HUMBOLDT PENGUINS OUTMANOEUVRING EL NIÑO

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Summary

We satellite-tracked five Humboldt penguins during the strong 1997/98 El Niño Southern Oscillation (ENSO) from their breeding island Pan de Azúcar (26°09′S, 70°40′W) in Northern Chile and related their activities at sea to satellite-derived information on sea surface temperature (SST), sea surface temperature anomaly (SSTA), wind direction and speed, chlorophyll a concentrations and statistical data on fishery landings.

We found that Humboldt penguins migrated by up to 895 km as marine productivity decreased. The total daily dive duration was highly correlated with SSTA, ranging from 3.1 to 12.5 h when the water was at its warmest (+4 °C). Birds travelled between 2 and 116 km every day, travelling further when SSTA was highest. Diving depths (maximum 54 m), however, were not increased with respect to previous years.

Two penguins migrated south and, independently of each other, located an area of high chlorophyll a concentration 150 km off the coast. Humboldt penguins seem to use day length, temperature gradients, wind direction and olfaction to adapt to changing environmental conditions and to find suitable feeding grounds. This makes Humboldt penguins biological *in situ* detectors of highly productive marine areas, with a potential use in the verification of trends detected by remote sensors on board satellites.

Key words: Humboldt penguin, *Spheniscus humboldti*, El Niño, Humboldt current, wind speed, day length, chlorophyll a, satellite telemetry, foraging, migration, sea surface temperature, dive.

Introduction

Humboldt penguins (*Spheniscus humboldti*) are top predators endemic to the area influenced by the cold, nutrient-rich Humboldt current on the west coast of South America. Their breeding colonies span the range between 5 and 42°S (Williams, 1995). Because of low population numbers (recent estimates indicate a world population of only approximately 13 000 birds), the species is considered to be vulnerable to endangered (Ellis et al., 1998; Bonn Convention on Migratory Species). One of the factors that severely affects the Humboldt penguin population is the recurring El Niño Southern Oscillation (ENSO). Breeding populations are reduced by 65–72 % during ENSO years (Hays, 1986), when upwelling of nutrient-rich, cold bottom water in the south-eastern Pacific Ocean is depressed.

The ENSO is the most important coupled ocean atmosphere phenomenon to cause global climate variability on an interannual time scale. The 1997/98 ENSO was one of the most intensive phenomena of this kind since the 1950s, and its anomalies reached a level only paralleled by the 1982/83 ENSO (Wolter and Timlin, 1998). The multivariate ENSO index (MEI), which is based on the six main observed variables over the tropical Pacific (sea-level pressure, zonal and meridional components of surface wind, sea surface temperature, surface air temperature and total cloudiness fraction of the sky), reached peak values of nearly +2.9 in July/August 1997 and again in February/March 1998. These values have been surpassed during the last 50 years only in early 1983 (Wolter and Timlin, 1998).

Humboldt penguins feed predominantly on anchovies (*Engraulis ringens*) and sardines (*Sardinops sagas*; Wilson et al., 1995; J. Hennicke, personal observations), patchily distributed, planktivorous cold-water shoaling fish normally found in the highly productive top 50 m of the water column (Arntz and Fahrbach, 1991). During El Niño events, however, anchovies concentrate in bodies of cold water close to shore, below the thermocline at depths of more than 100 m, or migrate to cold-water areas south of their normal distributional range (Arntz and Fahrbach, 1991; Arntz et al., 1991).

Because Humboldt penguins are considered sedentary, remaining close to their breeding localities year round (Croxall and Davis, 2000; but see Culik and Luna-Jorquera, 1997a,b), they should be unable to avoid El-Niño-related food shortages, which would explain high levels of ENSO-related mortality (Hays, 1986). However, many Humboldt penguins survive every ENSO event, which suggests that the species must have evolved mechanisms to deal with climate-dependent deprivation.

Within the framework of a long-term study on Humboldt penguins in northern Chile, we have previously determined

(Culik and Luna-Jorquera, 1997b; Culik et al., 1998) how these birds use their marine habitat during weak ENSO events (MEI<1; Wolter and Timlin, 1998). Here, we use these data as a baseline to investigate how Humboldt penguins respond to the ENSO avoidance strategies of their prey. Our study was aimed at detecting (i) whether Humboldt penguins breeding under ENSO conditions alter their foraging behaviour and, if so, how; (ii) whether the depression of the thermocline forces the birds to forage at deeper depths; (iii) whether Humboldt penguins migrate to follow their prey; and (iv) whether the birds employ environmental clues to find scarce food resources in the vast expanses of the ocean.

To answer these questions, we satellite-tracked five birds from their breeding island, Pan de Azúcar in northern Chile, during the strong 1997/98 ENSO and recorded their behaviour at sea. We determined the range of their foraging trips, daily dive duration and diving depth, and correlated these data with fishery landing statistics and satellite-derived information on sea surface temperature, wind speed and direction, as well as chlorophyll a concentrations in the surface waters off the Chilean coast.

Materials and methods

The breeding behaviour of free-living Humboldt penguins has been poorly studied (Williams, 1995). They nest in loose colonies and possibly breed in any month of the year. Most pairs lay two eggs, which are incubated for 41 days. Chicks are semi-altricial and nidiculous and are initially guarded by one of the parents while the other is foraging. Chicks are left unattended at the nest site after reaching a certain age (depending on breeding locality, climatic and oceanographic conditions), enabling both parents to forage simultaneously to meet the increasing demands of the chicks.

We used the Argos satellite system (Argos-CLS, Toulouse, France) to track five breeding birds (body mass at instrumentation 4200 ± 430 g) from Pan de Azúcar Island ($26°09'$S, $70°40'$W), 100 km north of Caldera, for 207 days between 2 December 1997 and 10 February 1998 (see Table 1). We employed three ST 10 PTT transmitters (Telonics, USA; packaged by Sirtrack, New Zealand) providing location and daily dive duration (salt-water timer) and two SDR 10 PTT satellite depth recorders (Wildlife Computers, USA) providing location and time at depth as well as depth histograms. The transmitters weighed approximately 130 g (dimensions 130 mm×60 mm×25 mm) and were equipped with a 220 mm×2 mm antenna placed at the centre of the devices at an angle of $45°$, facing backwards. The front of the PTT was streamlined according to Bannasch et al. (1994) to reduce hydrodynamic drag (see Culik et al., 1994).

After light sedation of the birds at their nest site using 0.25 ml of Ketavet (corresponding to a ketamine hydrochloride dose of 5 mg kg^{-1} body mass; Parke-Davis, Germany) injected into the pectoralis muscle (Luna-Jorquera et al., 1996), the units were attached to the feathers of the lower back using Tesa-Tape (Beiersdorf, Germany) and waterproof rubber cement (Pattex; Henkel, Germany) according to Wilson et al. (1997). After attachment, the units were coated with epoxy glue (Uhu, Germany) to protect them from abrasion. The complete procedure lasted approximately 15 min, after which the birds were returned to their nests.

Daily dive duration (ST 10 PTTs only) was determined from the salt-water timer and computed from a total of 164 penguin days at sea. Diving depths and durations (SDRs only) were transmitted as maximum values and as histograms summarizing dive data for the previous 6 h period. Six-hour summaries were recorded starting at 03:00, 09:00, 15:00 and 21:00 h local time every day, thereby covering night (21:00–03:00 h), dawn (03:00–09:00 h), midday (09:00–15:00 h) and dusk (15:00–21:00 h). Dive histograms were subdivided into 10 m depth intervals and accumulated the number of dives to that depth and the time spent in total at that depth for each interval. Total dive duration was recorded using a subdivision of 1 min intervals.

Penguin activity was related to satellite-derived and in situ recordings of sea surface temperature (SST), sea surface temperature anomaly (SSTA), wind speed and wind direction. Furthermore, we obtained satellite data on chlorophyll a concentrations and yearly fishery landing statistics. Chlorophyll a concentrations were computed from gridded (resolution 9 km×9 km) weekly mean sea-viewing wide-field-of-view sensor (SeaWifs) satellite data provided by the Earth Observing System Data and Information System (EOSDIS), Distributed Active Archive Center at Goddard Space Flight Center, which archives, manages and distributes this data set through funding from Earth Observing System of NASA's Mission to Planet Earth.

