

Horizontal niche partitioning of humpback and fin whales around the West Antarctic Peninsula: evidence from a concurrent whale and krill survey

Helena Herr¹ · Sacha Viquerat¹ · Volker Siegel² · Karl-Hermann Kock² · Boris Dorschel³ · Wilma G. C. Huneke³ · Astrid Bracher^{3,4} · Michael Schröder³ · Julian Gutt³

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Abstract A dedicated aerial cetacean survey was conducted concurrently to a standardised net trawl survey for krill in order to investigate distribution patterns of large whales and different krill species and to investigate relationships of these. Distance sampling data were used to produce density surface models for humpback (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*) around the West Antarctic Peninsula (WAP). Abundance for both species was estimated over two strata in the Bransfield Strait and Drake Passage. Distinct distribution patterns suggest horizontal niche partitioning of the two whale species around the WAP, with fin whales aggregating at the shelf edge of the South Shetland Islands in the Drake Passage and humpback whales in the Bransfield Strait. Krill biomass estimated from the concurrent krill

survey was used along with CTD data from the same expedition, bathymetric parameters and satellite data on chlorophyll-*a* and ice concentration to model krill distribution. Comparisons of the predicted distributions of both whale species with the predicted distributions of *Euphausia superba*, *Euphausia crystallorophias* and *Thysanoessa macrura* suggest a complex relationship rather than a straightforward correlation between krill and whales. However, results indicate that fin whales were feeding in an area dominated by *T. macrura*, while humpback whales were found in areas of higher *E. superba* biomass. Our results provide abundance estimates for humpback whales and, for the first time, fin whales in the WAP and contribute important information on feeding ecology and habitat use of these two species in the Southern Ocean.

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✉ Helena Herr
helena.herr@tiho-hannover.de

¹ Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover, Foundation, Werftstr. 6, 25761 Büsum, Germany

² Thünen-Institute of Sea Fisheries, Palmallee 9, 22767 Hamburg, Germany

³ Alfred Wegener Institute, Helmholtz Center for Polar and Marine Research, 27568 Bremerhaven, Germany

⁴ Institute of Environmental Physics, University Bremen, Otto-Hahn-Allee 1, 28359 Bremen, Germany

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Introduction

The Southern Ocean is well known for its krill-based ecosystem, sustaining large populations of marine birds and mammals (Steele 1970; Loeb et al. 1997; Nicol et al. 2006, 2008; Knox 2007). Many species of baleen whales undertake annual migrations to Antarctic waters to exploit the rich krill resources. In the Antarctic, they build up fat deposits to survive their long migration to subtropical and tropical waters where they breed but hardly feed for the remainder of the year (Lockyer and Brown 1981). Although whales are the largest and most conspicuous creatures of the Southern Ocean ecosystem, they are among the least studied (Ducklow et al. 2007).

Our current understanding of the large-scale (circum-Antarctic) distribution of whales in the Southern Ocean is mainly based on the Discovery expeditions in the 1920s and 1930s (Mackintosh and Wheeler 1929; Matthews 1938; Mackintosh 1942; Brown 1954), catch data series obtained from the whaling industry until 1979 and from the three circumpolar cetacean sighting surveys (CP I–III) carried out under the auspices of the International Whaling Commission's (IWC) International Decade of Cetacean Research (IDCR) and Southern Ocean Whale Ecosystem Research (SOWER) programmes (Branch and Butterworth 2001) from 1978/1979 to 2003/2004. Together, these data sets provide the most comprehensive available information on the circum-Antarctic distribution of cetacean species. Comparably little is known, however, about the distributions at smaller and more local scales.

Whale distribution has been linked to oceanographic and bathymetric parameters in many areas of the world (Tynan et al. 2005; Laran and Gannier 2008; Gill et al. 2011) including Antarctic waters (Friedlaender et al. 2006, 2011; Ribic et al. 2008; Ainley et al. 2011; Williams et al. 2014). For large baleen whales spending the summer months in the Southern Ocean, these parameters most likely serve as proxies for prey distribution, since feeding is the main reason for these species to perform seasonal migrations to Antarctic waters. Prey is thus likely to be a main driver of their distribution (Croll et al. 2005; Friedlaender et al. 2006). In the Southern Ocean, several euphausiid species, collectively referred to as 'krill', are the major prey resource for baleen whales (Steele 1970; Knox 2007; Nicol et al. 2008). Antarctic krill *Euphausia superba* often forms the overwhelming part of the krill biomass and is generally considered a keystone species in the Antarctic food web (Marrari 2008). It is the best studied species of krill in Antarctic waters (Daly and Macaulay 1988; Atkinson et al. 2012) and considered as the most important food source for baleen whales in the Southern Ocean (Steele 1970; Ducklow et al. 2007; Nicol et al. 2008). *E. superba* is known for schooling behaviour giving rise to large swarms (Everson 2000; Atkinson et al. 2012). For baleen whales as bulk feeders, swarming organisms are the most lucrative food resource (Goldbogen et al. 2013). Apart from *E. superba*, other Antarctic euphausiid species, namely *Euphausia crystallorophias* (also referred to as 'ice krill' or 'crystal krill') and *Thysanoessa macrura*, are also known as prey species for whales (Nemoto and Nasu 1958; Nemoto 1959; Steele 1970). Their distributions overlap with that of *E. superba*, and they can be very abundant and locally replace *E. superba* as the most abundant euphausiid (Makarov 1979; Daly and Zimmermann 2004). Yet, their role in the ecosystem and their

relationship to whales are even less understood than that of *E. superba* (Marrari 2008).

Krill is regularly surveyed in the Western Atlantic sector of the Southern Ocean during dedicated krill surveys by various nations both on a national basis and within the remit of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Nicol et al. 2000; Hewitt et al. 2004; Siegel et al. 2004; SC CCAMLR 2007; Wiebe et al. 2011). Nevertheless, information on krill distribution and abundance is rarely available on the same temporal and spatial scale as data on cetacean distribution and abundance. In some studies, hydroacoustic surveys for krill conducted concurrently to a ship-based cetacean survey have been used to obtain information on the distribution and abundance of whales in relation to zooplankton abundance (Murase et al. 2002; Friedlaender et al. 2006). However, such approaches usually lack detailed information on species composition of the zooplankton. They cannot distinguish euphausiid species and the ability to differentiate between krill and salps is limited, as salps have a frequency response similar to that of krill (Wiebe et al. 2010). Recent increases in salp (mainly *Salpa thompsoni*) biomass in the Southern Ocean (Atkinson et al. 2004) may lead to this species contributing to zooplankton masses to a large extent, while not being a target species of prey for baleen whales. A typical salp consists of 95 % water (Dubischar et al. 2006) and is unlikely to be a favourable food resource for marine mammals. In order to assess zooplankton biomass at species level, dedicated krill surveys use small pelagic trawls, such as the rectangular midwater trawl (RMT), for samples along a set grid of stations (Everson 2000; Atkinson et al. 2012). Krill distribution is estimated by interpolation of these dedicated point sampling schemes. However, such krill surveys rarely allow for concurrent dedicated cetacean surveys. Cetacean surveys require a constant minimum survey speed, a specified transect design and sufficient area coverage in order to obtain data that can be used for density estimation (Evans and Hammond 2004; Dawson et al. 2008). Concurrent marine mammal observations during krill surveys usually only allow for estimation of encounter rates as a measure for relative abundance (e.g. Santora et al. 2014).

During the *R/V Polarstern* expedition ANT 29-3, for the first time three key sets of data were collected simultaneously in the area of the West Antarctic Peninsula (WAP): cetacean sighting data from a dedicated helicopter survey, krill station samples and standardised oceanographic CTD sampling data. In this study, we use these data sets together with bathymetric parameters and satellite data on chlorophyll-*a* and sea ice concentration in order to investigate potential connections between the modelled distributions of cetaceans and krill.

Materials and methods

Setting

R/V Polarstern expedition ANT29-3 (22 January–18 March 2013) was a multidisciplinary research cruise which covered an area surrounding the tip of the Antarctic Peninsula (AP), comprising parts of the Bransfield Strait (BS), the Drake Passage (DP) and the Weddell Sea (WS) (Fig. 1) (cruise details in Dorschel et al. 2015). Both krill and cetacean surveys were conducted over the whole extent of the survey area (Fig. 1). Cetacean survey effort, however, was considerably reduced in the WS due to unfeasible weather conditions and wide areas of 100 % sea ice cover (NASA 2013) (Fig. 2). Analyses of cetacean distribution had to be restricted to BS and DP as WS provided too little effort and area coverage.

The marine ecosystem of the WAP is a highly productive area, known to support large populations of top predators, including many species of whales (Knox 2007; Ducklow et al. 2007). It extends from the Bellingshausen Sea to the northern tip of the AP. The shelf at the WAP is about 200 km wide and over-deepened with an average water depth of 430 m. Several glacial troughs cross the shelf (Arndt et al. 2013; Jerosch et al. 2015). BS is characterised by a 400-km-long and up to 2-km-deep chain of

three troughs between the South Shetland Island Arc and the AP. Ongoing rifting and subduction processes in the area cause ongoing volcanic and seismic activity (González-Casado et al. 2000), generally associated with biologically diverse habitats. The influence of waters from the Bellingshausen and Weddell Seas turns BS into a highly productive area (Lorenzo et al. 2002; Gonçalves-Araujo et al. 2015). Further offshore, in DP the continental slope continues beyond the shelf. The relatively flat shelf and the steeper slope are separated by the shelf break where the seafloor inclination increases abruptly. The continental slope is defined by steep, rapidly deepening bathymetry between the shelf and the deep sea (750–3000 m water depth). With regard to Antarctic marine ecosystem types defined by Treguer and Jacques (1992), BS can be attributed to the ‘Coastal and Continental Shelf Zone’ and the DP to the ‘Continental Shelf Edge and Slope’, consistent with respective bathymetry, ocean dynamics and water masses (Ducklow et al. 2007).

