



Finding food in the open ocean: foraging strategies in Humboldt penguins*

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Summary

Penguins are excellent "model" organisms allowing us to study the behaviour of marine homeotherms at sea. Penguins regularly return to their breeding colonies, enabling biologists to equip them with remote sensing devices such as physiological or behavioural data-loggers, radio- or satellite transmitters. Foraging trips at sea can last from days to weeks and after return of the birds to their breeding sites, the devices can easily be removed for analysis of on-board stored data, yielding a wealth of information. Investigation of penguin behaviour at sea becomes particularly revealing when other sources of information can be matched to the data set, such as satellite data on wind, temperature, ice cover, and chlorophyll-a concentrations.

Penguins and other marine homeotherms are true inhabitants of the high seas. Depending on the season, the marine behaviour varies: during reproduction, penguins are central-place foragers, and must return regularly to their nest to feed their chicks. During the remainder of the year, there are no constraints and the birds travel large distances at sea.

Breeding Humboldt penguins react to climatic change by varying their daily foraging range and dive duration. Similar to other representatives of the family Spheniscidae, Humboldt penguins avoid food shortages by migrating into more productive marine areas. Navigational clues such as daylength, sea surface temperature, local wind direction and olfaction might provide important aids in finding patchily distributed prey in the open ocean. DMS, a chemical compound produced by decaying algae, seems to be a further clue that indirectly points the way to feeding areas.

Key words: satellite, tracking, oceanography, El Niño, navigation

Introduction

Ecophysiological investigations of marine homeotherms, the whales, seals and marine birds, often revolve around a set of key questions:

- how is the marine habitat utilised?
- what is the food composition'?
- where and how is the prey captured?
- what physiological adaptations have been developed in order to deal with depth, cold or food provisioning of the offspring?
- how high is the energy return'?

- how do environmental factors such as food availability, climate and anthropogenic disturbances influence behaviour?
- how can we efficiently protect marine homeotherms?

The answers to these questions are among others important elements in finding solutions to the following problems faced by marine homeotherms:

- Oil pollution,
- Marine traffic and ensuing collisions with vessels,
- Uncontrolled and excessive fisheries (entanglement in nets, depletion of food resources by over-fishing),

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- Various forms of anthropogenic use of the marine environment, including the development of alternative energies such as offshore wind-farms.

Habitat use of penguins

During the breeding period, penguins are "Central place foragers". Because chicks must be fed at the nest site, the adults are forced to forage within relatively close proximity to their breeding island. At that time of the year, Humboldt penguins are found 90% of the time within a radius of 35 km of their breeding island (Culik et al., 1998; see below). Emperor penguins, however, have a large operational radius even during the breeding season. In a satellite-tracking study, Ancel et al. (1992) reported that these Antarctic birds can cover distances of up to 130 km by foot to reach a polynia (open sea water amidst pack-ice). Later on in the breeding season, the birds may cover distances of up to 1500 km in the search for the prey required to feed their chicks. Such large distances have also been reported for individual foraging trips in breeding king penguins (Culik et al., 1996).

At the beginning of winter, Antarctic emperor (*Aptenodytes forsteri*) and Adélie (*Pygoscelis adeliae*) penguins, sub-Antarctic king penguins (*Aptenodytes patagonicus*), and South American Magellanic penguins (*Spheniscus magellanicus*) regularly cover distances on the order of 1000 km and more between their breeding and wintering habitats (Ancel et al., 1992; Kooyman et al., 1996; Davis et al., 1996; Bost et al., 1997; Pütz et al., 2000). Magellanic penguins from the Falkland/Malvinas Islands leave the Patagonian shelf and reach shores as far North as Uruguay or Brasil (Pütz et al., 2000). Juvenile emperor penguins may even leave the area of the Antarctic treaty, moving North of the 60th parallel into the circumpolar current. These birds may only return to their breeding colonies after circumnavigating the whole Antarctic continent, a distance of roughly 20,000 km (Kooyman et al., 1996).

South American Humboldt penguins, however, were thought to be sedentary and remain close to their breeding localities year round (Williams, 1995; Croxall and Davis, 1999). As a consequence, they were supposedly unable to avoid climate-related food shortages. Regular, but unpublished observations of large numbers of Humboldt penguins returning to their breeding islands in spring or after an ENSO (El Niño Southern Oscillation) event, however, contradict this hypothesis (e.g. Araya and Todd, 1987). Evidence from sightings of ringed birds (H. Oyarzo, pers. comm.; Wallace et al., 1999) and from satellite tracking during the winter (Culik and Luna-Jorquera, 1997a) further confirms that Humboldt penguins travel long distances at sea.

The question arising from these observations on penguins is: how do these relatively small, flightless birds

find food in the vast expanses of the ocean? What are the environmental clues guiding them to their foraging areas? How do biotic and abiotic factors affect their behaviour at sea?

Humboldt penguins of Chile

Humboldt penguins (*Spheniscus humboldti*) are endemic to the Pacific coasts of Chile and Perú, an area influenced by the cold, nutrient-rich Humboldt current. Their breeding colonies span a range of 4500 km between 5 and 42 degrees southern latitude (Williams, 1995). Because of low population numbers, recent estimates indicate a world population of only ca. 13000 birds, Humboldt penguins are considered vulnerable to endangered (Ellis et al., 1998; Bonn Convention on Migratory Species, Appendix I). The factors that severely affect the population are 1) entanglement and drowning in nets (Simeone et al., 1999; Wallace et al., 1999), 2) overfishing, and 3) recurring food-shortage during El Niño Southern Oscillation (ENSO) events. The breeding population decreased by 72% in Chile and by 65% in Peru during the 1982-1983 ENSO (Hays, 1986; Araya and Todd, 1987), when upwelling of nutrient-rich, cold bottom water in the south-eastern Pacific Ocean was depressed.

Humboldt penguins feed predominantly on anchovies (*Engraulis ringens*) and sardines (*Sardinops sagax*; Wilson et al., 1995; Herling, 2001; Hennenke, 2001). These patchily distributed, planktivorous cold-water shoaling fish normally dwell in the highly productive top 50 m of the water column (Amtz and Fahrbach, 1991). During El Niño events, anchovy distribution changes dramatically. The fish concentrate: 1) in cold water eddies close to shore, 2) below the thermocline at depths >100 m, or 3) migrate to cold-water areas, south of their normal distributional range (Arntz and Fahrbach, 1991; Amtz et al., 1991). Because of the migratory behaviour of anchovies, their predators such as the Humboldt penguin would be expected to be migratory themselves.

