



ELSEVIER

Available online at [www.sciencedirect.com](http://www.sciencedirect.com)

SCIENCE @ DIRECT®

Deep-Sea Research I 51 (2004) 2091–2103

DEEP-SEA RESEARCH  
PART I

[www.elsevier.com/locate/dsr](http://www.elsevier.com/locate/dsr)

## Fine resolution 3D temperature fields off Kerguelen from instrumented penguins

Jean-Benoît Charrassin<sup>a,\*</sup>, Young-Hyang Park<sup>a</sup>, Yvon Le Maho<sup>b</sup>,  
Charles-André Bost<sup>b,1</sup>

<sup>a</sup>Muséum National d'Histoire Naturelle, Département des Milieux et Peuplements Aquatiques, USM 402/LODyC,  
43 rue Cuvier, 75231 Paris Cedex 05, France

<sup>b</sup>Centre d'Ecologie et Physiologie Energétiques, Centre National de la Recherche Scientifique, 3 rue Bequerel,  
F-67087 Strasbourg Cedex, France

Received 25 September 2003; received in revised form 12 July 2004; accepted 20 July 2004  
Available online 20 October 2004

### Abstract

The use of diving animals as autonomous vectors of oceanographic instruments is rapidly increasing, because this approach yields cost-efficient new information and can be used in previously poorly sampled areas. However, methods for analyzing the collected data are still under development. In particular, difficulties may arise from the heterogeneous data distribution linked to animals' behavior. Here we show how raw temperature data collected by penguin-borne loggers were transformed to a regular gridded dataset that provided new information on the local circulation off Kerguelen. A total of 16 king penguins (*Aptenodytes patagonicus*) were equipped with satellite-positioning transmitters and with temperature–time–depth recorders (TTDRs) to record dive depth and sea temperature. The penguins' foraging trips recorded during five summers ranged from 140 to 600 km from the colony and 11,000 dives > 100 m were recorded. Temperature measurements recorded during diving were used to produce detailed 3D temperature fields of the area (0–200 m). The data treatment included dive location, determination of the vertical profile for each dive, averaging and gridding of those profiles onto  $0.1^\circ \times 0.1^\circ$  cells, and optimal interpolation in both the horizontal and vertical using an objective analysis. Horizontal fields of temperature at the surface and 100 m are presented, as well as a vertical section along the main foraging direction of the penguins. Compared to conventional temperature databases (Levitus World Ocean Atlas and historical stations available in the area), the 3D temperature fields collected from penguins are extremely finely resolved, by one order finer. Although TTDRs were less accurate than conventional instruments, such a high spatial resolution of penguin-derived data provided unprecedented detailed information on the

\*Corresponding author. Tel.: +33 1 40 79 31 64; fax: +33 1 40 79 57 56.

E-mail address: [jbc@mnhn.fr](mailto:jbc@mnhn.fr) (J.-B. Charrassin).

<sup>1</sup>Present address: Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360 Villiers en Bois, France.

upper level circulation pattern east of Kerguelen, as well as the iron-enrichment mechanism leading to a high primary production over the Kerguelen Plateau.

© 2004 Elsevier Ltd. All rights reserved.

*Keywords:* Bio-logging; Kerguelen; Penguins; Regional circulation; Sea temperature

---

## 1. Introduction

The use of diving animals as cheap, autonomous, and efficient vectors of oceanographic instruments is an emerging field of bio-logging science. This approach accompanies a growing number of studies aiming to understand how marine predators utilize the marine environment, and to determine the importance of ocean physical parameters for their foraging success (e.g., Boyd and Arnbohm, 1991; Hindell et al., 1991; Weimerskirch et al., 1995; Georges et al., 2000; Block et al., 2001; Charrassin and Bost, 2001). For this purpose, one must record simultaneously behavioral and physical parameters, since physical data collected by conventional means are rarely available at the same temporal and spatial scales as those at which predators operate. Thanks to miniaturization of instruments and progress in electronics, biologists can now routinely monitor movements at sea and the diving activity of predators (birds and marine mammals), simultaneously with sea temperature. Using this method, it has been shown that marine predators forage preferentially at oceanographic discontinuities (oceanic fronts, thermoclines, sea-ice zones, etc.; Boyd and Arnbohm, 1991; Georges et al., 2000; Charrassin and Bost, 2001). From this, it has become apparent that physical data collected by animals and primarily dedicated to ecological research could also be used for purely oceanographic purposes (e.g., Wilson et al., 1994; Koudil et al., 2000; Boyd et al., 2001; Fedak, 2004). Indeed, pelagic animals generally travel several tens to hundreds of kilometers from their colonies and dive to 100–1500 m depth, so they can potentially sample relatively large oceanic areas in 3D space. Furthermore, marine predators exploit areas of high oceanic/biological interest that are generally remote and difficult to sample by conventional means.

Although this concept is now well recognized among the scientific community, including oceanographers, only a few studies have yet brought new information for oceanographic uses (Boehlert et al., 2001; Charrassin et al., 2002; Lydersen et al., 2002; Daunt et al., 2003; Fedak, 2004; Hooker and Boyd, 2003). As a follow-up of our preliminary report (Charrassin et al., 2002), we show here how temperature data collected by penguins allow a better understanding of the local circulation and high primary production in the Kerguelen region. The present paper aims (1) to demonstrate the local oceanographic interest of this approach based on a comparison with existing conventional data, and (2) to present in detail the methodology developed for analyzing animal-derived temperature data. From these bio-logging data, unprecedented high-resolution thermal fields of the upper ocean off Kerguelen have been obtained, enabling us to describe and understand the hitherto poorly known local circulation, in relation to the local productivity and penguins' habitat. The advantages and problems of using bio-logging data are also discussed.

