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Responses of seabirds, in particular prions (*Pachyptila* sp.), to small-scale processes in the Antarctic Polar Front

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Abstract

Small-scale distribution patterns of seabirds in the Antarctic Polar Front (APF) were investigated in relation to other biological, physical, and chemical features during the *ANT-XIII/2* research cruise of R.V. *Polarstern* from December 1995 to January 1996. The APF is characterized by steep gradients in sea-surface temperature and salinity. Within the APF, gradient zones were closely associated with elevated levels of primary production, chlorophyll-*a* (chl-*a*) concentrations, and zooplankton densities. Even broad-billed prions ('*Pachyptila vittata*-group'), which dominated the seabird community by 83% in carbon requirements, showed small-scale distributional patterns that were positively related to primary production, chl-*a*, and total zooplankton densities. The findings demonstrate a close, direct link between fine-scale physical processes in the APF and biological activity through several food web levels up to that of zooplankton-eating seabirds. Broad-billed prions appeared to forage on very small copepods (*Oithona* spp.) in close association with the front. Fish- and squid-eating predators showed poor correlations with small-scale spatial structures of the APF. However, in a wider band around the APF, most top predators did occur in elevated densities, showing gradual spatio-temporal diffusion of the impact of the APF on higher trophic levels. © 2002 Elsevier Science Ltd. All rights reserved.

1. Introduction

Seabirds live in a patchy, dynamic environment where prey is unevenly distributed. In their search for food, seabirds aggregate in certain areas where prey appears to be more abundant. Bird concen-

trations are often found around oceanic fronts (Haney and McGillivray, 1985; Heinemann et al., 1989; Hunt, 1990; Schneider, 1990; Veit et al., 1993; Pakhomov and McQuaid, 1996) but also in association with phenomena like sea-ice(-edges) or icebergs (Ainley et al., 1993; Van Franeker et al., 1997; Nicol et al., 2000). Frontal zones are often associated with high levels of biological activity derived from local production and/or from food transported to the front by converging water-

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masses (Murphy, 1995). However, it is only with limited success that small-scale seabird distribution has been directly related to processes at frontal zones (Abrams, 1985a; Ainley et al., 1992; Haney and McGillivray, 1985; Schneider et al., 1987; Van Franeker, 1992). For some Antarctic birds, Heinemann et al. (1989) did find a positive relation between their distributions and that of their prey krill *Euphausia superba*, but the relationship was absent in many other bird species, even in several specialized krill-predators. The lack of correlation may be due to differences in temporal and spatial scales of the occurrence of predators and prey and stochasticity of the availability of the prey or the occurrence of birds. It also has been shown that birds with different feeding ecologies react differently to frontal areas (Kinder et al., 1983; Harrison et al., 1990). So, in spite of a generally accepted pattern of aggregation of seabirds near frontal areas on a larger scale, the small-scale patterns and mechanisms leading to such aggregations are often unclear.

Here, we report on a top predator study in the *Antarctic Polar Front (APF)*. During December 1995 and January 1996, the German research vessel R.V. *Polarstern* undertook research in the Southern Ocean near the Greenwich meridian, travelling between Cape Town and Neumayer base in the Antarctic (voyage *ANT-XIII/2*; Bathmann et al., 1997a). This project was part of the Southern Ocean component of the Joint Global Ocean Flux Study (SO-JGOFS) and followed earlier work in the same area in October–November 1992 (*ANT-X/6*; Smetacek et al., 1997). An important part of the 1995/1996 cruise was dedicated to resolving features of primary production and carbon fluxes in the circumpolar APF. The APF here is characterized by steep but variable gradients in surface-water temperature and salinity (Whitworth and Nowlin, 1987; Veth et al., 1997), and patches of elevated primary production (Sullivan et al., 1993; De Baar et al., 1995; Bakker et al., 1997). During systematical small grid transects in the APF, we monitored seabird distributions simultaneously with continuous underway measurements of a number of abiotic and biotic variables. This paper discusses the spatial relationships between fine-scale seabird

aggregations in the APF and the physical and biological variables of the front.

2. Methods

2.1. Study area

Voyage *ANT-XIII/2* of R.V. *Polarstern* was conducted from 4 December 1995 to 24 January 1996. In between two long return transects from Cape Town south to Neumayer Station, the period from 23 December 1995 to 8 January 1996 was dedicated to study of the APF. Two grid-transects of different sizes were made (Fig. 1). First, we made a 'Coarse-Scale Grid' (Transect 6) with six parallel north–south legs crossing the APF in the area between 49°–52°S and 6°–12°E (area size $\pm 285 \times 380 \text{ km}^2$). Based on gradient observations, the northeastern corner was selected for a 'Fine-scale Grid' (Transect 8) with 11 parallel north–south legs over an area sized only about $130 \times 135 \text{ km}^2$. Reduced visibility and weather conditions resulted in poor coverage of seabird observations in the Coarse Grid. Therefore, this paper is focused on the analysis of the Fine Grid with only general reference to the Coarse Grid and adjacent areas (zones of 2° latitude ($\pm 220 \text{ km}$) to the north and to the south of the grid areas).

2.2. Top predators

Birds were counted within a transect band along the ship track, using contiguous time blocks of 10 min according to the snapshot method (Tasker et al., 1984; Van Franeker, 1994; Van Franeker et al., 1997). Transect width was 300 m, taken as 150 on each side of the track-line of the ship. Speed of the ship during the count can then be used to determine the area surveyed and the densities of animals encountered. As far as possible, censuses were conducted continuously from an open observation post-installed centrally on top of the bridge of *Polarstern* (about 21 m high). Only when glare on the water or other conditions hampered visibility, the transect width was reduced to 150 m on the one side of the ship with the best viewing conditions. Distances were estimated with a range

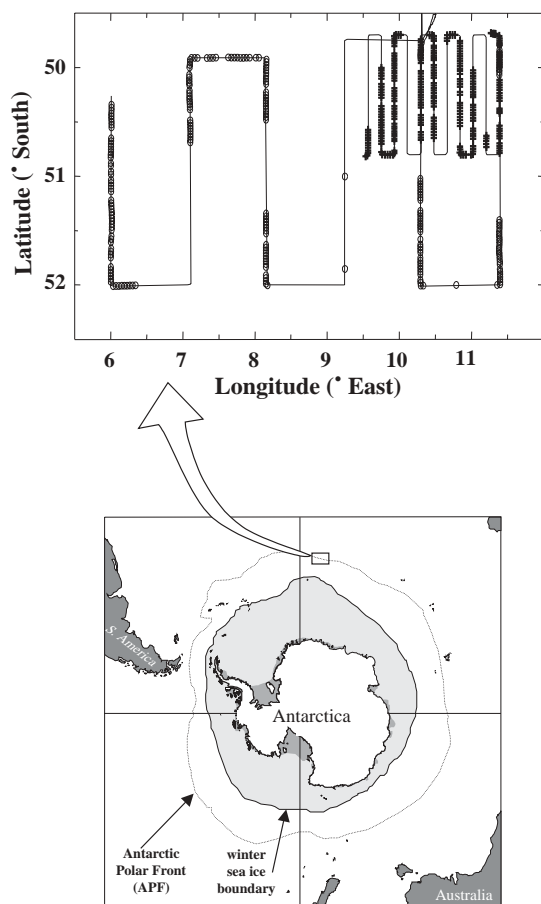


Fig. 1. Study area: Location, transect lay-out, and position of 10-min bird counts in the Coarse-Scale Grid (Transect 6, open circles for each count) and the Fine-Scale Grid (Transect 8, cross lines for each count) in the APF during *ANT-XIII/2*. Both grids were sailed from west to east. The large grid measured an area of $\approx 380 \times 285 \text{ km}^2$ and was transected by grid legs about 75 km apart, whereas the small grid measured about $135 \times 130 \text{ km}^2$ with grid legs about 13 km apart.

finder (Heinemann, 1981), calibrated by regular accurate distance measurements with a Leica Geovid binocular (laser system IR measurements). Flying directions and foraging events are usually recorded, but where large numbers occur in local aggregations without obvious movement or direction all birds are simply recorded as ‘milling’ (Spear et al., 1992) and quantitative records of individual foraging behaviour become impossible. Dense aggregations of large numbers of milling

birds were the dominant phenomenon during this study, so flying directions or frequencies of foraging events are not specified. Birds following or circling the ship were omitted from the counts.

