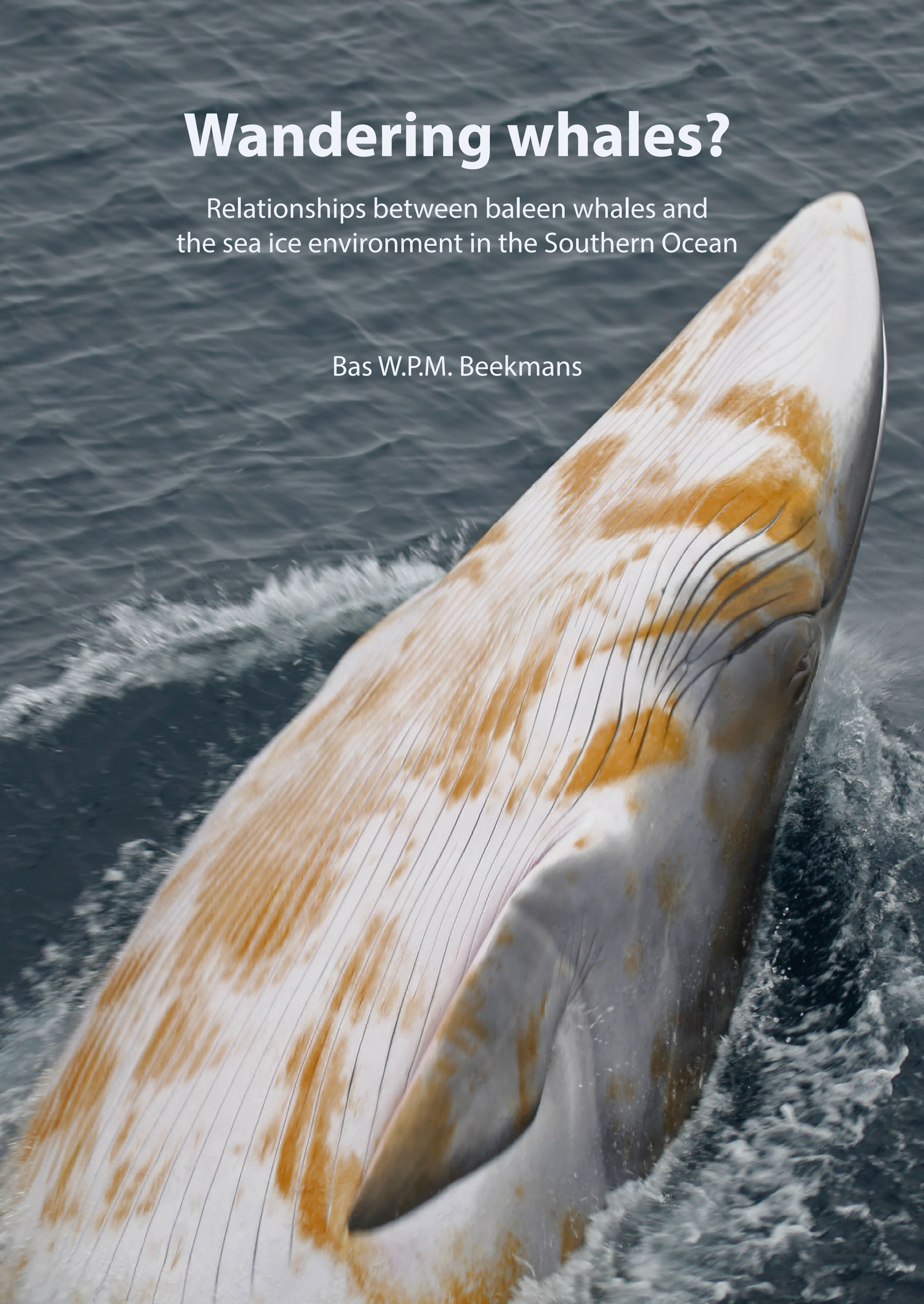
Wandering whales?

Relationships between baleen whales and the sea ice environment in the Southern Ocean

Bas W.P.M. Beekmans



Wandering whales?

Relationships between baleen whales and the sea ice environment in the Southern Ocean

Cover photo:	Minke whale breaching, Pine Island Bay, March 2008.
Photographer:	© Richard Turner, British Antarctic Survey (BAS)

Lay-out:	Nikki Vermeulen | Ridderprint BV
Printing:	Ridderprint BV | www.ridderprint.nl

Electronic version available at:
http://hdl.handle.net/11370/2e012223-f1b1-41c9-a7f0-eabbc7e729f7

ISBN 978-90-367-9504-3 (printed version)
ISBN 978-90-367-9503-6 (electronic version)

rijksuniversiteit
groningen

Wandering whales?

Relationships between baleen whales and the sea ice environment in the Southern Ocean

PhD thesis

to obtain the degree of PhD at the
University of Groningen
on the authority of the
Rector Magnificus Prof. E. Sterken
and in accordance with
the decision by the College of Deans.

This thesis will be defended in public on

Friday 24 February 2017 at 16.15 hours

by

Bas Wilhelmus Petrus Maria Beekmans

born on 22 January 1976
in Waalwijk

Supervisors

Prof. H.J.W. de Baar
Prof. U.V. Bathmann
Prof. E.J. Murphy

Co-supervisor

Dr. J. Forcada

Assessment Committee

Prof. A.G.J. Buma
Prof. P.J. Palsbøll
Prof. P.J.H. Reijnders

Contents

General introduction

1

Every summer, large baleen whales migrate into the Southern Ocean (Figure 1.1), which serves as a major feeding ground for a range of species. During the 20th century, most populations of baleen whales collapsed due to industrial whaling. More than 1.6 million baleen whales were killed in the Southern Hemisphere, the majority being caught in the Southern Ocean (Rocha et al., 2014). Some populations of baleen whales, including those of Antarctic blue and fin whales, were reduced to only a few percent of the pre-whaling population levels (Leaper and Miller, 2011). Populations of baleen whales in the Southern Hemisphere have shown signs of recovery since the moratorium on industrial whaling came into force in 1986 (Branch et al., 2004; Nicol et al., 2008; Leaper and Miller, 2011; Bejder et al., 2016). However, their fragile recovery could be hampered by a reduction in prey availability due to climate change (Nicol et al., 2008; Leaper and Miller, 2011).

One of the most pressing questions in the conservation and management of baleen whales is, therefore, how baleen whales will respond to future trends in the physical environment within the Southern Ocean. In order to answer this question, we need a much better understanding of the relationships between baleen whales, their prey and the physical environment. This introduction provides background information on these aspects, starting off with the Southern Ocean, and concludes with a formulation of the research questions for this thesis.

The Southern Ocean

In 2000, the International Hydrographic Organization recognised the Southern Ocean as a separate ocean and set its approximate northern limit at 60˚S. This northern limit has in fact not been formally accepted by all member states. More important and meaningful than this static limit is the natural dynamic boundary formed by the Subtropical Front (Figure 1.2). The Subtropical Front separates the subantarctic waters from the warmer and saltier subtropical waters (Orsi et al., 1995). The Subtropical Front mostly ranges from 40˚S to 45˚S in the South Atlantic Ocean and Indian Ocean, but it can extend to 30˚S in the South Pacific Ocean (Deacon, 1982). The five major water bodies within the Southern Ocean receiving specific names are the Weddell Sea, Scotia Sea, Bellingshausen Sea, Amundsen Sea and Ross Sea (Figure 1.1).

The Southern Ocean is characterised by two major surface currents, namely the Antarctic Coastal Current and the Antarctic Circumpolar Current, which are driven by wind force. The Antarctic Coastal Current is a counter-clockwise current close to the Antarctic continent. As it approaches the Antarctic Peninsula from the east, the surface current is deflected in a northerly direction. At this stage, surface waters come under the influence of westerly winds, which create a circumpolar clockwise current, named the Antarctic Circumpolar Current (ACC). The ACC has a range of width of 200-1,000km (Laws, 1985). The ACC is the largest current in the world, with volume transport ranging from 98 to 154 Sv [1] and mean volume transport estimated at 134 Sv (Whitworth, 1983; Whitworth and Peterson, 1985; Rintoul et al., 2001; Cunningham et al., 2003).

---

[1] The sverdrup (Sv) is a unit of measure of volume transport. 1 Sv equals 1 million cubic metres per second.

The volume transport of the Antarctic Coastal Current is much smaller and estimated at 10 to 15 Sv (Fahrbach and Beckmann, 2010).

The ACC is a collection of circumpolar fronts, including the Subantarctic Front (SAF), the Polar Front (PF), the Southern ACC Front (SACCF) and the Southern Boundary of the ACC (SBACC) (Orsi et al., 1995; Figure 1.2). All fronts are dynamic boundaries with positions exhibiting seasonal and interannual variability (Moore et al., 1999; Thorpe et al., 2002; Sokolov and Rintoul, 2009). At the Polar Front, northward flowing Antarctic surface water meets southward flowing water from the three largest oceans on our planet, i.e. the Atlantic, Pacific and Indian oceans. The Polar Front connects the three major oceans and has a mean latitude of about 50˚S (Laws, 1985). This front shows a strong sea surface temperature gradient which can be detected by remotely sensed data (Moore et al., 1997).

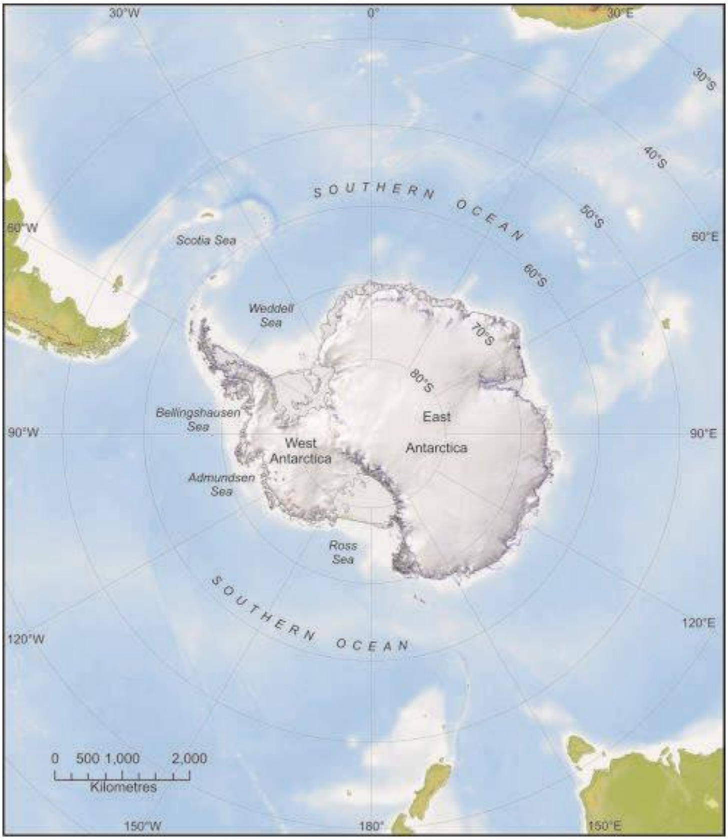


Figure 1.1. Map of the Southern Ocean and neighbouring areas (MAGIC department, British Antarctic Survey).

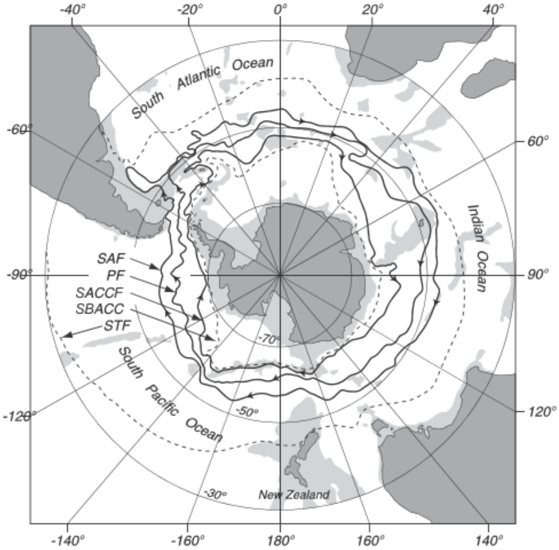


Figure 1.2. The major fronts in the Southern Ocean: STF = Subtropical Front, SAF = Subantarctic Front, PF = Polar Front, SACCF = Southern ACC Front and SBACC = Southern Boundary of the ACC. This figure is taken from Stewart (2008; his figure 13.13), which is a redrawn version of the original figure 11 of Orsi et al. (1995).

In addition to this horizontal water transport, vertical water transport in the form of strong upwelling occurs in the Southern Ocean. During upwelling, dense water mostly rises from a depth of roughly 2-3 km to the sea surface (Morrison et al., 2015). As much as 80% of deep water resurfaces in the Southern Ocean (Talley, 2013). Upwelling mainly occurs south of the ACC and near the coast. The upwelling water is rich in silica, iron and phosphate, which are nutrients needed for phytoplankton blooms (Ito et al., 2005).

One of the most prominent physical processes in the Southern Ocean is the seasonal melt and formation of sea ice. Maximum sea ice cover in winter is about 17 million km^2, while ice melting reduces the sea ice area to approximately 4 million km^2 in the austral summer (Zwally, 2002; Figure 1.3).

The ice melting leads to the formation of the marginal ice zone, defined (e.g. Arrigo et al., 1998) as the area where sea ice was present at the beginning of the month, but not at the end. The melt water in the marginal ice zone, being less dense than sea water because of its lower salinity, is found in a relatively stable layer at the sea water surface. On top of this, ice algae formerly trapped inside the ice are released during the melting process. The greater vertical water stability, together with the release of algae, creates algal blooms near the sea ice edge (e.g. Smith and Nelson, 1986). Therefore, the profound seasonal reduction in sea ice area is the engine of the sea ice ecosystem through its positive effect on primary productivity.

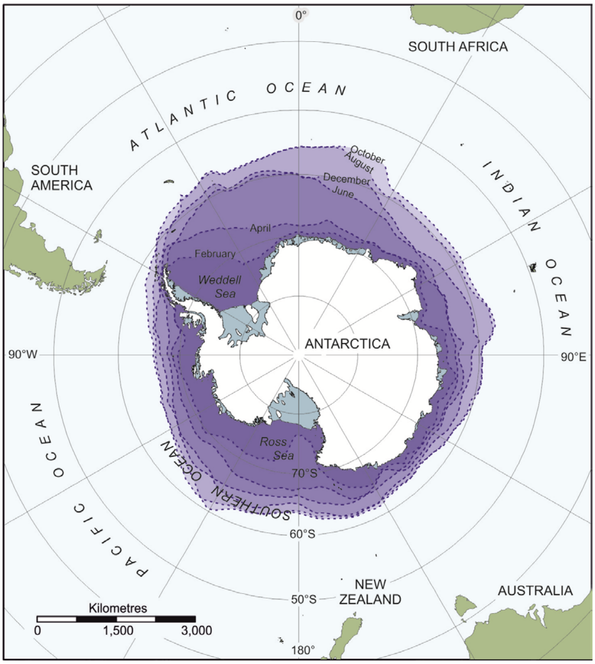


Figure 1.3. Average sea ice extent by month in the Southern Ocean (MAGIC department, British Antarctic Survey).

The extreme seasonality of the Southern Ocean is also expressed by its primary production. Daily primary production averaged over all Southern Ocean waters increases from about 60 mg C m^{-2} day^{-1} in August to an annual peak in December ranging from 325 to 425 mg C m^{-2} day^{-1}, after which it declines again in January. In general, daily primary production peaks about a month later (January – February) in the marginal ice zone than in the open ocean, since it takes time for the phytoplankton blooms to fully develop in the newly formed ice-free waters of the marginal ice zone (Arrigo et al., 2008).

Despite the surface waters being rich in available nitrate and phosphate, chlorophyll concentrations remain low and generally do not exceed 0.50 mg m^{-3} in most of the Southern Ocean (Comiso et al., 1993, Moore and Abbott, 2000). This makes the Southern Ocean the largest high-nutrient low-chlorophyll (HNLC) region in the world (Minas and Minas, 1992). Martin (1990) formulated the iron-hypothesis, which states that productivity of phytoplankton in the Southern Ocean is limited by deficiency of the trace nutrient iron. Intense phytoplankton blooms, with chlorophyll concentrations > 1.0 mg m^{-3}, regularly develop close to coastal regions and downstream of islands, where the dissolved iron from shelf sediments and glacial melt alleviates the HNLC conditions (Sullivan et al., 1993; Moore and Abbott, 2000; Borrione and Schlitzer, 2013). For instance, north of South Georgia, an island in the southwest Atlantic, large phytoplankton blooms with chlorophyll-*a* concentrations often exceeding 10 mg m^{-3} develop every year (Korb et al., 2004).

The International Whaling Commission, the international body charged with the conservation of whales and the management of whaling, divided the Southern Ocean into six Management Areas (Figure 1.4). These areas were mainly based on catch data, together with some sightings and markings data (Donovan, 1991).

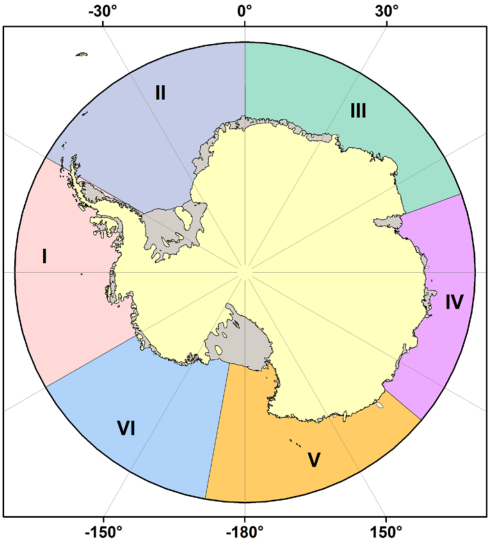


Figure 1.4. IWC Management Areas in the Southern Ocean (Mackintosh, 1942; Donovan, 1991).

Baleen whale species in the Southern Ocean

The order Cetacea consists of three groups of marine mammals, namely whales, dolphins and porpoises. Cetaceans are unrelated to the two other marine mammal groups, namely the sirenians (manatees and dugongs) and the pinnipeds (seals, sea lions and walruses). Sirenians are most closely related to elephants, while land carnivores (such as dogs and bears) are the closest relatives of pinnipeds. In contrast, cetaceans are most closely related to artiodactyls (even-toed ungulates) (Thewissen et al., 2009). Hippopotamuses are thought to be the closest living relatives of cetaceans (Nikaido et al., 1999; Gatesy and O'Leary, 2001).

Cetaceans originated approximately 50 million years ago (Milinkovitch and Thewissen, 1997). All modern cetaceans are obligate aquatic mammals: they cannot survive outside the water. However, paleontologists showed that the early cetaceans were amphibious, and that these whales evolved from early terrestrial artiodactyls (Gingerich et al., 2001; Thewissen et al., 2009). The fossil remains of the artiodactyl *Indohyus*, the closest relative to cetaceans found thus far, were discovered in the Himalaya mountains near the border between India and Pakistan. *Indohyus* was the size of a cat and resembled a small deer, as it had a long snout, long tail and long slender limbs (Thewissen et al., 2007, 2009).

All living cetaceans can be classified into the suborders Odontoceti (toothed whales, including dolphins and porpoises) and Mysticeti (baleen whales). These two suborders appeared about 35 million years ago (Fordyce, 2009). Odontocetes and mysticetes differ in various ways. Only odontocetes use echolocation for prey detection. In contrast to odontocetes, mysticetes do not possess teeth. Instead, mysticetes use baleen plates to filter small prey from the water. Furthermore, odontocetes have one blowhole, whereas mysticetes possess two blowholes. The sperm whale (*Physeter macrocephalus*), killer whale (*Orcinus orca*) and southern bottlenose whale (*Hyperoodon planifrons*) are examples of toothed whale species that can be encountered in the Southern Ocean.

Eight baleen whale species spend part of their life cycle in the Southern Ocean. These species are: Antarctic minke whale (*Balaenoptera bonaerensis*), dwarf minke whale (subspecies of the common minke whale, *B. acutorostrata*), humpback whale (*Megaptera novaeangliae*), blue whale (*B. musculus,* mainly the Antarctic blue whale, *B. musculus intermedia*), fin whale (*B. physalus*), sei whale (*B. borealis*), southern right whale (*Eubalaena australis*) and pygmy right whale (*Caperea marginata*). As minke whales, humpback whales and fin whales are the three species of interest within the other chapters of this thesis (Figure 1.5), this section will only provide information on these three species.

Distribution and migration

Antarctic and dwarf minke whales

Most species of baleen whales found in the Southern Ocean seasonally migrate between low-latitude winter breeding grounds and high-latitude summer feeding grounds. Baleen whales generally arrive in the Southern Ocean from December onwards. Seasonal migration is less well-defined for Antarctic minke whales than for most other baleen whales. Direct evidence of seasonal migration by minke whales consists of 'Discovery marks' recovered during the 1980s from two whales tagged in the Southern Ocean during previous decades. The whales were caught near Brazil, with sixty latitudinal degrees between the marking and recovery locations for one 'Discovery mark' (from 69°S to 6°S) (Buckland and Duff, 1989). In addition to this, the analysis of more than 7,000 mitochondrial and microsatellite DNA profiles revealed that a single Antarctic minke whale occurred in the Arctic in 1996 (Glover et al., 2010).

Breeding grounds for minke whales are dispersed and primarily located between 0-20°S in open waters (IWC, 1991; Kasamatsu et al., 1995; Zerbini et al., 1997; Best, 2007). Antarctic minke whales have been sighted within the pack ice region in austral winter during many surveys (e.g. Taylor, 1957; Ensor, 1989; Ribic et al., 1991; van Franeker, 1992; Thiele and Gill, 1999; Thiele et al., 2004). Furthermore, not all individuals may seasonally migrate, as Antarctic minke whales appear to occupy temperate waters of the south-western Indian Ocean throughout the year (Best, 2007). However, it is expected that most Antarctic minke whales have reached the Southern Ocean in January (Kasamatsu et al., 1995; Best, 2007).

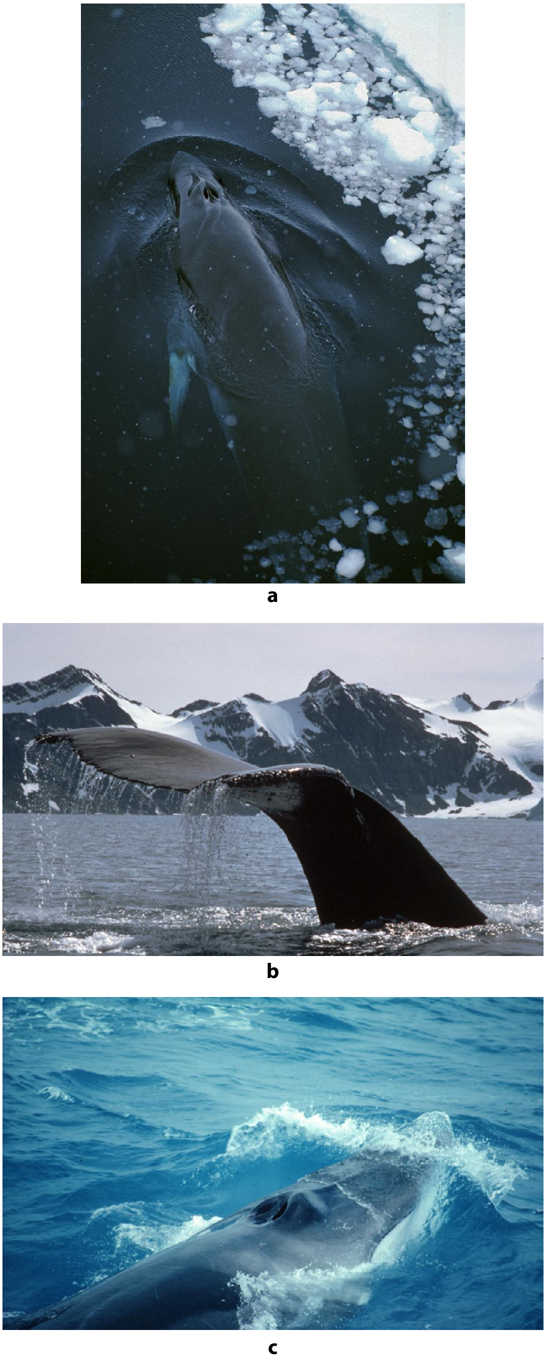


Figure 1.5. The three baleen whale species of interest for this thesis: a) Antarctic minke whale (© Roger Kidd, British Antarctic Survey), b) humpback whale (© Jeremy Colman, British Antarctic Survey), c) fin whale (© Tony Martin, British Antarctic Survey).

The migration patterns for dwarf minke whales are still largely unknown, as direct evidence of migration has not been reported. Individuals were exclusively sighted in the Southern Ocean between December and March, although this may largely reflect the high level of sighting effort during these months. Some reported sightings of dwarf minke whales were made off Brazil at 23°S in January. From this, Best (2007) suggested that not all dwarf minke whales may seasonally migrate, as some individuals stay in mid-low latitude waters during summer.

Humpback whales

The case for seasonal migration of baleen whales in the Southern Hemisphere is best documented for humpback whales via recovery of 'Discovery marks' (Rayner, 1940; Dawbin, 1966 and references therein), photo-identification (Stone et al., 1990; Gill and Burton, 1995; Garrigue et al., 2002; Stevick et al., 2004; Rasmussen et al., 2007), genetic analysis (Caballero et al., 2001; Engel et al., 2008) and satellite tagging (Zerbini et al., 2006). The IWC recognises seven breeding stocks for humpback whales (BS, named BSA through BSG) with whales showing seasonal migration to the Southern Ocean (IWC, 1998; Engel and Martin, 2009). Feeding grounds in the Southern Ocean have been identified for all breeding stocks, although this is still the focus for discussion (Leaper et al., 2008). Analysis of humpback whale catch data revealed a highly structured overall migration pattern in terms of timing of various groups characterised by gender and life history (Dawbin, 1966). Newly pregnant and resting females are generally the first to migrate southbound to the feeding grounds, followed by immature whales of both sexes, mature whales and lastly females in early lactation. Late lactating females are the first to leave the Southern Ocean for migration to the breeding grounds, followed by immatures, mature whales, resting females and late pregnant females.

Fin whales

Migration patterns of fin whales are the least known, compared to migration patterns of humpback and minke whales in the Southern Hemisphere. Fin whales seasonally migrate between Antarctic feeding areas in austral summer and lower latitudes in winter months, the latter situated in all oceans between 20 and 35˚S (Leatherwood and Reeves, 1983; Chapman, 1974). Like humpback whales, timing of migration differs by sexual class: pregnant females generally are the first group to arrive at and depart again from the Antarctic feeding grounds (Mackintosh, 1965; Mizroch et al., 1984). Thus far, fin whale calls were only detected from February to July by acoustic recording packages that were deployed year-round, which suggests that these whales may leave the Southern Ocean during austral winter (Širović et al., 2004, 2009).

Diet

Antarctic minke whales

Antarctic minke whales mostly feed on krill in the Southern Ocean, especially on Antarctic krill, *Euphausia superba* (Nemoto, 1959, 1970; Bushuev, 1986, 1991; Kawamura, 1980, 1994; Kato et al., 1989; Ichii and Kato, 1991; Ichii et al., 1998; Tamura and Konishi, 2009), which is by far the most abundant species. Although Antarctic krill is the dominant prey item for Antarctic minke whales in most regions, other krill species can be important secondary or even primary prey in some regions. Stomachs of Antarctic minke whales taken between 35°E-145°W in the Southern Ocean (management Areas III-East, IV, V and VI-West) revealed that Antarctic krill constituted between 85 and 100% of stomach contents weight (Tamura and Konishi, 2009). Ice krill, *Euphausia crystallorophias*, can be an important food item in shallow waters on the coastal shelf. For instance, *E. crystallorophias* was the only species found in 23 out of 38 non-empty stomachs of whales taken in Prydz Bay, between 67.5˚-69.2˚S and 73.5˚-77.3˚E (Bushuev, 1986). Furthermore, ice krill constituted 2.7 and 11.5% of stomach contents by weight, respectively, in Areas IV and V (Tamura and Konishi, 2009). In these Areas, ice krill were mainly found in whales taken in relatively shallow waters, in Prydz Bay and on the Ross Sea continental shelf (Tamura and Konishi, 2009). In the same study, *Thysanoessa macrura*, another krill species, formed the largest proportion of stomach weight, 6.8%, in Area VI-West (between 170 and 145°W). This krill species was also found in ~10-40% of stomachs of Antarctic baleen whales taken between 140-80°W (Areas VI and I, note that these numbers refer to rate of occurrence of *T. macrura* in whale stomachs instead of stomach contents weight) (Nemoto and Nasu, 1958; Nemoto, 1959). In contrast, between 105 and 115°E in the Southern Ocean, Antarctic krill was the only prey species found in stomachs of minke whales sampled in the ice-edge zone. In the offshore zone, this krill species still constituted 94% of stomach contents weight, although *T. macrura* was found more frequently than *E. superba* in net samples. This suggests that minke whales may selectively feed on *E. superba* in the Antarctic (Ichii and Kato, 1991). Other krill species occasionally found in stomachs of Antarctic minke whales included *Euphausia frigida* (Tamura and Konishi, 2009) and *Euphausia spinifera* (Ohsumi et al., 1970). Furthermore, other prey occasionally eaten by minke whales included the copepod species *Calanus tonsus*, the amphipod *Parathemisto gaudichaudi* and several fish species including *Myctophid* sp., *Notothenia* sp. and *Pleuragramma antarcticum* (Ohsumi et al., 1970; Bushuev, 1986, 1991; Tamura and Konishi, 2009). The latter fish species, *Pleuragramma antarcticum,* was the dominant prey item for some minke whales caught on the southeast part of the continental shelf in the Ross Sea in 1990/91(Ichii et al., 1998). In addition, small amounts of myctophid fish identified as *Kreffichthys anderssoni* were found in 13 out of 16 examined stomachs of dwarf minke whales (Kato and Fuyise, 2000).

Dominant length classes of krill eaten by minke whales vary per region and season. Both male and female minke whales taken in the Antarctic predominantly had small (10-20mm) to medium-sized (20-40mm) krill in their stomachs (Ohsumi et al., 1970). The dominant size class varied from 21 to 53mm in a study by Ichii et al. (1998), where Antarctic krill smaller than 30mm were found in most of Area V, except for the continental shelf in the Ross Sea. In the latter region, the dominant size class varied from 43 to 49mm. Considerable variability in dominant size class of krill in minke whale stomachs was also reported by Bushuev (1986), with dominant size classes ranging from 24-32mm to 40-52mm. Despite differences in krill size, the role of size selectivity in prey consumption is not well understood (but see Santora et al., 2010).

Humpback whales

Antarctic krill forms the staple diet for humpback whales foraging in the Southern Ocean. This krill species was exclusively found in 33 non-empty stomachs of humpback whales taken at South Georgia between 1925 and 1931. Examination of four whale stomachs revealed that the length of consumed krill ranged from 15 to 60mm, with dominant krill size classes between 25 and 50mm (Matthews, 1938). All seven non-empty stomachs of humpback whales taken in the Antarctic only contained unidentified krill, euphausiids (Nemoto, 1970). *Thysanoessa macrura* was also eaten by humpback whales taken between 130-110°W (Nemoto and Nasu, 1958), and a few fish were occasionally found that were possibly swallowed accidentally (Gaskin, 1972). Both Antarctic minke whales and humpback whales were rarely seen nearby longline vessels targeting Patagonian toothfish (*Dissostichus eleginoides*), suggesting that these whales do not preferentially feed on this fish species either (Kock et al., 2006). Being a main prey species, the distribution and aggregation patterns of Antarctic krill are likely to be a key determinant of humpback whale distribution (Nowacek et al., 2011).

Fin whales

Fin whales in the Southern Ocean are thought to almost exclusively feed on krill, with fish remains present in fewer than 1% of the more than 16,000 non-empty stomachs of fin whales taken between 1961 and 1965 by the Japanese whaling fleet (Kawamura et al., 1994; Nemoto, 1970). Fin whales preferably feed on medium-sized krill between 30 and 40mm (Nemoto, 1970), although like other mysticetes, they are likely to be opportunistic feeders and exploit large krill aggregations.

Antarctic krill

Since Antarctic krill (*Euphausia superba*) is the most important prey item of baleen whales foraging in the Southern Ocean, this section will focus on this particular krill species. A short summary of krill life history, together with an overview of the impact of sea ice on krill stocks follows.

Life history

Krill are generally divided into three groups: larvae, juveniles and adults (Marr, 1962), with twelve larval stages identified by Fraser (1936). Most krill spawning takes place between December and March, although timing and duration of spawning can vary substantially between different areas of the Southern Ocean (Spiridonov, 1995). Adult females migrate to offshore areas where they lay their eggs which then sink and hatch at depths of 500 to 1000 meters (Fraser, 1936; Marr, 1962; Hempel and Hempel, 1986). The larvae swim upwards and reach the surface water in about 30 days after the eggs were laid. By that time they reach the first feeding stage and need to find food within six days in order to survive (Nicol, 2006). In January/February, krill biomass is at its peak, as the krill stock consists of larvae, juveniles and adults. After March, the end of the spawning season, krill biomass declines sharply (Siegel, 2005).

In winter, pack ice extends across the Southern Ocean and becomes an important habitat for larval krill. The krill larvae live in close association with the sea ice and develop and grow by feeding on the community of microorganisms growing on the underside of the ice (Nicol, 2006). The winter diet of larval krill varies by region: heterotrophic organisms such as small copepods and protozoans are important dietary items for larval krill in the Lazarev Sea, whereas winter diet is mostly autotrophic for krill larvae in the waters west of the Antarctic Peninsula (Meyer et al., 2009; Meyer, 2012). At the end of the austral winter and through early spring, krill larvae reach the juvenile stage. During the winter to spring transition, heterotrophic flagellates and detrital material are important dietary components for both larval and juvenile krill in East Antarctica (Virtue et al., 2016).

It takes until spring in the second year after hatching for juveniles to reach full adult size and become mature. Adult krill feed on phytoplankton blooms that occur at the sea ice edge. In summer, adults migrate to the continental shelf break, whereas juveniles are found in more inshore waters (Nicol, 2006). Sub-adult and adult krill are dispersed across the Southern Ocean, including to areas which do not have winter pack ice cover, such as the waters near South Georgia. These adults feed on phytoplankton blooms in open water, but they can also feed on other prey items, including tintinnids and heterotrophic dinoflagellates (Schmidt et al., 2006). Furthermore, adult krill were found at depths between 200 and 2000 m in the Scotia Sea and were found on or near the seabed year-round and throughout their circumpolar range. Krill were feeding on detritus and copepods in these deeper waters and the benthic environment (Schmidt et al., 2011). Adult krill can survive the winter without or with little feeding. Laboratory experiments confirmed several overwintering mechanisms, including a reduction in metabolic activity of krill, slow growth or shrinkage and use of lipid reserves. These changes were triggered by food shortage only, and not by a changing light regime (Auerswald et al., 2015).

Impact of sea ice on krill stocks

Sea ice in part determines the life cycle of Antarctic krill and there is growing evidence of the importance of sea ice dynamics on krill biomass dynamics in the Southern Ocean. Siegel and Loeb (1995) reported a significant positive correlation between krill recruitment and the timing of sea ice retreat in the Elephant Island area between 1977 and 1994. Years with relatively late sea ice retreat corresponded with high krill recruitment in this region. Furthermore, strong recruitment of krill happened in years with higher than average ice cover (Siegel and Loeb, 1995). For waters west of the Antarctic Peninsula, years with poor recruitment success of krill had either an early sea ice retreat or late sea ice advance (Quetin and Ross, 2003). Low sea ice coverage and short sea ice duration can lead to late krill spawning (in March), possibly as a result of late krill gonadal development due to food deprivation (Siegel and Loeb, 1995; Siegel, 2005). Larvae that are born late in the spawning season have only a shorter portion of the summer season to grow and develop. Therefore, late krill spawning may result in higher probability of year-class failure (Siegel and Loeb, 1995).

Krill larvae feed on the sea ice community, which comprises microorganisms of several taxa including diatoms, dinoflagellates and foraminifera (Daly, 1990). The current view is that dense and long sea ice cover increases the availability of food for krill larvae required to successfully endure the winter season (Siegel and Loeb, 1995). Furthermore, the ice cover protects the krill larvae against predators. The combined effect of higher food availability and more protection from predators during winter leads to a higher immature krill biomass and, consequently, to higher recruitment in the year following a year with large sea ice coverage (Siegel and Loeb, 1995). Loeb et al. (1997) hypothesised that two or more succeeding winters with extensive and long sea ice coverage may amplify the positive effects on krill recruitment. Atkinson et al. (2004) studied krill densities in the southwest Atlantic region in summertime between 1926 and 2003, reporting positive correlations between krill densities in summertime and both the duration and extent of sea ice in the previous winter in the same area. In contrast to krill larvae, adult krill are able to store energy from phytoplankton blooms in autumn. Therefore, adult krill may benefit from a longer open water season, enabling them to increase their energy reserves before the winter starts, which may lead to a better chance at winter survival. However, krill recruitment, driven by the winter survival of larval and juvenile krill, is probably the population parameter most sensitive to environmental change (Flores et al., 2012).

Research questions and outline of this thesis

The main objective of this thesis is to investigate the relationships between baleen whale density and the physical-biological environment. In this thesis, density of baleen whales is defined as the number of baleen whales per km^2. Absolute abundance of baleen whales is the number of whales in a specific area, for instance the Scotia Sea, at a specific time. Density of baleen whales was estimated from visual observer data obtained during shipboard surveys, which were only conducted in open waters. Antarctic minke whales are the most abundant and best surveyed whale species of the Southern Ocean, and hence are selected as main study species for this thesis.

The estimates of whale density presented in this thesis are not corrected for availability bias, which is a negative bias due to a proportion of the animal population not being available for detection. This happens for instance when whales are submerged while the survey vessel passes. The availability bias due to diving activity is likely to be small for the three baleen whale species of interest for this thesis (Branch and Butterworth, 2001; Williams et al. 2006). However, for sperm whales and southern bottlenose whales, who can dive for long periods, availability bias is larger and should be taken into account when estimating density or abundance (Barlow, 1999).

For this thesis, I identified the most important aspects of the environment that are underlying the distributions of various baleen whale species, as suggested by spatial models of whale density in relation to environmental variables. Given the extreme seasonality of the Southern Ocean, of the krill, and of the seasonal presence of baleen whales, it can be assumed that density distributions of baleen whales are likely to be largely defined by baleen whale foraging behaviour and thus by aspects of the environment indirectly or directly related to food availability. The overarching hypothesis for this thesis is that whale density is higher close to transition zones, notably the sea ice edge, continental shelf and frontal systems, since these transition zones often show enhanced productivity of both phytoplankton and krill.

The following research questions are addressed in this thesis:

- Which aspects of the environment are related to density of Antarctic minke whales at the regional scale? This scale is defined as the area surveyed during a specific season (Chapter 2).
- How can the various relationships between density of Antarctic minke whales and the environment be characterised (Chapter 2)?
- How does sea ice affect the spatial and temporal variability in density of Antarctic minke whales in summertime (Chapter 3)?
- Which aspects of the environment are related to the density distributions of Antarctic minke whales, humpback whales and fin whales in the Scotia Sea and to what extent do their distributions differ (Chapter 4)?

Chapter 2 describes the spatial models used to analyse density distributions of Antarctic minke whales from sightings data collected during three circumpolar sets of surveys. The data used in this analysis came from a study that investigated only limited aspects of the physical environment and there was no sampling of zooplankton or other biological variables. To provide more information on the environment, a series of remotely sensed datasets were analysed. Environmental variables considered to be important drivers of minke whale density were assumed to be related to areas of high productivity. This is under the assumption that density distributions of Antarctic minke whales in various regions are mainly determined by their foraging behaviour. Chapter 3 examines the spatial and temporal variability in density of Antarctic minke whales, based on the spatial models described in Chapter 2. Circumpolar prediction maps of mean density of Antarctic minke whales are shown in Chapter 3. Furthermore, I investigated if, and to what extent, differences in mean density of minke whales could be explained by the amount of sea ice cover and seasonal change therein. Detailed relationships between density of baleen whales and the physical-biological environment within the Scotia Sea ecosystem are studied in Chapter 4. In addition to remotely sensed datasets, for this analysis I was able to consider in situ datasets representing both the physical environment and density distributions of Antarctic krill. Finally, Chapter 5 discusses how baleen whales may possibly respond to future trends in the sea ice environment, given what we can infer from the spatial models developed for this thesis.

REFERENCES

Arrigo, K.R., van Dijken, G.L. and Bushinsky, S. 2008. Primary production in the Southern Ocean, 1997-2006. *J. Geophys. Res.* 113(C8), C08004.

Arrigo, K.R., Worthen, D., Schnell, A. and Lizotte, M.P. 1998. Primary production in Southern Ocean waters. *J. Geophys. Res.* 103(C8): 15,587-15,600.

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

Auerswald, L., Meyer, B., Teschke, M., Hagen, W. and Kawaguchi, S. 2015. Physiological response of adult krill, *Euphausia superba*, to long-term starvation. *Pol. Biol.* 38: 763-780.

Barlow, J. 1999. Trackline detection probability for long-diving whales. pp. 209-221. *In*: G.W. Garner, S.C. Amstrup, J.L. Laake, B.F.J. Manly, L.L. McDonald and D.G. Robertson (eds.) *Marine mammal survey and assessment methods.* Balkema, Rotterdam. 287pp.

Bejder, M., Johnston, D.W., Smith, J., Friedlaender, A. and Bejder, L. 2016. Embracing conservation success of recovering humpback whale populations: evaluating the case for downlisting their conservation status in Australia. *Mar. Pol.* 66: 137-141.

Best, P.B. 2007. *Whales and dolphins of the southern African subregion*. Cambridge University Press, Cape Town. 338pp.

Borrione, I. and Schlitzer, R. 2013. Distribution and recurrence of phytoplankton blooms around South Georgia, Southern Ocean. *Biogeosciences* 10: 217-231.

Branch, T.A. and Butterworth, D.S. 2001. Southern Hemisphere minke whales: standardised abundance estimates from the 1978/79 to 1997/98 IDCR-SOWER surveys. *J. Cetacean Res. Manage.* 3(2): 143-174.

Branch, T.A., Matsuoka, K. and Miyashita, T. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. *Mar. Mamm. Sci.* 20(4): 726-754.

Buckland, S.T. and Duff, E.I. 1989. Analysis of the Southern Hemisphere minke whale mark-recovery data. *Rep. int. Whal. Commn.* Special issue 11: 121-143.

Bushuev, S.G. 1986. Feeding of minke whales, *Balaenoptera acutorostrata*, in the Antarctic. *Rep. int. Whal. Commn.* 36: 241-245.

Bushuev, S.G. 1991. Distribution and feeding of minke whales in Antarctic Area I. *Rep. int. Whal. Commn.* 41: 303-312.

Caballero, S., Hamilton, H., Jaramillo, C., Capella, J., Flórez-González, L., Olavarría, C., Rosenbaum, H., Guhl, F. and Baker, C.S. 2001. Genetic characterization of the Colombian Pacific coast humpback whale population using RAPD and mitochondrial DNA sequences. *Mem. Queensl. Mus.* 47(2): 459-464.

Chapman, D.G. 1974. Status of Antarctic rorqual stocks. pp. 218-238. *In*: W.E. Schevill (ed.) *The whale problem: a status report*. Harvard University Press, Cambridge. 419pp.

Comiso, J.C., McClain, C.R., Sullivan, C.W., Ryan, J.P. and Leonard, C.L. 1993. Coastal zone color scanner pigment concentrations in the Southern Ocean and relationships to geophysical surface features. *J. Geophys. Res.* 98(C2): 2419-2451.

Cunningham, S.A., Alderson, S.G., King, B.A. and Brandon, M.A. 2003. Transport and variability of the Antarctic Circumpolar Current in Drake Passage. *J. Geophys. Res.* 108(C5): 8084.

Daly, K.L. 1990. Overwintering development, growth, and feeding of larval *Euphausia superba* in the Antarctic marginal ice zone. *Limnol. Oceanogr.* 35(7): 1564-1576.

Dawbin, W.H. 1966. The seasonal migratory cycle of humpback whales. pp. 145-170. *In*: K.S. Norris (ed.) *Whales, dolphins and porpoises*. University of California Press, Berkeley, CA. 789pp

Deacon, G.E.R. 1982. Physical and biological zonation in the Southern Ocean. *Deep-Sea Res.* 29: 1-15.

Donovan, G.P. 1991. A review of IWC stock boundaries. *Rep. int. Whal. Commn.* (special issue) 13: 39-68.

Engel, M.H., Fagundes, N.J.R., Rosenbaum, H.C., Leslie, M.S., Ott, P.H., Schmitt, R., Secchi, E., Dalla Rosa, L. and Bonatto, S.L. 2008. Mitochondrial DNA diversity of the Southwestern Atlantic humpback whale (*Megaptera novaeangliae*) breeding area off Brazil, and the potential connections to Antarctic feeding areas. *Conserv. Genet.* 9: 1253-1262.

Engel, M.H. and Martin, A.R. 2009. Feeding grounds of the western South Atlantic humpback whale population. *Mar. Mamm. Sci.* 25(4): 964-969.

Ensor, P. H. 1989. Minke whales in the pack ice zone, East Antarctica, during the period of maximum annual ice extent. *Rep. int. Whal. Commn.* 39: 219-225.

Fahrbach, E. and Beckmann, A. 2010. Weddell Sea circulation. pp. 367-374. *In*: J.H. Steele, S.A. Thorpe and K.K. Turekian (eds.) *Ocean currents: a derivative of the encyclopedia of ocean sciences.* Academic Press, London. 627pp.

Flores, H., Atkinson, A., Kawaguchi, S., Krafft, B.A., Milinevsky, G., Nicol, S., Reiss, C., Tarling, G.A., Werner, R., Bravo Rebolledo, E., Cirelli, V., Cuzin-Roudy, J., Fielding, S., Groeneveld, J.J., Haraldsson, M., Lombana, A., Marschoff, E., Meyer, B., Pakhomov, E.A., Rombolá, E., Schmidt, K., Siegel, V., Teschke, M., Tonkes, H., Toullec, J.Y., Trathan, P.N., Tremblay, N., van de Putte, A.P., van Franeker, J.A. and Werner, T. 2012. Impact of climate change on Antarctic krill. *Mar. Ecol. Prog. Ser.* 458: 1-19.

Fordyce, R.E. 2009. Cetacean evolution. pp. 201-207. *In*: W.F. Perrin, B. Würsig and J.G.M. Thewissen (eds). *Encyclopedia of marine mammals*. Academic Press, London. 1352pp.

Fraser, F.C. 1936. On the development and distribution of the young stages of krill (*Euphausia superba*). *Discovery Rep.* 14: 1-192.

Garrigue, C., Aguayo, A., Amante-Helweg, V.L.U., Baker, C.S., Caballero, S., Clapham, P., Constantine, R., Denkinger, J., Donoghue, M., Flórez-González, L., Greaves, J., Hauser, N., Olavarría, C., Pairoa, C., Peckham, H. and Poole, M. 2002. Movements of humpback whales in Oceania, South Pacific. *J. Cetacean Res. Manage.* 4(3): 255-260.

Gaskin, D.E. 1972. Whales, dolphins and seals: with special reference to the New Zealand region. Heinemann Educational Books, London. 200pp.

Gatesy, J. and O'Leary, M.A. 2001. Deciphering whale origins with molecules and fossils. *Tr. Ecol. Evol.* 16(10): 562-570.

Gill, P.C. and Burton, C.L.K. 1995. Photographic resight of a humpback whale between western Australia and Antarctic Area IV. *Mar. Mamm. Sci.* 11(1): 96-100.

Gingerich, P.D., ul Haq, M., Zalmout, I.S., Khan, I.H. and Malkani, M.S. 2001. Origin of whales from early artiodactyls: hands and feet of Eocene Protocetidae from Pakistan. *Science* 293: 2239-2242.

Glover, K.A., Kanda, N., Haug, T., Pastene, L.A., Øien, N., Goto, M., Seliussen, B.B. and Skaug, H.J. 2010. Migration of Antarctic minke whales to the Arctic. *PloS ONE* 5(12): e15197.

Hempel, I. and Hempel, G. 1986. Field observations on the developmental ascent of larval *Euphausia superba* (Crustacea). *Pol. Biol.* 6: 121-126.

Ichii, T. and Kato, H. 1991. Food and daily food consumption of southern minke whales in the Antarctic. *Polar Biol.* 11: 479-487.

Ichii, T., Shinohara, N., Fujise, Y., Nishiwaki, S. and Matsuoka, K. 1998. Interannual changes in body fat condition index of minke whales in the Antarctic. *Mar. Ecol. Prog. Ser.* 175: 1-12.

Ito, T., Parekh, P., Dutkiewicz, S. and Follows, M.J. 2005. The Antarctic Circumpolar Productivity Belt. *Geophys. Res. Lett.* 32: L13604.

IWC. 1991. Annex E - Report of the sub-committee on Southern Hemisphere minke whales. *Rep. int. Whal. Commn.* 41: 113-131.

IWC. 1998. Annex G - Report of the sub-committee on comprehensive assessment of Southern Hemisphere humpback whales. *Rep. int. Whal. Commn.* 42: 170-182.

Kasamatsu, F., Nishiwaki, S. and Ishikawa, H. 1995. Breeding areas and southbound migrations of southern minke whales *Balaenoptera acutorostrata*. *Mar. Ecol. Prog. Ser.* 119: 1-10.

