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Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean

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ABSTRACT: Breeding grey-headed albatross *Thalassarche chrysostoma*, tracked from Marion Island (Prince Edward Islands) during November–December 1997 and January–February 1998, showed a strong association with mesoscale oceanographic features, as identified by sea surface height anomalies, in the southern Indian Ocean. During incubation, most birds foraged to the north of the island, at the edges of anomalies created by the Agulhas Return Current in the Subtropical Convergence and the Subantarctic zones. In contrast, during chick-rearing all tracked birds foraged to the southwest of the island, at the edges of anomalies along the South-West Indian Ridge. Previous work in this area has shown that these anomalies are in fact eddies that are created as the Antarctic Circumpolar Current crosses the South-West Indian Ridge. Diet samples taken during the chick-rearing period showed a predominance of fresh specimens of the predatory fish *Magnisudis prionosa* and the squid *Martialia hyadesi*. Myctophid fish and amphipods *Themisto gaudichaudii*, both known prey of *M. hyadesi*, were also well represented in our samples. Diet samples taken from tracked birds showed birds feeding at edges of positive anomalies returning with fresh specimens of *M. prionosa* and *M. hyadesi*. Predatory fish and squid are thus presumably concentrated at these features. Eddies formed at the South-West Indian Ridge have also been shown to drift closer to Marion Island, within the foraging range of penguins and seals breeding on Marion Island. We therefore suggest that these mesoscale oceanographic features may be an important component of the 'life-support' system enabling globally significant populations of seabirds and seals to breed at the Prince Edward Islands.

KEY WORDS: Albatross · Foraging ecology · Diet · Oceanography

INTRODUCTION

Pelagic seabirds, and especially albatross, display an extreme life history, with low reproductive rates, slow chick development, delayed onset of breeding and high adult survival (Warham 1996). Lack (1968) suggested that these breeding adaptations were the result of severe limitations on the rate at which adults could provide food to their chicks. These limits arise from the sparseness, patchiness and unpredictability of marine resources, as well as the large distances adults are required to travel to and from foraging areas (Ashmole 1971). It therefore follows that breeding birds should concentrate their foraging efforts in areas where resources are most predictable. Although foraging areas should ideally be located closest to their breeding colonies, in order to minimize time and energy required to travel to these areas, the closest foraging areas will also have the highest intra- and inter-specific

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competition and may also suffer local depletion first (Ricklefs 1990). It seems unlikely that pelagic seabirds and seals can deplete their stocks over the ocean as a whole, but it does seem reasonable that they are able to do this in the vicinity of their breeding colonies and in areas where prey becomes concentrated due to physical processes (Anderson & Ricklefs 1987).

Physical and biological processes in the ocean affect the distribution and abundance of plankton and nekton, which in turn affect the distribution of seabirds and marine mammals (Piontkovski et al. 1995, Pakhomov & McQuaid 1996). Studies have shown that seabirds are predictably concentrated at physical oceanographic features of different spatial scales, from tidal fronts through mesoscale eddies to latitudinal frontal systems, which all display increased prey availability (Haney et al. 1995, Pakhomov & McQuaid 1996, Rodhouse et al. 1996, Hunt et al. 1999). Once at an area of enhanced biological productivity, procellariforms may use odor trails or visual clues to locate concentrations of prey (Nevitt 1999).

Albatross living in the Southern Ocean are largely reliant on pelagic fish and squid (Cherel & Klages 1997). These prey items are patchily distributed and very little is known about the biological and environmental variables that govern their distribution (Cherel & Weimerskirch 1995). In this paper we demonstrate how grey-headed albatross, breeding at the sub-Antarctic Marion Island, are able to exploit mesoscale oceanographic features O(100 km) to O(1000 km) from their breeding locality, resulting from interactions between current systems and local bathymetry. In an attempt to understand more about the ecology of these oceanographic features, we describe the diet of these birds during the chick-rearing period, when birds showed a strong association with certain oceanographic features.

Physical environment

The Prince Edward Islands, of which Marion Island is the largest, lie in the Subantarctic, between the Subtropical Convergence to the north and the Antarctic Polar Front to the south (Lutjeharms & Valentine 1984). A secondary front, the Subantarctic Front, usually lies just to the north of the island group, but all 3 of these fronts exhibit considerable temporal changes in their latitudes (Lutjeharms 1990). Furthermore, a number of eddies of various sizes have been observed in the region, making it a complex physical environment (I.J.A. & J.R.E.L. unpubl.). Warmer, anti-cyclonic eddies were thought to come from north of the Subantarctic Front, and this has been borne out by the observed plankton content of such features (Froneman et al. 1999). The same holds true for colder, cyclonic eddies near the islands that seem to come from south of the Antarctic Polar Front. However, these eddies are not just vehicles for carrying foreign organisms; there is evidence that they intrinsically affect the primary productivity of their waters (e.g. Perissinotto & Duncombe Rae 1990, Ansorge et al. 1999, Froneman et al. 1999, Perissinotto et al. 2000) in ways that are not yet well understood.

The Subtropical Convergence has been shown to exhibit considerably enhanced levels of chlorophyll *a* and zooplankton standing stock, but this enhancement seems to occur at irregular intervals (Barange et al. 1998). This is true both in regions where this front is strongly developed (Pakhomov et al. 1994) and in regions where it is weaker (Barange et al. 1998). This enhancing effect is evident in colour observations from space (e.g. Lutjeharms et al. 1985, 1986, Weeks & Shillington 1994, Machu et al. 1999) as well as in *in situ* measurements (Allanson et al. 1981). However, it is not only the lowest trophic levels such as phytoplankton that are affected (Boden et al. 1988), but also fish and higher predators such as seabirds (Abrams 1983, 1985a, Abrams & Lutjeharms 1986, Abrams & Miller 1986).

