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Annual and seasonal changes in foraging site and diving behavior in Adélie penguins

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Abstract Foraging sites, diet, and diving behavior of chick-rearing Adélie penguins, *Pygoscelis adeliae*, in fast sea-ice areas were investigated during two consecutive seasons with contrasting sea-ice conditions. During 1995/1996, fast sea ice covered the foraging range of penguins during the whole breeding season. In contrast, during 1996/1997, sea ice covered the area in December 1996, but gradually thinned and finally broke up, so that open sea appeared along the coast during February 1997. Foraging sites were concentrated in a small area in 1995/1996 and spread over a wider area in 1996/1997 as more small open-water areas were available. In both seasons, parents traveled to more distant foraging sites as the season progressed and, consequently, the foraging-trip duration increased. In both years, *Euphausia superba* and *Pagothenia borchgrevinki* dominated the diet in the early part of the season, while later in the season penguins fed mainly on *E. superba* in 1995/1996 and *Pagothenia borchgrevinki* and *E. crystallorophias* in 1996/1997. In 1995/1996, penguins tended to dive deeper—albeit for a relatively shorter duration—when feeding mainly on krill compared to when feeding on fish. In 1996/1997, there was no difference in the dive depth and duration between krill- and fish-eating trips. Our results suggest that prey distribution changes annually and seasonally, probably according to sea-ice conditions, and that consequently penguins modify their foraging sites, diving patterns, and diet according to these changes.

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Introduction

Seabirds play an important role in the marine ecosystem in consuming large amounts of marine resources and quickly responding to changes in prey availability at various temporal and spatial scales (Cairns 1987; Montevecci 1993; Charrassin et al. 1998; Charrassin and Bost 2001). Foraging location of seabirds depends on the availability and predictability of prey (Weimerskirch et al. 1993; Irons 1998; Bost et al. 2002). Thus, simultaneous fine-scale information on the diving behavior and location of seabirds is of basic importance to understand their habitat use (Ancel et al. 1992; Rodary et al. 2000a). Activity recorders or radio transmitters have been used to study the foraging behavior of various species of seabirds (e.g., Wanless et al. 1990; Croll et al. 1992). Recently, small VHF transmitters and miniaturized data loggers have enabled us to study these two parameters simultaneously in a variety of free-ranging seabirds (Kato et al. 1998).

Adélie penguins (*Pygoscelis adeliae*) forage both in open sea and under sea ice (Ainley et al. 1998; Clarke et al. 1998; Rodary et al. 2000b). Sea-ice condition changes seasonally and also differs between years, which could be one of the factors affecting feeding sites, diet and depth-utilization patterns of penguins (Ainley et al. 1998; Clarke et al. 1998; Rodary et al. 2000b). Adélie penguins in Lützow-Holm Bay, Enderby Land are unique since they breed in an area covered by fast sea ice even during the austral summer. Their foraging sites are limited to small open-water areas surrounded by fast ice and are, therefore, more predictable than in the open sea (Watanuki et al. 1993, 1999). Diving behavior and feeding sites of Adélie penguins were measured simultaneously by using micro data loggers and VHF radio tracking in 1995/1996 (Watanuki et al. 1999) and 1996/1997. We report here the seasonal change and annual differences in the foraging behavior of Adélie penguins in Enderby Land, paying special attention to the variations in the diving behavior according to diet composition.

Materials and methods

The study was conducted at the Adélie penguin colony of Hukuro Cove in Lützow-Holm Bay (69°00′S, 39°39′E) during the 1995/1996 and 1996/1997 austral summers.

Foraging location and diving pattern (TRACK birds)

To determine simultaneously the foraging location and the diving behavior of birds, radio transmitters and two types of data loggers were attached to the lower back of chick-rearing Adélie penguins with epoxy glue and cable ties. These birds are referred to as the TRACK birds.

