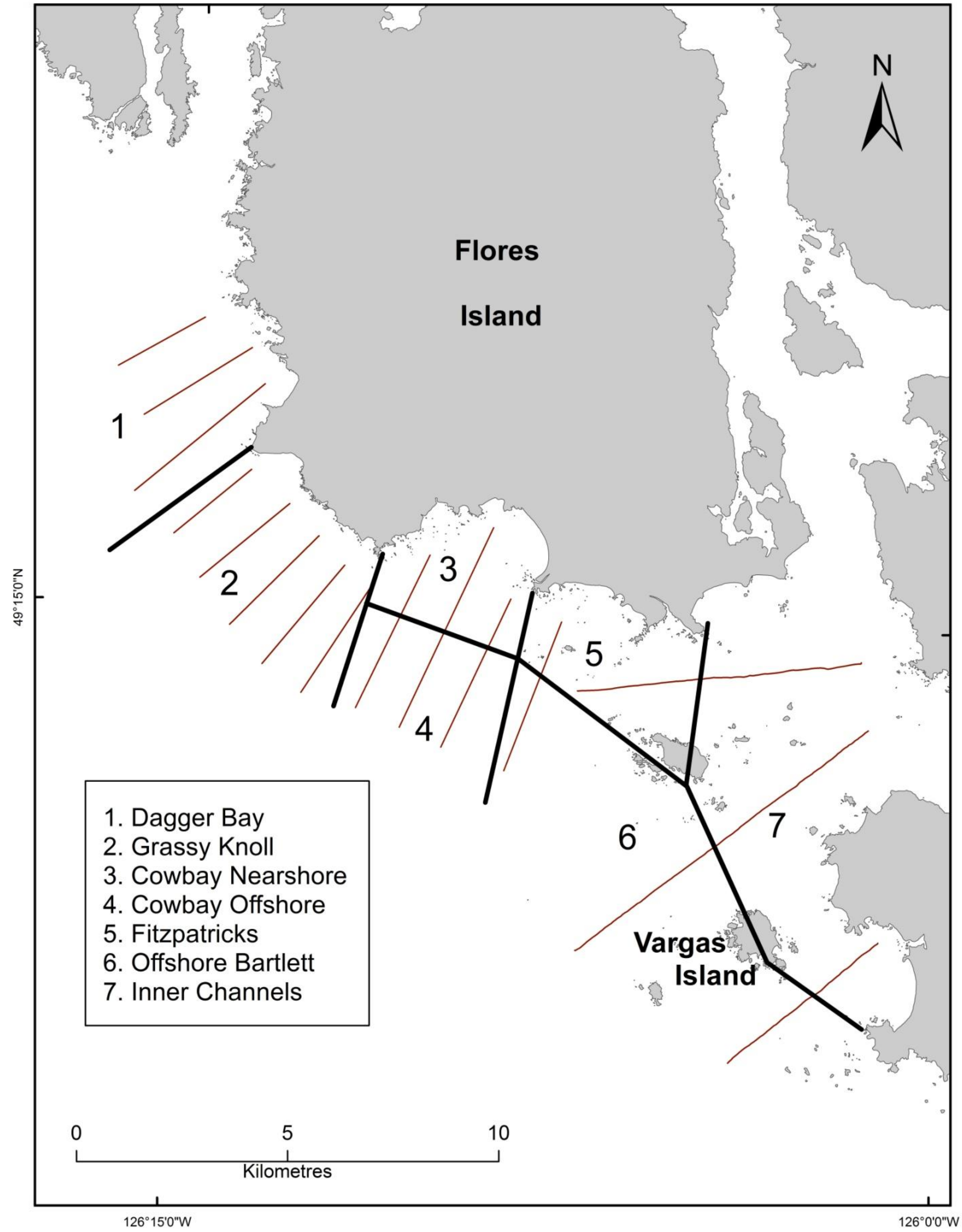


Figure 2.2: Classification areas used in qualitative descriptions of hotspot analysis.

Results

Nine survey sets (n=135 transects) were completed in 2007 and 8 (n=120 transects) in 2008 (Table 2.1). Behavioural data collected during the surveys suggest that the incubation period ended after 19 June in 2007 and after 17 June in 2008. The chick rearing period continued as late as 26 July in 2007 and 15 July in 2008, at which point the young were fledged and juveniles appeared in surveys.

Table 2.1: Marbled murrelet survey dates

Survey Set #	**2007Season**	**Chick-rearing Stage**	**Survey Set #**	**2008Season**	**Chick-rearing Stage**
1	May 23, 2007	inc	**10**	May 29, 2008	inc
2	June 8, 2007	inc	**11**	June 9, 2008	inc
3	June 19, 2007	inc	**12**	June 17, 2008	inc
4	June 26, 2007	c-r	**13**	June 27, 2008	c-r
5	July 13, 2007	c-r	**14**	July 11, 2008	c-r
6	July 26, 2007	flg	**15**	July 24, 2008	flg
7	August 1, 2007	flg	**16**	July 31, 2008	flg
8	August 9, 2007	flg	**17**	August 31, 2008	flg
9	August 13, 2007	flg			

When plotted temporally, data from both seasons show the same trend in number of individuals observed, with fluctuating total observations during incubation (2007 mean: 247.5, range: 98; 2008 mean: 244.5, range: 62), followed by consistently high observations during chick rearing (2007 mean: 252, range: 16; 2008 mean: 350.5, range: 3) and a significantly rapid decline in total number of individuals once juveniles had fledged (2007 mean: 43.5, range: 46; 2008 mean: 101.7, range: 47) (Figure 2.3). Despite this similarity, annual data were analysed separately due to variation in spatial distribution between seasons.

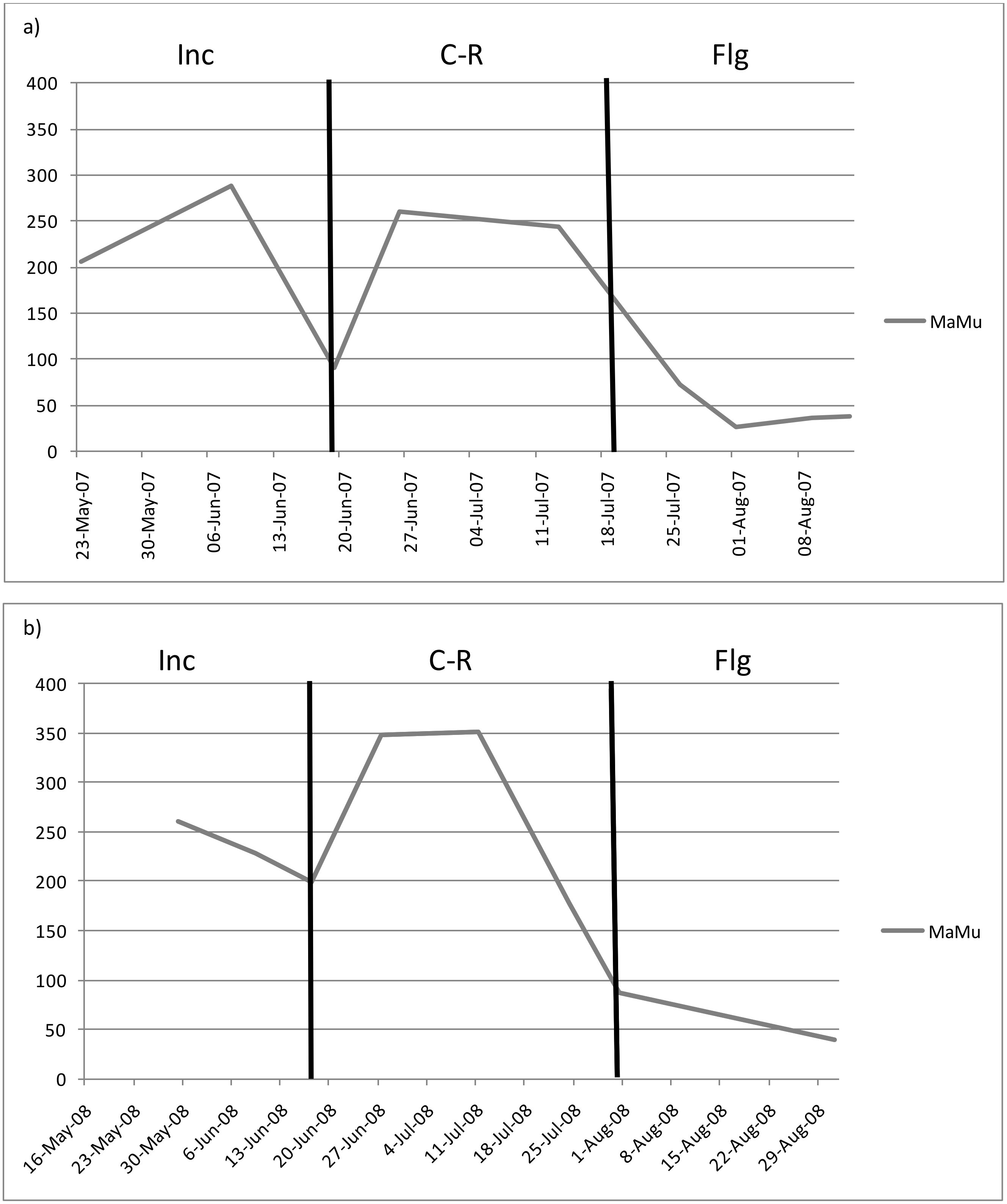


Figure 2.3: Total number of marbled murrelets observed in 2007 (a) and 2008 (b), aggregated by survey set. Black vertical lines represent divisions in the chick-rearing stage between incubation (inc) chick rearing (c-r) and fledged (flg) periods.

Global Spatial Autocorrelation

Global measures of spatial autocorrelation indicate no significant global spatial autocorrelation, confirming that large-scale influences are not affecting results at a local scale and giving greater confidence in tests of local spatial autocorrelation (Table 2.2).

Table 2.2: Global Moran's I statistics by time category; Significance measured at $p <= 0.05$.

Season		**Moran's I Index**	**Z-score**
2007	inc	0.14	0.83
	c-r	0.22	0.62
	flg	0.03	0.39
2008	inc	0.21	1.18
	c-r	0.02	0.52
	flg	-0.02	-0.14

Hotspot Analysis of Marbled Murrelet Foraging Habitat Use

A Getis-Ord G*i** statistic, calculated for both seasons and aggregated temporally by chick-rearing stage, identified clusters of significant positive spatial autocorrelation in all cases (Figure 2.4 – 2.6). During the incubation period in 2007 hotspots were situated mainly in the south-east part of the study area (areas 4, 6 and 7) while in 2008 hotspots were dispersed across the study area (areas 1, 3 and 6). During the chick rearing period, hotspots in both years were situated nearshore (2007: areas 1, 3, 5 and 7; 2008: areas 3, 5 and 7). During the fledged period, hotspots were minimal in 2007 (areas 2 and 7), with murrelets evenly distributed through most of the area. In 2008, more distinct hotspots were situated both near and offshore (areas 5 and 6).

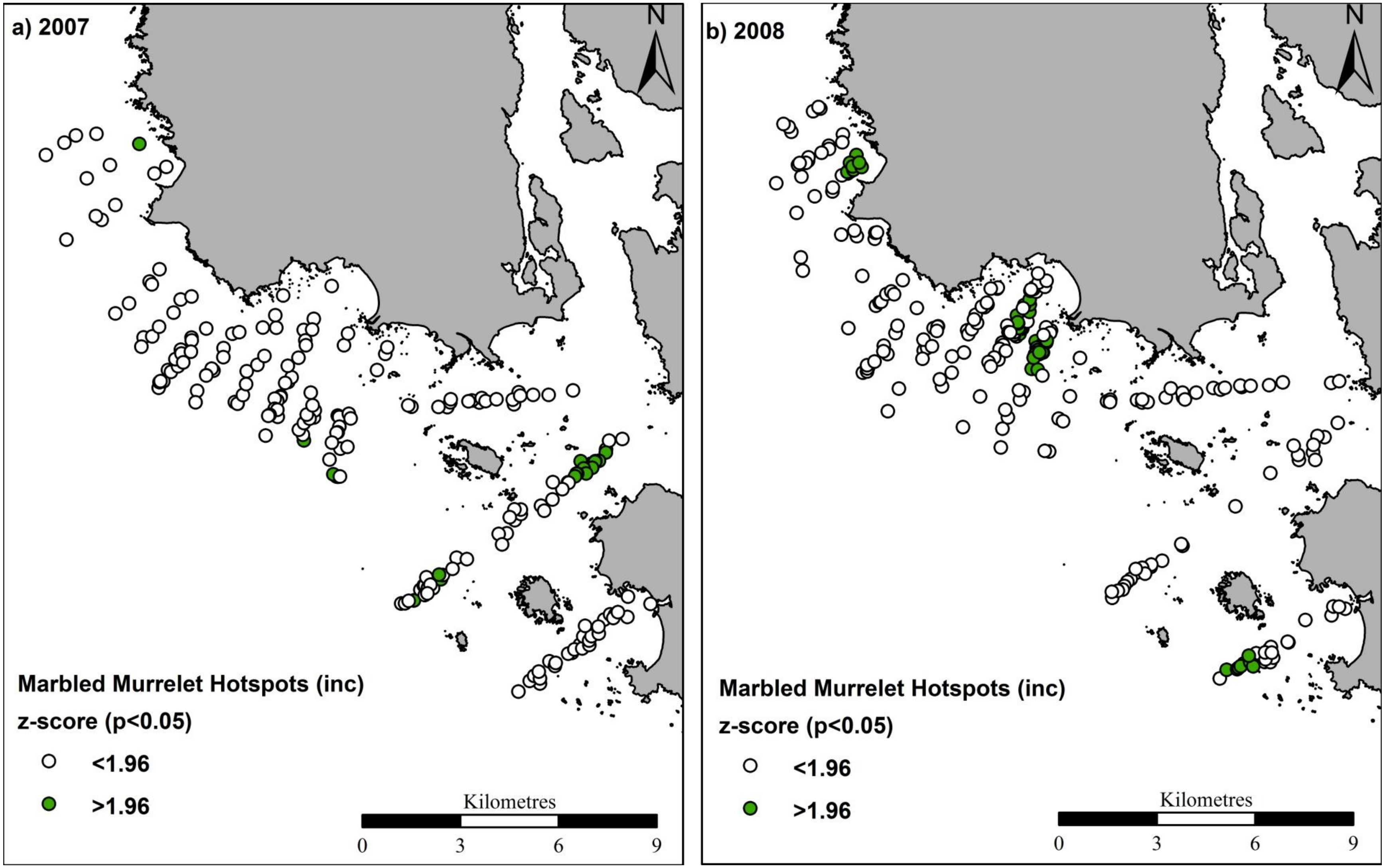


Figure 2.4: Marbled murrelet habitat use hotspots, identified by a Getis-Ord G*i** statistic, during murrelet incubation (inc), in 2007 (a) and 2008 (b). Test statistic critical value is +/- 1.96 at $p<0.05$.

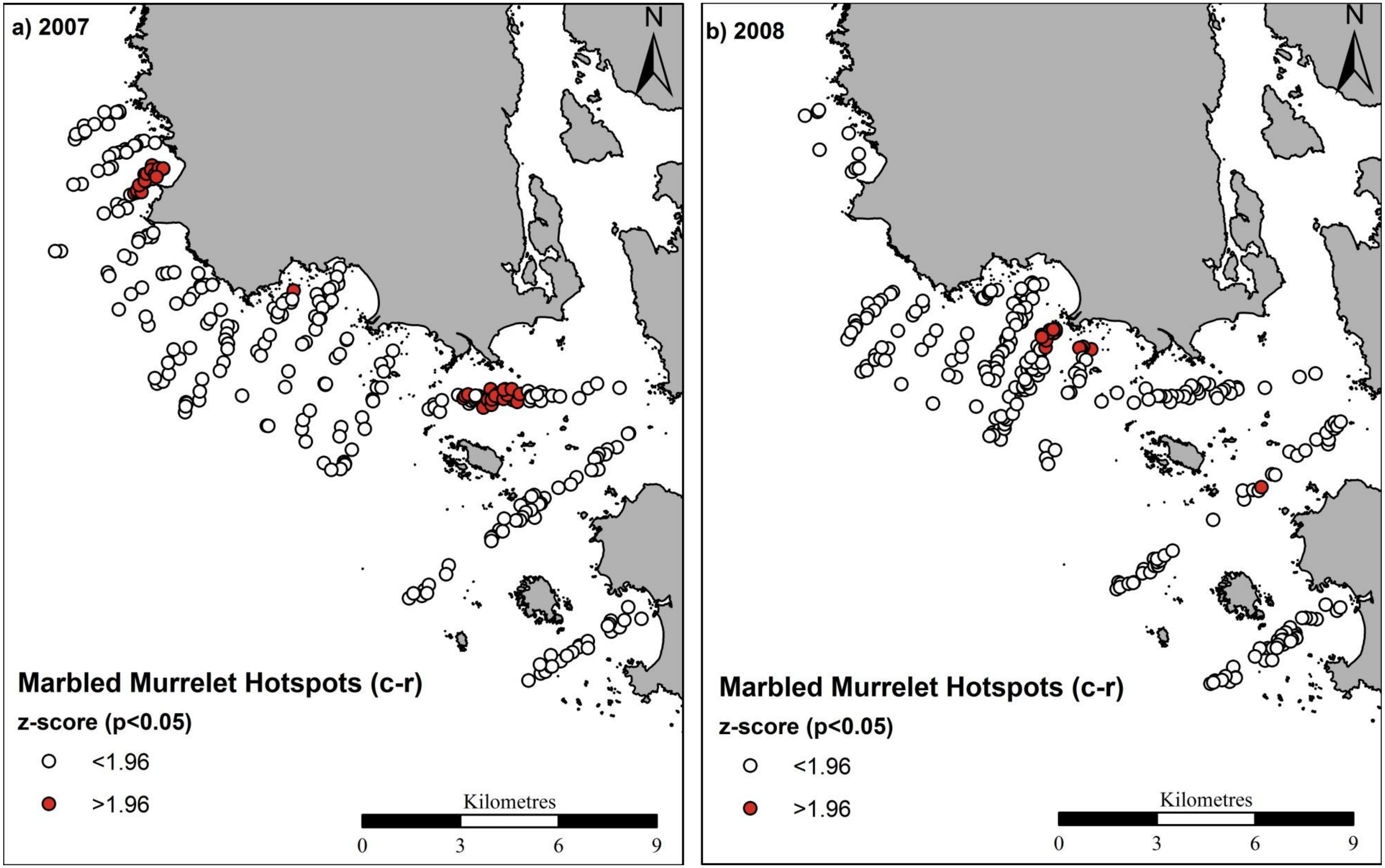


Figure 2.5: Marbled murrelet habitat use hotspots, identified by a Getis-Ord G*i** statistic, during murrelet chick rearing (c-r), in 2007 (a) and 2008 (b). Test statistic critical value is +/- 1.96 at $p<0.05$.

