Vol. 136: 37-50, 1996 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published June 6

Cephalopods and mesoscale oceanography at the Antarctic Polar Front: satellite tracked predators locate pelagic trophic interactions

P. G. Rodhouse*, P. A. Prince, P. N. Trathan, E. M. C. Hatfield, J. L. Watkins, D. G. Bone, E. J. Murphy, M. G. White

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, United Kingdom

ABSTRACT: Predator data and exploratory fishing in the Scotia Sea have revealed the presence of cephalopod stocks in the Antarctic Polar Frontal Zone (PFZ). This is a vast, remote region where large epipelagic cephalopods aggregate into highly mobile schools making them difficult to locate and sample. We used satellite tagged predators and shipboard acoustics for coarse and fine scale location of cephalopod concentrations, and sampled them with commercial and scientific nets to determine the relationship between cephalopod distribution and mesoscale oceanographic features at the PFZ. Satellite tags were attached to 9 grey-headed albatrosses *Diomedea chrysostoma*, breeding at Bird Island, South Georgia, to monitor foraging at sea in January-March 1994. A foraging area at the PFZ, north of South Georgia, was located, an acoustic survey undertaken and a fixed station established where acoustic targets were found. A net survey was carried out with a commercial pelagic trawl, a rectangular midwater trawl 25 m^2 (RMT25), a horizontal multiple plankton sampler and a neuston net. Acoustic layers were targeted and the RMT25 sampled 200 m layers to 1000 m in daylight and darkness. Cephalopods were simultaneously recovered from food samples fed to *D. chrysostoma* chicks at Bird Island. Two CTD transects, approximately normal to the major current flow, were undertaken across the PFZ and remote-sensed sea-surface temperature images from NOAA polar orbiting satellites were obtained aboard ship. The pelagic trawl sampled a cephalopod community that closely resembled that exploited by *D. chrysostoma*. The largest and most conspicuous species was the ommastrephid squid *Martialia hyadesi* which is the most important cephalopod prey species. Net-sampled *M. hyadesi* had been feeding on crustaceans and mesopelagic fish. The cephalopod community was sampled in a feature, interpreted as a warm core ring, in an area characterised by mesoscale features associated with the bathymetry of the northern end of the Northeast Georgia Rise and near a gap in the Falkland Ridge. The association of these mesoscale features with the bathymetry suggests that they may be predictable foraging locations for the cephalopods and their predators.

KEY WORDS: *Martialia hyadesi* · Acoustic targets · Warm core ring · Grey-headed albatross

INTRODUCTION

The Antarctic Polar Frontal Zone (PFZ) is a complex, circumpolar transition region between the Antarctic and sub-Antarctic surface waters characterised by the presence of eddies and meanders (Gordon et al. 1977). Recent research has revealed that the PFZ supports an important, but little known, trophic system. During the 'Discovery' expeditions it was found that the diet of several vertebrate predators, especially southern elephant seals *Mirounga leonina*, included large numbers of cephalopods (Harrison-Matthews 1929). At that time the krill/baleen whale trophic system in the Antarctic was of primary interest and krill *Euphausia superba* was amenable to the research methods of the day so this species dominated ecological research in the Southern Ocean for several decades.

*E-mail: p.rodhouse@bas.ac.uk

Examining the cephalopod prey of vertebrate predators breeding at South Georgia, Clarke & Prince (1981) found the diet of some species, notably grey-headed and black-browed albatrosses *Diomedea chrysostoma* and *D. melanophrys*, to be dominated by an ommastrephid squid which was later identified as *Martialia hyadesi* (Rodhouse & Yeatman 1990). Further research indicated that *M. hyadesi* is the major squid prey of *D. chrysostoma* and *D. melanophrys* (Rodhouse et al. 1990, Rodhouse & Prince 1993), that it is one of the most important species in the diet of *Mirounga leonina* (Rodhouse et al. 1992a) and is present in the diet of the wandering albatross *D. exulans* (Rodhouse et al. 1987). Japanese exploratory fishing at the PFZ subsequently caught commercial quantities of *M. hyadesi* to the west of Shag Rocks (Rodhouse 1991).

Although it is not possible to assess the size of the Scotia Sea stock, annual consumption of *Martialia hyadesi* by predators is estimated to be >326000 t (Rodhouse et al. 1993). Stomach contents of the specimens caught by the Japanese jiggers showed that they had been feeding on mesopelagic fish, especially the myctophid *Krefftichthys anderssoni* (Rodhouse et al. 1992c). Their diet is dominated in turn by copepods (Gerasimova 1990) so this large myctophid/cephalopod/higher predator trophic system may be partially or fully independent of the *Euphausia superba* system. Evidence is emerging elsewhere in the Southern Ocean of apparently large myctophid-based trophic systems at the PFZ (Adams & Klages 1987, Hindell 1988, Cherel & Ridoux 1992). During the 1980s a commercial fishery developed for myctophids (Filin et al. 1990, Sabourenkov 1990) and, until former Soviet Union vessels largely withdrew from the Antarctic, catches dominated the total fin-fish catch in the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) area. Remotely sensed Coastal Zone Colour Scanner images of the Southern Ocean reveal high concentrations of plant pigments in some sectors of the PFZ, notably in the north Scotia Sea area, highlighting the presence of algal blooms and indicating elevated levels of primary production (Comiso et al. 1993).

The PFZ is a vast, remote oceanic region and many of the epipelagic cephalopods are highly mobile so until recently there were insurmountable difficulties for scientific sampling. The acquisition of the British Antarctic Survey (BAS) research ship, RRS 'James Clark Ross' in 1990, with facilities for handling commercial size trawls, coincided with the BAS 'Higher Predator Studies Group' research on foraging, distribution and activity of albatross species at South Georgia using satellite tagging (Prince et al. 1992) and the installation of a satellite receiving station at Rothera Station, Adelaide Island (off the Antarctic Peninsula) which provides synoptic sea surface temperatures (SSTs) from advanced very high resolution radiometer (AVHRR) data for the region. Together these provided the first opportunity to locate and sample concentrations of macro-nekton and interpret ecological processes at the PFZ. Here we describe the results of an interdisciplinary research cruise in January/February 1994 to examine pelagic ecology and predator/prey relations in the north Scotia Sea. Satellite-tagged cephalopod predators, *Diomedea melanophrys* and especially *D. chrysostoma*, were tracked in the period before and during the cruise and an area of foraging activity identified in the PFZ to the north of South Georgia. The ship went to this region, carried out an acoustic search, identified an area of acoustic targets in the water column and undertook a series of net surveys. Synoptic SST images were collected concurrently with a high resolution CTD (conductivity/temperature/depth) survey of the area immediately following the biological sampling programme.

We were thus able to establish the relationship between the distribution of the cephalopod community, the satellite tagged predators and associated mesoscale oceanographic features at the PFZ. Although much information has been gathered in recent years on primary production and plankton processes at fronts (Le Fevre 1986), there are few data on trophic interactions, especially among the large pelagic fish and cephalopods (Olson et al. 1994). Cephalopods are currently the third most valuable species group in the world marine harvest after shrimp and tuna (FAO 1992). There are large stocks of cephalopods in the Southern Ocean that straddle the CCAMLR area and these are key species in an ecosystem supporting large numbers of higher predators breeding at South Georgia and other peri-Antarctic Islands. Knowledge of the ecology of these stocks is essential for the effective management of this ecosystem.

Several acronyms are used in this paper They are defined where they first appear and for convenience are listed here: AAZ: Antarctic Zone; ARIES: Antarctic Reception of Imagery for Environmental Studies; AVHRR. advanced very high resolution radiometer; BAS: British Antarctic Survey; CCAMLR: Commission for the Conservation of Antarctic Marine Living Resources; CTD: conductivity/temperature/depth; GIS: geographic information system; H-AMPS: horizontal-Antarctic multiple plankton sampler; LRL: lower rostral length; NOAA: National Oceanic and Atmospheric Administration; ML: mantle length; PFZ: Polar Frontal Zone; PTT: platform terminal transmitter; RMT25: rectangular midwater trawl 25 m^2; SAZ: Sub-Antarctic Zone; SST: sea surface temperature; XBT: expendable bathythermograph.