Kato, H. and Fuyise, Y. 2000. Dwarf minke whales: morphology, growth and life history with some analyses on morphometric variation among the different forms and regions. Paper SC/52/OS3 presented to the IWC Scientific Committee, June 2000 (unpublished). 30pp. [paper available from the Office of the IWC].

Kato, H., Hiroyama, H. Fujise, Y. and Ono, K. 1989. Preliminary report of the 1987/88 Japanese feasibility study of the special permit proposal for southern hemisphere minke whales. *Rep. int. Whal. Commn.* 39: 235-248.

Kawamura, A. 1980. A review of food of balaenopterid whales. *Sci. Rep. Whales Res. Inst.* 32: 155-197.

Kawamura, A. 1994. A review of baleen whale feeding in the Southern Ocean. *Rep. int. Whal. Commn.* 44: 261-271.

Kock, K-H., Purves, M.G. and Duhamel, G. 2006. Interaction between cetacean and fisheries in the Southern Ocean. *Polar Biol.* 29: 379-388.

Korb, R.E., Whitehouse, M.J. and Ward, P. 2004. SeaWiFS in the southern ocean: spatial and temporal variability in phytoplankton biomass around South Georgia. *Deep-Sea Res. II* 51: 99-116.

Laws, R.M. 1985. The ecology of the Southern Ocean. *American Scientist* 73(1): 26-40.

Leaper, R. Bannister, J.L., Branch, T.A, Clapham, P.J., Donovan, G.P., Matsuoka, K., Reilly, S. and Zerbini, A.N. 2008. A review of abundance, trends and foraging parameters of baleen whales in the Southern Hemisphere. Paper CCAMLR-IWC-WS-08/4 presented to the joint CCAMLR-IWC workshop to review input data for Antarctic marine ecosystem models, August 2008 (unpublished). 51pp. [paper available from the Office of the IWC].

Leaper, R. and Miller, C. 2011. Management of Antarctic baleen whales amid past exploitation, current threats and complex marine ecosystems. *Antarct. Sci.* 23(6): 503-529.

Leatherwood, S. and Reeves, R.R. 1983. *The Sierra Club handbook of whales and dolphins*. Sierra Club Books, San Diego. 302pp.

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

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. *Discovery Rep.* 22: 197-300.

Mackintosh, N.A. 1965. *The stocks of whales*. Fish. News (Books) Ltd., London. 232pp.

Marr, J.W.S. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discovery Rep.* 32: 33-464.

Martin, J.H. 1990. Glacial-interglacial CO_2 change: the iron hypothesis. *Paleoceanogr.* 5(1): 1-13.

Matthews, L.H. 1938. The humpback whale, *Megaptera nodosa*. *Discovery Rep.* 17: 7-92.

Meyer, B. 2012. The overwintering of Antarctic krill, *Euphausia superba*, from an ecophysiological perspective. *Polar Biol.* 35: 15-37.

Meyer, B., Fuentes, V., Guerra, C., Schmidt, K., Atkinson, A., Spahic, S., Cisewski, B, Freier, U., Olariaga, A. and Bathmann, U. 2009. Physiology, growth, and development of larval krill *Euphausia superba* in autumn and winter in the Lazarev Sea, Antarctica. *Limnol. Oceanogr.* 54(5): 1595-1614.

Milinkovitch, M.C. and Thewissen, J.G.M. 1997. Even-toed fingerprints on whale ancestry. *Nature* 388: 622-624.

Minas, H.J. and Minas, M. 1992. Net community production in “High Nutrient-Low Chlorophyll” waters of the tropical and Antarctic Oceans: grazing *vs* iron hypothesis. *Oceanologica Acta* 15(2): 145-162.

Mizroch, S.A., Rice, D.W. and Breiwick, J.M. 1984. The fin whale, *Balaenoptera physalus*. *Mar. Fish. Rev.* 46(4): 20-24.

Moore, J.K. and Abbott, M.R. 2000. Phytoplankton chlorophyll distributions and primary production in the Southern Ocean. *J. Geophys. Res.* 105(C12): 28,709-28,722.

Moore, J.K., Abbott, M.R. and Richman, J.G. 1997. Variability in the location of the Antarctic Polar Front (90°-20°W) from satellite sea surface temperature data. *J. Geophys. Res.* 102(C13): 27,825-27,833.

Moore, J.K., Abbott, M.R. and Richman, J.G. 1999. Location and dynamics of the Antarctic Polar Front from satellite sea surface temperature data. *J. Geophys. Res.* 104(C2): 3059-3073.

Morrison, A.K., Frölicher, T.L. and Sarmiento, J.L. 2015. Upwelling in the Southern Ocean. *Phys. Today* 68(1), 27-32.

Nemoto, T. 1959. Food of baleen whales with reference to whale movements. *Sci. Rep. Whales Res. Inst.* 14: 149-290.

Nemoto, T. 1970. Feeding patterns of baleen whales in the ocean. pp. 241-252. *In*: J.H. Steele (ed.) *Marine food chains*. Oliver and Boyd, Edinburgh. 552pp.

Nemoto, T. and Nasu, K. 1958. *Thysanoëssa macrura* as a food of baleen whales in the Antarctic. *Sci. Rep. Whales Res. Inst.* 13: 193-199.

Nicol, S. 2006. Krill, currents, and sea ice: *Euphausia superba* and its changing environment. *Bioscience* 56(2): 111-120.

Nicol, S., Worby, A. and Leaper, R. 2008. Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. *Mar. Freshw. Res.* 59: 361-382.

Nikaido, M., Rooney, A.P. and Okada, N. 1999. Phylogenetic relationships among cetartiodactyls based on insertions of short and long interspersed elements: hippopotamuses are the closest extant relatives of whales. *Proc. Natl. Acad. Sci. USA* 96: 10261-10266.

Nowacek, D.P., Friedlaender, A.S., Halpin, P.N., Hazen, E.L., Johnston, D.W., Read, A.J., Espinasse, B., Zhou, M. and Zhu, Y. 2011. Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. *PLoS ONE* 6(4): e19173.

Ohsumi, S., Masaki, Y. and Kawamura, A. 1970. Stock of the Antarctic minke whale. *Sci. Rep. Whales Res. Inst.* 22: 75-125.

Orsi, A.H., Whitworth III, T. and Nowlin Jr., W.D. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Res. I* 42(5): 641-673.

Quetin, L.B. and Ross, R.M. 2003. Episodic recruitment in Antarctic krill *Euphausia superba* in the Palmer LTER study region. *Mar. Ecol. Prog. Ser.* 259: 185-200.

Rasmussen, K., Palacios, D.M., Calambokidis, J., Saborío, M.T., Dalla Rosa, L., Secchi, E.R., Steiger, G.H., Allen, J.M. and Stone, G.S. 2007. Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biol. Lett.* 3(3): 302-305.

Rayner, G.W. 1940. Whale marking: progress and results to December 1939. *Discovery Rep.* 19: 245-284.

Ribic, C.A., Ainley, D.G. and Fraser, W.R. 1991. Habitat selection by marine mammals in the marginal ice zone. *Antarct. Sci.* 3(2): 181-186.

Rintoul, S.R., Hughes, C. and Olbers, D. 2001. The Antarctic Circumpolar Current system. *In*: G. Siedler, S. Griffies, J. Gould and J. Church (eds.) Ocean circulation and climate: a 21st century perspective. Academic Press, London. 904pp.

Rocha, Jr., R.C., Clapham, P.J. and Ivashchenko, Y.V. 2014. Emptying the oceans: a summary of industrial whaling catches in the 20th century. *Mar. Fish. Rev.* 76(4): 37-48.

Santora, J.A., Reiss, C.S., Loeb, V.J. and Veit, R.R. 2010. Spatial association between hotspots of baleen whales and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent predation. *Mar. Ecol. Prog. Ser.* 405: 255-269.

Schmidt, K., Atkinson, A., Petzke, K-J., Voss, M. and Pond, D.W. 2006. Protozoans as a food source for Antarctic krill, *Euphausia superba*: Complementary insights from stomach content, fatty acids and stable isotopes. *Limnol. Oceanogr.* 51(5): 2409-2427.

Schmidt, K., Atkinson, A., Steigenberger, S., Fielding, S., Lindsay, M.C.M., Pond, D.W., Tarling, G.A., Klevjer, T.A., Allen, C.S., Nicol, S. and Achterberg, E.P. 2011. Seabed foraging by Antarctic krill: Implications for stock assessment, bentho-pelagic coupling, and the vertical transfer of iron. *Limnol. Oceanogr.* 56(4): 1411-1428.

Siegel, V. 2005. Distribution and population dynamics of *Euphausia superba*: summary of recent findings. *Pol. Biol.* 29: 1-22.

Siegel, V. and Loeb, V. 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Mar. Ecol. Prog. Ser.* 123: 45-56.

Širović, A., Hildebrand, J.A., Wiggins, S.M., McDonald, M.A., Moore, S.E. and Thiele, D. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. *Deep-Sea Res. II* 51(17-19): 2327-2344.

Širović, A., Hildebrand, J.A., Wiggins, S.M. and Thiele, D. 2009. Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. *Mar. Mamm. Sci.* 25(1): 125-136.

Smith, Jr., W.O. and Nelson, D.M. 1986. Importance of ice edge phytoplankton production in the Southern Ocean. *Bioscience* 36(4): 251-257.

Sokolov, S., and Rintoul, S.R. 2009. Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts: 2. Variability and relationship to sea surface height. *J. Geophys. Res* 114: C11019.

Spiridonov, V.A. 1995. Spatial and temporal variability in reproductive timing of Antarctic krill (*Euphausia superba* Dana). *Pol. Biol.* 15: 161-174.

Stevick, P.T., Aguayo, A., Allen, J., Avila, I.C., Capella, J., Castro, C., Chater, K., Dalla Rosa, L., Engel, M.H., Félix, F., Flórez-González, L., Freitas, A., Haase, B., Llano, M., Lodi, L., Munoz, E., Olavarría, C., Secchi, E., Scheidat, M. and Siciliano, S. 2004. Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. *J. Cetacean Res. Manage.* 6(2): 109-113.

Stewart, R.H. 2008. *Introduction to physical oceanography*. Texas A&M University, College Station, Texas. 345 pp.

Stone, G.S., Flórez-Gonzalez, L. and Katona, S. 1990. Whale migration record. *Nature* 346: 705.

Sullivan, C.W., Arrigo, K.R., McClain, C.R., Comiso, J.C. and Firestone, J. 1993. Distributions of phytoplankton blooms in the Southern Ocean. *Science* 262: 1832-1837.

Talley, L.D. 2013. Closure of the global overturning circulation through the Indian, Pacific, and Southern Oceans: Schematics and transports. *Oceanography* 26(1): 80-97.

Tamura, T. and Konishi, K. 2009. Feeding habits and prey consumption of Antarctic minke whale (*Balaenoptera bonaerensis*) in the Southern Ocean. *J. Northw. Atl. Fish. Sci.* 42: 13-25.

Taylor, R.J.F. 1957. An unusual record of three species of whale being restricted to pools in Antarctic sea-ice. *Proc. Zool. Soc. Lond.* 129(3): 325-331.

Thewissen, J.G.M., Cooper, L.N., Clementz, M.T., Bajpai, S. and Tiwari, B.N. 2007. Whales originated from aquatic artiodactyls in the Eocene epoch of India. *Nature* 450: 1190-1195.

Thewissen, J.G.M., Cooper, L.N., George, J.C. and Bajpai, S. 2009. From land to water: the origin of whales, dolphins, and porpoises. *Evo. Edu. Outreach* 2: 272-288.

Thiele, D., Chester, E.T., Moore, S.E., Širovic, A., Hildebrand, J.A. and Friedlaender, A.S. 2004. Seasonal variability in whale encounters in the Western Antarctic Peninsula. *Deep-Sea Res. II* 51(17-19): 2311-2325.

Thiele, D. and Gill, P.C. 1999. Cetacean observations during a winter voyage into Antarctic sea ice south of Australia. *Antarct. Sci.* 11(1): 48-53.

Thorpe, S.E., Heywood, K.J., Brandon, M.A. and Stevens, D.P. 2002. Variability of the southern Antarctic Circumpolar Current front north of South Georgia. *J. Mar. Sys.* 37: 87-105.

van Franeker, J.A. 1992. Top predators as indicators for ecosystem events in the confluence zone and marginal ice zone of the Weddell and Scotia Seas, Antarctica, November 1988 to January 1989 (EPOS Leg 2). *Polar Biol.* 12: 93-102.

Virtue, P., Meyer, B., Freier, U., Nichols, P.D., Jia, Z., King, R., Virtue, J., Swadling, K.M., Meiners, K.M. and Kawaguchi, S. 2016. Condition of larval (furcilia VI) and one year old juvenile *Euphausia superba* during the winter-spring transition in East Antarctica. *Deep-Sea Res. II*. 131: 182-188.

Whitworth III, T. 1983. Monitoring the transport of the Antarctic Circumpolar Current at Drake Passage. *J. Phys. Oceanogr.* 13(11): 2045-2057.

Whitworth III, T. and Peterson, R.G. 1985. Volume transport of the Antarctic Circumpolar Current from bottom pressure measurements. *J. Phys. Oceanogr.* 15(6): 810-816.

Williams, R., Hedley, S.L. and Hammond, P.S. 2006. Modeling distribution and abundance of Antarctic baleen whales using ships of opportunity. *Ecology and Society* 11(1): 1. [online] URL: http://www.ecologyandsociety.org/vol11/iss1/art1/.

Zerbini, A.N., Andriolo, A., Heide-Jørgensen, M.P., Pizzorno, J.L., Maia, Y.G., VanBlaricom, G.R., DeMaster, D.P., Simões-Lopes, P.C., Moreira, S. and Bethlem, C. 2006. Satellite-monitored movements of humpback whales *Megaptera novaeangliae* in the Southwest Atlantic Ocean. *Mar. Ecol. Prog. Ser.* 313: 295-304.

Zerbini, A.N., Secchi, E.R., Siciliano, S. and Simões-Lopes, P.C. 1997. A review of the occurrence and distribution of whales of the genus *Balaenoptera* along the Brazilian coast. *Rep. int. Whal. Commn.* 47: 407-417.

Zwally, H.J., Comiso, J.C., Parkinson, C.L., Cavalieri, D.J. and Gloersen, P. 2002. Variability of Antarctic sea ice 1979-1998. *J. Geophys. Res.* 107(C5): 3041.

Generalised additive models to investigate environmental drivers of spatial density of Antarctic minke whales *(Balaenoptera bonaerensis)* in austral summer

Bas W.P.M. Beekmans
Jaume Forcada
Eugene J. Murphy
Hein J.W. de Baar
Ulrich V. Bathmann
Andrew H. Fleming

Published as:
Beekmans, B.W.P.M., Forcada, J., Murphy, E.J., de Baar, H.J.W., Bathmann, U.V. and Fleming, A.H. 2010. Generalised additive models to investigate environmental drivers of Antarctic minke whale (Balaenoptera bonaerensis) spatial density in austral summer. J. Cetacean Res. Manage. 11(2): 115-129.

Minor linguistic improvements were made to the published version.

2

ABSTRACT

There is a need to characterise the physical environment associated with the density of Antarctic minke whales in order to understand long-term changes in minke whale distribution and density in open waters of the Southern Ocean during austral summer months. To investigate environmental drivers of spatial density of Antarctic minke whales, we developed Generalised Additive Models (GAMs) based on line transect data collected for the International Decade of Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) programmes. The GAMs were fitted independently by survey year. Explained deviances ranged from 14.9% to 35.1%. Most models included covariates related to transition zones, such as distances to the continental shelf break and sea ice edge, both of which showed a predominantly negative relationship with whale density. This study suggests high variability in the relationships between Antarctic minke whale density and the environment. None of the selected covariates had a consistent qualitative relationship with density at either the circumantarctic or the regional scale. This in part may be explained by the changing ice-related boundaries of the surveys between years and hence differences in survey region. Another possible reason is that in absence of better data, most of the covariates considered were derived from remote sensing data. More localised surveys with comparable survey area conducted across the Southern Ocean, where whale sightings data are collected simultaneously with in situ non-biotic and prey data, are likely to provide a better assessment of the environmental determinants of whale density.

Keywords: Antarctic minke whale, Southern Ocean, distribution, ice, modelling, SOWER.

INTRODUCTION

The Southern Ocean is the most important feeding ground for Antarctic minke whales (*Balaenoptera bonaerensis*). Mainly during the austral summer months, these whales predominantly feed on krill (Kawamura, 1994) and are observed both within the pack ice region (e.g. Ensor, 1989; Ribic et al., 1991; van Franeker, 1992; Thiele and Gill, 1999; Thiele et al., 2002, 2005) and in the open ocean (e.g. Kasamatsu et al., 1988, 2000; Thiele et al., 2000; Murase et al., 2002; Friedlaender et al., 2006).

The Antarctic minke whale is currently the most abundant baleen whale species in the Southern Ocean, and is likely to be a major consumer of krill. During the austral summer, several hundred thousand Antarctic minke whales inhabit the Southern Ocean (Branch, 2006), although abundance estimates of Antarctic minke whales are currently under major review (Leaper et al., 2008; IWC, 2009). Estimates of annual circumpolar krill consumption by Antarctic minke whales are important to understand the role of minke whales in the marine ecosystems, including the interactions with potential competitors (e.g. Ainley et al., 2006). Krill consumption estimates by minke whales range between 35.5 (± 6.2) million tonnes per year (Armstrong and Siegfried, 1991) and 75 million tonnes per year (Everson, 2000). However, they are based on historic abundance estimates of Antarctic minke whales. Understanding how the changing environment affects minke whales and their prey is important to map changes in whale abundance and trends.

Several studies have reported regional trends in sea surface temperature and sea ice extent attributed to climate change in the Southern Ocean in the second half of the 20th century. This is especially true for the Bellingshausen-Amundsen Seas sector, with a marked increase in sea surface temperature (Meredith and King, 2005) and a strongly negative trend in sea ice extent (Zwally et al., 2002; Stammerjohn et al., 2008). The environmental variability may underlie long-term changes in density of Antarctic minke whales. For a better understanding of these long-term changes, we need to characterise the physical environment associated with Antarctic minke whale density dynamics.

From large-scale independent studies (e.g. Kasamatsu et al., 1988, 2000; Thiele et al., 2000; Murase et al., 2002), it is not clear which environmental variables determine the circumantarctic variability in Antarctic minke whale summer distribution and density. Only recently, studies on Antarctic minke whale distribution have been conducted at a smaller scale, and these indicate potentially complex spatial relationships between Antarctic minke whales and their prey (Friedlaender et al., 2006, 2009).

The International Whaling Commission (IWC) has conducted visual cetacean surveys in the Southern Ocean for almost 30 years under the IDCR (International Decade of Cetacean Research) and SOWER (Southern Ocean Whale and Ecosystem Research) programmes. This has resulted in three circumpolar sets of surveys, which were specifically designed for the visual detection of cetaceans with an emphasis on Antarctic minke whales and the environment. This is in contrast with multidisciplinary surveys, such as the CCAMLR 2000 (Commission for the Conservation of Antarctic Marine Living Resources, Reilly et al. (2004)) and SO GLOBEC surveys (Southern Ocean

Global Ocean Ecosystem Dynamics, Thiele et al., 2004; Friedlaender et al., 2006), which targeted specific study areas.

The IWC/IDCR-SOWER dataset is thus the only circumantarctic whale sightings dataset for the Southern Ocean that allows for a long-term large-scale analysis of spatio-temporal variability in minke whale density. To determine the environmental drivers of whale density, we analysed the data with the spatial modelling methodology developed by Hedley et al. (1999), and simple Generalised Additive Models (GAMs) (Wood, 2006). Input variables were derived from remote sensing data that are related to transition zones in the Southern Ocean. These zones are characterised by their enhanced productivity, such as the marginal ice zone (e.g. Smith and Nelson, 1986; Arrigo et al., 1998; Moore and Abbott, 2000) and frontal zones (e.g. Moore and Abbott, 2000). Bathymetric variables, sea surface temperature, chlorophyll *a* concentration and latitude were also considered as input for the spatial models.

With this analysis, we developed predictive spatial models for the summer density of Antarctic minke whales in open waters of the Southern Ocean at the regional scale, which is defined as the area surveyed during a specific season. In recent years, improved models have been developed to estimate summer abundance of Antarctic minke whales in the Southern Ocean (recently developed models are presented in Bravington and Hedley (2009), Cooke (2009) and Okamura and Kitakado (2009)). However, the models presented in this paper were not used for derivation of summer abundance estimates. Instead, the aim of our models was to identify aspects of the environment that underlie the density distribution of Antarctic minke whales at the regional scale, and to characterise the various relationships between minke whale density and the environment. Furthermore, we investigated if these relationships held at the circumantarctic scale.

MATERIALS AND METHODS

Study area and effort

The IWC/IDCR-SOWER programme has already completed three circumpolar (CP) sets of cetacean sighting surveys in the Southern Ocean, namely CPI (1978/79-1983/84), CPII (1985/86-1990/91) and CPIII (1991/92-2003/04). The IWC has divided the Southern Ocean into six Management Areas (Figure 2.1) (Mackintosh, 1942; Donovan, 1991), and Table 2.1 shows general information about the surveys analysed in this study in the context of the Management Areas. Coverage of most surveys was restricted to one Management Area, and some surveys covered sections of two Management Areas. Almost all open waters within the full latitudinal range from below 60°S to the sea ice edge were surveyed in CPIII. In contrast, the surveyed strata covered only about 65% and 81% of the range in CPI and CPII, respectively (Branch and Butterworth, 2001), with northern boundaries of the surveyed strata often at latitudes south of 60°S. During each survey, 2-4 vessels covered the open waters of the Southern Ocean, thereby excluding the pack ice region and polynyas (enclosed or semi-enclosed areas of open sea ice) within this region. The surveys varied in timing and duration, but were always conducted during austral summer, within a period from the end of December to the beginning of March of each season.

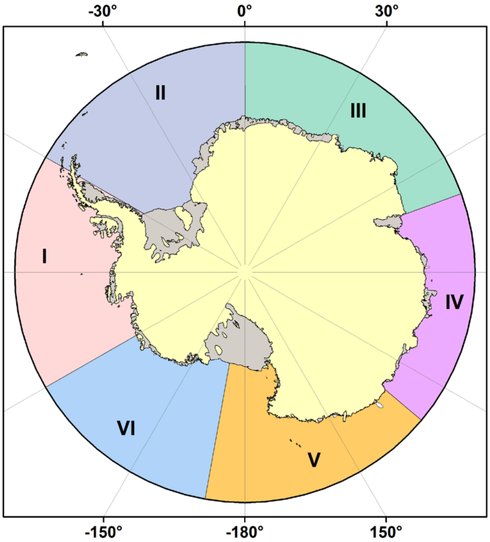


Figure 2.1. IWC Management Areas in the Southern Ocean (Mackintosh, 1942; Donovan, 1991). Ice shelves are represented by the grey areas. See Branch and Butterworth (2001) and Branch (2006) for detailed maps of the strata surveyed during the IDCR/SOWER programme.

Primary search effort, i.e. effort made when a vessel is in searching mode, was exclusively in closing mode for the surveys conducted between 1978/79 and 1984/85 and alternated between effort in closing mode and Independent Observer (IO) mode for surveys since 1985/86. In IO mode, the vessel stays on the cruise track line after a sighting, with the two observer teams on the primary and secondary platforms on full search effort. Meanwhile, the observers on the upper bridge track and identify the sighting. In contrast, in closing mode the survey vessel leaves the track line and approaches the sighted group(s) of whales for better school size estimation and species identification (Branch and Butterworth, 2001). See Branch and Butterworth (2001) and Branch (2006) for a more detailed description of the IWC/IDCR-SOWER surveys, including maps of the surveyed strata.

We did not consider the first surveys (1978/79 – 1980/81) because of the lack of environmental data from the satellite record needed to develop spatial models. Thus, spatial models were developed with line transect data from the 1981/82 – 2004/05 surveys. Total survey area ranged from 0.690 million km^2 (2001/02 survey) to 3.305 million km^2 (1985/86 survey). The lowest level of primary effort was 2,842 km (2000/2001 survey), while a maximum of 15,645 km primary effort was obtained during the survey in 1985/86. Table 2.1 summarises Antarctic minke whale sightings data under primary effort.

Table 2.1 Survey and Antarctic minke whale sighting information, grouped per IWC Management Area, south of 60°S. Sighting information refers to sightings made during primary effort and Independent Observer (IO) modes. Schools and sightings are standardised per unit primary effort and are given before truncation.

IWC Area[1]	Survey season	Survey period	Area size (10^6 km^2)	Primary effort (km)	IO effort (km)	Number of schools	Schools/ effort	Number of whales	Whales/ effort
Area I (120-60°W)	1982/83	1 Jan – 18 Feb 1983	1.099	8,938	n/a	616	0.069	1,546	0.173
	1989/90	28 Dec 1989 – 15 Feb 1990	1.473	10,192	5,635	608	0.060	1,208	0.119
	1993/94	29 Dec 1993 – 13 Feb 1994	2.290	9,002	4,601	314	0.035	608	0.068
	1999/2000	12 Jan 1999 – 14 Feb 2000	0.776	3,409	1,887	53	0.016	95	0.028
Area II (60°W-0)	1981/82	26 Dec 1981 – 8 Feb 1982	1.078	11,503	n/a	505	0.044	1,418	0.123
	1986/87	25 Dec 1986 – 9 Feb 1987	1.699	13,503	6,988	791	0.059	2,621	0.194
	1996/97	13 Jan – 17 Feb 1997	1.479	6,235	3,303	214	0.034	404	0.065
	1997/98	16 Jan – 15 Feb 1998	1.053	5,699	3,133	199	0.035	370	0.065
Area III (0-70°E)	1987/88	20 Dec 1987 – 27 Jan 1988	1.645	8,204	4,314	365	0.044	807	0.098
	1992/93	25 Dec 1992 – 2 Feb 1993	1.527	10,126	5,298	388	0.038	870	0.086
	1994/95	12 Jan – 27 Feb 1995	1.470	8,017	4,201	277	0.035	498	0.062
	2004/05	10 Jan – 27 Feb 2005	0.720	4,843	2,318	162	0.033	333	0.069
Area IV (70-130°E)	1984/85	28 Dec 1984 – 21 Feb 1985	1.105	11,436	n/a	370	0.032	904	0.079
	1988/89	28 Dec 1988 – 12 Feb 1989	1.622	12,957	4,767	476	0.037	1,361	0.105
	1998/99	20 Jan – 23 Feb 1999	1.329	7,288	3,933	186	0.026	432	0.059
Area V (130°E-170°W)	1985/86	22 Dec 1985 – 20 Feb 1986	3.305	15,645	8,101	1,184	0.076	2,752	0.176
	1991/92	27 Dec 1991 – 12 Feb 1992	1.522	6,872	3,834	637	0.093	1,491	0.217
	2001/02	25 Dec 2001 – 13 Feb 2002	0.690	3,397	1,879	136	0.040	392	0.115
	2002/03	22 Dec 2002 – 26 Feb 2003	1.653	7,332	3,892	265	0.036	580	0.079
	2003/04	21 Dec 2003– 1 March 2004	1.446	7,333	3,845	704	0.096	2,136	0.291
Area VI (170-120°W)	1983/84	3 Jan – 18 Feb 1984	2.516	7,701	n/a	194	0.025	431	0.056
	1990/91	2 Jan – 13 Feb 1991	1.912	6,734	4,020	187	0.028	357	0.053
	1995/96	10 Jan – 24 Feb 1996	1.531	6,298	3,222	227	0.036	379	0.060
	2000/2001	8 Jan – 22 Feb 2001	1.553	6,046	2,842	207	0.034	490	0.081

---

[1] In this table, as in subsequent tables, only the Management Areas were listed that were predominantly surveyed during a season. During most seasons, (part of) only one Management Area was surveyed. Three surveys were conducted in two Management Areas, namely the 1999/2000 survey (80-55°W, Areas I+II), 1994/95 survey (40-80°E, Areas III+IV) and 1995/96 survey (140-110°W, Areas VI+I).

The number of sighted Antarctic minke whale schools per km primary effort ranged from 0.016 (Area I, 1999/2000 survey) to 0.096 (Area V, 2003/04 survey). The number of sighted Antarctic minke whales per km primary effort ranged from 0.028 (Area I, 1999/2000 survey) to 0.291 (Area V, 2003/04 survey).

Whale sightings and detection probabilities

Following recommendations in Branch and Ensor (2001), Branch and Butterworth (2001) and Branch (2006), sightings coded as 04, 91 and 92 (all classified as "definitely minke whale") and 39 ("like minke whale") were extracted from the DESS (IWC Database-Estimation Software System) V3.52 database package (Strindberg and Burt, 2004), under the assumption that these sightings represented Antarctic minke whales. Dwarf minke whales, so far an unnamed subspecies of the common minke whale (*Balaenoptera acutorostrata*), also inhabit the Southern Ocean, and may be confused with Antarctic minke whales during shipboard surveys. However, probably less than 1% of minke whales in the Southern Ocean are dwarf minke whales (Leaper et al., 2008). Sightings used for this analysis were obtained in both closing and IO mode.

Some whale schools were sighted two or three times from different platforms during the survey and recorded as duplicates or triplicates, respectively. Each duplicate/triplicate was marked as either "definite", "possible", "remotely possible" or "uncertain". Only the first sighting of a duplicate/triplicate marked as "definite" was included. All other duplicates/triplicates were treated as distinct schools (Branch and Butterworth, 2001). Only sightings with activity codes considered suitable as defined in Table 3 of Branch (2006) were included in this analysis. Radial distances and angles were smeared using Method II of Buckland and Anganuzzi (1988). Selected sightings were further filtered by truncation of perpendicular distances at 1.5 nautical miles (nmi), after smearing (Branch and Butterworth, 2001).

Detection probabilities were estimated using Mark Recapture Distance Sampling (MRDS) methods implemented in Distance V5.0 release 2 (Thomas et al., 2006) and the MRDS package (V1.2.9) of Program R, V2.9.2 (R Development Core Team, 2008), which is part of Distance.
An MRDS detection function can be written as (Laake and Borchers, 2004):

$$p.\left(x,\ \underline{z}\right)=p.\left(0,\underline{z}\right)g.\left(x,\underline{z}\right) \tag{2.1}$$

where: $p.(x,\underline{z})$ = the probability that at least one of the observers detects a whale group at perpendicular distance x from the track line, given the vector $\underline{z}$ of sighting covariates (school size, sea state, etc);

$p.(0,\underline{z})$ = the probability that at least one of the observers detects a whale group on the track line (with perpendicular distance x = 0), given the covariate vector $\underline{z}$. The mark recapture (MR) component of the MRDS model is needed to estimate this probability;

$g.(x,\underline{z})$ = the probability that at least one of the observers detects a whale group at perpendicular distance x from the track line, given the covariate vector $\underline{z}$ and under the assumption that $g.(0,\underline{z}) = 1$. The distance sampling (DS) component of the MRDS model is needed to estimate this probability.

$p.(x,\underline{z})$ is derived from the individual detection functions in the following way (Laake and Borchers, 2004):

$$p.(x,\underline{z})=p_1(x,\underline{z})+p_2(x,\underline{z})\left[1-p_{1|2}(x,\underline{z})\right] \tag{2.2}$$

where: $p_j(x,\underline{z})$ = the probability that observer j detects a whale group at perpendicular distance x from the track line, given the covariate vector $\underline{z}$, for $j = 1$ or 2;

$p_{1|2}(x,\underline{z})$ = the conditional probability that observer 1 detects a whale group at perpendicular distance x from the track line, given that observer 2 detects the animal, for covariate vector $\underline{z}$.

To model the DS component, we considered the half-normal and hazard-rate key functions without any adjustment terms (see Buckland et al. (2001) for the formulae of these functions). The MR component as implemented in the MRDS package is the logistic model:

$$p_{j|3-j}(x,\underline{z})=\frac{\exp\left(\beta_0+\beta_1 z_1+\ldots+\beta_q z_q\right)}{1+\exp\left(\beta_0+\beta_1 z_1+\ldots+\beta_q z_q\right)} \tag{2.3}$$

where: $p_{j|3-j}(x,\underline{z})$ = the conditional probability that observer j detects a whale group at perpendicular distance x from the track line, given that observer (3-j) also detects the group, for sighting covariates $z_1, \ldots, z_q$;

$\beta_0, \ldots, \beta_q$ parameters to be estimated, with q = total number of covariates.

School size, sightability and sea state were considered as covariates for the detection-function models. All covariates were fitted as factor variables, with five levels for school size (i.e. 1, 2, 3-4, 5-9, 10+), four levels for sightability (2, 3, 4 and 5) and two levels for sea state (0 = Beaufort 0-2; 1 = Beaufort 3+) (Bravington and Hedley, 2009; Okamura and Kitakado, 2009). Model selection was based on Akaike's Information Criterion (AIC) (Akaike, 1973).

Only sightings of Antarctic minke whales collected during double platform effort in IO mode were used to model MR detection functions with the assumption of "point independence". This means that the individual detection probabilities $p_1(x,\underline{z})$ and $p_2(x,\underline{z})$ are independent at $x = 0$, but not necessarily elsewhere (Laake and Borchers, 2004). The $p.(0,\underline{z})$ values were only estimated for surveys since the 1985/86 season, which collected IO data, but not previously. Models for $p.(x,\underline{z})$ were fitted using all IO data pooled over the following Area(s): Areas I + II, Areas III + IV + VI and

Area V. Pooling was necessary to meet the recommendation of having at least 60 duplicate sightings, which is desirable for a good detection-function model (Buckland et al., 2001; Hedley et al., 2001). Detection-function models were fitted per vessel when sample size was appropriate.

The estimated $p.(0,\underline{z})$ values were smaller than 1 for all surveys conducted since 1985/86. Therefore, the $p.(0,\underline{z}) = 1$ assumption was also relaxed for the surveys between 1981/82 and 1984/85, for which IO data were not available. For these surveys, $g.(x,\underline{z})$ values were estimated by fitting detection functions to data collected under closing mode. As every vessel collected more than 60 sightings during each survey, detection-function models for $g.(x,\underline{z})$ were fitted per vessel and season. Values of $p.(0,\underline{z})$ were predicted with the detection-function models fitted to IO data in the same Areas. For instance, the detection-function model based on IO data pooled over Areas I + II was used to predict $p.(0,\underline{z})$ values for the 1982/83 survey, which was conducted in Area I. Estimates of $p.(x,\underline{z})$ for the early surveys were then derived from the individual components using equation (2.1). In this way, although IO data were not available for these surveys, sightings and covariate information collected during these surveys were used to determine the shape of the detection function.

Remote sensing data

The IWC/IDCR-SOWER surveys were specifically designed to detect cetaceans and relatively few non-biotic data were collected when compared to cruises under multi-disciplinary programmes such as SO GLOBEC and CCAMLR 2000. No observations were made on krill during the IWC/IDCR-SOWER cruises either and in situ biotic data are not available. Instead, remote sensing datasets were used for the derivation of potential environmental covariates needed to study the relationships between Antarctic minke whale density and their environment. Ocean depth and continental shelf break locations were obtained from the General Bathymetric Chart of the Oceans (GEBCO) dataset, at one lat-lon minute resolution (IOC et al., 2003). Sea ice concentrations were estimated from weekly passive microwave remote sensing data, derived from measurements obtained by the Scanning Multichannel Microwave Radiometer (SMMR) onboard the Nimbus-7 satellite and by the Special Sensor Microwave Imagers (SSM/I) onboard Defense Meteorological Satellite Program (DMSP) satellites F8, F11 and F13. Version 2 of the sea ice concentration data were used, released in September 2007, which had a 0.2° x 0.2° resolution (Cavalieri et al., 1996, updated 2006). Weekly 0.083° x 0.083° gridded chlorophyll *a* concentration data were derived from the NASA Sea-viewing Wide Field-of-view Sensor (SeaWiFS) dataset (http://oceancolor.gsfc.nasa.gov/SeaWiFS/). For sea surface temperature, Optimum Interpolation version 2 Sea Surface Temperature (hereafter called OISST) data (Reynolds and Smith, 1994; Reynolds et al., 2002) were used, provided on an approximately 7 day interval one-degree latitude-longitude grid (http://www.cdc.noaa.gov/data/gridded/data.noaa.oisst.v2.html). Frontal zone locations were obtained from two sources: firstly, positions were used of the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the Antarctic Circumpolar Current (SBACC) as identified by

Orsi et al. (1995), based on long-term datasets; secondly, sea surface velocities (SSV), a proxy for frontal zone location, were derived from absolute geostrophic velocities from AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data) on a weekly 1/3° x 1/3° Mercator grid based on altimetry instruments onboard the Topex/Poseidon, Jason-1, ERS and ENVISAT satellites.

Spatial models and potential covariates

Antarctic minke whale sightings were used in spatial models based on line transect data using GAMs from Wood (2006), as implemented in the R software library *mgcv* (V1.5-5). The count method developed by Hedley et al. (1999) was applied for which we divided the transect line into equal segments of ten nautical miles.

The number of Antarctic minke whales per segment area, N_i, was obtained using the following Horvitz-Thompson-like (Horvitz and Thompson,1952) estimator:

$$\hat{N}_i = \sum_j \frac{n_{i,j}}{\hat{p}.(x,\underline{z})_{i,j}} \tag{2.4}$$

where: $n_{i,j}$ = the number of minke whales within group *j* in segment *i*;

$\hat{p}.(x,\underline{z})_{i,j}$ = the estimated probability that at least one of the observers detects the *j*th group in segment *i*, at perpendicular distance *x* from the track line, given the covariate vector $\underline{z}$.

$\hat{N}_i$ was then used as the response variable for GAMs that assumed a logarithmic link-function and a Tweedie error distribution. Tweedie distributions are characterised by a variance that is proportional to the power θ of the mean (Peel et al., 2008). Within the package *mgcv* (Wood, 2006), the best value of θ was selected where $1<\theta<2$, based on the best possible fit according to standard diagnostic plots. Furthermore, we considered the quasi-Poisson and simple Poisson error distributions which are special cases of the more general Tweedie distribution (Peel et al., 2008).

The following GAM-model (Hedley et al., 1999) was used with the natural logarithm of the segment area as an offset variable:

$$E(\hat{N}_i) = \exp\left[\ln(A_i) + \theta_0 + \sum_r f_r(k_{i,r})\right] \tag{2.5}$$

where: A_i = segment area, equal to 2 l_i w (l_i = segment length, with w = 1.5 nm);

θ_0 = intercept;

$k_{i,r}$ = value of covariate *r* for segment *i*;

f_r = smoothed function (“smoother”) of covariate *r*.

Two different smoother function types were considered, namely isotropic smoothers and tensor product smoothers.

Potential covariates used in the spatial models were: closest distance to the sea ice edge, defined at 15% sea ice concentration (Tynan and Thiele, 2003), bathymetric depth and nearest distance to the continental shelf break, defined as the 1000m depth contour, SSV and closest distances to the SACCF and SBACC, OISST, chlorophyll *a*, latitude and longitude (latter two covariates both in degrees). The GAMs were fitted independently by survey year. Although the package *mgcv* can be used for automated model selection (Wood, 2008), we decided to use a somewhat ad hoc selection procedure, as we primarily aimed to identify important whale density – environment relationships with this study, instead of maximising explained deviance. Also, covariate interaction terms were not considered in this study. Model selection was based on minimisation of the Generalised Cross Validation (GCV) score, while excluding GAMs that generated extreme values of minke whale density.

To avoid overfitting, the degree of covariate smoothing was constrained by setting the argument gamma to 1.4 within the function “gam” of package *mgcv* (Wood, 2006, p. 256). Forward selection was used as a selection procedure: in each step, covariates were considered which had correlation coefficients smaller than 0.7 with the covariates that were already selected in the previous steps. In each step, the covariate was selected for which inclusion showed the largest increase in explained deviance. A new covariate was only retained if (i) it was significant, (ii) lowered the GCV score, and (iii) increased the amount of explained deviance by at least 4% (Southwell et al., 2008).

Predicted density maps

Spatial models were used to generate density surfaces of Antarctic minke whales for each Area and year, in regions encompassed by the surveyed strata. Density maps were used to examine the predictions of the selected models, e.g. to identify extreme values of predicted density, if present. Densities of Antarctic minke whales were only predicted for the surveyed strata, which were all in open waters of the Southern Ocean. Predicted density maps on a 0.2-degree latitude-longitude grid were plotted with ESRI ArcMap V9.2 (ESRI, 2006).

In order to compare the results between different surveys, whale density, $\widehat{D}_v$, was defined as $\widehat{N}_v/A_v$ the number of Antarctic minke whales per km^2 for grid cell *v*. The segment area per grid cell, A_v, was calculated using the South Pole Lambert Azimuthal Equal Area polar projection within program ArcMap. As surveys within a specific Area took place over weeks throughout the year, covariate values were estimated for the middle date of the overlapping survey period for surveys conducted within the same Area.

RESULTS

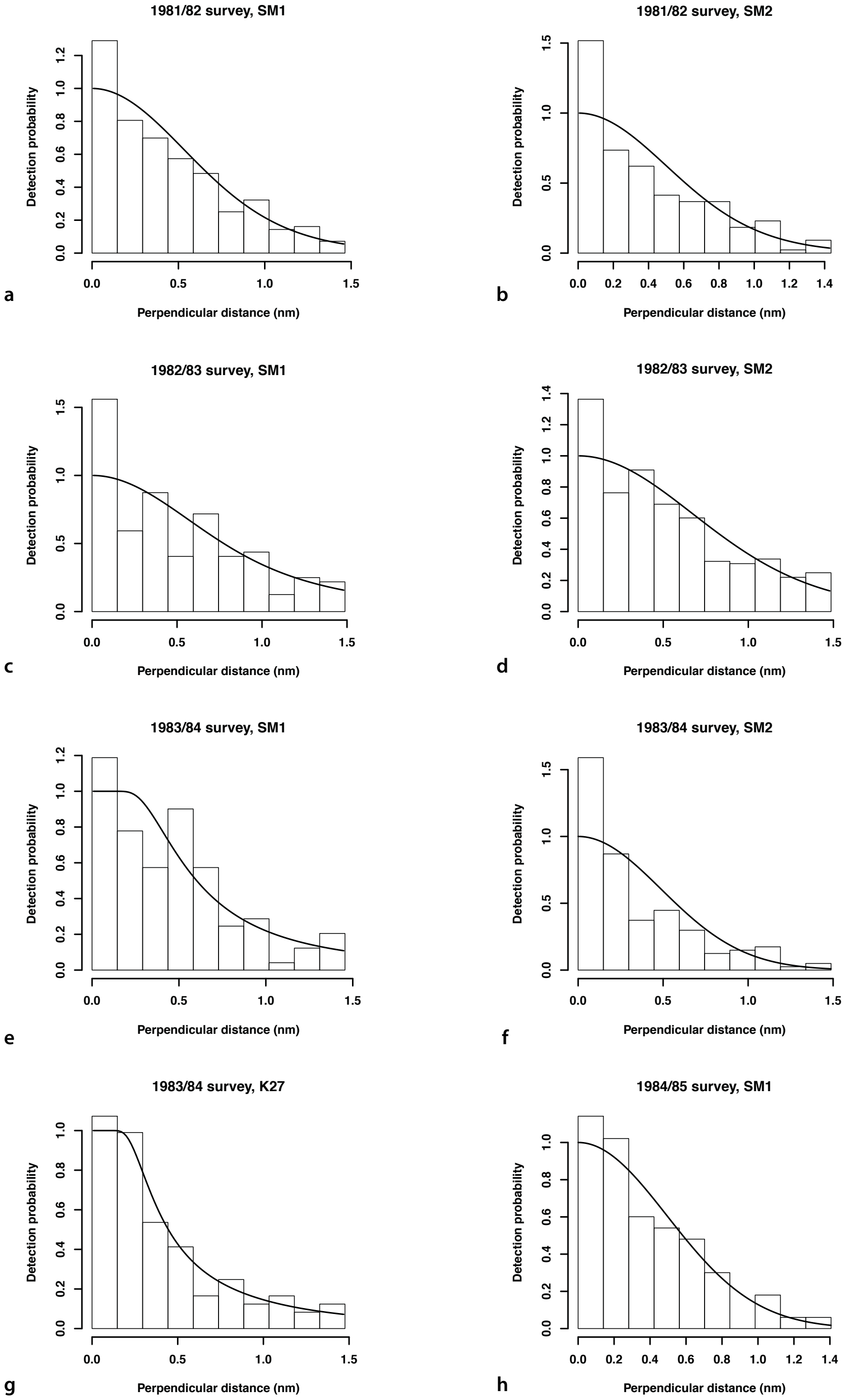
Whale sightings and detection probabilities

Tables 2.2 and 2.3 summarize the selected detection-function models and derived estimates of detection probability (also Figures 2.2 and 2.3). To illustrate the model selection process, Tables 2.4 and 2.5 list the detection-function model fits of the models that were successfully fitted. The $\bar{g}.(x)$ estimates for the surveys between 1981/82 and 1984/85 ranged from 0.392 (SE=0.048, vessel K27, 1983/84 survey) to 0.576 (SE=0.022, vessel SM2, 1982/83 survey). For these surveys, sea state data were only available for the 1984/85 survey. School size was the only sighting covariate apart from perpendicular distance that was frequently included in the models (Table 2.2), even though sightability and sea state were also considered as sighting covariates in some of the surveys (Table 2.4). The estimated $\bar{p}.(0)$ values for surveys conducted between 1985/86 and 2003/04 ranged from 0.561 (SE=0.027, vessels SM1+K27, Area V) to 0.724 (SE=0.031, vessel SM1, Areas III+IV+VI). Estimated $\bar{p}.(x)$ values ranged from 0.182 (SE=0.021, vessel SM2, Area V) to 0.338 (SE=0.019, vessels SM1+K27, Areas I+II). Group size was always selected in the models (Table 2.3). The MR component of some models included sea state as well, but sightability never improved model fit (Table 2.5).

Table 2.2 Summary of selected detection function models and derived $\bar{g}.(x)$ estimates for surveys between 1981/82 and 1984/85. $\hat{\bar{g}}.(x)$ is the estimated average detection probability derived from the detection function model which assumed $g(0)$=1. Detection function models were fitted per survey year and vessel.

Survey season	Area	Vessel	Number of sightings	Selected model	$\hat{\bar{g}}.(x)$ ± SE
1981/82	II	SM1	268	hn (*x*+*s*)	0.480 ± 0.021
		SM2	198	hn (*x*+*s*)	0.455 ± 0.022
1982/83	I	SM1	179	hn (*x*+*s*)	0.558 ± 0.032
		SM2	393	hn (*x*+*s*)	0.576 ± 0.022
1983/84	VI	SM1	120	hr (*x*+*s*)	0.492 ± 0.054
		SM2	165	hn (*x*)	0.410 ± 0.019
		K27	95	hr (*x*+*s*)	0.392 ± 0.048
1984/85	IV	SM1	73	hn (*x*)	0.438 ± 0.035
		SM2	162	hr (*x*+*s*)	0.565 ± 0.057
		K27	79	hn (*x*+*s*)	0.565 ± 0.047

Abbreviations: hn = half-normal model, hr = hazard-rate model, *x* = perpendicular distance, *s* = school size.


1981/82 survey, SM1
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0.0
0.5
1.0
1.5
a
Perpendicular distance (nm)
1981/82 survey, SM2
Detection probability
0.0
0.5
1.0
1.5
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
b
Perpendicular distance (nm)
1982/83 survey, SM1
Detection probability
0.0
0.5
1.0
1.5
0.0
0.5
1.0
1.5
c
Perpendicular distance (nm)
1982/83 survey, SM2
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
0.0
0.5
1.0
1.5
d
Perpendicular distance (nm)
1983/84 survey, SM1
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
1.2
0.0
0.5
1.0
1.5
e
Perpendicular distance (nm)
1983/84 survey, SM2
Detection probability
0.0
0.5
1.0
1.5
0.0
0.5
1.0
1.5
f
Perpendicular distance (nm)
1983/84 survey, K27
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.5
1.0
1.5
g
Perpendicular distance (nm)
1984/85 survey, SM1
Detection probability
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
h
Perpendicular distance (nm)

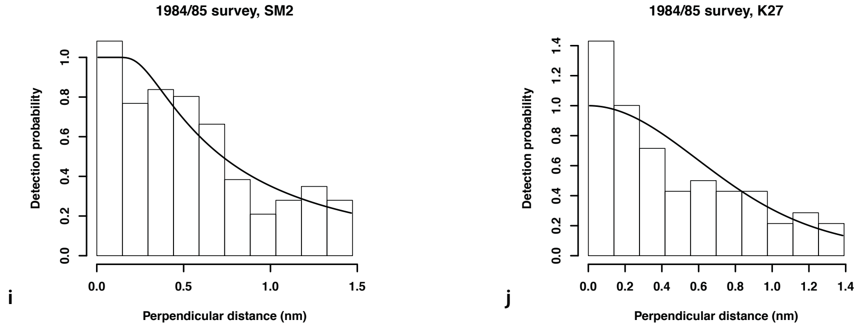


Figure 2.2. Plots of fitted detection functions and histograms of perpendicular distances for the surveys conducted on vessels SM1, SM2 and K27 between 1981/82 and 1984/85.