Cetacean survey

Aerial surveys for cetaceans were conducted with the helicopters (BO 105) on-board of *R/V Polarstern* between 25 January and 11 March 2013, using the ship as a platform of opportunity (compare Scheidat et al. 2011).

Fig. 1 Cruise track of *R/V Polarstern* expedition PS81 (black). The red lines represent all track lines covered by helicopter during the cetacean survey. Locations of all 50 stations which were sampled during the krill survey are indicated as yellow squares. Depth data from IBCSO (Arndt et al. 2013). (Color figure online)

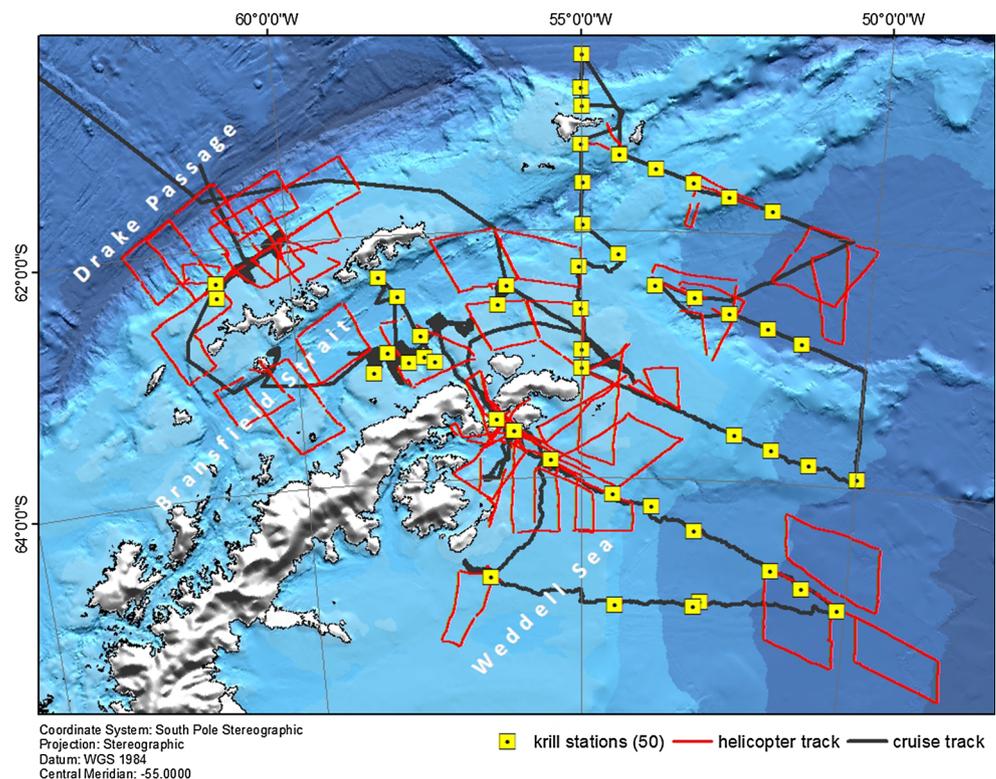
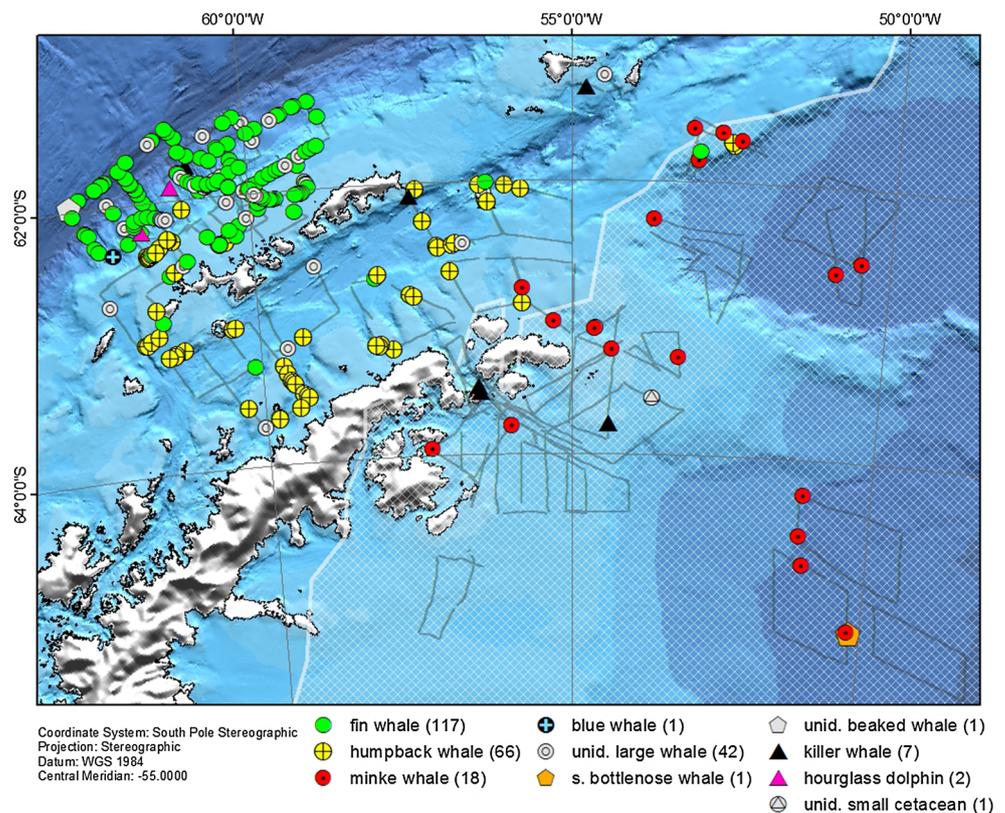


Fig. 2 Position of sightings of all cetacean groups made in observing mode ('on effort'). Each symbol represents a species as explained in the legend. The white shaded area depicts the area with at least 15 % ice coverage, with the white line representing the position of the edge of the 15 % marginal ice zone for 14 February 2013, i.e. the middle of the survey period. Tracks of the helicopter survey are indicated in light grey



Data collection followed line-transect distance sampling methodology (Buckland et al. 2001), yet surveys were planned in an *ad-hoc* manner rather than following a pre-designed sampling scheme. Weather conditions and ship's logistics permitting, track lines were designed around the current position of *R/V Polarstern*, aiming at achieving an adequate overall coverage of the survey area visited by the ship and applying basic principles of good survey design following Buckland et al. (2001) (e.g. random placement of starting point of transects, arbitrary orientation and placement of transects with respect to whale distribution). The basic design of each survey flight was a square of 4×40 nm transect lines, according to maximum endurance of the helicopters within the safety limits. Orientation of the first transect line was chosen randomly at a bearing between 0° and 90° in relation to the ship's track to either side. The following three transects were determined by rectangular angles. Furthermore, direction and placement of the squares were advised by the on-board meteorologists to ensure safe surveying and possible return to the ship at all times. Based on this advice, lengths of transects varied between 10 and 70 km. All covered track lines are shown in Fig. 1.

All survey flights were conducted at a constant altitude of 600 feet and a speed of 80–90 knots. Two observers

were positioned in the back of the helicopter and observed the area to the right and to the left side of the track line. As the helicopters were not equipped with bubble windows, the observers in the back were unable to observe the area directly underneath the helicopter, thus omitting approximately the closest 80 m to each side of the transect line, respectively. Therefore, a third observer was seated in the left front seat of the helicopter, which allowed a direct view onto the transect line through the front window of the helicopter. This way, the front observer covered the left part of the transect line not visible to the left observer in the back. Together, the left and front observers were able to provide full coverage of the left side of the transect line. Only the data from the completely surveyed left side of the helicopter were later considered for detection function modelling.

All data were entered directly into a computer running the AudioVOR software (Hiby and Lovell 1998), continuously storing GPS data obtained by a handheld GPS device (Garmin 72H) in intervals of 4 s. Data on environmental conditions (sea state, cloud cover, glare, ice coverage) were entered as assessed by the observers and sighting conditions rated by the observers as 'good', 'moderate', 'poor' or 'unacceptable'. All entries were continuously updated whenever any change therein occurred.

For each sighting of a cetacean, detailed information was recorded, including species, distance to transect (via declination angle) and group size. Inclinometers were used to measure the declination angle to each sighting; in addition, the bearing was recorded. The perpendicular distance of the sighting to the transect line was calculated post survey by trigonometry (based on the known flight altitude and the declination angle). This distance to the transect line is key input for detection function modelling and for the estimation of the effectively covered strip width (*esw*). If a sighting occurred and species or group size could not be determined immediately, the survey was halted (if overall flight endurance and weather conditions allowed) in order to approach the sighting for closer inspection (a procedure known as ‘closing mode’; Calambokidis and Barlow 2004; Strindberg and Buckland 2004). Once the required data were collected, the helicopter returned to the transect line and the survey was continued.

Krill survey

Zooplankton and krill investigations were carried out between 26 January and 2 March 2013. The survey period fell within the spawning season for Antarctic krill (Siegel and Loeb 1995). Along a transect design, 50 stations were sampled in BS, DP and WS (Fig. 1).