Wind reanalysis data were provided by the National Center for Environmental Prediction (NCEP) at the National Oceanic and Atmospheric Organisation (NOAA-CIRES) Climate Diagnostics Center, Boulder, Colorado, USA, from their Web site at http://www.cdc.noaa.gov/. Sea surface temperature data were provided by the International Research Institute for Climate Prediction from their homepage at http://iri.ucsd.edu/index.html. Fishery statistics were provided by the Chilean National Fisheries Service (SERNAP), in situ SST and SSTA data by the Hydrographic and Oceanographic Service of the Chilean Navy, and surface wind data by the Meteorological Service of the Chilean Navy, all located in Valparaíso, Chile.

Results

Between 2 December 1997 and 10 February 1998, we obtained 963 Argos locations from instrumented Humboldt penguins, 12 % of unknown accuracy (location classes A and B), 49 % with an accuracy of more than 1000 m (class 0) and 39 % with an accuracy less than 1000 m (classes 1–3; Taillade, 1992). From the location and sensor data, we derived foraging routes, distance travelled, dive duration and dive depth.

Foraging routes

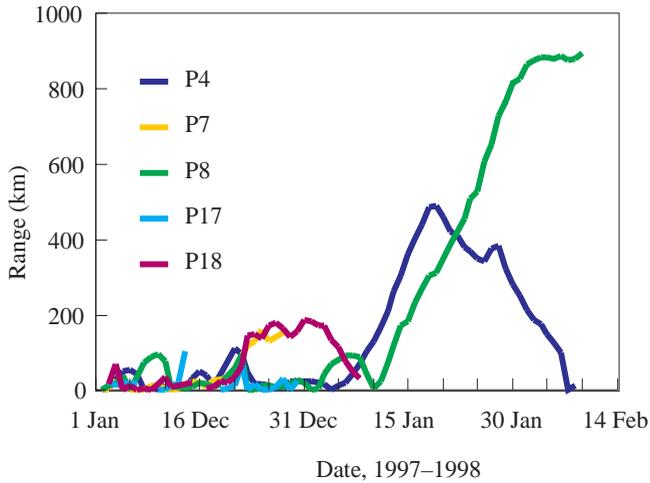Penguin activity during our study can be roughly divided

Fig. 1. Maximum range (km) of satellite-tracked Humboldt penguins from their breeding island Pan de Azúcar computed on a daily basis between December 1997 and February 1998. Until mid-December, penguins were central-place foragers, foraging close to their island. After 21 December, P7 and P18 left the island to forage almost 200 km away (see Fig. 2). Subsequently, P4 left the island on 6 January and P8 on 10 January (see Fig. 3).

to their colony after a maximum of 5 days at sea and were central-place foragers at that time, gathering food for their chicks in the close vicinity of the island.

In late December, two penguins foraged 160 km (P7) and 190 km (P18) away from Pan de Azúcar Island (Fig. 1), presumably after abandoning their chicks (Corporación Nacional Forestal, Copiapó, Chile, personal communication) and thus eliminating the necessity for regular returns to the nest. However, both penguins foraged in different areas: P7 swam north, remaining in close proximity to the shore, whereas P18 travelled south, searching as far as 50 km from the coast (Fig. 2), while the other three birds (P4, P7 and P17) continued the pattern observed in early December (Fig. 1). Because of dense cloud coverage, no satellite data on chlorophyll a concentrations are available for these dates and locations. Data reception from penguins P7, P17 and P18 terminated on 28 December, 30 December and 8 January, respectively. Mean travelling speed of all birds averaged 0.7 m s^{-1} between satellite locations (Table 1).

In early January 1998, penguins P4 and P8 left Pan de Azúcar Island travelling south. The maximum distance recorded between the birds and their colony was 490 km for P4 and 895 km for P8 (Fig. 1). However, while P4 returned to the island after 18 January, P8 continued its southern migration until we lost its track near Valparaíso on 10 February (Fig. 3).

into three periods (Fig. 1). In early December, foraging trips were mostly short (<100 km from the island). Birds returned
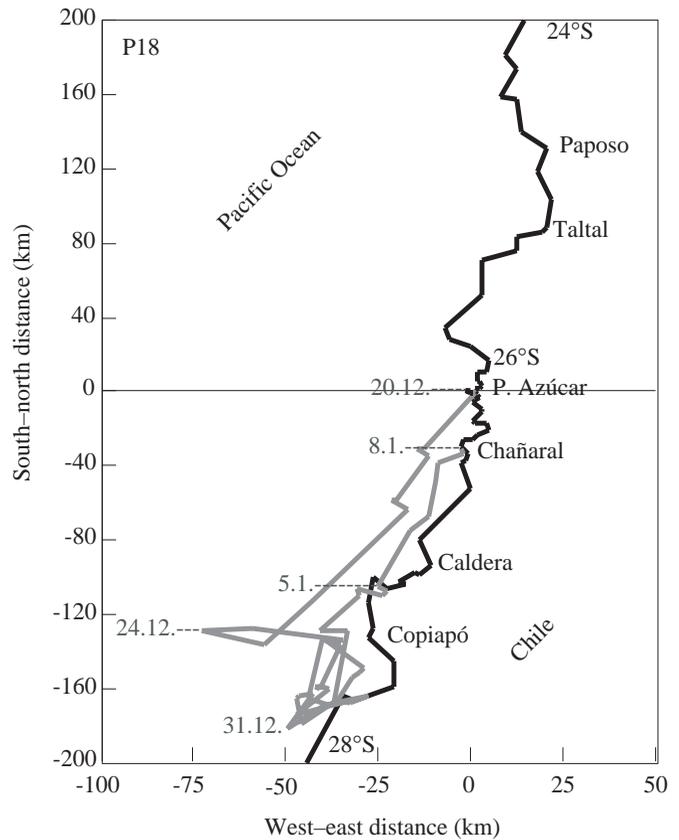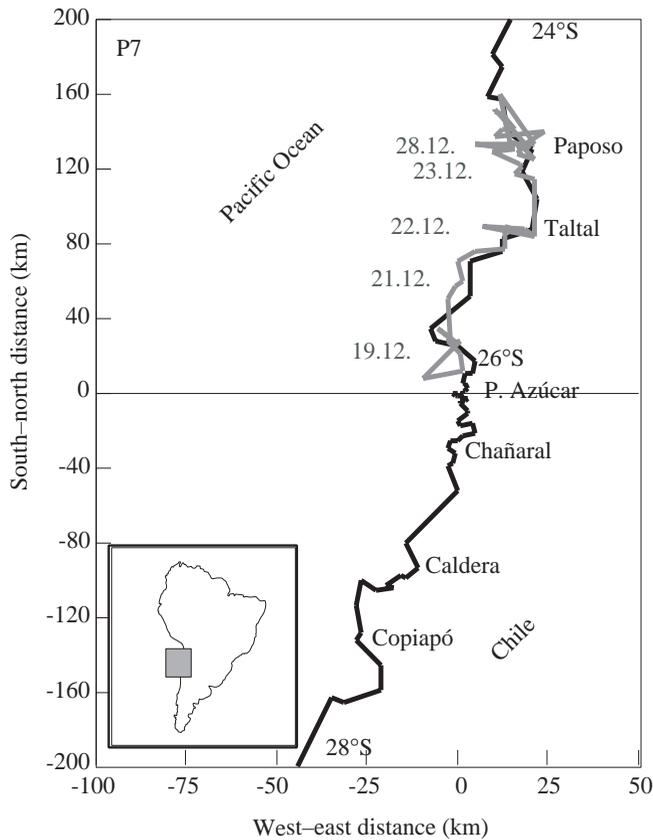

Fig. 2. Foraging trips of Humboldt penguins P7 and P18 during the second half of December 1997. While P7 foraged north of Pan de Azúcar Island (P. Azúcar), P18 travelled south. Transmissions stopped on 12 December for P7 and 8 January for P8.

Table 1. *Humboldt penguin telemetry study during the 1997–1998 El Niño Southern Oscillation*

PTT type	Body mass (kg)	Egg number	Sampling period	Number of locations	Location class 1–3* (%)	Travelling speed (m s^{-1})
PTT 04	4.015	2	2 Dec to 8 Feb	329	42	0.83±1.13
PTT 07	4.165	2	2 Dec to 28 Dec	118	40	0.66±0.86
PTT 08	3.515	2	2 Dec to 10 Feb	369	32	0.81±1.0
SDR 17	4.700	2	3 Dec to 30 Dec	49	57	0.48±0.93
SDR 18	4.600	2	3 Dec to 8 Jan	98	50	0.53±0.61

PTT refers to satellite transmitters with salt water timer. SDR refers to satellite depth recorders.