Table 2.3 Summary of selected detection function models and derived detection probability estimates for surveys between 1985/86 and 2003/04. Detection function models were fitted with Independent Observer (IO) sightings data from all surveys conducted in the following (sets of) Area(s): a) Areas I+II; b) Areas III, IV and VI; c) Area V. $\hat{\hat{p}}.(0)$ is the estimated average probability of sighting an Antarctic minke whale group on the survey line, derived from the mark recapture (MR) model. All MR models assumed point independence. $\hat{\hat{g}}.(x)$ is the estimated average detection probability derived from the distance sampling (DS) model which assumed $g(0)=1$. $\hat{\hat{p}}.(x)$ is the estimated average detection probability from the mark recapture distance sampling (MRDS) model.

Area	Vessel	Number of duplicate sightings	Selected model	$\hat{\hat{p}}.(0) \pm$ SE	$\hat{\hat{g}}.(x) \pm$ SE	$\hat{\hat{p}}.(x) \pm$ SE
I + II	SM1 + K27	119	hn (DS: $x+s$, MR: $x+s$)	0.672 ± 0.030	0.503 ± 0.017	0.338 ± 0.019
	SM2	135	hr (DS: $x+s$, MR: $x+s$)	0.696 ± 0.029	0.384 ± 0.028	0.267 ± 0.023
III + IV + VI	SM1	127	hr (DS: $x+s$, MR: $x+s+ss$)	0.724 ± 0.031	0.418 ± 0.045	0.303 ± 0.036
	SM2	167	hr (DS: x, MR: $x+s$)	0.721 ± 0.025	0.400 ± 0.034	0.289 ± 0.027
V	SM1 + K27	234	hr (DS: $x+s$, MR: $x+s+ss$)	0.561 ± 0.027	0.496 ± 0.034	0.278 ± 0.024
	SM2	152	hr (DS: $x+s$, MR: $x+s+ss$)	0.584 ± 0.031	0.313 ± 0.031	0.182 ± 0.021

Abbreviations: hn = half-normal model, hr = hazard-rate model, x = perpendicular distance, s = school size, ss = sea state.

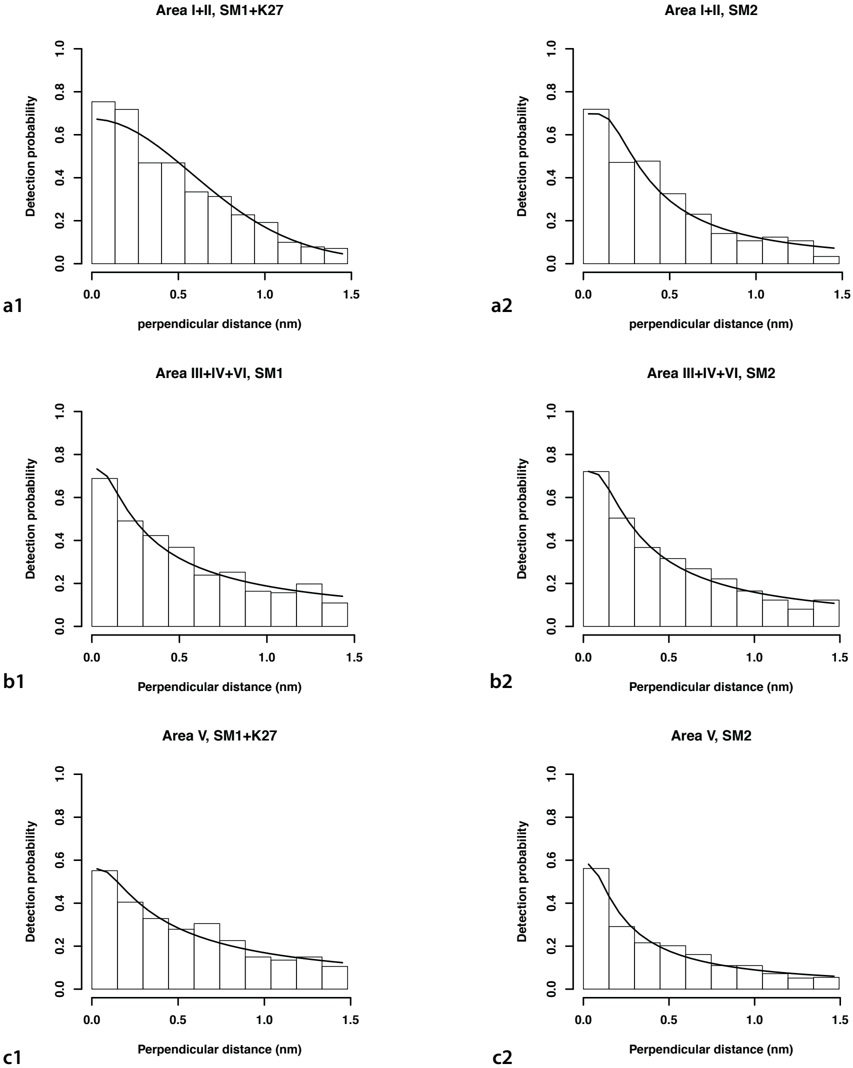


Figure 2.3. Plots of fitted detection functions and histograms of perpendicular distances for the surveys conducted on vessels SM1, SM2 and K27 between 1985/86 and 2004/05. Detection function models were fitted with independent observer (IO) sightings data from all surveys conducted in the following (sets of) Area(s): a) Areas I+II; b) Areas III, IV and VI; c) Area V.

Table 2.4 Detection-function model fits with AIC and ΔAIC for the surveys conducted between 1981/82 and 1984/85.

Survey season	Area	Vessel	Model	AIC	ΔAIC
1981/82	II	SM1	**hn (*x*+*s*)**	**60.8**	**0**
			hn (*x*+*sg*)	73.1	12.3
			hn (*x*)	74.9	14.1
		SM2	**hn (*x*+*s*)**	**22.6**	**0**
			hn (*x*)	28.8	6.2
			hn (*x*+*sg*)	30.5	7.9
			hn (*x*+*s*+*sg*)	31.0	8.4
1982/83	I	SM1	**hn (*x*+*s*)**	**79.8**	**0**
			hn (*x*+*s*+*sg*)	81.9	2.1
			hn (*x*)	94.6	14.8
			hn (*x*+*sg*)	94.7	14.9
		SM2	**hn (*x*+*s*)**	**194.2**	**0**
			hn (*x*+*sg*)	197.0	2.8
			hn (*x*+*s*+*sg*)	199.6	5.4
			hn (*x*)	204.2	10.0
1983/84	VI	SM1	**hr (*x*+*s*)**	**38.8**	**0**
			hr (*x*)	39.4	0.6
			hn (*x*)	40.5	1.7
			hr (*x*+*sg*)	41.2	2.4
			hr (*x*+*s*)	41.7	2.9
		SM2	**hn (*x*)**	**- 0.14**	**0**
			hn (*x*+*sg*)	1.81	2.0
			hn (*x*+*s*)	1.86	2.0
		K27	**hr (*x*+*s*)**	**5.1**	**0**
			hr (*x*+*s*+*sg*)	9.0	3.9
			hr (*x*+*s*)	11.7	6.6
			hr (*x*)	12.2	7.1
			hn (*x*)	21.6	16.5
1984/85	IV	SM1	**hn (*x*)**	**1.5**	**0**
			hn (*x*+*s*)	2.1	0.6
			hr (*x*)	3.1	1.6
			hn (*x*+*sg*)	3.4	1.9
			hn (*x*+*ss*)	3.5	2.0
		SM2	**hr (*x*+*s*)**	**78.9**	**0**
			hr (*x*)	94.1	15.2
			hn (*x*)	95.6	16.7
			hr (*x*+*ss*)	95.8	16.9
			hr (*x*+*sg*)	96.1	17.2

Abbreviations: hn = half-normal model, hr = hazard-rate model, *x* = perpendicular distance, *s* = school size, *sg* = sightability, *ss* = sea state. Selected models are in bold. Only models with good fits are listed.

Table 2.4 Detection-function model fits with AIC and ΔAIC for the surveys conducted between 1981/82 and 1984/85. *(Continued)*

Survey season	Area	Vessel	Model	AIC	ΔAIC
		K27	**hn (*x+s*)**	**29.3**	**0**
			hn (*x*)	31.0	1.7
			hn (*x+ss*)	31.9	2.6
			hn (*x+sg*)	32.3	3.0

Abbreviations: hn = half-normal model, hr = hazard-rate model, *x* = perpendicular distance, *s* = school size, *sg* = sightability, *ss* = sea state. Selected models are in bold. Only models with good fits are listed.

Table 2.5 Detection-function model fits with AIC and ΔAIC for the surveys conducted between 1985/86 and 2003/04.

Area	Vessel	Model	AIC	ΔAIC
I + II	SM1 + K27	**hn (DS: *x+s*, MR: *x+s*)**	**1242.9**	**0**
		hn (DS: *x+s+ss*, MR: *x+s*)	1245.9	3.0
		hn (DS: *x+s+sg*, MR: *x+s*)	1248.0	5.1
		hn (DS: *x+sg*, MR: *x+s*)	1250.1	7.2
		hn (DS: *x+ss*, MR: *x+s*)	1251.5	8.6
		hn (DS: *x*, MR: *x+s*)	1255.9	13
		hn (DS: *x*, MR: *x+s+ss*)	1257.0	14.1
		hn (DS: *x*, MR: *x+s+v*)	1257.7	14.8
		hn (DS: *x*, MR: *x+s+sg*)	1259.2	16.3
		hr (DS: *x*, MR: *x+s*)	1259.4	16.5
		hn (DS: *x*, MR: *x+ss*)	1291.6	48.7
		hn (DS: *x*, MR: *x*)	1291.7	48.8
		hn (DS: *x*, MR: *x+v*)	1292.6	49.7
		hn (DS: *x*, MR: *x+ sg*)	1296.1	53.2
	SM2	**hr (DS: *x+s*, MR: *x+s*)**	**1176.9**	**0**
		hr (DS: *x+sg*, MR: *x+s*)	1180.2	3.3
		hr (DS: *x*, MR: *x+s*)	1180.3	3.4
		hr (DS: *x+ss*, MR: *x+s*)	1182.3	5.4
		hn (DS: *x*, MR: *x+s*)	1191.1	14.2
		hn (DS: *x*, MR: *x+s+ss*)	1191.1	14.2
		hn (DS: *x*, MR: *x*)	1201.1	24.2
		hn (DS: *x*, MR: *x+ss*)	1202.0	25.1
III + IV + VI	SM1	**hr (DS: *x+s*, MR: *x+s+ss*)**	**1188.4**	**0**
		hr (DS: *x*, MR: *x+s+ss*)	1191.7	3.3
		hr (DS: *x+sg*, MR: *x+s+ss*)	1193.0	4.6
		hr (DS: *x+ss*, MR: *x+s+ss*)	1193.2	4.8
		hn (DS: *x*, MR: *x+s+ss*)	1206.3	17.9

Abbreviations: hn = half-normal model, hr = hazard-rate model, DS = Distance Sampling model, MR = Mark Recapture model, *x* = perpendicular distance, *s* = school size, *sg* = sightability, *ss* = sea state, *v* = vessel. Selected models are in bold. Only models with good fits are listed.

Table 2.5 Detection-function model fits with AIC and ΔAIC for the surveys conducted between 1985/86 and 2003/04. *(Continued)*

Area	Vessel	Model	AIC	ΔAIC
		hn (DS: *x*, MR: *x*+*s*)	1213.3	24.9
		hn (DS: *x*, MR: *x*+*s*+*sg*)	1215.3	26.9
		hn (DS: *x*, MR: *x*+*ss*)	1216.0	27.6
		hn (DS: *x*, MR: *x*)	1222.8	34.4
		hn (DS: *x*, MR: *x*+*sg*)	1224.2	35.8
III + IV +VI	SM2	**hr (DS: *x*, MR: *x*+*s*)**	**1588.4**	**0**
		hr (DS: *x*+*s*, MR: *x*+*s*)	1588.7	0.3
		hr (DS: *x*+*sg*, MR: *x*+*s*)	1590.4	2.0
		hr (DS: *x*+*ss*, MR: *x*+*s*)	1590.4	2.0
		hn (DS: *x*, MR: *x*+*s*)	1614.3	25.9
		hn (DS: *x*, MR: *x*+*s*+*ss*)	1615.3	26.9
		hn (DS: *x*, MR: *x*+*ss*)	1618.9	30.5
		hn (DS: *x*, MR: *x*+*s*+*sg*)	1621.1	32.7
		hn (DS: *x*, MR: *x*)	1624.8	36.4
		hn (DS: *x*, MR: *x*+*sg*)	1631.1	42.7
V	SM1 + K27	**hr (DS: *x*+*s*, MR: *x*+*s*+*ss*)**	**2373.6**	**0**
		hr (DS: *x*, MR: *x*+*s*+*ss*)	2380.6	7.0
		hr (DS: *x*+*sg*, MR: *x*+*s*+*ss*)	2391.2	17.6
		hr (DS: *x*+*ss*, MR: *x*+*s*+*ss*)	2392.2	18.6
		hn (DS: *x*, MR: *x*+*s*+*ss*)	2396.3	22.7
		hn (DS: *x*, MR: *x*+*ss*)	2445.3	71.7
		hn (DS: *x*, MR: *x*+*s*)	2447.3	73.7
		hn (DS: *x*, MR: *x*+*s*+*sg*)	2449.9	76.3
		hn (DS: *x*, MR: *x*)	2466.6	93.0
		hn (DS: *x*, MR: *x*+*sg*)	2468.1	94.5
	SM2	**hr (DS: *x*+*s*, MR: *x*+*s*+*ss*)**	**1291.9**	**0**
		hr (DS: *x*+*sg*, MR: *x*+*s*+*ss*)	1294.3	2.4
		hr (DS: *x*, MR: *x*+*s*+*ss*)	1296.9	5.0
		hr (DS: *x*+*ss*, MR: *x*+*s*+*ss*)	1298.5	6.6
		hn (DS: *x*, MR: *x*+*s*+*ss*)	1339.0	47.1
		hn (DS: *x*, MR: *x*+*s*)	1342.3	50.4
		hn (DS: *x*, MR: *x*+*ss*)	1361.9	70.0
		hn (DS: *x*, MR: *x*)	1365.4	73.5

Abbreviations: hn = half-normal model, hr = hazard-rate model, DS = Distance Sampling model, MR = Mark Recapture model, *x* = perpendicular distance, *s* = school size, *sg* = sightability, *ss* = sea state, *v* = vessel. Selected models are in bold. Only models with good fits are listed.

Spatial models and selected covariates

To illustrate goodness-of-fit, Figure 2.4 shows standard diagnostic plots for a fitted GAM using the *gam.check* function in package *mgcv*. Plots correspond to data collected during the 1981/82 survey and show patterns common to the majority of models fitted in this study. For instance, the QQ-plot (upper left panel) has a convex shape and the histogram of residuals (lower left panel) is right-skewed. Nevertheless, the distribution of predicted density of Antarctic minke whales for the 1981/82 survey corresponded broadly with the sightings distribution (Figure 2.5). The moderate model fit is the result of the high proportion of segments for which no schools were sighted: this proportion was often in excess of 70% for the various survey years. Methods specifically devised for zero-inflated data (R package *COZIGAM* 2.0-2, Liu and Chan, 2009) could not improve the results, due to non-convergence issues during the iteration process of model fitting.

GAM model descriptions are given in Table 2.6. We were not able to select a good model, based on spatial covariates which were the main focus of this analysis, for the 1995/96 and 2001/02 surveys. Seven out of ten potential covariates were included at least once in the selected GAMs: only SSV, chlorophyll *a* concentration and latitude were never selected. Of the environmental covariates, closest distance to the continental shelf break (*1000m-dist*), sea ice edge (*icedist*) and SACCF (*SACCFdist*) were most often included in the models.

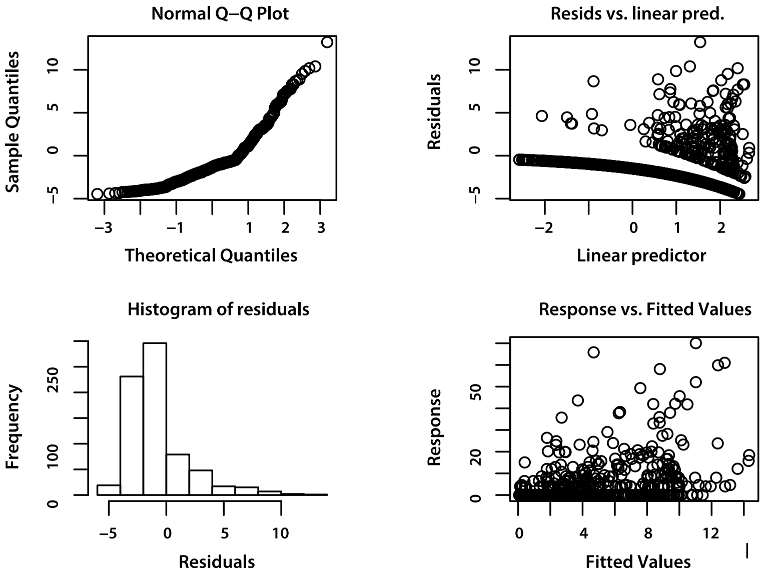


Figure 2.4. Standard diagnostic plots for the model based on the 1981/82 survey.

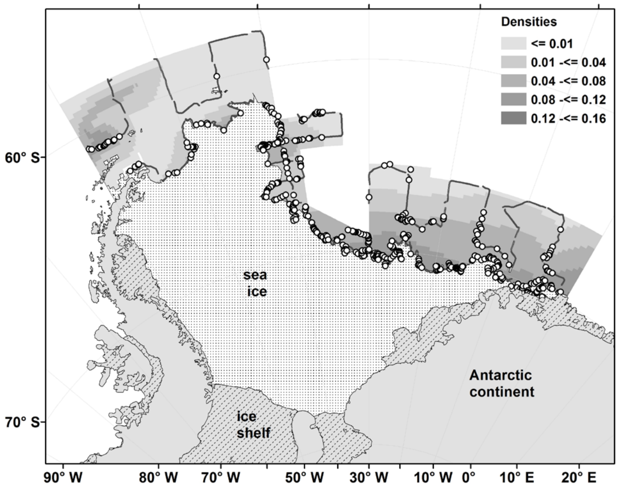


Figure 2.5. Prediction plot of density of Antarctic minke whales in the Weddell Sea sector (Area II) for the 1981/82 survey. Density, expressed in number of whales per km^2, was only predicted for surveyed strata. Sightings are represented by circles; survey effort is displayed by thick solid lines. The overlapping period for surveys conducted in Area II was 16 January – 8 February.

Table 2.7 shows selected model output. Explained deviances ranged from 14.9% to 35.1%, with a mean explained deviance of 25.3%. Table 2.7 highlights the highly variable nature of the relationships between whale density and the environment. Firstly, none of the covariates showed a consistent qualitative relationship with its effect on density of Antarctic minke whales. However, three covariates (*1000m-dist*, *icedist* and OISST) had a predominantly negative relationship with density. No dominant qualitative relationships were found for longitude, depth, *SACCFdist* or *SBACCdist*. Secondly, the selected models for every Management Area had variable sets of covariates. None of the covariates were selected in all surveys conducted in the same Management Area. *Icedist* was most often selected in models based on surveys in the Weddell Sea sector (Area II), a sector characterised by strong seasonal ice melt. Furthermore, *icedist* was non-significant for all models based on surveys in regions within the Bellingshausen/Amundsen Seas (Area I) and Indian Ocean sector (Area III). Areas I and III were characterised by relatively small sea ice coverage throughout the survey period. *1000m-dist* was most often selected in models based on surveys conducted in Area III.

Density distributions

The density distribution plots for Antarctic minke whales generated with the spatial models showed changes in whale density distribution throughout the years. As an example, Figure 2.6 shows the predicted density distributions within the Ross Sea sector (165°E-170°W) for the

1985/86 and 2003/04 surveys. For both surveys, relatively high densities of minke whales were predicted on or near the continental shelf. However, densities of minke whales higher than 0.2 whale per km^2 were exclusively predicted below 72°S for the 1985/86 survey (Figure 2.6a), whereas these densities were predicted within the 68°-72°S band for the 2003/04 survey (Figure 2.6b). These results suggest an important spatial and temporal heterogeneity in Antarctic minke whale density and distribution.

Table 2.6 Descriptions of selected models per area and survey year. Numbers between brackets in the "selected model" column refer to the covariate-specific number of degrees of freedom. Numbers between brackets in the error distribution column refer to the selected θ-value for the Tweedie error distribution. Model descriptions are given as fitted with the R software library *mgcv* (V1.5-5). All models included an offset variable which consisted of the natural logarithm of the segment area.

Area	Survey season	Selected model	Error distribution
I	1982/83	s(*longitude*, 2.6) + s(*1000m-dist*, 8.4)	Tweedie (1.3)
	1989/90	s(*OISST*, 3.0) + s(*SACCFdist*, 4.8)	Tweedie (1.4)
	1993/94	s(*longitude*, 8.7) + s(*1000m-dist*, 2.0)	Tweedie (1.2)
	1999/2000	s(*longitude*, 4.5) + s(*1000m-dist*, 1.0)	Tweedie (1.3)
II	1981/82	s(*icedist*, 3.0) + s(*SACCFdist*, 7.8)	Tweedie (1.1)
	1986/87	s(*longitude*, 7.2) + s(*depth*, 4.0)	Tweedie (1.3)
	1996/97	s(*longitude*, 4.0) + s(*icedist*, 3.0)	Tweedie (1.1)
	1997/98	s(*icedist*, 2.1) + s(*1000m-dist*, 4.0)	quasi-Poisson
III	1987/88	s(*longitude*, 8.4) + te(*1000m-dist*, 1.0)	Tweedie (1.1)
	1992/93	s(*longitude*, 4.0) + s(*1000m-dist*, 4.9)	Tweedie (1.1)
	1994/95	s(*OISST*, 6.1) + s(*1000m-dist*, 1.0) + te(*SACCFdist*, 1.8)	quasi-Poisson
	2004/05	s(*OISST*, 1.0) + s(*depth*, 4.0)	Tweedie (1.3)
IV	1984/85	s(*longitude*, 8.0) + te(*OISST*, 2.2) + s(*SBACCdist*, 5.0)	Tweedie (1.1)
	1988/89	s(*longitude*, 4.0) + s(*icedist*, 2.0)	Tweedie (1.3)
	1998/99	s(*longitude*, 4.0) + s(*1000m-dist*, 1.6)	Tweedie (1.3)
V	1985/86	s(*depth*, 4.0) + s(*1000m-dist*, 4.0)	Tweedie (1.2)
	1991/92	s(*1000m-dist*, 1.0) + s(*SACCFdist*, 7.0)	Tweedie (1.3)
	2002/03	s(*longitude*, 6.3) + s(*icedist*, 1.0)	Tweedie (1.1)
	2003/04	s(*OISST*, 4.0) + s(*SACCFdist*, 2.7)	Tweedie (1.2)
VI	1983/84	s(*longitude*, 2.5) + s(*1000m-dist*, 7.4)	Tweedie (1.2)
	1990/91	s(*icedist*, 2.0) + te(*SACCFdist*, 3.4)	quasi-Poisson
	2000/2001	s(*longitude*, 8.4) + s(*icedist*, 1.4)	quasi-Poisson

Abbreviations of the smoothers: s = isotropic smoother, te = tensor product smoother. Abbreviations of the covariates: *icedist* = closest distance to the sea ice edge (defined at 15% sea ice concentration), *OISST* = Optimally Interpolated Sea Surface Temperature, *1000m-dist* = closest distance to the continental shelf edge (defined at 1000m depth), *SACCFdist* = closest distance to the Southern Antarctic Circumpolar Current Front (SACCF), *SBACCdist* = closest distance to the Southern Boundary of the Antarctic Circumpolar Current (SBACC).

Table 2.7 Model output for the various surveys, grouped per IWC Area. The covariate columns show the relationships between a specific covariate and the effect of the specific covariate on density of Antarctic minke whales.

IWC Area	**Survey season**	**Explained deviance (%)**	**Covariates**						
			Longitude	*Icedist*	*OISST*	*Depth*	*1000m-dist*	*SACCF-dist*	*SBACC-dist*
Area I (120-60°W)	1982/83	21.5	∩				—		
	1989/90	22.0			—			∪	
	1993/94	30.5	NL				—		
	1999/2000	32.8	+				—		
Area II (60°W-0)	1981/82	27.3		—				NL	
	1986/87	26.4	NL			—			
	1996/97	23.7	—	∪					
	1997/98	35.1		—			+		
Area III (0-70°E)	1987/88	33.4	NL				—		
	1992/93	31.2	—				—		
	1994/95	33.5			—		—	—	
	2004/05	30.8			—	NL			
Area IV (70-130°E)	1984/85	17.0	NL		—				NL
	1988/89	28.2	∪	—					
	1998/99	20.9	NL				—		
Area V (130°E-170°W)	1985/86	19.5				—	∩		
	1991/92	14.9					—	NL	
	2002/03	17.4	NL	—					
	2003/04	24.8			—			∩	
Area VI (170-120°W)	1983/84	23.6	—				NL		
	1990/91	15.5		—				∪	
	2000/2001	27.3	NL	—					

Abbreviations of the covariates: *icedist* = closest distance to the sea ice edge (defined at 15% sea ice concentration), *OISST* = Optimally Interpolated Sea Surface Temperature, *1000m-dist* = closest distance to the continental shelf edge (defined at 1000m depth), *SACCFdist* = closest distance to the Southern Antarctic Circumpolar Current Front (SACCF), *SBACCdist* = closest distance to the Southern Boundary of the Antarctic Circumpolar Current (SBACC). Legend for the relationship characterisations: — = negative, + = positive, ∪ = minimum effect on density in middle of covariate range, ∩ = maximum effect on density in middle of covariate range, NL = complex non-linear relationship.

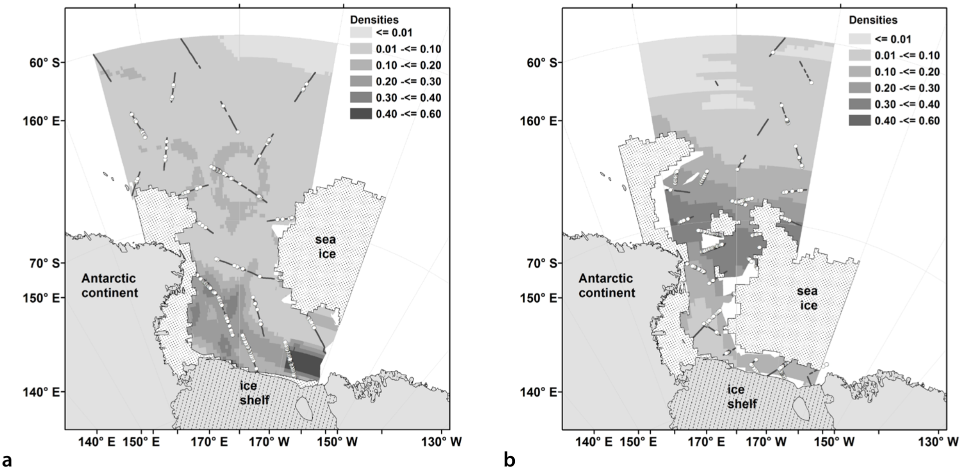


Figure 2.6. Prediction plots of density of Antarctic minke whales in the Ross Sea sector (Area V) for the 1985/86 survey (a) and 2003/04 survey (b). Density, expressed in number of whales per km^2, was only predicted for surveyed strata. Sightings in independent observer (IO) mode are represented by circles; survey effort in IO mode is displayed by thick solid lines. The overlapping period for surveys conducted in Area V was 27 December – 8 February.

DISCUSSION

Detection probabilities

Detection probability estimates as reported by Bravington and Hedley (2009) were closest to independent estimates reported by Burt et al. (2009), based on Buckland-Turnock (BT) mode experiments conducted during 2005/06 – 2007/08 (IWC, 2009). Therefore, we compared the estimates of detection probability in this study with those reported by Bravington and Hedley (2009); the estimates in Burt et al. (2009) were derived from a different dataset. As $\bar{p}.(0)$ estimates in Bravington and Hedley (2009) were only provided for the individual platforms, the estimates for $\bar{p}.(x)$ were compared with each other (Table 2.8). For the majority of CPII sightings, $\bar{p}.(x)$ estimates reported by the two studies were similar. Furthermore, $\bar{p}.(x)$ estimates were also similar for the two largest classes of CPIII sightings. These two classes contained only sightings of one-animal schools, and had sightability values of 3 and 4+, respectively. For almost all other classes of CPIII sightings, $\bar{p}.(x)$ estimates in this study were lower than those reported by Bravington and Hedley (2009). The exception were sightings of individual whales seen with sightability 2, which had a higher $\bar{p}.(x)$ estimate in our study.

The discrepancies in $\bar{p}.(x)$ estimates for various classes may be partly attributed to the different ways in which the two studies pooled IO sightings data. Furthermore, Bravington and Hedley (2009) developed a more sophisticated method for estimating detection probabilities, which takes school size errors into account. We checked whether the discrepancies in $\bar{p}.(x)$ estimates could affect presented model output by comparing the output of the models presented in this paper with models in which the $\bar{p}.(x)$ estimates reported by Bravington and Hedley (2009) were incorporated. We found that the model output in terms of covariate inclusion and the qualitative nature of covariate- whale density relationships remained the same. However, explained deviance was often somewhat lower for the models that incorporated the $\bar{p}.(x)$ estimates reported by Bravington and Hedley (2009). The aim of our study was to examine the relationships between whale density and the environment; the estimates of detection probability were not used for whale abundance estimation. Therefore, in our opinion, the detection probability estimates reported in this paper are sufficient for the purpose of this study.

Table 2.8 Comparison of estimates for $\bar{p}.(x)$ in this study, $\hat{\bar{p}}.(x)_{BE}$, with those reported by Bravington and Hedley (2009), $\hat{\bar{p}}.(x)_{BR}$. $\hat{\bar{p}}.(x)_{BR}$ is defined as $\widehat{ESW}_{BR}$ / 1.5 (truncation distance = 1.5 nmi), with $\widehat{ESW}_{BR}$ = estimated effective strip half-width as reported in Bravington and Hedley (2009). CP = circumpolar set, n = number of sightings in specific class. $\hat{\bar{p}}.(x)_{DIFF}$ = $\hat{\bar{p}}.(x)_{BE}$ minus $\hat{\bar{p}}.(x)_{BR}$. ESW_{BR} estimates are given for classes defined by sea state for CPII surveys, and for classes defined by sightability for CPIII surveys.

CP	Sea state	Sightability	School size	n	$\hat{\bar{p}}.(x)_{BE}$	$\widehat{ESW}_{BR}$	$\hat{\bar{p}}.(x)_{BR}$	$\hat{\bar{p}}.(x)_{DIFF}$
II	0-2		1	90	0.24	0.33	0.22	+0.02
			2	27	0.38	0.69	0.46	-0.08
			3-4	14	0.48	0.89	0.59	-0.11
			5-9	7	0.47	1.03	0.69	-0.22
			10+	3	0.71	1.30	0.87	-0.16
	3+		1	812	0.23	0.29	0.19	+0.04
			2	323	0.35	0.46	0.31	+0.04
			3-4	208	0.43	0.65	0.43	0
			5-9	73	0.44	0.69	0.46	-0.02
			10+	25	0.64	1.04	0.69	-0.05
III		4+	1	513	0.29	0.52	0.35	-0.06
			2	179	0.38	0.78	0.52	-0.14
			3-4	98	0.43	0.99	0.66	-0.23
			5-9	43	0.46	1.02	0.68	-0.22
			10+	17	0.50	1.38	0.92	-0.42
		3	1	521	0.24	0.41	0.27	-0.03
			2	176	0.33	0.64	0.43	-0.10
			3-4	121	0.40	0.85	0.57	-0.17
			5-9	44	0.42	0.91	0.61	-0.19
			10+	21	0.51	1.33	0.89	-0.38
		2	1	86	0.23	0.16	0.11	+0.12
			2	30	0.28	0.62	0.41	-0.13
			3-4	10	0.30	0.76	0.51	-0.21
			5-9	2	0.37	0.81	0.54	-0.17
			10+	1	0.63	0.98	0.65	-0.02

Exclusion of covariates in the GAMs

Most covariates considered for model selection were retained by the best models in various combinations (Table 2.6). Only SSV, chlorophyll *a* concentration and latitude were never selected in the best models. For the first two covariates, this may be due to limitations of the available remote sensing datasets: SSV data were not available for a wide band along the sea ice edge, which made it harder to detect a signal across the survey region, if there was any signal present; and chlorophyll *a* data were missing in a large proportion of the weekly grids due to cloud cover. The chlorophyll *a* range was also very small for some Areas (e.g. Area IV), which made it hard to detect any signal if present. Thus, it is not clear if a better spatial coverage of this covariate would improve the explanatory value of the models. Latitude was often highly correlated with other covariates, especially with *icedist* and *OISST*, and thus was often dropped in later steps of the model selection process.

Relationships with the environment

Covariates related to transition zones, such as *1000m-dist, icedist* and *SACCFdist*, were most often selected in the models. As transition zones often show enhanced productivity, the expected effect of these covariates on whale density would be smaller or more negative at greater distances to the boundaries of the zones (Tynan, 1998; Kasamatsu et al., 2000). In agreement, the covariate-density effect relationships for *1000m-dist* and *icedist* were predominantly negative. This suggested that density of Antarctic minke whales tended to be higher in regions closer to the continental shelf break and/or sea ice edge, often in colder waters (as *icedist* and OISST were often highly correlated, a selected model never included both *icedist* and OISST, with *icedist* having a clearer signal in more models). However, the covariate-density effect relationship for *SACCFdist* was often difficult to interpret, suggesting that the Antarctic Circumpolar Current may not be as important for Antarctic minke whales as it has been reported to be for larger baleen whales (Tynan, 1998).

Our study suggests that relationships between minke whales and their environment are best explored at a regional scale: spatial models did not show consistent relationships between the covariates and their effects on density at the circumantarctic scale. Circumantarctic relationships between minke whale density and their environment may be non-significant, while those relationships are significant at a regional scale.

Even within Management Areas, we could not detect consistent qualitative relationships between minke whale density and its environment over the various survey years. This in part may be explained by the changing ice-related boundaries of the surveys between years and hence differences in survey region. Another possible reason may be that only a limited number of environmental variables could be considered for this study. Other aspects of the environment that interact with the selected covariates, for which data were not available, may have changed throughout the years. In conjunction with this, the IWC/IDCR-SOWER surveys did not cover the pack ice region. Changes in the extent and heterogeneity of the pack ice may influence the distribution of Antarctic minke whales in the pack ice region (Thiele et al., 2005). We speculate that the pack ice quantity and quality may affect the density distribution of minke whales in open waters close to the sea ice edge as well. For instance, in years when the pack ice is more diverse in quality, shows more cracks, or encloses polynyas relatively in the proximity of the sea ice edge, Antarctic minke whales may move more easily into the pack ice region. In years when the pack ice close to the sea ice edge is more solid, the whales may be restricted in their movements into the pack ice region and stay in open waters close to the sea ice edge. In those years, the relationship between closest distance to the sea ice edge and its effect on density of Antarctic minke whales in open waters may be (more) negative. In order to have a better understanding of the relationship between minke whale density and its environment in the various sectors of the Southern Ocean, more aerial and shipboard surveys within the pack ice region are needed, ideally in combination with shipboard surveys in open waters in the same sector of the Southern Ocean (Hedley et al., 2007; Kelly et al., 2009).

Performance and application of spatial models

Most spatial models for density of Antarctic minke whales had moderate values for explained deviance. This was in part the result of the conservative selection method used in this study. The flexibility of the GAMs potentially leads to overfitting of the data (Forney, 2000; Hastie et al., 2005). While overfitting is not critical for prediction purposes, it did not improve the ability to describe the physical environment underlying the distribution of minke whales, which was the main objective of this analysis. In order to prevent overfitting, a covariate was only selected if it contributed at least 4% to the explained deviance of the model. Alternatively, Principal Components Analysis can be used to reduce the number of intercorrelated variables, and then the principal components can be interpreted as synthetic climatic covariates (Grosbois et al., 2008). However, this interpretation necessarily provides less fine-scale resolution when explaining the specific whale-environment relationships, and may not work well for covariate data sets with poor spatial resolution.

The performance of our models was probably also limited by the nature of the available environmental datasets from which we derived covariates. At this spatial scale, we could only consider remote sensing data and long-term frontal positions as covariate input for our models. Explained deviance of the models would probably increase if covariates could be included that more accurately reflect the environment, such as in situ data or remote sensing data at a higher resolution. For instance, explained deviances were 63.1% and higher for spatial models of baleen whales near the Western Antarctic Peninsula that included covariates derived from in situ chlorophyll *a* and acoustic zooplankton data (Friedlaender et al., 2006). In order to get a better understanding of the relationship between whale density and the environment, more localised surveys can be conducted during which whale sightings data will be collected simultaneously with in situ non-biotic and biotic (prey) data.

Nevertheless, given the limited possibilities for including environmental information in our models, model performance was satisfactory. Furthermore, models could be developed for surveys under considerably different environmental conditions, such as sea ice distribution and coverage, for the same time period (Figure 2.6). The predicted density maps (Figures 2.5 and 2.6) show both spatial and temporal variability in density of Antarctic minke whales. A more detailed description of these types of variability can be found in Chapter 3 of this thesis. We plan to further investigate the temporal variability in density at a regional scale across the Southern Ocean, by focusing on regional environmental features that were not captured by the models. Examples are regional sea ice extent during the survey and the degree of seasonal change therein. A better understanding of the temporal variability in whale density is needed for any scenario analysis of Antarctic minke whale density in the Southern Ocean under various climate regimes.

ACKNOWLEDGEMENTS

We are very grateful to the International Whaling Commission for providing us with the IWC/IDCR-SOWER whale sightings dataset. Furthermore, we would like to thank Jamie Tratalos and Peter Fretwell for providing GIS support. We thank Michael Meredith for oceanographic advice. We would also like to thank three anonymous reviewers for their helpful and thorough comments, which improved the manuscript substantially. The altimeter products were produced by Ssalto/Duacs and distributed by Aviso with support from Cnes. This project is funded by the EURopean Network of Excellence for Ocean Ecosystems Analysis (EUR-OCEANS) under project number WP4-SYSSO-1066. This paper contributes to the Ecosystems Programme, part of the Polar Science for Planet Earth framework of the British Antarctic Survey.

REFERENCES

Ainley, D.G., Ballard, G. and Dugger, K.M. 2006. Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. *Ecology* 87(8): 2080-2093.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. pp. 267-281. *In*: B. Petran and F. Csaaki (eds.) *Second international symposium on information theory*. Akadeemiai Kiadi, Budapest, Hungary. 451pp.

Armstrong, A.J and Siegfried, W.R. 1991. Consumption of Antarctic krill by minke whales. *Antarct. Sci.* 3(1): 13-18.

Arrigo, K.R., Worthen, D., Schnell, A. and Lizotte, M.P. 1998. Primary production in Southern Ocean waters. *J. Geophys. Res.* 103(C8): 15,587-15,600.

Branch, T.A. 2006. Abundance estimates for Antarctic minke whales from three completed circumpolar sets of surveys, 1978/79 to 2003/04. Paper SC/58/IA18 presented to the IWC Scientific Committee, June 2006 (unpublished). 28pp. [Paper available from the Office of the IWC].

Branch, T.A. and Butterworth, D.S. 2001. Southern Hemisphere minke whales: standardised abundance estimates from the 1978/79 to 1997/98 IDCR-SOWER surveys. *J. Cetacean Res. Manage.* 3(2): 143-174.

Branch, T. and Ensor, P. 2001. Recommended species code changes for minke and blue whale sightings for analysis of IDCR-SOWER surveys. Report of the Scientific Committee, Annex G, Appendix 8. *J. Cetacean Res. Manage. (Suppl.)* 3: 200-203.

Bravington, M.V. and Hedley, S.L. 2009. Antarctic minke whale abundance estimates from the second and third circumpolar IDCR/SOWER surveys using the SPLINTR model. Paper SC/61/IA14 presented to the IWC Scientific Committee, June 2009 (unpublished). 25pp. [Paper available from the Office of the IWC].

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. (eds.) 2001. *Introduction to distance sampling*. Oxford University Press, Oxford. 432pp.

Buckland, S.T. and Anganuzzi, A.A. 1988. Comparison of smearing methods in the analysis of minke sightings data from IWC/IDCR Antarctic cruises. *Rep. int. Whal. Commn.* 38: 257-263.

Burt, M.L., Ensor, P. and Borchers, D.L. 2009. Detection probability of Antarctic minke whales: analyses of the BT mode experiments conducted on the IWC-SOWER cruises 2005/06 – 2007/08. Paper SC/61/IA18 presented to the IWC Scientific Committee, June 2009 (unpublished). 14pp. [Paper available from the Office of the IWC].

Cavalieri, D., Parkinson, C., Gloersen, P. and Zwally, H.J. 1996, updated 2006. Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I passive microwave data. Boulder, Colorado USA: National Snow and Ice Data Center. Digital media.

Cooke, J.G. 2009. An integrated method for analysis of IDCR/SOWER data and TRANSIM simulated data sets. Paper SC/A09/AE6 presented to the IWC Workshop on minke whale abundance estimates using IWC/SOWER data, April 2009 (unpublished). 11pp. [Paper available from the Office of the IWC].

Donovan, G.P. 1991. A review of IWC stock boundaries. *Rep. int. Whal. Commn.* (special issue) 13: 39-68.

Ensor, P.H. 1989. Minke whales in the pack ice zone, East Antarctica, during the period of maximum annual ice extent. *Rep. int. Whal. Commn.* 39: 219-225.

ESRI. 2006. ArcMap 9.2. Environmental Systems Resource Institute, Redlands, California.

Everson, I. 2000. Role of krill in marine food webs – The Southern Ocean. pp. 194-201. *In:* I. Everson (ed.) *Krill: biology, ecology and fisheries*. Blackwell Science, Oxford. 384pp.

Forney, K.A. 2000. Environmental models of cetacean abundance: reducing uncertainty in population trends. *Cons. Biol.* 14(5): 1271-1286.

Friedlaender, A.S., Halpin, P.N., Qian, S.S., Lawson, G.L., Wiebe, P.H., Thiele, D. and Read, A.J. 2006. Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula. *Mar. Ecol. Prog. Ser*. 317: 297-310.

Friedlaender, A.S., Lawson, G.L and Halpin, P.N. 2009. Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. *Mar. Mamm. Sci.* 25(2): 402-415

Grosbois, V., Gimenez, O., Gaillard, J.-M., Pradel, R., Barbraud, C., Clobert, J., Møller, A. P. and Weimerskirch, H. 2008. Assessing the impact of climate variation on survival in vertebrate populations. *Biol. Rev.* 83: 357-399.

Hastie, G.D., Swift, R.J., Slesser, G., Thompson, P.M. and Turrell, W.R. 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. *ICES J. Mar. Sci.* 62: 760-770.

Hedley, S.L., Buckland, S.T. and Borchers, D.L. 1999. Spatial modelling from line transect data. *J. Cetacean Res. Manage.* 1(3): 255-264.

Hedley, S., Reilly, S., Borberg, J., Holland, R., Hewitt, R., Watkins, J., Naganobu, M. and Sushin, V. 2001. Modelling whale distribution: a preliminary analysis of data collected on the CCAMLR-IWC Krill Synoptic Survey, 2000. Paper SC/53/E9 presented to the IWC Scientific Committee, July 2001 (unpublished). 38pp. [Paper available from the Office of the IWC].

Hedley, S.L., Bravington, M.V., Gales, N. Kelly, N. and Peel, D. 2007. Aerial survey for minke whales off eastern Antarctica. Paper SC/59/IA2 presented to the IWC Scientific Committee, June 2007 (unpublished). 47pp. [Paper available from the Office of the IWC].

Horvitz, D.G. and Thompson, D.J. 1952. A generalization of sampling without replacement from a finite universe. *J. Am. Stat. Assoc.* 47: 663-685.

IOC, IHO and BODC. 2003. Centenary edition of the GEBCO Digital Atlas, published on CD-rom on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans, British Oceanographic Data Centre, Liverpool, UK.

IWC. 2009. Report of the Scientific Committee. Report IWC/61/Rep 1 presented to the IWC61 meeting, June 2009 (unpublished). 108pp. [Report available from the Office of the IWC].

Kasamatsu, F., Hembree, D., Joyce, G., Tsunoda, L., Rowlett, R. and 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. *Rep. int. Whal. Commn*. 38: 449-473.

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

Kawamura, A. 1994. A review of baleen whale feeding in the Southern Ocean. *Rep. int. Whal. Commn.* 44: 261-271.

Kelly, N., Peel, D., Pike, D., Bravington, M.V. and Gales, N. 2009. An aerial survey for Antarctic minke whales in sea ice off east Antarctica: a pilot study. Paper SC/61/IA3 presented to the IWC Scientific Committee, June 2009 (unpublished). 14pp. [Paper available from the Office of the IWC].

Laake, J.L. and Borchers, D.L. 2004. Methods for incomplete detection at distance zero. pp. 108-189. *In*: S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers and L. Thomas (eds.) *Advanced distance sampling*. Oxford University Press, Oxford. 416pp.

Leaper, R. Bannister, J.L., Branch, T.A., Clapham, P.J., Donovan, G.P., Matsuoka, K., Reilly, S. and Zerbini, A.N. 2008. A review of abundance, trends and foraging parameters of baleen whales in the Southern Hemisphere. Paper CCAMLR-IWC-WS-08/4 presented to the joint CCAMLR-IWC workshop to review input data for Antarctic marine ecosystem models, August 2008 (unpublished). 51pp. [Paper available from the Office of the IWC].

Liu, H. and Chan, K.-S. 2009. COZIGAM: constrained and unconstrained zero-inflated generalized additive models with model selection criterion. R package version 2.0-2. http:// CRAN.R-project.org/package=COZIGAM.

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. *Discovery Rep.* 22: 197-300.

Meredith, M.P. and King, J.C. 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys. Res. Lett.* 32, L19604.

Moore, J.K. and Abbott, M.R. 2000. Phytoplankton chlorophyll distributions and primary production in the Southern Ocean. *J. Geophys. Res.* 105(C12): 28,709-28,722.

Murase, H. Matsuoka, K., Ichii, T. and Nishiwaki, S. 2002. Relationship between the distribution of euphausiids and baleen whales in the Antarctic (35°E-145°W). *Polar Biol.* 25(2): 135-145.

Okamura, H. and Kitakado, T. 2009. Abundance estimates and diagnostics of Antarctic minke whales from the historical IDCR/SOWER survey data using the OK method. Paper SC/61/IA6 presented to the IWC Scientific Committee, June 2009 (unpublished). 58pp. [Paper available from the Office of the IWC].

Orsi, A.H., Whitworth III, T. and Nowlin Jr., W.D. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Res. I* 42(5): 641-673.

Peel, D., Kelly, N., Bravington, M.V. and Hedley, S.L. 2008. IWC 2008 title: Design of future SOWER voyages: an update. Paper SC/60/IA5 presented to the IWC Scientific Committee, June 2008 (unpublished). 11pp. [Paper available from the office of the IWC].

R Development Core Team. 2008. R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.r-project.org.

Reilly, S., Hedley, S., Borberg, J., Hewitt, R., Thiele, D., Watkins, J. and Naganobu, M. 2004. Biomass and energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean. *Deep-Sea Res. II* 51(12-13): 1397-1409.

Reynolds, R.W., Rayner, N.A., Smith, T.M., Stokes, D.C. and Wang, W. 2002. An improved in situ and satellite SST analysis for climate. *J. Clim*. 15: 1609-1625.

Reynolds, R.W. and Smith, T.M. 1994. Improved global sea surface temperature analyses using optimum interpolation. *J. Clim.* 7: 929-948.

Ribic, C.A., Ainley, D.G. and Fraser, W.R. 1991. Habitat selection by marine mammals in the marginal ice zone. *Antarct. Sci.* 3(2): 181-186.

Smith, Jr., W.O. and Nelson, D.M. 1986. Importance of ice edge phytoplankton production in the Southern Ocean. *Bioscience* 36(4): 251-257.

Southwell, C.J., Paxton, C.G.M., Borchers, D.L., Boveng, P.L., Nordøy, E.S., Blix, A.S. and De la Mare, W.K. 2008. Estimating population status under conditions of uncertainty: the Ross seal in East Antarctica. *Antarct. Sci.* 20(2): 123-133.

Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Yuan, X. and Rind, D. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño – Southern Oscillation and Southern Annular Mode variability. *J. Geophys. Res.* 113, C03S90.

Strindberg, S. and Burt, L. 2004. IWC Database-Estimation Software System (DESS) user manual. Research Unit for Wildlife Population Assessment, University of St Andrews, St Andrews.

Thiele, D. and Gill, P.C. 1999. Cetacean observations during a winter voyage into Antarctic sea ice south of Australia. *Antarct. Sci.* 11(1): 48-53.

Thiele, D., Chester, E.T. and Asmus, K. 2005. Antarctic sea ice: measuring habitat complexity, and seasonal and regional variability in habitat use for minke whales. Paper SC/57/E1 presented to the IWC Scientific Committee, June 2005 (unpublished). 21pp. [Paper available from the Office of the IWC].

Thiele, D., Chester, E. and Friedlaender, A. 2002. Antarctic sea-ice habitat for minke whales (*Balaenoptera acutorostrata* sp.). Results of a line transect survey in East Antarctica. Paper SC/54/IA6 presented to the IWC Scientific Committee, April 2002 (unpublished). 14pp. [Paper available from the Office of the IWC].

Thiele, D., Chester, E.T. and Gill, P.C. 2000. Cetacean distribution off Eastern Antarctica (80-150°E) during the Austral summer of 1995/1996. *Deep-Sea Res. II* 47(12-13): 2543-2572.