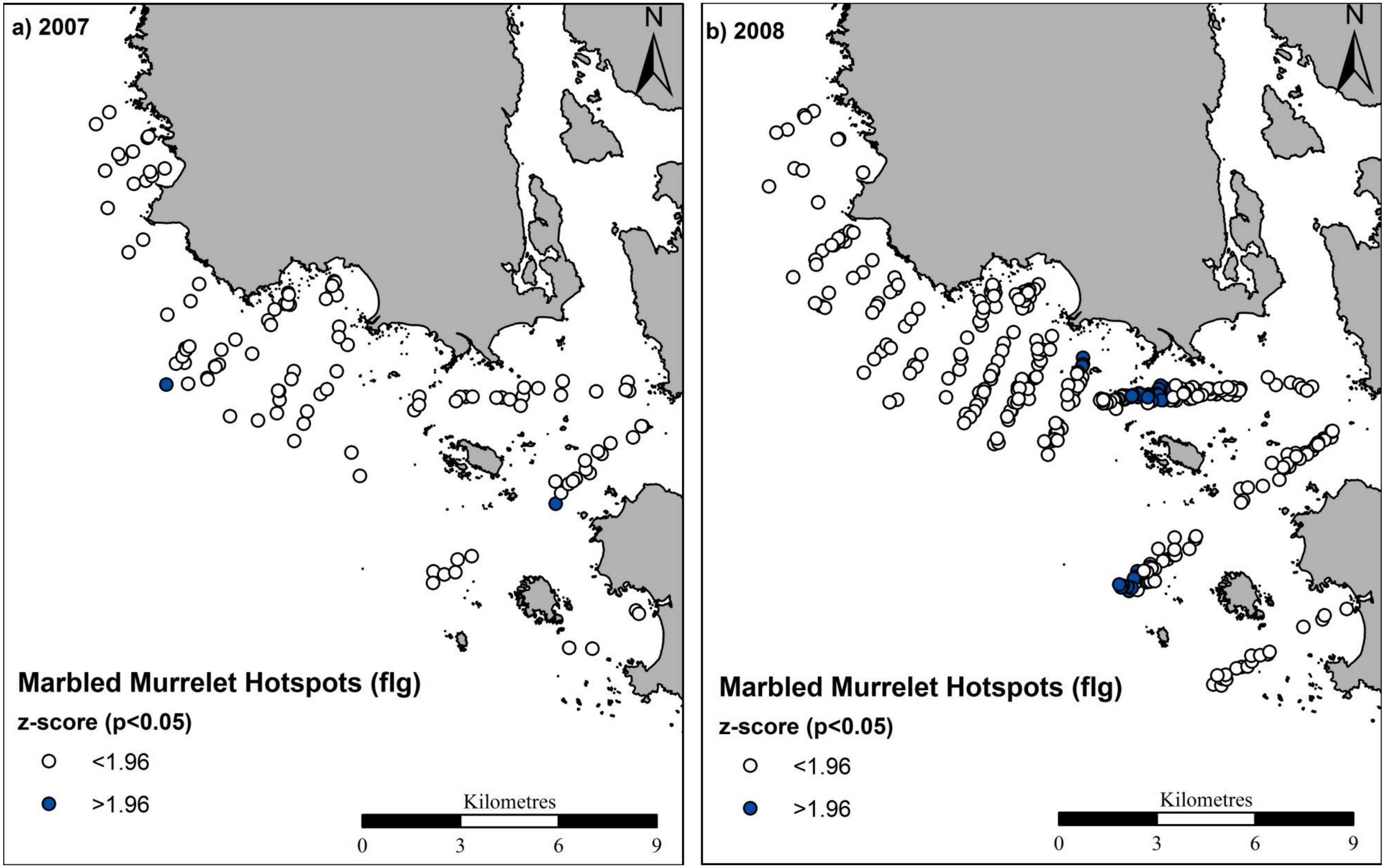


Figure 2.6: Marbled murrelet habitat use hotspots, identified by a Getis-Ord G*i** statistic, once the young are fledged (flg), in 2007 (a) and 2008 (b). Test statistic critical value is +/- 1.96 at $p<0.05$.

Discussion

Similar temporal patterns in marbled murrelet numbers for both field seasons suggest consistent seasonal trends in murrelet abundance in the study area, providing confidence in comparisons of spatial distribution between seasons. Within-season fluctuations were consistent in both seasons, with more individuals during the incubation and chick rearing periods, and declines at the beginning of fledging. In both seasons, the incubation period was marked by fluctuations in total birds observed per survey set, while during the chick-rearing period there were consistently high numbers. This pattern between seasons suggests that coarse scale environmental factors in the study area are not affecting marbled murrelet foraging behaviour.

The lack of spatial autocorrelation given by global Moran's I confirms that significant values found in subsequent measures of local spatial autocorrelation are not influence by global factors (Nelson & Boots 2008). Measures of local spatial autocorrelation found significant hot spots in all temporal categories for both field seasons. Fluctuations were observed in both size and location within- and between seasons. Between season comparisons of murrelet hot spots during incubation show only one instance where clusters were consistent in 2007 and 2008: a single cluster in Dagger Bay (Area 1). During the chick-rearing stage, murrelets in both years remained in habitat close to shore, with hot spots occurring in both years in areas 3, 5 and 7. Habitat use during the fledged stage was more dispersed, with no similarities in hot spot locations between years. This observed between-season variation, combined with similar results in both seasons of total murrelets and seasonal fluctuations, provides evidence that marbled murrelet foraging habitat use at this small scale is not consistent from year to year while the murrelets are subsistence feeding, even though overall murrelet presence is similar. Furthermore, while marbled murrelets are provisioning, habitat use patterns are much more consistent, feeding in nearshore coastal habitat, predominantly in sheltered bays (area 3) and inlets (area 5 and 7). Underlying and seasonally shifting variables in the study area appear to be influencing marbled murrelet habitat use at a local scale; coarse-scale influences cannot be inferred with the fine-scale spatial extent of the data collected.

Within season comparisons in 2007 show substantial shifts from incubation to chick rearing periods, and again from chick rearing to fledged periods, with distribution becoming very dispersed late in the season. Within-season fluctuation was observed in 2008, but with a constant clustering focused around the eastern part of nearshore Cow Bay (area 3) that did not occur in 2007. These results suggest that marbled murrelet habitat use does not remain constant over time, but rather fluctuates substantially as the season progresses. As juveniles hatch, adults no longer forage strictly for themselves, but also make several return trips to the nest with prey for their young. During the chick-rearing period results show that murrelet hot spots were situated closer to shore than those pre- and post-breeding. Breeding marbled murrelets in British Columbia, where nesting sites average 39 km from shore, have been observed foraging closer to shore than non-breeding adults (Lougheed 2000), which allows for energy savings by reducing travel time (Hull *et al.* 2001). Similar studies in northern California, where nesting sites averaged within 10 km from shore, did not have this variation in habitat use between provisioning and non-provisioning time periods (Hebert & Golightly 2008). These variations in foraging behaviour and habitat use patterns of marbled murrelets within their home range depict the need for conservation and management practices to rely not only on population-based studies of marbled murrelets, but also finer-scale, local studies of habitat use and behaviour within their home range, as well as more focused studies not just on population trends but foraging distribution and habitat interactions. Local marbled murrelet nesting habitat on Flores Island and the surrounding area has been found to be concentrated mainly around streams and inlets in valley bottoms with large spruce stands, and is negatively correlated with forest edge with lower tree densities and increased predator abundance (Rodway & Regehr 2002). This habitat type is consistent with the Cow Bay, Dagger Bay and Russell Channel areas of the study area, where the majority of hot spots were identified. Local conservation efforts would be more effective if their practices were based on observations and research conducted at a local scale, as site-specific factors can result in significant variations in foraging behaviour, foraging distribution, and breeding success.

In this study the total number of marbled murrelets observed in the study area was similar from year to year, but their spatial distribution has significant seasonal variation. The next step will be to identify what, if any, oceanographic variables, such as ocean temperature, salinity, and chlorophyll *a*, drive this spatial variation to generate these foraging hotspots.

Literature Cited

Azzalini, A. and N. Torelli. 2007. Clustering via nonparametric density estimation. *Statistics and Computing* 17: 71-80.

BC Conservation Data Centre. 2010. Conservation Status Report: *Brachyramphus marmoratus*. *B.C. Ministry of Environment*. Available: http://a100.gov.bc.ca/pub/eswp/ (accessed September 29, 2010).

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

Bibby, C.J., N.D. Burgess, D.A. Hill and S.H. Mustoe. 2000. *Bird census techniques 2nd edition,* California: Academic Press.

Block, W.M. and L.A. Brennan. 1993. The habitat concept in ornithology: Theory and Applications. In: *Ecology and conservation of the marbled murrelet,* Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, CA: US Forest Service. pp. 385-393.

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

Burger, A.E.1995. Marine distribution, abundance, and habitats of marbled murrelets in British Columbia. In *Ecology and conservation of the marbled murrelet,* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G. and J.F. Piatt (eds.), U.S. Department of Agricultre, Forestry Service General Technical Report PSW-152: 295-312.

Burger, A.E. 2002. Conservation assessment of marbled murrelets in British Columbia: a review of the biology, populations, habitat associations and conservation. *Technical report series No. 387,* Pacific and Yukon Region, BC: Canadian Wildlife Services.

Burkett, E.E. 1995. Marbled murrelet food habits and prey ecology. In *Ecology and conservation of the marbled murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, C.A.: U.S. Forest Service, pp.223-246.

Hebert, P.N. and R.T. Golightly. 2008. At-sea distribution and movements of nesting and non-nesting marbled murrelets *Brachyramphus marmoratus* in northern California. *Marine Ornithology,* 36: 99-105.

Hull, C.L. 1999. Marbled murrelet research in Desolation Sound, British Columbia. *Proceedings of the Biology and Management of Species and Habitats at Risk, Kamloops, BC*: 751-758.

Hull, C.L., Kaiser, G.W., Lougheed, C., Lougheed, L., Boyd, S. and F. Cooke. 2001. Intraspecific variation in commuting distance of marbled murrelets (*Brachyramphus marmoratus*): Ecological and energetic consequences of nesting further inland. *The Auk*, 118(4): 1036-1046.

Hunt, G.L. Jr. 1995. Oceanographic processes and marine productivity in waters offshore of marbled murrelet breeding habitat. In: *Ecology and conservation of the Marbled Murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, C.A.: U.S. Forest Service, pp.223-246.

Hunt, G.L., Russell, R.W., Coyle, K.O. and T. Weingartner. 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series*, 167: 241-259.

Hunt, G.L., Mehlum, F., Russell, R.W., Irons, D., Decker, M.B. and P.H. Becker. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. In: *Proceedings on the 22 International Ornithology Congress,* Adams, N.J. and R.H. Slotow (eds.), Durban: 2040-2056.

Kopach, B.W. 2004. Fine-scale circulation as a component of gray whale (*Eschrichtius robustus*) habitat in Clayoquot Sound, British Columbia. Thesis, University of Victoria, Victoria, B.C., Canada.

Krebs, J.R. and N.B. Davies. 1991. Behavioural ecology: An evolutionary approach, 4th edition. Blackwell Publishing.

Lougheed, C. 2000. Breeding chronology, breeding success, distribution and movements of marbled murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. *Technical report series No. 352*, Canadian Wildlife Service, Pacific and Yukon Region, Delta, BC: 1-89.

Nelson, S.K. 1997. Marbled murrelet (*Brachyramphus marmoratus*). In: *Birds of North America No. 276*, Poole, A. and F. Gill (eds.), Washington, DC: The American Ornithologists' Union. 32p.

Nelson, S.K. and T.E. Hamer. 1995. Nesting Biology and Behaviour of the Marbled Murrelet. *USDA Forest Service General Technical Report PSW-152:* 57-67.

Nelson, T.A. and B. Boots. 2008. Detecting spatially explicit hot spots in landscape-scale ecology. *Ecography,* 31(5): 556-566.

Ralph, C.J., Hunt, G.L., Raphael, M.G., and J.F. Piatt. 1995. Ecology and conservation of the marbled murrelet in North America: an overview. In *Ecology and conservation of the Marbled Murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, C.A.: U.S. Forest Service, pp.3-22.

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

Rodway, M.S. and H.M. Regehr. 2002. Inland activity and forest structural characteristics as indicators of marbled murrelet nesting habitat in Clayoquot Sound. In *Multi-scale studies of populations, distribution and habitat associations of marbled murrelets in Clayoquot Sound, British Columbia*, Burger, A.E. and T.A. Chatwin (eds.), Victoria, B.C.: British Columbia Ministry of Water, Land and Air Protection.

Rosenzweig, M.L. 1985. Some theoretical aspects of habitat selection. In: *Habitat selection in birds*, Cody, M.L. (ed.), Orlando: Academic Press. pp. 517-540.

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, 46: 337-365.

Strachan, G., McAllister, M. & C.J. Ralph. 1995. Marbled murrelet at sea and foraging behaviour. *USDA Forest Service General Technical Report PSW-152:* 247-253.

Thomas, J.W., Franklin, J.F., Gordon, J. and K.N. Johnson. 2006. The Northwest forest plan: Origins, components, implementation experience, and suggestions for change. *Conservation Biology*, 20(2): 277-287.

Chapter 3

Spatial and Temporal Variability in Oceanographic Conditions in a Marbled Murrelet Foraging Area

Introduction

The marbled murrelet spends the majority of its life foraging at sea, and breeding success depends heavily on the quality of prey it acquires from nearshore marine habitat (Burkett 1995). Under the *Species at Risk Act* the marbled murrelet (*Brachyramphus marmoratus*) is listed as "threatened" in Canada, with legal protection under the *Migratory Bird Convention Act* (1994). Population declines in BC (Kelson *et al.* 1995, Kelson & Mather 1999) have been attributed primarily to loss of old-growth nesting habitat, but also oil spills, gill net entanglements (Rodway *et al.* 1992, Kelson *et al.*1995, Ralph *et al.* 1995, Burger 2002), and ocean warming trends (Burger 2000). Food availability has been identified as a probable causal factor in California population declines (Peery *et al.* 2004).

Seabird distribution shares a close association with the distribution of prey in the ecosystem (Fauchald & Erikstad 2002, Becker & Beissinger 2003); in the case of the marbled murrelet, that prey includes planktivorous fish and zooplankton (Sealy 1975). Logistical and financial limitations to this study made it difficult to measure a very dynamic and patchy prey source with any accuracy, and alternative methods had to be explored. Oceanographic processes that influence the patterns of prey distribution and abundance can provide insight into prey dynamics when direct measures are not readily available (Tyler *et al.* 1993). High quality foraging sites can be predicted from recurrent oceanographic processes that drive prey distribution and aggregation in a region (Hunt 1995). Spatial and temporal variability in prey persistence and predictability should be reflected by the distribution patterns of seabirds (e.g. Briggs *et al.* 1987), and examining the scales over which birds aggregate allows us to infer which oceanographic processes are likely to be of trophic importance (Tyler *et al.* 1993), while considering variability in bird distribution and community over a range of temporal and spatial scales (Hunt & Schneider 1987).

Prey biomass is determined by survival, growth, reproduction and aggregation. Temperature and salinity directly influence growth and survival of both phytoplankton and zooplankton (Kalle 1971, Moloney *et al.* 1994, Spivak 1999, Berges *et al.* 2002, Daunt *et al.* 2003) and can be used as indicators of change in water condition over time (seasonal variation) and space (presence of fronts or barriers where prey may accumulate) (Pineda 1991, Daunt *et al.* 2003, Olson *et al.* 1994). Changes in oceanic temperatures, at scales of 100s of kilometres, affect ecosystems in the northeast Pacific (McGowan *et al.* 1998), including British Columbia (Freeland 1992). Ocean temperature fluctuations, due primarily to El Niño events but also resulting from subtle climatic fluctuations, including daylight hours or frequency of winter storms, are known to affect seabird habitat use and fecundity at nest sites (Hatch 1987, Ainley & Boekelheide 1990, Wilson 1991), including reduced breeding success and chick growth in wedge-tailed shearwaters (*Puffinus pacificus*) (Peck *et al.* 2004), degraded body conditions in blue petrels (*Halobaena carulea*) (Guinet *et al.* 1998), and decreased abundance of Atlantic Puffin prey (*Fratercula arctica*) (Durant *et al.* 2003). In 2005, anomalous atmospheric-oceanographic coupling in central California and southern British Columbia, causing poor upwelling-favourable winds and unusually warm sea-surface temperatures, resulted in unprecedented reproductive failures and redistribution of Cassin's Auklets (*Ptychoramphus* *aleuticus*) including complete abandonment of their breeding colony and only 8% nest success in British Columbia (Sydeman *et al.* 2006).

The effects of temperature fluctuations on marbled murrelet populations are not well understood. Murrelet prey, small schooling fish (Carter 1984) and invertebrates such as euphausiids (Burkett 1995), may be affected by temperature changes resulting in altered habitat use patterns (Ainley *et al.* 1995, Ralph *et al.* 1995). Research also suggests a negative relationship between marbled murrelet at-sea habitat use and rising oceanic temperature (Speckman *et al.* 2000). Transect counts of murrelets at 5 sites in British Columbia, sampled over 4 – 8 years at each site between 1979 and 1998, identified negative trends between murrelet abundance and temperature occurring at 3 sites, with statistical significance at 1 site. (Burger 1999).

Large oceanic currents determine regional marine habitat types and are responsible for a major portion of the seasonal variation in production on the coastal shelf of B.C. (Hunt 1995). However, marine waters within a few kilometres of the shore are the primary foraging habitats of marbled murrelets (Hunt 1995). In these areas, currents interacting with bathymetry can create upwelling that either enhances productivity, or causes organisms to accumulate because of behavioural responses to a physical gradient (Thomson 1981), and provide foraging sites for seabirds (Hunt 1995). In coastal waters, strong winds cause upwelling through the displacement of water near the coast by winds blowing parallel to the coastline and the displaced water is replaced by colder, nutrient rich water from depth (Price *et al.* 1987, Crawford & Thomson 1991). Along the open coast in areas such as British Columbia, these localized nearshore upwelling events provide regions of increased primary and secondary productivity and are expected to be the most important physical features in determining murrelet foraging opportunities (Hunt 1995). In Clayoquot Sound, ocean currents along the south and west coasts of Flores Island combined with strong tidal forces and freshwater inputs result in strong current velocities and converging fronts that promote phytoplankton upwelling and influence the distribution of invertebrates in the shallow nearshore marine environment (Kopach 2004).

The trophic linkages between elevated levels of primary productivity and increased zooplankton biomass are well known (Mackas *et al.* 1980, Durbin *et al.* 2003) as is the importance of these linkages to higher level predators such as seabirds (Hay 1992, Hunt 1995, Burger *et al.* 1997, Becker & Beissinger 2003, Burger 2003). The majority of abundant marine bird species on the west coast of Vancouver Island are either planktivorous or feed on small planktivorous fish (Mackas & Galbraith 1992) that are spatially influenced by phytoplankton density and distribution. The physical oceanographic processes controlling this primary production in the fjords and shallow coastal regions of British Columbia are highly seasonal, and in deeper fjords and sills the trophic pathways often include large net phytoplankton (primarily diatoms), large copepods, and finfish (Matthews & Heindel 1980) that are important prey for the small fish taken by marbled murrelets (Hunt 1995).

Studies of foraging patterns and behaviour in different regions, however, show varying results and demonstrate the high variability in marbled murrelet foraging behaviour and habitat use (Burkett 1995). To properly analyze and identify important foraging habitat of marbled murrelets in Clayoquot Sound, oceanographic and environmental conditions in areas where they forage must first be examined as to the impact they may have. Here I describe the spatial and temporal variation in ocean conditions in a marbled murrelet foraging habitat by examining ocean temperature, salinity, and chlorophyll *a* (chl *a*) levels.

Methods

Study Area

Clayoquot Sound occupies a straight-line distance of 90 kilometres along the west coast of Vancouver Island between Long Beach and Nootka Sound. The area reaches up to 35 kilometres inland, comprising 265,000 hectares of land and 85,000 hectares of narrow Pacific Ocean inlets. Data were collected in the area between Dagger Bay to the north and Ahous Bay to the south, including surveys out to 4-5 kilometres from the shoreline (Figure 3.1). The study area includes shallow and exposed rock reefs, sand and mud bays, and boulder and rock beds. Water depths range from 0 to 35 metres. The marine environment in Clayoquot Sound, and particularly that around Flores Island, is considered highly turbid with strong currents around the headlands and weaker flow in the bays. Flow direction is relatively constant in a northwest - southeast direction, and controlled by local bathymetry and tidal effects.

Data Collection

Measurements of temperature and chl *a* levels were made at 41 sampling stations in 2007 (Figure 3.2), and temperature, salinity, and phytoplankton levels at 9 sampling stations in 2008 (Figure 3.3). Sample sites for 2007 were chosen and measured as part of a second oceanographic study being conducted in the area. In 2008, sample sites were reduced, and their locations altered in order to attain better coverage of the study area while being logistically more efficient. At each sampling station, a Sea-Bird 19plus profiler CTD (Conductivity, Temperature, Depth) fitted with a “Wet-Labs” (ECO-AFL) fluorometre was deployed. CTD casts recorded physical and biological oceanographic variables: depth, temperature, salinity (2008 only) and chlorophyll *a* via fluorescence. Vertical profiles of temperature, salinity and chlorophyll *a* fluorescence were collected for the entire water column at each station. At each station, the CTD was lowered to the bottom at a freefall rate of approximately 1 m/s. Data from the downcast were used in the analysis, with measurements taken every 0.25 seconds. Accuracy of the Sea-Bird 19plus is 0.005˚C (range 5 to 35˚C), 0.0005 S/m (translates to 0.0048 psu) and 0.6m (resolution = 0.012m) (Sea-bird Electronics 2001). Fluorescence measurements, presented as chlorophyll *a* density, represent relative chlorophyll *a* concentrations as they were not calibrated against extracted chlorophyll *a* samples from the study area. A total of 16 full surveys and 1 partial survey were completed in 2007, and 8 full surveys and 1 partial survey were completed in 2008 (Table 3.1).