A standard RMT1 + 8 plankton net (Baker et al. 1973), an opening and closing net system in which two nets are combined in one framework, was used to collect krill samples from the upper 200 m of the water column. The mesh size of the larger 8 m² net and the smaller 1 m² net was 4.5 and 0.33 mm, respectively. This set-up served simultaneous sampling of larval and adult krill, as well as the epipelagic zooplankton components. The RMT was equipped with a time–depth recorder (TDR) to follow the track of the net during the double oblique tow. A calibrated flowmeter gave a measure of net speed during the haul as well as the total distance travelled. The flowmeter was mounted outside the net opening to avoid clogging which may reduce the efficiency. Total trawling time for the double oblique haul from 0–200–0 m was approximately 40 min (station list in Dorschel et al. 2015). The dependence of mouth angle to the vertical of net speed had been investigated for the RMT system (Pommeranz et al. 1982) to adjust the effective mouth opening of the net for the estimation of the volume of water filtered. The average filtered water volume of a standard RMT1 + 8 net tow was approximately 25,000 m³. Immediately after the tow, samples were sorted for Antarctic krill and other euphausiid species. These data were collected quantitatively from the RMT1 + 8, i.e. individual numbers of each species were counted. In cases when the sample size exceeded 1 L,

a representative subsample was taken with a Folsom plankton splitter and subsequently analysed.

Oceanographic data

Oceanographic data were collected with the ship’s CTD (Seabird 911+) between 26 January and 13 March 2013 at stations in BS, DP and WS. For details and station list, see Dorschel et al. (2015). The carousel connected to the CTD held 24 Niskin bottles of 12 L, and the accuracy of the sensors was 2 mK for temperature, 0.002 psu for salinity, 1 dbar for pressure and 1.34 $\mu\text{mol kg}^{-1}$ for oxygen concentration. For the purposes of this study, data on temperature, salinity and oxygen at 200 m depth were interpolated over a grid of 6.25 km spacing, in accordance with the resolution of the sea ice data also used for analyses (see below). CTD sample distribution in the study area did not allow interpolation throughout the entire study area, but left a gap in the western part of DP and to a lesser extent in the middle and east of BS.

Data analyses

Cetaceans

Distance sampling methods were used to estimate the probability of detection as a function of distance from the transect line (Buckland et al. 2001). Species-specific detection functions were modelled for humpback whales (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*), as only these species provided the number of detections required ($n > 40$) for a robust detection function (Buckland et al. 2001). Sighting data were analysed using the software package ‘Distance’ (Miller 2015) in R version 3.0.1 (R Core Team 2015). A multiple covariate distance sampling (MCDS) framework was used to estimate the detection function (Marques and Buckland 2004), assuming that detection on the track line is 100 %, i.e. $g(0) = 1$. Covariates tested in the MCDS analyses included group size and sighting conditions, sea state and local sea ice concentration as judged by the observers. Visually judged ice concentration was included at the detection function modelling stage of the analyses to test whether increasing complexity in the visual field may decrease the probability that a sighting is made. Satellite data-based ice cover (*AMSR_ice*) was later used at the modelling stage to test for ecological relevance in cetacean occurrence. Perpendicular distances were truncated to exclude sightings beyond 1300 m for humpback whales and 1000 m for fin whales, respectively. Only data from the left side (collected by the left and front observers) were used for detection function modelling, since, as

mentioned above, the right side of the track line could not be fully covered by observers. Furthermore, only sightings from ‘good’ or ‘moderate’ sighting conditions were included for fitting the detection function. Half-normal and hazard-rate keys using no adjustment terms of the detection function were tested, and selection of the best model was based on Akaike’s information criterion (AIC; Akaike 1974).

Each data point of the cetacean survey was annotated with water depth (from IBCSO, Arndt et al. 2013) and derived bathymetric slope and local ice concentration (from daily 6.25-km—resolution satellite remote sensing data; Daily AMSR2 Sea Ice Maps, <http://www.meer.eisportal.de>; Spreen et al. 2008).

A density surface modelling approach was used to produce predictions of density and distribution of humpback and fin whales related to environmental covariates. Aerial survey data were aggregated into 241 segments with an average length of 31.75 km (minimum: 14.90 km, maximum: 62.39 km). We used the detection functions obtained in the previous step to estimate the effective strip widths (*esw*) of each segment, thus calculating the effectively covered area per segment. We then used the ‘dsm’ package (Miller et al. 2014) for R (R Core Team 2015), to test negative binomial density surface models (dsm) of smooths of *x* and *y* (projected longitude and latitude values, respectively) interactions, satellite data-based ice cover (*AMSR_ice*), water depth (*depth_m*), bathymetric slope (*slope*) and combinations of these (using the effectively covered area as offset) against a null model. Model selection was based on their unbiased risk estimator score (*UBRE*, see Craven and Wahba 1979) and deviance explained (*dev.exp*). We applied a conversion factor of the density estimates of 0.5, since only half of the effective strip width (*esw*) was actually observed and accounted for in the modelling of the detection function (see above). Predictions of densities of humpback and fin whales were conducted over a regular grid (6.25 × 6.25 km, ~40 km² cell area).

Krill

In order to model krill distribution for the whole survey area, water depth and local ice cover were assigned to each krill station in the same manner as for the cetacean survey data. In addition, we assigned daily satellite chlorophyll-*a* concentrations (from merged OC-CCI Chl-*a* data; ESACCI-OC-L3S product, ~4 km, version 2, <http://www.oceancolour.org>; OC-CCI 2015) to a 10-km buffer around each krill station. As the daily coverage of chlorophyll-*a* was not always available for each station, we extracted daily values for a time period of 3 days before and after the actual krill station deployment in order to increase the

number of available chlorophyll-*a* measurements for each station. We then calculated the average, the standard deviation and the linear trend of chlorophyll-*a* concentration for the resulting time span of 7 days for each of the 50 stations. As additional input, we collated oceanographic data (temperature, oxygen concentration, salinity, at 200 m depth, respectively) from the oceanographic survey using the same 10-km buffer around each krill station. We then produced a model-based estimate of *E. superba*, *E. crystallorophias* and *T. macrura* biomass for our study area using a generalised additive modelling approach. Using the gam function of the ‘mgcv’ package (Wood 2011) for R (R Core Team 2015), we tested negative binomial biomass models of smooths of *x* and *y* interactions (*x,y*), temperature at 200 m depth (*temp200*), salinity at 200 m depth (*sal200*), oxygen at 200 m depth (*oxy200*), satellite data based ice cover (*AMSR_ice*), water depth (*depth_m*) and combinations of these against a null model. Due to the small sample size ($n \leq 50$), model selection was based on the restricted maximum likelihood score (REML; Wood 2011) and deviance explained (*dev.exp*). Predictions of biomass of *E. superba*, *E. crystallorophias* and *T. macrura* were conducted over a grid of 6.25 × 6.25 km cell size (~40 km² cell area).

Comparison of predicted krill and cetacean patterns

We produced plots of predicted humpback and fin whale densities, respectively, against the predicted biomass of all three krill species in order to compare distribution patterns.

Results

Cetacean data

Survey results

During 22 days with feasible weather conditions, 40 survey flights were accomplished, covering 7633 km on effort (i.e. in observing mode). Strong winds, high sea states, fog or low cloud cover prevented flights on the remaining days, often for several days in a row. This left gaps in our area coverage, in particular of some parts of WS (Figs. 1, 2). A total of 256 cetacean sightings comprising 640 individuals were recorded, and seven cetacean species were identified (Table 1; Fig. 2). Fin whales (117 sightings, 337 individuals) and humpback whales (66 sightings, 127 individuals) made up the majority of sightings and were the only species providing enough sightings for further distance sampling analyses. All humpback and fin whales were sighted west of the AP in BS and DP. In BS, humpback whales accounted for most of the sightings, while in DP, fin whales

Table 1 Numbers of group sightings and sighted individuals per species for the whole survey

Species	# Sightings	# Individuals	Group size		
			Mean	Min	Max
Humpback whale (<i>Megaptera novaeangliae</i>)	66	127	1.92	1	6
Fin whale (<i>Balaenoptera physalus</i>)	117	337	2.88	1	60
Antarctic minke whale (<i>Balaenoptera bonaerensis</i>)	18	33	1.83	1	7
Blue whale (<i>Balaenoptera musculus</i>)	1	1	1.00	1	1
Killer whale (<i>Orcinus orca</i>)	7	74	10.57	3	21
Hourglass dolphin (<i>Lagenorhynchus cruciger</i>)	2	9	4.50	4	5
Southern bottlenose whale (<i>Hyperoodon planifrons</i>)	1	2	2.00	2	2
Unidentified beaked whale	1	3	3.00	3	3
Unidentified baleen whale	42	58	1.38	1	3
Unidentified small cetacean	1	1	1.00	1	1
Total	256	640	1.92	1	6

predominated (Fig. 2). Both species were observed feeding. For humpback whales, bubble net feeding was observed on several occasions (Fig. 3). Fin whales in DP were observed forming large groups of up to 60 animals feeding (Fig. 4).