## 2. Material and methods

### 2.1. *Birds and instrumentation*

The fieldwork took place from 1998 to 2002 at Kerguelen Islands (Indian sector of the Southern Ocean), at the king penguin colony of Ratmanoff. The colony is located on the eastern side of the archipelago and contains ~50,000 breeding pairs (Weimerskirch et al., 1988). The study was conducted every year between late January and late March on breeding birds at the brooding stage (i.e., with chicks younger than 3 weeks), as part of a long-term project on the foraging behavior of

king penguins. A total of 16 birds were equipped with an Argos satellite platform transmitter terminal (PTT, model ST-10, Telonics, USA) to track the movements at sea (Fig. 1), and a time–temperature–depth recorder (TTDR; model Wildlife Computers Mk5 ( $n = 2$  trips) or Mk7 ( $n = 14$  trips), USA) to record diving behavior and sea temperature. The number of birds equipped was 1, 4, 6, and 5 for the years 1998, 1999, 2000 and 2002, respectively. Instruments were attached in a lower back position to reduce drag (Bannasch et al., 1994), and were glued to the feathers using a cyanoacrilate adhesive (Loctite 420). Animals were equipped after their departure from the nest, just before they reached the sea. All instruments were removed upon retrieval after the foraging trips.

When animals were at sea, depth was sampled every 2 or 5 s, and temperature was sampled every 5, 10 or 20 s depending on sensors used. Depth was recorded with a 2 m resolution. The resolution of the different TTDR temperature sensors varied from 0.1 to 0.3 °C. In order to reduce the response time of the temperature sensor, all TTDRs were modified so that the temperature probe protruded slightly from the unit, resulting in a response time of 24 s.

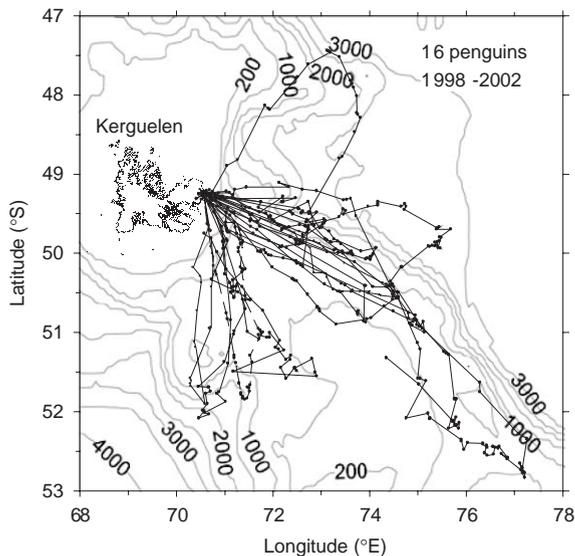


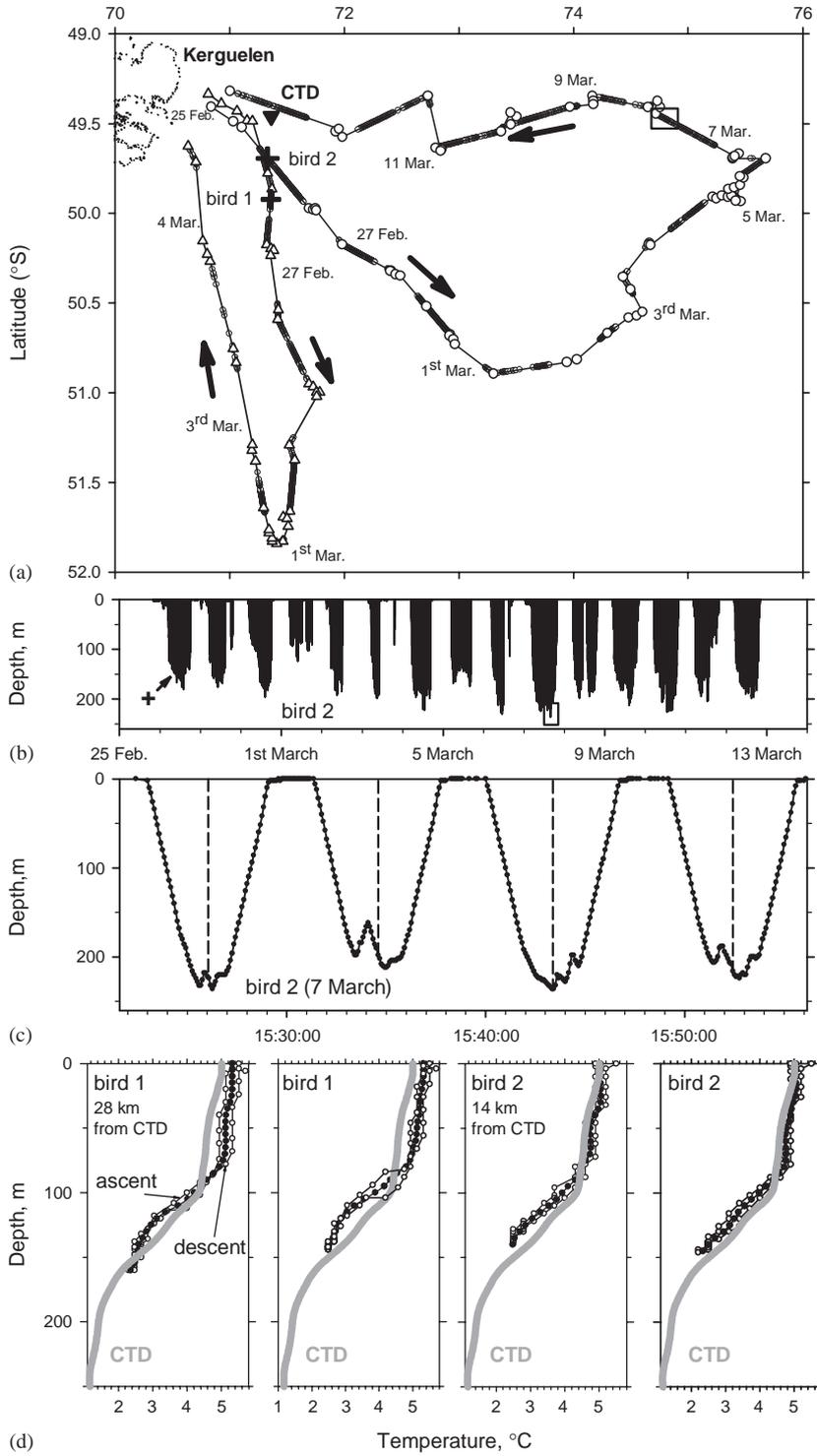
Fig. 1. Argos tracks of 16 penguins followed in February–March between 1998 and 2002. Animals were also equipped with a TTDR.

