MODELING THE FORAGING HABITAT OF HUMPBACK WHALES

by

Luciano Dalla Rosa

B.Sc. in Oceanography, Universidade Federal do Rio Grande, 1995
M.Sc. in Biological Oceanography, Universidade Federal do Rio Grande, 2000

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ABSTRACT

Knowing how species will respond to environmental variability and climate change requires understanding the factors that influence their distribution and movement patterns. I investigated the processes that drive individuals to concentrate in specific areas of their home range by modeling encounter rates of humpback whales (*Megaptera novaeangliae*) in relation to environmental variables using GIS tools, generalized additive models, and remote sensing and *in situ* data. I conducted this work at two foraging areas: the coastal waters of British Columbia, Canada, and the Bransfield and Gerlache Straits, Antarctica.

Humpback whales in British Columbia were strongly associated with latitude and bathymetric features. The relationships with remotely sensed variables reflecting primary productivity were not consistent, but higher numbers of whales seemed to be associated with higher productivity. In fact, the highest concentrations of humpback whales appeared to reflect areas where concentration and retention processes lead to higher biological productivity, including south Dixon Entrance, middle and southwestern Hecate Strait and off Juan de Fuca Strait.

Humpback whales in the Southern Ocean also preferred areas of enhanced biological productivity. In Gerlache Strait, humpback whales were associated with areas of higher chlorophyll-*a* concentration in the central and northern sections of the strait, which also corresponded to relatively higher temperatures and shallower mixed layer depths for the *in situ* data. In Bransfield Strait, humpback whales appeared to prefer the near-frontal zones and the deep basins, where surface waters are influenced by the Bransfield Current.

Interannual variability in both humpback and minke whale encounter rates in Gerlache Strait was correlated with the Oceanic Niño Index, the oceanic component of ENSO.

In addition to investigating species-habitat relationships with statistical models, I conducted the first study to describe the satellite-monitored movements of humpback whales on their feeding grounds along the Antarctic Peninsula. Results showed considerable individual variation in direction, speed and range of movements, and an overall pattern characterized by short- and long-distance movements between presumed foraging areas with relatively short residency times.

All told, the results of my research show that humpback whale distribution within foraging habitat is influenced by physical and biological variables that enhance biological productivity.

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CO-AUTHORSHIP STATEMENT

Data presented in Chapters 2, 3 and 4 were collected in collaboration with various colleagues. All GIS work, data analyses and the preparation of the manuscripts presented in this thesis were conducted by me; this includes the previously published Chapter 4.

1. General introduction

1.1. Species-habitat relationships

Several theories and hypotheses have evolved in the study of animal-habitat relationships to explain observed patterns and predict the distribution of animals. One of the leading theories predicts that good and poor habitats are equally suitable to individuals within populations increasing to maximum sustainable levels (Krebs 1994). This theory, known as the ideal free distribution (Fretwell & Lucas 1970) has been used to explain the habitat selected by a number of species, including herring gulls (*Larus argentatus*) (Pierotti 1982), mallard ducks (*Anas platyrhynchos*) (Harper 1982), bumblebees (*Bombus flavifrons*) (Pyke 1980) and humans (*Homo sapiens*) (Sokolowski et al. 1999), and has proven effective in predicting the distribution of fish in spatially heterogeneous habitats (Schilling 2005). The ideal free distribution theory is also consistent with the distribution of Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia (Heithaus & Dill 2002, Heithaus & Dill 2006). However, it apparently fails to explain the distribution of species such as humpback (*Megaptera novaeangliae*) and common minke whales (*Balenoptera acutorostrata*) (Heithaus & Dill 2002).

Humpback whales and other migratory species tend to move annually from breeding to feeding grounds where prey densities may or may not be high. As such, they may require minimum thresholds of prey density to optimize energy intake (Heithaus & Dill 2002). This would be consistent with the resource concentration hypothesis (Root 1973) that attempted to explain why habitat patches containing large amounts of resources tend to have higher densities of insects. The resource concentration hypothesis predicts that population density should be positively correlated with patch area. However, attempts to test this hypothesis found insects to have large positive correlations between patch area and population density, with birds having moderately large correlations, and small mammals having correlations near zero (Connor et al. 2000).

The ideal free distribution theory and the resource concentration theory, along with several other theories and hypotheses, originate from terrestrial ecology. In many cases it remains to be determined if these theories can explain the distribution of aquatic species or whether new theories are needed to explain aquatic species-habitat relationships. Marine and terrestrial ecosystems operate at different spatial and temporal scales and have different general directions of trophic processes (Steele 1995). Such differences are likely to impact the organisms that inhabit each domain (Sims 2003).

Understanding species-habitat relationships contributes to ecological theory and has significant implications for applied ecology. Conserving any species by establishing marine protected areas or other management measures requires such knowledge. Climate change is now widely accepted as a reality (e.g. Oreskes 2004, IPCC 2007), and the only way to better understand and predict how species will be affected is through having a better understanding of how species interact with their habitat.

The marked growth of computer power in recent years has led to the development of new statistical techniques and integration between GIS tools and environmental models. This in turn has improved analyses of species distributions in relation to the environment. However, a better comprehension is still needed of the spatial and temporal scales at which ecological phenomena influence patterns of species occurrences before these occurrences can be predicted with high levels of accuracy (Scott et al. 2002). The wide variety of predictive habitat distribution models include envelope models, classification and regression trees (CART), neural networks, Bayesian models, generalized linear and generalized additive models (GLM and GAM) and their extensions with random terms (GLMM and GAMM), among others (Guisan & Zimmermann 2000, Austin 2002, Wood 2006). The choice of type of model to use will depend on statistical considerations and on the objectives of the study (Guisan & Zimmermann 2000).

1.2. Research objectives

The main goal of my thesis was to investigate **the processes that drive individuals to concentrate in specific areas of their home range.** I addressed this from a marine environment perspective using the humpback whale as a focal species within two study sites: the foraging grounds of British Columbia and the Antarctic Peninsula. Recognizing the limitations associated with data from a relatively cryptic and widely distributed species living in a dynamic environment, I used generalized additive models (GAMs) to address the following three hypotheses that might explain humpback whale distributions:

1. Higher densities of humpback whales are positively correlated with areas of higher biological production.
2. Annual or seasonal changes in the distribution of humpback whales are related to changes in oceanographic processes and, consequently, primary production and prey availability.
3. The parameters and underlying processes determining humpback whale distribution may differ between the two study areas due to differences in feeding habits.

The GAMs I used to test these hypotheses were formulated with cetacean survey data and environmental variables, including remote sensing and oceanographic data. I also used the GAMs to gain insight into the temporal and spatial scales at which the biotic and abiotic parameters affect the distribution of large whales; and considered whether primary production and other explanatory variables can be used to predict humpback whale distribution. In addition, I attempted to quantify how humpback whales respond to climate variability and to gradients of environmental resources such as primary productivity; and determined the movement patterns and habitat use of satellite-monitored humpback whales around the Antarctic Peninsula.

1.3. Species, study sites and research question justifications

Recent studies suggest that abiotic factors, such as the melting of sea ice due to global warming and increasing UV radiation associated with reduced ozone layer, can substantially affect the marine ecosystem (Tynan & DeMaster 1997, Walther et al. 2002). The extent of sea ice causes fluctuations of krill abundance (Loeb et al. 1997), but the effect of this fluctuating prey biomass on cetacean distribution is unknown. Identifying such effects on cetaceans requires understanding the relationships between cetaceans and the physical and biological marine environment. This can be achieved by determining the mechanisms that affect whale abundance and distribution, and by identifying cetacean habitats and distribution patterns. Such studies may yield referential parameters to monitor trends and oscillations in the abundance and distribution of both the predators and their prey, and their reactions to environmental changes. They therefore constitute important steps for managing and conserving cetacean species.

Past studies have attempted to relate the distributions of cetacean species to physiographic (e.g. Woodley & Gaskin 1996, Baumgartner 1997), physical (e.g. Woodley & Gaskin 1996, Ferrero et al. 2002) and biological (e.g. Fiedler et al. 1998, Reid et al. 2000) variables, with only a few studies considering all three types of features together (e.g. Jaquet & Whitehead 1996, Baumgartner et al. 2001, Friedlaender et al. 2006) or at different scales (e.g. Jaquet & Whitehead 1996, Croll et al. 1998).

The humpback whale is a cosmopolitan and highly migratory species found in all oceans. It is known to migrate seasonally from winter breeding and calving grounds in tropical or subtropical waters to feeding grounds in temperate or high-latitude waters, where it spends spring, summer and autumn (Chittleborough 1965, Dawbin 1966). Site fidelity to relatively discrete feeding grounds is well documented for populations of humpback whales in the North Pacific (Baker et al. 1986, Perry et al. 1990, Calambokidis et al. 2001) and in the North Atlantic (Katona & Beard 1990, Stevick et al. 2003). Recent studies in the Southern Ocean indicate that some individuals may also show fidelity to feeding grounds of the Antarctic Peninsula (Dalla Rosa et al. 2001, Stevick et al. 2004).

In the Southern Hemisphere, the diet of the humpback whale is composed of euphausiids, primarily *Euphausia superba* (Matthews 1937). In the Northern Hemisphere, however, humpback whales prey on euphausiids of more than one genus, and also feed on a variety of schooling fish, including herring (*Clupea* sp.), mackerel (*Scomber scombrus*), sand lance (*Ammodytes* sp.), sardines (*Sardinops* or *Sardinella* sp.), anchovies (*Engraulis mordax*), and capelin (*Mallotus villosus*) (e.g. Watkins & Schevill 1979, Payne et al. 1986, Clapham et al. 1997).

The humpback whale is an appropriate animal model to test and address the questions and hypothesis I proposed due to its coastal distribution on feeding grounds for a relatively large period of the year, and the existence of many recovering populations (e.g. Clapham & Mead 1999). This species is common off British Columbia, with a wide distribution along the coast, including sheltered bays and straits (e.g. Gregr & Trites 2001, Williams & Thomas 2007), areas with potentially high anthropogenic impacts. Coastal British Columbia and Southeast Alaska constitute a unique feeding habitat for humpback whales, especially considering the numerous inlets and channels where the whales can be found and the variety of potential prey species available to them. The Antarctic Peninsula is also characterized by several inlets and islands, but has a simpler food web. Comparing these two distinct environments might improve comprehension of the relationships between whales and their environment. Comparisons of systems remain a valuable and now accepted means of evaluating and debating ecological generalizations (Pace 2001).

Few studies have been undertaken on the interaction between humpback whales and their feeding ground habitat. In the North Atlantic, Payne et al. (1986) studied humpback whale distribution on Georges Bank and the Gulf of Maine in relation to densities of the sand eel (*Ammodytes americanus*) and suggested that humpback whale distribution was not regulated by prey distribution alone. Kenney et al. (1996) identified shifts in cetacean distributions, including humpback whales, relative to trends in finfish abundance in the Gulf of Maine/Georges Bank. In the northeast North Pacific, Calambokidis et al. (2004) examined distribution of humpback whales in relation to depth, distance from shore, and sea surface temperature (SST) off the northern Washington coast. Moore et al. (2002)

investigated cetacean distribution and relative abundance in the Bering Sea with reference to oceanographic domains.

In the Southern Hemisphere, Kasamatsu et al. (2000) investigated cetacean distribution and encounter rates on feeding grounds in relation to SST, distance from ice edge and sea floor-slope type in Antarctic waters, but did not include the interior waters of Bransfield and Gerlache Straits, where high densities of humpback whales regularly occur (e.g. Secchi et al. 2001). They found no association between the densities of humpback and minke whales, and no relationship between humpback whales and SST or sea floor type. Reid et al. (2000) examined the relationships between densities of whales and Antarctic krill in a small area north of South Georgia, and observed positive correlations at the largest scale (80x100 km), which weakened at smaller scales. Thiele et al. (2000) made a qualitative analysis of cetacean distribution in relation to physical and biological features off eastern Antarctica during the Austral summer of 1995/96. Reilly et al. (2004) estimated krill consumption by baleen whales in the South Atlantic sector of the Southern Ocean. Friedlander et al. (2006) found relationships between whale distribution (humpback + minke) and distance to ice edge, bathymetric slope and zooplankton acoustic volume backscatter in the Marguerite Bay area (western Antarctic Peninsula), in autumn 2001 and 2002.

Gregr and Trites (2001) predicted the critical habitat of five whale species, including humpback whales, in coastal waters of British Columbia, using whaling records for the period 1948-1967 and six predictor variables (month, depth, slope, depth class, sea surface temperature and salinity). Their humpback whale models showed low correlation coefficients due to either small sample size, partitioning of data into monthly time scales, or because the association with the predictor variables was relatively weak and other factors were better predictors. However, their annual model confirmed strong affinity of humpback whales for coastal waters. They also pointed out the necessity of conducting field studies to improve predictions and the need to take a multiscale approach to investigate the predictors and the scales over which they operate. Hamazaki (2002) developed prediction models for 13 cetacean species, including humpback whales, for the mid-western North Atlantic Ocean, but also used only oceanographic and topographic variables as predictors. His model predicted seasonal shifts in habitat. Very few habitat models are available for humpback whales that include other potentially important predictors, such as primary and secondary production, depth of mixed layer and proximity to eddies and fronts. Yet statistically defendable habitat models are needed to guide conservation and management decisions and to understand how environmental changes will ultimately affect the distribution of humpback whales.

Making inferences from habitat models is limited to the range of data used to develop the predictive models (e.g. Hamazaki 2002), so current data are necessary to make inferences about the present status and habitat use of humpback whales in waters of coastal British Columbia. Studying the movement patterns and habitat use of individual whales can complement information obtained from the habitat models from survey data, as it may give different insights on the nature of relationships with the habitat. While the first provides information on individual whale behavior ranging from a few days to several weeks, habitat models from survey data are based on a series of snapshots of part of the population.

1.4. Thesis structure

My thesis is organized into five chapters. This first chapter includes a general introduction, the research questions and a general background to the research I undertook. The next three chapters consist of independent studies written for publication in peer-reviewed journals. In Chapter 2, I investigate the distribution and relative abundance of humpback whales in relation to environmental variables in British Columbia using generalized additive models. In Chapter 3, I follow the same habitat modeling approach to study humpback whales in the western Antarctic Peninsula. Some repetition in the methods sections of Chapters 2 and 3 was therefore necessary, as well as between the general background in Chapter 1 and the introductions in Chapters 2 and 3. In Chapter 4, I investigate the movements and habitat use of satellite-tagged humpback whales around the Antarctic Peninsula. This chapter was published in the journal Polar Biology (Dalla Rosa et al. 2008). In Chapter 5, I summarize my findings and present concluding remarks regarding my proposed research questions. I finish this chapter with a discussion of potential caveats in my research and with recommendations for future research.

1.5. References

Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling 157:101-118

Baker CS, Herman LM, Perry A, Lawton WS, Straley JM, Wolman AA, Kaufman GD, Winn HE, Hall JD, Reinke JM, Ostman J (1986) Migratory movement and population structure of humpback whales, *Megaptera novaeangliae*, in the central and eastern North Pacific. Marine Ecology Progress Series 31:105-119

Baumgartner MF (1997) The distribution of Risso's dolphin (*Grampus griseus*) with respect to the physiography of the northern Gulf of Mexico. Marine Mammal Science 13:614-638

Baumgartner MF, Mullin KD, May LN, Leming TD (2001) Cetacean habitats in the northern Gulf of Mexico. Fishery Bulletin 99:219-239

Calambokidis J, Steiger GH, Ellifrit DK, Troutman BL, Bowlby CE (2004) Distribution and abundance of humpback whales (*Megaptera novaeangliae*) and other marine mammals off the northern Washington coast. Fishery Bulletin 102:563-580

Calambokidis J, Steiger GH, Straley JM, Herman LM, Cerchio S, Salden DR, Urban J, Jacobsen JK, von Ziegesar O, Balcomb KC, Gabriele CM, Dahlheim ME, Uchida S, Ellis G, Miyamura Y, de Guevara PL, Yamaguchi M, Sato F, Mizroch SA, Schlender L, Rasmussen K, Barlow J, Quinn TJ (2001) Movements and population structure of humpback whales in the North Pacific. Marine Mammal Science 17:769-794

Chittleborough RG (1965) Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). Australian Journal of Marine and Freshwater Research 16:33-128

Clapham PJ, Leatherwood S, Szczepaniak I, Brownell RL (1997) Catches of humpback and other whales from shore stations at Moss Landing and Trinidad, California, 1919-1926. Marine Mammal Science 13:368-394

Clapham PJ, Mead JG (1999) *Megaptera novaeangliae*. Mammalian Species 604:1-9

Connor EF, Courtney AC, Yoder JM (2000) Individuals-area relationships: the relationship between animal population density and area. Ecology 81:734-748

Croll DA, Tershy BR, Hewitt RP, Demer DA, Fiedler PC, Smith SE, Armstrong W, Popp JM, Kiekhefer T, Lopez VR, Urban J, Gendron D (1998) An integrated approach to the foraging ecology of marine birds and mammals. Deep-Sea Research Part II: Topical Studies in Oceanography 45:1353-1371

Dalla Rosa L, Secchi ER, Kinas PG, Santos MCO, Martins MB, Zerbini AN, Bethlem CBP (2001) Photo-identification of humpback whales, *Megaptera novaeangliae*, off the Antarctic Peninsula from 1997/98 to 1999/2000. Memoirs of the Queensland Museum 47:555-561

Dalla Rosa L, Secchi ER, Maia YG, Zerbini AN, Heide-Jorgensen MP (2008) Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula. Polar Biology 31:771-781

Dawbin WA (1966) The seasonal migratory cycle of humpback whales. In: Norris K (ed) Whales, Dolphins and Porpoises. University of California Press, Berkeley, p 145-170

Ferrero RC, Hobbs RC, Van Blaricom GR (2002) Indications of habitat use patterns among small cetaceans in the Central North Pacific based on fisheries observer data. The Journal of Cetacean Research and Management 4:311-321

Fiedler PC, Reilly SB, Hewitt RP, Demer D, Philbrick VA, Smith S, Armstrong W, Croll DA, Tershy BR, Mate BR (1998) Blue whale habitat and prey in the California Channel Islands. Deep-Sea Research Part II: Topical Studies in Oceanography 45:1781-1801

Fretwell SD, Lucas HL (1970) On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:136-156

Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. Marine Ecology Progress Series 317:297-310

Gregr EJ, Trites AW (2001) Predictions of critical habitat for five whale species in the waters of coastal British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 58:1265-1285

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

Hamazaki T (2002) Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, USA to Nova Scotia, Canada). Marine Mammal Science 18:920-939

Harper DGC (1982) Competitive foraging in mallards: ideal free ducks. Animal Behavior 30:575-584

Heithaus MR, Dill LM (2002) Feeding strategies and tactics. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, New York, p 412-422

Heithaus MR, Dill LM (2006) Does tiger shark predation risk influence foraging habitat use by bottlenose dolphins at multiple spatial scales? Oikos 114:257-264

IPCC (2007) Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds.)] Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Jaquet N, Whitehead H (1996) Scale-dependent correlation of sperm whale distribution with environmental features and productivity in the South Pacific. Marine Ecology Progress Series 135:1-9

Kasamatsu F, Matsuoka K, Hakamada T (2000) Interspecific relationships in density among the whale community in the Antarctic. Polar Biology 23:466-473

Katona SK, Beard JA (1990) Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. Reports of the International Whaling Commission (Special Issue)12:295-305

Kenney RD, Payne PM, Heinemann DW, Winn HE (1996) Shifts in Northeast Shelf cetacean distributions relative to trends in Gulf of Maine / Georges Bank finfish abundance. In: Sherman K, Jaworski NA, Smayda T (eds) The Northeast Shelf Ecosystem: Assessment, Sustainability and Management. Blackwell Science, Cambridge, p 169-196

Krebs CJ (1994) Ecology: The Experimental Analysis of Distribution and Abundance, Harper Collins College Publishers, New York

Loeb V, Siegel V, HolmHansen O, Hewitt R, Fraser W, Trivelpiece W, Trivelpiece S (1997) Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. Nature 387:897-900

Matthews LH (1937) The humpback whale, *Megaptera nodosa*. Discovery Reports 17:7-92

Moore SE, Waite JM, Friday NA, Honkalehto T (2002) Cetacean distribution and relative abundance on the central-eastern and the southeastern Bering Sea shelf with reference to oceanographic domains. Progress in Oceanography 55:249-261

Oreskes N (2004) Beyond the ivory tower: the scientific consensus on climate change. Science 306:1686

Pace ML (2001) Prediction and the aquatic sciences. Canadian Journal of Fisheries and Aquatic Sciences 58:63-72

Payne PM, Nicolas JR, O'Brien L, Powers KD (1986) The distribution of the humpback whale, *Megaptera novaeangliae*, on Georges Bank and in the Gulf of Maine in relation to densities of the sand eel, *Ammodytes americanus*. Fishery Bulletin 84:271-278

Perry A, Baker CS, Herman LM (1990) Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. Reports of the International Whaling Commission (Special Issue) 12:307-317

Pierotti R (1982) Habitat selection and its effect on reproductive output in the herring gull in Newfoundland. Ecology 63:854-868

Pyke GH (1980) Optimal foraging in bumblebees. Calculation of net rate of energy intake and optimal patch choice. Theoretical Population Biology 17:232-246

Reid K, Brierley AS, Nevitt GA (2000) An initial examination of relationships between the distribution of whales and Antarctic krill (*Euphausia superba*) at South Georgia. The Journal of Cetacean Research and Management 2:143-149

Reilly S, Hedley S, Borberg J, Hewitt R, Thiele D, Watkins J, Naganobu M (2004) Biomass and energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 51:1397-1409

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleraceae*). Ecological Monographs 45:95-120

Schilling NS (2005) Survival of the fittest: fish in patchy environments show ideal free distribution (IFD). Eukaryon 1:11-16

Scott JM, Heglund J, Morrison ML, Haufler JB, Raphael MG, Wall WA, Samson FB (eds) (2002) Predicting Species Occurrences: Issues of Accuracy and Scale, Island Press, Washington

Secchi ER, Dalla Rosa L, Kinas PG, Santos MCO, Zerbini AN, Bassoi M, Moreno IB (2001) Encounter rates of whales around the Antarctic Peninsula with special reference to humpback whales, *Megaptera novaeangliae*, in the Gerlache Strait: 1997/98 to 1999/2000. Memoirs of the Queensland Museum 47:571-578

Sims DW (2003) Tractable models for testing theories about natural strategies: foraging behavior and habitat selection of free-ranging sharks. Journal of Fish Biology 63(Supplement A):53-73

Sokolowski MBC, Tonneau F, Freixa I Baque EF (1999) The ideal free distribution in humans: An experimental test. Psychonomic Bulletin and Review 6:157-161

Steele JH (1995) Can ecological concepts span the land and ocean domains? In: Powell TM, Steele JH (eds) Ecological Time Series. Chapman & Hall, New York, p 5-19

Stevick PT, Aguayo A, Allen J, Avila IC, Capella J, Castro C, Chater K, Dalla Rosa L, Engel MH, Felix F, Florez-Gonzalez L, Freitas A, Haase B, Llano M, Lodi L, Munoz E, Olavarria C, Secchi E, Scheidat M, Siciliano S (2004) Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. The Journal of Cetacean Research and Management 6:109-113

Stevick PT, Allen J, Berube M, Clapham PJ, Katona SK, Larsen F, Lien J, Mattila DK, Palsboll PJ, Robbins J, Sigurjonsson J, Smith TD, Oien N, Hammond PS (2003) Segregation of migration by feeding ground origin in North Atlantic humpback whales (*Megaptera novaeangliae*). Journal of Zoology 259:231-237

Thiele D, Chester ET, Gill PC (2000) Cetacean distribution off Eastern Antarctica (80-150 degrees E) during the Austral summer of 1995/1996. Deep-Sea Research Part II: Topical Studies in Oceanography 47:2543-2572

Tynan CT, DeMaster DP (1997) Predictions of Antarctic climatic and ecological response to global warming and ozone depletion. Reports of the International Whaling Commission 47:953-989

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389-395

Watkins WA, Schevill WE (1979) Aerial observation of feeding-behavior in 4 baleen whales - *Eubalaena glacialis*, *Balaenoptera borealis*, *Megaptera novaeangliae*, and *Balaenoptera physalus*. Journal of Mammalogy 60:155-163

Williams R, Thomas L (2007) Distribution and abundance of marine mammals in the coastal waters of BC, Canada. The Journal of Cetacean Research and Management 9:15-28

Wood SN (2006) Generalized Additive Models: An Introduction with R, Chapman and Hall/CRC Press, Boca Raton, Florida

Woodley TH, Gaskin DE (1996) Environmental characteristics of North Atlantic right and fin whale habitat in the lower Bay of Fundy, Canada. Canadian Journal of Zoology 74:75-84

2. Distribution and relative abundance of humpback whales in relation to environmental variables in coastal British Columbia and adjacent waters[1]

2.1. Introduction

Humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific feed from California to western Alaska (Perry et al. 1990). They are common off British Columbia (BC) from spring to fall and are widely distributed along the coast (Gregr et al. 2000, Williams & Thomas 2007).

Most of what is known about humpback whales in coastal British Columbia originates from whaling records. Humpback whales, as well as sperm (*Physeter macrocephalus*), fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), and blue (*Balaenoptera musculus*) whales were intensively hunted during commercial whaling, between 1908 and 1967 (Nichol & Heise 1992, Gregr et al. 2000). Additional information obtained mainly through photo-identification studies has shown movements and migratory destinations and provided estimates of abundance (Darling et al. 1996, Urbán-Ramirez et al. 2000, Calambokidis et al. 2008, Rambeau 2008). The Canadian Department of Fisheries and Oceans (DFO) maintains a catalogue of humpback whales seen in BC waters containing over 2,000 individuals photographed between 1989 and 2006. In recent years, systematic line-transect surveys have also been conducted to estimate cetacean abundance, including humpback whales, in inshore BC waters (Williams & Thomas 2007).

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[1] A version of this chapter will be submitted for publication. Dalla Rosa L, Ford JKB and Trites AW. Distribution and relative abundance of humpback whales in relation to environmental variables in coastal British Columbia and adjacent waters.

Concerns about the potential effects of climate change (IPCC 2007) on the recovery of North Pacific humpback whales (Calambokidis & Barlow 2004, Calambokidis et al. 2008) can not be properly addressed without a better understanding of species-habitat relationships. Unfortunately, such studies on humpback whales and their habitat are still rare in most regions, including the feeding grounds of the eastern North Pacific. Humpback whales seem to be associated with bathymetry in the Bering Sea (Moore et al. 2002) and off the northern Washington coast, where they also prefer relatively colder waters in comparison to other offshore species found in the area (Calambokidis et al. 2004). In the northern California Current System, sea surface temperature (SST), depth and distance to the alongshore upwelling front were the most important variables in a multiple logistic regression model for humpback whales during late spring 2000, and sea surface salinity, latitude and depth were the most important predictors during summer of the same year (Tynan et al. 2005). Depth and distance, SST and fluorescence in the top 50 m of the nearest Aleutian pass resulted in the most significant correlations with humpback whale occurrence along the Aleutian Islands in 2000 and 2001 (Sinclair et al. 2005). Nevertheless, additional habitat modeling studies involving multi-year surveys and a wide range of explanatory variables are necessary to identify what oceanographic processes influence the distribution of humpback whales.

Gregr & Trites (2001) produced predictive habitat models for five whale species, including humpback whales, in BC coastal waters, using whaling records for the period 1948-1967 and six predictor variables (month, depth, slope, depth class and climatologies of SST and salinity). Their humpback whale models showed low correlation coefficients due to either small sample size or relatively weak association with the predictor variables.

However, their annual model confirmed strong association of humpback whales with coastal waters (Gregr & Trites 2001). Inferences of predictive habitat models are limited to the range of data (e.g. Hamazaki 2002, Redfern et al. 2006), so habitat models based on contemporary data are necessary to make inferences about the present distribution and habitat use of humpback whales in BC waters. This is vital for providing scientific advice towards identifying critical habitat of humpback whales under DFO guidelines.

The currents and ocean structure along the BC coast, particularly in the semi-protected northern shelf region, are shaped by deep-sea processes, tides, winds and estuarine processes (Thomson 1981). Therefore, waters with coastal, offshore or mixed properties may be found in the region, resulting in a dynamic oceanographic environment. In light of this, it is desirable to implement habitat models that include not only fixed physiographic variables, but also other potentially important predictors, such as primary productivity and proximity to eddies and fronts, at different spatial and temporal scales.

We sought to investigate the distribution and relative abundance of humpback whales in BC waters in relation to a range of environmental variables, including oceanographic and remote sensing data, using GIS and generalized additive models (GAMs). We hypothesize that the higher densities of humpback whales will be positively correlated with areas of enhanced biological productivity driven by physical forcing.

2.2. Material and methods

2.2.1. Data collection

2.2.1.1. Surveys

Data on cetacean distribution were obtained during six surveys conducted between 2004 and 2006 off the coast of British Columbia, including the waters of Queen Charlotte Sound, Hecate Strait and Dixon Entrance, and the offshore waters on the west coast of the Queen Charlotte Islands, Vancouver Island and Washington State (Fig. 2.1). Five surveys were conducted during spring and fall months aboard vessels from the Department of Fisheries and Oceans (DFO), Canada. The first three of these surveys were part of the ‘Structure of Populations, Levels of Abundance, and Status of Humpbacks’ (SPLASH) project (Calambokidis et al. 2008), aimed primarily at photo-identification and genetic studies. The only summer survey, in July-August 2005, was part of a joint Canadian and U.S. Pacific hake survey aboard the NOAA ship *Miller Freeman* (MF), which was used as a platform of opportunity for cetacean observations. Survey periods and vessels are detailed in Table 2.1.

Table 2.1 – Survey periods and vessels used in the collection of cetacean sighting data.

Cruise	Year	Season	Period	Vessel
1	2004	Spring	10 – 23 May	CCGS *John P. Tully*
2	2004	Fall	14 – 21 October	CCGS *John P. Tully*
3	2005	Spring	10 – 21 May	CCGS *Vector*
4	2005	Summer	19 July – 10 August	NOAA *Miller Freeman*
5	2006	Spring	29 April – 20 May	CCGS *Tanu*
6	2006	Fall	21– 29 October	CCGS *John P. Tully*

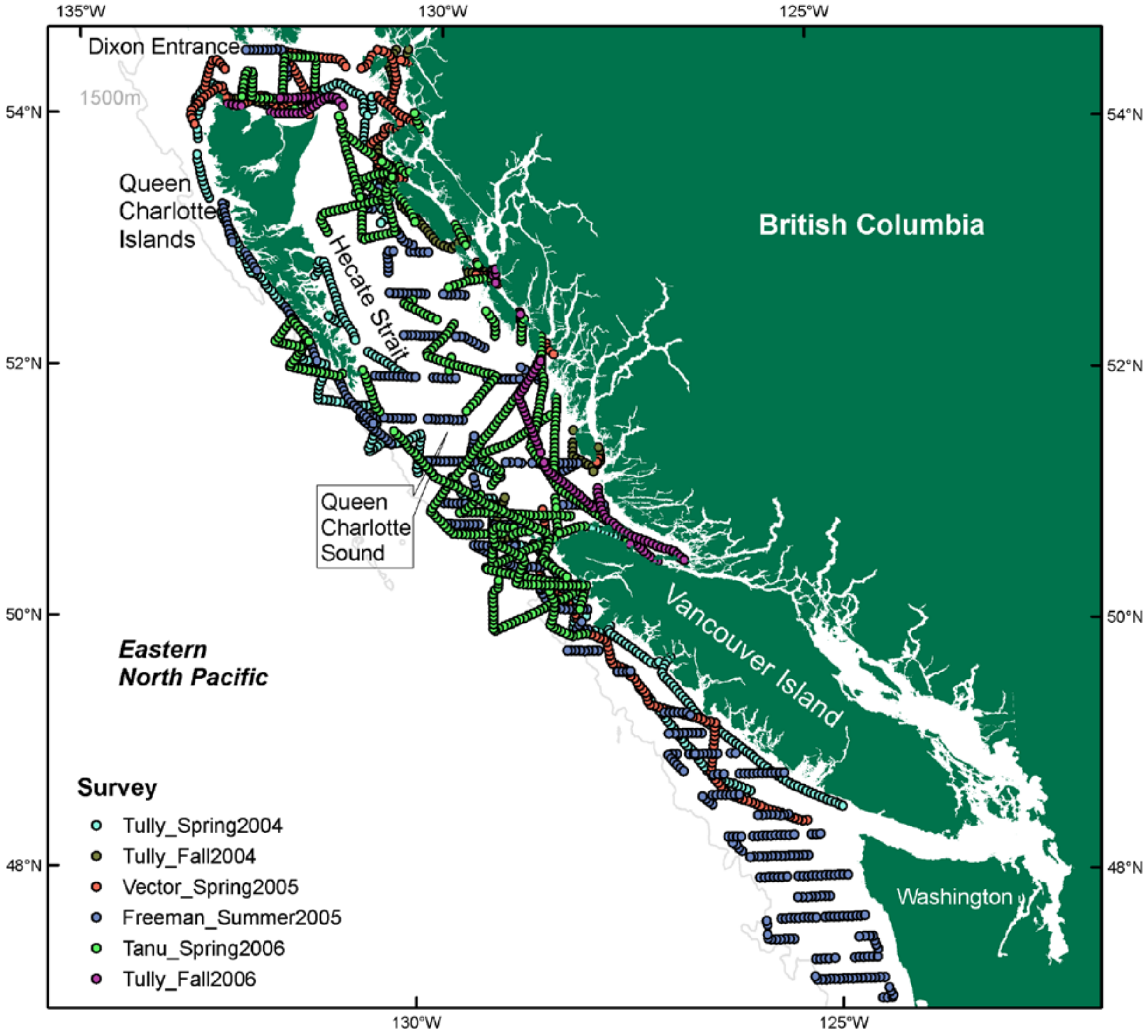


Fig. 2.2 – Cetacean surveys conducted off the coast of British Columbia between 2004 and 2006.

2.2.1.2. Effort and sighting data

Although surveys were non-systematic, searching effort followed strict criteria while vessels were in transit. Trained observers on port and starboard scanned with 7x50 Fujinon binoculars and naked eye from about 10 degrees on the other side of the ship’s bow to 90 degrees on their side. Fujinon 25x150 binoculars (“big eyes”) were occasionally used by the primary observers, and tended to be used by auxiliary observers to help with species identification or group size estimation. The observers rotated through port, starboard and data recorder positions every 30 or 40 minutes, depending on the cruise, with a minimum 2-hour rest period which varied according to the number of extra observers on the cruise. For the MF cruise, the only two observers that were available at each leg worked together, with one observer reporting sightings to the other, who acted as data recorder. Port and starboard positions were switched every 30 minutes, and resting took place during fishing operations and CTD casts.

The ship's position, course and speed were continuously recorded on a laptop computer connected to the ship's GPS unit. Sightings and environmental conditions were recorded on datasheets on the first three cruises and in Logger 2000, IFAW's data logging software, on the remaining cruises. Sighting data included time, location, ship's true heading, number of reticles from the horizon to the sighting, bearing to the sighting, species identification, number of animals (best, minimum and maximum estimates), sighting cue and other comments. Weather and sea conditions (e.g. Beaufort sea state, swell height and visibility) were recorded on every observer rotation and when conditions changed. Searching effort was carried out only in good conditions, i.e., up to Beaufort 5 and with visibility of 3 nautical miles or higher. Observation platforms ranged in height from 8.2 m (*Vector*) to 15.5 m (*John P. Tully*).

Radial distance to each sighting was calculated from binocular reticle readings and platform height (Lerczak & Hobbs 1998, see also associated Errata), and corrected based on distance to land when the coastline was at shorter distances than the horizon. The location of each whale group was then estimated from bearing and radial distance to the sighting and the ship’s true heading at the moment of the sighting. On-effort sightings and tracklines were imported into geodatabases in ArcGIS 9.2 (ESRI, Redlands, CA). Tracklines were divided into 4-km segments. If a segment at the endpoint of a trackline was shorter than 2 km, it was added to the previous segment; otherwise, it was left as a separate segment. Each sighting was assigned to the closest segment. Segments were therefore the sampling unit, and the number of whales per segment represented encounter rates.

2.2.2. Environmental data

A series of GIS layers was produced or imported into ArcGIS containing physiographic, remote sensing and climatological datasets on a BC Albers equal area projection (Table 2.2).

Bathymetry data were obtained from a 75-m digital elevation model (DEM) produced by the Geological Survey of Canada (Pacific), Natural Resources Canada, Sidney, BC (Fig. 2.2A). A 250-m DEM of the Cascadia region (http://geopubs.wr.usgs.gov/open-file/of99-369/) was also used for the southern portion of the study area not covered by the first dataset. Bathymetric slope (Fig. 2.2B) and 100-m and 200-m contour lines were originated from the DEMs using Spatial Analyst’s slope and contour tools, respectively, in ArcGIS.

Table 2.2 – Environmental variables sampled along survey segments and their corresponding names and transformation (if any) for the data analyses. Note that not all variables were considered in the modeling process (see methodology for more details).

Environmental variable	Unit	Temporal resolution	Transfor-mation	Reference name (s)
Latitude	m	--	none	Lat
Longitude	m	--	none	Lon
Depth	m	--	log	logDepth
Slope	degree	--	log	logSlope
Distance to land	m	--	square root	sqrtdistland
Distance 100-m isobath	m	--	square root	sqrtcontour100m
Distance 200-m isobath	m	--	square root	sqrtcontour200m
Sea surface temperature	^{o}C	Seasonal	none	SST_s
		Monthly	none	SST_m
		8-day	none	SST_w
Distance to SST fronts	m	8-day	square root	sqrtdistfront_w
Front probability index	prob.	Monthly		sqrtfrontspi_m
Chlorophyll *a*	mg/m3	Monthly	log	logchla_m logchla_mlag
		8-day	log	logchla_w logchla_wlag logchla_wmerged logchla_wmerged_lag
Net primary production	mgC/m^2/d	Monthly	log	logNPP_m logNPP_mlag
		8-day	log	logNPP_w logNPP_wlag
Sea surface height deviation	m	Monthly	none	SSHdev
Tidal speed	RMS	Climatology	log	logtidal_veloc
Salinity (model)		Climatology	exponential	expsal_surf
			exponential	expsal_bottom
Temperature (model)	^{o}C	Climatology	none	temp_surf
			none	temp_bottom

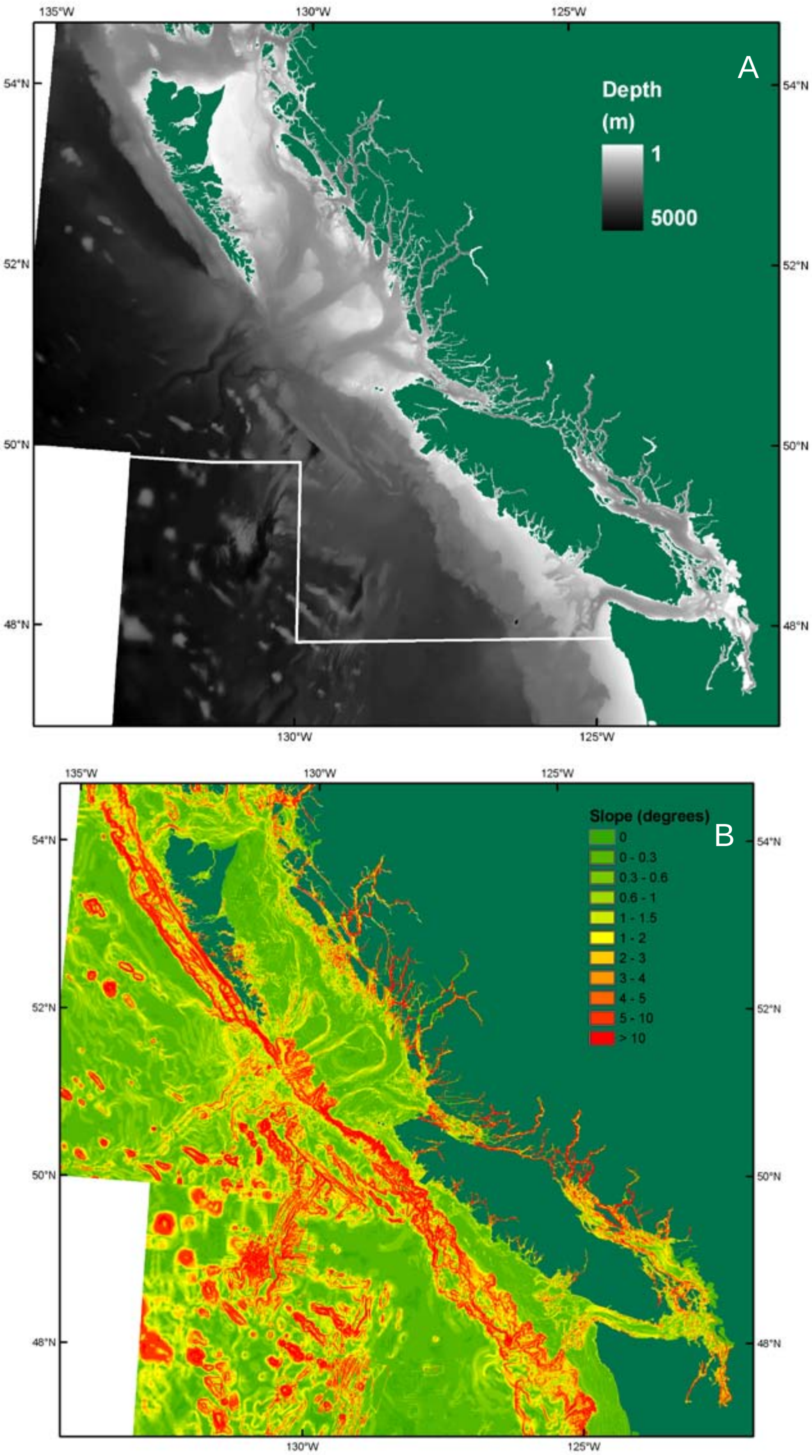


Fig. 3.2 – A) Digital elevation models used in this study. The white line divides the 75-m resolution (upper) from the 250-m resolution DEM (lower); B) Slope raster (in degrees) produced from the DEMs.

Chlorophyll *a* (chl-*a*) concentration (mg/m^3) was used as a proxy for primary productivity, and was obtained as seasonal, monthly and 8-day images from the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the Aqua satellite (available at http://oceancolor.gsfc.nasa.gov/). These chl-*a* images consisted of the binned product, a 4.63-km resolution dataset stored in an equal area projection. Each image was re-projected, clipped and exported as point data to an ASCII file using the SeaDAS 5.1 software, an image analysis package for ocean color data. Subsequently, each file was imported to a point geodatabase in ArcGIS and converted to raster (Fig. 2.3A). In addition, two mapped (equal-angle grid) chl-*a* image products were also downloaded: a MODIS rolling 32-day ~4-km composite and an 8-day MODIS-SeaWiFS (Sea-viewing Wide Field-of-view Sensor) ~9-km merged image. These were imported to ArcGIS using the Marine Geospatial Ecology Tools (MGET) (Roberts et al. in review). The merged product has potentially increased image coverage, a desirable feature particularly with 8-day images which tend to be more affected by cloud coverage. Maximum chl-*a* concentration values in mapped images are scaled down to 64.56 mg/m^3, whereas the original maximum values are kept in the binned images.

Sea surface temperature (SST) was obtained as seasonal, monthly and 8-day MODIS 4.63-km binned data (Fig. 2.3B), and processed in the same way as the chl-*a* binned product. Fronts were identified in the SST raster images using MGET, which implements the Cayula & Cornillon (1992) single-image edge detection algorithm. Custom settings in the parameters of the algorithm which produced better results with the MODIS images included a histogram window size of 16x16 and a histogram window stride of 4 pixels. Weak fronts with mean temperature difference of less than 0.375^{o}C were not included.

The fronts in the output rasters were converted to polylines to allow calculation of Euclidean distances between each effort segment and the closest front (Fig. 2.4A).