Thiele, D., Chester, E.T., Moore, S.E., Širovic, A., Hildebrand, J.A. and Friedlaender, A.S. 2004. Seasonal variability in whale encounters in the Western Antarctic Peninsula. *Deep-Sea Res. II* 51(17-19): 2311-2325.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. and Marques, T.A. 2006. Distance 5.0. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.

Tynan, C. and Thiele, D. 2003. Report on Antarctic ice edge definition by the ad hoc Working Group on ice data collection in the Antarctic. Paper SC/55/E19 presented to the IWC Scientific Committee, May 2003 (unpublished). 1pp. [Paper available from the Office of the IWC].

Tynan, C.T. 1998. Ecological importance of the Southern Boundary of the Antarctic Circumpolar Current. *Nature* 392: 708-710.

van Franeker, J.A. 1992. Top predators as indicators for ecosystem events in the confluence zone and marginal ice zone of the Weddell and Scotia Seas, Antarctica, November 1988 to January 1989 (EPOS Leg 2). *Polar Biol*. 12: 93-102.

Wood, S.N. 2006. *Generalized Additive Models: an introduction with R.* Chapman & Hall, New York. 391pp.

Wood, S.N. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. *J. R. Statist. Soc. B* 70(3): 495-518.

Zwally, H.J., Comiso, J.C., Parkinson, C.L., Cavalieri, D.J. and Gloersen, P. 2002. Variability of Antarctic sea ice 1979-1998. *J. Geophys. Res.* 107(C5), 3041.

Sea ice as environmental driver of spatial and temporal variability in summer density of Antarctic minke whales

Bas W.P.M. Beekmans
Jaume Forcada
Eugene J. Murphy
Hein J.W. de Baar
Ulrich V. Bathmann
Andrew H. Fleming

3

ABSTRACT

The Southern Ocean is expected to be greatly influenced by climate change in the future. In order to predict the effect of these changes on Antarctic minke whales, we need to know how their distribution is currently influenced by physical and biological drivers. To answer this question we applied Generalised Additive Models (GAMs) to a circumpolar 24-year time series of ship-borne data collected by the International Whaling Commission (IWC). The GAMs were fitted independently by survey year with the environment mostly represented by remotely sensed data. Estimates of mean whale density ranged from 0.002 to 0.138 whales/km^2. Particular areas of the Ross Sea, Weddell Sea and Prydz Bay contained relatively high whale densities for several sets of surveys. Most open water areas with high predicted whale densities were found close to the sea ice edge and, in some years, the continental shelf break. We identified eight regions which were surveyed at least three times. In three out of eight regions, mean whale densities differed significantly between survey years. Furthermore, we found significant positive relationships between mean whale density and three sea ice variables, i.e. total and mean daily change in sea ice cover during spring/early summer and summer sea ice cover. We speculate that the percentage of summer sea ice cover and its average daily change during spring and early summer may determine higher mean density of minke whales through a positive effect on mainly Antarctic krill in certain regions of the Southern Ocean, such as the South Atlantic sector. However, regional qualitative differences were found in the relationships between mean density of minke whales and sea ice variables presented in this study. These regional differences suggest a more complex interaction between sea ice and other aspects of the minke whale environment, such as a positive interaction between closest distances to the sea ice edge and the continental shelf break.

Keywords

Antarctic minke whale, distribution, density, sea ice, Southern Ocean, spatial modelling

INTRODUCTION

A good understanding of the spatio-temporal relationships between Antarctic minke whales *Balaenoptera bonaerensis* and their environment is required to predict how these whales may react to future changes in their environment. The Southern Ocean is the main feeding ground for baleen whales, including Antarctic minke whales (Laws, 1977), in the Southern Hemisphere. During austral summer months in these waters, the animals primarily forage on Antarctic krill *Euphausia superba* (Ichii and Kato, 1991; Kawamura, 1994). Although Antarctic minke whales are often associated with sea ice, with the highest densities of whales close to the sea ice edge, they also occur in open waters away from the ice (Kasamatsu et al., 1998, 2000; Thiele et al., 2000; Murase et al., 2002). This study will focus on open waters of the Southern Ocean where a series of extensive surveys have been undertaken.

Since the early 1980s, some areas of the Southern Ocean have experienced substantial warming and a decrease in summer sea ice cover, while summer sea ice cover has increased in other areas over time. The western Antarctic Peninsula region is one of the most rapidly warming regions on the planet (Vaughan et al., 2003), with a near 3°C rise in annual mean atmospheric temperature between 1951 and 2000 (Turner et al., 2005) and a more than 1°C summer warming of surface waters in the Bellingshausen Sea between 1955 and 1994 (Meredith and King, 2005). In addition, the West Antarctic Ice Sheet experienced an annual mean temperature increase of 2.4°C between 1958 and 2010 (Bromwich et al., 2013). For austral summer months (January-March), trends in sea ice extent for the period 1979-2013 are negative in the Bellingshausen/ Amundsen Seas and positive in the eastern Weddell and western Ross Seas (Zwally et al., 2002; Turner et al., 2016). Trends in sea ice season duration for 1979-2004 show a similar pattern, with a shorter sea ice season for the western Antarctic Peninsula/ southern Bellingshausen Sea region and a longer sea ice season for the western Ross Sea region (Stammerjohn et al., 2008). Sea surface temperatures for the Southern Ocean are expected to increase through the rest of the 21st century. However, the expected rise in sea surface temperature in the Southern Ocean is likely lower than the expected global mean rate of temperature increase (Christensen et al., 2013; IPCC, 2013).

Both sea ice conditions and sea surface temperature are positively correlated with aspects of regional Antarctic krill populations in the South Atlantic sector. Summer krill recruitment in the waters near Elephant Island and the South Shetland Islands is positively correlated with sea ice extent in the Bellingshausen Sea and west Antarctic Peninsula region during the preceding winter (Siegel and Loeb 1995; Loeb et al., 1997; Brierley et al., 1999; Hewitt et al., 2003). At South Georgia, changes in krill biomass have been related to regional sea surface temperatures and sea ice extent (Brierley et al., 1999; Murphy et al., 2007; Fielding et al., 2014). Furthermore, summer krill (numerical) density in the Southwest Atlantic shows a positive relationship with sea ice cover and duration in the same region during the previous winter (Atkinson et al., 2004). The relationships are complex, which can generate lags in the relationships between variability in regional oceanic and ice conditions and changes in krill abundance and biomass. For instance, Murphy et al. (2007)

reported an increase in biomass of Antarctic krill near South Georgia, 12-24 months after a warm spring in the South Atlantic. Changes in sea ice dynamics are likely to affect regional populations of minke whales through changes in the physical and biological habitats, which are probably accompanied by changes in prey distribution and abundance (Nicol et al., 2008).

For almost 30 years, the International Whaling Commission (IWC) has conducted visual shipboard surveys under the IDCR (International Decade of Cetacean Research) and SOWER (Southern Ocean Whale and Ecosystem Research) programmes in all sectors of the Southern Ocean (Matsuoka et al., 2003). These IWC/IDCR-SOWER surveys were designed to visually detect cetaceans, with a special emphasis on Antarctic minke whales to estimate their abundance. This has resulted in three complete circumpolar (CP) sets of surveys, namely CPI (1978/79-1983/84), CPII (1985/86-1990/91) and CPIII (1991/92-2003/04). Abundance estimates of Antarctic minke whales are substantially lower for CPIII than for the other two circumpolar sets of surveys (Branch, 2006a). However, it is unclear whether the lower estimates reflect a real decline in the number of Antarctic minke whales or result from changes in survey design or analysis methods (Branch, 2006b). Examining changes in the physical environment that influence whales and their distribution is an effective way to investigate the potential factors that control whale density, and address some of the uncertainty.

We developed spatial models for summer density of Antarctic minke whales in open waters of the Southern Ocean based on data collected during the IWC/IDCR-SOWER surveys. In this paper we present composite circumpolar prediction maps of the density of Antarctic minke whales, to show regions with relatively high predicted densities of minke whales. We used regional prediction maps to study changes in density distributions of minke whales over time and to characterise the physical environment associated with relatively high predicted whale density. For selected regions across all sectors of the Southern Ocean, we estimated mean density of whales for the surveys conducted within the specific region and analysed the variance of these mean predicted densities in relation with variables describing the sea ice environment.

MATERIALS AND METHODS

Study area and effort

The IWC has divided the Southern Ocean into six Management Areas (Figure 3.1) (Mackintosh, 1942; Donovan, 1991). During each survey, 2-4 vessels covered the open waters of each Management Area, thereby excluding the pack ice region and polynyas within this region. We decided not to develop spatial models for the first three surveys of the programme, conducted during the 1978/79-1980/81 field seasons, as the selected satellite records for those seasons did not contain sea ice concentration and sea surface temperature data that were comparable to data available in subsequent years. From these later datasets, potential predictors of whale density could be derived that are deemed important for this analysis. Thus, we developed spatial models using line transect data collected during the 1981/82 – 2004/05 surveys.

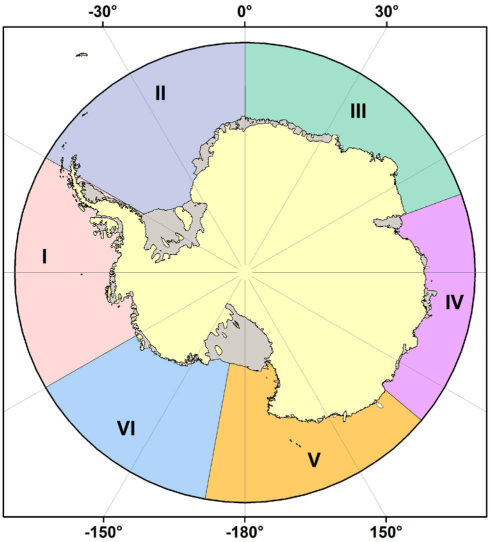


Figure 3.1. IWC management Areas in the Southern Ocean (Mackintosh, 1942; Donovan, 1991). See Branch and Butterworth (2001) and Branch (2006a) for detailed maps of the strata surveyed during the IDCR/SOWER programme.

One out of six IWC management Areas (Figure 3.1) was at least partly surveyed during each field season. The surveys varied in timing and duration, but were always conducted during the austral summer, between the end of December to the beginning of March of each season. The surveys covered areas ranging from 0.690 million km^2 (2001/02 survey) to 3.305 million km^2 (1985/86 survey). Survey effort was lowest (3,409 km) for the 1999/2000 survey in Area I, and highest (15,645 km) for the 1985/86 survey in Area V. The number of sighted Antarctic minke whale schools per km effort ranged from 0.016 (Area I, 1999/2000 survey) to 0.096 (Area V, 2003/04 survey). The number of sighted Antarctic minke whales per km effort ranged from 0.028 (Area I, 1999/2000 survey) to 0.291 (Area V, 2003/04 survey). A more detailed description of the surveys underlying the spatial models is given in Matsuoka et al. (2003).

Whale sightings and detection probabilities

During shipboard surveys, observers could confuse Antarctic minke whales with dwarf minke whales, an unnamed subspecies of the common minke whale (*Balaenoptera acutorostrata*). However, probably less than 1% of the minke whales in the Southern Ocean are dwarf minke whales (Leaper et al., 2008). Therefore, we extracted sightings coded as 04, 91 and 92 (all classified as "definitely minke whale") and 39 ("like minke whale") from the DESS (IWC Database-Estimation Software System) V3.52 database package (Strindberg and Burt, 2004), under the assumption that these sightings represented Antarctic minke whales (Branch and Ensor, 2001; Branch and Butterworth, 2001; Branch, 2006a). We used sightings collected during either Independent

Observer (IO) or closing mode. In IO mode, the vessel keeps following the track line after a sighting, with the two observer teams on the primary and secondary platform on full search effort. Meanwhile, the observers on the upper bridge track and identify the sighting. In contrast, in closing mode the vessel leaves the track line and approaches the sighting, thereby adjourning search effort. Sometimes whale schools were sighted two or three times during the survey and recorded as duplicates or triplicates in DESS, respectively. Each duplicate/triplicate was coded as either "definite", "possible", "remotely possible" or "uncertain". We only included the first sighting of a "definite" duplicate/triplicate. Duplicates/triplicates coded otherwise were treated as sightings of distinct schools (Branch and Butterworth, 2001). We used Method II of Buckland and Anganuzzi (1988) to smear radial distances and angles to account for rounding errors in sighting angles and distances. After smearing, sightings were truncated at 2.8 km perpendicular distance (Branch and Butterworth, 2001).

For the estimation of detection probabilities, we used Mark Recapture Distance Sampling (MRDS) methods as implemented in Distance 5.0 release 2 (Thomas et al., 2006) and the package *mrds* (V1.2.9) of program R., V.2.9.2 (R Development Core Team, 2008). An MRDS detection function consists of a distance sampling (DS) and mark recapture (MR) component (Laake and Borchers, 2004). For the DS component, we considered the half-normal and hazard-rate key functions without any adjustment terms (Buckland et al., 2001). We assumed "point independence" for the MR component (Laake and Borchers, 2004) and considered school size, sightability and seastate as covariates for both components. See Chapter 2 of this thesis for a detailed description of the methodology used for estimating detection probabilities.

Remote sensing data

Limited non-biotic data were collected during the above described cruises and zooplankton was not sampled. Therefore, remote sensing datasets are the best available complementary sources of spatially explicit data available to examine the relationship between whale density and the physical environment.

Sea ice concentrations were based on weekly passive microwave remote sensing data, derived from measurements made by the Scanning Multichannel Microwave Radiometer (SMMR) onboard the Nimbus-7 satellite and by the Special Sensor Microwave Imagers (SSM/I) onboard Defense Meteorological Satellite Program (DMSP) satellites F8, F11 and F13. We used version 2 of the sea ice concentration data, released in September 2007, which had a 0.2° x 0.2° resolution (Cavalieri et al., 1996, updated 2006). For sea surface temperature, we used Optimum Interpolation version 2 Sea Surface Temperature (hereafter called OISST) data (Reynolds and Smith, 1994; Reynolds et al., 2002), provided on an approximately 7 day interval one-degree latitude-longitude grid (ftp://ftp.emc.ncep.noaa.gov/cmb/sst/oisst_v2/). We obtained bathymetric data from the General Bathymetric Chart of the Oceans (GEBCO) dataset, at a latitude-longitude resolution of one minute (IOC et al., 2003). Eight-day average 0.083° x 0.083° gridded chlorophyll *a* concentration data were derived from the NASA Sea-viewing Wide Field-of-view Sensor (SeaWiFS) dataset (http://oceancolor.gsfc.nasa.gov/SeaWiFS/). We obtained information on frontal zone positions from two sources. Firstly, we used positions of the Southern Antarctic Circumpolar Current Front (SACCF) and the Southern Boundary of the Antarctic Circumpolar Current (SBACC) as identified and defined by Orsi et al. (1995), based on long-term datasets. Secondly, we considered sea surface velocities (SSV) derived from absolute geostrophic velocities provided by AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data) on a weekly 1/3° x 1/3° Mercator grid based on measurements by altimetry instruments onboard the Topex/Poseidon, Jason-1, ERS and ENVISAT satellites. The two datasets were complementary: SSV data reflected the conditions during the time of survey more accurately; however, these data were only available from October 1992 onwards. In contrast, the mean frontal zone positions presented by Orsi et al. (1995) could be used for all surveys, under the assumption that these mean positions were still representative for frontal positions during the time of more recent surveys.

Spatial models and potential covariates

Sightings of Antarctic minke whales were used as input for spatial models based on line transect data. We used Generalised Additive Model (GAM) methodology developed by Wood (2006) and implemented in the R software library *mgcv* (V1.5-5). The count method developed by Hedley et al. (1999) was applied; we divided the transect line into equal segments of ten nautical miles survey effort. We estimated N_i, the number of Antarctic minke whales per segment area, using the following Horvitz-Thompson-like (Horvitz and Thompson, 1952) estimator:

$$\hat{N}_i = \sum_j \frac{n_{i,j}}{\hat{p}.(x,\underline{z})_{i,j}} \tag{3.1}$$

where: $n_{i,j}$ = the number of minke whales within group *j* in segment *i*;
$\hat{p}.(x,\underline{z})_{i,j}$ = the estimated probability that at least one of the observers detects the *j*th group in segment *i*, at perpendicular distance *x* from the track line, given the covariate vector $\underline{z}$.

See Chapter 2 of this thesis for more details on estimation of N_i. In this study, $\hat{N}_i$ was the response variable for GAMs that assumed a logarithmic link-function and a Tweedie distribution. The variance of a Tweedie distribution is proportional to the power θ of the mean. We also considered the quasi-Poisson and simple Poisson error distributions which are special cases of the more general Tweedie distribution (Peel et al., 2008). The GAMs in this study had the following structure (Hedley et al., 1999), with the natural logarithm of the segment area as an offset variable:

$$E(\hat{N}_i)=\exp\left[\ln(A_i)+\theta_0+\sum_r f_r\left(k_{i,r}\right)\right] \tag{3.2}$$

where: A_i = segment area, equal to 2 l_i w (l_i = segment length, with w = 1.5nm);
θ_0= intercept;
$k_{i,r}$ = value of covariate r for segment i;
f_r = smoothed function ("smoother") of covariate r.

Two different smoother function types were considered, namely isotrophic smoothers and tensor product smoothers. We considered the following potential covariates as input for the spatial models: closest distance to the sea ice edge (*icedist*, defined at 15% sea ice concentration (Tynan and Thiele, 2003)), OISST, bathymetric depth and nearest distance to the continental shelf break (*1000m-dist*, defined as the 1000m depth contour), SSV and closest distances to the SACCF and SBACC (*SACCFdist* and *SBACCdist*), chlorophyll *a* concentration, latitude and longitude (latter two covariates both in degrees).

The GAMs were fitted independently by survey year. We based model selection on maximisation of the explained deviance and minimisation of the Generalised Cross Validation (GCV) score and excluded models that generated extreme values of minke whale density because of sparse coverage of the covariate range. The GAMs have a tendency to overfit the data (Forney 2000, Hastie et al., 2005), thus we constrained the degree of smoothing by setting the argument gamma to 1.4 within the function "gam" of package *mgcv* (Wood, 2006, p. 256). We used forward covariate selection: in each step, covariates were considered which had correlation coefficients smaller than 0.7 with the covariates that were already selected in previous steps to avoid collinearity problems. In each step, we only retained the covariate for which inclusion showed the largest increase in explained deviance compared to the model from the previous step. A new covariate was only retained if it was (i) significant, (ii) lowered the GCV score and (iii) increased the deviance explained by at least 4% (Southwell et al., 2008).

Circumpolar and regional predicted Antarctic minke whale density maps

The selected spatial models were used for generation of density surfaces of Antarctic minke whales for surveyed strata within each management Area, mainly below 60°S. We standardised the results by defining whale density $\hat{D}_p$ as $\hat{N}_p/A_p$, the estimated number of Antarctic minke whales per km^2 for grid cell p. All maps were plotted on a 0.2° x 0.2° grid with ESRI ArcMap V9.3.1 (ESRI, 2009). We calculated the segment area per grid cell, A_p, using the South Pole Lambert Azimuthal Equal Area polar projection within ArcMap. For each cell p, we calculated effort, which was defined as the number of years the particular cell was included in the surveyed strata. Furthermore, we estimated the mean and standard deviation of density for each cell p. The latter variable could only be estimated for cells that were surveyed multiple times (effort > 1). The circumpolar maps for effort, mean density and standard deviation of density were created with two aims. The first aim was to gain insight in the degree of spatial variability in density of minke whales at the circumpolar scale. The second aim was to identify regions with relatively high predicted densities of minke whales within the Southern Ocean. These regions were all in open waters, i.e. they were not covered with sea ice at the time of survey. The selected GAMs were based on surveys that had an overlapping time period from 20 January to 27 January. For each survey, we derived covariate values for this time period within the survey season and used these values as input for the generation of predicted densities. As such, the resulting circumpolar maps summarised output of models fitted with data from surveys in various Management Areas conducted in different years.

In addition, we created regional predicted density maps in order to characterise the environment for the areas with relatively high predicted whale density. Furthermore, we used these maps to compare density distributions in the same region for the different surveys conducted within the specific region. For each surveyed stratum, we derived covariate values for the middle date of the stratum-specific survey period. This way, the covariate values more closely resembled the average environmental conditions experienced during the survey.

Estimation of mean predicted density of Antarctic minke whales

We identified regions, defined by their longitudinal ranges, that were surveyed at least three times under the IWC/IDCR-SOWER programme between 1981/82 and 2004/05. In order to investigate the temporal variability in density of Antarctic minke whales, we calculated mean predicted density ($\hat{\bar{D}}_p$) for these regions, based on covariate values for the middle date of the stratum-specific survey periods.

Over the years, survey design has changed for the IWC/IDCR-SOWER surveys. Almost all open waters within the full latitudinal range from below 60°S to the sea ice edge were surveyed in CPIII. In contrast, the surveyed strata covered only about 65% and 81% of the open water area in CPI and CPII, respectively (Branch and Butterworth, 2001). Especially the open water area at greater distance from the sea ice edge, at lower latitudes, was relatively poorly covered by the earlier surveys. As density of minke whales often tends to decrease with lower latitude (Kasamatsu et al., 1988, 1996), not taking into account the change in survey design could introduce a negative bias in mean predicted density for the CPIII surveys. Therefore, we only estimated mean predicted density for a surveyed area within a specific distance from the estimated location of the sea ice edge on the middle date of the stratum-specific survey period. We set the distance limit at 212 km, which was the minimum distance between the northern boundary of the strata surveyed and the estimated location of the sea ice edge for the 1982/83 survey, for which this minimum distance was smallest among the surveys. The distance limit was equal for all surveys included in this study.

Variance estimation

We used a nonparametric bootstrap, a resampling method, on both stages of detection probability estimation and GAM fitting to obtain variance estimates for mean density of Antarctic minke whales for each area of interest and survey year. We bootstrapped the data by stratum (n = 1000 bootstrap samples) and considered days on effort as sampling unit. Days with only a few segments were pooled with the preceding or following days to form one sampling unit. This way, the number of resampled segments would be similar for all bootstraps while preserving the spatial structure of the original dataset. We used day of survey as sampling unit for strata that had at least ten sampling units after pooling. For strata with fewer than ten sampling units, we used a moving-blocks bootstrap (Efron and Tibshirani, 1993) with block length of 92.6 km (five segments). The resulting bootstrap estimates were slightly biased and required rescaling. Thus, we multiplied the bootstrap estimates by the ratio of the original mean density estimate to the mean of the bootstrap estimates. The coefficient of variation was defined as the standard deviation of the rescaled bootstrap estimates divided by the original mean density estimate (Clarke et al., 2003).

Derivation of regional sea ice variables

For each region and survey, we identified the following sea ice variables:

1) *Icemax* = maximum sea ice cover within the region for the period September (before the survey) until the middle date of the survey period. We calculated *icemax* for the same time of year for all surveys within the specific region. Unit: km^2.
2) *Icemiddle* = summer sea ice cover within the region at the middle date of the survey period. Unit: km^2.
3) *Icechange* = change in sea ice cover within the region, defined as (1) minus (2). Unit: km^2.
4) *Icechangedaily* = mean daily change in sea ice cover (unit: km^2/day) within the region. As time periods varied for the surveys conducted in the same region, so did the middle dates of the surveys. Changes in sea ice cover as defined under (3) could be the result of both sea ice dynamics and timing of survey. Therefore, ice change was better calculated as the mean daily change in sea ice cover, which is the sea ice variable under (3) divided by the number of days within the time period between the date of maximum sea ice cover and middle date of the survey.

Spatial and temporal variability in mean predicted density estimates of Antarctic minke whales

In order to detect significant differences in mean density estimates of minke whales for a specific region, we carried out *z*-tests for all combinations of surveys conducted within that region by calculating *z*-values defined as (Buckland et al., 2001):

$$\frac{\left(\hat{D}_0 - \hat{D}_1\right)}{\sqrt{\left\{\widehat{SD}\left(\hat{D}_0\right)\right\}^2 + \left\{\widehat{SD}\left(\hat{D}_1\right)\right\}^2}} \tag{3.3}$$

where: $\hat{D}_i$ = mean whale density estimate within region-specific distance limit for survey *i*
$\widehat{SD}$ = standard deviation of the rescaled bootstrap estimates for mean density

As the distribution of rescaled bootstrap estimates is approximately normal, two mean density estimates are significantly different from each other at the 5% level if $|z| > 1.96$.

We used analysis of variance (ANOVA) with mean density as response variable to test trends and relationships between mean density and sea ice related variables for significance. We defined *trend* as a numeric variable, for which the number sequence followed the chronological order of the surveys conducted within a specific region. Other potential covariates were: *region* as a factor variable, *period* (number of days between the date of maximum sea ice cover and the middle date of the survey) and the four sea ice variables as earlier mentioned. The mean densities were weighted by their inverse variance. We used the Akaike Information Criterion (AIC) as selection criterion (Akaike, 1973). We selected the ANOVA which included only significant covariates and for which ΔAIC < 2 with ΔAIC defined as the difference between the AIC of a fitted model and the minimal AIC for all fitted models.

RESULTS

Detection probabilities

Mark recapture data were not collected during the surveys conducted between 1981/82 and 1984/85. Therefore, only average detection probabilities of detecting a whale school within 2.8 km (1.5 nautical miles) could be directly estimated from the distance sampling data collected during these surveys, under the assumption that all whale schools were detected on the transect line. These detection probabilities ranged from 0.392 (SE=0.048) to 0.576 (SE=0.022). School size was the only covariate often included in the detection function models, apart from perpendicular distance. Both components of the MRDS detection function could be directly estimated from data collected during the surveys between 1985/86 and 2003/04. Average detection probabilities of detecting a whale school on the transect line, estimated from the MR component, ranged from 0.561 (SE = 0.027) to 0.724 (SE = 0.031) for these surveys. School size was always selected as a variable in the MR component, and in some detection function models this component included sea state as well. The average probability of detecting a whale school within 2.8 km from the survey vessel ranged from 0.182 (SE=0.021) to 0.338 (SE=0.019). The inclusion of sightability as a covariate never improved model fit. More detailed results from the distance sampling analysis can be found in chapter 2 of this thesis.

Spatial models and selected covariates

We fitted simple GAMs which had explained deviances ranging from 14.9% to 35.1%; the mean explained deviance was 25.3%. We were not able to select a good model based on environmental covariates for the 1995/96 and 2001/02 surveys. The selected GAMs consisted of combinations of seven out of ten potential covariates: only SSV, chlorophyll *a* concentration and latitude were never selected. Of the environmental covariates, closest distance to the continental shelf break

(*1000m-dist*), sea ice edge (*icedist*) and SACCF (*SACCFdist*) were most often included in the models. The GAM output highlighted the highly variable nature of the relationships between minke whale density and its environment. Selected models for the same Management Area included different sets of environmental covariates. Furthermore, none of the environmental covariates had a consistent qualitative effect on minke whale density. However, three covariates (*1000m-dist*, *icedist* and OISST) showed a predominantly negative relationship with density. The Eastern Ross Sea region (170-140°W) was surveyed three times, but we could not fit a good model for the 1995/96 survey conducted in this region. Instead, we fitted a simple GAM with only latitude and longitude as isotrophic smoothers for this survey, which enabled us to include the Eastern Ross Sea region in the ANOVA model selection.

Circumpolar maps

Figures 3.2a-c are circumpolar maps of effort, mean density and standard deviation of density, summarising three circumpolar sets of surveys. Most of the Southern Ocean was surveyed two or three times within the 1981/82 – 2004/05 time period. Only parts of the open ocean between 60-80°W and 170°E-170°W were surveyed four times (Figure 3.2a). The circumpolar map of mean predicted density of Antarctic minke whales (Figure 3.2b) shows a heterogeneous distribution of whale density. Mean whale density was lower than 0.12 whales/km^2 for most surveyed areas north of 65°S. Mean densities higher than 0.24 whales/km^2 were mostly found south of 70°S, close to the sea ice edge and close to or on the continental shelf. Mean densities higher than 0.18 whales/km^2 were often found in areas that were only surveyed once. Examples are the areas in the Weddell Sea (between 25-40°W, below 67°S), and in the Indian Ocean sector (between 60-70°W, below 65°S). However, mean densities higher than 0.18 whales/km^2 were also found on the continental shelf in the Ross Sea (between 165°E-170°W, south of ~70°S), most of which was surveyed two or three times. Most of the highest standard deviations were found in this area as well (Figure 3.2c). Mean whale density was low in parts of the Indian Ocean sector (particularly in the 30-50°E and 80-130°E regions), and in the eastern Ross Sea/western Amundsen Sea (140-160°W) (Figure 3.2b).

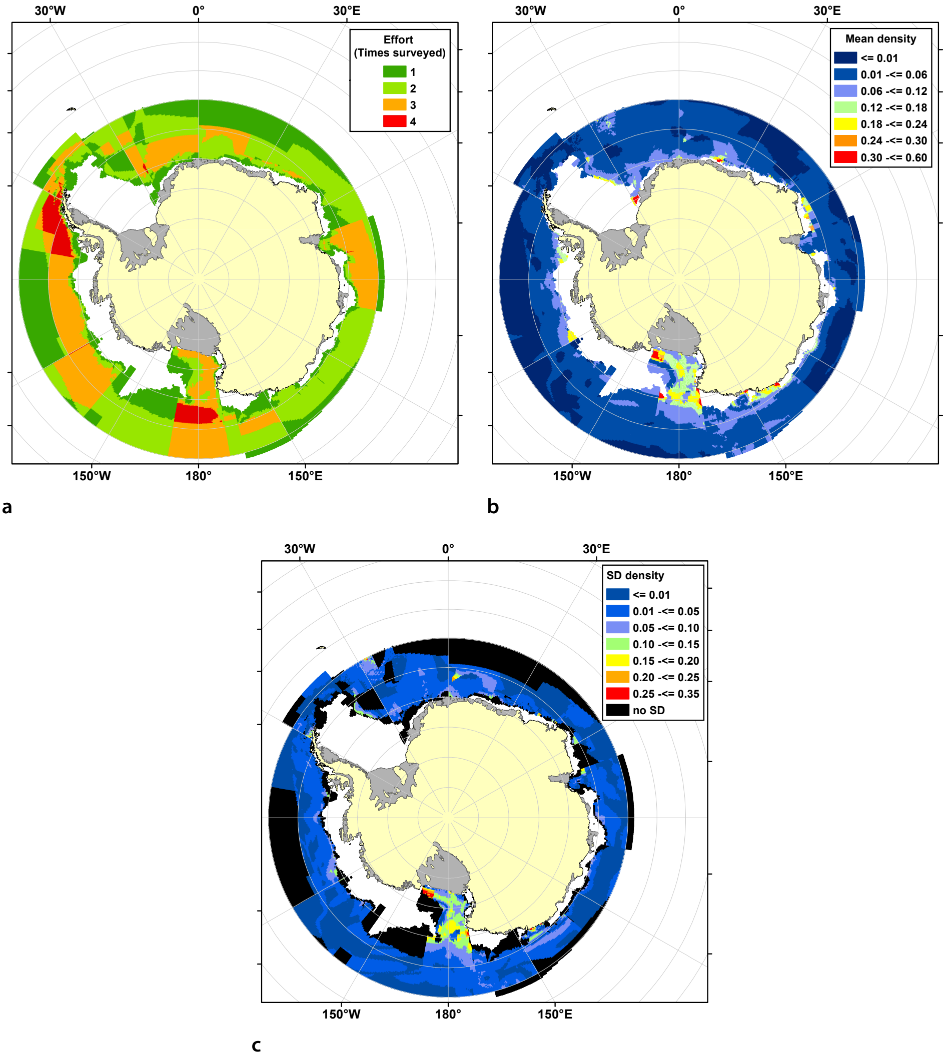
Regional spatial variability

We identified eight regions that were surveyed at least three times (Table 3.1). In this section we describe the spatial distributions of predicted densities of Antarctic minke whales per region for each survey year.

Amundsen Sea, Bellingshausen Sea, Western Antarctic Peninsula region (region 1, 110-60°W)

For 1982/83, 1989/90 and 1993/94, predicted densities of Antarctic minke whales above 0.10 whales/km^2 are largely found close to the sea ice edge, but with different longitudinal ranges by survey. The plot for 1982/83 (Figure 3.3a) shows predicted densities of Antarctic minke whales above 0.10 whales/km^2 within the 80-110°W region, relatively close to the continental shelf.

For 1989/90, this longitudinal range stretches from 70-110°W (Figure 3.3b), in relatively cold waters (below 0°C). Furthermore, whale densities above 0.10 whales/km^2 within 70-85°W were exclusively on the continental shelf for this survey. The 1993/94 model predicted relatively high densities in shallow waters between 65-85°W, on or close to the continental shelf and SBACC (Figure 3.3c). Whale densities never exceeded 0.05 whales/km^2 for 1999/2000 (Figure 3.3d).



a

b

c

Figure 3.2. Circumpolar prediction plots of a) survey effort, b) mean density of Antarctic minke whales and c) standard deviation of density for surveys conducted from 1981/82 to 2004/05. The dark grey area is the ice shelf region, white area surrounding the continent was unsurveyed area, mostly due to sea ice cover during the time of survey. Mean densities are shown for surveyed strata and based on environmental data during the overlapping period for all surveys, i.e. 20-27 January of each year.

Table 3.1. Mean predicted densities of Antarctic minke whales with corresponding standard deviations (SDs) and coefficients of variation (CVs) for eight selected regions in the Southern Ocean. The mean predicted densities were computed for all open waters within 212 km from the estimated position of the sea ice edge during the time of the survey. Mean density values with different superscripts within a region differ significantly.

IWC Area	Region	Longitudinal range region	Survey	Mean predicted whale density (whales/km^2)	Mean predicted whale density bootstrap (whales/km^2)	SD rescaled whale density bootstrap	CV rescaled whale density bootstrap (SD/ original mean estimate)
I	1	110-60°W	1982/83	0.056^{a}	0.060	0.015	0.266
			1989/90	0.039^{a}	0.041	0.014	0.360
			1993/94	0.038^{a}	0.042	0.016	0.414
II	2.1	60-30°W	1981/82	0.032^{a}	0.032	0.010	0.312
			1986/87	0.049^{a}	0.049	0.016	0.336
			1997/98	0.053^{a}	0.055	0.033	0.630
	2.2	30°W-0	1981/82	0.073^{a}	0.076	0.017	0.234
			1986/87	0.078^{a}	0.079	0.016	0.201
			1996/97	0.041^{a}	0.049	0.021	0.516
III	3	0-20°E	1987/88	0.088^{a}	0.089	0.034	0.386
			1992/93	0.151^{a}	0.156	0.043	0.285
			2004/05	0.020^{b}	0.023	0.008	0.398
IV	4	80-100°E	1984/85	0.028^{a}	0.035	0.009	0.333
			1988/89	0.007^{b}	0.006	0.004	0.526
			1998/99	0.034^{ab}	0.032	0.016	0.462
V	5	165°E-170°W	1985/86	0.130^{a}	0.117	0.025	0.194
			1991/92	0.086^{a}	0.108	0.048	0.564
			2003/04	0.138^{a}	0.151	0.071	0.511
VI	6.1	170-140°W	1983/84	0.049^{a}	0.054	0.016	0.331
			1990/91	0.002^{b}	0.002	0.001	0.312
			1995/96	0.029^{a}	0.023	0.009	0.310
	6.2	140-120°W	1983/84	0.016^{a}	0.019	0.007	0.445
			1990/91	0.031^{a}	0.032	0.011	0.351
			2000/2001	0.036^{a}	0.050	0.025	0.694

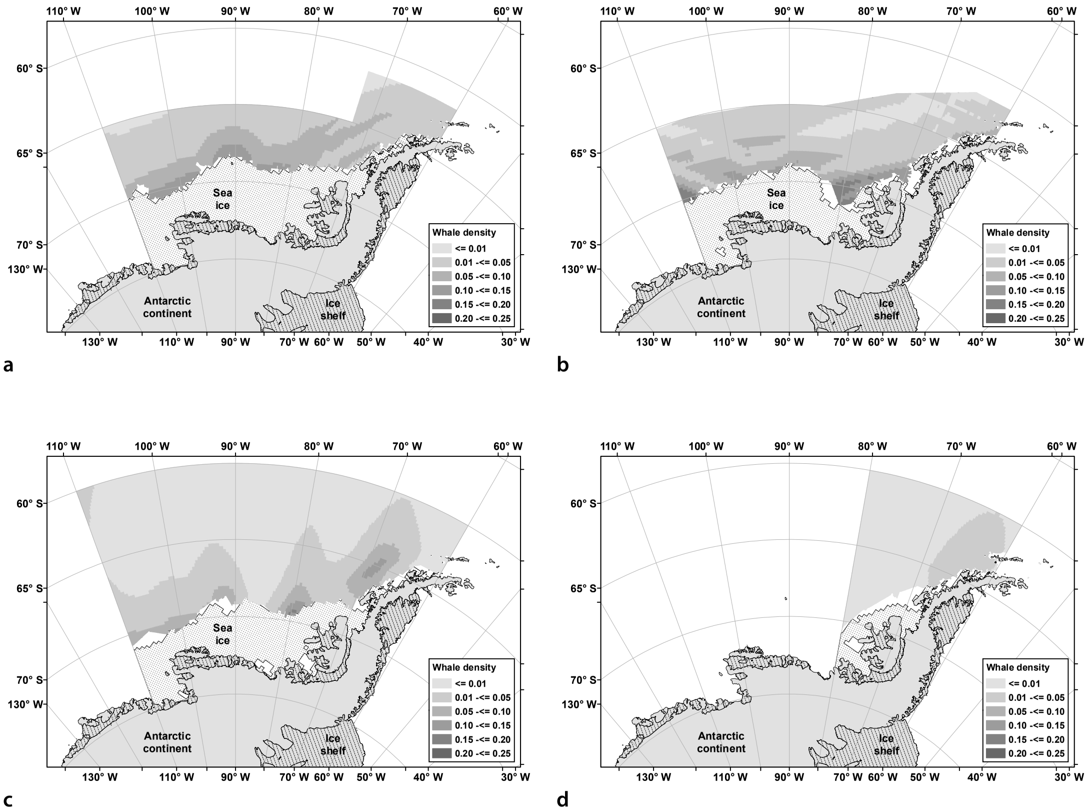


Figure 3.3. Prediction plots of Antarctic minke whale density for surveys conducted in the Amundsen Sea, Bellingshausen Sea and Western Antarctic Peninsula region (region 1, 60-110°W) within IWC management Area I. a) 1982/83 survey, b) 1989/90 survey, c) 1993/94 survey, d) 1999/2000 survey. The grey striped area is the ice shelf region, white dotted areas represent sea ice within 60-110°W (Figs 3a-c) or 60-80°W (Fig 3d). Densities are shown for surveyed strata and based on environmental data during the middle date of the stratum-specific survey period. As the displayed sea ice cover was derived for the middle date of the survey, some maps show white areas between the southern boundary of the surveyed area and the northern boundary of the sea ice.

Western Weddell Sea (region 2.1, 30-60°W)

Densities were all lower than 0.15 whales/km^2 for the 1981/82 survey (Figure 3.4a). The prediction map for 1986/87 (Figure 3.4b) shows two areas with densities above 0.15 whales/km^2, both in proximity of sea ice. One area was north of the Antarctic Peninsula, in shallow waters. The other area, with all predicted densities above 0.20 whales/km^2, was smaller and below 73°S, close to the continental shelf in cold waters (below -1.0°C). For 1997/98, the largest continuous area with whale density above 0.15 whales/km^2 was found between 30-40°W, in the proximity of sea ice in relatively cold waters (Figure 3.4c).

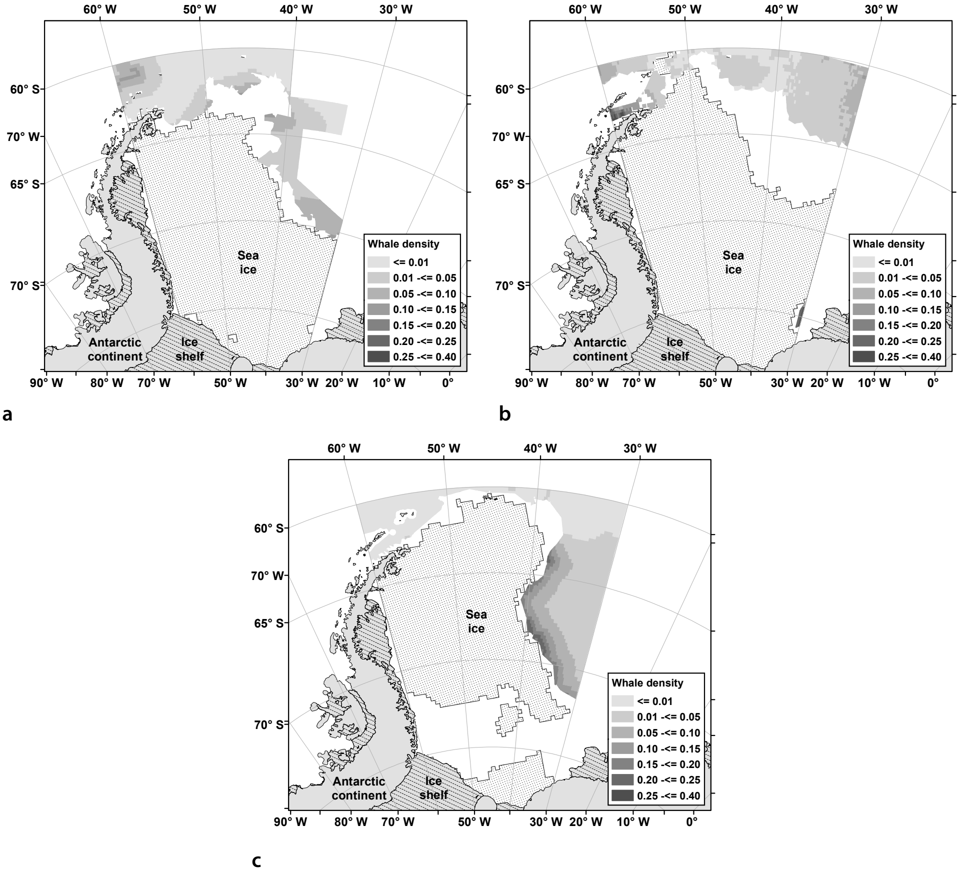


Figure 3.4. Prediction plots of Antarctic minke whale density for surveys conducted in the western Weddell Sea (region 2.1, 30-60°W) within IWC management Area II. a) 1981/82 survey, b) 1986/87 survey and c) 1997/98 survey. The grey striped area is the ice shelf region, white dotted areas represent sea ice within 30-60°W. Densities are shown for surveyed strata and based on environmental data during the middle date of the stratum-specific survey period. As the displayed sea ice cover was derived for the middle date of the survey, some maps show white areas between the southern boundary of the surveyed area and the northern boundary of the sea ice.

Eastern Weddell Sea, western Lazarev Sea (region 2.2, 0-30°W)

The density plot for 1981/82 (Figure 3.5a) shows whale densities above 0.09 whales/km^2 across most of the longitudinal range, close to the sea ice edge. Furthermore, these densities were predicted close to the continental shelf break between 0-11°W. For 1986/87, whale densities above 0.12 whales/km^2 were mainly found close to the sea ice edge and over or nearby the continental shelf (Figure 3.5b). It was only during this survey that sea ice retreat made it possible to survey waters south of 74°S, which had predicted whale densities above 0.15 whales/km^2. For 1996/97, whale densities above 0.06 whales/km^2 were mostly found within a narrow band below 70°S, close to the sea ice, near the continental shelf and in cold waters (Figure 3.5c).

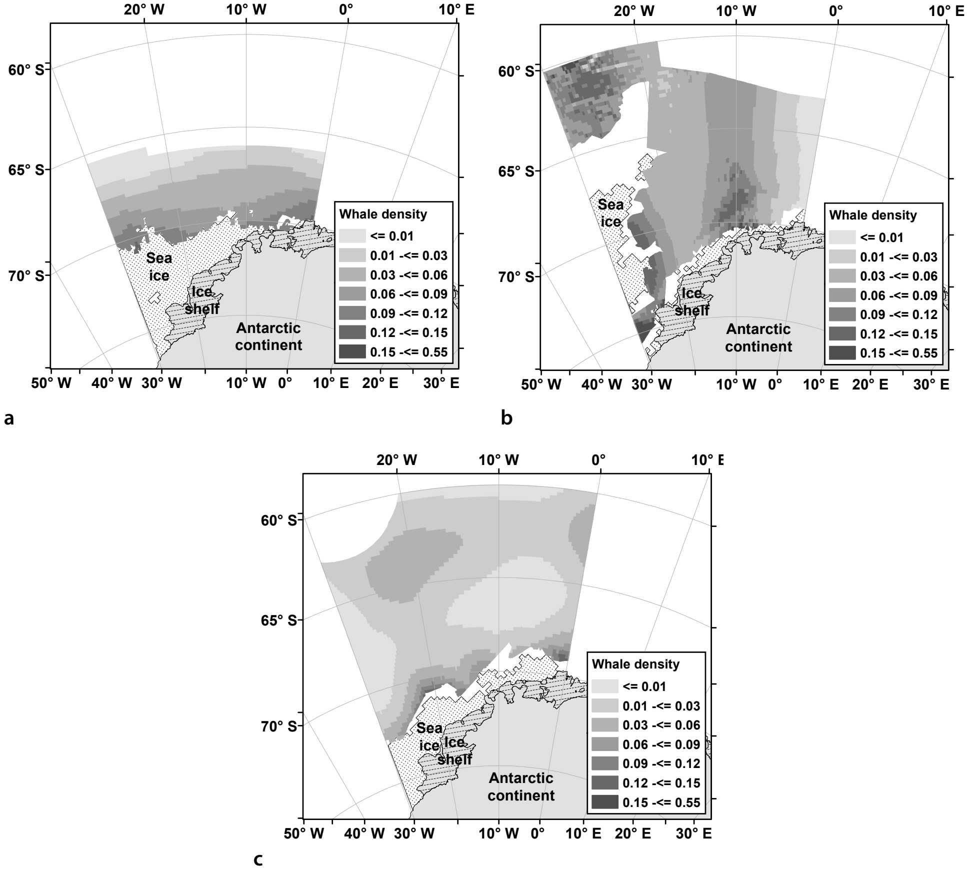


Figure 3.5. Prediction plots of Antarctic minke whale density for surveys conducted in the eastern Weddell Sea and western Lazarev Sea (region 2.2, 0-30°W) within IWC management Area II. a) 1981/82 survey, b) 1986/87 survey and c) 1996/97 survey. The grey striped area is the ice shelf region, white dotted areas represent sea ice within 0-30°W. Densities are shown for surveyed strata and based on environmental data during the middle date of the stratum-specific survey period. As the displayed sea ice cover was derived for the middle date of the survey, some maps show white areas between the southern boundary of the surveyed area and the northern boundary of the sea ice.

Eastern Lazarev Sea (region 3, 0-20°E)

The density plot for 1987/88 (Figure 3.6a) shows whale densities above 0.18 whales/km^2 only below 68°S, close to the sea ice and ice shelves. The model for 1992/93 predicted relatively high whale densities (above 0.18 whales/km^2) below 65°S between 0-6°E (Figure 3.6b), relatively close to the sea ice edge at the time of the survey. The southern boundary of the surveyed strata was generally at lower latitudes for the 1992/93 survey compared to 1987/88 and 2004/05. For 2004/05, whale densities above 0.12 whales/km^2 were only between 68-70°S and 15-20°E, in relatively cold waters close to the sea ice edge (Figure 3.6c). A large proportion of the area surveyed during 2004/05 had densities below or equal to 0.01 whales/km^2.

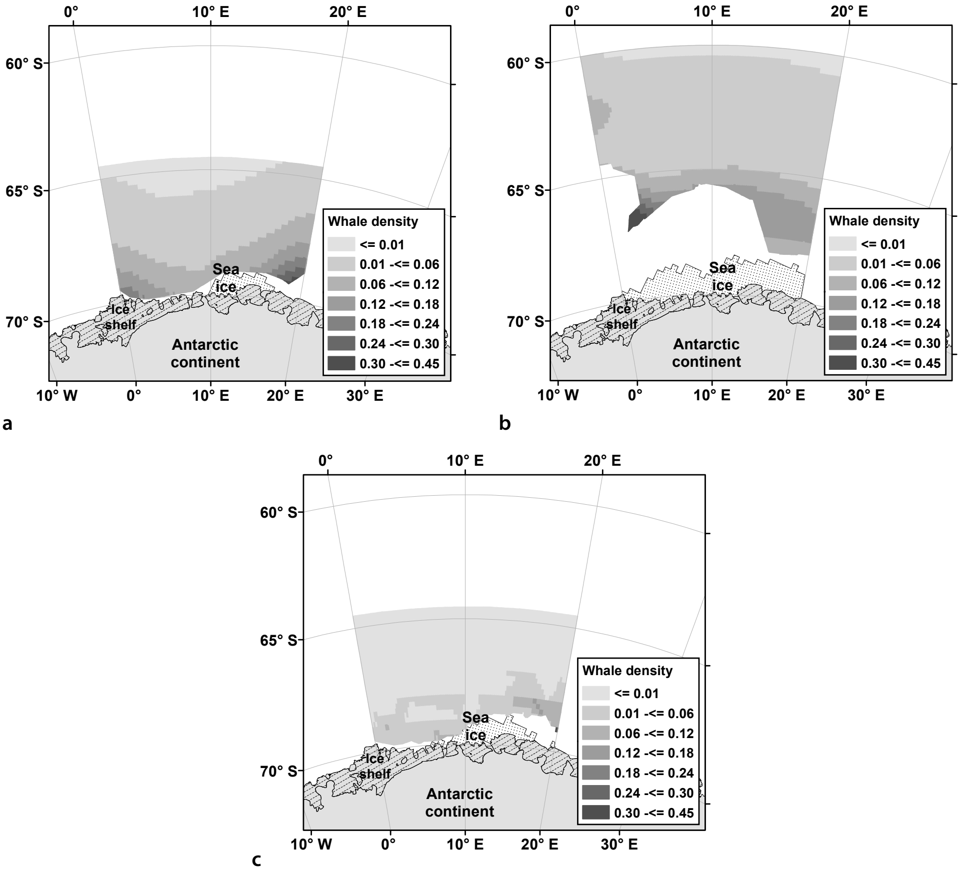


Figure 3.6. Prediction plots of Antarctic minke whale density for surveys conducted in the eastern Lazarev Sea (region 3, 0-20°E) within IWC management Area III. a) 1987/88 survey, b) 1992/93 survey and c) 2004/05 survey. The grey striped area is the ice shelf region, white dotted areas represent sea ice within 0-20°E. Densities are shown for surveyed strata and based on environmental data during the middle date of the stratum-specific survey period. As the displayed sea ice cover was derived for the middle date of the survey, some maps show white areas between the southern boundary of the surveyed area and the northern boundary of the sea ice.