In 1995/1996, KS-type data loggers (Little Leonardo, Tokyo) and transmitters were attached in early, mid-, and late January, and retrieved after 3 days of radio tracking (Watanuki et al. 1999). The KS-type logger is cylindrical, 19 (diameter)×70 mm, weighing 36 g in air (including battery), and has a flash memory of 0.5 Mbyte in which data were stored with 12-bit resolution, giving absolute and relative accuracies of 1 and 0.1 m. In 1996/1997, NIPR-type data loggers (Little Leonardo, Tokyo) and transmitters were attached to birds in late December 1996 and retrieved in late January 1997. The NIPR-type logger is cylindrical, 14 (diameter)×84 mm, 26 g in air (including battery), and has a flash memory of 0.5 Mbyte in which data were stored with 8-bit resolution, giving absolute and relative accuracies of 1 and 0.5 m. Birds were radio tracked on 26/27 December, 5–7, 15–17 and 26/27 January. In both years, cylindrical radio transmitters (12×50 mm, weighing 10 g in air, with a 20-cm aerial; ATS, USA) were used.

Directions of radio signals were monitored every 30 min from 0900 to 2100 hours by a seven-element two-stack Yagi antenna with FT-290 mkII receiver (Yaesu Musen, Tokyo) on a hill behind the colony (A: 25 m altitude in Fig. 1) and at Cape Koyubi (B: 40 m altitude). Birds' locations were determined by the triangulation method and the system could cover at least 5 km range. By allowing 5 degrees of direction resolution, space resolution was 100–200 m in general, but could be more than 500 m depending on the distance and direction. Signals were received only when the aerial of the transmitter was in the air, i.e., when birds were on the ice or swimming at the water surface, so that an interruption in the signal could be defined as the consequence of the birds' diving activity. Bird positions were sometimes determined by direct observation from land. Water depths at the foraging sites were obtained from the bathymetric charts of Moriwaki and Yoshida (2002).

Data loggers recorded depth at 2-s intervals in both years. After loggers were retrieved, data were downloaded onto a computer. Maximum dive depth and dive duration were calculated for each dive >1 m. Maximum dive depth and dive duration in dive sequences with position data were analyzed. We assumed that birds foraged at the same site when a dive sequence was continuous.

Prey type and diving patterns (PREY birds)

To examine the effect of prey type on diving behavior, stomach contents of Adélie penguins equipped with data loggers were collected after a single foraging trip. These birds were not radio tracked and are further referred to as PREY birds.

Breeding penguins were caught after leaving their nests and data loggers were attached to their lower back in December and January. Three types of data loggers were used; KS-type in 1995/1996, NIPR-type and UWE-type (Little Leonardo, Tokyo) in 1996/1997. The UWE-type logger is cylindrical, 20×102–107 mm, weighing 50–66 g in air (including battery), and has a flash memory of 1 Mbyte in which data are stored with 12-bit resolution, giving absolute and relative accuracies of 1 and 0.1 m. All loggers were set to record depth every second. When birds returned to the colony, they were recaptured before they could feed their chicks. Data loggers were retrieved and food samples were collected by stomach flushing (Wilson 1984). About 1 l of warm seawater was introduced into the stomach through a soft plastic tube. The stomach of each bird was flushed three to five times until the regurgitated water became clear. The samples were drained with a set of 1-mm and 4-mm mesh-size sieves and weighed. Prey items larger than 4 mm were sorted into two krill species (*Euphausia superba* and *E. crystallorophias*), fish and amphipods. Each item was weighed and the percentage mass composition was calculated.