MATERIALS AND METHODS

Satellite tagging and food sampling predators. In 1993 and 1994 *Diomedea chrysostoma* and *D. melanophrys* from the breeding colonies at Bird Island, off the northwest end of South Georgia, were tagged with Toyocom 2038 microwave platform terminal transmitters (PTTs) weighing between 65 and 75 g PTTs were attached using the method described by Prince et al. (1992). In 1993, from late January to early March, a total of 9 *D. chrysostoma* and 11 *D. melanophrys* albatross tracks were obtained from adults foraging at sea. For *D. chrysostoma* 1307 locations were obtained from 63 foraging trips and for *D. melanophrys* 2071 position fixes were obtained from 67 foraging trips. Fourteen meals delivered to *D. chrysostoma* and 12 to *D. melanophrys* chicks by adults bearing PTTs were either observed directly while the chick was being fed or collected from the adult using the method described by Prince (1980). Cephalopods in the samples were identified by comparison of lower beaks, gladii and soft parts with samples caught by nets and jigs in the Scotia Sea (Rodhouse 1989, 1990, Rodhouse & Yeatman 1990) and by reference to Clarke (1986). Lower rostral lengths (LRL) of beaks were measured to 0.1 mm with Vernier calipers and allometric equations given by Clarke (1986), Rodhouse & Yeatman (1990) and Rodhouse et al. (1992c) used to estimate mantle length (ML). Satellite position fixes during the foraging trips indicated the tracks taken by the adults and the approximate area where the prey was obtained.

In 1994 five PPTs were deployed on *Diomedea chrysostoma* in January, during the 4 wk preceeding the sampling programme in February, in order to locate an area where foraging was concentrated and to identify an appropriate survey site. *D. chrysostoma* only were used for this purpose as their diet contains a higher proportion of cephalopods (Prince 1980) of which *Martialia hyadesi* contributes about 90% of the biomass (Rodhouse et al. 1990). A total of 435 position fixes were recorded, from 17 foraging trips, of which 8 were completed by the start of the sampling programme.

Concurrent with the 1994 net sampling programme, food samples were collected from a total of 37 *Diomedea chrysostoma* and 38 *D. melanophrys* returning to the colonies at Bird Island. Samples were taken at approximately weekly intervals starting on 28 January with up to 10 samples from each species collected on each day. Methods of collection and analysis of cephalopod material were as for 1993.

PTT data handling. PTT data from the tagged *Diomedea chrysostoma* were relayed to Toulouse, France, via the Argos satellite system, sent daily to BAS headquarters in Cambridge and transmitted to the RRS 'James Clark Ross' On the ship, the PTT positional information was loaded into PC Arc/Info (ESRI), a geographic information system (GIS). The delay between a position fix and the data being processed on board ship was 4 to 24 h. Plots of individual predator foraging trips were generated by the GIS, as well as a compilation plot of all trips made to the PFZ. During the 24 h prior to the start of the acoustics and net sampling programme the positions of 3 *D. chrysostoma* foraging at the PFZ were plotted at 4 h intervals. Following the acoustic transects a fixed station was established among these position fixes, at 49° 48' S, 37° 28' W.

Acoustics. ***Equipment:*** Acoustic data were collected with a Simrad EK500 echo-sounder and integrator operating at frequencies of 38 and 120 kHz through hull-mounted transducers. Calibration of the echo-sounder system was carried out at Leith Harbour, South Georgia, on 7 January and 17 February 1994. Calibration procedures followed those of Foote et al. (1987) and Simrad (1992) whereby a target sphere of known backscattering cross-section was suspended below each transducer in turn.

Integrated data were collected during transects and net hauls from a depth of 10 m below the transducer to a depth of either 250 or 850 m below the transducer. All integrated data were logged to PC using a custom programme written in Labwindows. Continuous records of the ping-by-ping records were printed onto 2 paper charts; the first recorded 38 and 120 kHz data from 10 to 250 m, the second recorded 38 kHz between 10 and 1000 m. Echo-integrator summary tables were printed on the first paper chart at 2.5 min intervals.

Survey design: A series of zig-zag acoustic transects, coupled with surface oceanographic measurements and predator observations, were made along the frontal zone through areas where satellite-tagged *Diomedea chrysostoma* were foraging (Fig. 1).

Data processing: Integrated data were processed and viewed using custom modules of the Application Visualization System (Socha et al. 1996) and spurious data points definitely attributable to non-biological targets removed. The data were compensated for background noise using the technique described in detail in Watkins et al. (1996), loaded into an Oracle data base and merged with latitude and longitude for the beginning of each integration period.

Net sampling. ***Pelagic trawl:*** Larger cephalopods were sampled with an Ymuiden Stores (Netherlands) 2800 pelagic trawl (head rope: 93.2 m; side rope: 85.5 m; foot rope: 105 m). Two double oblique hauls of 2 h duration each were made through the fixed station (Fig. 2), one during daylight to 1000 m and the other during darkness (defined by local sunrise and sunset) to 300 m. A further 2 h haul targeting acoustic marks was made to a depth of ca 100 m in darkness.

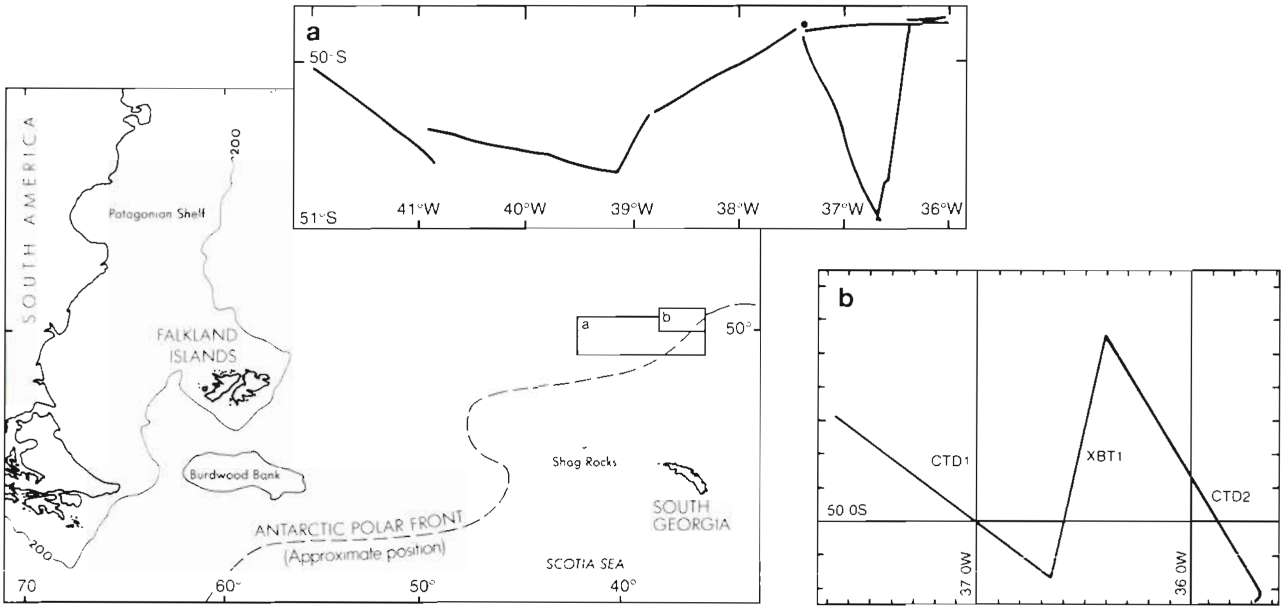

Fig. 1. Map of southwest Atlantic showing South Georgia and approximate position of Antarctic Polar Front. Inset a: acoustic transects at the Polar Frontal Zone in relation to the position of the fixed station of the sampling programme; inset b: CTD and XBT transects

Rectangular midwater trawl 25 m² (RMT25): Smaller cephalopods were sampled with an opening/closing rectangular midwater trawl with a design aperture of 25 m^2 (RMT25) (Piatkowski et al. 1994). At the fixed station each 200 m layer from the surface to 1000 m was sampled by nominal 1 h downward oblique tows, twice in daylight and once in darkness. Volume filtered ranged between 131 and 279×10^3 m^3 (mean 209 ± 53) according to Wormuth & Roper's (1983) recommendation. A further 7 hauls targetting acoustic layers were made as follows: (1) 50 m, 30 min, daylight (×2); (2) 300 to 350 m, 45 min, daylight; (3) 375 to 400 m, 20 min, daylight; (4) 600 m, 30 min, daylight; (5) 50 m, 15 min, darkness; (6) 50 to 100 m, 15 min, darkness.

Horizontal-Antarctic multiple plankton sampler (H-AMPS): The opening/closing H-AMPS with a mouth aperture of 2 m^2 and a mesh size of 1.5 mm was deployed in a vertical series. At the fixed station each 100 m layer from the surface to 600 m was sampled by nominal 30 min downward oblique tows twice in daylight and once in darkness.

Neuston net: A rectangular frame net with a mouth aperture of 1 m^2 and a mesh size of 5 mm was deployed in the surface layer from the foredeck. Six daylight and 6 darkness hauls of 30 min each were carried out in the course of the study.