Marine mammals were recorded using both strip- and line-transect methods (Hiby and Hammond, 1989), but encounters in the APF grids were too few to allow meaningful analysis at the spatial scales used for birds. Mammal observations will only be discussed in general terms with reference to the larger area.

Carbon requirements of top predators can be calculated by allometric formulae based on the average body mass of each species. For Southern Ocean seabirds, species-specific Field Metabolic Rates (FMR: in kJ/day) can be calculated as $\text{FMR} = 8.01 \times M^{0.704}$ (Nagy, 1987; M is the body mass in grams, mainly taken from Croxall and Gaston (1988) and listed in Table 1). From FMR, the daily food requirement per individual of a bird species was calculated assuming an average energetic value of 4.5 kJ/g fresh food and an assimilation efficiency of 75%. For the conversion of fresh food to carbon intake, we assumed 10% carbon content in the fresh food. Densities as calculated from the 10-min counts can then be used to estimate total food- or carbon-consumption figures for separate species or the top predator community as a whole. For further details see Van Franeker et al. (1997).

Species identifications were not always possible: if such was the case, species are lumped in the lowest possible taxon (see Table 1). In general, we have used names as in Harrison (1983) and for example did not follow recent albatross taxonomy (Robertson and Nunn, 1997). The prions or whalebirds form a particular problematic bird group in field identification and taxonomy (Warham, 1990). All prions recorded in this study appeared to belong to the group of broad-billed prions (the ‘*Pachyptila vittata* aggregate’), which includes the Broad-billed Prion (*P. vittata*), Salvin’s Prion (*P. salvini*), and Antarctic Prion (*P. desolata*). We suspect that the prions in our APF study area were Antarctic Prions, but will refer to them as ‘broad-billed prions’ (the ‘*P. vittata* -group’).

Table 1

Summary of transect information and bird observations during transects in and near the Antarctic Polar Front

| | Fine-Scale Grid (Transect 8) | Coarse-Scale Grid (Transect 6) | Zone 2° south of the APF grids | Zone 2° north of the APF grids | |
|-------------------------------------|------------------------------------|--------------------------------------|--------------------------------------|-----------------------------------|--|
| Census dates | 1–5 Jan '96 | 24–29 Dec '95 | 10 Dec–18 Jan | 8 Dec–12 Jan | |
| Latitudinal range (°S) | 49°40'–50°49' | 49°26'–52°00' | 52°00'–54°00' | 47°30'–49°30' | |
| Longitudinal range(°E) | 9°30'–11°23' | 6°00'–11°24' | –0°16'–10°22' | 6°29'–12°34' | |
| Water temp. range | 3.1–5.4°C | 2.4–5.5°C | 0.1–3.7 | 3.5–5.8°C | |
| Nr. of 10 min counts | 269 | 233 | 121 | 64 | |
| Surface counted (km ²) | 199.4 | 194.8 | 127.6 | 53.7 | |
| Seaweed density | 0.196 | 0.128 | 0.071 | 0.037 | |
| Bird densities (n/km ²) | Fine scale | Coarse scale | Zone 2° south | Zone 2° north | Scientific name (body mass in g) |
| Broad-billed prions | 18.12 | 9.02 | 1.76 | 0.15 | <i>Pachyptila vittata</i> group (162) |
| Soft-plumaged Petrel | 0.94 | 0.60 | 0.27 | 0.17 | <i>Pterodroma mollis</i> (310) |
| Great Shearwater | 0.37 | 0.19 | 0.04 | + | <i>Puffinus gravis</i> (834) |
| Black-bellied Stormpetrel | 0.24 | 0.42 | 0.21 | 0.04 | <i>Fregatta tropica</i> (56) |
| White-headed Petrel | 0.17 | 0.08 | + | 0.06 | <i>Pterodroma lessonii</i> (750) |
| Kerguelen Petrel | 0.08 | 0.02 | 0.11 | | <i>Pterodroma brevirostris</i> (360) |
| White-chinned Petrel | 0.05 | 0.02 | 0.01 | 0.02 | <i>Procellaria aequinoctialis</i> (1270) |
| Sooty Shearwater | 0.05 | | | + | <i>Puffinus griseus</i> (787) |
| Diving Petrel sp. | 0.04 | 0.05 | 0.06 | | <i>Pelecanoides</i> sp. (134) |
| Gray Petrel | 0.02 | 0.03 | 0.01 | + | <i>Procellaria cinerea</i> (1040) |
| Giant Petrel sp. | 0.01 | + | 0.02 | + | <i>Macronectes</i> sp. (4500) |
| Gray-headed Alb. | 0.01 | 0.01 | 0.02 | 0.04 | <i>Diomedea chrysostoma</i> (3790) |
| Black-browed Alb. | 0.01 | + | 0.02 | 0.02 | <i>Diomedea melanophris</i> (3790) |
| Wandering Alb. | 0.01 | 0.03 | + | + | <i>Diomedea exulans</i> (8730) |
| Cape Petrel | 0.01 | 0.01 | 0.02 | + | <i>Daption capense</i> (425) |
| Arctic Skua | 0.01 | 0.01 | | | <i>Stercorarius parasiticus</i> (536) |
| Little Shearwater | 0.01 | | | 0.06 | <i>Puffinus assimilis</i> (225) |
| Antarctic Skua | + | + | 0.008 | + | <i>Catharacta lonnbergi</i> (1536) |
| Yellow-nosed Alb. | + | + | | | <i>Diomedea chlororhynchus</i> (2060) |
| Eudyptes penguin sp. | + | 0.015 | | | <i>Eudyptes</i> sp. (3650) |
| Light-m. Sooty Alb. | + | 0.005 | + | + | <i>Phoebetria palpebrata</i> (2840) |
| Great-winged Petrel | + | | | | <i>Pterodroma macroptera</i> (560) |
| Wilson's Stormpetrel | + | | | | <i>Oceanites oceanicus</i> (36) |
| Sooty Albatross | | 0.005 | | 0.019 | <i>Phoebetria fusca</i> (2510) |
| Art/Ant/Ker Tern | | + | | | <i>Sterna sp medium</i> (120) |
| Blue Petrel | | | 0.008 | | <i>Halobaena caerulea</i> (200) |
| Chinstrap Penguin | | | + | | <i>Pygoscelis antarctica</i> (4150) |
| Southern Fulmar | | | + | | <i>Fulmarus glacialis</i> (775) |
| Totals birds | Fine scale | Coarse scale | Zone 2° south | Zone 2° north | |
| Density (n/km ²) | 20.12 | 10.48 | 2.55 | 0.56 | |
| Biomass (kg/km ²) | 3.98 | 2.30 | 0.70 | 0.42 | |
| Food-req. (kg/km ² /day) | 1.98 | 1.06 | 0.29 | 0.12 | |
| C-cons. (kg/km ² /day) | 0.20 | 0.11 | 0.03 | 0.01 | |

Bird species listed according to abundance in the Fine-Scale Grid.

2.3. Additional data

In association with each 10-min top predator count, visual observations were made of weather and sea conditions. A wide range of further variables is continuously monitored by automatic sensors on board *Polarstern* and data are stored in the ship's POLDAT database system on VAX computer. Among these are positional data, speed, heading, water depth, a range of weather data, and surface water properties such as temperature and salinity at a depth of 8 m (ships pump). We pooled POLDAT data for 10-min time frames to allow direct comparison with top predator data.

2.4. Phytoplankton and primary production

As an assessment of the standing stock of phytoplankton, concentrations of chlorophyll-*a* (Chl-*a*) were measured underway by fluorescence methods according to Bathmann et al. (1997b). The water was taken from the ship's pump at 8 m depth, the same as used for temperature and salinity measurements. For the purpose of this paper, continuous fluorescence measurements originally averaged over 5-min periods, were paired to 10-min averages for direct comparability with bird data. The in vivo Chl-*a* fluorescence measurements were made with a Turner-Design flow-through fluorometer. The fluorometer readings were converted into Chl-*a* concentrations based on measurements of extracted pigment from triplicate 1 l subsamples taken every 3 h during the duration of the cruise. Extracted Chl-*a* and phaeopigments were determined after filtration of 1 l of seawater onto GF/F filters. The filters were placed in 90% (v/v) acetone/water and homogenized in a cell mill for 5 min. Fluorometric measurements were performed before and after acidification with two drops of 1 N HCl (Strickland and Parsons, 1972; Evans et al., 1987). Filters were measured within a few days on board.