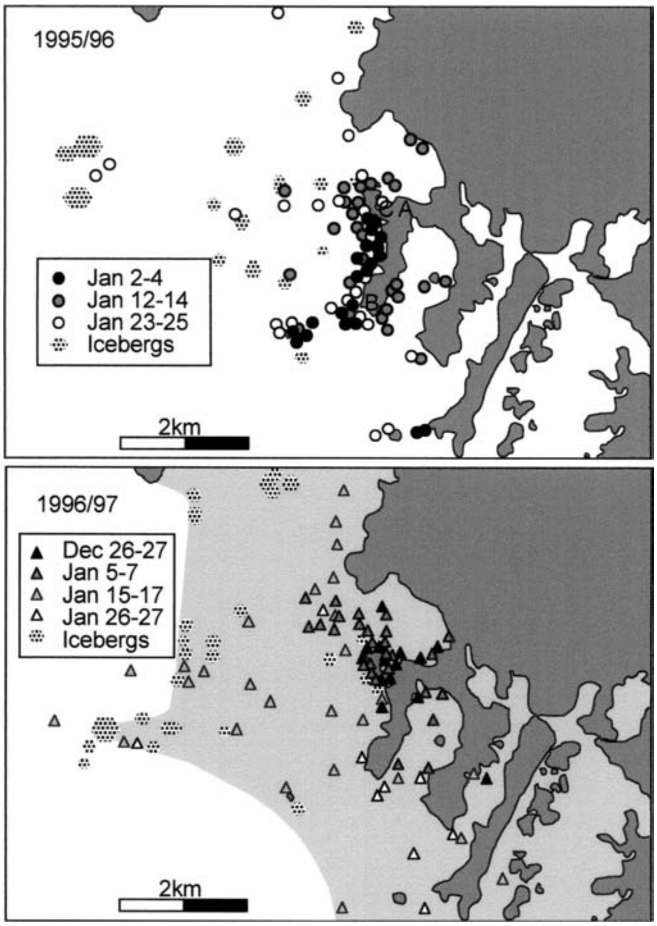

Fig. 1 Foraging sites determined by radio telemetry in 1995/1996 and 1996/1997. Each *dot* represents a single fix from a single bird. Sea was covered by sea ice and *grey area* indicates the area covered with thin sea ice in late December 1996. *A*, *B*: radio-tracking points, *C*: colony site

In order to measure the foraging-trip duration, nest attendance of TRACK and PREY birds was observed for 72 h in late December, early January and mid-late January in 1996/1997.

Seasonal and annual differences were tested by ANOVA and post-hoc test (Fisher's PLSD) and regressions were compared by ANCOVA using Statview 5.0 (SAS Institute, USA). Values are presented as mean ± SD. For all statistical tests, the threshold was 5%.

Results

Sea-ice condition

Lützow-Holm Bay was covered by fast sea ice in which some icebergs were trapped. The ice edge was about

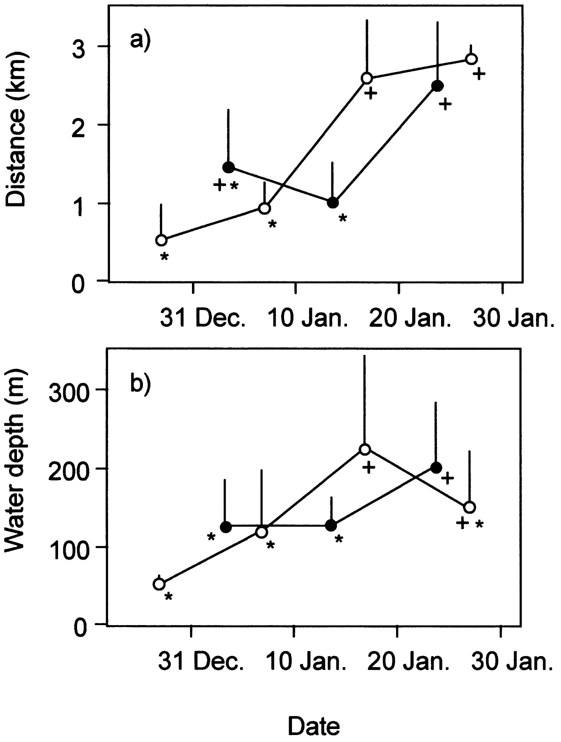

Fig. 2a, b Mean distance between colony and foraging sites (**a**) and mean water depth of the foraging sites (**b**) in 1995/1996 (*filled circles*) and 1996/1997 (*unfilled circles*). *Vertical bars* show 1 standard deviation. Values with same symbols are not significantly different (ANOVA and post-hoc test)

70 km away from the colony in mid–December in both years. About 1 m of thick, fast sea ice covered more than 95% of the birds' feeding area throughout the breeding season in 1995/1996. In 1996/1997, a 2- to 3-km-wide band of thinner ice ran along the coast in late December (Fig. 2 in Endo et al. 2002). The sea ice got thinner during the summer and finally broke up so that a 3-km-wide band of open sea appeared along the coast in February but fast sea ice still covered most of the bay.

