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Seasonal variability in whale encounters in the Western Antarctic Peninsula

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Abstract

Cetacean sighting surveys were conducted as part of nine multidisciplinary research cruises over late summer, autumn and winter of 2 years (2001–2003) during the Southern Ocean Global Ocean Ecosystems (SO GLOBEC) program. Sea-ice cover differed markedly between years, with apparent effects on cetacean distribution. No ice was present until late June in 2001, while the previous winter sea ice never fully retreated (>30% cover) during the 2002 or 2003 summer, thus increasing the proportion of thicker and more complex ice, including multi-year floes. Humpback (237 sightings; 537 individuals) and minke (103 sightings: 267 individuals) whales were the most commonly detected species. Data from seven comparable cruises were used to identify habitat for minke and humpback whales over five geographically distinct spatial divisions in the study area. In all years, both species were predominantly found in near coastal habitat, particularly in the fjords where complex habitat likely concentrated prey. In 2002 and 2003 the presence of sea ice provided additional feeding habitat, and the numbers of minkes (in winter) and humpbacks (late summer and autumn) in the area doubled compared with 2001. Humpbacks in particular were concentrated at the ice boundaries during late summer and autumn, while minke numbers increased in the winter that followed and occupied ice-covered areas along the entire shelf edge. Important resource sites for these species are mainly located in near-coastal areas and are used in all years, but when ice margins exist and intersect with resource sites they attract much larger numbers of animals due to the dynamics between sea ice and prey.

1. Introduction

The core objective of the International Whaling Commission's (IWC) collaborative research in the

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Antarctic is to investigate how spatial and temporal variability in the physical and biological environment influences cetaceans (IWC 2000). The IWC participated in the Southern Ocean Global Ocean Ecosystems Dynamics (SO GLOBEC) studies in the Western Antarctic Peninsula (WAP) to contribute to this objective. The multidisciplinary framework and scale of the SO GLOBEC program provided a rare opportunity to investigate cetacean patterns of occurrence concomitant with data collected across physical and biological domains.

Programs of cetacean research have been conducted along the Antarctic Peninsula for many years, but most have focused on areas north of the SO GLOBEC study site (Stone and Hamner, 1988; van Franeker, 1992; Pankow and Kock, 2000; Olavierra et al., 2003). Cetacean sightings data have also been collected from the offshore, shelf and fjord regions to the north and west of Marguerite Bay during the austral summer, as part of the United States (US) Long Term Ecological Research (LTER) program (LTER unpublished data) and also on the IWC International Decade of Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) circumpolar surveys (Kasamatsu et al., 2000). These surveys included portions of the WAP region (IWC Management Area I 60°W–120°W), in the austral summers of 1982/83, 1989/90, 1993/94, 1999/00, 2000/01 (Branch and Butterworth, 2001). Marguerite Bay has never been surveyed during IWC circumpolar surveys (Branch and Butterworth, 2001; Kasamatsu et al., 2000; Matsuoka et al., 2003). Those IWC surveys rarely approached the shelf in this area, and no cetacean sightings have been reported from the WAP SO GLOBEC study area (Kasamatsu et al., 2000). Reports of cetacean surveys in this region outside the spring and summer seasons or within the pack ice are rare (Joiris, 1991; Aguayo-Lobo, 1994).

Marguerite Bay is located in the central Western Antarctic Peninsula (WAP) (Fig. 1). It is a large embayment open to the continental shelf (~100 nm wide) to the west, abutting a steep shelf slope and waters over 3000 m. The bay is bordered to the north by Adelaide Island, and to the south by Alexander Island. The eastern edge of the bay is the main Peninsular land mass. A coastal fjord system, formed by near-shore islands close to the steep mountains and glaciers of the continent, extends from the east side of Adelaide Island to Anvers Island in the north. Marguerite Bay is bisected in the south by a deep trough (Marguerite Trough) that extends across the shelf in the west and lies along the northern edge of Alexander Island. This trough extends all the way into the bay and ends in a glacier-filled sound (George VI Sound). The overall bathymetric environment of Marguerite Bay is complex, and comprises many shoals, minor troughs and deep holes and ridges. The southern boundary of the Antarctic Circumpolar Current flows in a northwesterly direction against the continental shelf here, causing warm-water intrusions throughout the year (Smith, D. A. et al., 1999).

The combination of complex bathymetry and oceanographic processes in this region produces very high-velocity currents and small gyres in some parts of the bay (Smith et al., 1999, Beardsley et al., 2004), that may concentrate and entrain zooplankton such as krill in particular areas (Lawson et al., 2004; Ashijan et al., 2004). This area was chosen for multidisciplinary research into the physical and biological factors that contribute to enhanced krill growth, reproduction, recruitment and survivorship (Hofmann et al., 2002) for two reasons: unusually high krill production (Lascara et al., 1999) and predictable winter sea-ice cover (Jacobs and Comiso, 1997).

Krill (*Euphausia superba and E. sp.*) form a significant component of baleen whale diet in the Antarctic (Kawamura, 1994), and relationships between the distribution of these predators and that of their prey have been shown at broad (~100 to 1000s of km) spatial scales for the Antarctic (Tynan, 1998; Reid et al., 2000; Thiele et al., 2000; Murase et al., 2002). So far, strong associations between baleen whale and krill distributions have not been shown at smaller (10s of km) spatial scales (Pankow and Kock, 2000; Reid et al., 2000). This may be due to the difficulty of integrating data for predator and prey species that both have patchy distributions (van Franeker et al., 2002). In the Antarctic, the patchiness of whale distributions

