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The importance of oceanographic fronts to marine birds and mammals of the southern oceans

C.A. Bost [a,*], C. Cotté [a], F. Bailleul [a], Y. Cherel [a], J.B. Charrassin [b], C. Guinet [a], D.G. Ainley [c], H. Weimerskirch [a]

[a] *Centre d'Etudes Biologiques de Chizé, CEBC-CNRS UPR 1934, F-79360, Villiers en Bois, France*
[b] *Département Milieux et Peuplements Aquatiques, Muséum National d'Histoire Naturelle, 43 rue Cuvier, 75231 Paris Cedex 05, France*
[c] *H. T. Harvey and Associates, 983 University Avenue, Bldg D, Los Gatos CA 95032 USA*

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ABSTRACT

During the last 30 years, at-sea studies of seabirds and marine mammals in the oceans south of the Subtropical Front have described an association with major frontal areas. More recently, the advancement in microtechnology has allowed the tracking of individuals and investigations into how these marine predators actually use the frontal zones. In this review, we examine 1) the relative importance to apex predators of the different frontal zones in terms of spatial distribution and carbon flux; 2) the processes that determine their preferential use; and 3) how the mesoscale dynamics of frontal structures drive at-sea foraging strategies of these predators. We review published results from southern waters and place them in a broader context with respect to what has been learned about the importance of fronts in oceans farther north.

Some fronts constitute important boundaries for seabird communities in southern waters. At a mesoscale the maximum values of seabird diversity and abundance correspond to the location of the main fronts. At-sea surveys show a strong curvilinear correlation between seabird abundance and sea surface temperatures. High mean species richness and diversity for whales and seabirds are consistently associated with the southern water mass boundary of the Antarctic Circumpolar Current, the Subtropical Front and the Subantarctic Front; in the case of the Polar Front mean seabird densities are more variable. At small-scales, variation in seabird occurrence has been directly related to the processes at fronts in a limited number of cases. A significant positive relation was found between some plankton feeding species and frontal temperature gradient–phytoplankton variables.

Telemetric studies have revealed that several apex predators (penguins, albatrosses, seals) perform long, directed foraging trips either to the Subtropical front or Polar Front, depending on locality. Seabirds with low flight costs, such as albatrosses, are able to reach fronts at long distances from colonies, showing variable foraging strategies as a function of the distances involved. Diving birds such as King penguins, that travel at a higher cost and lower speed, rely on the predictable spatial distribution of mesopelagic fish found close to the Polar Front. They may use the currents associated with eddies as oceanographic cues in the active search for frontal zones. Once in these areas they dive preferentially in and below the depth of the thermocline where catches per unit effort are high. Elephant seals concentrate foraging activity principally inside or at the boundary of cyclonic eddies. These mesoscale features appear to offer exceptional productivity favourable for foraging by various diving top predators.

The connection between biophysical parameters at fronts and predators is likely to be made through biological enhancement. Top predators appear to forage at locations where prey are advected by physical processes and others where prey are produced locally. Long-term research on at-sea distributions and demographic parameters of top predators are essential to assess the consequences of potential shift in front distributions in relation to global warming. Such environmental changes would add to the impact of fish extraction by the industrial fisheries on the southern food webs.

1. Introduction

Physical processes play a large role in affecting the abundance and distribution of oceanic organisms (Pakhomov et al., 1994; Hunt et al., 1999; Pollard et al., 2002). They offer the physical structure within which phytoplankton and trophic food webs may develop (Mann and Lazier, 1991). Most important in foodweb development is the mesoscale variability and heterogeneity of physical processes (Lima et al., 2002). This concerns especially the southern Indian, Atlantic, Pacific and Southern oceans, subdivided into distinct circumpolar regions by marked fronts. Such physical discontinuities of coarse scale

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[*] Corresponding author. Tel.: +33 5 49 09 96 09; fax: +33 5 49 09 65 26.
E-mail address: bost@cebc.cnrs.fr (C.A. Bost).

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(up to 100 km width) exhibit high, horizontal spatial gradients in current speed, temperature, salinity and density, as well as enhanced vertical circulation associated with bathymetric features (Deacon, 1933, 1982; Franks, 1992; Belkin and Gordon, 1996). Increased marine productivity and biomass, sometime at exceptional levels with respect to interfrontal waters masses, often characterize frontal zones (Lutjeharms et al., 1985; Ainley and DeMaster, 1990; Pakhomov et al., 1994; Hunt et al., 1999).

It is well known that apex predators associate with fronts where they find favourable feeding conditions whatever the oceanic system (Bering Sea: Kinder et al., 1983; North Atlantic: Brown and Gaskin, 1988; Gulf Stream: Haney, 1986a,b; Eastern Tropical Pacific: Briggs et al., 1987; California Boundary Current System: Hoefer, 2000; Ainley et al., 2005). Two main nonexclusive hypotheses have been proposed to explain why fronts are important determinants of predators' at-sea distributions. First, prey supply can be increased at the fronts because of enhancement of local primary production. Second, the higher aggregation of marine organisms may result from prey transport to the fronts by convergence processes (Hunt et al., 1990; Murphy, 1995; Hunt et al., 1999; Spear et al., 2001; van Franecker et al., 2002).

In southern waters the logistics of at-sea studies can be exceedingly difficult, particularly true due to the distances from home ports involved in this work, rough seas and high seasonality. Consequently, at-sea studies on predators and fronts have been limited in space and time although, fortunately, several works have been conducted within tightly coordinated multidisciplinary cruises at regional scales (e.g. Ainley et al., 1994; Nicol et al., 2000; van Franecker et al., 2002). Over the same time period, the exponential development of bio-logging and the use of remote sensing technologies have provided considerable insight into the association between predators and fronts. These studies have reported in great detail on how individually tracked seabirds and mammals use fronts (Bost et al., 1997; Croll et al., 1998; Georges et al., 2000; Boehlert et al., 2001; Boyd et al., 2001; Charrassin and Bost, 2001; Weimerskirch et al., 2002; Wilson et al., 2002; Charrassin et al., 2004; Bailleul et al., 2007a). Several studies have also monitored the diving activity or feeding success of the individually tracked predators in relation to oceanic features (Bost et al., 1997; Wilson et al., 2002; Lea and Dubroca, 2003; Weimerskich, 2007). Diving predators equipped with miniaturized devices to simultaneously record oceanographic parameters (temperature and salinity) have provided information on both the location of areas of biological interest explored and the *in situ* physical features of the frontal zones (Boehlert et al., 2001; Charrassin and Bost, 2001; Charrassin et al., 2002, 2004; Sokolov et al., 2006; Bailleul et al., 2007a). However, very few studies have included contemporaneous real time, reliable, sessions in which prey were sampled.

In this paper, we review studies of the relationship between top predators and fronts in the Southern Ocean north to the subtropics, following definitions in Deacon (1933). This includes the southern zones of the Indian, Atlantic and Pacific Oceans, from the Subtropical Front to the limit of the Antarctic continent, thus encompassing the Antarctic Circumpolar Current and several associated oceanic fronts. This review builds on, as well, the huge amount of work that has been accomplished on association of these predators with frontal zones elsewhere in the world for a longer time period (e.g., Wynne-Edwards, 1935; van Oordt and Kruijt, 1953; Pocklington, 1979; Ainley and Boekelheide, 1984; Ainley et al., 1984; Ribic and Ainley, 1988/89; Hunt et al., 1990; Veit and Hunt, 1992; Ainley et al., 1994; Hunt et al., 1999; van Franecker et al., 2002).

We attempt to provide new insights into seemingly simple but actually complex questions: Why do apex predators strongly associate with frontal zones? Do marine predators forage at fronts because they respond to physical properties associated with prey and/or because of some change in biotic factors (i.e., merely food)? We will first examine the relative importance to top predators of the different frontal zones in the context of their diet and feeding ecology. Through an at-sea perspective we shall assess top predator frontal association from a macro- to the fine scale. We use information from at-sea surveys to point out some possible mechanisms for the observed association. Then, by using findings from bio-logging, we shall describe distinct foraging strategies in relation to fine- to mesoscale physical processes that determine the preferential use of fronts.