Foraging site and dive depth (TRACK birds)

In 1995/1996, data loggers and radio transmitters were deployed on eight, eight, and seven birds rearing chicks from separate nests on 1, 11, and 22 January 1996, respectively. Data loggers were retrieved from all but one bird, which made a long trip (> 5 days) after 22 January and was not recaptured. In all sessions, no chick died during the 3-day radio tracking period.

In 1996/1997, data loggers and radio transmitters were simultaneously deployed on both mates of four pairs on 23 and 24 December 1996, and were retrieved between 20 and 31 January 1997 from six birds. Two pairs lost their whole brood in late January and one individual from each pair was not recaptured. One bird lost its transmitter on 13 January and one logger stopped several hours after being deployed.

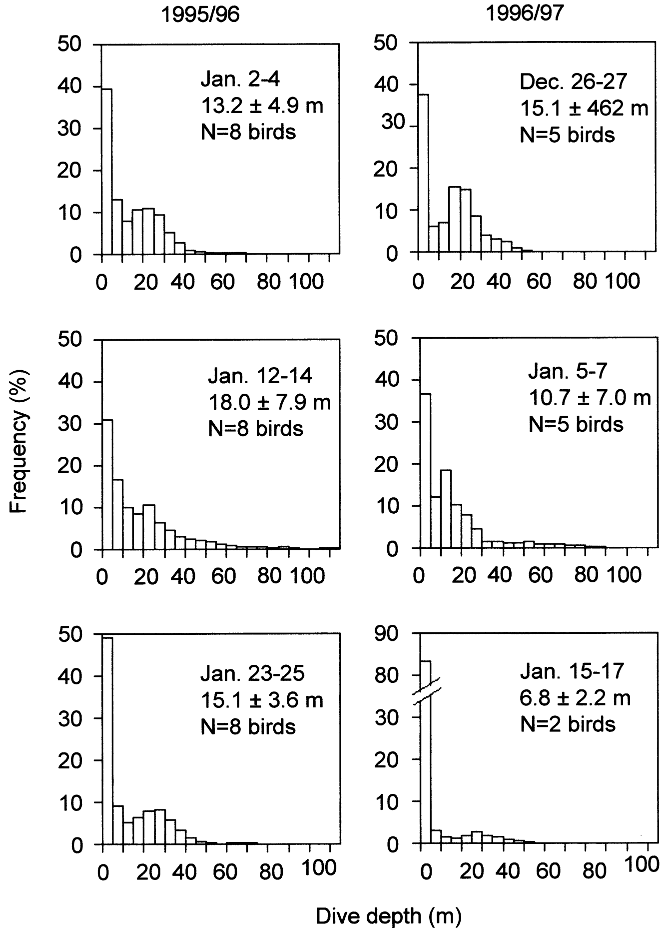

Fig. 3 Frequency distribution of maximum dive depth of TRACK birds. Values are mean ± SD

Foraging sites were determined at 87 and 79 points in 1995/1996 and 1996/1997, respectively. Adélie penguins foraged mostly in small areas of open water along the shore, and also around islets or icebergs (Fig. 1). They commuted between colony and foraging sites by walking on the ice. Foraging sites were concentrated in small areas in 1995/1996 and spread wider in 1996/1997. In both years, parents tended to visit foraging sites closer to the colony in late December and early January and then farther afield in late January (Fig. 2a, $F_{(6,38)} = 12.9$, $P < 0.01$). Foraging sites with deeper depths were visited in late January (Fig. 2b, $F_{(6,\ 38)} = 4.7$, $P < 0.01$). Mean dive depth did not show any significant difference between seasons and between years ($F_{(5,\ 28)} = 1.7$, $P = 0.17$), but the proportion of shallow dives < 5 m increased later in the season, especially in 1996/1997 (Fig. 3).