## 2.2. Data analysis

While depth and temperature were recorded continuously in time, the Argos system only provided a limited number of locations per day (Fig. 2). The bad Argos location data were filtered out following Wienecke and Robertson (1997) and Bost et al. (2002). Briefly, for a given location, average swimming speed was determined by taking the root mean square of the travel speeds from the previous two and to the next two locations from the point in question. We excluded data that gave an average swimming speed higher than  $14 \text{ km h}^{-1}$ , i.e., the mean maximal swimming velocity of king penguins (Kooyman and Davis, 1987).

In order to assign a geographical position to each dive (Fig. 2a), the TTDR record and the Argos record of each bird were first aligned in time. The time of each dive was calculated as the midpoint between the beginning and the end of the dive (Fig. 2c). The location of each dive was then determined using a time-based linear interpolation between two consecutive Argos fixes, assuming that penguins swim with a constant speed between two fixes (Koudil et al., 2000; Boehlert et al., 2001; Boyd et al., 2001; Charrassin et al., 2002; Fig. 2a).

Temperature data recorded by diving predators are characterized by their vertical and horizontal heterogeneity. The following treatment was aimed at homogenizing the data both vertically and horizontally. For each dive, temperature data recorded during descending and ascending phases were projected separately on a vertical axis corresponding to the mean time of the dive, sorted, and resampled at a 5-m depth interval using Gaussian interpolation with a 5-m depth-scale. The resulting data for descent and ascent were then averaged (Fig. 2d). In order to avoid a highly variable surface heating effect, temperature for the first 10 m were set constant and equal to the temperature at 10 m. This procedure has several practical advantages. First, the original data with continuously changing locations during each dive are transformed into fixed location data, in much the same fashion as conventional ship-based station measurements. Second, the mixing of the descending and ascending phases of the record tends to minimize the errors associated with the



response time of temperature sensors. Note that due to the delay of sensors' response to varying temperatures of the water column, the descending (or ascending) profile is biased to higher (or lower) temperatures (Fig. 2d). Due to horizontal movements of penguins, the ascent phase of dives could be through a slightly different water column than that during the descent phase. Considering a mean dive angle of  $45^\circ$  for a very deep dive (Pütz et al., 1998), say 300 m, the maximum horizontal distance between the beginning and the end of each dive should be 600 m. Given the scale that we are interested in ( $> 10$  km), such a small displacement has been neglected when averaging temperatures for descent and ascent phases of the dives. Third, the vertical interpolation scheme used filters out any fluctuations of vertical lengthscales much shorter than 5 m, a scale poorly resolved by TTDR measurements made every 5–20 s, as mentioned previously. It also yields regularly gridded data in the vertical.

We checked the effect of this treatment by comparing the data collected by a standard conductivity–temperature–depth (CTD) device from a ship at a time series station CLIOKER (Park, unpublished document, 2002), with those recorded by TTDRs carried by two penguins diving in the vicinity of the CTD station. For logistic reasons, we could not attach the TTDRs directly on the CTD device. We selected four deep dives from our penguin dataset that were the closest from the CTD station both in time and space. The selected “penguin” stations were located at 28 km (bird 1) and 14 km (bird 2) from the CTD station and took place 11 days later (Fig. 2a, d). The resulting mean absolute difference between the treated penguin profiles and the CTD

was  $0.33 \pm 0.18^\circ\text{C}$  (maximum  $0.72^\circ\text{C}$ ). Despite the slight discrepancy in time and location, the two types of measurements give quite similar profiles, permitting the penguin stations to correctly resolve the main features of the water column (temperature and thickness of the surface mixed layer (SML) and of the thermocline) (Fig. 2d).

Since the penguins tend to forage intensively in specific areas, and travel across other areas during transit, the density of data is highly variable over the region explored. This uneven data density may affect mapping of a horizontal temperature distribution using an interpolation method, because high-density areas will have a greater “weight” than those of low-density. To give each area the same importance, and to avoid a mass of stations too closely located, we put vertical temperature profiles on a corresponding  $0.1^\circ \times 0.1^\circ$  ( $11 \text{ km} \times 7 \text{ km}$ ) cell and averaged the values found within each cell at each 5 m depth interval. The resulting cell stations at 100 m depth together with the original data density (in color scale) are shown in Fig. 3. Note that the spatial distribution of these stations is highly irregular, with most of stations being concentrated along the eastern escarpment of the Kerguelen Plateau.

Before mapping horizontal temperature distributions at different depths, these irregularly distributed cell station data were interpolated on a  $0.25^\circ \times 0.25^\circ$  ( $28 \text{ km} \times 18 \text{ km}$ ) regular grid, using an optimal interpolation scheme. Briefly, this scheme consists of four steps. First, a latitude-dependant linear temperature surface or “trend” at each depth is computed. Second, temperature anomalies at every cell stations are obtained by subtracting the computed temperature trend. Third, interpolated temperature anomalies on

Fig. 2. Example of a dataset collected from instrumented penguins, preliminary data treatment, and comparison with a CTD: (a) Argos track of two king penguins foraging east of Kerguelen in summer 2002. Large dots and triangles indicate Argos fixes for each bird, and small dots indicate positions of individual dives obtained after a time-based interpolation of the dives between two consecutive fixes. The crosses indicate the positions of the penguin temperature profiles that were compared to the CTD (black triangle). (b) Diving activity of bird 2 during the same foraging trip, recorded by a TTDR. The plus sign indicates the dives selected for comparison with the CTD. (c) Details of the diving profile of bird 2, corresponding to the position and dives indicated by a small box shown in (a) and (b). The vertical dashed lines indicate the midpoint of each dive used for determining the dive position (see Section 2). Black dots indicate depth and temperature measurements recorded simultaneously every 5 s. (d) Vertical profiles of temperature from two consecutive dives of bird 1 and bird 2, and CTD profile recorded 11 days before and  $\sim 30$  km apart. Small circles indicate raw data recorded during descent and ascent. Black dots indicate temperature data after initial treatment (averaging of downcast and upcast followed by Gaussian filtering and resampling every 5 m).