The standing stock of phytoplankton, as measured by Chl-*a*, is not necessarily an appropriate measure for the primary production that takes place at the moment of sampling. Therefore, we use the undersaturation of carbon dioxide in the

surface water as compared to air concentrations as a measure of *total primary production* (Bakker et al., 1997). The partial pressure of CO₂ in air ($f\text{CO}_{2\text{air}}$) and in water ($f\text{CO}_{2\text{water}}$) was measured using a home-built extraction unit/analyser including a Li-Cor (LI-COR, Model 6252) infrared analyser (Stoll, 1994). Air was pumped through Dekabon tubing from the crows nest to the laboratory, water was taken from the ship's pump at 8 m depth and led through an equilibrator (Bakker et al., 1997). The system is calibrated using reference gases, which in turn had been calibrated vs. National Oceanic and Atmospheric Administration (NOAA) certified standard gas mixtures (accurate to 0.01 ppm) before and after the cruise. The CO₂ undersaturation is defined as $\delta\text{CO}_2 = f\text{CO}_{2\text{air}} - f\text{CO}_{2\text{water}}$. Data are averaged over 10-min periods. In order to uncouple primary production from the standing stock of phytoplankton, we define *primary-production rate* as the ratio of δCO_2 per unit Chl-*a* (atm/g/l) in the water.

2.5. Zooplankton

Underway measurements of a range of variables were possible during ANT XIII/2 by the deployment of sensors mounted on the towed profiling vehicle SeaSoar (Pollard, 1986). SeaSoar was towed behind the ship at 8 knots (4 m/s), undulating between the surface and 350 m every few km. ANT XIII/2 was the first cruise during which an Optical Plankton Counter (OPC) (Herman, 1988) was mounted on SeaSoar (Pollard et al., 2002). The OPC counts and records the sizes of particles with Equivalent Spherical Diameters (ESD) between 250 μm and about 12 mm. Calibration is discussed in detail by Pollard et al. (2002). For the purpose of this paper our interest lies in the spatial patterns in the upper surface layer. To avoid bias from occasional air bubbles very close to the surface (top few metres) and to maximize available data given that the SeaSoar occasionally turned before it reached the surface, we shall here use data sampled in the 8 m depth range between 17 and 25 m depth. Data were thus binned at successive intervals of latitude approximately spanning 0.049° (5.5 km). The counts have been normalized to counts/m³ by dividing by the volume of water

that passed through the OPC in each bin. ESD was used to split the counts into three size classes, nominally 250–500, 500–1000, and >1000 μm ESD. When we report on total counts (n/m^3) these are dominated by the smallest size classes. Greatest confidence in our spatial patterns should be given to the data in the two smaller size classes, as in the larger size class the number of individuals per bin in the APF surface layers becomes small for statistics on spatial distributions. For specific details on size frequencies and distributions, derived from larger data-sets and full depth ranges, see Pollard et al. (2002).

2.6. Statistics

Regressions with linear and exponential models were used to analyse relations between variables that were normally distributed (Lane, 1993). The linear models were fitted using a least-sum-of-squares method (Lane, 1993, p. 366), while the exponential models were fitted with a maximum likelihood method (Lane, 1993, p. 434). Whenever dependent variables were not normally distributed, General Linear Models (GLM) were used to analyse their relations with other variables (Lane, 1993, pp. 413–434). The distribution of the variable was then assumed to be quasi-poisson, and the logarithm was used as link-function. In order to analyse exponential relations between variables, which are not normally distributed, an exponential parameter was introduced in the GLM, which was estimated iteratively (Lane, 1993, pp. 426–427).

The time scales, and therefore also the spatial scales, of the data collection of the different variables were not always identical. In order to cross-relate the geographical distribution of different variables, the data were gridded with a kriging method (Cressie et al., 1991). This procedure resulted in a set of interpolated values of each variable on designated gridnodes, which were spaced identically for all variables. The number of designated gridnodes used in the statistical analyses will be discussed in the results section on spatial autocorrelation.

The gridded data also can be used to produce contour maps. These were produced with the

program Surfer (Version 6.02 for Windows). Contour maps are based on gridmaps with 2200 gridnodes. With the option ‘terrain modelling’ in this program it is also feasible to calculate gradients of variables in space. Using this method a gradient is defined as being the angle between the surface of the contour map and the flat surface. Hence, no gradient is 0° , an infinite gradient is 90° . In calculations relating physics to biology, we have not used actual temperatures or salinities, but the gradients.

2.7. Spatial autocorrelation

Autocorrelation is a common problem whenever analysing seabird census data gathered on a cruise track (Schneider, 1990; Schneider and Bajdik, 1991). When a data-set shows autocorrelation this means that an observation in a certain 10-min count is more likely to have a similar density to a count adjacent to it than to one farther down the track (Cliff and Ord, 1973). Autocorrelation indicates that the observations are spaced in a smaller scale than the spatial extent of the physical or biological structures that are being analysed. The same structures may thus be sampled repeatedly and ‘pseudo-replication’ may be the result (Hurlbert, 1984). When analysing a data-set that shows autocorrelation within variables, the relations between variables are likely to show exaggerated significance of the cross-correlations. Conclusions based on such an analysis may be overstated. Autocorrelation also shows the extent of spatial structures in the data-set (Cliff and Ord, 1973), and this may be used to analyse the spatial clustering of the density of variables. For the analysis of the spatial autocorrelation we used the statistical program Genstat[®] (Wilson and Welham, 1993).

3. Results

Observations of seabirds were made in 296 standard 10-min counts during the Fine-Scale Grid (Transect 8) from 1 to 5 January 1996. Because of day-light limitations, blocks of top predator counts are alternated with periods

without observations (Fig. 1). Table 1 summarizes transect information and results from all top predator observations and makes a comparison to data from the Coarse-Scale Grid (Transect 6) in the APF and the bordering zones of 2°C latitude to the north and to the south. Because our focus is on seabirds that feed in the upper surface layers, we selected subsets of data from other measurements specifically for the surface. For this reason we used data on physics and phytoplankton from water collected continuously by the ship's pump at 8 m depth, rather than SeaSoar data. Zooplankton were sampled by SeaSoar on a different scale, which resulted for example in 253 data points for zooplankton densities in the Fine-Scale Grid.

Because we selected data for surface layers, our graphical presentations and calculations on spatial patterns may differ from those in other papers in this issue (e.g., Pollard et al., 2002; Strass et al., 2002a, b; Vélez et al., 2002) which often deal with deeper water layers (e.g., around the temperature minimum at 150–200 m depth) or integrate data over larger depth ranges. Surface and subsurface structures of the APF may be widely separated (Read et al., 2002).

3.1. Sea-surface temperature and salinity

Surface-water temperature and salinity showed a clear north–south pattern, indicating the surface position of the front (Fig. 2 for the Coarse-Scale Grid; Fig. 3 for the Fine-Scale Grid). The temperature decreased north to south, with two areas showing steeper temperature gradients: there was an east–west band at $\approx 50^{\circ}\text{S}$, with a diversion going south at $\approx 10^{\circ}\text{E}$. Salinities in the surface water increased north to south, with gradients being strongest in a spatial pattern similar to that of water temperature. The Fine-Scale Grid, shown by the inserted rectangle in Fig. 2, was positioned over the area with the steepest gradients, viz. the strongest 'Frontal' characteristics. Based on subsurface characteristics Strass et al. (2002b) described the area as a meander structure of the APF with a cold cyclonic eddy located to its south.