In 1996/1997, foraging sites of the same birds were monitored throughout the season. Each bird tended to keep similar traveling directions to reach their foraging sites (Fig. 4). For instance, 4M went northward; 3M and 3F went northwestward; 1M went southwestward, and 2F and 2M went southward. Although mates of pairs nos. 2 and 3 showed the same preferences in foraging

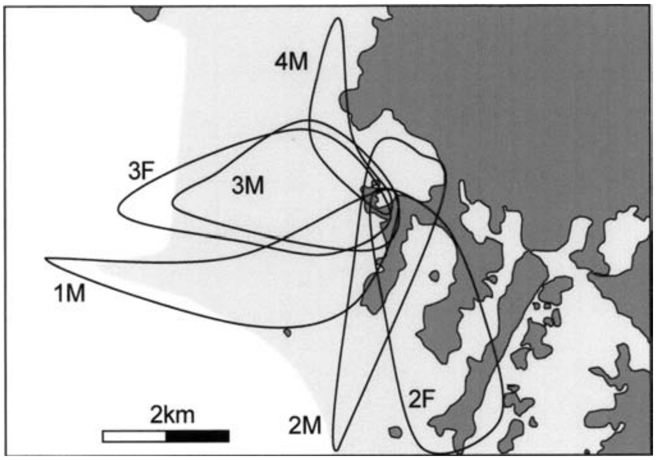

Fig. 4 Foraging ranges of individual Adélie penguins determined by radio telemetry in 1996/1997. The *lines* define maximum distances of the birds from the colony throughout the season

direction, they left the colony separately and foraged at different sites.

Prey and diving pattern (PREY birds)

Data loggers were deployed on 9, 20, 10, 10, 10, and 9 PREY birds on 27 December in 1995, 5, 15 January, 29 December in 1996, and 8 and 18 January in 1997, respectively. Nine, 20, 9, 10, 10, and 5 loggers were retrieved after 1 foraging trip and 9, 19, 7, 9, 9, and 3 of them recorded reliable data with stomach samples collected. Five stomach samples were collected from birds without logger deployment on 31 January in 1996.

Mean maximum dive depth was deeper, and mean dive duration was longer in 1995/1996 (26.7 ± 15.9 m, 96.5 ± 25.9 s) than in 1996/1997 (12.4 ± 7.3 m, 47.7 ± 17.1 s) (two-way ANOVA, depth; $F = 7.5$, $P < 0.01$, duration; $F = 31.8$, $P < 0.01$) but these parameters did not show any significant seasonal change within years (depth; $F = 0.6$, $P = 0.6$, duration; $F = 2.2$, $P = 0.1$).

Parents brought between 28 and 1,002 g of food to their chicks (Table 1). Food mass did not show any seasonal difference (ANOVA, $F_{(3,38)} = 0.9$, $P = 0.45$ in 1995/1995, $F_{(2,27)} = 1.2$, $P = 0.31$ in 1996/1997) or between years ($F_{(1,70)} = 1.9$, $P = 0.17$). Diet consisted mainly of two species of krill (*E. superba* and *E. crystallorophias*) and fish, both in 1995/1996 and 1996/1997. Fish were mostly juvenile and young *Pagothenia borchgrevinki*. In addition, some *Gymnodraco acuticeps*, *Trematomus bernacchii*, *T. newnesi*, *Acanthodraco dewitti*, *Dissostichus mawsoni*, and *Pleuragramma antarcticum* were found occasionally. The size of *Pagothenia borchgrevinki* was smaller in 1996/1997 than in 1995/1996 (T. Iwami, unpublished data). Small individuals of *E. superba* were more numerous, and mean length of *E. crystallorophias* was smaller in 1996/1997 than in 1995/1996 (Endo et al. 2002). In both years, *E. superba* and *Pagothenia borchgrevinki* were the main dietary items until mid-January. The proportion of fish decreased and *E. superba* became predominant in late January 1996. In 1997, the proportion of *E. superba* decreased and that of *E. crystallorophias* increased in late January. Amphipods were minor items in the diet but occurred more often in 1996/1997 than in 1995/1996.