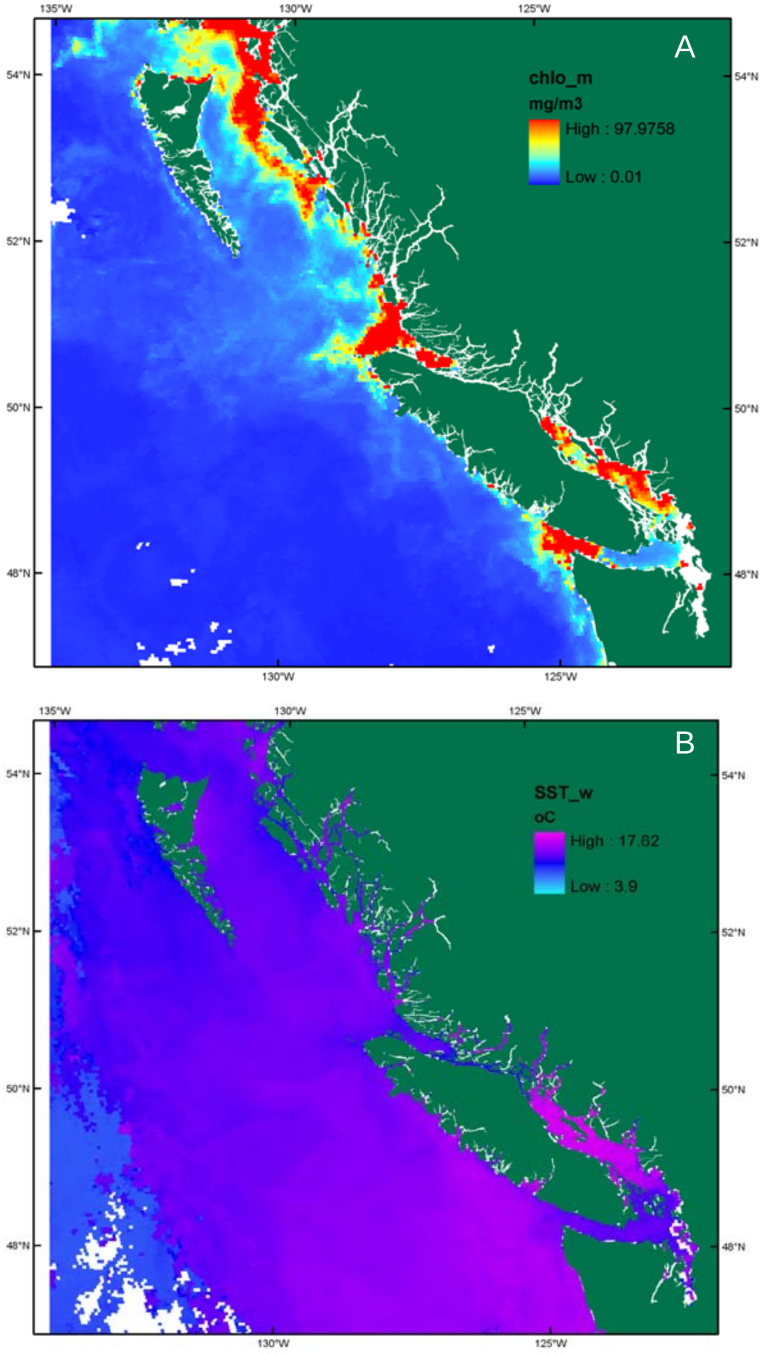
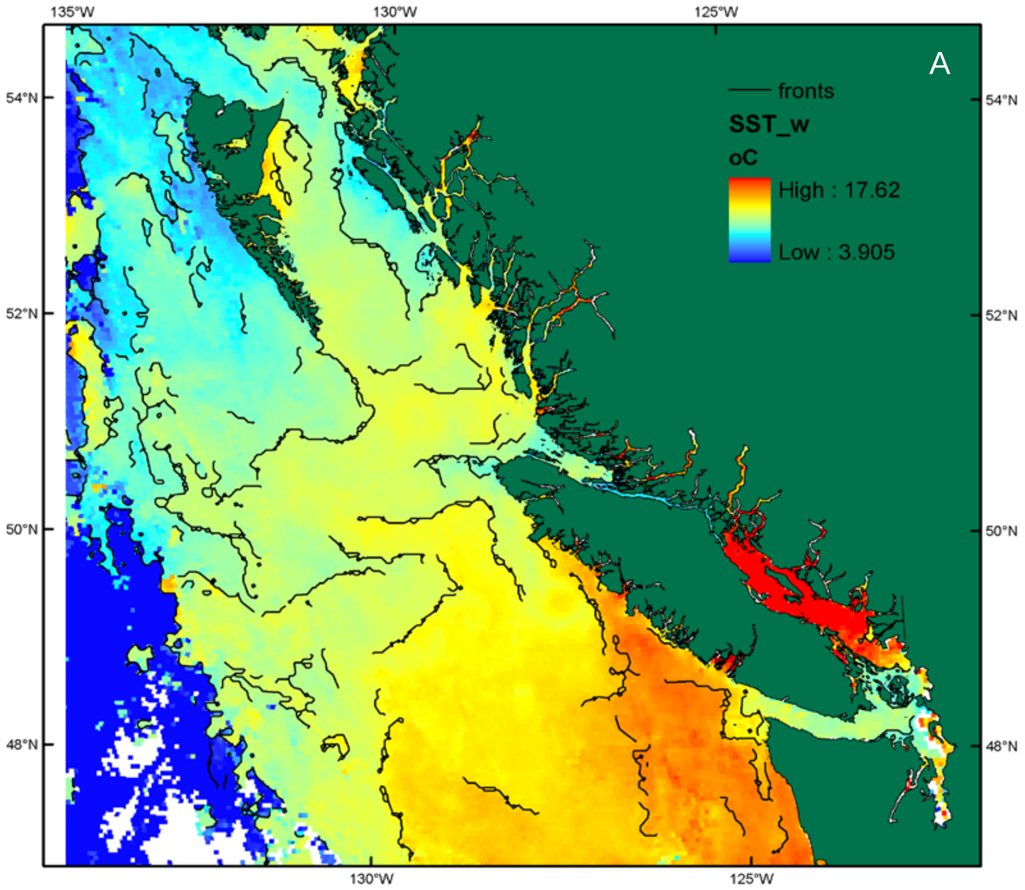


Fig. 2.4 – Example of A) a monthly chlorophyll *a* image obtained from the MODIS 4.63-km resolution binned product; B) 8-day SST image obtained the MODIS 4.63-km resolution binned product.



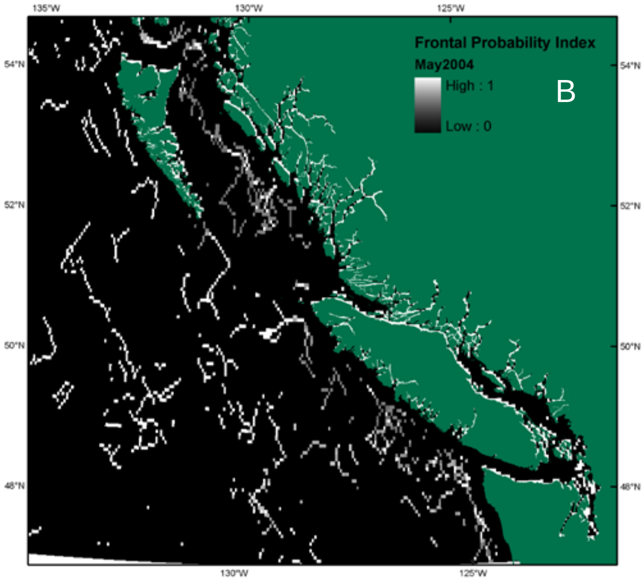


Fig. 2.5 – A) Thermal fronts identified on an 8-day SST raster of 16-23 May 2004. The SST image is the same presented in figure 2.3B, with a different color representation to give a better idea of the performance of the algorithm; B) example of image containing oceanic front probabilities for May 2004.

The Oceanic Front Probability Index (NOAA CoastWatch Program) is an experimental dataset produced by applying an edge detection algorithm to daily SST images from the Geostationary-orbiting Operational Environmental Spacecraft (GOES) satellites (Breaker et al. 2005). The index is calculated as the number of times a pixel is classified as a front (gradient > 0.375^{o}C) divided by the number of cloud-free days for the given time period. These data were acquired as monthly composites mapped to an equal angle grid (~5.5-km resolution) in Arcview gridded format. Each file was then imported to an ArcGIS raster and re-projected (Fig. 2.4B).

Monthly and 8-day net primary production (NPP) was obtained from the Ocean Productivity website (http://www.science.oregonstate.edu/ocean.productivity/). The selected product uses the Vertically Generalized Production Model (VGPM) (Behrenfeld & Falkowski 1997) as the standard algorithm, where net primary production is a function of chl-*a*, available light, and the photosynthetic efficiency, which is temperature-dependent. The resulting ~9-km resolution NPP estimates (Fig. 2.5A) were based on SeaWiFS chl-*a* values and on sea surface temperature from the Advanced Very High Resolution Radiometer (AVHRR).

Sea surface height deviation (SSHd) from the AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data) program was obtained as monthly averages at a 0.25-degree resolution (Fig. 2.5B). SSHd, or sea level anomaly, is the difference between measured SSH and the expected mean SSH (see Ducet et al. 2000 for more details).

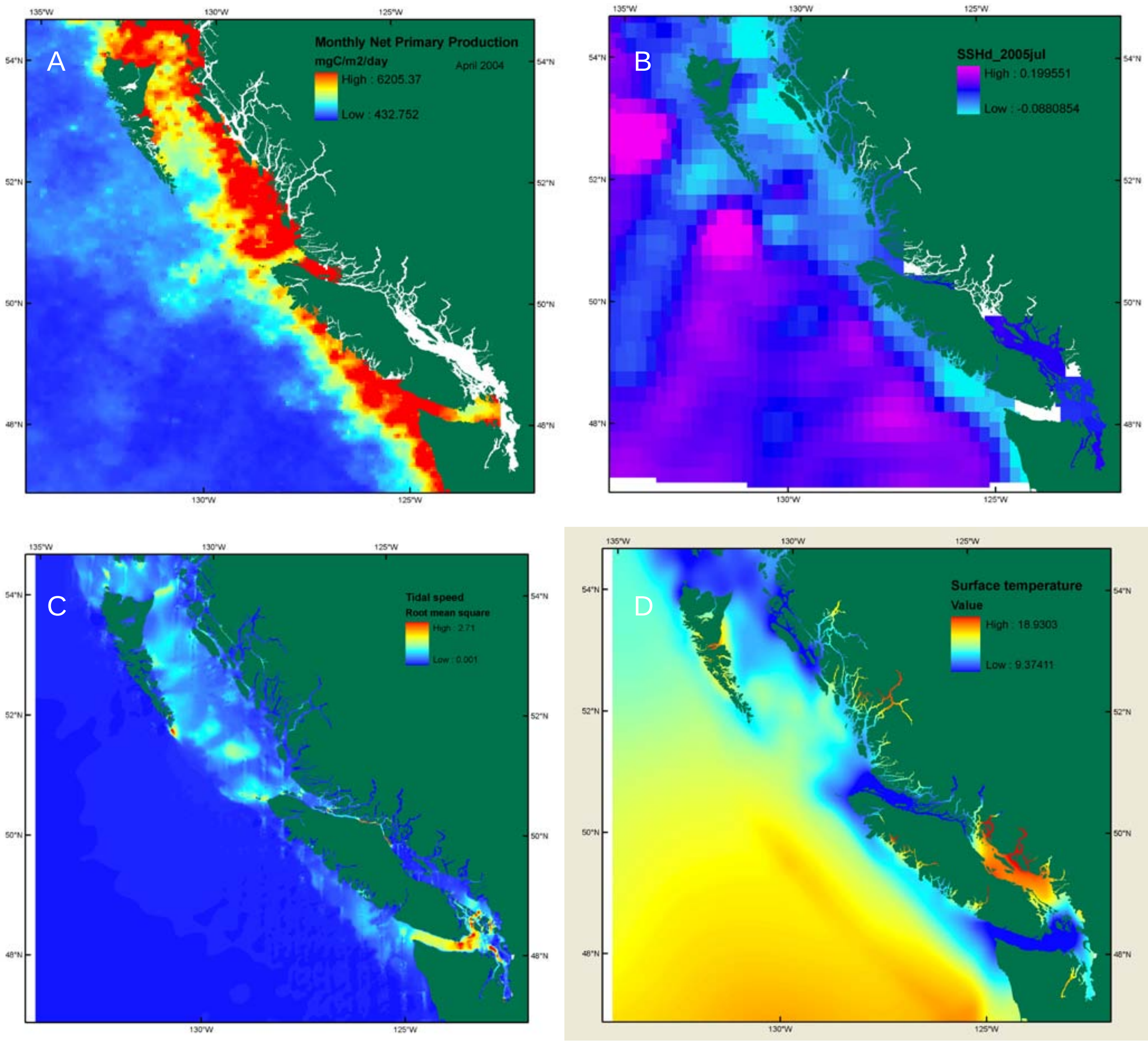


Fig. 2.6 – A) Example of a ~9-km monthly image of net primary production (NPP) based on the Vertically Generalized Production Model (VGPM); B) Example image of monthly sea surface height deviation (SSHd) from the AVISO program for July 2005; C) Tidal speeds for the study area; D) Climatology of summer surface temperature for the study area.

Five additional explanatory variables were extracted from datasets in a circulation model for the Northeastern Pacific Ocean maintained by Dr. Mike Foreman (Institute of Ocean Sciences, Sidney, British Columbia). These include the root mean square of tidal speeds (RMS tidal speed) and four climatologies: bottom and surface summer temperature and bottom and surface summer salinity. These data were imported to point geodatabases in ArcGIS and interpolated to 500-m^2 resolution rasters using Spatial Analyst's inverse distance weighting (IDW) (Figs. 2.5C-D).

2.2.3. Sampling environmental data

The GIS layers containing the environmental variables were sampled at each segment in two different ways: 1) all distances to features were measured as the shortest straight-line distance from the midpoint of the segment to the feature; and 2) all rasters were sampled as the mean value of 5 points, i.e., the values extracted at the midpoint and at the vertices of a 2x2-km box placed over the midpoint following the segment's orientation angle. This latter approach aimed at providing a more balanced sampling for those segments falling near the margins of adjacent raster pixels with different values and whose searching effort certainly included at least part of them. The chl-*a* and NPP layers were sampled according to their corresponding time periods but also with time lags that included the previous month for the monthly data and a 2-week prior for the 8-day data.

Some environmental data to be used as explanatory variables in the models were not available for the inland waters of the Inside Passage and adjacent channels; therefore, segments and observations made in those areas were not included in the analyses.

2.2.4. Data analyses

2.2.4.1. Statistical modeling

Exploratory data analysis was conducted to identify outliers (e.g. boxplots) and other potential problems in the data that could affect model fitting (Zuur et al. 2007). Most explanatory variables were transformed to attain an even spread of values. Depth, slope, chl-*a* and NPP values were log-transformed and distances to features were square-root transformed (Table 2). Additionally, pairplots of all explanatory variables were produced to identify correlated variables (see example in Fig. 2.6). The variable with lower spatial/temporal resolution or coverage was dropped from further analyses when two variables were found to be highly correlated ($r > 0.75$). This approach avoided multicollinearity, which could have led to model performance issues (Zuur et al. 2007), and also identified and eliminated covariates that were not ecologically meaningful if put together in the same model, given their similar explanatory power (e.g. monthly and 8-day SST).

Humpback whale encounter rates were modeled as a function of environmental variables using Generalized Additive Models (GAMs) (Hastie & Tibshirani 1990). GAMs are semiparametric models where the dependent variable is linked to an additive predictor through a nonlinear link function. The goal was, therefore, to investigate nonlinear relationships between humpback whale distribution and relative abundance and the environmental variables. A quasi-Poisson error distribution with variance proportional to the mean was used to account for overdispersion. With a logarithmic link function, the general model structure was:

$$\log(\mathrm{E}[n_i]) = \sum_k s_k(z_{ik}) + \mathrm{offset}(\log[\mathrm{seg\_length}]_i)$$

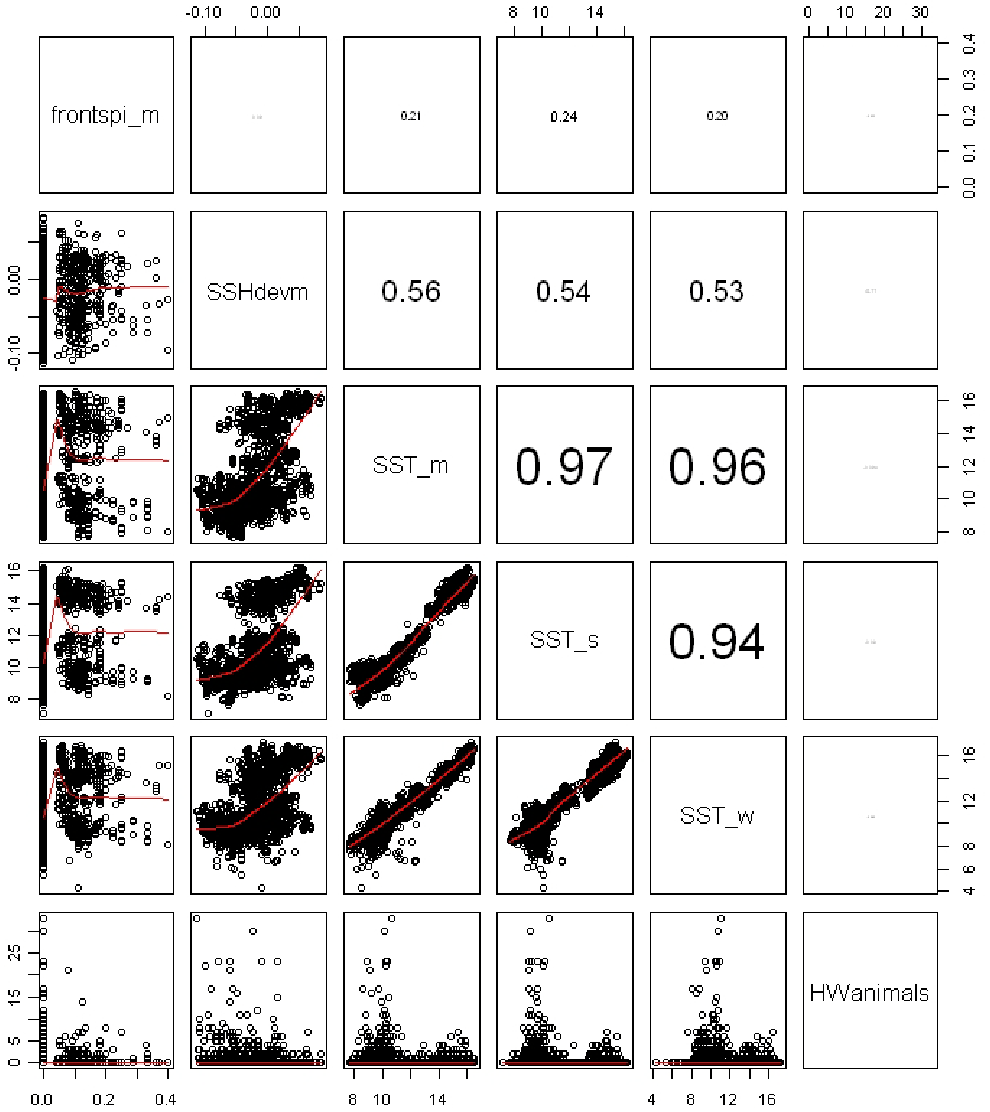


Fig. 2.7 – Example of pairplots produced for identifying highly correlated explanatory variables during the exploratory data analysis.

where s_k are smooth functions of the explanatory covariates, and z_{ik} is the value of the k^{th} explanatory covariate in the i^{th} segment. The length of each segment was included as an offset, so that the encounter rates could be modeled as count data.

GAMs were fitted using the mgcv package v. 1.4-1 for the statistics program R (Wood 2001). The degree of smoothness of model terms was estimated as part of fitting using penalized regression splines and parameters selected by generalized cross validation (GCV). Due to the tendency of GAMs to overfit, the argument gamma = 1.4 was used (Kim & Gu 2004), inflating the effective degrees of freedom by 1.4 in the GCV score (Wood 2006). Also, the basis dimension parameter, k, was set to 8, thereby limiting the maximum allowable degrees of freedom of each term to 7 and further avoiding overfitting by restraining the wiggliness of the smoothing functions of the model terms, which leads to more ecologically defensible functions.

The mgcv package does not have a function to account for missing values of the covariates; therefore, segments containing missing values of one of the explanatory variables were automatically excluded from model fitting.

Model selection was based on GCV scores (Wood 2001, 2006), percentage deviance explained and a visual examination of residual plots, and followed a backwards selection procedure. First, model terms were dropped, one at a time, if the approximate 95% confidence interval of the smoothing function contained zero everywhere and, if by dropping the term, the GCV score also dropped. Next, each remaining term was also tested for lower GCV values and improvements in deviance explained and residual plots. Very small increases in GCV scores did prevent a variable from being dropped if it resulted in a simpler model with similar or improved explanatory power, as measured by the % deviance explained, or if an improvement in residual plots was observed. Competing models were not compared with a formal statistical test either because the models started with different sets of variables (one of the explanatory variables was replaced by another variable which was highly correlated), or because the models were not nested.

Spatial autocorrelation in the residuals was investigated through a variogram analysis using the geoR package v. 1.6-22 for R (Ribeiro & Diggle 2001). One of the model assumptions is that residuals are independently distributed. Violation of this assumption, which would suggest the need for a different type of model, was assessed by comparing the empirical variogram of deviance residuals with the Monte Carlo envelope of empirical variograms computed from 300 independent random permutations of the residuals, holding the corresponding locations fixed (Diggle & Ribeiro 2007).

2.2.4.2. Predicting encounter rates of humpback whales

Maps of predicted encounter rates of humpback whales were produced to verify if the overall predicted distribution pattern throughout the study area matched with the observed distribution. A 4.63x4.63-km grid was generated for the study area and values for all explanatory variables selected in the final 3-year model were extracted at the midpoint of each grid cell. The resolution of the grid was chosen to be the same as the best resolution remote sensing data used. Encounter rates were predicted for each grid cell by the final 3-year model with the *predict.gam* function in mgcv and plotted for visualization. Three time periods corresponding to the larger surveys in each year were selected to visually verify if predicted areas of high whale densities matched with the overall observed patterns. Single survey or year models (see below for the exception of the MF survey) were not used for prediction because the limited range of some explanatory variables in the fitted models would result in extrapolation and unreliable predictions when applied to the whole study area.

2.2.4.3. Spatial modeling of humpback whale abundance – 2005 summer survey

Given the wide range of the MF survey, the density of humpback whales in the study area during the summer of 2005 was estimated following the distance sampling methodology (Buckland et al. 2001). Horizontal angles to the sightings had been rounded to the nearest 5^o, so a smearing technique was used by randomly selecting an angle within a 10^o smearing zone centered on the recorded angle (see Buckland et al. 2001). Next, perpendicular distances to the sightings were calculated by multiplying the radial distance by the sine of the horizontal angle. A detection function was then estimated from the perpendicular distances using program Distance 5.0 Release 2 (Thomas et al. 2006). The best detection function was selected using Akaike's Information Criterion (AIC) (Akaike 1985). Finally, the area effectively surveyed on each segment was calculated by multiplying the segment's length by twice the effective strip half-width (ESW), obtained from the detection function. This allowed the density to be modelled instead of encounter rates (e.g. Hedley et al. 1999, Marques 2001, Hedley & Buckland 2004).

A GAM model was then fitted to the survey data. Model structure was similar to the encounter rate models, except that the offset in this case was the effective surveyed area per segment. Also, since the detection function was estimated for sightings (and not individuals), regardless of group size, the response variable was the number of groups sighted in each segment instead of the number of animals. A similar prediction grid described above was used, except for the exclusion of the Juan the Fuca Strait and offshore areas farther than around 100 km from the west coast. Humpback whale abundance was calculated by multiplying the predicted abundance of groups in each grid cell by the expected group size (from a size-bias regression in the detection function estimation process), and summing all values over the entire grid.

The variance of the abundance estimate was estimated using the jackknife procedure (Efron & Stein 1981), with each day of searching effort as the resampling unit. Therefore, several abundance estimates were produced by leaving one day out at a time and repeating at each iteration the whole process described above from detection function and group size estimation to model fitting. The 95% confidence interval was obtained assuming a log-normal distribution (Buckland et al. 2001). The bootstrap method (Efron & Tibshirani 1993) was also implemented, but did not perform well and was, therefore, discontinued. Williams et al. (2006) also used the jackknife due to poor performance of other resampling methods.

2.3. Results

2.3.1. Surveys

Humpback whales were observed on all surveys throughout the study area (Fig. 2.7), and were the most commonly sighted large cetacean species in BC, followed by fin whales. The largest whale concentrations during individual surveys were observed east of Moresby Island (in the Queen Charlotte Islands = QCI), over the edge of the trough located in the middle of Hecate Strait, and in the southern portion of Dixon Entrance (north of QCI).

A total of 541 humpback whale groups and 1,041 individuals were recorded during 2,167 segments of searching effort. However, due to missing values of some environmental variables, 2,041 survey segments (8,144 km) were used in the analyses (Table 2.3).

Table 2.3 – Total number of humpback whale groups and individuals sighted on each cruise along the survey segments used in the models. Note that segments with missing environmental variables are not accounted for here.

Cruise	Segments	HW groups	HW individuals
1	420	167	308
2	103	61	197
3	232	44	64
4	532	88	127
5	663	145	294
6	91	29	43
Total	2,041	534	1,033

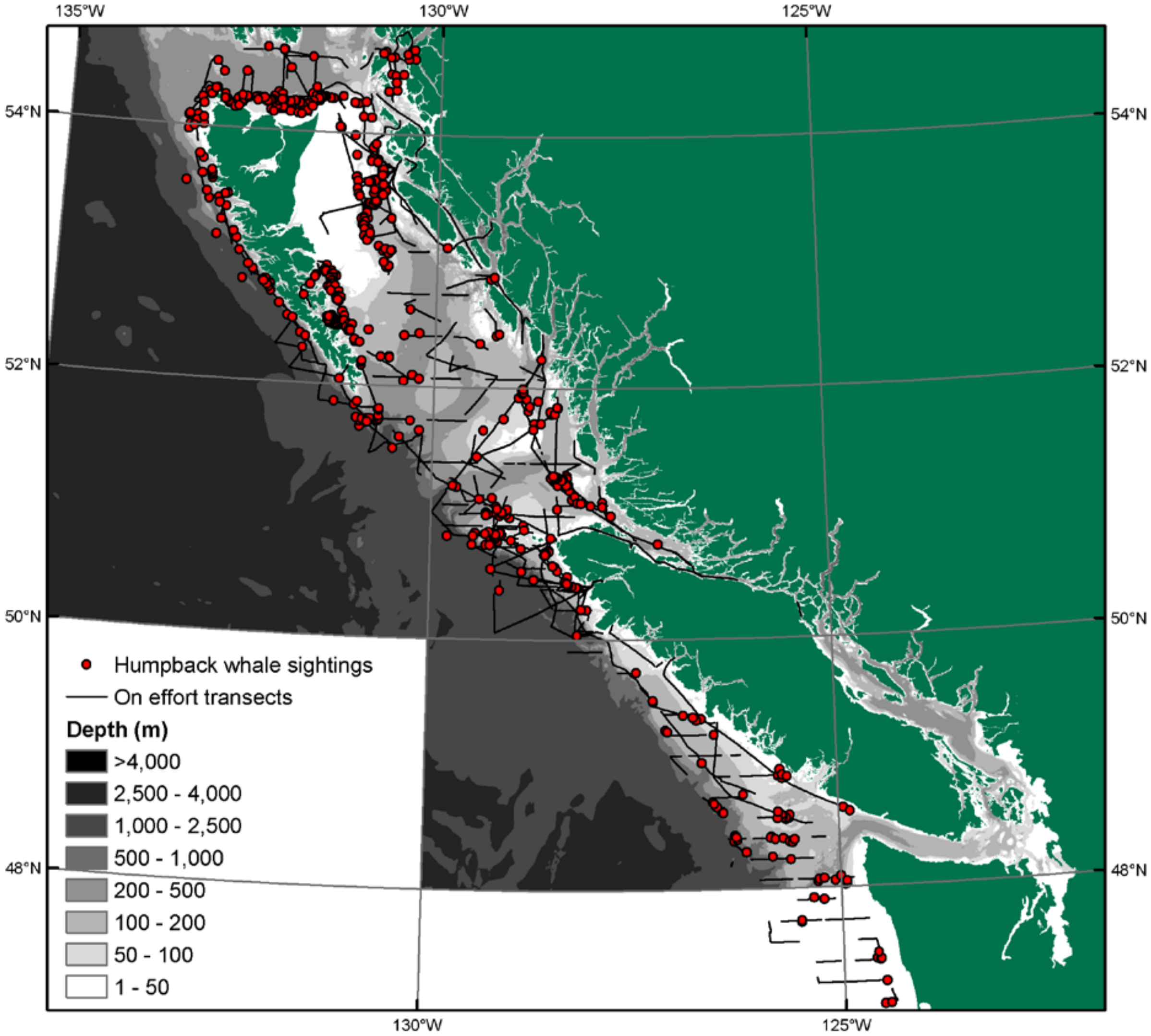


Fig. 2.8 – Locations of humpback whale groups (red dots) sighted during six surveys conducted between 2004 and 2006. Survey tracklines and bathymetry are also shown.

2.3.2. Generalized additive models (GAMs)

The combined 3-year GAM containing data from the six surveys resulted in 12 selected explanatory variables, an adjusted R-square of 0.27 and 39.2% of explained deviance (Table 2.4). All smooth functions for this model indicated non-linear relationships (Fig. 2.8). The smooth function for latitude (which represents the variation of the fitted response surface holding all other predictors fixed) showed a marked relationship with humpback whale encounter rates. A first peak occurred between 47^{o}30’ and 48^{o}30’N, off the Olympic Peninsula, followed by a drop that reached the lowest value around 50^{o}N, just south of the Brooks Peninsula. Encounter rates then steadily increased northward,

Table 2.4 – GAM results for the combined 3-year and the individual year models. The selected explanatory variables in each model are identified as factors (F) or smooth functions (S) along with their estimated degrees of freedom in parentheses and approximate p-value significance. Empty spaces correspond to non-selected variables and dashes represent variables that were not part of the initial model. Competing models (‘b’) are included for 2004 and 2006. Percent deviance explained and R^2 adjusted for all models are also presented.

Variable	3-year GAM	2004	2004(b)	2005	2006	2006(b)
Year	**F**	-	-	-	-	-
Month	F *			-	-	-
Lat	**S** (6.47)	**S** (6.38)	-	**S** (6.33)	**S** (6.09)	**S** (5.25)
SST_w	**S** (6.85)	-	**S** (6.58)		**S** (5.9)	**S** (5.85)
logDepth	**S** (4.73)	**S** (6.54)	**S** (5.57)	**S** (4.39)	**S** (6.83)	**S** (6.77)
logSlope	**S** (6.25)	**S** (6.95)	**S** (6.97)	**S** (4.06)	**S** (6.76)	
logchla_m	**S** (6.2)	-	-	-	**S** (7)	**S** (7)
logchla_mlag		**S** (6.94)	**S** (7)		S (4.66)*	
logchla_wmerged			**S** (2.76)	S (2.86)**	**S** (6.34)	**S** (6.53)
logNPP_mlag	**S** (6.09)		S (5.06)**		**S** (5.31)	**S** (5.31)
logNPP_wlag		**S** (6.11)	**S** (6.95)	-		
logtidal_speed			S (1.69)**	**S** (6.46)	-	-
sqrtdist100m	**S** (4.26)	**S** (5.46)	**S** (6.37)	**S** (1)^{l}	**S** (5.15)	**S** (5.06)
sqrtdist200m		**S** (6.79)	**S** (6.89)		**S** (6.4)	**S** (6.48)
sqrtdistland					**S** (4.66)	**S** (4.65)
sqrtdistfront_w	**S** (5.8)	**S** (6.59)	**S** (6.98)	**S** (5.53)	**S** (6.8)	**S** (6.89)
sqrtfrontspi_m			S (1)^{l}**			**S** (3.39)
SSHdev		**S** (6.35)		**S** (6.83)		
expsal_surf	**S** (5.92)	**S** (6.97)	**S** (6.33)	**S** (6.85)	**S** (6.73)	**S** (6.87)
temp_surf	**S** (4.77)			**S** (2.65)	**S** (5.99)	**S** (5.97)
% Deviance explained	39.2	75.5	75.9	42	62.9	61.3
R^2 adjusted	0.27	0.76	0.74	0.31	0.65	0.56

* = $p < 0.05$; ** = $p < 0.01$; all other terms in bold => $p < 0.001$; l = linear term

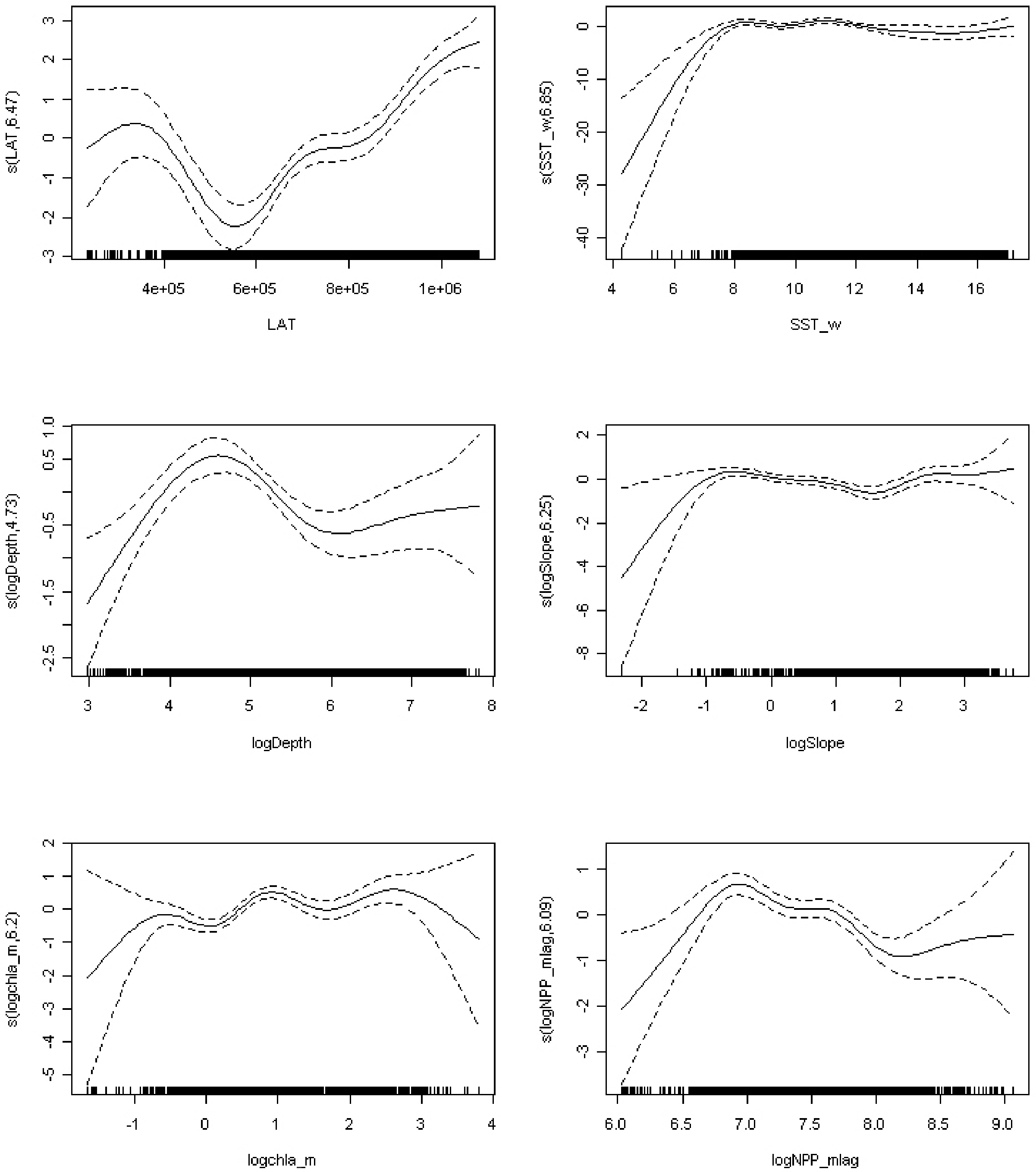
with latitude having a positive effect again around 52^{o}20'N, the same latitude of Juan Perez Sound. The highest fitted values were obtained north of 54^{o}N (Fig. 2.8), the area corresponding to Dixon Entrance.

Humpback whales appeared to be strongly associated with bathymetry. Encounter rates were higher between 50 and 200 m of depth (peak around 110 m) and, accordingly, were also higher around 2.5 km and dropped with increasing distance from the 100-m isobath. Slope was also significant, but the functional form was not so conspicuous. The steep curve increase from flat bottom was likely an artifact of the variable transformation, given that it represents a variation of only 0.3 degrees, and has considerable uncertainty associated with it (see 95% confidence limits). After that point, the curve slowly decreased to around the 4.5 degree mark and started increasing again towards the steeper slopes (Fig. 2.8).

The smooth curve for monthly chl-*a* appeared to indicate a slight increase in encounter rates with increasing chl-*a* values, up to at least 20 mg/m^3, with the middle peak corresponding to about 2.7 mg/m^3. The relationship with lagged monthly NPP, on the other hand, indicated higher concentrations of whales in areas with relatively lower productivity in the previous month (peak around 990 mgC/m^2/day). The 8-day SST showed a negative effect at lower temperatures, with slightly higher encounter rates at around 8 and 11^{o}C, and the climatology of summer surface temperature presented a peak around 13^{o}C. The function for distance to weekly fronts suggested an initial drop in encounter rates from zero to 2.5 km, followed by an increase to around 15 km, and a further increase with higher distances from the fronts (Fig. 2.8). This last increase was likely caused by the very high encounter rates observed close to shore, east of Moresby

Island during the survey in May 2004, and the absence of fronts detected nearby. However, detecting fronts in nearshore areas with several fjords was problematic given the spatial and temporal resolution of the SST data used.

Fig. 2.9 – Model terms for the 3-year generalized additive model (GAM) of humpback whale relative abundance. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. Y-axis = fitted function with estimated degrees of freedom in parenthesis; x-axis = variable range with rug plots indicating sampled values. The partial effects of factor variables are also included.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2
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0
-1
-2
-3
4e+05
6e+05
8e+05
1e+06
LAT
s(SST_w,6.85)
0
-10
-20
-30
-40
4
6
8
10
12
14
16
SST_w
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0.5
-0.5
-1.5
-2.5
3
4
5
6
7
8
logDepth
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2
0
-2
-4
-6
-8
-2
-1
0
1
2
3
logSlope
s(logchla_m,6.2)
2
1
0
-1
-2
-3
-4
-5
-1
0
1
2
3
4
logchla_m
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-3
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6.5
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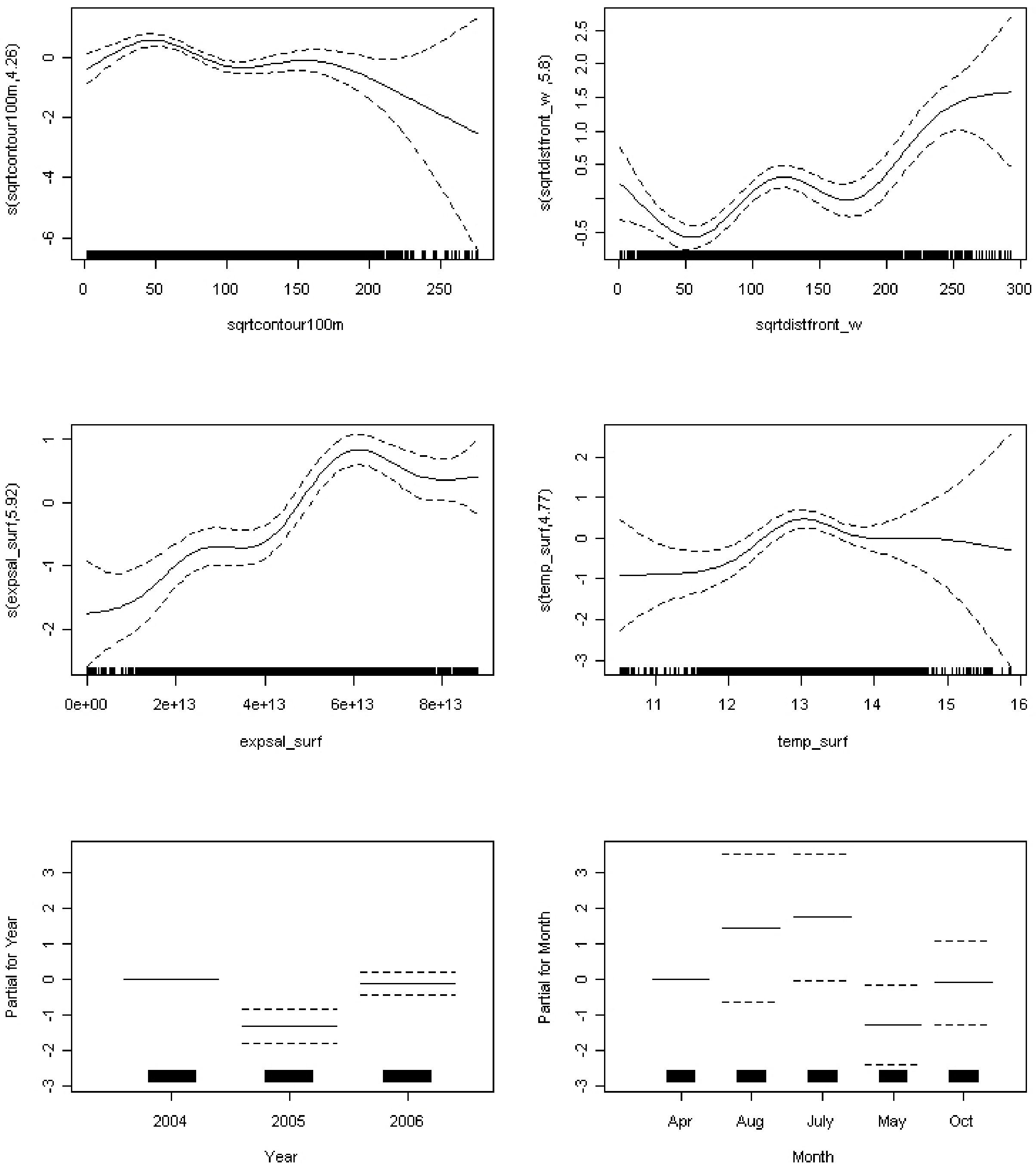
7.5
8.0
8.5
9.0
logNPP_mlag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-4
-6
0
50
100
150
200
250
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2.0
1.5
1.0
0.5
-0.5
0
50
100
150
200
250
300
sqrtdistfront_w
s(expsal_surf,5.92)
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0
-1
-2
0e+00
2e+13
4e+13
6e+13
8e+13
expsal_surf
s(temp_surf,4.77)
2
1
0
-1
-2
-3
11
12
13
14
15
16
temp_surf
Partial for Year
3
2
1
0
-1
-2
-3
2004
2005
2006
Year
Partial for Month
3
2
1
0
-1
-2
-3
Apr
Aug
July
May
Oct
Month

Fig. 2.8 – cont.

Higher humpback whale encounter rates were also associated with higher climatology values of summer surface salinity. The categorical variables year and month were both selected. The partial for year indicated a significant negative effect of 2005 relative to 2004 and 2006, whereas the partial for month resulted in significant effects of May and July.

Since the selection of year as a factor in the 3-year model suggested potential differences among years, individual year models, each containing two surveys, were also fitted to the data.

The 2004 GAM resulted in 10 explanatory variables, an adjusted R-square of 0.76 and 75.5% deviance explained (Table 2.4). The estimated smooth functions of latitude, slope and distance to the 100-m isobath were quite similar to those obtained in the 3-year model (Fig. 2.9). The function for depth, however, indicated higher humpback whale encounter rates between 120 and 400 m. The lagged monthly chl-*a* curve showed two peaks, one at around 1.65 mg/m^3 and a higher one around 16 mg/m^3. The smooth term for the 8-day NPP with a two week lag was also similar in shape to the lagged monthly NPP from the 3-year model, including a peak around the same value, except for the clear drop at values larger than 3,000 mgC/m^2/day. Encounter rates of whales increased with increasing distance to fronts and with higher values of summer surface salinity. There were also more whales either around 13 km or further than 40 km from the 200-m isobath. The smooth term for SSH deviation reached a peak just below zero and then increased again at positive values (Fig. 2.9).