Within Indian Ocean sector (region 4, 80-100°E)

The density plot for 1984/85 (Figure 3.7a) shows whale densities above 0.06 whales/km^2 for 62-65.5°S across the longitudinal range of this region, close to the sea ice edge and in relatively cold waters. All whale densities predicted by the 1988/89 model were below or equal to 0.03 whales/km^2 (Figure 3.7b). For this season, none of the predicted densities north of 63°S were higher than 0.01 whales/km^2. For 1998/99, the areas with density above 0.06 whales/km^2 were in the middle of the region, between 85-95°E (Figure 3.7c).

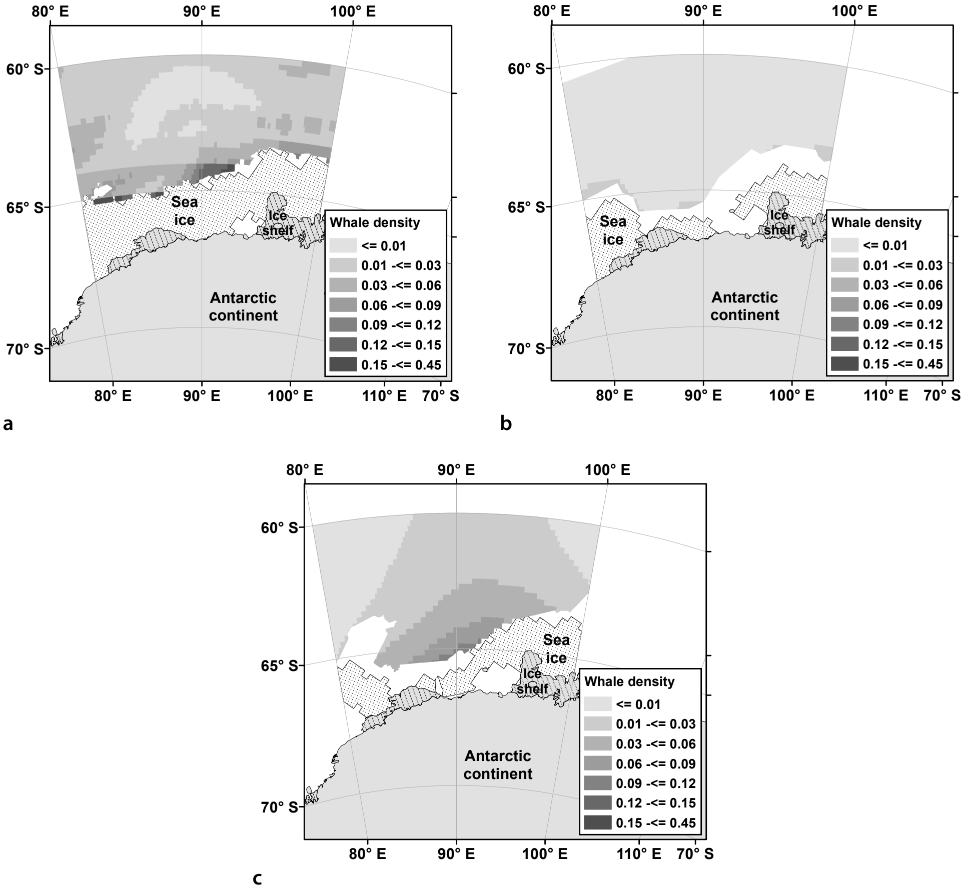


Figure 3.7. Prediction plots of Antarctic minke whale density for surveys conducted within the Indian sector of the Southern Ocean (region 4, 80-100°E) within IWC management Area IV. a) 1984/85 survey, b) 1988/89 survey and c) 1998/99 survey. The grey striped area is the ice shelf region, white dotted areas represent sea ice within 80-100°E. Densities are shown for surveyed strata and based on environmental data during the middle date of the stratum-specific survey period. As the displayed sea ice cover was derived for the middle date of the survey, some maps show white areas between the southern boundary of the surveyed area and the northern boundary of the sea ice.

Western Ross Sea (region 5, 165°E-170°W)

The density plot for 1985/86 (Figure 3.8a) shows extensive areas with high whale densities (above 0.18 whales/km^2) south of 72°S, on or close to the continental shelf. Effort in this region during the 1991/92 survey was only south of 65°S. For 1991/92, relatively high predicted whale densities (above 0.18 whales/km^2) were found across the whole latitudinal range, often in proximity of the sea ice edge at the time of survey (Figure 3.8b). The model for 2003/04 predicted one extensive area with whale densities above 0.18 whales/km^2, namely within the 67-75°S band (Figure 3.8c) on or near the continental shelf break.

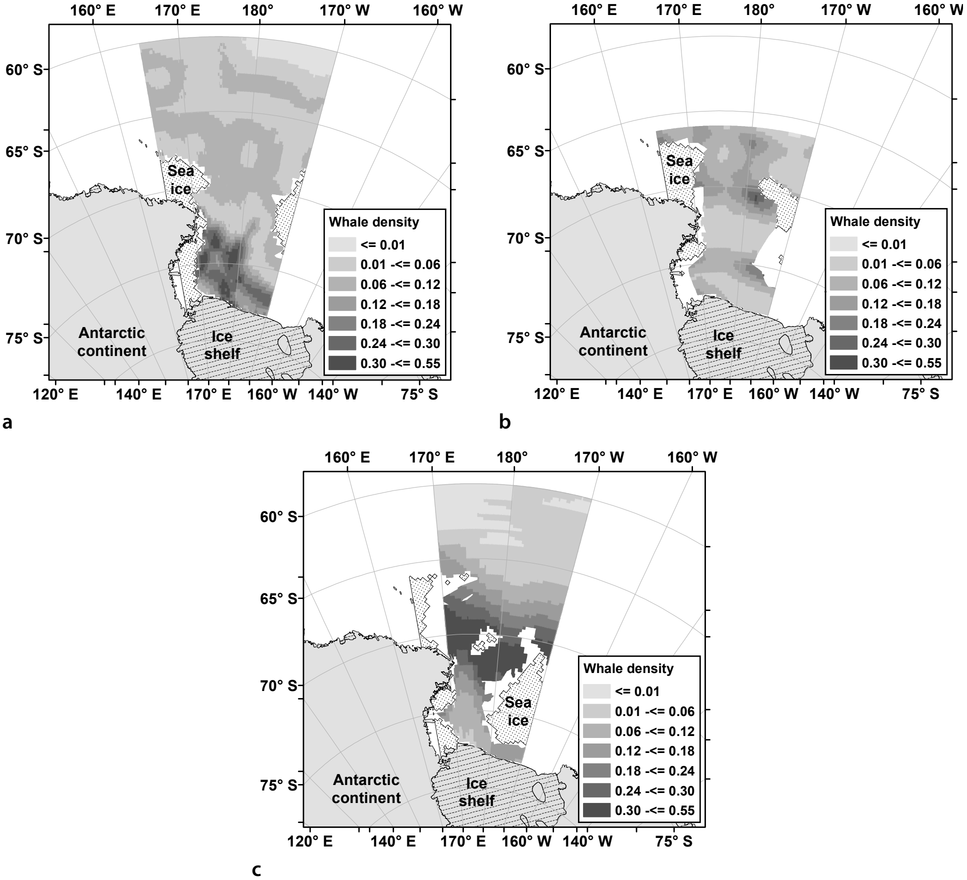


Figure 3.8. Prediction plots of Antarctic minke whale density for surveys conducted in the western Ross Sea (region 5, 165°E-170°W) within IWC management Area V. a) 1985/86 survey, b) 1991/92 survey and c) 2003/04 survey. The grey striped area is the ice shelf region, white dotted areas represent sea ice within 165°E-170°W. Densities are shown for surveyed strata and based on environmental data during the middle date of the stratum-specific survey period. As the displayed sea ice cover was derived for the middle date of the survey, some maps show white areas between the southern boundary of the surveyed area and the northern boundary of the sea ice.

Eastern Ross Sea (region 6.1, 140-170°W)

Only the model for 1983/84 predicted whale densities above 0.075 whales/km^2 in this region. These densities were mainly found south of 69°S, in proximity of the sea ice during the time of survey. Predicted whale densities north of 65°S were above 0.050 whales/km^2 at moderate distance to the SBACC (Figure 3.9a). Effort in this region during the 1990/91 survey was only north of 67°S, due to extensive sea ice cover. For this survey, whale densities above 0.050 whales/km^2 were predicted across most of the latitudinal range, close to the sea ice edge or near the SACCF (Figure 3.9b).

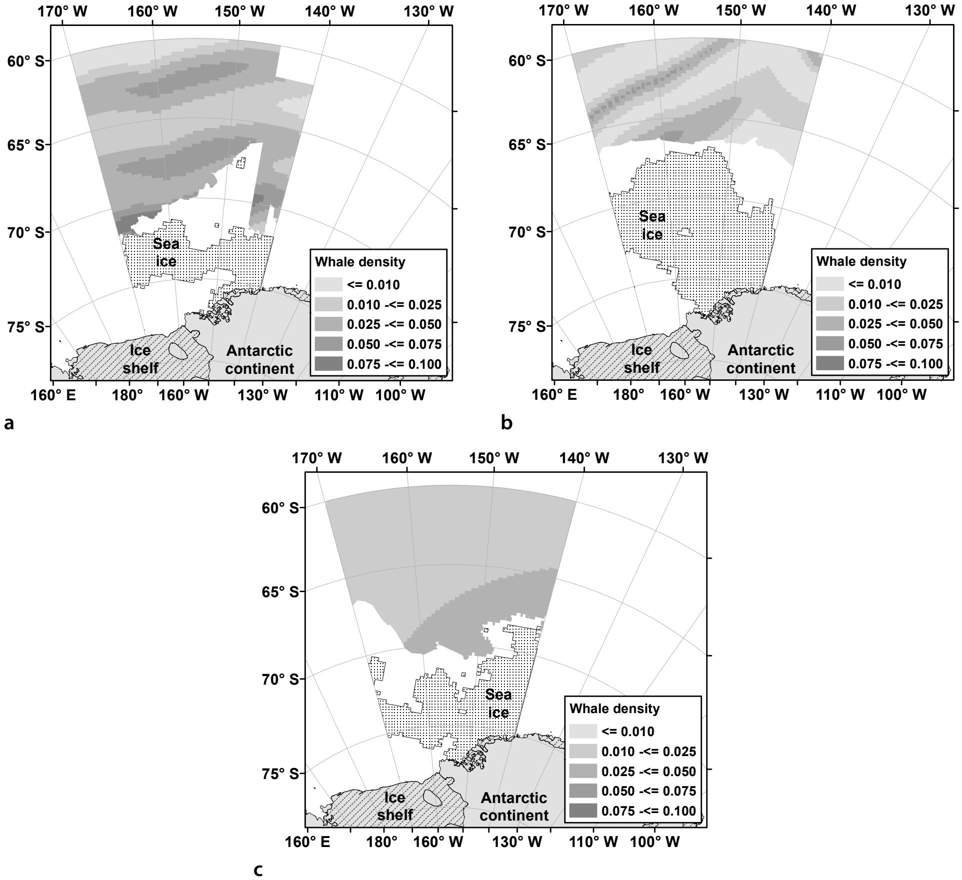


Figure 3.9. Prediction plots of Antarctic minke whale density for surveys conducted in the eastern Ross Sea (region 6.1, 140-170°W) within IWC management Area VI. a) 1983/84 survey, b) 1990/91 survey and c) 1995/96 survey. The grey striped area is the ice shelf region, white dotted areas represent sea ice within 140-170°W. Densities are shown for surveyed strata and based on environmental data during the middle date of the stratum-specific survey period. As the displayed sea ice cover was derived for the middle date of the survey, some maps show white areas between the southern boundary of the surveyed area and the northern boundary of the sea ice.

The density map for the 1995/96 survey suggests low spatial variability: all predicted whale densities were below 0.050 whales/km^2, with relatively high densities predicted south of ~65°S, relatively close to sea ice (Figure 3.9c).

Central Marie Byrd Land open water region (region 6.2, 120-140°W)

The density map for 1983/84 shows low spatial variability, with all predicted whale densities below 0.06 whales/km^2. Only between 130-140°W, whale densities were above 0.03 whales/km^2, in relatively cold waters (OISST < 0.5°C) (Figure 3.10a).

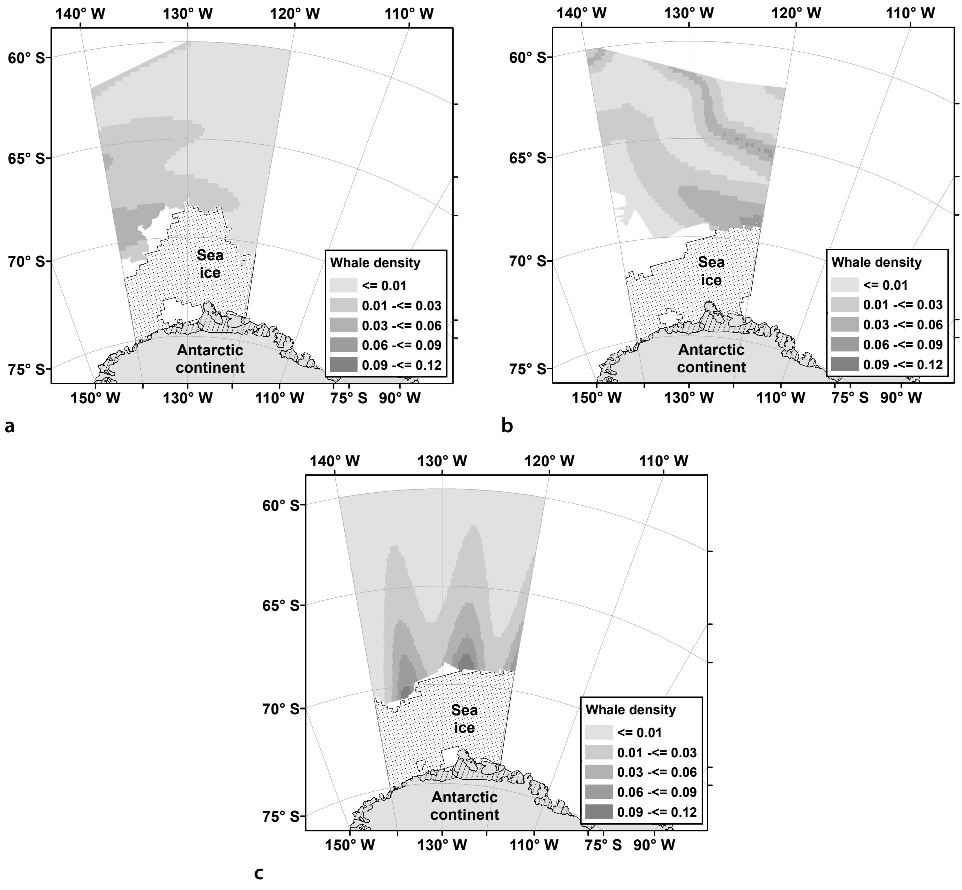


Figure 3.10. Prediction plots of Antarctic minke whale density for surveys conducted in the central Marie Byrd Land open water region region (region 6.2, 120-140°W) within IWC management Area VI. a) 1983/84 survey, b) 1990/91 survey and c) 2000/2001 survey. The grey striped area is the ice shelf region, white dotted areas represent sea ice within 120-140°W. Densities are shown for surveyed strata and based on environmental data during the middle date of the stratum-specific survey period. As the displayed sea ice cover was derived for the middle date of the survey, some maps show white areas between the southern boundary of the surveyed area and the northern boundary of the sea ice.

The model for 1990/91 predicted densities above 0.06 whales/km^2 close to the sea ice or SACCF (Figure 3.10b). Only for 2000/2001 were whale densities above 0.09 whales/km^2, in proximity of the sea ice (Figure 3.10c).

Temporal variability in mean density estimates of Antarctic minke whales

Mean density ranged from 0.002 (western Amundsen Sea, 1990/91 survey) to 0.138 (western Ross Sea, 2003/04 survey) Antarctic minke whales/km^2, indicating high spatial variability between regions (Table 3.1). The highest mean whale density was in the 0-20°E region in the Lazarev Sea for 1992/93. The second and third highest mean densities were in the 165°E-170°W region of the Ross Sea for 1985/86 and 2003/04. Some regions showed much higher variability in mean density over the years than other regions. The largest absolute difference in mean whale density was observed in the 0-20°E region in the Lazarev Sea (mean density of 0.020 whales/km^2 for 2004/05 compared to 0.151 whales/km^2 for 1992/93). The eastern Ross Sea (region 6.1, 170-140°W) showed the largest relative difference in mean density (mean density of 0.002 whales/km^2 for 1990/91 compared to 0.049 whales/km^2 for 1983/84). The coefficients of variation (CVs) ranged from 0.194 to 0.694 (Table 3.1). Region 1 in the Amundsen Sea - Bellingshausen Sea - Western Antarctic Peninsula region (60-110°W) had the lowest absolute difference in mean density, with mean density ranging from 0.038 to 0.056 minke whales/km^2 for the various surveys.

For three out of eight regions (regions 1, 2.2 and 3), mean density of Antarctic minke whales was lowest for the most recent survey (Table 3.1). On the other hand, the regions 2.1 and 6.2 showed a monotonous increase in mean density over the years. For three regions (region 3, 4 and 6.1), *z*-tests indicated significant differences in mean density between at least two surveys conducted in the specific region.

Table 3.2 specifies the input values of the potential covariates considered for the ANOVA. The different models and their AIC and ΔAIC values are displayed in Table 3.3. The best model included *region* and *icechange* as covariates, with a positive relationship between *icechange* and mean density of minke whales. Of the four sea ice covariates, both *icechange* and *icemiddle* had a significant positive relationship with mean minke whale density ($P < 0.05$). Furthermore, the positive relationship between *icechangedaily* and mean whale density was significant at the 10% level.

Table 3.2. Input values of potential covariates considered for the ANOVA-analysis. Only column headings in italics refer to potential covariates.

IWC Area	*Region* (*label*)	Survey season	*Trend*	Date max sea ice cover	Middle date survey	*Period* (days)	Mean density (whales/km^2)	*Icemax* (km^2)	*Icemiddle* (km^2)	*Icechange* (km^2)	*Icechangedaily* (km^2/day)
I	110 - 60°W	1982/83	1	07/09/1982	25/01/1983	140	0.056^{a}	1753949	616588	1137361	8124
	(1)	1989/90	2	07/09/1989	22/01/1990	137	0.039^{a}	1353480	462158	891322	6506
		1993/94	3	07/09/1993	21/01/1994	136	0.038^{a}	1312684	531380	781304	5745
II	60-30°W	1981/82	1	20/09/1981	17/01/1982	119	0.032^{a}	2290685	1240960	1049995	8823
	(2.1)	1986/87	2	20/09/1986	17/01/1987	119	0.049^{a}	2276019	1435708	840311	7061
		1997/98	3	20/09/1997	31/01/1998	133	0.053^{a}	2300946	1163135	1137811	8555
	30°W-0	1981/82	1	20/09/1981	17/01/1982	119	0.073^{a}	1851286	281637	1569649	13190
	(2.2)	1986/87	2	20/09/1986	17/01/1987	119	0.078^{a}	1851286	157902	1693384	14230
		1996/97	3	20/09/1996	31/01/1997	133	0.041^{a}	1851286	171649	1679637	12629
III	0-20°E	1987/88	1	21/09/1987	08/01/1988	119	0.088^{a}	1044328	16501	1027827	8637
	(3)	1992/93	2	21/09/1992	14/01/1993	115	0.151^{a}	1044328	85030	959298	8342
		2004/05	3	21/09/2004	03/02/2005	135	0.020^{b}	1044328	25743	1018585	7545
IV	80-100°E	1984/85	1	21/09/1984	09/02/1985	141	0.028^{a}	727057	163173	563884	3999
	(4)	1988/89	2	21/09/1988	20/01/1988	121	0.007^{b}	699597	102302	597295	4936
		1998/99	3	21/09/1998	06/02/1999	138	0.034^{ab}	726513	116752	609761	4419
V	165°E - 170°W	1985/86	1	28/09/1985	21/01/1986	115	0.130^{a}	1381342	181754	1199588	10431
	(5)	1991/92	2	28/09/1991	21/01/1992	114	0.086^{a}	1431965	181473	1250492	10969
		2003/04	3	28/09/2003	25/01/2004	119	0.138^{a}	1329587	234552	1095035	9202
VI	170-140°W	1983/84	1	07/09/1983	26/01/1984	141	0.049^{a}	2056209	306798	1749411	12407
	(6.1)	1990/91	2	07/09/1990	23/01/1991	138	0.002^{b}	1855902	773770	1082132	7842
		1995/96	3	07/09/1995	02/02/1996	148	0.029^{a}	1646573	451489	1195084	8075
	140-120°W	1983/84	1	07/09/1983	26/01/1984	141	0.016^{a}	893111	308209	584902	4148
	(6.2)	1990/91	2	07/09/1990	23/01/1991	138	0.031^{a}	1058420	272550	785870	5695
		2000/2001	3	07/09/2000	30/01/2001	145	0.036^{a}	1068140	325569	742571	5121

Explanations of the column headings: *region* = longitudinal range and label of region for which the covariate values were computed, Date max sea ice cover = date for which *icemax* was computed, Middle date survey = date for which *icemiddle* was computed, *period* = the number of days between the middle date of the survey and the date for which *icemax* was computed, Mean density = mean predicted density of minke whales (see Table 3.1), *Icemax* = maximum sea ice cover within the region for the period September (before the survey) until the middle date of the survey period, *Icemiddle* = sea ice cover within the region at the middle date of the survey period, *Icechange* = change in sea ice cover within the region, defined as *icemax* minus *icemiddle*, *Icechangedaily* = mean daily change in sea ice cover, defined as *Icechange/period*. *Region* was a factor variable. Mean density values with different superscripts within a region differ significantly.

Table 3.3. Specifications and results for the fitted ANOVA-models. Cov1 * Cov2 = both covariates (Covs) were included separately, together with their interaction terms, Cov1 : Cov2 = interaction term between two covariates.

ANOVA specification	p-value	AIC	ΔAIC
region + icechange	< 0.01 (*region*), 0.033 (*icechange*)	-108.1289	0
*region * icechange*	< 0.01 (*region*), 0.051 (*icechange*), 0.555 (*region : icechange*)	-107.9422	0.1867
region + icemiddle	< 0.01 (*region*), 0.040 (*icemiddle*)	-107.5339	0.5950
region + icechangedaily	< 0.01 (*region*), 0.091 (*icechangedaily*)	-105.3241	2.8048
region + period	< 0.01 (*region*), 0.129 (*period*)	-104.3978	3.7311
region	<0.01 (*region*)	-102.5893	5.5396
region + trend	< 0.01 (*region*), 0.844 (*trend*)	-100.6533	7.4756
region + icemax	< 0.01 (*region*), 0.860 (*icemax*)	-100.6410	7.4879

DISCUSSION

Comparing mean densities for different surveys

The IWC/IDCR-SOWER programme is one of the longest running large-scale programmes for shipboard detection of cetaceans. As the vessels did not survey within the pack ice region, the highly dynamic nature of sea ice in the Southern Ocean has resulted in differences in areal coverage and timing of the surveys, which we had to address in our comparison of mean densities for the various regions. This was problematic for two reasons. First, the common geographic area was very small for some regions, due to the high interannual variability in the location of the sea ice edge (e.g. Figures 3.6a-c). Second, the mean density of whales in an area depends on the ecological importance of that specific area to the species, which may vary for a common geographic area between surveys. For example, the southern boundary of a common geographic area in region 3 would align with the southern boundary of the 1992/93 survey, as its location of the sea ice edge during the survey is more northerly than for the other surveys in this region (Figures 3.6a-c). This would mean that the common geographic area would not cover large parts of the marginal ice zone, and thus would not include many high densities, for 1987/88. As a result, the mean density for 1987/88 would be much lower than for 1992/93, which would merely be a reflection of change in areal coverage instead of ecological change. For a more ecologically meaningful comparison, we only compared mean whale density for the area within a distance limit to the estimated location of the sea ice edge during the time of survey.

The surveys from 1994/95 to 2000/01 and in 2004/05 started later in the summer than other surveys (Branch, 2006b). This change in timing of survey improved the chances of the ice edge receding before the survey started, which eased the task of cruise track design (Branch and Butterworth, 2001). When we assume the date of maximum sea ice extent to be at the same day in the year for the various surveys in the region, a survey conducted later in the summer would have a higher probability of having low *icemiddle* and high *icechange* values, as there would be more time for the sea ice to melt until the middle date of the survey. Therefore, we defined the variable *icechangedaily*, which was the variable *icechange* corrected for timing of the survey. After correction, only a marginally significant relationship remained between *icechangedaily* and mean density, although *icechange* was the ice covariate included in the selected model.

Spatial variability

The circumpolar density maps showed high spatial variability in Antarctic minke whale density, especially in the Ross Sea (Figure 3.2b). In general, most open water areas with high whale densities were found close to the sea ice edge. However, proximity to the sea ice edge is not the only factor underlying high whale densities. For some surveys, densities higher than 0.3 whales/km^2 close to the sea ice edge were only on or close to the continental shelf, especially for region 2.2 (eastern Weddell Sea) in 1986/87 (Figure 3.5b), region 3 in 1992/93 (Figure 3.6b) and region 5 in 1985/86 and 2003/04 (Figures 3.8a+c). The only band with relatively high densities for 2003/04 (Figure 3.8c) was found in the proximity of the continental shelf break. Densities were also relatively high in these type of waters in region 1 for 1993/94 (Figure 3.3c). These findings are in agreement with Murase et al. (2002) who reported high minke whale densities in the Indian Ocean sector where the sea ice edge coincided with the continental slope. The continental shelf break may form an important feeding ground for Antarctic minke whales in these years, as adult krill are often found close to the continental shelf break in summer (Nicol, 2006). However, Atkinson et al. (2008) estimated mean krill density over the shelf-slope areas (water depth <2000m) to be only 1.65 times that over the deep ocean at the circumpolar scale. In our study, high minke whale densities were not exclusively found on or close to the continental shelf (exceptions are for instance the high densities for 1992/93 (Figure 3.6b) and 1984/85 (Figure 3.7a)), suggesting a more complex relation between environmental factors and minke whale distribution.

The circumpolar maps show that predicted minke whale densities were consistently high in the 165°E-170°W region in the Ross Sea (Figure 3.2b). This region is an exceptionally productive area in the Southern Ocean, partly because of a large polynya (region of open water surrounded by sea ice) forming over the largest continental shelf region in the Antarctic during spring and summer. The polynya begins to expand rapidly in November, extends to the northwest and east, and turns into a post-polynya when the surrounding sea ice has disappeared in at least one direction (Arrigo, 2007). By mid-January, much of the continental shelf in the Ross Sea is free of sea ice (Smith et al., 2007, 2012). High concentrations of cetacean biomass (mainly Antarctic minke whales and killer whales, *Orcinus orca*) were reported in the marginal ice zone surrounding the Ross Sea post-polynya in December (Ainley, 1985; Karnovsky et al., 2007). As little is known about the abundance and distribution of the zooplankton in the Ross Sea, especially on the continental shelf (Deibel and Daly, 2007; Cuzin-Roudy et al., 2014), zooplankton sampling in this region would be useful to assess if the high predicted whale densities within this region are determined by high prey densities, and which are the predominant prey species.

Our study suggests that the density distribution of Antarctic minke whales is not stable in much of the Southern Ocean between years. Antarctic minke whales mostly use the Southern Ocean as feeding ground in the summer and are thus less restricted in movements than central place foraging predator species that aggregate in breeding colonies. Therefore, minke whales probably have more freedom to respond to dynamic processes in their environment, such as the retreat of sea ice in summer, which may have resulted in relatively high variability in their density distributions. This mobility makes assessment of the Antarctic minke whale population more challenging, particularly in the light of changes in areal coverage between surveys of the same region.

Temporal variability

In only three out of eight regions, mean density of minke whales was lowest for the most recent survey. The ANOVA did not detect a time trend in mean whale density (Table 3.3). This result appears to contradict the conclusion by Branch (2006a), who reported an appreciably lower circumpolar abundance estimate of minke whales for the CPIII surveys compared to the CPII surveys. However, our results are difficult to compare with those reported by Branch (2006a), mainly for two reasons. Firstly, Branch (2006a) assumed that all minke whale schools on the survey line were detected (Branch and Butterworth, 2001), while we relaxed this assumption and estimated detection probabilities using distance sampling techniques that accounted for non-detection of minke whale schools on the survey line. More importantly, the regions used for comparison of minke whale density in this study differed from the total surveyed area. Branch (2006a)'s purpose was to obtain the best abundance estimate of minke whales for the whole Southern Ocean, including surveyed areas at lower latitude. In contrast, the goal of our study was to explain spatial and temporal variability in mean whale density. In this context, it is best to compare mean density for areas that are similar in their ecological importance for Antarctic minke whales, only within a certain distance to the sea ice edge. For most regions of our study, this distance limit partially or wholly excluded northern surveyed strata. Furthermore, we only compared mean density for regions that were surveyed three times. Each region in this study encompassed 20-30 degrees in longitude, its longitudinal range often smaller than the longitudinal range of total area surveyed in a season.

Although we could not detect an overall trend in mean density of minke whales, several regions had the lowest mean whale density for the most recent survey, while others showed a monotonous, albeit small, increase in mean density over time. However, the detection of regional trends in whale density was hampered by the low temporal resolution of the IDCR/SOWER dataset, as each region was only surveyed 3-4 times in a 24-year time span (Matsuoka et al., 2003). If the goal of the IDCR/SOWER programme is to detect possible regional trends in whale density, it would probably be better to increase the sampling frequency by focusing sampling effort on certain regions instead of the whole Southern Ocean. Regions of interest may be regions that had relatively high predicted whale densities for several surveys (such as in region 3 and region 5) or regions that showed significant trends in sea ice extent and season duration (region 1 and region 5, Zwally et al., 2002; Stammerjohn et al., 2008).

The selected ANOVA-model suggested that the variability in mean density of minke whales is in part region-specific. Furthermore, both seasonal change in sea ice cover (*icechange*) and sea ice cover experienced during the survey itself (*icemiddle*) showed a significant relationship ($P < 0.05$) with mean density. After correction for timing of survey, a significant relationship ($P < 0.10$) between mean daily change in sea ice cover (*icechangedaily*) and mean density remained. The significant positive relationships between sea ice covariates and mean density suggested that sea ice dynamics may underlie temporal variability in whale density.

The selected ANOVA-model suggested a positive relationship between *icechangedaily* and mean density. In spring, sea ice melt is followed by dense phytoplankton blooms near the ice edge in open, iron-enriched waters (Smetacek and Nicol, 2005). Adult krill is thought to feed on these blooms (Nicol, 2006) and both immature and mature krill concentrated in a large phytoplankton bloom north of the sea ice edge in the Scotia and Weddell Sea in one spring season (Daly and Macaulay, 1991). Furthermore, a positive and significant correlation was found between the rate of sea ice retreat in spring and phytoplankton biomass and productivity in a study at the circumpolar scale (Nicol et al., 2006). However, regional differences in this relationship were found, with this correlation being strongly positive in Prydz Bay, the Ross Sea, the Western Antarctic Peninsula region and the Weddell Sea, and a weak correlation elsewhere (Constable et al., 2003; Nicol et al., 2006, 2008).

We speculate that the percentage of summer sea ice cover and its mean daily change during spring and early summer (as represented by *icemiddle* and *icechangedaily*, respectively) may drive higher krill biomass and consequently higher mean whale density in summer. In several regions in the South Atlantic, regional abundance of krill in summer shows a positive relationship with sea ice cover in the previous winter (Siegel and Loeb, 1995; Loeb et al., 1997; Brierley et al., 1999; Hewitt et al., 2003; Atkinson et al., 2004) and duration of winter sea ice (Atkinson et al., 2004). Although these studies show that the history and timing of the sea ice retreat are important drivers for krill summer biomass in South Atlantic, we are not aware of studies linking regional krill summer biomass with the percentage of ice coverage and the speed of seasonal sea ice melt. Furthermore, it must be noted that these relationships do not hold at the circumpolar scale (Atkinson et al., 2008; Nicol et al., 2008). This inconsistency may also be reflected by the regional qualitative differences in relationships between minke whale density and variables related to the sea ice environment found in this study (Table 3.2).

As zooplankton was not sampled during the IDCR/SOWER cruises it is not possible to determine the biological mechanism behind the sea ice-whale density relationships, i.e. whether years with relatively high seasonal changes in sea ice cover or large sea ice cover during time of survey were also characterised by relatively high prey abundance. For a better understanding of the relationships between Antarctic minke whales and their prey species, simultaneous sampling of krill and minke whales is essential. Zooplankton sampling with a Continuous Plankton Recorder (CPR) during SOWER cruises, as is currently done under the Southern Ocean CPR (SO-CPR) programme (Hosie et al., 2003), could provide this kind of data.

One potentially important unknown is the proportion of minke whales that were in the pack ice and thus unavailable for detection during the IWC/IDCR-SOWER surveys. Minke whales can perform extensive foraging dives under the sea ice, during which they ingest prey in small gulps (Friedlaender et al., 2014). The lower mean whale densities found in some regions of the Southern Ocean for the most recent surveys may just as well be the result of a higher proportion of minke whales residing in the pack ice during time of survey in recent years (Branch, 2006b; Leaper et al., 2008). We did not find a negative linear relationship between mean minke whale density and sea ice cover as represented by *icemiddle*. However, we predicted high minke whale densities near the continental shelf edge in region 2.2 for the 1986/87 survey (Figure 3.5b), in waters that were covered by sea ice during the 1981/82 and 1996/97 surveys (Figures 3.5a+c). Thus, the proportion of animals available for detection may be dependent on the proportion of continental shelf in the region that is exposed during the survey. For future work, it would be of interest to consider the total area of exposed continental shelf during the survey as a covariate for the ANOVA-model. Furthermore, other aspects of the pack ice, such as its quality (Thiele et al., 2005) and the presence and size of polynyas, may have an impact on whale densities in open water as well. Only by conducting more aerial and shipboard surveys in the pack ice region (Kelly et al., 2011, 2014; Herr et al., 2014), preferably in combination with shipboard surveys in open waters within the same region, can we estimate if and to which extent changes in mean predicted whale density in open waters are driven by changes in the pack ice region.

In summary, our study indicated that sea ice is an important driver for both the spatial and temporal variability in density of minke whales. We found significant positive relationships between mean whale density and daily change in sea ice cover during spring/early summer. Another positive relationship was found between mean whale density and sea ice cover during time of survey, in summer. The lower estimated mean densities of minke whales for some regions within the Southern Ocean in recent years may be attributed to changes in seasonal sea ice retreat and summer sea ice cover. More frequent sampling of whales in selected regions, preferably together with continuous zooplankton sampling, is required for a better understanding of the ways in which the environment drives the summer distribution and abundance of Antarctic minke whales in open waters of the Southern Ocean.

ACKNOWLEDGEMENTS

We are very grateful to the International Whaling Commission for providing us with the IWC/IDCR-SOWER whale sightings dataset. Furthermore, we would like to thank Jamie Tratalos and

Peter Fretwell for providing GIS support. We thank Michael Meredith for oceanographic advice. The altimeter products were produced by Ssalto/Duacs and distributed by Aviso with support from the Centre national d'études nationales (Cnes). This project was supported by the EURopean Network of Excellence for Ocean Ecosystems Analysis (EUR-OCEANS) under project number WP4-SYSSO-1066, by the British Antarctic Survey and by the University of Groningen. This paper contributes to the Ecosystems Programme, part of the Polar Science for Planet Earth framework of the British Antarctic Survey.

REFERENCES

Ainley, D.G. 1985. Biomass of birds and mammals in the Ross Sea. pp. 498-515. *In:* W.R. Siegfried, P.R. Condy and R.M. Laws (eds.) *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin. 700pp.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. pp. 267-281. *In*: B. Petran and F. Csaaki (eds.) *Second international symposium on information theory*, Akadeemiai Kiadi, Budapest, Hungary. 451pp.

Arrigo, K.R. 2007. Physical control of primary productivity in Arctic and Antarctic polynyas. pp. 223-238. *In:* W.O. Smith, Jr., D.G. Barber (eds.) *Polynyas: windows to the world*. Elsevier Science, Amsterdam. 474pp.

Atkinson, A., Siegel, V., Pakhomov, E. and 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, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A. and Fleming, A.H. 2008. Oceanic circumpolar habitats of Antarctic krill. *Mar. Ecol. Prog. Ser.* 362: 1-23.

Branch, T.A. 2006a. Abundance estimates for Antarctic minke whales from three completed circumpolar sets of surveys, 1978/79 to 2003/04. Paper SC/58/IA18 presented to the IWC Scientific Committee, June 2006 (unpublished). 28pp. [Paper available at the Office of the IWC]

Branch, T.A. 2006b. Possible reasons for the appreciable decrease in abundance estimates for Antarctic minke whales from the IDCR/SOWER surveys between the second and third circumpolar sets of cruises. Paper SC/58/IA4 presented to the IWC Scientific Committee, June 2006 (unpublished). 8pp. [Paper available at the Office of the IWC]

Branch, T.A. and Butterworth, D.S. 2001. Southern Hemisphere minke whales: standardised abundance estimates from the 1978/79 to 1997/98 IDCR-SOWER surveys. *J. Cetacean Res. Manage.* 3(2): 143-174.

Branch, T.A. and Ensor, P. 2001. Recommended species code changes for minke and blue whale sightings for analysis of IDCR-SOWER surveys. Report of the Scientific Committee, Annex G, Appendix 8. *J. Cetacean Res. Manage. (Suppl.)* 3: 200-203.

Brierley, A.S., Demer, D.A., Watkins, J.L., Hewitt, R.P. 1999. Concordance of interannual fluctuations in acoustically estimated densities of Antarctic krill around South Georgia and Elephant Island: biological evidence of same-year teleconnections across the Scotia Sea. *Mar. Biol.* 134: 675-681.

Bromwich, D.H., Nicolas, J.P., Monaghan, A.J., Lazzara, M.A., Keller, L.M., Weidner, G.A. and Wilson, A.B. 2013. Central West Antarctica among the most rapidly warming regions on Earth. *Nature Geoscience* 6: 139-145.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. (eds.) 2001. *Introduction to distance sampling*. Oxford University Press, Oxford. 432pp.

Buckland, S.T. and Anganuzzi, A.A. 1988. Comparison of smearing methods in the analysis of minke sightings data from IWC/IDCR Antarctic cruises. *Rep. int. Whal. Commn.* 38: 257-263.

Cavalieri, D., Parkinson, C., Gloersen, P. and Zwally, H.J. 1996, updated 2006. Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I passive microwave data. Boulder, Colorado USA: National Snow and Ice Data Center. Digital media.

Christensen, J.H., Krishna Kumar, K., Aldrian, E., An, S.-I., Cavalcanti, I.F.A., de Castro, M., Dong, W., Goswami, P., Hall, A., Kanyanga, J.K., Kitoh, A., Kossin, J., Lau, N.-C., Renwick, J., Stephenson, D.B., Xie, S.-P. and Zhou, T. 2013. Climate phenomena and their relevance for future regional climate change. pp. 1217-1308. *In*: T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.) *Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, NY, USA. 1535pp.

Clarke, E.D., Spear, L.B., McCracken, M.L., Marques, F.F.C., Borchers, D.L., Buckland, S.T. and Ainley, D.G. 2003. Validating the use of generalized additive models and at-sea surveys to estimate size and temporal trends of seabird populations. *J. Appl. Ecol.* 40(2): 278-292.

Constable, A.J., Nicol, S. and Strutton, P.G. 2003. Southern Ocean productivity in relation to spatial and temporal variation in the physical environment. *J. Geophys. Res.* 108(C4), 8079.

Cuzin-Roudy, J., Irisson, J.-O., Penot, F., Kawaguchi, S. and Vallet, C. 2014. pp. 309-320. Southern Ocean euphausiids. *In*: C. de Broyer, P. Koubbi, H.J. Griffiths, B. Raymond, C. d'Udekem d'Acoz, A. van de Putte, B. Danis, B. David, S. Grant, J. Gutt, C. Held, G. Hosie, F. Huettman, A. Post and Y. Ropert-Coudert. *Biogeographic atlas of the Southern Ocean.* Scientific Committee on Antarctic Research, Cambridge, United Kingdom. 498 pp.

Daly, K.L. and Macaulay, M.C. 1991. Influence of physical and biological mesoscale dynamics on the seasonal distribution and behavior of *Euphausia superba* in the Antarctic marginal ice zone. *Mar. Ecol. Prog. Ser.* 79: 37-66.

Deibel, D. and Daly, K.L. 2007. Zooplankton processes in Arctic and Antarctic polynyas. pp. 271-322. *In:* W.O. Smith, Jr. and D.G. Barber (eds). *Polynyas: windows to the world*. Elsevier Science, Amsterdam. 474pp.

Donovan, G.P. 1991. A review of IWC stock boundaries. *Rep. int. Whal. Commn.* (special issue) 13: 39-68.

Efron, B. and Tibshirani, R.J. 1993. *An introduction to the bootstrap*. Chapman & Hall, London. 456pp.

ESRI. 2009. ArcMap 9.3.1. Environmental Systems Resource Institute, Redlands, California.

Fielding, S., Watkins, J.L., Trathan, P.N., Enderlein, P., Waluda, C.M., Stowasser, G., Tarling, G.A. and Murphy, E.J. 2014. Interannual variability in Antarctic krill (*Euphausia superba*) density at South Georgia, Southern Ocean:1997-2013. *ICES J. Mar. Sci.* 71(9): 2578-2588.

Forney, K.A. 2000. Environmental models of cetacean abundance: reducing uncertainty in population trends. *Cons. Biol.* 14(5): 1271-1286.

Friedlaender, A.S., Goldbogen, J.A., Nowacek, D.P., Read, A.J., Johnston, D. and Gales, N. 2014. Feeding rates and under-ice foraging strategies of the smallest lunge feeder, the Antarctic minke whale (*Balaenoptera bonaerensis*). *J. Exp. Biol.* 217: 2851-2854.

Hastie, G.D., Swift, R.J., Slesser, G., Thompson, P.M. and Turrell, W.R. 2005. Environmental models for predicting oceanic dolphin habitat in the Northeast Atlantic. *ICES J. Mar. Sci.* 62: 760-770.

Hedley, S.L., Buckland, S.T. and Borchers, D.L. 1999. Spatial modelling from line transect data. *J. Cetacean Res. Manage.* 1(3): 255-264.

Herr, H., Kelly, N., Viquerat, S., Kock, K.-H., Williams, R., Scheidat, M., Lehnert, L.S. and Siebert, U. 2014. Overview of five German helicopter surveys provide insight into spatio-temporal variability of minke whale densities in ice. Paper SC/65b/IA16 presented to the IWC Scientific Committee, May 2014 (unpublished). 15pp. [Paper available from the office of the IWC].

Hewitt, R.P., Demer, D.A., Emery, J.H. 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. *Aquat. Living Resour.* 16(3): 205-213.

Horvitz, D.G. and Thompson, D.J. 1952. A generalization of sampling without replacement from a finite universe. *J. Am. Stat. Assoc.* 47: 663-685.

Hosie, G.W., Fukuchi, M. and Kawaguchi, S. 2003. Development of the Southern Ocean Continuous Plankton Recorder survey. *Prog. Oceanogr.* 58: 263-283.

Ichii, T. and Kato, H. 1991. Food and daily food consumption of southern minke whales in the Antarctic. *Polar Biol*. 11: 479-487.

IOC, IHO and BODC. 2003. Centenary edition of the GEBCO Digital Atlas, published on CD-rom on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans, British Oceanographic Data Centre, Liverpool, UK.

IPCC. 2013. Annex I: atlas of global and regional climate projections [G.J. van Oldenborgh, M. Collins, J. Arblaster, J.H. Christensen, J. Marotzke, S.B. Power, M. Rummukainen and T. Zhou (eds.)]. *In*: T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.) *Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, NY, USA.

Karnovsky, N., Ainley, D.G. and Lee, P. 2007. The impact and importance of production in polynyas to top-trophic predators: three case histories. pp. 391-410. *In:* W.O. Smith, Jr., D.G. Barber (eds.) *Polynyas: windows to the world*. Elsevier Science, Amsterdam. 474pp.

Kasamatsu, F., Hembree, D., Joyce, G., Tsunoda, L., Rowlett, R. and 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. *Rep. int. Whal. Commn*. 38: 449-473.

Kasamatsu, F., Joyce, G.G., Ensor, P. and Mermoz, J. 1996. Current occurrence of baleen whales in Antarctic waters. *Rep. int. Whal. Commn.* 46: 293-304.

Kasamatsu, F., Ensor, P. and Joyce, G.G. 1998. Clustering and aggregations of minke whales in the Antarctic feeding grounds. *Mar. Ecol. Prog. Ser.* 168: 1-11.

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

Kawamura, A. 1994. A review of baleen whale feeding in the Southern Ocean. *Rep. int. Whal. Commn.* 44: 261-271.

Kelly, N., Peel, D. and Bravington, M.V. 2014. Distribution and abundance of Antarctic minke whales in sea ice regions of East Antarctica: a summary of results. Paper SC/65b/IA15 presented to the IWC Scientific Committee, May 2014 (unpublished). 22pp. [Paper available from the office of the IWC].

Kelly, N., Peel, D., Bravington, M.V. and Gales, N. 2011. Analysis of minke whale sighting data from aerial surveys over pack ice in East Antarctica. Paper SC/63/IA3 presented to the IWC Scientific Committee, May-June 2011 (unpublished). 19pp. [Paper available from the office of the IWC].

Laake, J.L. and Borchers, D.L. 2004. Methods for incomplete detection at distance zero. pp. 108-189. *In*: S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers and L. Thomas (eds.) *Advanced distance sampling*. Oxford University Press, Oxford. 416pp.

Laws, R.M. 1977. Seals and whales of the Southern Ocean. *Phil. Trans. R. Soc. Lond. B*. 279: 81-96.

Leaper, R. Bannister, J.L., Branch, T.A., Clapham, P.J., Donovan, G.P., Matsuoka, K., Reilly, S. and Zerbini, A.N. 2008. A review of abundance, trends and foraging parameters of baleen whales in the Southern Hemisphere. Paper CCAMLR-IWC-WS-08/4 presented to the joint CCAMLR-IWC workshop to review input data for Antarctic marine ecosystem models, August 2008 (unpublished). 51pp. [Paper available from the Office of the IWC].

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

Mackintosh, N.A. 1942. The southern stocks of whalebone whales. *Discovery Rep.* 22: 197-300.

Matsuoka, K., Ensor, P., Hakamada, T., Shimada, H., Nishiwaki, S., Kasamatsu, F. and Kato, H. 2003. Overview of minke whale sightings surveys conducted on IWC/IDCR and SOWER Antarctic cruises from 1978/79 to 2000/01. *J. Cetacean Res. Manage* 5(2): 173-201.

Meredith, M.P. and King, J.C. 2005. Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys. Res. Lett. 32*: L19604.

Murase, H. Matsuoka, K., Ichii, T. and Nishiwaki, S. 2002. Relationship between the distribution of euphausiids and baleen whales in the Antarctic (35°E-145°W). *Polar Biol.* 25(2): 135-145.

Murphy, E.J., Trathan, P.N., Watkins, J.L., Reid, K., Meredith, M.P., Forcada, J., Thorpe, S.E., Johnston, N.M. and Rothery, P. 2007. Climatically driven fluctuations in Southern Ocean ecosystems. *Proc. R. Soc. B* 274: 3057-3067.

Nicol, S., Worby, A. and Leaper, R. 2008. Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. *Mar. Freshwater Res.* 59: 361-382.

Nicol, S. 2006. Krill, currents, and sea ice: *Euphausia superba* and its changing environment. *Bioscience* 56(2): 111-120.

Nicol, S., Worby, A.P., Strutton, P.G. and Trull, T.W. 2006. Oceanographic influences on Antarctic ecosystems: a summary of observations and insights from East Antarctica (0°-150°E). pp. 1493-1534. *In*: A. Robinson and K. Brink (eds.) *The sea vol. 14B: the global coastal ocean*. Harvard University Press, Cambridge, MA. 810pp.