Cephalopod mantle length (ML) was measured to 1 mm. If only the head was recovered the beak lower rostral length (LRL) was measured to 0.1 mm and ML estimated using equations in Clarke (1986), Rodhouse & Yeatman (1990) and Rodhouse et al. (1990). Maturity was defined according to Lipinski (1979). Stomach contents were identified visually and data reported as percent occurrence (proportion of the total specimens of each cephalopod species in which each prey type was found).

Oceanographic data. Two CTD (Neil Brown Mk III) transects were undertaken to characterise the mesoscale oceanographic regime of the area. These transects were specifically sited across the region of biological interest, and were determined from the position of foraging predators fitted with PTT satellite tags. The orientation of the transects was a compromise between running as normal as possible to the major current flow and the local isobaths. CTD Transect 1 started at 49° 42' S, 37° 41' W and finished at 50° 10' S, 36° 39' W; CTD Transect 2 started at 49° 27' S, 36° 26' W and finished at 50° 13' S, 35° 40' W. Transects 1 and 2 consisted of 10 and 11 CTD stations respectively, with both having a nominal 10 km spacing between stations. The depths of the CTD casts varied; all casts were to at least 1000 m with intermittent profiles to near bottom. Expendable Bathythermographs (XBTs) (T7: range 760 m) were deployed approximately half way between the CTD stations and also at a nominal 5 km spacing on passage between CTD Transects 1 and 2 (XBT Transect 1). This crossed the major current flow in an oblique direction, but nevertheless added extra oceanographic coverage for the area.

At each CTD station water bottle samples were taken at standard depths between the surface and 200 m; additional samples were also taken at depths between 200 m and the bottom of the cast.

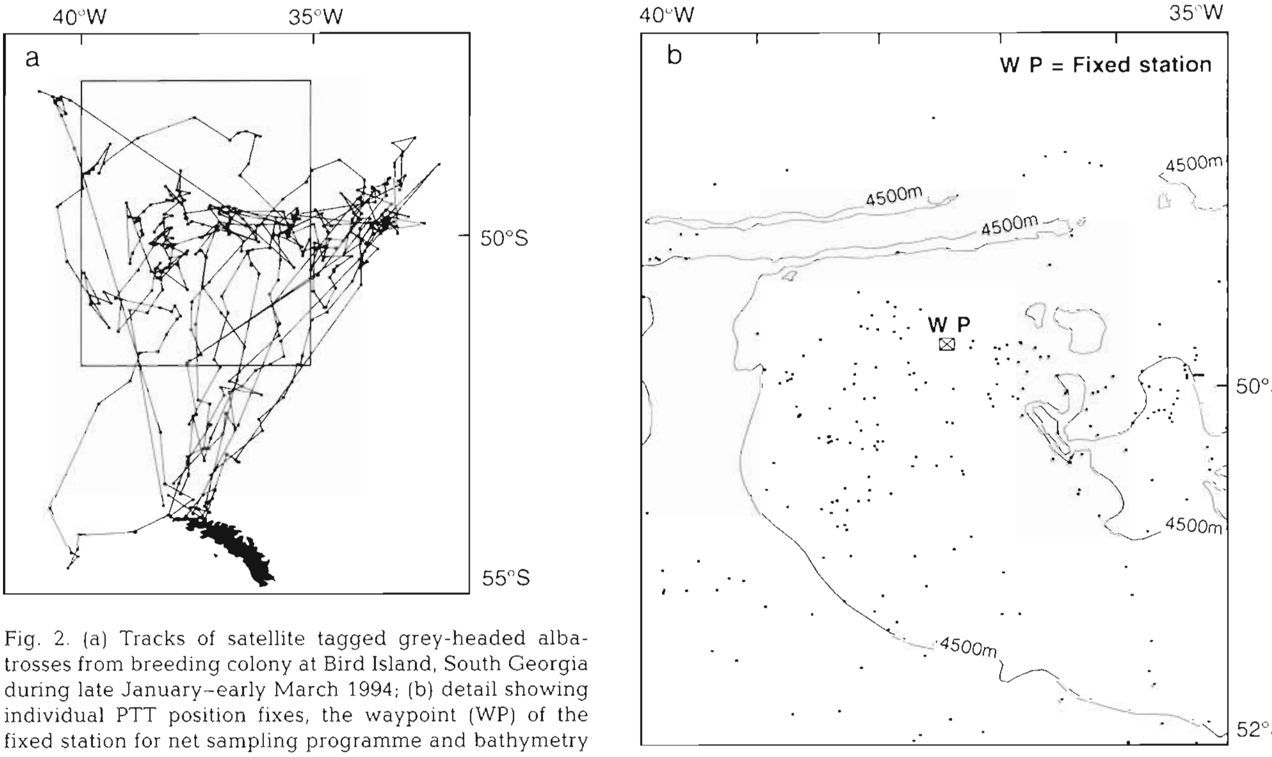

Fig. 2. (a) Tracks of satellite tagged grey-headed albatrosses from breeding colony at Bird Island, South Georgia during late January–early March 1994; (b) detail showing individual PTT position fixes, the waypoint (WP) of the fixed station for net sampling programme and bathymetry

Remotely sensed sea surface temperature. Remotely sensed SST images were obtained during the cruise from ARIES (Antarctic Reception of Imagery for Environmental Studies). These images were obtained from NOAA polar orbiting satellites using infra-red sensors operating at 11 µm and sensors operating in the visible spectrum. Images were transmitted to the ship providing information over substantial parts of the PFZ to the north of South Georgia. The images were transformed to a standard polar-stereographic projection and loaded onto the workstation GIS (Arc/Info ERSI).

RESULTS

Satellite tagging and food sampling predators

Cephalopods recovered from regurgitations of tagged *Diomedea chrysostoma* and *D. melanophrys* in 1993 are given in Table 1. The cephalopod prey of *D. chrysostoma* was dominated by *Martialia hyadesi* with a mean mantle length (ML) of 242 mm. PTT position fixes showed that all birds returning with *M. hyadesi* had been foraging at the PFZ to the north of South Georgia within a rectangle defined by 50 to 52° S and 34 to 42° W. Although *M. hyadesi* is usually an important element of the squid prey of *D. melanophrys* at Bird Island (Rodhouse & Prince 1993), none was recovered from these samples.

Of the 8 completed foraging trips by *Diomedea chrysostoma* tracked in 1994 prior to the sampling programme, 7 were made to the PFZ to the north of South Georgia. The 8th was made to the south and is not considered further here. The 7 tracks made to the PFZ are shown in Fig. 2 along with a larger scale plot of individual PTT position fixes. Spacing of fixes indicates that the birds were travelling to the north and concentrating their foraging along the east/west axis of the PFZ at a latitude of ~50° S.

Cephalopods recovered from regurgitations of untagged *Diomedea chrysostoma* and *D. melanophrys* feeding their chicks at Bird Island in 1994 are given in Fig. 3. The cephalopod prey of both species was dominated by *Martialia hyadesi* and smaller numbers of *Galiteuthis glacialis*. There was no significant difference (t-test: $p > 0.10$) between the mean ML of *M. hyadesi* from the 2 species of albatross. Nor was there any significant difference ($p > 0.10$) between the mean ML of *M. hyadesi* from *D. melanophrys* in 1994 and those from *D. chrysostoma* in 1993. The mean ML of *M. hyadesi* from *D. chrysostoma* in 1994 was significantly less than from the same species in 1993 (t-test: $p < 0.01$), but the difference of 23 mm was small.

Table 1 Cephalopods recovered from food samples delivered to chicks at Bird Island, South Georgia (Antarctic) by satellite-tagged grey-headed and black-browed albatrosses between late January and early March 1993

Cephalopod species	Grey-headed albatross Estimated ML, mm (range)	Mean	n	Black-browed albatross Estimated ML, mm (range)	Mean	n
Gonatus antarcticus	243		1			
Moroteuthis knipovitchi				279		1
Martialia hyadesi	218-306	242	10			
Galiteuthis glacialis	207		1			
Parelodene turqueti				60		1

Acoustics

The vertical pattern at the fixed station consisted of 3 main layers of acoustic targets (Fig. 4). A shallow layer, usually about 20 to 50 m thick, was found between 10 and 100 m throughout most of the study period. A deep layer about 100 to 150 m thick was found centred around depths of 600 to 700 m. A 3rd layer was frequently found between the deep and shallow layers. The depth and thickness of this middle layer was quite variable but a typical daytime depth layer was 300 to 400 m. However, during some daylight net hauls there was no obvious middle layer visible on the echo-chart. The thickness of the middle layer also varied from <20 to 150 m but overall density was usually the least of the 3 layers. At times, mostly during daylight, very dense, relatively small targets were found either imbedded within the middle layer (Fig. 4a) or within the top 100 m (Fig. 4b).