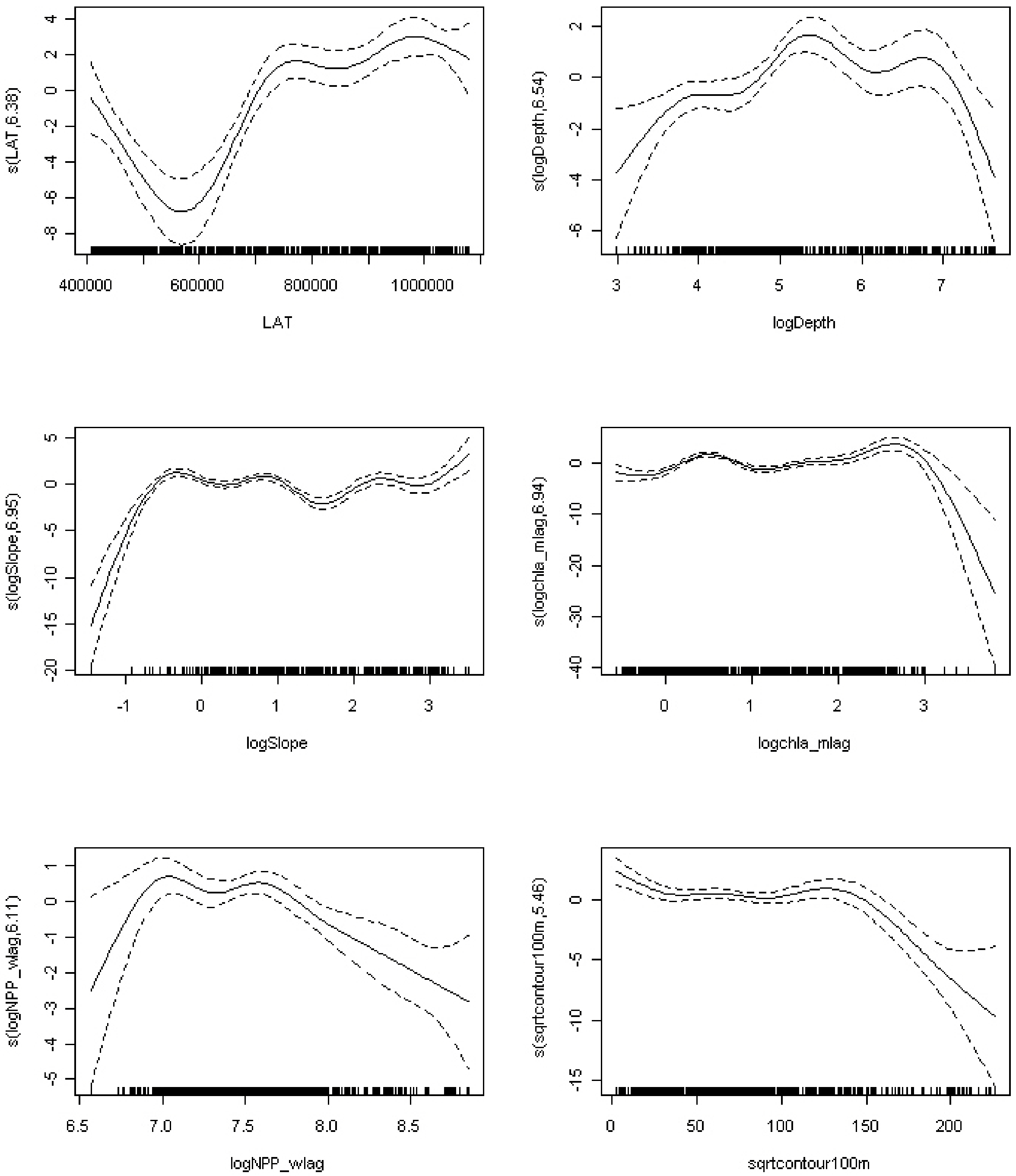


Fig. 2.10 – Model terms for the 2004 generalized additive model (GAM) of humpback whale relative abundance. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. Y-axis = fitted function with estimated degrees of freedom in parenthesis; x-axis = variable range with rug plots indicating sampled values.

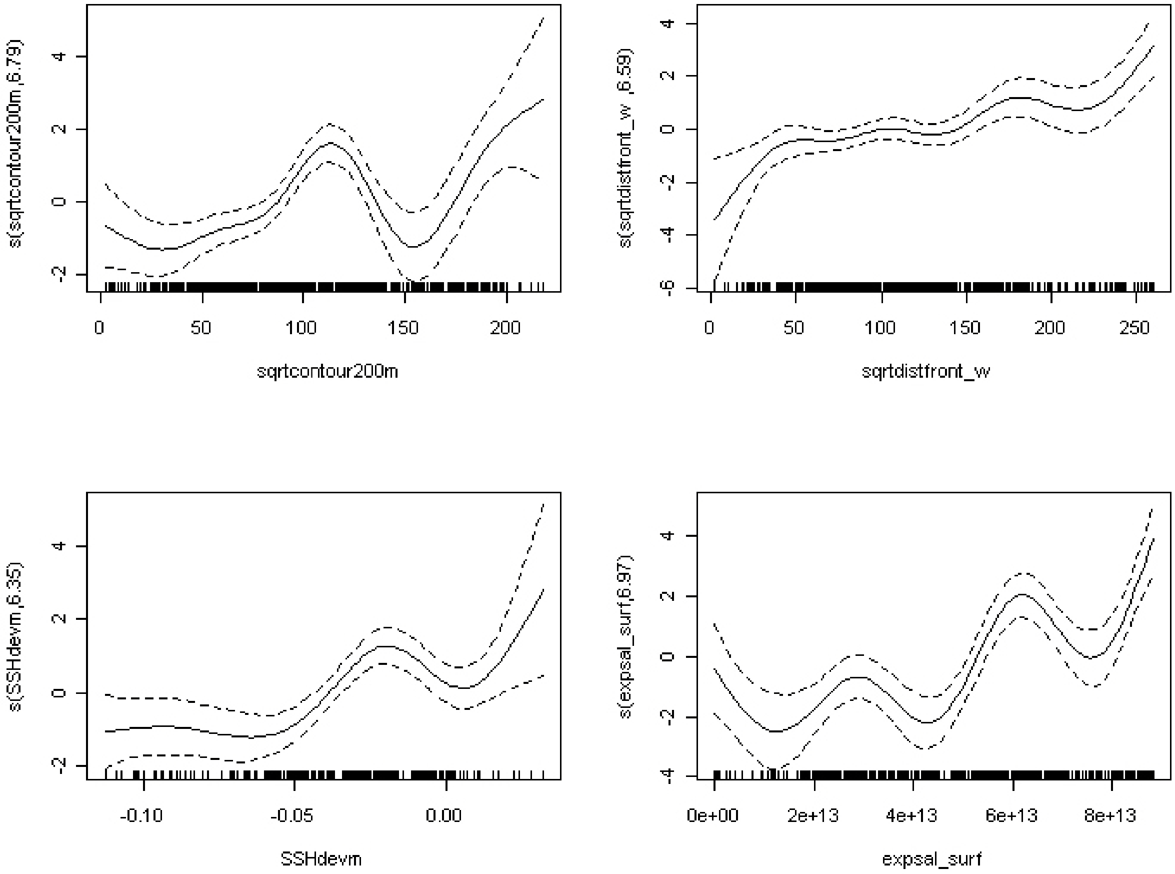


Fig. 2.9 – cont.

A competing model for 2004 replacing latitude with 8-day SST resulted in similar explanatory power, but with a larger number of variables. This model contained, besides SST, another four variables not selected on the previous model, and SSH was dropped (Table 2.4).

The 2005 GAM resulted in 10 explanatory variables, an adjusted R-square of 0.31 and 42% deviance explained (Table 2.4). Latitude presented a similar functional form to the previous models (Fig. 2.10).

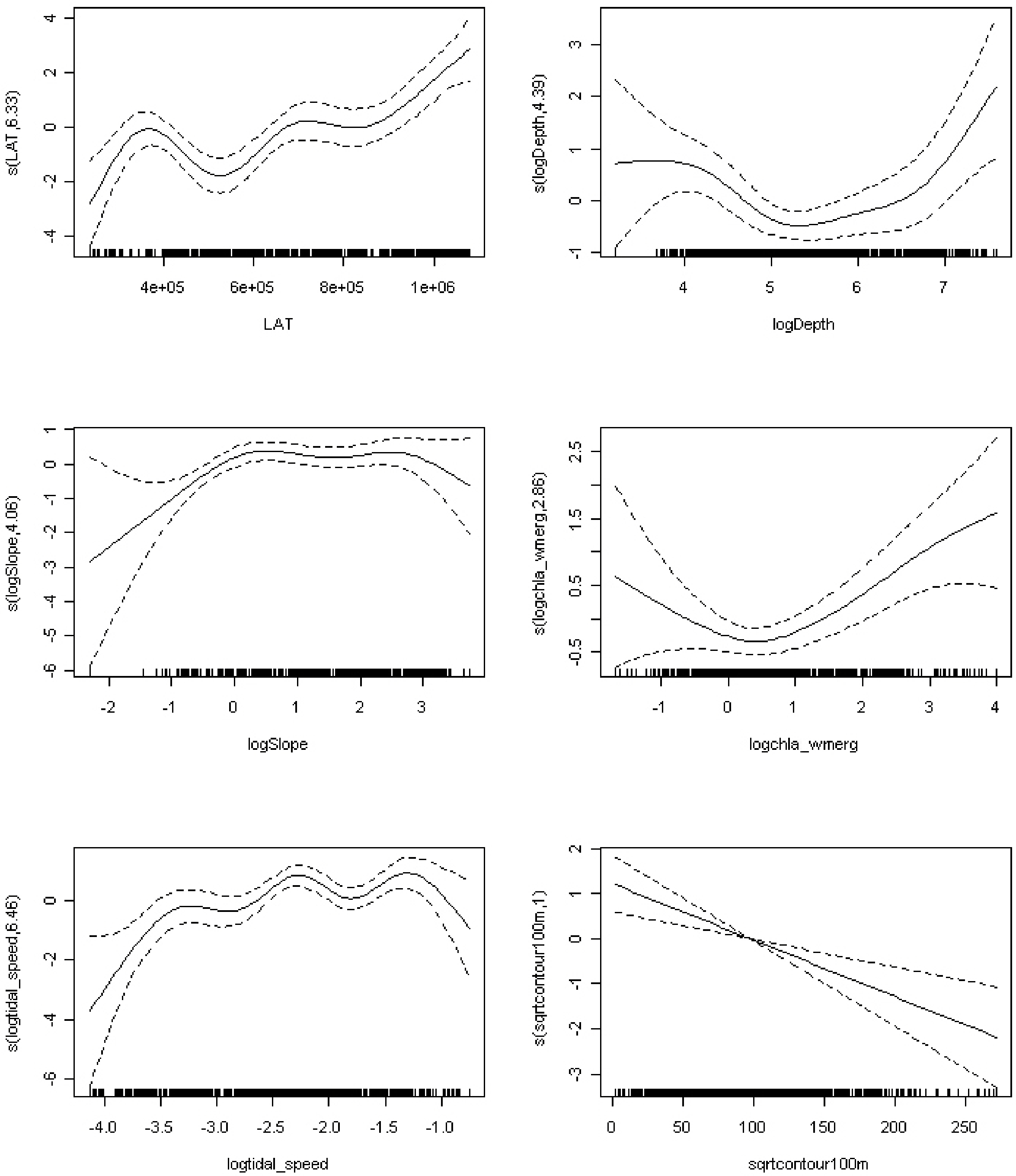


Fig. 2.11 – Model terms for the 2005 generalized additive model (GAM) of humpback whale relative abundance. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. Y-axis = fitted function with estimated degrees of freedom in parenthesis; x-axis = variable range with rug plots indicating sampled values.

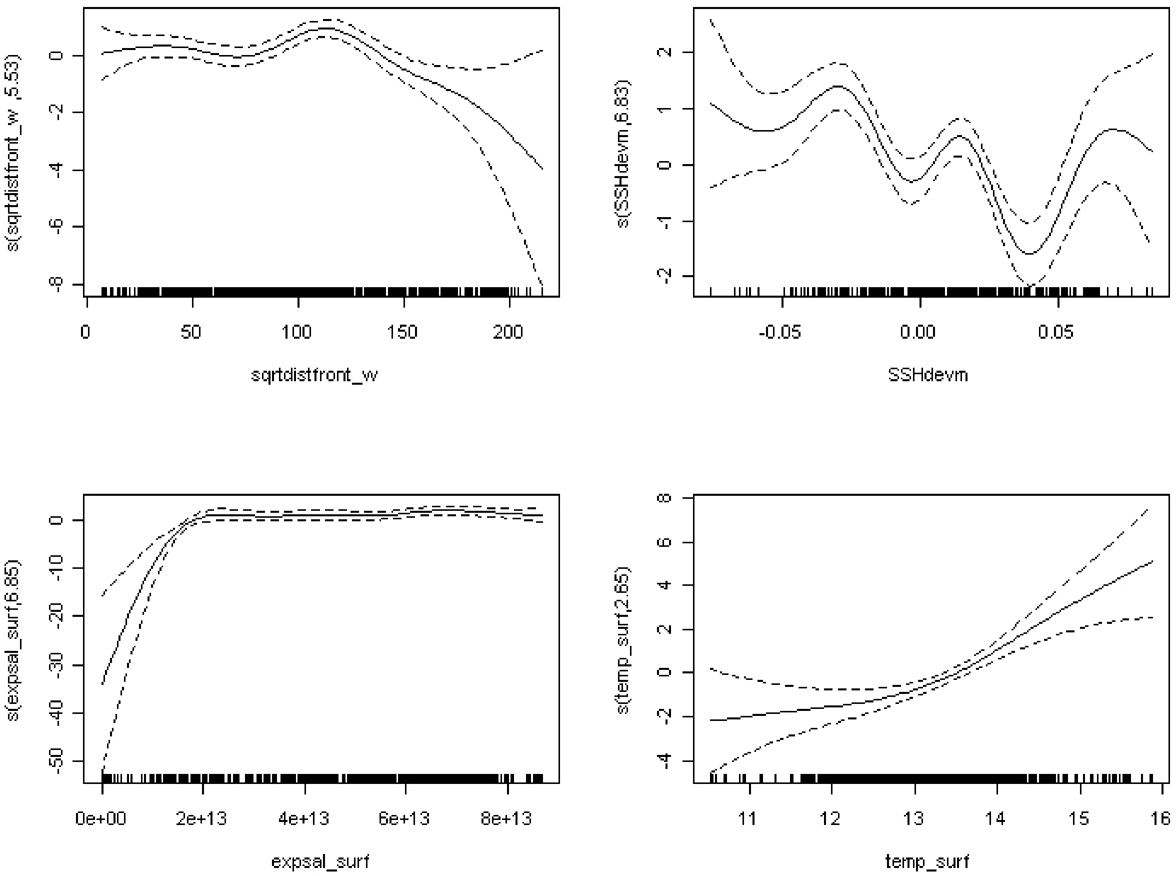


Fig. 2.10 – cont.

Humpback encounter rates were higher at depths up to about 120 m and greater than about 600 m, and decreased linearly with distance from the 100-m isobath. The smooth curve of slope peaked around 1 degree and remained relatively constant. Higher encounter rates were also associated with higher values of chl-*a* (8-day merged), areas of higher summer surface temperatures and, apparently, faster tidal speeds. The curve for distance to fronts remained relatively constant at closer distances, with a slight peak around 15 km and a conspicuous drop afterwards. SSH deviation yielded a wiggly curve with three peaks and summer surface salinity had a negative effect at lower values and stabilized around 30.6 psu (Fig. 2.10).

The 2006 GAM resulted in 10 explanatory variables, an adjusted R-square of 0.65 and 62.9% deviance explained (Table 2.4). Humpback whale encounter rates in 2006 were lower on the segments south of 51^{o}N and higher on the northernmost ones, as in the previous years (Fig. 2.11). The SST curve suggested lower encounter rates at temperatures below 8^{o}C, however with a lot of uncertainty due to few samples in that range. Encounter rates were higher around 150 and 500 m of depth, and apparently decreased sharply over the steepest slopes. The smooth terms of lagged monthly and 8-day merged chl-*a* yielded similarly shaped curves suggesting higher encounter rates at both lower and upper ranges, with a peak in the middle for the latter. The curve of monthly chl-*a* also indicated there were more whales at the lower range of values, but with an apparent (given the wide confidence interval) decrease at the upper range. The lagged monthly NPP resulted in a bi-modal curve almost opposite in shape to the lagged monthly chl-*a*. The shape of the 'distance to 100 m' curve was similar to its equivalent term in the 3-year and 2004 models. The smooth term for distance to land and to the 200-m isobath showed peaks in encounter rates around 40 and 32 km, respectively. Higher humpback encounter rates were also associated with areas with an average summer surface temperature around 13^{o}C, similarly to the 3-year model, and an average summer surface salinity around 31.9 psu. The smooth curve of distance to fronts indicated that whales were more common very close to fronts (under 2.5 km), and less common around 35 km and beyond 65 km (Fig. 2.11).

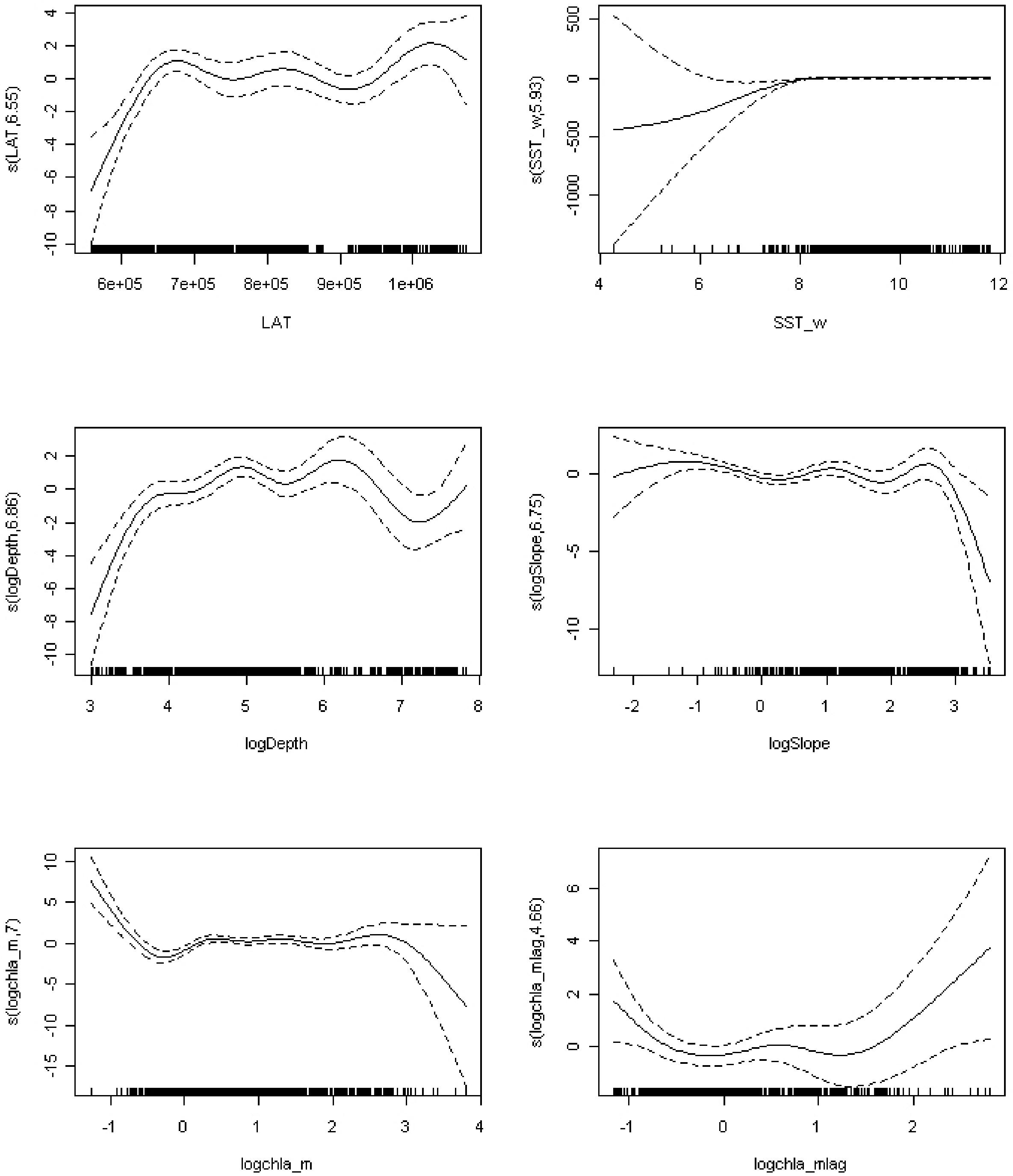
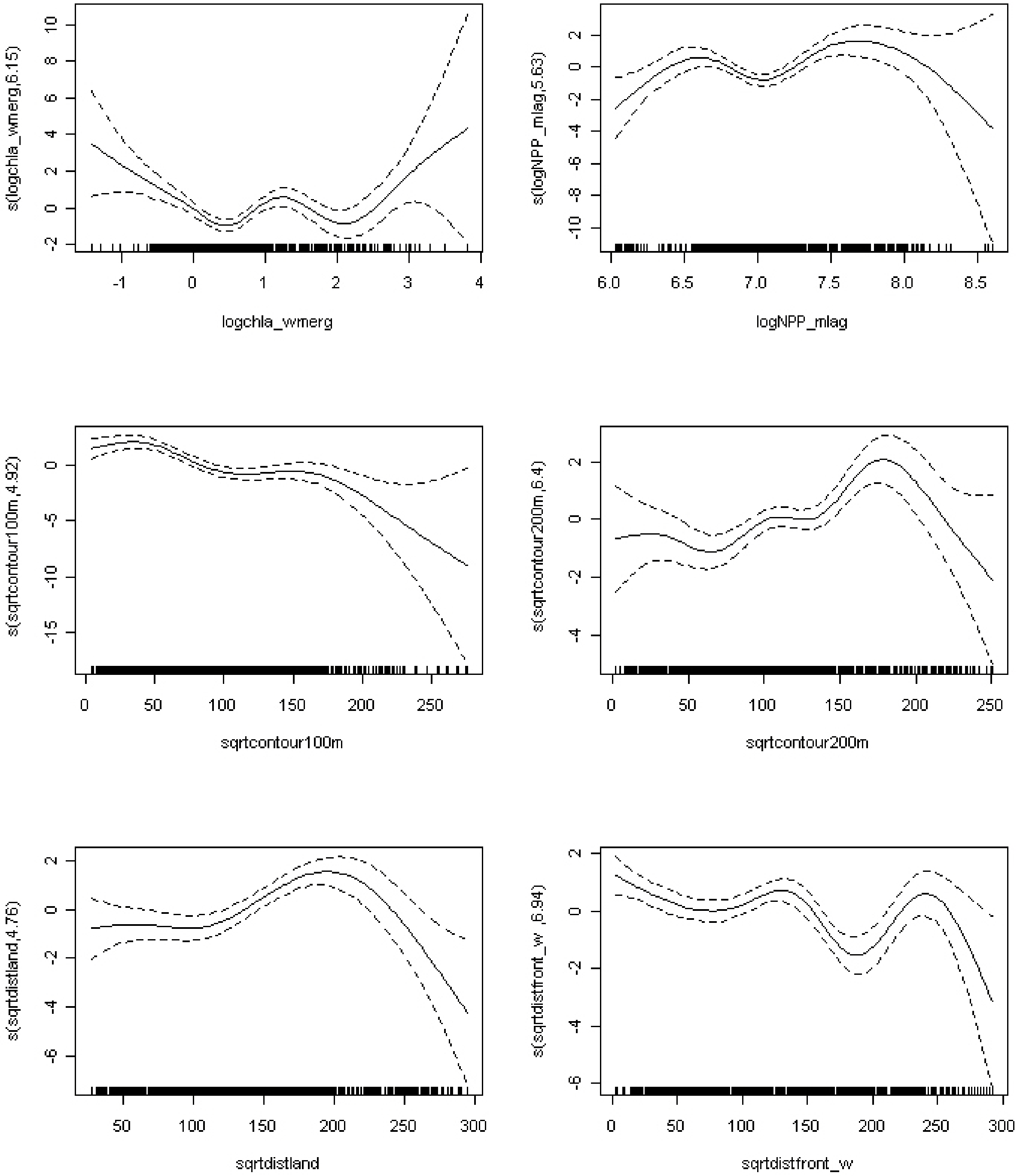


Fig. 2.12 – Model terms for the 2006 generalized additive model (GAM) of humpback whale relative abundance. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. Y-axis = fitted function with estimated degrees of freedom in parenthesis; x-axis = variable range with rug plots indicating sampled values.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4
6
8
10
-1
0
1
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3
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s(logNPP_mlag,5.63)
-10
-8
-6
-4
-2
0
2
6.0
6.5
7.0
7.5
8.0
8.5
logNPP_mlag
s(sqrtcontour100m,4.92)
-15
-10
-5
0
0
50
100
150
200
250
sqrtcontour100m
s(sqrtcontour200m,6.4)
-4
-2
0
2
0
50
100
150
200
250
sqrtcontour200m
s(sqrtdistland,4.76)
-6
-4
-2
0
2
50
100
150
200
250
300
sqrtdistland
s(sqrtdistfront_w,6.94)
-6
-4
-2
0
2
0
50
100
150
200
250
300
sqrtdistfront_w

Fig. 2.11 – cont.

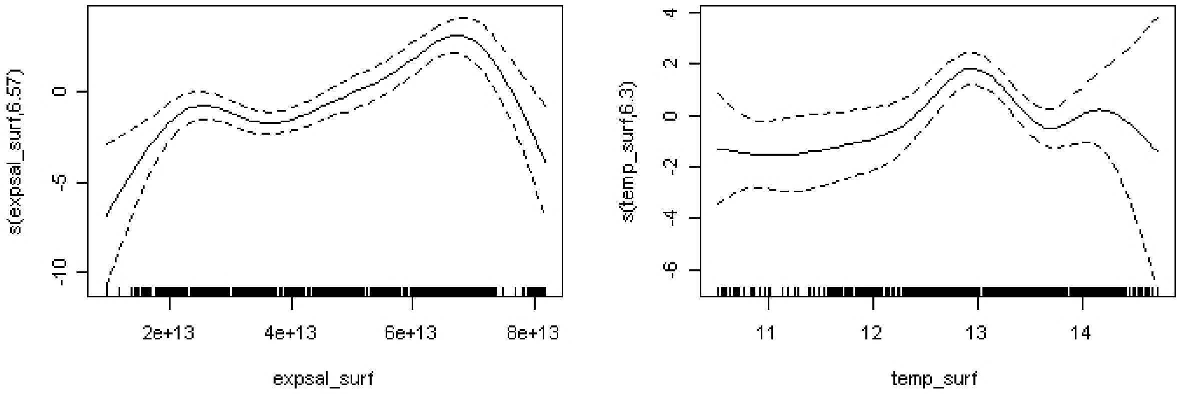

Fig. 2.11 – cont.

In the competing 2006 GAM, two explanatory variables were dropped and a smooth function for the frontal probability index was added (Table 2.4). The shape of this function suggested higher encounter rates in areas with higher probability of front occurrence. The same trend for this variable was observed on the 2004b GAM.

There was no evidence of significant spatial autocorrelation on the residuals of any of the models, as the semivariance was within the boundaries of the Monte Carlo envelopes on all variograms (Fig. 2.12 A-D).

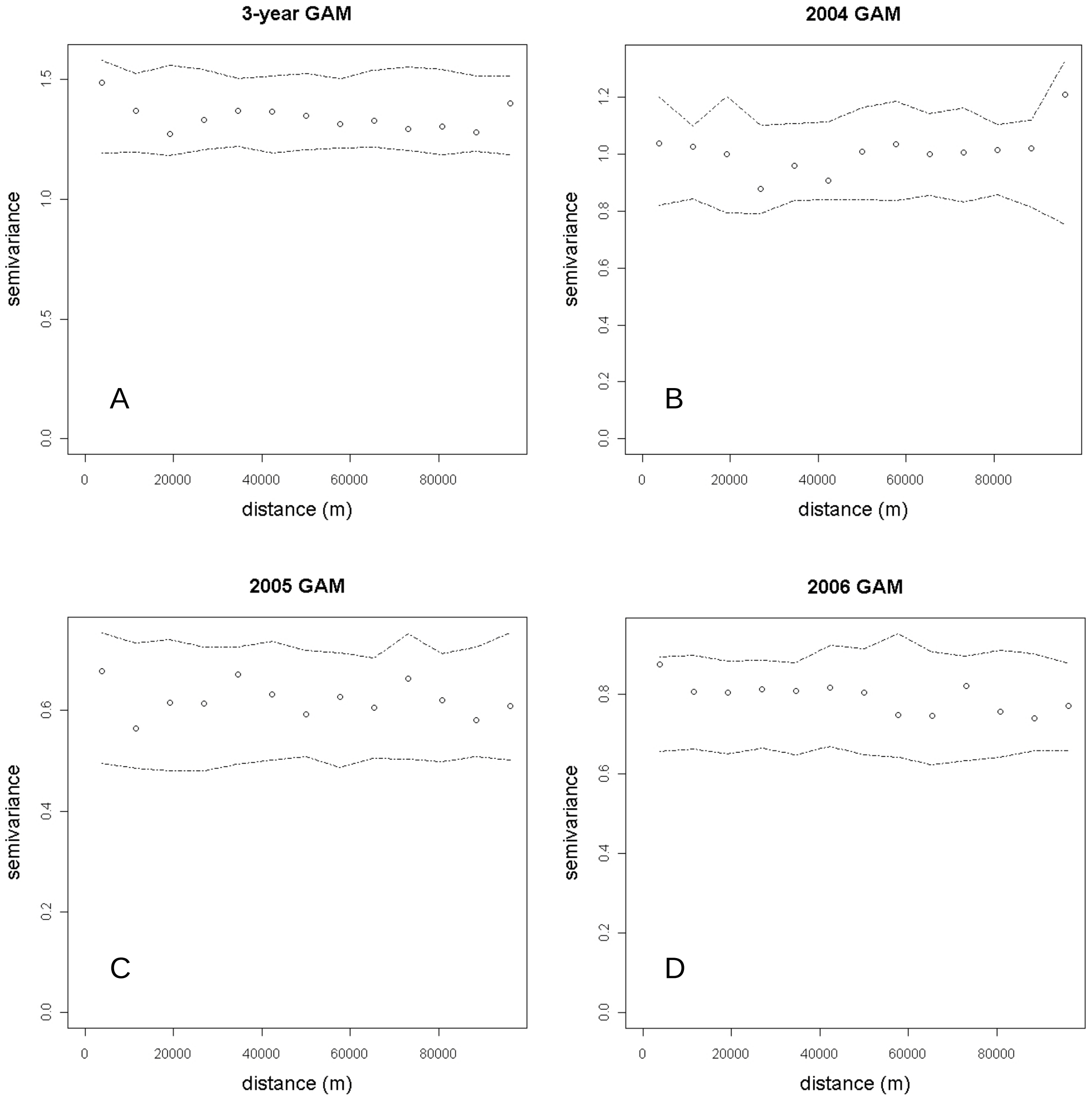

Fig. 2.13 A-D – Binned variograms with Monte Carlo envelopes of deviance residuals of the selected GAM models.

2.3.3. Predicted encounter rates

The predicted humpback whale encounter rates from the 3-year GAM compare favorably with the overall distribution patterns observed during the surveys (Fig. 2.13A-C). All areas where the highest concentrations were observed were consistently identified in the predictions. There seems to be some edge effect on the northernmost limit of the map, which could be fixed by adding longitude to the model. However, that would also increase the influence of spatial variables in the model, potentially affecting the effect of the explanatory variables more directly related to the physical and biological processes.

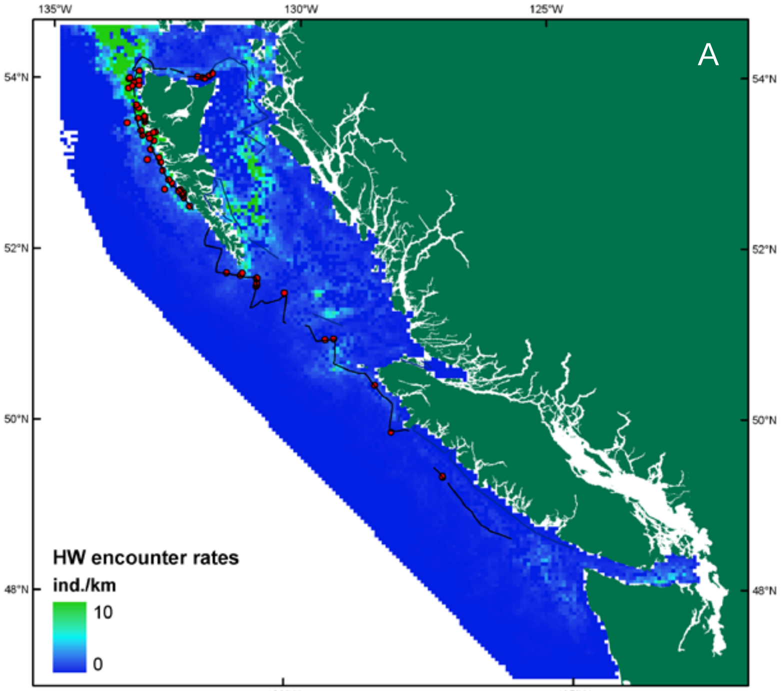

Fig. 2.14 – Predicted humpback whale encounter rates for (a) 8-15 May 2004, (b) 20-27 July 2005 and (c) 9-16 May 2006 obtained from the 3-year GAM model. Actual sightings and effort during these periods are included for comparison. Note that the color bars of the three images are not on the same scale.

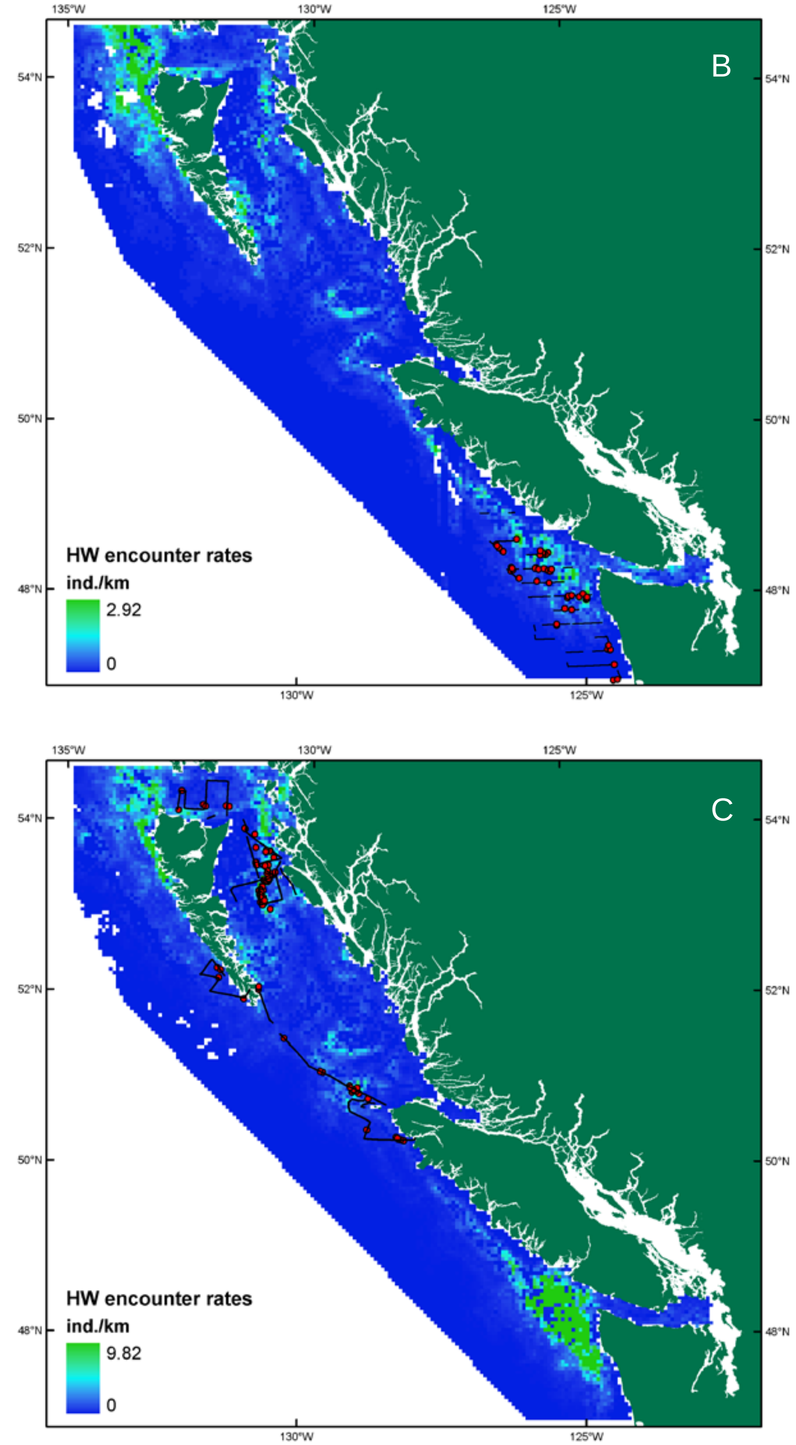
135°W
130°W
125°W
B
54°N
52°N
50°N
48°N
HW encounter rates
ind./km
2.92
0
130°W
125°W
135°W
130°W
125°W
C
54°N
52°N
50°N
48°N
HW encounter rates
ind./km
9.82
0
130°W
125°W

Fig. 2.13 – cont.

2.3.4. Spatial modeling – 2005 summer survey

A total of 88 groups of humpback whales (127 individuals) were observed during 2,124 km of searching effort. The best fitting detection function was a half-normal key function with cosine adjustments of second and third orders (Fig. 2.14). The estimated effective strip width (ESW) was 2.69 km (SE = 0.41), and the expected group size was 1.30 (SE = 0.05). The selected GAM model for the number of humpback whale groups contained the following smooth terms of explanatory variables, including their estimated degrees of freedom: s(Lon, Lat, 17.72) + s(logchla_w_merg, 3.16) + s(distland, 1.29) + s(sqrtdistfront_w, 4.6) + s(temp_surf, 2.68) (Appendix 1). The explanatory power of this model was relatively low as a consequence of reducing the maximum allowable number of degrees of freedom for model terms to avoid unrealistically high variance estimates. Deviance explained was 26.8% and the adjusted R-square was 0.14. Spatial autocorrelation was not present in the deviance residuals as indicated by the variogram analysis.

The predicted abundance of humpback whales in the study area during 20-27 July 2005 was 1,840 individuals (95% CI = 1,408 – 2,771). The prediction was made for a particular week given the presence of two explanatory variables based on weekly data in the model. The corresponding map of predicted densities is shown in Fig. 2.15. The model seems to predict relatively well throughout most of the study area, identifying areas where higher concentrations of whales were observed during the survey. However, there is an edge effect around the latitude of northern Vancouver Island which was likely created by extending the predicted surface outside the range of the actual survey. Also, predicted densities in Dixon Entrance and northwestern Queen Charlotte Islands could be underestimates due to reduced survey effort that occurred in these areas because of fog.

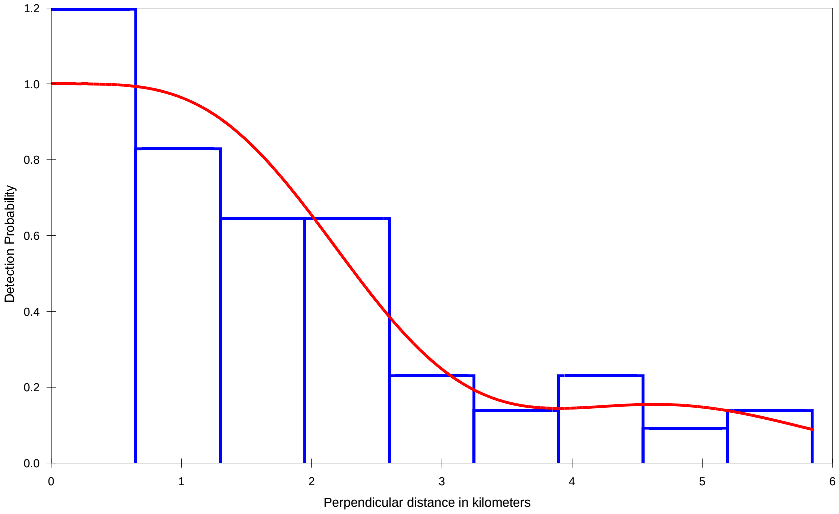

Fig. 2.15 – Detection function fitted to perpendicular distance data of humpback whale groups sighted off British Columbia and Washington State during the summer of 2005.

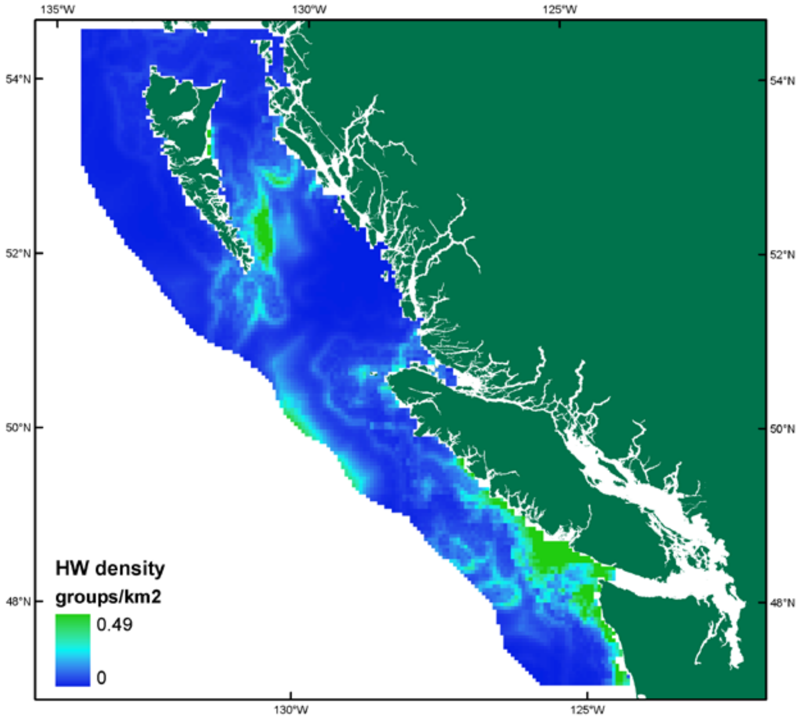

Fig. 2.16 – Density surface of humpack whales predicted by the spatial model constructed for the *Miller Freeman* survey, in 2005.

2.4. Discussion

2.4.1. Distribution patterns

The humpback whale was the most common large cetacean species in our surveys, as in other studies in the region (Williams & Thomas 2007) or elsewhere in shelf waters of the eastern North Pacific feeding grounds (e.g. Calambokidis & Barlow 2004, Tynan et al. 2005, Zerbini et al. 2006). The exceptions are the Bering Sea, where fin whales are more abundant (Moore et al. 2002), or some localized areas like the Channel Islands, where blue whales predominate (Fiedler et al. 1998).

Two of the largest concentrations of humpback whales were observed around the Queen Charlotte Islands (QCI), in areas where high densities of sightings have been previously reported: southwestern Hecate Strait, from photo-identification (Cetacean Research Program, Pacific Biological Station, Nanaimo, unpublished data) and line-transect (Williams & Thomas 2007) surveys; and southern Dixon Entrance, from opportunistic boat surveys (J.K.B. Ford, unpublished data). Sightings made off the Olympic Peninsula during the 2005 summer survey were more numerous in the area east of Barkley Canyon and between La Perouse Bank and Nitnat Canyon, and on the shelf edge near the southern portion of Juan de Fuca Canyon (see Fig. 2.13B). These observations agree with the distribution patterns reported by Calambokidis et al. (2004) from line-transect surveys conducted between 1997 and 2002.

As our surveys were not systematic and synoptic, we were unable to detect shifts in whale distribution among areas or changes in overall abundance, either within or between years. However, high variability in encounter rates was observed on the local scale, such as in the southern Dixon Entrance over the five surveys that crossed this area. We explored this variability in our habitat models by relating it to the dynamic variables from the weekly remote sensing images, and also by including month and year as factors in the 3-year GAM.

2.4.2. Environmental variables and oceanographic processes

Our models indicate that humpback whales were strongly associated with latitude and bathymetric features, including depth, slope and distance to isobaths. A number of studies have shown associations between latitude and cetacean distribution, either in terms of geographical ranges (e.g. Weir et al. 2001), latitudinal gradients (e.g. Forney & Wade 2006), or as representing particular physiographic features (e.g. Tynan et al. 2005). Regardless of the type of association, latitude is always a proxy for some biological or physical property that ultimately affects distribution, such as prey availability or a physiologically limiting factor (e.g. temperature). The seasonal increase in biological productivity towards high latitudes favors the use of mid- and high-latitude areas by migratory baleen whales during their feeding season (Gaskin 1982). Therefore, on a large scale, the general pattern of increasing relative abundance with latitude observed in our models may partially reflect a latitudinal gradient of increased whale biomass towards the Arctic. Two subpopulations of humpback whales occupy our study area: the Eastern North Pacific subpopulation ranges from California to Washington, and the Central North Pacific subpopulation inhabits British Columbia and Alaska (Calambokidis et al. 2001). Current abundance estimates are around 1,400-1,700 for the California-Oregon area, 200-400 for Washington-southern British Columbia, and 3,000-5,000 for northern British Columbia and southeast Alaska (Calambokidis et al. 2008, see also Rambeau 2008).

From a regional perspective, however, the latitudinal differences may reflect the amount of suitable habitat available to the humpback whales. That is, if humpbacks prefer mid-shelf waters, as we suggest below, then the latitudinal variation in the extent of shelf area along the BC coast seems to explain the observed pattern well. The lower encounter rates in our models occur off the northwestern side of Vancouver Island, where the shelf is relatively narrow. On a wider shelf, more of the primary production remains on shelf and becomes available to the coastal food web (Ware & Thomson 2005). And although mean annual chl-*a* and zooplankton concentrations and mean resident fish yields are higher off Washington-southern BC than in northern BC (Ware & Thomson 2005), the total area of ocean habitat with coastal influence is larger in the latter, which may provide more opportunities for humpbacks of finding predictable prey aggregations.