Since 1994 we have conducted a long-term study on Humboldt penguins in the center of their geographic range in Northern Chile, and since 1998 we have also worked at the southern limit of their range. We have determined how these birds use their marine habitat during "normal" summers (Luna-Jorquera, 1996; Culik and Luna-Jorquera, 1997b; Culik et al., 1998) and used this dataset as a baseline to investigate their ENSO-response strategies in 1997-1998 (Culik et al., 2000).

Data loggers and satellite transmitters

The use of electronic devices to monitor the behaviour and physiology of free-ranging animals is a rapidly developing technique. Due to improvements in the minia-

turisation of satellite transmitters and data-loggers, monitoring the location, physiology and behaviour is becoming increasingly easy for smaller species. At the same time, satellite-derived information on sea-surface temperature, wind speed and direction, ice-coverage and chlorophyll-a concentrations in surface waters enables marine biologists to relate animal behaviour to biotic and abiotic environmental conditions. Applications of these new techniques have been reported for elephant seals in Campagna et al. (2000), for Weddell seals in Davis et al. (1999) and for Humboldt penguins in Culik et al. (2000).

Penguins are comparatively easy to handle, as they can be restrained on the nest. In the case of Humboldt penguins, the birds have to be approached slowly and sedated at the nest site. We used 0.25 ml Ketavet, corresponding to a ketamine hydrochloride (Parke-Davis, Germany) dose of 5 mg kg⁻¹ body mass. This was injected into the pectorales muscle via a syringe mounted on a ca. 1 m long aluminum "applicator" (Luna-Jorquera et al., 1996, 2000), which allowed us to maintain a larger minimum approach distance.

Argos satellite transmitters (Taillade, 1992) were attached dorsally to the feathers of the lower back using Tesa-Tape (Beiersdorf, Germany) and waterproof rubber cement as in Wilson et al. (1997). The devices were placed slightly aft of the line of maximum girth and oriented parallel to the antero-posterior axis of the birds. Care was taken not to obstruct the oil glands situated at the base of the tail. After attachment, the units were coated with epoxy glue to protect them from abrasion. The complete procedure lasted approx. 15 minutes after which the birds were returned to their nest site.

Field work was conducted in Northern Chile at Pan de Azúcar Island, Pan de Azúcar National Park (26°09'S, 70°40'W) during three summers and one winter between 1994 and 1998. In total, we tracked 14 Humboldt penguins (Table 1): a) two birds between Nov. 1994-Jan. 1995, b) two birds between Nov. 1995-Jan. 1996, c) five penguins between Dec. 1997-Feb. 1998

and d) five birds between March - July 1996, respectively.

We used either: 1) ST 10 PTT transmitters (Telonics, USA; packaged by Sirtrack, New Zealand) providing location and daily dive duration (salt water timer), or 2) SDR 10 PTT satellite depth recorders (Wildlife Computers, USA) providing location and time at depth as well as depth histograms. Transmitters weighed ca. 130 g (dimensions 130 x 60 x 25 mm). They were equipped with a 220 x 2 mm antenna placed at the center of the devices at an angle of 45°, facing back. The front of the PTT's was streamlined according to Bannasch et al., (1994) to reduce hydrodynamic drag (c.f. Culik et al., 1994).

Daily dive duration (ST 10 PTT's only) was determined from the salt water timer. Diving depths and durations (SDR's only) were transmitted as maximum values as well as histograms summarizing dive data for the previous 6 h period, starting at 3:00 AM every day. 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 per 6 hour interval with a resolution of 1 minute (i.e. numbers of dives < 1 min could be separated from dives > 1 min).

Oceanographic variables

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 fishery landing statistics:

SST and SSTA data were provided by the International Research Institute for Climate Prediction from their homepage at <http://iri.ucsd.edu/index.html>.

In situ SST and SSTA data were made available by the Hydrographic and Oceanographic Service, and surface wind data by the Meteorological Service, Chilean Navy, Valparaiso, Chile.

Table 1. Details of satellite transmitter deployments in Humboldt penguin migratory research conducted during the breeding season at Pan de Azúcar Island, Northern Chile. The number of locations per day depends on pre-set transmission rates, satellite overpass frequencies and satellite availability, among other factors. Location class 1-3 corresponds to an accuracy of 1000 m or better (Taillade, 1992). Other locations were obtained with less accuracy. ST = Telonics, SDR = Wildlife Computers, seasons: s = summer, w = winter.

Bird nr.	PTT type (seasons)	Body Mass (g)	Sampling Period	Locations (n / d)	Class 1-3 (%)	on/off (h)
1	ST (s)	—	10.11.94-19.12.94	4.16	39	24/ 0
2	ST (s)	—	22.11.94-03.01.95	3.05	39	16/ 8
3	ST (s)	4 650	15.11.95-29.12.95	1.78	39	16/ 8
4	ST (s)	4 750	15.11.95-24.01.96	1.68	39	16/ 8
5	ST (s)	4 015	02.12.97-08.02.98	4.84	42	10/14
6	ST (s)	4 165	02.12.97-28.12.97	4.53	40	10/14
7	ST (s)	3 515	02.12.97-10.02.98	5.27	32	10/14
8	SDR (s)	4 700	03.12.97-30.12.97	1.81	57	24/ 0
9	SDR (s)	4 600	03.12.97-08.01.98	2.72	50	24/ 0

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, from their Web site at <http://www.cdc.noaa.gov/>.

Chlorophyll-a concentrations were computed from gridded (resolution 9 x 9 km) weekly mean Sea-viewing Wide Field of View Sensor (SeaWiFS) satellite data as 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.

Finally, statistics on fishery landings were provided by the Chilean National Fisheries Service (SERNAP), Valparaiso, Chile.