2. Definition of fronts

The location of fronts and macroscale water masses of the southern regions of the Indian, Atlantic and Pacific oceans, together with major islands discussed in the present paper, are shown in Fig. 1. Three major fronts lie on a north-south gradient as follows: the Subtropical Front (STF), the Subantarctic Front (SAF) and the Polar Front (PF) (Orsi et al., 1995; Belkin and Gordon, 1996). The STF delimits the northern limit of the Antarctic Circumpolar Current (ACC) (Orsi et al., 1995) and corresponds to the boundary of the Southern Ocean (following Deacon, 1933). The Subantarctic Zone (SAZ) lies north of the Southern Ocean (Deacon, 1982; Lutjeharms and Valentine, 1985; Orsi et al., 1995). The PF separates the Antarctic Zone from the Polar Frontal Zone (PFZ). This front marks where Antarctic Surface Waters sink below the warmer Subantarctic Waters (Deacon, 1982). The PF has been defined as the northernmost extent of the subsurface temperature minimum of 2 °C, which corresponds to SST of 4–5 °C in summer (Park et al., 1993, 1998). The PFZ is bordered on the south by the PF and the SAF on the north (Belkin and Gordon, 1996). Finally the northern limit of the pack-ice defines the limit of the cold Antarctic Zone and coincides approximately with the southern boundary of the ACC. Within this zone, the southern part of the Antarctic Circumpolar Current (SBF) is characterized by a series of gyres, rather than directional floe (Nicol et al., 2000). It corresponds to the poleward extent of the shoaled nutrient-rich Upper Circumpolar Deep Water (Orsi et al., 1995). Close to the Antarctic, continental shelf breaks such as the shelf break of the Ross Sea and the Antarctic Slope Front (ASF) are areas of key importance in biological production (Ainley and DeMaster, 1990; Smith et al., 2007).

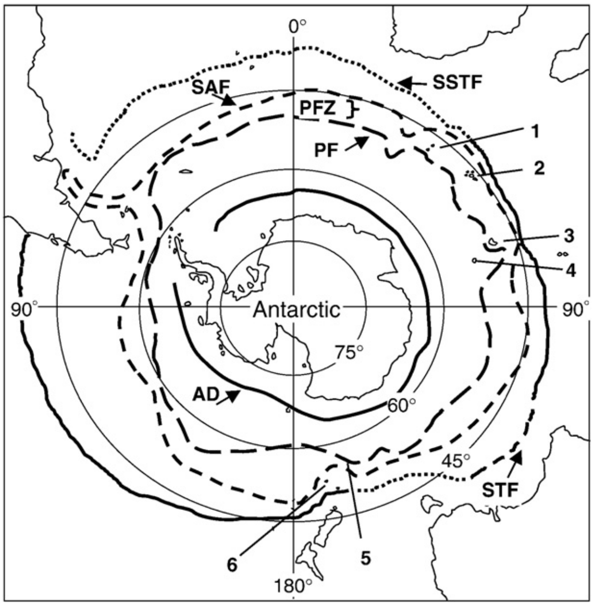

Fig. 1. Location of the main fronts and oceanic zones of the Southern Ocean (from Orsi et al., 1995; Belkin and Gordon, 1996; Park and Gambéroni, 1997). SSTF: South Subtropical Front; STF: Subtropical front; SAF: Subantarctic Front; PF: Polar Front; AD: Antarctic Divergence or southern boundary of the ACC. Numbers refer as following: 1: Marion and Prince Edward Islands; 2: Crozet Islands; 3: Kerguelen Archipelago; 4: Heard and McDonald Islands; 5: Macquarie Island; 6: Campbell Island.

3. Data used

We have considered studies published during the past 50 years on at-sea distribution and foraging ecology of top predators. So far, most of the at-sea studies have been made in the southern zone of the Atlantic with however intensive work conducted also in the Ross Sea and in the southern zone of the Indian Ocean. Few studies concern the 75% of the remaining water masses around the Antarctic continent (Woehler et al., 2003). In addition we have gathered information from 34 biologging studies conducted on the movements of several predators (fur seals, elephant seals, albatrosses, penguins). Predators' diet information in relation to their at-sea distribution remains poorly known, and perhaps not satisfactory to be categorizing diet based on the limited land-based studies (Ridoux, 1994). These studies also mostly concern breeding birds tied to foraging for offspring, i.e. during a limited portion of the annual cycle. In an attempt to distinguish the main trophic niche of the species communities over extended periods, we have also used data from recent stable isotope studies when available (Cherel et al., 2006).

4. At-sea distribution and foraging ecology of top predators from ship surveys

4.1. Macroscale level

Many studies have pointed out the existence of seabird assemblages related to distinct water masses (Ribic and Ainley, 1988/89; Wahl et al., 1989; Ribic and Ainley, 1997). Accordingly, each biogeographical zone being considered herein (i.e., the Subtropical, Subantarctic, Polar Frontal and Antarctic zones) holds particular seabird assemblages (South Atlantic: Abrams, 1985a; Ainley et al., 1994; Veit, 1995; South Pacific: Ainley and Boekelheide, 1984; East Antarctica: Woehler et al., 2003; Raymond and Woehler, 2003). Overall, the steepness of horizontal temperature and salinity gradients of surface waters, the distance to the ice edge, and ice type determine the changes observed in avifaunal composition (Pocklington, 1979; Ainley and Boekelheide, 1984; Abrams, 1985a; Ainley et al., 1994; Veit, 1995). Few studies have investigated whether these seabird assemblages result from a common response to specific physical features of the water masses, or whether they actually are ‘communities’ of co-evolved members (Ainley et al., 1994; Ribic and Ainley, 1997).

4.1.1. South Atlantic Ocean

In the South Atlantic Ocean, four geographically distinct clusters based on seabird composition were pointed out (Veit, 1995). Importantly, each cluster corresponds to a major zone, including the Patagonian Shelf, the SAZ, the PFZ and the zone north of the SAF (i.e. in the Subtropical Zone). The number of seabird species in the SAZ (43) is higher than in the Patagonian Shelf (27), the PFZ (30) or the SZ (Subtropical Zone, 28 species). Birds aggregate in larger numbers near the fronts with sharp breaks in species composition. As noted by Abrams (1985a), who worked in waters off southern Africa, as much as 40% of the variation in seabird abundance can be explained in terms of environmental gradients (barometric pressure, salinity, air and water temperature, wind strength).

South of the APF, in the Scotia–Weddell confluence region (56–66°S; 70–38°W), three assemblages of seabird species have been identified (Ainley et al., 1994). One is associated with the pack-ice. Another includes the species using the adjacent open ocean. Still another includes species found far away within the PFZ. This latter assemblage appears similar to that described in the PFZ identified in the South Atlantic during summer (Veit and Hunt, 1991).

4.1.2. South Pacific Ocean

Large overlaps in seabird species occur in the Pacific Ocean between the ice-free waters of the Antarctic Zone and the Subantarctic and between the Subantarctic and the Subtropical Zone. Overall the avifaunas in Subantarctic and Subtropical waters are less distinctive than those in the Antarctic or in tropical waters (Ainley and Boekelheide, 1984; Ainley et al., 1984). Thus the APF and the STF are clearly not the classical avifaunal barriers expected at least in the South Pacific. Once south of the APF, the pack-ice edge is a much more effective boundary with clearly distinctive avifauna compared to Antarctic open waters, Subantarctic and tropical waters. The PF appears to be a more effective avifaunal barrier only in the Drake Passage where an extreme sharp horizontal gradient in water density occurs.

4.1.3. Southeast Indian Ocean

In the sector East of Antarctica (Prydz Bay) three seabird assemblages were pointed out from a cluster analysis of at sea-observations collected over 20 years on the avian community (Woehler et al., 2003). Assemblage 1 is consistent with the influx, presence and departure of the 9 resident breeding species. Assemblage 3 is dominated by non-breeding summer visitors visiting Prydz Bay from sub-Antarctic and temperate localities. Assemblage 2 results of the overlap in time and space of these 2 assemblages. It comprises all 26 species/taxa reported from Prydz Bay and is most observed in mid summer in areas with less than 9% ice. Overall a stability of these assemblages was reported over the study period (Woehler et al., 2003).

4.2. Mesoscale level (10 s to 100 s of km)

4.2.1. Antarctic shelf break fronts

In the Antarctic, numerous studies have shown the importance of ice edge habitats and of the Marginal Ice Zone, as well as the importance of shelf break or the Antarctic Slope Front (ASF) fronts, to marine predators (e.g. Ainley and Jacobs, 1981; Ribic and Ainley, 1988; Ainley and DeMaster, 1990; Ribic et al., 1991; Ainley et al., 1994). Upwelling of Circumpolar Deep Water along the continental slopes greatly increases local marine productivity. High seabird biomass has been reported over the ASF in a number of instances: Ross Sea (Ainley and Jacobs, 1981; Ainley et al., 1984; Veit and Braun, 1984); Amundsen and Bellingshausen seas (Ainley et al., 1998); Weddell–Scotia confluence (Veit and Hunt, 1992); Western boundary of the Antarctic Peninsula, South Shetland Islands and off the eastern coast of South America (Veit and Braun, 1984; Ainley and DeMaster, 1990). Importantly such fronts correspond to distinct boundaries between pelagic seabird communities (Veit and Braun, 1984; Ainley et al., 1984; Ainley, 1985; Ainley and DeMaster, 1990).