All investigations of this type have shown that there is considerably higher mesoscale variability related to frontal systems than in other regions of the Southern Ocean. This has been shown from statistical investigations using accumulated hydrographic data (Lutjeharms & Baker 1980), from the movement patterns of surface drifters (Daniault & Menard 1985) and from satellite altimetry (e.g. Cheney et al. 1983). Investigations that have focused on the Subtropical Convergence have demonstrated that much of the variability here is due to the prevalence of eddies (Lutjeharms & Valentine 1988). It has subsequently been shown that the intensity of mesoscale variability at the Subtropical Convergence diminishes from a peak south of Africa to a low value at ~70°E (Lutjeharms & Ansorge in press), suggesting that the prevalence and intensity of eddies at this front would also decrease.

Secondary regions of high variability are found coincident with the Antarctic Polar Front, where the core of the Antarctic Circumpolar Current crosses mid-ocean ridges (Lutjeharms & Baker 1980, Colton & Chase 1983). This is particularly relevant to the environment of the Prince Edward Islands. These islands lie just downstream of the South-West Indian Ridge, which is crossed by the core of the Antarctic Circumpolar Current at about 50° S, 30° E (Read & Pollard 1993). Altimetric observations have shown that this specific location is a region of extraordinarily high mesoscale variability (e.g. Chenney et al. 1983, Wakker et al. 1990, Snaith & Robinson 1996) that extends eastwards to the vicinity of the islands (see Fig. 2). The key

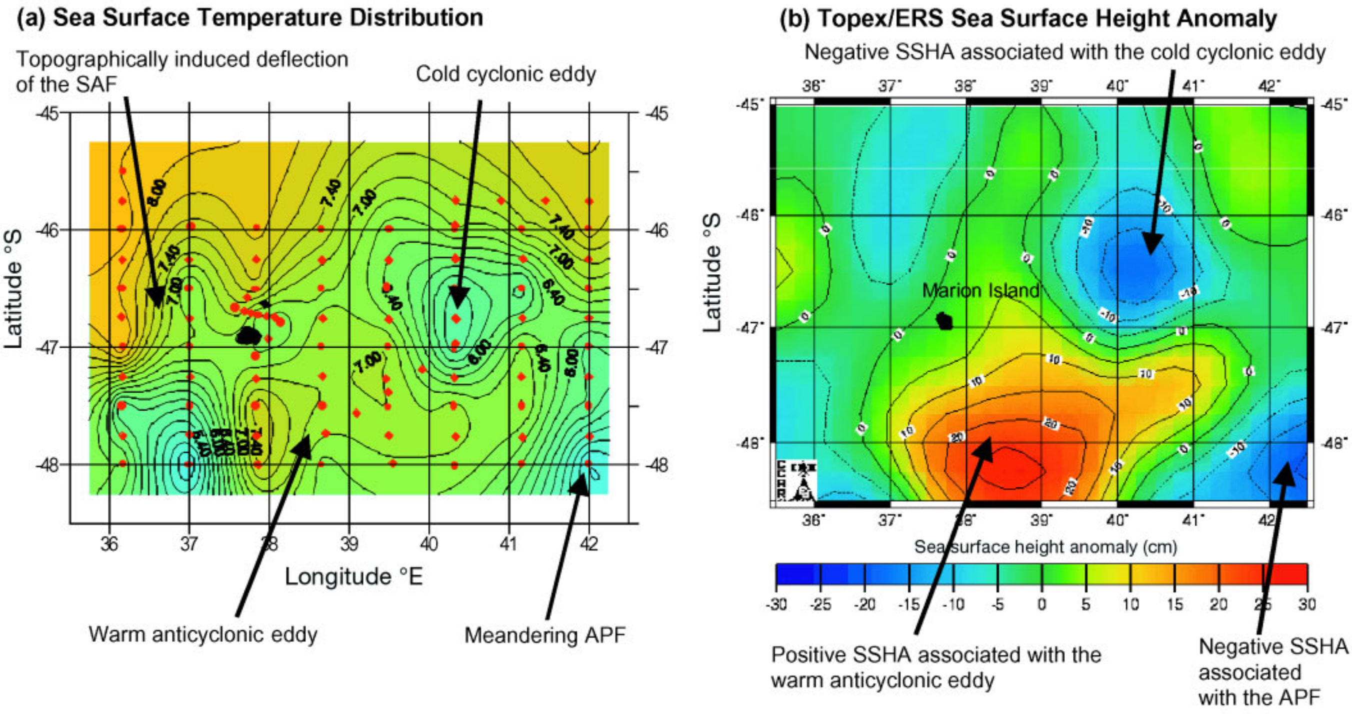

Fig. 1. (a) Sea surface temperature distribution as determined by a hydrographic survey and (b) blended TOPEX/ERS sea surface height anomaly (SSHA) data. Cold cyclonic and warm anticyclonic eddies are clearly visible as positive and negative anomalies in the TOPEX/ERS. APF = Antarctic Polar Front

question, from the point of view of marine organisms, is whether the unusually high variability at this location is due to meandering of the current or to the spawning of eddies. Hydrographic investigation of some of the features originating here and seen in altimetry (I.J.A. & J.R.E.L. unpubl.) show that they are indeed eddies (Fig. 1) that are created at the ridge and subsequently move towards and past the Prince Edward Islands. It seems that this area at the South-West Indian Ridge is the major source of eddies near