"Normal" summers of 1994-95 and 1995-96

Locations obtained from Humboldt penguins P 1 and P2 during the 1994-1995 breeding season, and on birds P3 and P4 during the 1995-1996 season (Fig. 1) show no specific foraging areas. During both seasons, the penguins remained within 95 km of the coast and all foraging trips were within a strip extending from 31 km South to 98 km North of the island. The maximum area covered was therefore 12,255 km².

Diving behaviour

A detailed analysis of a foraging trip of penguin P 1 between Dec. 5-7, 1994 is shown in Fig. 1 (top right). During this trip, the bird was located 16 times by Argos-satellites. The bird left the island on the morning of Dec. 5, and spent the night at sea. After foraging the

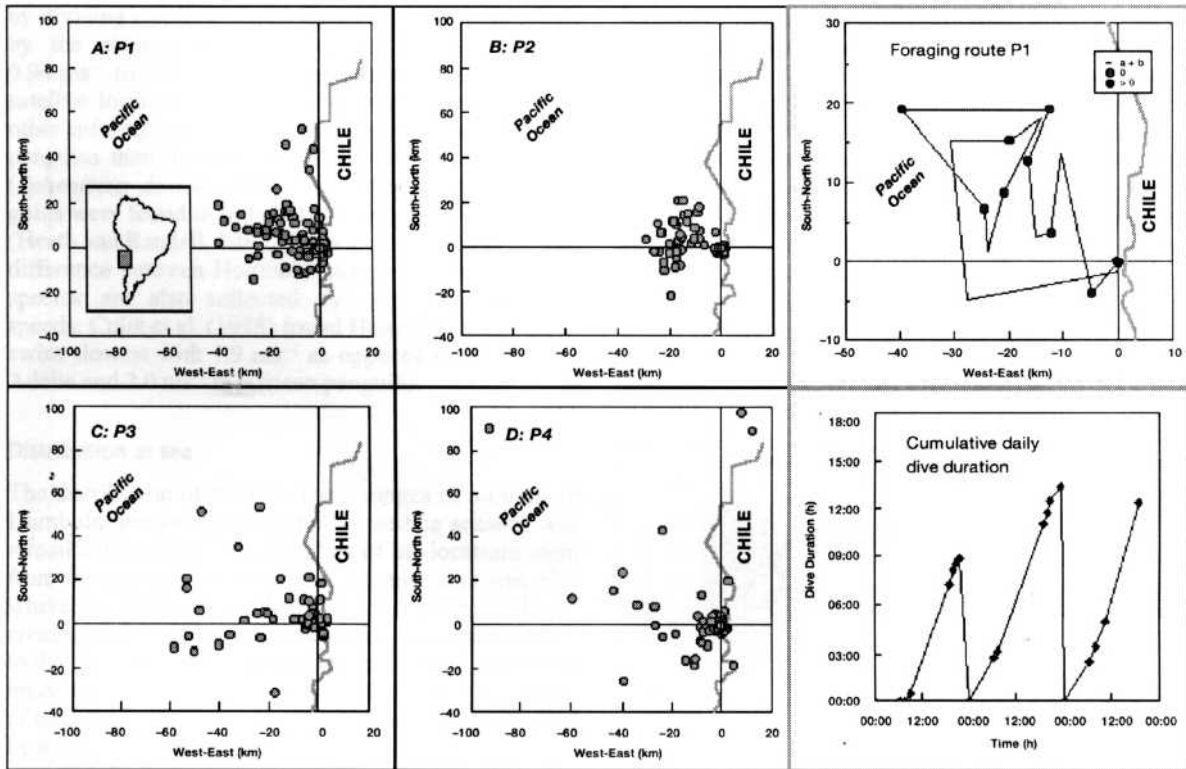


Fig. 1. Left: Distribution of all satellite positions obtained from Humboldt penguins P1 and P2 during the 1994-1995 (top, A and B, respectively) and P3 and P4 during the 1995-1996 (bottom, C and D, respectively) breeding seasons. The Chilean coastline is situated on the right and Pan de Azúcar island (not visible) is at the origin of the x and y axes (mod. from Culik and Luna-Jorquera 1997b). Right: Details of a foraging trip of penguin P1 during Dec 5-7, 1994 (top). Location quality is indicated by the symbol used, location classes > 0 correspond approx. to an accuracy of < 1000 m. During this foraging trip, P1 covered an area of 1,200 km². While the penguin was at sea, the salt water switch timed cumulative daily dive duration (bottom) which amounted to 13.5 h on Dec. 6 (mod. from Culik and Luna-Jorquera 1997b).

whole next day, the animal spent a second night at sea in the same area and also foraged during the third day. P1 finally returned to the island on the evening of the 3rd day. During the entire trip (57.7 h), the bird covered an area of 30 x 40 km (1,200 km²). Diving activity during this trip was obtained via the salt water timer on the transmitter (Fig 1, bottom right).

Wilson et al. (1989) found that African penguins dived for a mean period of 10 h per day during the breeding season whereas time under-water in Humboldt penguins at Chañaral island, central Chile, amounted to 7.1 h per day. The data we obtained from birds P1 and P2 compares well. We found that bird no. 1 spent on average 9.0 h submerged per day (range 1:29 to 13:25 h, 25 days at sea) while P2 spent on average 7.8 h submerged per day at sea (range 1:55 to 13:26 h, 36 days at sea).

Travelling speeds

Mean travelling speed of the penguins was determined by dividing the distance traversed between 2 locations by the elapsed time. Mean travelling speed was 0.94 ms⁻¹ (n = 154). Travelling speeds measured from satellite locations are lower than estimates based on other information and seem to be lower in Humboldt penguins than in other species. The African penguin (*Spheniscus demersus*) and similar-sized Adélie penguins were found to travel at a mean speed of 1.2 ms⁻¹ (Heath and Randall, 1989; Davis and Miller, 1992). The difference between Humboldt penguins and these two species are also reflected by different swimming speeds: Culik et al. (1998) found Humboldt penguins to swim slowest with 1.9 ms⁻¹ as opposed to 2.2 ms⁻¹ in Adélie and 2.0 ms⁻¹ in African penguins.