4.2.1.1. Ross Sea. The Ross Sea's continental shelf (170°–150°W) is the largest of the Antarctic and the most spatially extensive region of high productivity in the Southern Ocean. Shelf break occurs deeper than 200 m, with lower slope reaching 3000 m depth (Smith et al., 2007). Here, seabird density and biomass are >10 fold greater than in adjacent waters (Veit and Braun, 1984). Some bird biomasses ranging from 50 to 150 kg/km^2 have been found (Ainley, 1985). The dominant species inshore of the ASF are the Wilson' storm petrel *Oceanites oceanicus*, Snow petrel *Pagodroma nivea*, Antarctic petrel *Thalassoica antarctica*, Adelie penguin *Pygoscelis adeliae* and emperor penguin *Aptenodytes forsteri*. The Dove prion *Pachyptila desolata*, Light-mantled Sooty albatross *Phoebetria palbebrata* and Mottled petrel *Pterodroma mollis* are observed only offshore from the front (Veit and Braun, 1984). The biomass of sea mammals (Crabeater seals *Lobodon carcinophagus*) and whales are also elevated close to the ASF (Ainley, 1985; Ackleys et al., 2003; Ainley et al., 2007). Higher turbulence and biomass in waters of the shelf and upper slope and oceanic frontal structure probably drives greater biological productivity and concentration of target prey, such as the Antarctic krill *Euphausia superba* for marine mammals and birds (Ackleys et al., 2003; Ainley et al., 2007).

4.2.1.2. Amundsen Sea (130°–100°W) and Bellingshausen Sea (100°–60°W). In these two seas, a variety of subsurface fronts occur on both sides of the shelf break, at shallower depths from west to east and with warmer and saltier waters on the northern sides. These fronts are more restricted in their vertical dimension and have a smaller horizontal temperature gradient than those from the Ross Sea. As a consequence, seabird density and biomass are much lower (Ainley et al., 1998). In the Amundsen Sea, the seabird distribution is quite similar to that in the Ross Sea, with higher bird biomass at shelf break front. Conversely, in the Bellingshausen Sea, seabird biomass does not differ over the front and the continental shelf. This may be related to a greater stratification of the water column over the shelf and/or more plentiful coastal resources.

4.2.1.3. The Weddell–Scotia confluence. To the north and east of the Orkney Islands (60°35′S, 45°30′W), the Weddell–Scotia confluence corresponds to the interface of the ACC and the Weddell Sea Gyre. This abrupt horizontal transition between two distinct water masses (+2.0 °C to −1.5 °C in the upper 400 m) is biologically important (Veit and Hunt, 1992; Ainley et al., 1994). Elevated seabird numbers have been reported near this front at the steepest physical gradients. Overall, fronts close to the colonies and over insular slopes are important summer feeding grounds to some local Antarctic species such as Chinstrap penguins *Pygoscelis antarctica* and Fulmars *Fulmarus glacialoides* but also to subantarctic species (Veit and Braun, 1984; Ainley et al., 1994). The Confluence is important to seabirds and marine mammals in the winter as well (Ribic et al., 1991; Ainley et al., 1994).

4.2.2. Oceanic fronts

4.2.2.1. Seabird. In the South Atlantic, the highest mean seabird species richness and diversity were reported at the STF and SAF, respectively, with squid- and plankton-feeders peaking at the STF and the PF (Griffiths et al., 1982). The maxima of seabird abundances occur as a series of Gaussian distribution curves with the highest values observed in the vicinity of the STF. Over the PF some very variable mean seabird densities have been reported during summer (2 to 20 individual/km). Up to 400 prions/km^2 were observed in the South Atlantic during transects from Cape-Town to Antarctica. Likewise high density signals associated with the STF and SAF have been reported in the South Pacific (Ainley and Boekelheide, 1984).

At the STF and PF, macroplankton biomass is higher than in the interfrontal zones (Pakhomov et al., 1994). These two fronts differ in their biological activities. The STF is an area of higher primary production (El-Sayed, 1994) and therefore supports higher pelagic macroplankton stocks than does the PF (Pakhomov and Froneman, 2000). This latter is considered to be a region with marked seasonal changes (Pakhomov et al., 1994). In contrast, the productivity of the STF is more uniform (El Sayed, 1988; Comiso et al., 1993). These differences in productivity and predictability may explain the attraction of the STF for seabirds.

Species differences exist in the use of these fronts, depending on body size and diet. Large species, such as albatrosses and gadfly petrels, that partially depend on squid (Cherel and Klages, 1998) dominate seabird biomass near the STF (Griffiths et al., 1982). Prions dominate near the PF and are numerous at the STC. These small species feed primarily on macrozooplankton throughout the year (Cherel et al., 2006). Species more flexible in their diet (such as Kerguelen petrel *Pterodroma brevirostris*) are most numerous at the PF southward (Griffiths et al., 1982; Ainley et al., 1994).

To sum up, the maximum values of seabird diversity and abundances coincide with oceanic fronts, as defined by SST. Few studies report elevated seabird abundance at the PF, the highest mean seabird species richness and diversity being reported at the STF and SAF, respectively. The variances explained by SST gradients, however, are usually <20% (Abrams, 1985a). One explanation is the mismatch between the spatial scale at which seabird abundance is observed and the spatial scale of physical gradients (Schneider, 1990). This mismatch results from the length of the causal chain from the physical process to prey including the intermediate two-step chains, i.e. fronts to prey and prey to seabird (Schneider, 1990).

4.2.2.2. Whales. Mesoscale whale distribution has been directly related to oceanographic features at the SBF. The circumpolar distribution of baleen whales and sperm whales *Physeter macrocephalus* during summer reflects the high latitude penetration of the nutrient-rich Upper Circumpolar Deep Water transported eastward by the ACC. At the southern boundary, Upper Circumpolar Deep Water upwells and replenishes nutrients necessary to sustain primary production and planktonic food webs. Therefore, the highest concentrations of Blue whales *Balaenoptera musculus*, Humpback whales *Megaptera novaeangliae*, Fin whales *B. physalus* and Minke whales (*B. bonarensis*) have been found south of the southern boundary, including a strong association with the SBF (Ainley et al., 2007), reflecting the distribution patterns of their main prey, the Antarctic Krill (Tynan, 1998; Nicol et al., 2000). Along the coastline, ocean circulation processes drive the sea-ice extent and associated biological productivity from phytoplankton to whales through krill. Where the coastal current becomes wider, the boundary occurs farther offshore and generates greater sea-ice extent. As a consequence, the area of krill availability for the whales will be larger, encompassing the southern limit of the boundary (Nicol et al., 2000).

North of the Southern Ocean, whales may also benefit from favourable feeding conditions. Thus Sei whales *B. borealis* are concentrated close to the STF (Cotté et al., unpublished data). Prey composition of Sei whales is diverse and amounts to about 80 different species, dominated by copepods (Budylenko, 1978). This wide range of food is most pronounced in warmer waters where species richness is high, especially for copepods (Errhif et al., 1997). In the southern Indian Ocean, the highest density of large cetaceans has been found along the southern flank of the Kerguelen Plateau and northern edge of the Princess Elizabeth Trough. Here, the distribution of whales (mostly Sperm whales, northern Minkes whales *B. acutorostrata* and Humpback whales) coincides with the mean position of the southern front of the ACC and the southern boundary of the ACC. The topographic steering effect of these features of the ACC at this place of the Kerguelen Plateau brings shoaled, nutrient-rich Upper Circumpolar Deep Water to an higher latitude than in adjacent basins (Tynan, 1997). High density areas of Humpback Whales, Southern right Whales *Eubalaena australis*, male Sperm Whales, and Bottlenose Whales *Hyperoodon planifrons* occur along the wide meander of the southern boundary of the ACC between 80–110° (Matsuoka et al., 2003). Whales may here benefit from predictably enhanced marine productivity due to high macronutrient levels in the surface mixed layer, the isopycnal shoaling in cyclonic eddies, the presence of a complex bathymetry, and advection of a tongue of ice northward along the eastern side of the plateau (Tynan, 1997).

4.2.3. Eddies

The role of mesoscale eddies in feeding success of top predators of the Southern Ocean has been recently emphasized (Nel et al., 2001; Cotté et al., 2007; Bailleul et al., 2007a). Eddies are characterized by increase in marine productivity and zooplankton biomass relative to adjacent waters (Seki et al., 2001; Polovina et al., 2004; Hyrenbach et al., 2006). The upwelling and down welling processes induced by eddy vorticity induce aggregation of prey (Olson and Backhus, 1985; Hyrenbach et al., 2006). Myctophid fish tend to concentrate along the periphery of warm, anti-cyclonic eddies where a much higher biomass of zooplankton and micronekton is found (Olson and Backhus, 1985; Pakhomov et al., 1994; Pakhomov and Froneman, 2000; Hyrenbach et al., 2006). Crustaceans may be forced to move upward in decaying warm eddies to stay at their preferred temperature. Predators of myctophid such as the southern baracudina *Magnisudis prionosa* and the cephalopod *Martiala Hyades* also occur here (Nel et al., 2001).