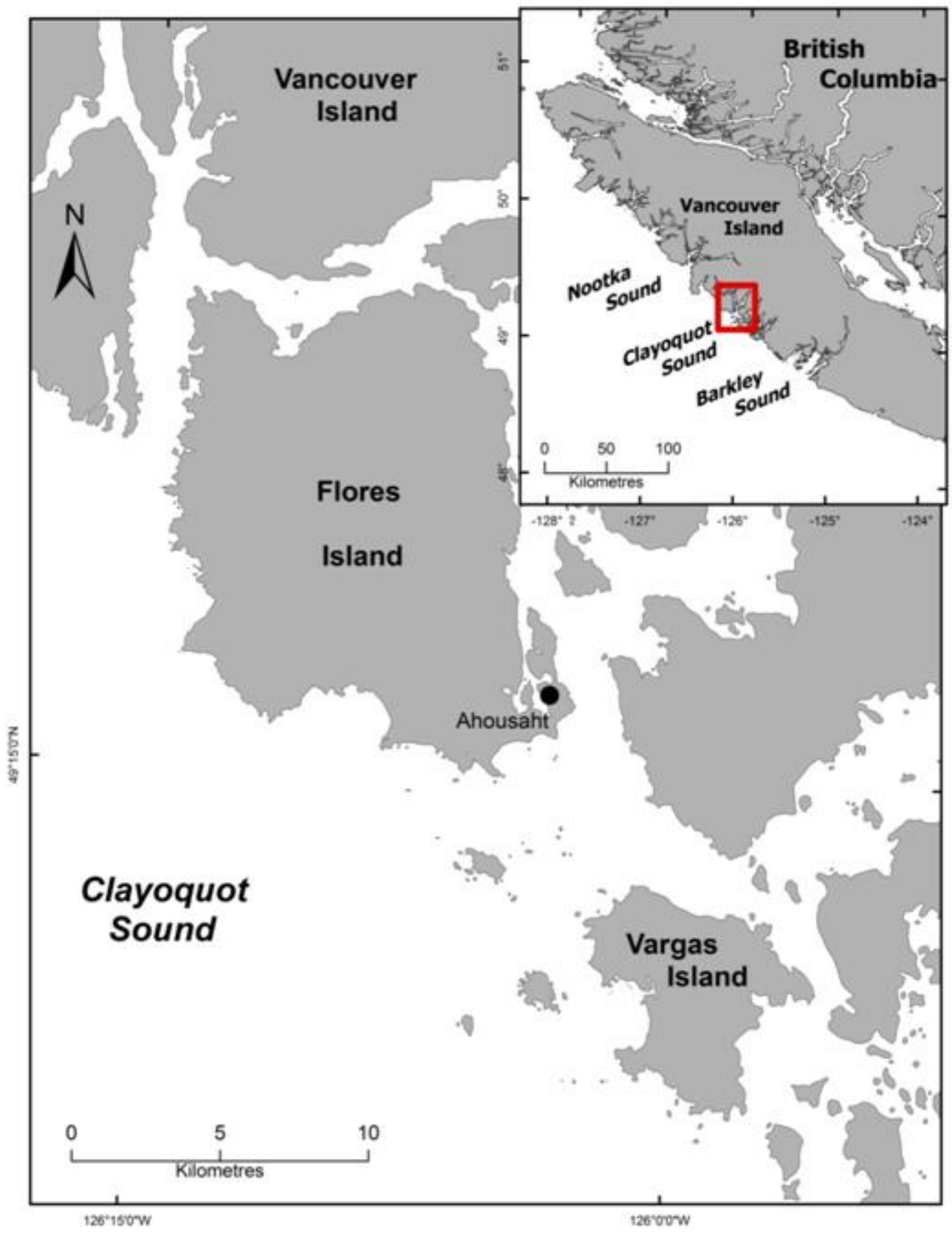


Figure 3.1: Study area along the west coast of Vancouver Island.

Data Analysis

CTD/fluorometre data were processed using Sea-Bird Electronics data processing software package version 5.31a (Sea-Bird Electronics, Inc. 2001). Initial data processing included the removal of all data points associated with priming of the water pump (first 45 seconds of analysis, or 180 samples). Data points were consolidated into 1 metre segments. For statistical analysis, all full surveys were analyzed separately to examine spatial variation within the study area, and pooled over sampling days to analyze within- and between-season variation. Mean chl *a*, temperature and salinity levels in the upper 12 metres of the water column, the depth at the shallowest site, are used for all statistical tests. Salinity data is analyzed in 2008 only, as data from 2007 was unavailable.

Data were pooled into 3 temporal categories, based on behavioural observations conducted during marbled murrelet surveys: incubation (inc), chick-rearing (c-r), and fledged (flg) (Table 3.1). Incubation refers to all data collected before hatching, when adults are foraging strictly for subsistence. Chick-rearing includes data collected between the time that juveniles are born and fledged, when adults are provisioning for their young. The beginning of this stage was determined when adults carried prey at the surface to transport to the nest. Fledged includes all data collected after juveniles appeared in the study area, identified by their plumage.

Finally, comparisons are presented between marbled murrelet spatial and temporal abundance (Chapter 2) and variability in CTD data, both within and between seasons, to identify any potential influence oceanographic conditions may exert on murrelet habitat use in the study area.

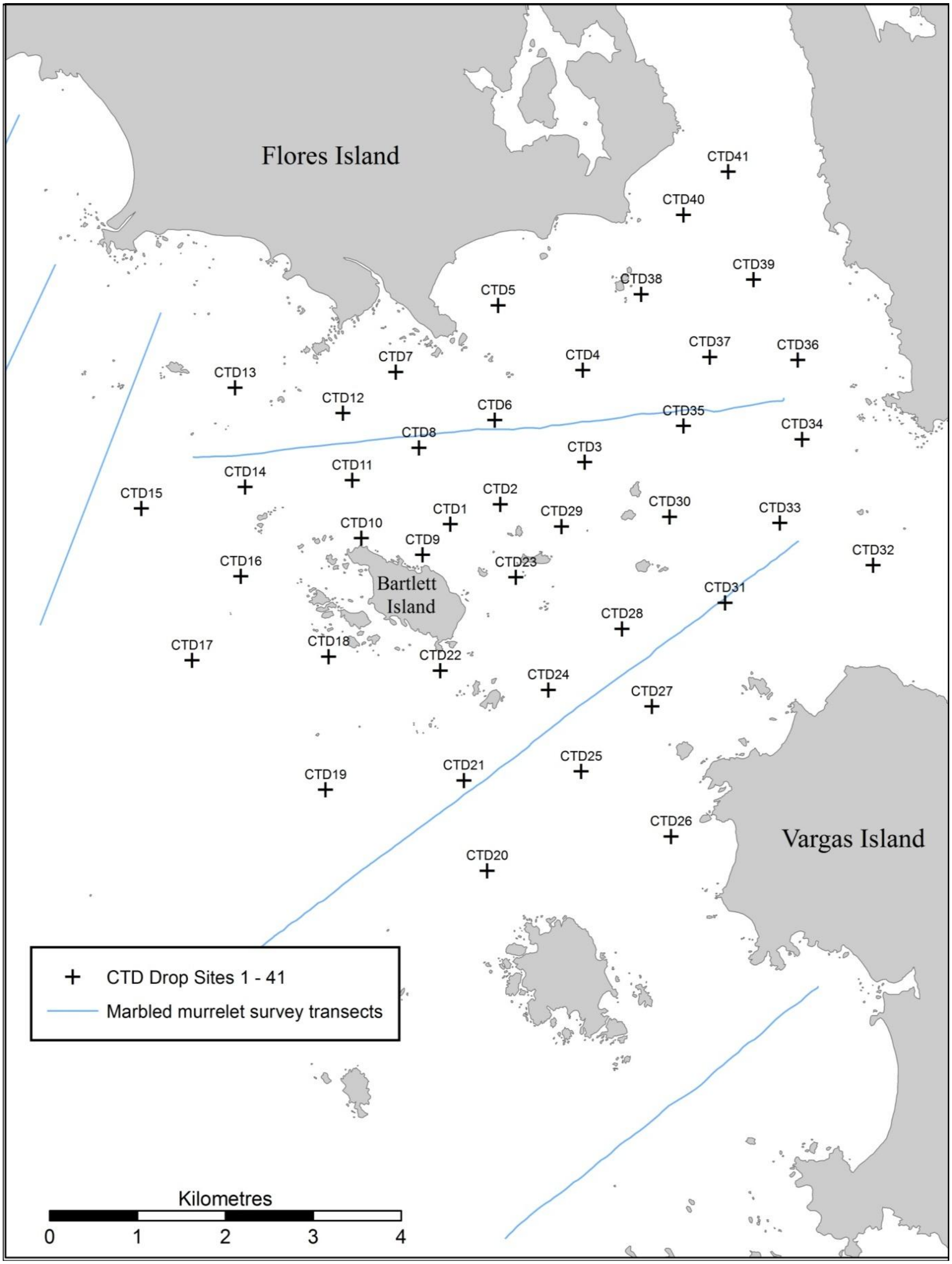


Figure 3.2: CTD drop sites sampled in 2007

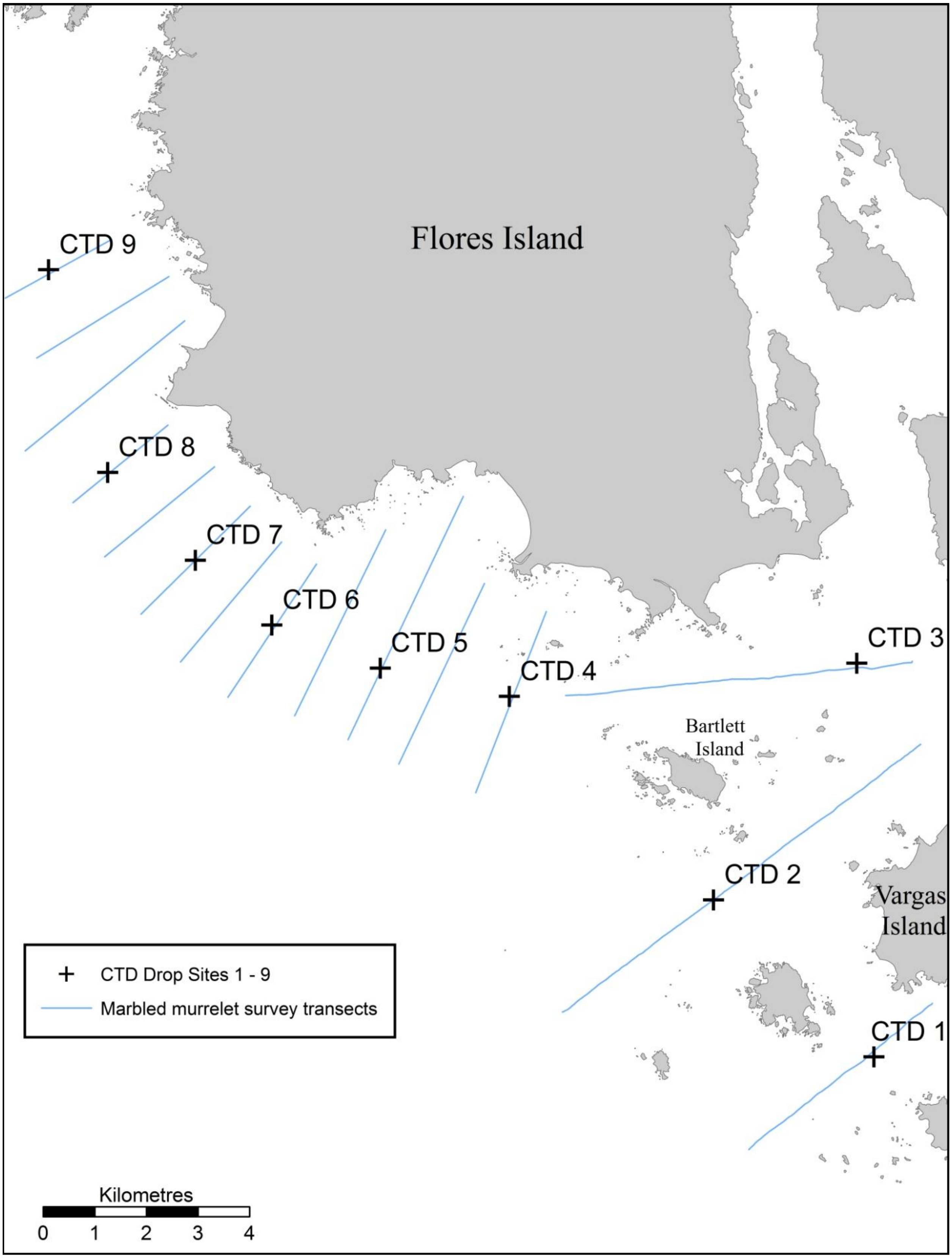


Figure 3.3: CTD drop sites sampled in 2008.

Table 3.1: CTD sampling timeline; each survey consists of 41 sampling stations in 2007 and 9 sampling stations in 2008. Surveys are grouped temporally into 3 categories: Incubation (Inc.), Chick-rearing (C-R) and Fledged (Flg).

Survey Number	**Date**	**Chick-rearing Stage**
1	May 26, 2007	Inc
2	June 03, 2007	Inc
3	June 13, 2007	Inc
4	June 22, 2007	C-R
5	June 25, 2007	C-R
6	July 04, 2007	C-R
7	July 07, 2007	C-R
8	July 14, 2007	C-R
9	July 16, 2007	C-R
10	July 25, 2007	C-R
11	July 29, 2007	Flg
12	August 09, 2007	Flg
13	August 12, 2007	Flg
14	August 21, 2007	Flg
15	August 25, 2007	Flg
16	August 30, 2007	Flg
17	May 29, 2008	Inc
18	June 09 - June 12, 2008	Inc
19	June 17 - June 18, 2008	C-R
20	June 27 - July 01, 2008	C-R
21	July 11 - July 16, 2008	C-R
22	July 24 - July 25, 2008	Flg
23	July 31 - August 03, 2008	Flg
24	August 31 – September 02, 2008	Flg

Results

Spatial Variation

Spatial variation in mean temperature was minimal in both years of study. Mean values are plotted across each sampling station, aggregated into three chick-rearing stages for 2007 (Figure 3.4 a-c) and 2008 (Figure 3.4 d-f). Results from an analysis of variance (ANOVA) at $p<0.05$ for all stations in each category show no significant differences (Table 3.2).

Table 3.2: Results of Analysis of Variance for Water Temperature for all sampling stations, aggregated into incubation (inc), chick-rearing (c-r) and fledged (flg) time categories.

Water Temperature (˚C)							
Season	Chick-rearing Stage	n	x	sd	df	f	p
2007	Inc	113	10.4435	0.393144	40	1.069	0.395
	C-R	283	12.33571	0.791376	40	0.136	1.000
	Flg	244	13.03587	0.681488	40	0.630	0.958
2008	Inc	18	9.378841	0.393487	8	0.656	0.718
	C-R	27	9.645815	0.530755	8	1.966	0.111
	Flg	27	11.12188	0.73513	8	0.274	0.966

Spatial variation in mean salinity was also minimal. Mean values are plotted across each sampling station, aggregated into three time categories for 2008 (Figure 3.5). Results from ANOVA for all stations in each category show no significant differences (Table 3.3).

Table 3.3: Results of Analysis of Variance for Water Salinity for all sampling stations, aggregated into incubation (inc), chick-rearing (c-r) and fledged (flg) time categories.

Salinity (psu)							
Season	Chick-rearing Stage	n	mean	sd	df	f	P
2008	Inc	18	34.27736	0.471666	8	2.943	0.064
	C-R	27	34.61331	0.432092	8	1.058	0.432
	Flg	27	35.63431	0.47191	8	0.697	0.690

Mean chlorophyll *a* concentrations exhibited no significant spatial variation. Mean values are plotted across each sampling station, aggregated into three time categories for 2007 (Figure 3.6 a-c) and 2008 (Figure 3.6 d-f). Results of ANOVA for all stations in each category show no significant differences (Table 3.4).

Table 3.4: Results of Analysis of Variance for chl *a* density for all sampling stations, aggregated into incubation (inc), chick-rearing (c-r) and fledged (flg) time categories.

chl *a* (mg/L)							
Season	Time Category	n	mean	sd	df	f	p
2007	Inc	113	5.577874	1.652427	40	0.559	0.976
	C-R	283	3.423489	2.517179	40	0.799	0.801
	Flg	244	4.532329	2.608506	40	0.943	0.572
2008	Inc	18	6.282872	2.50798	8	0.286	0.954
	C-R	27	7.687144	4.166927	8	0.532	0.817
	Flg	27	11.78468	12.37613	8	0.068	1.000

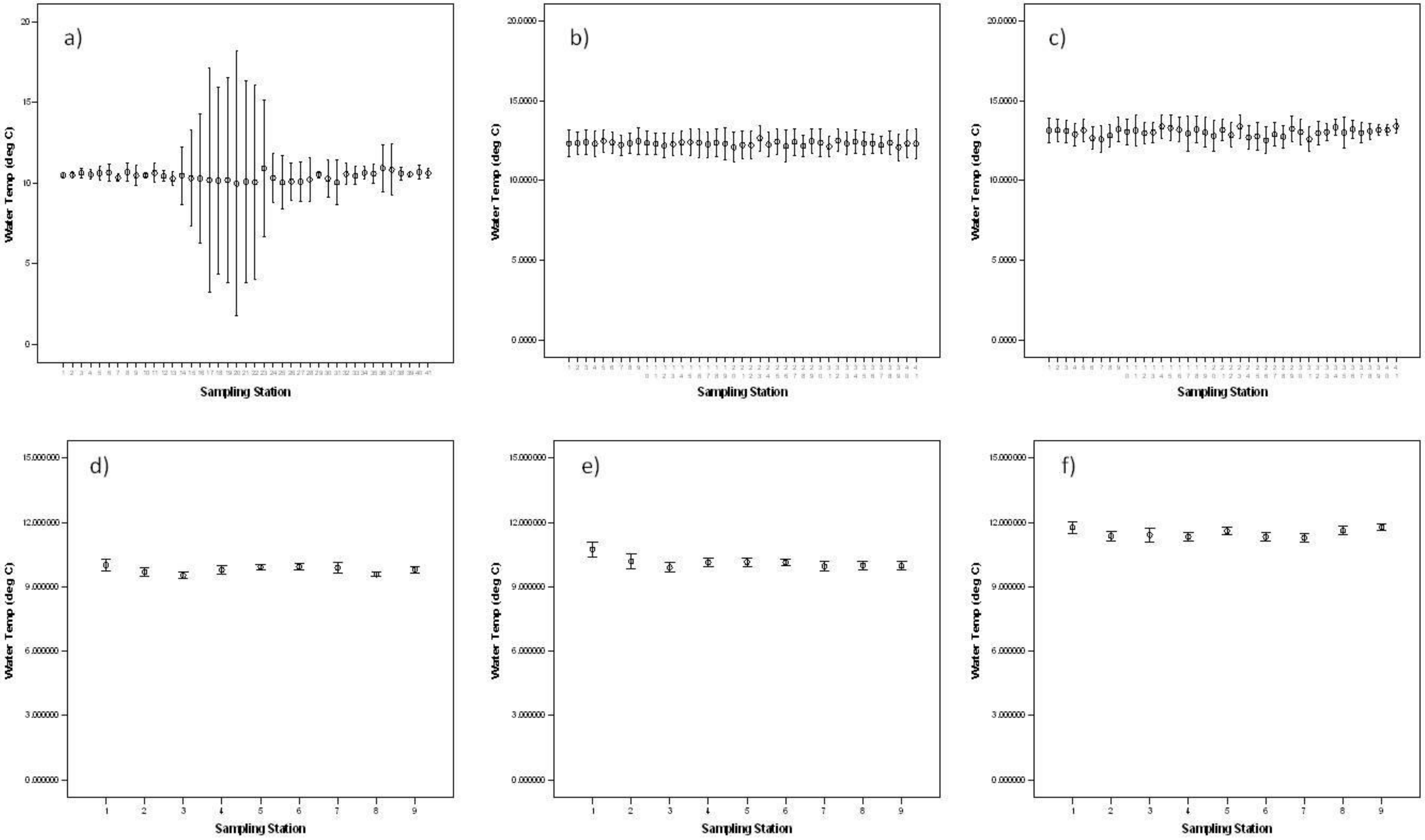


Figure 3.4: Mean water temperature, measured through the water column at 41 stations in 2007 (a-c) and 9 stations in 2008 (d-f). Bars delineate +/-1 standard error. Data grouped by chick-rearing stage; inc (a,d), c-r (b,e), and flg (c,f).