Distribution at sea

The distribution of the maximum ranges of all marked Humboldt penguins during both breeding seasons was remarkably similar (Fig. 2). Most of the locations stem from the vicinity of the island, because this was also where the penguins went to rest, thus presumably increasing the likelihood of successful data transmission to the satellites. Foraging range and duration during the breeding season reflect the availability and proximity of their major food sources and the constraints imposed by the needs of their chicks. Consequently, both parameters can be highly variable within the same species. Foraging ranges of Humboldt penguins varied both in time and between birds and ranged between 2 and 92 km (4-day means). Although birds did not seem to prefer particular areas (which was confirmed in more detail by VHF-telemetry; Culik et al., 1998), their distribution at sea allowed us to determine the distance

from the island where they were most likely to be encountered. In total, 90% of all satellite locations came from a range of 35 km around the island (50% within 5 km). This compares well to estimates from African penguins: Wilson et al. (1989) found that adults with small and medium sized chicks foraged within an average range of 11 and 15 km of their nesting island, respectively, and a census of penguins at sea (Wilson et al., 1988) confirmed that, during the breeding season, 50% of the birds were within 3 km of the coast.

The close proximity of Humboldt penguin foraging areas to the Chilean coast is related to the distribution of their main prey, clupeid-type pelagic school fish such as the anchovy. Because Chilean anchovy landings amounted to 2.7 million metric tons in 1994, with ca. 25% of the annual catch from regions adjacent to Pan de Azúcar Island (SERNAP, 1994), one of our questions was whether fisheries affect Humboldt penguin behaviour at sea.

If authorities restricted fishing to outside a 35 km radius around breeding islands this could improve the survival chances of Humboldt penguins during "nonnal" breeding seasons (see below).

Foraging parameters and fish availability

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 certain radius whose magnitude depends on visibility conditions, we expected that the birds increase linear distance (measured indirectly via travelling distance and daily dive duration) as prey densities decrease, to maximize the volume of water searched. To test this hypothesis, we computed the 4-day mean daily dive duration for each bird

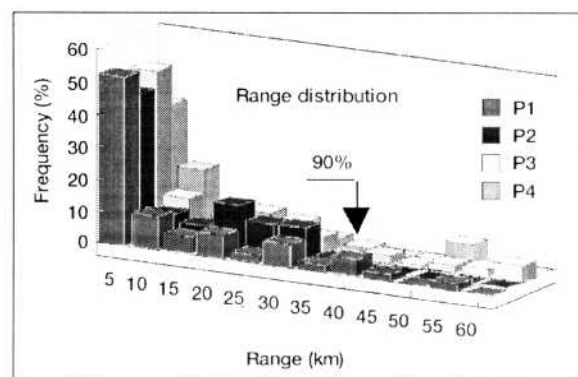


Fig. 2. Penguin distribution at sea during the "normal" summers of 1994-1995 and 1995-1996. Fifty percent of the locations stem from an area with a 5 km radius around the breeding island and 90% of all locations were obtained within a radius of 35 km (modified from Culik and Luna-Jorquera 19976).

and correlated this parameter with fishery landings at nearby Caldera (SERNAP, 1995, 1996, 1997), the best available data on prey availability in the region.

We also assumed that sea surface temperature anomaly (SSTA) represents an independent measurement of marine productivity, which itself depends on the upwelling of cold, nutrient-rich water. SSTA is the deviation of the actual mean weekly sea surface temperature from the average of the previous 10 years and its magnitude represents a good indicator of the intensity of ENSO-phenomena (Fahrbach et al., 1991). High SSTA values should therefore reflect poor upwelling and nutrient conditions, with negative effects on marine productivity and fishery landings.

During the 1994-1995 season, the SSTA was positive all along the Pacific Coast of South America (BAC, 1996) and averaged 1 °C higher than normal. Similarly, sea level measurements at Caldera were 4 cm above average (BAC, 1996). SSTA and fishery landings were negatively correlated (Pearson correlation analysis, $R = -0.998$, $p < 0.001$), indicating that marine productivity is indeed related to SSTA and negatively affected by a positive anomaly.

Mean Humboldt penguin foraging effort was highly correlated ($R = 0.675$, $p < 0.001$, $n = 37$) between the 2 birds (P1 and P2). Both birds therefore appeared to react simultaneously to some extrinsic factor. The correlation between their daily dive duration and fishery landings was negative and highly significant ($R = -0.79$ and -0.68 for P1 and P2, respectively, $p < 0.001$): The birds increased their foraging effort at a time when fish availability decreased. Finally, penguin foraging effort was positively correlated with SSTA values ($R = 0.79$ and 0.69 , P1 and P2, respectively, $p < 0.001$), and so the behaviour of Humboldt penguins at sea appears to be affected by SSTA.

In contrast, the breeding season of 1995-1996 was characterized by SSTA conditions moderately (0.5 °C) colder than normal. SSTA and sea level signals were weak (BAC 1996) and correlation between the parameters stated above were not significant in all cases ($p > 0.05$).

El Niño summer of 1997-1998

Foraging areas

Between December 2, 1997 and February 10, 1998 we obtained a total of 963 Argos locations from instrumented Humboldt penguins. Penguin activity can be roughly divided into 3 periods (Fig. 3).

I) In early December 1997, Humboldt penguins remained close to the island, foraging either North or South of Pan de Azúcar, a behaviour also observed in 1994-1995 and 1995-1996 (Fig. 1). Similar to the be-

haviour during "normal" years reported above, 90% of all locations obtained between Dec. 2-21, 1997 were within a radius of 55 km around the island. Comparison of the two distributions (Kolmogorov-Smirnov two-sample test) showed that the difference was not significant between the years ($p > 0.05$). 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 tending their offspring in December 1997. They commented, however, that the birds were "making long foraging trips", which indicates that foraging conditions at that time were already sub-optimal.

II) In late December 1997 anchovy landings in Chile's 1st and 2nd region (North of Pan de Azúcar island) collapsed, but remained at the same level in region 3 (Fig. 6). Foraging strategies adopted by the 5 satellite-tracked Humboldt penguins were variable: two penguins (P6 and P9) foraged further away, as far as 160 and 190 km from the island, while three of the birds remained in the vicinity (< 100 km away). As a consequence, compared to early December, the distribution of the birds around the island changed between December 21, 1997 and January 10, 1998. Most records (>50%) occurred in a radius >45 km from the island, and the distribution differed significantly from previous years (Kolmogorov-Smirnov two-sample test, $p < 0.001$).