4.3. Small scale level (<10 s of km)

4.3.1. Small scale distribution patterns

Within oceanic fronts of southern waters, variation in the small-scale distribution of seabirds has been explained directly by physical and biological processes only in a limited number of cases. One case involved intensive interdisciplinary surveys at the PF near the Greenwich Meridian in conjunction with the Joint Global Ocean Flux Study (van Franecker et al., 2002). Overall, the highest seabird densities were those of plankton feeders (up to 400 individual/km^2), concentrated at steep temperature gradients. Squid and fish feeders, however, were much less abundant than plankton feeders, and showed little correlation with the physical patterns at this scale. At a wider spatial scale (49–52°S and 6–12°E), seabird densities generally respond to increased productivity in the PF. Broad-billed prion (*Pachyptila vittata*), one of the commonest species feeding at the subsurface on small copepods, exhibited a remarkable, positive association with frontal temperature gradients–phytoplankton variables in spite of the front dynamics. Prions were reported in highest densities (average: 18.1/km^2) in the 4 °C isotherm area during summer. The spatial coherence of the front appears to persist enough to allow the development of zooplankton stocks at an energetically relevant threshold for these predators (van Franecker et al., 2002). Less clear relationships were found with larger zooplankton (>500 µm) in the Southern Drake passage and Brandsfield Strait (Heineman et al., 1989).

4.3.2. Insular fronts

Although spatially restricted, insular fronts are biologically important, increasing both the marine productivity and trophic transfer rates (El Sayed et al., 1979; Wolanski and Hammer, 1998; Ainley and DeMaster, 1990). Non-flying diving predators whose foraging range is limited are particularly associated with insular fronts. For example, high densities of Macaroni penguins *Eudyptes chrysolophus* and Antarctic fur seals *Arctocephalus gazella* forage in the area of upwelling fronts along the northwest coast of South Georgia (Croxall et al., 1985). Prions also actively feed there on prey probably forced to the surface by strong tidal current (Reid et al., 1997). Another example was found, around the Prince Edward archipelago (47°S, 38°E), where continuous advection of prey for top predators results from consistently high winds that increase the effect of the eastward flowing ACC. This advection appears sufficient to compensate for the daily consumption of euphausiids over the shelf by plankton feeders (mostly eudyptid penguins *Eudyptes*) but not to support the feeding activity of myctophid consumers (King penguins *Aptenodytes patagonicus*) (Perissinotto and McQuaid, 1992). Finally, at the western side of the Crozet shelfbreak (46°S, 50°E), about 80 km off Hog Island, a significant upwelling occurs and induces dense aggregation of feeding prions (Stahl, 1983).

4.4. Comparison with the Arctic Ocean

In contrast to the Antarctic region, the Arctic continental shelf break fronts are of secondary importance for pelagic biological production and predator concentration. This is mainly because of shallower bathymetry and less active currents (Ainley and DeMaster, 1990; Hunt, 1991; Hunt et al., 1999). Midshelf fronts (inner and middle shelf) have been identified as relevant for carbon flux to marine predators that concentrate here (Schneider and Hunt, 1982). The importance of midshelf fronts has not yet been investigated in much detail in the Southern Ocean (Ainley and DeMaster, 1990). Oceanic fronts are particularly important for the feeding ecology of numerous plankton feeders in the Arctic, especially auks (Nettelship and Evans, 1985; Schneider, 1990; Hunt et al., 1999). Here the fronts interact with the bathymetry in shallow waters to induce predictable surface features aggregating prey (Hunt et al., 1999). The closer proximity of such physical discontinuities to the breeding colony (usually <200 km) is of key importance for these diving foragers with limited range.

At a broader scale, the role of oceanic fronts differs between the two polar regions for two main reasons. First, biological activity at Southern Ocean fronts is less important. This activity must be considered with respect to background productivity of the surrounding water masses (Ainley and DeMaster, 1990). Second, in the Southern Ocean, the fronts occur over larger spatial scales. They are usually more distant from the breeding colonies because of the scarcity of potential breeding sites (islands). Seabirds must then travel farther to remoter areas than northern species (Hunt et al., 1999). They compensate by their ability to use strong winds for gliding (albatrosses, petrels, prions) or by fast swimming as large penguins do (at much higher cost, however, than economical gliding and soaring activities; Butler, 2000).

4.5. Comparison with the North Atlantic Ocean

Gulf Stream eddies play a key trophic role in the North Atlantic (e.g. Haney, 1986a,b). These eddies are small and episodic physical features consisting of an entrained warm filament and a cold cyclonic core. Here seabird species show strong affinities for single water mass. Bridled terns *Sterna anaethetus* associate with warm filaments of the Gulf Stream (Haney, 1986a), similar to the association reported for these species (and the Sooty tern *Sterna fuscata*) with mesoscale eddies in the southern Indian Ocean (Hyrenbach et al., 2006). Deep diving cetaceans such as beaked and sperm whales use shelf edge and Gulf Stream waters off the northeast American coast (Waring et al., 1993, 2001). Because eddies of the Gulf Stream exhibit strong gradients in physical (SST gradients) and biotic (chlorophyll concentration) properties, it is difficult to point out the most important environmental features attracting predators.

4.6. Comparison with the tropics

The significance of fronts to apex predators differs strongly between the southern oceans and the tropics (Ballance and Pitman, 1999). First there are fewer opportunities in tropical areas (sea surface temperature >23 °C, Ballance and Pitman, 1999) for physical forcing because of the scarcity of shelf systems, excluding the occurrence of shelf break fronts (Longhurst and Pauly, 1987). Second, at a large scale, seabirds are associated generally more with current systems than with water masses (Ribic et al., 1997). Like in the Southern Ocean however thermocline depth and topography plays a major role in prey aggregation in the tropics and in the structuring of habitats of seabird guilds (Ballance and Pitman, 1999; Ballance et al., 2001; Charrassin and Bost, 2001; Vilchis et al., 2006). Planktivores respond to the fronts like in the Southern Ocean whereas piscivores can be unaffected by a front's presence. They are however strongly dependant to depth and intensity of the thermocline i.e. the front corresponding to the subsurface horizontal boundary especially with respect to its depth and intensity (semi-permanent Equatorial Front, eastern tropical Pacific, Spear et al., 2001). Overall the highest densities of fish-eating species predicted by models correspond to areas with a sharp thermocline or a well stratified water column which are also favourable areas for foraging tunas and dolphins (Ballance et al., 2001; Spear et al., 2001). The difference between piscivores vs planktivores seabird seem to reflect the process inducing the availability of their prey (Spear et al., 2001). The best habitat model of plankton-feeding seabirds corresponds to areas of cool surface waters well mixed waters with a much shallower thermocline (<30 m) that concentrate prey at the surface. To catch their prey (flying fish, squids), tropical seabirds use the activities of commensal tunas and dolphins found in close association with the horizontal thermocline boundary (Ballance et al., 2001; Spear et al., 2001). Some differences in water clarity between the tropics and the Antarctic waters (lower vs. higher productivity, respectively) also play an important role in prey accessibility. In Antarctic waters, more turbid water favour a greater concentration of prey in the upper layers of the water (prey being more hidden) in association with strong temperature/density gradients and higher local primary productivity (Ainley, 1977; Spear et al., 2001).

Numerous studies have reported seabird–eddy associations in tropical and subtropical waters. Recently these associations were investigated in the subtropical Indian Ocean by comparing the presence/absence and abundance of the most abundant taxa in relation to the main environmental variables (Hyrenbach et al., 2006). Seabirds using eddies are more strongly associated with habitat parameters such as warm SST and distance from the closest breeding colony. To determine the respective influence of biotic and physical parameters of eddies on seabird foraging behaviour it is important to deal with confounding factors such SST gradients and associated chlorophyll concentration. It is also necessary to consider processes at smaller scale (ephemeral convergences and divergences) which in turn concentrate prey and their predators. Finally the seabird–eddy association must be considered in the larger scale patterns of mesoscale variability across the basins oceanographic context (Hyrenbach et al., 2006) as already pointed out for some subantarctic predators (Cotté et al., 2007; Bailleul et al., 2007a).

4.7. Seasonal changes in frontal use by seabirds

Few studies have had the opportunity to investigate temporal changes in the structure of seabird community at southern fronts.

4.7.1. Scotia–Weddell confluence

Two seabird assemblages occur during winter (Ainley et al., 1994): the pack ice assemblage with Antarctic species and the near ice open water assemblage that includes some true PFZ species (diving petrel *Pelecanoides* spp., Kerguelen and Blue petrels *Halobanea coerulea*). During spring, three assemblages have been reported: the pack-ice assemblage, a near to ice assemblage including the winter open water assemblage (with the addition of Fairy prion *Pachyptyla turtur* and Black-Bellied storm petrel *Fregetta tropica*, two true PFZ species) and a far-from ice open water assemblage (including White-chinned petrel *Procellaria aequinoctalis* and Light-Mantled, Grey headed *Diomedea chrysostoma* and Black-Browed albatross *Diomedea melanophrys*). In autumn, the open water assemblage includes near to and far from ice species (albatrosses). As a result, the number of species in the open-water assemblage is higher than in winter. The pack-ice assemblage is quite similar to the spring situation. To summarize, ice dependant species maintain their association with their habitat all year round. In contrast, the two open-water assemblages (including birds from the PFZ) exhibited important seasonal changes. Open-water species, which are not adapted to exploit ice resources, vacate high latitudes of the Southern Ocean in winter at a time when marine productivity falls to a minimal level (Ainley et al., 1994).