With 18 sightings and 33 individuals, Antarctic minke whales (*Balaenoptera bonaerensis*) were the third most

frequently sighted species, however not providing sufficient sightings for robust detection function modelling. All Antarctic minke whales were sighted in WS, in waters with higher ice concentration compared with the west side of the AP. Apart from minke whales, only a few sightings of killer whales (*Orcinus orca*) and one sighting of Southern bottlenose whales (*Hyperoodon planifrons*) were recorded



Fig. 3 Feeding humpback whales observed in the Bransfield Strait. *Upper left*: bubble curtain produced by humpback whales to aggregate prey organisms; *upper right*: four humpback whales diving

up, lunge feeding, *lower left and right*: humpback whale surface feeding, engulfing prey-laden water. Photographs: Helena Herr

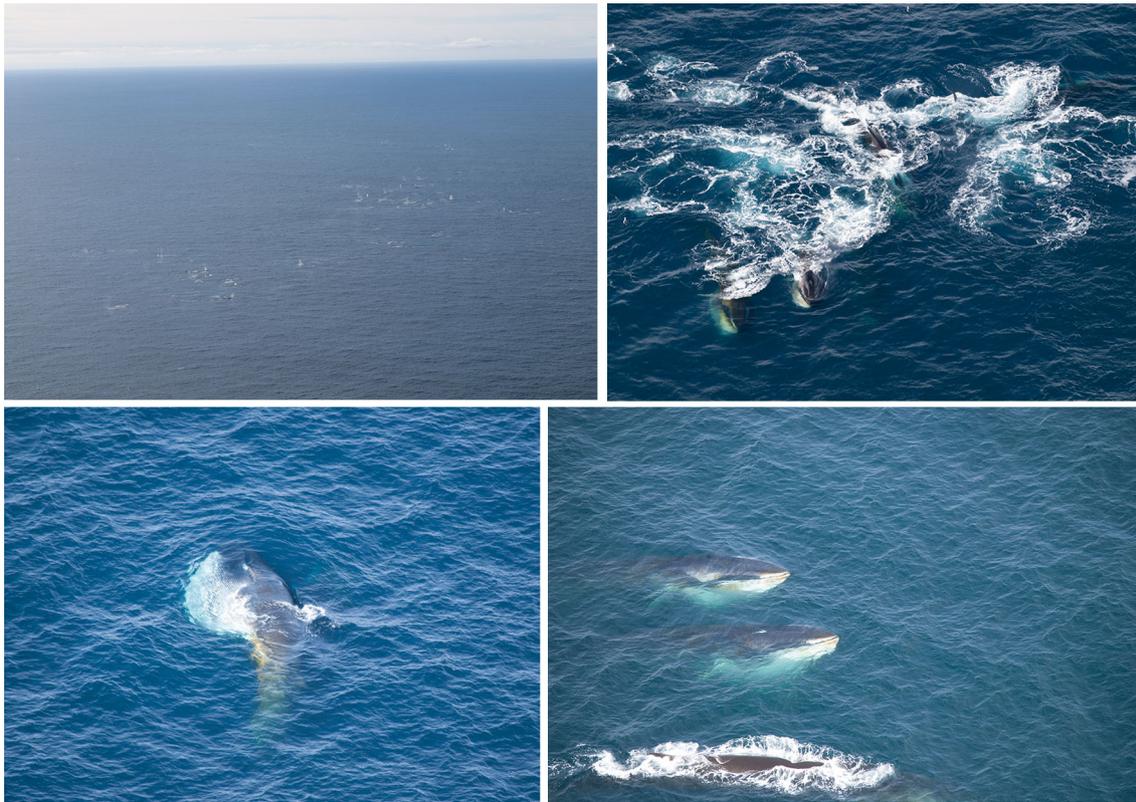


Fig. 4 Feeding fin whales observed in the Drake Passage. *Upper left*: overview of the aggregation of 60 fin whales, with a calm sea surface sprinkled with whale blows, *upper right*, close-up of part of the feeding aggregation, showing three fin whales surface feeding; *lower*

left: fin whale with stretched buccal cavity filled with prey-laden water, *lower right*: three fin whales diving up with stretched buccal cavities in a lunge feeding event. Photographs: Helena Herr (*upper 2* pictures) and Carsten Rocholl (*lower 2* pictures)

east of the AP in WS. WS was covered by ice throughout the survey period with an unusual northerly extension of the sea ice zone for the time of the year (NASA 2013).

Detection functions

Detection functions were based on 47 humpback and 80 fin whale sightings. The best detection function model for humpback whales used a half-normal key function without covariates and right truncation of data at 1300 m. For fin whales, the inclusion of subjective sighting conditions (a factor variable taking 2 levels ‘good’ and ‘moderate’) and a right truncation at 1000 m yielded the best model (see Fig. 5).

Density surface models

A summary of all tested models for humpback and fin whales is given in Table 2. After visual inspection of humpback whale models 2 and 4 (both incorporating *AMSR_ice* as covariate), we decided to exclude these models due to large standard error bands in response to *AMSR_ice* that included 0 throughout the covariate range

(Online Resource 1). Since all humpback and fin whale sightings occurred in ice-free regions and areas for prediction were largely ice free, the slight improvement in model fit with ice coverage (*AMSR_ice*) as covariate over water depth (*depth_m*) is a redundant feature that only emphasises the absence of both humpback and fin whales from ice covered areas in the east of the AP. Water depth as a covariate performed almost equally as good and was thus preferred over *AMSR_ice* in all cases. For humpback whales, the chosen model included parametric smooths of x and y interactions and a smooth of water depth, explaining 83.2 % of deviance (for model plot see Online Resource 2). The model with the lowest *UBRE* score and highest deviance explained (85.3 %) for fin whales also included parametric smooths of x and y interactions and a smooth of water depth (Online Resource 3) (Table 2).

Distribution and abundance

Using these models, we produced predicted distribution maps for fin and humpback whale densities in BS and DP (Figs. 6, 7). For WS, effort and area coverage were not sufficient to justify extrapolation of the modelling results to

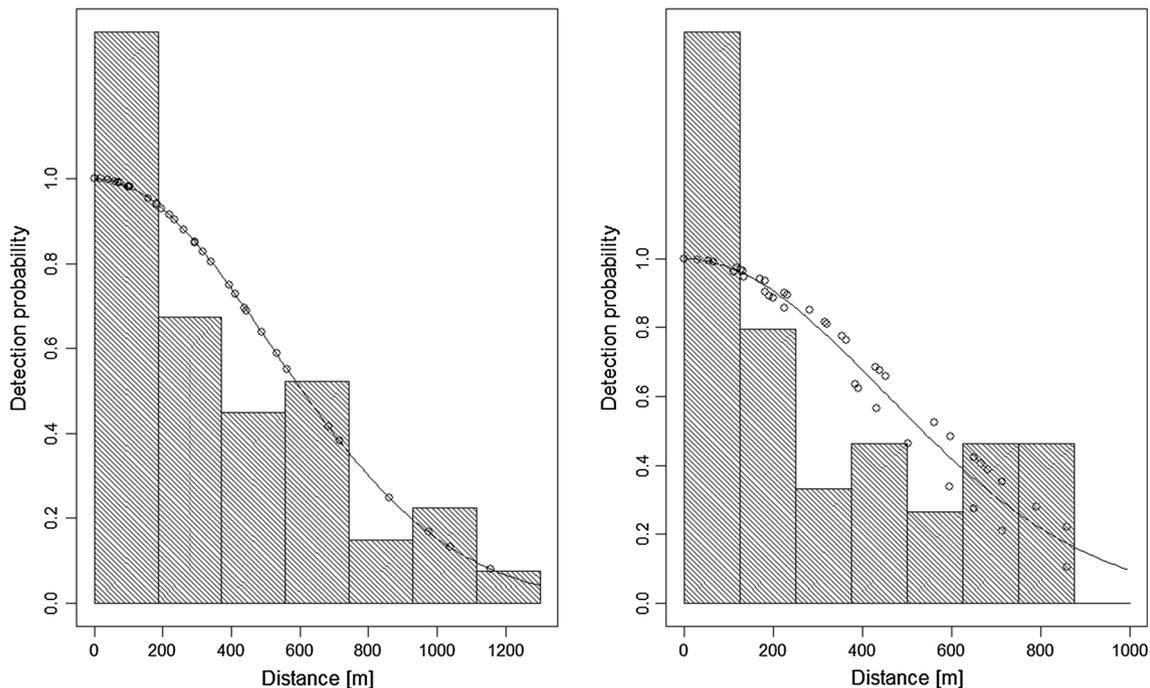


Fig. 5 Detection functions for humpback whales (*left graphic*) and fin whales (*right graphic*) based on 47 and 80 sightings, respectively. The underlying data sets were right truncated at 1300 m for humpback whales and at 1000 m for fin whales. No covariates were

used in the humpback whale model, while a model using subjective sighting conditions ('good' and 'moderate') as a covariate yielded the best result for fin whales

this area, especially since neither humpback nor fin whale sightings were recorded in WS. Estimated abundances for both species in BS and DP are given in Table 3. Highest densities (0.056 ind/km²; 95 % CI 0.017–0.094) for humpback whales were predicted in BS with an estimate of 3024 (95 % CI 944–5105) individuals. High fin whale densities were predicted in DP (0.114 ind/km²; 95 % CI 0.053–0.181) with a total of 4898 (95 % CI 2221–7575) predicted individuals.

Krill survey

Five krill (euphausiid) species were caught during the survey with *E. superba*, *E. crystallophias* and *T. macrura* being the predominant species (Table 4). *Euphausia triacantha* and *Euphausia frigida* were only found north of the South Shetland/Elephant Islands in small numbers. Antarctic krill *E. superba* was caught on 48 of the 50 RMT stations with a total of more than 136,000 individuals. Overall mean density of Antarctic krill for the entire survey area was 109 ind/1000 m³. The high standard deviation (SD = 204) showed a highly skewed distribution of krill abundance; 41 % of all krill were caught in just three hauls on the southern shelf of BS. A geographical difference was observed for the abundance of krill between the outflow areas of the WAP and WS.

E. crystallophias was only found in relatively low numbers in the southern BS and in greater densities on the shelf of the western WS. *T. macrura* was concentrated more in offshore areas to the north in the DP, although it was present at most stations in the survey.

Krill modelling

Due to the small sample size ($n = 50$ krill stations), we restricted the complexity of the models to two variables and no interactions (except for the spatial interaction). A negative binomial model including a smooth of the spatial interaction (x , y) and water temperature at 200 m depth (*temp200*) yielded the best model for *E. superba*, explaining 32.6 % of deviance between the 48 stations, for which both measures (*temp200* and spatial components x and y) were available (Fig. 8). The best model for *E. crystallophias* was a smooth of water temperature at 200 m depth (*temp200*) and water depth (*depth_m*), explaining 85.1 % of deviance between the 48 stations, for which both parameters were available (Fig. 9). For *T. macrura*, a smooth of the spatial interaction (x , y) was chosen as the best model, explaining 52.5 % of deviance between the 50 stations (Fig. 10; Table 5). Model plots are given in Online Resources 4–6.