The 3 acoustic layers appeared to occupy 3 distinct depth zones with little overlap during either day or night. At sunset (21:00 h) on 8 February 1994 we observed the deep layer dividing. The lower part remained centred around 600 m while the upper migrated up towards the middle layer. At the same time the mid layer appeared to diffuse. By 22:30 h this upward migrating layer had reached 300 to 400 m, replacing the middle layer in the water column, and then starting to scatter and become very diffuse.

Acoustic backscatter from organisms within the 3 layers was typically in the range −69 to −75 dB at 38 kHz. For animals such as squid, with a target strength (TS) of around −45 to −50 dB (Arnaya et al. 1989a, b), this would correspond to a numerical density of 0.01 to 1 animals 100 m^{-3}.

Cephalopods from net samples

The 4 nets caught a total of 109 specimens of pelagic squid representing 10 species (Fig. 3). The largest and most conspicuous was *Martialia*

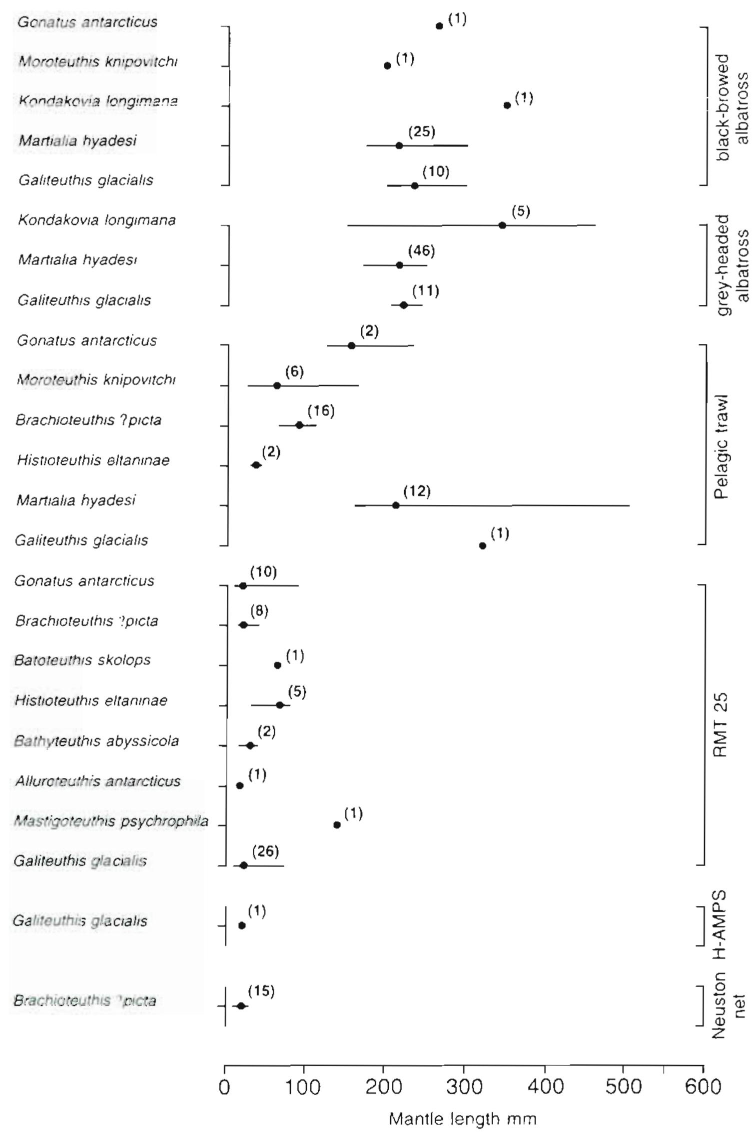

Fig. 3. Cephalopods from research net hauls at Antarctic Polar Frontal Zone and from predators sampled at Bird Island in February 1994 (median mantle length and range; mantle length estimated from beak lower rostral length in the case of predator samples)

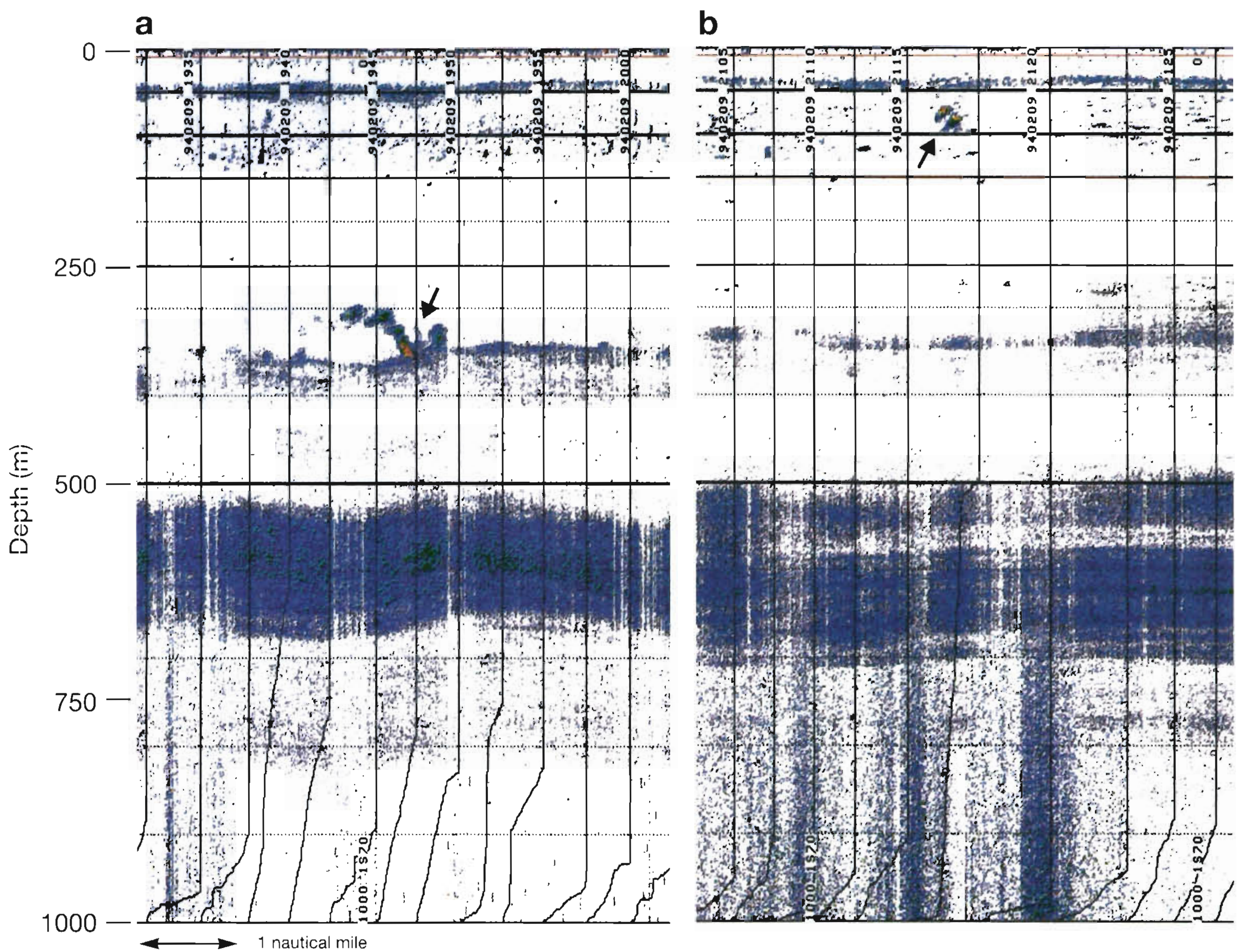

Fig. 4. Echograms produced by EK500 echo-sounder operating at 38 kHz. (a) General pattern of 3 acoustic layers (blue area) and dense targets (arrowed yellow/red area) in mid afternoon (16:45 h local) imbedded in middle layer at around 350 m. (b) Echogram with dense targets (arrowed yellow/red area) in top 100 m taken in evening (18:20 h local). Note that annotated time on echograms is GMT (= local + 3 h)

hyadesi, caught with the pelagic trawl. Most specimens fell in the size range 161 to 248 mm ML and there was a single much larger specimen with a ML of 506 mm. This could not be identified with certainty because the head was stolen by an albatross as the net came aboard but the shape of the mantle and fins, along with the characteristic purple skin, left little doubt as to its identity. The male:female ratio of the sample was 1:2. The smaller specimens of both sexes were all at maturity stage II (immature). The single large specimen (ML = 506 mm) was a female at maturity stage III (preparatory). Most specimens were removed from meshes in the wings of the net and few reached the cod-end, suggesting that the net considerably undersampled the population. There was no significant difference (t-test: $p > 0.10$) between the ML of *M. hyadesi* caught by the net (excluding the 506 mm ML specimen) and those sampled from *Diomedea chrysostoma*. The mean ML of *M. hyadesi* caught by the net was 23 mm less than those from black-browed albatrosses and this difference was significant (t-test: $p < 0.05$).