III) By mid-January 1998 conditions had deteriorated even further and the shift in foraging strategies of individuals P6 and P9 was accompanied by nest desertion. Only 312 Humboldt penguins were counted in January 1998 as opposed to 2,276 birds in January 1997. This tendency was confirmed by Paredes and Zavalaga (1998) who observed that at Punta San Juan, Perú

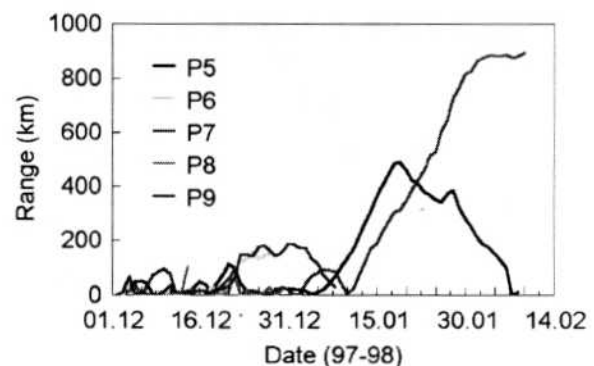


Fig. 3. Maximum range (km) of Humboldt penguins from their breeding island during the ENSO event between Dec. 1997 and Feb. 1998. Until mid-December, penguins foraged close to Pan de Azúcar Island. After Dec. 21, P6 and P9 left the island to forage almost 200 km away. P5 and P7 left the island on January 6 and 10, respectively (Fig. 4) (mod. from Culik et al., 2000).

(15.5 °S), all chicks were deserted by January 1998. Penguin numbers there declined from ca. 3,600 (in normal years) to only 670 individuals, 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, pers. comm.). Further South, at Pajaro Niho Island / Algarrobo (33 °21 'S, 71°40'W), the size of the breeding population was already by reduced to one third in December 1997 as opposed to "normal" years. Throughout the duration of our study, prey availability in Chilean waters, as derived from fishery statistics, decreased (SERNAP, 1997; 1998; 1999). In January 1998, Chilean industrial anchovy landings (24,735 t) were reduced by 84% as opposed to January 1997 (158,867 t) and by 50% as opposed to December 1997 (50,359 t). This was due to the collapse of fisheries in northern Chile (Fig. 6, region 1). Pan de Azúcar is located at the border between 2nd and 3d Region, and Fig. 6 shows that in January, anchovy catch North of Pan de Azúcar was very low. After January 1998, landings in central Chile (Region 4 and 5) increased, reflecting the southward migration of the fish shoals.

Between Jan 6-10, both P5 and P7 also abandoned breeding and began to migrate southward (Figs. 3 to 5). Anchovy landings suggest that the food situation to the north of very poor at that time Pan de Azúcar island was deteriorating by then (Fig. 6; 1st and 2nd Region) and that, as suggested by Arntz and Fahrbach (1991) and Arntz et al. (1991), anchovy stocks had migrated southward. This is confirmed by trends in anchovy landings in Chile's 4th and 5th region, which started to increase by January and February, respectively. While no 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, as opposed to only 5 tons in December 1997 (SERNAP, 1997; 1998). This supports the hypothesis that penguin migration was a consequence of anchovy migratory behaviour.

Foraging parameters and oceanographic variables

During the time the penguins carried their PTT's, their daily travelling distance was highly variable (range 2 to 116 km). As before, the 7d-running mean of daily travelling distance was significantly correlated with sea

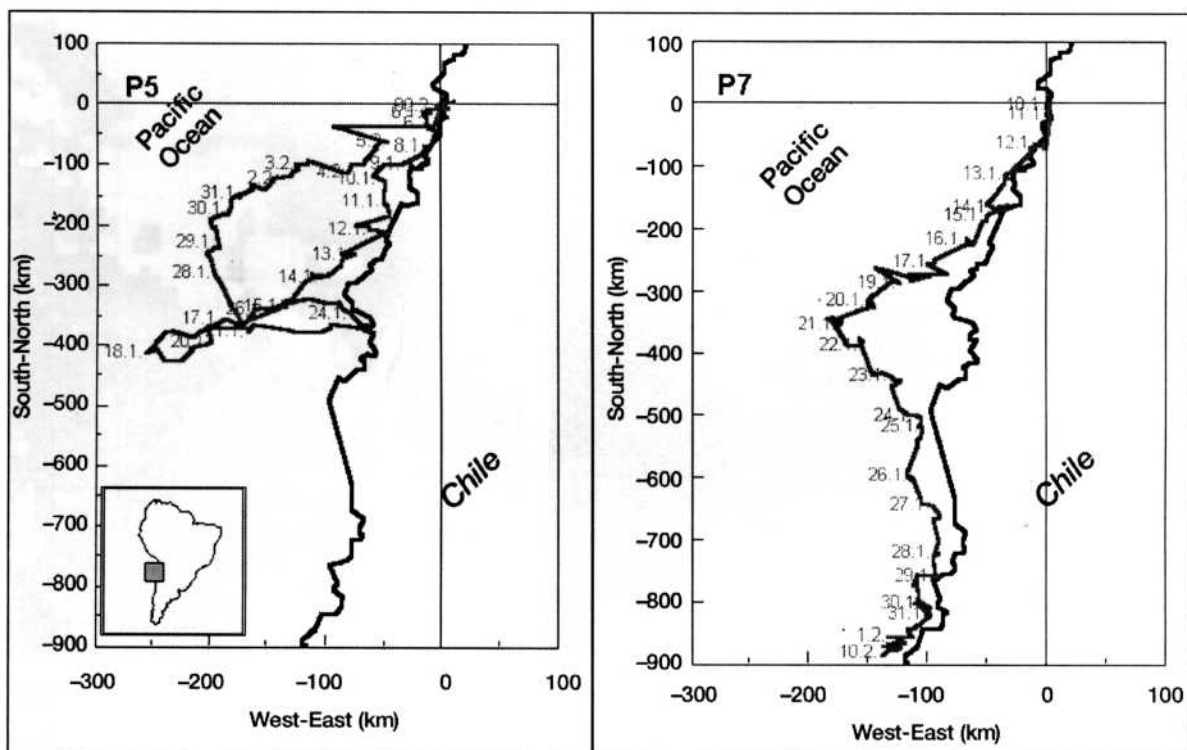


Fig. 4. Foraging trips of penguins P5 and P7, after January 6 and 10, 1998, respectively. Both birds first travelled South in close proximity of the coast and headed South-West after crossing the 28 °S parallel. While P5 returned to Pan de Azúcar on February 8th, P7 continued South to 34 °S. Data transmission ended while P7 was 895 km south of Pan de Azúcar Island (mod. from Culik et al., 2000).