3.2. δCO_2 and chlorophyll-*a*

For further variables, we concentrate on the Fine-Scale Grid (Transect 8). Patterns of undersaturation of CO_2 in the surface water in the small grid are shown in Fig. 4A. Since δCO_2 is defined as

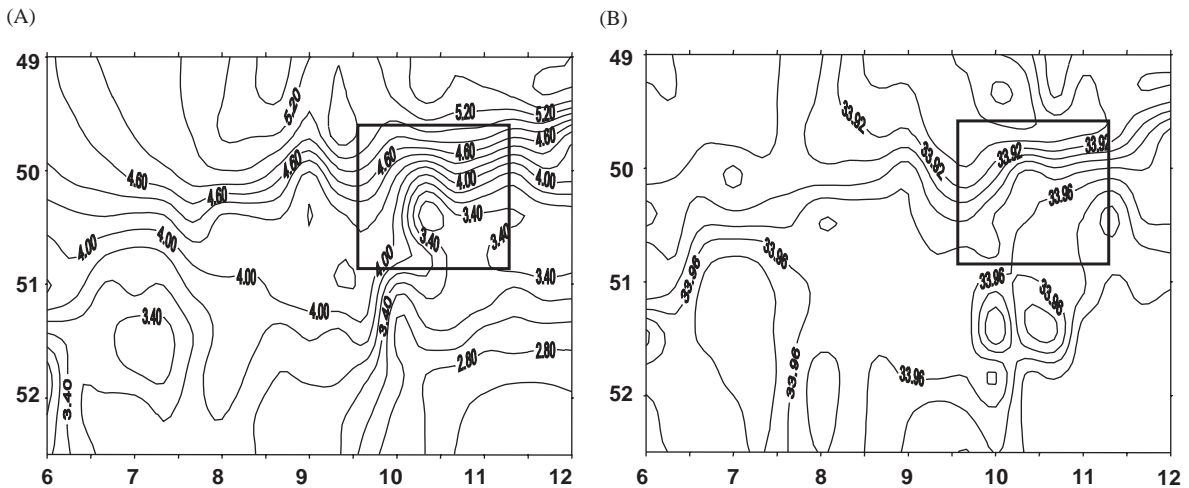


Fig. 2. Coarse-Scale Grid (Transect 6) physics: (A) temperature ($^{\circ}\text{C}$) and (B) salinity (0/00) patterns in the surface water (8 m depth) showing the larger structure of the APF in relation to the later Fine-Scale Grid (inserted rectangle; see Fig. 3). Axes scaled by whole $^{\circ}\text{S}$ and $^{\circ}\text{E}$.

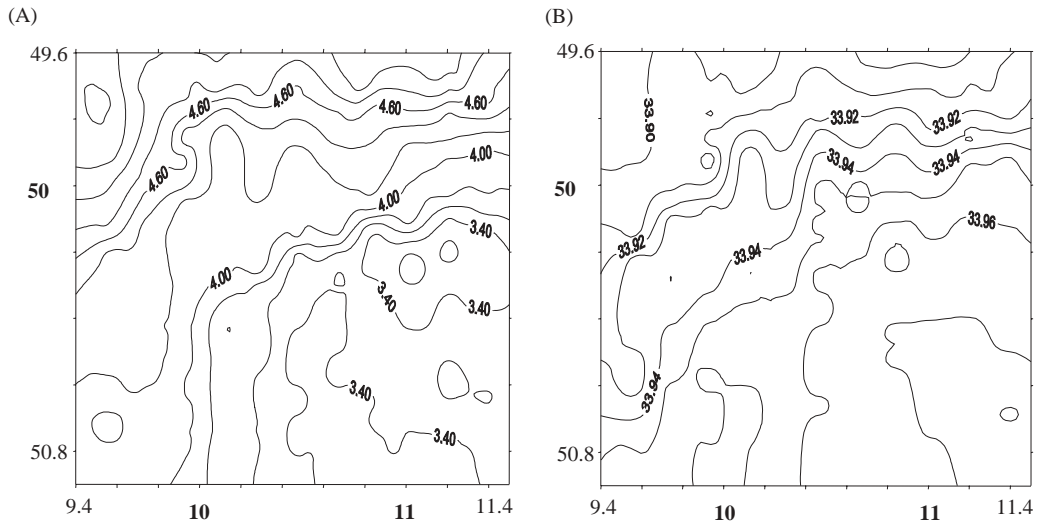


Fig. 3. Fine-scale Grid (Transect 8) physics: (A) temperature ($^{\circ}\text{C}$) and (B) salinity (0/00) patterns in the surface water at 8 m depth. Axes scaled by bold print whole degrees of latitude and longitude, with intermittent subdivisions in decimals. Scaling has been omitted in further graphs of the Fine-Scale Grid area.

$f\text{CO}_{2\text{air}} - f\text{CO}_{2\text{water}}$, positive values of δCO_2 indicate undersaturation of the water as a consequence of CO_2 uptake by phytoplankton growth. Darker colours in Fig. 4A thus correspond to higher total primary production. The highest undersaturation is located in the north-west part. The average δCO_2 is $-0.373 \mu\text{atm}$ (range -14.45 to $+17.72 \mu\text{atm}$). Relatively low productivity values are suggested for the south-east part, and in a 'finger'-shaped intrusion in the west part of the survey area. A very similar spatial pattern results if primary-production rate is mapped (primary production per unit chlorophyll; not shown).

Patterns in surface phytoplankton standing stock, as shown by the Chl-*a* distribution (Fig. 4B), are similar to those of δCO_2 , with again minimum values in the south-east and in a finger-shaped intrusion in the west. The distribution of chlorophyll patterns in the Fine-Scale Grid shows enhanced concentrations along the meandering stream of the Polar Front in the north and a southward tongue, with diatoms being the dominating phytoplankton forms (Smetacek et al., 2002). The average concentration of Chl-*a* in the Fine-Scale Grid was $1.06 \mu\text{g/l}$ (range from 0.46 to $2.25 \mu\text{g/l}$). Chl-*a* concentrations in the Coarse-

Scale Grid were significantly lower (*t*-test, $p < 0.001$) at an average of $0.86 \mu\text{g/l}$ and range of 0.28 – $2.37 \mu\text{g/l}$.

3.3. Zooplankton

Zooplankton, measured by OPC counts on SeaSoar, were counted in different size classes. The density distribution of zooplankton of all size classes shows a minimum at the south-east corner and in the well-defined finger-shaped area in the west, and maximum densities were encountered in the north and in a band diagonally across the survey area (Fig. 4C). Similar distributional patterns resulted if separate size classes were mapped. In terms of relative abundances of different size classes, the smallest zooplankton (OPC diameter $< 0.5 \text{ mm}$) are superabundant (nearly 75%), with hardly any contribution to numbers by the largest size class ($> 1 \text{ mm}$). However, in terms of volume/biomass, the medium and large size classes gain considerably in importance (Table 2). Volumes were calculated assuming particles in each size class to be spheres with a radius of half the average OPC diameter of the size class (375, 750, and $2000 \mu\text{m}$). The volume ratio between different size