Among the other species of squid the largest were also caught by the pelagic trawl, followed in order of decreasing size by the RMT25, H-AMPS and neuston net. There was little overlap between the size ranges sampled by the different nets (Fig. 5). The RMT25 caught the greatest number of species but did not sample 2 species, *Martialia hyadesi* and *Moroteuthis knipovitchi*, which were only caught with the pelagic trawl.

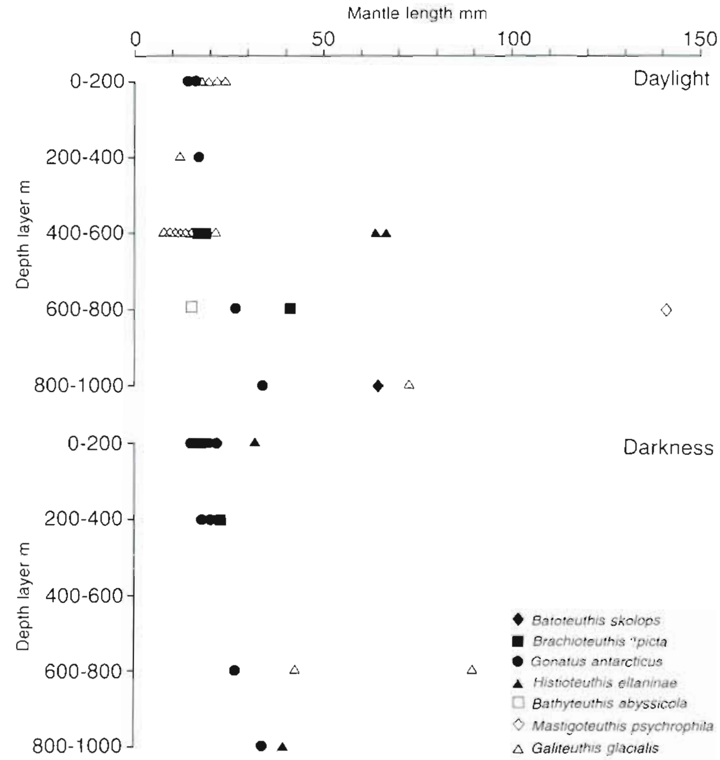

Fig. 6. Vertical distribution of cephalopods at the Antarctic Polar Frontal Zone in February 1994, sampled by the RMT25

The commonest species in the net samples was *Brachioteuthis ?picta*, which is rarely, if ever, taken by albatrosses. *Galiteuthis glacialis* was caught by all nets, except the neuston net, and was present in the regurgitations of both albatross species; the single specimen from the pelagic trawl was of similar size to the samples from albatrosses. *Gonatus antarcticus* was caught by the 2 larger nets as well as by a *Diomedea melanophrys* and those from the pelagic trawl and the albatross were of similar size.

The RMT25 vertical series (Fig. 6) showed that smaller *Gonatus antarcticus* and *Galiteuthis glacialis* are present throughout the water column to 1000 m. There is some evidence that *Brachioteuthis ?picta* and *Histioteuthis eltaninae* make an upward vertical migration in darkness. Specimens of *Batoteuthis skolops*, *Bathyteuthis abyssicola* and *Mastigoteuthis psychrophila* were all caught at depths >600 m.

The data from nets that targeted specific layers are given in Table 2. The neuston net and the RMT25 catches were similar in composition to those made at the same depths with the RMT25 during the vertical series. The pelagic trawl caught relatively large specimens of *Gonatus antarcticus*, *Moroteuthis knipovitchi*,

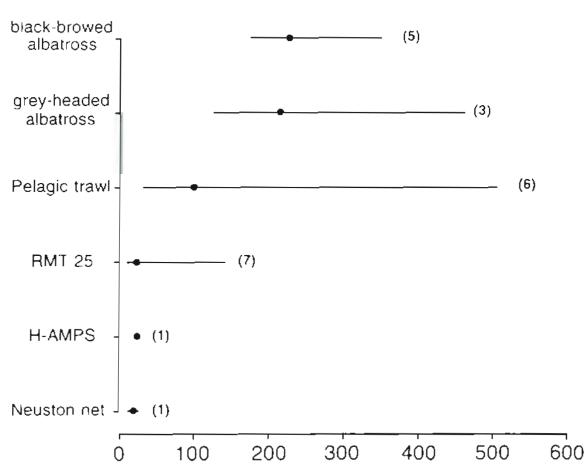

Fig. 5. Comparison of size of cephalopods and numbers of species from predators sampled at Bird Island and by nets at the Antarctic Polar Frontal Zone in February 1994 (median mantle length and range; mantle length estimated from beak lower rostral length in the case of predator samples)

Table 2. Cephalopods caught by pelagic trawl, RMT25 and neuston net targeting acoustic layers at the Antarctic Polar Frontal Zone in February 1994

Cephalopod species	Number of specimens	Mantle length, mm (range)
Neuston net surface (darkness)		
Brachioteuthis ?picta	15	12–24
RMT25 375 to 400 m (daylight)		
Galiteuthis glacialis	6	15–23
RMT25 600 m (daylight)		
Brachioteuthis ?picta	3	18–25
Galiteuthis glacialis	4	16–24
Histioteuthis eltaninae	2	67–79
Pelagic trawl 0 to 100 m (darkness)		
Gonatus antarcticus	1	124
Moroteuthis knipovitchi	5	48–62
Brachioteuthis ?picta	15	77–111
Martialia hyadesi	8	175–214
Galiteuthis glacialis	1	320

Brachioteuthis ?picta, *Martialia hyadesi* and *Galiteuthis glacialis* in the 0 to 100 m layer in darkness. Most of the *M. hyadesi* (66%) that were caught with the pelagic net were taken in that haul.

Cephalopod stomach contents

Stomach contents of each cephalopod species are given in Table 3. Crustaceans were the most frequent group, being present in all stomachs with contents, and they were the only prey present in all but 2 species of squid, *Martialia hyadesi* and *Histioteuthis eltaninae*. No crustaceans other than amphipods and copepods were identified. *Euphausia superba* was absent from the stomach contents. *M. hyadesi* also had remains of unidentifiable myctophid and squid species, and one specimen of *H. eltaninae* had cephalopod remains in the stomach.

Oceanographic data

On the basis of thermohaline stratification, 3 distinct water types can be distinguished to the north of South Georgia (Gordon et al. 1977). Features characteristic of the 3 water types are indicated on the temperature/salinity plots for the CTD transects (Fig. 7).

Sub-Antarctic Zone. The SAZ is characterised by a gradual increase in salinity with depth. There is no temperature minimum (T-min), although there is a rapid decrease in temperature between 100 and 300 m. Below this broad layer the water is nearly isothermal to 1000 m. In Fig. 7 the rapid decrease in temperature is indicated by SAZ-dt, and the nearly isothermal layer by SAZ-il.

Polar Frontal Zone. The PFZ may be identified by numerous density compensating temperature and salinity inversions. These layers extend from approximately 100 to 400 m. Below this layer, salinity gradually increases with depth, whereas temperature gradually decreases. In Fig 7 examples of the mesoscale variability associated with the temperature and salinity inversions are indicated by PFZ-dci.

Antarctic Zone. The AAZ is characterised by a well developed T-min. Below the T-min, the salinity gradu-

Table 3. Percentage occurrence of prey types in the stomach contents of cephalopods caught at Antarctic Polar Frontal Zone in February 1994 (crustaceans = all crustaceans including those identified to lower taxon; copepod = copepods not identified to species)

Cephalopod species	Fish (Myctophidae)	Crustaceans	Copepod	Copepod *Euchaeta* sp.	Amphipod *Themisto gaudichaudii*	Amphipod *Primno macropa*	Cephalopod	Stomach empty
Gonatus antarcticus ML 67–79 mm, n = 2		50			50			50
Moroteuthis knipovitchi ML 57–166 mm, n = 6		83			17			17
Brachioteuthis ?picta ML 31–111 mm, n = 20		81	20	10	57			19
Batoteuthis skolops ML 65 mm, n = 1								100
Histioteuthis eltaninae ML 67–79 mm, n = 2	50	50					50	
Bathyteuthis abyssicola ML 43 mm, n = 1								100
Martialia hyadesi ML 161–506 mm, n = 10	27	100				9	27	
Mastigoteuthis psychrophila ML 141 mm, n = 1								100
Galiteuthis glacialis 42–91 mm, n = 3								100