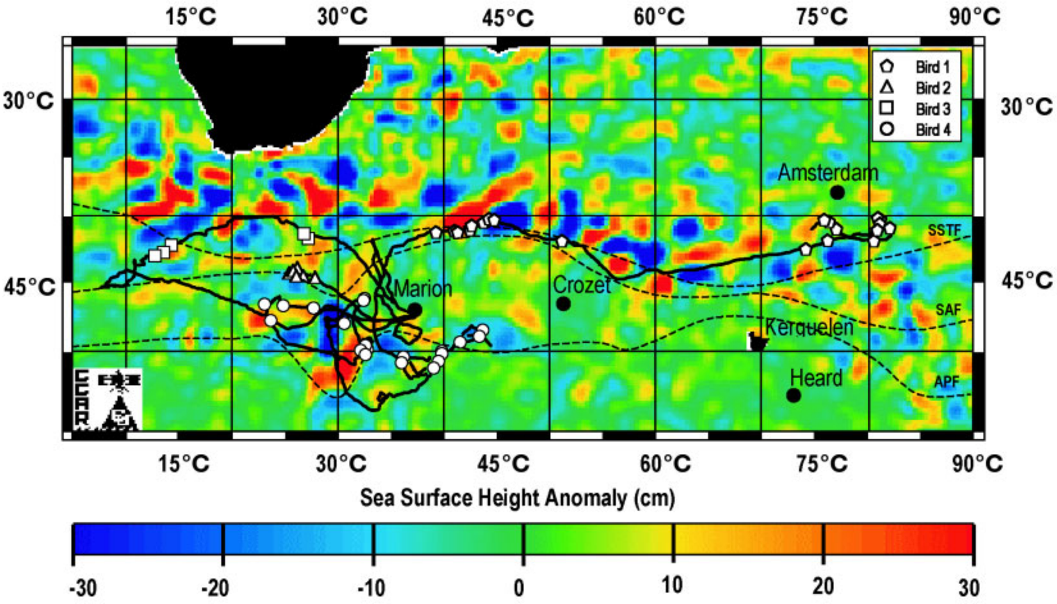

Fig. 2. Foraging tracks of 4 birds tracked from Marion Island by means of PTTs during the incubation stage. Symbols indicate birds moving at <10 km h^{-1} during the daytime, probably foraging. Dashed lines indicate approximate positions of major fronts (Belkin & Gordon 1996). SSTF = southern extent of Sub-Tropical Front, SAF = Sub-Antarctic Front, APF = Antarctic Polar Front

the islands and thus might be of considerable importance to the ecology of the region.

MATERIALS AND METHODS

Breeding grey-headed albatross were tracked using: (1) ST10 Platform Transmitter Terminals (PTTs), manufactured by Telonics (USA) and packaged by Sirtrack Limited (NZ); and, (2) pillbox Geo-Locating Sensors (GLS) manufactured by Driesen and Kern (DE). The methods by which these devices provide position fixes for the birds are described in Nel et al. (2000). PTTs provided successful locations at ~2 h intervals, with a normal accuracy of <5 km, while GLS only give 2 position fixes per 24 h period, with an accuracy of ~40 km.

The PTTs and GLS weighed <100 g and were attached to feathers on the back of the birds (between the wings) by means of adhesive tape. During late incubation (24 November to 17 December 1997) 2 males and 2 females were tracked for a total of 56 d using PTTs. Birds were captured immediately after they had been relieved of their incubation shift by their mates, and were taken to the side of the colony, where the devices were attached. Attachment took 10 to 15 min. During early chick-rearing (post-brooding, 20 January to 5 February 1998) 3 males and 3 females were tracked for a total of 61 d and 15 complete foraging trips, using 2 PTTs (on 1 male and 1 female) and 4 GLS (on 2 males and 2 females). Devices were attached to adults immediately after they had completed feeding their chick and were left on for successive foraging trips.

Movement data were plotted and spatially analysed using ARCVIEW GIS Version 3.0a (ESRI, Redlands, CA). All location classes were considered for analysis, unless the location proved to be implausible according to predicted maximum flying speeds by Pennycuik (1982). Distances were calculated using an equidistant azimuthal (south pole) projection. As grey-headed albatross generally forage during the day and rest on the surface during the night (Huin & Prince 1997), we considered plots of birds moving at <10 km h^{-1} during daylight hours to be indicative of concentrated foraging in an area. This is consistent with theoretical models that predict that high frequency of prey capture leads to an increase in complexity of movement and decreased velocity in order to maximise search effort in profitable areas (Knoppien & Reddingius 1985).

Data were analysed in relation to weekly satellite-derived TOPEX sea surface height anomaly data, available from the 'Colorado Centre for Astrodynamics Research' (CCAR) (http://www-ccar.colorado.edu). The TOPEX derived sea surface height anomaly represents a statistical measure of temporal variations in major current systems, caused by either mesoscale eddy activities, such as meandering and eddy shedding, displacement of current axes or fronts, or changing speed and direction of currents (Park & Gamberoni 1995). Regions of high mesoscale variability correlate closely with either the terminal region of a major western boundary current, such as the Agulhas Current or the Gulf Stream, or where the Antarctic Circumpolar Current interacts with prominent bottom topography, such as in the Drake Passage or at the Crozet-Kerguelen Plateau in the Southern Ocean (Lutjeharms & Baker 1980). The launch of TOPEX/POSEIDON in 1992 has resulted in continual mapping of global sea surface topography, from which surface geostrophic currents can be computed. Persistent attempts in the past, using infrared imagery to ascertain the circulation pattern in the Southern Ocean, have been foiled by almost continuous cloud cover. An advantage of using satellite altimetry is its ability to penetrate through cloud cover.

Thirty diet samples were collected from grey-headed albatross chicks between 25 January and 16 April 1998. Chicks were induced to regurgitate by inverting them over a bucket immediately after they had been fed by their parents. No ill effects of this procedure were noticed. Six diet samples were taken from chicks that had been fed by tracked parents. Four of these samples yielded fresh prey items that could be related to a specific tracked foraging trip. These nests were under constant surveillance during the daylight hours and none of these chicks had been fed by the other parent for at least 24 h prior to sampling. Prey items were judged to be fresh if fresh pieces of the flesh of the item were found in the sample.