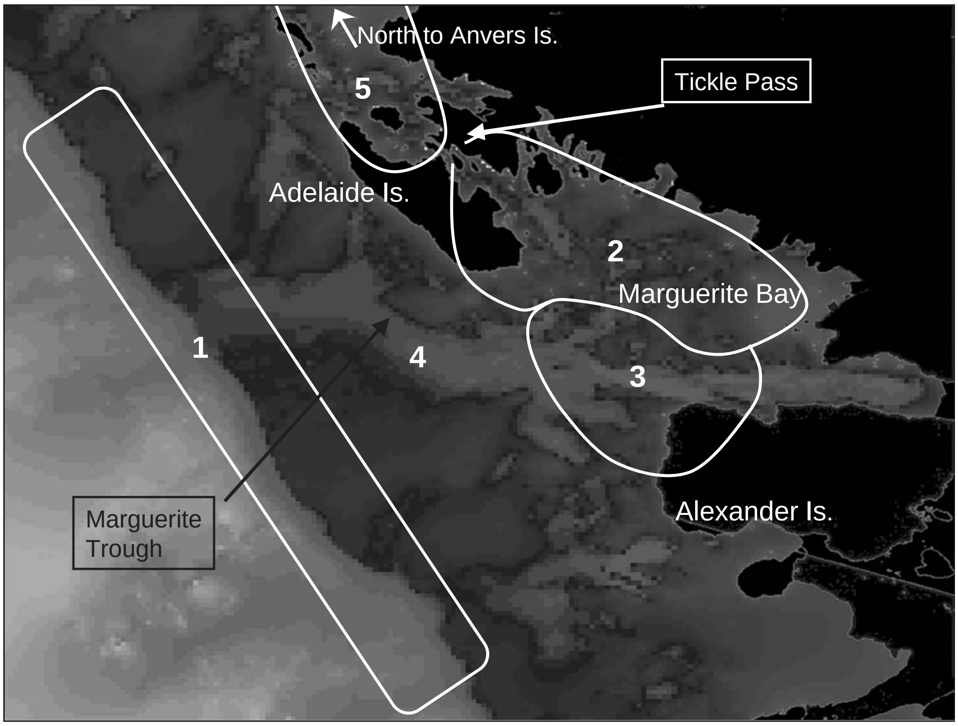

Fig. 1. Study area around Marguerite Bay with bathymetry. Spatial divisions used in analysis: shelf edge (SD 1), inner shelf (SD 2), southern inner shelf (SD 3), outer shelf (SD 4) and coastal fjord area (SD 5).

is further compounded by low densities of many species due to the depletion of populations during commercial whaling.

Krill population dynamics have been linked to variability in sea ice conditions in a number of studies (Fraser and Hofmann, 2003; and summarized in Constable et al., 2003), and winter ice extent is known to affect krill survival and abundance in the following season (Daly, 1990; Siegel and Loeb, 1995; Loeb et al., 1997; Nicol et al., 2000; Constable et al., 2003). High densities of krill, baleen whales and other predators have been observed at 'ice margins' or 'ice edges' (de la Mare, 1997; Ainley et al., 1998; Ferguson et al., 2000; Brierly et al., 2002; van Franeker et al., 2002), and particularly where ice habitat coincides with certain physical features and biological processes such as complex bathymetry, gyres, eddies, warm-water intrusions, high-velocity currents, high productivity, troughs, ridges, slopes, shelf edges, and other features which, alone or in combination, produce upwelling or concentration of nutrients and prey (Daly and Macaulay, 1991; Ribic et al., 1991; Plotz et al., 1991; Ichii et al., 1998; Murase et al., 2002). In general, habitat complexity is reported to result in increased diversity and abundance for many species (Bartholomew et al., 2000). Marguerite Bay and the surrounding area have complex habitat features, as well as a predictably high krill abundance. We therefore expected that significant numbers of baleen whales would be present there, and that the distribution of krill and krill predators would reflect the spatial complexity of the Marguerite Bay area.

Our central objective here was to investigate seasonal changes in distribution and concentration of minke and humpback whales, and to relate this to variability in feeding habitat associated with bathymetric and sea-ice features. Our analyses were focused on minke and humpback whales because they are often found in association with sea ice, and because of the relatively low numbers of other cetacean species observed. Sea-ice conditions and krill abundance differed greatly between 2001 and 2002 (Ashijan et al., 2004; Lawson et al., 2004), which provided a strong foundation for comparison of cetacean distribution and relative abundance between years.

2. Materials and methods

The SO GLOBEC research program in the WAP was conducted over two years commencing March 2001 and finishing in March 2003 (Table 1). Three sampling protocols were developed for research cruises: survey grid, process studies and mooring deployments (see Hofmann et al., 2004, for detail of cruise tracks and descriptions of survey types). Four survey cruises were conducted aboard the *RVIB Nathaniel B Palmer (NBP)*, comprised of multidisciplinary sampling of the entire study area along pre-determined grid lines except when sea ice made this impossible. Four process cruises were conducted aboard the *RV Laurence M. Gould (LMG)*. At process sites a range of sampling and experimental activities occurred (e.g. seal foraging and tagging (Burns et al., 2004), penguin tagging and diet studies, zooplankton sampling (Lawson et al., 2004). Surveys for cetaceans were conducted whenever the vessel transited between sampling sites. The *RV Laurence M. Gould (LMG)* have also used for three mooring cruises to deploy and retrieve a series of oceanographic and cetacean passive acoustic moorings along the outer shelf and inshore regions. Visual surveys for cetaceans were conducted as the vessel transited through the study area. The *RV Polarstern* conducted one cruise in this study area, but these data have not been used in statistical analyses. Sightings are reported here only to provide seasonal context of humpback whale presence for late April/May 2001, due to the large concentrations seen in southern MB on a single helicopter survey.

2.1. Data collection

One or two trained cetacean observers were placed on each cruise to search along all survey grid lines and transits between process, mooring and other sampling sites (Table 1). Observers searched an arc 180° ahead of the vessel whenever the ship was in transit, usually by naked eye, but sometimes augmented by Fujinon 7 × 50 binoculars. Zeiss 20 × binoculars were used to aid in species identification. Search effort was occasionally interrupted while observers attempted to positively identify species or note unusual sightings. Data were recorded using a laptop computer based sighting program (Wincruz Antarctic[1]) that also logged GPS position, ship course and speed. The Wincruz program catalogued search effort, number of observers on effort, weather and sea-state information (Beaufort sea state, swell height and direction), cetacean sightings (time, ship's position, angle and distance from vessel, species identification, group size, presence of ice) and ancillary data. A group is defined here as two or more cetaceans, broadly coordinating their behavior and direction of movement. Best, high and low estimates of group size were recorded for each sighting, and where more than one observer made an estimate, the final record was arrived at by consensus.