4.7.2. Southern Indian Ocean

Seasonal surveys across the SAF and PFZ show important changes in species use of frontal areas during the course of the year (Stahl et al., 1985). During winter, the seabird biomass is relatively low over almost all water masses including the STF, SAF and PF. The seabird biomass is similar over Subantarctic and Antarctic waters, with most petrel species (White-chinned petrels, Prions, Storm petrels) almost completely disappear from these areas. Albatrosses (Yellow-nosed *Diomedea chlororhynchos*, Wandering *Diomedea exulans* and Sooty *Phoebetria fusca* albatrosses) are also much less abundant at this time. Foraging zones of the different species are more segregated than in summer. In spring and early summer, the seabird biomass over cold waters of the PFZ becomes much higher than over northern Subtropical waters. Between the beginning and the end of summer, the bulk of seabird biomass moves to the south, possibly because of the delayed vertical migration of zooplankton at higher latitude (Stahl et al., 1985).

A detailed study reports the seasonal use of southern fronts by Short tailed shearwaters *Puffinus tenuirostris*. It is based on 23 years of at-sea surveys in the Indian Ocean between Australia and East Antarctica (Woehler, 1997; Woehler et al., 2006). Between the end of winter and early summer, a prominent peak of shearwater density is associated with the PF. From late spring to early autumn, a second peak in the densities is observed close to the AD. As summer progresses, a southward and westward shift of the shearwaters distribution up to the ice edge limit is observed. At this time, the birds are still constrained by the presence of pack-ice. As the Marginal Ice Zone retreats southward, the shearwaters forage over the Antarctic continental shelf. The role of AD still remains to be separated from those of the shelf break and marginal ice zones. It is likely however that these physical processes act in synergy to increase prey availability for these predators at a key period of their breeding cycle. This southward shift corresponds to the hatching period, i.e. an increase in the energy demand to their chicks. The higher productivity of the Marginal Ice Zone at his time may explain why these predators paradoxally forage south of the PF in late summer, thousands of kilometres away (Woehler et al., 2006).

4.8. Carbon flux to marine predators in the frontal zones

Estimations of the consumption of marine resources by predator communities of southern waters are speculative because of the multiple biases involved. This includes a lack of data about primary production in large areas and seasonal changes in marine productivity, limited information about predators diet, energetic costs of behaviours and energetic content of prey, habitat use and abundance, and the use of theoretical values of energy requirement and assimilation efficiency (Ainley, 1985; Croxall et al., 1985; Guinet et al., 1996; Woehler, 1997; van Franeker et al., 1997). Keeping in mind these inherent limitations, the annual carbon consumption by seabirds can be roughly estimated between 0.070 to 0.095 g C/m^2/y in the area of the PF (Abrams, 1985b; van Francker et al., 2002). This corresponds to only 0.01–0.1 of the whole primary production. The carbon flux to birds was found higher at the PF than at the STF. Such carbon fluxes, however, are five to ten times lower than values estimated in sea ice areas (Weddell Sea) where whale and seal populations contribute much more significantly to the total carbon flux (van Franeker et al., 1997).

5. Top predator foraging activities in frontal areas: contribution of individual tracking studies

Individual tracking of breeding marine birds and mammals has revealed that fronts can be major areas for foraging activities during the breeding season. Some species exhibit a combined feeding strategy exploiting both frontal zones over deep waters and neritic zones. Finally, some predators forage extensively in certain areas dominated by complex interactions between the proximity of a front, bathymetry and advection by currents.

5.1. Flying seabirds: albatrosses

The remarkable power-saving of gliding flight results in a relatively low energetic cost of movements that enables albatrosses and petrels to forage at large distances from their breeding colonies. Species specific differences in the use of the marine environment exist with some species being specialized in the exploitation of fronts (Weimerskirch, 1998; BirdLife International, 2004).

5.1.1. Black-browed albatross and Grey-headed albatross

Black browed and Grey-headed albatrosses breed together at several localities, including South Georgia (South Atlantic Ocean, 54°15′S, 36°45′W), Kerguelen (South Indian Ocean, 49°15′S, 69°35′E) and Macquarie (southwest corner of the Pacific Ocean, 54°30′S, 158°60′E, Fig. 2). Satellite-tracked Black-browed albatrosses from Kerguelen and Campbell Island (South Pacific, 52°32′S, 169°80′E) depended strongly on the PF for food acquisition. At South Georgia, where the species relies extensively on krill and fish, no specific association with the PF was found (Prince et al., 1998). There, Black-browed albatrosses mostly divide their time at-sea between distinct shelf areas in the North and South of this island the northwest edge of the continental shelf of South Orkney Islands and the oceanic PFZ to the North (Prince et al., 1998).

Kerguelen Black browed albatrosses rely mostly on fish and perform commuting trips, often moving in a straight line to some specific areas over the outer shelf and inner shelf break that almost coincides with the closely-located PF (about 40 km off the coast; Cherel et al., 2000). At Campbell Island, these birds show a combined feeding strategy exploiting both the extensive surrounding shelf area together with the oceanic environment. However, in contrast to Kerguelen, the PF is located 1500 km to the south of the island (Waugh et al., 1999). After a series of short trips over the continental shelf where they rely on fish, the same individuals visit the PF during longer trips (Fig. 2). During these trips, they feed mostly on cephalopods such as *Martiala hyadesi*. Thus, the importance of the PF for these albatrosses leads to contrasted foraging strategies, depending on PF location relative to that of the breeding colony. Strategies range from short trips only at Kerguelen to an alternation of short and long trips at Campbell Island. The use of such a two-fold strategy is common for albatrosses and petrels rearing chicks (Weimerskirch et al., 1994), allowing Campbell Black browed albatrosses, to feed their chick frequently with food caught on the shelf break (fishes) and to restore their body reserves in the productive PF waters far away the colony.

Grey-headed albatrosses at all localities appear to be even more dependent on the PF than Black browed albatrosses. They may concentrate as much as 70% of their time at sea, relying on the same cephalopod prey as Black browed albatrosses. Such a distinction in the use of oceanic habitats by these two species suggests a spatial segregation that is still poorly understood (Waugh et al., 1999). For Grey-headed albatrosses, birds appear to use different foraging strategies according to the stage of the breeding cycle. Incubating albatrosses from Marion island (South Indian Ocean, 46°64′S, 37°44′E) concentrate their foraging activities at the edge of positive and negative sea surface height anomalies that are likely to be eddies as a result of the interaction between the Agulhas return current and the Madagascar ridge (Nel et al., 2001). They exploit these small scale features in the STF and the SAZ. In contrast, chick-rearing birds forage mostly around negative height anomalies south of the PF and no foraging trip was observed to the STF at that time. Diet samples from tracked albatrosses showed that birds travel to exploit the edge of warm eddies where they caught mostly the predatory fish *Magnisudis prionosa* and the squid *Martiala hyades*. These two prey species are predators of myctophid fish (which are also present in the albatross diet) and may be more concentrated at both warm and cold eddies because of a much higher available biomass of zooplankton and micronekton (Pakhomov et al., 1994; Pakhomov and Froneman, 2000). At South Georgia, a preliminary investigation indicated that Grey-headed albatrosses show a similar foraging behaviour at warm eddies (Rodhouse et al., 1996).

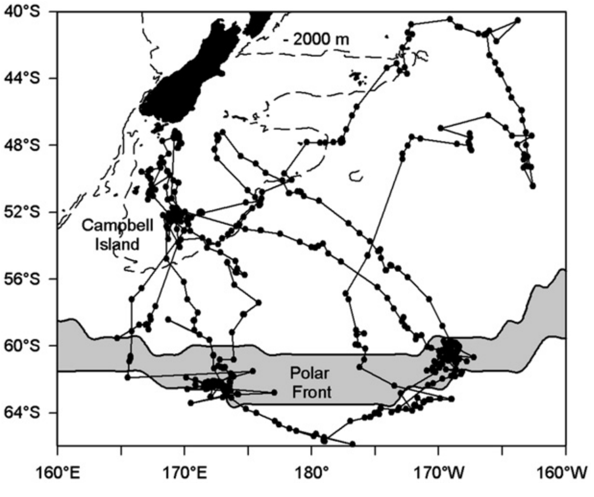

Fig. 2. Oceanic foraging trips of Black-Browed albatrosses from Campbell Island, Pacific Southern Ocean (from Waugh et al., 1999). The Polar Front position was determined from contemporaneous monthly SST data base (IGOSS Integrated Global Ocean Services System, Reynolds et al., 2002).

5.2. Diving predators

Tracking studies have shown that diving predators are highly specialized in the use of fronts. Because they exploit the three dimensions of the water column, they can take advantage of vertical physical discontinuities at fronts and have access to deeper dwelling prey than flying birds.