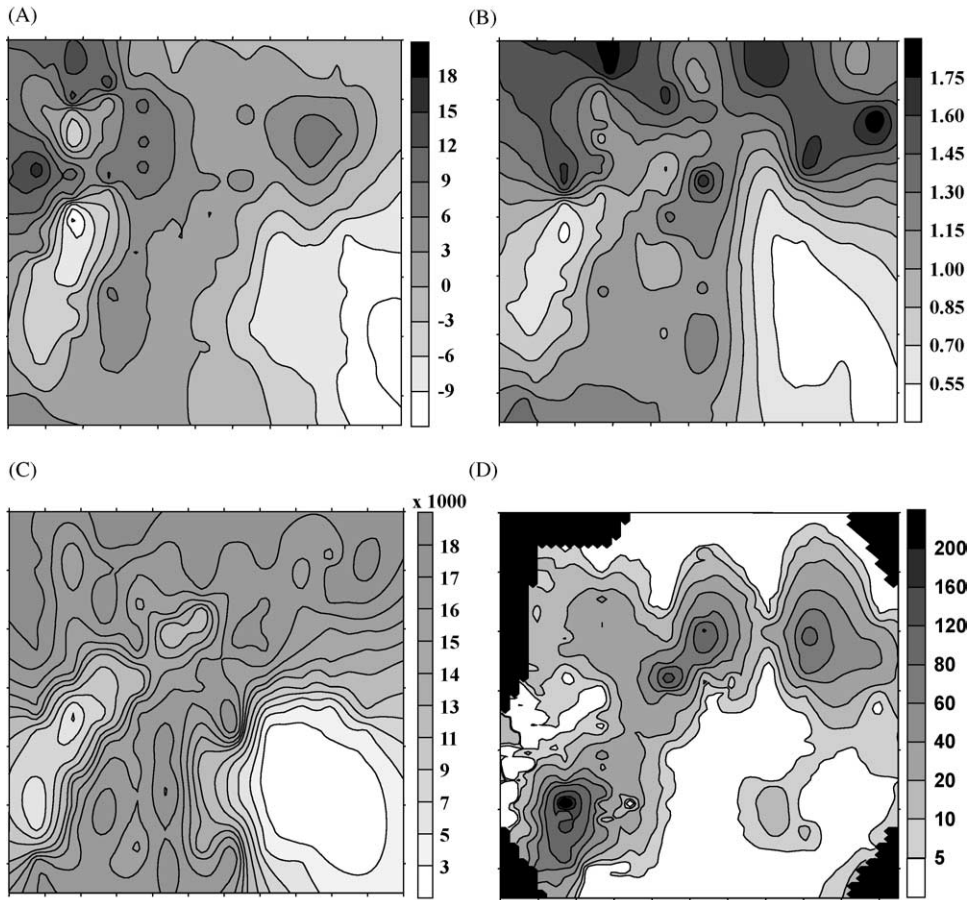


Fig. 4. Biology in the upper surface layer of the Fine-Scale Grid area. Scales of latitude and longitude as in Fig. 3. (A) Primary production as derived from undersaturation of CO₂ in the surface water at 8 m depth ($\delta\text{CO}_2 = f\text{CO}_{2\text{air}} - f\text{CO}_{2\text{water}}$; μatm). (B) Phytoplankton stocks as derived from concentration of Chl-*a* in surface water at 8 m depth (in $\mu\text{g/l}$). (C) Zooplankton stocks by density (n/m^3) of all sizes of zooplankton in the surface layer (17–25 m depth). Smaller sizes dominate. (D) Seabird density (all species, n/km^2). NB: the black, non-mapped corner areas result from insufficient data points nearby to calculate realistic grid values.

Table 2
Average abundance and biovolume for different zooplankton size classes in the surface layer of the Fine-Scale Grid

| Zooplankton Size class | Density | | Volume | |
|---------------------------|--------------------|-------|------------------------------|-------|
| | (n/m^3) | (%) | (mm^3/m^3) | (%) |
| 250–500 μm | 9194 | (73) | 275 | (20) |
| 500–1000 μm | 3310 | (26) | 731 | (52) |
| > 1000 μm | 96 | (1) | 402 | (28) |
| All sizes | 12600 | (100) | 1408 | (100) |

classes may be assumed to be proportionate to ratios in biomass and carbon contents.

For further details on depth distributions of different sizes and biovolumes, see Table 2 and Fig. 8 in Pollard et al. (2002), indicating that the larger size classes of zooplankton were particularly rare in the upper few metres in the APF. Data from areas near the ice edge showed that larger zooplankton like euphausiids are detected by the OPC, so we are certain that these were uncommon in the APF, and particularly so near the surface.

Net-catches indicated that zooplankton were mainly copepods and copepodites, with adults of the cyclopoid copepod *Oithona* spp. dominating the <0.5 mm size class. A variety of copepod species occurred in the larger classes (Pollard et al., 2002).

3.4. Seabirds

In the Fine-Scale Grid, 23 different seabird species were identified (Table 1). Seventeen of these are included in density counts, but six others were only seen outside the transect-bands or crossed it in between the snapshot counts. Tubenosed seabirds dominated in the APF, with only few individuals of other bird groups (skua's, terns, penguins). Table 1 summarizes similar data for the adjacent areas.

The combined density of all birds in the Fine-Scale Grid ranged from 0 to 388 individuals per km² in different counts and averaged at about 20 birds/km², with median less than 7/km². The density distribution showed a distinct pattern, with higher densities occurring more or less along the areas with relatively steep temperature gradients (Fig. 4D). Only six species occurred in more than 5% of the 10-min counts in the Fine-Scale Grid: Black-bellied Stormpetrel (*Fregatta tropica*), White-headed Petrel (*Pterodroma lessonii*), Kerguelen Petrel (*P. brevirostris*), Soft-Plumaged Petrel (*P. mollis*), broad-billed prion (*P. vittata*-group), and Great Shearwater (*Puffinus gravis*). These species showed different distributional patterns in the Fine-Scale Grid (Figs. 5A–F). Four types of distribution may be distinguished:

- (i) maximum densities in the south-east area of the small grid (i.e. on the cold side of the front): Black-bellied Stormpetrel and the White-headed Petrel;
- (ii) no clear pattern in densities: the Kerguelen Petrel and the Soft-plumaged Petrel;
- (iii) maximum densities along the temperature gradient: the broad-billed prion;
- (iv) maximum densities in the 'finger'-shaped area in the west: the Great Shearwater.

Of these species, the broad-billed prion occurred in highest densities (average, 18.12/km²; median,

3.86/km²; range, 0–384/km²), and concentrated in the area of the 4°C isotherm.

3.5. Spatial autocorrelation

In order to assess the extent of the autocorrelation within our data-set, we analysed a part of it that contained consecutive 10-min counts, collected in ≈4 h ($n = 25$, covered distance ≈65 km). Data for broad-billed prions and Chl-*a* were analysed over the same spatial scale and can therefore be compared directly. Broad-billed prions show autocorrelation to an extent of 5–10 km, while for Chl-*a* this occurs to about the distance of 15 km (Fig. 6). Seabirds are of main interest in the current research, and therefore the data-sets were corrected for the spatial autocorrelation of the broad-billed prions. This implies that data points used for regression analyses were calculated by gridding procedures with gridnodes spaced at ±15 km distance, with no overlap in the areas of integration (integration over 0.45 of the radial distance between gridnotes). These procedures assured that the data-set for broad-billed prions showed no significant autocorrelation. All other variables were gridded with the same procedure to obtain a data-set for analysis of cross-relations between all variables. Remaining effects of different autocorrelation scales among other variables are deemed to be of minor importance in the relations.

3.6. Regression and correlation analyses

We analysed relationships between variables by means of regression analyses or General Linear Model (GLM) procedures (Tables 3 and 4 and Discussion). Results from these analyses are expressed as the percentage of variance or deviance of the dependent variable that is explained by the independent variable. However, many other studies report correlation coefficients (see for instance Abrams, 1985 and Griffiths et al., 1982). In a correlation analysis the form of the relation is not taken into account and thus provides less information than a regression analysis. For comparative purposes, we applied correlation as well as regression analyses to our major

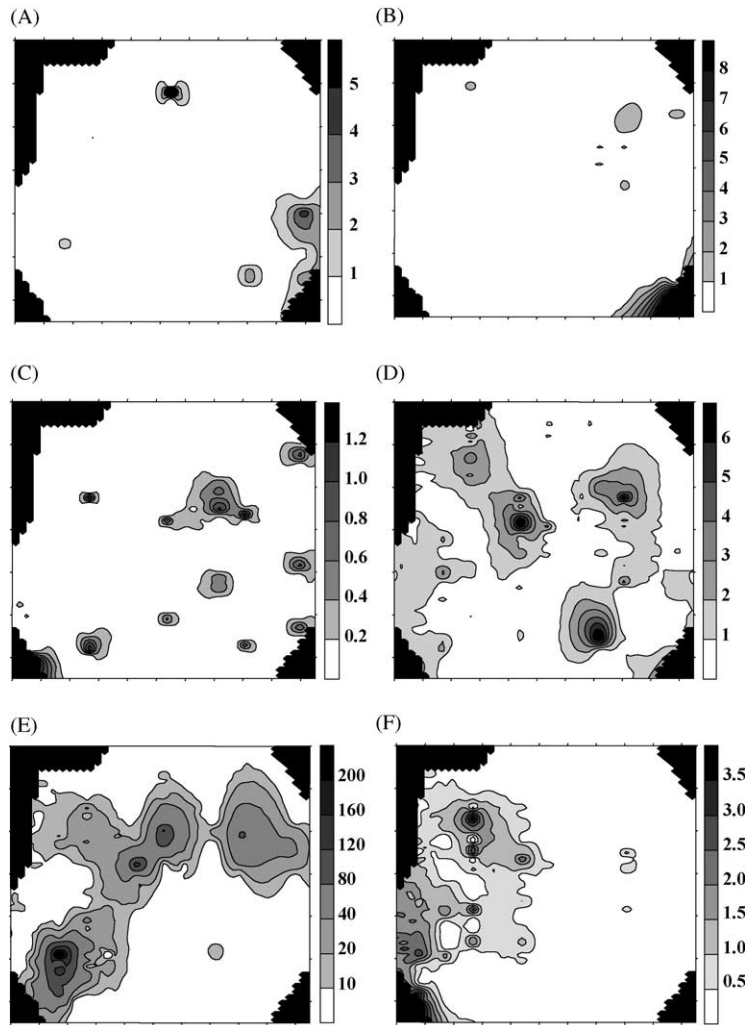


Fig. 5. Fine-scale Grid: density distributions (n/km^2) of seabird species that occurred in more than 5% of the 10-min counts. Black areas in corners reflect insufficient data for mapping. Latitude and longitude scaling as in Fig. 3. (A) Black-bellied Stormpetrel. (B) White-headed Petrel. (C) Kerguelen Petrel. (D) Soft-plumaged Petrel. (E) Broad-bellied prior. (F) Great Shearwater.