Values for speed are means ± S.D.

*Location class 1–3 are better than 1000 m (Taillade, 1992).

Travelling distance

During the time the penguins carried their PTTs, their daily travelling distance was highly variable (range 2–116 km). To account for foraging trip duration and intermittent nest attendance in December and to smooth the data set, we computed the 7-day running mean of daily travelling distance (Fig. 4B). This variable was significantly correlated with SSTA (7-day running mean, in °C) in three of the birds (Table 2), indicating that Humboldt penguins had to travel significantly farther to encounter prey when water temperatures increased (reflecting a lack of cold, nutrient-rich bottom water), with a positive slope of 3–8.7 km °C^{-1}.

Dive duration

Mean daily dive duration (7-day running mean), obtained *via* PTTs, was significantly correlated with local SSTA data (Table 3). Dive durations increased by 1.6–2.5 h °C^{-1} positive temperature anomaly in the three birds. We found that when SSTA values were low, at the beginning of December 1997 (Fig. 4A), penguins invested approximately 4 h daily under water to find prey (Fig. 4C); at the time of highest SSTA values in late January 1998, daily dive duration reached values as high as 12.5 h.

Using SDR tags on P17 and P18, dive duration was recorded with a resolution of 1 min. On average, 85.3 % (for P17) and
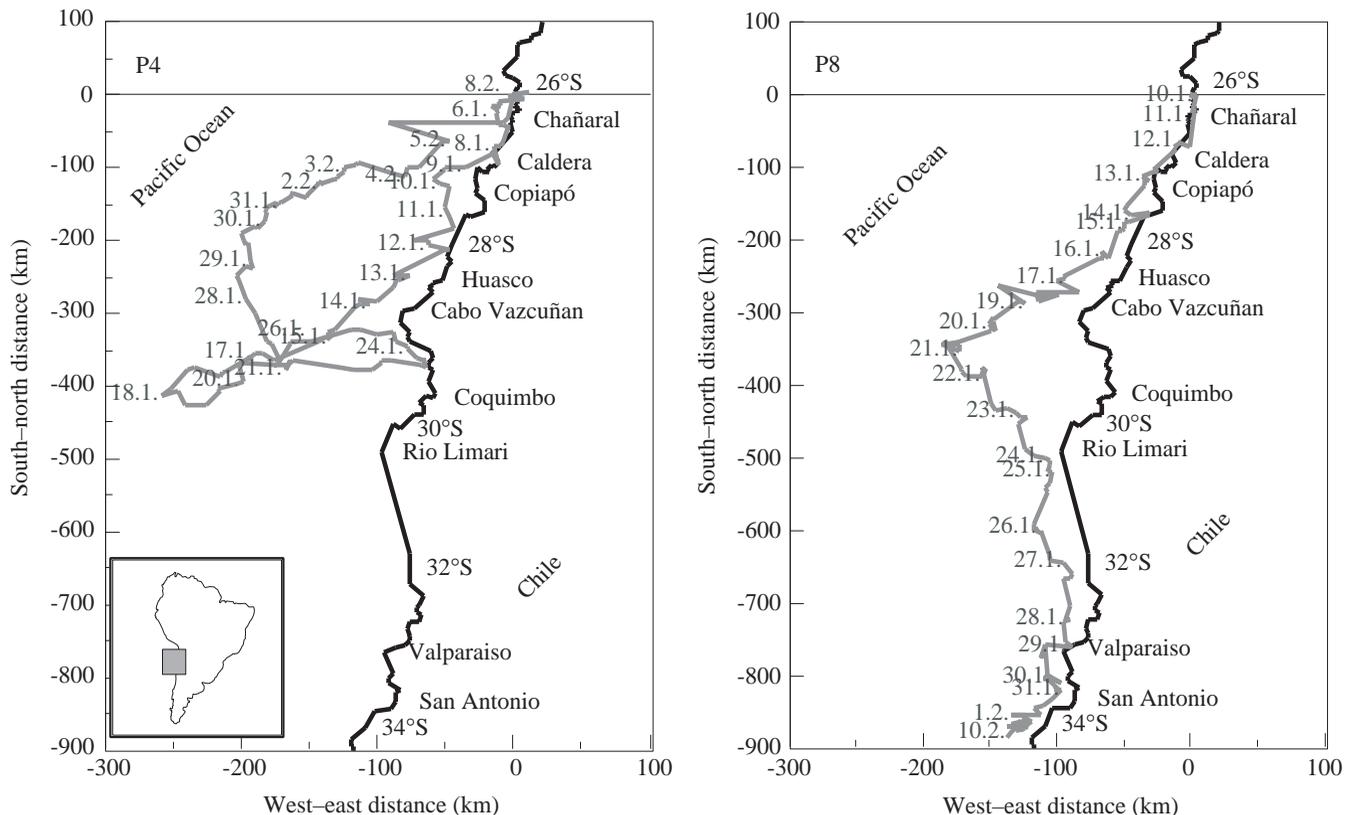

Fig. 3. Foraging trips of penguins P4 after 6 January 1998 and of P8 after 10 January 1998. Both penguins first travelled south in close proximity to the coast and headed southwest after crossing the 28°S parallel. While P4 returned to Pan de Azúcar Island (P. Azúcar) on 8 February, P8 continued south to 34°S, and its PTT stopped transmitting 895 km from Pan de Azúcar Island.
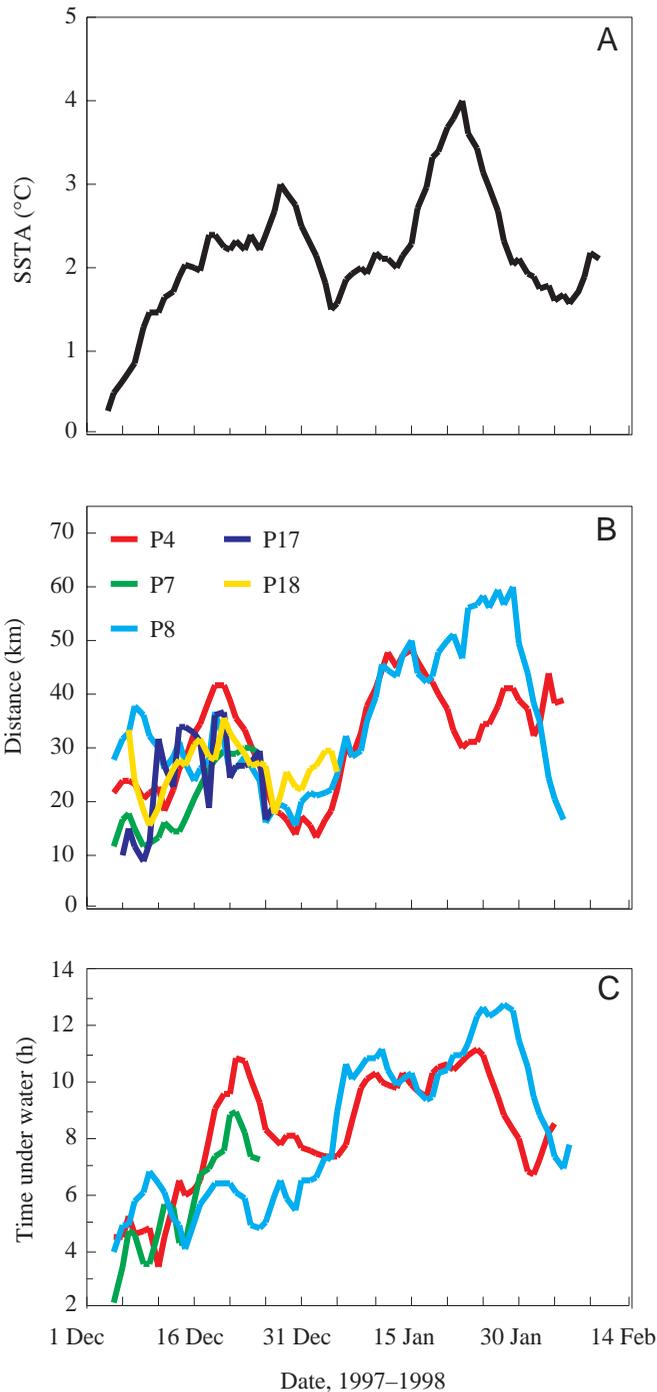
Fig. 4. Sea surface temperature anomaly (SSTA in °C) measured at Caldera, Chile (7-day running mean), reached a peak in late December 1997 and again in mid-January 1998 (A). Daily distance travelled (B) by Humboldt penguins (7-day running mean) paralleled SSTA data, and the two were significantly correlated for three penguins (see Table 2). Daily dive duration (time under water; C) in penguins P4, P7 and P18 was also highly correlated (see Table 3) with SSTA. Because sea surface temperatures were close to normal in early December, the birds spent only approximately 4 h under water per day. This figure rose to 12.5 h by mid-January as the deviation from normal SSTA values reached +4 °C.