Table 2 All tested models for humpback and fin whales

Model	Formula	UBRE	Dev.exp
<i>Humpback whale models</i>			
Model 0	Nhat \sim 1	1.6798	0.000
Model 1	Nhat \sim s(x, y)	-0.2397	0.812
Model 2	Nhat \sim s(x, y) + s(AMSR_ice)	-0.3179	0.854
Model 3	Nhat \sim s(x, y) + s(depth_m)	-0.2772	0.832
Model 4	Nhat \sim s(x, y) + s(AMSR_ice) + s(depth_m)	-0.3417	0.873
Model 5	Nhat \sim s(AMSR_ice)	0.5068	0.455
Model 6	Nhat \sim s(depth_m)	0.8369	0.338
Model 7	Nhat \sim s(AMSR_ice) + s(depth_m)	0.1845	0.598
Model 8	Nhat \sim s(slope)	2.0031	0.105
Model 9	Nhat \sim s(x,y) + s(slope)	0.4251	0.761
<i>Fin whale models</i>			
Model 0	Nhat \sim 1	1.8636	0.000
Model 1	Nhat \sim s(x, y)	-0.4364	0.844
Model 2	Nhat \sim s(x, y) + s(AMSR_ice)	-0.4253	0.843
Model 3	Nhat \sim s(x, y) + s(depth_m)	-0.4333	0.853
Model 4	Nhat \sim s(x, y) + s(AMSR_ice) + s(depth_m)	-0.4227	0.852
Model 5	Nhat \sim s(AMSR_ice)	0.3794	0.524
Model 6	Nhat \sim s(depth_m)	1.5047	0.150
Model 7	Nhat \sim s(AMSR_ice) + s(depth_m)	0.1039	0.641
Model 8	Nhat \sim s(slope)	1.8947	0.149
Model 9	Nhat \sim s(x,y) + s(slope)	0.2589	0.752

Best models are given in bold; formula denotes the actual formula passed to the dsm; UBRE is a metric scoring the fit of a model (the lower, the better); *dev.exp* is a measure of how much of the observed values are predicted by the model (the higher the value, the more of variation is explained)

Humpback whale model 3 was chosen over models 2 and 4 due to large standard error bands in response to AMSR_ice that included 0 throughout the covariate range

Comparison of predicted patterns of cetacean and krill abundance

Humpback whales seemed to be associated with medium biomass of *E. superba* (Fig. 11), while fin whales were predicted in areas with low *E. superba* biomass (Fig. 12). Comparison of cetacean densities with *E. crystallorophias* biomass distribution did not indicate any relationship. Fin whales occurred in areas for which a high biomass of *T. macrura* was predicted. The observed relationships were also reflected in the correlation of whale densities and total krill biomass.

Discussion

This study provides model-based abundance estimates for humpback whales and fin whales in the WAP. These are the first abundance estimates for both species derived from aerial surveys in the Southern Ocean. These abundance estimates are minimum estimates. They were not corrected for availability, i.e. detection on the track line was assumed

to be $g(0) = 1$. It is unlikely, however, that all animals on the track line are detected during any survey and $g(0)$ is very likely to be <1 (Marsh and Sinclair 1989). Minimal abundances, however, provide at least a minimum estimate of the number of whales present in the area at the time of the survey (January–March 2013).

For fin whales, this is the first abundance estimate in the WAP. Little is known with regard to fin whale abundance and distribution, habitat use and seasonal migration in the Southern Ocean. Fin whales presumably perform seasonal migrations to the Southern Ocean in order to feed on krill, but it is unknown where fin whales migrate from and where their breeding grounds are located (Leaper and Miller 2011). Fin whales are considered as an offshore species. They are assumed to be extensively distributed in latitudes between 40°S and 60°S (Reilly et al. 2013). These were not surveyed during the IDCR/SOWER assessments, which current circumpolar abundance estimates are based on (Branch and Butterworth 2001). For IWC management area I, comprising WAP, only 3, 8 and 3 sightings of fin whales were recorded in the austral summers of 1982/1983, 1989/1990 and 1993/1994, respectively (Branch and

Fig. 6 Predicted humpback whale density and positions of actual humpback whale (*Megaptera novaeangliae*) sightings (×) during the aerial survey. The prediction area is subdivided into two strata: Drake Passage (DP) and Bransfield Strait (BS), for which abundances were predicted separately

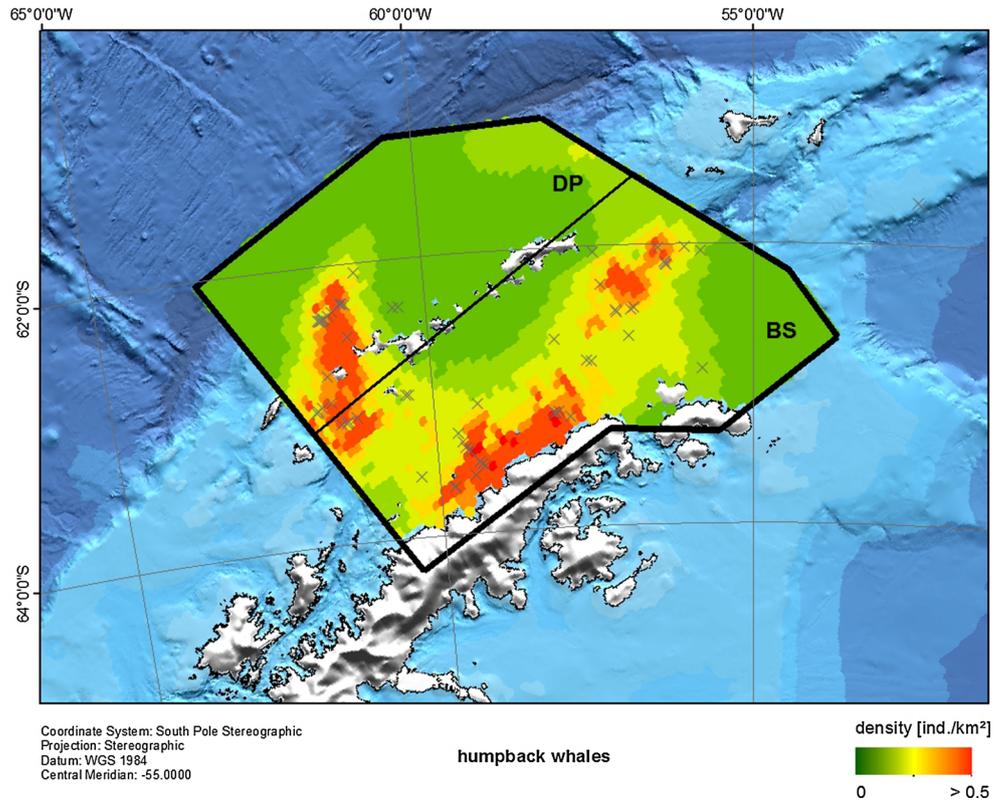


Fig. 7 Predicted fin whale (*Balaenopter physalus*) density and positions of actual fin whale sightings (×). The prediction area is subdivided into two strata: DP and BS, for which abundances were predicted separately