Our goal was to detect cetaceans whenever possible, so search effort was conducted over a broad range of weather conditions. The majority of Antarctic species are medium to large whales, with cues that can be detected in relatively high Beaufort sea states (Thiele et al., 2000). Search effort was terminated when observers determined that visibility was too poor due to some combination of adverse weather conditions that precluded detection of most species (i.e. strong winds, fog, large swell, confused swell, high sea state). Cetaceans were identified to the lowest taxonomic level possible. A positive species identification was made only when there was certainty.

2.2. Data analysis

To compare variability in cetacean distributions across multiple surveys of a geographically

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[1] Wincruz Antarctic is a free software program developed by Robert Holland at the Southwest Fisheries Science Centre, La Jolla, USA, for cetacean surveys in the Antarctic. The software is available at http://mmdshare.ucsd.edu/software.html.

Table 1
SO GLOBEC cruises 2001–2003 with cetacean sighting survey data

Vessel/cruise acronym	Cruise dates	Purpose
R/V Laurence M. Gould/LMG 0103	18 March–13 April 2001	Mooring cruise (Initial deployments)
RV Polarstern/AntXVIII5b	14 April–7 May 2001	Survey and ice/krill process cruise
RVIB Nathaniel B. Palmer/NBP 0103	24 April–5 June 2001	Survey cruise
RVIB Nathaniel B. Palmer/NBP 0104	24 July–31 Aug 2001	Survey cruise
R/V Laurence M. Gould/LMG 0201A	6 Feb–3 March 2002	Mooring cruise (Retrieve and deploy)
R/V Laurence M. Gould/LMG 0203	7 April–21 May 2002	Process cruise
RVIB Nathaniel B. Palmer/NBP 0202	9 April–21 May 2002	Survey cruise
RVIB Nathaniel B. Palmer/NBP 0204	31 July–18 Sept 2002	Survey cruise
R/V Laurence M. Gould/LMG 0302	12 Feb–17 March 2003	Final mooring cruise (Retrieval)

complex study area, we: (a) divided the study area into biologically meaningful zones within which total effort was pooled; (b) treated sections of sighting survey effort as statistical samples; (c) adjusted sighting survey counts by the duration of effort within defined spatial divisions; (d) selectively pooled some cruises and areas for separate analyses; (e) separated some cruises completely when they could not easily be used in analyses; and (f) tested hypotheses of independence and homogeneity, rather than for differences in abundance or density.

The study area was divided into four subregions based upon potentially biologically important locations (Fig. 1). These spatial divisions (SD) included: the *shelf edge* (SD 1); the *inner shelf* waters inside Marguerite Bay and around the southern tip of Adelaide Island, generally with depths of 100–400 m (SD 2); the *southern inner-shelf waters* including the mouth and southern part of Marguerite Bay, and Marguerite Trough (SD 3); the outer shelf (SD 4) Additionally, sighting effort was pooled in order to allow adequate overall survey time in the *coastal fjord* area from near Anvers Island in the north (64°00'S), to Tickle Pass at Adelaide Island (SD 5).

Sighting survey effort was not continuous along entire cruise tracks, but occurred only when the vessel was transiting between points during daylight, and where sea and weather conditions did not critically affect visibility. For analysis, survey periods of varying length "on effort" (time spent on visual survey) were treated as independent "shifts". "Off effort" temporal discontinuities allowed shifts to be viewed as samples within each spatial division The fact that the coincidence of timing for each shift with geographic position was not planned addresses concerns about sampling bias (Quinn and Keough, 2002). Shifts were considered separate, or independent, if the end of one recorded survey period was separated by more than one hour from the beginning of the next. Shifts were eliminated or truncated if they did not fit wholly within a particular spatial division. Consequently, sighting data were standardized by the duration of effort for each shift, and then the adjusted counts for each spatial division were summed.

Once adjusted for effort, counts for each "sample" were then grouped within "cells" of a table formed by each combination of cruise and spatial division (Fig. 2). Several cells in Part A (Fig. 2) are empty, as the result of two distinct occurrences, where (1) the cruise track did not cover that combination, or there was little or no effort there, or (2) the combinations did not exist, e.g., because fast ice prevented access to areas during winter 2002 in Marguerite Bay. Sampling effort in a division for each cruise was determined to be significant if it exceeded 5 h in total (~0.2 days): any cell with less than this was counted as missing (only NBP 0104 division 5). Fig. 2 also includes the two cruises (Polarstern AntXVIII5b and LMG 0302) where effort was not directly comparable with the other cruises: these were not used in statistical analyses, but provided

		SPATIAL DIVISION	**1**	**2**	**3**	**4**	**5**
A	Summer 2001	LMG 0103	▒╲		▒╲	▒╲	
	Autumn 2001	Polarstern AntXVIII5b	-----	-----	-----	-----	-----
B	Autumn 2001	NBP 0103	╲				✕
C	Winter 2001	NBP 0104	▒	▒╲	▒	▒	✕
D	Summer 2002	LMG 0201A		╲	╲		
E	Autumn 2002	NBP 0202/LMG 0203					
F	Winter 2002	NBP 0204	▒	✕	✕	▒	▒╲
	Summer 2003	LMG 0302	-----	-----	-----	-----	-----

Fig. 2. Analysis of whale sightings as table frequencies. Counts (per 24 h) within each voyage by spatial division combination are entered as cell frequencies for statistical analysis (Part A). Cruises with dashes were not included in statistical analyses. Missing cells (missing survey grid data) in the table are due to (1) combinations where there was no significant sampling effort (cells shown crossed), and (2) where no sighting were recorded for a particular combination (dark shaded for humpback whales, diagonally striped for minke whales).

additional supporting data for some locations within the study area.