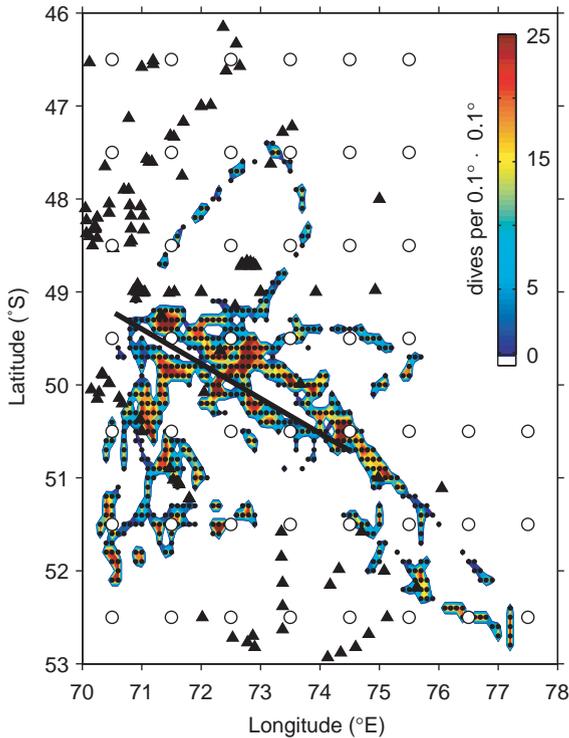


Fig. 3. Distribution of the penguin stations obtained by averaging individual deep dives ( $>100$  m) on a  $0.1^\circ \times 0.1^\circ$  cell (black dots), together with the original dive frequency within each cell (color scale whose upper limit corresponds to numbers of dives per cell comprised between 25 and 120); circles designate data points of the Levitus Atlas World Ocean (1994); triangles indicate historical hydrographic stations.

our regular grid are estimated by objective analysis (Bretherton et al., 1976; Emery and Thomson, 1998). This analysis requires a priori knowledge of the temperature's covariance function and uncorrelated error variance. The normalized covariance function or the spatial correlation function  $S(x)$  is assumed to be an isotropic, exponentially decaying function of the form:  $S(x) = a \exp(-x^2/b^2) + \varepsilon$ . Here,  $a$  is a normalized signal variance at a point of estimation ( $x = 0$ ),  $b$  is a decorrelation length scale, and  $\varepsilon$  is a normalized uncorrelated error variance. These coefficients have been estimated by minimizing the rms difference between the model correlation function  $S(x)$  and the experimental correlation function computed from the actual temperature anomaly field, which yields  $a = 0.61$ ,

$b = 110$  km, and  $\varepsilon = 0.39$ . Finally, a gridded temperature field is obtained by adding the linear temperature trend and the objectively interpolated anomaly field. Plotting was limited to the area where the estimated error variance does not exceed 50% of the total variance. To build a vertical temperature section along the penguins' main foraging path, data at each depth were projected onto a predetermined axis (thick line in Fig. 3), using a similar scheme but with different parameters ( $a = 0.50$ ,  $b = 40$  km, and  $\varepsilon = 0.50$ ) estimated from the high-density penguin data in the vicinity of the main foraging path. Note that our interpolation scheme is not very sensitive to the choice of  $a$  and  $\varepsilon$  for the overall structure of the field, but it yields an increasingly finer field with decreasing value of  $b$ , as expected. For consistency purpose, the historical station data and Levitus data were also treated in the same manner.

### 3. Results

#### 3.1. Penguins movements and data distribution

Data are presented as mean  $\pm$  standard deviation, unless otherwise stated. The trip duration of all penguins examined was  $9.3 \pm 4.5$  days (range 4–21 days;  $n = 16$  birds with a total of 150 days at sea) and the distance traveled by the penguins from the colony was  $310 \pm 119$  km (range 139–613 km) (Fig. 1). The total number of Argos locations was 525, with  $3.7 \pm 1.7$  locations per bird per day. This corresponds to a distance between two fixes of  $19.4 \pm 26.2$  km. Penguins dived continuously during daylight and a total of 11,000 dives  $\geq 100$  m were recorded. The mean dive depth for dives  $\geq 100$  m was  $148 \pm 32$  m (mean maximum dive depth  $222 \pm 34$  m, range 178–272 m).

The map of dives  $>100$  m shows that dives are heterogeneously distributed, with areas of high ( $>20$  dives per cell) and low density (Fig. 3). There are two areas without any dives, in the northern part of the study region, and in the south-central part where bottom depths are  $<500$  m.

These dives provided 604 vertical profiles, averaged within cells of  $0.1^\circ \times 0.1^\circ$  (11 km  $\times$  7 km). They were calculated from  $18 \pm 18$  initial

dives per cell (range 1–120 dives). These penguin stations are extremely dense, especially along the main foraging path, and surpass in number by an order of magnitude as compared to Levitus World Ocean Atlas (1994) data points and historical hydrographic stations. For a visual comparison, these latter stations are shown superimposed in Fig. 3, together with penguin stations.

Temperature data from the Levitus Atlas (1994) have a  $1^\circ \times 1^\circ$  resolution (indicated by circles). This regular distribution has been obtained by interpolating sparse historical data that were scattered in space and gathered over the past 50 years in the study area (only 25 “source” stations were used for the Levitus Atlas in the study area for the February–March period; Levitus and Boyer, 1994). Individual hydrographic stations from a historical database presently available for us in the study area are more numerous than Levitus data, but still there is a very limited number of observations, with only 50 stations (indicated by triangles) dispersed irregularly with a number of data holes.

### 3.2. Temperature map from the penguins: comparison with historical data

The penguins 3D temperature database was used to build a sea surface temperature (SST) map (Fig. 4a) and a temperature map at 100 m depth (Fig. 4b). The SST map, which in reality has been constructed using temperatures at 10 m depth for the reason given in Section 2.2, shows that two water masses exist in the area east of Kerguelen, with warm waters in the northern and western part of the area, and cold waters in the south-east along the eastern escarpment of the Kerguelen Plateau. The 100 m map shows more clearly the presence of a cold water tongue pointing northwestward along the eastern escarpment (black arrow in Fig. 4b). This subsurface cold water originating from the south (Park et al., 1998; Charrassin et al., 2002) penetrates farther north than its surface expression, and its presence can be felt as far north as  $49^\circ\text{S}$ , close to the Ratmanoff colony.