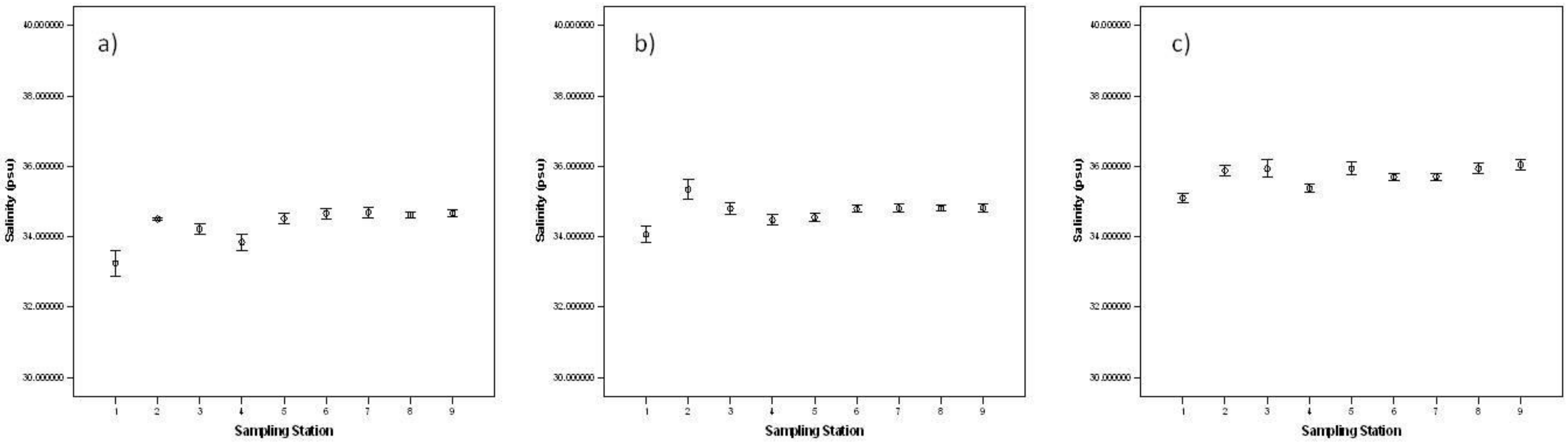


Figure 3.5: Mean water salinity, measured through the water column at 9 stations in 2008, grouped by chick-rearing stage; inc (a), c-r (b), and flg (c). Bars delineate +/-1 standard error.

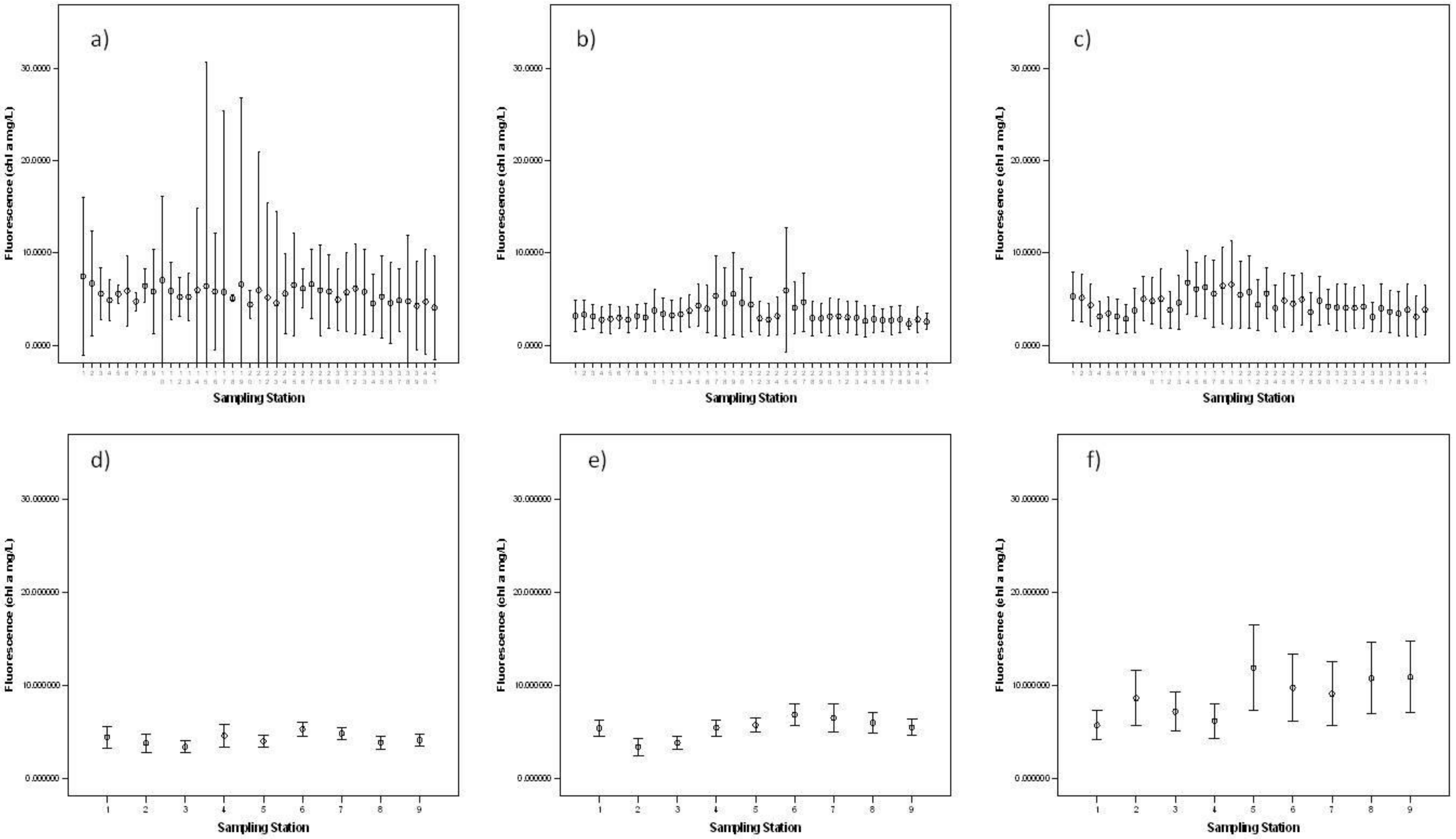


Figure 3.6: Mean chl *a* density, measured through the water column at 41 stations in 2007 (a-c) and 9 stations in 2008 (d-f). Bars delineate +/-1 standard error. Data grouped by chick-rearing stage; inc (a,d), c-r (b,e), and flg (c,f).

Temporal Variation

Mean water temperature values of all stations are plotted across survey dates for 2007 and 2008 surveys, depicting an upward trend in water temperatures between May 26 and August 30, 2007 (range: 5.3962) and May 29 and August 31, 2008 (range: 3.5270) (Figure 3.7). A one-way ANOVA found significant temporal variation in 2007 (n = 640, df = 15, f = 325.891, p = 0.000) and in 2008 (n = 72, df = 7, f= 52.920, p = 0.000). Tukey's multiple comparison test points to a gradual upward trend in temperature: in 2007 surveys 1, 2 and 3 were similar in mean, surveys 6, 8, 9, 10, 11, 12, 15 and 16 were similar in mean, and surveys 4, 5, 7, 13 and 14 were each significantly different from all others. In 2008 surveys 1, 2, 3 and 5 were similar in mean, surveys 4, 6 and 8 were similar in mean, and survey 7 was significantly different from all others.

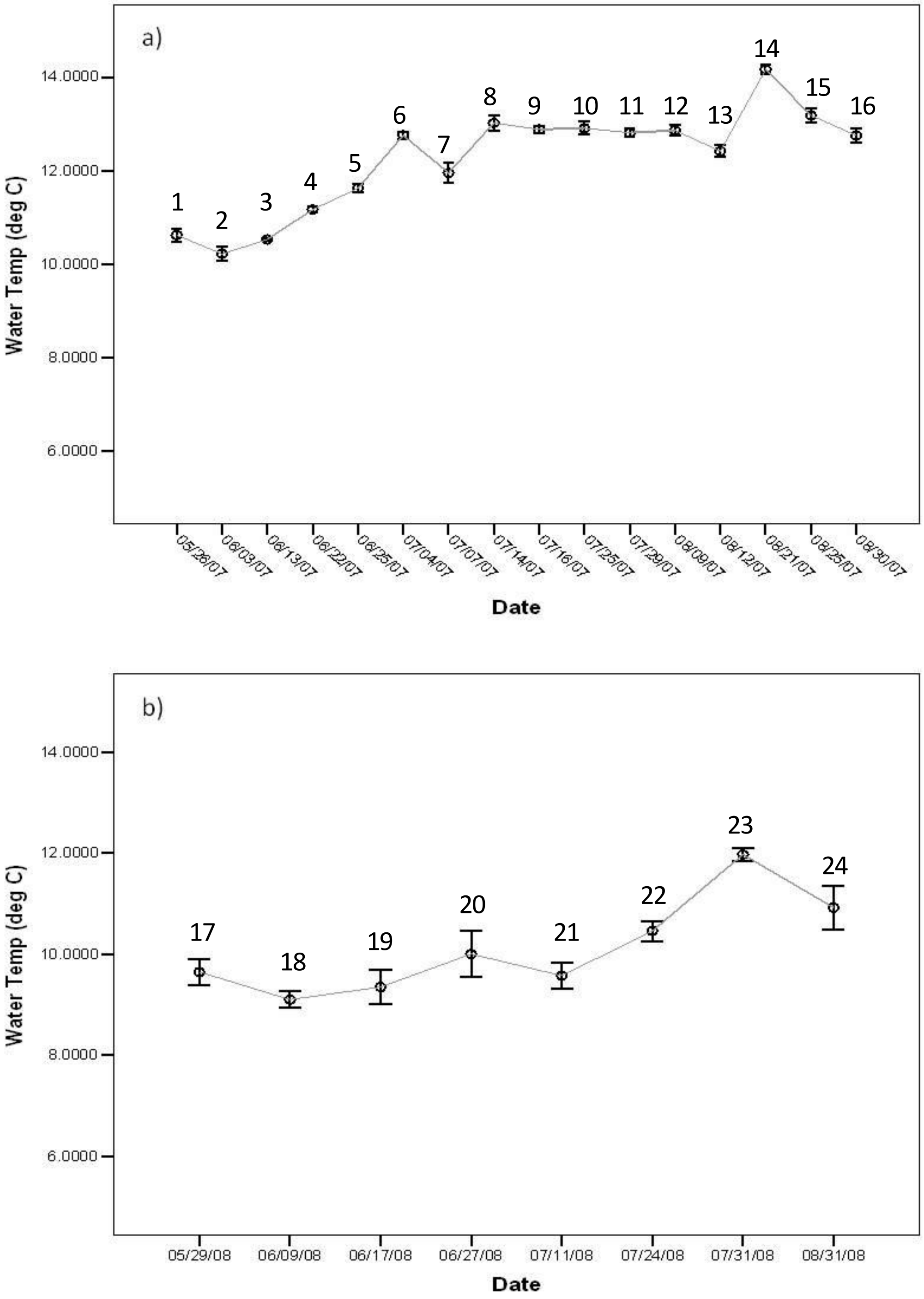


Figure 3.7: Mean water temperature of all sampling stations in 2007 (a) and 2008 (b). Bars delineate +/-1 standard error.

Mean water salinity values of all stations are plotted across survey dates for 2008 surveys, depicting a slight upward trend in salinity levels May 29 and August 31, 2008 (range: 4.1668) (Figure 3.8). A one-way ANOVA found significant temporal variation (n = 72, df = 7, f = 30.828, p = 0.000). Tukey's multiple comparison test shows a gradual upward trend in temperature; surveys 1, 2, and 3 were similar in mean, surveys 4, 5 and 8 were similar in mean, and surveys 6 and 7 were similar in mean.

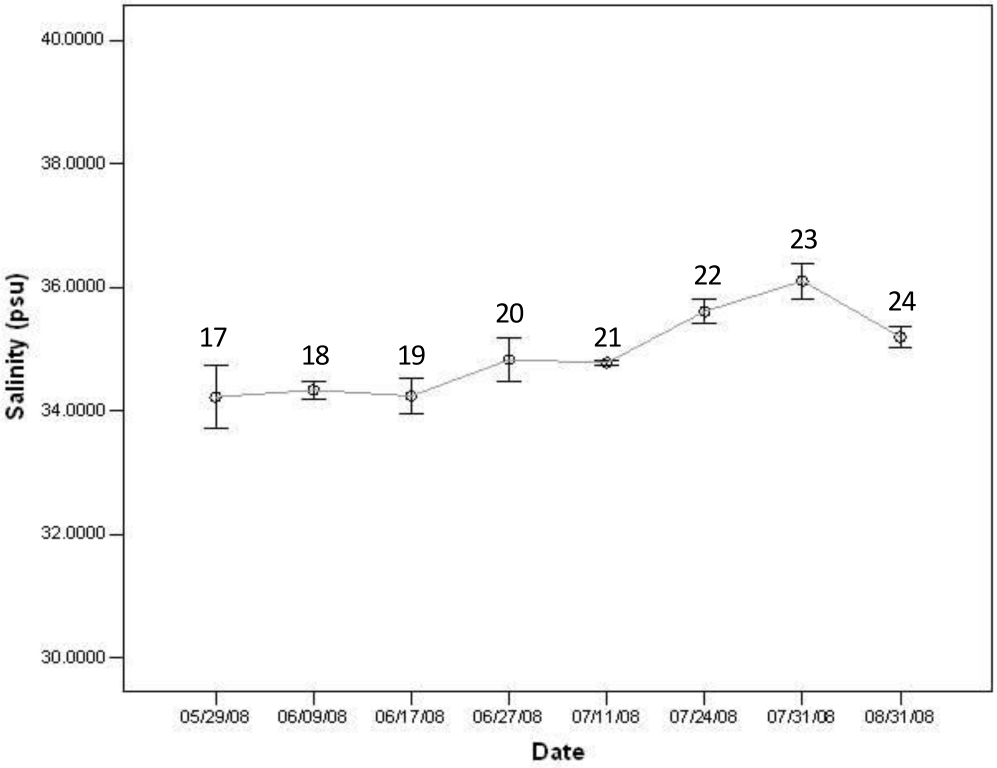


Figure 3.8: Mean water salinity of all sampling stations in 2008. Bars delineate +/-1 standard error.

Mean chl *a* values of all stations are plotted across survey dates for 2007 and 2008 surveys, depicting a rising and falling trend in chlorophyll *a* densities between May 26 and August 30, 2007 (range: 21.2183) and more prominent rising and falling between May 29 and August 31, 2008 (range: 36.2678) (Figure 3.9). A one-way ANOVA found significant temporal variation in 2007 (n = 640, df = 15, f = 66.512, p = 0.000) and in 2008 (n = 72, df = 7, f = 59.960, p = 0.000). Tukey's multiple comparison test points shows a series of peaks and troughs. In 2007 surveys 6, 7, 10 and 13 were similar in mean, surveys 9 and 15 were similar in mean, surveys 11 and 14 were similar in mean, surveys 1, 3, and 5 were similar in mean, surveys 2 and 8 were similar in mean, and survey 4 and survey 12 were both significantly different from all others. In 2008 surveys 2, 4 and 8 were similar in mean, surveys 1, 3, 5 and 7 were similar in mean, and survey 6 was significantly different from all others.

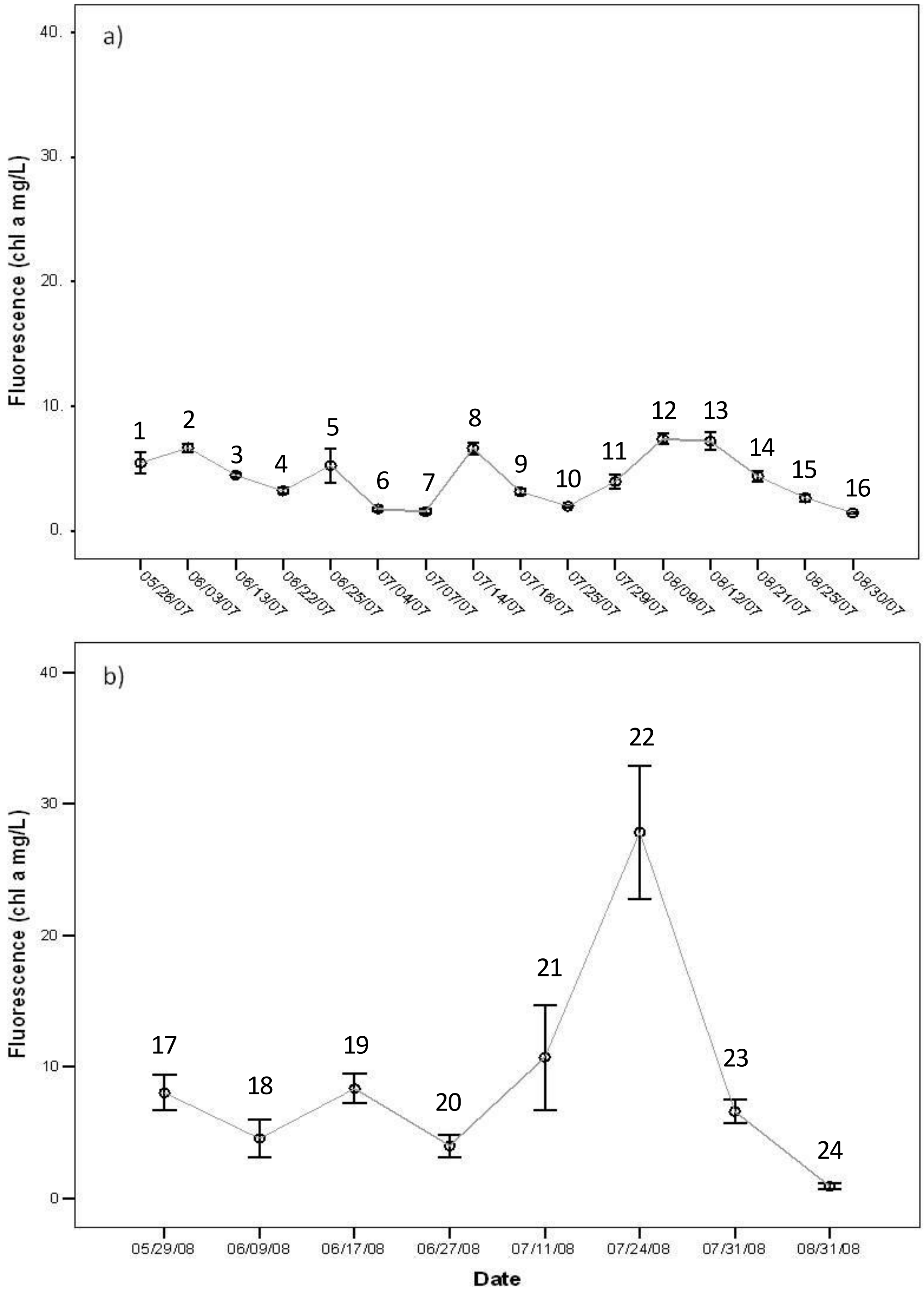


Figure 3.9: Mean chl *a* density of all sampling stations in 2007 (a) and 2008 (b). Bars delineate +/-1 standard error.

To examine temporal correlations between fluctuations in marbled murrelet abundance and CTD measures in the study area, data is plotted over the field season for 2007 and 2008, comparing patterns between marbled murrelet presence and temperature, salinity and chl *a* density. When compared with ocean temperatures, averaged by survey set, in both 2007 and 2008, and average salinity in 2008, no discernible pattern is present between fluctuating values of murrelets and temperature or salinity (Figure 3.10, 3.11). Comparison of temporal fluctuations in marbled murrelet abundance and chl *a* densities also revealed no correlating patterns in either year, with similar trends in marbled murrelet abundance in both years, but different patterns emerging in chl *a* levels in each year (Figure 3.12, 3.13).