variable-combinations. There appears to be a predictable relationship between correlation coefficients and percentages of explained variance in our data, which may be expressed as: $CC = 0.77 \times (1 - 0.97^{PV})$ ($P < 0.001$, CC = correlation coefficient; PV = percentage explained variance). This equation may be applied to all detailed regression analyses shown in Tables 3 and 4 to translate our results to approximate correlation coefficients.

4. Discussion

The seabird densities in our Fine-Scale Grid over the APF ranged from 0 to almost 400 ind/ km^2 . The arithmetic mean density (20.12 ind/ km^2) is amongst the highest recorded in the APF (Abrams, 1985b; Pakhomov and McQuaid, 1996), in spite of the large distances to the nearest potential breeding grounds. Distance to colony would be irrelevant if non-breeders had prevailed

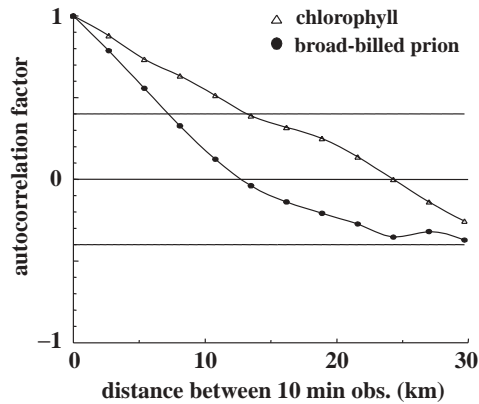


Fig. 6. Autocorrelation within a series of 25 directly bordering 10-min observations on the cruise track, as a function of the distance between the observations. Each dot represents an observation-lag (first lag compares observations 1–2, 2–3, etc.; second lag compares observations 1–3, 2–4, etc.). For observations between the solid lines the autocorrelation is not different from 0% at 95% confidence interval (Wilson and Welham, 1993).

Table 3

Regression analyses of relationships between variables in the Fine-Scale Grid (Transect 8) listed are level of significance (% variance accounted for; *degree of freedom*)

| | Temperature gradient | δCO_2 | Chl- <i>a</i> | $\delta\text{CO}_2/\text{Chl-}a$ | Zooplankton all sizes |
|----------------------------------|--------------------------|---------------------------|---------------------------|----------------------------------|--------------------------|
| δCO_2 | *** (58;35) | | | | |
| Chl- <i>a</i> | *** (58;34) ^g | *** (58;47) ^g | | | |
| $\delta\text{CO}_2/\text{Chl-}a$ | *** (68;34) ^c | *** (94;47) | *** (82;47) | | |
| Zooplankton all sizes | *** (57;35) ^g | *** (77;55) ^{eg} | *** (92;50) ^{eg} | *** (85;47) ^{eg} | |
| 250–500 μm | *** (45;35) ^g | *** (69;55) ^{eg} | *** (90;50) ^{eg} | *** (81;47) ^{eg} | *** (90;61) |
| 500–1000 μm | *** (62;35) ^g | *** (70;55) ^{eg} | *** (73;50) ^{eg} | *** (69;47) ^{eg} | *** (74;61) |
| > 1000 μm | *** (26;35) ^g | *** (31;55) ^{eg} | *** (26;50) ^{eg} | *** (30;47) ^{eg} | *** (45;61) |
| b.b. prion all records | ** (11;33) ^g | *** (21;46) ^g | ** (15;49) ^{eg} | *** (24;46) ^{eg} | n.s. (5;49) ^g |
| b.b. prion pos. records | ** (23;32) ^g | *** (24;41) ^g | ** (27;43) ^{eg} | *** (32;41) ^g | ** (14;43) ^g |

Note: Two data-sets were analysed for broad-billed prions: one including ('b.b. prions all records') and one excluding ('b.b. prion positive records') gridnodes where broad-billed prion density was zero.

***, $p \leq 0.001$; **, $0.001 < p \leq 0.01$; *, $0.01 < p \leq 0.05$; n.s., $p > 0.05$.

^cExponential relation.

^gRegression with GLM (see methods).

Table 4

Details of relationships between broad-billed prions and zooplankton size classes

| | Zooplankton (250–500 μm) | Zooplankton (500–1000 μm) | Zooplankton (> 1000 μm) | Zooplankton all sizes |
|-------------------------|--------------------------------------|---------------------------------------|-------------------------------------|--------------------------|
| b.b. prion all records | * (10;49) ^g | n.s. (0;49) ^g | n.s. (0;49) ^g | n.s. (5;49) ^g |
| b.b. prion pos. records | ** (20;43) ^g | n.s. (2;43) ^g | n.s. (0;43) ^g | ** (14;43) ^g |

**, $0.001 < p \leq 0.01$; *, $0.01 < p \leq 0.05$; n.s., $p > 0.05$.

^gRegression with GLM (see methods).

in our study, but in mid summer non-breeders are expected to have advanced stages of primary moult, and such was not observed among our major species. Of the potential breeding locations, only Bouvet Island is relatively close at ± 700 km, but this location supports only marginal populations of broad-billed prion and Black-bellied Stormpetrel and none of the other major species in this study (Mehlum, 1986; Bakken, 1991). Other potential origins such as the islands of Tristan da Cunha and Gough to the north-west (Williams, 1984; Fraser et al., 1988), Prince Edward and Marion to the northeast (Williams, 1984) and South Sandwich to the southwest (Croxall et al., 1984; Convey et al., 1999), are all at distances of 2000–2500 km away. South Georgia, the stronghold of the Antarctic Prion *P. desolata* with an estimated population of 22 million pairs (Croxall et al., 1984), is over 3000 km away. Because of the

large distance to breeding grounds, and the lack of directional movement among observed birds (see methods), it is not likely that our numbers or distributional patterns were influenced by commuting birds (Ribic and Ainley, 1997). Many birds in our high-density patches were actively feeding. Thus, the distributional pattern of seabirds in the area may be considered to reflect patterns of food availability and consumption.

4.1. Carbon consumption by the top predator community in the APF

The seabird community in our APF grids and nearby areas was completely dominated by procellariiform (tube-nosed) seabirds. The same was recorded during nearby APF crossings in spring 1992, although with slightly more penguin observations (Van Franeker et al., 1997). The pattern of seabird carbon requirements in the Fine-Scale Grid (Fig. 7) is very similar to the density distribution, with maximum requirements in a belt crossing the grid from the east to the west along about 50°S, plus a diversion going southwest from $\approx 10^{\circ}50'E$. The arithmetic mean of the carbon flux to the seabird community in the Fine-Scale Grid is 0.20 mg C/m²/day (Table 1). This represents about 0.03% of the estimated daily primary production

during our study (585 mg mg C/m²/day; Strass et al., 2002a). Assuming similar bird densities year-round (the major species are more or less resident in the Southern Ocean), this translates to an annual carbon consumption of 0.07 g C/m²/year close around the APF. Abrams (1985b) reported a similar annual carbon flux of 0.095 g C/m²/year for the APF. These are high values for an open-water deep-ocean system, and compare to the lower end of the range of continental-shelf-based systems (Diamond et al., 1993). In the Barents Sea, seabirds are estimated to consume 0.05 g C/m²/year (Sakshaug, 1997). Carbon consumption by birds in the Coarse-Scale Grid was only half of that in the fine grid, and reduced by an order of magnitude at further distance from the front (Table 1).