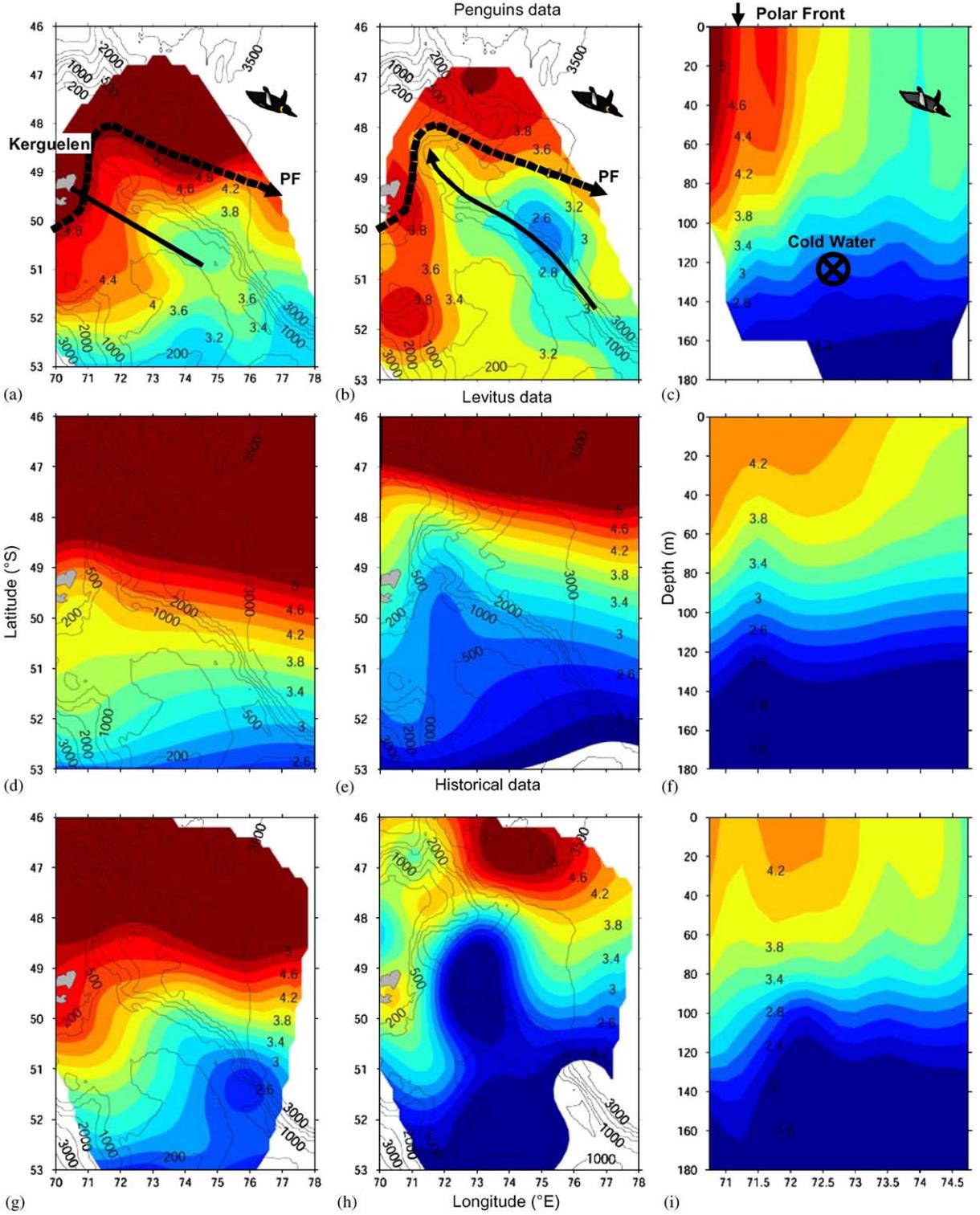
The presence of such cold water tongue following the eastern escarpment is not clear from the historical data. The Levitus maps show warm

waters in the north and cold waters in the south, but the water masses are distributed independently of the bathymetry (Fig. 4d). Indeed, the surface map shows temperatures changing according to a quasi-meridional gradient, with near-zonally aligned isotherms, without showing any small-scale features. The Levitus 100 m map shows a cold subsurface water mass lying over the whole southern part of the Kerguelen Plateau, characterized by isotherms running quasi-perpendicularly to the NW-orientated eastern escarpment (Fig. 4e).

The historical station data maps are slightly more detailed, and somewhat closer to the penguin-derived maps, with the presence of a warm water mass along the western part of the area (Fig. 4g). However, the importance of the eastern escarpment for the circulation of the cold water tongue seen from the penguin map is not so apparent from these data, because the cold waters are widespread over the southern plateau (Fig. 4h). The maps constructed from individual historical stations show an intermediate pattern between the penguin-derived maps and the Levitus maps.

### 3.3. Vertical section from the penguins: comparison with historical data

Fig. 4c shows a vertical temperature distribution obtained from penguin data along a SE section from the Ratmanoff colony, which forms the major route most commonly occupied by foraging penguins. Surface temperature increases rapidly towards the colony where the above-mentioned warm waters ( $>5^\circ\text{C}$ ) penetrate deeply along the continental slope west of  $71^\circ\text{E}$ . A steep inclination of subsurface isotherms between  $72^\circ$  and  $73^\circ\text{E}$  indicates the boundary between warm inshore waters and cold offshore waters. The latter waters are relatively homogenous ( $\sim 3.5^\circ\text{C}$ ) in the upper 80 m, forming a SML. Below this SML, the temperature decreases rapidly to reach  $2.2^\circ\text{C}$  at  $\sim 180$  m, forming a cold thermocline layer. The thermocline layer isotherms east of  $73^\circ\text{E}$  are found  $\sim 40$  m shallower than those at  $71^\circ\text{E}$ , consistent with the northward advection of the subsurface cold water tongue along the eastern escarpment, as mentioned previously.