Table 2. *Regression of daily travelling distance against sea surface temperature anomaly for all Humboldt penguins*

Penguin	a	b	r	N	P
P4	3	24.8	≤0.05	63	0.07
P7	8.7	5.3	≤0.6	21	<0.01
P8	6.9	19.6	≤0.16	63	<0.01
P17	8.5	8.3	≤0.31	22	<0.01
P18	0	26.3	0	30	0.9

Daily travel distance, TD (in km), is a 7-day running mean.
Sea surface temperature anomaly, SSTA (in °C), is a 7-day running mean.
The equation is TD=aSSTA+b.

Table 3. *Regression of mean daily dive duration against sea surface temperature anomaly for penguins P4, P7 and P8*

Penguin	a	b	r	N	P
P4	2	3.7	≤0.56	62	<0.01
P7	2.5	1.3	≤0.68	21	<0.01
P8	1.6	4.5	≤0.21	64	<0.01

Daily dive duration, DDD (in h), is a 7-day running mean.
Sea surface temperature anomaly, SSTA (in °C), is a 7-day running mean.
The equation is DDD=aSSTA+b.

75.5 % (for P18) of all dives (per 6 h interval) were shorter than 1 min. However, as shown in Fig. 5, both penguins mostly dived for short periods (<1 min) at night (21:00–03:00 h), when dive times longer than 1 min accounted for only 1.5 % (P17) and 4.5 % (P18) of total dives. During daylight, many dives were longer and 15–30 % of dives exceeded a duration of 1 min.

Dive depth

Depth utilization of foraging Humboldt penguins P17 and P18 could only be monitored using SDR tags until 30 December 1997 (for P17) and 8 January 1998 (for P18). During that time, the birds did not dive deeper than 54 m (maximum depth) and 98.8 % of all dives were shallower than 30 m (Fig. 6). Depth distribution (here, 100 % corresponds to all dives recorded in 24 h) shows that the majority of dives were recorded during the daylight hours. At night, i.e. between 21:00 and 03:00 h, these Humboldt penguins dived rarely (4.1 % of all dives recorded in 24 h for P17 and 2.6 % for P18) and never deeper than 10 m. During the day, the deepest dives were centred around noon (i.e. between 09:00 and 15:00 h local time), when penguins dived most frequently (36.2 % of all dives for P17 and 38.9 % for P18).

Orientation and chlorophyll a

While penguins P4 and P8 travelled south in January 1998 (Fig. 3), they encountered lower sea surface temperatures which, at that time, decreased by 0.7 °C per degree latitude
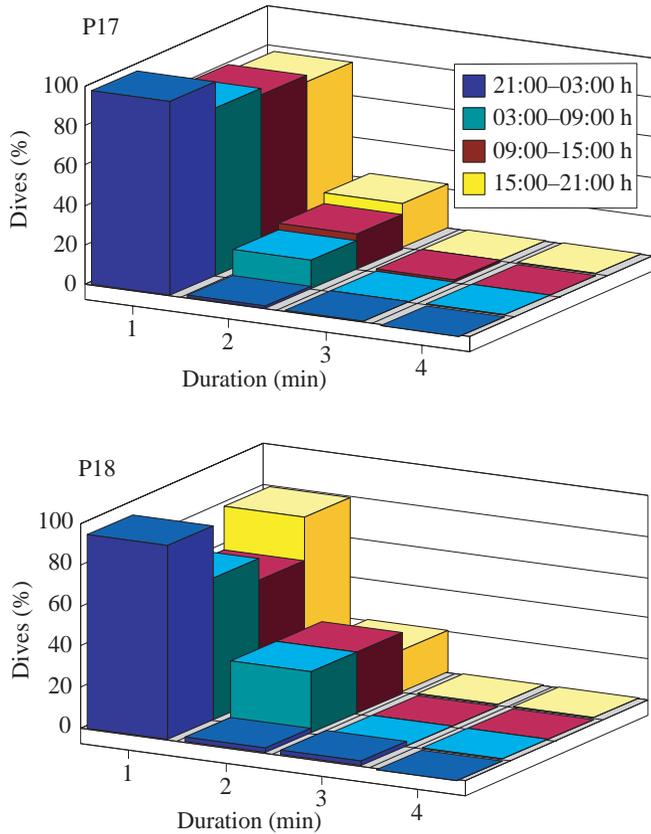
Fig. 5. Frequency distribution (percentage, based on a 6 h period) of dives lasting 0–1, 1–2, 2–3 and 3–4 min during every 6 h recording interval. At night (21:00–03:00 h), dives were mostly short (<1 min); longer dives were recorded only during daylight hours.
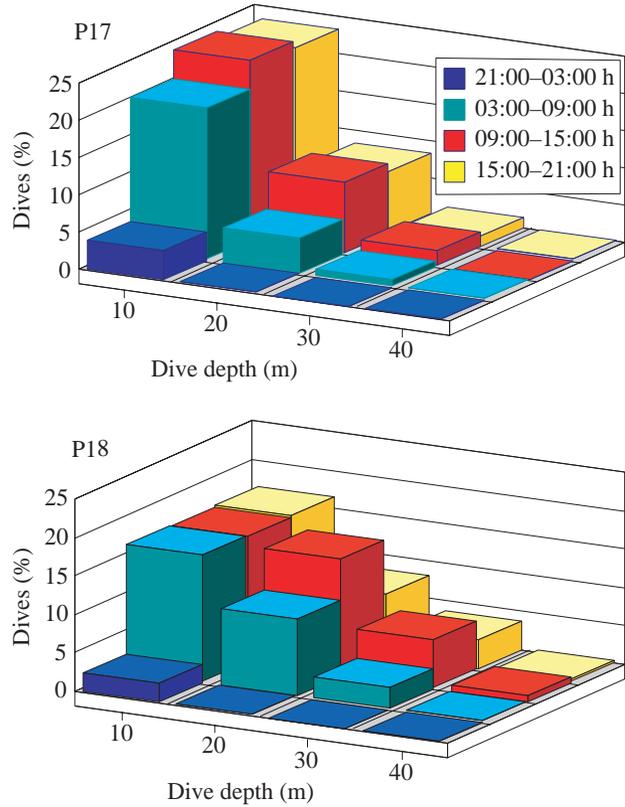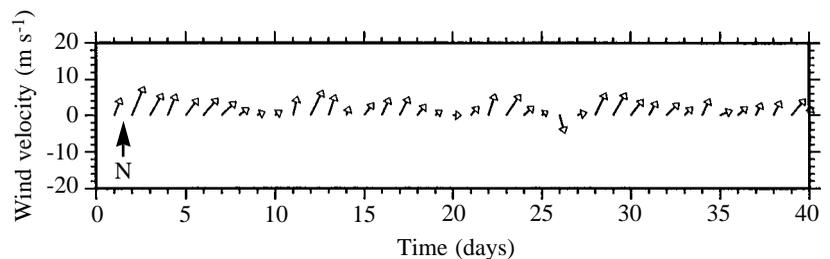
Fig. 6. Frequency distribution (percentage, based on a 24 h day) of dives to particular depth strata (0–10 m, 10–20 m, etc.). At night, penguins rarely dived, and dives were shallower than 10 m. Diving activity during the day peaked at around midday, when diving depths were greatest.

(Hydrographic and Oceanographic Service of the Chilean Navy, Valparaíso, Chile, personal communication).

The birds changed heading (Fig. 3) on 12 January (P4) and 14 January (P8), swimming directly into the wind, which blew steadily from 210° (southsouthwest) at speeds of 1.5–8 m s^{-1} (Fig. 7). Independently of each other, both penguins localized an area of high (4 mg m^{-3}) chlorophyll a concentration (at 29°S, 72.5°W) 150 km from the coast (Fig. 8), on 17 January (P4) and 21 January (P8).