Oceanographic fronts follow the descriptions of Belkin & Gordon (1996), and 'thermal zones' referred to in the text are defined as follows: the Sub-Tropical Frontal Zone (STFZ) is the broader extent of the Sub-Tropical Front (STF); the Sub-Antarctic Zone (SAZ) extends from the Sub-Antarctic Front (SAF) to the southern extent of the STF; and the Polar Frontal Zone (PFZ) extends from the Antarctic Polar Front (APF) to the SAF. See Fig. 2 for the approximate positions of these fronts.

RESULTS

Foraging movements in relation to physical oceanographic features

During incubation, 3 of the 4 birds moved north of the island to forage in the vicinity of the STFZ and the SAF (Fig. 2). All 3 of these birds appeared to initially forage at the interface between positive and negative sea surface height anomalies. Bird 1 foraged for 3.2 d at the edge of a large positive anomaly, situated in the

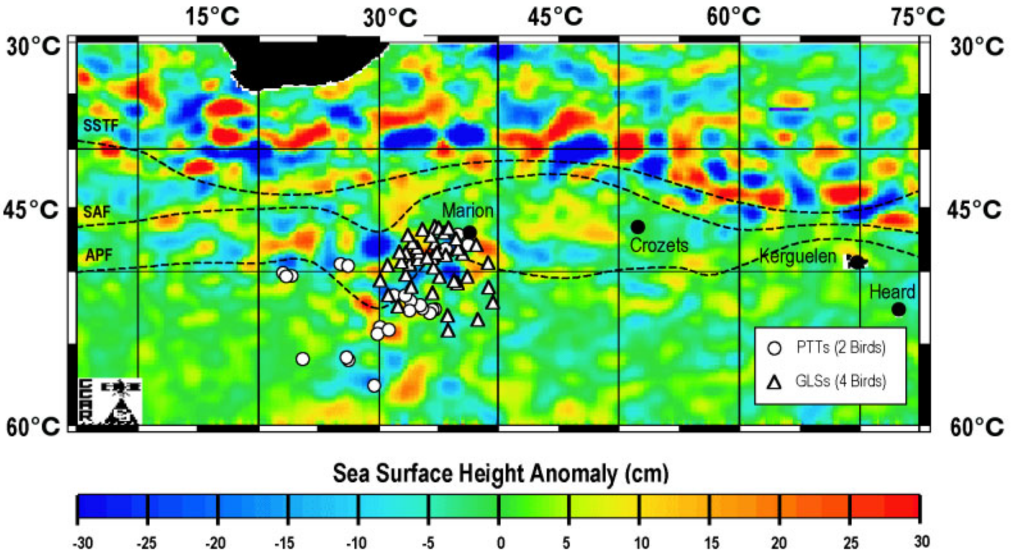

Fig. 3. Foraging distribution of 6 grey-headed albatrosses tracked from Marion Island (by means of 2 PTTs and 4 GLS) during the chick-rearing stage. All GLS positions shown; for PTTs, only positions where birds moving at <10 km h^{-1} during daylight (probably foraging) are shown. Dashed lines indicate approximate positions of major fronts (Belkin & Gordon 1996). SSTF = Southern extent of Sub-Tropical Front, SAF = Sub-Antarctic Front, APF = Antarctic Polar Front

STFZ ~750 km north of Marion Island, before moving farther east, tracking the string of positive and negative anomalies at the STFZ all the way to Amsterdam Island. Birds 2 and 3 moved northwestwards simultaneously and foraged around the same positive anomaly within the SAZ, ~1000 km northwest of Marion Island. Unfortunately the device on Bird 2 stopped functioning after it had foraged here for 3.5 d. Bird 3

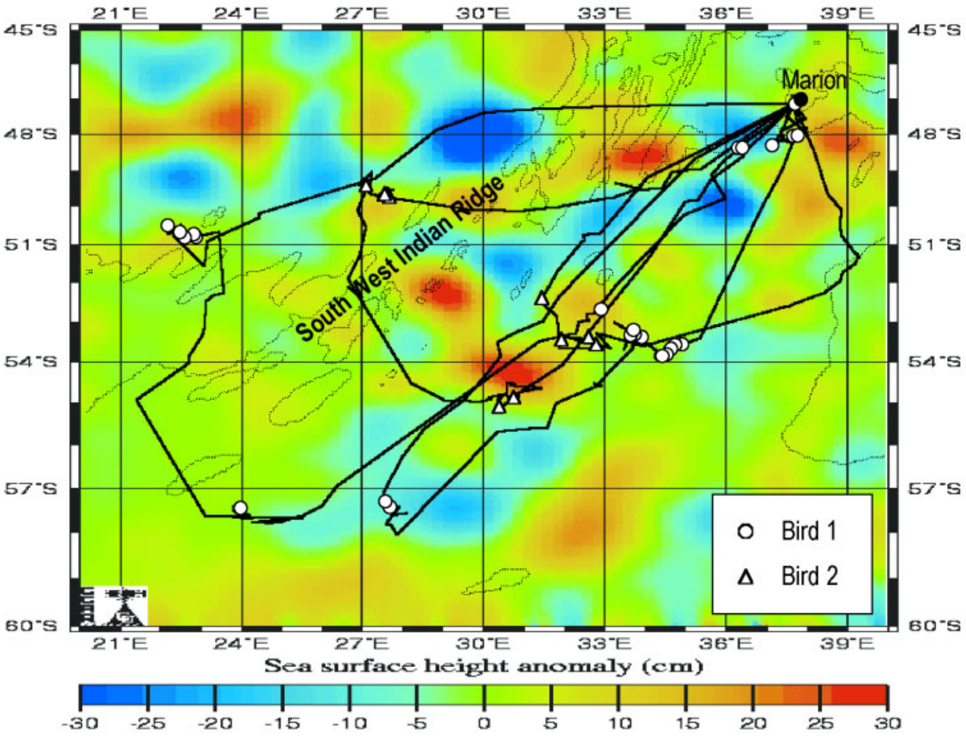

Fig. 4. Foraging tracks from Marion Island, using PTTs during chick-rearing stage. Symbols indicate birds moving <10 km h^{-1} during daytime, probably foraging. Tracks overlayed onto TOPEX/ERS satellite altimetry image. Dotted lines indicate 4000 m depth contour

continued in a westerly arc, passing over the STFZ before moving slightly southwards to forage at the edge of a large negative anomaly in the SAZ. The fourth bird displayed a highly erratic foraging track restricted mostly to the PFZ. However, much of its foraging activity was also concentrated around the edges of positive and negative anomalies.