Using calculation methods as in Van Franeker et al. (1997), our few observations of marine mammals lead to rough estimates for mammal carbon consumption in these areas as: Fine Grid 0.11; Coarse Grid 0.07; zone south 0.09; and zone north 0.00 mg C/m²/day. Species involved were Hourglass Dolphin *Lagenorhynchus cruciger*, Fin Whale *Balaenoptera physalus*, Humpback Whale *Megaptera novaeangliae*, unidentified small whale, and a Fur Seal *Arctocephalus* sp. Observations were too few to allow spatial analysis.

Annual primary production in the APF has been estimated to be 83 g C/m²/year (Wefer and Fischer, 1991). At that level, carbon consumption rates by the top predator community (birds and mammals) in and near the APF are in the order of 0.01–0.1% of primary production. Such values are in agreement with those for open-water zones in the Southern Ocean in an earlier study (cf. Table 4 in Van Franeker et al., 1997).

4.2. Broad-billed prions

The distribution pattern of the bird carbon requirements in the Fine-Scale Grid is dominated by broad-billed prions. Figs. 8A and B show two north–south cross-sections of the APF zone (cross-sections through Fig. 7, split into carbon consumption by the broad-billed prion and that of all other birds). The section along 10°46'E shows a transect leg with relatively few birds: here the

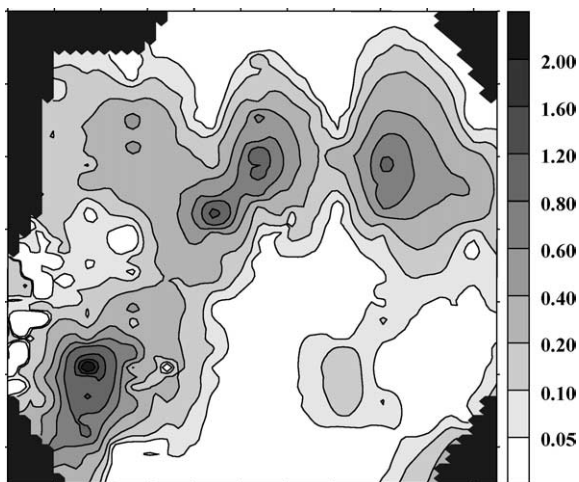


Fig. 7. Carbon consumption by seabirds in the Fine-Scale Grid area (mg C/m²/day). Latitude and longitude scaling as in Fig. 3.

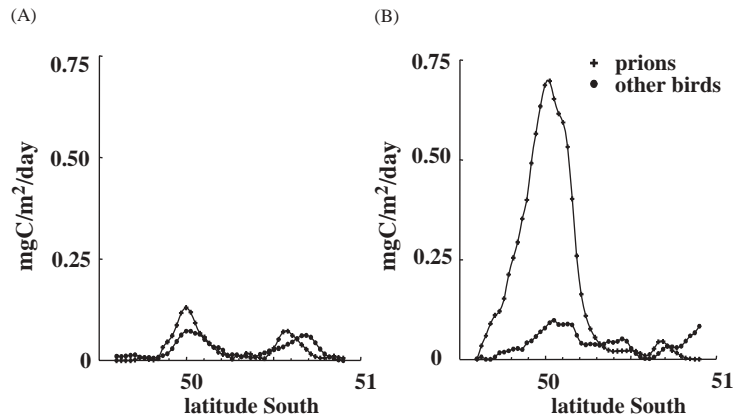


Fig. 8. North-south cross-sections of Fig. 7 at two longitudes (A) 10°46'E and (B) 11°04'E, showing separate carbon requirements of the broad-billed prions as the main consumers, and the remainder of the seabird community, in the Fine-Scale Grid (gridded data).

broad-billed prion represents about 50% of the total carbon requirements. However, only a bit further west, along 11°04'E, its carbon requirement exceeds that of all other species more than five times. The figures emphasize the patchy nature of distributions even within a strong front like the APF.

For the whole Fine-Scale Grid, broad-billed prions represented 83% of the total carbon requirement. Broad-billed prion variance explains $\approx 96\%$ of the requirements of the total bird community. Thus, broad-billed prions not only require most of the carbon in this area, but also determine the spatial distribution of the community carbon requirement. Because of the importance of the broad-billed prion in the distribution of the seabird density and carbon requirements, we will discuss this species in more depth, and relate its distribution to other variables.

4.3. Food web structure

With available data, we can consider a simplified food web of phytoplankton production to zooplankton and ultimately seabirds, as driven by physical characteristics of the APF. Our focus is on the surface layer only, which can have aberrant spatial patterns from analyses of other depth ranges. Large zooplankton, fish, and cephalopods form an important intermediate food web level for

seabirds (Croxall, 1987; Rodhouse and White, 1995; Rodhouse et al., 1996) of which data are lacking in our study. Nevertheless, small copepod-sized zooplankton being an important prey of prions (Prince, 1980; Gartshore et al., 1988; Klages and Cooper, 1992; Liddle, 1994; Reid et al., 1997), we will relate the distribution of broad-billed prions to the data that we do have and will discuss the relevance of this analysis. Evidently, this is a simplification of complicated food web interactions (Lavigne, 1996).

Water temperature and salinity in our study area showed a distinctive pattern of relatively steep gradients (Figs. 2 and 3). The converging water-masses also were visualized by the concentrated occurrence of floating patches of seaweed (Table 1). The spatial pattern of the temperature gradient seemed to be followed by that of high primary production (δCO_2 ; Fig. 4A), and indeed regression analysis confirmed a highly significant linkage between the phenomena (Table 3). Furthermore, a highly significant relationship existed between total primary production (δCO_2) and the standing stock of phytoplankton (Table 3). Strass et al. (2002b) show the same for depth-integrated values and describe that meandering within the Polar Front and stabilization of the upper water column resulted in development of high phytoplankton biomass. The primary production per unit phytoplankton ($\delta\text{CO}_2/\text{Chl-}a$) was

also significantly related to phytoplankton standing stock and temperature gradient of the water (Table 3). In other words, zones with the steepest physical gradients spatially coincide with the highest primary-production rates (production per unit Chl-*a*), high standing stocks of algae, and high total primary production.

Although some sort of time lag may be anticipated, stocks of phytoplankton-grazing zooplankton are expected to respond to situations of productive and dense phytoplankton stocks and high total primary production. Results of regression analyses (Table 3) confirmed that indeed densities of all zooplankton size classes showed highly significant relationships to phytoplankton abundance/productivity and the physical gradients in the surface water.

The broad-billed prion showed significant positive relations with the frontal temperature gradients and phytoplankton variables, but less clearly so with zooplankton densities: there is a positive relation (Fig. 9), but not significant (Table 3; broad-billed prions all records). Lack of significance could have several backgrounds. Prey density is not necessarily the same as prey availability for birds (Heinemann et al., 1989). Also, there may be threshold levels in prey density (e.g., Mehlum et al., 1999) and bird density

(Schneider, 1990) before bird concentrations build up. Finally, there will be a time lag before prey concentrations are detected by birds. Such delay in response will exist in spite of the fact that seabirds use sophisticated cues such as olfaction to detect prey (Nevitt et al., 1995, 1999a, b).

For prions, Nevitt (2000) showed that dimethylsulfide (DMS) is an attractive odour: DMS is produced by phytoplankton when grazed by zooplankton.

Quantitative relationships between birds and the environment may be clearer above initial trigger levels of prey density or initial predator density. If we simply define initial bird density as above zero (Table 3; broad-billed prions positive records) the relationship between prions and zooplankton (all sizes OPC) is significant. The existence of a threshold level in zooplankton density is suggested by Fig. 9, but its proper quantification in the prion-zooplankton relationship would require data collection at even considerably finer scales than was possible in our study, with continuous zooplankton records in the top metre of the water surface.

Closer analysis of the relations between broad-billed prions and different size classes of zooplankton (Table 4) shows that the positive link mainly exists in the smallest zooplankton: the relationship is significant in the size class of 250–500 μm OPC diameter also when zero records of prions are included in the analysis.