Orsi, A.H., Whitworth III, T. and Nowlin Jr., W.D. 1995. On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep-Sea Res*. *I* 42(5): 641-673.

Peel, D., Kelly, N., Bravington, M.V. and Hedley, S.L. 2008. IWC 2008 title: Design of future SOWER voyages: an update. Paper SC/60/IA5 presented to the IWC Scientific Committee, June 2008 (unpublished). 11pp. [Paper available at the Office of the IWC].

R Development Core Team. 2008. R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.r-project.org.

Reynolds, R.W., Rayner, N.A., Smith, T.M., Stokes, D.C. and Wang, W. 2002. An improved in situ and satellite SST analysis for climate. *J. Clim*. 15: 1609-1625.

Reynolds, R.W. and Smith, T.M. 1994. Improved global sea surface temperature analyses using optimum interpolation. *J. Clim.* 7: 929-948.

Siegel, V. and Loeb, V. 1995. Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Mar. Ecol. Prog. Ser.* 123: 45-56.

Smetacek, V. and Nicol, S. 2005. Polar ocean ecosystems in a changing world. *Nature* 437: 362-368.

Smith, Jr., W.O., Ainley, D.G., Cattaneo-Vietti, R. and Hofmann, E.E. 2012. The Ross Sea continental shelf: regional biogeochemical cycles, trophic interactions, and potential future changes. pp. 213-242. *In*: A.D. Rogers, N.M. Johnston, E.J. Murphy and A. Clarke (eds.) *Antarctic ecosystems: an extreme environment in a changing world*. Wiley-Blackwell, Oxford. 538pp.

Smith, Jr., W.O., Ainley, D.G. and Cattaneo-Vietti, R. 2007. Trophic interactions within the Ross Sea continental shelf ecosystem. *Phil. Trans. R. Soc. B.* 362: 95-111.

Southwell, C.J., Paxton, C.G.M., Borchers, D.L., Boveng, P.L., Nordøy, E.S., Blix, A.S. and De la Mare, W.K. 2008. Estimating population status under conditions of uncertainty: the Ross seal in East Antarctica. *Antarct. Sci.* 20(2): 123-133.

Stammerjohn, S.E., Martinson, D.G., Smith, R.C., Yuan, X. and Rind, D. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño – Southern Oscillation and Southern Annular Mode variability. *J. Geophys. Res.* 113, C03S90.

Strindberg, S. and Burt, L. 2004. IWC Database-Estimation Software System (DESS) user manual. Research Unit for Wildlife Population Assessment, University of St Andrews, St Andrews.

Thiele, D., Chester, E.T. and Asmus, K. 2005. Antarctic sea ice: measuring habitat complexity, and seasonal and regional variability in habitat use for minke whales. Paper SC/57/E1 presented to the IWC Scientific Committee, June 2005 (unpublished) 21pp. [Paper available at the Office of the IWC].

Thiele, D., Chester, E.T. and Gill, P.C. 2000. Cetacean distribution off Eastern Antarctica (80-150˚E) during the Austral summer of 1995/1996. *Deep-Sea Res. II* 47(12-13): 2543-2572.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B. and Marques, T.A. 2006. Distance 5.0. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK.

Turner, J., Hosking, J.S., Marshall, G.J., Phillips, T. and Bracegirdle, T.J. 2016. Antarctic sea ice increase consistent with intrinsic variability of the Amundsen Sea Low. *Clim. Dyn.* 46(7): 2391-2402.

Turner, J., Colwell, S.R., Marshall, G.J., Lachlan-Cope, T.A., Carleton, A.M., Jones, P.D., Lagun, V., Reid, P.A. and Iagovkina, S. 2005. Antarctic climate change during the last 50 years. *Int. J. Climatol.* 25: 279-294.

Tynan, C. and Thiele, D. 2003. Report on Antarctic ice edge definition by the ad hoc Working Group on ice data collection in the Antarctic. Paper SC/55/E19 presented to the IWC Scientific Committee, May 2003, Berlin. 1pp. [Paper available from the Office of the IWC]

Vaughan, D.G., Marshall, G.J., Connolley, W.M., Parkinson, C., Mulvaney, R., Hodgson, D.A., King, J.C., Pudsey, C.J. and Turner, J. 2003. Recent rapid regional climate warming on the Antarctic Peninsula. *Clim. Change* 60: 243-274.

Wood, S.N. 2006. *Generalized Additive Models: an introduction with R.* Chapman & Hall, New York. 391pp.

Zwally, H.J., Comiso, J.C., Parkinson, C.L., Cavalieri, D.J. and Gloersen, P. 2002. Variability of Antarctic sea ice 1979-1998. *J. Geophys. Res.* 107(C5), 3041.

Species-specific responses of baleen whales to bottom-up environmental drivers within the Scotia Sea ecosystem

Bas W.P.M. Beekmans
Jaume Forcada
Eugene J. Murphy
Hein J.W. de Baar
Ulrich V. Bathmann

4

ABSTRACT

The Scotia Sea and adjacent waters support large populations of top predators, including baleen whales, that mainly forage on Antarctic krill *Euphausia superba*. We developed Generalised Additive Models for whale density to identify the main bottom-up drivers underlying the distributions of Antarctic minke whales *Balaenoptera bonaerensis*, humpback whales *Megaptera novaeangliae* and fin whales *B. physalus*. Covariates considered during model selection were either directly representing or indirectly related to krill, and included average density of krill, sea surface velocity, sea water temperature and closest distances to the coast, fronts and sea ice edge. High predicted densities had wider geographic coverage for Antarctic minke whales than for the other two baleen whale species. Furthermore, high densities for fin whales mainly occurred close to the continental shelf away from the coast, while high humpback whale densities occurred only in waters north to northwest of the Antarctic Peninsula. Only density of Antarctic minke whales was significantly positively related to average density of krill. Both density of humpback whales and average krill density showed a significantly negative relationship with distance from the coast within the first 200 km, possibly indicating a positive relationship between density of humpback whales and average krill density within this coastal range. The different predicted spatial density distributions, together with the different sets of bottom-up drivers underlying these distributions, may be indicative of different foraging strategies for the various baleen whale species within the Scotia Sea region. For example, minke and humpback whales may prefer juvenile krill, which is mostly found in the southwest of the Scotia Sea, whereas fin whales prefer (sub)adult krill found in deeper waters.

INTRODUCTION

The Scotia Sea ecosystem is one of the most productive regions in the Southern Ocean, largely because of relatively unusual water mass dynamics (Murphy et al., 2007). Strong currents meet, mix and stratify within the Scotia Sea region (Thorpe et al., 2007), thereby creating optimal conditions in terms of supply of both major and trace nutrients and sufficient light exposure for large summer phytoplankton blooms (Holm-Hansen et al., 2004). These blooms in turn enable high secondary productivity, especially of Antarctic krill (Miller and Hampton, 1989; Atkinson et al., 2004, 2008). Large marine predators, including several baleen whale species, feed on this krill (Reid et al., 2000; Hedley et al., 2001; Širović et al., 2006).

Antarctic krill occupies a wide range of habitats within the Scotia Sea. High krill concentrations are found in waters less than 1000m deep (Miller and Hampton 1989; Murphy et al., 1997), with maximum values in the shelf break region (Murphy et al., 1997; Trathan et al., 1998; Trathan et al., 2003). On the other hand, large amounts of krill were found in off-shelf regions of the Scotia Sea (Marr 1962; Atkinson et al., 2004; Hewitt et al., 2004; Siegel, 2005; Tarling et al., 2009). Antarctic krill reaches its northernmost extent in this ecosystem, with high krill densities occurring north of 53°S (Murphy et al., 2004, 2007, 2012). Advection is an important determinant of krill distribution within the Scotia Sea, and can explain the unusually large amounts of krill found in off-shelf regions (Hofmann and Murphy, 2004; Thorpe et al., 2007). However, the question remains whether Antarctic krill distribution is solely dependent on water currents. An alternative view is that krill distribution can, at least partly, be explained by its active swimming behaviour, with only spawning females found in off-shelf regions in austral summer, while juvenile krill are mainly found in shallow waters (Nicol, 2006; Nicol et al., 2008). A southward directed active migration to spawning grounds could be possible although there is no direct evidence for such a strategy in the Scotia Sea (Atkinson et al., 2008; Murphy et al., 2012).

The Antarctic krill stock in the Scotia Sea is about half the total estimated stock of Antarctic krill (Atkinson et al., 2004). This species plays a key role within the Scotia Sea foodweb, supporting large populations of higher trophic level predators, such as penguins, seals and baleen whales. Not surprisingly, in the past this particular ecosystem supported a large, and at its time modern, whaling industry. Vessels were mainly operating from land stations based on South Georgia, with most whales taken between 1904 and the mid-1930s. Whaling had a dramatic impact on populations of baleen whales at South Georgia: local populations of humpback and blue whales were commercially extinct by 1915 and 1936, respectively (Clapham and Baker, 2002). Today, the Scotia Sea serves as a feeding ground for western South Atlantic humpback whales (Engel and Martin, 2009). Furthermore, other large baleen whales, notably blue whales, fin whales and southern right whales were detected by acoustic and visual surveys conducted in the Scotia Sea region (Hedley et al., 2001; Širović et al., 2006).

The CCAMLR 2000 survey was the first collaborative field programme between the scientific committees of the International Whaling Commission (IWC) and the Commission for the

Conservation of Antarctic Marine Living Resources (CCAMLR) (Reilly et al., 2004). The survey was conducted in Area 48, a fishery and management area extending through the Scotia Sea and waters northwest of the Antarctic Peninsula. The primary aim of the CCAMLR 2000 survey was to obtain a better estimate of krill biomass in this Area (Watkins et al., 2004). Although survey design and protocols were set up to meet this target, the survey also provided an opportunity to collect whale sightings data simultaneously. Cetacean observers from the IWC Scientific Committee collected whale sightings data onboard three out of four vessels that participated in the survey, i.e. the R.R.S. *James Clark Ross*, the R.V. *Yuzhmorgeologiya* and the R.V. *Kaiyo Maru*. Furthermore, in situ data on sea water temperature, salinity and water depth were collected.

The CCAMLR 2000 survey data offer a unique opportunity to investigate relationships between density of baleen whales and the physical-biological environment, represented by a suite of environmental variables. Species of interest were minke whales (*Balaenoptera bonaerensis*), humpback whales (*Megaptera novaeangliae*), fin whales (*B. physalus*) and southern right whales (*Eubalaena australis*). Compared to a similar spatial modelling study by Hedley et al. (2001), we considered more environmental variables, such as sea surface velocity and sea surface height. These physical upper ocean features are thought to be indirectly linked to krill distribution. Furthermore, we included improved estimates of krill density in our analysis, based on more recent models for krill target strength, a measure for the efficiency with which krill scatters sound. The improved estimates of krill density were thought to better represent the distribution of krill.

MATERIALS AND METHODS

Survey area

The CCAMLR2000 survey covered two large strata, Antarctic Peninsula (AP) and Scotia Sea (SS), and three smaller strata around the South Shetlands Islands (SSI), South Orkney Islands (SOI) and South Georgia (SG), respectively (Figure 4.1).

Datasets

Effort and whale sightings data

Two survey modes were used for the collection of whale sightings data during the CCAMLR 2000 survey, i.e. Primary mode and BT mode. In Primary mode, one cetacean observer team was operational. On the *Yuzhmorgeologiya*, this team consisted of three observers (including a “Recorder”), while two observers searched for whales in Primary mode onboard of the other two vessels. In BT mode, two cetacean observer teams, each consisting of two observers, were on search effort on two separate observation platforms on the same vessel, i.e. the Primary platform and the Tracking platform (Buckland and Turnock, 1992). The observer team on the Primary platform searched for cetaceans using the Primary mode survey protocol.

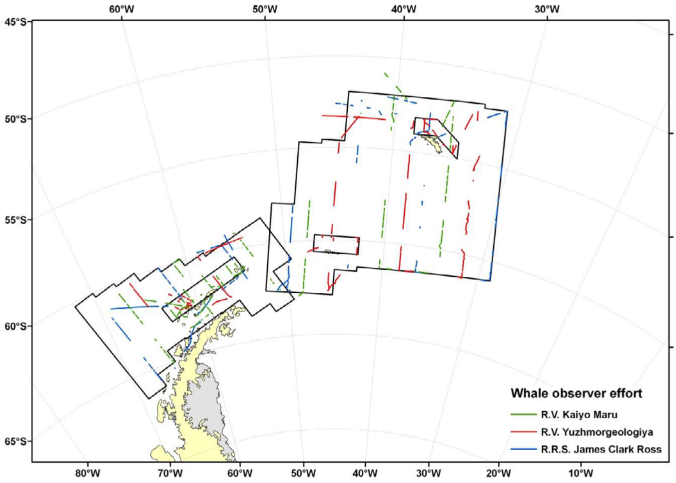


Figure 4.1. Whale observer effort onboard the three vessels (R.V. *Kaiyo Maru*, R.V. *Yuzhmorgeologiya* and R.R.S. *James Clark Ross*) which participated in the CCAMLR2000 survey. The various coloured lines show parts of the survey line where at least one observer team was on-effort. The boxes show the five strata surveyed by the various vessels: two large strata (left: Antarctic Peninsula, right: Scotia Sea) and three smaller strata (from left to right: in the proximity of South Shetland Islands, South Orkney Islands and South Georgia, respectively).

The observer team on the Tracking platform consisted of a “Tracker” and a “Recorder”. The BT mode is an asymmetric survey mode, in which the observers on the Primary platform are not informed of sightings made by observers on the Tracking platform. The BT mode is preferable over Primary mode (IWC, 2000) because the BT mode potentially leads to more accurate estimates of whale density. Only BT mode enables the collection of duplicate sightings, i.e. sightings of the same whale schools made by two different observer teams, which can be used to estimate *p(0)*, the probability of detecting a whale school on the transect line by at least one of the observer teams. Due to logistic constraints, the number of observers and observer teams varied per vessel (Reilly et al., 2004). Two observers formed one team on the R.V. *Kaiyo Maru*, and, therefore, data collection onboard this vessel was in Primary mode only. Four and six observers were onboard the R.V. *Yuzhmorgeologiya* and the R.R.S. *James Clark Ross*, respectively. On these two ships, search effort alternated between Primary mode and BT mode. More detailed information on the data collection protocol can be found in Reilly et al. (2004). Total observer effort was 9,839 km distance covered, consisting of 6,539 km in Primary Mode and 3,300 km in BT Mode.

Table 4.1 summarises the CCAMLR 2000 sightings that the observers attributed to the four baleen whale species of interest. We assumed that the category “unidentified large baleen whale” represented sightings of animals which were either a humpback, fin or southern right whale. Following Reilly et al. (2004), we did not consider the taxonomic categories “unidentified large whale” and “unidentified whale” as these sightings potentially included toothed whales, such as sperm whales (*Physeter macrocephalus*) and southern bottlenose whales (*Hyperoodon planifrons*).

Table 4.1. On-effort sightings of baleen whales (sightings made by observers on full search effort) per vessel in the CCAMLR 2000 survey region derived from validated sightings data. For each baleen whale species or taxonomic category, the number of sighted schools and animals are listed.

Species name or taxonomic category	R.R.S. *James Clark Ross*		R.V. *Yuzhmorgeologiya*		R.V. *Kaiyo Maru*		Total	
	Schools	**Whales**	**Schools**	**Whales**	**Schools**	**Whales**	**Schools**	**Whales**
Minke whale	16	23	0	0	6	14	22	37
Like minke whale	25	43	30	56	21	49	76	148
Undetermined minke whale	4	6	9	14	7	8	20	28
Humpback whale	97	209	30	53	38	77	165	339
Like humpback whale	4	7	6	7	10	23	20	37
Fin whale	30	75	7	17	12	53	49	145
Like fin whale	3	3	7	33	5	39	15	75
Southern right whale	16	26	0	0	6	13	22	39
Like southern right whale	1	1	0	0	1	2	2	3
Unidentified large baleen whale	22	29	48	98	36	67	106	194

Remote sensing environmental data

Both remote sensing data and in situ environmental data were used in this study. Remote sensing datasets included datasets of sea ice concentration, sea surface temperature, sea surface velocity (SSV), sea surface height (SSH) and chlorophyll *a* concentration, in combination with bathymetric depth for the same geographic position. Sea ice concentrations were estimated from passive microwave data, derived from measurements obtained by the Scanning Multichannel Microwave Radiometer (SMMR) onboard the Nimbus-7 satellite and by the Special Sensor Microwave Imagers (SSM/I) onboard Defense Meteorological Satellite Program (DMSP) satellites F8, F11 and F13. We used Version 2 of the sea ice concentration data, released in September 2007, which had a 0.2° x 0.2° resolution and were provided as daily data on a 7 day interval (Cavalieri et al., 1996, updated 2006). Bathymetric depth values were derived from the General Bathymetric Chart of the Oceans (GEBCO) dataset, at a latitude-longitude resolution of one minute (IOC et al., 2003). For sea surface temperature, we used Optimum Interpolation version 2 Sea Surface Temperature (hereafter called OISST) data (Reynolds and Smith, 1994, Reynolds et al., 2002), provided on an approximately 7 day interval one-degree latitude-longitude grid (http://www.cdc.noaa.gov/data/gridded/data.noaa.oisst.v2.html). Mean SSV values were derived from near-surface drifter data for the period 1994-2007, provided by the Global Drifter Program (http://www.aoml.noaa.gov/phod/dac/gdp.html). Velocity data obtained from these drifters were corrected for inertial currents, slow bias, Ekman drift, Stokes' drift and geostrophic velocity anomaly to generate a mean SSV field. The derived mean velocities were binned at the 1/3 Mercator grid resolution as used for Aviso (Archiving, Validation and Interpretation of Satellite Oceanographic data) data products (Sally Thorpe, pers. comm.). We extracted SSV anomaly data from the delayed time absolute geostrophic anomaly dataset, distributed by Aviso on a 1/3 x 1/3º Mercator grid as daily data on a weekly interval (accessed on December 19, 2009). The geostrophic velocity anomalies were added to the mean SSV field to obtain an absolute SSV field on the 1/3 Mercator grid. For SSH values, we used the "upd" Delayed Time – Maps of Absolute Dynamic Topography (DT-MADT) Aviso dataset (accessed on February 2, 2010), provided as daily data on a weekly interval (Sally Thorpe, pers. comm.). We extracted 0.083º x 0.083º gridded chlorophyll *a* (Chl-concentration data from the NASA Sea-viewing Wide Field-of-view Sensor (SeaWiFS) dataset (http://oceancolor.gsfc.nasa.gov/SeaWiFS). This dataset, consisting of eight-day composite chlorophyll *a* concentration values corresponded well with shipboard measurements conducted during the CCAMLR 2000 survey, especially for concentrations smaller than 1.0 mg m^{-3}, which was the case for the majority of chlorophyll concentration values (Holm-Hansen et al., 2004). The SeaWiFS eight-day composite datasets were partly incomplete due to cloud cover. Therefore, we used 16-day composite chlorophyll *a* concentration values for the CCAMLR 2000 survey.

In situ environmental data

During the CCAMLR 2000 survey, each vessel sampled two Conductivity-Temperature-Depth (CTD) stations a day. For this study, 0.25° x 0.25° gridded data on water temperature, salinity and density at various depths (sea surface, 50, 100, 200 and 300m) were considered, based on iso-surfaces derived from these CTD data (Hedley et al., 2001). Furthermore, we used the SACCF and SBACC contours derived from these CTD data by Brandon et al. (2004). Acoustic data on Antarctic krill were collected with the Simrad EK500 echosounder onboard all four ships (three ships earlier mentioned and the R.V. *Atlantida*) during the CCAMLR 2000 survey (Hewitt et al., 2004). The echosounder was connected to hull-mounted 38, 120 and 200 kHz transducers. Continuous sampling occurred with 2s ping intervals (Hewitt et al., 2004). For the identification of Antarctic krill, the dual-frequency dB-difference technique (Madureira et al., 1993a, b) was applied using a fixed 2-16 dB window (Watkins and Brierley, 2002) for the difference between the mean volume backscattering strength (S_v) at two frequencies ($\Delta S_v = S_{v,\ 120\ kHz} - S_{v,\ 38\ kHz}$). This analysis resulted in a series of integrated backscattering areas attributed to Antarctic krill (s_A), expressed in units of Nautical Area Scattering Coefficient (NASC, $m^2\ n.mi^{-2}$; MacLennan et al., 2002). The s_A-values were converted to biomass of Antarctic krill by applying the stochastic distorted-wave Born approximation (SDWBA) model for krill target strength (Conti and Demer, 2006; see also Demer and Conti 2003a, b, 2005). This SDWBA model is based on a study by McGehee et al. (1998) on target strength of krill, which is a measure for the efficiency with which krill scatters sound. For krill orientation the $N(11°, 4°)$ distribution was used, which provided the best fit with CCAMLR 2000 krill data (CCAMLR, 2005; Conti and Demer, 2006).

Cetacean detection probabilities

We used Method II of Buckland and Anganuzzi (1988) to smear radial distances and angles, to correct for rounding errors in sighting distances and angles. Furthermore, we excluded sightings made under very poor sighting conditions (sightability = 1), which meant we discarded three sightings. In addition, we excluded three sightings that were collected under non-standardised effort on February 10, 2000.

Only 18 duplicate sightings were recorded in BT mode during the CCAMLR 2000 survey, which meant that we could not apply Mark Recapture Distance Sampling (MRDS) analysis to estimate *p(0)* for this survey. This type of analysis requires about 60 duplicate cetacean detections (Hedley et al., 2001; Laake and Borchers, 2004). However, we used Multiple Covariate Distance Sampling (MCDS) methods (Marques and Buckland, 2004) as implemented in Distance 5.0 release 2 (Thomas et al., 2010) and the package *mrds* (V1.3.8) of Program R, V2.10.1 (R Development Core Team, 2009) to test which covariates affected the detection of whales.

We fitted detection-function models to two groups of CCAMLR 2000 sightings data independently. The first sightings group contained only sightings of minke whales, including "undetermined" and "like" sightings of minke whales. The second group contained sightings of humpback whales, fin whales, southern right whales (including "like" categories for these three species) and unidentified large baleen whales (Hedley et al., 2001; Reilly et al., 2004). For both groups, we considered the following covariates potentially affecting the detection of whales: effort mode, stratum, vessel, school size, sightability, sea state and swell. All potential covariates were treated as discrete values, with five levels for school size (i.e. 1, 2, 3-4, 5-9 and 10+), four levels for sightability (2, 3, 4 and 5), two levels for sea state (0 = Beaufort 0-2, 1 = Beaufort 3+) and two levels for swell (0 = swell code 0-2 (low swell) and 1 = swell code 3+). In addition, we tested whether model fit improved when species as a covariate was included in the detection-function model for pooled sightings of large baleen whales (second group). We considered both half-normal and hazard-rate key functions without polynomial adjustment terms (Buckland et al., 2001). Selection of all detection-function models was based on Akaike's Information Criterion (AIC)(Akaike, 1973).

Potential covariates

Table 4.2 shows all variables considered as potential covariates in this study, together with their corresponding datasets and abbreviations used throughout this manuscript. *Icedist* is the closest distance to the sea ice edge, defined at 15% sea ice concentration (Tynan and Thiele, 2003). The covariate *1000m-dist* is the closest distance to the continental shelf break, the latter shelf break is represented by the 1000m depth contour. For defining the positions of fronts in both surveys, we extracted contours at 17 and 6 dynamic cm from SSH data to derive positions of the SACCF and SBACC, respectably (Hugh Venables, pers. comm.). The minimal distances to these contours are called *SACCFdist_SSH* and *SBACCdist_SSH* in this study. We also considered the minimal distances to the SACCF and SBACC contours (*SACCFdist_CTD* and *SBACCdist_CTD*) derived by Brandon et al. (2004). These contours better represent the positions of these fronts during the CCAMLR survey, as they were based on CTD data collected during this survey.

Several covariates were represented by datasets that were partly incomplete. Firstly, the gridded SSV datasets had low coverage in some regions, especially in the 50º-30ºW region below 60ºS. Therefore, we only retrieved SSV values for locations within 35 km distance of a SSV grid point. By applying this distance limit, we could include SSV values for locations with nearby SSV grid points. Secondly, the frontal contours derived by Brandon et al. (2004) did not encompass the whole survey region, which meant *SACCFdist_CTD* had missing values for locations west of 68ºW and for the region between 33.2º-30.6ºW, north of 53ºS. Locations west of 67ºW had missing values for *SBACCdist_CTD*. Finally, missing values for krill density (*krilldens*) represented days during which krill were not sampled acoustically while detecting cetaceans. To account for these covariates in our spatial models, we created dummy variables with missing values (0 = missing value, 1 = numeric value). This way, we could still consider these covariates.

Table 4.2. Variables considered as potential covariates during model selection.

Potential covariate	Definition	Unit
Icedist	Closest distance to the sea ice edge (15% sea ice concentration)	km
OISST	Optimally Interpolated Sea Surface Temperature	ºC
Depth	Bathymetric depth	m
1000m-dist	Closest distance to the continental shelf break (1000m depth contour)	km
SSVmean	Mean sea surface velocity	m s^{-1}
SSVanom	Anomaly sea surface velocity	m s^{-1}
SSVabs	Absolute sea surface velocity	m s^{-1}
SACCFdist_SSH	Closest distance to the SACCF, defined at SSH = 17 dyn. cm	km
SBACCdist_SSH	Closest distance to the SBACC, defined at SSH = 6 dyn. cm	km
Coastdist	Closest distance to the coastline	km
SACCFdist_CTD	Closest distance to the SACCF, contour derived by Brandon et al. (2004)	km
SBACCdist_CTD	Closest distance to the SBACC, contour derived by Brandon et al. (2004)	km
Temptop	Sea water temperature at surface level	ºC
temp50m	Sea water temperature at 50m depth	ºC
temp100m	Sea water temperature at 100m depth	ºC
temp200m	Sea water temperature at 200m depth	ºC
temp300m	Sea water temperature at 300m depth	ºC
Wdtop	Water density at surface level	kg m^{-3}
wd50m	Water density at 50m depth	kg m^{-3}
wd100m	Water density at 100m depth	kg m^{-3}
wd200m	Water density at 200m depth	kg m^{-3}
wd300m	Water density at 300m depth	kg m^{-3}
Saltop	Sea water salinity at surface level	-
sal50m	Sea water salinity at 50m depth	-
sal100m	Sea water salinity at 100m depth	-
sal200m	Sea water salinity at 200m depth	-
sal300m	Sea water salinity at 300m depth	-
Logmeanchl	Natural logarithm of mean chlorophyll	-
Logavgkrill	Natural logarithm of average krill density	-

Abbreviations: SACCF = Southern Antarctic Circumpolar Current Front; SBACC = Southern Boundary of the Antarctic Circumpolar Current; SSH = Sea Surface Height.

Principal component analysis

A large number of covariates were considered for the spatial models based on the CCAMLR 2000 survey. We used Principal Component Analysis (PCA) methods implemented in the *FactorMineR* package (Lê et al., 2008) to study which covariates were highly correlated with the two major Principal Components (PCs) which explained most of the variance. Furthermore, we generated 95% confidence regions within the individuals factor map for these two Principal Components to study whether the various species-specific categories of baleen whale density were significantly different from each other.

Spatial model of the average density of krill

Acoustic sampling of krill is limited to the water volume underneath the vessel. As a result, estimates of krill density could only be derived for every nautical mile on the transect line where the Echosounder was operational, which covers a small portion of the survey area. If krill density underlies the distribution of baleen whales, we need to estimate krill density for the unsampled regions between transect lines, in order to predict whale density for the whole survey area. However, krill density per nautical mile is highly variable, with density estimates per nautical mile sometimes differing by three orders of magnitude. Therefore, we estimated the average krill density per 0.25° x 0.25° grid cell (Hedley et al., 2001). The Generalised Additive Model (GAM) for average krill density had the following structure:

$$\mathrm{E}\left(\widehat{K}_v\right) = \exp\left[\gamma_0 + \sum_q f_q\left(m_{v,q}\right)\right] \tag{4.1}$$

where: $\hat{K}_v$ = estimated average krill density per 0.25° x 0.25° grid cell v;
γ_0 = intercept;
$m_{v,q}$ = value of covariate q for grid cell v;
f_q = smoothed function ("smoother") of covariate q.

Furthermore, we assumed a logarithmic link-function and a Tweedie error distribution. The variance of a Tweedie distribution is proportional to the power θ of the mean (Tweedie, 1984). We considered Tweedie error distributions with various values of θ, thus allowing for more flexibility than considering only (quasi-)Poisson error distributions, which are special cases of the Tweedie distribution (Peel, 2008). For model fitting, we used the GAM methodology developed by Wood (2006, 2008) that was implemented in the R software library *mgcv* (V1.6-1). Model selection was based on minimisation of the Generalised Cross Validation (GCV) score and maximisation of the explained deviance. Models that generated extreme values of average krill density were excluded. The degree of smoothing was constrained by setting the argument gamma to 1.4 within the function "gam" of package *mgcv*. We used forward model selection: in each step we retained the covariate for which its inclusion led to the largest increase in explained deviance. A new covariate was only retained if (i) it was significant, (ii) lowered the GCV score and (iii) increased the explained deviance by at least 4% (Southwell et al., 2008). To avoid multicollinearity effects, we only considered covariates having correlation coefficients smaller than 0.7 with the covariates that were already selected in previous steps. Furthermore, if a covariate was included with a correlation coefficient larger than 0.7 with one of the first two principal components, we did not consider the other covariates anymore that were strongly correlated with the specific principal component. We could have used the principal components as synthetic covariates to consider during model selection. However, the resulting relationships between a principal component and estimated average krill density were difficult to interpret. Therefore, the principal components were not considered during model selection.

Spatial models of baleen whale density

We developed spatial models for baleen whale species with a sufficient number of sightings. For the CCAMLR 2000 survey, this was the case for Antarctic minke whales, humpback whales and fin whales. Only 22 groups of southern right whales were detected during this survey, mostly in waters near South Georgia and very rarely in other locations. We included all species-specific "undetermined" and "like" sightings in the spatial models to increase sample size.

We applied the count method developed by Hedley and Buckland (2004) and divided the transect line into equal segments of three nautical miles survey effort. We estimated N_i, the number of species-specific baleen whales per segment area, with the following Horvitz-Thompson-like estimator (Horvitz and Thompson, 1952):

$$\widehat{N}_i = \sum_j \frac{n_{i,j}}{\hat{p}.(x,\underline{z})_{i,j}} \tag{4.2}$$

where: $n_{i,j}$ = the number of species-specific baleen whales within group j in segment i;
$\hat{p}.(x,\underline{z})_{i,j}$ = the estimated probability that at least one of the observers detects the jth group in segment i, at perpendicular distance x from the track line, given the covariate vector $\underline{z}$.

The spatial models of baleen whale density had the following structure (Hedley and Buckland, 2004):

$$\mathrm{E}\left(\widehat{N}_i\right) = \exp\left[\ln(A_i) + \theta_0 + \sum_r f_r\left(k_{i,r}\right)\right] \tag{4.3}$$

where: A_i = segment area, equal to 2 l_i w (l_i = segment length, with w the species-specific truncation distance for sightings);
θ_0 = intercept;
$k_{i,r}$ = value of covariate r for segment i;
f_r = smoother of covariate r.

The model selection procedure for the GAM fitting was the same as used for selection of the average krill density GAM, described in the previous section.

RESULTS

Detection functions and distance sampling

Sightings of minke whales collected during the CCAMLR 2000 survey were truncated at 1.1 nautical mile (nmi). Table 4.3 lists all fitted detection-function models for minke whales. Hazard-rate models did not provide good model fits. Instead, the AIC-selected half-normal model included effort mode, swell, stratum and vessel as covariates (Figure 4.2a). Truncation distance was 3.5 nmi for sightings of large baleen whales. Although this truncation distance is quite large, too many sightings would have been omitted if the sightings data were truncated more. Table 4.4

gives an overview of all fitted detection-function models for large baleen whales. The selected hazard-rate model included sightability, species, vessel and stratum as covariates (Figure 4.2b).

Table 4.3. Detection-function model fits with AIC and ΔAIC for sightings of minke whales, including "undetermined minke whale" and "like minke whale", made during the CCAMLR 2000 survey. Sightings were truncated at 1.1 nmi. Only models with good fits are listed.

Model	AIC	ΔAIC
hn ($x + ef + sw + st + v$)	-44.1	0
hn ($x + ef + sw + st$)	-42.4	1.7
hn ($x + ef + sw + st + v + ss$)	-42.1	2.0
hn ($x + ef + sw + st + v + s$)	-40.8	3.3
hn ($x + ef + sw + v$)	-40.6	3.5
hn ($x + ef + sw + st + v$)	-40.5	3.6
hn ($x + ef + sw + st + v$)	-40.4	3.7
hn ($x + ef + sw$)	-39.6	4.5
hn ($x + ef + sw + st + v + sg$)	-39.6	4.5
hn ($x + ef + sw + ss$)	-38.0	6.1
hn ($x + ef + sw + st + v$)	-37.8	6.3
hn ($x + ef + v$)	-37.6	6.5
hn ($x + ef + sw + st + v$)	-37.3	6.8
hn ($x + ef + sw + s$)	-36.2	7.9
hn ($x + ef + sw + sg$)	-36.1	8.0
hn ($x + ef + st$)	-35.9	8.2
hn ($x + ef + ss$)	-35.1	9.0
hn ($x + ef + sg$)	-34.1	10.0
hn ($x + ef$)	-34.0	10.1
hn ($x + sw$)	-32.5	11.6
hn ($x + ef + s$)	-31.6	12.5
hn ($x + v$)	-30.1	14.0
hn ($x + sg$)	-26.4	17.7
hn (x)	-26.3	17.8
hn ($x + st$)	-25.4	18.7
hn ($x + ss$)	-24.9	19.2
hn ($x + s$)	-22.8	21.3

Abbreviations: hn = half-normal model, x = perpendicular distance, ef = effort mode, s = school size, sg = sightability, ss = sea state, sw = swell, st = stratum, v = vessel.

Table 4.4. Detection-function model fits with AIC and ΔAIC for sightings of large baleen whales, including species-specific "like" categories, made during the CCAMLR 2000 survey. Sightings were truncated at 3.5 nmi. Only models with good fits are listed.

Model	AIC	ΔAIC
hr (*x* + *sg* + *sp* + *v* + *st*)	661.6	0
hr (*x* + *sg* + *sp* + *v*)	663.0	1.4
hr (*x* + *sg* + *sp* + *v* + *sw*)	663.8	2.2
hr (*x* + *sg* + *sp* + *v* + *ss*)	664.9	3.3
hr (*x* + *sg* + *sp* + *v* + *ef*)	665.0	3.4
hr (*x* + *sg* + *sp* + *v* + *s*)	665.4	3.8
hr (*x* + *sg* + *sp* + *sw*)	669.3	7.7
hn (*x* + *sg* + *sp* + *v* + *s*)	671.3	9.7
hr (*x* + *sg* + *sp* + *st*)	671.6	10.0
hn (*x* + *sg* + *sp* + *v*)	673.3	11.7
hn (*x* + *sg* + *sp* + *v* + *st*)	673.9	12.3
hn (*x* + *sg* + *sp* + *v* + *sw*)	674.4	12.8
hn (*x* + *sg* + *sp* + *v* + *ss*)	674.5	12.9
hr (*x* + *sg* + *sp*)	674.6	13.0
hr (*x* + *sg* + *sp* + *ef*)	674.7	13.1
hn (*x* + *sg* + *sp* + *v* + *ef*)	674.7	13.1
hr (*x* + *sg* + *sp* + *ss*)	676.5	14.9
hn (*x* + *sg* + *sp* + *sw*)	676.5	14.9
hn (*x* + *sg* + *sp* + *st*)	677.9	16.3
hr (*x* + *sg* + *v*)	678.5	16.9
hr (*x* + *sg* + *sp* + *s*)	678.8	17.2
hn (*x* + *sg* + *sp*)	679.1	17.5
hn (*x* + *sg* + *sp* + *s*)	679.8	18.2
hn (*x* + *sg* + *sp* + *ss*)	679.8	18.2
hn (*x* + *sg* + *sp* + *ef*)	681.0	19.4
hr (*x* + *sg* + *sw*)	682.1	20.5
hr (*x* + *sg* + *st*)	682.7	21.1
hr (*x* + *sg*)	683.2	21.6
hr (*x* + *sg* + *ef*)	683.3	21.7
hn (*x* + *sg* + *v*)	684.1	22.5
hr (*x* + *sg* + *ss*)	685.1	23.5
hn (*x* + *sg*)	685.4	23.8
hn (*x* + *sg* + *ss*)	685.4	23.8
hn (*x* + *sg* + *st*)	685.5	23.9
hn (*x* + *sg* + *sw*)	685.8	24.2
hn (*x* + *sg* + *ef*)	686.8	25.2
hr (*x* + *sp*)	687.1	25.5
hn (*x* + *sp*)	688.5	26.9

Abbreviations: hn = half-normal model, hr = hazard-rate model, *x* = perpendicular distance, *ef* = effort mode, *s* = school size, *sg* = sightability, *sp* = species, *ss* = sea state, *sw* = swell, *st* = stratum, *v* = vessel.

Table 4.4. Detection-function model fits with AIC and ΔAIC for sightings of large baleen whales, including species-specific "like" categories, made during the CCAMLR 2000 survey. Sightings were truncated at 3.5 nmi. Only models with good fits are listed. *(Continued)*

Model	AIC	ΔAIC
hr (*x* + *sg* + *s*)	689.9	28.3
hn (*x* + *sg* + *s*)	691.8	30.2
hr (*x* + *sw*)	694.4	32.8
hr (*x* + *st*)	694.7	33.1
hn (*x* + *st*)	694.8	33.2
hn (*x* + *sw*)	696.6	35.0
hr (*x*)	697.7	36.1
hr (*x* + *v*)	698.5	36.9
hn (*x*)	698.7	37.1
hr (*x* + *ef*)	699.5	37.9
hn (*x* + *ss*)	699.7	38.1
hr (*x* + *ss*)	699.7	38.1
hn (*x* + *ef*)	700.6	39.0
hn (*x* + *v*)	700.9	39.3
hr (*x* + *s*)	703.3	41.7
hn (*x* + *s*)	705.8	44.2

Abbreviations: hn = half-normal model, hr = hazard-rate model, *x* = perpendicular distance, *ef* = effort mode, *s* = school size, *sg* = sightability, *sp* = species, *ss* = sea state, *sw* = swell, *st* = stratum, *v* = vessel.

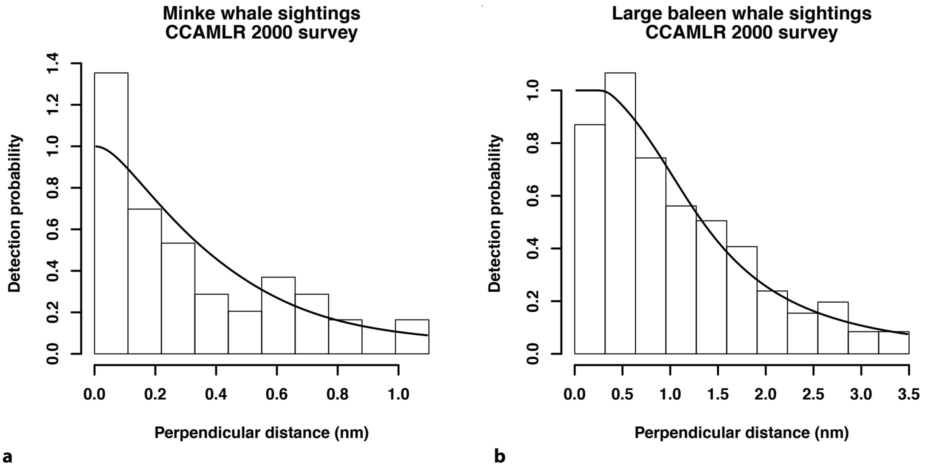


Figure 4.2. Plots of selected detection functions and histograms of perpendicular distances for Antarctic minke and large baleen whales, respectively. Three baleen whale species were defined as large baleen whales, namely humpback whales, fin whales and Southern right whales.

Principal component analysis

Table 4.5 shows the correlation matrix for the five major principal components (PCs) based on the PCA applied to CCAMLR 2000 environmental data. The first PC (PC1) accounted for 46.8% of total variation in the original environmental covariates, and the second PC (PC2) accounted for a further 14.6% of variation. Most of the abiotic in situ covariates (sea water temperature, water depth and salinity at various depths), together with OISST, were strongly correlated with PC1. The PC2 was highly correlated with covariates that represented closest distance to the coast (*coastdist*) and to fronts (*SACCFdist_SSH*, *SBACCdist_SSH* and *SACCF_CTD*) (Figure 4.3). Although the first two PCs explained more than 60% of the total variation in the environmental data, we decided not to use the PCs as potential covariates since relationships between whale density and PCs are often difficult to interpret. Instead, after selecting a covariate in the spatial models that correlated strongly with one of the two major PCs, we did not consider the other covariates anymore that also showed correlation coefficients in excess of 0.7 with the specific PC.

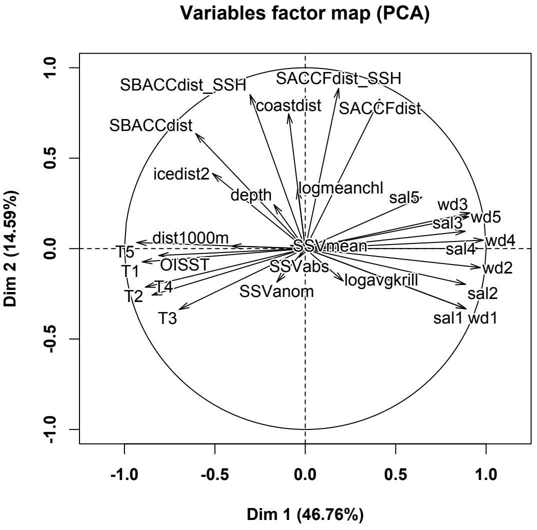


Figure 4.3. Principal component analysis' variables factor map for the CCAMLR 2000 data. All covariate abbreviations can be found in Table 4.3.

Figure 4.4 shows the PCA individuals factor map for the first two PCs with 95% confidence ellipses for the four groups of baleen whale species (minke whale, humpback whale, fin whale and southern right whale). None of the confidence ellipses showed an overlap with confidence ellipses of other species, with respect to the first two major PCs. Furthermore, each ellipse was centered at a very different combination of PC values, suggesting that the species categories of baleen whale sightings were all significantly different from each other. The ellipses for humpback and southern right whale sightings were furthest apart from each other, with most sightings of humpback whales found in segments with positive PC1 and negative PC2 values, while most sightings of southern right whales had negative PC1 and positive PC2 values. The non-overlapping confidence ellipses encouraged us to develop species-specific spatial models of baleen whale density.

Table 4.5. Correlation matrix for the five major principal components (PCs) based on Principal Component Analysis applied to CCAMLR 2000 environmental data.

Potential covariate	PC1	PC2	PC3	PC4	PC5
icedist	-0.51	0.42	-0.01	0.29	0.37
OISST	**-0.81**	-0.04	-0.07	0.25	0.21
depth	-0.17	0.24	0.67	0.34	-0.10
1000m-dist	-0.41	0.01	0.65	0.32	-0.14
SSVmean	-0.08	0.02	0.64	-0.51	0.49
SSVanom	-0.16	-0.19	0.49	-0.02	-0.33
SSVabs	-0.03	-0.05	0.69	-0.47	0.46
SACCFdist_SSH	0.18	**0.89**	-0.18	-0.23	-0.10
SBACCdist_SSH	-0.31	**0.85**	-0.17	-0.15	-0.04
coastdist	-0.09	**0.75**	0.47	0.19	-0.13
SACCFdist_CTD	0.41	**0.83**	-0.09	-0.14	-0.08
SBACCdist_CTD	-0.61	0.64	-0.28	-0.03	0.09
temptop	**-0.90**	-0.07	-0.19	0.11	0.17
temp50m	**-0.89**	-0.21	-0.21	0.08	0.21
temp100m	**-0.70**	-0.34	0.27	0.22	-0.09
temp200m	**-0.85**	-0.26	-0.07	0.19	0.22
temp300m	**-0.93**	0.03	0.05	0.18	0.02
wdtop	**0.89**	-0.33	-0.01	-0.04	-0.01
wd50m	**0.97**	-0.11	0.04	-0.01	-0.01
wd100m	**0.91**	0.20	0.02	0.21	0.16
wd200m	**0.98**	0.05	0.04	0.07	0.01
wd300m	**0.90**	0.18	0.03	0.25	0.19
saltop	**0.89**	-0.33	-0.01	-0.04	-0.01
sal50m	**0.89**	-0.20	-0.06	0.03	0.08
sal100m	**0.88**	0.10	0.15	0.32	0.13
sal200m	**0.96**	0.01	0.04	0.14	0.07
sal300m	0.64	0.28	0.06	0.48	0.29
logmeanchl	-0.04	0.33	0.07	-0.02	0.21
logavgkrill	0.21	-0.18	-0.42	0.09	0.41
Percentage of overall variance	46.76	14.59	9.44	5.51	4.55

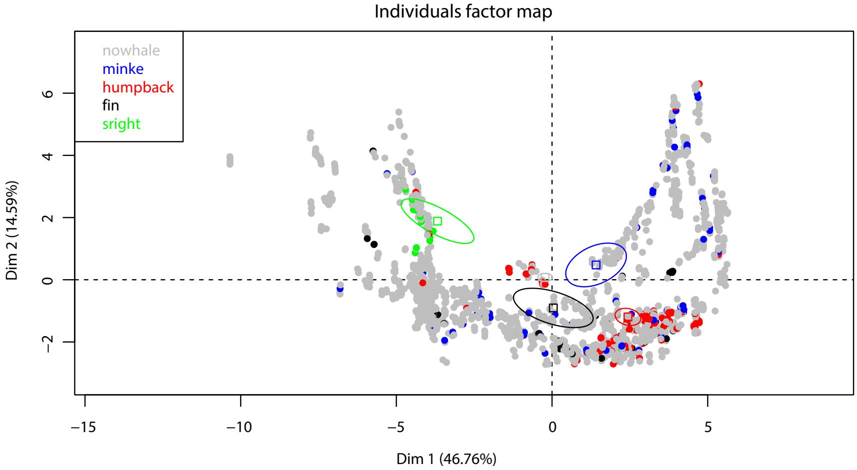


Figure 4.4. Principal component analysis' individuals factor map for the first two principal components, based on CCAMLR 2000 data, with 95% confidence ellipses for the four groups of baleen whale species (minke whale, humpback whale, fin whale and southern right whale), together with segments that did not include any of these whales (in grey).

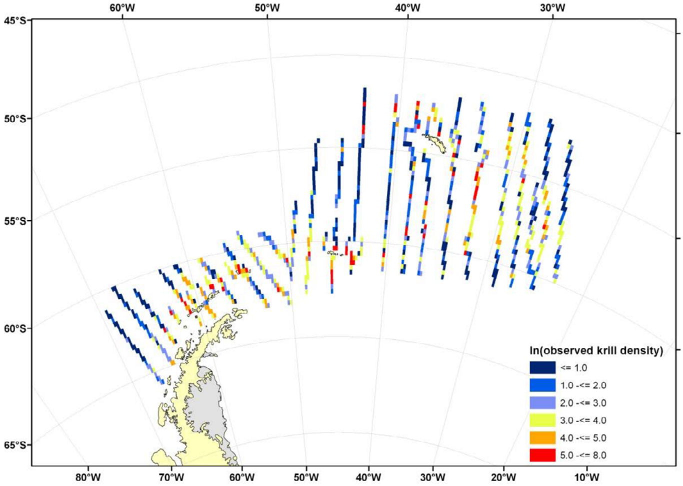


Figure 4.5. Distribution of natural logarithms taken from observed krill densities, averaged within each 0.25° x 0.25° grid cell, for the transect lines on which krill were acoustically sampled.

Spatial model of the average density of krill

The distribution of average observed krill density still shows high, albeit reduced, variability (Figure 4.5). Relatively high average krill densities were observed in the northern waters off the Western Antarctic Peninsula, near the South Orkney Islands, in the waters northwest off South Georgia and in waters in the middle of the Scotia Sea, between 32-32ºW and 55-57ºS.

The selected spatial model for average krill density explained 36.2% of the deviance. Closest distance to the coast (*coastdist*), sea surface temperature derived from CTD stations (*temptop*) and absolute sea surface velocity (*SSVabs*) were included in the selected model. Figure 4.6 shows smoother plots of these covariates. Predicted densities of krill were higher in onshore waters, especially within 130 km from the coast. A positive effect on predicted krill density was found in waters with surface temperatures of ~0.5-1.5ºC, while predicted krill density was lower for sea surface temperatures between 1.5-3.0ºC. Absolute sea surface velocity had a positive effect on predicted krill density for the 0.15-0.25 m/s range, and a negative effect for waters with higher absolute sea surface velocities (waters with absolute velocities higher than 0.45 m/s were poorly represented).