The relationships with bathymetry shown in our models suggest that humpback whales in BC waters prefer shelf waters between 50 and about 200 m of depth, especially near the 100-m contour. Where positive correlations with deeper depths were observed, they appeared to be related to areas with a narrow shelf (e.g. west coast of QCI) or deep channels (e.g. Juan Perez Channel, east Moresby Island) and cross-shelf canyons (e.g. off Juan de Fuca Strait). This idea is supported by the positive correlations within shorter distances to the 100-m isobath alone, or in combination with slope and distance to the shelf break. Calambokidis et al. (2004) reported a mean depth and distance to shelf break of 144 m and 8.4 km, respectively, for 153 humpback whale sightings made off the Olympic Peninsula. In the northern California Current System, humpback whales occurred over the slope in late spring, but were concentrated at water depths of 50-100 m over the Heceta Bank and off Cape Blanco in summer (Tynan et al. 2005). In the Bering

Sea, humpbacks were primarily seen on the middle shelf (50-100 m depth), and also in deeper waters near the Unimak Pass (Moore et al. 2002), one of the Aleutian passes with the highest number of humpback whale sightings (Sinclair et al. 2005).

Bottom topography plays a determinant role on the oceanographic processes that lead to enhanced productivity in coastal regions. Through sometimes complex interactions with tidal flow, wind stress and ocean currents, bathymetry is the basis for such enrichment processes as tidal mixing and shelf-break upwelling, and also facilitates concentration and retention processes by simply acting as a physical barrier or by altering water flows (e.g. Taylor column over a submarine bank) and promoting frontal zones (Bakun 1996). It is therefore not surprising that explanatory variables related to bottom topography were consistently selected in our models.

The preference of humpback whales for shelf waters in BC is presumably related to the horizontal distribution of prey, but may also be influenced by the energetic cost of diving and foraging efficiency. Dive depths of foraging humpback whales correlate significantly with dive and surface durations, as well as with ventilation patterns (Dolphin 1987b, c), such that shallower dives should be more efficient than deeper dives when prey densities are comparable. In support of this, humpback whales tend to lunge feed on the upper boundary of dense aggregations of euphausiids (Goldbogen et al. 2008). In Frederick Sound, Alaska, humpback whales have been observed to dive as deep as 150 m in waters averaging over 300 m deep with dense euphausiid patches as deep as 200 m (Dolphin 1987a, c). Humpback whales should, therefore, benefit energetically by feeding in areas with shallower bottom depths where the vertical diel migration of euphausiids is depth limited and prey may be concentrated closer to the surface.

The concentrations of whale sightings off the Olympic Peninsula in summer 2005, mentioned above, are located on what appears to be the edge of the Juan de Fuca Eddy (Appendix 2). This seasonal and semi-permanent cyclonic feature is formed off the entrance of Juan de Fuca Strait in summer (Freeland & Denman 1982), as a consequence of the geostrophic adjustment to doming isopycnals that arise from tidal or wind upwelling off Cape Flattery (Foreman et al. 2008). Its presence has been linked to enhanced phytoplankton biomass and primary productivity (Marchetti et al. 2004) and to increased biomass of euphausiids, pelagic fish and seabirds (Simard & Mackas 1989, McFarlane et al. 1997, Burger 2003). The whales observed could have been taking advantage of this feature given that edges of eddies may help concentrate euphausiids and pelagic fish such as herring (Johnston et al. 2005). During CTD/rosette and acoustic survey lines run across shelf at about the same area in 1991, Mackas et al. (1997) recorded the highest densities of euphausiids and Pacific hake between the 100- and 150-m isobaths, in a region of upward-domed isotherms and isohalines about 15 km from a strong surface front, and under a band of high chl-*a* concentration.

The shapes of the estimated smooth functions of chl-*a* and net primary productivity (NPP) were not consistent. The time-lagged NPP variables showed positive effects in the relatively lower to middle range of log values in two models (3-year and 2004), and in the upper range of values of the 2006 model. The different chl-*a* smoothed functions resulted in positive effects in the upper range of log values in all models and for most variables. The exception was the monthly chl-*a* for the 2006 GAM, although this model also included two other chl-*a* variables with positive effects in both upper and lower range of log values. Therefore, higher encounter rates of whales generally seemed to be associated with high primary production. Indeed, the areas with highest concentrations of humpback whales typically showed high chl-*a* concentrations in our satellite images.

There are at least four reasons why chl-*a* might not always be a good predictor of baleen whale distribution. First, grazing by herbivores can substantially reduce phytoplankton standing stocks (Strom et al. 2001). Second, phytoplankton can be advected away from the producing area by wind, currents and eddies (e.g. Hofmann & Murphy 2004); Third, there may be higher phytoplankton concentrations at intermediate depths if vertical mixing is not strong enough (Denman et al. 1985, Prézelin et al. 2004), which are not detected by satellite sensors scanning surface waters; and finally, the spatial and temporal scale of the study may not be the most appropriate (e.g. Jaquet 1996). Spatial and temporal lags between peaks of phytoplankton and zooplankton biomass ultimately affect large whale occurrence and distribution (e.g. Croll et al. 2005). Differences in oceanographic processes throughout the BC coastal areas might therefore have led to the variability observed. Potential inaccuracies of satellite derived chl-*a* estimates and modeled NPP (Falkowski & Woodhead 1992) combined with using variables with different spatio-temporal resolutions and time lags in our models could further explain some of the variability in our results.

As our surveys occurred at different time of year, seasonal events such as wind-driven upwelling could be another source of variability in our models, particularly for variables related to primary productivity. Coastal upwelling occurs along eastern boundary areas such as the west coast of Vancouver Island during northwesterly winds, typical of summertime conditions (Thomson 1981). Even within a season, the onset and duration of coastal upwelling varies considerably. For instance, upwelling indices calculated by the

Pacific Fisheries Environmental Laboratory (NOAA) for the area off Juan de Fuca Strait were positive for the period of our 2004 and 2006 spring surveys, but negative for the 2005 spring survey. The index also indicated that upwelling continued in this area in the fall of 2006, but apparently not in the fall of 2004. Additional surveys would be required to investigate the effects of the seasonality and within-season variation of upwelling events on humpback whale distribution in BC waters.

We had predicted that the concentration of chl-*a* would correlate better with humpbacks and their prey in areas where concentration and retention processes prevail. This appears to be the case in the southwestern Hecate Strait region, which typically has the highest estimated chl-*a* concentrations of the Gwaii Haanas National Marine Conservation Area (southern QCI). Phytoplankton blooms sometimes originate in this area (Robinson et al. 2004) of complex topography and coastline where three-dimensional simulation modeling indicates important particle retention at 30 and 100 m depths (Robinson et al. 2005). Comparisons of surface chl-*a* concentrations measured at Queen Charlotte Sound, Hecate Strait and Dixon Entrance suggested no significant differences between years or between sites, and showed a strong spring bloom and a weaker fall bloom (McQueen & Ware 2006). Analyses of the IOS zooplankton database comparing euphausiid biomass among Queen Charlotte Sound (QCS), Hecate Strait (HS) and Dixon Entrance (DE) suggested no between-site differences using ANOVA, but sample variance was large, and a non-parametric test (Kruskall-Wallis) suggested significant differences: QCS > DE > HS (McQueen & Ware 2006). Euphausiids peaked later in the summer and fall (McQueen & Ware 2006).

Sea surface temperature did not appear to have a strong influence on whale encounter rates, except for the negative effect in waters colder than 8°C. The slightly bimodal SST smooth curve of the 3-year GAM apparently reflects the lower values encountered in Dixon Entrance and the higher values elsewhere.

Fronts are regions of enhanced horizontal gradients in temperature, salinity, density and other physical properties, often leading to enhanced phytoplankton, zooplankton and fish biomass (Mann & Lazier 1996, Sharples & Simpson 2001). Consequently, cetaceans may also be attracted to these frontal systems, either oceanic or shelf and slope fronts (e.g. Gaskin 1982, Bluhm et al. 2007, Doniol-Valcroze et al. 2007). Humpback whales, for instance, appeared to be associated with the inside edge of the coastal upwelling front of the northern California Current System in June 2000 (Tynan et al. 2005). The distributions of blue, fin and humpback whales were also highly correlated with thermal fronts in the northern Gulf of St. Lawrence (Doniol-Valcroze et al. 2007). These authors observed, however, that most whales were not directly on top of the frontal areas. They hypothesized that this spatial lag could either occur because fronts are not necessarily straight lines under the surface, or because it takes time for passive prey to be aggregated by the fronts.

Except for the 2004 GAM, all of our models suggest that SST fronts had positive effects on whale distribution within distances of up to about 20 km. However, further increases in modeled encounter rates with longer distances were noted in both the 3-year and 2004 models, apparently as a consequence of problems with detection of frontal systems (and not necessarily a true absence of fronts). The temporal and spatial resolution of the SST images was too coarse to reliably detect alongshore fronts in areas with complex coastline, such as the east Moresby area. Similar issues with coastal front mapping were reported by Breaker et al. (2005). Ideally, daily 1-km resolution satellite images should be used to capture the fast dynamics and fine-scale resolution of these areas very close to shore. Nevertheless, the edge detection algorithm we used frequently identified several of the recurring thermal features described for the region (see example in Fig. 2.6), such as the Dogfish Banks Front, the mainland coastal upwelling in the eastern Hecate Strait, the Cape Scott upwelling front, tidal jets at Cape St. James and the Haida Front (Jardine et al. 1993, Crawford et al. 1995, Belkin & Cornillon 2003).

During our study, relatively high densities of humpback whales were observed over the edge of the trough in the middle of Hecate Strait. This area is bordered on the west by the Dogfish Banks Front, a tidal mixing and seasonally reversing front over shallow depths (Jardine et al. 1993) containing the highest near-surface concentrations of chl-*a*, nutrients, diatoms and copepods of the region (Perry et al. 1983). This front was also identified by Belkin & Cornillon (2003) as the northern part of a well-defined front, from July through March, between 52.5 and 54^{o}N. Northwesterly winds lead to coastal upwelling along the eastern shores of Hecate Strait (Jardine et al. 1993), bordering therefore the east side of the trough.

Tidal streams and non-tidal currents at Dixon Entrance are generally characterized by the intrusion of cold high-salinity water on the southern portion and strong seaward flow of brackish water on the northern side, with a counterclockwise vortex in the middle of the channel (Thomson 1981). We suspect that this circulation favors concentration and retention processes on the south side, and further investigation is warranted. An exploratory inspection of average humpback whale encounter rates against average values of remote sensing images for this area resulted in no apparent correlations, except for higher encounter rates with higher mean surface temperature (data not shown).

The values of the summer climatologies of sea surface temperature and salinity corresponding to positive effects in our models are spread throughout most of the shelf areas, except for Dixon Entrance and, in the case of salinity, for some areas near the mainland. Therefore, these values appear to simply reinforce the strong association of humpback whales with shelf waters. Sea surface height deviation, although selected in two models, did not appear to yield any interpretable results, with positive effects between -5 and 3 cm.

2.4.3. Modeling considerations

The explanatory power of the 3-year GAM was lower than that of the single-year models. This was expected because the full dataset added additional variability to be explained. However, using the full dataset also provided more confidence in the results, as it reduced the chance of selecting spurious covariates. The year models were still a useful means to obtain a snapshot of potentially different conditions and correlations that could have disappeared in the 3-year model. In this context, we interpreted our results primarily in terms of what the models and groups of variables told us in aggregate. The selection of several explanatory variables in our models suggests the relationship between humpback whales and their environment is complex. Interactions between explanatory variables were not tested in our models due to the large number of covariates investigated. Although they can potentially improve model fit (Wood 2006), they can also lead to complicated and uninterpretable functions, particularly if interactions are not expected a priori.

The partial effects of year and month in the 3-year GAM could potentially represent inter-annual and inter-seasonal differences in whale encounter rates. Nevertheless, we cannot rule out the possibility that these differences were caused, in fact, by the non-synoptic nature of the surveys. The fall surveys, for instance, were limited in range, and there was only one summer survey.

2.4.4. Predicted encounter rates

The 3-year GAM appeared to perform well for the purpose of identifying the main areas of humpback whale concentration. It is unclear, however, if this model would be able to predict important shifts in whale distribution or perform well against new datasets. This logical next step was beyond the scope of our study.

2.4.5. Spatial modeling — 2005 summer survey

Our estimated abundance of humpback whales in BC (~ 1,840) is within the plausible range of other studies in the region. Williams & Thomas (2007) estimated 1,310 humpback whales (755-2,280) for the inshore coastal waters of BC's Inside Passage in 2004 and 2005. Abundance estimates from mark-recapture models applied to photo-identification data suggest around 2,000 individuals for BC waters (Rambeau 2008). Nevertheless, caution is necessary with the lower survey effort in Dixon Entrance and northwest Queen Charlotte Islands, which may have resulted in underestimation for that region. Furthermore, the summer of 2005 was known for delayed upwelling favorable winds that resulted in a positive temperature anomaly and a negative anomaly in chl-*a* and primary productivity (Kudela et al. 2006), a scenario that might also have affected whale abundance.

2.4.6. Conclusions

We modeled humpback whale encounter rates in coastal British Columbia and adjacent waters with respect to oceanographic and physiographic data using GAMs. Humpback whales were strongly associated with latitude and bathymetric features, indicating a preference for shelf waters. Distance to SST fronts and salinity (climatology) were also constantly selected as explanatory variables in the models. The shapes of smooth functions estimated for variables based on chl-*a* concentration or net primary productivity with different temporal resolutions and time lags were not consistent, even though higher numbers of whales seemed to be associated with higher primary productivity in all models and for most variables. These and other selected explanatory variables may reflect areas of enhanced biological productivity that favor top predators.

Areas where we observed high concentrations of humpback whales are generally associated with topographically induced oceanographic processes that are known to influence the patchy distribution of euphausiids, an important prey of humpback whales (e.g. Clapham et al. 1997). Off Vancouver Island, for example, euphausiids form dense aggregations over the steep slopes of the shelf break and the edges of the midshelf banks. These areas are characterized by complex topography, domed isopycnals and slower cross-shelf flows (Mackas et al. 1997). The interaction between varying winds, tidal flows and the diverse topographic features on the BC coast likely create distinct conditions to concentrate prey. Thus whales may select habitat based on previous experience and foraging success (Weinrich 1998), and may also use their knowledge of current tides and winds to choose predictable habitats that might be reached within hours.

Few studies have combined GIS with satellite images in cetacean habitat modeling, and fewer have used dynamic variables such as sea surface fronts, and high-resolution spatial and temporal data. To our knowledge, we incorporated explanatory variables from sources that have not been previously tested in cetacean habitat models, and have shown the value of using remotely sensed data when *in situ* oceanographic samples are unavailable. We cannot over stress the need to undertake finer-scale studies to shed light on how humpback whales interact with prey fields and different oceanographic processes. The challenge is to integrate these fine-scale studies into habitat models that take advantage of remote sensing data and provide knowledge on broader scale distribution patterns at the population level.

Our study indicates the presence of at least three important regions for humpback whales along the BC coast: 1) southern Dixon Entrance and northwestern QCI; 2) middle and southwestern Hecate Strait; and 3) the region off Juan de Fuca Strait. Increased survey effort on the west coasts of the QCs and VI is needed to affirm the relative importance of these regions. Further humpback whale research in BC waters should also couple systematic surveys with oceanographic sampling in the inside mainland channels where remote sensing data are not appropriate. Studies are also needed on feeding habits to investigate preferences and interactions with prey.

2.5. References

Akaike H (1985) Prediction and entropy. In: Atkinson AC, Fienberg SE (eds) A celebration of statistics. Springer, New York, p 1-24

Bakun A (1996) Patterns in the ocean : ocean processes and marine population dynamics. California Sea Grant College System, National Oceanic and Atmospheric Adminstration in cooperation with Centro de Investigaciones Biológicas del Noroeste (Mexico), San Diego

Behrenfeld MJ, Falkowski PG (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnology and Oceanography 42:1-20

Belkin IM, Cornillon P (2003) SST fronts of the Pacific coastal and marginal seas. Pacific Oceanography 1:90-113

Bluhm BA, Coyle KO, Konar B, Highsmith R (2007) High gray whale relative abundances associated with an oceanographic front in the south-central Chukchi Sea. Deep-Sea Research II: Topical Studies in Oceanography 54:2919-2933

Breaker LC, Mavor TP, Broenkow WW (2005) Mapping and monitoring large-scale ocean fronts off the California Coast using imagery from the GOES-10 geostationary satellite, Publ. T-056, California Sea Grant College Program, University of California, San Diego, La Jolla (Available at http://repositories.cdlib.org/csgc/rcr/Coastal05_02)

Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL, Thomas L (2001) Introduction to distance sampling: estimating abundance of biological populations, Oxford University Press, London

Burger AE (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

Calambokidis J, Barlow J (2004) Abundance of blue and humpback whales in the eastern North Pacific estimated by capture-recapture and line-transect methods. Marine Mammal Science 20:63-85

Calambokidis J, Falcone EA, Quinn TJ, Burdin AM, Clapham PJ, Ford JKB, Gabriele CM, LeDuc R, Mattila D, Rojas-Bracho L, Straley JM, Taylor BL, Urbán R. J, Weller D, Witteveen BH, Yamaguchi M, Bendlin A, Camacho D, Flynn K, Havron A, Huggins J, Maloney N, Barlow J, Wade PR (2008) SPLASH: Structure of populations, levels of abundance and status of humpback whales in the North Pacific, Final report for Contract AB133F-03-RP-00078 prepared by Cascadia Research for U.S. Dept of Commerce

Calambokidis J, Steiger GH, Ellifrit DK, Troutman BL, Bowlby CE (2004) Distribution and abundance of humpback whales (*Megaptera novaeangliae*) and other marine mammals off the northern Washington coast. Fishery Bulletin 102:563-580

Calambokidis J, Steiger GH, Straley JM, Herman LM, Cerchio S, Salden DR, Urban J, Jacobsen JK, von Ziegesar O, Balcomb KC, Gabriele CM, Dahlheim ME, Uchida S, Ellis G, Miyamura Y, de Guevara PL, Yamaguchi M, Sato F, Mizroch SA, Schlender L, Rasmussen K, Barlow J, Quinn TJ (2001) Movements and population structure of humpback whales in the North Pacific. Marine Mammal Science 17:769-794

Cayula J-F, Cornillon P (1992) Edge detection algorithm for SST images. Journal of Atmospheric and Oceanic Technology 9:67-80

Clapham PJ, Leatherwood S, Szczepaniak I, Brownell RL (1997) Catches of humpback and other whales from shore stations at Moss Landing and Trinidad, California, 1919-1926. Marine Mammal Science 13:368-394

Crawford WR, Woodward MJ, Foreman MGG, Thomson RE (1995) Oceanographic features of Hecate Strait and Queen Charlotte Sound in summer. Atmosphere-Ocean 33:639-681

Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. Marine Ecology Progress Series 289:117-130

Darling JD, Calambokidis J, Balcomb KC, Bloedel P, Flynn K, Mochizuki A, Mori K, Sato F, Suganuma H, Yamaguchi M (1996) Movement of a humpback whale (*Megaptera novaeangliae*) from Japan to British Columbia and return. Marine Mammal Science 12:281-287

Denman K, Forbes R, Mackas DL, Hill S, Sefton H (1985) Ocean ecology data report British Columbia Coastal Waters 29 June - 10 July 1983., Canadian Data Report of Hydrography and Ocean Sciences 36. Institute of Ocean Sciences, Dept. of Fisheries and Oceans, Sidney, BC

Diggle PJ, Ribeiro PJ (2007) Model-based geostatistics, Springer-Verlag, New York

Dolphin WF (1987a) Dive behavior and estimated energy-expenditure of foraging humpback whales in Southeast Alaska. Canadian Journal of Zoology 65:354-362

Dolphin WF (1987b) Prey densities and foraging of humpback whales, *Megaptera novaeangliae*. Experientia (Basel) 43:468-471

Dolphin WF (1987c) Ventilation and dive patterns of humpback whales, *Megaptera novaeangliae*, on their Alaskan feeding grounds. Canadian Journal of Zoology 65:83-90

Doniol-Valcroze T, Berteaux D, Larouche P, Sears R (2007) Influence of thermal fronts on habitat selection by four rorqual whale species in the Gulf of St. Lawrence. Marine Ecology Progress Series 335:207-216

Ducet N, Le Traon P-Y, Reverdin G (2000) Global high resolution mapping of ocean circulation from TOPEX/Poseidon and ERS-1 and -2. Journal of Geophysical Research 105:19477-19498

Efron B, Stein C (1981) The jackknife estimate of variance. The Annals of Statistics 9:586-596

Efron B, Tibshirani RJ (1993) An introduction to the bootstrap, Chapman and Hall, London

Falkowski PG, Woodhead AD (eds) (1992) Primary productivity and biogeochemical cycles in the sea, Plenum Press, New York

Fiedler PC, Reilly SB, Hewitt RP, Demer D, Philbrick VA, Smith S, Armstrong W, Croll DA, Tershy BR, Mate BR (1998) Blue whale habitat and prey in the California Channel Islands. Deep-Sea Research Part II: Topical Studies in Oceanography 45:1781-1801

Foreman MGG, Callendar W, MacFadyen A, Hickey BM, Thomson RE, Di Lorenzo E (2008) Modeling the generation of the Juan de Fuca Eddy. Journal of Geophysical Research-Oceans 113

Forney KA, Wade PR (2006) World-wide abundance and density of killer whales. In: Estes J (ed) Whales, whaling and ecosystems. University of California Press, Berkeley, p 143-160

Freeland HJ, Denman KL (1982) A topographically controlled upwelling center off southern Vancouver Island. Journal of Marine Research 40:1069-1093

Gaskin DE (1982) The ecology of whales and dolphins. Heinemann, London

Goldbogen JA, Calambokidis J, Croll DA, Harvey JT, Newton KM, Oleson EM, Schorr G, Shadwick RE (2008) Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. Journal of Experimental Biology 211:3712-3719

Gregr EJ, Nichol L, Ford JKB, Ellis G, Trites AW (2000) Migration and population structure of northeastern Pacific whales off coastal British Columbia: An analysis of commercial whaling records from 1908-1967. Marine Mammal Science 16:699-727

Gregr EJ, Trites AW (2001) Predictions of critical habitat for five whale species in the waters of coastal British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 58:1265-1285

Hamazaki T (2002) Spatiotemporal prediction models of cetacean habitats in the mid-western North Atlantic Ocean (from Cape Hatteras, North Carolina, USA to Nova Scotia, Canada). Marine Mammal Science 18:920-939

Hastie TJ, Tibshirani RJ (1990) Generalized additive models, Chapman and Hall, New York

Hedley SL, Buckland ST (2004) Spatial models for line transect sampling. Journal of Agricultural Biological and Environmental Statistics 9:181-199

Hedley SL, Buckland ST, Borchers DL (1999) Spatial modelling from line transect data. The Journal of Cetacean Research and Management 1:255-264

Hofmann EE, Murphy EJ (2004) Advection, krill, and Antarctic marine ecosystems. Antarctic Science 16:487-499

IPCC (2007) Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds.)] Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Jaquet N (1996) How spatial and temporal scales influence understanding of sperm whale distribution: A review. Mammal Review 26:51-65

Jardine ID, Thomson KA, Foreman MG, LeBlond PH (1993) Remote sensing of coastal sea-surface features off northern British Columbia. Remote Sensing of Environment 45:73-84

Johnston DW, Westgate AJ, Read AJ (2005) Effects of fine-scale oceanographic features on the distribution and movements of harbour porpoises *Phocoena phocoena* in the Bay of Fundy. Marine Ecology Progress Series 295:279-293

Kim YJ, Gu C (2004) Smoothing spline Gaussian regression: more scalable computation via efficient approximation. Journal of the Royal Statistical Society Series B-Statistical Methodology 66:337-356

Kudela RM, Garfield N, Bruland KW (2006) Bio-optical signatures and biogeochemistry from intense upwelling and relaxation in coastal California. Deep Sea Research Part II: Topical Studies in Oceanography 53:2999-3022

Lerczak JA, Hobbs RC (1998) Calculating sighting distances from angular readings during shipboard, aerial, and shore-based marine mammal surveys. Marine Mammal Science 14:590-598

Mackas DL, Kieser R, Saunders M, Yelland DR, Brown RM, Moore DF (1997) Aggregation of euphausiids and Pacific hake (*Merluccius productus*) along the outer continental shelf off Vancouver Island. Canadian Journal of Fisheries and Aquatic Sciences 54:2080-2096

Mann KH, Lazier JRN (1996) Dynamics of marine ecosystems, 2nd ed. Blackwell Science, Boston

Marchetti A, Trainer VL, Harrison PJ (2004) Environmental conditions and phytoplankton dynamics associated with *Pseudo-nitzschia* abundance and domoic acid in the Juan de Fuca eddy. Marine Ecology Progress Series 281:1-12

Marques FFC (2001) Estimating wildlife distribution and abundance from line transect surveys conducted from platforms of opportunity. Ph.D. Thesis, University of St. Andrews, St. Andrews, Scotland

McFarlane GA, Ware DM, Thomson RE, Mackas DL, Robinson CLK (1997) Physical, biological and fisheries oceanography of a large ecosystem (west coast of Vancouver Island) and implications for management. Oceanologica Acta 20:191-200

McQueen D, Ware D (2006) Handbook of physical, chemical, phytoplankton, and zooplankton data from Hecate Strait, Dixon Entrance, Goose Island bank and Queen Charlotte Sound, Canadian Data Report of Fisheries and Aquatic Sciences 1162

Moore SE, Waite JM, Friday NA, Honkalehto T (2002) Cetacean distribution and relative abundance on the central-eastern and the southeastern Bering Sea shelf with reference to oceanographic domains. Progress in Oceanography 55:249-261

Nichol LM, Heise KA (1992) The historical occurrence of large whales off the Queen Charlotte Islands, Queen Charlotte City, South Moresby/Gwaii Haanas National Park Reserve, Canadian Parks Service: 68.

Perry A, Baker CS, Herman LM (1990) Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. Reports of the International Whaling Commission (Special Issue)12:307-317

Perry RI, Dilke BR, Parsons TR (1983) Tidal mixing and summer plankton distributions in Hecate Strait, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 40:871-887

Prézelin BB, Hofmann EE, Moline M, Klinck JM (2004) Physical forcing of phytoplankton community structure and primary production in continental shelf waters of the Western Antarctic Peninsula. Journal of Marine Research 62:419-460

Rambeau AL (2008) Determining abundance and stock structure for a widespread migratory animal : the case of humpback whales (*Megaptera novaeangliae*) in

British Columbia, Canada. M.Sc. Thesis, University of British Columbia, Vancouver

Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD, Good C, Barlow J, Kaschner K, Baumgartner MF, Forney KA, Ballance LT, Fauchald P, Halpin P, Hamazaki T, Pershing AJ, Qian SS, Read A, Reilly SB, Torres L, Werner F (2006) Techniques for cetacean-habitat modeling. Marine Ecology Progress Series 310:271-295

Ribeiro PJ, Diggle PJ (2001) geoR: A package for geostatistical analysis. R News 1:15-18

Roberts JJ, Best BD, Dunn DC, Treml EA, Halpin PN (in review) Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. Environmental Modelling & Software. Available online: <http://mgel.env.duke.edu/tools>

Robinson CLK, Gower JFR, Borstad GA (2004) Twenty years of satellite observations describing phytoplankton blooms in seas adjacent to Gwaii Haanas National Park Reserve, Canada. Canadian Journal of Remote Sensing/Journal Canadien de Teledetection 30:36-43

Robinson CLK, Morrison J, Foreman MGG (2005) Oceanographic connectivity among marine protected areas on the north coast of British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 62:1350-1362

Sharples J, Simpson JH (2001) Shelf-sea and slope fronts. In: Steele JH, Turekian KK, Thorpe SA (eds) Encyclopedia of ocean sciences. Elsevier Science Ltd, London, p 2759-2768

Simard Y, Mackas DL (1989) Mesoscale aggregations of euphausiid sound scattering layers on the continental shelf of Vancouver Island. Canadian Journal of Fisheries and Aquatic Sciences 46:1238-1247

Sinclair EH, Moore SE, Friday NA, Zeppelin TK, Waite JM (2005) Do patterns of Steller sea lion (*Eumetopias jubatus*) diet, population trend and cetacean occurrence reflect oceanographic domains from the Alaska Peninsula to the central Aleutian Islands? Fisheries Oceanography 14:223-242

Strom SL, Brainard MA, Holmes JL, Olson MB (2001) Phytoplankton blooms are strongly impacted by microzooplankton grazing in coastal North Pacific waters. Marine Biology 138:355-368

Thomas L, Laake JL, Strindberg S, Marques FFC, Buckland ST, Borchers DL, Anderson DR, Burnham KP, Hedley SL, Pollard JH, Bishop JRB, Marques TA (2006) Distance 5.0. Release 2. Research Unit for Wildlife Population Assessment, University of St Andrews, UK (Available at http://wwwruwpast-andacuk/distance/)

Thomson RE (1981) Oceanography of the British Columbia coast, Canadian Special Publication of Fisheries and Aquatic Sciences 56, National Research Council, Ottawa

Tynan CT, Ainley DG, Barth JA, Cowles TJ, Pierce SD, Spear LB (2005) Cetacean distributions relative to ocean processes in the northern California Current System. Deep-Sea Research Part II: Topical Studies in Oceanography 52:145-167

Urbán-Ramirez J, Jaramillo L A, Aguayo L A, Ladron De Guevara P P, Salinas Z M, Alvarez F C, Medrano G L, Jacobsen JK, Balcomb KC, Claridge DE, Calambokidis J, Steiger GH, Straley JM, von Ziegesar O, Waite JM, Mizroch S, Dahlheim ME, Darling JD, Baker CS (2000) Migratory destinations of humpback whales wintering in the Mexican Pacific. The Journal of Cetacean Research and Management 2:101-110

Ware DM, Thomson RE (2005) Bottom-up ecosystem trophic dynamics determine fish production in the Northeast Pacific. Science (Washington) 308:1280-1284

Weinrich M (1998) Early experience in habitat choice by humpback whales (*Megaptera novaeangliae*). Journal of Mammalogy 79:163-170

Weir CR, Pollock C, Cronin C, Taylor S (2001) Cetaceans of the Atlantic Frontier, north and west of Scotland. Continental Shelf Research 21:1047-1071

Williams R, Hedley SL, Hammond PS (2006) Modeling distribution and abundance of Antarctic baleen whales using ships of opportunity. Ecology and Society 11(1):1

Williams R, Thomas L (2007) Distribution and abundance of marine mammals in the coastal waters of BC, Canada. The Journal of Cetacean Research and Management 9:15-28

Wood SN (2001) mgcv: GAMs and generalized ridge regression for R. R News 1:20-25

Wood SN (2006) Generalized additive models: an introduction with R, Chapman and Hall/CRC Press, Boca Raton, Florida

Zerbini AN, Waite JM, Laake JL, Wade PR (2006) Abundance, trends and distribution of baleen whales off Western Alaska and the central Aleutian Islands. Deep-Sea Research Part I: Oceanographic Research Papers 53:1772-1790

Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data, Springer, New York

3. Environmental factors influence the distribution and relative abundance of humpback whales in waters of the Antarctic Peninsula[2]

3.1. Introduction

Studies of species-habitat relationships are fundamental for understanding distribution and movement patterns, for identifying and predicting species responses to environmental changes, and for supporting management and conservation initiatives (Guisan & Zimmermann 2000). The Southern Ocean has long been considered an ideal place to investigate ecological relationships as it encompasses relatively simplified marine ecosystems (Knox 2006). Nevertheless, the underlying processes determining the abundance and distribution of several species in this region, particularly of marine mammals, are not well understood.

It may be difficult to establish the relationship between marine mammals and their habitat because of the heavy exploitation in the Southern Hemisphere compared to other species, and the potential confounding effects of recent regional climate change on post-harvest recovery (Ducklow et al. 2007, Trathan et al. 2007). For example, the humpback whale, *Megaptera novaeangliae,* was exploited to the point that several populations were severely depleted (Mackintosh 1965, Findlay 2001). Most humpback whale populations have shown signs of recovery since protection in 1966 (Reilly et al. 2008), but may now be facing another threat, as the Antarctic Peninsula region is experiencing one of the fastest rates of climate change on Earth (Vaughan et al. 2003, Turner et al. 2005, Clarke et al. 2007, IPCC 2007).

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[2] A version of this chapter will be submitted for publication. Dalla Rosa L, Secchi ER, Garcia CAE, Garcia VMT, Mata MM, Kinas PG. Environmental factors influence the distribution and relative abundance of humpback whales in waters of the Antarctic Peninsula.

Recent studies suggest that sea ice melting from regional warming and increasing UV radiation due to a reduced ozone layer can substantially affect marine ecosystems (Walther et al. 2002). Changes in sea ice extent may result in fluctuations of the abundance of krill, *Euphausia superba* (Siegel & Loeb 1995, Loeb et al. 1997), the primary prey of humpback whales and other baleen whales in the Southern Ocean (Matthews 1937, Mackintosh 1970, Kawamura 1994). In fact, krill densities have declined significantly in the western Antarctic Peninsula and the southwest Atlantic Ocean concurrent with declining winter sea ice (Atkinson et al. 2004), as have some populations of krill and ice-dependent penguins in the western Antarctic Peninsula (Ducklow et al. 2007). The effects of climate change and variability on marine mammals are not so clear, but are also expected in Southern Ocean ecosystems given the strong physical forcing and evident links with upper-trophic levels (Trathan et al. 2007). Possible climate-related population changes in Antarctic and sub-Antarctic regions have been reported for Antarctic fur seals, *Arctocephalus gazella* (e.g. Forcada et al. 2005) and southern elephant seals, *Mirounga leonina* (e.g. McMahon & Burton 2005). Unfortunately, in the case of cetaceans, the lack of precise and long-term data on population parameters and the need for a better understanding of the associations with the physical and biological environment have prevented these types of assessments.

Few studies have examined humpback whale distribution in relation to their foraging habitat, and even fewer have modeled these relationships (Tynan et al. 2005). In the Southern Hemisphere, assessments between foraging humpback whales and environmental features have included qualitative analyses with physical and biological variables (Thiele et al. 2000), quantitative analyses with physiographic and physical variables (Kasamatsu et al. 2000, Nicol et al. 2000) and habitat modeling of combined humpback and minke whales using physiographic, physical and biological explanatory variables (Friedlaender et al. 2006). These studies consisted of single or two-year surveys. As such, some of the observed patterns may represent unique environmental conditions at the time of the surveys. Habitat models, in particular, should also be produced with longer time series to capture some of the inherent biological variability. This would likely increase the predictive power of the models and more accurately portray the species functional responses to environmental features and processes.

The high cost and logistical demand of running multidisciplinary surveys in the Southern Ocean may explain why so few studies have synchronized cetacean surveys with *in situ* oceanographic data collection (e.g. Nicol et al. 2000, Friedlaender et al. 2006). The increasing quality and availability of remote sensing data should complement *in situ* data, and may be a reasonable alternative to collecting oceanographic data from ships when resources are limited. The use of remote sensing data is indeed growing in cetacean habitat modeling (Redfern et al. 2006).

Bransfield and Gerlache Straits, off the Antarctic Peninsula, represent important humpback whale feeding grounds and valuable sites for ecological studies. Relatively large numbers of humpback whales occupy these straits in austral summer months (Secchi et al. 2001, Williams et al. 2006). Individual whales have been observed in different years (Dalla Rosa et al. 2001, Dalla Rosa et al. 2004) and others are known to have spent several weeks within a season (Dalla Rosa et al. 2008) in the area. This growing population of humpback whales breeds and calves along the western coast of

South America, and migrates annually to feeding grounds along the Antarctic Peninsula (Olavarría et al. 2000, Stevick et al. 2004, Branch 2006, Rasmussen et al. 2007).

We investigated the distribution and relative abundance of humpback whales in Bransfield and Gerlache Straits in relation to environmental variables and processes using remote sensing and concurrent *in situ* oceanographic data, GIS tools and generalized additive models (GAMs). We also examined the interannual variability in whale encounter rates in Gerlache Strait at a coarser spatial-scale, by testing for correlations with climate indices and averaged values of environmental variables.

3.2. Material and methods

3.2.1. Study area

Our two study sites were located west and north of the Antarctic Peninsula. Bransfield Strait (ca. 62°S to 63°45'S) is roughly 400 by 100 km and is bounded on the north by the South Shetland Islands and on the south by the Antarctic Peninsula. The western end of Bransfield Strait is delimited by relatively shallow waters less than 500 m deep, and the eastern end is connected to the Weddell Sea. Three deep basins separated by sills less than 1500 m deep mark the northern section of the strait (Hofmann et al. 1996). Two across-shelf depressions about 500-600 m deep form the only northern connections to deeper waters of the Drake Passage (Fig. 3.1).

Gerlache Strait (ca. 63°45'S to 65°S) is a narrow corridor about 175 km long and 7-40 km wide, located to the southwest of Bransfield Strait, between Anvers and Brabant Islands and the Antarctic Peninsula. The southern and middle sections of the strait connect to the Bellingshausen Sea through Bismarck Strait and Schollaert Channel/Dallman Bay, respectively. The northern section of Gerlache Strait provides another deep water connection to Bransfield Strait (Fig. 3.1).

3.2.2. Data collection

3.2.2.1. Surveys

During the austral summers of 1998-2006, cetacean surveys to investigate whale distribution and relative abundance were conducted by the Projeto Baleias/Brazilian Antarctic Program in Bransfield and Gerlache Straits, near the Antarctic Peninsula (Fig. 3.1). All surveys were conducted onboard the 75-meter long Oceanographic and Supply

Vessel (NApOc) '*Ary Rongel*', from the Brazilian Navy, at a cruising speed in the range of 10 knots. Surveys in Gerlache Strait were systematic and dedicated, whereas surveys in Bransfield Strait took place during transit passes, multidisciplinary studies or dedicated line transects. Only surveys conducted in the months of January and February were included in our study. This accounted for most of the data and also avoided the influence of migration timing on our analyses. Furthermore, for the period 1998-2000, we only included surveys in Gerlache Strait..

Between 2003 and 2005, concurrent cetacean and oceanographic data were collected as part of a multidisciplinary study by the *Grupo de Oceanografia de Altas Latitudes* (GOAL – "High Latitude Oceanography Group"). In Bransfield Strait, a grid of CTD (conductivity, temperature, depth) casts with water sampling (Carousel) was conducted 5-10 km apart during a period of about seven to nine days (Fig. 3.2), and the cetacean searching effort was done between the daylight casts during favorable conditions. In Gerlache Strait, the cetacean survey covered the whole area in a single day and was run non-stop, while the oceanographic sampling was completed over one and a half to two days during day and night (Fig. 3.2).

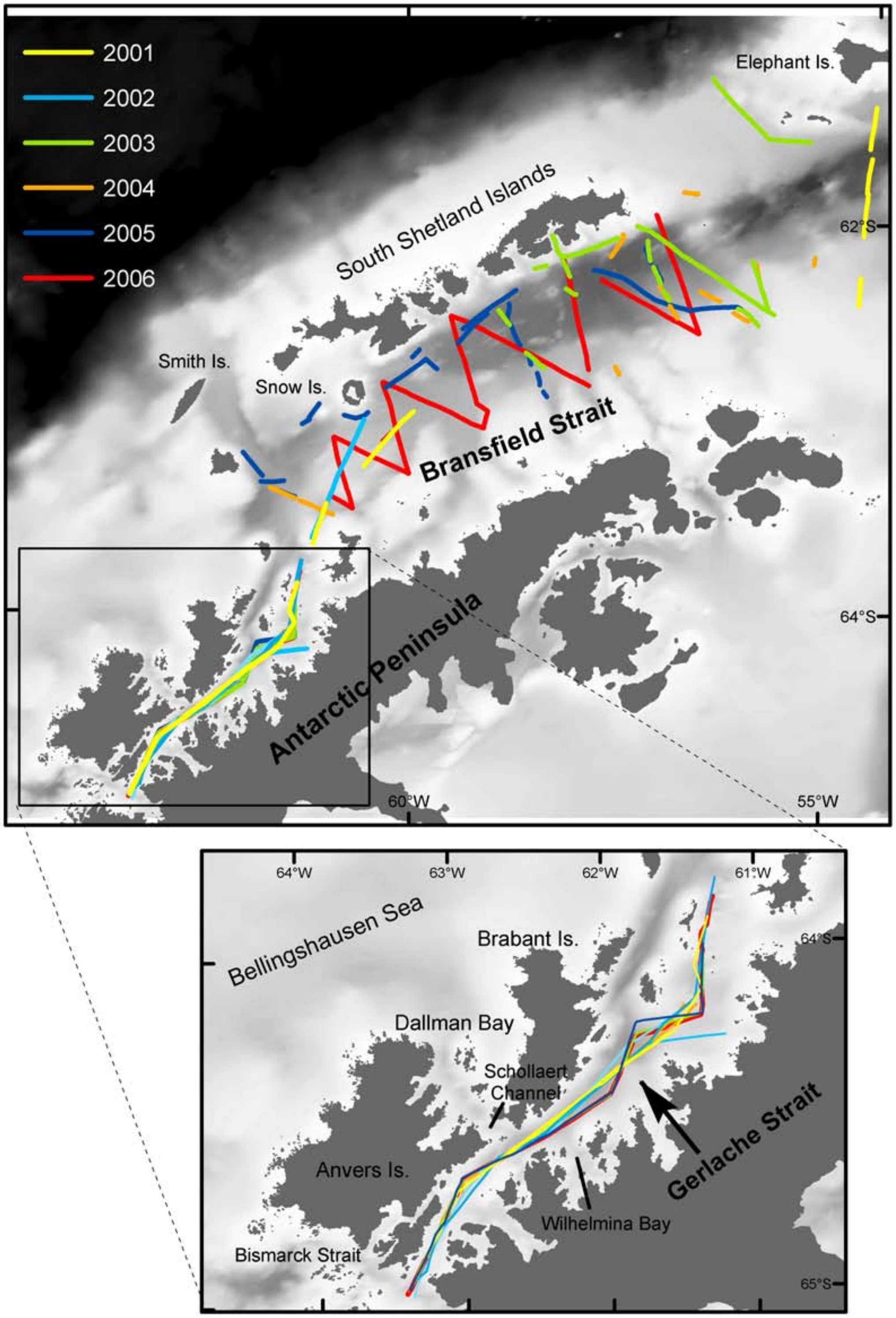


Fig 3.17 – Study area and survey tracklines along the Antarctic Peninsula during 2001-2006.

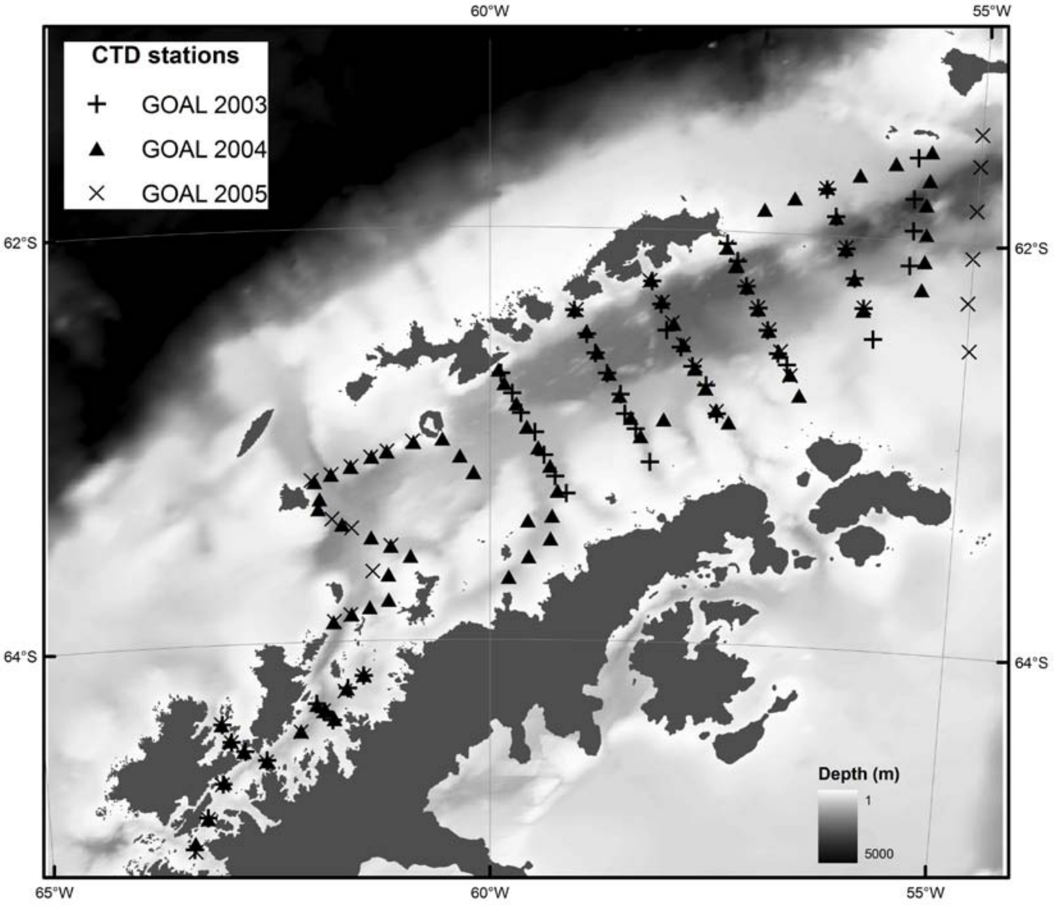


Fig. 3.18 – Locations of oceanographic sampling stations (CTD-Carousel) conducted in Bransfield and Gerlache Straits during 2003-2005.