The presence of zero or missing values (Goodman, 1968) strongly influences the way in which data are analyzed, because too many prevent meaningful hypothesis tests. Here, LMG 0203 and NBP 0202 could be combined because their temporal extents were nearly coincident, and this eliminated a missing cell in the table. The influence of other missing cells on statistical tests was minimized by separating the table into subsets for analysis.

For statistical analyses, sightings (for cruises A–F in Fig. 2) were treated as a multinomial experiment, i.e. counts adjusted for effort were treated as frequencies allocated to each cell within the full table (Ramsey and Schaeffer, 1996). Analysis tested hypotheses using chi-squared statistics for homogeneity or goodness of fit on separable ‘sub-tables’, with tests of quasi-independence for the full table (Quinn and Keough, 2002). Where there was the potential for compounding error due to repeated tests on the same data, Bonferroni type corrections (Quinn and Keough, 2002) were not deemed necessary because evidence in favour of rejecting null hypotheses was always either very strong or very weak. Specifically, null hypotheses for sub-tables were that across-division patterns of frequencies (i.e. effort-adjusted counts) do not change between cruises. Then, using the additive property of χ^2 statistics (Goodman, 1968), results for the sub tables were combined to test the equivalent null hypothesis for the full table. The prior analysis of sub-tables allowed complex interactions between the spatial and temporal components of observed frequencies to be explored. Because hypothesis tests for independence or homogeneity do not involve directly comparing estimates of, e.g., density between different times or area, the different spatial extents of the divisions to which counts were assigned have no effect on the outcome.

The analyses for humpback and minke whale habitat use were conducted independently both to address different sets of hypotheses and because the patterns of missing values and zero frequencies required tables to be separated and/or pooled differently. Humpbacks were seen throughout most of the study area on four cruises (NBP 0103–Autumn 2001, LMG 0201a–Summer 2002, LMG 0203/NBP 0202–Autumn 2002) so data were combined into a 3×4 cell table with the four SDs around Marguerite Bay. A separate test for homogeneity of frequencies was done for SD 5 for LMG 0201a and LMG 0203/NBP 0202. Sightings for winter cruises were not included in statistical analysis because of the pattern of zero values.

A different approach was taken for minke whales, because they were seen in the study area during all seasons, on all cruises. The zero frequencies (especially in LMG 0103) were addressed by separating the full table by year, then differentially pooling each year across spatial divisions. This allowed the separate examination and then comparison of the change in the pattern of distribution in each year. Since 2001 and 2002 were very different in terms of extent and timing of pack-ice formation: we hypothesized that pack ice was an important habitat for minke whales, hence we expected the distribution of minkes through the year to respond to pack ice.

Finally, there was the problem of missing survey grid data, for NBP 0204 (in Winter, 2002), because at this time fast ice covered the inner shelf and southern inner shelf (SD 2 and 3) around Marguerite Bay. Hence, for 2001, the shelf edge and outer shelf (SD 1 and 4) were pooled, and SD 2 and 3 also were pooled within each cruise, forming a 2×3 sub-table. The coastal fjord area (SD 5) could not be included because there was no (or very little) effort there for NBP 0103 and NBP 0104 (2001). For 2002, SD 2 and 3 were not included in the sub-table, leaving SD1 and 4, which were largely covered by pack ice by Autumn 2002. A further test was done for SD 2–4 between May 2001 and May 2002.

3. Results

Ten cetacean species (fin whale *Balaenoptera physalus*, sei whale *Balaenoptera borealis*, blue whale *Balaenoptera musculus* sp., minke whale *Balaenoptera bonaerensis and B. acutorostrata sub species*, killer whale *Orcinus orca*, humpback whale *Megaptera novaeangliae*, sperm whale *Physeter macrocephalus*, hourglass dolphin *Lagenorhynchus cruciger*, Ziphiidae and various categories of ‘unidentified’ cetaceans) were detected on nine cruises (Table 2). Humpback and minke whales were by far the most numerous species.

Table 2
Cetacean species, total number of sightings/groups and individuals for all (nine) SO GLOBEC cruises 2001–2003 south of 60°S

Species (common name)	No. of groups	No. of animals
Humpback whale	356	848
‘like’ humpback	14	34
Antarctic minke and undetermined minke	137	331
‘like’ minke whale	17	29
All unidentified cetacean categories	94	198
Killer whale	17	172
Fin whale	3	12
‘like’ fin whale	9	24
Sei whale	6	30
‘like’ sei whale	1	3
Ziphiidae	5	15
Hourglass dolphin	4	19
Sperm whale	2	3
‘like’ blue whale	1	1
Total	666	1719

Overall survey effort was 650 h for the seven statistically analysed cruises (Fig. 3). Total search effort per cell ranged up to 62 h (NBP 0202 SD 4), and total effort per division ranged from 79 (SD 3) to 232 h (SD 4). Additionally, for LMG 0302 there was over 55 h survey effort in the study area . The Polarstern cruise (April/May 2001) conducted only a brief survey of the study area, but did include helicopter survey of the inner shelf (SD 2), where a large concentration of humpbacks was seen. Two cruises ancillary to the analyses, but important for their contribution of additional distribution data are the Polarstern ANTXVII5b and LMG 0302 cruises. Sightings recorded on these cruises were 20 sightings of 90 individual humpbacks (20:90 this is standard notation for recording number of sightings/groups and number of individual whales and will be used from now on in the text), 9:11 minkes (LMG 0302) and 16 sightings of 38 humpbacks, 15 sightings of 28

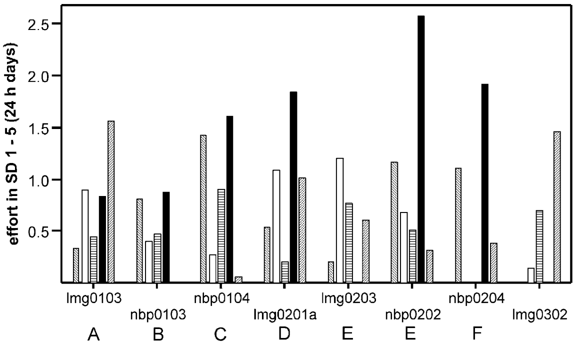

Fig. 3. Effort (24 h day equivalents) for SD 1–5, all cruises except Polarstern (total eight cruises). A–F as per Fig. 2.

minkes (Polarstern). Sighting summaries for all cruises in the analysis (A-F Table 2) include 103 minke sightings of 267 individuals and 237 humpback sightings of 537 individuals; by far the highest proportion of these were in the coastal fjords (SD 5). Sightings corrected for effort were: minkes (87.36:225.26); humpbacks (196.92:423.11).