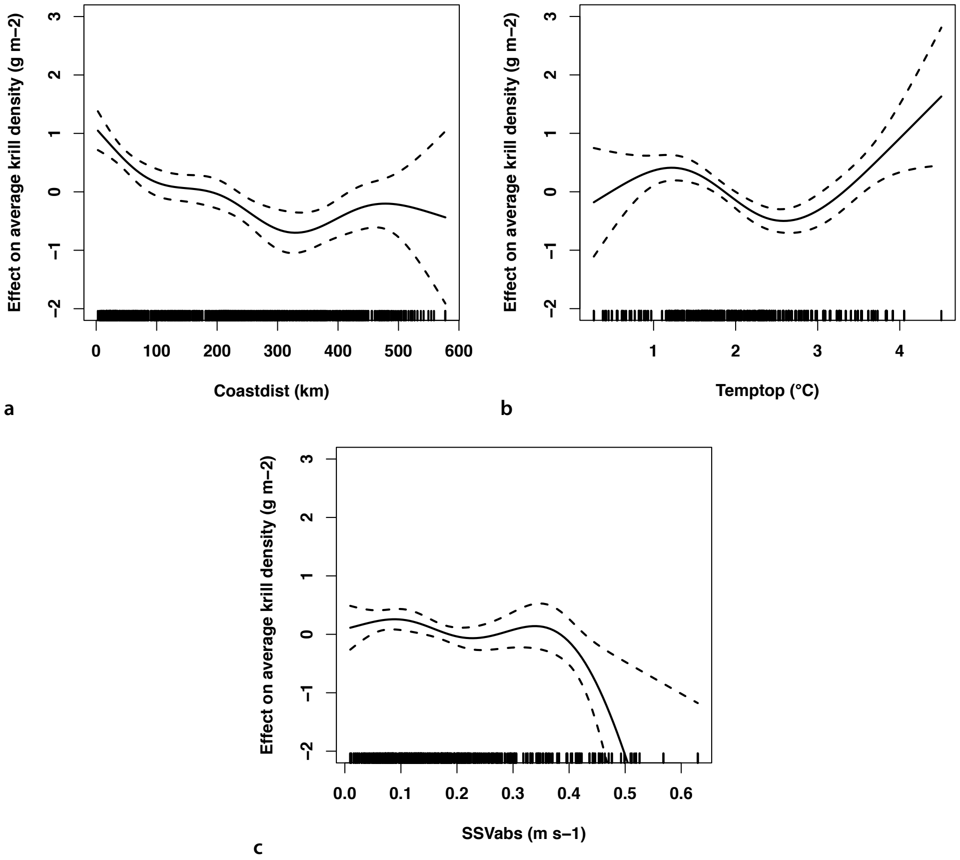


Figure 4.6. Smoother plots for the selected covariates in the spatial model of average krill density. The dashed upper and lower lines are placed at two standard errors above and below the smoother estimate. Covariate abbreviations: *coastdist* = closest distance to the coastline; *temptop* = sea surface temperature; *SSVabs* = absolute sea surface velocity.

Figure 4.7 shows a distribution map of the natural logarithms of predicted krill densities for the CCAMLR 2000 strata. In general, the predicted average krill density did correspond quite well with the observed values for average krill density. High values for both predicted and observed average krill densities were found near the South Shetland Islands and South Orkney Islands. However, cells with high observed average krill densities northwest of South Georgia and in the middle of the Scotia Sea (near 35ºW), also reported by Hewitt et al. (2004), only had moderate average krill density values predicted by the model. Regions representing high predicted average krill densities were more smoothed out than in the observed average krill density map (Figure 4.7 compared to Figure 4.5). These more smoothed results are due to the inclusion of only three covariates in the selected spatial model for average krill density.

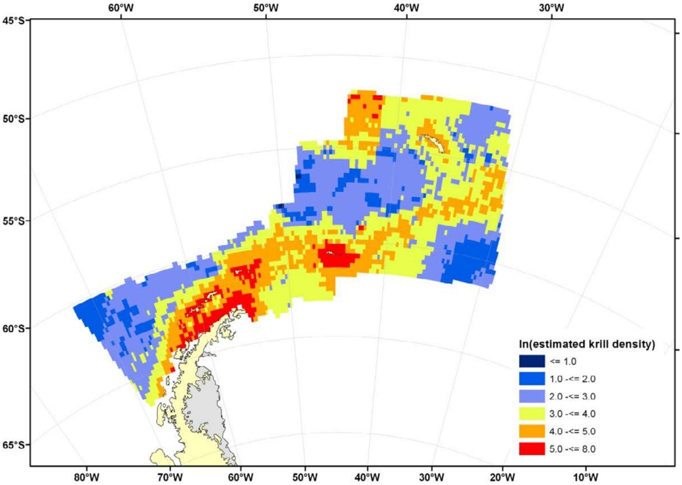


Figure 4.7. Distribution of natural logarithms taken from estimated krill densities, predicted for each 0.25° x 0.25° grid cell, for the CCAMLR 2000 strata with cetacean observers on effort.

Spatial models of baleen whale density

Since southern right whales were only encountered in waters southwest of South Georgia, and the number of detected schools for this species was relatively low (less than 25), we decided not to develop a spatial model for this particular species. Therefore, the below section only describes selected spatial models for minke whales, humpback whales and fin whales.

Minke whale density

The selected spatial model for minke whale density explained 19.7% of the deviance and included the following covariates: sea water temperature at 100m depth (*temp100m*), the natural logarithm of average krill density (*logavgkrill*), closest distance to the SACCF (*SACCFdist*) and bathymetric depth. Figure 4.8 shows smoother plots of these covariates. Densities of minke whales were highest for waters with *temp100m*-values below -0.2ºC. A positive effect on minke whale density was found for high average krill density (natural logarithm values in excess of 4.0). Furthermore, densities of minke whales were highest in proximity of the SACCF and a positive effect on minke whale density was found for waters with bathymetric depths ranging between ~1000m and 3000m. The prediction plot for minke whale density (Figure 4.11a) shows that the region with most sightings, northwest of the Antarctic Peninsula, did contain relatively high predicted minke whale densities (> 0.05 whales/km^2). The highest densities of minke whales were predicted for waters (south)west of the South Orkney Islands, yet unfortunately the limited survey effort in this region did not result in any minke whale sighting. The number of minke whales sighted in the Scotia Sea stratum was quite low, which was reflected by the low predicted densities (mostly lower than 0.05 whales/km^2) within this stratum.

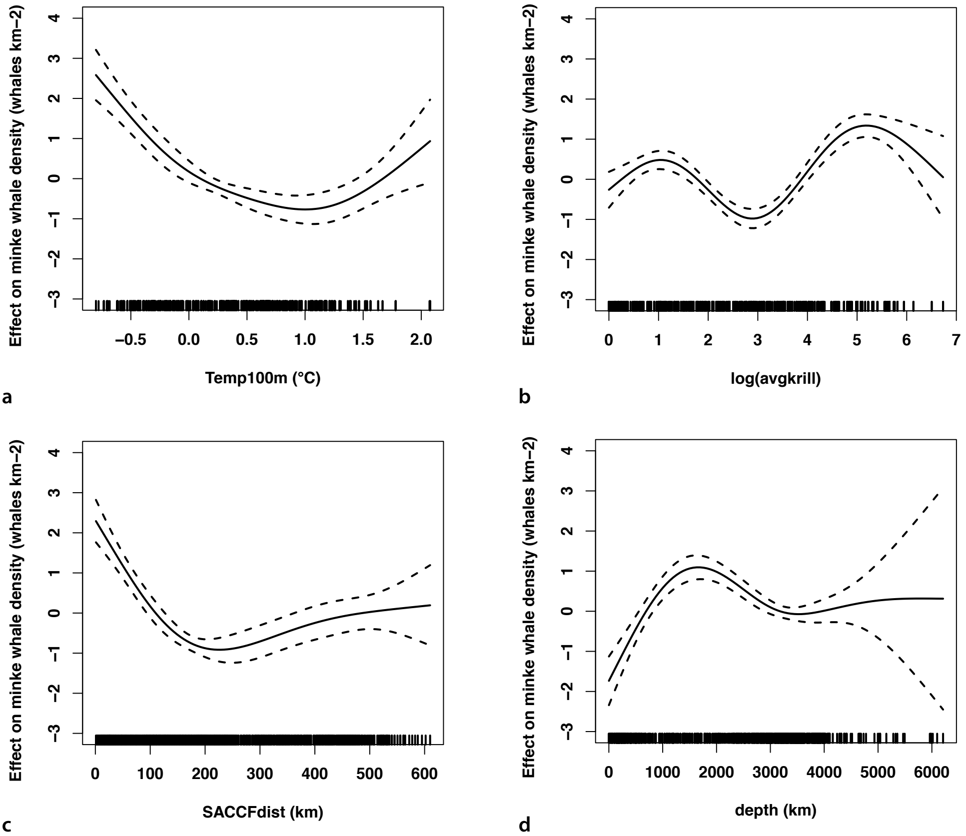


Figure 4.8. Smoother plots for the selected covariates in the spatial model of minke whale density. The dashed upper and lower lines are placed at two standard errors above and below the smoother estimate. Covariate abbreviations: *temp100m* = sea water temperature at 100m depth; *logavgkrill* = natural logarithm of average krill density per 0.25°x0.25° grid cell; *SACCFdist* = closest distance to the Southern Antarctic Circumpolar Current Front.

Humpback whale density

The selected spatial model for humpback whale density included only closest distance to the coast (*coastdist*) and in situ sea water temperature (*temptop*), and explained 34.2% of the deviance. Smoother plots of these two covariates are given in Figure 4.9. Density of humpback whales was relatively high in proximity of the coast and further than about 400m away from the coast, with the *coastdist*-smoother having a global minimum around 200m. Waters with sea surface temperatures between ~1.0 to 2.5ºC had a relatively high density of humpback whales. Most sightings of humpback whales were recorded in the waters north to northwest of the Antarctic Peninsula, and in the northeast corner of the Scotia Sea stratum. Densities in these two regions were also predicted to be high by the selected model (Figure 4.11b). One region with predicted densities between 0.01 and 0.04 whales/km^2 in the Scotia Sea (~35-40ºW, ~57-59ºS) did not contain any humpback whale sightings. Predicted densities were also somewhat higher southwest of South Georgia, but we could not verify this with sightings due to lack of effort. All predicted densities for humpback whales were below 0.06 whales/km^2, while minke whale predicted densities were between 0.10 and 0.20 whales/km^2 in a few localities. This confirmed the highest local abundance of this species.

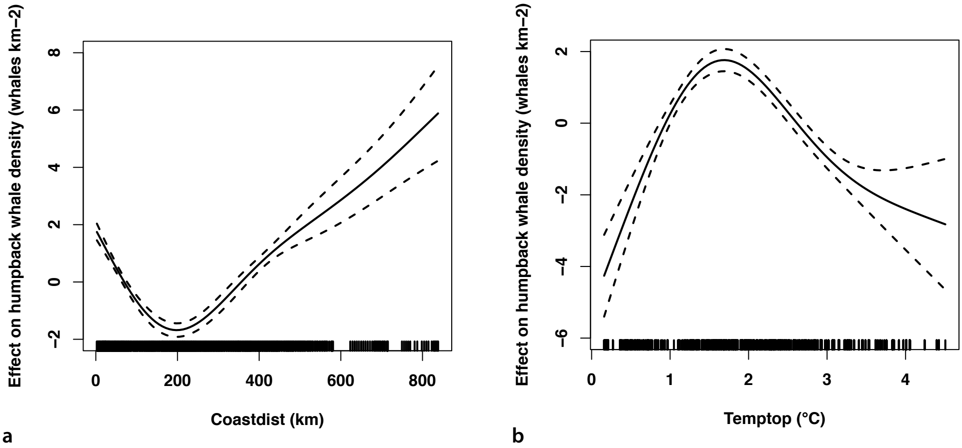


Figure 4.9. Smoother plots for the selected covariates in the spatial model of humpback whale density. The dashed upper and lower lines are placed at two standard errors above and below the smoother estimate. Covariate abbreviations: *coastdist* = closest distance to the coastline; *temptop* = sea surface temperature.

Fin whale density

Explained deviance was 26.0% for the selected fin whale model, which included sea surface temperature (*OISST*), closest distance to the continental shelf (*1000m-dist*) and closest distance to the SBACC (*SBACCdist_SSH*) as covariates. The smoother plot for OISST (Figure 4.10) shows a negative effect on fin whale density for waters with sea surface temperatures below ~2.0°C while the effect was positive for *OISST*-values higher than 4.0°C (although sea surface temperatures above 5.0°C were poorly represented). Densities of fin whales were relatively high within 100m of the continental shelf and 200m distance to the SBACC (Figure 4.10). Predicted densities of fin whales were generally lower than 0.04 whales/km^2 (Figure 4.11c). The largest region with relatively high densities (between 0.01 and 0.04 whales/km^2) was found between 60 and 45°W and coincided with recorded sightings. Fin whales were hardly sighted in the Scotia Sea, which was confirmed by the low predicted densities.

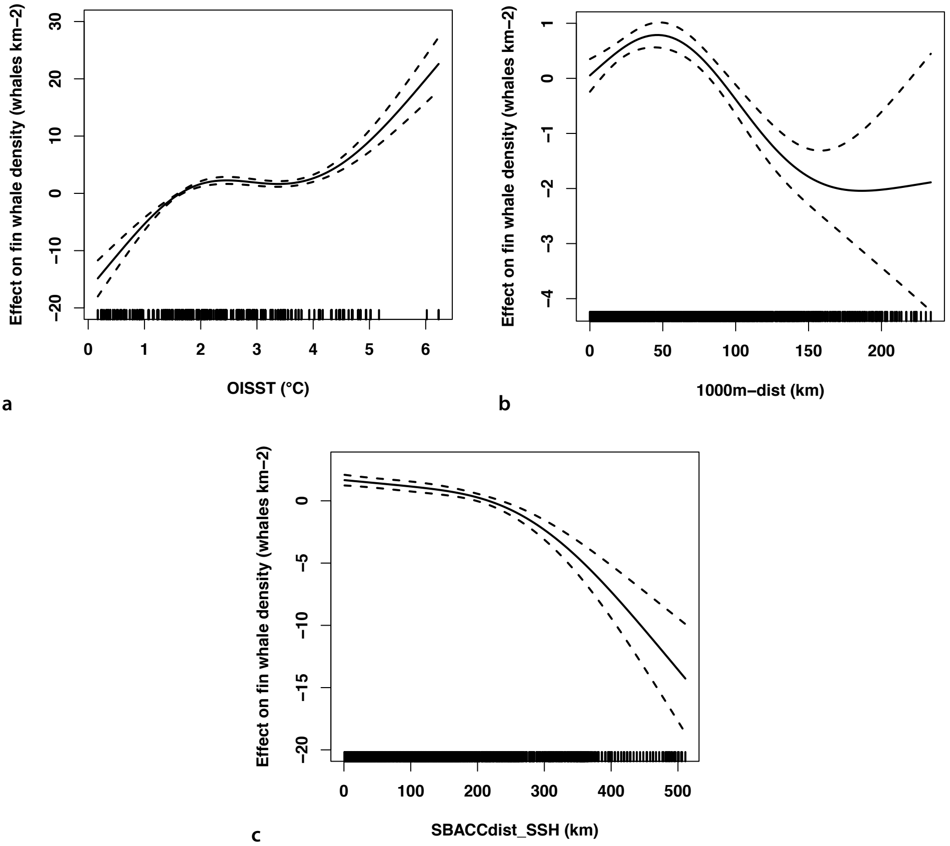


Figure 4.10. Smoother plots for the selected covariates in the spatial model of fin whale density. The dashed upper and lower lines are placed at two standard errors above and below the smoother estimate. Covariate abbreviations: *OISST* = Optimally Interpolated Sea Surface Temperature; *1000m-dist* = closest distance to the continental shelf (defined at 1000m depth); *SBACCdist_SSH* = closest distance to the Southern Boundary of the Antarctic Circumpolar Current. Location derived from Sea Surface Height (SSH) data.

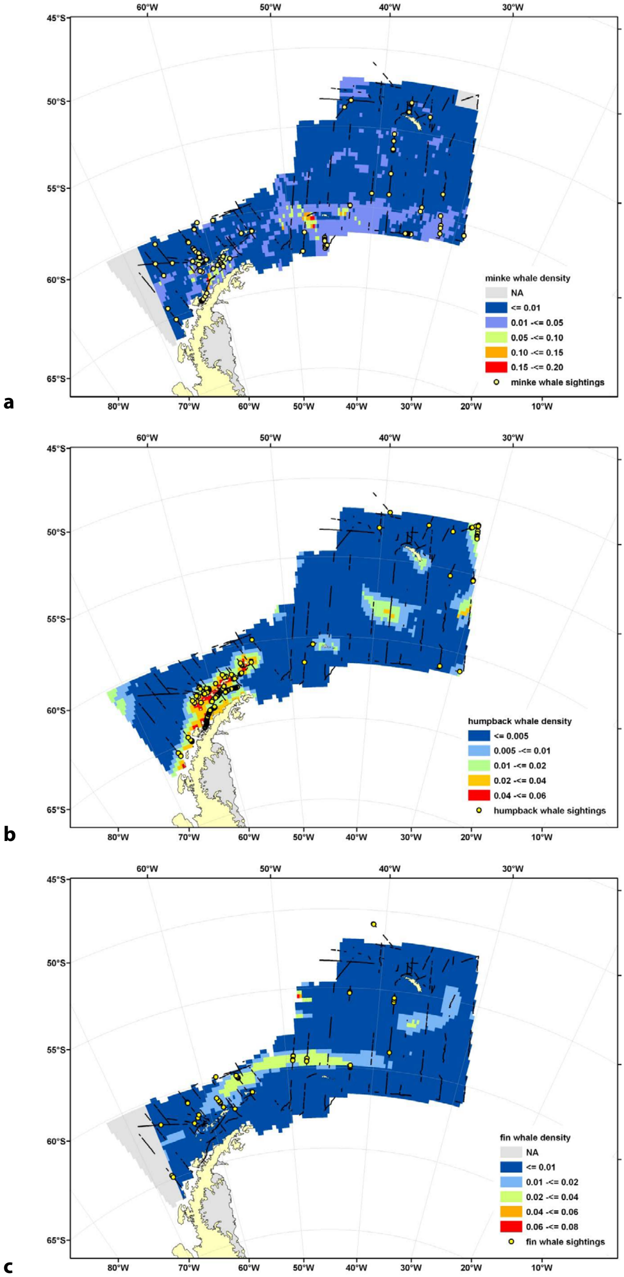


Figure 4.11. Predicted density (whales/km^2) maps for Antarctic minke whales (*Balaenoptera bonaerensis*), humpback whales (*Megaptera novaeangliae*) and fin whales (*B. physalus*), generated by species-specific spatial models based on CCAMLR2000 shipboard sightings data. The density maps for Antarctic minke and fin whales include grey regions, due to missing values for *SACCFdist* and *SBACCdist_SSH*, respectively. Legends show different density scales for the various species.

DISCUSSION

Our study shows large differences in predicted density patterns for Antarctic minke whales, humpback whales and fin whales within the Scotia Sea region. Firstly, prediction maps suggest a more widespread high density distribution for Antarctic minke whales compared to the other whale species (note the different scale for the predicted density map for minke whales). These other whale species include southern right whales for which density could not be estimated, but all the sightings of southern right whales aggregated around South Georgia. Secondly, predicted densities of both Antarctic minke and humpback whales were relatively high in the waters north to northwest of the Antarctic Peninsula, whereas predicted density of fin whales did not exceed 0.01 whales/km^2 (the lowest density class) for these particular waters.

The highest densities of Antarctic minke whales were predicted for waters (south)west of the South Orkney Islands (Figure 4.11a). Unfortunately, we could not verify this result due to a lack of survey effort in this region. However, we predicted high densities of Antarctic krill for this region (Figure 4.7), which had a positive effect on predicted density of Antarctic minke whales. In addition, waters in this region were relatively cold (values for *temp100m* lower than -0.20˚C) and had bathymetric depths ranging between ~1500 and 2500m. The combination of these environmental factors led to the predicted high densities of Antarctic minke whales in this region.

Stomach analysis studies show Antarctic krill being the staple diet for the three species of baleen whales in the Southern Ocean (Matthews, 1938; Ohsumi et al., 1970; Nemoto, 1970; Kawamura, 1980, 1994). However, even though these three whale species share interest in the same prey, this does not necessarily have to result in similar whale density distributions. Species of baleen whales may differ in their foraging behaviour and target different types of krill aggregations. Friedlaender et al. (2009) found for Marguerite Bay, western Antarctic Peninsula, that sightings of minke whales were associated with krill aggregations generally found at larger depth and with a higher mean biomass density compared to the aggregations with which humpback whale sightings were associated. Furthermore, the same authors reported that aggregations of krill associated with minke whales were more variable in size compared to the aggregations associated with humpback whales. The more widespread density distribution for minke whales in the Scotia Sea region could indicate that this species targets a wider range of habitats suitable for krill aggregations of various sizes.

Apart from the size of krill aggregations, baleen whales might prefer aggregations of krill dominated by a specific life history stage. Atkinson et al. (2006) reported a general gradient in population structure across the Scotia Sea region. Immature krill was dominant in the southwest, while subadult and adult krill were relatively abundant in the northeast. Furthermore, highest daily growth rates were reported for stations with populations dominated by small, immature or subadult krill (Atkinson et al., 2006; Tarling et al., 2006). The availability of a predictable food supply in the vicinity of the South Shetland Islands is the simplest explanation for high densities of Antarctic minke and humpback whales in these waters. However, this warrants the question why the density distribution of fin whales does not show the same pattern. An alternative explanation is that minke whales and humpback whales prefer juvenile krill, which is mostly found in the southwest of the Scotia Sea, whereas fin whales prefer subadult and adult krill found in deeper waters. Similarly, Santora et al. (2010) found that humpback whales were associated with small juvenile krill, whereas fin whales were associated with large mature krill near the South Shetland Islands.

Surprisingly, only the selected spatial model for minke whales includes average krill density as a covariate, with density of minke whales being significantly higher for the upper end of the average krill density spectrum. For the selected spatial model of humpback whale density, the inclusion of closest distance to the coast (*coastdist*) as a covariate may indirectly represent a positive relationship between humpback whale density and average krill density. Smoother function plots show that both densities decline significantly with increasing distance from the coast within the 200 km range (Figures 4.6 and 4.9). The low number of fin whale sightings may be an explanation for not finding the expected positive relationship with average krill density, even though other strong qualitative relationships with non-biological variables were included in the selected spatial model.

Average krill density may not be the best descriptive variable of spatial relationships between baleen whales and their prey. Recent studies show that krill can aggregate in 'superswarms', which are very dense, localised aggregations (Tarling et al., 2009). Nowacek et al. (2011) reported a congregation of humpback whales foraging on a 'superswarm' in inshore waters of Marguerite Bay. Similarly, both aggregation area and packing concentration were larger for swarms within 50 m of the shoreline, compared to swarms in offshore waters for the Scotia Sea region (Klevjer et al., 2010). The steep decline in the *coastdist*-smoother plot for humpback whales could be indicative of humpback whales specifically targeting these 'superswarms', or other coastal areas that promote higher density of krill.

Covariates related to advection processes were included in spatial models for minke and fin whale density. Both models include an expected decline in whale density with increasing distance from strong currents. For Antarctic minke whales, the SACCF appears to be more important (*SACCFdist*-smoother plot, Figure 4.8), while closest distance from the SBACC was included in the spatial model of fin whale density (*SBACCdist_SSH*-smoother plot, Figure 4.10). A relationship between humpback whale density and currents is possibly indirectly included in the *coastdist*--smoother, as both the SACCF and SBACC are relatively close to the coast for the western part of the Scotia Sea (Brandon et al., 2004). These findings agree with Tynan (1998) who found that the highest concentrations of catches of both fin whales and humpback whales coincided with the SBACC from late spring to midsummer between 1932 and 1961.

Even after considering a large number of potential bottom-up drivers, the explained deviance of the selected models was relatively low to moderate. For these models, only potential bottom-up drivers were considered, assuming that density distributions of baleen whales are solely determined by foraging behaviour. However, even though baleen whales migrate to the

Southern Ocean to feed, they do not necessarily have to forage all the time. Furthermore, the Scotia Sea region is expected to undergo rapid change, and maybe even experience a shift from a krill-dominated to a copepod-dominated or salp-dominated ecosystem (Murphy et al., 2007). Therefore, we need to study the flexibility of baleen whale foraging behaviour which affects the variability of their density distributions. In order to do this, more interdisciplinary surveys need to be conducted in the Scotia Sea region in subsequent years, to confirm whether the distribution patterns as described in this chapter are exemplary for the Scotia Sea region, or only characteristic for the austral summer of 2000. An alternative way to study the flexibility of baleen whale foraging behaviour is to develop models with various sets of behavioural rules, as has been done for Antarctic krill (Thorpe et al., 2007). Model output in the form of distribution patterns can be compared with predicted density maps, to discover the most plausible behavioural rule for each baleen whale species.

ACKNOWLEDGEMENTS

We would like to thank all officers, crew and scientists involved in the CCAMLR 2000 survey for conducting this survey and collecting the data used for this analysis. We are grateful to CCAMLR for providing all data sets. We would like to thank Sharon Hedley and Carole Durussel for their information and comments on the whale sightings data. The frontal positions derived from CTD data were kindly provided by Mark Brandon. Sophie Fielding performed the analysis of krill acoustic data and provided the processed data. The SSV data were given by Sally Thorpe, and Hugh Venables commented on which SSH-values to use for identifying fronts. The altimeter products were produced by SSalto/Duacs and distributed by Aviso, with support from Cnes (http://www.aviso.oceanobs.com/duacs/). This research is funded by the EURopean Network of Excellence for Ocean Ecosystems Analysis (EUR-OCEANS) under project number WP4-SYSSO-1066 and by the University of Groningen. This chapter contributes to the Ecosystems Programme, part of the Polar Science for Planet Earth framework of the British Antarctic Survey.

REFERENCES

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. pp. 267-281. *In*: B. Petran and F. Csaaki (eds.) *Second international symposium on information theory*, Akadeemiai Kiadi, Budapest, Hungary. 451pp.

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

Atkinson, A., Shreeve, R.S., Hirst, A.G., Rothery, P., Tarling, G.A., Pond, D.W., Korb, R.E., Murphy, E.J. and Watkins, J.L. 2006. Natural growth rates in Antarctic krill (*Euphausia superba*): II. Predictive models based on food, temperature, body length, sex and maturity stage. *Limn. Oceanogr.* 51(2): 973-987.

Atkinson, A., Siegel, V., Pakhomov, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A., Fleming, A.H. 2008. Oceanic circumpolar habitats of Antarctic krill. *Mar. Ecol. Prog. Ser.* 362: 1-23.

Brandon, M.A., Naganobu, M., Demer, D.A., Chernyshkov, P., Trathan, P.N., Thorpe, S.E., Kameda, T., Berezhinskiy, O.A., Hawker, E.J. and Grant, S. 2004. Physical oceanography in the Scotia Sea during the CCAMLR 2000 survey, austral summer 2000. *Deep-Sea Res. II* 51(12-13): 1301-1321.

Buckland, S.T. and Anganuzzi, A.A. 1988. Comparison of smearing methods in the analysis of minke whale sightings data from IWC/IDCR Antarctic cruises. *Rep. int. Whal. Commn.* 38: 257-263.

Buckland, S.T. and Turnock, B.J. 1992. A robust line transect method. *Biometrics* 48(3): 901-909.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. and Thomas, L. (eds.) 2001. *Introduction to distance sampling*. Oxford University Press, Oxford. 432pp.

Cavalieri, D., Parkinson, C., Gloersen, P. and Zwally, H.J. 1996, updated 2006. Sea ice concentrations from Nimbus-7 SMMR and DMSP SSM/I passive microwave data. Boulder, Colorado USA: National Snow and Ice Data Center. Digital media.

CCAMLR. 2005. Report of the first meeting of the subgroup on acoustic survey and analysis methods (SG-ASAM). SC-CCAMLR-XXIV/BG/3.

Clapham, P. J. and Baker, C.S. 2002. Modern whaling. pp. 1239-1243. *In*: Perrin, W.F., Würsig, B. and Thewissen, J.G.M. (eds.) *Encyclopedia of marine mammals*. Academic Press, San Diego. 1352pp.

Conti, S.G. and Demer, D.A. 2006. Improved parameterization of the SDWBA for estimating krill target strength. *ICES J. Mar. Sci.* 63(5): 928-935.

Demer, D.A. and Conti, S.G. 2003a. Reconciling theoretical versus empirical target strengths of krill: effects of phase variability on the distorted-wave Born approximation. *ICES J. Mar. Sci.* 60(2): 429-434.

Demer, D.A. and Conti, S.G. 2003b. Validation of the stochastic distorted-wave Born approximation model with broad bandwidth total target strength measurements of Antarctic krill. *ICES J. Mar. Sci.* 60(3): 625-635.

Demer, D.A. and Conti, S.G. 2005. New target-strength model indicates more krill in the Southern Ocean. *ICES J. Mar. Sci.* 62(1): 25-32.

Engel, M.H. and Martin, A.R. 2009. Feeding grounds of the western South Atlantic humpback whale population. *Mar. Mamm. Sci.* 25(4): 964-969.

Friedlaender, A.S., Lawson, G.L. and Halpin, P.N. 2009. Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. *Mar. Mamm. Sci.* 25(2): 402-415.

Hedley, S.L. and Buckland, S.T. 2004. Spatial models for line transect sampling. *J. Agric. Biol. Env. Stat.* 9(2): 181-199.

Hedley, S., Reilly, S., Borberg, J., Holland, R., Hewitt, R., Watkins, J., Naganobu, M. and Sushin, V. 2001. Modelling whale distribution: a preliminary analysis of data collected on the CCAMLR-IWC Krill Synoptic Survey, 2000. Paper SC/53/E9 presented to the IWC Scientific Committee, July 2001 (unpublished). 38pp. [Paper available from the Office of the IWC].

Hewitt, R.P., Watkins, J., Naganobu, M., Sushin, V., Brierley, A.S., Demer, D., Kasatkina, S., Takao, Y., Goss, C., Malyshko, A., Brandon, M., Kawaguchi, S., Siegel, V., Trathan, P., Emery, J., Everson, I. and Miller, D. 2004. Biomass of Antarctic krill in the Scotia Sea in January/February 2000 and its use in revising an estimate of precautionary yield. *Deep-Sea Res. II* 51(12-13): 1215-1236.

Hofmann, E.E. and Murphy, E.J. 2004. Advection, krill, and Antarctic marine ecosystems. *Antarct. Sci.* 16(4): 487-499.

Holm-Hansen, O., Kahru, M., Hewes, C.D., Kawaguchi, S., Kameda, T., Sushin, V.A., Krasovski, I., Priddle, J., Korb, R., Hewitt, R.P. and Mitchell, B.G. 2004. Temporal and spatial distribution of chlorophyll-*a* in surface waters of the Scotia Sea as determined by both shipboard measurements and satellite data. *Deep-Sea Res II* 51(12-13): 1323-1331.

Horvitz, D.G. and Thompson, D.J. 1952. A generalization of sampling without replacement from a finite universe. *J. Am. Stat. Assoc.* 47: 663-685.

IOC, IHO and BODC. 2003. Centenary edition of the GEBCO Digital Atlas, published on CD-rom on behalf of the Intergovernmental Oceanographic Commission and the International Hydrographic Organization as part of the General Bathymetric Chart of the Oceans, British Oceanographic Data Centre, Liverpool, UK.

IWC, 2000. Report of the SOWER 2000 workshop. *J. Cetacean Res. Manage.* 2(Suppl.): 321-346.

Kawamura, A. 1980. A review of food of balaenopterid whales. *Sci. Rep. Whales Res. Inst.* 32: 155-197.

Kawamura, A. 1994. A review of baleen whale feeding in the Southern Ocean. *Rep. int .Whal. Commn.* 44: 261-271.

Klevjer, T.A., Tarling, G.A. and Fielding, S. 2010. Swarm characteristics of Antarctic krill *Euphausia superba* relative to the proximity of land during summer in the Scotia Sea. *Mar. Ecol. Prog. Ser.* 409: 157-170.

Laake, J.L. and Borchers, D.L. 2004. Methods for incomplete detection at distance zero. pp. 108-189. *In*: S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers and L. Thomas (eds.) *Advanced distance sampling*. Oxford University Press, Oxford. 416pp.

Lê, S., Josse, J. and Husson, F. 2008. FactoMineR: An R package for multivariate analysis. *J. Stat. Softw.* 25(1): 1-18.

MacLennan, D.N., Fernandes, P.G. and Dalen, J. 2002. A consistent approach to definitions and symbols in fisheries acoustics. *ICES J. Mar. Sci.* 59(2): 365-369.

Madureira, L.S.P., Everson, I. and Murphy, E.J. 1993a. Interpretation of acoustic data at two frequencies to discriminate between Antarctic krill (*Euphausia superba* Dana) and other scatterers. *J. Plankton Res.* 15(7): 787-802.

Madureira, L.S.P., Ward, P. and Atkinson, A. 1993b. Differences in backscattering strength determined at 120 and 38 kHz for three species of Antarctic macroplankton. *Mar. Ecol. Prog. Ser.* 93: 17-24.

Marques, F.F.C. and Buckland, S.T. 2004. Covariate models for the detection function. pp. 31-47. *In*: S.T. Buckland, D.R. Anderson, K.P. Burnham, J.L. Laake, D.L. Borchers and L. Thomas (eds). *Advanced distance sampling*. Oxford University Press, Oxford. 416pp.

Marr, J.W.S. 1962. The natural history and geography of the Antarctic krill (*Euphausia superba* Dana). *Discov. Rep.* 32: 33-464.

Matthews, L.H. 1938. The humpback whale, *Megaptera nodosa*. *Discovery Rep.* 17: 7-92.

McGehee, D.E., O'Driscoll, R.L. and Traykovski, L.V.M. 1998. Effects of orientation on acoustic scattering from Antarctic krill at 120 kHz. *Deep-Sea Res. II* 45(7): 1273-1294.

Miller, D.G. and Hampton, I. 1989. Biology and ecology of the Antarctic krill (*Euphausia superba* Dana): a review. *BIOMASS Scientific Series* 9: 1-66.

Murphy, E.J., Thorpe, S.E., Watkins, J.L. and Hewitt, R. 2004. Modeling the krill transport pathways in the Scotia Sea: spatial and environmental connections generating the seasonal distribution of krill. *Deep-Sea Res II* 51: 1435-1456.

Murphy, E.J., Watkins, J.L., Trathan, P.N., Reid, K., Meredith, M.P., Thorpe, S.E., Johnston, N.M., Clarke, A., Tarling, G.A., Collins, M.A., Forcada, J., Shreeve, R.S., Atkinson, A., Korb, R., Whitehouse, M.J., Ward, P., Rodhouse, P.G., Enderlein, P., Hirst, A.G., Martin, A.R., Hill, S.L., Staniland, I.J., Pond, D.W., Briggs, D.R., Cunningham, N.J. and Fleming, A.H. 2007. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. *Phil. Trans. R. Soc. B* 362: 113-148.

Murphy, E.J., Watkins, J.L, Trathan, P.N, Reid, K., Meredith, M.P., Hill, S.L., Thorpe, S.E., Johnston, N.M., Clarke, A., Tarling, G.A, Collins, M.A., Forcada, J., Atkinson, A., Ward, P., Staniland, I.J., Pond, D.W., Cavanagh, R.A., Shreeve, R.S., Korb, R.E., Whitehouse, M.J., Rodhouse, P.G., Enderlein, P., Hirst, A.G., Martin, A.R., Briggs, D.R., Cunningham, N.J. and Fleming, A.H. 2012. Spatial and temporal operation of the Scotia Sea ecosystem. pp. 160-212. *In*: A.D. Rogers, N.M. Johnston, E.J. Murphy and A. Clarke (eds.) *Antarctic ecosystems: an extreme environment in a changing world.* Wiley-Blackwell, Oxford. 538 pp.

Nemoto, T. 1970. Feeding patterns of baleen whales in the ocean. pp. 241-252. *In*: J.H. Steele (ed.) *Marine food chains*. Oliver and Boyd, Edinburgh. 552pp.

Nicol, S. 2006. Krill, currents, and sea ice: *Euphausia superba* and its changing environment. *BioScience* 56(2): 111-120.

Nicol, S., Worby, A. and Leaper, R. 2008. Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. *Marine and Freshwater Research* 59: 361-382.

Nowacek, D.P., Friedlaender, A.S., Halpin, P.N., Hazen, E.L., Johnston, D.W., Read, A.J., Espinasse, B., Zhou, M. and Zhu, Y. 2011. Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. *PLoS ONE* 6(4): e19173.

Ohsumi, S., Masaki, Y. and Kawamura, A. 1970. Stock of the Antarctic minke whale. *Sci. Rep. Whales Res. Inst.* 22: 75-125.

Peel, D., Kelly, N., Bravington, M.V. and Hedley, S.L. 2008. IWC 2008 title: Design of future SOWER voyages: an update. Paper SC/60/IA5 presented to the IWC Scientific Committee, June 2008 (unpublished). 11pp. [Paper available at the Office of the IWC].

R Development Core Team. 2009. R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. URL http://www.R-project.org.

Reid, K., Brierley, A.S. and Nevitt, G.A. 2000. An initial examination of relationships between the distribution of whales and Antarctic krill *Euphausia superba* at South Georgia. *J. Cetacean Res. Manage.* 2(2): 143-149.

Reilly, S., Hedley, S., Borberg, J., Hewitt, R., Thiele, D., Watkins, J. and Naganobu, M. 2004. Biomass and energy transfer to baleen whales in the South Atlantic sector of the Southern Ocean. *Deep-Sea Res. II* 51 (12-13): 1397-1409.

Reynolds, R.W., Rayner, N.A., Smith, T.M., Stokes, D.C. and Wang, W. 2002. An improved in situ and satellite SST analysis for climate. *J. Clim.* 15: 1609-1625.

Reynolds, R.W. and Smith, T.M. 1994. Improved global sea surface temperature analyses using optimum interpolation. *J. Clim.* 7: 929-948.

Santora, J.A., Reiss, C.S., Loeb, V.J. and Veit, R.R. 2010. Spatial association between hotspots of baleen whales and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent predation. *Mar. Ecol. Prog. Ser.* 405: 255-269.

Siegel, V. 2005. Distribution and population dynamics of *Euphausia superba*: summary of recent findings. *Pol. Biol.* 29:1-22.

Širović, A., Hildebrand, J.A. and Thiele, D. 2006. Baleen whales in the Scotia Sea during January and February 2003. *J. Cetacean Res. Manage.*8(2): 161-171.

Southwell, C.J., Paxton, C.G.M., Borchers, D.L., Boveng, P.L., Nordøy, E.S., Blix, A.S. and De la Mare, W.K. 2008. Estimating population status under conditions of uncertainty: the Ross seal in East Antarctica. *Antarct. Sci.* 20(2): 123-133.

Tarling, G.A., Shreeve, R.S., Hirst, A.G., Atkinson, A., Pond, D.W., Murphy, E.J. and Watkins, J.L. 2006. Natural growth rates in Antarctic krill (*Euphausia superba*): I. Improving methodology and predicting intermolt period. *Limnology and Oceanography* 51(2): 959-972.

Tarling, G.A., Klevjer, T., Fielding, S., Watkins, J., Atkinson, A., Murphy, E., Korb, R., Whitehouse, M. and Leaper, R. 2009. Variability and predictability of Antarctic krill swarm structure. *Deep-Sea Res. I* 56(11): 1994-2012.

Thomas, L., Buckland, S.T., Rexstad, E.A., Laake, J.L., Stringberg, S., Hedley, S.L., Bishop, J.R.B., Marques, T.A. and Burnham, K.P. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *J. Appl. Ecol.* 47(1): 5-14.

Thorpe, S.E., Murphy, E.J. and Watkins, J.L. 2007. Circumpolar connections between Antarctic krill (*Euphausia superba* Dana) populations: investigating the roles of ocean and sea ice transport. *Deep-Sea Res. I* 54: 792-810.

Trathan, P.N., Brierley, A.S., Brandon, M.A., Bone, D.G., Goss, C., Grant, S.A., Murphy, E.J. and Watkins, J.L. 2003. Oceanographic variability and changes in Antarctic krill (*Euphausia superba*) abundance at South Georgia. *Fish. Oceanogr.* 12(6): 569-583.

Trathan, P.N., Everson, I., Murphy, E.J. and Parkes, G.B. 1998. Analysis of haul data from the South Georgia krill fishery. *CCAMLR Science* 5: 9-30.

Tweedie, M.C.K. 1984. An index which distinguishes between some important exponential families. pp. 579-604. *In*: J.K. Ghosh and J. Roy (eds.) *Statistics: applications and new directions. Proceedings of the Indian Statistical Institute Golden Jubilee International Conference*. Indian Statistical Institute, Calcutta. 609pp.

Tynan, C. and Thiele, D. 2003. Report on Antarctic ice edge definition by the ad hoc Working Group on ice data collection in the Antarctic. Paper SC/55/E19 presented to the IWC Scientific Committee, May 2003 (unpublished). 1pp. [Paper available from the Office of the IWC].

Tynan, C.T. 1998. Ecological importance of the Southern Boundary of the Antarctic Circumpolar Current. *Nature* 392: 708-710.

Watkins, J.L. and Brierley, A.S. 2002. Verification of the acoustic techniques used to identify Antarctic krill. *ICES J. Mar. Sci.* 59: 1326-1336.

Watkins, J.L., Hewitt, R., Naganobu, M. And Sushin, V. 2004. The CCAMLR 2000 survey: a multinational, multi-ship biological oceanography survey of the Atlantic sector of the Southern Ocean. *Deep-Sea Res. II* 51 (12-13): 1205-1213.

Wood, S.N. 2006. *Generalized Additive Models: an introduction with R*. Chapman & Hall, New York. 391pp.

Wood, S.N. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. *J. R. Statist. Soc. B* 70(3): 495-518.

Synthesis and reflections on future research

5

One of the most pressing questions in baleen whale conservation and management is how baleen whales will respond to future trends in the physical environment within the Southern Ocean. To answer this question, we need to gain a much better understanding of baleen whale behaviour in relation to the environment. More specifically, a large unknown is their ability to respond to longer-term changes in the sea ice environment and corresponding changes in prey availability (Tynan and DeMaster, 1997). In absence of prey availability data, one way to indirectly study this question is to examine past density distributions of baleen whales and model how their densities were associated with aspects of their environment that are consistent with potential changes in prey availability. Firstly, the variability in density distributions provides information on how each baleen whales species occupies a certain area of interest. Secondly, associations found between species-specific baleen whale density and the environment may give us a better idea of the relationships and mechanisms underlying these associations (Nicol et al., 2008). Thirdly, studying density distributions of different baleen whale species in the same area of interest can provide insight into how species differ in their foraging behaviour. The degree of overlap in foraging behaviour could indicate potential conflicts of interest when prey availability and distributions shift.

In this chapter, I will discuss what we can infer from the spatial models developed for this thesis to partly fill this knowledge gap. Firstly, I will briefly give an overview of the sea ice environment and predicted trends therein. Secondly, I will give an overview of what we can infer from the spatial models developed for this thesis regarding the relationships between baleen whale density and the environment. Finally, I will explore possible responses of baleen whale species to predicted long-term change in the sea ice environment.

Predicted trends in the sea ice environment

One of the most prominent physical processes in the Southern Ocean is the seasonal sea ice melt and formation, which is related to extreme seasonality. Maximum sea ice cover in winter is about 17 million km^2, while ice melting reduces the sea ice area to approximately 4 million km^2 in the austral summer (Zwally, 2002). A consequence of the ice melting process is the formation of the marginal ice zone, defined (e.g. Arrigo et al., 1998) as the area where sea ice was present at the beginning of the month, but not at the end. The melt water in the marginal ice zone is less dense than sea water because of its lower salinity, and thus is found in a relatively stable layer at the sea water surface. This promotes vertical stability and phytoplankton growth when phytoplankton is more exposed to sunlight. On top of this, ice algae formerly trapped inside the ice are released during the melting process. The greater vertical water stability, together with the release of algae, creates algal blooms near the sea ice edge (e.g. Smith and Nelson, 1986). Therefore, daily primary productivity is relatively higher in the marginal ice zone compared to the open ocean (Arrigo et al., 1998). The profound seasonal reduction in sea ice area is the engine that drives the sea ice ecosystem through its positive effect on primary productivity, micro- and mesozooplankton, and ultimately Antarctic krill, a keystone component of Antarctic marine ecosystems.

Large changes are predicted for the sea ice, which will affect primary productivity, krill, and ultimately may affect baleen whales. Current model studies suggest a 24-33% decrease in annual average total sea ice cover by 2100, with the largest decrease predicted for the Weddell Sea in late summer (Arzel et al., 2006; Bracegirdle et al., 2008; Mayewski et al., 2009). The projected decrease in sea ice extent between 1986-2005 and 2081-2100 ranges from 16 to 67% in February, although Collins et al. (2013) expressed low confidence in these model projections. A result of this scenario would be a lower expected primary production within both the sea ice and marginal ice zones. However, total primary production within the Southern Ocean is expected to increase, since the expected gain in primary production within the open ocean is much higher than the loss of primary production within the two ice zones (Arrigo and Thomas, 2004). It is unclear what the implications of the negative trend in sea ice cover will be for krill abundance, distribution and swarm organisation, as the mechanistic relationship between primary production and krill is not well established. Under conditions of even ice melting, the alleged 25% reduction in sea ice cover during the 1960s (de la Mare, 1997) equals a less than 10% decrease in the length of the sea ice edge (Brierley et al., 2002). The sea ice edge is considered to be suitable habitat for krill, with postlarval density of Antarctic krill reported to be significantly higher under the ice at a distance of approximately 10-80 m from the ice edge than in open waters in the Lazarev Sea in summer (Flores et al., 2012). Furthermore, the macrozooplankton biomass within this band under the ice was dominated by Antarctic krill during the same expedition (Flores et al., 2011). Brierley et al. (2002) reported elevated summer krill densities further south from the ice edge as well, with krill densities between 1 and 13 kilometres south from the ice edge being up to five times higher than krill densities in open waters in the Weddell Sea. Therefore, a decline in the length of the sea ice edge may lead to lower krill abundance in the marginal ice zone. However, most krill live in the open ocean at moderate density (Atkinson et al., 2008) and the open ocean area is expected to increase as the sea ice declines. Thus, the lower krill abundance in the marginal ice zone may be in part compensated for by an increase of krill biomass in the open ocean area. Since the marginal ice zone is also an important source of young krill to the open ocean, the mechanisms of krill advection need to be considered as part of this process.

Given that sea ice is crucial to the viability of this system, how will the various baleen whale species respond to expected trends in the sea ice environment? To answer this question, we need to improve our understanding of the relationships between distribution patterns of baleen whale density and aspects of the environment that relate to whale food availability. More specifically, we need to understand whether the associations found between baleen whale density and the physical environment signify prey-predator relationships.

Relationships between baleen whale density and the environment

In this section, I revisit the questions stated in the Introduction chapter of this thesis.

Which aspects of the environment are related to density of Antarctic minke whales at the regional scale? How can the various relationships between density of Antarctic minke whales and the environment be characterised?

The spatial models described in Chapter 2 most often included environmental aspects related to transition zones, notably the sea ice edge, continental shelf and frontal systems. The density of Antarctic minke whales tended to be higher in regions closer to the sea ice edge and/or continental shelf break, often in colder waters. The relationship between density of minke whales and distance to the Southern Antarctic Circumpolar Current Front was often non-linear. Furthermore, only one model included distance to the Southern Boundary of the Antarctic Circumpolar Current, which suggests that the Antarctic Circumpolar Current may not be that important for minke whales. Transition zones often show enhanced productivity of both phytoplankton and krill, thus the higher density of minke whales in proximity of transition zones is probably related to higher krill density. Predominantly negative relationships with minke whale density were found for sea surface temperature and distances to the sea ice edge and continental shelf. However, none of the selected aspects of the environment had a consistent qualitative relationship with density at either the circumantarctic or the regional scale.

The selected spatial models did not include interactions between environmental aspects. For instance, Murase et al. (2002) reported high densities of minke whales in regions where the sea ice edge coincided with the continental shelf break in the Indian Ocean sector. These findings suggest a possible interaction effect between distance to the sea ice edge and distance to the continental shelf break. It would be interesting to see if the spatial models could improve by including interaction terms, but care must be taken to avoid overfitting.

How does sea ice affect the spatial and temporal variability in density of Antarctic minke whales in summertime?

Predicted density maps for Antarctic minke whales (Chapter 3) show that spatial density distributions of Antarctic minke whales are highly heterogeneous, with whale densities being particularly high in the Ross Sea, Weddell Sea and Prydz Bay, and very low densities for the Bellingshausen-Amundsen Sea. These regional differences in whale density coincide with differences in area of the marginal ice zone: the Bellingshausen-Amundsen Sea has the smallest marginal ice zone of all Southern Ocean sectors. Furthermore, the combined areas of the marginal ice zones of the Ross Sea and Weddell Sea constitute more than 70% of the total area of the marginal ice zone found in the Southern Ocean in January (and more than 55% in February) (Arrigo et al., 1998, 2008).

The temporal variability in mean density of Antarctic minke whales is in part region-specific (Chapter 3). In only three out of eight regions, mean density was lowest for the most recent survey, while other regions showed a monotonous, albeit small, increase in mean density over time. Both summer sea ice cover (experienced during the survey) and total change in sea ice cover during austral spring and summer showed significantly positive relationships with mean density of Antarctic minke whales. After correction for timing of survey, a significantly positive relationship between mean daily change in sea ice cover and mean whale density remained. We speculate that a larger amount of summer sea ice cover and/or a larger mean daily change in sea ice cover during spring and early summer may lead to higher krill biomass and consequently higher mean density of Antarctic minke whales during summer. These findings strongly suggest that the amount of sea ice cover, and especially seasonal change, affects density of Antarctic minke whales at the regional scale. Unfortunately, we could not directly study predator-prey relationships at the circumpolar, or even the regional scale, since data on krill density were not collected during the SOWER surveys. Therefore, we could only obtain indirect evidence of a positive relationship between minke whale density and krill biomass based on analysis of SOWER data.