During small chick-rearing, all 6 tracked birds moved south-west of the island and foraged here on 15 separate foraging trips (Fig. 3). This was despite the large positive anomalies at the STFZ still being well developed. On closer inspection of the fine-scale movements of PTT-tracked foraging trips (Fig. 4), we see that most foraging activity was concentrated on the edges of 2 closely associated positive anomalies at ~52° to 55° S and 30° to 34° E (~750 to 950 km away). Both PTT-tracked birds foraged in this area on successive foraging trips and both were also present in the area simultaneously. Foraging activity was also recorded at the interface of anomalies located closer to the island (between 100 and 400 km away). The edge of a positive anomaly just 100 km south of the island was visited on 3 out of 4 foraging trips made by the same bird. Foraging activity during longer foraging trips was concentrated around negative anomalies south of the APF (~1300 to 1800 km away). Most foraging activity was located on either side of the Southwest Indian Ridge. Foraging trips were also very directed during this stage. Birds flew rapidly and directly to an oceanographic feature before slowing down and starting to search for food.

General diet during the chick-rearing period

Fish (59 %) and cephalopods (32 %) were the major constituents of the solid fraction stomach contents. Crustaceans only contributed 3 % by drained mass. The most common fish species, both by relative abundance and frequency of occurrence was *Magnisudis prionosa* (Paralepididae), occurring in 30 % of samples (Appendix 1). This was also the largest fish prey item. The smaller myctophids were the second most common family and were represented in 27 % of samples. The most frequently occurring and largest squid prey species was *Kondakovia longimana* (Appendix 1). However, few of these specimens were fresh and this species was probably over-represented due to large beaks being retained for longer periods in the stomachs of chicks (Berruti & Harcus 1978). The second most frequently occurring species was the slightly smaller ommastrephid *Martialia hyadesi*, which was found in 47 % of the samples. 27 % of these specimens were very fresh (i.e. the beak was still attached to the whole squid, the crown of arms, or embedded in the buccal mass). The smaller *Chiroteuthis* sp. and *Histioteuthis eltaninae* both occurred in 33 % of the samples. *Chiroteuthis* sp. was also the most abundant squid. The cranchiid *Galiteuthis glacialis* was also represented in 30 % of the samples.

Decapod shrimps were found in 40 % of the samples (Appendix 1). These were mostly *Pasiphaea scotia*, while 2 larger *Austropandalus grayi* were also found in 2 separate samples. One complete *A. grayi* measured 215 mm. Euphausiids were found in 16 % of the samples. All specimens that could be identified to species level were *Euphausia superba*.

Large numbers of amphipods (mostly *Themisto gaudichaudii*) were found in 27 % of the samples. Amphipods were also found within the stomach of an unidentified fish.

Diet items associated with particular foraging tracks

Four diet samples, taken from the chicks of tracked adults yielded fresh prey items. The tracks relating to these samples are shown in Fig. 5. It is simple to associate an oceanographic feature with prey items acquired in Track 1 (Fig. 5a) and Track 3 (Fig. 5c), as these birds only foraged at a single type of feature (i.e. edges of warm eddies located ~900 and 400 km away respectively). The main prey item of both these foraging trips was the large fish *Magnisudis prionosa*. Both diet samples also contained fresh specimens of myctophids (*Electrona subaspera* and *Gymnoscopelus piabilis*) and the decapod shrimp *Pasiphaea scotia*. This procedure is slightly more problematic with Track 2 (Fig. 5b) as this bird foraged at 2 main locations. However, as most foraging time was spent at the edge of a positive anomaly, at the main area of variability (53° S, 33° E) and this is also the location at which the bird from Track 1 (Fig. 5a) captured 4 specimens of *M. prionosa* at the same time, it is most likely that this is where the specimen of *M. prionosa* in this sample was captured. The specimen of the squid *Martialia hyadesi* could have been captured at either the warm or the cold core eddy; however, given the frequency of very fresh specimens of this species recorded in our diet samples (Appendix 1), and the fact that Rodhouse et al. (1996) recorded this species in association with warm eddies at the APF in the Scotia Sea, it is most likely that this species was captured at the closer positive anomaly. *Euphausia superba* only occurs south of the APF (Pakhomov et al. 1994). It is thus most likely that it was this species that was captured at the cold core eddy (farther south). The bird from Track 4 (Fig. 5d) foraged at the edge of the positive anomaly just south of the island (~100 km away) and captured 5 very fresh specimens of the smaller squid *Chiroteuthis* sp. A single specimen of *M. hyadesi* was also recovered from this sample.