surface temperature anomaly (SSTA, 7d running mean, in °C) in 3 of the birds (P6, P7 and P8, $p < 0.001$). Daily travelling distance increased with temperature by a factor of 3 to 8.7 km per °C (SSTA), respectively. Penguin foraging effort was expected to increase in response to anchovy and sardine reaction to warming temperatures, i.e. preference for colder bodies of water and therefore migration to cold-water eddies and/or greater depths (Arntz and Fahrbach, 1991; Arntz et al., 1991). Our results show that during the 1997-1998 ENSO-event foraging effort (daily travelling distance as determined from satellite fixes and daily dive duration) was highly correlated with SSTA, confirming that Humboldt penguins have to work significantly harder to obtain food when SSTA increases. During the 1997-1998 ENSO-event, daily dive duration (7d-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. This is the net time under water, to which pauses required for respiration and recovery at the surface have to be added. These amount to ca. 20% of dive time (Culik et al., 1998) and thus total foraging activity in the birds summed up to 15 h per day. Consid-

ering that in mid-December at 26 °S the number of hours from sunrise to sunset amount to ca. 14 h per day (Baur, 1970), high SSTA values forced Humboldt penguins to forage non-stop, from dusk to dawn, making full use of daylight hours. Comparison of mean daily dive durations during the 1997/98 season (7.8 h) with those of 1994/95 (5.5 h) indicates that Humboldt penguins had to invest significantly more time for foraging during the 1997/98 ENSO-event than in "normal" years (Kolmogorov-Smirnov test, $n = 244$, $p < 0.001$).

Arntz et al. (1991) found that, under ENSO conditions, anchovies and sardines are substantially lighter (by 30 and 15% respectively), and their lipid content is reduced by as much as 56% because of deteriorated feeding conditions. Consequently, the mass of food required for Humboldt penguins to balance their high energy investments while foraging under severe ENSO-conditions is considerably higher as opposed to "normal" years (Luna-Jorquera and Culik, 2000). Because of lower energy gain per fish caught, the number of fish ingested has to also be substantially higher during ENSO. This factor therefore aggravates ENSO-related food shortage even further.

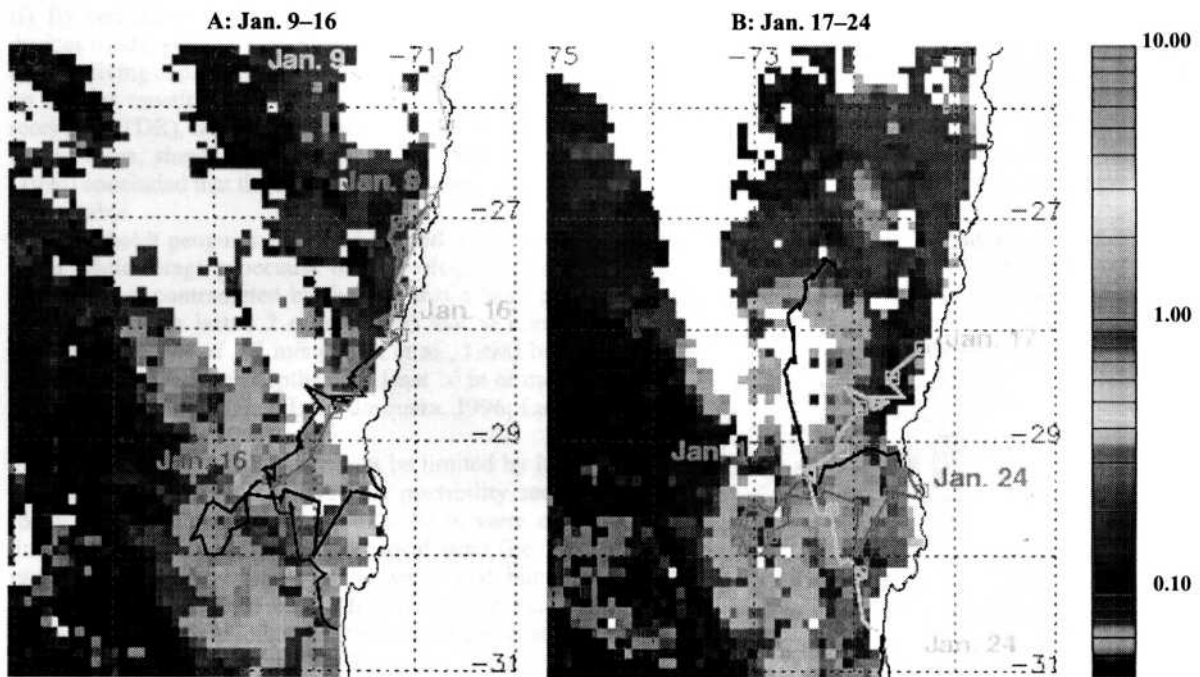


Fig. 5. (A) Foraging trips of penguins P5 and P7 between Jan. 9 and Jan. 16, 1998. Fractions of the penguin routes corresponding to the underlying composite image of chlorophyll-a concentrations (in mg m^{-3}) are marked in red (P5) and yellow (P7) respectively. Penguin tracks of the following 7 d period are coloured in black (P5) and violet (P7) respectively. (B) Foraging trip of penguins P5 and P7 and chlorophyll-a concentrations between Jan. 17 and Jan. 24, 1998. Fractions of the penguin routes corresponding to the underlying composite image of chlorophyll-a concentrations (in mg m^{-3}) are marked in red (P5) and yellow (P7) respectively. Penguin tracks of the following 7 d period are coloured in black (P5) and violet (P7) respectively. Independent of each other, both birds located a patch of high chlorophyll-a concentrations, situated at 29.5 °S and 72.5 °W (mod. from Culik et al., 2000).