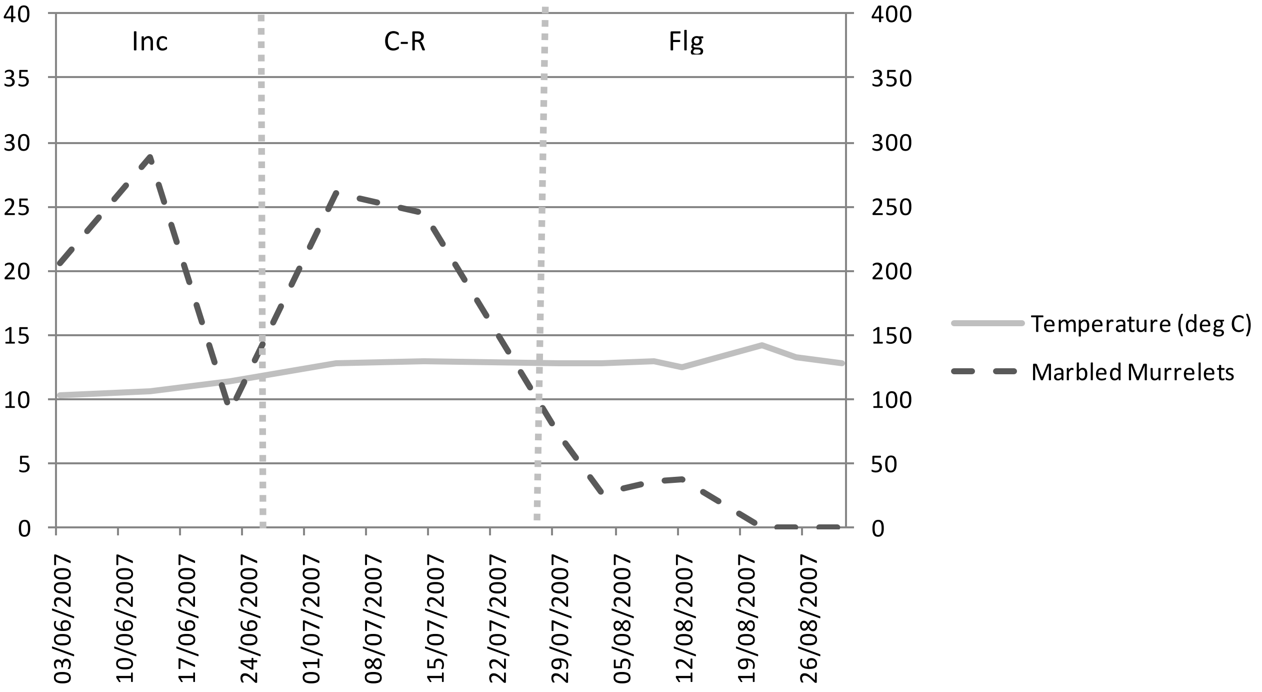


Figure 3.10: Average temperature trends compared with number of marbled murrelets observed over the 2007 field season.

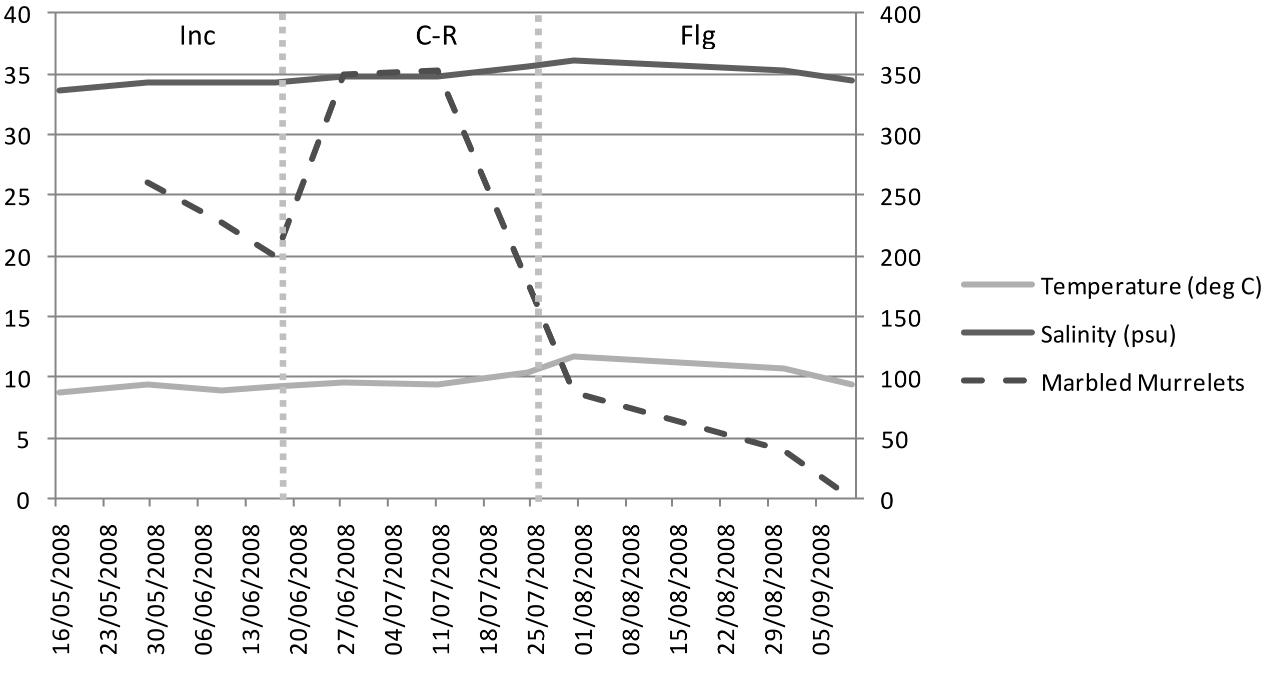


Figure 3.11: Average temperature and salinity trends compared with number of marbled murrelets observed over the 2008 field season.

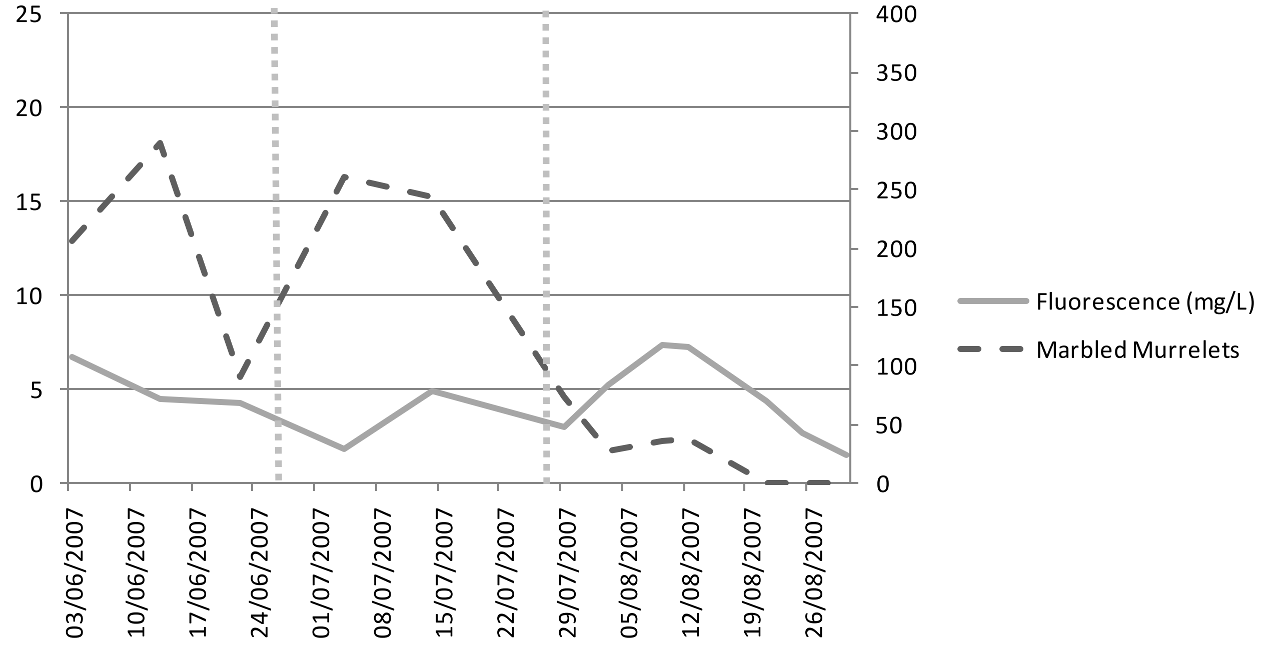


Figure 3.12: Average chl *a* trends compared with number of marbled murrelets observed over the 2007 field season.

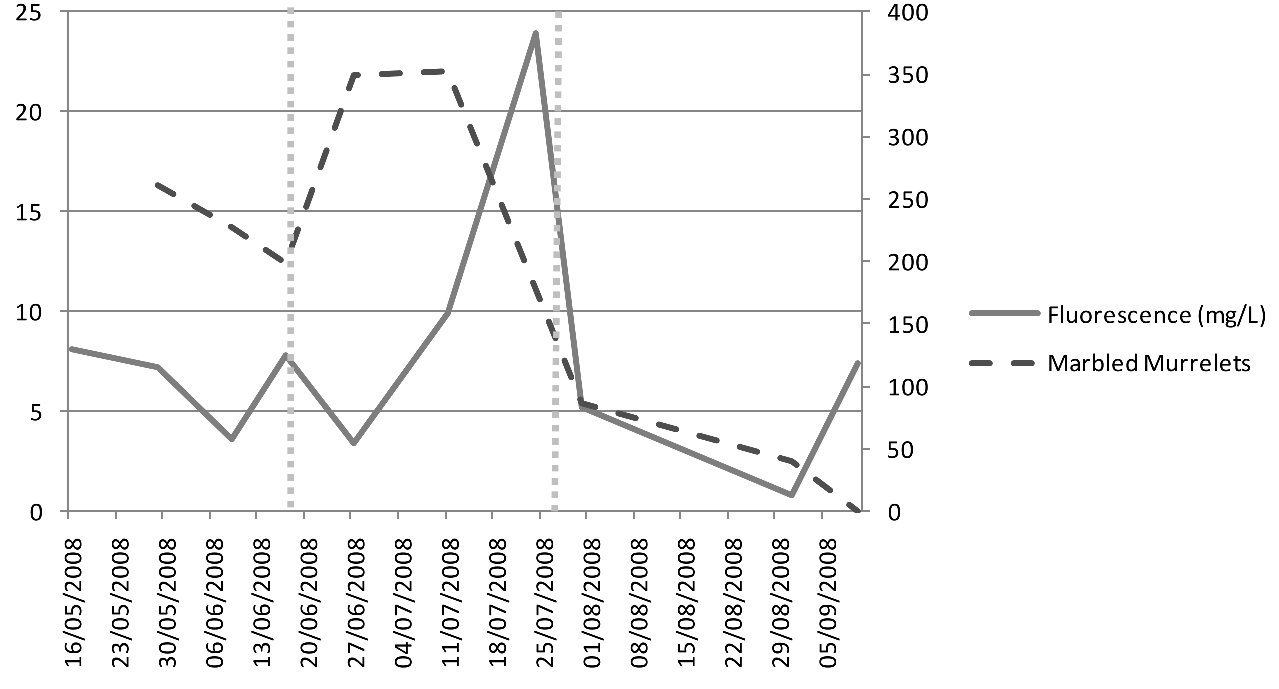


Figure 3.13: Average chl *a* trends compared with number of marbled murrelets observed over the 2008 field season.

Discussion

In both 2007 and 2008, variables measured in the study area showed no significant variation between sampling stations in all three time periods. These results suggest that, within the Clayoquot Sound study area, ocean temperature, water salinity and chlorophyll *a* densities are spatially ubiquitous. Due to this lack of clustering, these factors do not play a significant role in driving marbled murrelet habitat use within the study area, at levels that can be measured here.

The overall trend of consistent water temperature over both field seasons follows an expected trend during the summer of surface warming due to longer days and more intense insolation with fewer storms. Salinity also followed a similar trend in 2008. When compared with temporal fluctuations in marbled murrelet presence within the study area for 2007 (Figure 3.10) and 2008 (Figure 3.11), neither variable illustrates a correlation in temporal variance, suggesting that seasonal trends in coastal ocean temperature and salinity do not affect marbled murrelet foraging presence in the study area. Though studies have found a negative relationship between the at-sea presence of marbled murrelets and rising ocean temperatures (Burger 1999, Speckman *et al.* 2000), they are conducted over large areas with few sampling sites and insufficient samples collected to conduct any statistical testing (e.g. Burger 1999). Data in this study, collected more rigorously over a smaller area, was not subject to variations in coarser ocean conditions during the two years of study.

Chl *a* densities show similar trends in 2007 and 2008, with higher overall densities in 2008. In both season, chl *a* densities progressed through a series of peaks and troughs, representing productivity blooms that are characteristic of the area (Kerr 2005). As the phytoplankton blooms are taken up into the system, chl *a* levels drop. When compared with temporal fluctuations in marbled murrelet presence in 2007 (Figure 3.13) and 2008 (Figure 2.14), marked differences in the timing of chl *a* peaks between 2007 and 2008, especially the late-summer bloom that is evident near 12 August 2007 and 05 September 2008, are not reflected in the presence of marbled murrelets in these years. This would suggest that phytoplankton densities are not having an effect on marbled murrelet abundance in the study area, and other factors must be influencing marbled murrelets to forage in the study area.

A similar trend in marbled murrelet presence over the course of both field seasons suggests a pattern in the foraging behaviour of the murrelets of the Clayoquot Sound area. This pattern appears to be more closely tied to breeding stages than oceanic and habitat conditions, seen with the rise in attendance that coincides with the need to provision their young (after 17 June 2007 and 19 June 2008) followed by a significant decline in attendance following the fledging of their young (after 13 July 2007 and 11 July 2008). While significant fluctuations in chl *a* density did occur during both years of study, these fluctuations do not appear to alter the temporal pattern of marbled murrelet habitat use within the Clayoquot Sound study area. This, combined with the ubiquitous spatial distribution of primary productivity in this area suggests that prey is the driving influence affecting the spatial distribution of marbled murrelets in Clayoquot Sound, and ocean temperature, salinity and phytoplankton densities do not fluctuate, spatially or temporally, at a level that is sufficient to identify ideal foraging habitat.

Oceanographic measurements of temperature, salinity and primary productivity collected during this study were unable to serve as alternatives to direct measures of prey distribution when identifying important foraging habitat for the marbled murrelet. The consistent within-season use of this habitat in both years, combined with a spatial homogeneity in primary productivity, provides the potential for a large prey base from which the murrelets can feed.

Due to the extent of logging that has occurred in both Nootka Sound to the north and Barkley Sound to the south, which restricts nesting habitat, the marine coastline of Clayoquot Sound, next to which terrestrial nesting habitat abounds, provides forage for a large number of murrelets, and the impacts of a natural or anthropogenic disaster, such as the Nestucca oil spill that killed approximately 56,000 seabirds off Vancouver Island and northern Washington in 1988-89 (Burger 1992), could have a profound impact not only in direct mortality, but in degradation of coastal marine and estuarine habitat. Further studies of prey distribution and abundance in the nearshore marine environment are necessary to understand the underlying forces that drive marbled murrelet distribution, aggregation, behaviour and survival across their entire home range. However, at the same time extenuating factors must also be considered that may influence distribution and behaviour under locally based circumstances, such as feeding relationships with other seabirds (e.g. Ronconi 2008) and even marine mammals. This is addressed in the next chapter.

Literature Cited

Ainley, D.G., Allen, S.G. and L.B. Spear. 1995. Offshore occurrence patterns of marbled murrelets in central California. In *Ecology and conservation of the marbled murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, C.A.: U.S. Forest Service, pp.361-369.

Ainley, D.G. and R.J. Boekelheide (eds.). 1990. *Seabirds of the Farallon Islands: Ecology, dynamics, and structure of an upwelling-system community*. Stanford University Press, Stanford, C.A.

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

Berges, J.A., Varela, D.A. and P.J. Harrison. 2002. Effects of temperature on growth rate, cell composition and nitrogen metabolism in the marine diatom *Thalassiosira pseudomana* (Bacillariophyceae). *Marine Ecology Progress Series*, 225: 139-146.

Briggs, K.T., Tyler, W.B., Lewis, D.B. and D.R. Carlson. 1987. Bird communities at sea off California: 1975 to 1983. *Studies in Avian Biology*, 11: 1-74.

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

Burger, A.E. 1999. Bird in Hot Water: Responses by marbled murrelets to variable ocean temperatures off southwestern Vancouver Island. *Proc. Biology and Management of Species and Habitats at Risk*, Kamloops, B.C.

Burger, A.E. 2000. Bird in hot water: responses by marbled murrelets to variable ocean temperatures off southwest Vancouver Island. In *Proceedings of a Conference on the Biology and Management of Species and Habitats At Risk*, *Kamloops, BC, 15-19 February 1999. Volume 2*, Darling, L.M. (Ed), Victoria: BC Ministry of Environment, Lands and Parks & Kamloops: University College of the Cariboo, pp. 723-732.

Burger, A.E. 2002. Conservation assessment of Marbled Murrelets in British Columbia: review of the biology, populations, habitat associations and conservation of this threatened species. Delta, B.C.: Canadian Wildlife Service, Pacific and Yukon Region, British Columbia Technical Report Series No. 387.

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

Burger, A.E., Booth, J.A. and K.H. Morgan. 1997. A preliminary identification of processes and problems affecting marine birds in coastal and offshore areas of British Columbia. *Canadian Wildlife Service, Pacific and Yukon Region, Technical Report Series*, 277: 110p.

Burkett, E.E. 1995. Marbled murrelet food habits and prey ecology. In *Ecology and conservation of the marbled murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, C.A.: U.S. Forest Service, pp.223-246.

Carter, H.R. 1984. At-sea biology of the marbled murrelet in Barkley Sound, B.C. Thesis, University of Manitoba, Winnipeg, M.B., Canada.

Crawford, W.R. and R.E. Thomson. 1991. Physical oceanography of the western Canadian continental shelf. *Continental Shelf Research* 11(8-10): 669-683.

Daunt, F., Peters, G., Scott, B., Gremillet, D. and S. Wanless. 2003. Rapid response recorders reveal interplay between marine physics and seabird behaviour. *Marine Ecology Progress Series,* 255: 283-288.

Durant, J.M., Anker-Nilssen, T. and N.C. Stenseth. 2003. Trophic interactions under climate fluctuations: the Atlantic Puffin as an example. *Proceedings of the Royal Society of London,* 270: 1461-1466.

Durbin, E.G., Campbell, R.G., Casas, M.C., Ohman, M.D., Niehoff, B., Runge, J. And M. Wagner. 2003. Interannual variation in phytoplankton blooms and zooplankton productivity and abundance in the Gulf of Maine during winter. *Marine Ecology Progress Series*, 254: 81-100.

Fauchald, P. And K.E. Erikstad. 2002. Scale-dependent predator-prey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. *Marine Ecology Progress Series*, 231: 279-291.

Freeland, H.J. 1992. They physical oceanography of the west coast of Vancouver Island. In *The ecology, status and conservation of marine shoreline birds of the west coast of Vancouver Island,* Vermeer, K., Butler, R.W. and K.H.Morgan (eds.), Occasional Paper No. 75. Ottawa, O.N.: Canadian Wildlife Service, pp.10-14.

Guinet, C., Chastel, O., Koudil, M., Durbec, J.P. and P. Jouventin. 1998. Effects of warm sea-surface temperature anomalies on the blue petrel at the Kerguelen Islands. *Proceedings of the Royal Society of London,* 265: 1001-1006.

Hatch, S.A. 1987. Did the 1982-1983 El Niño – Southern Oscillation affect seabirds in Alaska? *Wilson Bulletin,* 99: 468-474.

Hay, R.B. 1992. The oceanic habitats of seabirds: Their zonal distribution off Vancouver Island, British Columbia, Canada. *Journal of Biogeography,* 19(1): 67-85.

Hunt, G.L. Jr. 1995. Oceanographic processes and marine productivity in waters offshore of marbled murrelet breeding habitat. In *Ecology and conservation of the Marbled Murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, C.A.: U.S. Forest Service, pp.223-246.

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

Kalle, K. 1971. Salinity: General introduction. In *Marine Ecology: A comprehensive, integrated treatise on life in oceans and coastal waters. Volume 1: Environmental factors, part 2.* Kinne, O. (ed.), London: Wiley-Interscience, pp. 683-688.

Kelson, J., Manley, I. and H. Carter. 1995. Decline of the Marbled Murrelet in Clayoquot Sound, British Columbia: 1982-1993. *Northwest Naturalist,* 76: 90-105.

Kelson, J. and M.H. Mather. 1999. At-sea population size and distribution of Marbled Murrelets (*Brachyramphus marmoratus*) in Clayoquot Sound, British Columbia: 1982-1996. In *Inventory of Marbled Murrelets in Clayoquot Sound, 1997*. Nanaimo: Unpublished report, Ministry of Environment, Lands and Parks, Vancouver Island Regional Office. pp. 54-75.

Kerr, K.A. 2005. Nearshore oceanography and planktonic prey (Family Porcellanidae) of gray whales, *Eschrichtius robustus*, in Clayoquot Sound, British Columbia. Thesis, University of Victoria, Victoria, B.C., Canada.

Kopach, B.W. 2004. Fine-scale circulation as a component of gray whale (*Eschrichtius robustus*) habitat in Clayoquot Sound, British Columbia. Thesis, University of Victoria, Victoria, B.C., Canada.

Mackas, D.L. and M. Galbraith. 1992. Zooplankton on the west coast of Vancouver Island: Distribution and availability to marine birds. In *The ecology, status and conservation of marine shoreline birds of the west coast of Vancouver Island,* Vermeer, K., Butler, R.W. and K.H.Morgan (eds.), Occasional Paper No. 75. Ottawa, O.N.: Canadian Wildlife Service, pp.15-21.