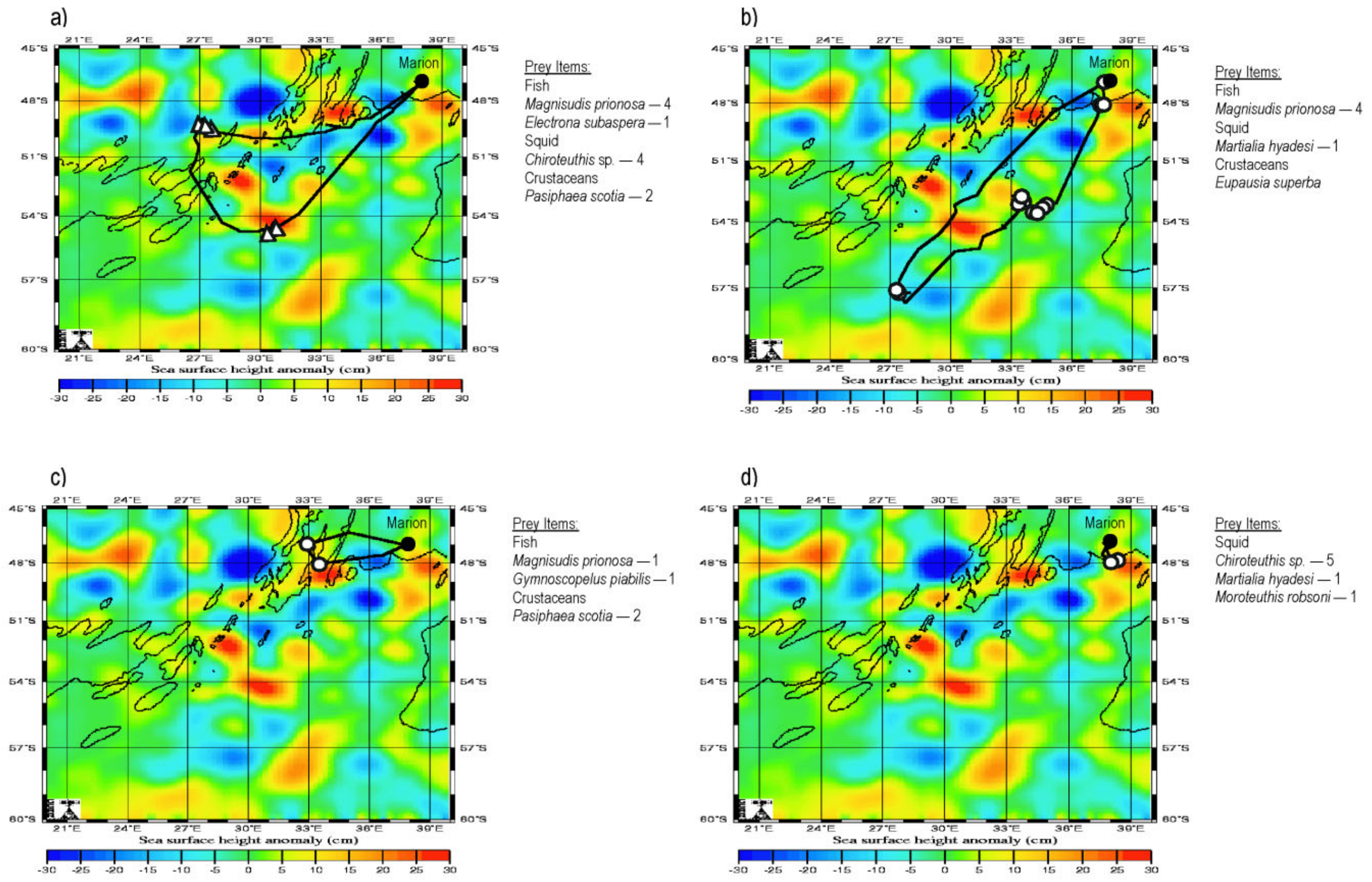

Fig. 5. Tracks from Marion Island during chick-rearing stage. Fresh prey items recovered from chicks shown next to relevant track. Symbols indicate bird moving <10 km h^{-1} during daylight, probably foraging. Dotted lines indicate position of 4000 m depth contour

DISCUSSION

Foraging movements in relation to physical oceanographic features

Grey-headed albatross tracked from Marion Island showed a strong association with oceanographic features expressed as positive and negative sea surface height anomalies, both during the incubation and chick-rearing stages. Interestingly, most foraging activity was concentrated at the edges of these anomalies or at the interface between positive and negative anomalies. During incubation, most birds preferred to exploit oceanographic features to the north of the island, in the STFZ and the SAZ. We cannot say unequivocally that these features, as seen in the altimetry, are eddies, but the results of previous hydrographic research in the region (e.g. Lutjeharms & Valentine 1988, Lutjeharms 1990) gives us confidence that this is the case. These features are formed largely as a result of the interaction between the Agulhas Return Current and bathymetric features such as the Madagascar Ridge (Pollard & Read 2001).

By contrast, during chick-rearing no foraging trips were made to the STFZ, despite oceanographic features still being well developed here, but were instead made exclusively to the southwest of the island. Most foraging activity occurred at the edges of altimetric features located to the south-west of the island and either side of the South-West Indian Ridge. A number of such mesoscale features have been investigated hydrographically (Ansorge et al. unpubl. ms.) and in all cases it has been shown that they are eddies. This area, to the leeward side of the South-West Indian Ridge was also used extensively by elephant seals *Mirounga leonine* tracked from Marion Island (Jonker & Bester 1998). Grey-headed albatross breeding on South Georgia have also been shown to forage at warm eddies in the PFZ, which occur predictably due to bathymetric features (Rodhouse et al. 1996). It is worth noting that although many of the eddies occurring on the South-West Indian Ridge, both cyclonic and anti-cyclonic, have been shown to eventually drift by the Prince Edward Islands (Ansorge et al. 2000), the birds preferred to utilize recently formed eddies. This suggests that the biological content of these eddies may change with time and/or that eddies located closer to the island experience higher levels of competition and local depletion by the large populations of non-aerial and less mobile predators (i.e. fur seals and penguins) breeding on Marion Island (see discussion of diets in next section).