Chlorophyll a concentrations decreased after 17 January, and both penguins continued their foraging search (Fig. 8). While P4 first remained in the area, returned to the coast and then headed north to return to Pan de Azúcar Island, P8 continued its southbound migration until we lost its track near Valparaíso on 10 February, 895 km from Pan de Azúcar Island.

Fishery statistics

Throughout our study, prey availability, derived from fishery statistics (SERNAP, 1997, 1998), decreased. In January 1998, Chilean industrial anchovy landings (24 735 tons) were reduced by 84 % compared with January 1997 (158 867 tons) and by 50 % compared with December 1997 (50 359 tons). Pan de Azúcar Island is located at the border between the second and third regions shown in Fig. 9, which illustrates that, in January, the anchovy catch north of Pan de Azúcar was very low. After January 1998, landings increased in the southern regions of Chile (regions 3–5), reflecting the southward migration of the shoals.

On a more detailed scale (Fig. 10), the initial southward migration of anchovies caused landings in Chañaral, 30 km south of Pan de Azúcar Island, to increase from November

Fig. 7. Wind speed and direction (from satellite information) at sea surface level in January and early February 1998 computed for 30°S and 72.5°W. Note the mostly constant southwesterly wind direction, with westerly winds on 20 and 25 January and the northerly wind on day 26 (corresponding to 26 January).
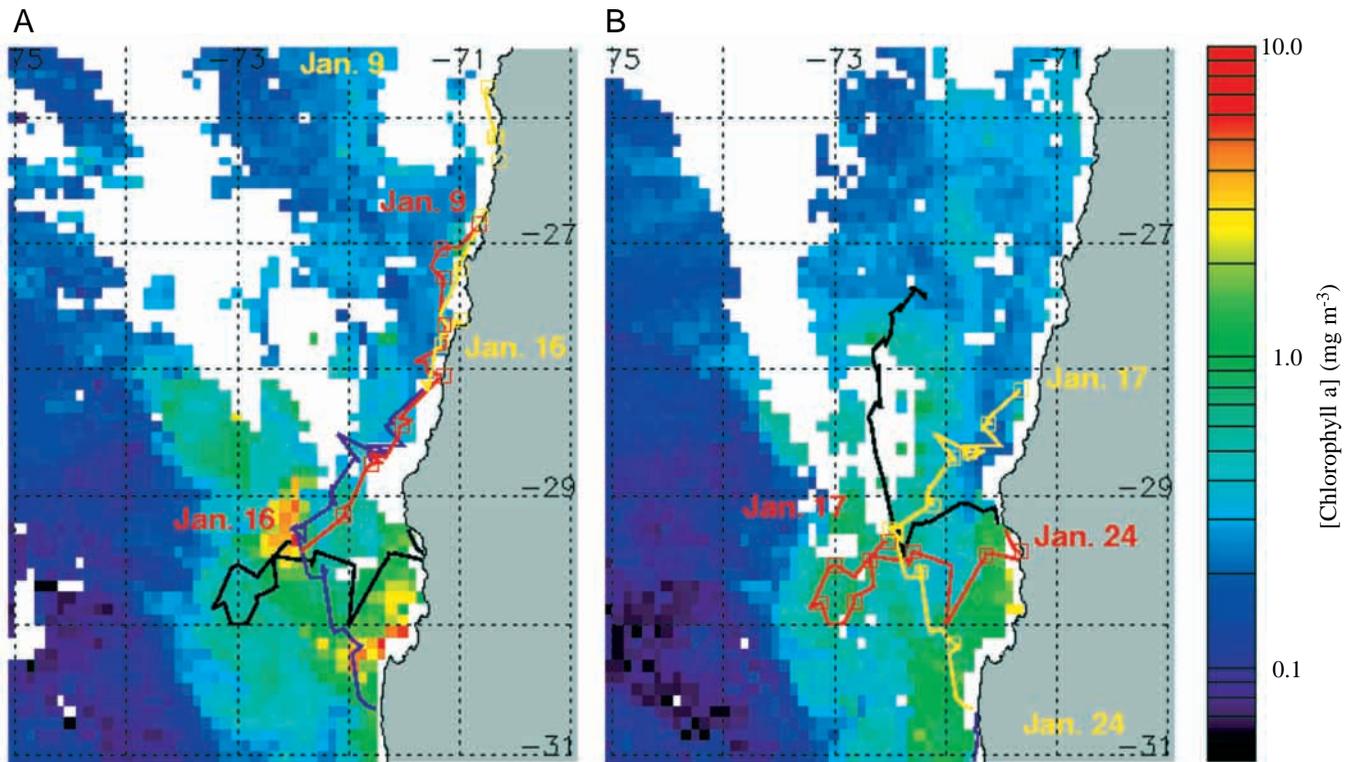
Fig. 8. (A) Foraging trips of penguins P4 and P8 between 9 and 16 January 1998. Fractions of the penguin routes corresponding to the composite image of chlorophyll a concentration (in mg m^{-3}) are coloured in red (P4) and yellow (P8), respectively, while the penguin tracks of the following 7-day period are coloured in black (P4) and violet (P8). (B) Foraging trip of penguins P4 and P8 and chlorophyll a concentrations between 17 and 24 January 1998.

1997 to January 1998 and to collapse in February 1998. February landings were also reduced in Caldera, 100 km South of Pan de Azúcar, whereas landings in Coquimbo, 400 km south of Pan de Azúcar, increased during that period (Fig. 10).

Discussion

Foraging area

In early December 1997, Humboldt penguins resident on Pan de Azúcar remained close to the island (Fig. 1), foraging in a northerly or southerly direction, a behaviour reported previously during the breeding season (Culik and Luna-Jorquera, 1997b). In both 1994/95 and 1995/96, Humboldt penguins carrying satellite transmitters remained within 95 km of the island while gathering food for themselves and their chicks, with no preference for particular foraging areas (Culik and Luna-Jorquera, 1997b). This was later confirmed by Culik et al. (1998), who used VHF-telemetry and found that, on the same day, individual birds foraged independently of each other in different directions.

Previous studies conducted during the breeding season have shown that 90 % of all Humboldt penguin locations at sea were in an area of 20–35 km radius around Pan de Azúcar Island (Culik and Luna-Jorquera, 1997b; Culik et al., 1998). Although in the present study 90 % of all locations obtained between 2

and 21 December 1997 were within a radius of 55 km around the island, a comparison of the two distributions (Kolmogorov–Smirnov two-sample test) showed that the difference was not significant between the years (P=0.523). This result agrees with the report of Paredes and Zavalaga (1998) who found that, in Punta San Juan, Perú (15.5°S), Humboldt penguins with medium-sized chicks were still feeding their offspring in December 1997, 'making long foraging trips'. This comment indicates, however, that foraging conditions at that time were already suboptimal.

In January 1998, anchovy landings in Chile's first and second regions (North of Pan de Azúcar Island) decreased, but landings remained at the same level in region 3 (Fig. 9). The foraging strategies adopted by the five satellite-tracked Humboldt penguins varied: two penguins (P7 and P18, Figs 1, 2) foraged further away, as far as 160 and 190 km from the island, while three of the birds remained in the vicinity. As a consequence, the distribution of the birds around the island between 21 December 1997 and 10 January 1998 changed in comparison with the distribution in early December. Most locations (more than 50 %) were now obtained from a radius of more than 45 km from the island. For that period, the distribution of locations was significantly different from those of previous years (Kolmogorov–Smirnov two-sample test, P<0.001).