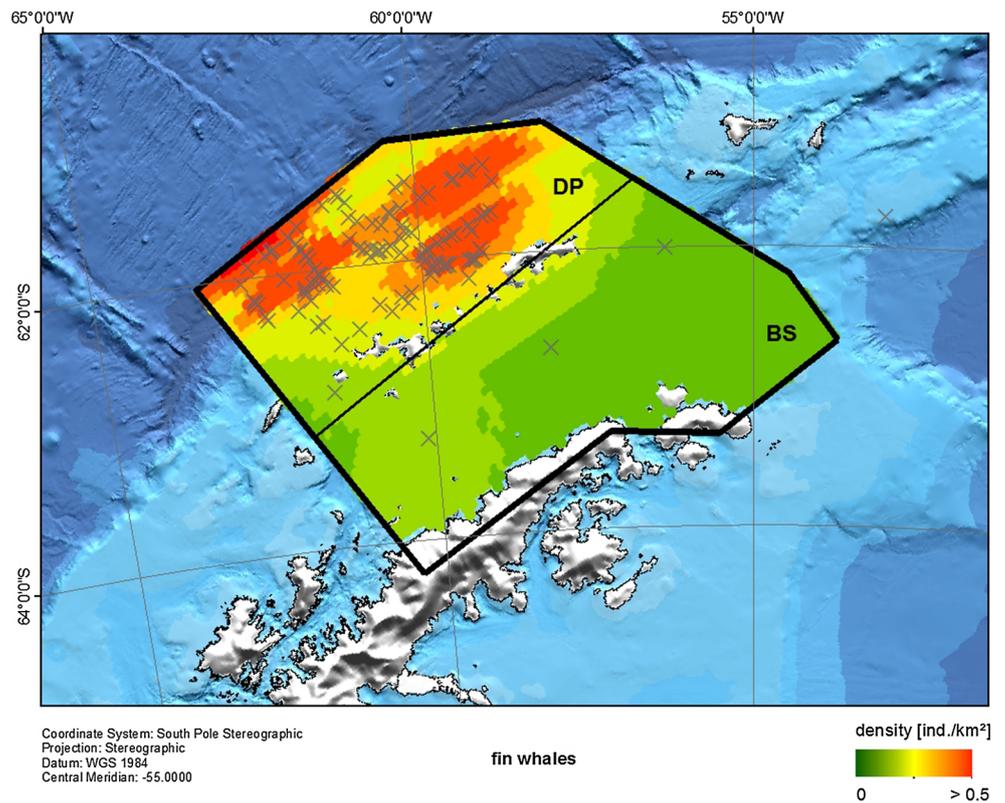


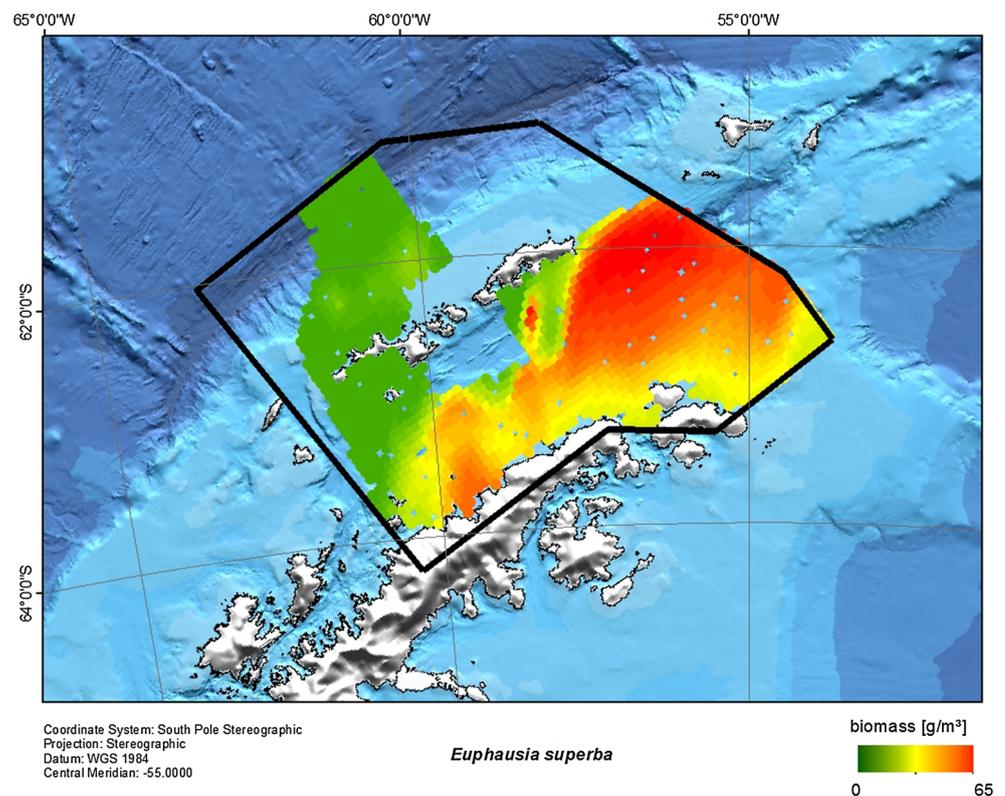
Table 3 Predicted densities and abundance for humpback (*Megaptera novaeanglia*) and fin whales (*Balaenoptera physalus*) in DP and BS during the time of the survey

Species	Stratum	Density (ind/km ²)	95 % CI _{density}	Abundance (N)	95 % CI _{abundance}
Humpback whales	DP	0.022	0.006–0.038	934	263–1605
	BS	0.056	0.017–0.094	3024	944–5105
Fin whales	DP	0.117	0.053–0.181	4898	2221–7575
	BS	0.002	0.000–0.004	94	0–210

Table 4 Biomass of *Euphausia superba*, *Euphausia crystallorophias* and *Thysanoessa macrura* from krill catches along all 50 stations sampled during the krill survey

	<i>E. superba</i>	<i>E. crystallorophias</i>	<i>T. macrura</i>	Total biomass
Biomass (g/m ²)	327.58	6.40	311.82	645.80
Share of total biomass (%)	50.7	0.01	48.3	100

Fig. 8 Plot of predicted biomass of *Euphausia superba*. Main effects were a smooth of x and y and temperature at 200 m depth. Gaps in the prediction are a result of lack of information on temperature at 200 m depth from the oceanographic data set in these areas



Butterworth 2001). In 2006/2007, Scheidat et al. (2011) recorded 10 fin whale sightings in the WAP area. Large aggregations of fin whales in the WAP area with notably large group sizes have only recently been reported (Burkhard and Lanfredi 2012 (unpublished data), Santora et al. 2014), tentatively suggesting the emergence of a new hot spot area for fin whales in late austral summer. Our results provide the first estimate of abundance for fin whales aggregating in this area. Based on IDCR/SOWER data from 1991 to 2004, circumpolar fin whale abundance south of 60°S was estimated at 5445 (95 % CI 2000–14,500)

individuals (Leaper and Miller 2011). For the total area South of 30°S, 15,178 fin whales were estimated in 1983 (Reilly et al. 2013). Trends and growth rates of the fin whale population as well as the current population status, however, are unknown. The IUCN continues listing fin whales as ‘endangered’ (Reilly et al. 2013). Our estimated abundance of 4898 (95 % CI 2221–7575) fin whales in DP suggests that a substantial number of Southern Hemisphere fin whales aggregate in this area north of the South Shetland Islands in late summer to feed. Whether these newly observed aggregations are indicative of rising fin whale

Fig. 9 Plot of predicted biomass of *Euphausia crystallorophias*. Main effects were temperature at 200 m depth and water depth (note that biomass scale differs from that of the other two depicted krill distribution maps). Gaps in the prediction are a result of lack of information on temperature at 200 m depth from the oceanographic data set in these areas

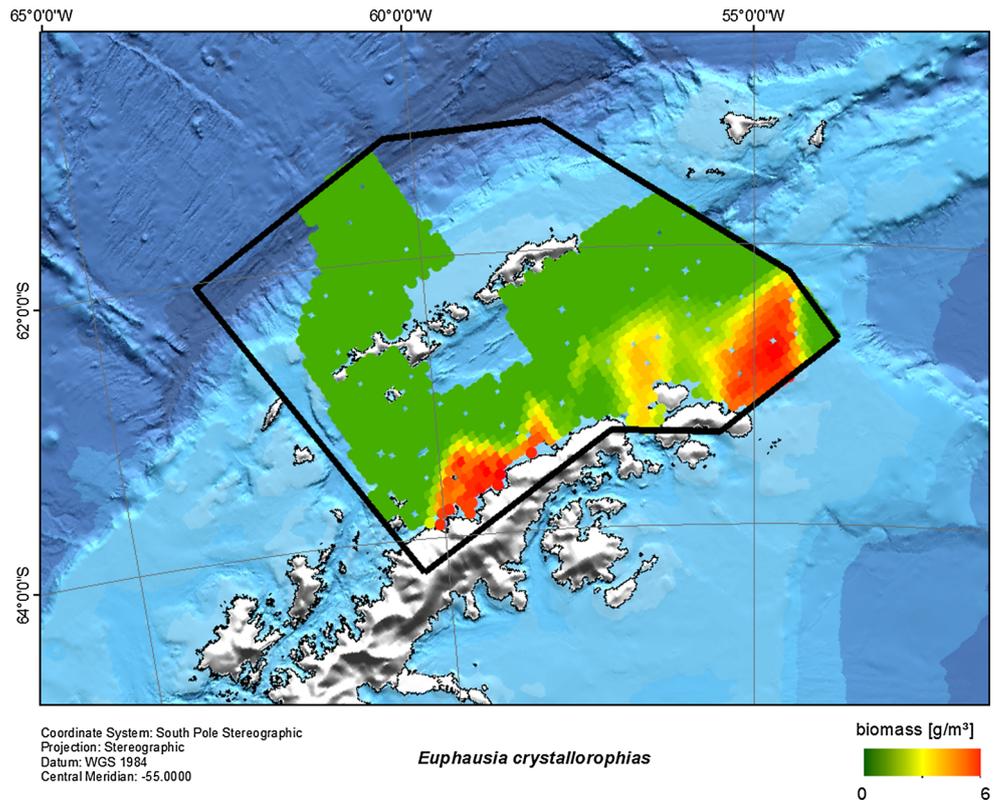


Fig. 10 Plot of predicted biomass of *Thysanoessa macrura* at the time of the survey. Main effect for the prediction was a smooth of x and y

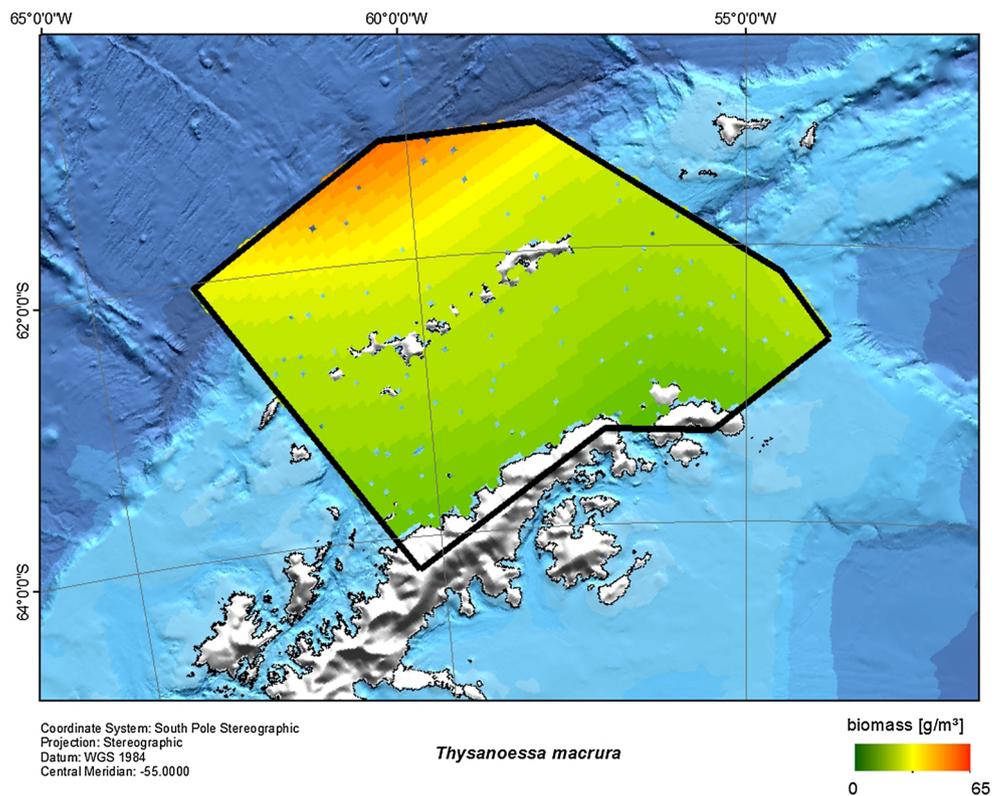


Table 5 Overview of models tested for prediction of krill distribution in the survey area; formula gives the model call for the generalised additive model; *REML* gives the restricted maximum likelihood score of each model (lower scores indicate better fit, but as a relative measure are not comparable between different data sets, i.e. different

species models can only be compared between models for the same species); *dev.exp* is a measure of how much of the observed values are predicted by the model (the higher the value, the more of variation is explained)