5.2.1. Fur seals

Satellite-tracked female Subantarctic fur seals *Arctocephalus tropicalis* from Amsterdam Island were found to forage mainly at the STF (Georges et al., 2000) and to follow the seasonal latitudinal variation of this front (Beauplet et al., 2004). Their foraging habitat is associated with the northern limit of the STF during early summer, located 60 to 130 km south of Amsterdam Island. In winter, as the STF migrates 250 km north of Amsterdam Island, fur seals increase their foraging range up to 530 km from the island.

At Kerguelen, lactating Antarctic fur seals *Arctocephalus gazella* target mainly waters along the shelf break that are associated with the eastern side of the PF (Guinet et al., 2001; Lea and Dubroca, 2003). Analysis of the thermal signature recorded by the logger carried by the seals is in good agreement with the location of the PF, suggesting enhanced availability of their myctophid prey there. At South Georgia, female Antarctic fur seals exhibit four categories of spatially well-defined trips (Staniland et al., 2004). Short intermediate location trips are concentrated in the frontal region associated with an up-welling where the fur seal dive deep. The three other categories occurred within South Georgia shelf water (Short Shallow-location trips), far toward the west (long intermediate-location trips) and shallow shelf water (long deep-location trips).

5.2.2. Elephant seals

The PFZ constitutes an important foraging sector for the Kerguelen population of Elephant seals *Mirounga leonina*. This species undertakes long migrations throughout the southern waters in search of prey (Fig. 3) and they regularly dive to ~400–1500 m. Four distinct behavioural strategies have been reported: a) pelagic foragers that spend most of their time travelling along frontal areas within the ACC; b) seals within the PFZ that undertake a pronounced diurnal vertical migration associated with a temperature minimum at night and a temperature maximum during the day, while seals within the SAF zone record no diurnal temperature variation; c) other seals that were coastal benthic foragers, spending most of their time diving to the seafloor along the Antarctic continental shelf edge; and finally, d) the

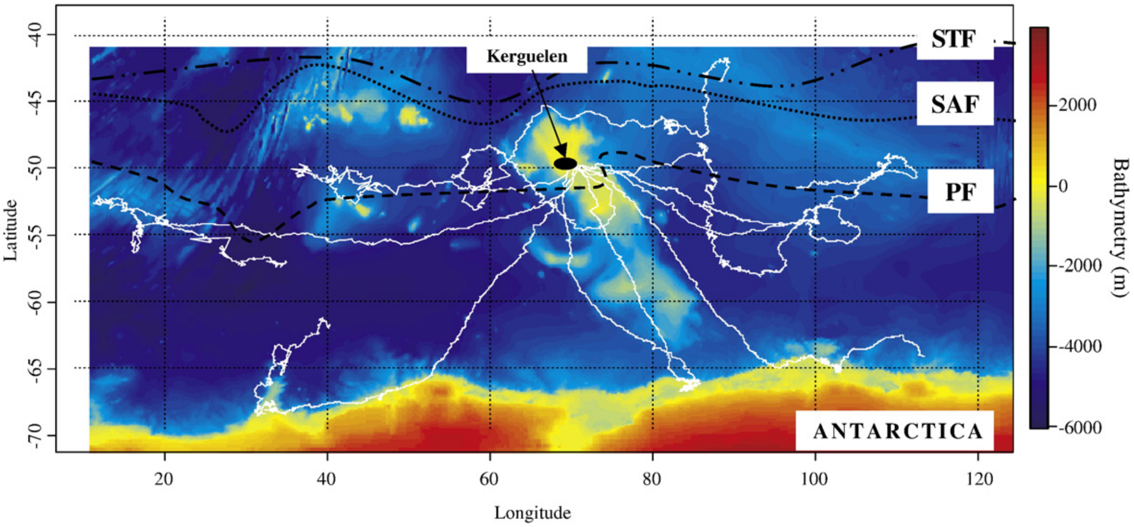

Fig. 3. Example of eight different trips (solid white line) of Elephant seals through the Southern Ocean. PF: Polar Front; SAF: Subantarctic Front; STF: Subtropical Front (Sources: Belkin and Gordon, 1996; Park and Gambéroni, 1997). The source of bathymetry is ETOPO5 database.

ice-edge pelagic foragers that spend most of their time in the vicinity of the pack-ice edge.

Monitoring the changes in drift rate of the seals (a proxy for body composition) allows distinguishing periods of relative fattening from periods when seals become leaner (Biuw et al., 2003). By correlating these changes with oceanographic physical parameters and behavioural strategies, it is possible to characterise important feeding "hotspots" (Biuw et al. 2007). Concerning the Atlantic sector, most of these spots are within the ACC and illustrate the importance of the PF as a main foraging area. In the Indian and Pacific sectors, a greater proportion of the females are found foraging along the ice edge and a smaller proportion within frontal structures, mainly at the PF (Bailleul et al., 2007a,b). Theses differences in foraging preferences between populations illustrate the plasticity of individuals and populations in their reliance on fronts.

Within the PF area, Elephant seals are confronted to specific oceanographic features such as eddies. Cold cyclonic eddies (cold-core) can issue from the PF. Warmer anticylonic eddies (warm-core) can come from north of the SAF (Nel et al., 2001). Satellite-tracked individuals preferentially followed the edge of eddies. The current directions within eddy field do not seem to influence the movements of seals that swim without any preference with and against the current. Moreover, seals dived deeper inside several, but not all, cyclonic eddies and they focused their foraging activity mainly inside or at their edges. By contrast, no behavioural changes were observed inside anticyclonic eddies (Bailleul et al., 2007a). Mesoscale eddies may offer opportunities for exceptional local productivity favourable to top predators such as elephant seals. In general, enhanced upwellings occurred inside cyclonic eddies and predators would be expected to dive shallower inside this kind of structure. However, both cyclonic and anticyclonic eddies may embody either upwellings or downwellings, depending on whether they are forced eddies or free eddies (Bakun, 2006). In cyclonic free eddy issued from the PF the vertical flow that occurs inside the eddy is mainly downward, which is in agreement with elephant seals diving in the deep. Therefore, diving behaviour of elephant seals could be explained by the presence of free eddies within the PFZ.

5.2.3. Penguins

Several penguin species, such as Macaroni, Royal and King penguins, are known to rely on the PFZ for feeding. All foraging activities of the middle-sized Royal penguin *Eudyptes schlegeli* occur within the PFZ south of Macquarie Island where they breed (Hull et al., 1997). The closely related Macaroni penguins from South Georgia (one of the main populations of the species, Woehler, 1995) travel during incubation toward the PF and the Maurice Edwing Bank (a micro-continental rise east of the Falkland Islands) at a mean distance varying from 376 km (females) to 572 km (males) during trips lasting about two weeks. At this breeding stage, their foraging ranges (especially the males) encompass the PFZ, i.e. an area north of the PF (Trathan et al., 2000) and south of the SAF. During the brood phase, both sexes forage over the continental shelf much closer to nesting areas (Barlow and Croxall, 2002).

5.2.4. King penguins as a study case

The most detailed accounts of the use of oceanographic front features by diving birds are those of the King penguin from various breeding localities. These penguins are among the major avian predators of the southern waters in terms of population size and prey consumption (Woehler, 1995). Stable isotope data strongly suggest that, over their whole geographic range, King penguins are always specialized predators in summer, targeting myctophid fish in waters of the PF (Cherel et al., 2002, 2007 and unpublished data).

Whatever the breeding location, King penguins exploit frontal zones and especially the PF in a consistent way. Two distinct oceanographic contexts have been reported: a) the use of highly dynamic frontal regions far away from the breeding colonies (Crozet, South Indian Ocean: Bost et al., 1997; Guinet et al., 1997; Macquarie Island: Wienecke and Robertson, 2006); and b) foraging in areas dominated by complex interactions between the proximity of a front, bathymetry and advection currents (Kerguelen: Koudil et al., 2000; Bost et al., 2002; Charrassin et al., 2002; Heard: Wienecke and Robertson, 2006; South Georgia: Rodhouse et al., 1996; Pütz, 2002).

5.2.4.1. King penguin at Crozet (46°40′ S, 51°90′E). The Crozet population is the only one where the use of frontal zones by a top predator has been investigated over the annual breeding cycle (Charrassin and Bost, 2001). King penguins here strongly rely in summer on two remote frontal zones lying about 400 km away, either south (PF) or north east (SAF) of the colony in deep oceanic waters. Most of the satellite tracked birds head south toward the PF where they end their outward trip (Fig. 4).