The overall pattern of distribution of humpback and minke whales is evident in Fig. 4(A)–(E). Humpback whales were detected throughout late summer and autumn of both years. Detections were much higher in 2002 and distribution appeared to follow the position of the pack-ice edge. For example in 2001 humpbacks were concentrated in the inner shelf area (SD 2) (Fig. 4A), while in 2002, although some large groups were found in one area of the inner shelf (SD 2), humpback aggregations were seen in the southern inner shelf area (SD 3) in association with the pack ice margin, with smaller groups scattered over the outer shelf (SD 4) (Fig. 4B). The late summer 2003 cruise (LMG 0302) also recorded the largest concentrations of humpbacks near ice margins in the coastal fjords (SD 5) and in the southern inner shelf, where this intersected the pack ice margin (SD 3) (Fig. 4C). Notably, one pair of humpback whales was seen on 4 August 2002 near Anvers Island (64° 53.15S 64°08.37W).

Minke whales were seen on every survey. During late summer and autumn of 2001 and 2002, most minke whales were found in the coastal fjords (SD 5), although sightings were lower for 2002. During 2001, there were fewer minke sightings on winter surveys, while in 2002 numbers increased during winter and were significantly higher than in 2001. Winter distributions of minke whales were concentrated at two sites: one very close to the shelf edge, and one in the Marguerite Trough. In 2001 most were seen at one location on the shelf edge (Fig. 4D), while in 2002 they occupied a much greater area of the shelf edge (Fig. 4E). Standardizing by effort did not generally affect this pattern of occurrences, i.e. where there were many sightings, there were still many sightings with the correction. Two cruises ancillary to the analyses, but important for additional distribution data are the Polarstern ANTXVII5b and LMG 0302 cruises. Sightings recorded on these cruises were 20:90 humpbacks, 9:11 minkes (LMG 0302) and 16:38 humpbacks, 15:28 minkes (Polarstern). For all cruises in the analysis (Fig. 2) minke sightings with 103 groups and 267 individuals (103:267) and humpback whales are 237 groups and 537 individuals (237:537): by far the highest proportion of these were in the coastal fjords (SD 5). When corrected for effort, i.e. expressed as sightings per day added for each spatial division, the totals are: minkes (87.36:225.26); humpbacks (196.92:423.11) (Fig. 5A–D).

3.1. Humpback whale seasonal occurrence and habitat selection

Humpback whale distribution was restricted to the inner shelf and coastal fjord area in late Summer 2001 (SD 2 and 5). They were detected

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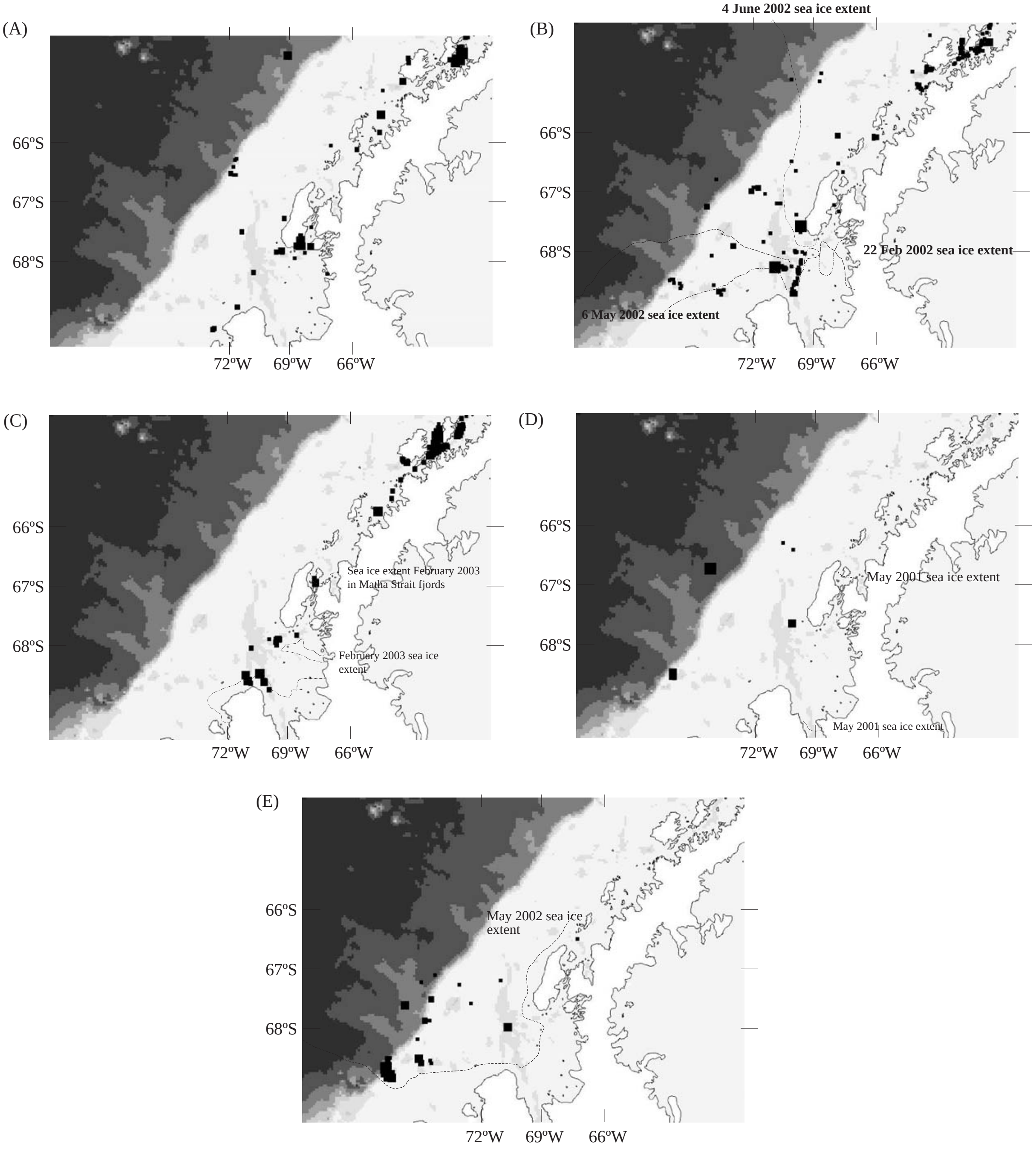
Fig. 4. Whale sightings from cetacean sighting surveys in the SO GLOBEC Western Antarctic Peninsula study area. All sightings represented by black filled squares. (A) Humpback whales March 2001–June 2001 (symbol size represents group size for each sighting: groups size categories are 1, 2, 3, 4, 5 or 6 whales). There was no sea ice in the study area until after June 2001. (B) Humpback whales February 2002–May 2002 (symbol size represents group size for each sighting: groups size categories are 1–2, 3–4, 5–6, 7–8, 9–10, 11–12 whales). Sea-ice extent for February 22 2002, 6 May 2002 and 4 June 2002 represented by solid line. May ice extent comprised more than one third brash marginal ice zone at outer edge—diffuse ice edge; while February sea-ice extent had a distinct boundary of sheet ice. (C) Humpback whales LMG 0302 February 2003–March 2003 in the SO GLOBEC Western Antarctic Peninsula (symbol size represents group size for each sighting: groups size categories are 1, 2, 3, 4, 5, 6 whales). Sea-ice extent for cruise period marked with dashed lines. (D) Minke whales July 2001–August 2001 (symbol size represents group size for each sighting: groups size categories 1, 2 or 3 whales). Pre-winter sea-ice extent is shown by a dashed line for comparison with 2002. In both 2001 and 2002 sea ice covered the entire bay and shelf when winter cruises were conducted. Ice thickness, ridging and the percentage of multi year floes changed between years, with 2002 having thicker ice, more ridging and more multi-year floes than 2001. (E) Minke whales August 2002–September 2002 (symbol size represents group size for each sighting: groups size categories are (1, 2, 3 or 4 whales).