Which aspects of the environment are related to the density distributions of Antarctic minke whales, humpback whales and fin whales in the Scotia Sea and to what extent do their distributions differ?

For the Scotia Sea ecosystem, where we could consider variables derived from krill acoustic data, we did find a significantly positive relationship between minke whale density and average krill density (Chapter 4). Only for the Scotia Sea ecosystem did sightings data allow us to study density distributions of several baleen whale species using line transect based methods. Furthermore, different sets of variables representing bottom-up drivers were selected for the three baleen whale species. For minke whale density, the selected spatial model included variables representing sea water temperature, average krill density, closest distance to the SACCF and bathymetric depth. The selected spatial model of humpback whale density included distance to the coast and sea water temperature. The spatial model of fin whale density suggested that sea surface temperature, closest distance to the continental shelf and closest distance to the SBACC were related to fin whale density in the Scotia Sea. Only for Antarctic minke whales did we find a significantly positive relationship with their main prey (Chapter 4). The relatively high densities of humpback whales in proximity of the coast may indirectly represent a positive relationship between humpback whale density and average krill density, since distance to the coast was included in the selected model for average krill density. Predicted density distributions were markedly different for the three baleen whale species (Antarctic minke whales, humpback whales and fin whales).The species-specific whale density distributions also suggest that different baleen whale species target krill aggregations that differ in size and life history class composition (Chapter 4). Relatively high densities were most widespread for Antarctic minke whales, which indicates that this species forages in a larger variety of habitats, inhabited by krill aggregations that are highly variable in size. In concordance with this, Friedlaender et al. (2009) reported a larger variation in the size of krill aggregations associated with Antarctic minke whales compared to those in the vicinity of humpback whales, in Marguerite Bay on the western Antarctic Peninsula. Densities of both minke and humpback whales were relatively high in the southwest of the Scotia Sea, in waters inhabited by mostly juvenile krill, while fin whales may prefer subadult and adult krill found in deeper waters. This degree of habitat segregation and prey preference between whale species (see also Santora et al., 2010) has implications for their different responses to trends in the environment.

Possible responses of baleen whale species to trends in the environment

In this section, I will explore possible responses of baleen whale species to a negative trend in annual mean sea ice cover. This section needs to be considered as highly speculative, since we have only just begun to understand how baleen whales exploit their environment, and the long-term data series required to test and validate these ideas are not available. Since sea ice melt triggers algal blooms and sea ice provides a habitat for krill larvae to overwinter, at first glance a decrease in sea ice cover will lead to a decrease in krill biomass, and thus to less food being available for baleen whales. The lower availability of prey for baleen whales may potentially have a negative impact on the fragile recovery of populations of baleen whales in the Southern Ocean. However, this does not necessarily have to be the case.

Firstly, a negative trend in annual average total sea ice cover reduces the pack ice zone, which is the only zone that is exploited by Antarctic minke whales as only this baleen whale species is able to successfully penetrate the pack ice. When the pack ice zone becomes smaller, which implies a larger open ocean area, more foraging area will be available for larger baleen whale species. Especially humpback whales may benefit from this, since they preferentially forage on the continental shelf. Fin whales, which generally prefer deeper waters, may be the last species to move to higher latitude areas that were previously covered by sea ice.

Secondly, the opening up of the pack ice zone for large baleen whales can give them access to polynyas, which are often characterised by high krill productivity. As Brierley et al. (2002) pointed out, the decline in sea ice edge length may be more important for krill availability than the decline in sea ice cover. Even though climate models generally suggest a decline in sea ice cover, much less is known about how future regional warming may affect total sea ice edge length. Regional warming can also lead to more temporary polynyas in the pack ice, and a corresponding increase in sea ice edge length, which could increase primary and secondary productivity as well. It could even be possible, although quite unlikely, to have an increase in sea ice edge length for the larger area available to baleen whale foraging under a regime of uneven ice melt.

Finally, a decrease of annual average total sea ice area can be accompanied by a larger seasonal decrease in sea ice area and thus, at least temporarily, in a larger marginal ice zone which may be associated with higher primary and secondary productivity and higher density of minke whales at the regional level (as discussed in Chapter 3). However, climate model outputs suggest that the projected negative trend in annual mean sea ice cover is mostly driven by a negative trend in sea ice cover for the austral winter and spring (Bracegirdle et al., 2008). This could result in a smaller seasonal change in sea ice cover, simply because the differences between winter and summer sea ice cover become smaller. In addition, the projected long-term southward shift in the mean latitude of the summer sea ice edge (Collins et al., 2013) may lead to lower primary productivity in the marginal ice zone due to lower light intensity at higher latitudes. Furthermore, another possibility is that the marginal ice zone area will peak earlier in the season, for instance in November. This may result in a mismatch between a peak in krill availability and baleen whale density, since baleen whales generally arrive in the Southern Ocean from December onwards, constrained by the duration of their breeding cycle in other oceans.

Predicted changes in sea ice cover will not only impact krill productivity and biomass, but will also probably lead to a change in krill distribution. Northward and eastward sea-ice-associated transport from the southern Scotia Sea and western Antarctic Peninsula regions may be important in replenishing krill stocks in the Scotia Sea (Murphy et al., 2007; Thorpe et al., 2007). A continuation of regional warming for the western Antarctic Peninsula region with corresponding decrease in sea ice cover may lead to disruption of these pathways of transport. This will negatively impact krill stocks in the Scotia Sea, on which many baleen whale species depend.

Baleen whales may only target krill aggregations above a certain density threshold level, to outweigh the costs of foraging (Dolphin, 1987; Piatt and Methven, 1992). Thus far, studies have only started to associate types of krill aggregations with aspects of the environment (see Klevjer et al., 2010). Krill 'superswarms' are very dense aggregations of krill that can stretch over one kilometre in length. Krill 'superswarms' accounted for more than 56% of estimated krill abundance in the Scotia Sea in January and February 2003 (Tarling et al. 2009). We hardly know how, and under which conditions, these 'superswarms' are formed, that in turn attract large whale aggregations (Nowacek et al., 2011). Changes in sea ice cover and melt may have an impact on krill aggregation behaviour and thus on the number and distribution of krill swarms that are sufficiently dense for baleen whales to forage on. A similar problem exists for predicting the response of baleen whales to changing sea ice conditions in the Arctic Ocean, where arctic cod is an abundant food supply in late summer. During this period, arctic cod forms large aggregations which are crucial for baleen whale foraging. Tynan and DeMaster (1997) speculate that regional changes in sea ice cover may lead to redistribution of arctic cod and thus will affect marine mammal distributions and maybe even their migrational patterns. More insight into the aggregation behaviour of keystone species such as Antarctic krill and Arctic cod is probably crucial to predict if and how baleen whales will redistribute in response to changing ice conditions in polar ecosystems.

Environmental change in the sea ice environment may lead to the emergence of new food competitors for krill, such as salps (pelagic tunicates). The salp species *Salpa thompsoni* is an omnivorous filter feeder and prefers warmer open waters, thereby avoiding sea ice. Traditionally, the spatial distributions of *S. thompsoni* and *E. superba* hardly overlapped at high latitudes in the Southern Ocean (Nicol et al., 2000). However, especially since the 1980s, *S. thompsoni* has increased its abundance in the Southern Ocean (Loeb et al., 1997; Atkinson et al., 2004) and expanded its range southward. Foxton (1966) reported a belt of dense salp concentrations between 45 and 60˚S, based on data collected during the Discovery expeditions conducted between 1925 and 1951. However, the distribution of *S. thompsoni* was extended to high latitudes between 1980 and 1998. Within this time period, *S. thompsoni* was found in the southern parts of the Bellingshausen, Weddell and Lazarev Seas and the belt of dense salp concentrations extended to ~65˚S (Pakhomov et al., 2002). A more recent study showed that *S. thompsoni* and *E. superba* co-occurred at some stations in the western Antarctic Peninsula (Bernard et al., 2012). At a single station in the south, *S. thompsoni* formed a large salp bloom in 2009 and was considered the dominant grazer. If the warming trend continues, salps may become key grazers in the western Antarctic Peninsula region (Bernard et al., 2012) and may directly compete for food with krill in the long-term (Loeb et al., 1997; Pakhomov et al., 2002).

Increased glacial melting may be an overlooked threat to Antarctic krill. Glacial melting leads to a discharge of sediment-laden meltwater into coastal surface waters. Fuentes et al. (2016) studied mass strandings of krill on the southern coast of King George Island, South Shetlands Islands, between 2003 and 2012. Stomachs of dead krill from these strandings contained more than two times the volume of sediment particles, compared to stomachs of living krill. Feeding experiments showed that large quantities of sediment particles negatively affected feeding and nutrient absorption by krill. Therefore, Fuentes et al. (2016) postulated that the ingestion of large sediment particles, which most likely originated from glacial melting, is the primary cause of the mass strandings of krill. An expected increase in glacial melting may thus lead to more mass strandings of krill in coastal ecosystems in the Southern Ocean.

Even if we have sufficient understanding of how phytoplankton and krill will respond to long-term change in the sea ice environment, this knowledge is still not sufficient to predict baleen whale redistributions. Firstly, baleen whales do not operate in a two-species predator-prey system: instead they are after the same food source as seabirds and seals. Baleen whales do have a few advantages over these other top predator groups. Baleen whales can forage more easily in offshore waters and their foraging trips can take longer since they do not have to return to a land-based colony to feed their young. This allows them more time to travel and detect new krill aggregations. Also, baleen whales do not depend on the sea ice for breeding and thus a negative trend in sea ice cover will not directly affect their population birth rate. However, increased local competition between the various top predator groups can be expected at these polar higher latitudes, if local seabird or seal colonies experience higher food stress. Trivelpiece et al. (2011) attributed the population increases of Adélie (*Pygoscelis adeliae*) and chinstrap penguins (*Pygoscelis antarctica*) at breeding colonies in the Scotia Sea region from the 1930s to the 1970s to the removal of baleen whales and krill-eating seals in the 19th to mid-20th centuries. The authors hypothesised that recovering krill-eating whale and seal populations have led to a decline in the amount of krill available to penguin populations in the Scotia Sea region during the last decades. Ainley et al. (2006) presented evidence for competition between Adélie penguins and minke whales in the western Ross Sea. During the 2003-2004 and 2004-2005 seasons, Adélie penguins and minke whales were foraging together on ice krill under the ice ringing a polynya near an Adélie penguin colony. The foraging trips of the Adélie penguins lengthened when minke whales were regularly seen by mid-January. The longest foraging trips by penguins corresponded with the highest incidence of whales, and the penguin foraging trips shortened again when minke whales left the polynya. Furthermore, the penguin diet switched from ice krill to silverfish (*Pleurogramma antarcticum*) by mid-January, presumably due to ice krill depletion in the polynya region (Ainley et al. 2006).

Secondly, baleen whale species may compete with each other if there is a substantial decline in food supply, however, competition between species is extremely difficult to study in the field. Thus far, studies have only provided circumstantial evidence for size-based predation (Friedlaender et al., 2009; Santora et al., 2010; Chapter 4). If there will be a southward shift in krill biomass, fin whales may shift their foraging range to higher latitudes as well. This could lead to increased local competition between baleen whale species.

Finally, the recovery of baleen whale populations following the moratorium on industrial whaling will likely have large effects on future population trajectories of krill, seals and penguins. Modelling studies by Murphy (1995) and Mori and Butterworth (2006) predicted a negative impact of whale recovery on krill biomass and seal and penguin populations. However, these analyses did not include the potentially positive effects of baleen whales on primary productivity via iron fertilisation. Baleen whales recycle iron in the surface waters through their faeces (Smetacek and Nicol, 2005; Smetacek, 2008) , which can contain more than ten million times as much iron than Antarctic surface waters (Nicol et al., 2010). Model estimates by Lavery et al. (2014) suggested that Southern Ocean productivity would be promoted by blue whales recovering to pre-exploitation population levels. Ratnajarah et al. (2016) estimated that a pre-exploitation population of blue whales could have enhanced mean primary productivity by 0.3 g C m^{-2} yr^{-1}, compared to a mean primary productivity estimate of about 57 g C m^{-2} yr^{-1} for the entire Southern Ocean (Arrigo et al., 2008). Pre-exploitation populations of fin whales and humpback whales could have contributed 0.19 and 0.03 g m^{-2} yr^{-1} to mean primary production, respectively. Although these contributions to primary production are quite small when averaged across the entire Southern Ocean, iron fertilisation by baleen whales may impact primary productivity at local scales, for instance in feeding areas (Ratnajarah et al., 2016). Thus, the negative effects of recovering baleen whale populations on seal and penguin populations due to reduced krill availability may be somewhat mitigated by enhanced primary productivity at local scales.

The limits of spatial modelling

An important limitation of spatial models is the explanatory power of the available variables selected to describe the environment. At the end of chapter 2, the suggestion is made that explained deviance would increase after considering in situ variables during selection of spatial models for minke whales. However, explained deviances (EDs) did not exceed 35% for the spatial models for which a plethora of in situ covariates were considered (Chapter 4), and this upper limit was the same for the spatial models that only included remotely sensed covariates. Furthermore, the selected spatial model of minke whale density for the Scotia Sea region (which included in situ covariates) had an ED of less than 20% (Chapter 4), while the majority of the SOWER spatial models (which only included remotely sensed covariates) had EDs in excess of 20% (Chapter 2). Several explanations can be given for this relatively low ED for the Scotia Sea model. Firstly, it is possible that the in situ datasets do not provide much extra information compared to the remotely sensed covariates. Secondly, other important in situ variables may not have been considered. Thirdly, it is possible that the spatial models for the Scotia Sea ecosystem cannot be readily compared to models developed for the whole Southern Ocean, since the former ecosystem is not so much dominated by sea ice, but more by currents and frontal systems. However, the relatively low explained deviance for models based on high quality datasets in a well-studied area does raise the question how much of the variability in whale density can be explained by robust spatial models.

A major direction the whale modelling scientific community has moved into is developing theoretical optimal models for minke whale abundance (Okamura and Kitakado, 2010; Bravington, 2011). While the move to increasingly complex (spatial) models is probably unavoidable, I question whether these models alone can provide the understanding required to make robust predictions of the impacts of future change. With more detailed datasets, the spatial models will improve our understanding of associations between baleen whale density and aspects of the environment at finer scales. However, one important element that is lacking in these models, and which is crucial to predict baleen whale response to environmental change, is whale behaviour. We need to answer questions such as:

- How far away can baleen whales detect swarms? If they can detect swarms at long distances, this will increase their probability in finding krill swarms in time in case they do not happen to be at regions that historically had high krill densities.
- What kind of information do baleen whales use for effective foraging? Do they only use simple cues such as the sea ice edge? Or do they use a combination of information sources, such as visual or auditory cues from krill swarms, together with the presence of seals and/or seabirds?
- How do the various baleen whale species forage in a three-dimensional environment? Krill swarms probably display evasive behaviour towards top predators. They may be able to keep themselves out of reach of baleen whales by moving to deeper waters. Studying

> diving profiles of baleen whales could provide information on these and other aspects of predator-prey dynamics. For instance, humpback whales performed shallow feeding dives during night-time hours, after krill migrated vertically into larger and less dense patches near the sea surface, in the near shore waters of the Western Antarctic Peninsula. These whales rested during the day and targeted denser, more compact patches of krill in the afternoon, when krill was in deeper waters (Friedlaender et al., 2016).

Specially designed visual shipboard surveys dedicated to the detection of whales are less frequently done these days, due to financial and logistic constraints. Instead, passive monitoring methods are perhaps more promising. Acoustic recording packages have already been used at four different areas around Antarctica, namely the Western Antarctic Peninsula, the Scotia Sea, Eastern Antarctica and the Ross Sea (Širović et al., 2004, 2009) for the detection of blue whales and fin whales. In recent years, methods have been developed to estimate density of sperm whales and humpback whales from acoustic surveys (Whitehead et al., 2009; Horrocks et al., 2011; Horrocks and Rueffer, 2014). It may thus be possible to develop new methodology for estimating density of baleen whales from passively recorded acoustic data. Another exciting new technique is automated infrared detection of whales with 360º rotating cameras (Zitterbart et al., 2011, 2013). These cameras can detect whale blows when the whales are at the sea surface. This offers the opportunity to detect baleen whales during the night, which is particularly interesting since Antarctic krill swarms show a vertical migration pattern, moving closer to the sea surface during the night. Although challenging to conduct in the field, baleen whales could be tagged with satellite-relayed data loggers. For instance, data loggers deployed on southern elephant seals from the Kerguelen population have revealed that the majority of the animals display different foraging behaviour in the presence of eddies (Dragon et al., 2010). If technical limitations are overcome, future data loggers could include acoustic recording devices, opening up new ways to explore the environment from the whales' point of view. Even with all these technical advances, much is still to be learned by conducting traditional behavioural studies with observers on board. Regular trips to important foraging areas in shallow waters can show observers unexpected behavioural interactions between baleen whales, other top predators and their prey.

REFERENCES

Ainley, D.G., Ballard, G. and Dugger, K.M. 2006. Competition among penguins and cetaceans reveals trophic cascades in the western Ross Sea, Antarctica. *Ecology* 87(8): 2080-2093.

Arrigo, K.R. and Thomas, D.N. 2004. Large scale importance of sea ice biology in the Southern Ocean. *Antarct. Sci.* 16(4): 471-486.

Arrigo, K.R., van Dijken, G.L. and Bushinsky, S. 2008. Primary production in the Southern Ocean, 1997 – 2006. *J. Geophys. Res.* 113(C8), C08004.

Arrigo, K.R., Worthen, D., Schnell, A. and Lizotte, M.P. 1998. Primary production in Southern Ocean waters. *J. Geophys. Res.* 103(C8): 15,587-15,600.

Arzel, O., Fichefet, T. and Goosse, H. 2006. Sea ice evolution over the 20th and 21st centuries as simulated by current AOGCMs. *Ocean Modell.* 12: 401-415.

Atkinson, A., Siegel, V., Pakhomov, E. and 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, E.A., Rothery, P., Loeb, V., Ross, R.M., Quetin, L.B., Schmidt, K., Fretwell, P., Murphy, E.J., Tarling, G.A and Fleming, A.H. 2008. Oceanic circumpolar habitats of Antarctic krill. *Mar. Ecol. Prog. Ser.* 362: 1-23.

Bernard, K.S., Steinberg, D.K. and Schofield, O.M.E. 2012. Summertime grazing impact of the dominant macrozooplankton off the Western Antarctic Peninsula. *Deep-Sea Res I* 62: 111-122.

Bracegirdle, T.J., Connolley, W.M. and Turner, J. 2008. Antarctic climate change over the twenty first century. *J. Geophys. Res.* 113, D03103.

Bravington, M. 2011. A hybrid spatial-and-hazard-prob model for SOWER minke data. Paper SC/63/IA15 presented to the IWC Scientific Committee, June 2011, Tromsø, Norway (unpublished). 5pp. [Paper available from the Office of the IWC].

Brierley, A.S., Fernandes, P.G., Brandon, M.A., Armstrong, F., Millard, N.W., McPhail, S.D., Stevenson, P., Pebody, M., Perrett, J., Squires, M., Bone, D.G. and Griffiths, G. 2002. Antarctic krill under sea ice: elevated abundance in a narrow band just south of the ice edge. *Science* 295: 1890-1892.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J.-L., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W.J., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A.J. and Wehner, M. 2013. Long-term climate change: projections, commitments and irreversibility. pp. 1029-1136. *In*: T.F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.) *Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, NY, USA. 1535pp.

de la Mare, W.K. 1997. Abrupt mid-twentieth-century decline in Antarctic sea-ice extent from whaling records. *Nature* 389: 57-60.

Dolphin, W.F. 1987. Prey densities and foraging of humpback whales, *Megaptera novaeangliae*. *Experientia* 468-471.

Dragon, A.-C., Monestiez, P., Bar-Hen, A. and Guinet, C. 2010. Linking foraging behaviour to physical oceanographic structures: Southern elephant seals and mesoscale eddies east of Kerguelen Islands. *Prog. Oceanogr.* 87: 61-71.

Flores, H., van Franeker, J.-A., Cisewski, B., Leach, H., van de Putte, A.P., Meesters, E.H.W.G., Bathmann, U. and Wolff, W.J. 2011. Macrofauna under sea ice and in the open surface layer of the Lazarev Sea, Southern Ocean. *Deep-Sea Res II* 58: 1948-1961.

Flores, H., van Franeker, J.A., Siegel, V., Haraldsson, M., Strass, V. Meesters, E.H., Bathmann, U. and Wolff, W.J. 2012. The association of Antarctic krill *Euphausia superba* with the under-ice habitat. PLoS ONE 7(2): e31775.

Foxton, P. 1966. The distribution and life-history of *Salpa thompsoni* Foxton with observations on a related species, *Salpa gerlachei* Foxton. *Discovery Rep.* 34: 1-116.

Friedlaender, A.S., Lawson, G.L. and Halpin, P.N. 2009. Evidence of resource partitioning between humpback and minke whales around the western Antarctic Peninsula. *Mar. Mammal Sci.* 25(2): 402-415.

Friedlaender, A.S., Johnston, D.W., Tyson, R.B., Kaltenberg, A., Goldbogen, J.A., Stimpert, A.K., Curtice, C., Hazen, E.L., Halpin, P.N., Read, A.J. and Nowacek, D.P. 2016. Multiple-stage decisions in a marine central-place forager. *R. Soc. Open Sci.* 3: 160043.

Fuentes, V., Alurralde, G., Meyer, B., Aguirre, G.E., Canepa, A., Wölfl, A.-C., Hass, H.C., Williams, G.N. and Schloss, I.R. 2016. Glacial melting: an overlooked threat to Antarctic krill. *Sci. Rep.* 6, 27234.

Horrocks, J., Hamilton, D.C. and Whitehead, H. 2011. A likelihood approach to estimating animal density from binary acoustic transects. *Biometrics* 67: 681-690.

Horrocks, J. and Rueffer, M. 2014. A Bayesian approach to estimating animal density from binary acoustic transects. *Comp. Stat. Data Anal.* 80: 17-25.

Klevjer, T.A., Tarling, G.A. and Fielding, S. 2010. Swarm characteristics of Antarctic krill *Euphausia superba* relative to the proximity of land during summer in the Scotia Sea. *Mar. Ecol. Prog. Ser.* 409: 157-170.

Lavery, T.J., Roudnew, B., Seymour, J., Mitchell, J.G., Smetacek, V. and Nicol, S. 2014. Whales sustain fisheries: blue whales stimulate primary production in the Southern Ocean. *Mar. Mamm. Sci.* 30(3): 888-904.

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

Mayewski, P.A., Meredith, M.P., Summerhayes, C.P., Turner, J., Worby, A., Barrett, P.J., Casassa, G., Bertler, N.A.N., Bracegirdle, T., Naveira Garabato, A.C., Bromwich, D., Campbell, H., Hamilton, G.S., Lyons, W.B., Maasch, K.A., Aoki, S., Xiao, C. and Van Ommen, T. 2009. State of the Antarctic and Southern Ocean climate system. *Rev. Geophys.* 47(1): RG1003.

Mori, M. and Butterworth, D.S. 2006. A first step towards modelling the krill-predator dynamics of the Antarctic ecosystem. *CCAMLR Science* 13: 217-277.

Murphy, E.J., Watkins, J.L., Trathan, P.N., Reid, K., Meredith, M.P., Thorpe, S.E., Johnston, N.M., Clarke, A., Tarling, G.A., Collins, M.A., Forcada, J., Shreeve, R.S., Atkinson, A., Korb, R., Whitehouse, M.J., Ward, P., Rodhouse, P.G., Enderlein, P., Hirst, A.G., Martin, A.R., Hill, S.L., Staniland, I.J., Pond, D.W., Briggs, D.R., Cunningham, N.J. and Fleming, A.H. 2007. Spatial and temporal operation of the Scotia Sea ecosystem: a review of large-scale links in a krill centred food web. *Phil. Trans. R. Soc. B* 362: 113-148.

Murphy, E.J. 1995. Spatial structure of the Southern Ocean ecosystem: predator-prey linkages in Southern Ocean food webs. *J. Anim. Ecol.* 64(3): 333-347.

Nicol, S., Bowie, A., Jarman, S., Lannuzel, D., Meiners, K.M. and Van der Merwe, P. 2010. Southern Ocean iron fertilization by baleen whales and Antarctic krill. *Fish and fisheries* 11: 203-209.

Nicol, S., Pauly, T., Bindoff, N.L., Wright, S., Thiele, D., Hosie, G.W., Strutton, P.G. and Woehler, E. 2000. Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. *Nature* 406: 504-507.

Nicol, S., Worby, A., Leaper, R. 2008. Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. *Mar. Freshwater Res.* 59: 361-382.

Nowacek, D.P., Friedlaender, A.S., Halpin, P.N., Hazen, E.L., Johnston, D.W., Read, A.J., Espinasse, B., Zhou, M. and Zhu, Y. 2011. Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. *PLoS ONE* 6(4): e19173.

Okamura, H. and Kitakado, T. 2010. Abundance estimates of Antarctic minke whales from the historical IDCR/SOWER survey data using the OK method. Paper SC/62/IA3 presented to the IWC Scientific Committee, June 2010 (unpublished). 35pp. [Paper available from the Office of the IWC]

Pakhomov, E.A., Froneman, P.W. and Perissinotto, R. 2002. Salp/krill interactions in the Southern Ocean: spatial segregation and implications for the carbon flux. *Deep-Sea Res II* 49: 1881-1907.

Piatt, J.F. and Methven, D.A. 1992. Threshold foraging behaviour of baleen whales. *Mar. Ecol. Prog. Ser.* 84: 205-210.

Ratnarajah, L., Melbourne-Thomas, J., Marzloff, M.P., Lannuzel, D., Meiners, K.M., Chever, F., Nicol, S. and Bowie, A.R. 2016. A preliminary model of iron fertilisation by baleen whales and Antarctic krill in the Southern Ocean: sensitivity of primary productivity estimates to parameter uncertainty. *Ecol. Modelling* 320: 203-212.

Santora, J.A., Reiss, C.S., Loeb, V.J. and Veit, R.R. 2010. Spatial association between hotspots of baleen whales and demographic patterns of Antarctic krill *Euphausia superba* suggests size-dependent predation. *Mar. Ecol. Prog. Ser.* 405: 255-269.

Širović, A., Hildebrand, J.A., Wiggins, S.M., McDonald, M.A., Moore, S.E. and Thiele, D. 2004. Seasonality of blue and fin whale calls and the influence of sea ice in the Western Antarctic Peninsula. *Deep-Sea Res. II* 51: 2327-2344.

Širović, A., Hildebrand, J.A., Wiggins, S.M. and Thiele, D. 2009. Blue and fin whale acoustic presence around Antarctica during 2003 and 2004. *Mar. Mamm. Sci.* 25(1): 125-136.

Smetacek, V. 2008. Are declining Antarctic krill stocks a result of global warming or of the decimation of the whales? pp. 46-83. *In*: C.M. Duarte (ed.) *Impacts of global warming on polar ecosystems*. Fundación, Madrid. 192pp.

Smetacek, V. and Nicol, S. 2005. Polar ocean ecosystems in a changing world. *Nature* 437:362-368.

Smith, Jr., W.O. and Nelson, D.M. 1986. Importance of ice edge phytoplankton production in the Southern Ocean. *Bioscience* 36(4): 251-257.

Tarling, G.A., Klevjer, T., Fielding, S., Watkins, J., Atkinson, A., Murphy, E., Korb, R., Whitehouse, M. and Leaper, R. 2009. Variability and predictability of Antarctic krill swarm structure. *Deep-Sea Res I* 56(11): 1994-2012.

Thorpe, S.E., Murphy, E.J. and Watkins, J.L. 2007. Circumpolar connections between Antarctic krill (*Euphausia superba* Dana) populations: investigating the roles of ocean and sea ice transport. *Deep-Sea Res. I* 54: 792-810.

Trivelpiece, W.Z., Hinke, J.T., Miller, A.K., Reiss, C.S., Trivelpiece, S.G. and Watters, G.M. 2011. Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. *PNAS* 108(18): 7625-7628.

Tynan, C.T. and DeMaster, D.P. 1997. Observations and predictions of Arctic climatic change: potential effects on marine mammals. *Arctic* 50(4): 308-322.

Whitehead, H. 2009. Estimating abundance from one-dimensional passive acoustic surveys. *J. Wildlife Manage.* 73(6): 1000-1009.

Zitterbart, D.P., Kindermann, L. and Boebel, O. 2011. MAPS: An automated whale detection system for mitigation purposes. *SEG Expanded Abstracts* 30: 67.

Zitterbart, D.P., Kindermann, L., Burkhardt, E. and Boebel, O. 2013. Automatic round-the-clock detection of whales for mitigation from underwater noise impacts. *PLoS ONE* 8(8): e71217.

Zwally, H.J., Comiso, J.C., Parkinson, C.L., Cavalieri, D.J. and Gloersen, P. 2002. Variability of Antarctic sea ice 1979-1998. *J. Geophys. Res.* 107(C5): 3041.

English summary
Dutch summary
Affiliations of co-authors
Acknowledgements
Biography

Summary

The Southern Ocean is a major feeding ground for baleen whale species in the Southern Hemisphere, including Antarctic minke whales, humpback whales and fin whales. These three whale species feed predominantly on Antarctic krill, which is a key species in Southern Ocean foodwebs. During austral spring and summer, the melting of sea ice leads to the formation of the marginal ice zone, defined as the area where sea ice was present at the beginning of the month, but not at the end. The seasonal phytoplankton blooms that develop following the retreat of sea ice are dominated by diatoms and allow rapid growth and development of juvenile and adult krill. Each summer large baleen whales migrate into the Southern Ocean to these regions of retreating sea ice to feed on krill. This makes the marginal ice zone a crucial habitat for large baleen whales.

Current climate model studies suggest a decrease in annual average total sea ice cover of up to 33% by 2100. To predict how baleen whales will respond to long-term change in the physical environment, we need to understand the relationships between baleen whale distribution and abundance, their prey and the physical environment. All spatial models developed for this thesis were based on line transect data collected during large scale visual shipboard surveys, conducted in open waters between 1981 and 2005 during austral summer.

Chapter 2 describes the spatial generalised additive models (GAMs) that we developed for investigating the relationships between minke whale density (number of baleen whales per km^2) and the physical environment. The models were based on whale sightings data and remotely sensed environmental data from three circumpolar sets of surveys. The model analyses suggested that minke whale density in open waters tends to be higher close to transition zones, notably the sea ice edge and continental shelf. The spatial models suggested high variability in the relationships between Antarctic minke whale density and the physical environment between years. None of the selected environmental aspects showed a consistent qualitative relationship with density at either the circumpolar or the regional scale.

Chapter 3 shows predicted density maps for Antarctic minke whales. Whale densities were particularly high in the Ross Sea, Weddell Sea and Prydz Bay, and densities were very low for the Bellingshausen-Amundsen Sea. These regional differences in whale density coincide with differences in area of marginal ice zone. In addition to this, we found a significant positive relationship between mean whale density and total change in sea ice cover during austral spring and summer. These findings strongly suggest that the amount of sea ice cover, and especially its seasonal change, affects Antarctic minke whale density at the regional scale.

Chapter 4 describes detailed habitat modelling for Antarctic minke, humpback and fin whales in the Scotia Sea. Available data for this region included both whale sightings and concurrent in situ non-biotic data and krill acoustic data, collected during a large scale survey in 2000. Only the density of minke whales was significantly positively related to the density of krill. High density areas were more widespread for Antarctic minke whales than for the other two whale species. The modelling suggests that the different baleen whale species may target krill aggregations that

differ in life history class composition. Densities of minke and humpback whales were relatively high in the southwest of the Scotia Sea, in waters inhabited by juvenile krill, while high fin whale densities were found in deeper waters predominantly inhabited by subadult and adult krill.

Chapter 5 explores and discusses possible responses of baleen whale species to predicted long-term change in the sea ice environment. A long-term predicted decrease in mean annual sea ice cover might lead to a decrease in krill biomass, and thus to less food being available for baleen whales. However, this does not necessarily have to be the case. A reduction in the pack ice region implies a larger open ocean area, thus more foraging area will become available for larger baleen whales such as humpback and fin whales, which hardly penetrate the pack ice zone. Furthermore, the marginal ice zone may increase regionally, which may lead to higher primary and secondary productivity and thus to higher baleen whale density at the regional level.

Current knowledge regarding the impact of long-term changes in sea ice conditions on productivity is not sufficient to predict how these changes affect baleen whale distribution and abundance. For instance, changes in the physical environment may affect the number and distribution of krill swarms sufficiently dense for baleen whales to forage on. However, we hardly know under which conditions dense krill swarms are formed. Furthermore, if high productivity areas for krill move to higher latitudes, increased local competition can be expected between baleen whales and land-based colony breeders such as seabirds and seals. Finally, increased local competition between baleen whale species may follow a potentially large long-term decline in their food supply.

We need to get a better understanding of whale behaviour in order to predict baleen whale response to environmental change. We hardly know what kind of information baleen whales use for effective foraging, how far away they can detect krill swarms and how they forage in a three-dimensional environment. Recent advances in passive monitoring techniques, such as acoustic recording packages and infrared detection of whales, are promising. Whale density can be estimated from acoustic data, which may also allow to sample baleen whales in harsh weather conditions often experienced in the Southern Ocean. Finally, future data loggers could include acoustic recording devices, opening up new ways to explore the environment from the whales' point of view.

Samenvatting

De Zuidelijke IJszee is een belangrijke voedselplek op het zuidelijk halfrond voor baleinwalvissen, zoals Antarctische dwergvinvissen, bultruggen en gewone vinvissen. Deze drie walvissoorten foerageren vooral op Antarctisch krill, een cruciale soort binnen het voedselweb van de Zuidelijke IJszee. Het smelten van het zeeijs in de lente leidt tot het ontstaan van de Marginale IJszone, gedefinieerd als het gebied waar zeeijs aanwezig is aan het begin van de maand, maar niet meer op het eind van de betreffende maand. De seizoensgebonden planktonbloei, die ontstaat na terugtrekking van het zeeijs, wordt gedomineerd door diatomeëen (eencellige algen) en zorgt voor een snelle groei en ontwikkeling van juveniel en volwassen krill (kleine ongewervelde, garnaalachtige zeedieren). Elke zomer migreren grote baleinwalvissen naar gebieden van terugtrekkend zeeijs in de Zuidelijke IJszee om zich te voeden met krill. De Marginale IJszone is daarom een cruciale leefomgeving voor grote baleinwalvissen.

Huidige klimaatmodelstudies suggereren een afname in het jaarlijks gemiddelde totale zeeijsoppervlak van maximaal 33% in 2100. Om te kunnen voorspellen hoe baleinwalvissen zullen reageren op lange termijn veranderingen in de fysieke omgeving dienen we de relaties tussen baleinwalvissen, hun prooi en de fysieke omgeving te begrijpen. Alle ruimtelijke modellen ontwikkeld voor dit proefschrift waren gebaseerd op lijntransect-gegevens verzameld tijdens visuele surveys aan boord van schepen. Deze surveys werden alleen uitgevoerd op open zee in de zomer tussen 1981 en 2005.

Hoofdstuk 2 beschrijft de ruimtelijke Gegeneraliseerde Additieve Modellen (GAMs) die we ontwikkeld hebben om de relaties te onderzoeken tussen de dichtheid van Antarctische dwergvinvissen (aantal baleinwalvissen per km^2) en de fysieke omgeving. De modellen waren gebaseerd op visuele waarnemingen van walvissen en satellietgegevens van de leefomgeving voor drie groepen circumpolaire surveys. Modelresultaten suggereren dat de dichtheid van Antarctische dwergvinvissen in open wateren hoger is dichtbij een overgangszone, zoals de zeeijsrand en het continentaal plat. De ruimtelijke modellen suggereren een hoge variabiliteit in de relaties tussen de dichtheid van Antarctische dwergvinvissen en de fysieke leefomgeving voor de verschillende jaren. Geen van de geselecteerde milieufactoren liet een consistente kwalitatieve relatie zien met walvisdichtheid, noch op de circumpolaire noch op de regionale schaal.

Hoofdstuk 3 geeft kaarten weer met voorspelde dichtheden voor Antarctische dwergvinvissen. Dichtheden van walvissen waren erg hoog in de Ross Zee, Weddell Zee en Prydz Bay, en dichtheden waren zeer laag voor de Bellingshausen-Amundsen Zee. Deze regionale verschillen in walvisdichtheden vallen samen met verschillen in grootte van de Marginale IJszone. Verder vonden we een significant positieve relatie tussen gemiddelde walvisdichtheid en totale verandering in zeeijsoppervlak gedurende de lente en zomer. Deze bevindingen suggereren sterk dat de hoeveelheid zeeijsoppervlak, en vooral seizoensverandering hierin, de dichtheid van Antarctische dwergvinvissen sterk beïnvloedt op regionale schaal.

Hoofdstuk 4 beschrijft gedetailleerde modellen voor de leefomgeving van Antarctische dwergvinvissen, bultruggen en gewone vinvissen in de Scotiazee. Voor deze regio zijn visuele waarnemingen van walvissen beschikbaar, evenals in situ non-biotische gegevens en akoestische gegevens van krill, verzameld tijdens een grote survey die gehouden werd in 2000. Alleen de dichtheid van Antarctische dwergvinvissen was significant positief gerelateerd aan de dichtheid van krill. Hoge dichtheden waren wijder verspreid voor Antarctische dwergvinvissen dan voor de andere twee soorten baleinwalvissen. Modelresultaten suggereren dat de verschillende soorten baleinwalvissen mogelijk voorkeur hebben voor krill aggregaties met een specifieke samenstelling van levensfases. Dichtheden van Antarctische dwergvinvissen en bultruggen waren relatief hoog in het zuidwesten van de Scotiazee, in wateren met juveniel krill, terwijl hoge dichtheden van gewone vinvissen gevonden werden in diepere wateren die vooral bewoond worden door jongvolwassen en volwassen krill.

Hoofdstuk 5 verkent en bediscussieert de mogelijke manieren waarop de baleinwalvissen kunnen reageren op voorspelde lange termijn veranderingen in de zeeijsomgeving. Op het eerste gezicht kan een afname van het jaarlijks gemiddelde totale zeeijsoppervlak op de lange termijn leiden tot een afname in de biomassa aan krill, en dus tot minder voedsel dat beschikbaar is voor baleinwalvissen. Dit hoeft echter niet per se het geval te zijn. Een afname van het pakijsgebied impliceert een groter open water gebied, waardoor het foerageergebied toeneemt voor grotere baleinwalvissen, zoals bultruggen en gewone vinvissen, die nauwelijks doordringen in het pakijsgebied. Verder kan het zeeijsoppervlak regionaal een grotere seizoensverandering doormaken. De resulterende grotere Marginale IJszone kan leiden tot een hogere primaire en secundaire productiviteit en dus tot een hogere dichtheid van baleinwalvissen op regionaal niveau.

Onze huidige kennis wat betreft de gevolgen van lange termijn veranderingen in zeeijs op de productiviteit zal niet toereikend zijn om te kunnen voorspellen hoe deze veranderingen zullen inwerken op de verspreiding van baleinwalvissen en hun aantallen. Veranderingen in de fysieke leefomgeving kunnen invloed hebben op de hoeveelheid en verspreiding van krillzwermen, waarvan de dichtheid groot genoeg is voor de baleinwalvissen om op te foerageren. We weten echter nauwelijks onder welke omstandigheden dichte krillzwermen gevormd worden. Als verder gebieden met een hoge productiviteit aan krill zich verplaatsen naar hogere breedtegraden, dan kan men verwachten dat de competitie lokaal op deze breedtegraden toeneemt tussen baleinwalvissen en koloniebroeders op het land, zoals zeevogels en zeehonden. Tenslotte kan de lokale competitie tussen de verschillende soorten baleinwalvissen toenemen als gevolg van een mogelijke substantiële afname in het voedselaanbod op lange termijn.

We hebben een veel beter begrip nodig van het foerageergedrag van walvissen om te kunnen voorspellen hoe baleinwalvissen zullen reageren op verandering in hun leefomgeving. We weten nauwelijks wat voor soort informatie baleinwalvissen gebruiken om effectief te foerageren, vanaf welke afstand ze krillzwermen kunnen detecteren en hoe de verschillende soorten baleinwalvissen foerageren in een driedimensionale omgeving. Recente ontwikkelingen in passieve monitoringstechnieken, zoals akoestische opname apparatuur en infrarood detectie van walvissen, zijn veelbelovend. Nieuwe methoden zijn ontwikkeld om walvisdichtheden te schatten uit gegevens verzameld tijdens akoestische surveys, waardoor we baleinwalvissen ook kunnen onderzoeken tijdens slechte weersomstandigheden die vaak voorkomen in de Zuidelijke IJszee. Tenslotte zouden zenders in de toekomst ook akoestische opname-apparatuur kunnen bevatten, zodat de leefomgeving op nieuwe manieren verkend kan worden, vanuit het perspectief van de walvissen.

Affiliations of co-authors

Hein J.W. de Baar

1. Koninklijk Nederlands Instituut voor Onderzoek der Zee (NIOZ)/ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, the Netherlands
2. University of Groningen, Department Ocean Ecosystems, P.O. Box 11103, 9700 CC Groningen

Jaume Forcada, Eugene J. Murphy & Andrew Fleming:

British Antarctic Survey, High Cross, Madingley Road, Cambridge, CB3 0ET, United Kingdom

Ulrich V. Bathmann

Leibniz-Institute for Baltic Sea Research, Seestraße 15, 18119 Rostock, Germany

Acknowledgements

The whales that were born in the year that I started this PhD-project have already reached their maturity as I am writing this last section of my thesis. During this time period, I have met many colleagues that helped me with my research and writing of this thesis. I am honoured to have been supervised by four advisors. Although this was challenging at times, your contributions definitely helped to improve my research and thesis especially since you all have different backgrounds and knowledge regarding the Southern Ocean. I would like to thank you all for your dedication, your willingness to help me, your knowledge and experience that I could benefit from and your patience during this project.

Hein, I would like to thank you for the opportunity you have given me to start this project. You believed in me and kept expressing this belief throughout the whole project. Furthermore, your knowledge of the Southern Ocean is truly amazing, and I enjoyed the discussions we had as an ecologist versus an oceanographer. To you, the concept of 'whale density' is horrifying, and I must admit it is a strange term, even though it is commonly used by ecologists. During the end of the project, while writing the last sections of the thesis, you really helped me with careful reading and commenting on the manuscript and I am truly grateful for your dedication to help me finish the project, even when you sacrificed your free time for it.

Jaume, you are truly one of a kind, and I mean this in the best possible way. You are 'merely' mentioned as the co-supervisor at the title page, where those familiar with the Dutch PhD system very well know this in fact is the primary supervisor as agreed before and during the entire project. You introduced me to spatial modelling, advanced statistics and R software. You helped me during all phases of the project and I was, and still am, amazed how much you care for detail. I must admit that, in the beginning of the project, I did not quite understand your attention to detail, but I learned that detailed and concise writing is crucial for effective and clear communication. When I first met you, you showed me your fresh bite-mark of a fur seal on your upper arm, which told me you are in your element when you are South. I hope many successful field seasons will follow for you. It was also very special to (finally) meet someone with an equally bad taste in movies, music and comic books. You are a good friend and I hope we will see each other again after the defence.

Eugene, you helped me a lot during my project as well. I thoroughly enjoyed the conversations we had during my time at BAS. Your profound knowledge of the Southern Ocean ecosystem helped me to see the bigger picture. I am sorry I have not listened to your advice to wrap up writing the thesis as soon as possible after my move to the Netherlands, but I hope you enjoy the end result. You have always supported me very well, and I sincerely thank you for all your time and effort put into this thesis.

Uli, sehr herzlichen Dank für Ihre Zusammenarbeit und Supervision. I also sincerely thank you for your kind hospitality during my stay at AWI in Bremerhaven, which I thoroughly enjoyed. During this stay, you gave me a tour on the Polarstern, a German research icebreaker. I noticed this really was your second home, you knew every nook and cranny of it. I have learned a lot about krill from you, and I would like to thank you for your willingness to share your expertise and knowledge.

Apart from this splendid collaborative supervisory team, I would like to thank many more. First of all, I would like to thank all my colleagues at the British Antarctic Survey for being so hospitable, friendly and warm to me. You definitely made my stay in Cambridge very pleasant and supported me whenever I needed it. I was a privilege to have met you and I wish you all the best, in Cambridge and down South. Special thanks to Claire, Clare, Jamie and Rachel for sharing an office and many good laughs during the tea breaks. I really enjoyed our time at the office; you made me feel very welcome at BAS. I would also like to thank Sandra Goddard, Nadine Johnston, Amanda McEvoy, and Paul Rodhouse for supporting me as a student at BAS.

This project required quite some effort to obtain funding. The first proposal I wrote regarding baleen whales in the Southern Ocean was not selected, unfortunately. Ruben and Helias, you gave me the opportunity to write this proposal at the Institute of Environmental Sciences (CML), and I would like to thank you for that, since those first steps were crucial to obtain funding with a second, re-written proposal. I hope you are happy to see this project being finished successfully.

When I moved back to the Netherlands, after completing the research, I worked at the Resource Ecology Group (REG) in Wageningen. The writing of the thesis still needed to be finished as well, which was challenging, to say the least. Herbert and Sip, I would like to thank you for your help and your incredible support for me, more than I deserved. Ignas, you coached me through the writing process, which helped me a lot to get the thesis back on track. I hope you enjoy the end result, for which you should all take credit.

During the last phase of the project, I had the pleasure of administrative support from Cindy van Boggelen who answered all my questions about how to deal with regulations and Hora Finita the PhD workflow system at the University of Groningen. You told me I was your first PhD-student, I hope many more will follow, and I am sure you will be a great help to them as well.

This modelling project could not have been realized without the data provided by the IWC and CCAMLR. I would like to thank both organisations for this, and for all the effort behind the collection and processing of these data. In particular, I would like to thank Greg Donovan, Helen Coulson and Andrea Cooke for their guidance through the process of my first publication. Funding for this project was provided by EUR-OCEANS and the University of Groningen, for which I am grateful. I would also like to thank EUR-OCEANS for organising the summer schools and meetings that I attended during my studies.

Of course, I should not forget my friends who were always there to support me and provided the much needed distraction from the thesis work. I would like to mention them in random order: Thierry, Ania and Tamara, Bart and Vio, Cleo and Wouter, Jan and Trees, Richard, Olaf and Danny. You were there for me, and I am sure it must be refreshing not having to ask the question anymore of when the project will be finished.

I would like to express my sincerest thanks to my brothers and my parents for all their support, patience and love. You were there to help me through this project, and I will be there for you when you need some help in return.

Lastly, I would like to thank the whales for swimming out there in the vast Southern Ocean. If I may offer some criticism, you could have provided more assistance in reducing uncertainty by breaching more often. However, from your point of view, there is no uncertainty regarding your existence. You are simply out there, and I hope this will be the case for many years to come.

Bas Beekmans

Nieuwkuijk, januari 2017

Biography

Bas Wilhelmus Petrus Maria Beekmans was born in Waalwijk, the Netherlands, on 22 January, 1976. In 1994, he achieved his high school degree at d'Oultremontcollege in Drunen, after which he studied Economics at Tilburg University for two years. In 1996, he moved to 's-Hertogenbosch, to study Animal Husbandry and Health Care at the HAS University of Applied Sciences, where he obtained a BSc degree in 2001. During this study, he did an internship at SAD-AFAG in Foça, Turkey, to investigate the effects of the Mediterranean monk seal (*Monachus monachus*) on small-scale fishery in Foça.

He started studying Biology at Leiden University in 2001. During this study, he did an internship at the Whitehead Lab at Dalhousie University, Halifax, Canada. During this internship, he compared two computer assisted matching methods for the photo-identification of sperm whales (*Physeter macrocephalus*). He also wrote an MSc-thesis about the possible effects of sperm whales on the biological pump. This thesis was written at the Institute of Environmental Sciences (CML) in Leiden, the Netherlands. After obtaining his MSc degree at Leiden University (Biology, specialisation Environmental Sciences, *cum laude*) in 2004, he worked at CML as a teaching assistant, and as assistant coordinator for Europhlukes, a European Cetacean Photo-ID System and Database. In 2005, he was research consultant for a marine fisheries campaign, organised by the World Wildlife Fund for Nature (WWF) in Zeist. He was also team coordinator for a group of WWF volunteers in Leiden.

In 2006, Bas moved to the British Antarctic Survey (BAS), Cambridge, United Kingdom, for a PhD-project on the impact of changes in the sea ice environment on baleen whales in the Southern Ocean. The PhD-research included the analysis of large datasets by applying spatial modelling, distance sampling and Geographic Information System (GIS) techniques. The project was part of the EUR-OCEANS European Network of Excellence. The EUR-OCEANS acronym stands for *EURopean research on OCean Ecosystems under Anthropogenic and Natural ForcingS*. From 2010 to 2012, he worked as a quantitative ecologist at the Resource Ecology Group (REG) at the Wageningen University and Research Centre (Wageningen UR). His work included the analysis of geese count data, while simultaneously working on the PhD-thesis. After finishing the PhD-thesis in 2016, Bas starting working as a consultant for DIKW Intelligence in Nieuwegein, thereby moving into the world of data science and big data.