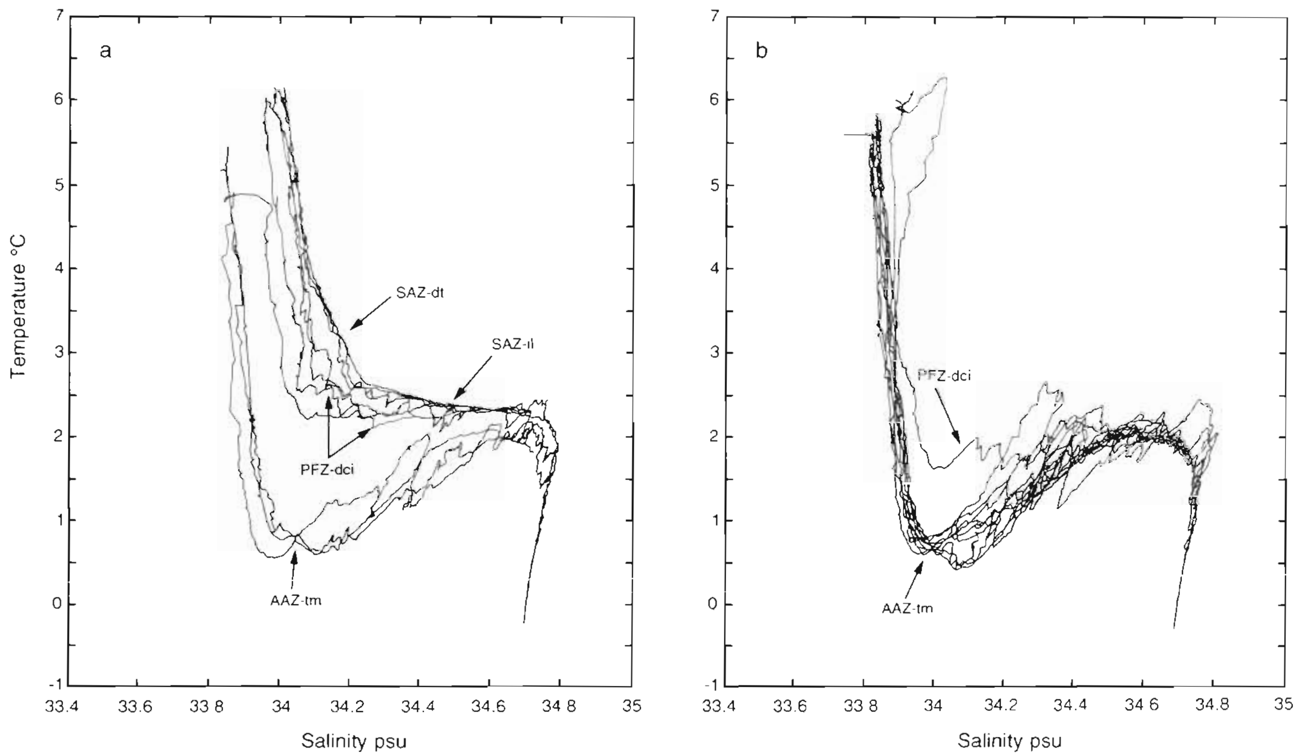

Fig. 7. (a) Temperature/salinity (T/S) plot along CTD Transect 1; (b) T/S plot along CTD Transect 2 (dt: decrease in temperature; il: isothermal layer; dci: density compensated inversions layers; tm: temperature minimum)

ally increases with depth. The T-min is indicated by AAZ-tm in Fig. 7.

Temperature and salinity profiles along the transects indicate substantial mesoscale variability. AAZ water was found towards the southern end of both CTD Transect 1 and XBT Transect 1 and across the centre of CTD Transect 2, whilst SAZ water occurred to the north of CTD Transect 1; PFZ water was found on all transects. Substantial vertical variability is also evident, with interleaving of the main water types.

The density profiles (σt) along CTD Transects 1 and 2 (Fig. 8) are not consistent with crossing a single mesoscale hydrographic feature, but suggest that a complex feature or set of features was sampled. From CTD Transect 1, the isopycnals (σt surfaces) indicate strong density differences, with the 27.4 kg m^{-3} surface occurring at 200 m toward the southern end of the transect, compared to 400 m at the centre and 350 m at the northern end. Such a density gradient is indicative of an easterly flow at the southern end of the transect and a westerly flow at the northern end. In comparison, along CTD Transect 2, the 27.4 surface is at 300 m at the southern end of the transect, at 200 m near the centre and at 250 m at the northern end. Such density gradients indicate an easterly flow at the northern end of the transect and a westerly flow at the southern end. The horizontal displacement of the

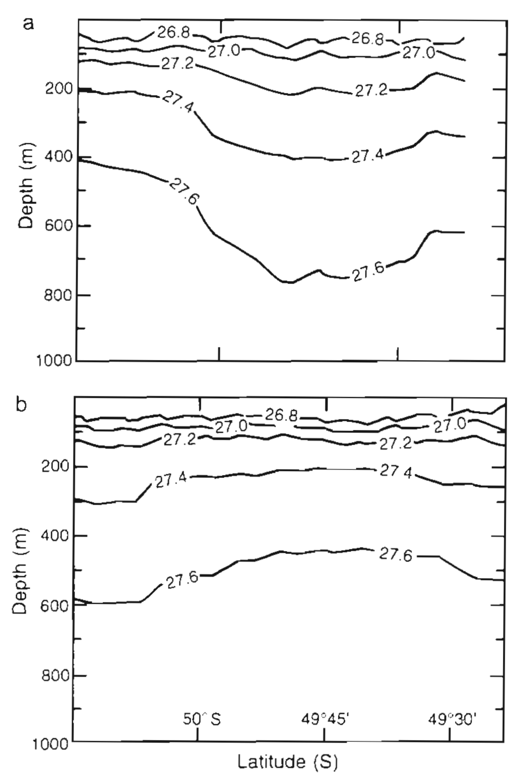

Fig. 8. (a) Density profile (σt) Transect 1; (b) density profile (σt) Transect 2

ship whilst on station during the transects was also consistent with these flows.

Calculation of geostrophic flow at 200 m (referenced to 1000 m) confirms the existence of these flows, with velocities approaching 0 cm s^{-1} on CTD Transect 2, to as much as 40 cm s^{-1} on CTD Transect 1.

Remotely sensed sea surface temperature

A SST image timed at the start of CTD Transect 2 is shown in Fig. 9. The image is entirely consistent with the oceanographic data collected on the ship and provides considerable clarification of the PFZ.

To the north of South Georgia, the area covered by CTD Transects 1 and 2 is largely cloud free. In this area the PFZ includes a large number of mesoscale features over the northern end of the Northeast Georgia Rise and near the gap in the Falkland Ridge. The meander or eddy at 37° 30' W, 50° 00' S matches very closely with CTD Transect 1; and suggests the existence of a warm core ring with approximate dimensions 140 × 80 km. The AAZ water passing east of this meander streams out over the gap in the Falkland Ridge. The middle of CTD Transect 2 cuts across the AAZ water, whilst the southern end lies close to a further mesoscale feature situated at 35° 00' W, 50° 00' S.