3.2.2.2. Effort and sighting data

Cetacean observations were made from the exterior wings of the bridge, at a platform height of 12 m above sea level. Searching effort was carried out only in favorable weather conditions (Beaufort ≤ 5 and visibility ≥ 3 nm). Observers rotated through port, data recorder, starboard and resting positions every 30 minutes. Port and starboard observers scanned with 7x50 binoculars and, to a lesser degree, with naked eye from about 10 degrees on the other side of the ship's trackline to 90 degrees on their side. Searching effort was higher towards the trackline.

Sighting data included date/time, coordinates, ship's true heading, number of reticles from the horizon to the sighting, bearing to the sighting, species identification, number of whales and sighting cue. Weather and sea conditions (Beaufort sea state, swell height, visibility, cloud coverage/precipitation and sun glare) were recorded on every observer rotation and when conditions changed.

The radial distance to each sighting was calculated from the reticle measurement and platform height (Lerczak & Hobbs 1998), and corrected for distance to land when the coastline was within shorter distances than the horizon. The location of each whale group was then estimated from bearing and radial distance to the sighting and the ship's true heading at the moment of the sighting.

On-effort tracklines were imported to a geodatabase in ArcGIS 9.2 (ESRI, Redlands, CA) and divided into 4-km segments. If a segment at the endpoint of a trackline was shorter than 2 km, it was added to the previous segment; otherwise, it was left as a separate segment. On-effort sightings were also imported to a geodatabase and assigned to the closest segment. Segments were the sampling unit in the habitat modeling analyses.

3.2.3. Environmental data

GIS layers consisting of physiographic, remote sensing and *in situ* oceanographic data were produced or imported into projected space in ArcGIS. The environmental variables sampled from these layers are shown in Table 3.1.

Table 3.5 – Environmental variables sampled along survey segments and their corresponding transformation and reference names.

Environmental variable	Unit	Temporal resolution	Transformation	Reference name (s)*
Physiographic				
Latitude	M	--	none	Lat
Longitude	M	--	none	Lon
Depth	M	--	log or none	logdepth, depth
Slope	degree	--	log	logSlope
Distance to land	M	--	square root	sqrtDistland
Distance 200-m isobath	M	--	square root	sqrtContour200m
Distance 500-m isobath	M	--	square root	sqrtContour500m
Remote sensing				
Sea surface temperature	^{o}C	Seasonal	none	SST_s
		Monthly	none	SST_m
		8-day	none	SST_w
Distance to SST fronts	M	Monthly	square root	sqrtdistfront_m
Chlorophyll *a*	mg/m3	Monthly	log	logchla_m logchla_mlag
		8-day	log	
Net primary production	mgC/m^2/d	Monthly	log	
		8-day	log	
Sea surface height deviation	M	Monthly	none	SSHd
In situ				
Chlorophyll *a*	mg/m3	--	log	logChla_max; logChla_surf
Salinity	Psu	--	None	Sal(depth): Sal_surf; Sal100; Sal200; Sal300; Sal_bot
Water temperature	^{o}C	--	none	T(depth):T_surf; T100; T200; T300; T_bot; Tmax200;
Mixed layer depth	M	--	log	MLD

* Reference names for some of the variables not included in the models were discarded

3.2.3.1. Bathymetric data

The 2-minute gridded global relief data Etopo2v2 was combined with bathymetry data from the Marine Trackline Geophysics Data to produce a higher resolution bathymetry raster for the study area (Fig. 3.1, Appendix 3). Both databases are available from the National Geophysical Data Center (http://www.ngdc.noaa.gov). Point data extracted from Etopo2v2 and from over 100 cruises and nearly 300,000 soundings conducted in the area were imported to a geodatabase in ArcGIS. Depth values were then log-transformed to approach normality and interpolated to a 500-m grid using kriging and the Geostatistical Analyst to account for spatial structure in the data and to identify and eliminate outliers representing tracks with erroneous locations and depths. Bathymetric slope and depth contours were calculated using ArcGIS Spatial Analyst’s slope and contour tools, respectively, applied to the final bathymetry.

3.2.3.2. Remote sensing data

Seasonal, monthly and 8-day composite images of sea surface temperature (SST) from the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the Aqua satellite (available at http://oceancolor.gsfc.nasa.gov/) were obtained for the period 2003-2006. These images consisted of the 4.63-km level 3 binned product (equal-area projection), and were re-projected, clipped and exported as point data using the SeaDAS 5.1 software (SeaDAS Development Group, NASA Goddard Space Flight Center). Files were then imported to a point geodatabase in ArcGIS and converted to rasters. In addition, SST images from the Advanced Very High Resolution Radiometer (AVHRR)

Pathfinder V5 (NOAA/NESDIS/NODC and University of Miami) were obtained for the period 1998-2002 at a resolution of ~ 5 km.

Thermal fronts were identified in the SST raster images using the Cayula & Cornillon (1992) single-image edge detection algorithm in the Marine Geospatial Ecology Tools (MGET)(Roberts et al. in review). Custom settings in the parameters of the algorithm included a mean temperature difference ≥ 0.375°C, a histogram window size of 16x16 and a histogram window stride of 4 pixels. Fronts in the output rasters were converted to polylines for the calculation of Euclidean distances between each effort segment and the closest front.

Seasonal, monthly and 8-day composite images of chlorophyll-*a* (chl-*a*) concentration (mg/m^3) were obtained as MODIS 4.63-km binned data for 2003-2006, and as Sea-viewing Wide Field-of-view Sensor (SeaWiFS) 9.26-km binned data (also available at http://oceancolor.gsfc.nasa.gov/) for 1998-2002. These data were processed like the MODIS SST product. Two mapped (equal-angle grid) chl-*a* image products were also downloaded: a ~4-km MODIS or ~9-km SeaWiFS rolling 32-day composite and a ~9-km MODIS-SeaWiFS merged image (monthly and 8-day). The potential increase in coverage by the merged product may be important in areas constantly affected by cloud coverage such as the high latitudes. All mapped images were imported to ArcGIS using the MGET tools.

Monthly and 8-day net primary production (NPP) data were obtained from *Ocean Productivity* (http://www.science.oregonstate.edu/ocean.productivity/) at ~9-km resolution. The selected product uses the Vertically Generalized Production Model (VGPM)(Behrenfeld & Falkowski 1997) as the standard algorithm, where NPP is a function of chl-*a*, available light, and the photosynthetic efficiency which is temperature-dependent. The NPP estimates were based on chl-*a* and SST values from SeaWiFS and AVHRR sensors, respectively.

Sea surface height deviation (SSHd) data from the AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data) program were obtained as monthly averages at a 0.25-degree resolution.

3.2.3.3. In situ oceanographic data

Vertical profiles of salinity and temperature were taken with a CTD-Carousel system (Seabird 911+ with 5-liter Niskin bottles). Chl-*a* concentration (mg/m^3) was determined from water samples collected at the surface and at several depths up to 150 m following methods described in Garcia et al. (2008).

The hydrographic and chl-*a* measurements were imported to point geodatabases in ArcGIS and interpolated to raster surfaces of 4-km cell size using Spatial Analyst's inverse distance weighting (IDW) method. Raster layers of temperature and salinity were produced for surface, bottom and the depths of 100, 200 and 300 m.

GIS layers of deep temperature maxima below 200 m (Tmax200) were also produced (see example in Fig. 3.3). This can be used to identify water masses such as the Upper Circumpolar Deep Water (Prézelin et al. 2004). Chl-*a* concentration values were interpolated at the surface and at maximum values. The mixed layer depth (MLD), defined as the depth at which the temperature change from the value at a depth of 10 m is 0.2^{o}C (de Boyer Montégut et al. 2004), was calculated at each station and values were interpolated as above. Because of the 1-m resolution vertical profiles, there was no need to vertically interpolate MLD depths.

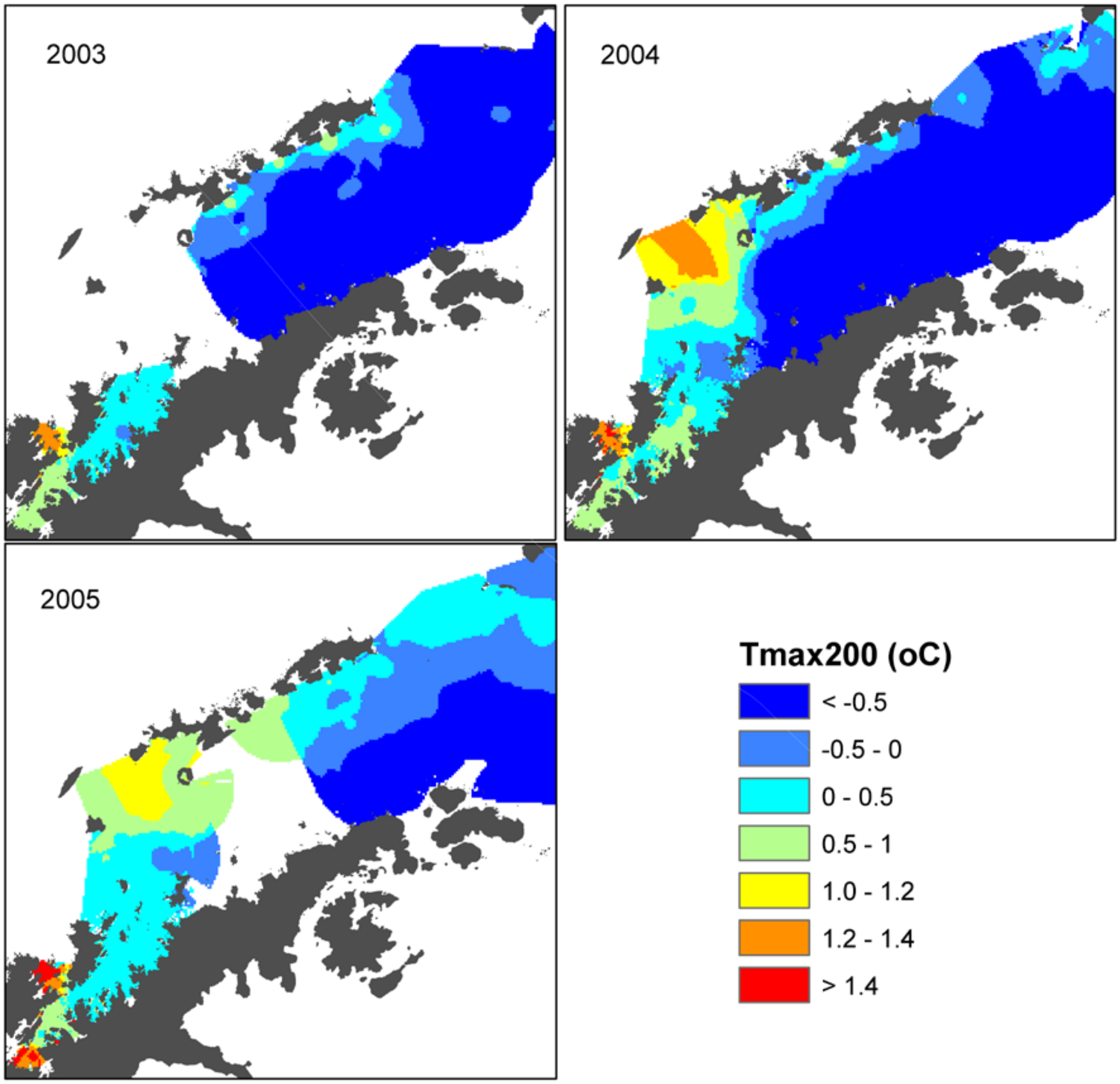


Fig. 3.19 – Isosurfaces of temperature maxima below 200 m (Tmax200) for the years 2003-2005 in Gerlache and Bransfield Straits. Note the colder water of Weddell Sea origin (dark blue).

3.2.4. Sampling GIS layers

The raster surfaces containing the environmental variables from remote sensing were sampled at each segment by taking the mean of values extracted at the midpoint and at the vertices of a 2x2-km box placed over the midpoint following the segment's orientation angle. This approach aimed to provide more even sampling of segments falling near the margins of adjacent raster cells that were also within searching radius by including values from them. The chl-*a* and NPP layers were also sampled with time lags that included the previous month for the monthly data and a 2-week prior for the 8-day data. Distances to features were measured as the shortest straight-line distance from the midpoint of the segment to the feature. The isosurfaces created from the *in situ* measurements were sampled at the midpoint of each segment.

3.2.5. Data analyses

3.2.5.1. Habitat modeling

Prior to model fitting, outliers and other potential problems were identified by graphical exploratory analysis of the data (e.g. Zuur et al. 2007). Most explanatory variables were transformed to approach an even distribution of values: depth, slope, chl-*a* and NPP values were log-transformed; distances to features were square-root transformed (Table 3.1). Pairplots were produced for all variables, and the variable with lower spatio-temporal resolution or coverage from highly correlated ($r > 0.7$) pairs was dropped from further analyses. This approach avoided using similar variables with similar explanatory power in the models, which could lead to multicollinearity issues.

Encounter rates of humpback whale groups were modeled as a function of environmental variables using Generalized Additive Models (GAMs)(Hastie & Tibshirani 1990). These semiparametric models are widely used to investigate nonlinear relationships between species distributions and abundance, including cetaceans, and their environment (Redfern et al. 2006). A quasi-Poisson error distribution with variance proportional to the mean was used to account for overdispersion. Model structure, with a logarithmic link function, was:

$$\log(\mathrm{E}[n_i]) = \sum_k s_k(z_{ik}) + \mathrm{offset}(\log[\mathrm{seg\_length}]_i)$$

where s_k are smooth functions of the explanatory covariates, and z_{ik} is the value of the k^{th} explanatory covariate in the i^{th} segment. For the encounter rates to be modeled as count data, the length of each segment was included as an offset.

GAMs were fitted using mgcv v. 1.4-1 for R (Wood 2001). This package estimates the degree of smoothness of model terms as part of fitting using penalized regression splines and parameters selected by generalized cross validation (GCV). The effective degrees of freedom were inflated by 1.4 (gamma) in the GCV score to avoid overfitting (Kim & Gu 2004, Wood 2006). The basis dimension parameter (k) was set to 8. This procedure limited the maximum allowable degrees of freedom of each term to 7 and further avoided overfitting by restraining the wiggliness of the smoothing functions of the model terms, leading to more ecologically defensible functions. Segments containing missing values of one of the explanatory variables were automatically excluded from model fitting because the mgcv package does not handle missing values. A backwards model selection procedure was performed based on GCV scores (Wood 2006), percentage of deviance explained and a visual examination of residual plots. Model terms were dropped, one at a time, if the approximate 95% confidence interval of the smoothing function contained zero everywhere and, if by dropping the term, the GCV score also dropped (Wood 2001). Next, each remaining term was also tested for lower GCV values and improvements in deviance explained or residual plots.

Our models assumed that residuals were independently distributed. Violation of this assumption, or spatial autocorrelation, was assessed through a variogram analysis using the geoR package v. 1.6-22 for R (Ribeiro & Diggle 2001). The empirical variogram of deviance residuals was compared with the Monte Carlo envelope of empirical variograms computed from independent random permutations of the residuals, holding the corresponding locations fixed (Diggle & Ribeiro 2007).

Models were fitted separately to Bransfield and Gerlache Strait data due to differences in survey effort and design that could affect the results. Surveys were more numerous and were run systematically in Gerlache Strait. Furthermore, they followed the main channel along the strait implying that depth gradients were not broadly sampled, and therefore bathymetry would likely not be a good predictor of whale distribution in our models for Gerlache Strait. These differences could lead to improper selection of covariates related to bathymetry if both datasets were analyzed together. Also, the covariate based on distance to fronts was only considered in the analyses for the Bransfield Strait region due to front detection issues (see Chapter 2). Separate models were also fitted for covariates based on remote sensing and in situ oceanographic data, as the latter were only available for three consecutive years (2003-2005).

The three additional years (1998-2000) available for Gerlache Strait were not included in the modeling process to avoid potential biases from assigning whale locations to the wrong segments, since reticle readings were not available for all sightings in this period. Nevertheless, they were considered in the following section.

3.2.5.2. Interannual variation in whale relative abundance in Gerlache Strait with respect to climate indices and averaged environmental variables

The non-parametric Spearman's rank correlation test was used to investigate potential associations between whale encounter rates and climate indices and averaged environmental variables in Gerlache Strait between 1998 and 2006. Overall encounter rates (individuals per nautical mile surveyed) of humpback and minke whales were calculated by month. Three monthly climate indices were obtained from NOAA Climate Prediction Center (http://www.cpc.ncep.noaa.gov/): 1) the Oceanic Niño Index (ONI), computed as a three-month running mean of ERSST v3b SST anomalies in the Niño 3.4 region (5^{o}N-5^{o}S, 120^{o}-170^{o}W), based on the 1971-2000 base period; 2) the Southern Oscillation Index (SOI), computed from fluctuations in the sea level pressure difference between Tahiti and Darwin, Australia; and 3) the Antarctic Oscillation Index (AAO), computed from surface pressure anomalies poleward of 20^{o}S. ONI and SOI represented the oceanic and atmospheric components of the El Niño Southern Oscillation (ENSO), respectively. The other environmental variables consisted of the mean values of remotely sensed variables (SST and chl-*a*) sampled along survey tracklines (see Section 3.2.4)

3.3. Results

3.3.1. Surveys

3.3.1.1. Gerlache Strait

A total of 444 groups of humpback whales (899 individuals) were recorded during nine survey years and 1,220 nm of searching effort in Gerlache Strait (Table 3.2). Humpback whale locations during the 2001-2006 surveys used in the habitat models are shown in Fig. 3.4. A high proportion of sightings occurred in the middle section of the strait, between Schollaert Channel and Wilhelmina Bay, and towards the northeast.

Table 3.6 – Cetacean surveys conducted in Gerlache Strait between 1998 and 2006, including effort (in nautical miles), total number of humpback whale (HW) groups and individuals sighted, and number of segments used for sampling explanatory variables. Surveys included in the habitat models are shown in bold. Data for the period 1998-2000 have been presented in Secchi et al. (2001).

Survey	Date	Effort (nm)	HW groups	HW individuals	Segments
1a	25-Jan-1998	50.95	9	15	24
1b	27-Jan-1998	20.03	9	34	11
2a	3-Feb-1998	70.73	25	44	33
2b	4-Feb-1998	55.30	14	26	27
3a	27-Jan-1999	59.57	14	33	29
3b	29-Jan-1999	29.72	4	8	14
3c	1-Feb-1999	66.49	12	26	31
4	9-Jan-2000	68.16	8	18	31
5	**3-Feb-2001**	**63.39**	**18**	**42**	**30**
6	**26-Feb-2001**	**86.12**	**20**	**36**	**40**
7a	25-Jan-2002	39.70	22	50	18
7b	**29-Jan-2002**	**84.69**	**34**	**64**	**39**
8	**23-Feb-2002**	**92.01**	**60**	**136**	**43**
9	**21/2-Feb-2003**	**79.43**	**22**	**45**	**36**
10a	15-Jan-2004	41.55	12	25	19
10b	19-Jan-2004	16.13	20	41	7
10c	**20-Jan-2004**	**64.68**	**25**	**49**	**30**
11	**24-Jan-2005**	**91.85**	**80**	**147**	**42**
12a	**25-Jan-2006**	**96.49**	**28**	**48**	**45**
12b	27-Jan-2006	43.60	8	12	20

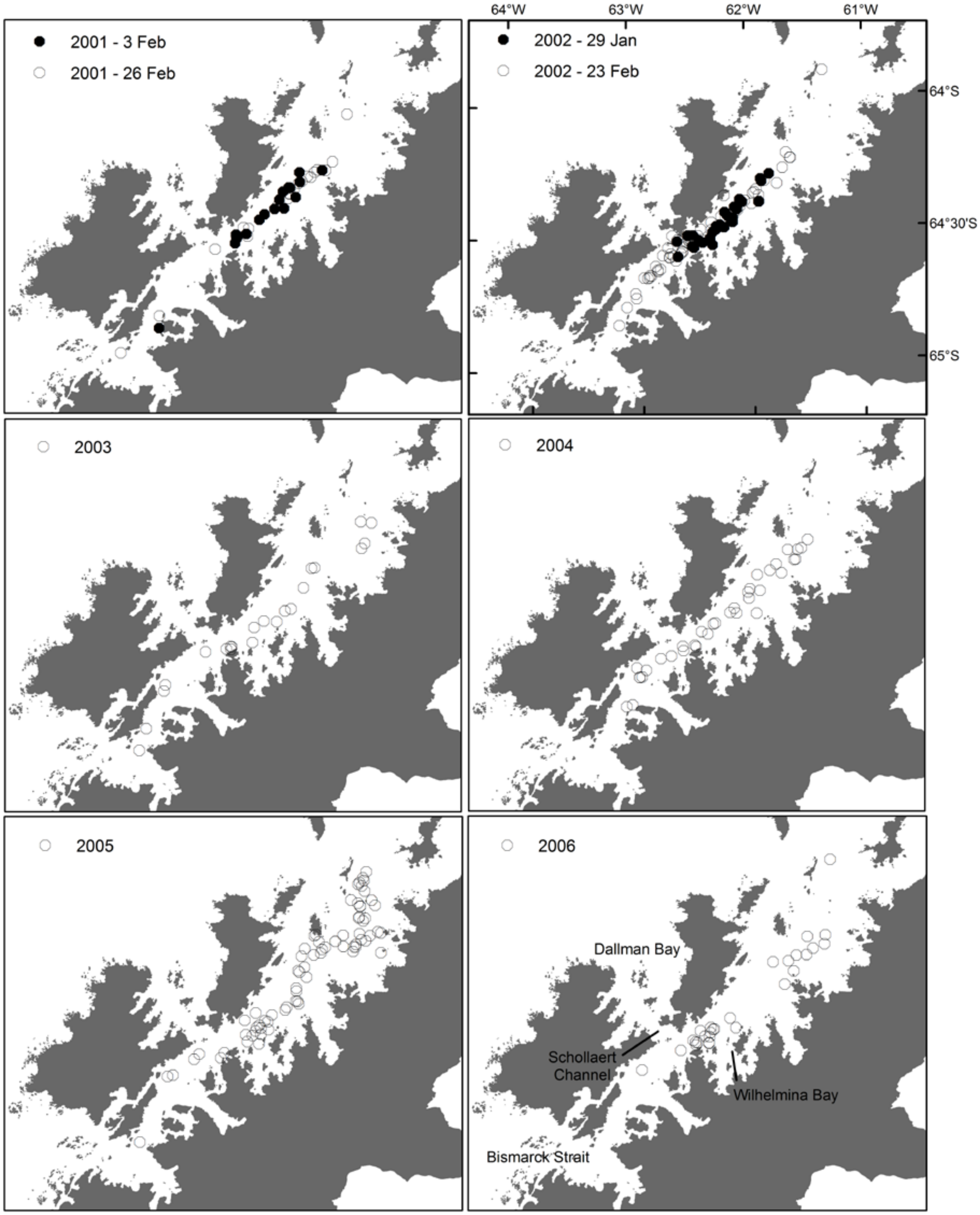


Fig. 3.20 - Locations of humpback whale groups sighted during January-February cetacean surveys conducted in Gerlache Strait between 2001 and 2006. Only surveys included in the habitat models are shown.

3.3.1.2. Bransfield Strait

A total of 245 humpback whale groups (462 individuals) were recorded during six survey years and 862.27 nm of searching effort in Bransfield Strait (Table 3.2; Fig. 3.5).

Table 3.7 – Survey effort and number of humpback whale groups and individuals sighted during January-February 2001-2006 in Bransfield Strait. The number of segments used for sampling explanatory variables is included.

Year	Period	Effort (nm)	HW groups	HW individuals	Segments
2001	21 Jan-3 Feb	83.77	19	33	39
2002	19 Jan	40.10	0	0	19
2003	14-31 Jan	179.21	39	81	83
2004	21-29 Jan	62.86	16	32	28
2005	25 Jan-9 Feb	178.13	64	118	83
2006	24 Jan-9 Feb	318.20	107	198	147

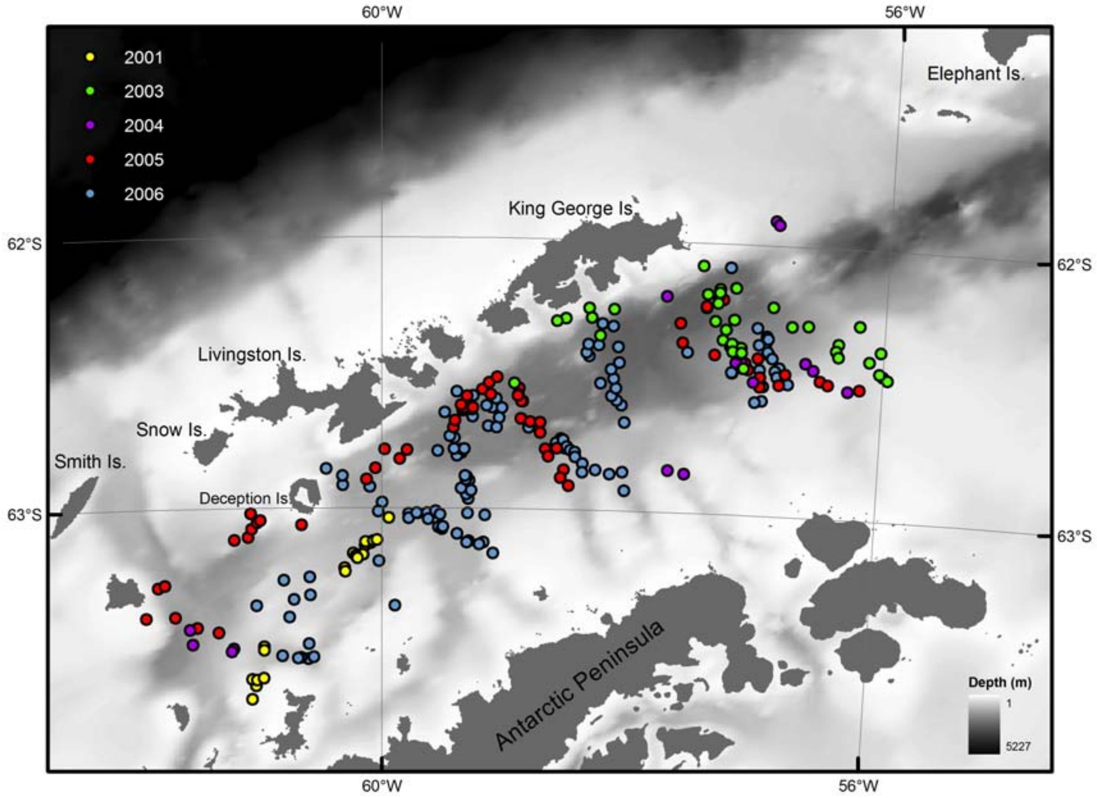


Fig. 3.21 – Location of humpback whale groups sighted during 2001-2006 surveys in Bransfield Strait.

3.3.2. Habitat modeling

3.3.2.1. Remote sensing variables

The generalized additive model (GAM) containing data from the eight surveys in Gerlache Strait resulted in six selected explanatory variables, an adjusted R^2 of 0.41 and 45.9% of explained deviance (Table 3.4). Except for logSlope, which decreased linearly with increasing logged value, all smooth functions for this model indicated non-linear relationships (Fig. 3.6), where each smooth function represents the variation of the fitted response surface holding all other predictors fixed. The model suggests that encounter rates of humpback whales were lower at the lower values and peaked at the mid logged values of both monthly chl-*a* and lagged monthly chl-*a* (Fig. 3.6). The smooth function for seasonal SST showed a positive effect on humpback whale numbers around 1^oC. Humpback whale numbers were also lower in the southernmost portion of Gerlache Strait and peaked near the latitude of Schollaert Channel, decreasing slowly towards the north (Fig. 3.6). The partial effect for year indicates interannual variation in encounter rates that could not be explained by the other variables, with strong positive effects in particular for 2002 and 2005 in relation to 2001 (Fig. 3.6).

The GAM with remote sensing data for Bransfield Strait resulted in six explanatory variables, an adjusted R^2 of 0.17 and 24.5% of explained deviance (Table 3.4). The estimated smooth functions of monthly SST and distance to weekly SST fronts showed positive effects around 1.5^oC and at closer distances to the fronts, respectively (Fig. 3.7). The model also suggests that humpback whale encounter rates increased linearly with depth (with a positive effect over depths deeper than 1000 m) and peaked around 40 km from land (mostly the South Shetland Islands, Fig. 3.7). Humpback whale numbers apparently decreased linearly with increasing logged values of monthly chl-*a*, and were also lower at the northern portion of Bransfield Strait (Fig. 3.7).

Variogram analyses of the residuals of the above models showed no evidence of spatial auto-correlation.

Table 3.8 – Results of generalized additive models based on physiographic and remote sensing data for Gerlache (GS) and Bransfield (BS) Straits. The selected explanatory variables in each model are identified as factors (F) or smooth functions (S) along with their estimated degrees of freedom in parentheses and approximate p-value significance. Empty spaces correspond to non-selected variables and dashes represent variables that were not part of the initial model.

Variable	GS	BS
logDepth		S(1)*
logSlope	S(1)*	
sqrtContour500m	-	
sqrtDistLand		S(2.11)$^{\cdot}$
logchla_m	S(2.43)*	S(1)$^{\cdot}$
logchla_mlag	S(2.97)**	
SST_season	S(4.65)**	-
SST_m		S(3.54)**
SST_w	-	
sqrtdistfront_w	-	S(5.24)$^{\cdot}$
SSHdevm	-	
Lat	**S(6.30)**	**S(4.68)**
Year	F: **Year2002,** Year2003**, **Year2004, Year2005,** Year2006*	-
% Deviance explained	45.9	24.5
R^2 adjusted	0.41	0.17
n	252	385

$^{\cdot}$ = p < 0.1; * = p < 0.05; ** = p < 0.01; all other terms in bold => p < 0.001
S(1) = linear term
n = number of segments in the selected model

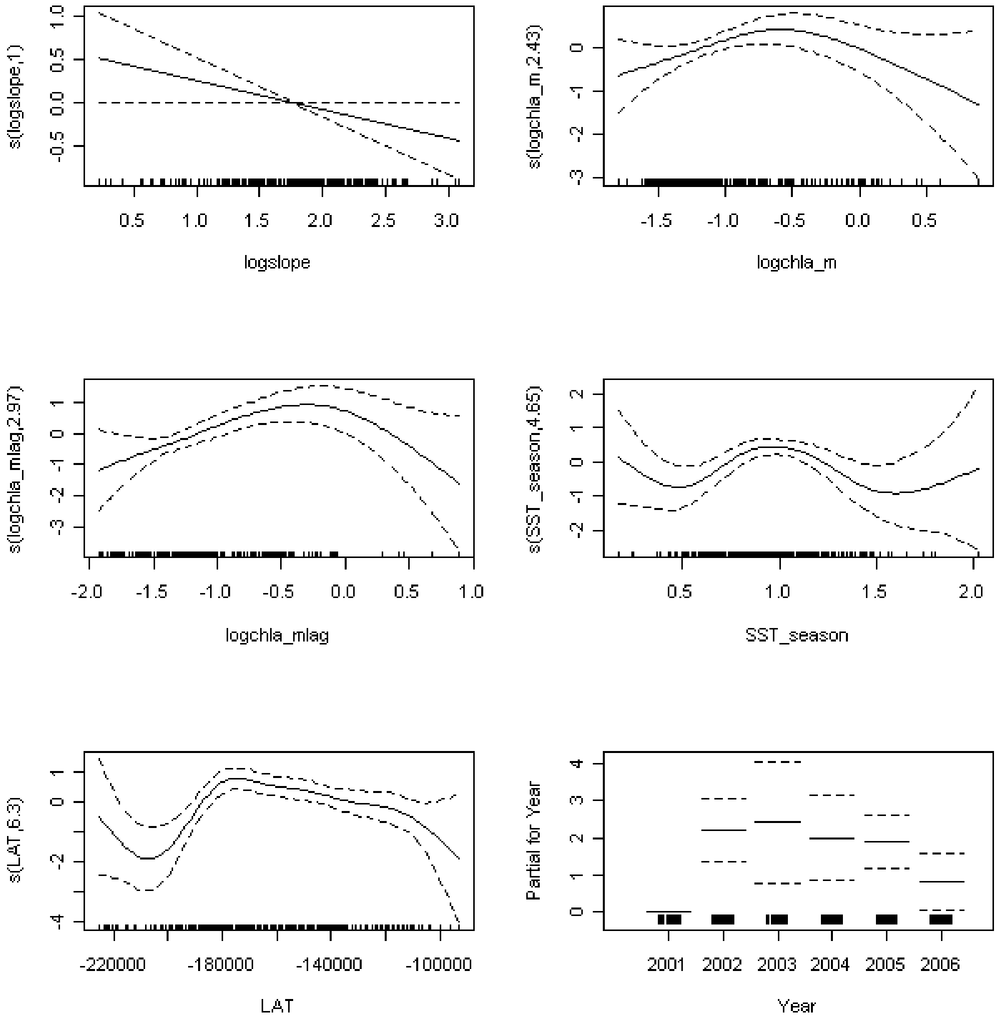


Fig. 3.22 – Model terms of the selected generalized additive model (GAM) of humpback whale relative abundance for Gerlache Strait, based on physiographic and remotely sensed explanatory variables. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. Y-axis = fitted function with estimated degrees of freedom in parenthesis; x-axis = variable range with the short parallel bars on the x-axis (rug plots) indicating sampled values. The partial effect of year is also included.

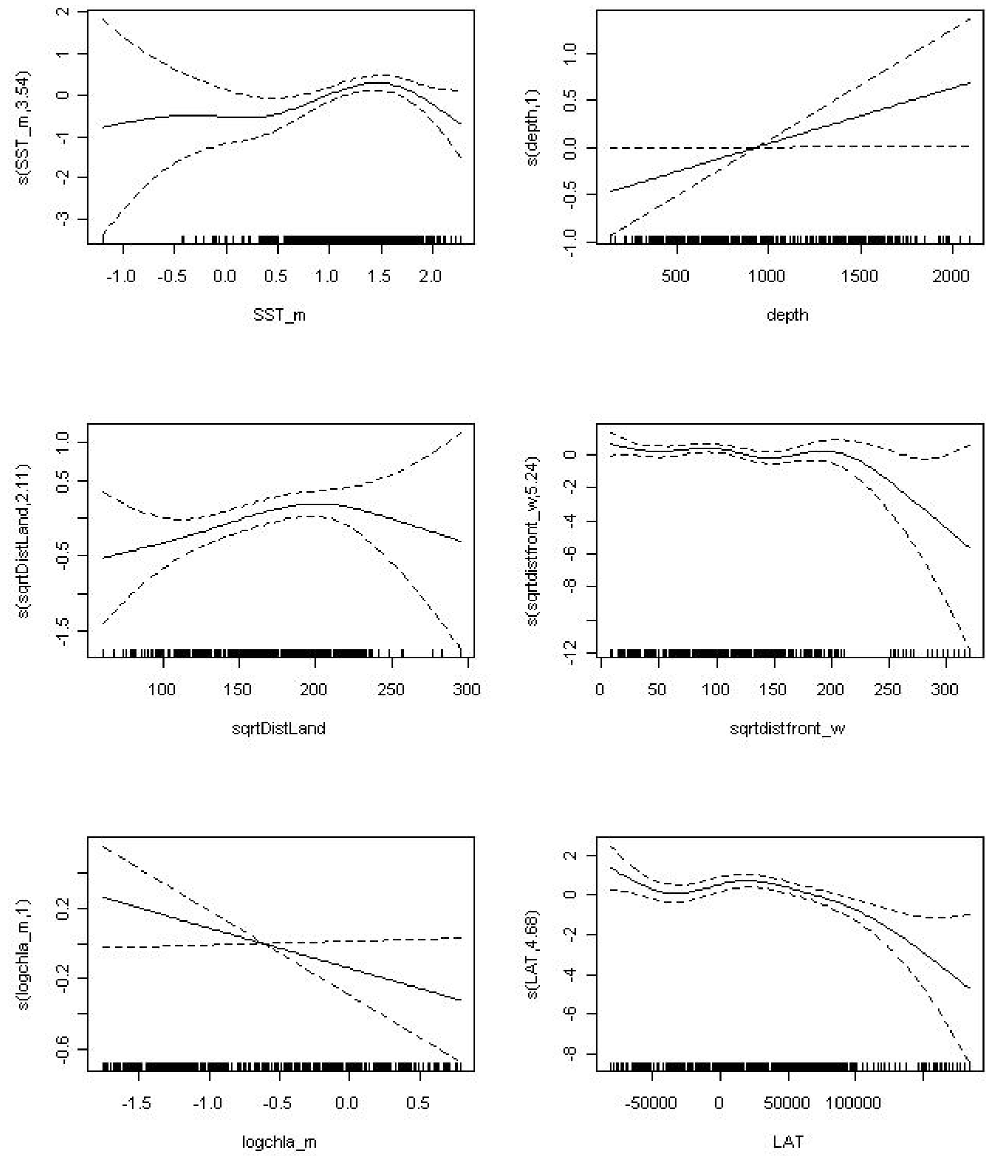


Fig. 3.23 – Model terms of the selected generalized additive model (GAM) of humpback whale relative abundance for Bransfield Strait, based on physiographic and remotely sensed explanatory variables. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. Y-axis = fitted function with estimated degrees of freedom in parenthesis; x-axis = variable range with rug plots indicating sampled values.

3.3.2.2. In situ (CTD) oceanographic variables

Of the three oceanographic cruises conducted in Gerlache Strait, the highest chl-*a* values in 2005 were associated with shallower mixed layer depth (MLD) and higher SST values (Fig. 3.8). MLD values decreased with Year, while both chlorophyll-a maxima and SST ranged about the same in 2003 and 2004, and were markedly higher in 2005. With respect to latitude, the highest chl-*a* values of 2005 occurred in the middle and northern sections of the Strait, while SST showed a similar signature along the Strait, with lower temperatures in the southern section, and the higher values of 2005 represented by a separate line (Fig 3.8). Given that chl-*a* maxima, MLD and SST were highly correlated, these variables were only tested in separate models for Gerlache Strait. It should be noted, however, that these alternative models were not compared with a formal statistical test because model selection started with different sets of variables. Models with a by-year argument were also included for chl-*a* and SST, to verify whether the observed relationship between humpback whales and these variables was the same for the three years, or their increased values in 2005 had an effect on the smoothing function.

The best fitting GAM for Gerlache Strait with CTD data resulted in three explanatory variables, including SST with a by-year argument, sea surface salinity (SSS) and latitude (model 4, Table 3.5). The explained deviance and adjusted R^2 for this model were 45.6% and 0.53, respectively. The estimated smooth functions of latitude, SSS and SST:2004 resulted in linear terms with positive effects towards increasing values (Fig. 3.9D; Table 3.5). Humpback whale numbers peaked around 3^oC in 2005, and no effect was observed for SST in 2003.

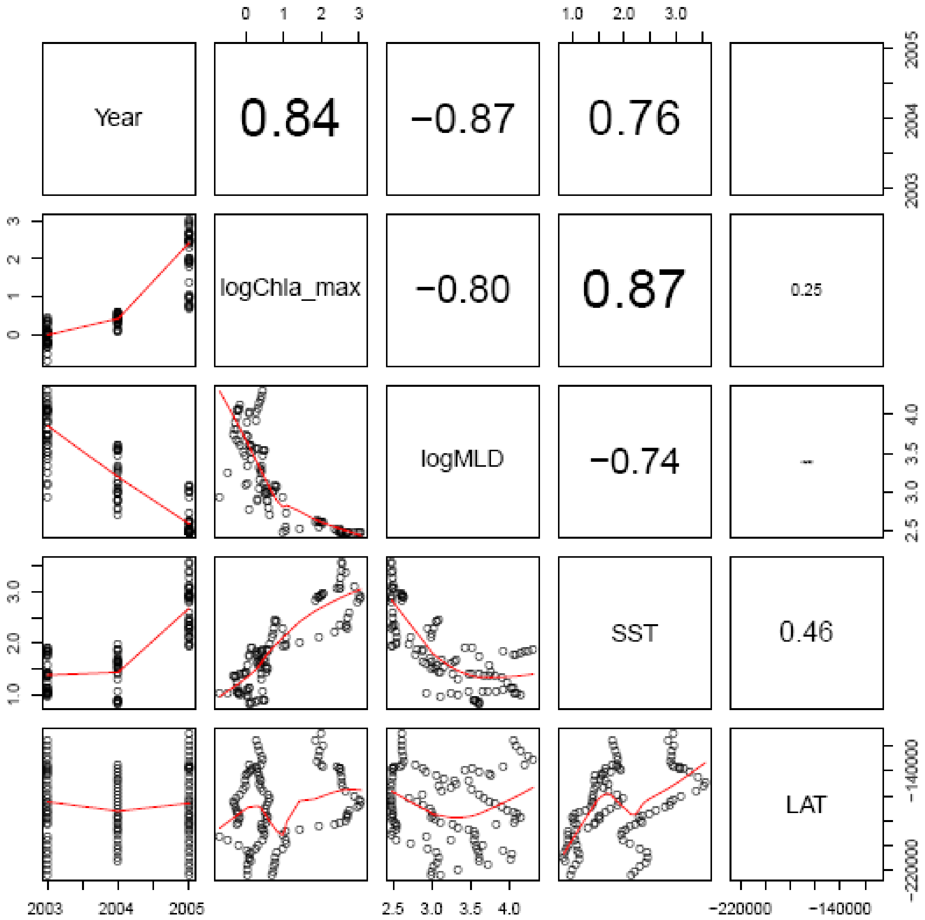


Fig. 3.24 – Correlations between pairs of some oceanographic variables sampled along transects in Gerlache Strait between 2003 and 2005. Year and latitude are included to show temporal and spatial patterns in the variables.

The other three GAMs for Gerlache Strait resulted in two selected explanatory variables, one of which consisted of a linear term for latitude identical for all (Fig. 3.9A). The effect of chl-*a* maxima on humpback whale numbers increased linearly with log values in model 1 (Fig. 3.9B), while the effect of MLD decreased almost linearly in model 3 (Fig. 3.9C), as expected from the inverse correlation between these two variables. Humpback whale numbers also appeared to have increased with increasing chl-*a* values when examined by year, although this relationship resulted in significant approximate p-values only for 2003 (Fig. 3.9A).

Table 3.9 – Results of generalized additive models based on physiographic and *in situ* oceanographic data for Gerlache (GS) and Bransfield (BS) Straits, and both datasets combined (GS + BS). The selected explanatory variables in each model are identified as factors (F) or smooth functions (S) along with their estimated degrees of freedom in parentheses and approximate p-value significance. Empty spaces correspond to non-selected variables and dashes represent variables that were not part of the initial model.

Variable	GS				BS	BS + GS
	Model 1	Model 2	Model 3	Model 4		
logDepth						
sqrtDistLand					S(1.31)**	
logChla_max	**S (1)**	-	-	-		**S**(1)
logChla_max (by year)	**-**	S(1.95):2003* S(1.15):2004 S(1):2005 $^{\cdot}$	-	-	-	-
logMLD	-	**-**	**S (1.35)**	-	S(1)	
T_surf (SST) (by Year)	**-**	-	-	S(1): 2003 S(1): 2004* **S(2.93)**:2005	-	-
Tmax200					S(1)**	
Sal_surf				**S**(1)		S(1.02) $^{\cdot}$
Sal_bot						
Lat	**S (1)**	**S (1)**	**S (1)**	S (1.11)**	S(2.38)*	**S(2.79)**
logSlope	-	-	-	-	S(2.38)	
sqrtContour500m	-	-	-	-		
Area (GS or BS)	-	-	-	-	-	F: GS**
% Deviance explained	34.9	40.3	35.9	45.6	20.9	25.3
R^2 adjusted	0.429	0.465	0.451	0.53	0.182	0.311
n	108	108	108	108	182	316

$^{\cdot}$ = $p < 0.1$; * = $p < 0.05$; ** = $p < 0.01$; all other terms in bold => $p < 0.001$

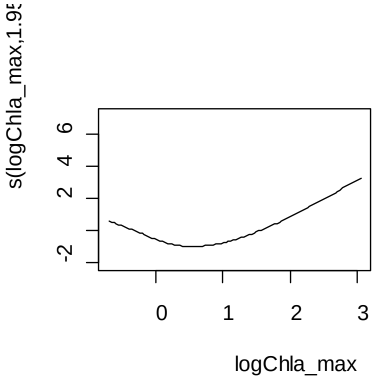
S(1) = linear term; *n* = number of segments in the selected model

The GAM with CTD data for Bransfield Strait resulted in five explanatory variables, an adjusted R^2 of 0.18 and 20.9% of explained deviance (Table 3.5). The estimated smooth functions of slope and latitude suggest negative effects at the flatter and most northerly regions of the strait, respectively (Fig. 3.10). The effect of deep temperature maxima below 200 m (Tmax200) increased linearly with increasing temperature, being positive about -0.2°C and above. Distances from land larger than about 22 km also had a positive effect on humpback whale encounter rates, and the effect of MLD appeared to decrease linearly with increasing depth, though its approximate p-value was not significant (Fig. 3.10).