There thus appear to be 2 areas of high variability within the foraging range of grey-headed albatross: (1) the STFZ to the north of the island, and (2) the area where the ACC crosses the South-West Indian Ridge to the south west of the island. These 2 areas are at a similar distance from the island, and positive and negative anomalies were present in these areas during both the incubation and chick-rearing stages (Figs 2 & 3). It is thus unclear why birds would switch to foraging exclusively to the south of the island during chick-rearing. The most plausible explanation is that, although the main area of variability to the southwest of the island occurs at ~700 to 900 km from the island, eddies appear to persist closer to the island as well (Fig. 4, Ansorge et al. 2000). Weimerskirch (1999) showed that shorter foraging trips for albatross were aimed primarily at meeting the energetic demands of the chick, while longer foraging trips resulted in the adult regaining its body condition. Foraging to the south of the island along the South-West Indian Ridge gives the adults a choice of several warm and cold eddies at a range of distances from the island and state of degradation or local depletion by less mobile predators. The selected foraging area will be a compromise between the energetic needs of the chick and the body condition of the parent. During incubation birds are away from the island for far longer periods (Nel et al. 2000) and are not under the constraint of needing to return to their breeding locality in order to feed a chick at regular intervals. This allows adults to forage further from the island and be more selective about their foraging area.

General diet during chick rearing

Diet samples, taken from a larger sample of birds (n = 30) during the chick-rearing period revealed a predominance of species associated with the SAZ and PFZ, thus confirming that the adults were foraging exclusively to the south of the island during this period. Little is known about the biology and distribution of the most frequently occurring fish species, *Magnisudis prionosa* (Gon & Heemstra 1990), although it has been recorded in the diets of grey-headed and black-browed albatross *Thalassarche melanophrys* at South Georgia (Reid et al. 1996), as well as in the diets of several other sub-Antarctic species known to feed mainly in the PFZ, including king penguins *Aptenodytes patagonicus* (Hindell 1988), Antarctic fur seals *Arctocephalus gazella* and Subantarctic fur seals *Arctocephalus tropicalis* (Green et al. 1990, Klages & Bester 1998). Four of the 6 myctophids found in our samples (*Electrona antarctica*, *Electrona carlsbergi*, *Gymnoscopelus bolini*, *Krefftichthys andersoni*) only occur in the upper water column at or south of the APF (Gon & Heemstra 1990). To date, little is known about the fish stocks in the SAZ and PFZ. The limited number of acoustic and trawling surveys conducted in the Atlantic sector of the Southern Ocean indicate that during the austral summer high myctophid stocks are associated with the APF and southern parts of the PFZ (Filin et al. 1991, Pakhomov et al. 1994, 1996).

The most frequently occurring fresh prey item, the ommastrephid squid *Martialia hyadesi*, is strongly associated with the APF (Rodhouse et al. 1992) and has also been found to associate with warm eddies that form at the APF in the Scotia Sea (Rodhouse et al. 1996). This species has major potential for commercial exploitation (Rodhouse 1997). *M. hyadesi* is a major squid prey of the mollymawk albatross species (genus *Thalassarche*) breeding across the entire Southern Ocean (Rodhouse et al. 1990, Ridoux 1994, Waugh et al. 1999). Knowledge of the environmental variables that influence its abundance and distribution are therefore of utmost importance.

Prey items associated with particular oceanographic features

The data suggest that birds were feeding at the edges of sea surface height anomalies mostly on larger predators (e.g. the fish *Magnisudis prionosa* and the squid *Martialia hyadesi*), which are presumably attracted by the presence of potential prey such as myctophids and crustaceans (e.g. decapod shrimps). These in turn could have been attracted by elevated stocks of copepods, amphipods (particularly *Themisto gaudichaudii*) and euphausiids, which were also well represented in our samples. Small amphipods (mainly *T. gaudichaudii*) and euphausiids are the most consistent components in the diet of adult Antarctic myctophids (Koslov & Tarverdieva 1989). Furthermore, amphipods were found in a stomach of an unidentified fish in one of our albatross diet samples. Although this is a single opportunistic record, it confirms the structure of the food chain suggested above. Continuous acoustic measurements in this region clearly indicated that the biomass of large plankton and micronekton (>20 mm in length) was consistently elevated at both warm and cold eddies (Pakhomov & Froneman 2000). Although the acoustic data do not discriminate species, these findings provide first evidence that positive and negative sea surface height anomalies (sensu warm and cold eddies) might contain elevated stocks of potential prey for epipelagic fish and squid, which in turn are preyed upon by grey-headed albatross. Rodhouse et al. (1996) reported that grey-headed albatross tracked from South Georgia while exploiting warm eddies at the PFZ fed mainly on the squid *M. hyadesi*. Sampling in these areas using pelagic trawls revealed that these squid were feeding mainly on myctophids, which presumably become concentrated by warm eddies. Myctophids, euphausiids and amphipods, especially *T. gaudichaudii*, are also the major prey items of the squid *M. hyadesi* at the APF in the Scotia Sea (Rodhouse et al. 1992). Rodhouse & White (1995) demonstrated that in the Scotia Sea the dominant predators in the epipelagic system at the PFZ were squid. Our data suggest that a predatory fish, *M. prionosa*, may also be an important member of the epipelagic predator community at the PFZ in the Southern Indian Ocean.

Exactly how positive and negative sea surface height anomalies (sensu warm and cold eddies) concentrate prey near the surface is unknown at the moment. However, Wiebe (1982) demonstrated that slope-water euphasiids move downwards in decaying cold eddies in an attempt to stay in their preferred environment. It is thus possible that crustaceans might be forced to move upwards in decaying warm eddies in order to stay in their preferred environment. This would make them accessible to epipelagic predators and initiate a trophic chain ending with top predators breeding on the Prince Edward Islands. It has recently been demonstrated that eddies spawned off the major frontal systems are rich in zooplankton/micronekton standing stock (Craddock et al. 1992, Wiebe & Youce 1992, Pakhomov et al. 1994, Pakhomov & Perissinotto 1997). The eddies may persist for up to 6 mo (Lutjeharms & Gordon 1987, Lutjeharms & Valentine 1988) and exhibited elevated primary productivity at the edges (Dower & Lucas 1993, Froneman et al. 1999). Eddies are therefore regarded as important vehicles in transporting unique or dense zooplankton communities, providing ideal feeding grounds for top predators (Sugimoto & Tameishi 1992, Barange et al. 1998). However, physical mechanisms and trophic links within eddies are as yet poorly understood and will be the subject of future research in the region southwest of the Prince Edward Islands.