Species	Model	Formula	<i>REML</i>	<i>Dev.exp</i> (%)	Sample size
<i>E. superba</i>	s_0	superba ~ 1	126.24	0.00	50
	s_1	superba ~ s(x,y) + s(temp200)	110.09	32.61	48
	s_2	superba ~ s(x,y)	123.13	24.59	50
	s_3	superba ~ s(temp200)	114.49	17.75	48
	s_4	superba ~ s(AMSR_ice)	125.29	1.31	49
	s_5	superba ~ s(sal200)	115.74	12.00	48
	s_6	superba ~ s(oxy200)	115.01	13.8	48
<i>E. crystallorophias</i>	c_0	crystall ~ 1	18.81	0.00	50
	c_1	crystall ~ s(temp200) + s(depth_m)	4.79	85.14	48
	c_2	crystall ~ s(temp200)	8.39	70.67	48
	c_3	crystall ~ s(depth_m)	13.33	46.33	50
	c_4	crystall ~ s(AMSR_ice)	12.54	33.93	49
	c_5	crystall ~ s(sal200)	17.73	2.58	48
	c_6	crystall ~ s(oxy200)	12.09	57.60	48
<i>T. macrura</i>	t_0	tmac ~ 1	143.00	0.00	50
	t_1	tmac ~ s(x,y)	134.34	52.47	50
	t_2	tmac ~ s(AMSR_ice)	138.02	14.95	49
	t_3	tmac ~ (temp200)	132.20	14.03	48
	t_4	tmac ~ s(depth_m)	141.76	20.80	50
	t_5	tmac ~ s(sal200)	134.29	8.08	48
	t_6	tmac ~ s(oxy200)	132.61	19.90	48

The best models, given in bold, were chosen based on *REML* score and explained deviance

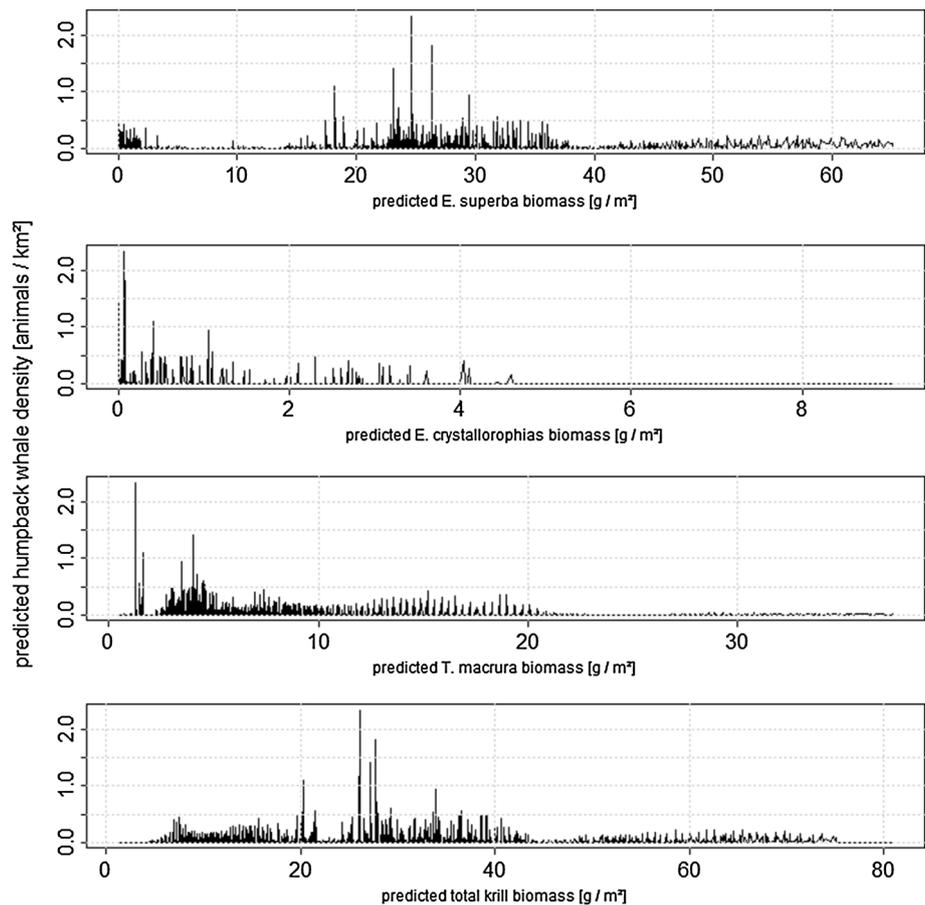
numbers in the Southern Hemisphere needs to be the matter of further investigation. The latest estimates of fin whale abundance are at least 13 years out of date (Leaper and Miller 2011), and information on the recovery status is lacking. Our results for fin whale distribution and abundance contribute important information about population numbers and habitat use of this endangered species. The abundance estimate may serve for future comparison and as base line data for this area. Plus, it suggests that a more detailed assessment of fin whale abundance and recovery status of the population should be completed.

Comparably more knowledge exists on humpback whales (Leaper and Miller 2011). They are the best studied baleanopterids in the Southern Ocean (Reilly et al. 2008; Leaper and Miller 2011). Humpback whales exhibit a coastal distribution with both their feeding and breeding grounds mainly located in continental shelf waters (Clapham 2002). They are thus more accessible for research and observation than fin whales. Seven major humpback whale breeding stocks (A–G) migrating to Antarctic waters in the austral summer are currently recognised (IWC 1998; Reilly et al. 2008). Their nearshore breeding areas are located in the Atlantic, Indian Ocean and Pacific. Their feeding areas

in the Southern Ocean cannot be delineated with much precision (Reilly et al. 2008), but humpback whales feeding along the WAP likely belong to breeding stock G (Dalla Rosa et al. 2008; Zerbini et al. 2011; IWC 2015), wintering off the west coast of Central and South America (Stevick et al. 2004; Dalla Rosa et al. 2008; Secchi et al. 2011). BS is considered an important feeding ground for humpback whales of breeding stock G (Dalla Rosa et al. 2008), which is one of the less studied of the seven breeding stocks (Secchi et al. 2011). Based on data from a shipboard survey in January/February 2006, Secchi et al. (2011) reported densities of ~ 0.10 ind/km² (95 % CI 0.07–0.13)¹ in BS. Our estimated abundance for humpback whales in BS of 0.06 (95 % CI 0.02–0.1) is lower; however, the associated confidence intervals signify that the two estimates are not significantly different from each other. Aerial surveys are known to yield lower encounter rates compared to ship surveys. This is due to the much higher survey speed of the observation platform, which shortens the time window available to detect a whale and

¹ In the original publication given as 0.18 individuals/nm² (95 % CI 0.14–0.24).

Fig. 11 Predicted humpback whale (*Megaptera novaeangliae*) densities versus predicted biomass of Antarctic krill (*Euphausia superba*), Ice krill (*Euphausia crystallophias*), *Thysanoessa macrura* and total krill biomass (from top to bottom)

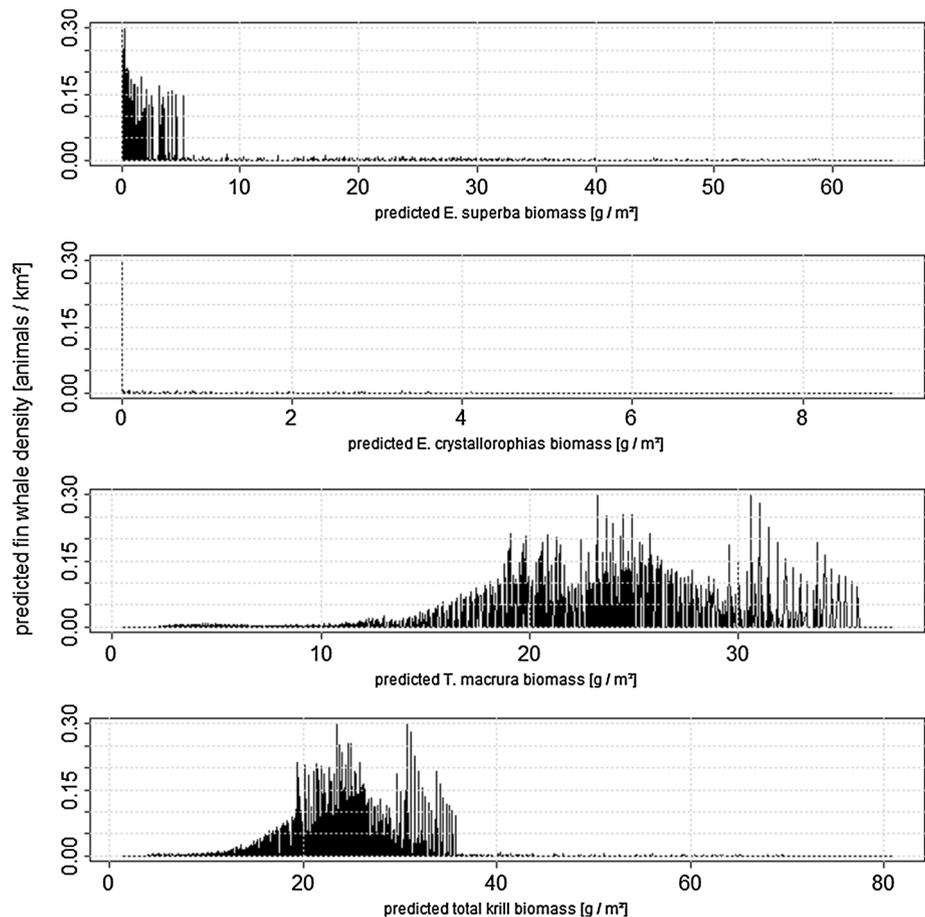


hence more whales on the track line are missed. Moreover, humpback whales have been shown to be highly mobile around the WAP and to move in and out of the BS (Curtice et al. 2015). Therefore, variation in abundance at any observed time can be expected.