The GAM with the combined CTD datasets for Bransfield and Gerlache Straits resulted in four explanatory variables, an adjusted R^2 of 0.31 and 25.3% of explained deviance (Table 3.5). Linear terms for chl-*a* maxima and SSS indicate that humpback whale numbers increased with increasing values of these variables (Fig. 3.11). The effect of latitude peaked around Deception Island (~ 63°S), and the partial for area suggests higher encounter rates of humpback whales occurred in Gerlache Strait during the three-year period (Fig. 3.11).

Fig. 3.25 – Model terms of alternative generalized additive models (GAMs) of humpback whale relative abundance for Gerlache Strait, based on physiographic and *in situ* oceanographic explanatory variables (2003-05). A) model 2; B) Chl-a term of model 1; C) MLD term of model 3; D) model 4. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. Y-axis = fitted function with estimated degrees of freedom in parenthesis; x-axis = variable range with rug plots indicating sampled values.

A



Variogram analyses of the residuals of the above models showed no evidence of spatial auto-correlation.

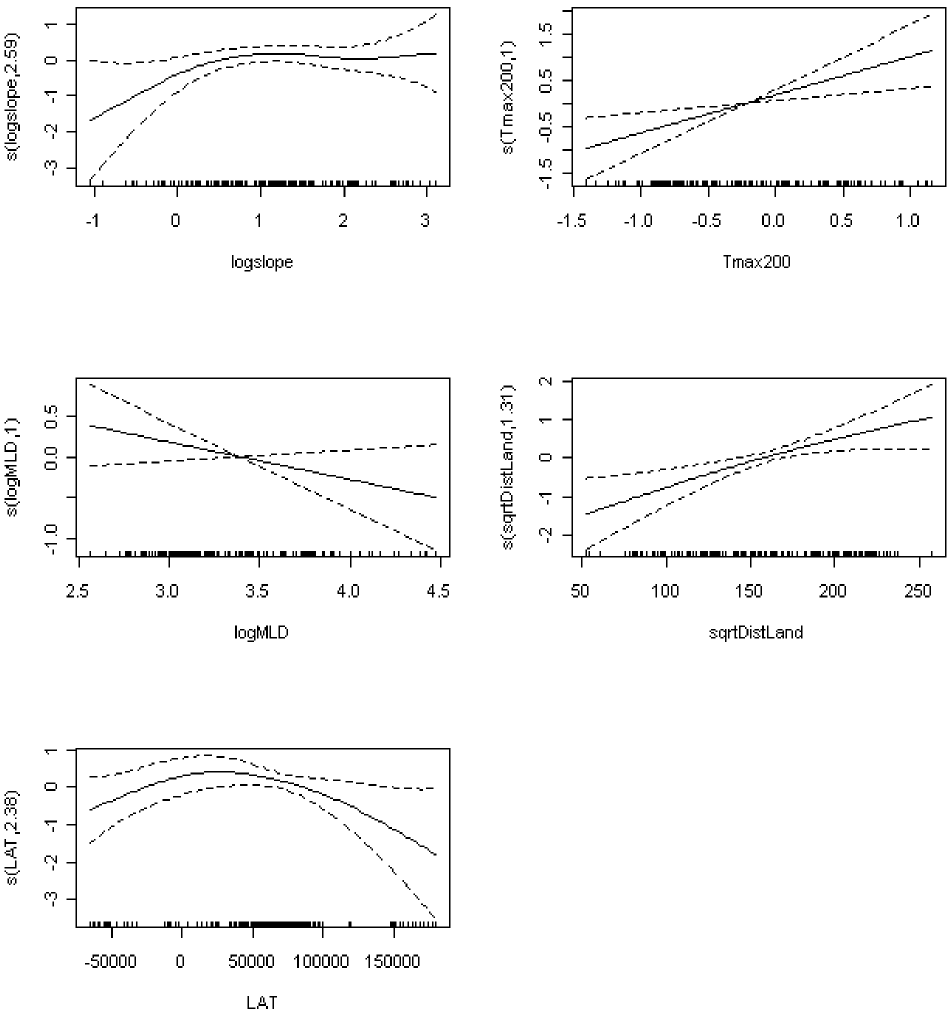


Fig. 3.26 – Model terms of the selected generalized additive model (GAM) of humpback whale relative abundance for Bransfield Strait, based on physiographic and *in situ* oceanographic explanatory variables (2003-05). Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. Y-axis = fitted function with estimated degrees of freedom in parenthesis; x-axis = variable range with rug plots indicating sampled values.

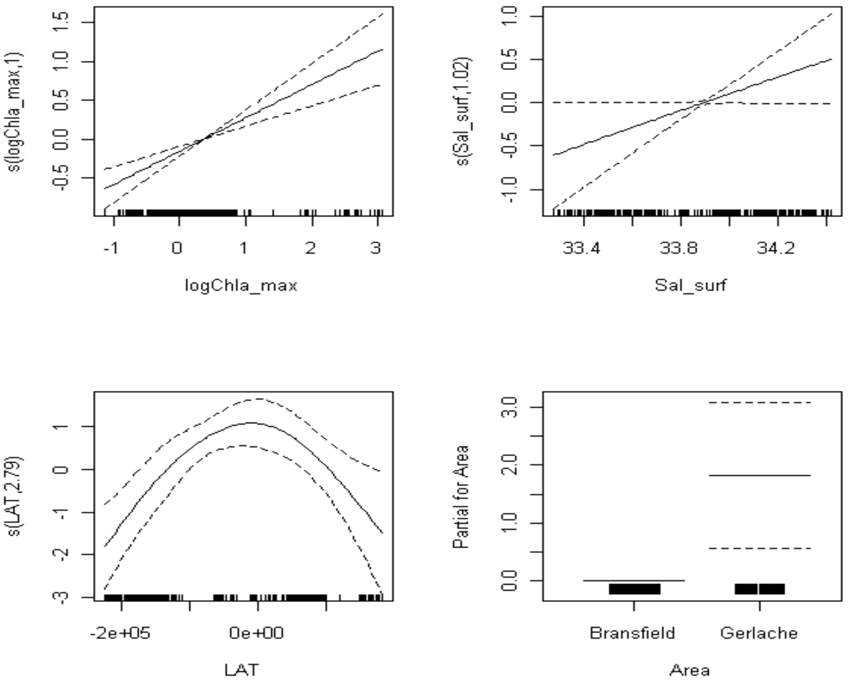


Fig. 3.27 – Model terms of the selected generalized additive model (GAM) of humpback whale relative abundance for Gerlache and Bransfield Straits combined, based on physiographic and *in situ* oceanographic explanatory variables (2003-05). Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. Y-axis = fitted function with estimated degrees of freedom in parenthesis; x-axis = variable range with rug plots indicating sampled values. The partial effect of area is also included.

3.3.3. Interannual variation in whale relative abundance in Gerlache Strait

Encounter rates (ERs) of humpback whales in Gerlache Strait were positively correlated with ONI (Spearman's $\rho = 0.601$; $p < 0.05$; Table 3.6). Lower ERs were associated with the cold phase (La Niña), while higher ERs appeared to be associated with warm and, most likely, neutral phases (Fig. 3.12A). Taking the absolute values of ONI, which places relatively stronger events (cold or warm) together, slightly improved the correlation (Spearman's $\rho = -0.636$; $p < 0.05$; Table 3.6), suggesting that humpback whale ERs may actually be associated with smaller absolute values of ONI, i.e., the neutral phase (Fig. 3.12B). No correlations occurred between humpback whale ERs and the other indices or the environmental variables (Appendix 4), although ERs appeared to be higher towards higher averaged monthly SST values (Table 3.6).

Minke whale ERs, on the other hand, were negatively correlated with ONI, and positively correlated with chl-*a* concentration in the previous month (Table 3.6). The highest ERs occurred during cold phases, whereas three surveys with no minke whale sightings occurred during warm phases (Fig. 3.12C).

Table 3.10 – Results of Spearman's rank correlation analysis between encounter rates (individuals/nautical mile) of humpback (HW_ER) and minke (MinkeER) whales and climate indices and averaged environmental variables in Gerlache Strait between 1998 and 2006. P-values are located on the upper half of the table, with significant ones in bold. Spearman's ρ values on the lower half. All tests with 10 d.f. and $\alpha = 0.05$.

	HW_ER	MinkeER	ONI	absONI	SOI	AAO	SST_m	Chla_m	Chla_mlag
HW_ER	-	0.4	**0.0386**	**0.026**	0.276	0.746	0.085	0.417	0.125
MinkeER	-0.268	-	**0.0095**	0.467	0.109	0.339	0.467	0.467	**0.0292**
ONI	0.601	-0.711	-	-	**0.0014**	0.167	0.118	0.059	**0.0114**
absONI	-0.636	-0.232	-	-	0.354	0.746	0.125	0.795	0.983
SOI	-0.343	0.486	-0.811	-0.294	-	0.542	0.276	**0.026**	**0.0019**
AAO	-0.105	0.303	-0.427	-0.105	0.196	-	0.713	0.762	0.404
SST_m	0.517	-0.232	0.476	-0.469	-0.343	-0.119	-	0.931	0.276
Chla_m	-0.259	0.232	-0.559	-0.084	0.636	0.098	0.028	-	0.08
Chla_mlag	-0.469	0.627	-0.699	-0.007	0.797	0.266	-0.343	0.524	-

ONI = Oceanic Niño Index; abs = absolute value; SOI = Southern Oscillation Index;
AAO = Antarctic Oscillation Index

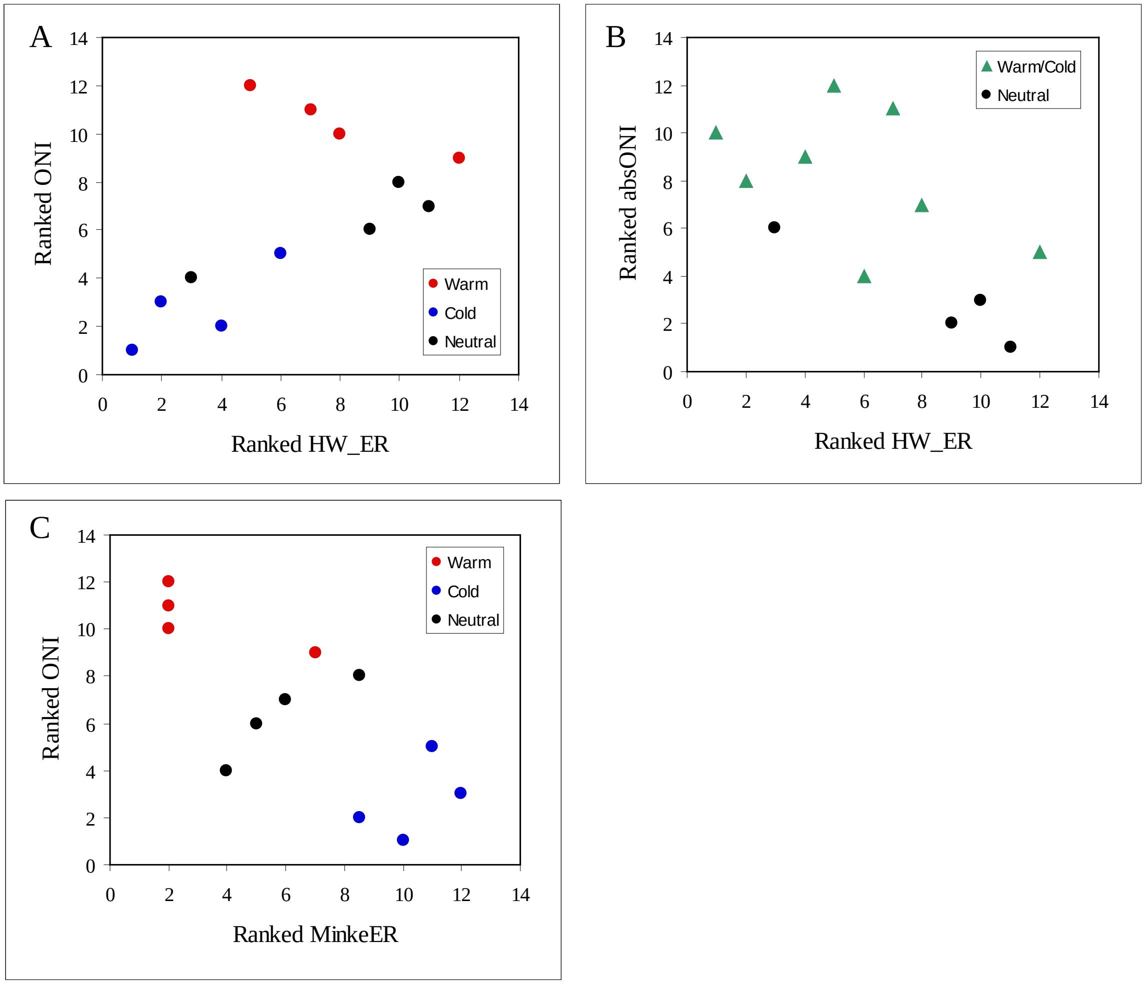


Fig. 3.28 – Plots of ranked Oceanic Niño Index (ONI) versus ranked whale encounter rates in Gerlache Strait during 1998-2006: A) ONI vs. humpback whale encounter rates; B) absolute values of ONI vs. humpback whale encounter rates; C) ONI vs. minke whale encounter rates. Dots are colored to indicate cold La Niña (blue), warm El Niño (red) or either (green) episodes. Neutral phases are represented by black dots.

3.4. Discussion

We modeled several years of data to establish the relationship between environmental features, oceanographic processes and the distribution and relative abundance of humpback whales in waters of the Antarctic Peninsula. Resulting models revealed significant associations that generally reflected the presence of whales in areas of increased biological productivity. They also suggest a mechanism that may explain interannual variability in whale numbers and distribution.

To our knowledge, our study is the first to model cetacean habitat across multiple years in the Southern Ocean using GIS tools and statistical models applied to remote sensing and *in situ* oceanographic data. The time span of our research, particularly the systematic surveys in Gerlache Strait, also allowed us to examine the interannual variability in whale encounter rates with respect to climate indices and showed evidence that the teleconnections between ENSO and the Antarctic Peninsula may possibly influence the distribution of top predators in this region.

3.4.1. Gerlache Strait

The best fitting models for Gerlache Strait explained about 45% of the deviance, with either type of data (remote sensing or *in situ* explanatory variables). Only the number of selected variables was smaller and the adjusted R^2 was higher for the model based on *in situ* variables and fewer surveys (three years as opposed to six years). Considering the observed interannual variability in environmental variables, and the lack of variables related to prey biomass, the resulting models seem to have good explanatory power.

The GAMs suggest, based on estimated smooth functions of chl-*a* concentration values from both remote sensing and *in situ* data, that higher numbers of humpback whales were associated with higher primary productivity in Gerlache Strait. Whale numbers were also strongly associated with latitude, being higher in the middle and northern sections of the strait, and suggesting, therefore, that these areas were more productive.

The Gerlache Strait is a highly productive area (Holm-Hansen & Mitchell 1991, Castro et al. 2002, Rodríguez et al. 2002) with values analogous to those of upwelling zones (Lorenzo et al. 2002) having heterogeneous physical characteristics (Rodríguez et al. 2002) and interannual variability in both physical and biological parameters (Hofmann et al. 1996, Ross et al. 1996, García et al. 2002). There have been few studies on krill biomass and distribution during the austral summer in Gerlache Strait. The more recent studies in this area have focused primarily on mesozooplankton (e.g. Cabal et al. 2002), or krill abundance in winter, when large aggregations were observed compared to offshore areas (Nordhausen 1994, Zhou et al. 1994). Nevertheless, important krill biomass has been detected in this area during the austral summer (Montú et al. 1994, Siegel & Kalinowski 1994, Ross et al. 1996), including the so-called ‘superswarms’ (Cram et al. 1979), and it contains one of the highest mean krill densities of the Antarctic Peninsula (see Fig. 14a in Atkinson et al. 2008). Also, northern Gerlache Strait was proposed as an important nursery area for krill (Huntley & Brinton 1991).

The high productivity of Gerlache Strait is influenced by the hydrography and circulation in the region. The shallower southern section of the strait is usually occupied by cold Antarctic Surface Water (AASW), with potential intrusions of Upper

Circumpolar Deep Water (UCDW) below it, coming from the Bellingshausen Sea through Bismarck Strait. These intrusions of UCDW are not seasonal, but episodic in nature, and occur when the southern boundary of the Antarctic Circumpolar Current (ACC) floods over the shelf and through across-shelf channels, bringing warm and nutrient-rich waters to the coast and enhancing biological production (Hofmann et al. 1996, Prézelin et al. 2000). The area to the north is typically occupied by upper and lower layers of Transitional Zonal Waters of Bellingshausen Sea (TBW) and Weddell Sea (TWW) influence, respectively (García et al. 2002). Intrusions of UCDW may also occur in the middle section of the strait, through Dallman Bay and Schollaert Channel (García et al. 2002), as it also appears to be the case during this study (see for example Fig. 3.3).

The confluence and potential mixing of waters in the middle zone, shaped by topographic features, divides Gerlache into two areas with distinct physical properties, and may be responsible for enhancing the biological productivity of the area. Hydrographic stations conducted at the latitude of the Schollaert Channel frequently contain the highest levels of primary productivity in the Gerlache Strait (Rodríguez et al. 2002, Pollery 2005). Therefore, we hypothesize that the physical setting at this area of Gerlache Strait consistently enhances primary productivity, attracting predictable and large concentrations of zooplankton which, in turn, attract large numbers of their most significant predator in the area, the humpback whale. This would explain the peak in humpback whale numbers around this latitude, as suggested by the GAM with remote sensing data and also evident for most of the surveys by looking at the distribution of whales (see Fig. 3.4). Further evidence for the resource predictability of this specific area comes from the interannual resightings of four photo-identified individuals within distances of less than 6 nm, three of them in consecutive years and one four years apart (Dalla Rosa et al. 2004, unpublished data).

As surface currents flow to the northeast towards Bransfield Strait (Niiler et al. 1990, Zhou et al. 2002), it is also possible that part of the biological production near the Schollaert Channel area is transported further northeast, adding to the already favorable conditions of the northeastern sector, such as stratified waters and shallow MLDs (see discussion below). Humpback whales instrumented with satellite tags in the middle sector of Gerlache Strait generally travelled to the northeast as they were leaving the area (Dalla Rosa et al. 2008), possibly searching for predictable krill patches.

The steady increase in overall humpback whale encounter rates between 2003 and 2005 matched an increase in both chl-*a* concentrations and SST in the same period, particularly in 2005, when whale numbers were also considerably higher. This partially explains the strong linear relationship between whales and chl-*a* maxima suggested by one of the GAM models with *in situ* data (Fig. 3.9B), as this relationship also accounts for some of the interannual variability in the explanatory variables. The same variable explored by year in a GAM still suggests a positive effect towards increasing values, although variable and not so conspicuous (Fig. 3.9A). This should be more realistic as the linear relationship would likely have changed had the oceanographic surveys continued the following year. In 2006, higher chl-*a* concentrations occurred in the region according to the remote sensing data, but considerably lower numbers of humpback whales were recorded than in the previous year in Gerlache Strait. The same observation applies to the *in situ* SST, which resulted in the best fitting GAM (Fig. 3.9D). The association between humpback whales and higher SST and SSS values in Gerlache appears to be related to the presence of TBW, which is present in the middle and northern sectors. The AASW, present in the southwestern end, is typically colder and less saline due to ice melting.

Some level of variability would undoubtedly be expected in whale distribution and encounter rates given the interannual variability in both primary and secondary productivity in waters of the Antarctic Peninsula, including Gerlache Strait. The positive partial effects of all years in relation to 2001 in the GAM with remote sensing data, especially of 2002 and 2005, when the highest numbers of whales were recorded, reflect variability that could not be explained by the available explanatory variables. Nevertheless, the overlapping effects for the period 2002-2005 appear to suggest that the other explanatory variables were able to account for most of the interannual variability in whale numbers among these years.

The negative correlation between MLD and chl-*a* concentration observed in this study had been previously reported for the northern Gerlache Strait and southwestern Bransfield Strait, with massive phytoplankton blooms observed in mid-summer with upper mixed layers < 20 m (Mitchell & Holm-Hansen 1991). Castro et al. (2002) and Lorenzo et al. (2002) found a similar pattern in this area, with chl-*a* maxima and increased phytoplankton biomass associated with the shallower upper mixed layers. Shallow MLDs less than 25 m deep are common in the Southern Ocean during summer months, mainly due to the freshwater flux from the Antarctic Continent (Kara et al. 2003). In fact, melt water stabilization and protection from high winds, which lead to shallow MLDs and a stratified water column, are considered important factors for the development and maintenance of high levels of primary productivity around the Antarctic Peninsula (Mitchell & Holm-Hansen 1991, Ducklow et al. 2007). The shallow MLD prevents nutrients and phytoplankton from sinking to depths below the euphotic zone and, therefore, helps enhancing the primary productivity. Melt water from glaciers is also an important source of nutrients in coastal waters of the Southern Ocean, including Gerlache Strait (Martin et al. 1990, Dierssen et al. 2002).

The negative association between humpback whale numbers and slope suggested by the GAM with remote sensing data is likely a consequence of the survey lines running mostly along the channel, in the deeper parts, and of the higher whale densities towards the northern and wider sector of the strait.

3.4.2. Bransfield Strait

The best fitting GAMs for Bransfield Strait explained 21-25% of the deviance, with either type of data. This suggests that one or more important explanatory variables were missing in the models, the more obvious of which would be prey distribution. Moreover, it may also be that the spatio-temporal scales of the explanatory variables were not fine enough to capture the variability, particularly as whales were widely distributed throughout most of the survey region. Nevertheless, some significant relationships that likely indicate areas of high prey concentration and availability were identified.

The associations with selected physiographic variables (depth, distance to land and latitude) in the GAM with remote sensing data suggest that the higher densities of humpback whales in the Bransfield Strait occur in the southwestern end of the strait and over the deep basins of the strait, in the area protected from the Drake Passage by the South Shetland Islands. Although the lower survey effort at the northernmost part of the study area could have produced some bias in the smooth function of latitude, two transect lines run in that area in different years produced no sightings of humpback whales. The general circulation in the western Bransfield Strait is characterized by a northward surface flow of the Gerlache Current that enters along the deep channel on the southwestern end. This current then meets the Bransfield Current flowing northeastward along the southern continental margin of the South Shetland Islands (Niiler et al. 1991, Hofmann et al. 1996), over waters deeper than 750 m (Zhou et al. 2002). Due to a southwestward counter flow near the central axis of Bransfield Strait, small cyclonic eddies form at the southern edge of the Bransfield Current over the deep basins, providing a retention mechanism for zooplankton in the region (Zhou et al. 2002). Therefore, both Bransfield and Gerlache currents appear to be important features determining the distribution of humpback whales in the region.

The same GAM also suggests that the highest concentrations of humpback whales occurred within closer distances to SST fronts and in relatively warmer surface waters. Two major hydrographic fronts have been described for the Bransfield Strait. One that separates the relatively warmer and fresher TBW, located on the northern margin and associated with the Bransfield Current, from the colder and saltier TWW, located on the southern margin and with a southwestern flow (Niiler et al. 1991, García et al. 1994, Vázquez et al. 2007, Catalán et al. 2008). The other is the Bransfield Front, a slope front that extends along the southern South Shetlands continental slope and separates TBW or TWW from waters on the archipelago’s shelf (García et al. 2002, Vázquez et al. 2007). These frontal zones and the Bransfield-Gerlache confluence appear to be the most productive areas within Bransfield Strait (e.g. Hernández-León et al. 2000, Castro et al.

2002, Lorenzo et al. 2002). North of the South Shetland Islands, the highest krill concentrations occur at a frontal zone (Ichii et al. 1998).

Subsurface maxima in chl-*a* concentrations (Garibotti et al. 2003) or heavy krill grazing pressure (Varela et al. 2002) might explain the negative linear correlation between humpback numbers and monthly (surface) chl-*a* suggested by the GAM with remote sensing data. The latter is more likely given the high correlation between surface chl-*a* and integrated chl-*a* (Holm-Hansen & Mitchell 1991, Varela et al. 2002), primary productivity (Varela et al. 2002) or chl-*a* maxima (this study) that has been observed in Bransfield and Gerlache Straits. A relatively tight coupling between surface and depth integrated chl-*a* has also been observed further southwest, in shelf waters of the west Antarctic Peninsula (Smith et al. 1996). Nevertheless, monthly averaging of remotely-sensed values, which may be affected by intra-seasonal variability or cloud coverage, or confounding with other explanatory variables cannot be ruled out as potential causes for the resulting smooth function.

The linear positive effect of temperature maxima below 200 m on humpback whale numbers in the GAM with *in situ* data suggests that the whales may be associated to areas with modified CDW. Intrusions of CDW occur between Smith and Snow Islands, on the western Bransfield Strait, and may be detected as relatively higher temperatures in subsurface waters (> 200 m) on this area and along the northern margin of the strait (Niiler et al. 1991, Hofmann et al. 1996). This model also suggests a negative linear correlation with MLD, though non-significant. Interestingly, however, Reiss et al. (2009) reported shallower upper MLDs in 2006 than in previous years in the nearby Elephant

Island, which coincides with the higher humpback whale encounter rates that were observed in that year compared to previous years in Bransfield Strait (see Table 3.3).

3.4.3. Model combining Gerlache and Bransfield Straits

The model combining data from Gerlache and Bransfield straits showed similar explanatory power to the Bransfield models, indicating that the higher number of segments in the latter likely had an effect on the performance of the model. The positive correlation of chl-*a* concentration with humpback whale numbers and the generally higher encounter rates in Gerlache Strait suggested by this model conform to studies conducted in both areas that point to higher biological production in the Gerlache Strait (e.g. Burkholder & Sieburth 1961, Lorenzo et al. 2002, Morán & Estrada 2002, Varela et al. 2002).

3.4.4. Interannual variability in Gerlache Strait and climate indices

A rapidly growing literature has shown that ENSO teleconnections affect the marine ecosystem of the Antarctic Peninsula. ENSO events induce interannual variability in the Antarctic Dipole, a high-latitude climate mode characterized by out-of-phase sea ice and SST anomalies in the South Pacific and South Atlantic (Yuan & Martinson 2001, Yuan 2004). During a La Niña event, an anomalous low pressure system develops in the South Pacific and is associated with enhanced northerly winds, higher temperatures and a strengthening of the Polar Front (PF) jet near the Antarctic Peninsula. The changed temperature advection pattern in the atmosphere and the SST anomalies cause the sea ice to retreat poleward (Yuan 2004). El Niño conditions have an opposite effect, including the formation of a high pressure cell, a weaker PF jet in the South Pacific, weaker northerly winds in the Antarctic Peninsula, and sea ice advance (Yuan 2004). Other associated changes include movements of the Southern Antarctic Circumpolar Current Front along with eastward (La Niña) versus westward (El Niño) flow and mixing processes on the northern tip of the Antarctic Peninsula (Loeb et al. 2009), as well as increased upwelling of UCDW on the shelf of the western Antarctic Peninsula during La Niña (Martinson et al. 2008). The AAO, or Southern Annular Mode (SAM), can also lead to variability or even add to the effects of ENSO, as the Antarctic Peninsula responds similarly to a La Niña during strong positive phases of SAM (Martinson et al. 2008, Stammerjohn et al. 2008).

The positive correlation between chl-*a* and SOI observed in this study agrees with Loeb et al. (2009), who also found positive correlations of sea ice extent and ONI, krill larvae and sea ice extent, and one-year-lag positive correlations of chl-*a* and sea ice extent, krill abundance and ONI, among others, in the Antarctic Peninsula. Given this one-year-lag for factors that influence food availability, in addition to the three- to five-year frequency of ENSO events (e.g. Loeb et al. 2009), and the suggested eight-year cycle in krill biomass in the vicinity of the South Shetland Islands (Hewitt et al. 2003), caution is needed when trying to interpret the observed correlation between humpback or minke whale encounter rates and ONI based on a nine-year study. Nevertheless, if climate variability affects prey biomass and distribution, then some signal is likely to be visible relative to whale distribution.

One confounding factor is that variability in whale distribution in Gerlache Strait may reflect changes specific to this relatively small area. This means that an increase in whale numbers here could reflect a decrease in the adjacent Bransfield Strait, and not necessarily a uniform change in distribution throughout the western Antarctic Peninsula. For instance, krill biomass in 2002 was the lowest for the period 1998-2002 in northern Bransfield Strait (e.g. Hewitt et al. 2003), coinciding with no humpback whale sightings in a 40-nm transect in Bransfield Strait and one of the highest encounter rates observed in Gerlache Strait (see Tables 3.2 and 3.3). In 2006, when the model for the 8-year krill cycle would have predicted high krill biomass near the South Shetland Islands (see Hewitt et al. 2003), humpback whale encounter rates were higher in Bransfield than in Gerlache Strait (Secchi et al. in press, also this study).

Examining our results in the above context, a few non-exhaustive hypotheses could be proposed to explain the observed correlations:

1) The lower sea ice duration and extent along the western Antarctic Peninsula during La Niña events provides extended ice-free habitat for the whales. Reduced ice coverage allows the population to disperse more in search for food than it would during an icy El Niño phase, resulting in lower encounter rates of humpback whales in Gerlache Strait.

Thiele et al. (2004) reported higher numbers of humpback whales in late summer and fall of 2002 and 2003 in comparison to 2001 in the western Antarctic Peninsula, which they suggested was linked to variation in sea ice extent. Although 2001 had no sea ice in the region, sea ice never fully retreated in the following two years (especially in 2002), possibly providing additional krill habitat near ice margins and attracting more whales (Thiele et al. 2004). This seems to be a sensible hypothesis for their study area, but may not explain the variability we observed in the summer-ice-free Gerlache Strait. Our results also show higher encounter rates for 2002 in relation to 2001, but not for 2003, when summer sea ice extent was relatively low off the western Antarctic Peninsula. It therefore appears that an “ice-pushing” hypothesis related to ENSO variability deserves further examination. This simple hypothesis, however, does not consider the complex krill-sea ice interactions, and does not seem to explain the differences in encounter rates for 2006 between Bransfield and Gerlache straits.

2) Humpback whale numbers in Gerlache Strait could be reduced as they spread themselves over a larger area if cold La Niña events, particularly those following El Niño events, increased krill biomass throughout the Antarctic Peninsula. The inverse could be true for El Niño periods, when lower krill biomass would drive individuals to areas with more predictable food resources, such as Gerlache Strait.

3) The anomalies related to both cold and warm phases of ENSO affect the productivity of Gerlache Strait relative to other areas. This would explain the apparently higher humpback whale encounter rates during neutral phases, as opposed to the warm phases (see Figs 3.12 A-B).

As for the minke whales, which appear to be heavily dependent on the pack-ice (e.g. Kasamatsu et al. 1988, Kasamatsu et al. 2000), their virtual absence in Gerlache Strait during El Niño and increased presence during La Niña events is likely related to sea ice availability. The reduction of their preferred habitat around the Antarctic Peninsula during La Niña phases could drive individuals to the more protected inshore waters of the Antarctic Peninsula, where prey availability may be more predictable. Conforming to this hypothesis, lower densities of minke whales have been recorded further south and southwest of the study area during years of less extensive sea ice coverage (Kasamatsu et al. 2000, Thiele et al. 2004).

Stone & Hamner (1988) reported higher encounter rates of humpback whales inside bays rather than in the open waters of Gerlache Strait during fall 1986. This pattern, however, could be driven by the movements of krill into the bays during fall and winter. During our summer surveys, frequent searches into several bays primarily for photo-identification and biopsy sampling efforts provided no evidence of important aggregations that could bias our estimates of relative abundance for the strait.

The many possible interactions between climate forcing and the marine environment make the interpretation of ENSO linkages with the Southern Ocean biota a complex matter (Turner 2004). It becomes even more difficult to disentangle and explain the potential factors and effects as we move up the food chain. Moreover, local scales may have different responses among them or from the broader scale. Continuing systematic cetacean surveys in Gerlache Strait is warranted to confirm the observed relationship between whale relative abundance and the ENSO variability and should help to better understand the effects of climate variability on the marine ecosystem of the Antarctic Peninsula, in particular of the top predators.

3.5. References

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature 432:100-103

Atkinson A, Siegel V, Pakhomov EA, Rothery P, Loeb V, Ross RM, Quetin LB, Schmidt K, Fretwell P, Murphy EJ, Tarling GA, Fleming AH (2008) Oceanic circumpolar habitats of Antarctic krill. Marine Ecology Progress Series 362:1-23

Behrenfeld MJ, Falkowski PG (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnology and Oceanography 42:1-20

Branch TA (2006) Humpback abundance south of 60°S from three completed sets of IDCR/SOWER circumpolar surveys. Paper SC/A06/HW6 presented to the IWC Scientific Committee (unpublished)

Burkholder PR, Sieburth JM (1961) Phytoplankton and chlorophyll in the Gerlache and Bransfield Straits of Antarctica. Limnology and Oceanography 6:45-52

Cabal JA, Alvarez-Marques F, Acuna JL, Quevedo M, Gonzalez-Quiros R, Huskin I, Fernandez D, del Valle CR, Anadon R (2002) Mesozooplankton distribution and grazing during the productive season in the Northwest Antarctic Peninsula (FRUELA cruises). Deep-Sea Research Part II: Topical Studies in Oceanography 49:869-882

Castro CG, Rios AF, Doval MD, Perez FF (2002) Nutrient utilisation and chlorophyll distribution in the Atlantic sector of the Southern Ocean during Austral summer 1995-96. Deep-Sea Research Part II: Topical Studies in Oceanography 49:623-641

Catalán IA, Morales-Nin B, Company JB, Rotllant G, Palomera I, Emelianov M (2008) Environmental influences on zooplankton and micronekton distribution in the Bransfield Strait and adjacent waters. Polar Biology 31:691-707

Cayula J-F, Cornillon P (1992) Edge detection algorithm for SST images. Journal of Atmospheric and Oceanic Technology 9:67-80

Clarke A, Murphy EJ, Meredith MP, King JC, Peck LS, Barnes DKA, Smith RC (2007) Climate change and the marine ecosystem of the western Antarctic Peninsula. Philosophical Transactions of the Royal Society B-Biological Sciences 362:149-166

Cram DL, Agenbag JJ, Hampton I, Robertson AA (1979) Protea cruise, 1978: The general results of the acoustics and remote sensing study, with recommendations for estimating the abundance of krill (*Euphausia superba* Dana). South African Journal of Antarctic Research 9:3-14

Dalla Rosa L, Freitas A, Secchi ER, Santos MCO, Engel MH (2004) An updated comparison of the humpback whale photo-id catalogues from the Antarctic Peninsula and the Abrolhos Bank, Brazil. Paper SC/56/SH16 presented to the IWC Scientific Committee (unpublished)

Dalla Rosa L, Secchi ER, Kinas PG, Santos MCO, Martins MB, Zerbini AN, Bethlem CBP (2001) Photo-identification of humpback whales, *Megaptera novaeangliae*, off the Antarctic Peninsula from 1997/98 to 1999/2000. Memoirs of the Queensland Museum 47:555-561

Dalla Rosa L, Secchi ER, Maia YG, Zerbini AN, Heide-Jorgensen MP (2008) Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula. Polar Biology 31:771-781

de Boyer Montégut C, Madec G, Fischer AS, Lazar A, Iudicone D (2004) Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. Journal of Geophysical Research-Oceans 109

Dierssen HM, Smith RC, Vernet M (2002) Glacial meltwater dynamics in coastal waters west of the Antarctic peninsula. Proceedings of the National Academy of Sciences of the United States of America 99:1790-1795

Diggle PJ, Ribeiro PJ (2007) Model-based geostatistics. Springer-Verlag, New York

Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC, Stammerjohn SE, Vernet M, Fraser W (2007) Marine pelagic ecosystems: The West Antarctic Peninsula. Philosophical Transactions of the Royal Society B-Biological Sciences 362:67-94

Findlay KP (2001) A review of humpback whale caches by modern whaling operations in the Southern Hemisphere. Memoirs of the Queensland Museum 47:411-420

Forcada J, Trathan PN, Reid K, Murphy EJ (2005) The effects of global climate variability in pup production of Antarctic fur seals. Ecology 86:2408-2417

Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. Marine Ecology Progress Series 317:297-310

García MA, Castro CG, Rios AF, Doval MD, Roson G, Gomis D, Lopez O (2002) Water masses and distribution of physico-chemical properties in the Western Bransfield Strait and Gerlache Strait during Austral summer 1995/96. Deep-Sea Research Part II: Topical Studies in Oceanography 49:585-602

García MA, Lopez O, Sospedra J, Espino M, Gracia V, Morrison G, Rojas P, Figa J, Puigdefabregas J, Arcilla AS (1994) Mesoscale variability in the Bransfield Strait region (Antarctica) during austral summer. Annales Geophysicae-Atmospheres Hydrospheres and Space Sciences 12:856-867

Garcia VMT, Garcia CAE, Mata MM, Pollery RC, Piola AR, Signorini SR, McClain CR, Iglesias-Rodriguez MD (2008) Environmental factors controlling the phytoplankton blooms at the Patagonia shelf-break in spring. Deep-Sea Research Part I: Oceanographic Research Papers 55:1150-1166

Garibotti IA, Vernet M, Ferrario ME, Smith RC, Ross RM, Quetin LB (2003) Phytoplankton spatial distribution patterns along the western Antarctic Peninsula (Southern Ocean). Marine Ecology Progress Series 261:21-39

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

Hastie TJ, Tibshirani RJ (1990) Generalized additive models, Chapman and Hall, New York

Hernández-León SC, Almedia C, Portillo-Hahnefeld A, Gomez M, Montero I (2000) Biomass and potential feeding, respiration and growth of zooplankton in the Bransfield Strait (Antarctic Peninsula) during austral summer. Polar Biology 23:679-690

Hewitt RP, Demer DA, Emery JH (2003) An 8-year cycle in krill biomass density inferred from acoustic surveys conducted in the vicinity of the South Shetland Islands during the austral summers of 1991-1992 through 2001-2002. Aquatic Living Resources 16:205-213

Hofmann EE, Klinck JM, Lascara CM, Smith DA (1996) Water mass distribution and circulation west of the Antarctic Peninsula and including Bransfield Basin. In: Ross RM, Hofmann EE, Quetin LB (eds) Foundations for ecological research west of the Antarctic Peninsula, Antarctic Research Series, Vol 70. American Geophysical Union, Washington, p 61-80

Holm-Hansen O, Mitchell BG (1991) Spatial and temporal distribution of phytoplankton and primary production in the western Bransfield Strait region. Deep-Sea Research Part a: Oceanographic Research Papers 38:961-980

Huntley M, Brinton E (1991) Mesoscale variation in growth and early development of *Euphausia superba* Dana in the western Bransfield Strait region. Deep-Sea Research Part a: Oceanographic Research Papers 38:1213-1240

Ichii T, Katayama K, Obitsu N, Ishii H, Naganobu M (1998) Occurrence of Antarctic krill (*Euphausia superba*) concentrations in the vicinity of the South Shetland Islands: relationship to environmental parameters. Deep-Sea Research Part I: Oceanographic Research Papers 45:1235-1262

IPCC (2007) Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds.)] Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA

Kara AB, Rochford PA, Hurlburt HE (2003) Mixed layer depth variability over the global ocean. Journal of Geophysical Research-Oceans 108:24:21

Kasamatsu F, Ensor P, Joyce GG, Kimura N (2000) Distribution of minke whales in the Bellingshausen and Amundsen Seas (60 degrees W-120 degrees W), with special reference to environmental/physiographic variables. Fisheries Oceanography 9:214-223

Kasamatsu F, Hembree D, Joyce G, Tsunoda L, Rowlett R, Nakano T (1988) Distribution of cetacean sightings in the Antarctic: results obtained from the IWC/IDCR minke whale assessment cruises, 1978/79 to 1983/84. Reports of the International Whaling Commission 38:449-487

Kawamura A (1994) A review of baleen whale feeding in the Southern Ocean. Reports of the International Whaling Commission 44:261-271

Kim YJ, Gu C (2004) Smoothing spline Gaussian regression: more scalable computation via efficient approximation. Journal of the Royal Statistical Society Series B-Statistical Methodology 66:337-356

Knox GA (2006) The biology of the Southern Ocean, CRC Press, Boca Raton

Lerczak JA, Hobbs RC (1998) Calculating sighting distances from angular readings during shipboard, aerial, and shore-based marine mammal surveys. Marine Mammal Science 14:590-598

Loeb V, Siegel V, HolmHansen O, Hewitt R, Fraser W, Trivelpiece W, Trivelpiece S (1997) Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. Nature 387:897-900

Loeb VJ, Hofmann EE, Klinck JM, Holm-Hansen O, White WB (2009) ENSO and variability of the Antarctic Peninsula pelagic marine ecosystem. Antarctic Science 21:135-148

Lorenzo LM, Arbones B, Figueiras FG, Tilstone GH, Figueroa FL (2002) Photosynthesis, primary production and phytoplankton growth rates in Gerlache and Bransfield Straits during Austral summer: cruise FRUELA 95. Deep-Sea Research Part II: Topical Studies in Oceanography 49:707-721

Mackintosh NA (1965) The stocks of whales, Fishing News (Books) Ltd, London

Mackintosh NA (1970) Whales and krill in the twentieth century. In: Holdgate MW (ed) Antarctic ecology, Vol 1. Academic Press, London, p 95-212

Martin JH, Gordon RM, Fitzwater SE (1990) Iron in Antarctic waters. Nature 345:156-158

Martinson DG, Stammerjohn SE, Iannuzzi RA, Smith RC, Vernet M (2008) Western Antarctic Peninsula physical oceanography and spatio-temporal variability. Deep-Sea Research Part II: Topical Studies in Oceanography 55:1964-1987

Matthews LH (1937) The humpback whale, *Megaptera nodosa*. Discovery Reports 17:7-92

McMahon CR, Burton HR (2005) Climate change and seal survival: evidence for environmentally mediated changes in elephant seal, *Mirounga leonina*, pup survival. Proceedings of the Royal Society B-Biological Sciences 272:923-928

Mitchell BG, Holm-Hansen O (1991) Observations and modeling of the Antarctic phytoplankton crop in relation to mixing depth. Deep-Sea Research Part a: Oceanographic Research Papers 38:981-1007

Montú M, Gloeden IM, Resgalla Jr C, Loureiro Fernandes LF (1994) Krill populations in the Bransfield Strait and neighbouring areas during the summers of 1983, 1984, 1985 and 1987. Nauplius 2:107-121

Morán XAG, Estrada M (2002) Phytoplanktonic DOC and POC production in the Bransfield and Gerlache Straits as derived from kinetic experiments of C-14 incorporation. Deep-Sea Research Part II: Topical Studies in Oceanography 49:769-786

Nicol S, Pauly T, Bindoff NL, Wright S, Thiele D, Hosie GW, Strutton PG, Woehler E (2000) Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. Nature 406:504-507

Niiler PP, Amos A, Hu JH (1991) Water masses and 200 m relative geostrophic circulation in the western Bransfield Strait region. Deep-Sea Research Part a: Oceanographic Research Papers 38:943-959

Niiler PP, Illeman J, Hu JH (1990) RACER: Lagrangian drifter observations of surface circulation in the Gerlache and BransÞeld Straits. Antarctic Journal of the United States 25:134-137

Nordhausen W (1994) Winter abundance and distribution of *Euphausia superba*, *E. crystallorophias*, and *Thysanoessa macrura* in Gerlache Strait and Crystal Sound, Antarctica. Marine Ecology Progress Series 109:131-142

Olavarría C, Baker CS, Medrano L, Aguayo A, Caballero S, Flórez-González L, Capella J, Rosenbaum HC, Garrigue C, Greaves J, Jenner M, Jenner C, Bannister JL (2000) Stock identity of Antarctic Peninsula humpback whales inferred from mtDNA variation. Paper SC/52/IA15 presented to the IWC Scientific Committee (unpublished)

Pollery RCG (2005) Disponibilidade e distribuição dos nutrientes e clorofila-a nas águas adjacentes à Península Antártica (Verões de 2000/01, 2001/02 e 2002/03). Ph.D. Thesis, Universidade Federal Fluminense

Prézelin BB, Hofmann EE, Mengelt C, Klinck JM (2000) The linkage between Upper Circumpolar Deep Water (UCDW) and phytoplankton assemblages on the west Antarctic Peninsula continental shelf. Journal of Marine Research 58:165-202

Prézelin BB, Hofmann EE, Moline M, Klinck JM (2004) Physical forcing of phytoplankton community structure and primary production in continental shelf waters of the Western Antarctic Peninsula. Journal of Marine Research 62:419-460

Rasmussen K, Palacios DM, Calambokidis J, Saborio MT, Dalla Rosa L, Secchi ER, Steiger GH, Allen JM, Stone GS (2007) Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. Biology Letters 3:302-305

Redfern JV, Ferguson MC, Becker EA, Hyrenbach KD, Good C, Barlow J, Kaschner K, Baumgartner MF, Forney KA, Ballance LT, Fauchald P, Halpin P, Hamazaki T, Pershing AJ, Qian SS, Read A, Reilly SB, Torres L, Werner F (2006) Techniques for cetacean-habitat modeling. Marine Ecology Progress Series 310:271-295

Reilly SB, Bannister JL, Best PB, Brown M, Brownell Jr RL, Butterworth DS, Clapham PJ, Cooke J, Donovan GP, Urbán J, Zerbini AN (2008) *Megaptera novaeangliae*. In: IUCN 2009. IUCN Red List of Threatened Species. Version 2009.1. available at www.iucnredlist.org.