The data presented in this paper provide the first insights into the nature and importance of these physical oceanographic features to top predators in this region. The findings of this study further demonstrate that productive eddies occurred at a range of distances from the island. Eddies that occur closer to the island could also be important for non-aerial predators breeding on Marion Island (i.e. penguins and seals). These species are not able to cover the vast distances covered by albatross, but are able to exploit resources occurring further down in the water column. Myctophids, which become concentrated at warm eddies (Rodhouse et al. 1996), dominate the diets of both King Penguins and fur seals at Marion Island (Adams & Klages 1987, Klages & Bester 1998). Furthermore, king penguins tracked from nearby Crozet Island showed that breeding birds made long directed foraging trips (indicative of a predictable food resource) to the PFZ

(Jouventin et al. 1994). Finally, elephant seals tracked from Marion Island also showed intensive foraging activity on the leeward side of the Southwest Indian ridge. We therefore suggest that this area of high mesoscale eddy activity, created by the ACC crossing the South-West Indian Ridge, could be an important component of the 'life-support system' for numerous globally significant populations of seabirds and seals breeding on Marion Island.

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Appendix 1. Relative abundance, frequency of occurrence and estimated lengths and masses of prey items identified in diet samples collected during chick-rearing period at Marion Island, 1998. Unid.: unidentified

Taxa	Relative abundance	Frequency of occurrence (Total) (%)	Frequency of occurrence (Fresh) (%)	Estimated length (mm) (Fish=TL, Squid=ML, Crus=CL)		Estimated mass (g)	
				Mean	Range	Mean	Range
FISH	75	90	63				
Family Macrouridae	2	3	3				
Cynomacrurus piriei	1	3	3				
Unid. Macrouridae	1	3					
Family Myctopidae	14	27	10				
Electrona antarctica	4	3		103.8 ± 38.2	70.7–136.9	20.5 ± 18.2	4.7–36.2
Electrona carlsbergi	1	3		58.2		3.58	
Electrona subaspera	1	3	3	92.5		14.9	
Gymnoscopelus bolini	2	3					
Gymnoscopelus piabilis	1	3	3	167.9		99.9	
Gymnoscopelus sp.	1	3					
Krefftichthys andersoni	3	7		44.5 ± 2.4	41.7–45.9	0.878 ± 0.14	0.71–0.96
Unid. Myctophidae	1	3	3	52			
Family Paralepididae							
Magnisudis prionosa	39	30	20	452.5 ± 68.6	198.2–624.4	321.6 ± 48.7	140.9–443.7
Family Photichthydae							
Photichthys argenteus	2	7	7	309.5		126.3	
Unid. Fish	18	53	33	324.4 ± 76.3	270–378		
SQUID	315	97	68				
Family Chiroteuthidae							
Chiroteuthis sp.	66	33	7	111.4 ± 10.7	82.3–150.8	36.1 ± 10.4	13.9–86.3
Family Cranchiidae							
Galiteuthis glacialis	65	30		219 ± 13.5	187.6–248.7	93.2 ± 14.3	62.9–126.6
Family Gonatidae							
Gonatus antarcticus	8	20		290.4 ± 12.1	270.6–304.9	178.6 ± 28.6	134.1–214.1
Family Histioteuthidae							
Histioteuthis eltaninae	14	33	3	62.2 ± 11.1	44.1–90.8	86.5 ± 31.0	44.8–175.7
Family Mastigoteuthidae							
M*astigoteuthis psychrophila*	3	7		164.9 ± 41.4	117.4–193.0	203.3 ± 116.8	69.9–287.7
Family Neoteuthidae							
Alluroteuthis antarctica	14	30	3	147.1 ± 31.6	70.4–202.0	389.5 ± 210.5	38–898.9
Family Ommastrephidae							
Martialia hyadesi	46	47	27	233.3 ± 35.5	150–287.7	227.5 ± 105.9	60.9–445.6
Family Onychoteuthidae	61	60	10				
Konakovia longimana	47	53	10	387.8 ± 110.7	149.3–533.7	1 648 ± 957.3	87.5–3556.1
Moroteuthis ingens	1	3		600.4		2625.6	
Moroteuthis robsoni	3	7		309.1 ± 26.5	284.5–337.1	766.3 ± 104.0	671.8–877.6
Family Psychroteuthidae							
Psychroteuthis glacialis	1	3		26.2		90.9	
Unid. squid	47	43					
CRUSTACEANS	174	70	70				
Amphipoda	116	27	27				
Themisto guadichaudii	114	20	20				
Unidentified amphipods	2	7	7	29.5 ± 4.9	26–33		
Decapoda	18	40	40				
Austopandalus grayi	2	7	7	69.5 ± 7.8	64.0–75.0		
Pasiphaea scotia	10	23	23	33.3 ± 6.3	24.0–40.0		
Unidentified decapods	6	9	9				
Euphausiacea	36	17	17				
Euphausia superba	4	3	3				
Unid. euphausiids	32	13	13				
Isopoda							
Unid. Isopods	4	13					
OTHER	10	20	7				
Goose barnacles	4	3	3				
Penguin feathers	3	10					
Jelly fish	2	7	7				
Mammal lung and stomach	1	3	3				

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