The most recent abundance estimate for breeding stock G is 9687 (8520–10,202) individuals (IWC 2015). Our estimate of 3024 (95 % CI 944–5105) humpback whales in BS supports BS as an important feeding ground for breeding stock G, as previously suggested by Dalla Rosa et al. (2008). BS might at times hold a large proportion of individuals of breeding stock G. Therefore, special attention needs to be paid with regard to increasing krill fisheries and tourism activities in this area which seems to be of great importance for the sustenance of the stock. Humpback whales are the first baleen whale species nearing pre-exploitation numbers. Breeding stock G is assumed to have recovered to 93 % (95 % CI 74–98 %) of its pre-exploitation level (IWC 2015). Preserving important feeding grounds is central for the species' full recovery and conservation of these whales in the Southern Ocean.

The spatial predictions for humpback and fin whale densities reveal distinct species-specific distribution patterns at the time of the survey (January–March 2013). Fin whale densities are highest in DP, while humpback whales predominate in BS. The predictions reflect the positions of the recorded sightings very well. These results indicate at least temporal habitat segregation between humpback and fin with no overlap in their distribution patterns. This provides an indication of a horizontal niche separation between the two species. As suggested by Friedlaender et al. (2009) for Antarctic minke whales and humpback whales, sympatric whale species feeding on krill may have evolved some form of resource partitioning mechanism to avoid interspecific competition for prey. In the case of Antarctic minke whales and humpback whales, both species prefer coastal habitats on the shelf of the AP region (Friedlaender et al. 2009). They appear to feed on krill in different depth ranges in the water column, indicating vertical niche segregation (Friedlaender et al. 2006, 2009, 2011). The results of our study suggest a horizontal niche separation between humpback and fin whales, with

Fig. 12 Predicted fin whale (*Balaenoptera physalus*) densities versus predicted biomass of Antarctic krill (*E. superba*), Ice krill (*E. crystallophias*), *Thysanoessa macrura* and total krill biomass (from top to bottom)



humpback whales preferring the coastal parts of BS and fin whales residing in habitats around the shelf edge in DP.

The predicted distributions of different krill species at the time of the survey (Figs. 8, 9, 10) reflect patterns that are in line with the general theory about krill distribution in the WAP (Daly and Macaulay 1988; Wiebe et al. 2011). *E. superba* is the most widely distributed and dominant species on the shelf, *E. crystallophias* occurs sporadically in smaller aggregations near the coast, and *T. macrura* occurs predominantly beyond the shelf edge. Despite a comparatively small number of samples (i.e. 50 krill stations), we were able to produce reasonable predictions of the distribution of krill at the time of the survey. The available sample size, however, restricted our choice of model terms to two parameters per model at most. While we were unable to explore any interaction between oceanographic parameters, the selected models produced robust results with few covariates. It is recommended that further studies be undertaken to increase the number of krill samples available to enable a more thorough modelling of krill distribution and abundance in the area.

Krill at the WAP undergo seasonal variations in distribution and abundance (Siegel 1988; Lascara et al. 1999) which is influencing the distribution and abundance of the predators preying on them (Curtice et al. 2015). Several studies suggest that whales might be able to identify physical features of the ocean that may lead them towards enriched prey abundances (Murase et al. 2002; Friedlaender et al. 2006, 2009; Santora et al. 2014). For example, recurrent and tidally predictable availability of krill occurrence has been shown to make areas highly attractive for whales (Cotté and Simard 2005). There are reoccurring hot spots for krill predator occurrence independent of changes in both the physical environment and prey distribution (Friedlaender et al. 2011; Santora and Veit 2013). Probably, thresholds of minimum krill density rather than interactions along gradients are more likely to describe the relationship between whales and their prey. For example, Piatt and Methven (1992) described threshold feeding behaviour for baleen whales in relation to densities of fish swarms. Friedlaender et al. (2006) found a persistent, strong, positive relationship between increasing

zooplankton volume (based on backscatter data) and relative whale abundance beyond a minimum threshold value. It is possible that whales recorded during our survey were feeding on small, locally restricted krill patches that were not detected by the net sampling survey for krill. Moreover, high densities of whales in an area may have an impact on local krill density due to the feeding activity of the whales (Santora et al. 2010).

Both cetacean species were observed feeding on numerous occasions during the survey (Figs. 3, 4). While we cannot discern what the animals were feeding on, fin whales were most abundant in areas of highest *T. macrura* biomass. Therefore, it is likely that fin whales were mainly feeding on *T. macrura*. Nemoto and Nasu (1958) described *T. macrura* as a prey species of fin whales. Furthermore, *T. macrura* is known to form large aggregations (Daly and Macaulay 1988) with local densities comparable to *E. superba*, making *T. macrura* attractive for exploitation by bulk feeding whales (Goldbogen et al. 2013). Fin whales are known to have a broad diet (Reilly et al. 2013), opportunistically feeding on aggregated prey species with a preference for areas with complex water circulation, such as in upwelling areas around continental shelf edges, within eddies and fronts (Johnston et al. 2005; Santora et al. 2014). Fin whale hot spots in DP have been described in association with aggregations of *E. superba* (Santora et al. 2010, 2014). Santora et al. (2010) suggested size-dependent *E. superba* predation by fin whales, with a preference for swarms of large mature *E. superba*. In summer, these predominantly occur around the shelf edge region north of the South Shetland Islands in DP, while smaller juvenile *E. superba* is found in more coastal areas (Siegel 1988; Siegel and Loeb 1995; Siegel et al. 2004). Our results indicate that fin whales were likely feeding on aggregated *T. macrura* rather than *E. superba* at the time of the survey. These findings suggest that fin whales are less particular with regard to prey species and size but rather opportunistically feed on aggregating krill around the shelf edge. What role *T. macrura* plays as prey for fin whales in the Southern Ocean in comparison with *E. superba*, and if *T. macrura* is regularly preyed on by aggregating fin whales around the shelf edge of the South Shetland Islands should be the subject of further investigation. Recently, several non-lethal techniques including genetic methods provide means to determine prey species and composition of baleen whales (Witteveen et al. 2011; Ryan et al. 2013). Together with additional concurrent krill and dedicated cetacean surveys in the area, important information on the role of *T. macrura* and fin whales in the Southern Ocean ecosystem could be obtained in the future.

Humpback whales show a less clear relationship to either of the sampled krill species. The model predictions suggest that humpback whales occur in all areas regardless

of how large the predicted krill biomass is, with a tendency of higher densities of humpback whales occurring in areas of medium *E. superba* biomass. At individual and breeding stock level, humpback whales have been shown to return to the same feeding grounds every year (IWC 1998). At a population level, humpback whales seem to have adopted migration patterns and foraging strategies leading them to areas likely providing, on average, sufficient amounts of prey. Dalla Rosa et al. (2008) showed that humpback whales in the WAP area regularly move in short- and long-distance movements between presumed foraging areas with relatively short residency times. This is probably, at least partly, due to local depletion of krill abundance. Santora et al. (2010) suggested that baleen whales may be able to deplete the abundance of the local prey at small spatial scales. As mentioned above, it is likely that humpback whales were exploiting krill occurrences beyond a certain density threshold, not driven by highest prey density. Moreover, Santora et al. (2010) suggested that humpback whales have a preference for small juvenile krill mainly residing in the shelf waters of the BS, as opposed to large, fast swimming mature krill, mainly found further offshore. Whether size-dependent predation is a driver of humpback whale distribution, or humpback whales feed on krill sizes most available in their preferred habitat cannot be determined on the basis of our study.

Conclusion

This study marks the first time that ship-based helicopter surveys were used to provide model-based abundance estimates for fin whales and humpback whales in the WAP. The predictions suggest that the area serves as a feeding ground for a substantial number of animals of both species, representing a large proportion of current population estimates. Furthermore, species-specific distribution patterns of humpback and fin whales showed habitat segregation suggesting horizontal niche separation between the two species on the WAP. Comparisons with krill abundance distribution presented a rather complex relationship between whales and krill biomass. The clearest correlation was found for fin whales, suggesting that at the time of the survey, fin whales were almost exclusively feeding on *T. macrura*. In the light of increasing effort by the commercial krill fishery (Nicol et al. 2008) and climate change-related effects on krill biomass (Atkinson et al. 2004; Nicol et al. 2008), dedicated surveys that target both krill and their main predators, such as baleen whales, need to be undertaken concurrently to monitor and ensure that habitats in the Southern Ocean will continue to support a humpback whale population that has just touched pre-exploitation numbers (IWC 2015). We also need to strengthen our

efforts to investigate the ecology and feeding strategies of Southern Hemisphere fin whales, since little is known about their connection to and dependency on local prey stocks. Our survey shows that a joint effort, making use of all available data from a multidisciplinary research cruise, can extend the knowledge from isolated information on species distribution to local ecosystem assessment.

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