only once during winter 2002 Fig. 2: C and F), in the extreme north of the coastal fjord area (SD 5). The hypothesis of non-independence between spatial divisions and the cruises outside winter was thus supported by the lack of sightings on LMG 0103 (Fig. 2): their distribution was restricted to the inner shelf and coastal fjord area in late Summer 2001 (SD 2 and 5).



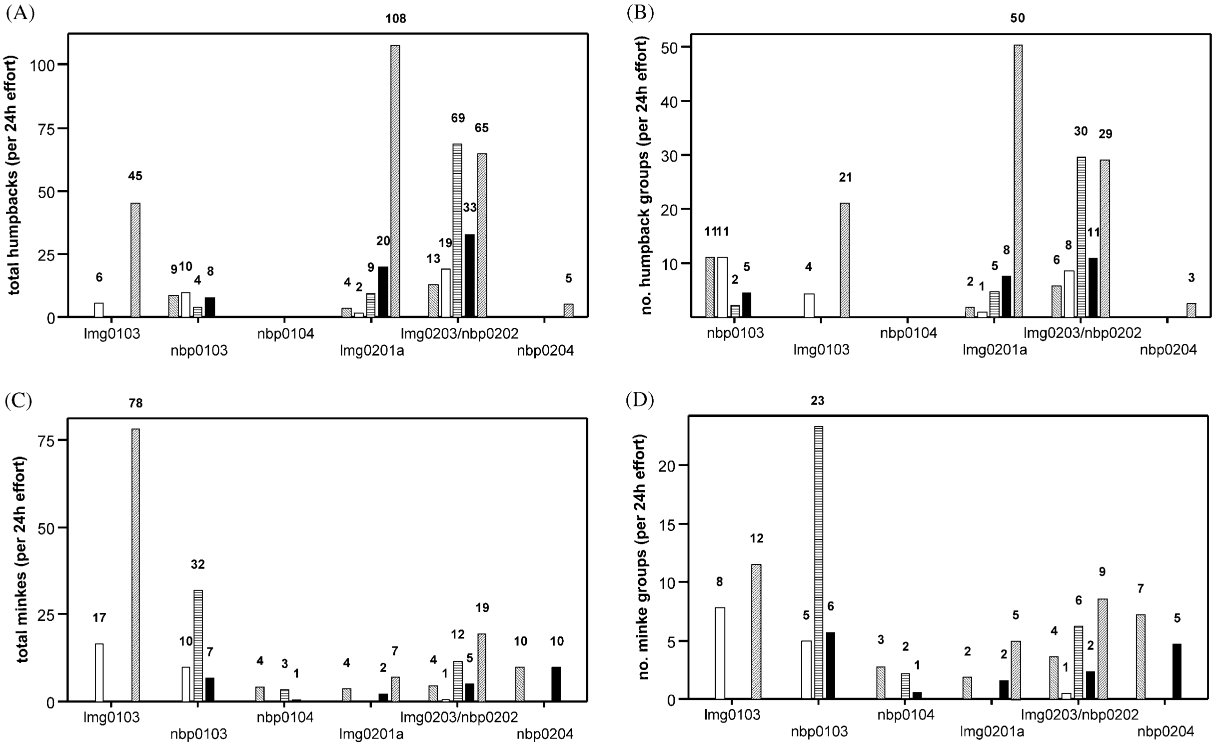


Fig. 5. Individuals and groups in SD 1–5 corrected for effort: (A) total humpbacks (no. individuals), (B) total humpbacks (no. groups), (C) total minkes (no. individuals) and (D) total minkes (no. groups).