Fine scale adjustments of at-sea movements of King penguins travelling to the PF was investigated from SST gradient and geostrophic currents associated with eddies (Cotté et al., 2007). In contrast to Elephant seals, penguin movements while searching for eddies

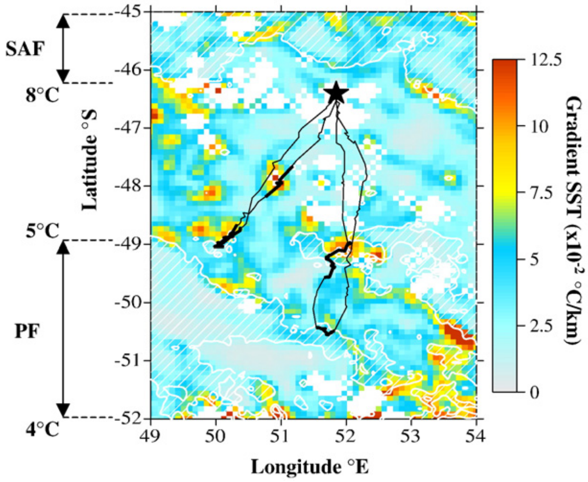

Fig. 4. Foraging trips of 2 King penguins (14–27 February 2004) from Crozet islands, South Indian Ocean, in relation to a weekly situation of sea surface temperature (SST) and SST gradients from satellite data (18–26 February 2004). Bold segments indicate central phases of the trips. Hatched areas correspond to the fronts (PF: Polar front, SAF: Subantarctic front) delimited by white lines defining the surface isotherms (between 4 and 5 °C for the PF and between 8 and 11 °C for the SAF, Park et al., 1993). The white area corresponds to the cloud coverage. The star indicates the position of the Crozet Archipelago.

coincide with the underlying current directions. There is no trend in deviation of bearing direction in the central phase of the trip, i.e. when the foraging activity is the highest. Importantly, while travelling toward the PF, the currents are at least one order of magnitude lower than penguin velocity. Once at the edge of an eddy, all trips are clockwise or anticlockwise relative to the prevailing intense current. Adjustments in swimming direction argue that the mesoscale circulation pattern might be a useful cue for foraging King penguins, despite the large difference between their swimming velocity and current amplitude (Cotté et al., 2007). As Elephant seals, penguins also benefit first from upwellings at the centre and from convergences (horizontal concentrations) at the edge of cyclonic eddies, and second, from enhanced concentrations of prey at shallow depths in anticyclonic eddies due to an elevation of isopycnals there (Polovina et al., 2006).

On average King penguins spend 33% of their trip duration at the PF (Bost et al., 1997). Prey are clearly more available for King penguins there, with foraging effort and foraging success (dive frequencies and prey ingestion rate) being greater at the PF than during the transit phases (C.A. Bost, unpubl. data). Foraging King penguins typically dive to the thermocline or deeper. Importantly, they typically dive to decreasing depths when travelling toward the PF as a response to the shallower thermocline (Charrassin and Bost, 2001). Prey are thus apparently more accessible with increasing distance travelled from the island. Myctophid fish appear closer to the surface and in more dense concentrations at the PF (Sabourenkov, 1991; Pakhomov et al., 1994), where the temperature in the lower part of the thermocline is close to the thermal optimum (2.6–5 °C, Hulley, 1990) of myctophids preyed upon during summer by King penguins (*Electrona carlsbergi* and *Krefftichthys anderssoni*; Cherel and Ridoux, 1992). Then, by diving consistently within and below the thermocline, King penguins rely on predictably-distributed prey.

Incubating and brooding King penguins travel quickly during the transit phases to the PF with a mean maximal foraging range of 540 km and 340 km, respectively. Incubating birds generally travel to the centre of the PF or to its southern side, whereas brooding birds usually stop at its northern side. During the long incubation trips (12 to 22 days), penguins are less time-constrained than during brooding but they need to re-build their body reserves after the long incubation shifts during which they fast ashore. Their choice to use waters beyond the south side of the PF strongly suggests a higher prey availability in this area. Available data on myctophid distribution in the southern Atlantic Ocean indicate large concentrations of *Electrona carlsbergi* at the southern edge of the front (Kozlov et al., 1991).

Except in spring, King penguins exhibit all year long the above described foraging pattern at the PF, using strong vertically stratified regions and typically diving to the thermocline to avoid the Surface Mixed Layer (SML). During autumn, they dive deeper in relation to a thicker SML (100 m) by contrast to summer (80 m) (Fig. 5). This

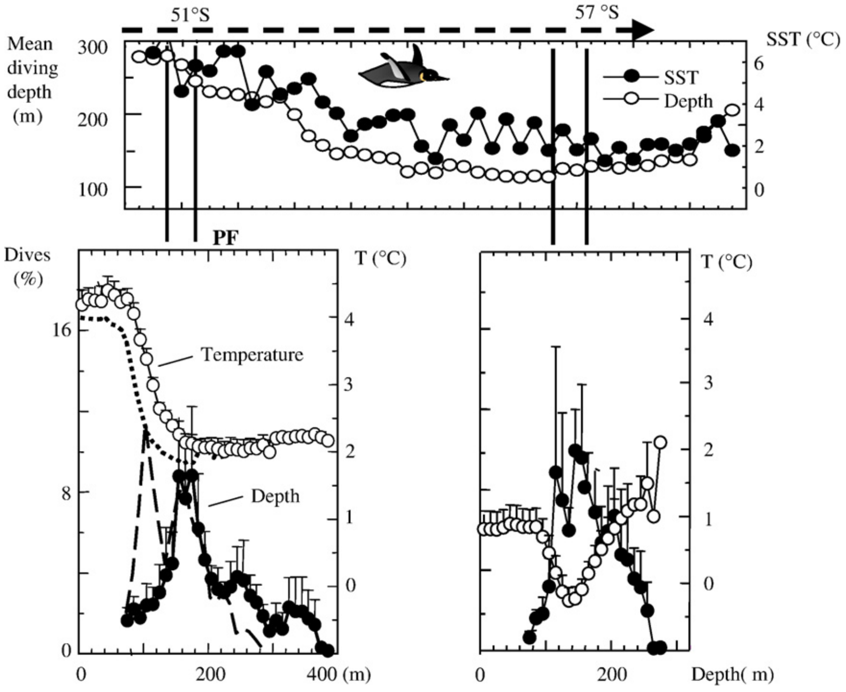

Fig. 5. Top: diving depths of King penguins from Crozet Islands during their autumn trips in relation to SST. Bottom: dive frequency (closed symbols) in relation to the thickness of the Surface Mixed Layer (open symbols) and autumn foraging areas within the Polar Frontal Zone (left: transit phase of the trip) and outside it (right: central phase of the trip). The dotted curves (bottom left) correspond to the summer records of temperature profile (dotted) and dive frequencies (long dash).

suggests that myctophids are less accessible within the SML than below it. As the season progresses, penguins travel towards Antarctic waters south of the PF and they gradually increase their foraging range until midwinter. At the southern limit of their foraging range (57° to 60.6°S, i.e. close to the ice-edge), King penguins find again a thermal discontinuity (inversed) less deep than at the PFZ at this time of the year.

At any time of the annual cycle, these long distance foragers and deep divers track thermal discontinuities below the SML. Because of their diving and travelling abilities, King penguins use distant but predictable frontal areas such as the PF to catch myctophid fishes, one of the most important trophic resources of the southern waters. This foraging strategy may have evolved as a result of the thinning of the SML and a more accessible thermocline by heading south (Charrassin and Bost, 2001).

5.2.4.2. King penguin at Macquarie Island (54°30′ S, 158°60′ E). The oceanic area surrounding Macquarie Island is dominated by the ACC. Three main currents carry most of the ACC: the SAF, the PF and the Southern ACC (Orsi et al., 1995). The extensive Campbell plateau deviates the position of the fronts more than 5° south to the east of Macquarie. When leaving Macquarie Island to forage, King penguins consistently travel to the southeast where their foraging strategy is strongly influenced by oceanographic features (Sokolov et al., 2006). At the macroscale, penguins forage near the PF where they feed close to and between the northern and southern branches of the PF for almost the entire duration of their trips in summer.

5.2.4.3. King penguin at Kerguelen (48°40′–50°00′ S; 68°45′–70°58′ E) and Heard Islands (53°06′ S, 73°31′ E). The Kerguelen archipelago and its extensive shelf lie in the southern Indian Ocean, 1400 km southeast of Crozet Islands. At Kerguelen, King penguins forage closer to the colonies than at Crozet because of the closer proximity of the PF. Park and Gambéroni (1997) provided evidence that the PF skirts the Kerguelen archipelago from the south and passes just southeast of the islands, following the inner part of the continental slope along the shelf break between the 200 m and 500 m isobaths. King penguins generally follow a path to the southeast up to 300 km from their colony, mainly along the eastern edge of the shelf (Bost et al., 2002). After having crossed the PF at 71° and the strong associated current, they forage mostly over the wide shallow plateau (500–1000 m) and along the shelf break. They encounter a cold northwest flowing current, in opposition to the general eastward flow of the ACC (Charrassin et al., 2002; Roquet et al., 2009-this issue). This current results from a tidal current–bottom interaction. It also generates internal tides that favour iron enrichment by vertical mixing, leading to a high primary production observed over the plateau (Blain et al., 2007). In addition, the thermocline is located closer to the surface (80 m) providing favourable diving conditions. Shallower dives recorded at Kerguelen during chick rearing (mean diving depth: 120 m versus 160 m recorded for Crozet birds) are probably determined by the shallower thermocline there (Koudil et al., 2000; Charrassin et al., 2002).