The 1997/98 breeding season was poor at Pan de Azúcar

Fig. 9. Anchovy landing statistics for Chilean regions 1 (north) to 5 (south) between October 1997 and April 1998. Region 1 stretches approximately from 19 to 22°S, region 2 from 22 to 26°S, region 3 from 26 to 29°S, region 4 from 29 to 32°S and region 5 from 32 to 34°S. Note the increase in landings from north to south and as the season progressed.
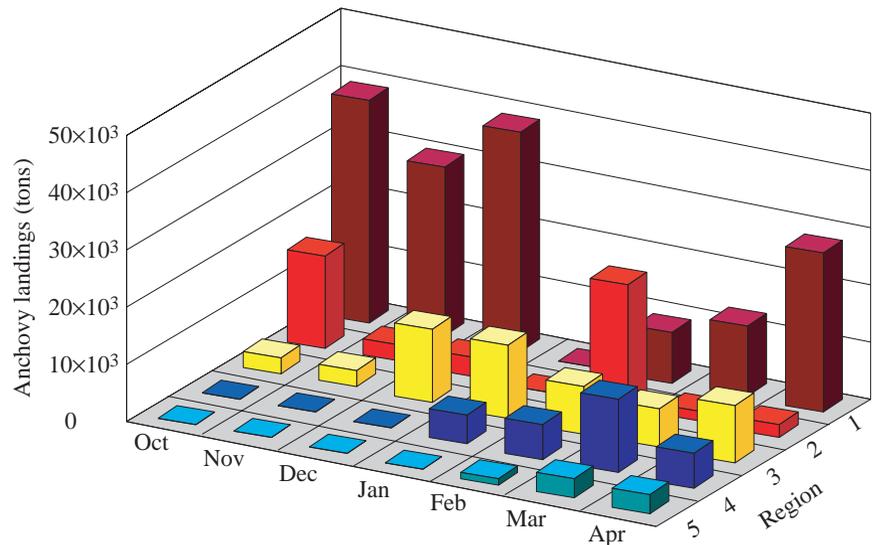
Island in general, and the shift in foraging stategies of P7 and P18 was accompanied by nest desertion. Only 312 Humboldt penguins were counted at Pan de Azúcar Island in January 1998 compared with 2276 birds in January 1997 (CONAF, personal communication). This was confirmed by Paredes and Zavalaga (1998), who observed that, at Punta San Juán, Perú (15.5°S), all chicks were deserted by January 1998. Penguin numbers at Punta San Juán declined from approximately 3600 (in normal years) to only 670, the 'location of the missing penguins being unknown' (Paredes and Zavalaga, 1998). No fishmeal factory was processing anchovies in December and January, because these fish were not available to purse-seine fishery (C. B. Zavalaga, personal communication). Further south, at Pajaros Niños Islands (33°S), only one-third of the penguins counted in December 1996 were breeding towards the end of December 1997 (A. Simeone, personal communication).

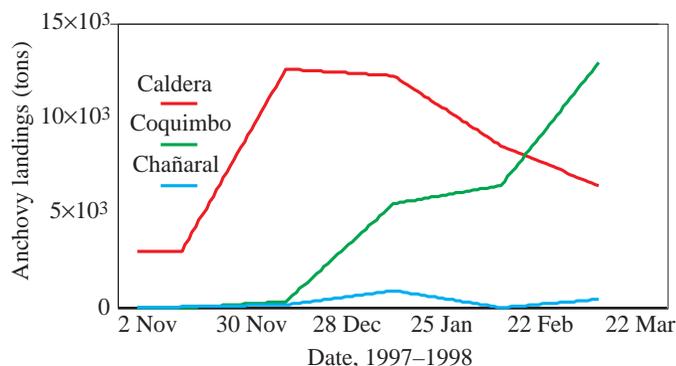Between 6 and 10 January, both P4 and P8 also abandoned

breeding and began their southward migration (Figs 1, 3). Anchovy landings suggest that the food situation around Pan de Azúcar Island was deteriorating by then (Figs 9, 10) and that, as suggested by Arntz and Fahrbach (1991) and Arntz et al. (1991), anchovy stocks migrated southwards. Anchovy landings started to increase by January in the fourth region and by February in the fifth region (Fig. 9). While no anchovy landings were reported for regions 6 and 7, landings in region 8 (Constitución, 36°S or 1000 km south of Pan de Azúcar Island) reached 28 000 tons by March 1998 compared with only 5 tons in December 1997 (SERNAP, 1997, 1998), which further supports the hypothesis that penguin migration was a consequence of southbound anchovy migratory behaviour.

Foraging variables and oceanographic variables

The sea surface temperature anomaly (SSTA) is the deviation of the actual mean weekly sea surface temperature from the average of the previous 10 years, and its magnitude is a good indicator of the intensity of the ENSO phenomenon (Fahrbach et al., 1991). Because of the reaction of anchovies and sardines to rising temperatures, i.e. their preference for colder bodies of water and therefore migration to cold-water eddies and/or deeper depths (Arntz and Fahrbach, 1991; Arntz et al., 1991), we expected Humboldt penguin behaviour to be directly associated with SSTA.

Penguins rely mostly on their sense of vision when capturing prey (Wilson, 1995). Assuming that a penguin can monitor a cylindrical body of water with a radius whose magnitude depends on visibility conditions, the birds would be expected to increase their linear distance (i.e. travelling distance and distance under water) as prey densities decreased to maximize the volume of water searched and thereby increase their chances of encountering food. Our results show that this is exactly what happened during the 1997/98 ENSO. A comparison of daily travelling distance, determined from satellite fixes, and of daily dive duration, derived from SSTA, revealed statistically significant correlations (Tables 2, 3;

Fig. 10. Anchovy landing statistics for three Chilean fishery harbours to the south of Pan de Azúcar Island: Caldera (100 km south), Coquimbo (400 km south) and Chañaral (30 km south). The next harbour to the north where anchovies are landed is Antofagasta (400 km north, not shown).

Fig. 4) and suggests that Humboldt penguins have to work significantly harder to obtain food when SSTA increases.

A similar trend had been observed during the 1994/95 study: as SSTA values increased by 0.5 °C, fishery landings decreased and penguin effort under water, measured *via* satellite transmitters, increased from a 4-day average daily dive duration of 3 h to 7.5 h (Culik and Luna-Jorquera, 1997b). Because mean daily dive durations during the 1997/98 season (7.8 h) were significantly higher (Kolmogorov–Smirnov test, $N=244$, $P<0.001$) than in 1994/95 (5.5 h), this further indicates that during the 1997/98 ENSO Humboldt penguins had to invest more time in foraging than during normal years.

During the 1997/98 ENSO, daily dive duration (7-day average) of Humboldt penguins ranged from 4 h at the beginning of the season to 12.5 h when SSTA values (+4 °C) were highest (Fig. 4C). This is the net time under water, to which pauses required for respiration and recovery at the surface must be added. These amount to approximately 20 % of dive time (Culik and Luna-Jorquera, 1998), and the total foraging activity of the birds was therefore 15 h per day. Considering that in mid-December at 2 °S day length between sunrise and sunset is approximately 14 h (Baur, 1970), the high SSTA values forced the Humboldt penguins to forage non-stop, from dusk to dawn, and to make full use of daylight.

Energy balance

Foraging penguins invest time, effort and most of all energy to obtain food, and the amount of energy invested has to be balanced by the energy gained if the birds are not to starve. In a recent paper, Luna-Jorquera and Culik (2000) calculated the energetic requirements of foraging Humboldt penguins (foraging metabolic rate, FMR, J kg^{-1}) which relate to body temperature (T_b, in °C), water temperature (T_a, in °C), the duration of resting at the surface (t_{rest}, in s), foraging time (t_{forage}, in s) and travelling time (t_{travel}, in s):

$$\text{FMR} = 5.95 \times 0.05(T_b - T_a)t_{rest} + 12t_{travel} + 18.3t_{forage}.$$

Using this equation, the energetic costs of foraging Humboldt penguins can be modelled using our data and the following assumptions (Luna-Jorquera and Culik, 2000): (i) that time below the surface correponds to 18 % travelling and 82 % foraging; (ii) that T_b is 39 °C and T_a is 19 °C under ENSO conditions; and (iii) that a Humboldt penguin (body mass 4.2 kg) rests at sea for the remainder of a 24 h foraging day.

We find that, when SSTA values reached a maximum, a Humboldt penguin invested 4300 kJ day^{-1} while foraging at sea (12.5 h daily dive duration). This is at least 50 % more than at the beginning of the 1997/98 season, when foraging costs were 2800 kJ day^{-1} bird^{-1} (4 h daily dive duration), if the bird did not return to land sooner.