Compared to this penguin section, the Levitus section (Fig. 4f) is featureless, with its isotherms being nearly horizontal. It thus misses completely the vertical structure associated with the warm water concentration toward the islands and the northward advection of the subsurface cold water between 72° and 73°E. The historical station data section (Fig. 4i) better resembles the penguin section although details are somewhat different. For example, the warm surface water west of 71°E is much colder (by up to 1 °C) and less well marked in the historical data section. Also, the subsurface cold water tongue in this section is shifted farther west compared to the penguin section. This is probably because of a very limited number of historical hydrographic stations available in the area. The overall temperature increase in the penguin section as compared to the Levitus and historical station data is noticeable, which seems to be related to a recent warming, although this topic is beyond the scope of the present study. Note only that the mean rms interannual variability of penguin-derived temperatures on the section amounts to ~0.3 °C, a value marginally detectable from the animal-borne sensors.

#### 4. Discussion

##### 4.1. Characteristics of penguins-derived temperature data

The most remarkable feature of the temperature data obtained employing foraging penguins is their very high spatial density. This is a consequence of the continuous diving activity of the penguins, and of the propensity of most individuals to explore similar foraging areas. Thus, when several birds and years are combined, some areas are sampled with a large number of dives (up to 120 dives

within a cell of 0.1° × 0.1°). Most birds foraged in one main region (mainly along the eastern edge of the Kerguelen Plateau), but, interestingly, a few of them showed a different behavior and headed toward the south or the north. While atypical, these tracks are of some value because they considerably enlarged the sampled area.

Such high-density of data allowed the construction of a database having a very fine-scale resolution of ~10 km, which is one order of magnitude finer than that from conventional hydrographic database (e.g., Levitus climatology, Levitus and Boyer, 1994; Fig. 4d–f). Moreover, such climatology has been constructed from generally sparse observations, especially in the Southern Ocean, thus using a wide radius (500 km) of influence for interpolation. Only large-scale features greater than 500 km will therefore be observed from that interpolation. This reflects the difficulty in sampling hydrological data in the Southern Ocean, mainly due to cost and logistic limitations. Therefore, it is generally impossible from climatology or historical data to map small-scale features of a few tens of kilometers that could affect the foraging behavior of diving predators. We have shown here that the penguin-derived dataset can present an efficient alternative for describing such a fine scale, upper-layer thermal structure of the predator's habitat.

The second aspect of temperature data obtained with this type of TTDR concerns the slow response time of temperature sensors and their far lower accuracy (0.3 °C) compared to a standard oceanographic device, CTD. This is not surprising because of the limited size of TTDR units (placed on the animals back), which restricts the space for accommodating larger, more accurate and faster electronic components, and because TTDRs were not originally designed for conventional oceanography (Wilson et al., 2002). We have shown that

←  
 Fig. 4. Top panels: horizontal distributions of temperature at the surface (a) and at 100 m depth (b), and vertical section of temperature along the main foraging axis (c), mapped from penguin data. Solid line in (a) indicates the axis along which the vertical section was mapped. The position of the Polar Front (PF; dash line) is given after Park et al. (1998). The arrow in (b) indicates the direction of the cold water tongue. Middle and bottom panels: same as the top panels, but for the Levitus World Ocean Atlas (1994) (d–f), and historical hydrographic data (g–i), respectively. To keep a homogeneous color scale among maps, a 2–5 °C temperature range was applied to all maps. Only areas where the estimated error variance is smaller than 50% of the total variance from an objective analysis are shown.

some of the related problems such as the shift in profiles between descent and ascent could reasonably well be remedied by our data treatment. It is also clearly shown that the weakness of low accuracy is largely compensated by an incomparable number of penguin stations compared to traditional oceanographic stations. In particular, by averaging and transforming the penguin dive data located closely within  $\sim 10$  km each others into cell stations, and considering the 18 dives per cell on the average, the mean standard error of our penguin station data should be  $\sim 0.07^\circ\text{C}$  ( $= 0.3/\sqrt{18}$ ). Although not sufficient compared to standard oceanographic criteria, this accuracy is found to be of practical use to delineate major horizontal and vertical structures of surface water masses in such a poorly exploited area as ours. Nevertheless, there is no doubt that faster and more accurate sensors are required for small-sized diving animals, and some are already available (Daunt et al., 2003).

Finally, the penguins tended to forage along a privileged route, leaving certain zones unvisited, thus yielding a highly non uniform sampling distribution within a given study area. This undesired characteristic of penguin data, though inevitable, would lead to a biased mean temperature field if original data were used for mapping. Our cell averaging scheme may compromise with this biased foraging tendency, reducing greatly the otherwise “overweight” the interpolation scheme would exert on the mean field, thus diminishing at least partly the expected bias in the estimated mean field.

#### 4.2. New information for regional circulation

The high spatial resolution of the penguin-derived data provided unprecedented detailed information on the upper level circulation pattern east of Kerguelen. These data allowed us to (1) better understand the surface circulation of the Polar Front east of Kerguelen, and (2) provide evidence for a subsurface current circulating northwestwardly along the eastern edge of the Kerguelen Plateau.