As this smallest zooplankton size class seems too minute to be consumed by birds, a closer evaluation is warranted. Copepods are an important part of the diet of broad-billed prions (Prince, 1980; Klages and Cooper, 1992; Liddle, 1994). Small cyclopid copepods of mainly *Oithona* spp dominated our smallest OPC size class (Pollard et al., 2002). Would prions be able to forage on such small prey?

Assuming that OPC measurements represent the diameter of a sphere equivalent in volume to that of the particle measured (ESD-see methods), we should attempt to translate this to actual copepod morphology. Using length–weight relationships for several calanoid types of copepods (Klein Breteler et al., 1982; Klein Breteler pers. inf.; Mizdalsky, 1988), it may be estimated that the

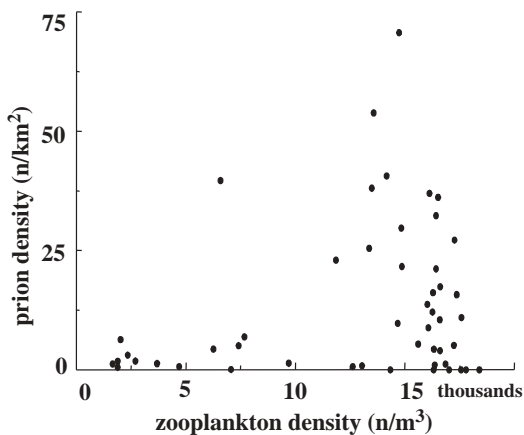


Fig. 9. Relation between zooplankton densities (all sizes) in the surface water and the density of broad-billed prions in the Fine-Scale Grid area, suggesting threshold levels in prey density or initial predator density.

Table 5

Estimates for calanoid copepod dimensions in different OPC size classes (freshweight estimated from sphere volume)

| OPC diameter ESD (μm) | Freshweight (mg) | Copepod length (mm) (cephalothorax + urosome) | Copepod width (mm) (cephalothorax) |
|---------------------------------------|---------------------|--|---------------------------------------|
| 250 | 0.008 | 0.47 | 0.11 |
| 500 | 0.065 | 1.00 | 0.22 |
| 1000 | 0.523 | 2.11 | 0.47 |
| 2000 | 4.187 | 4.50 | 1.00 |

body length (cephalothorax + urosome) of a copepod would be about twice its measured ESD (Table 5) whereas cephalothorax-width is slightly below half its ESD. Copepods in our smallest size class would thus measure between 0.5 and 1 mm in length, not including the (often substantial) antennae and tail-elongations.

Broad-billed prions possess lamellae in the bill like the filter plates in baleen whales (Warham, 1990; Klages and Cooper, 1992), which allow them to filter feed for small zooplankton like copepods. Minimum lengths of copepods in diet samples of broad-billed prions have been recorded as 0.7 mm in *P. vittata* (Klages and Cooper, 1992) to 0.9 mm in *P. desolata* (Prince, 1980); average lengths in samples were 1.7 mm and higher.

From bill morphology, Klages and Cooper (1992) concluded that *P. vittata* has a filter mesh size of 0.16 mm between the numerous lamellae. Within the group of broad-billed prions, they suggested that *P. desolata* was a less efficient filter feeder because it has a smaller bill with fewer lamellae, whereas *P. salvini* takes an intermediate position. Recent measurements (Norbert Klages, pers. commun.) in two *P. desolata* from Bouvet Island demonstrated gaps between lamellae of 0.19 and 0.20 mm, and 0.16 mm in a *P. salvini* from Marion Island. Using a 1:4 width to length ratio in copepods (Table 5), all three 'broad-billed' prions may thus be able to feed efficiently on copepod prey with lengths from around 0.8 mm upwards. Taking into account that extremities of copepods (antennae, legs, and tail elongations) were not included in size calculations in Table 5, we conclude that in our study area broad-billed prions were feeding on zooplankton in the 250–500 μm OPC size class and that the significant relationship in Table 4 represents a direct causal trophic link.

Broad-billed prions also feed on larger zooplankton and partly fish, sometimes even predominantly (Gartshore et al., 1988; Reid et al., 1997). The lack of significance in relations between broad-billed prions and larger zooplankton in Table 4 could be explained by lower abundance of larger zooplankton, rendering seizing of individual larger prey less attractive than filter feeding on the smallest zooplankton. Closer evaluation of available OPC data for the top 0–5 m surface layer suggests that abundance of the smallest OPC size class remains similar or increases all the way to the surface, but that larger size classes increasingly avoid the upper surface and do not show nocturnal migration into that layer (Pollard et al., 2002). Thus, our usage of OPC data from 17–25 m depths (to obtain complete coverage) is even likely to overestimate the abundance of larger zooplankton (ESD > 500 μm) in the surface layer of the water where broad-billed prions are able to feed. As indicated, the OPC does measure presence of larger zooplankton, which was demonstrated by measurements far south of the APF. This supports the idea that it was only the zooplankton in the 250–500 μm OPC size class that determined the distributional pattern of the broad-billed prions. Non-significance of the relationships to the larger OPC classes does not mean that feeding on larger zooplankton did not occur; it only indicates that variability in densities of larger zooplankton in the APF were not the primary determinants of broad-billed prion distribution. Our analyses thus show a remarkable spatial coherence on a small-scale (within few tens of kilometres) between physical frontal gradients in the APF and the simplified food web up to the level of small zooplankton feeding seabirds.

At this small spatial scale one might expect that time lags for responses between different trophic levels would obscure detectability of the patterns. Apparently, in spite of dynamic interactions between currents, wind and waves, the spatial coherence of the APF gradient zones persists over sufficient time to allow phyto- and zooplankton stocks to build up to levels exploitable by seabirds. Once these occur in a structured pattern, prions can respond rapidly because of their speed of movement and advanced searching techniques such as olfaction.

4.4. The wider region and other top predators

Insufficient data are available to conduct similar analyses in the Coarse-Scale Grid (Transect 6). However, we can compare the relations between Chl-*a* levels and zooplankton abundance (OPC, all sizes) in both the grid areas (Fig. 10). The regression lines appear similar and the asymptotes of the different lines are not significantly different. This indicates that spatial patterns and food web structure of the Fine-Scale Grid are likely to be valid in the Coarse-Scale Grid as well.

None of the other five regular seabird species in the Fine-Scale Grid (Figs. 5A–D and F) showed a distributional pattern as clear cut as that of the broad-billed prion, and low densities impair quantitative analyses. However, for all these five species, it is clear that they do not concentrate

along the narrow steep gradient zone of the APF in a manner similar to the broad-billed prion. Dietary preferences of all five species are mainly squid and fish, with only a minor crustacean component (Prince and Morgan, 1987; Marchant and Higgins, 1990; Del Hoyo et al., 1992), so one to several trophic levels above the zooplankton preyed on by broad-billed prions. Apparently, these higher prey levels do not, on the scale considered, concentrate along the narrow gradient zone of the APF, at least not near the surface. Why they do not is unclear to us: mobile predators like fish would be expected to exploit similar types of prey as broad-billed prions (copepod-sized zooplankton).

However, on a wider spatial scale it is evident that all trophic levels respond to increased productivity in the APF. Most numerically important bird species show decreasing densities away from the front (Table 1) and as discussed, carbon consumption by the total bird and mammal community follows that pattern. Time lags between responses by subsequent trophic levels, in combination with the dynamic nature of the APF will gradually diffuse spatial patterns and food web relations. Tackling such issues in more detail will require considerable effort because of sampling problems in quantitative surveys of macroplankton, fish and squid, and decreasing predator densities when stepping up the trophic ladder.

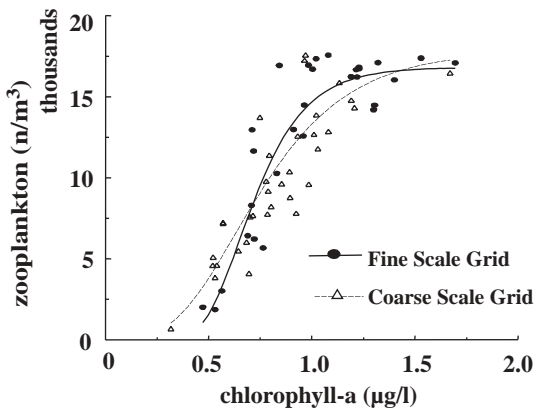


Fig. 10. Chl-*a* to zooplankton relations in the Fine- and Coarse-Scale Grid.

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