At nearby Heard Island, a strong current from the southern ACC circulates from west to east, sweeping the south end of the island. The penguins mostly forage at the south end of the Eastern Trough over deep waters. There is a strong current flow to the north across the trough probably providing predictable prey concentrations (Wienecke and Robertson, 2006).

6. Conclusions and perspectives

6.1. Why are fronts so profitable to predators?

So far, multidisciplinary approaches to the relationships between top predator foraging behaviour and frontal structures have been much more limited in Southern waters than in the Northern Hemisphere. However, results from the southern studies, combined with bio-logging, have demonstrated that predators rely extensively on fronts that are predictable in time and space. These structures include macroscale latidudinal frontal systems, mesoscale eddies, and tidal currents at smaller spatial scales. Some fronts, such as those overlying the Antarctic Continental slope, appear so profitable that they consistently attract seabirds from several hundred kilometres away.

At-sea studies have been successful in relating predator abundance to frontal physical parameters, but have had limited success in relating predator distribution to prey biomass. At the mesocale level, southern seabirds clearly respond to increased productivity and prey abundance at the fronts, as in other marine ecosystems (Schneider and Duffy, 1985; Hunt et al., 1990; Fauchald et al., 2000; Ainley et al., 2005). Results from bio-logging have also provided indirect evidence of higher resource predictability at mesoscale fronts. At smaller scales however, relationships are less clear, thus underlining the limits of our understanding of the predators' habitats. Several hypotheses can be advanced to explain this small scale mismatch. First, we do not evaluate prey abundance in the same conditions as predators (Ainley et al., 2005). Second, the lower abundance of some zooplankton species may result in a lower attraction for such predators. Prey density threshold level may be required before birds aggregate significantly (Schneider, 1990; Hunt et al., 1999). Finally, predictability is time-dependent. The time lag in the causal chain linking physical features to prey may be long enough to prevent detection of crustacean swarms and fish schools. In addition, predictability of prey at fronts might be ephemeral, i.e. over a time scale of days to weeks. This is suggested by available tracking studies as seabirds appear to return rarely right to the same place within the frontal area (Weimerskich, 2007).

In the Southern Ocean we still know too little about the origin of increased prey availability in the frontal areas to answer the question: do predators rely mostly on prey concentrated here because of advection processes or do they rely mostly on production-related increases in prey biomass? In the Arctic, when the structure of the frontal zone is the prime factor inducing prey concentration, the association between physical parameters and seabird flocks occurs at small spatial and temporal scales (Hunt et al., 1999). In the Southern Ocean, top predators appear to forage as much on prey advected by physical processes as on locally produced prey. The strong association of some avian predators with frontal temperature gradients (plankton feeders: prions; diving predators: king penguins) suggests indeed a key role of the physical processes to induce prey aggregations.

6.2. Finding prey at the frontal area

Seabirds constitute the group whose movements toward the frontal zones have been the best documented. All studied species and populations, however, do not necessarily rely on frontal processes to acquire food. Birds that use fronts extensively feed mostly on small prey aggregated in patchily distributed swarms (i.e. euphausiids, myctophids).

Specific foraging modes and movements occur at different spatial scales during trips to fronts. At mesoscale, birds generally use commuting type movements, corresponding to a displacement from the colony with a particular bearing and high speed until reaching a particular area close to the front or within it (Weimerskich, 2007). This commuting trip strongly suggests that seabirds have knowledge of the front location and that resources there are predictable. We do not know if this behaviour is genetically inherited or the result of experience. At a fine scale level, the birds will increase their turning rate, adopting an “Area Restricted Searching behaviour” (ARS) with a generally decreased speed (Fauchald et al., 2000; Pinaud and Weimerskirch, 2005). This behavior corresponds to an environment where the probability of prey capture may be higher. At this time diving birds also increase their foraging effort in terms of dive rate and time spent by sector (Bost et al., 1997; Charrassin and Bost, 2001). After a certain time spent at the frontal zone, the bird returns generally by a direct path to the breeding colony. The variability in the duration of presence at the frontal zone, i.e. at the limit of the foraging range, suggests that the energetic gain differs among the individuals. Foraging decisions are indeed state dependent (MacNamara and Houston, 1996). In addition, the time spent at sea off the colony may approach a threshold indicating the need to relieve the partner at the nest or to feed the chick. A second broad type of foraging movement is a looping trip, where the bird does not reach the frontal zone with a fixed bearing. It makes stops one or more times that may correspond to eddies where ARS behaviour occurs (Weimerskich, 2007).

At finer scale, we still rarely know if predators rely more on biotic cues of the front (i.e. congeners, prey) and/or visuals cues to locate an appropriate foraging habitat. In a study of kittiwakes *Rissa tridactyla*, it was found that they foraged more in areas suitable for the existence of prey than in areas where prey schools were actually visible (Ainley et al., 2003; Ford et al., 2007). Physical cues, thus, are important, and may be obtained from degree of contrast of habitat and discontinuities at the sub-surface, such as a change in wave height, SST, current strength, or colour of the sea. Predators would first locate a favourable habitat and then would search actively for prey (see also Ainley et al., 2005). Flying seabirds can also strongly rely on olfactive cues to detect prey aggregation (Nevitt et al., 2002). The presence of diving predators coming to the surface to breathe may also be a good indicator of the frontal zone. Diving predators explore the three dimensions of the water column when travelling towards a predictable front and they could gain information about prey abundance beneath them more easily than flying foragers. Works on King penguin suggests that diving foragers might use currents associated with eddy activity as oceanographic cues in an active search for physical discontinuities in frontal zones.

How warm and cold eddies lead predators to increase their foraging effort at the limit of these physical features is still unknown. Much remains to be learned about how seabirds such as albatrosses can access their fast moving, often mesopelagic or even benthic prey, at the eddies (Nel et al., 2001). Advection of prey might be involved, for example in the case of dead post-spawning buoyant squids.

6.3. Future work

A better understanding of the functioning of oceanographic processes and structures in the frontal zones is crucial to improve our knowledge of top predator behaviour. For this purpose, the use of recently developed towed sensor arrays to record oceanographic parameters in real time in conjunction with continuous top predator surveys appears highly promising. Such a method could considerably help to understand the extent to which seabirds respond to physical versus biotic parameters and finally to explain spatial variations in their occurrence (Ainley et al., 2005).

Top predators are more often associated with strong than weak fronts (Schneider et al., 1987). It would be then relevant to investigate further how latitudinal variation in the signals of physical parameters changes the role of physical processes as factors concentrating top predator prey (Hunt et al., 1999). Studies simultaneously tracking predators and sampling their prey across fronts should better tell us why some eddies attract predators whereas others do not. More data on prey abundance/distribution and marine predator association with fine-scale oceanographic processes especially at oceanic fronts are also required as recommended by the GLOBEC program. These studies have to be carried on with a scale-dependency approach to habitat selection (Schneider, 1993; Fauchald and Erikstad, 2002). The response of subsurface plankton feeders would be especially relevant to investigate further (Hunt et al., 1992; Goss et al., 1997).

Bio-logging studies were mainly conducted on pinnipeds and large seabird species. One can expect that progress in the miniaturization of telemetric technologies (GPS, Argos transmitters) will allow investigations into how small flying, plankton feeders species such as prions and small petrels use the frontal zones. Despite the huge amount of information provided on individual movements by bio-logging techniques, we know almost nothing about how seabirds and marine mammals find favourable areas and how they adjust their search to find prey. Direct observations of flying seabirds, or the use of new generations of loggers, such as still and video cameras, may help to clarify these questions in the future. Bio-logging studies have revealed large differences in frontal utilization among populations and individuals. Further work is needed to understand the consequences of this plasticity on individual fitness. Investigating in detail the role of learning in the use of fronts and eddies would be especially promising (Weimerskich, 2007). In this perspective, it will be highly relevant to investigate the behaviour of individually tracked predators in areas where eddies occur consistently and persistently at the same locations.

The warming trend observed in the Southern Ocean is expected to increase the amplitude of interannual variations in sea surface temperatures, thus inducing a latitudinal shift of fronts (Moore et al., 1999). It can be hypothesized that a southward shift of the PF will induce a shift in the foraging areas of several key apex predators. As a consequence, this shift would lead to an increase in foraging effort and ultimately induce a population declined of these species (Inchausti et al., 2003). It is, however, unclear whether species with distinct foraging strategies would react similarly or not to a variation in the fronts locations. Such environmental changes would add to the severe impact of fish extraction by the industrial fisheries on the southern food webs (Ainley and Blight, in prep.). Long-term research on at-sea distributions and demographic parameters of top predators are therefore essential to assess the consequences of a potential shift in front distribution.

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