Since the typical energy content of anchovies is 5.93 kJ g^{-1} wet mass (Fitzpatrick et al., 1988), and the assimilation efficiency of Humboldt penguins can be taken as 77 % (Guerra, 1992), we can convert FMR into fish-equivalents (FI, g) using: FI=0.218FMR. Thus, foraging Humboldt penguins would have had to consume 610 g of anchovies per day to balance their foraging costs at the beginning of the season, and this would have increased to 940 g day^{-1} when SSTA values were maximal. However, these calculations are simplistic, because Arntz et al. (1991) found that, under ENSO conditions, anchovies and sardines were substantially lighter (by 30 and 15 % respectively) and their lipid content was reduced by as much as 56 % because of poor feeding conditions. Consequently, the mass of food required for Humboldt penguins to balance their energy investments while foraging under severe ENSO conditions might have been considerably higher and, because of lower energy gain per fish caught, the number of fish ingested substantially higher than under these assumptions.

Diving depth

During the 1997/98 ENSO, the distance travelled and time under water increased (see above). Penguins are positively buoyant, which precludes rest below the surface (Williams, 1995), so time under water is directly related to distance swum. Our data can therefore be interpreted such that, as SSTA increased, Humboldt penguins increased their search effort in both the horizontal and vertical planes.

We hypothesized that, during normal years, the thermocline, which lies at depths of 40 m or less (Arntz and Fahrbach, 1991), constitutes a natural barrier for the maximum diving depth of Humboldt penguins feeding on planktivorous fish. This was confirmed by the maximum depth of 53 m measured during the breeding seasons of 1994 and 1995 (Luna-Jorquera, 1996; Luna-Jorquera and Culik, 1999). Because anchovies dive to deeper strata during ENSO, following the depression of the thermocline to 100 m and more (Arntz and Fahrbach, 1991; Arntz et al., 1991; BAC, 1998), we expected that in 1997/98 Humboldt penguins would follow their prey and also dive deeper.

However, our data show that this was not the case and that, as in previous years, the maximum depth reached by the birds was 54 m. Several factors could be responsible for this behaviour. (i) The period during which we were able to obtain depth data was very short, because the devices stopped transmitting on 30 December 1997 and 8 January 1998. Thus, our dive data might not have included the strongest response of the birds to ENSO. (ii) The devices used were too large and had an impact on the diving capabilities of the birds. Device effects have been discussed in detail elsewhere (Wilson and Culik, 1992), and the size of the SDRs employed here, together with the antenna required for data transmission, might have caused significant drag and thus have limited the aerobic dive time of the birds (Culik and Wilson, 1991). However, on the basis of similar travelling speeds recorded using time/depth recorders (TDRs), radiotransmitters and PTTs differing in mass, shape and antenna design, Culik et al. (1998) concluded that device effects on Humboldt penguins from these methods were comparable.

(iii) Humboldt penguins might be limited to the upper water strata while foraging because of physiological limitations. This is contradicted by the fact that a considerable percentage of

dives lasted 2 min (Fig. 5) and that at normal swimming speeds of $1.7\,m\,s^{-1}$ (Culik et al., 1998), the birds should be able to reach depths of at least 70 m or more, depending on dive angle (Luna-Jorquera, 1996; Luna-Jorquera and Culik, 1999).

(iv) Maximum diving depths might be limited by the availability of light or by water turbidity. The latter is supported by the fact that all dives deeper than 10 m occurred during the daylight hours, i.e. between 03:00 and 21:00 h local time (Figs 5, 6). Penguins are visual hunters (Wilson, 1995) and do not seem to rely on other senses, such as echolocation or mechanical stimuli, to locate prey (Dehnhardt et al., 1998). Therefore, their foraging behaviour at sea might be limited by visibility, unlike that of fur seals (*Arctocephalus australis*), which increase both their mean and maximum dive depths during ENSO conditions (Majluf, 1991).

(v) Because water depth was not a limiting factor for dive depths, the 500 m isobath being less than 15 km from the coast (GEBCO, 1984), and because other penguin species of similar size dive considerably deeper (Williams, 1995), the 0–50 m layer could present foraging Humboldt penguins with better feeding conditions (i.e. higher average encounter probability per unit volume) than deeper layers (Zamon et al., 1996) even during ENSO years. This is supported by anecdotal evidence presented by Arntz and Fahrbach (1991), who report that 'in 1982 several shoals (of anchovies, sardines and silverside *Odontesthes regia*) moved into shallow waters, such that the purse seiners, which need a minimum of 50 m water depth, could not follow them'. Indeed, as shown in Figs 2 and 3, our satellite-tagged penguins spent a large proportion of their time close to the coast.

Orientation at sea and chlorophyll a levels

ENSO-related southward migration of top predators relying on the Humboldt current ecosystem has been observed previously in fur seals (Guerra and Portflitt, 1991) and guano birds such as Guanay cormorants (*Phalacrocorax bougainvillii*), boobies (*Sula variegata*) and pelicans (*Pelecanus thagus*) (Arntz and Fahrbach, 1991). During the 1997/98 ENSO, A. Simeone (personal communication) recorded 'thousands of Guanay cormorants moving southwards, with 5000 birds on Dec. 21 and 15 000 birds on Dec. 26, 1997, at Algarrobo (33.5°S)'.

At the time when both Humboldt penguins P4 and P8 began their southward migration, the multivariate ENSO index (MEI) had almost reached its maximum, and sea surface temperature anomaly (SSTA) values were also rising. The southbound migration of both penguins might have directly followed the migration of their prey (Figs 9, 10) and/or the birds may have been 'lured' towards the south by other factors.

As the birds reached higher latitudes, sea surface temperatures decreased by 0.7 °C (Hydrographic and Oceanographic Service of the Chilean Navy, Valparaíso, Chile, personal communication) and day length increased by approximately 4 min (Time Service Department, US Naval Observatory, Washington, DC, USA: http://tycho.usno. navy.mil/srss.html) per 100 km (approximately 1° latitude).

Because cold temperatures are favoured by both sardines and anchovies (Arntz et al., 1991) and since longer days allow penguins to forage for longer, both factors may have positively reinforced the southward migration of the birds.

An additional clue for the orientation of the penguins at sea was the wind field, which we computed from satellite data for the sector 30°S and 72.5°W (Fig. 7). Winds blew steadily from the southsouthwest, and the heading of both P4 and P8 along the Chilean coast was, therefore, into the wind, which might have transported olfactory clues towards the migrating birds.

Olfactory clues play a role in orientation and navigation in pigeons and presumably other bird species (Wallraff, 1996) and dimethyl sulphide, a naturally occurring scented compound produced by phytoplankton in reaction to grazing by zooplankton (Bürgermeister et al., 1990), has been shown to attract procelariiform seabirds (Nevitt et al., 1995). Fig. 8A shows that P4 and P8 left the coast on 12 and 14 January, respectively, near approximately 28°S, and then swam in a southwesterly direction into the wind (Fig. 7) to reach an area of high chlorophyll a concentration. The foraging tracks of both birds, although separated by 4 days, were closely parallel, and both pointed towards the same 'hot spot' in the vicinity of a sea mount (GEBCO, 1984). We hypothesize that an olfactory clue such as dimethyl sulphide could have played a role in leading both penguins towards these high phytoplankton concentrations.

However, while P4 arrived just as the 'hot spot' disappeared, P8 arrived too late (Fig. 8B). As indicated by consistently high daily dive durations and travelling distances, neither of the birds seems to have been able to derive much advantage from reaching this area, and both birds then continued their migration. While P4 continued to explore the coast at the same latitude as the 'hot spot' had occupied and then returned to area of the 'hot spot' before heading north again, P8 migrated southeast towards the coast and higher phytoplankton concentrations in the south. Fishery statistics (Fig. 9) indicate that both strategies might have been equally successful: anchovy landings in February 1998 reached a maximum in region 2, and landings in the south (regions 4 and 5) were also substantial at that time.

Although B. C. Zavalaga (personal communication) observed that by March 1998 the population of Humboldt penguins at Punta San Juán, Perú, had not recovered, the birds might still have been foraging in more productive areas at that time. Recent Chilean census data will become available in late 2000. Only then can the long-term impact of the 1997–98 ENSO on the Humboldt penguin population be assessed.

To conclude, Humboldt penguins react to climatic change by varying their daily foraging range and dive duration and avoid El-Niño-related food shortages by migrating into more productive marine areas. This makes Humboldt penguins biological *in situ* detectors of highly productive marine areas, with a potential use in confirming, on the ground, trends detected by remote sensors on board satellites (see Ancel et al., 1992; Sims and Quayle, 1998). Navigational clues could be provided by day length, sea surface temperature, local wind

direction and olfaction, important aids in finding patchily distributed prey under El Niño conditions. Our continuing studies will now evaluate how Humboldt penguins at the southern end of the distributional range of the species reacted to the 1997/98 ENSO (J. Hennicke and B. M. Culik, in preparation) and whether dimethyl sulphide can induce foraging behaviour in Humboldt penguins (S. Hagemann and B. M. Culik, in preparation).