Mackas, D.L., Louttit, G.C. and M.J. Austin. 1980. Spatial distribution of zooplankton and phytoplankton in British Columbian coastal waters. *Canadian Journal of Fisheries and Aquatic Sciences,* 37(10): 1476-1487.

Matthews, J.B.L. and B.R. Heimdal. 1980. Pelagic productivity and food chains in fjord systems. In *Fjord Oceanography,* Freeland, H.J., Farmer, D.M. and C.D. Levings (eds.), New York: Plenum Publication Corp, pp. 377-398.

McGowan, J.A., Cayan, D.R. and L.M. Dorman. 1998. Climate-ocean variability and ecosystem response in the northeast Pacific. *Science,* 281: 210-217.

Moloney, C.L., Botsford, L.W. and J.L. Largier. 1994. Development, survival and timing of metamorphosis of planktonic larvae in a variable environment: the Dungeness crab as an example. *Marine Ecology Progress Series* 113: 61-79.

Olson, D.B., Hitchock, G.L., Mariano, A.J., Ashjian, C.J., Peng, G., Nero, R.W. and G.P. Podesta. 1994. Life on the edge: Marine life and fronts. *Oceanography,* 7(2): 52-60.

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

Peck, D.R., Smithers, B.V., Krockenberger, A.K. and B.C. Congdon. 2004. Sea surface temperature constrains wedge-tailed shearwater foraging success within breeding seasons. *Marine Ecology Progress Series,* 281: 259-266.

Pineda, J. 1991. Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. *Science,* 253: 548-551

Price, J.F., Weller, R.A. and R.R. Schudlich. 1987. Wind-driven ocean currents and Ekman transport. *Science*, 238(4833): 1534-1538.

Ralph, C.J., Hunt, G.L., Raphael, M.G., and J.F. Piatt. 1995. Ecology and conservation of the marbled murrelet in North America: an overview. In *Ecology and conservation of the Marbled Murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, C.A.: U.S. Forest Service, pp.3-22.

Rodway, M.S., Carter, H.R., Sealy, S.G. and R.W. Campbell. 1992. Status of the Marbled Murrelet in British Columbia. In *Status and conservation of the Marbled Murrelet in North America*, Carter, H.R. & Morrison, M.L. (Eds.), Proceedings of the Western Foundation of Vertebrate Zoology 5, pp. 17-41.

Ronconi, R.A. 2008. Patterns and processes of marine habitat selection: Foraging ecology, competition and coexistence among coastal seabirds. Thesis, University of Victoria, Victoria, B.C., Canada.

Sea-Bird Electronics, 2001. SEASOFT-Win32: SBE Data Processing-Win 32 User’s Manual. Software Version 5.24 and later. Sea-Bird Electronics, Inc., Bellevue, Washington.

Sealy, S.G. 1975. Aspects of the breeding biology of the Marbled Murrelet in British Columbia. *Bird-Banding*, 46: 141-154.

Speckman, S.G., Springer, A.M., Piatt, J.F. and D.L. Thomas. 2000. Temporal variability in abundance of marbled murrelets at sea in southeast Alaska. *Waterbirds*, 23(3): 364-377.

Spivak, E.D. 1999. Effects of reduced salinity on juvenile growth of two co-occurring congeneric grapsid crabs. *Marine Biology,* 134: 249-257.

Sydeman, W.J., Bradley, R.W., Warzybok, P., Abraham, C.L., Jahncke, J., Hyrenbach, K.D., Kousky, V., Hipfner, J.M. and M.D. Ohman. 2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: Unusual atmospheric blocking? *Geophysical Research Letters*, 33: L22S09, 5 pp.

Thomson, R.E. 1981. Oceanography of the British Columbia Coast. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 56: 292 pp.

Tyler, W.B., Briggs, K.T., Lewis, D.B. and R.G. Ford. 1993. Seabird distribution and abundance in relation to oceanographic processes in the California Current System. In *the status, ecology, and conservation of marine birds of the North Pacific,* Vermeer, K., Briggs, K.T., Morgan, K.H. and D. Siegel-Causey (eds.) Canadian Wildlife Service Special Publication, Ottawa, pp. 48-60.

Wilson, U.W. 1991. Responses of three seabird species to El Niño events and other warm episodes on the Washington coast, 1979-1990. *The Condor,* 93: 853-858.

Chapter 4

Marbled Murrelets Foraging with Gray Whales

Introduction

Optimal foraging theory states that an individual or species will forage in such a way as to find, capture and consume food as time-efficiently as possible (MacArthur & Pianka 1966). It is argued that selection is an iterative and competitive process whereby outcomes, expressed as phenotypes, represent the best balance of costs and benefits (Krebs & Davies 1991). So, not only prey availability, but prey type is a factor driving foraging distribution and behaviour. Much of optimal foraging theory attempts to explain how the distribution, abundance and quality of food influence distribution, habitat use and movements of birds (Pyke *et al.* 1984). In the case of marbled murrelets, an individual should proceed from items of highest harvest per unit of expenditure to those of lowest, proceeding in a hierarchical system of prey and site selection based on the abundance and quality of prey (MacArthur & Pianka 1966). Anything that increases availability or reduces expenditures of energy may find its way into the foraging behaviour of a predator.

One such behaviour, kleptoparasitism is traditionally defined as the deliberate stealing by an animal of prey that has already been captured by another (Furness 1987), and develops where there are large concentrations of hosts, where large quantities of prey are available and carried in large, discrete masses, prey is available in a predictable manner, and is visible to the kleptoparasite (Brockman & Barnard 1979). Six inter-specific associations exist that may lead to kleptoparasitism: 1) association based on predation, 2) association based on mobbing, 3) association based on mixed-species flocks, 4) association based on mixed species nesting colonies, 5) association based on ‘beating’, and 6) association based on scavenging (Brockman & Barnard 1979). Beating occurs when an animal takes advantage of the feeding activities of other species that frighten or dislodge food. This commensal kleptoparasitic association may result if the host’s foraging habits are predictable (Brockman & Barnard 1979), or if the prey becomes readily visible (Brockman & Barnard 1979, Harrison 1979, Au & Pitman 1986). The host may then provide an increased rate of prey capture and allow for an individual to exploit the resource, with benefits especially in provisioning during the breeding season.

Many species of marine birds forage in association with other marine predators, including fish (Colblentz 1985, Au & Pitman 1986, Safina 1990) and marine mammals (Evans 1982, Au & Pittman 1986, Pitman & Balance 1992, Vermeer *et al.* 1992). In these associations, seabirds benefit from access to small fish forced to the surface, or by retrieval of scraps from larger prey torn apart by the predators.

Many studies have documented foraging relationships between seabirds and cetaceans (Au & Pitman 1986, Mehlum *et al.* 1998, Camphuysen & Webb 1999, Camphuysen *et al.* 2006). Gray whales (*Eschrichtius robustus*) are a marine predator with which marine birds have been associated (Harrison 1979, Obst & Hunt 1990). Harrison (1979) documented 9 species of marine birds in the Bering Sea, including 4 species of alcid (parakeet auklet (*Aethia psittacula*), crested auklet (*Aethia cristatella*), least auklet (*Aethia pusilla*) and horned puffin (*Fratercula corniculata*)), feeding on zooplankton in mud plumes released to the surface by feeding gray whales (*Eschrictius robustus*). Obst & Hunt (1990) observed that seabirds in the Bering Sea were associated with 66% of feeding gray whales (63 of 95 individuals or groups of whales) and postulated that whale generated food is an important ecological factor for several locally breeding species. Surf scoters (*Melanitta perspicillata*) have also been noted in Puget Sound, Washington, taking advantage of feeding gray whales that dislodge prey, mainly ghost shrimp *Neotrypaea californiensis,* in the benthic and subtidal sediment layers (n=19 scoters, Anderson & Lovvorn 2008).

There have been to date no reports of marbled murrelets (*Brachyramphus marmoratus*) feeding in association with gray whales. Marbled murrelets are known to feed on a variety of prey, including euphausiids, mysids, and small fish (Sealy 1975). The importance of different prey types has been linked to time of year and location. For instance, in British Columbia small schooling fish, primarily Pacific sand lance (*Ammodytes hexapterus*), dominate the diet during nestling and fledging periods, and euphausiids (Family *Euphausiidae*) during the winter and early spring (Sealy 1975, Carter 1984, Vermeer 1992). However, marbled murrelets have also been observed to forage opportunistically (Evans 1982, Burkett 1995).

Both gray whales and marbled murrelets feed along the west coast of North America (Oliver *et al.* 1984, Sumich 1984, Weitkamp *et al.* 1992, Dunham & Duffus 2001). In Clayoquot Sound (Figure 1), gray whales forage primarily on swarms of epibenthic mysids (Mysidae) (Dunham & Duffus 2001, 2002). During the summer months, these foraging bouts occur around kelp beds and rocky reefs. This habitat is also important for foraging marbled murrelets. How marbled murrelets are associated with foraging gray whales is not well understood. Here, I seek to explore the relationship between marbled murrelets and foraging gray whales. By examining the feeding numbers and behaviours of marbled murrelets in both the presence and absence of gray whales in Clayoquot Sound, the notion of a functional feeding association can be investigated.

Methods

Study Area

Clayoquot Sound is located along the west coast of Vancouver Island (Figure 4.1), reaching up to 35 kilometres inland and comprising 265,000 hectares of land and 85,000 hectares of narrow inlets. Data for this study were collected in Cow Bay, along the southwest coast of Flores Island (49º15'N, 126 º10'W) between Siwash Point in the west and the Fitzpatrick Islands to the east (Figure 4.2). Cow Bay contains numerous shallow reefs commonly used by both gray whales and marbled murrelets. The coastline is characterized by rocky shores and kelp beds with intermittent sandy beaches and cobble bays, and the central and eastern portions of Cow Bay are exposed to prevailing summer wind waves and northwest swells.

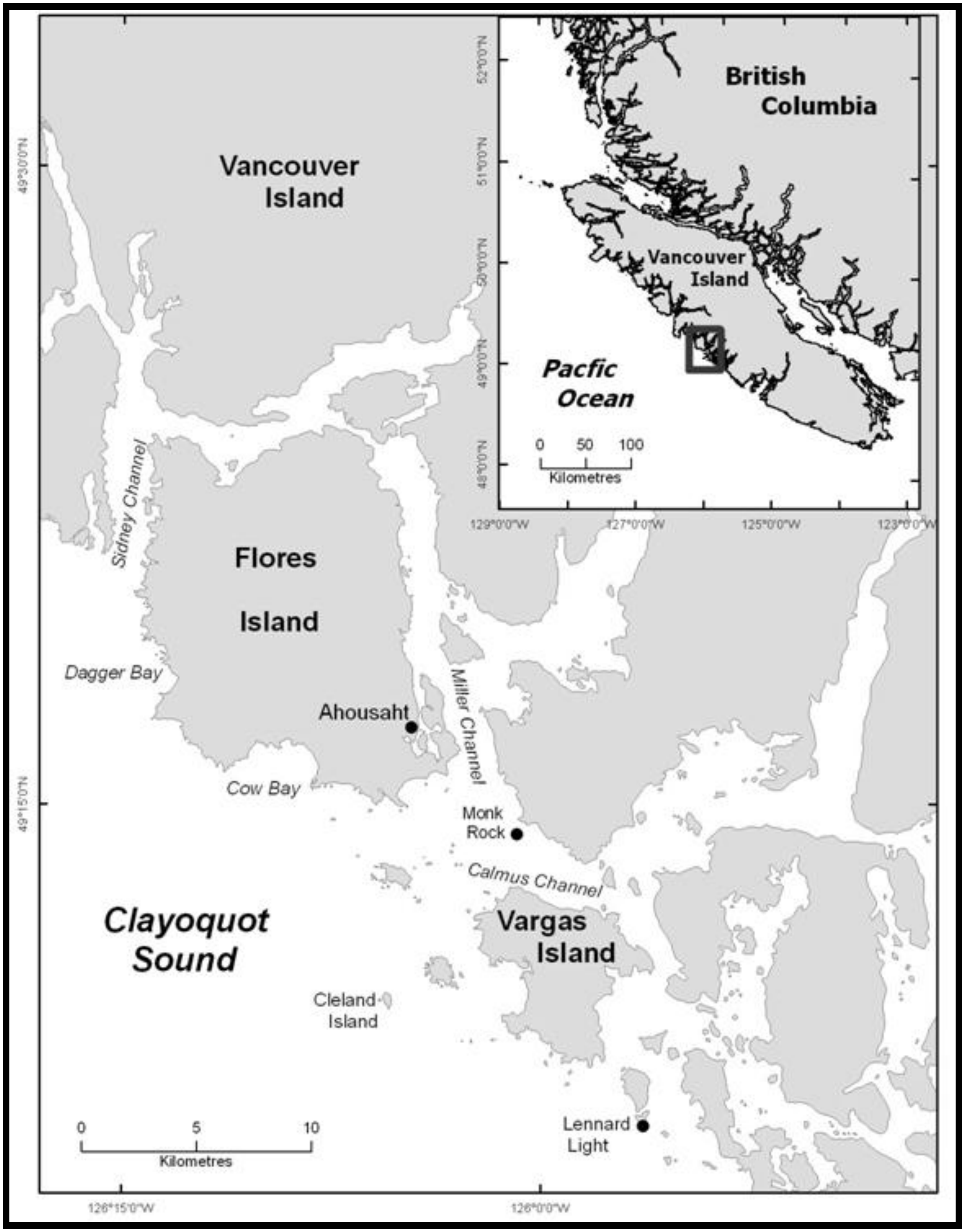


Figure 4.1: Research study area, Clayoquot Sound, British Columbia.

Data Collection

Boat-based surveys were conducted from a 6.5m aluminum vessel along a fixed-width transect with a 600m inclusion zone (i.e. to 300m from either side of the vessel), representing the limit beyond which seabird species identification is no longer reliable (Bibby *et al.* 2000) (Figure 4.2). Survey transects were oriented along roughly the 10-metre depth contour as this depth has demonstrated to be an important attribute to foraging whales utilizing these waters (Laskin 2010). Continuous observations were made of both marbled murrelets and gray whales, with two observers scanning 180 degrees on either side of the vessel for both marbled murrelets and gray whales. Marbled murrelets feeding in the presence of gray whales were documented on three of three surveys in 2006 (8 June, 9 June and 12 June), and two of eight surveys in 2008 (26 June and 14 July). Attributes recorded for each observation included location of the research vessel, bearing and range to the bird(s)/whale(s) observed, date, time, and sea state. Murrelet behaviour (foraging or resting) was also recorded.

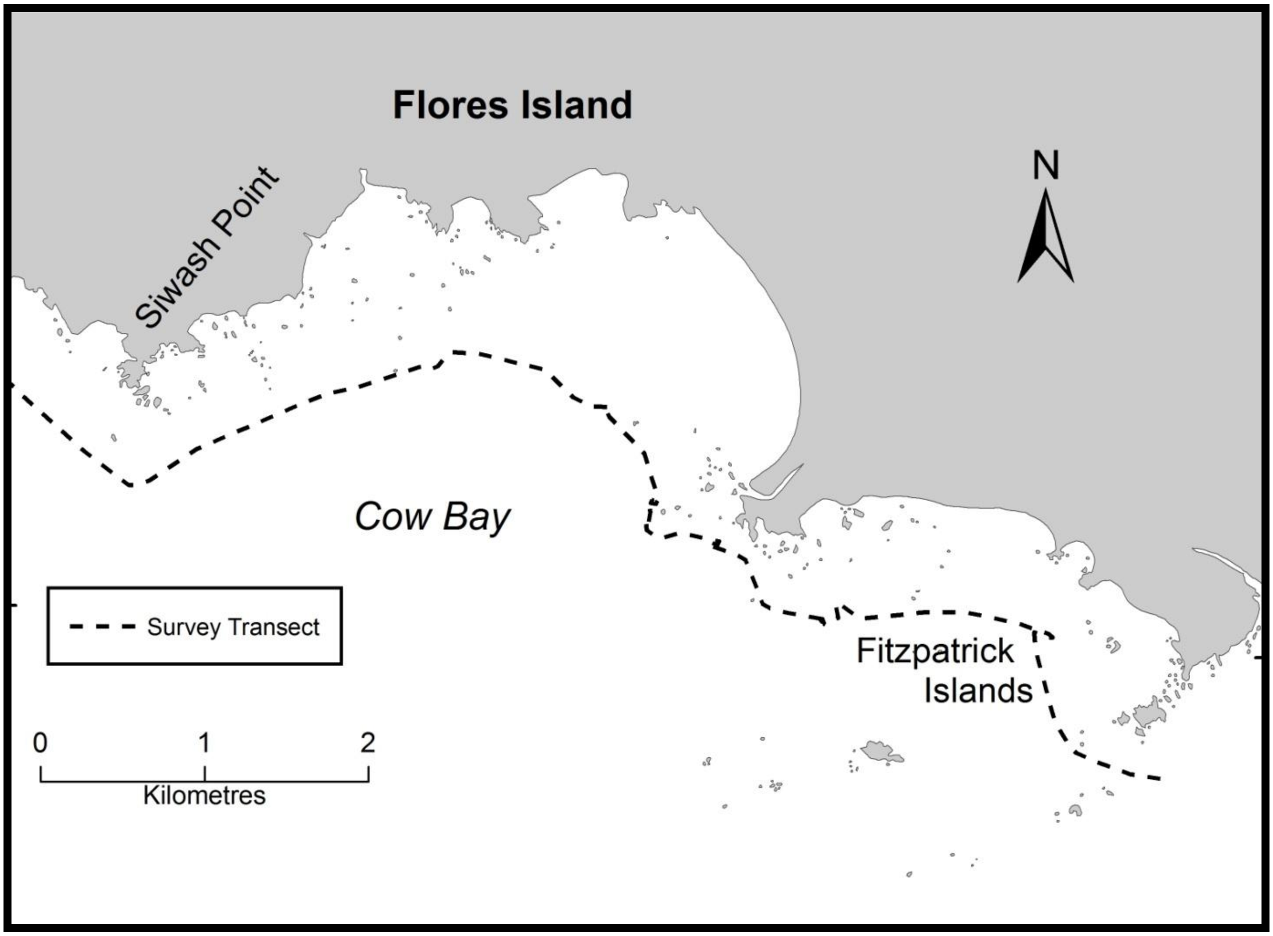


Figure 4.2: Cow Bay, along the South coast of Flores Island; foraging habitat for both marbled murrelets and gray whales.

Data Analysis

To analyse the spatial relationship between marbled murrelets and gray whales, a point pattern analysis approach was adopted. Local spatial autocorrelation was measured using a join count statistic (Alstadt *et al.* 2008), which assesses spatial patterns in binary data from adjacent sampling units or regions (Upton & Fingleton 1985). The observed join count statistic counts the number of adjacent points in the data set (i.e. murrelets, M, and gray whales, G) and assesses positive spatial autocorrelation in data points of the same category (i.e. two marbled murrelet points) resulting in a positive z-score, and positive spatial autocorrelation in data points of opposing categories (i.e. marbled murrelet and gray whale) resulting in a negative z-score. The result is a measure of positive spatial autocorrelation, with values greater than 0 signifying more clustering in points of the same category than would be expected by random distribution, and values less than 0 signifying higher clustering in points of opposing categories than would be expected by random distribution (Fortin *et al.* 2002). This study focuses on the results of join counts between points of opposing values, calculated by the equation:

$$\mathrm{MG} = \tfrac{1}{2} \sum_i \sum_j w(i,j)(x_i - x_j)^2$$

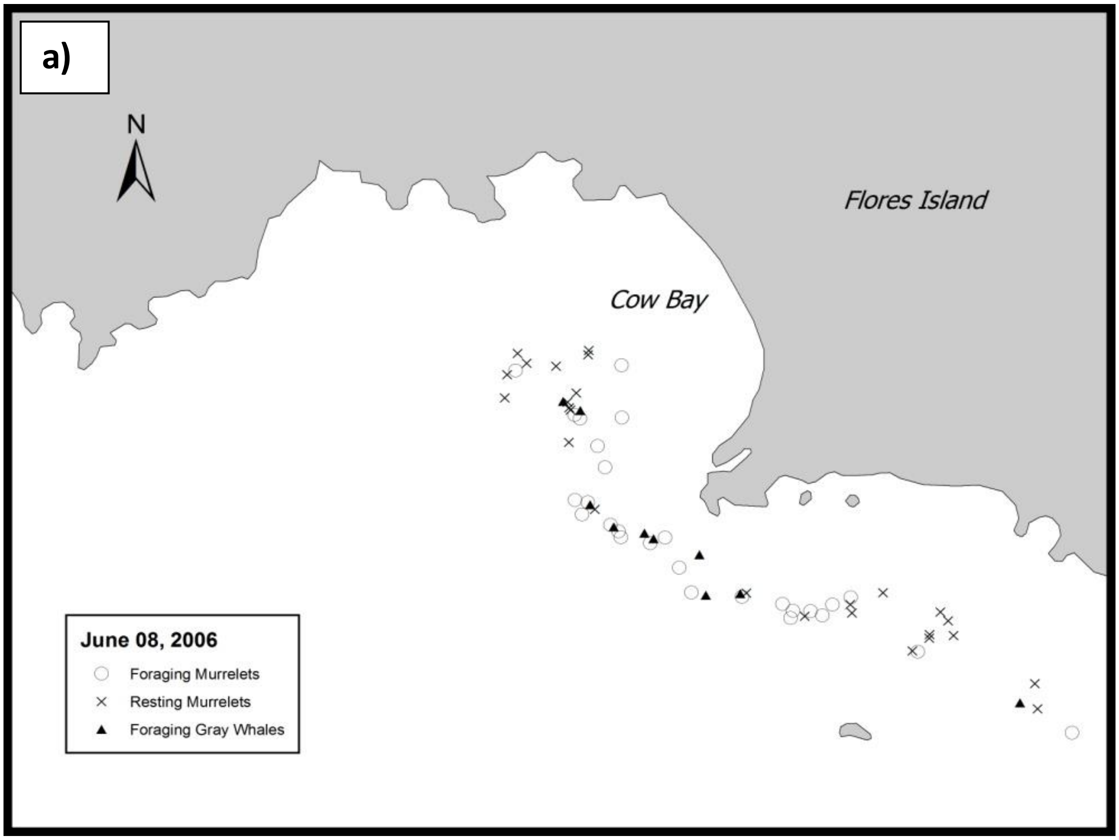
Where $x\ (i,j)$ is the binary value, 1 for black, 0 for white, and $w(i,j)$ is the binary weight, identified from an N x N spatial weights matrix, and is assigned a 1 if two points are within a set distance threshold, and a 0 if otherwise (Alstadt *et al.* 2008). Calculations were done at 100, 200 and 300 metre thresholds to evaluate the extent of influence that the gray whales exhibited. The 300 metre threshold was used as a maximum based on the detectability of murrelets in the study area, and individuals sighted beyond 300 metres are said to be acting independently.