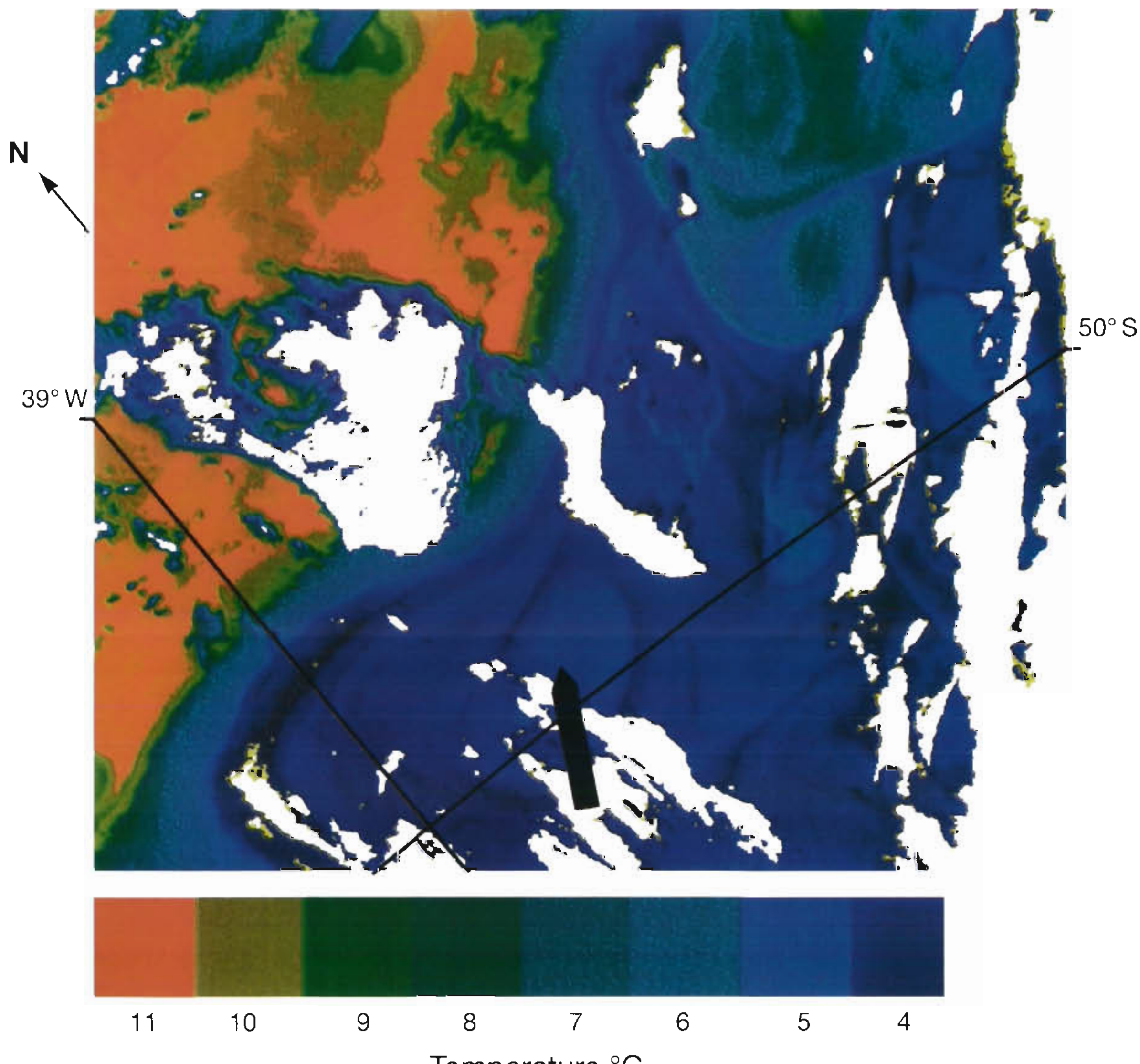

Fig. 9. False colour AVHRR image of sea surface temperature showing mesoscale features over northern end of Northeast Georgia Rise near the gap in the Falkland Ridge. Meander or eddy at 37° 30' W, 50° 00' S, within which the cephalopod community was sampled, is indicated with an arrow. Area covered by image is approximately 610 × 550 km

DISCUSSION

We have demonstrated that it is possible to use satellite-tagged foraging seabirds to identify the location of their cephalopod prey, to locate associated acoustic marks and sample their prey using a commercial scale pelagic trawl. We have discovered that *Diomedea chrysostoma* and possibly *D. melanophrys*, feeding their chicks at Bird Island with *Martialia hyadesi* and associated squid species, are primarily foraging in the vicinity of the PFZ. Furthermore, the cephalopod community was found in the same area as transitory mesoscale oceanographic features possibly related to the bathymetry of the North Scotia Ridge and Falkland Plateau. The apparent association of the mesoscale oceanographic features with the bathymetry suggests that they may be predictable foraging locations for the cephalopods and their predators.

The cephalopod community in the upper 100 m of the water column sampled with the pelagic trawl at night in the region of the PFZ where the albatrosses were foraging agrees well, both in terms of species composition and size range, with food samples collected from adult albatrosses at Bird Island during the present study, in 1993 and in earlier comprehensive studies of the cephalopod prey of these albatross species (Clarke & Prince 1981, Rodhouse et al. 1990, Rodhouse & Prince 1993). The albatrosses' prey is largely comprised of *Martialia hyadesi* with small numbers of other species. Of these, *Galiteuthis glacialis*, *Gonatus antarcticus* and *Histioteuthis eltaninae* were caught in the pelagic net and *Alluroteuthis antarcticus* was caught in the RMT25. Other squid species, *Kondakovia longimana* and *Chiroteuthis* sp., are of minor importance in the albatrosses' diet. They were not caught during the present study but have been sampled by nets in earlier studies in the PFZ (Rodhouse 1991, Rodhouse & Piatkowski 1995). However, the most frequent squid in the net samples, *Brachioteuthis ?picta*, is entirely absent from the albatrosses' diets. This is a relatively small species, and thus may not be of interest to albatrosses, although it is numerically the most abundant species of squid in the diet of southern elephant seals (Rodhouse et al. 1992a).

The pelagic net caught only a small number of *Martialia hyadesi* but exploratory jigging trials at the PFZ in 1989 (Rodhouse 1991) have shown that high densities of the species occur in the region. Furthermore, the South Georgia population of *Diomedea chrysostoma* has been reliably estimated to consume some 14 000 to 19 000 t of *M. hyadesi* per annum and other, less reliable, estimates of consumption by other predator species in the Scotia Sea are much higher (Rodhouse et al. 1993). The brief sampling with the pelagic net described here undoubtedly underestimated densities of the highly mobile and aggregated *M. hyadesi* at the PFZ.

Although the pelagic net caught a relatively small number of *Martialia hyadesi*, it revealed information that has not previously been available about the species from samples caught by commercial squid jiggers. The largest specimens sampled previously have been <340 mm ML whereas the pelagic trawl caught a specimen of >500 mm ML during the present study. The specimen from the trawl was a female that had not reached full sexual maturity which supports the conclusion, derived from statolith ageing studies, that *M. hyadesi* has a life span of more than 1 yr, possibly 2 (Rodhouse 1991, Rodhouse et al. 1994b). The life cycle of *M. hyadesi* is poorly understood. The small numbers of young juveniles caught on the edge of the Patagonian Shelf in the vicinity of the Falkland Islands (Rodhouse et al. 1992b) suggest that spawning takes place in the northwestern part of the Scotia Sea. There are 2 known areas of distribution of the early adult phase, the PFZ and the Patagonian Shelf edge. However, there is no information about distribution of juveniles or the large squid in what is presumed to be the 2nd year of the life cycle.

The presence of *Martialia hyadesi* and other cephalopod species associated with a warm core ring at the PFZ (Fig. 9) is consistent with observations elsewhere that mesoscale distribution of pelagic squid, especially ommastrephids, is related to frontal systems, and in particular to the eddy structure at fronts (Sugimoto & Tameishi 1992). Furthermore there is evidence that the distribution of another cephalopod predator, the sperm whale *Physeter catodon*, is associated with warm core rings on the northern edge of the Gulf Stream (Waring et al. 1993). At the PFZ the pelagic nekton community is dominated by small crustaceans, larger myctophid fish, the tunicate *Salpa thompsoni* and cnidarians (Piatkowski et al. 1994, Rodhouse et al. 1994a, F. Pagès, M. G. White, P. G. Rodhouse unpubl.). Smaller cephalopods prey on the crustaceans but the presence of larger *M. hyadesi* appears to be associated with the high densities of myctophid fish. Warm core rings presumably provide favourable conditions for the community that the cephalopods exploit.

At the PFZ the dominant top predators in the epipelagic system are cephalopods and not fish (Rodhouse & White 1995). The composition of the PFZ pelagic fish community is characterised by the absence of epipelagic families and typical members of the pelagic food-web in temperate and tropical seas. In the South Pacific there is an oceanic epipelagic fish community and some members of this, notably the slender tuna *Allothunnus fallai* (Yatsu 1995) and the Peruvian jack mackerel *Trachurus symmetricus murphyi* (Elizarov et al. 1993), extend into Sub-Antarctic waters but do not penetrate south of the Sub-Antarctic Front into the PFZ. There is no evidence that epipelagic fish are present in the PFZ in the Atlantic sector. Explanations for the absence of epipelagic fish in Antarctic waters, reviewed by Eastman (1993), include physiological constraints on white and red muscle physiology, the lack of a swim bladder in the predominant suborder of Antarctic fish, the Notothenioidei, and the highly seasonal food supply which would limit planktivores. There is no information on cephalopod muscle physiology at low temperatures. Buoyancy constraints may be minimised in ommastrephid and other muscular squid because they have no bones, they possess a large oil-filled digestive gland and they generate hydrodynamic lift with their fins and swimming keels. These constraints are eliminated in the bathyscaphoid cranchiids which possess ammoniacal coelomic fluids, and in species with ammoniacal musculature such as the histioteuthids.

The life cycles of *Martialia hyadesi* and other cephalopods at the PFZ are poorly understood and the ecology of this region has received scant attention from biological oceanographers. It is an important system for several Antarctic higher predators and has apparent potential to support commercial fisheries. Understanding the relationship between cephalopod life cycles and variability within the physical oceanographic regime of the PFZ is an important requirement for the rational management of this ecosystem.