References

Ancel, A., Kooyman, G. L., Ponganis, P. J., Gendner, J.-P., Lignon, J., Mestre, X., Huin, N., Thorson, P. H., Robisson, P. and LeMaho, Y. (1992). Foraging behaviour of emperor penguins as a resource detector in winter and summer. *Nature* **360**, 336–338.

Arntz, W. E. and Fahrbach, E. (1991). *El Niño – Klimaexperiment der Natur.* Basel, Switzerland: Birkhäuser Verlag.

Arntz, W. E., Pearcy, W. G. and Trillmich, F. (1991). Biological consequences of the 1982–83 El Niño in the Eastern Pacific. In *Ecological Studies*, vol. 88, *Pinnipeds and El Niño* (ed. F. Trillmich and K. A. Ono), pp. 22–44. Heidelberg: Springer Verlag.

BAC (1998). Boletín de Alerta Climático, Instituto Oceanográfico de la Armada, Guayaquil Ecuador, vol. 88: http://www.inocar.mil.ec/homepage/ccmm/cpps/bacboletines.htm.

Bannasch, R., Wilson, R. P. and Culik, B. (1994). Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J. Exp. Biol.* **194**, 83–97.

Baur, F. (1970). *Meteorologisches Taschenbuch.* Leipzig, Germany: Akademische Verlagsgesellschaft Geest und Portig KG.

Bürgermeister, S., Zimmermann, R. L., Georgii, H.-W., Bingemer, H. G., Kirst, G. O., Janssen, M. and Ernst, W. (1990). On the biogenic origin of dimethylsulfide: relation between chlorophyll, ATP, organismic DMSP, phytoplankton species and DMS distribution in Atlantic surface water and atmosphere. *J. Geophys. Res.* **95**, 20607–20615.

Croxall, J. P. and Davis, L. S. (2000). Penguins: paradoxes and patterns. In *Proceedings of the Third International Penguin Conference, Cape Town* (ed. J. Cooper) (in press).

Culik, B., Bannasch, R. and Wilson, R. P. (1994). External devices on penguins: how important is shape? *Mar. Biol.* **118**, 353–357.

Culik, B. M., Luna, G., Correa, H. V. and Oyarzo, H. (1998). Humboldt penguins monitored *via* VHF-telemetry. *Mar. Ecol. Prog. Ser.* **162**, 279–288

Culik, B. M. and Luna-Jorquera, G. (1997a). The Humboldt penguin: a migratory bird? *J. Orn.* **138**, 325–330.

Culik, B. M. and Luna-Jorquera, G. (1997b). Satellite-tracking of Humboldt penguins (*Spheniscus humboldti*) in Northern Chile. *Mar. Biol* **128**, 547–556.

Culik, B. M. and Wilson, R. P. (1991). Swimming energetics and performance of instrumented Adélie penguins (*Pygoscelis adeliae*). *J. Exp. Biol.* **158**, 355–368.

Dehnhardt, G., Mauck, B. and Bleckmann, H. (1998). Seal whiskers detect water movements. *Nature* **394**, 235–236.

Ellis, S., Croxall, J. P. and Cooper, J. (1998). (eds) *Penguin Conservation Assessment and Management Plan.* Report. Apple Valley, MN 55124 USA: IUCN/SSC Conservation Breeding Specialist Group.

Fahrbach, E., Trillmich, F. and Arntz, W. (1991). The time sequence and magnitude of physical effects of El Niño in the Eastern Pacific. In *Ecological Studies*, vol. 88, *Pinnipeds and El Niño* (ed. F. Trillmich and K. A. Ono), pp. 8–21. Heidelberg: Springer Verlag.

Fitzpatrick, L. C., Guerra, C. and Aguilar, R. (1988). Energetics of reproduction in the desert nesting sea gull (*Larus modestus*). *Estud. Oceanol.* **7**, 33–39.

GEBCO (1984). *General Bathymetric Chart of the Oceans.* Canada: Ministry of Supply and Services.

Guerra, C. (1992). *Efectos de la Nidificación Estival/Invernal sobre Parámetros Seleccionados de la Historia de Vida del Pingüino de Humboldt (*Spheniscus humboldti*).* Chile: Proyecto FONDECYT 90-0599.

Guerra, C. G. and Portflitt, G. (1991). El Niño effects on pinnipeds in northern Chile. In *Ecological Studies*, vol. 88, *Pinnipeds and El Niño* (ed. F. Trillmich and K. A. Ono), pp. 47–54. Heidelberg: Springer Verlag.

Hays, C. (1986). Effects of the El Niño on Humboldt penguin colonies in Perú. *Biol. Conserv.* **36**, 169–180.

Luna-Jorquera, G. (1996). Balancing the energy budget for a warm-blooded bird in a hot desert and cold seas: The case of the Humboldt penguin. PhD thesis, University of Kiel, Germany.

Luna-Jorquera, G. and Culik, B. M. (1999). Diving behaviour of Humboldt penguins (*Spheniscus humboldti*) in Northern Chile. *Mar. Orn.* (in press).

Luna-Jorquera, G. and Culik, B. M. (2000). Metabolic rates of swimming Humboldt penguins. *Mar. Ecol. Prog. Ser.* (in press).

Luna-Jorquera, G., Culik, B. M. and Aguilar-Pulido, R. (1996). Capturing Humboldt Penguins (*Spheniscus humboldtii*) with the use of an anaesthetic. *Mar. Orn.* **24**, 47–50.

Majluf, P. (1991). El Niño effects on pinnipeds in Perú. In *Ecological Studies*, vol. 88, *Pinnipeds and El Niño* (ed. F. Trillmich and K. A. Ono), pp. 55–61. Heidelberg: Springer Verlag.

Nevitt, G. A., Veit, R. R. and Kareiva, P. (1995). Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. *Nature* **376**, 680–682.

Paredes, R. and Zavalaga, C. B. (1998). Overview of the effects of El Niño1997–98 on Humboldt penguins and other seabirds at Punta San Juán, Perú. *Penguin Conserv.* **11**, 5–7.

SERNAP (1997,1998). *Servicio Nacional de Pesca: Anuario Estadístico de Pesca.* Valparaíso, Chile: Ministerio de Economía, Fomento y Reconstrucción.

Sims, D. W. and Quayle, V. A. (1998). Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature* **393**, 460–464.

Taillade, M. (1992). Animal tracking by satellite. In *Wildlife Telemetry: Remote Monitoring and Tracking of Animals* (ed. I. G. Priede and S. M. Swift), pp. 149–160. London: Ellis Horwood Ltd.

Wallraff, H. G. (1996). Seven theses on pigeon homing deduced from empirical findings. *J. Exp. Biol.* **199**, 105–111.

Williams, T. D. (1995). *The Penguins.* Oxford: Oxford University Press.

Wilson, R. P. (1995). Foraging ecology. In *The Penguins* (ed. T. D. Williams), pp. 81–106. Oxford: Oxford University Press.

Wilson, R. P. and Culik, B. M. (1992). Packages on penguins and device-induced data. In *Wildlife Telemetry: Remote Monitoring and Tracking of Animals* (ed. I. G. Priede and S. M. Swift), pp. 573–580. London: Ellis Horwood Ltd.

Wilson, R. P., Duffy, D. C., Wilson, M.-P. and Araya, B. (1995). Aspects of the ecology of species replacement in Humboldt and Magellanic penguins in Chile. *Gerfaut* **85**, 49–61.

Wilson, R. P., Pütz, K., Peters, G., Culik, B. M., Scolaro, J. A., Charrassin, J.-B. and Ropert Coudet, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl. Soc. Bull.* **25**, 101–106.

Wolter, K. and Timlin, M. S. (1998). Measuring the strength of ENSO – how does 1997/98 rank? *Weather* **53**, 315–324.

Zamon, J. E., Greene, C. H., Meir, E., Demer, D. A., Hewitt, R. and Sexton, S. (1996). Acoustic characterization of the three-dimensional prey field of foraging chinstrap penguins. *Mar. Ecol. Prog. Ser.* **131**, 1–10.