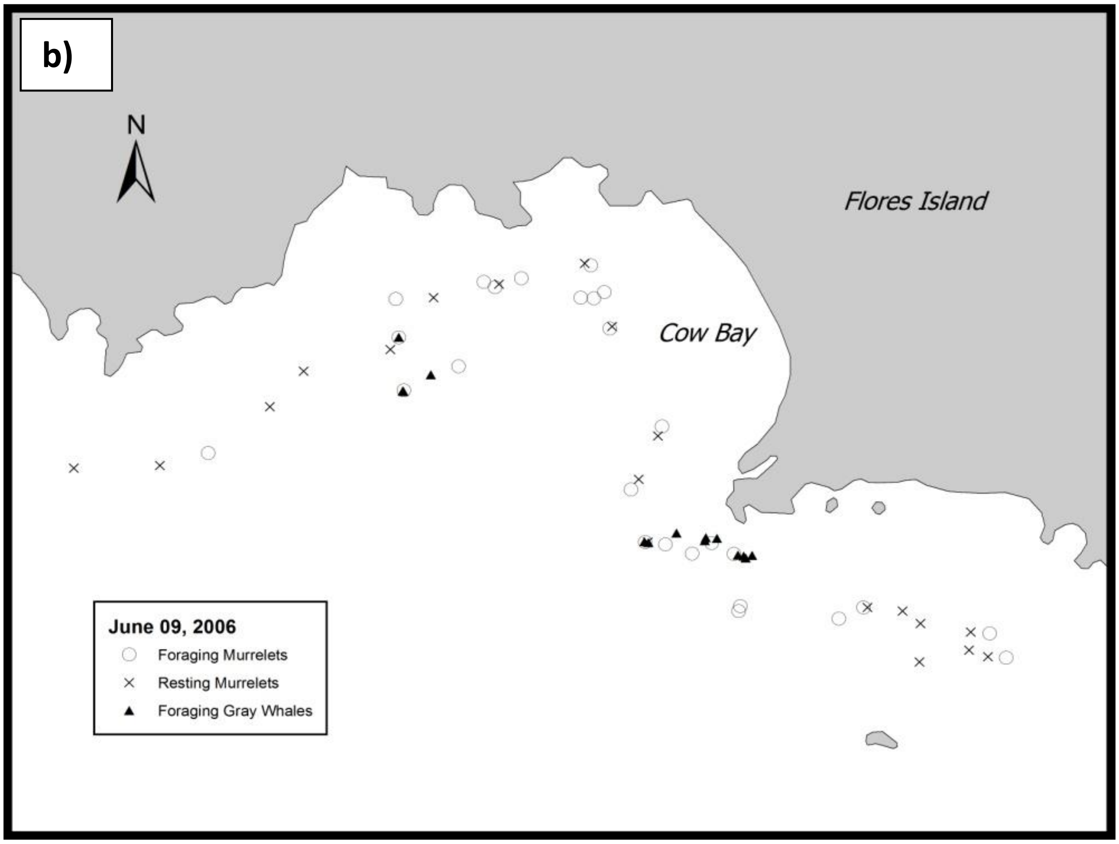
Results

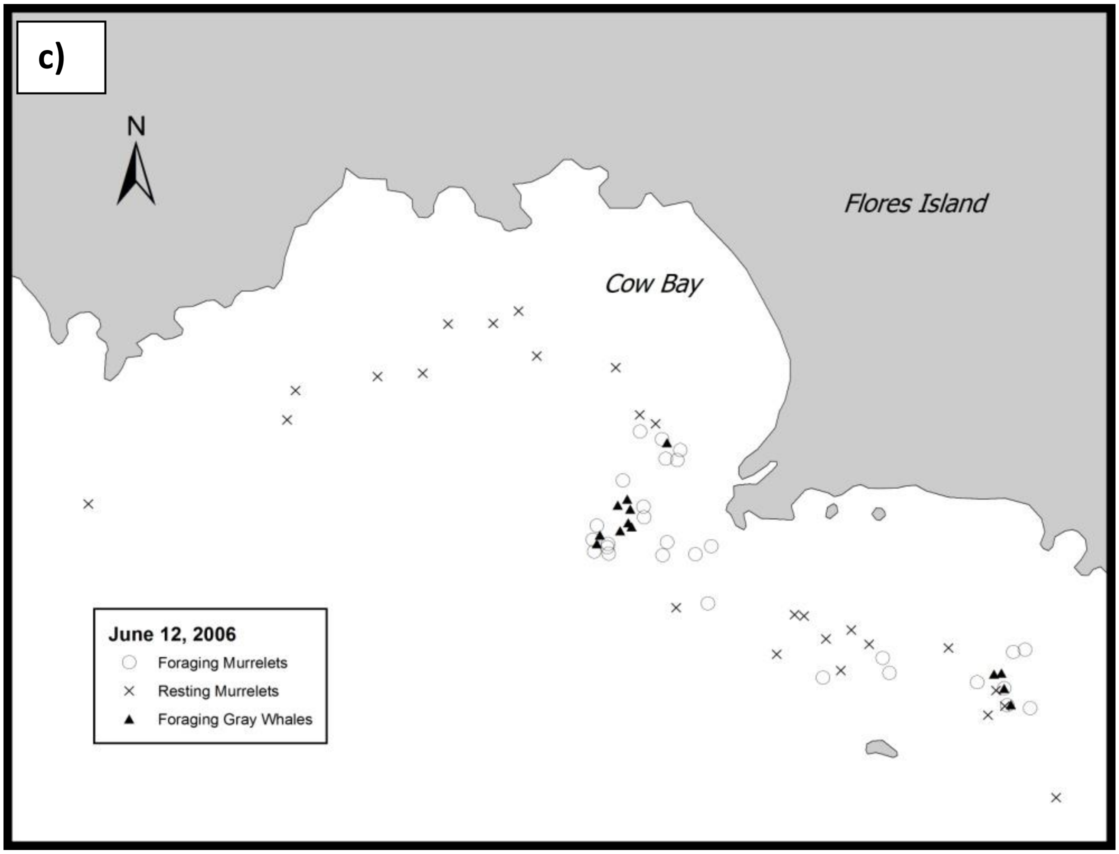
In 2006, 39 gray whales were present in the study area. Over three surveys, a total of 258 marbled murrelets were observed foraging in association with gray whales and 88 were observed in non-whale-associated foraging (Figures 4.3a-c, Table 4.1). In 2008, 5 gray whales were located foraging in Cow Bay. In two surveys, 34 marbled murrelets were observed foraging with gray whales and 102 in non-whale-associated foraging (Figures 4.3d-e, Table 4.1). Surveys conducted in 2007 revealed no instances where marbled murrelets were engaged in foraging with gray whales. In this year few gray whales were found foraging (approximately 3 individuals) (Feyrer 2010), and the likelihood of observing any relationship was low as whales were rarely seen.

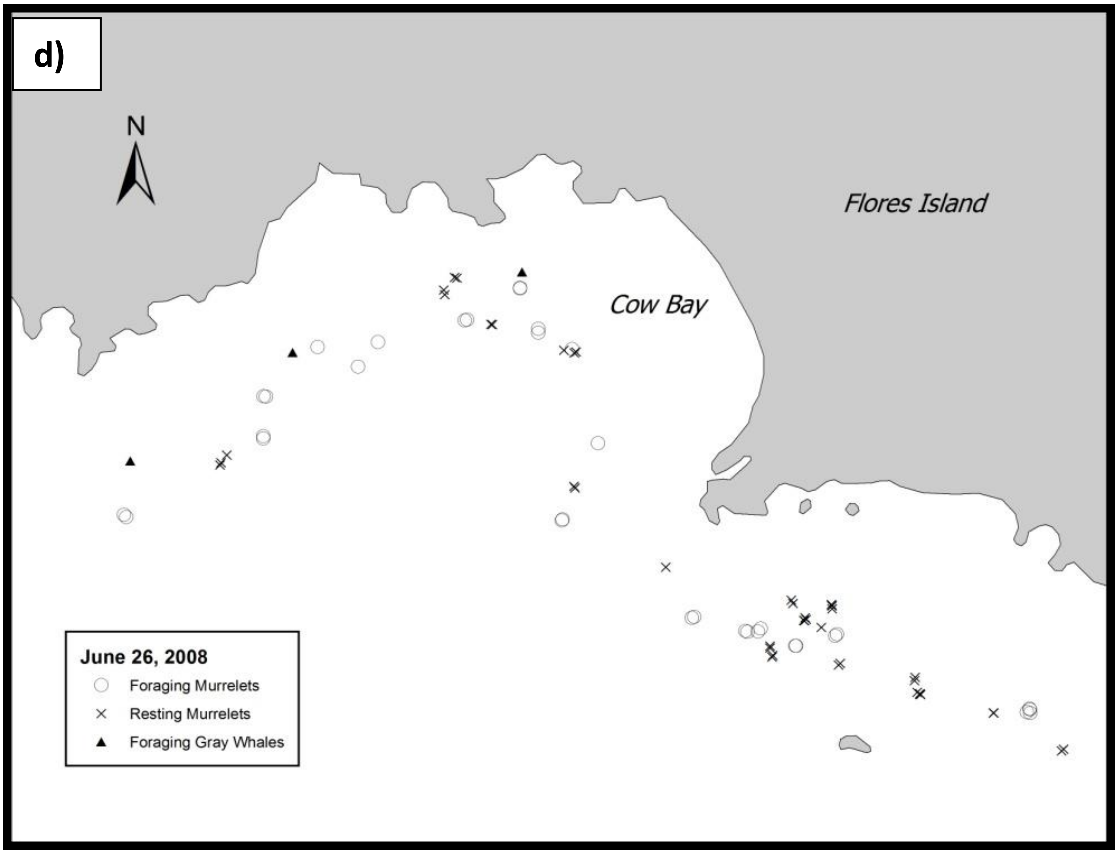
Table 4.1: Observed feeding associations between Marbled Murrelets (MaMu) and Gray Whales in Cow Bay, Clayoquot Sound, June 2006.

Date	Location of event	Total feeding Gray Whales	Total Murrelets feeding with whales	Total Murrelets feeding: no whales
08/06/06	49º 15.28’N 126º 8.33’W	10	81	36
09/06/06	49º 15.41’N 126º 9.19’W	16	94	34
12/06/06	49º 15.20’N 126º 8.18’W	13	83	18
26/06/08	49º 15.20’N 126º 8.18’W	3	22	47
14/07/08	49º 15.20’N 126º 8.18’W	2	12	55


a)
N
Flores Island
Cow Bay
June 08, 2006
○ Foraging Murrelets
× Resting Murrelets
▲ Foraging Gray Whales


b)
N
Flores Island
Cow Bay
June 09, 2006
○ Foraging Murrelets
× Resting Murrelets
▲ Foraging Gray Whales


c)
N
Flores Island
Cow Bay
June 12, 2006
○ Foraging Murrelets
× Resting Murrelets
▲ Foraging Gray Whales


d)
N
Flores Island
Cow Bay
June 26, 2008
○ Foraging Murrelets
× Resting Murrelets
▲ Foraging Gray Whales

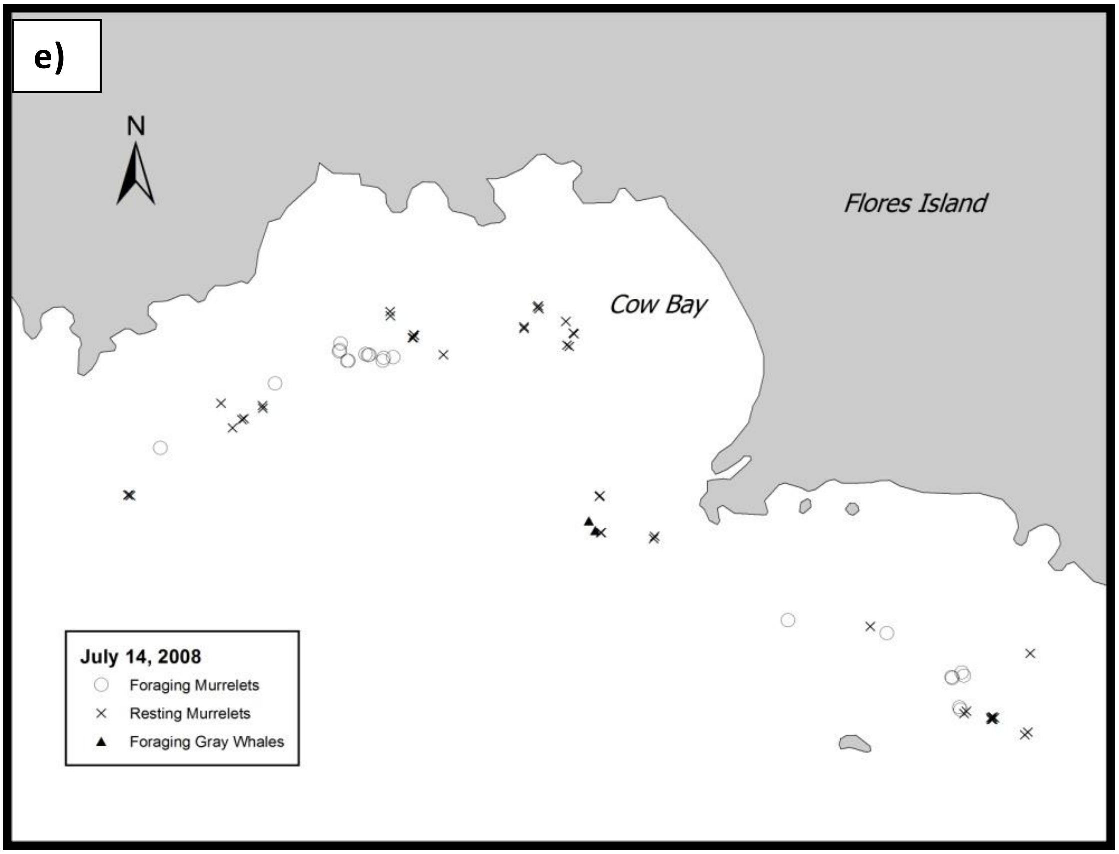


Figure 4.3: Distribution of gray whales and marbled murrelets across the study area, 08 June (a) 09 June (b) and 12 June (c), 2006 and 26 June (d) and 14 July (e), 2008. Maps depict the distribution of foraging gray whales, and foraging and resting marbled murrelets observed along a single survey, conducted east to west (see Figure 3.2 for survey track).

Based on the distribution of point data (Figure 4.3 a-e), join count statistics for all marbled murrelets in the study area showed significant positive spatial autocorrelation between murrelet and gray whale points in 2006 at 100, 200 and 300 metre thresholds (Tables 4.2 – 4.4), indicating a greater relationship between marbled murrelets and gray whales than would be expected under complete spatial randomness. No significant spatial autocorrelation was found in 2008 (Tables 4.2 – 4.4).

Table 4.2: Join count statistics results; 100m threshold.

Date	Total Murrelets	Total Gray Whales	Observed Joins	Expected Joins	*Z* (p=0.1)
06/08/2006	117	10	47	98.667	**-1.5357**
06/09/2006	128	16	30	58.110	**-1.1557**
06/12/2006	101	13	23	42.991	**-1.1644**
06/26/2008	50	3	4	6.6248	-0.4167
07/14/2008	67	2	4	7.1174	-0.4338

Table 4.3: Join count statistics results; 200m threshold.

Date	Total Murrelets	Total Gray Whales	Observed Joins	Expected Joins	*Z* (p=0.1)
06/08/2006	117	10	53	112.58	**-1.3281**
06/09/2006	128	16	50	99.711	**-1.1223**
06/12/2006	101	13	49	101.62	**-1.2667**
06/26/2008	50	3	7	8.2233	-0.0833
07/14/2008	67	2	24	42.179	-0.0741

Table 4.4: Join count statistics results; 300m threshold.

Date	Total Murrelets	Total Gray Whales	Observed Joins	Expected Joins	*Z* (p=0.1)
06/08/2006	117	10	81	167.71	**-1.5357**
06/09/2006	128	16	94	129.38	**-1.1557**
06/12/2006	101	13	83	117.80	**-1.1644**
06/26/2008	50	3	15	13.333	0.0687
07/14/2008	67	2	24	42.179	-0.0741

Discussion

Results for 2006 show that marbled murrelets respond to the presence of gray whales by foraging in spatially clustered groups centred on gray whale feeding sites. This fine-scale spatial association suggests that gray whales act as a cue to the presence of prey, and in their presence marbled murrelets will aggregate and feed. Of the total observations in 2006, 75% of marbled murrelets were seen feeding with gray whales suggesting an increased feeding effort in the presence of whales in that year.

Results for 2008 failed to show a significant correlation between marbled murrelets and gray whales similar to 2006. This foraging relationship was observed during the spring and early summer, when gray whales are feeding heavily on mysids, often in close proximity with each other. In 2008, there were fewer gray whales in the study area, and significantly lower densities of mysid prey available (Feyrer 2010). Of the total observations in 2008, 26% of murrelets were seen feeding within 300 metres of gray whales; a 67% decrease from 2006. This lack of consistency between years of murrelets taking advantage of feeding gray whales suggests that an underlying factor is driving annual resource selection and foraging behaviour, such as the availability of other prey. The decreased number of gray whales found feeding in the study area in 2008 also confirms that marbled murrelets are likely to take advantage of the cue to an available prey source, but only when the number of gray whales present is high enough to make this foraging behaviour energetically efficient, such as years where finfish abundance is low.

Gray whales in the Bering Sea have been documented bringing from depth food that would otherwise be unavailable to seabirds, and several species of seabird have been identified foraging in association with these whales (Harrison 1979, Obst & Hunt 1990). Correlations between gray whale locations and foraging seabirds found in studies by Harrison (1979) and

Obst & Hunt (1990) further suggest the potential for gray whales to act as cues to the presence of large quantities of invertebrate prey. This relationship likely serves to increase net energy gain for the marbled murrelets during chick provisioning. Gray whales feeding in groups create these ephemeral opportunities for the murrelets by disorienting and/or bringing large quantities of mysids closer to the surface, allowing murrelets easier access to prey (Obst & Hunt 1990) and improving breeding conditions, as well as egg production in female murrelets (Janssen *et al.* 2009).

Although further research is required, mysids disturbed by feeding gray whales may represent an opportunistic yet important nestling period prey source for marbled murrelets in this area. Later in the summer when the whales disperse as they deplete the mysid prey base (Dunham & Duffus 2001), this relationship is less likely to occur. Survey efforts from May – September of 2007 and 2008 revealed that once fledging occurred (29 July 2007 and 26 July 2008) these events ceased, signifying the importance of this association during chick rearing when adult energy inputs must remain high.