Reiss CS, Hewes CD, Holm-Hansen O (2009) Influence of atmospheric teleconnections and Upper Circumpolar Deep Water on phytoplankton biomass around Elephant Island, Antarctica. Marine Ecology Progress Series 377:51-62

Ribeiro PJ, Diggle PJ (2001) geoR: A package for geostatistical analysis. R News 1:15-18

Roberts JJ, Best BD, Dunn DC, Treml EA, Halpin PN (in review) Marine Geospatial Ecology Tools: An integrated framework for ecological geoprocessing with ArcGIS, Python, R, MATLAB, and C++. Environmental Modelling & Software. Available online: <http://mgel.env.duke.edu/tools>

Rodríguez J, Jiménez-Gómez F, Blanco JM, Figueroa ML (2002) Physical gradients and spatial variability of the size structure and composition of phytoplankton in the Gerlache Strait (Antarctica). Deep-Sea Research Part II: Topical Studies in Oceanography 49:693-706

Ross RM, Quetin LB, Lascara CM (1996) Distribution of Antarctic krill and dominant zooplankton west of the Antarctic Peninsula. In: Ross RM, Hofmann EE, Quetin LB (eds) Foundations for ecological research west of the Antarctic Peninsula, Antarctic Research Series, Vol 70. American Geophysical Union, Washington, p 199-218

Secchi ER, Dalla Rosa L, Kinas PG, Nicolette RF, Rufino AMN, Azevedo A (in press) Encounter rates and abundance of humpback whales, *Megaptera novaeangliae*, in Gerlache and Bransfield Straits, Antarctic Peninsula. The Journal of Cetacean Research and Management

Secchi ER, Dalla Rosa L, Kinas PG, Santos MCO, Zerbini AN, Bassoi M, Moreno IB (2001) Encounter rates of whales around the Antarctic Peninsula with special reference to humpback whales, *Megaptera novaeangliae*, in the Gerlache Strait: 1997/98 to 1999/2000. Memoirs of the Queensland Museum 47:571-578

Siegel V, Kalinowski J (1994) Krill demography and small-scale processes: a review. In: El-Sayed SZ (ed) Southern Ocean ecology: The BIOMASS perspective. Cambridge University Press, New York, p 145-163

Siegel V, Loeb V (1995) Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. Marine Ecology Progress Series 123:45-56

Smith RC, Dierssen HM, Vernet M (1996) Phytoplankton biomass and productivity in the western Antarctic Peninsula region. In: Ross RM, Hofmann EE, Quetin LB (eds) Foundations for ecological research west of the Antarctic Peninsula, Antarctic Research Series, Vol 70. American Geophysical Union, Washington, p 333-356

Stammerjohn SE, Martinson DG, Smith RC, Iannuzzi RA (2008) Sea ice in the western Antarctic Peninsula region: Spatio-temporal variability from ecological and climate change perspectives. Deep-Sea Research Part II: Topical Studies in Oceanography 55:2041-2058

Stevick PT, Aguayo A, Allen J, Avila IC, Capella J, Castro C, Chater K, Dalla Rosa L, Engel MH, Felix F, Florez-Gonzalez L, Freitas A, Haase B, Llano M, Lodi L, Munoz E, Olavarria C, Secchi E, Scheidat M, Siciliano S (2004) Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. The Journal of Cetacean Research and Management 6:109-113

Stone GS, Hamner WM (1988) Humpback whales *Megaptera novaeangliae* and southern right whales *Eubalaena australis* in Gerlache Strait, Antarctica. Polar Record 24:15-20

Thiele D, Chester ET, Gill PC (2000) Cetacean distribution off Eastern Antarctica (80-150 degrees E) during the Austral summer of 1995/1996. Deep-Sea Research Part II: Topical Studies in Oceanography 47:2543-2572

Thiele D, Chester ET, Moore SE, Sirovic A, Hildebrand JA, Friedlaender AS (2004) Seasonal variability in whale encounters in the Western Antarctic Peninsula. Deep-Sea Research Part II: Topical Studies in Oceanography 51:2311-2325

Trathan PN, Forcada J, Murphy EJ (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. Philosophical Transactions of the Royal Society B-Biological Sciences 362:2351-2365

Turner J (2004) The El Nino-Southern Oscillation and Antarctica. International Journal of Climatology 24:1-31

Turner J, Colwell SR, Marshall GJ, Lachlan-Cope TA, Carleton AM, Jones PD, Lagun V, Reid PA, Iagovkina S (2005) Antarctic climate change during the last 50 years. International Journal of Climatology 25:279-294

Tynan CT, Ainley DG, Barth JA, Cowles TJ, Pierce SD, Spear LB (2005) Cetacean distributions relative to ocean processes in the northern California Current System. Deep-Sea Research Part II: Topical Studies in Oceanography 52:145-167

Varela M, Fernandez E, Serret P (2002) Size-fractionated phytoplankton biomass and primary production in the Gerlache and south Bransfield Straits (Antarctic

Peninsula) in Austral summer 1995-1996. Deep-Sea Research Part II: Topical Studies in Oceanography 49:749-768

Vaughan DG, Marshall GJ, Connolley WM, Parkinson C, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Climatic Change 60:243-274

Vázquez E, Ameneiro J, Putzeys S, Gordo C, Sangra P (2007) Distribution of meroplankton communities in the Bransfield Strait, Antarctica. Marine Ecology Progress Series 338:119-129

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389-395

Williams R, Hedley SL, Hammond PS (2006) Modeling distribution and abundance of Antarctic baleen whales using ships of opportunity. Ecology and Society 11

Wood SN (2001) mgcv: GAMs and generalized ridge regression for R. R News 1:20-25

Wood SN (2006) Generalized additive models: an introduction with R. Chapman and Hall/CRC Press, Boca Raton, Florida

Yuan X (2004) ENSO-related impacts on Antarctic sea ice: a synthesis of phenomenon and mechanisms. Antarctic Science 16:415-425

Yuan X, Martinson DG (2001) The Antarctic dipole and its predictability. Geophysical Research Letters 28:3609-3612

Zhou M, Niiler PP, Hu JH (2002) Surface currents in the Bransfield and Gerlache Straits, Antarctica. Deep-Sea Research Part I: Oceanographic Research Papers 49:267-280

Zhou M, Nordhausen W, Huntley M (1994) Adcp measurements of the distribution and abundance of euphausiids near the Antarctic Peninsula in winter. Deep-Sea Research Part I: Oceanographic Research Papers 41:1425-1445

Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data, Springer, New York

4. Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula[3]

4.1. Introduction

The humpback whale, *Megaptera novaeangliae*, is a highly migratory species found in all major oceans, from low-latitude breeding and calving grounds in the winter to temperate and high-latitude feeding grounds between spring and fall (Dawbin 1966). Its migration is the longest of any mammal (Stone et al. 1990; Stevick et al. 2004; Rasmussen et al. 2007).

In the Southern Hemisphere, seven geographically isolated humpback whale Breeding Stocks (A to G) are recognized by the International Whaling Commission (IWC 1998, 2006). Waters of the western Antarctic Peninsula have been identified as feeding grounds for the eastern South Pacific (Peru, Ecuador, Colombia, Panama and Costa Rica) population based on photo-identification and molecular genetic data (Stone et al. 1990; Stevick et al. 2004; Rasmussen et al. 2007; Olavarría et al. 2000). On the other hand, the lack of photographic matches between whales from the Antarctic Peninsula and the breeding grounds off Brazil (Stevick et al. 2004; Dalla Rosa et al. 2004) indicate the western Antarctic Peninsula region is not used as a feeding ground by whales from the western South Atlantic, as previously hypothesized (e.g. Slijper 1962; IWC 1998). In fact, satellite telemetry studies have recently demonstrated that whales wintering off

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[3] A version of this chapter has been published. Dalla Rosa L, Secchi ER, Maia YG, Zerbini AN, Heide-Jørgensen MP (2008) Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula. Polar Biology 31(7): 771-781.

Brazil migrate to feeding destinations in the Scotia Sea, near South Georgia and the South Sandwich Islands (Zerbini et al. 2006a, b).

Photo-identification studies have also shown that humpback whales have strong site fidelity to the Antarctic Peninsula region (Dalla Rosa et al. 2001, 2004), and that at least part of the population wintering in the eastern South Pacific does not migrate to the Antarctic, but feeds in the Magellan Strait area (Acevedo et al. 2007). However, despite extensive research effort in the area around the Antarctic Peninsula (e.g. Secchi et al. 2001, 2006; Thiele et al. 2004; Williams et al. 2006), virtually nothing is known about the movement patterns of humpback whales in this area. Dalla Rosa et al. (2001) reported two within-season resightings of humpback whales in 1998. The first was photographed off King George Island on 22 January, and the second was photographed in Bismarck Strait (southern end of Gerlache Strait) on 27 January. Both individuals were photographed together in Gerlache Strait on 7 March, 335 and 71 km away, respectively, from their previous sighting locations. Knowledge of such movements has important ecological and management implications, as it can provide insights into how whales use their feeding habitat and assist in defining stock boundaries and in designing proper surveys for stock assessment.

Satellite telemetry has been successfully used to investigate behavior (e.g. Laidre et al. 2003), associations with environmental features (e.g. Baumgartner and Mate 2005; Etnoyer et al. 2006), habitat use, migration and movement patterns (e.g. Mate et al. 1998, 1999; Heide-Jørgensen et al. 2003; Zerbini et al. 2006), home range (Heide-Jørgensen et al. 2002) and stock discreteness (Heide-Jørgensen et al. 2006) of cetacean species.

In this paper we investigate the movement patterns and habitat use of humpback whales instrumented with satellite transmitters in Gerlache Strait and Dallman Bay (63.8^oS to 65^oS; 61^oW to 63.5^oW), Antarctic Peninsula, in January of 2004-06.

4.2. Material and methods

Tags consisted of Wildlife Computers' SPOT3 (2004), SPOT4 (2005) and SPOT5 (2006) satellite-linked radio transmitters housed in a surface-mounted stainless steel can ('mini-can'—MC) or in an implantable (IM) stainless steel cylinder. Each transmitter was attached to a titanium or stainless steel anchoring system equipped with foldable barbs and a triangular sharp tip. Tags used in 2004 were programmed to transmit every day, and the ones used in 2005 and 2006 were duty-cycled to transmit every fourth day and every other day, respectively. The number of transmissions was limited to 300 per day in all tags, and transmission time was between 0:00 and 23:00 hours for the mini-can and 7:00-22:00 hrs for the implantable tags. The expected total number of transmissions for each tag was about 20,000 based on the battery configurations used: 2xM1 for mini-can and 1xAA for implantable tags.

Tag deployment was conducted from an inflatable boat with a mounted wooden standing platform using an 8 m long fiberglass pole. Whales were approached with caution by first observing their surface activity patterns. Tagging was only attempted on large individuals and when they were parallel to the boat from about a 4-5 m distance. A skin sample was collected simultaneously with tag deployment by a biopsy tip attached to the pole or, alternatively, with a crossbow and a modified dart. Skin samples were used for DNA extraction and sex determination following methods described in Sambrook et al. (1989), Bérubé and Pasbøll (1996) and Shaw et al. (2003). Fluke and dorsal fin photographs of the tagged animals were taken for individual identification.

Locations were obtained using the Argos System (ARGOS 1990). Each location was coded by Service Argos according to predicted accuracy. In order of increasing quality, location classes (LC) B, A and 0 have no associated error prediction, and LC 1, 2 and 3 are predicted to be within 1, 0.35 and 0.15 km of the true position, respectively. Locations used for analyzing movement patterns and distance traveled were selected based on the following criteria: (1) only good quality locations (LC 1-3) were selected, (2) daily average positions were calculated when good locations were not available, and (3) locations were removed from the dataset if travel speed between two consecutive locations exceeded 12km/h. This value was selected based on maximum speeds reported for humpback whales (e.g. Tyack 1983; Bauer 1986; Frankel et al. 1995). Straight great-circle distances between consecutive points were transformed into minimum distances around land masses if underestimation was noticeable from tracks over land, particularly for the duty cycled tags. The rate of travel (km/d) was calculated as the total distance traveled between locations divided by the number of days elapsed between locations. Individual mean speeds (km/h) were also computed for the two whales with daily transmissions (and therefore with larger sample sizes) using only segments between consecutive locations of LC 2 or 3 that were at least 20 minutes and no more than 4 hours apart for improved accuracy.

The coastline data were extracted from the Antarctic Digital Database version 4.1 (Scientific Committee on Antarctic Research 2003). Regional sea ice concentration maps using data from the Advanced Microwave Scanning Radiometer (AMSR-E) with the ARTIST sea ice algorithm (ASI version 5.2) (Spreen et al. 2007) were obtained from the Institute of Environmental Physics, University of Bremen (http://www.iup.uni-bremen.de).

Area usage was investigated by estimating the 95% fixed kernel home range with least squares cross-validation and the minimum convex polygon (MCP) using the Home Range Tools extension (Rodgers et al. 2005) in ArcGIS 9.1 (ESRI, Redlands, CA). When more than one good quality position was available per day, average daily positions were used to minimize autocorrelation bias in home range calculations (e.g. Heide-Jørgensen et al. 2002). Since this procedure reduced sample size considerably, individual area usage could only be estimated for six individuals with more than 30 days of tracking. Furthermore, for the kernel estimates of whales with duty-cycled tags, one pseudo-location (e.g. Frydman and Gales 2007) was added midway along the track between each pair of every-other-day locations assuming constant speed and straight line of travel between them. This method places data in the same temporal resolution (one daily position) allowing for better comparisons among individuals and partially reducing the bias in kernel estimation due to sample size differences. Also, considering the long distances that humpback whales may travel in a single day, it adds biological significance to the lower resolution data by taking into account information present in their tracks. The kernel smoothing should help reduce biases associated with likely deviations from straight-line tracks. Two pseudo-locations for one individual were added on a path around land. Pseudo-locations were not included in the MCP home ranges as they would not have any effect on these estimates. An overall summer area usage combining all individual ranges overlaid was also computed to give an idea of minimum area use for this population. Areas where land overlapped with the home range were subtracted from the estimates.

4.3. Results

We tagged eleven humpback whales in January 2004-06 (Table 4.1). Sex was determined for six individuals, of which five were females. Whales with IM tags and with MC tags were tracked for 4-20 days and for 32-80 days, respectively. One tag never transmitted. A total of 3,951 locations were received, of which 1,295 were used to analyze movement patterns.

Estimates of traveled distances for nine individuals ranged from 223 to 4,356 km (mean = 1,415 km, SD = 1,343 km). Travel rates ranged from 17 to 75 km/d (mean = 32 km/d, SD = 16). The mean speed and standard error using only small segments between LC 2-3 was 2.26 ± 0.17 km/h ($n = 85$) for whale 20683 and 4.03 ± 0.27 km/h ($n = 51$) for whale 20689 ($p < 0.001$; Z-Test; $Z = -5.52$).

Marked individual variation was observed in direction, speed and range of movements. All whales tagged in Gerlache Strait (GS) between $63^{o}59'$S and $64^{o}45'$S left this area within 3 to 10 days, and all except two moved initially north to Bransfield Strait (BS). Only two whales returned to GS at some point during their monitored period.

Table 4.11 – Satellite transmitters deployed on humpback whales, *Megaptera novaeangliae*, in Gerlache Strait, Antarctic Peninsula, between 2004 and 2006. Distances and speeds were rounded to the closest integer.

Whale ID (Tag no.)	Sex	Tag type	Duty cycling	Deployment Date	Tagging location	Tag longevity (d)	No. of locations received	No. of locations used	Distance traveled (km)	Speed (km/d)
20683	-	MC	none	17 Jan 04	64°28.61'S 62°11.90'W	72	1,931	612	2,733	39
20689	-	MC	none	17 Jan 04	64°31.86'S 62°16.92'W	59	1,021	306	4,356	75
20691	-	MC	none	17 Jan 04	64°35.27'S 62°32.37'W	-	-			
21809	-	IM	e4d	19 Jan 05	64°09.55'S 61°22.04'W	13	26	8	312	28
24639	-	IM	e4d	23 Jan 05	64°44.44'S 63°01.67'W	13	43	24	223	19
24640	F	IM	e4d	24 Jan 05	63°59.56'S 61°18.46'W	20	32	15	418	23
26715	F	IM	e4d	20 Jan 05	64°23.00'S 62°54.60'W	4	5	1	-	-
63375	F	MC	eod	24 Jan 06	64°25.68'S 62°04.75'W	39	206	61	636	18
63376	M	MC	eod	26 Jan 06	64°32.11'S 62°32.84'W	33	86	20	1,235	40
63377	F	MC	eod	27 Jan 06	64°33.91'S 62°12.50'W	32	173	56	525	17
63378	F	MC	eod	27 Jan 06	64°35.86'S 62°11.02'W	80	428	192	2,298	29
Total						365	3,951	1,295	12,736	
Mean (SD)						36.5 (24.8)			1,415 (1,343)	32 (16)

MC ‘*mini can*’, *IM* implantable, *e4d* every fourth day, *eod* every other day

Whale 20683 stayed near the tagging location, in the northern section of GS for the first 10 days, and then it moved north to the boundary with BS, where it stayed for a week (Fig. 4.1 and 4.2). Finally, it traveled back through GS and Schollaert Channel into Dallman Bay and its open-sea section, where it moved erratically the remaining 47 days of the tracking period, except for two days when it ventured back into mid-GS. Whale 20689, on the other hand, left GS three days after the instrumentation and moved north nearby to Deception Island, in BS, before traveling south to the Biscoe Archipelago, where it stayed for five days (Fig. 4.2). Then it traveled 1,300 km to the southwest in 12 days (at an average 108 km/d) reaching its southernmost position at 71^{o}30.7'S, 81^{o}58.7'W on 16 February 2004, near an area with patches of sea-ice. After 9 days in this area, it moved on a round clockwise turn towards the Marguerite Bay area, where it spent 8 days before starting to move southwest along the shore, 3 days prior to the end of transmissions. The speed of whale 20689 averaged 43 km/d at presumed foraging patches characterized by erratic movements and 109 km/d during travel between these sites.

Whale 21809, tagged in northern GS, was in the middle of BS about 60 km east of Deception Island four days later (Fig. 4.3). Whale 24639, on the other hand, was tagged in southern GS and moved out into an open area in the Bellingshausen Sea (Fig. 4.3). It was the only whale to exit GS through its southern section, but also the only one tagged in this area of the strait. Whale 24640, tagged in northern GS, moved south around the west side of Brabant and Anvers Islands, then traveled through Bismarck Strait and back north through GS until transmissions ended about 28 km from its tagging location (Fig. 4.3). Whale 26715 was the only individual tagged outside of GS and it was still inside Dallman Bay four days after tag deployment, when it stopped transmitting (Fig. 4.3).

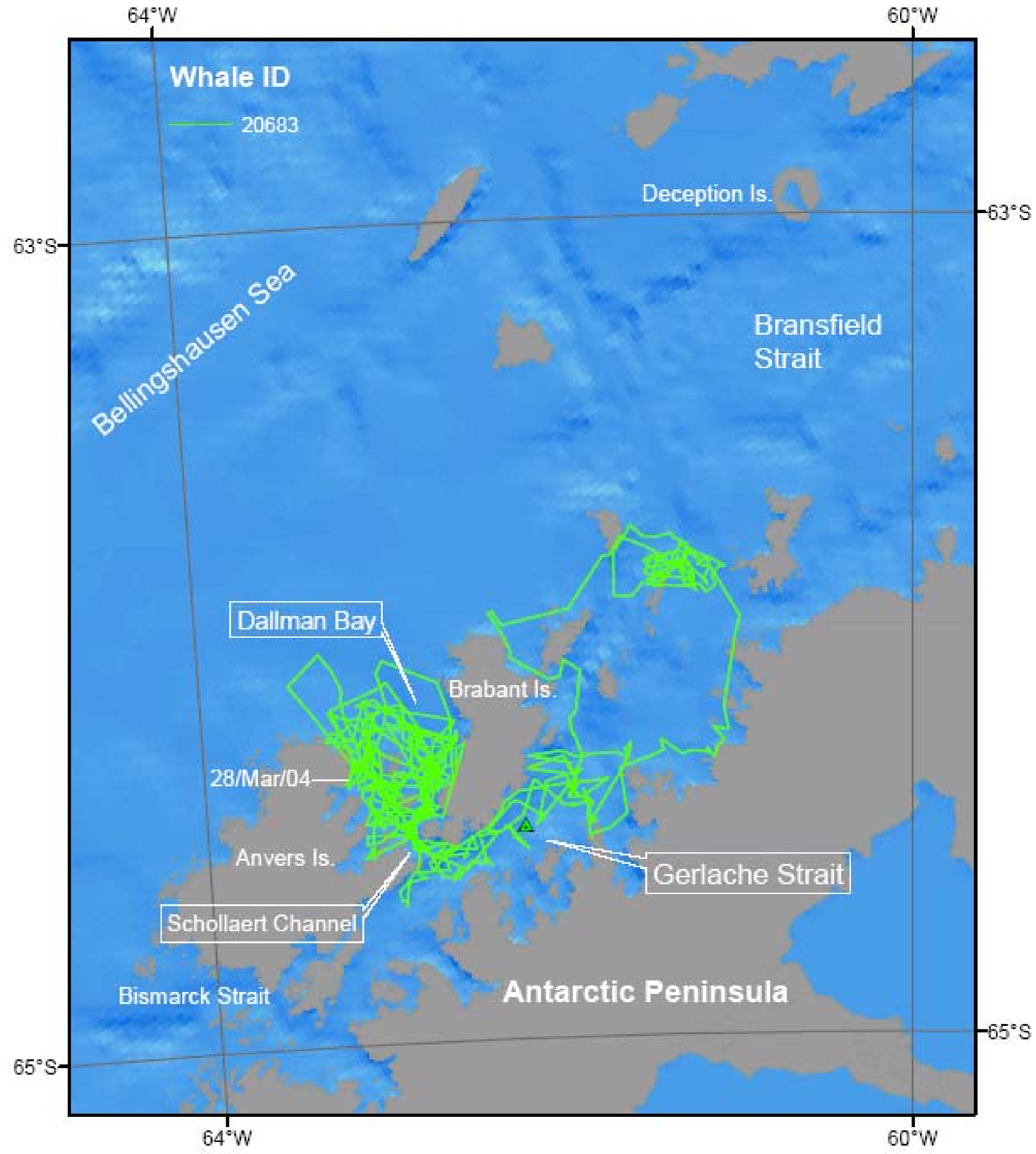


Fig. 4.29 – Track of humpback whale # 20683 tagged in the Gerlache Strait in January 2004. Triangle indicates tagging location

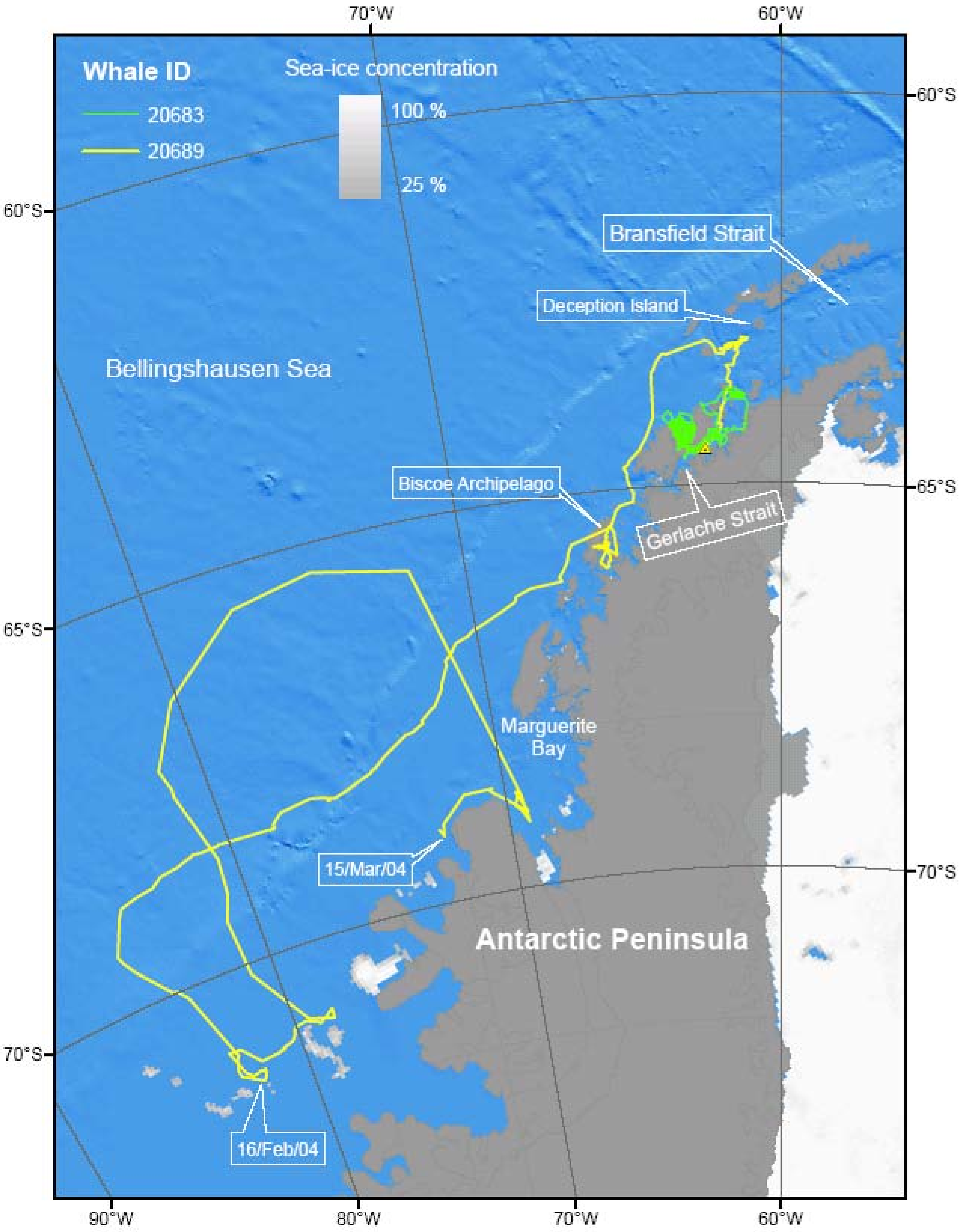


Fig. 4.30 – Track of humpback whale # 20689 tagged in the Gerlache Strait in January 2004. The track of whale # 20683 is also included to better represent the difference in the range of movements between the two whales. Sea-ice concentration on 16 Feb 2004 is shown along with the whale location on that date. Triangle indicates tagging location

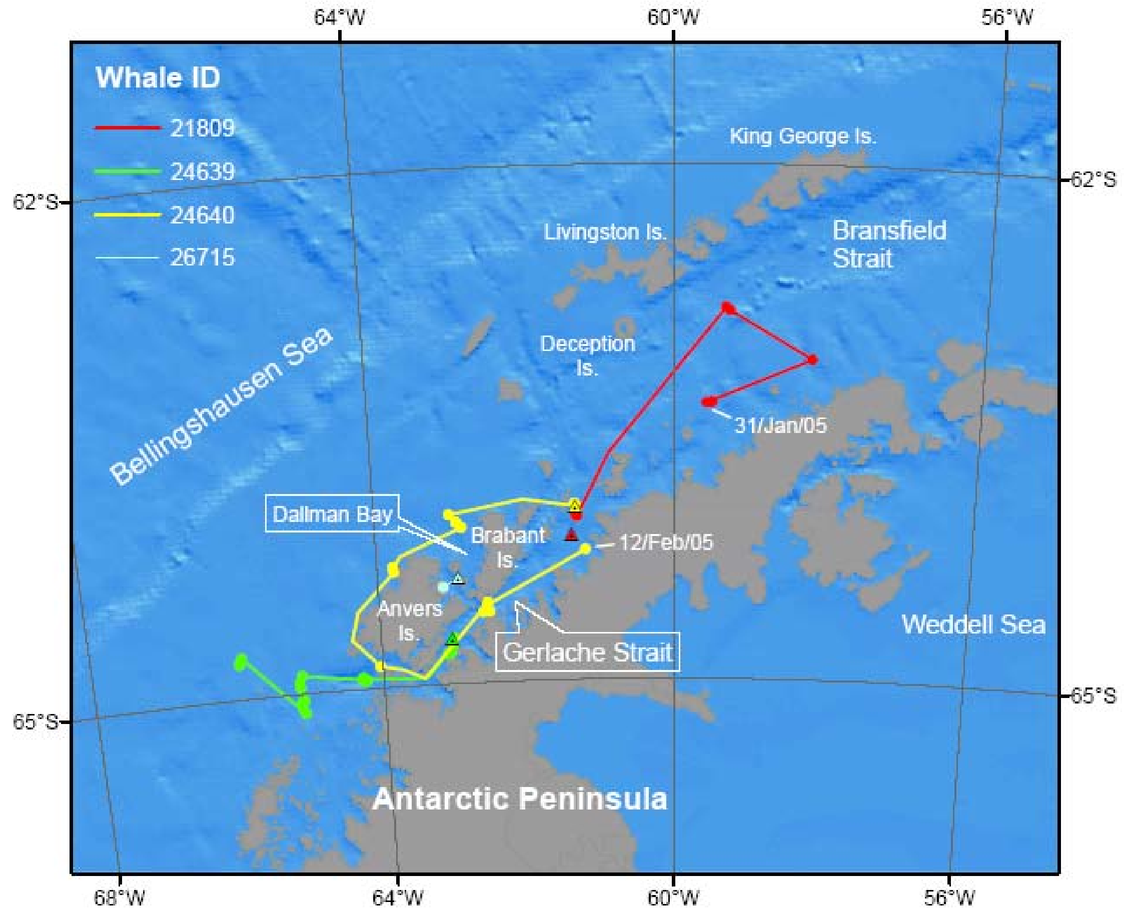


Fig. 4.31 – Tracks of humpback whales tagged with satellite transmitters in the Gerlache Strait and Dallmann Bay in January 2005. Triangles indicate tagging location

Whales 63375 and 63377, which were tagged three days and 16.5 km apart, moved into BS with a time lag of about 6 days (Fig. 4.4). However, both individuals followed a very similar path until they were north of Deception Island. Their time lag was only 2 days near this island, but increased again to 6 days near Livingston Island. Whale 63377 was about 70 km south of King George Island when transmissions ended, while whale 63375 was very close to continental land in the southeast section of BS when transmissions ceased almost a week later. Whale 63376 left GS about 7-8 days after being tagged, and once it reached an area close to the Peninsula in BS, it traveled 637 km northeast across the strait and east into the Weddell Sea to a location (63^{o}09’S; 50^{o}14’W) near an area covered by sea-ice (Fig. 4.5) in 16 days (40 km/d). This individual then returned to an area near the eastern side of the Antarctic Peninsula four days later, when transmissions ceased. Whale 63378 traveled north into southern BS about 9 days after it was tagged, then it moved to an area north of Brabant Island, where it stayed for 8 days, and after that it reached an area off Dallmann Bay for 10 days (Fig. 4.5). On 5 March 2006 it started traveling south at a speed of 42 km/d reaching its southernmost position 849 km later on 25 March at the entrance of Marguerite Bay (68^{o}43’S; 69^{o}47’W). This whale started moving back northwards 6 days later and it may have attempted to pass through ‘The Gullet’ channel between Adelaide Island and the mainland. However, sea-ice images suggest that the channel was closed during that period, perhaps forcing the whale to turn around and bypass Adelaide Island to head straight to the Biscoe Archipelago area, where it stayed from 8 April to the end of transmissions on 16 April 2006 (Fig 4.5).

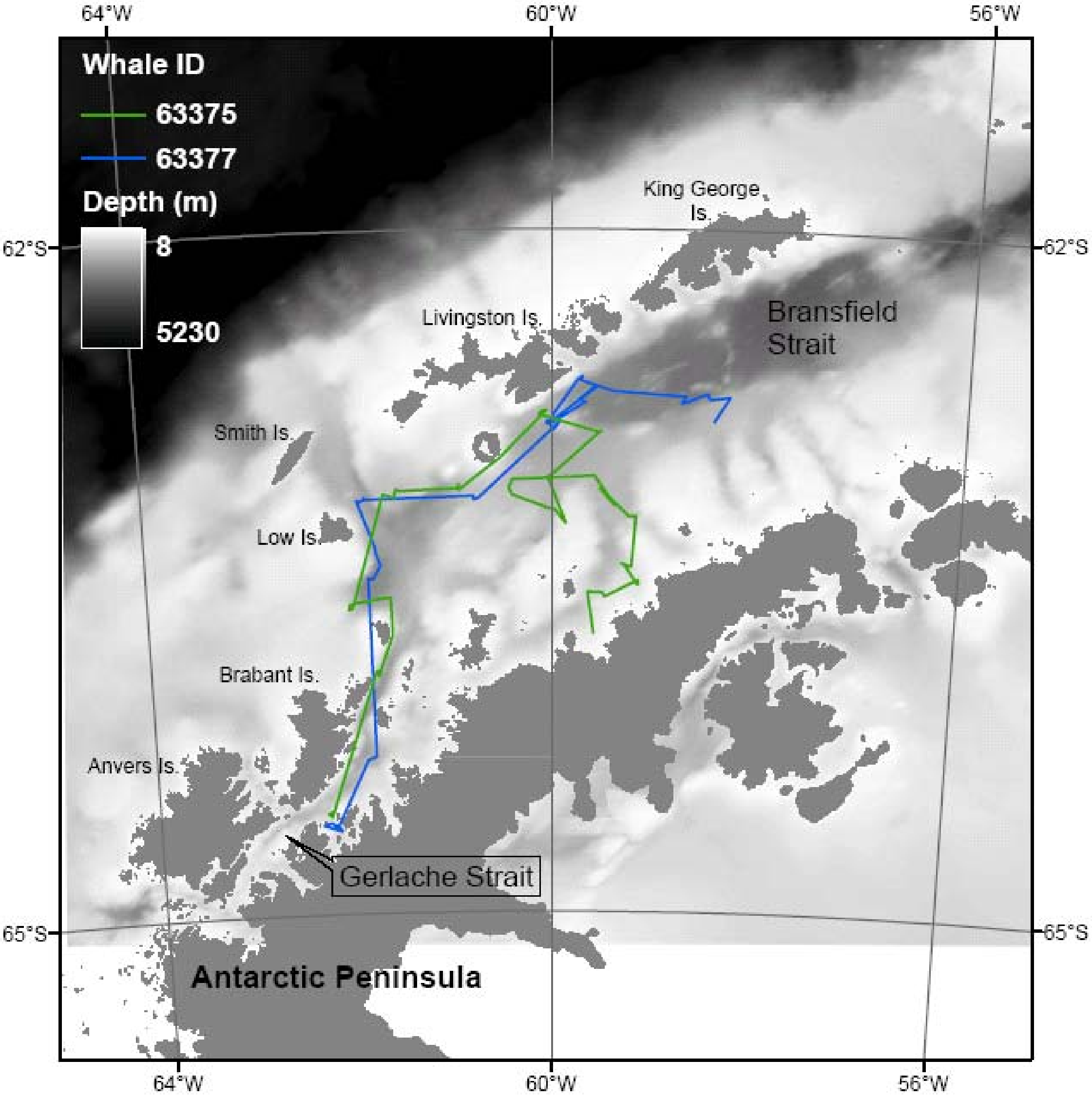


Fig. 4.32 – Tracks of humpback whales (# 63375 and 63377) tagged in the Gerlache Strait in January 2006. Note: figure from original paper was modified to include improved bathymetry (see Chapter 3).

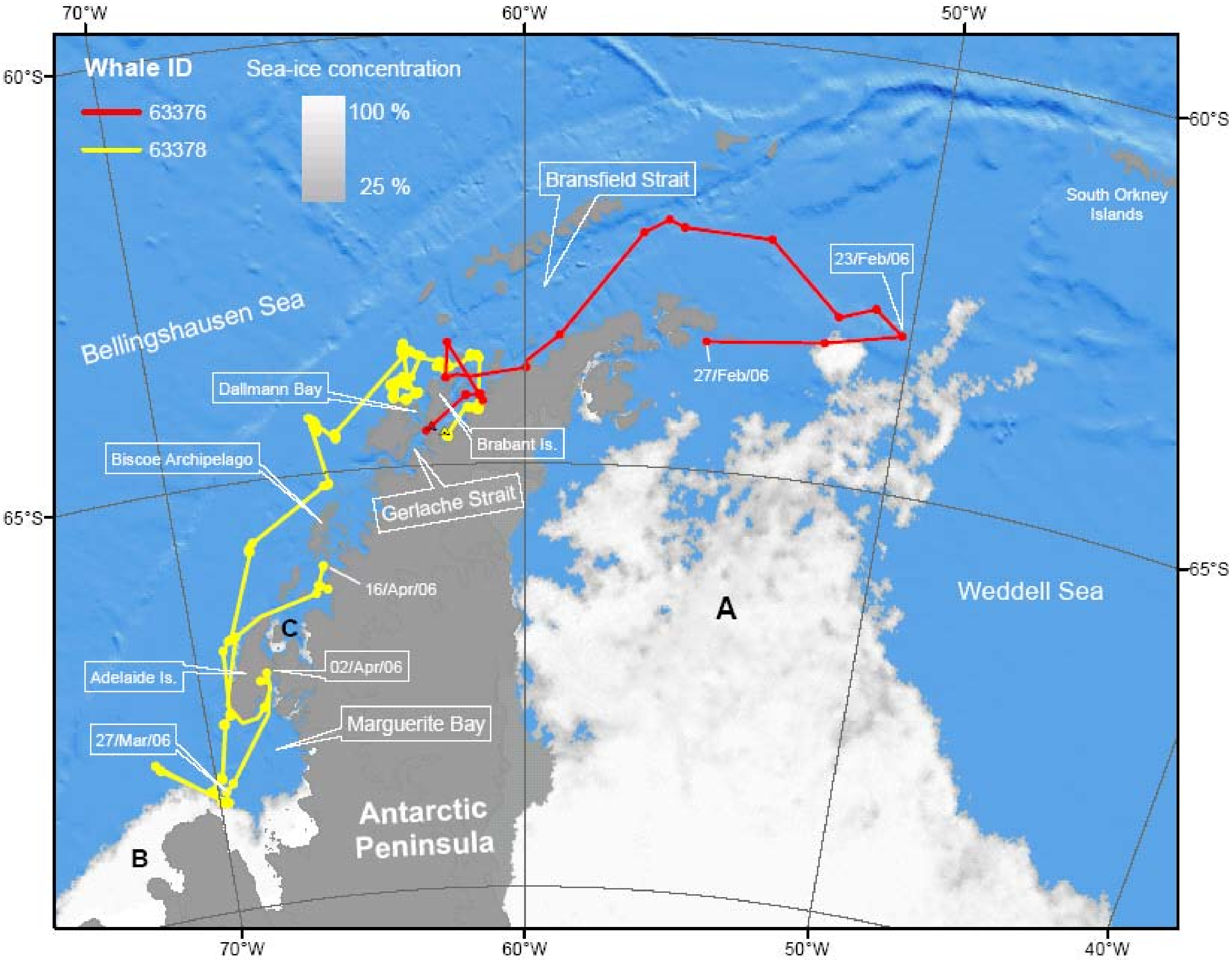


Fig. 4.33 – Tracks of humpback whales (# 63376 and 63378) tagged in the Gerlache Strait in January 2006. Sea-ice fields correspond to the following dates with nearby whale locations: (A) 23 February 2006; (B) 27 March 2006; and (C) 2 April 2006. Triangles indicate tagging location

Area usage based on the MCP estimator varied from 4,782 to 407,583 km^2 with a mean of 97,709 km^2 and a total overlaid area of 480,825 km^2. The 95% kernel calculations ranged from 2,771 to 172,356 km^2 with a mean of 48,193 km^2 and a total area of 239,501 km^2 (Table 4.2). The wide variation in these estimates, which in part is caused by differences in sample size and the complex coastline, is still present after estimates are rated by the number of tracking days, indicating individual variation in area use. The limited movements of whale 20683, which had the second longest tracking period, resulted in the smallest area usage by far. And the broad movements of whale 20689 resulted in very large estimates when compared to the other individuals.

Table 4.12 – Estimates of area usage (km^2) based on the minimum convex polygon (MCP) and the 95% fixed kernel home range with least squares cross-validation (95% kernel) for six humpback whales satellite monitored near the Antarctic Peninsula in 2004-2006. Rates of area usage (km^2/d) and an estimate of summer area usage combining all individual home ranges overlaid are also provided.

Whale ID	MCP	n_1	95% Kernel	$n_2 = d$	MCP/d	95% Kernel/d
20683	4,782	69	2,771	72	66	38
20689	407,583	57	172,356	59	6,908	2,921
63375	15,763	19	20,024	37	426	541
63376	71,669	16	57,647	31	2,312	1,860
63377	16,723	16	5,851	31	539	189
63378	69,735	40	30,508	79	883	386
All overlaid	480,825		239,501			

n_1 and n_2 number of average daily positions used in the MCP and 95% kernel estimates, respectively; d number of days between first and last transmission

4.4. Discussion

The longevity of MC tags was greater than that of IM tags in the present study. Nevertheless, IM tags were expected to last longer since they were duty-cycled to transmit at longer intervals, therefore saving battery, and also because they were designed to cause less drag when whales moved. We believe they fell off sooner because they were not properly attached to the whales.

The observed individual variation in the movement pattern of humpback whales suggests important individual differences in foraging strategies. Except for whale 20683, residency time in specific areas was limited (up to 10 days), possibly reflecting the depletion of local krill patches below a required threshold or some other dynamic process that might affect prey fields and influence the animal's decision on whether to stay longer in an area or not. That includes Gerlache Strait (GS), an important feeding area for humpback whales, where site fidelity is demonstrated by several inter-annual resightings, some within a few kilometers of each other (Dalla Rosa et al. 2004), and where high encounter rates are commonly observed (e.g. Secchi et al. 2001). Therefore, in general, humpback whales do not stay in the same place for extended periods of time, but rather present fluid movements. This observation is also evident from a similar study in the Northern Hemisphere, where satellite telemetry was used to observe movement patterns of humpback whales on their feeding ground in West Greenland (see Heide-Jørgensen and Laidre in press). Movements between foraging sites involve adjacent patches (commuting) or more distant regions with a different set of oceanographic conditions (ranging) (see Stern 2002). The short-range movements between northern GS and southwestern Bransfield Strait (BS) and the long-distance movements between southwestern BS and Marguerite Bay and other distant sites are examples of these two types of displacements.

Most whales moved initially north to BS instead of south through Bismarck Strait or west through Schollaert Channel, suggesting a common pattern. The wider northern exit of GS and the influence of waters from the Bellingshausen and Weddell Seas (Hofmann et al. 1996, García et al. 2002) which turn northern GS and southwestern BS into highly productive areas (e.g. Ross et al. 1996, Lorenzo et al. 2002) might be driving this pattern. All four whales tagged in GS in 2006 moved into BS within up to nine days after being tagged, between 28 January and 5 February. This period coincides with the higher encounter rate of humpback whales observed in BS as compared to GS between late January and early February 2006 (Secchi et al. 2006). The similar routes taken by whales 63375 and 63377 into BS seem to be associated with the bathymetry of the region, i.e., both tracks followed the deep channel connecting GS and BS and the deeper basins of BS. This region is characterized by a northward surface flow of the GS current that meets the BS current flowing northeastward along the southern continental margin of the South Shetland Islands (Zhou et al 2002).

The distances traveled and travel rates obtained from the Argos locations correspond to minimum estimates. Long directional movements, such as those characteristic of migrating whales, yield better estimates than more erratic movements of feeding animals. This is particularly true for the tracks with coarser resolution from whales with duty-cycled tags. Nevertheless, satellite telemetry can provide better estimates than other methods previously used (e.g. Discovery marks, photo-identification and genotyping). Travel rates estimated from photo-identification/genotype matches typically lack precise information on departure and arrival dates to specific locations, while speeds measured on site either from shore-based observations or by following animals with a boat correspond to short temporal and fine spatial scales, and, in the latter case, potentially distressed animals. As expected, whales with wider ranges yielded proportionally larger distance and speed estimates, which were also affected by the duty-cycling frequency. The distance traveled by whale 20689 seems remarkable for a whale in the feeding grounds, and its average travel rate of 75 km/d is comparable to that of migrating whales. Travel rates ranging from 63 to 100 km/d were reported for humpback whales that migrated southward in the South Atlantic (Zerbini et al. 2006a, b), although these same individuals traveled between 18 and 30 km/d in the feeding grounds. The average speed of 108 km/d maintained by whale 20689 during a 12-day period traveling offshore is also similar to the average of 120 km/d reported by Mate et al. (1998) for three North Pacific humpback whales tracked for up to 15 days during their initial migration from Hawaii. However, when we partition whale 20689's track into presumed foraging sites and traveling between these sites, the difference in effective movement is clearly shown in the corresponding travel rate estimates (43 and 109 km/d, respectively). In this case, the lower value approaches those estimated for whales 20683 (predominantly erratic movements) and 63376 (more directional movements but lower resolution data). Average daily speeds between 10 and 55 km/d, with considerably higher speeds during long-distance or offshore movements, were recorded for satellite-monitored humpback whales in the feeding grounds of West Greenland (Heide-Jørgensen and Laidre in press).