Dive depth

We had 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 planctivorous fish. The maximum depth of 53 m measured during the breeding seasons of 1994 and 1995 (Luna-Jorquera, 1996; Luna-Jorquera and Culik, 1999) supports this hypothesis. Because anchovies dive to greater depths during ENSO, following the depression of the thermocline to 100 m or more (Arntz and Fahrbach, 1991; Arntz et al., 1991; BAC, 1998), we expected that Humboldt penguins would follow their prey and equally dive deeper in 1997-1998.

However, we found that, as in previous years, the maximum depth reached by the birds during the 1997-1998 ENSO was 54 m. Several factors could be responsible for this behaviour.

I) The period during which we obtained depth data was very short, because Satellite depth records stopped transmission on Dec. 30, 1997 and Jan 8, 1998. Thus, our dive data might not have included the strongest response of the birds to ENSO.

II) By comparison to previous studies, the telemetric devices used could have been too large, thereby impairing the diving capabilities of the birds. However, based on similar travelling speeds recorded via time-depth recorders (TDR), radio-transmitters, and PTT's differing in mass, shape and antenna design, Culik et al. (1998) concluded **that the effects** of these methods were comparable.

III) Humboldt penguins might be limited to shallower water while foraging because of physiological limitations. This is contradicted by the fact that a large percentage of dives lasted 2 minutes and that at normal swimming speeds of 1.7 m/s (Culik et al., 1998) birds should be able to reach depths of at least 70 m or more, depending on dive angles (Luna-Jorquera, 1996; Luna-Jorquera and Culik, 1999).

IV) Maximum diving depths might be limited by light availability or water turbidity. This possibility seems likely because all dives deeper than 10 m were conducted between 3 AM and 9 PM local time (i.e. between dusk and dawn). Penguins are visual hunters (Wilson, 1995) and do not seem to rely on other senses to locate prey, such as echolocation or mechanical stimuli (e.g. Dehnhardt et al., 1998). Therefore, their foraging behaviour at sea might be limited by visibility, as opposed to fur seals (*Arctocephalus australis*), which increase both their mean and maximum dive depths during ENSO conditions (Majluf, 1991).

V) Because water depth did not restrict dive depths - the 500 m isobath (depth line) was less than 15 km from the coast (GEBCO, 1984) - and because other penguin

species of similar size dive considerably deeper (Williams, 1995), the top 50 m could present foraging Humboldt penguins with better feeding conditions (i.e. higher encounter probability per unit volume) than deeper layers (Zamon et al., 1996) even during ENSO years. Anecdotal evidence supports this. Arntz and Fahrbach (1991) reported 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 Fig. 4 and 5, satellite-tagged penguins spent a large proportion of their time in close vicinity of the coast.

Orientation and Chlorophyll a

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 bougainvillhi*), Peruvian boobies (*Sula variegata*) and Chilean pelicans (*Pelecanus thagus*) (Arntz and Fahrbach, 1991). In December 1997, Simone (1997) recorded 20,000 southbound Guanay cormorants at Algarrobo.

When both Humboldt penguins P5 and P7 began their southward migration, the ENSO-phenomenon had almost reached its maximum (BAC, 1998) but SSTA values were still rising. The southbound migration of both penguins might have directly followed the migration of their prey (Fig. 6), and/or the birds may have been 'lured' southward 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, Val-

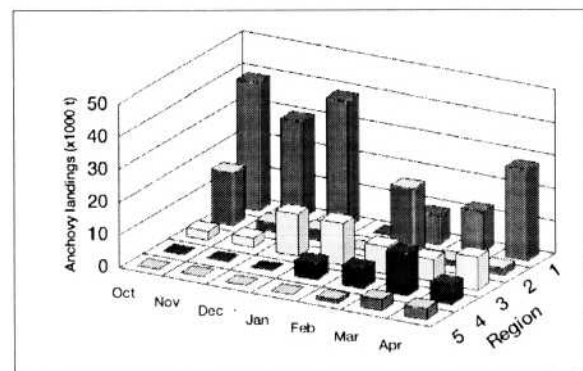


Fig. 6. Anchovy landing statistics for Chilean regions I (North) to V (South) between October 1997 and April 1998. Region I stretches approximately from 19--22 °S, region 2 from 22--26 °S, region 3 from 26-29 °S, region 4 from 29-32 °S and region 5 from 32-34 °S. Note the increase in landings from North to South and as the season progressed (mod. from Culik et al., 2000).

paraiso, Chile, pers. comm.) and day length increased by ca. 4 min per 100 km (ca. 1 degree latitude). Because cold temperatures are favoured by both sardines and anchovies (Arntz et al., 1991), and because longer days allow penguins to forage longer, both factors may have positively reinforced the southward migration of both penguins.

However both P5 and P7 left the coast on Jan 12 and 14, respectively, near approx. 28 °S and then swam in a south-westerly direction, into the wind to reach an area of high chlorophyll-a concentrations (Fig. 5A). The foraging tracks of both birds, although separated by 4 days, were highly parallel, and both pointed towards the same "hot spot", in the vicinity of a sea mount (GEBCO, 1984). We hypothesized, that an olfactory clue could have played a role in leading both penguins towards these high phytoplankton concentrations.

However, while P5 arrived just in time to "see" the "hot spot" disappear, P7 arrived too late (Fig. 5B). As indicated by invariably high daily dive durations and travelling distances, neither of the birds seems to have been able to derive much advantage from reaching this area of high chlorophyll - a concentration and both birds continued their migration afterwards. While P5 explored the coast at the same latitude as the transient "hot spot" and then returned to that area before heading North again, P7 migrated South-East towards the coast and higher phytoplankton concentrations in the South. Fishery statistics (Fig. 6) indicate that both strategies might have been equally successful: Anchovy landings in February 1998 reached a high in region 2, and landings in the South (regions 4 and 5) were also substantial at that time.

C.B. Zavalaga (pers. comm.) observed that by March 1998 the population of Humboldt penguins at Punta San Judn, Perú, had not recovered. However, rather than having died of starvation, some of the birds might still have been foraging in more productive areas at that time. Rapid recovery of the Chilean breeding population after the 1982-1983 ENSO suggested that migration plays an important role (Araya and Todd, 1987).