Literature Cited

Alstadt, J., Chen, D. & A. Getis. 2008. Point pattern analysis version 1.0a online software. San Diego State University. Available online at http://www.nku.edu

Anderson, E.M. and J.R. Lovvorn. 2008. Gray whales may increase feeding opportunities for avian benthivores. *Marine Ecology Progress Series*, 360: 291-296.

Au, D.W.K. and R.L. Pitman. 1986. Seabird interactions with dolphins and tuna in the eastern tropical Pacific. *The Condor*, 88: 304-317.

Bibby, C.J., Burgess, N.D., Hill, D.A. and S.H. Mustoe. 2000. Bird census techniques 2nd edition. California: Academic Press.

Brockman, H.J. and C.J. Barnard. 1979. Kleptoparasitism in birds. *Animal Behaviour*, 27: 487-514.

Burkett, E.B. 1995. Marbled Murrelet food habits and prey ecology. In *Ecology and conservation of the Marbled Murrelet. General technical report PSW-GTR-152.* Ralph, C.J., Hunt, G. L., Raphael, M.G., and J.F. Piatt (Eds.), Albany, CA: U.S. Forest Service, pp. 223–246.

Camphuysen, C.J. and A. Webb. 1999. Multi-species feeding associations in North Sea seabirds: jointly exploiting a patchy environment. *Ardea*, 87(2): 177-198.

Camphuysen, C.J., Scott, B.E. and S. Wanless. 2006. Distribution and foraging interactions of seabirds and marine mammals in the North Sea: multispecies foraging assemblages and habitat-specific feeding strategies. In *Top predators in marine ecosystems: their role in monitoring and management*. Boyd, I.L., Wanless, S. and C.J. Camphuysen (Eds.), Cambridge University Press, pp. 82-97.

Carter, H.R. and S.G. Sealy. 1984. Marbled Murrelet (*Brachyramphus marmoratus*) mortality due to gill-net fishing in Barkley Sound, British Columbia. In *Marine birds: their feeding ecology and commercial fisheries relationships*, Nettleship, D.N., Sanger, G.A. & P.F. Springer (Eds.), Canadian Wildlife Service Special Publication. Ottawa: Minister of Supply and Services, pp. 212-220.

Colblentz, B.E. 1985. Mutualism between Laughing Gulls *Larus atricilla* and epipelagic fishes. *Cormorant*, 13: 61-62.

Dunham, J.S. and D.A. Duffus. 2001. Foraging patterns of Gray Whales in central Clayoquot Sound, British Columbia, Canada. *Marine Ecology Progress Series*, 223: 299-310.

Dunham, J.S. and D.A. Duffus. 2002. Diet of Gray Whales (*Eschrichtius robustus*) in Clayoquot Sound, British Columbia, Canada. *Marine Mammal Science*, 18: 419-437.

Evans, P.G.H. 1982. Associations between seabirds and cetaceans: a review. *Mammal Review*, 12: 187-206.

Feyrer, L.J. 2010. The foraging ecology of gray whales in Clayoquot Sound: Interactions between predator and prey across a continuum of scales. Thesis, University of Victoria, Victoria, B.C., Canada.

Fortin, M-J., M.R.T. Dale and J. Hoef. 2002. Spatial analysis in ecology, Vol. 4. In: *Encyclopedia of Environmentrics*, El-Shaarawi, A.H. and W.W. Piegorsch (Eds.). Chichester, U.K. pp. 2051-2058.

Furness, R.W. 1987. Kleptoparasitism in seabirds. In: *Seabirds: feeding ecology and role in marine ecosystems*. Croxall, J.P. (ed.), Cambridge University Press. pp. 77-100.

Harrison, C.S. 1979. The association of marine birds and feeding Gray whales. *The Condor*, 81: 93-95.

Janssen, M.H., Arcese, P., Kyser, T.K., Bertram, D.F., Tranquilla, L.M., Williams, T.D. and D.R. Norris. Pre-breeding diet, condition and timing of breeding in a threatened seabird, the Marbled Murrelet *Brachyramphus marmoratus*. *Marine Ornithology,* 37: 33-40.

Kelson, J., Manley, I. and H. Carter. 1995. Decline of the Marbled Murrelet in Clayoquot Sound, British Columbia: 1982-1993. *Northwest Naturalist,* 76: 90-105.

Kelson, J. and M.H. Mather. 1999. At-sea population size and distribution of Marbled Murrelets (*Brachyramphus marmoratus*) in Clayoquot Sound, British Columbia: 1982-1996. In *Inventory of Marbled Murrelets in Clayoquot Sound, 1997*. Nanaimo: Unpublished report, Ministry of Environment, Lands and Parks, Vancouver Island Regional Office. pp. 54-75.

Krebs, J.R. and N.B. Davies. 1991. Behavioural ecology: An evolutionary approach, 4th edition. Blackwell Publishing.

Laskin, D.N. 2007. A marine GIS case study of micro-scale gray whale (*Eschrichtius robustus*) habitat-use off Vancouver Island, British Columbia. M.Sc. thesis, University of Calgary, Calgary, Alberta.

MacArthur, R.H. and E.R. Pianka. 1966. On optimal use of a patchy environment. *The American Naturalist*, 100: 603-609.

Mehlum, F., Hunt, G.L.Jr., Decker, M.B. and N. Nordlund. 1998. Hydrographic features, cetaceans and the foraging of thick-billed murres and other marine birds in the northwestern Barents Sea. *Arctic*, 51(3): 243-252.

Nelson, T.A. and B. Boots. 2008. Detecting spatial hot spots in landscape ecology. *Ecography,* 31(5): 556-566.

Obst, B.S. and G.L. Hunt. 1990. Marine birds feeding at Gray Whale mud plumes in the Bering Sea. *The Auk*, 107: 678-688.

Oliver, J.S., Slattery, P.N., Silbertstein, M.A. and E.F. O'Connor. 1984. Grey whale feeding on dense ampeliscid community near Bamfield, British Columbia. *Canadian Journal of Zoology*, 62: 41-49.

Ord, J.K. and A. Getis. 2001. Testing for local spatial autocorrelation in the presence of global autocorrelation. *Journal of Regional Science,* 41: 411 – 432.

Pitman, R.L. and L.T. Balance. 1992. Parkinson's Petrel distribution and foraging ecology in the eastern Pacific: aspects of an exclusive feeding relationship with dolphins. *The Condor,* 94:825-835.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecological Systems*, 15: 523-575.

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

Sealy, S.G. 1975. Aspects of the breeding biology of the Marbled Murrelet in British Columbia. *Bird-Banding*, 46: 141-154.

Sumich, J.L. 1984. Gray Whales along the Oregon coast in summer, 1977–1980. *Murrelet*, 65:33–40.

Upton, G.J.G. and B. Fingleton. 1985. Spatial Data Analysis by Example, Vol. 1: Point Pattern and Quantitative Data. New York: Wiley.

Vermeer, K., Morgan, K.H. and G.E.J. Smith. 1992. Habitat analysis and co-occurrence of seabirds on the west coast of Vancouver Island. In *The ecology, status, and conservation of marine and shoreline birds on the west coast of Vancouver Island.* Vermeer, K., Butler, R.W., Morgan, K.H. (Eds.), Occasional Paper No. 75. Delta, BC: Canadian Wildlife Service, pp. 78-85.

Weitkamp, L.A., Wissmar, R.C., Simenstad, C.A., Fresh, K.L. and J.G. Odell. 1992. Gray Whale foraging on Ghost Shrimp (Callianassa californiensis) in littoral sand flats of Puget Sound, USA. *Canadian Journal of Zoology*, 70: 2275–2280.

Chapter 5

Summary

The goal of this thesis was to address three questions: 1) Are there any spatial and/or temporal patterns associated with the distribution of marbled murrelets foraging in the nearshore coastal waters of Clayoquot Sound; 2) Can measures of oceanographic conditions across a marbled murrelet foraging area be used to identify ideal marbled murrelet foraging habitat in a situation where direct measures of prey are unavailable; 3) How does the presence of a large predator, the gray whale, affect the spatial distribution of foraging marbled murrelets in a nearshore environment?

Marbled murrelets were abundant in the study area in both years of study, exhibiting a similar pattern in the overall number of individuals that forage in Clayoquot Sound over the breeding season (Chapter 2). The spatial distribution of murrelets within each season, however, showed that spatial clustering in habitat use varies significantly from year to year early and late in the breeding season when murrelets are subsistence feeding. During the chick-rearing stage, when adults are provisioning for their young, hotspots were consistent in both years with murrelets foraging in nearshore areas of Cow Bay and Russell Channel, demonstrating the importance of nearshore coastline as foraging habitat during this chick-rearing stage.

Variations in spatial distribution between years during incubation and fledged stages of the breeding season suggest underlying environmental forces driving habitat use in the study area. Previous studies have found that the most significant force affecting murrelet habitat selection is the abundance and distribution of prey (Becker & Beissinger 2003). Pacific sand lance (*Ammodytes hexapterus*), the predominant prey of the marbled murrelet (Carter 1984), is a highly mobile species that is difficult to monitor in an open water system. However, spatial and temporal variability in prey abundance and distribution should be reflected by the distribution patterns of seabirds (e.g. Briggs *et al.* 1987), and examining the scales over which birds aggregate may allow for inference into which oceanographic processes are influencing this prey variability.

In Chapter 3, oceanographic measures of salinity, temperature and primary productivity collected at sampling stations across the study area were examined for their capacity to explain the patterns in spatial distribution found in Chapter 2. Samples collected in concert with marbled murrelet surveys showed that all variables are ubiquitous across the study area, with no significant variation between sites during either field season. The ability of these oceanographic variables to serve as alternatives to direct measurements of prey density and distribution is insufficient in this case. The distribution of marbled murrelets observed in this study depicts a response to a prey source that occurs in patches across the study area. This study has demonstrated that this patchy distribution is not present at the primary production level, but begins at the next level (invertebrates and small finfish).

Temporal patterns in temperature, salinity and primary productivity also proved insufficient to explain fluctuations in marbled murrelet presence over either field season. Temperature and salinity remained consistent over the field season despite fluctuations in the number of murrelets observed. Chlorophyll *a* densities occurred in significant peaks and troughs, and varied considerably between years, while trends in the number of marbled murrelets observed were consistent between years, with predictable increases and decreases in total murrelets observed per survey set. These opposing trends indicate that fluctuations in chlorophyll *a* densities were not affecting seasonal fluctuations in marbled murrelet abundance in the study area, and suggest that, even at lower-than-average levels, productivity did not decline to the point of affecting murrelet foraging behaviour. Furthermore, the consistent seasonal trend in marbled murrelet abundance suggests that, at a fine scale, behaviour is influenced more by breeding stage than oceanic conditions.

This thesis highlights the importance of local-scale research relating to population dynamics and behaviour. Chapter 4 emphasizes this point by examining the potential impact that another predator, the gray whale, has on marbled murrelet foraging behaviour. Data collected in 2006 suggest that marbled murrelets responded to the presence of feeding gray whales by foraging in spatially significant clusters focused around these feeding sites. Though anecdotal observations of seabird-whale interactions have been reported, this is the first documentation of marbled murrelets exhibiting kleptoparasitic behaviour towards another species, and appears to be a locally-occurring phenomenon observed only in the one of two years where zooplankton abundance, and therefore gray whale presence was high. Lower than average numbers of gray whales present in 2007 and 2008 resulted in an inability to measure this relationship, with no significant spatial association recorded.

The overarching goal of this thesis is to explore the relationship that exists between marbled murrelets and their marine coastal habitat. Population declines in this species have been attributed to loss of their old-growth nesting habitat (Naslund *et al.* 1995, Bahn & Newsom 1999, Zharikov *et al.*2007), resulting in a significant focus on the terrestrial nesting component of the marbled murrelet home range (e.g. Naslund 1993, Kuletz *et al.* 1995, Bradley & Cooke 2001, Meyer & Miller 2002, Raphael *et al.* 2002, Peery *et al.* 2004, Baker *et al.* 2006). This has led to a lack of research examining the marine component of the marbled murrelet home range, and only now are we beginning to understand the processes driving marbled murrelet at-sea abundance, distribution and behaviour. Studies of at-sea distribution have often focused over large areas, and have often generalized habitat in order to analyse population fluctuations. Though important in conservation and management efforts, the small-scale relationships that exist between marbled murrelets and their foraging habitat have been overlooked.

The majority of provincial marine parks and conservation areas on Vancouver Island consist of small areas of coastal and marine habitat established on an *ad hoc* basis (Short 2005) including two provincial parks within the Clayoquot Sound study area: Flores Island Marine Protected Area and Vargas Island Protected Area (Figure 5.1). It seems obvious that conservation and management efforts implemented at a local scale should be supported by research conducted at the local scale, but much of our understanding of population dynamics and marbled murrelet habitat requirements is derived from research conducted at the regional level, compiled from data across the west coast of Vancouver Island and British Columbia. Though the objectives of the Flores and Vargas Island protected areas, prior to establishment, were not to protect marbled murrelet foraging habitat, their encompassing of murrelet feeding grounds, especially during the chick-rearing period when murrelets were consistently found close to shore, allows for local conservation and management efforts to be effective. The improved understanding of the impact that gray whales can have on marbled murrelet foraging patterns can also be used to further improve murrelet conservation efforts, and emphasizes the importance of understanding the ecological structure of an ecosystem in conservation and management practice.

In this thesis I present findings on marbled murrelet at-sea distribution in Clayoquot Sound, and begin to examine possible forces driving this distribution. However, this is only a first step towards understanding the relationship between marbled murrelets and the marine environment. Future studies should seek to establish reliable methods of monitoring the abundance and distribution of small finfish, the primary prey source of most seabirds on the west coast of Vancouver Island. Though large-scale studies have found relationships between oceanographic variables and marbled murrelet habitat use, at a local scale these variables become more homogenous, and unable to account for patterns in marbled murrelet distribution. Understanding these patterns is the key to steering conservation efforts in a direction that will improve the status of this threatened little seabird.

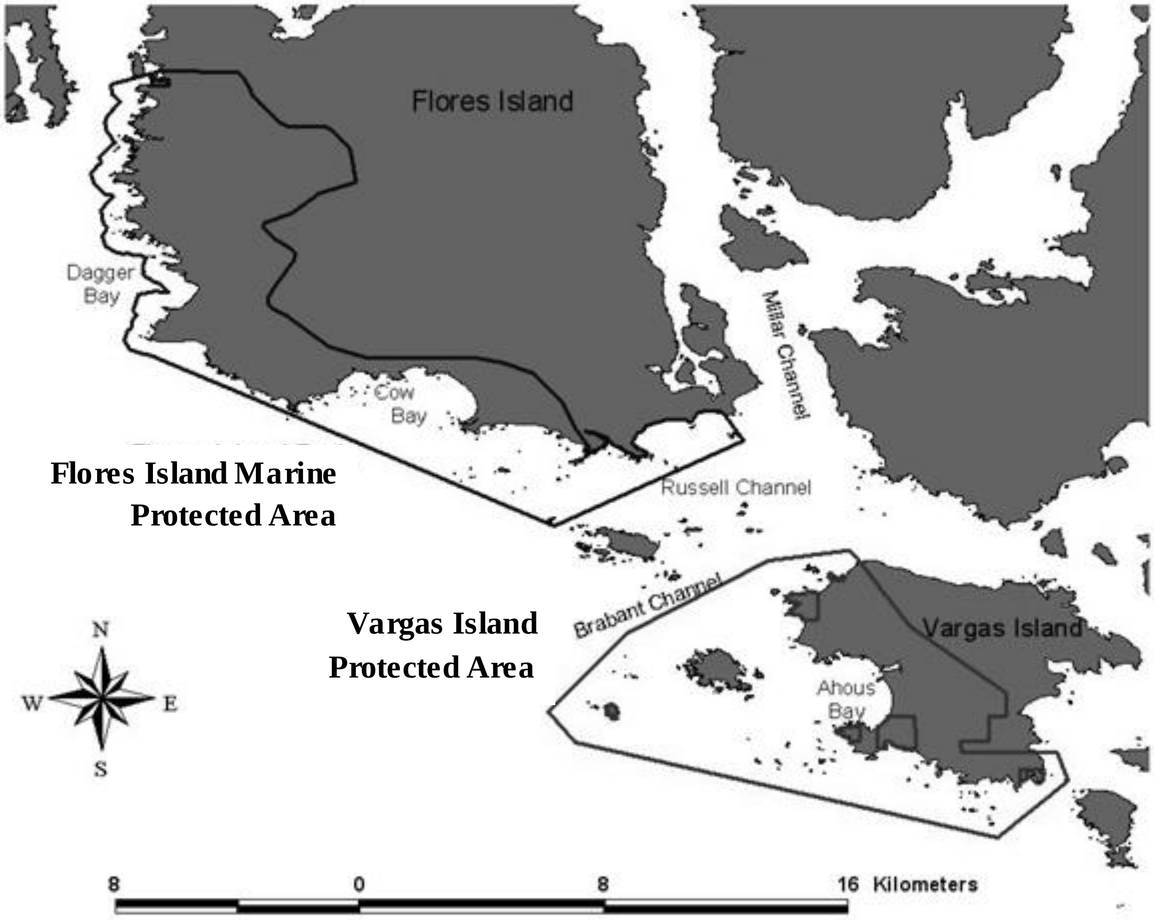


Figure 5.1: Clayoquot Sound study area depicting boundaries of Flores Island marine protected area and Vargas Island protected area.

Literature Cited

Bahn, V. and D.N. Newsom. 1999. Marbled murrelet as target species for land management in coastal British Columbia. *Proc. Biology and Management of Species and Habitats at Risk*, Kamloops, B.C.

Baker, L.M., Peery, M.Z., Burkett, E.E., Singer, S.W., Suddjian, D.L. and S.R. Beissinger. 2006. Nesting habitat characteristics of the marbled murrelet in central California redwood forests. *Journal of Wildlife Management*, 70(4): 939-946.

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

Bradley, R.W. and F. Cooke. 2001. Cliff and deciduous tree nests of marbled murrelets in southwestern British Columbia. *Norhtwestern Naturalist*, 82(2): 52-57.

Briggs, K.T., Tyler, W.B., Lewis, D.B. and D.R. Carlson. 1987. Bird communities at sea off California: 1975 to 1983. *Studies in Avian Biology*, 11: 1-74.

Carter, H.R. and S.G. Sealy. 1984. Marbled Murrelet (Brachyramphus marmoratus) mortality due to gill-net fishing in Barkley Sound, British Columbia. In *Marine birds: their feeding ecology and commercial fisheries relationships*, Nettleship, D.N., Sanger, G.A. & P.F. Springer (Eds.), Canadian Wildlife Service Special Publication. Ottawa: Minister of Supply and Services, pp. 212-220.

Feyrer, L.J. 2010. The foraging ecology of gray whales in Clayoquot Sound: Interactions between predator and prey across a continuum of scales. Thesis, University of Victoria, Victoria, B.C., Canada.

Kuletz, K.J., Marks, D.K., Naslund, N.L., Goodson, N.J. and M.B. Cody. 1995. Inland habitat suitability for the marbled murrelet in southcentral Alaska. In *Ecology and conservaton of the marbled murrelet*, Ralph, C.J., Hunt, G.L., Raphael, M.G. and J.F. Piatt (eds.), General Technical Report PSW-GTR-152. Albany, CA: U.S. Forest Service, pp. 141-150.

Meyer, C.B. and S.L. Miller. 2002. Use of fragmented landscapes by marbled murrelets for nesting in southern Oregon. *Conservation Biology*, 16(3): 755-766.

Naslund, N.L. 1993. Why do marbled murrelets attend old-growth forest nesting areas year-round? *The Auk*, 110(3): 594-602.

Naslund, N.L., Kuletz, K.J., Cody, M.B. and D.K. Marks. 1995. Tree and habitat characteristics and reproductive success at marbled murrelet tree nests in Alaska. *Northwestern Naturalist*, 76(1): 12-25.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Becker, B.H., Burkett, E. and T.D. Williams. 2004. Individual and temporal variation in inland flight behaviour of marbled murrelets: Implications for population monitoring. *The Condor,* 106(2): 344-353.

Raphael, M.G., Mack, D.E., and B.A. Cooper. 2002. Landscape-scale relationships between abundance of marbled murrelets and distribution of nest habitat. *The Condor,* 104: 331-342.

Short, C.J. 2005. A multiple trophic level approach to assess ecological connectivity and boundary function in marine protected areas: A British Columbia example. Thesis, University of Victoria, Victoria, B.C., Canada.

Zharikov, Y., Lank, D.B. and F. Cooke. 2007. Influence of landscape pattern on breeding distribution and success in a threatened alcid, the marbled murrelet: model transferability and management implications. *Journal of Applied Ecology,* 44: 748-759.