Significantly more humpback whales were found in summer 2002 than in autumn 2002 in the coastal fjords (SD 5) ($\chi^2 = 10.79 > \chi^2_{0.001,1}$,for individuals$\chi^2 = 5.726 > \chi^2_{0.05,1}$) for groups. In late summer, the majority of humpbacks were found in the coastal fjords (SD 5) (50.42:107.75), 75% of the total. This is concordant with LMG 0103 at a similar time in 2001 (21.14:45.49) 89% of the total, although for this cruise, humpbacks were seen throughout the coastal fjord area (SD 5). In 2002 they were mainly seen in the far north of SD 5. The Polarstern helicopter surveys confirmed the presence of aggregations of humpback whales (38 individuals in groups of 2–4), near the south east coast of Adelaide Island, and in bays around Anvers Island in early May 2001.

While many humpbacks (33% of individuals) were still found in the coastal fjord area (SD 5) in Autumn 2002 (29.08:64.62), the distribution between divisions was more uniform than in 2001. In Autumn 2002, most (80%) humpbacks were found in SD 5 and the southern inner shelf area (SD 3) (29.65:68.66). This cruise went mainly through and along the edge of pack ice (Fig. 4B), in the inner shelf area (SD 2) and SD 3, and relative densities were much higher here in 2002 (87.77 versus 14.19 individuals) than in the equivalent (ice-free) areas in 2001 (Fig. 4A). The average group size for humpbacks was higher in 2002 and 2003 than in 2001 (Fig. 4A, B).

The test for the 4 × 3 cell table provided very strong evidence to reject the null hypothesis of independence between the four spatial divisions around Marguerite Bay and the cruises ($\chi^2 = 35.242 > \chi^2_{0.001,6}$ for individuals; $\chi^2 = 24.176 > \chi^2_{0.001,6}$ for groups). Examination of cell expected values showed that this could be attributed to cell differences between LMG 0203/NBP 0202 (Autumn 2002) and both the autumn 2001 and summer 2002 cruises. A test for the table combining both the previous sub-table and the non-missing cells for SD 5 then provided very strong evidence to reject the null hypothesis of quasi-independence ($\chi^2 = 45.538 > \chi^2_{0.001,7}$ and $\chi^2 = 29.901 > \chi^2_{0.001,7}$ for groups sighted) between spatial divisions and sampling times for humpback whales.

In March 2003 (LMG 0302) large numbers (20 sightings of 90 whales) of humpbacks were again found in the inner shelf, southern inner shelf and coastal fjord areas (SD 2,3 and 5) (there was little effort away from the coast in SD1, on this cruise). More individuals (56, 62%) were observed in the coastal fjords (SD 5); however, this proportion dropped when corrected for effort (28%). Sampling by shift was not strictly comparable with previous cruises: effort in SD 2 was less than the a priori threshold for significance of 0.2, but this was an artifact of an inability to assign shifts as occurring wholly within the spatial divisions used on previous cruises.

3.2. *Minke whale seasonal occurrence and habitat selection*

By far the largest number of minkes were observed in the coastal fjords (SD 5) on LMG 0103 (18:122, 11.53:78.16 per 24 h effort). This included two large feeding groups encountered in Matha Strait, north of Adelaide Island (~100 animals), which dispersed after several hours. Many fewer minkes were seen on the equivalent cruise in 2002 (LMG 0201a) (Fig. 4), although most were still seen in SD 5. With SD 5 excluded from the 2001 sub-table, there were many zero frequencies for minkes in the full cruise by spatial division table, indicating that minke distributions were relatively localized within the period covered by each cruise. The highest proportion of minke whale sightings occurred in autumn in both 2001 and 2002. 66% and 45% of the overall effort-corrected totals for their respective within-year sub tables.

There was strong evidence to reject the null hypothesis of independence between cruises and spatial division groupings for total individuals seen (for 2001, $\chi^2 = 14.72 > \chi^2_{0.001,2}$; for 2002, $\chi^2 = 22.92 > \chi^2_{0.001,4}$), as well as for number of groups seen for both years (2001, $\chi^2 = 8.881 > \chi^2_{0.001,2}$; 2002, $\chi^2 = 13.78 > \chi^2_{0.001,4}$). The null hypothesis of quasi-independence for the table combining both years was also rejected ($\chi^2 = 9.49 > \chi^2_{0.001,6}$ for total number; $\chi^2 = 22.591 > \chi^2_{0.001,6}$ for groups). The single zero-values in both these tables contributed greatly to this result: i.e., no minkes were in the shelf edge or outer shelf areas (SD 1 and 4) in March 2001, and none were found in the coastal fjords (SD 5) in winter 2002.

The test for independence for the 3 × 2 complete table for the inner, inner southern and outer shelf (SD 2–4) autumn cruises reused cells from the previous analyses. A statistically significant result would need to be corrected for potentially compounding type I error (Quinn and Keough, 2002); however, there was no evidence that the null hypothesis of independence for spatial divisions across the two years should be rejected, neither for individuals ($\chi^2 = 4.05 < \chi^2_{0.05,2}$), nor groups ($\chi^2 = 0.733 < \chi^2_{0.05,2}$). In other words, the relative distribution of minke whales in and around Marguerite Bay during autumn appears to have been similar in 2001 and 2002 for those spatial divisions, although the densities were higher in 2001.

There were differences in the seasonal pattern of minke whale distribution between years, and the difference in analytical treatment between years is partly due to this. Interannual differences for the combined table were largely due to the large number of minkes found inshore (SD 2, 3) in 2001. However, examining the full data for cruises A–F before it was pooled for statistical tests (Fig. 5C, D) also shows the effect of the high number of minkes seen in SD 5 on LMG 0103, and the missing cells (Fig. 2, Part A), where there was insignificant effort, i.e. no data to be compared with equivalent times or spatial divisions. The most obvious interannual pattern is that minke whales were more dispersed, in pack ice, in winter 2002.