Plankton: a clue for foraging Humboldt penguins?

An additional clue for the orientation of southbound Humboldt penguins P5 and P7 was the wind field, which we computed from satellite data for the sector 30 °S and 72.5 °W. Winds blew steadily from South-South West. The heading of both P5 and P7 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). Dimethyl sulfide (DMS), a naturally occurring scented compound liberated by phytoplankton during cell-lysis (Bürgermeister et al., 1990), has previously been shown to attract procelariiform seabirds at sea (Nevitt et al., 1995).

To investigate whether DMS could indeed serve as a navigational clue for Humboldt penguins, we conducted a simple experiment. At Hagenbeck's Tierpark in Hamburg we conditioned Humboldt penguins to DMS (Hagemann, 2000). From 30 min prior to normal feeding times (9:00 and 12:00) until feeding occurred (9:30 and 15:30), penguins were exposed to aerial DMS

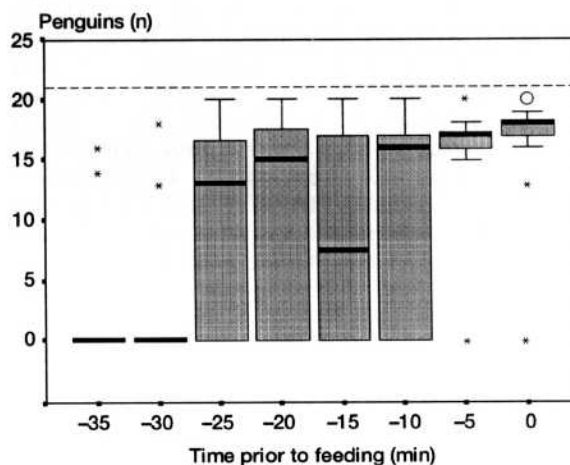


Fig. 7. Number of Humboldt penguins (median) engaged in "anticipatory" behaviour in Hagenbeck's Tierpark in Hamburg prior to feeding at normal feeding hours. The number of active birds increases from one 5-minute interval to the next and reaches a peak immediately prior to feeding (mod. from Hagemann, 2000).

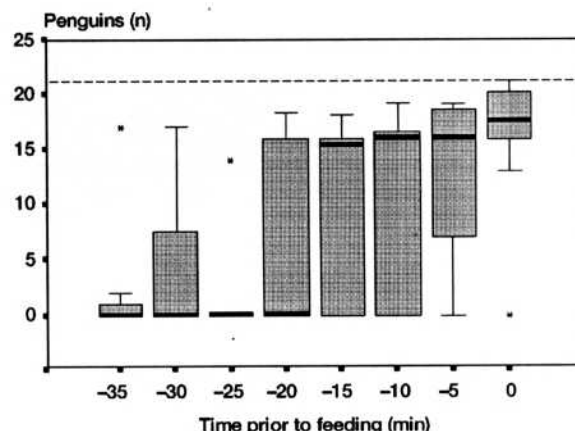


Fig. 8. Number of Humboldt penguins (median) engaged in anticipatory feeding behaviour outside normal feeding times. The birds were exposed to DMS (starting at t = -30) as the only clue signaling the temporal proximity of a feeding event. Time in 5-min intervals (mod. from Hagemann, 2000).

concentrations $10 \text{ nmol} \cdot \text{m}^{-3}$ comparable to values recorded at sea (Bürgermeister et al., 1990). The behaviour of the birds was recorded simultaneously by a closed-circuit TV monitoring system.

Three weeks after the onset of this conditioning experiment, we began to analyse bird behaviour. Within the 30 min prior to feeding, the birds showed increasing levels of activity, peaking immediately before oral administration of the food (Fig. 7). However, the clues allowing the penguins to sense the coming feeding event could have been many, ranging from hunger, internal clock, behaviour and numbers of human spectators, behaviour of the seals in the nearby cage, as well as to the DMS scent itself.

To separate these clues from the signal of the DMS scent, we randomly varied feeding times. The only reliable clue for the upcoming feeding event became, therefore, the DMS scent presented 30 min before feeding. Bird behaviour indicates that the DMS scent alone was sufficient to initiate the same "anticipatory" behaviour observed before (Fig. 8). The two distributions were not significantly different (Kolmogorov-Smirnov test, $p > 0.05$). In contrast, feeding birds outside their "normal" times without DMS as a clue resulted in a lack of activity changes (Fig. 9).

From this experiment and from the tracks recorded on Humboldt penguins P5 and P7 during ENSO off Chile we conclude that phytoplankton could indeed, via DMS, offer navigational clues. Penguins might have learned to associate the scent of decaying phytoplankton with productivity, i.e., the presence of planktivorous fish. Whether this is truly so, however, would have to be tested in a field experiment using DMS at sea, upwind from a Humboldt penguin colony.

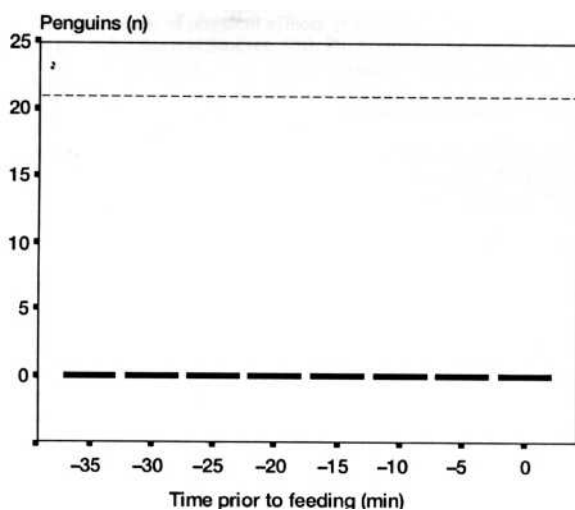


Fig. 9. Outside normal feeding hours Humboldt penguins (median) show no "anticipatory" behaviour when no clues, including DMS, are present prior to feeding (mod. from Hagemann, 2000).

While we have identified DMS as one potential olfactory aid in penguin navigation at sea, there must be others. How else can emperor penguins find open water polynias after travelling on foot for up to 130 km? This research field of animal navigation still offers a large number of very interesting and scientifically rewarding questions.

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