Previous studies have indicated that the Polar Front rounds the Kerguelen Islands from the

south to flow northward just east of the islands along the 200–500 m isobaths. This scheme has been inferred from the subsurface  $2^\circ\text{C}$  minimum at 200 m based on a few stations available in the area (Park et al., 1993; Park and Gambéroni, 1997). Supporting information has been also provided by SeaWiFS satellite images of chlorophyll concentration, showing a plume of chlorophyll-poor waters from the west penetrating the chlorophyll-rich waters, while meandering around the eastern flank of the islands along the 200–500 m isobaths (Park et al., 2002; black arrow in Fig. 5). These images depict the path of a strong current associated with the Polar Front passing nearby the eastern continental shelf break east of Kerguelen. Here, our penguin map strongly supports this pattern by showing a belt of high-temperature waters advected from the southwest and following the bottom topography, especially

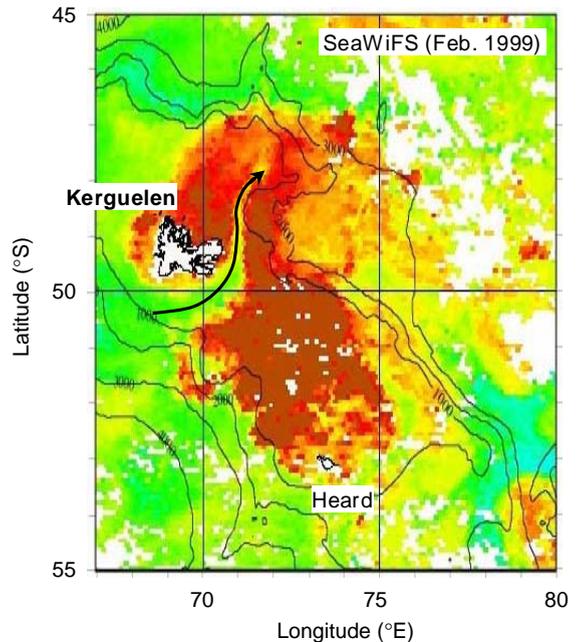


Fig. 5. Monthly composite of SeaWifS chlorophyll images for February 1999 (from Park et al., 2002). Dark red regions indicate high chlorophyll concentrations. The arrow indicates the path of the strong current associated with the Polar Front after Park et al. (1998), also evidenced by a plume of chlorophyll-poor waters from the west penetrating the chlorophyll-rich waters.

the 200–500 m isobaths just east of the islands. The vertical temperature section of Fig. 4c shows more clearly the Polar Front's position at  $\sim 71^\circ\text{E}$ , to the west of which can be seen the deeply penetrating high-temperature waters  $> 5^\circ\text{C}$ . The clearest surface signature of the Polar Front in the area is a slight decrease in temperature at the front, related to its origin farther south. A steep horizontal temperature gradient with cold waters to the east corresponds, by geostrophy, to the subsurface expression of a northward flow. Since the vertical section precisely crosses the 200–500 m isobaths at  $71^\circ\text{E}$ , such a northward flow should coincide with the Polar Front described by (Park et al., 1993; Park and Gambérone, 1997). To sum up, the finely resolved penguin maps confirm previous studies of the Polar Front, but with a greater refinement of both horizontal and vertical thermal structures of the front.

Second, this penguin dataset has evidenced a subsurface cold water mass flowing northwestwardly. The NW flow should exist because cold waters originate from the south, and the cold tongue visible on the 100 m map follows the NW-orientated eastern edge of the Kerguelen Plateau (Fig. 4b). Charrassin et al. (2002) suggested that this northwestward flow of subsurface cold water is consistent with the tidal residual circulation resulting from a tidal current–bottom topography interaction (Robinson, 1983). This interaction generating a counterclockwise (in the southern hemisphere) along slope current should be the most likely forcing mechanism explaining the observed subsurface current circulating in the apparently paradoxical NW direction. Indeed, the latter is totally opposed to the dominant direction of both the westerly winds and the ACC.

Here, our vertical section brings a strong additional support to the existence of this NW subsurface cold current (Fig. 4c). Indeed, by geostrophy, the steep inclination of subsurface isotherms below 80 m between  $72^\circ$  and  $73^\circ\text{E}$  hints at the existence of a subsurface current flowing northward. This location corresponds precisely to the area where the abrupt escarpment (1000–3000 m isobaths) is orientated in the N–S direction, consistent with the above-mentioned residual current's pathway. Charrassin et al.

(2002) argued that the tidal current–bottom topography could also generate internal tides (Le Provost et al., 2001) that promote the iron enrichment process by vertical mixing, leading to a high primary production over the plateau (see SeaWiFS image in Fig. 5). This is one of the working hypotheses that will be tested during the coming oceanographic survey “KEOPS” in 2005 (S. Blain, unpublished document, 2002), which aims at understanding the role of iron in the primary production over the Kerguelen Plateau. Further field experiments and numerical modeling studies are needed to quantify and understand the apparently complicated circulation around Kerguelen. However, it is worth emphasizing that the complexity of the circulation within the limited study area has been revealed largely thanks to the extremely high-density dataset obtained from penguins.

To conclude, this study shows that even with moderately accurate devices, it is possible to obtain original information using foraging animals. These data are of particular value because they concern areas that had previously been only poorly sampled, but which are important in terms of biomass and biological activity. Future development of better equipment (faster, more accurate, and sampling other parameters such as salinity (Daunt et al., 2003; Fedak, 2004; Hooker and Boyd, 2003) is therefore extremely promising for both the biological and oceanographic communities.

## Acknowledgements

We thank the Institut Polaire Français (IPEV), the Terres Australes et Antarctiques Françaises (TAAF), the Programme Environnement and GDRE 1069 (CNRS), and the Programme Gestion et Impact du Changement Climatique (MEDD) for financial and logistical support. We also thank Thierry Zorn, Wilfrid Bonneau, Nicolas Lecomte, Julien Baudat, Nicolas Caviale and Vivien Chartendraul for expert data collection in the field. We are grateful to Vincent Carrière and to the Captain and crew of R.V. *La Curieuse* for conducting the CTD experiment. Isabelle Durand

helped in analyzing the data and drawing the figures. Sascha Hooker made useful comments on an earlier version of the manuscript