Acknowledgements. We thank Tricia Gilmour, Carolyn Simon, John Croxall, Andy Wood, Keith Reid, Nick Huin, Mark Brandon and Andy Clarke (BAS Marine Life Sciences Division), Tom Lachlan-Cope and Richard Siddans (BAS Remote Sensing Group) and the ship's company RRS 'James Clark Ross' for their various contributions to this research. Development of the work station GIS was funded in part by the Worldwide Fund for Nature (UK). We thank 3 anonymous referees for their constructive criticism.

LITERATURE CITED

Adams NJ, Klages NT (1987) Seasonal variation in the diet of the king penguin (*Aptenodytes patagonicus*) at sub-Antarctic Marion Island. J Zool Lond 212:303–324

Arnaya IN, Sano N, Iida K (1989a) Studies on acoustic target strength of squid III. Measurements of the mean target strength of small live squid. Bull Fac Fish Hokkaido Univ 40:100–115

Arnaya IN, Sano N, Iida K (1989b) Studies on acoustic target strength of squid IV. Measurements of the mean target strength of relatively large-sized live squid. Bull Fac Fish Hokkaido Univ 40:169–180

Cherel Y, Ridoux V (1992) Prey species and nutritive value of food fed during summer to King Penguin *Aptenodytes patagonica* chicks at Possession Island, Crozet Archipelago. Ibis 134:118–127

Clarke MR (1986) A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford

Clarke MR, Prince PA (1981) Cephalopod remains in the regurgitations of black-browed and grey-headed albatrosses at South Georgia. Br Antarct Surv Bull 54:1–7

Comiso JC, McClain CR, Sullivan CW, Ryan JP, Leonard CL (1993) Coastal zone color scanner pigment concentrations in the Southern Ocean and relationships to geophysical surface features. J Geophys Res 98:2419–2451

Eastman JT (1993) Antarctic fish biology. Academic Press, San Diego

Elizarov AA, Grechina AS, Kotenev BN, Kuzetsov AN (1993) Peruvian jack mackerel, *Trachurus symmetricis murphyi*, in the open waters of the South Pacific. J Ichthyol 33: 86–103

FAO Fisheries Department (1992) Marine fisheries and the law of the sea: a decade of change. Special chapter (revised) of the State of Food and Agriculture 1992. FAO Fisheries Circular No. 853. FAO, Rome

Filin AA, Gorchinsky KV, Kiseleva VM (1990) Biomass of myctophids in the Atlantic sector of the Southern Ocean as estimated by acoustic surveys. SC-CCAMLR-SSP/7· 417–431

Foote KG, Knudsen HP, Vestnes G, MacLennan DN, Simmonds EJ (1987) Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Coop Res Rep 144:1–69

Gerasimova OV (1990) Feeding and food intake of *Electrona carlsbergi* (Tåning, 1932) Myctophidae. SC-CCAMLR-SSP/7:411–416

Gordon AL, Georgi DT, Taylor HW (1977) Antarctic Polar Frontal Zone in the Western Scotia Sea—Summer 1975. J Phys Oceanogr 7:309–328

Harrison-Matthews L (1929) The natural history of the elephant seal. Discovery Rep 1:235–255

Hindell MA (1988) The diet of the king penguin *Aptenodytes patagonicus* at Macquarie Island. Ibis 130:193–203

Le Fevre J (1986) Aspects of the biology of frontal systems. Adv Mar Biol 23:163–299

Lipinski M (1979) Universal maturity scale for the commercially important squids. The results of maturity classification of the *Illex illecebrosus* population for the years 1973–77. ICNAF Research Document 79/2/38, Serial 5364

Olson DB, Hitchcock GL, Mariano AJ, Ashjian CJ, Peng G, Nero RW, Podesta GP (1994) Life on the edge: marine life and fronts. Oceanography 7:52–60

Piatkowski U, Rodhouse PG, White MG, Bone DG, Symon C (1994) Nekton community of the Scotia Sea as sampled by the RMT25 during austral summer. Mar Ecol Prog Ser 11:13–28

Prince PA (1980) The food and feeding ecology of grey-headed albatross *Diomedea chrysostoma* and black-browed albatross *D. melanophrys*. Ibis 122:476–488

Prince PA, Wood AG, Barton T, Croxall JP (1992) Satellite tracking of wandering albatrosses (*Diomedea exulans*) in the South Atlantic. Antarct Sci 4:31–36

Rodhouse PG (1989) Pelagic cephalopods caught by nets during the Antarctic research cruises of the Polarstern and Walther Herwig, 1984–87. Arch FischWiss 39:111–121

Rodhouse PG (1990) Cephalopod fauna of the Scotia Sea at South Georgia: potential for commercial exploitation and possible consequences. In: Kerry K, Hempel G (eds) Antarctic ecosystems. Ecological change and conservation. Springer, Berlin, p 289–298

Rodhouse PG (1991) Population structure of *Martialia hyadesi* (Cephalopoda: Ommastrephidae) at the Antarctic Polar Front and the Patagonian Shelf. Bull Mar Sci 49:404–418

Rodhouse PG, Arnbom TR, Fedak MA, Yeatman J, Murray AWA (1992a) Cephalopod prey of the southern elephant seal *Mirounga leonina* L. Can J Zool 70:1007–1015

Rodhouse PG, Clarke MR, Murray AWA (1987) Cephalopod prey of the wandering albatross *Diomedea exulans*. Mar Biol 96:1–10

Rodhouse PG, Croxall JP, Prince PA (1993) Towards an assessment of the stock of the ommastrephid squid *Martialia hyadesi* in the Scotia Sea: data from predators. In: Okutani T, O'Dor RK, Kubodera T (eds) Recent advances in cephalopod fisheries biology. Tokai University Press, Tokyo, p 433–440

Rodhouse PG, Hatfield EMC, Symon C (1992b) Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. Mar Ecol Prog Ser 89:183–195

Rodhouse PG, Piatkowski U (1995) Fine-scale distribution of juvenile cephalopods in the Scotia Sea and adaptive allometry of the brachial crown. Mar Biol 124:111–117

Rodhouse PG, Piatkowski U, Murphy EJ, White MG, Bone DG (1994a) Utility and limits of biomass spectra: the nekton community sampled with the RMT25 in the Scotia Sea during austral summer. Mar Ecol Prog Ser 112:29–39

Rodhouse PG, Prince PA (1993) Cephalopod prey of the black-browed albatross *Diomedea melanophrys* at South Georgia. Polar Biol 13:373–376

Rodhouse PG, Prince PA, Clarke MR, Murray AWA (1990) Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. Mar Biol 104:353–362

Rodhouse PG, Robinson K, Gajdatsy SB, Daly HI, Ashmore MJS (1994b) Growth, age structure and environmetal history in the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Antarctic Polar Frontal Zone and on the Patagonian Shelf edge. Antarct Sci 6: 259–267

Rodhouse PG, White MG (1995) Cephalopods occupy the ecological niche of epipelagic fish at the Antarctic Polar Frontal Zone. Biol Bull 189:77–80

Rodhouse PG, White MG, Jones MRR (1992c) Trophic relations of the cephalopod *Martialia hyadesi* (Teuthoidea: Ommastrephidae) at the Antarctic Polar Front. Mar Biol 114:415–421

Rodhouse PG, Yeatman J (1990) Redescription of *Martialia hyadesi* Rochebrune and Mabille, 1889 (Mollusca: Cephalopoda). Bull Br Mus (Nat Hist), Zool 56:135–143

Sabourenkov EN (1990) Mesopelagic fish of the Southern Ocean—summary results of recent Soviet studies. SC-CCAMLR-SSP/7:433–457

Simrad (1992) Simrad EK500 scientific echo sounder, P2170E edn. Simrad, Horten

Socha DG, Watkins JL, Brierley AS (1996) A visualization-based post processing system for analysis of acoustic data. ICES J Mar Sci 53:335–338

Sugimoto T, Tameishi H (1992) Warm-core rings, streamers and their role on the fishing ground formation around Japan. Deep Sea Res 39(Suppl 1):S183–S201

Waring GT, Fairfield CP, Ruhsam CM, Sano M (1993) Sperm whales associated with Gulf Stream features off the northeastern USA shelf. Fish Oceanogr 2:101–105

Watkins JL, Brierley AS (1996) A post-processing technique to remove background noise from echo-integration data. ICES J Mar Sci 53:339–344

Wormuth JH, Roper CFE (1983) Quantitative sampling of oceanic cephalopods by nets: problems and recommendations. Biol Oceangr 2:357–377

Yatsu A (1995) Zoogeography of the epipelagic fishes in the South Pacific Ocean and the Pacific sector of the Subantarctic, with special reference to the ecological role of slender tuna, *Allothunnus fallai*. Bull Natl Res Inst Far Seas Fish 3:1–145

This article was submitted to the editor

Manuscript first received: October 25, 1995
Revised version accepted: January 4, 1996