4. Discussion

The ecology of Marguerite Bay is probably influenced both by habitat complexity and by the effects of regional oceanographic and sea ice processes (e.g., Antarctic Circumpolar Current intrusions onto the MB shelf, timing, nature and extent of sea ice) on the fauna. The marked seasonal and interannual variability in this environment observed over the two years of this study had apparent effects on cetacean distribution in and around the bay.

The results of these surveys showed humpback and minke whales using primarily near-coastal habitat (SD2, 3 and 5) in the late summer and autumn. When sea ice was present, its boundary provided an additional area of concentration, particularly for humpback whales. Both species were found in greater numbers during seasons where a sea ice boundary existed over the inner, and southern inner shelf areas of Marguerite Bay. For humpbacks, this was evident throughout late summer and autumn in years where sea ice was present across the inner shelf (2002 and 2003). Also, in winter, minke whales were found in greater numbers on the shelf in 2002 compared to 2001. The single winter sighting of one pair of humpback whales in the northern part of the coastal fjords in early August of 2002 is notable, since this provides solid evidence that members of this species can remain in this part of the Antarctic during winter. All humpback whales are presumed to migrate out of the Antarctic prior to winter (Dawbin, 1997), yet this has been challenged by Brown et al. (1995) with evidence of possible sex segregated migration off the East coast of Australia. The sex of the pair of humpbacks sighted in winter during this study could not be determined.

Hypothesis tests supported the assumption that whale distributions vary on a seasonal basis and between years. There was complex non-independence in the relationship between sampling location and cruise (or time of year), both within 2001 and 2002 and between cruises compared across the 2 years. Despite strong qualifications because of uncertainty over the effects of any interaction between varying effort and sampling location, spatial and temporal heterogeneity is clearly apparent for both minkes and humpbacks. A component of this is broad, taxon-specific behavior, i.e. the rarity of humpbacks over winter due to migration, and the association of minkes with pack ice in winter. However, it is clear that the distribution of whales changed markedly between years, between spatial divisions, and with the extent and nature of sea-ice cover, and that this likely reflects changes in the distribution and abundance of prey.

In the regions we surveyed, it appears that there are 'resource sites' that are important locations for baleen whale feeding during summer and autumn in years with or without ice. These sites were in the coastal fjord area, particularly Matha Strait and south eastern Adelaide Island; southwest Adelaide Island, north and northwest Alexander Island; the shelf edge; and around the Marguerite Trough. These localities had in common some of the following features: complex bathymetry, high velocity currents, small to medium gyres and eddies (Beardsley et al., 2004). We hypothesize that combinations of these features form a complex habitat that functions to enhance the concentration of zooplankton, and that this explains the strong seasonal and interannual association between these locations and the distribution of humpback and minke whales.

Reports of linkages between marine vertebrate distributions and physical features in the Antarctic, such as oceanographic fronts and gyres, which concentrate prey, also appear in much of the recent literature (Ainley, 1985; de la Mare, 1997; Tynan, 1997, 1998; van Franeker et al., 2002; Thiele et al., 2000; Wilson et al., 2001). Sea-ice processes play an integral role in the lives of Antarctic marine biota, whether they be permanent (e.g., krill, penguins, minke, killer and some other species of whales), or temporary (migrating seabirds and some whales) residents (Tonnessen and Johnsen, 1982; Ainley, 1985; Trathan et al., 1996; Ichii et al., 1998; Nicol et al., 2000; Barbraud et al., 2000; Wilson et al., 2001; Barbraud and Weimerskirch, 2001; Brierley et al., 2002; Murase et al., 2002).

A complex series of events determines sea-ice formation and structure (Allison, 1997). A sea-ice environment that forms relatively rapidly (2001 winter) will be more homogenous than one that has formed over many months (2002). The slower ice cover forms, and the older the ice involved, the more time it is exposed to the destructive effects of sea and weather conditions, and thus more areas will be ridged and broken, creating more diverse habitats. Krill have been shown to congregate under ridged ice (Eicken, 1992) and concentrations of zooplankton (particularly krill, *E. superba*) have been reported as being significantly higher at some Antarctic ice boundaries (Ichii, 1990; Brierley et al., 2002).

In this study we see that when ice cover is present, as in 2002, resource sites remain important, but ice margins, edges, boundaries, or areas where these intersect with resource sites, attract much larger numbers of animals (particularly, but not exclusively humpbacks); i.e. they become 'enhanced resource sites'.

Examination of cell structure within analysed tables showed significant differences between the groups and the total number of individuals, suggesting that degree of aggregation changes seasonally, and potentially with annual ice conditions. Since baleen whales found in and around ice boundaries were usually engaged in feeding behaviour, aggregation at ice edges or boundaries is probably a manifestation of a direct link between ice as habitat for krill and a trophic response by their predators. In both years of this study, krill predators other than cetaceans (seabirds and seals) were generally found in higher abundance in the same areas as whales (Chapman et al., 2004), providing support for a link between habitat complexity and a greater diversity and abundance of fauna (Eicken, 1992; Bartholomew et al., 2000). The presence of large concentrations of krill predators feeding at sea-ice margins in the study area in 2002 supports the suggestion by Brierley et al. (2002) and others of a strong positive relationship between the sea-ice edge and krill densities.

The distribution of humpback and minke whales on the Antarctic feeding grounds is therefore likely to be influenced by both short and long-term changes in the distribution and dynamics of sea ice. The availability and abundance of baleen whale prey will be affected by variability in sea ice conditions, particularly in regions of the Antarctic where annual sea-ice extent is being reduced or increasing (Zwally et al., 2002). This variability directly influences the population dynamics, distribution and abundance of many krill predators in localized areas, as well as at regional and circum-Antarctic scales (van Franeker, 1992; Trathan et al., 1996; Smith, et al., 1999a,b; Barbaud and Weimerskirch, 2001; Croxall et al., 2002; Kato et al., 2002; Fraser and Hofmann 2003). Similar responses are likely for baleen whale populations that feed in the Antarctic, and therefore the implications of such environmental change need to be considered in the management and conservation of these species in the Southern Ocean.

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