The mean swimming speeds computed for whales 20683 and 20689 using only segments between the best quality locations represent more accurate estimates and reflect well the difference in the range of movements of both animals. Again, the mean speed of whale 20689 is consistent with other reported humpback whale speeds. An average migratory speed of 4.74 km/h was estimated for the fastest documented migration in the North Pacific (Gabriele et al. 1996), and an average swimming speed of 4.44 km/h was calculated from shore-based observations in Hawaiian wintering grounds (Bauer 1986). The mean speeds of migrating humpback whales estimated from acoustic and visual observations off the east coast of Australia were 2.5 km/h and 4.0 km/h for singing and non-singing whales, respectively (Noad and Cato 2007). These estimates are similar to the mean speed of whales 20683 (2.26 km/h) and 20689 (4.03 km/h). From these comparisons, our results suggest that swimming speeds of humpback whales vary according to individual behavioral patterns and not necessarily to common patterns differing among migratory corridors and breeding and feeding grounds.

Movements of humpback whales monitored during this study have implications for stock structure. The Antarctic Peninsula is located directly to the south of South America, so populations wintering on either side of this continent could potentially feed near the Peninsula. In 1997, the IWC Scientific Committee suggested that the stock boundary separating the feeding grounds associated with Breeding Stocks A (wintering off Brazil) and G (wintering off western Central and South America) should be placed at 60^{o}W (IWC 1998). Subsequently, in light of new genetic and photo-identification data (e.g. Olavarría et al. 2000, Dalla Rosa et al. 2004), this boundary was moved east to 50^{o}W (IWC 2006). The tracks of one whale tagged in 2005 and three in 2006 crossed the 60^{o}W meridian, confirming the lack of a biological meaning for the previous boundary. In addition, one individual (whale 63376), a male, traveled eastward of the Antarctic

Peninsula nearly to 50^{o}W, the new proposed boundary. This individual was on an eastward path and apparently turned around when it reached a sea-ice fringe, so it is reasonable to assume that it would have probably continued further east had it not found a physical barrier. In this respect, it is noteworthy that the easternmost tracking position of whale 63376 (63^{o}09.1’S, 50^{o}13.7’W) is located 172 km southeast of the resighting location (62^{o}11.1'S, 52^{o}51.1'W), in February 2001, of a humpback whale first photographed in February 2000 in a position 732 km to the east (61^{o}50.5’S, 38^{o}48.8’W) (Dalla Rosa et al. 2004). This resighting, therefore, suggests that some individuals may cross the new proposed 50^{o}W boundary. Furthermore, there were no matches between 15 and 983 individuals photo-identified in the Weddell Sea and off Brazil, respectively (Dalla Rosa et al. 2004). Satellite-monitored humpback whales wintering off Brazil migrated southeastwards to 32-33^{o}W, east of South Georgia, and one whale reached as far south as the South Sandwich Islands (~58^{o}S, 26^{o}W), where it remained for several months (Zerbini et al. 2006a). None of the whales tracked by Zerbini et al. (2006a, b) migrated towards the Antarctic Peninsula or the Weddell Sea. Results from satellite telemetry were further supported by photo-identification as individuals seen near South Georgia and the South Sandwich Islands were matched to whales wintering off Brazil (e.g. Stevick et al 2006). While further investigation is necessary due to sample sizes, we hypothesize from the above information that the Weddell Sea area south of the South Orkney Islands (60^{o}36’S, 45^{o}32’W) and west of ~35^{o}W is occupied by whales from Breeding stock G, and that whales from Breeding stock A are unlikely to use this area, or rarely do so. Alternative hypotheses include a partial overlap between these two stocks in the feeding grounds in the Weddell Sea, around the 50^{o}W boundary and further east, or a spatial but not temporal overlap in this region either within or between seasons. However, there are currently no data to support or reject either of these hypotheses.

Low densities of humpback whales have been observed in the Weddell Sea (Projeto Baleias/PROANTAR, unpublished data), possibly as a consequence of the variable sea-ice conditions characteristic of the region (Venegas and Drinkwater 2001). Humpback whales may be common near ice margins (e.g. Thiele et al. 2004), but they avoid entering the pack ice. Sea-ice coverage in the Weddell Sea often reaches 60^{o}S and the western tip of the Peninsula during the feeding season, creating a natural barrier to the whales. As a result, use of this area by humpback whales may vary within and between seasons, depending on sea-ice extent.

The accuracy of home range estimates is affected by sample size and sampling interval (Kernohan et al. 2001). Therefore, considering differences in the number of locations used and that the whale tracking periods did not cover their whole feeding season, our home range calculations are only intended to represent individual area use during the tracking period and a minimum estimate of summer home range. Autocorrelation between sequential average daily positions was detected in our analyses of area use by indexes based on time to independence (TTI) (see Swihart and Slade 1997). Sub-sampling data to a larger interval of one location every four days did not result in independent observations either. However, we must note that the TTI test has little value when animal movements are not centered around one focal use area (Kernohan et al. 2001), as this will produce unrealistically long TTI (McNay et al. 1994). In addition, although autocorrelation may lead to underestimation of home range size, the use of statistically independent intervals that result in loss of important biological information may also underestimate home range, in which case autocorrelated data may provide a more accurate estimate (Reynolds and Laundré 1990). The use of pseudo-locations allowed us to include areas used by the whales that otherwise would be missed in the kernel density calculations. Rates of area use per tracking day provided a better idea of area use given the variable tagging duration and suggested that the estimates for whales 20689 and 63376 are likely positively biased, in particular the MCP estimates.

4.5. Conclusions

Our study shows that humpback whales can travel extensive distances in the feeding grounds as part of their foraging strategy, and that individual movement patterns are highly variable near the Antarctic Peninsula. While photo-identification data suggest that site fidelity to the Gerlache Strait is high, our telemetry data indicate that use of area may be fluid, with short residency times and frequent movements of whales among neighboring or distant feeding sites. Travel rate estimates are lower at presumed foraging sites, characterized by erratic movements, than during traveling between these sites. We also show that humpback whales may displace from the western Antarctic Peninsula to the Weddell Sea, and we suggest, based on available information, that the current boundary between the feeding grounds associated with Breeding Stocks A and G should be reconsidered.

4.6. References

Acevedo J, Rasmussen K, Félix F, Castro C, Llano M, Secchi ER, Saborío MT, Aguayo-Lobo A, Haase B, Scheidat M, Dalla Rosa L, Olavarría C, Forestell P, Acuña P, Kaufman G, Pastene L (2007) Migratory destinations of the humpback whales from Magellan Strait feeding ground, Chile. Mar Mamm Sci 23(2): 453-463, doi:10.1111/j.1748-7692.2007.00116.x

Argos. 1990. User’s manual. Service Argos. Landover, MD, USA. 267pp.

Bauer GB (1986) The behavior of humpback whales in Hawaii and modifications of behavior induced by human interventions. Ph.D. dissertation, University of Hawaii, Hawaii (unpublished)

Baumgartner MF, Mate BR (2005) Summer and fall habitat of North Atlantic right whales (*Eubalaena glacialis*) inferred from satellite telemetry. Can J Aquat Sci 62:527-543

Bérubé M, Palsbøll P (1996) Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. Mol Ecol 5:283-287

Dalla Rosa L, Secchi ER, Kinas PG, Santos MCO, Martins MB, Zerbini AN, Bethlem CBP (2001) Photo-identification of humpback whales, *Megaptera novaeangliae*, off the Antarctic Peninsula from 1997/98 to 1999/2000. Mem Queensl Mus 47(2):555-561

Dalla Rosa L, Freitas A, Secchi ER, Santos MCO, Engel MH (2004) An updated comparison of the humpback whale photo-id catalogues from the Antarctic Peninsula and the Abrolhos Bank, Brazil. Paper SC/56/SH16 presented to the IWC Scientific Committee (unpublished)

Dawbin WH (1966) The seasonal migratory cycle of humpback whales. In Whales, dolphins and porpoises K. Norris (Ed) University of California Press, Berkeley & Los Angeles, pp 145-170

Etnoyer P, Canny D, Mate BR, Morgan LE, Ortega-Ortiz JG, Nichols WJ (2006) Sea-surface temperature gradients across blue whale and sea turtle foraging trajectories off the Baja California Peninsula, Mexico. Deep Sea Res II 53(3-4):340-358

Frankel AS, Clark CW, Herman LM, Gabriele CM (1995) Spatial distribution, habitat utilization, and social interactions of humpback whales, *Megaptera novaeangliae*, off Hawaii, determined using acoustic and visual techniques. Can J Zool 73(6):1134-1146

Frydman S, Gales N (2007) HeardMap: Tracking marine vertebrate populations in near real time. Deep-Sea Res II 54:384-391

Gabriele CM, Straley JM, Herman LM, Coleman RJ (1996) Fastest documented migration of a North Pacific humpback whale. Mar Mamm Sci 12(3):457-464

Garcia MA, Castro CG, Ríos AF, Doval MD, Rosón G, Gomis D, López O (2002) Water masses and distribution of physico-chemical properties in the Western Bransfield Strait and Gerlache Strait during Austral summer 1995/96. Deep-Sea Res II 49:585–602

Heide-Jørgensen MP, Dietz R, Laidre KL, Richard P (2002) Autumn movements, home ranges, and winter density of narwhals (*Monodon monoceros*) tagged in Tremblay Sound, Baffin Island. Polar Biol 25(5):331-341

Heide-Jørgensen MP, Dietz R, Laidre KL, Richard P, Orr J, Schmidt HC (2003) The migratory behaviour of narwhals (*Monodon monoceros*). Can J Zool 81(8):1298-1305

Heide-Jørgensen MP, Laidre KL, Jensen MV, Dueck L, Postma LD (2006) Dissolving stock discreteness with satellite tracking: Bowhead whales in Baffin Bay. Mar Mamm Sci 22(1):34-45

Heide-Jørgensen MP, Laidre KL (In press) Autumn space-use patterns of humpback whales (*Megaptera novaeangliae*) in West Greenland. J Cetacean Res Manage

Hofmann EE, Klinck JM, Lascara CM, Smith DA (1996) Hydrography and circulation west of the Antarctic Peninsula and including Bransfield Strait. In: Ross R, Hofmann E, Quetin L (eds.) Foundations for Ecological Research West of the Antarctic Peninsula. Amer Geophys Union, Antarctic Res Ser 70:61–80

International Whaling Commission (1998) Annex G – Report of the sub-committee on comprehensive assessment of Southern Hemisphere humpback whales. Rep int Whal Comm 48:170-182

International Whaling Commission (2006) Report of the Workshop on the Comprehensive Assessment of Southern Hemisphere Humpback Whales. Document SC/58/Rep 5 (unpublished)

Kernohan BJ, Gitzen RA, Millspaugh JJ (2001) Analysis of animal space use and movements. In: Millspaugh JJ, Marzluff JM (eds.) Radio Tracking and Animal Populations. Academic Press, San Diego, pp 125–166

Laidre KL, Heide-Jørgensen MP, Dietz R, Hobbs RC, Jørgensen OA (2003) Deep-diving by narwhals *Monodon monoceros*: differences in foraging behavior between wintering areas? Mar Ecol Prog Ser 261:269-281

Lorenzo LM, Arbones B, Figueiras FG, Tilstone GH, Figueroa FL (2002) Photosynthesis, primary production and phytoplankton growth rates in Gerlache and Bransfield Straits during Austral summer: cruise FRUELA 95. Deep-Sea Res II 49:707–721

Mate BR, Gisiner R, Mobley J (1998) Local and migratory movements of Hawaiian humpback whales tracked by satellite telemetry. Can J Zool 76(5):863-868

Mate BR, Lagerquist BA, Calambokidis J (1999) Movements of North Pacific blue whales during the feeding season off southern California and their southern fall migration. Mar Mamm Sci 15(4):1246-1257

McNay RS, Morgan JA, Bunnell FL (1994) Characterizing independence of observations in movements of Columbian black-tailed deer. J Wildl Manage 58: 422–429

Noad MJ, Cato DH (2007) Swimming speeds of singing and non-singing humpback whales during migration. Mar Mamm Sci 23(3): 481-495, doi: 10.1111/j.1748-7692.2007.02414.x

Olavarría C, Baker CS, Medrano L, Aguayo A, Caballero S, Flórez-González L, Capella J, Rosenbaum HC, Garrigue C, Greaves J, Jenner M, Jenner C, Bannister JL (2000) Stock identity of Antarctic Peninsula Humpback whales inferred from mtDNA variation. Paper SC/52/IA15 presented to the IWC Scientific Committee (unpublished)

Rasmussen K, Palacios DM, Calambokidis J, Saborío MT, Dalla Rosa L, Secchi ER, Steiger GH, Allen JM, Stone GS (2007) Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. Biol Lett 3:302-305, doi:10.1098/rsbl.2007.0067

Reynolds TD, Laundré JW (1990) Time intervals for estimating pronghorn and coyote home ranges and daily movements. J Wildl Manage 54(2):316-322

Rodgers AR, Carr AP, Smith L, Kie JG (2005) HRT: Home Range Tools for ArcGIS. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Ross RM, Quetin LB, Lascara CM (1996) Distribution of Antarctic krill and dominant zooplankton west of the Antarctic Peninsula. In: Ross R, Hofmann E, Quetin L (eds.) Foundations for Ecological Research West of the Antarctic Peninsula. Amer Geophys Union, Antarctic Res Ser 70:199–217

Sambrook J, Fritsch EF and Maniatis T (1989) Molecular Cloning: a Laboratory Manual. 2nd edition. Cold Spring Harbor Lab. Press, New York

Secchi ER, Dalla Rosa L, Kinas PG, Santos MCO, Zerbini AN, Bassoi M, Moreno IB (2001) Encounter rates of whales around the Antarctic Peninsula with special reference to humpback whales, *Megaptera novaeangliae*, in the Gerlache Strait: 1997/98 to 1999/2000. Mem Queensl Mus 47(2):571-578

Secchi ER, Dalla Rosa L, Kinas PG, Nicolette RF, Azevedo AF, Maia YG (2006) Abundance of humpback whale, *Megaptera novaeangliae*, in the Gerlache and Bransfield straits, Antarctic Peninsula region. Paper SC/A06/HW43 presented to the IWC Scientific Committee (unpublished)

Shaw CN, Wilson PJ, White BN (2003) A reliable molecular method of gender determination for mammals. J Mamm 84(1):123–128

Slijper EJ (1962) Whales. Hutchinson & Co., London

Spreen G, Kaleschke L, Heygster G (2007) Sea ice remote sensing using AMSR-E 89 GHz channels. J Geophys Res 113, C02S03, doi: 10.1029/2005JC003384

Stern SJ (2002) Migration and movement patterns. In: Perrin WF, Würsig B, Thewissen JGM (eds.) Encyclopedia of Marine Mammals. Academic Press, San Diego, pp 742-748

Stevick PT, Aguayo A, Allen J, Avila IC, Capella J, Castro C, Chater K, Dalla Rosa L, Engel MH, Félix F, Florez-Gonzalez L, Freitas A, Haase B, Llano M, Lodi L, Muñoz E, Olavarria C, Secchi ER, Scheidat M, Siciliano S (2004) Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. J Cetacean Res Manage 6(2):109-113

Stevick PT, Pacheco de Godoy L, Mcosker M, Engel MH, Allen J (2006) A note on the movement of a humpback whale from Abrolhos Bank, Brazil to South Georgia. J Cetacean Res Manage 8(3):297-300

Stone GS, Florez-Gonzalez L, Katona S (1990) Whale migration record. Nature 346:705

Swihart RK, Slade NA (1997) On testing for independence of animal movements. J Agricult Biol Environ Stat 2:48-63

Thiele D, Chester ET, Moore SE, Širovic A, Hildebrand JA, Friedlaender AS (2004) Seasonal variability in whale encounters in the Western Antarctic Peninsula. Deep-Sea Res II 51:2311-2325

Tyack P (1983) Differential response of humpback whales, *Megaptera novaeangliae*, to playback of song or social sounds. Behav Ecol Sociobiol 13:49-55

Venegas SA, Drinkwater MR (2001) Sea ice, atmosphere and upper ocean variability in the Weddell Sea, Antarctica. J Geophys Res-Oceans 106(C8):16747-16765

Williams R, Hedley SL, Hammond PS (2006) Modeling distribution and abundance of Antarctic baleen whales using ships of opportunity. Ecol & Soc 11(1):1 [online] url: http://www.ecologyandsociety.org/vol11/iss1/art1/

Zerbini AN, Andriolo A, Heide-Jørgensen MP, Pizzorno JL, Maia YG, Vanblaricom GR, Demaster DP, Simões-Lopes PC, Moreira S, Bethlem C (2006a) Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the southwest Atlantic Ocean. Mar Ecol Prog Ser 313:295-304

Zerbini AN, Andriolo A, Heide-Jørgensen MP, Moreira S, Pizzorno JL, Maia YG, Bethlem C, Vanblaricom GR, Demaster DP (2006b) What does satellite telemetry tell us about the stock identity and feeding grounds of humpback whales in the western South Atlantic Ocean? Paper SC/A06/HW46 presented to the IWC Scientific Committee (unpublished)

Zhou M, Niiler PP, Hu J-H (2002) Surface current in the Bransfield and Gerlache Straits measured by surface Lagrangian drifters. Deep-Sea Res I 46:267–280

5. Conclusions

The main goal of my research was to investigate the processes that drive individuals to concentrate in specific areas of their home range. I addressed this by modeling the encounter rates of humpback whales in relation to environmental variables and processes at two foraging areas and found that humpback whales tended to be associated with areas of enhanced biological productivity driven by physical forcing. As outlined in the following sections, my findings are based on advanced sampling and modeling techniques that come with some caveats. My research also leads to new and remaining questions to be answered through further study.

5.1. Summary of findings

In Chapter 2, I investigated the distribution and relative abundance of humpback whales in relation to environmental variables in British Columbia waters using GIS, remote sensing data and generalized additive models (GAMs). The models suggested that humpback whales in British Columbia were strongly associated with latitude and bathymetric features, including depth, slope and distance to the 100-m isobath, while relationships with variables based on chl-*a* concentration or net primary productivity were not consistent. Nevertheless, higher numbers of whales seemed to be associated with higher primary productivity for some models, and the regions that stood out with the highest concentrations of humpback whales did appear to reflect areas of higher biological productivity. These areas included south Dixon Entrance, middle and southwestern Hecate Strait, and the region off Juan de Fuca Strait.

In Chapter 3, I also modeled the distribution and relative abundance of humpback whales with respect to environmental variables using GAMs, but this time in Antarctica in the Bransfield and Gerlache Straits. Besides using remote sensing data, I also produced models based on hydrographic and chl-*a* data collected *in situ* during a three-year multidisciplinary study. The models for Gerlache Strait suggested that higher numbers of humpback whales were associated with areas of higher chl-a concentration in the central and northern sections of the strait, which in the case of the *in situ* data also corresponded to relatively higher temperatures and shallower mixed layer depths. The models for Bransfield Strait suggested that the numbers and distribution of humpback whales were associated with the deep basins, where there is influence of the Bransfield Current at the surface, and near frontal zones. Combining the Bransfield and Gerlache data into a single model with *in situ* data also pointed to higher numbers of humpback whales being associated with higher chl-*a* maximum values, and to higher encounter rates in Gerlache Strait. Interannual variability in both humpback and minke whale encounter rates in Gerlache Strait was correlated with the Oscillation Niño Index, the oceanic component of ENSO.

The work I conducted in Chapter 4 was the first satellite telemetry study of cetaceans tagged in the Southern Ocean, and the first to describe the detailed movements of humpback whales on their feeding grounds along the Antarctic Peninsula. Whales were tracked from 4 to 80 days (mean = 36.5 days). Distance estimates for nine individuals ranged from 223 to 4,356 km with corresponding travel rates ranging from 17 to 75 km/day. The overall pattern consisted of short- and long-distance movements between presumed foraging areas with relatively short residency times. Travel rates were lower at these sites, characterized by erratic movements, than during traveling between them. Some individuals showed extensive movements, a pattern that, to my knowledge, was previously unknown for humpback whales on their feeding grounds. Area usage for six individuals based on the 95% fixed kernel home range with least squares cross-validation ranged from 2,771 to 172,356 km^2. Results of this study also have implications for stock structure definition of Southern Hemisphere humpback whales.

5.2. Evaluation of research hypotheses

My thesis research addressed three hypotheses:

Hypothesis 1. Higher densities of humpback whales are positively correlated with areas of higher biological production.

The results in Chapters 2 and 3 support this hypothesis, especially the models for the Antarctic Peninsula region. For instance, humpback whale numbers were positively correlated with higher chl-*a* concentrations both within and between seasons in Gerlache Strait. The highest density of humpback whales in Bransfield Strait was recorded when the highest chl-*a* concentrations were observed in that region. The general pattern in the movements of the satellite monitored individuals was also consistent with areas of known biological productivity, such as the northern Gerlache Strait and the southwestern Bransfield Strait.

While the relationships between humpback whales and chl-*a* and NPP values were not always consistent with this hypothesis for the BC study, the associations with latitude and bathymetric features in this area do support it. For instance, the areas with predicted high concentrations of whales from the 3-year GAM are known areas of high biological productivity, usually characterized by complex bathymetry, as pointed out in the discussion of Chapter 2. The associations with the 100-m isobath also seem indicative of areas where concentration and retention processes enhance biological productivity.

Hypothesis 2. Annual or seasonal changes in the distribution of humpback whales are related to changes in oceanographic processes and, consequently, primary production and prey availability.

Due to the non-systematic nature of the BC surveys, it was not possible to address this hypothesis with the analyses in Chapter 2. Nevertheless, data in Chapter 3 support this hypothesis. The increase in humpback whale encounter rates over the 3-year period (2003-2005) of the multidisciplinary study in Gerlache Strait matched with an increase in chl-*a* concentration and SST, especially in 2005, and a decrease in MLD during the same period. This hypothesis is also supported by the correlation between humpback whale encounter rates and ONI in Gerlache Strait, since ENSO is known to affect both atmospheric and oceanographic processes in the Antarctic Peninsula region, which in turn affect primary and secondary productivity.

Hypothesis 3. The parameters and underlying processes determining humpback whale distribution may differ between the two study areas due to differences in feeding habits.

Although I initially intended to conduct a direct comparison between the two regions, the difficulties in obtaining comparable datasets both in terms of survey design and availability and quality of explanatory variables made it an impractical task.

One difference between the two studies is that humpback whale numbers and distribution were explained by a greater number of explanatory variables in the BC than in the Antarctic. It is not clear, however, if this was due to differences in foraging habits or strategies, or simply a consequence of the larger area and higher heterogeneity (due to seasonality or not) of the oceanographic processes along the BC coast. I believe the latter is more likely, because the areas with the highest concentrations of humpback whales during the BC surveys were characterized by individuals presumably feeding on euphausiids (based on frequent observations of flick-feeding behavior), as they do in the Antarctic.

In both study areas, the processes leading to areas of enhanced productivity are clearly affected by bottom topography, which might explain why bathymetric variables were constantly selected in the models. Two possibly important differences are the deeper continental shelf of the Antarctic Peninsula and the influence of two quite different water masses, the Bellingshausen and Weddell seas. On the other hand, tidal mixing is a definitely important process along the BC coast, but may not be the case for the study area along the Antarctic Peninsula. Strong tidal mixing does occur in Southern Ocean areas such as the Ross Sea and southern Weddell Sea shelf breaks, but apparently not in most shelf areas of the western Antarctic Peninsula (Beckmann & Pereira 2003). So, it appears that different physical forcing may be responsible for the concentration and retention features in the two regions, and these features, frequently in the form of fronts and eddies, are ultimately responsible for attracting large numbers of whales.

5.3. Potential caveats

I did not include prey biomass or another measure of prey availability as explanatory variables in my models because these data were not available. This might be a limitation for improved predictions and understanding of the factors driving whale distribution, and should be pursued in future studies. Nevertheless, due to the patchy and dynamic distribution of the prey, a multi-spatial-scale approach may be necessary to investigate the relationship of prey biomass with whale distribution. For instance, Torres et al. (2008) found that fine-scale models of dolphin habitat selection in coastal areas predicted better with environmental variables than with prey data as explanatory variables.

Generalized additive models (GAMs) are still relatively new, and several statistical improvements have been made in the last few years (see Wood 2006). In addition to that, other alternatives or variations to the regular GAMs have emerged and seem promising modeling techniques, including Bayesian GAMs (e.g. Fahrmeir & Lang 2001, Brezger & Lang 2006) and generalized additive mixed models (GAMMs), for spatially auto-correlated data (Wood 2006).

Weather conditions are one of the most common limiting factors during cetacean surveys. Indeed, poor weather accounts for part of the irregular sampling during my study, especially in the Bransfield Strait area and off the west coast of British Columbia. The only solution to overcome this type of problem is to wait out the bad weather, or repeat the missed transect lines during favorable conditions. Unfortunately, this option is rarely feasible due to ship time constrains. It was only possible a couple of times in Gerlache Strait. Also, multidisciplinary research with a single vessel requires setting priorities and accepting compromises. For example, the oceanographic sampling in Bransfield Strait during 2003-2005 was not disrupted except during extreme weather, and it continued overnight, so cetacean observations could not be optimized for those circumstances.

Remote sensing data are significantly affected by cloud cover, particularly in the high latitudes. This is why the 8-day chl-*a* composites could not be chosen over the monthly composites in the Antarctic Peninsula region. This is obviously not ideal given the known variability in phytoplankton biomass. On the other hand, a monthly composite where individual pixels were sampled several times by the satellite sensor may point to areas that were on average more productive and may be able to indirectly account for the gap between increases in primary and secondary producers in a local area. Cloud formation not only affects remote sensing, but together with ice cover and wind seems to be responsible for the observed decline in summer surface chl-*a* in the southwestern Bransfield Strait over the past 30 years, and for substantial increases further south with decreased cloud formation (Montes-Hugo et al. 2009).

Satellite tagging of large cetaceans still has two major limitations: attachment and battery longevity. As tags are built smaller to increase chances of staying attached for longer periods, battery duration becomes a limiting factor. Also, contrary to tagging of seals and other species that can be handled for tag attachment, acquisition of data for long-range or migratory movements has to be done separately from data on dive profiles due to tag size limits. The latter is usually done with suction-cup tags, a less intrusive method that requires that animals be followed from a distance and tags be retrieved for data downloading, which results in shorter monitoring periods (e.g. Goldbogen et al. 2008). Technological improvements (miniaturization of tags, longer lasting batteries and better anchoring systems) will hopefully soon allow using both types of tags together and even use the whales as oceanographic samplers of the water column with the conductivity–temperature–pressure satellite relay data loggers, as is currently possible with seals (e.g. Charrassin et al. 2008).

5.4. Future research

Concurrent hydroacoustic and net prey sampling along with systematic surveys for habitat modeling studies should be pursued in both British Columbia and the Antarctic, as this would be a next step to further improve our understanding of humpback whale distribution and habitat selection.

The systematic cetacean surveys in Gerlache Strait should be continued to verify whether the correlations I observed between humpback and minke whale encounter rates and the Oceanic Niño Index hold for larger datasets, and to investigate the hypotheses proposed in Chapter 3. Moreover, these systematic surveys consist of the longest duration cetacean dedicated dataset for the Antarctic Peninsula region and, therefore, their continuation is warranted to investigate the potential effects of climate change on cetacean populations.

Investigating individual-habitat associations and resource selection (e.g. Conner & Plowman 2001, Erickson et al. 2001) of the satellite-monitored humpback whales in the Southern Ocean (see Chapter 4) is part of a longer term research program I am involved in. I am looking forward to deploying additional satellite tags to increase sample size. I am also considering using state-space models (e.g. Jonsen et al. 2005, Jonsen et al. 2007) or the behavioral change point analysis (BCPA) (Gurarie et al. 2009) in future analyses of movement data to deal with transmission gaps and to potentially identify behavioral states.

Use of other types of statistical models, as mentioned in the previous section, should also be considered in future studies, including testing potential improvements to GAM selection and model fitting. In addition to that, I believe that there is a strong need for new methods of model evaluation, in particular for models based on count data.

My research demonstrated the advantages of using online databases available to the scientific community from reliable sources such as government and non-government institutions. During the development of my thesis, several new products based on remote sensing data were launched and others improved in quality and resolution. Along with that, new tools to analyze these types of data have been developed. As datasets become available at finer temporal and spatial resolutions, this will provide researchers with a suite of options for studying the habitat of marine species, particularly in remote regions where multidisciplinary studies are more difficult to implement both financially and logistically.

I look forward, in particular, to having access to higher resolution data on sea surface height (SSH), which would allow important hydrographic features such as warm- and cold-core eddies and confluence zones to be identified and tracked (e.g. Davis et al. 2002). High resolution SSH data are already available for some regions, such as the Gulf of Mexico. It would also be valuable to investigate the potential influence of tidal mixing on whale distribution in the Antarctic Peninsula region by including data on tidal speeds, which were not readily available at the time of my analyses.

In conclusion, my research improved current understanding of cetacean-habitat relationships through advanced sampling and modeling techniques. This resulted in new information about the distribution, habitat selection and movements of foraging humpback whales. My findings on the interannual variability of humpback whale numbers and the association of humpback whales with areas of enhanced biological productivity through physical forcing should lead to better predictions and evaluation of the effects of environmental variability and climate change on cetacean distributions.

5.5. References

Beckmann A, Pereira AF (2003) Lateral tidal mixing in the Antarctic marginal seas. Ocean Dynamics 53:21-26

Brezger A, Lang S (2006) Generalized structured additive regression based on Bayesian P-splines. Computational Statistics & Data Analysis 50:967-991

Charrassin JB, Hindell M, Rintoul SR, Roquet F, Sokolov S, Biuw M, Costa D, Boehme L, Lovell P, Coleman R, Timmermann R, Meijers A, Meredith M, Park YH, Bailleul F, Goebel M, Tremblay Y, Bost CA, McMahon CR, Field IC, Fedak MA, Guinet C (2008) Southern Ocean frontal structure and sea-ice formation rates revealed by elephant seals. Proceedings of the National Academy of Sciences of the United States of America 105:11634-11639

Conner LM, Plowman BW (2001) Using Euclidean distances to assess nonrandom habitat use. In: Millspaugh JJ, Marzluff JM (eds) Radio Tracking and Animal Populations. Academic Press, San Diego, p 275-290

Davis RW, Ortega-Ortiz JG, Ribic CA, Evans WE, Biggs DC, Ressler PH, Cady RB, Leben RR, Mullin KD, Wursig B (2002) Cetacean habitat in the northern oceanic Gulf of Mexico. Deep-Sea Research Part I: Oceanographic Research Papers 49:121-142

Erickson WP, McDonald TL, Gerow KG, Howlin S, Kern JW (2001) Statistical issues in resource selection studies with radio-marked animals. In: Millspaugh JJ, Marzluff JM (eds) Radio Tracking and Animal Populations. Academic Press, San Diego, p 211-242

Fahrmeir L, Lang S (2001) Bayesian inference for generalised additive mixed models based on Markov random field priors. Applied Statistics 50:201-220

Goldbogen JA, Calambokidis J, Croll DA, Harvey JT, Newton KM, Oleson EM, Schorr G, Shadwick RE (2008) Foraging behavior of humpback whales: kinematic and respiratory patterns suggest a high cost for a lunge. Journal of Experimental Biology 211:3712-3719

Gurarie E, Andrews RD, Laidre KL (2009) A novel method for identifying behavioural changes in animal movement data. Ecology Letters 12:395-408

Jonsen ID, Myers RA, Flemming JM (2005) Robust statespace modeling of animal movement data. Ecology and Society 86:2874-2880

Jonsen ID, Myers RA, James MC (2007) Identifying leatherback turtle foraging behaviour from satellite telemetry using a switching state-space model. Marine Ecology Progress Series 337:255-264

Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE, Schofield O (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the Western Antarctic Peninsula. Science 323:1470-1473

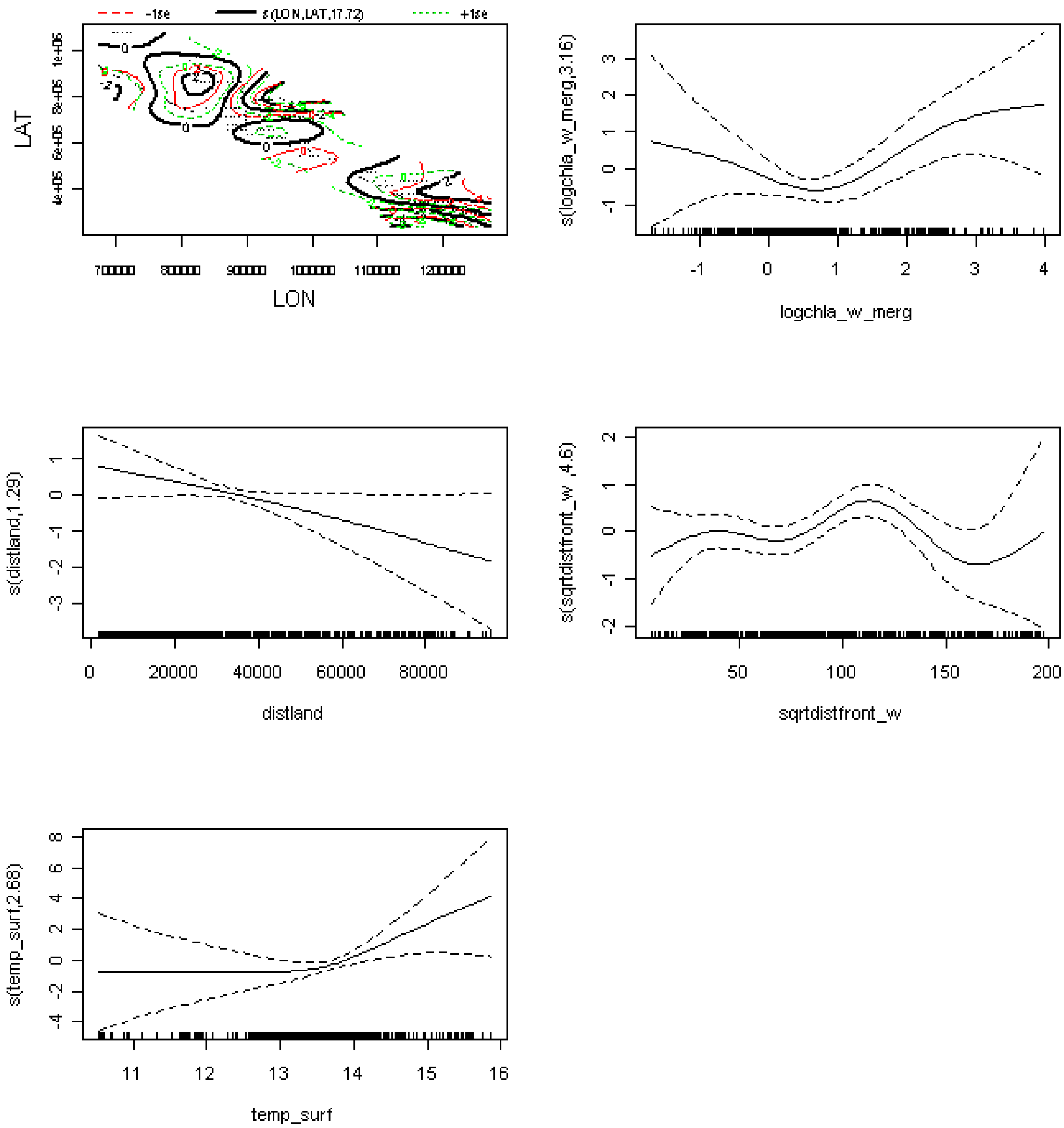
Torres LG, Read AJ, Halpin P (2008) Fine-scale habitat modeling of a top marine predator: do prey data improve predictive capacity? Ecological Applications 18:1702-1717

Wood SN (2006) Generalized Additive Models: An Introduction with R, Chapman and Hall/CRC Press, Boca Raton, Florida

APPENDICES

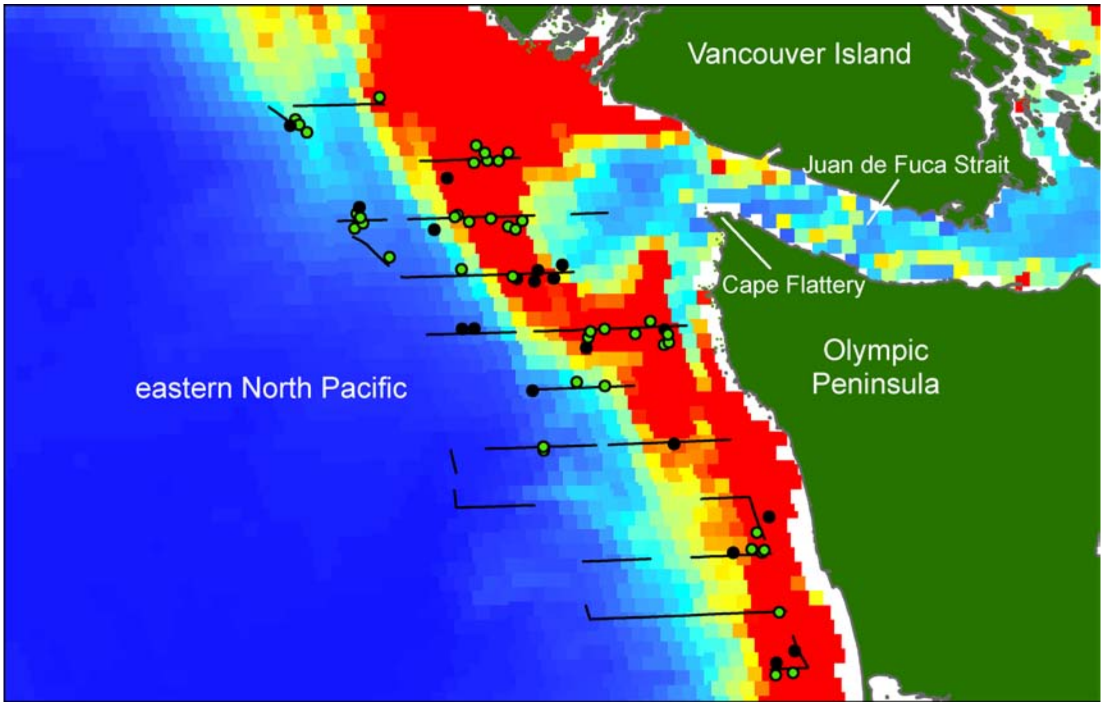
Appendix 1

Model terms for the summer 2005 GAM of the number of humpback whale groups. Estimated smooth functions (solid lines) with 95% confidence interval (dashed lines) are shown for each explanatory variable. Y-axis = fitted function with estimated degrees of freedom in parenthesis; x-axis = variable range with rug plots indicating sampled values



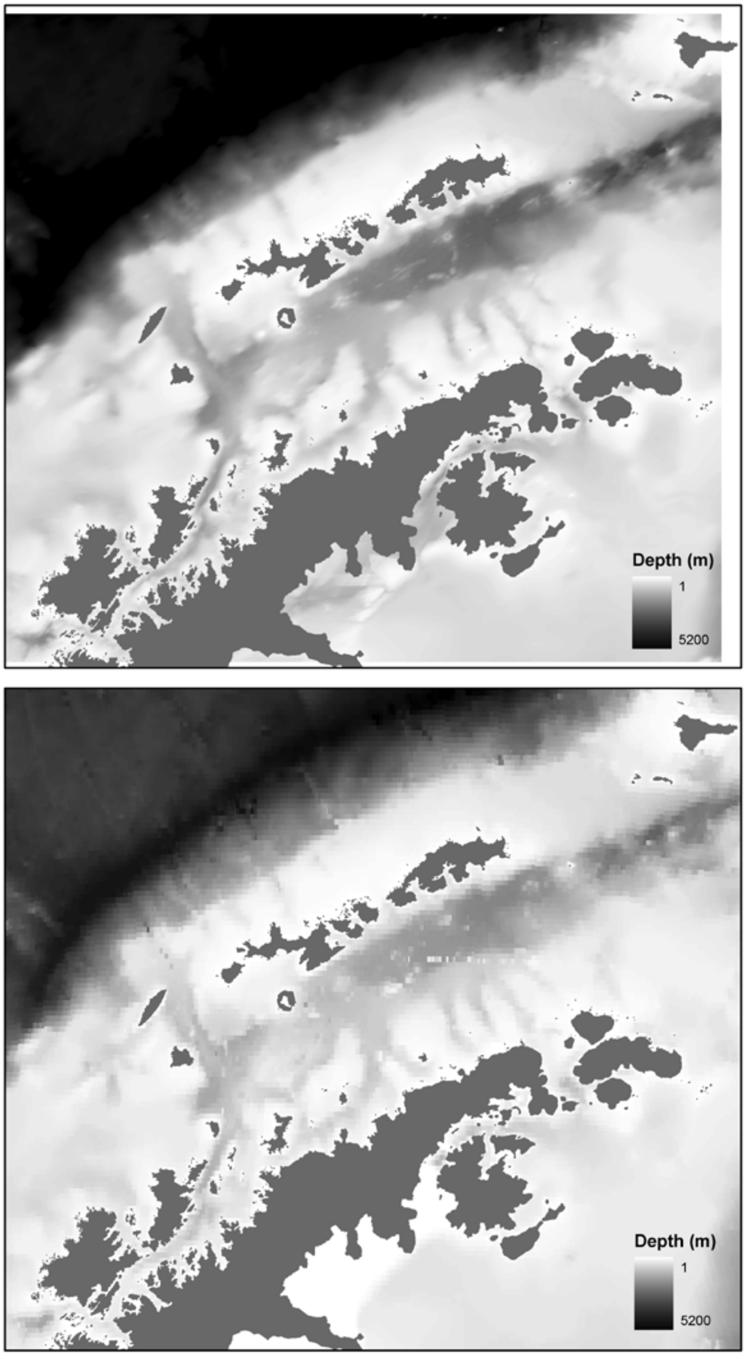
Appendix 2

Locations of humpback (green dots) and unidentified (black dots) whales sighted off the Olympic Peninsula during 20-26 July 2005 on board the *Miller Freeman*, overlaid on a MODIS chlorophyll image for that week. Notice how whale sightings concentrate around the edge of what appears to be the semi-permanent Juan de Fuca Eddy. On effort tracklines are also shown.



Appendix 3

Improved 500-m resolution bathymetry map of the study region (top), constructed from the 2’ gridded global relief data Etopo2v2 and the Marine Trackline Geophysics Data, with nearly 300,000 soundings in the area, using geostatistics and interpolation techniques. The Etopo 2v2 map is also shown for comparison (bottom).



Appendix 4

Encounter rates (individuals/nautical mile) of humpback (HW_ER) and minke (MinkeER) whales, along with climate indices and averaged environmental variables along transect lines in Gerlache Strait between 1998 and 2006. Warm (red) and cold (blue) events based on the Oceanic Niño Index (ONI) are indicated.

Year: Month	HW_ER	Minke_ER	ONI	SOI	AAO	SST_m	Chla_m	Chla_mlag
1998 Jan	0.48	0	2.32	-5.4	0.41	1.364	0.286	0.295
1998 Feb	0.56	0	1.96	-4.4	0.39	1.082	0.245	0.238
1999 Jan	0.46	0.11	-1.5	3.2	1.00	0.877	0.885	0.703
1999 Feb	0.39	0.26	-1.17	1.2	0.46	0.881	0.277	1.241
2000 Jan	0.26	0.23	-1.66	1.1	1.27	0.944	0.432	0.428
2001 Feb	0.52	0.25	-0.54	2.4	-0.26	1.327	0.468	0.634
2002 Jan	0.92	0.02	-0.1	0.7	0.75	1.476	0.553	0.272
2002 Feb	1.48	0.04	0.08	1.5	1.33	1.208	0.275	0.584
2003 Feb	0.57	0	0.88	-2	-0.36	1.079	0.211	0.168
2004 Jan	0.94	0.11	0.38	-2.8	0.81	1.255	0.265	0.218
2005 Jan	1.60	0.06	0.61	0.4	-0.13	1.140	0.491	0.317
2006 Jan	0.42	0.01	-0.79	2.9	0.34	1.113	0.628	0.448

SOI = Southern Oscillation Index; AAO = Antarctic Oscillation Index; SST_m = monthly composite of sea surface temperature (^{o}C) from AVHRR/MODIS; Chla_m = monthly composite of chlorophyll-a concentration (mg/m^{3}) from SeaWiFS/MODIS; Chla_mlag = previous month Chla_m