## References

- Bannasch, R., Wilson, R.P., Culik, B., 1994. Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *Journal of Experimental Biology* 194, 83–96.
- Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L.H., Seitz, A., Walli, A., Fudge, D., 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293, 1310–1314.
- Boehlert, G.W., Costa, D.P., Crocker, D.E., Green, P., O'Brien, T., Levitus, S., Le Bœuf, B.J., 2001. Autonomous pinniped environmental samplers; using instrumented animals as oceanographic data collectors. *Journal of Atmospheric Research and Oceanic Technology* 18, 1882–1893.
- Bost, C.-A., Zorn, T., Le Maho, Y., Duhamel, G., 2002. Feeding of diving predators and diel vertical migration of prey: king penguins' diet versus trawl sampling at Kerguelen Islands. *Marine Ecology Progress Series* 227, 51–61.
- Boyd, I.L., Arnborn, T., 1991. Diving behaviour in relation to water temperature in the Southern Elephant Seal: foraging implications. *Polar Biology* 11, 259–266.
- Boyd, I.L., Hawker, E.J., Brandon, M.A., Staniland, I.J., 2001. Measurement of ocean temperatures using instruments carried by Antarctic fur seals. *Journal of Marine Systems* 27, 277–288.
- Bretherton, F.P., Davis, R.E., Fandry, C.B., 1976. A technique for objective analysis and design of oceanographic experiments applied to MODE-73. *Deep-Sea Research* 23, 559–581.
- Charrassin, J.-B., Bost, C.-A., 2001. Utilization of the oceanic habitat by king penguins over the annual cycle. *Marine Ecology Progress Series* 221, 285–297.
- Charrassin, J.-B., Park, Y.-H., Le Maho, Y., Bost, C.-A., 2002. Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecology Letters* 5, 317–319.
- Daunt, F., Peters, G., Scott, B., Grémillet, D., Wanless, S., 2003. Rapid-response recorders reveal interplay between marine physics and seabird behaviour. *Marine Ecology Progress Series* 255, 283–288.
- Emery, W.J., Thomson, R.E., 1998. *Data Analysis Method in Physical Oceanography*. Pergamon Press, Oxford 634pp.
- Fedak, M., 2004. Marine animals as platforms for oceanographic sampling: a “win/win” situation for biology and operational oceanography. *Proceedings of the International Symposium on Bio-Logging Science*, Tokyo. *Memoirs of the National Institute of Polar Research*, special issue, in press.
- Georges, J.Y., Bonadonna, F., Guinet, C., 2000. Foraging habitat and diving activity of lactating Subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. *Marine Ecology Progress Series* 196, 291–304.
- Hindell, M.A., Burton, H.R., Slip, D.J., 1991. Foraging areas of southern elephant seals, *Mirounga leonina*, as inferred from water temperature data. *Australian Journal of Marine and Freshwater Research* 42, 115–128.
- Hooker, S.K., Boyd, I.L., 2003. Salinity sensors on seals: use of marine predators to carry CTD dataloggers. *Deep-Sea Research Part I* 50, 927–939.
- Kooyman, G.L., Davis, R.W., 1987. Diving behavior and performance, with special reference to penguins. In: Croxall, J.P. (Ed.), *Seabirds, Feeding Ecology and Role in Marine Ecosystems*. Cambridge University Press, Cambridge, pp. 63–75.
- Koudil, M., Charrassin, J.-B., Le Maho, Y., Bost, C.-A., 2000. Seabirds as monitors of upper-ocean thermal structure: king penguins at the Antarctic Polar Front, east of Kerguelen sector. *Comptes Rendus de l'Académie des Sciences, Paris, Serie III* 323, 377–384.
- Le Provost, C., Carrere, L., Gaspar, P., Le Traon, P.Y., Lyard, F., Ponte, R., 2001. Ocean response to short-period atmospheric and tidal forcings. *AVISO Newsletter* 8, 75–77.
- Levitus, S., Boyer, T., 1994. *World Ocean Atlas, vol. 3: Temperature*. NOAA, US Department of Commerce.
- Lydersen, C., Nols, O.A., Lovell, P., McConnell, B.J., Gammelsrod, T., Hunter, C., Fedak, M.A., Kovacs, K.M., 2002. Salinity and temperature structure of a freezing Arctic fjord—monitored by white whales (*Delphinapterus leucas*). *Geophysical Research Letters* 29 (23), 2119–2123.
- Park, Y.-H., Gambèroni, L., 1997. Cross-frontal exchange of Antarctic intermediate water and Antarctic bottom water in the Crozet basin. *Deep-Sea Research Part II* 44, 963–986.
- Park, Y.-H., Gambèroni, L., Charriaud, E., 1993. Frontal structure, water masses, and circulation in the Crozet Basin. *Journal of Geophysical Research* 98, 12361–12385.
- Park, Y.-H., Charriaud, E., Fieux, M., 1998. Thermohaline structure of the Antarctic surface water/winter water in the Indian sector of the Southern Ocean. *Journal of Marine Systems* 17, 5–23.
- Park, Y.-H., Pollard, R.T., Read, J.F., Leboucher, V., 2002. A quasi-synoptic view of the frontal circulation in the Crozet Basin during the Antares-4 cruise. *Deep-Sea Research Part II* 49, 1822–1842.
- Pütz, K., Wilson, R.P., Charrassin, J.-B., Raclot, T., Lage, J., Le Maho, Y., Kierspel, M.A.M., Culik, B.M., Adelung, D., 1998. Foraging strategy of king penguins (*Aptenodytes patagonicus*) during summer at the Crozet Islands. *Ecology* 79, 1905–1921.
- Robinson, I.S., 1983. Tidally induced residual flows. In: Johns, B. (Ed.), *Physical Oceanography of Coastal and Shelf Seas*. Elsevier, Amsterdam, pp. 321–356.
- Weimerskirch, H., Zotier, R., Jouventin, P., 1988. The avifauna of Kerguelen Islands. *Emu* 89, 15–29.
- Weimerskirch, H., Wilson, R.P., Guinet, C., Koudil, M., 1995. Use of seabirds to monitor sea-surface temperatures and to validate satellite remote-sensing measurements in the Southern Ocean. *Marine Ecology Progress Series* 126, 299–303.

- Wilson, R.P., Culik, B.M., Bannasch, R., Lage, J., 1994. Monitoring Antarctic environmental variables using penguins. *Marine Ecology Progress Series* 106, 199–202.
- Wilson, R.P., Grémillet, D., Syder, J., Kierspel, M.A.M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J.A., Bost, C.A., Plötz, J., Nel, D., 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* 228, 241–261.
- Wienecke, B.C., Robertson, G., 1997. Foraging space of Emperor Penguins *Aptenodytes forsteri* in Antarctic shelf waters in winter. *Marine Ecology Progress Series* 159, 249–263.