Either krill or fish dominated in most of the stomach samples: 44% and 46% of samples contained more than 70% of krill (krill-eating trips) and fish (fish-eating trips) by mass, respectively (Fig. 5). Mean dive depth and duration of both krill-eating trips and fish-eating trips in 1995/1996 were greater than those in 1996/1997 (Table 2). Mean dive depth and duration of krill-eating trips were greater than those of fish-eating trips in 1995/1996, though there was no difference in diving pattern between krill- and fish-eating trips in 1996/1997 (Table 2). Mean dive depth and duration were linearly correlated for both krill-eating trips and fish-eating trips in each year (Fig. 6). In 1995/1996, the slope of linear

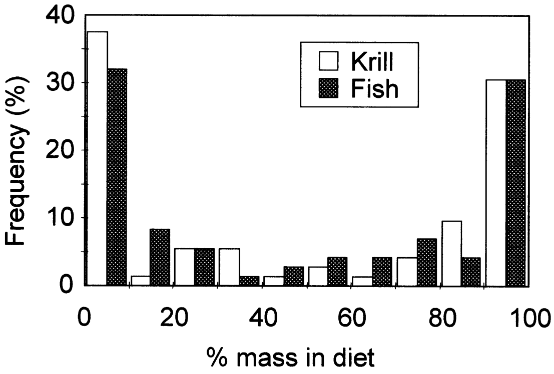

Fig. 5 Frequency distribution of percentage of krill and fish in diet ($N = 72$). Diet data of both years were combined

Table 1 Food mass and the percentage of each prey mass, *Euphausia superba*, *E. crystallorophias*, amphipods, and fish. Values are mean ± SD. Data in 1995/1996 were taken from Watanuki et al. (1999)

Period	*N*	Food mass (g)	% *E. superba*	% *E. crystallorophias*	% amphipods	% fish
1995/96						
29–30 Dec.	9	294.8 ± 157.8	36.2 ± 39.8	0.0	0.5 ± 0.9	63.3 ± 39.5
6–8 Jan.	20	364.5 ± 171.0	36.2 ± 35.9	16.0 ± 23.1	0.2 ± 0.5	47.7 ± 39.0
17–19 Jan.	8	385.9 ± 304.7	27.0 ± 34.5	14.6 ± 28.0	0.1 ± 0.1	58.4 ± 43.7
31 Jan.	5[a]	480.0 ± 100.3	71.0 ± 36.5	5.8 ± 4.0	0.1 ± 0.1	23.2 ± 38.0
1996/97						
31 Dec.–1 Jan.	9	320.4 ± 184.5	47.7 ± 44.6	1.0 ± 1.6	3.3 ± 9.4	49.3 ± 41.7
9–11 Jan.	9	224.1 ± 151.9	40.7 ± 42.4	11.7 ± 27.7	11.1 ± 32.2	36.6 ± 41.3
20–24 Jan.	12	346.5 ± 201.7	17.5 ± 22.6	24.3 ± 36.8	2.3 ± 6.2	55.9 ± 37.9

[a] Food sample was collected from birds without data logger

Table 2 Mean maximum dive depth and duration of krill-eating trips and fish-eating trips of Adélie penguins. Values are mean ± SD with sample size in *parentheses*. Results of ANOVA are shown as *F* and *P* values

	Krill		Fish		*F*, *P*	
	Depth (m)	Duration (s)	Depth (m)	Duration (s)	Depth (m)	Duration (s)
1995/1996	39.1 ± 15.9 (14)	106.8 ± 30.1 (14)	16.5 ± 4.6 (17)	88.1 ± 18.8 (17)	31.5, < 0.01	4.5, 0.04
1996/1997	14.4 ± 7.2 (9)	52.2 ± 14.1 (9)	10.0 ± 7.1 (8)	42.6 ± 19.7 (8)	1.6, 0.22	1.4, 0.26
F, *P*	18.9, < 0.01	25.7, < 0.01	7.7, 0.01	31.0, < 0.01		

regression did not differ but the intercepts were larger for fish-eating trips than krill-eating trips, and fish-eating trips were submerged longer at any depth (ANCOVA, $F_{(1,28)} = 9.5$, $P < 0.01$). In 1996/1997, there was no difference in slope and intercept between krill- and fish-eating trips. Relationships between mean dive depth and duration did not differ according to the species composition of krill in the diet.

Trip duration

The trip duration of TRACK birds and PREY birds in late December, early and mid/late January in 1996/1997 was examined by two-way ANOVA (Table 3). Trip duration was not different between groups ($F_{(1,\ 31)} = 0.05$, $P = 0.8$) and among time intervals ($F_{(2,\ 31)} = 1.5$, $P = 0.2$).

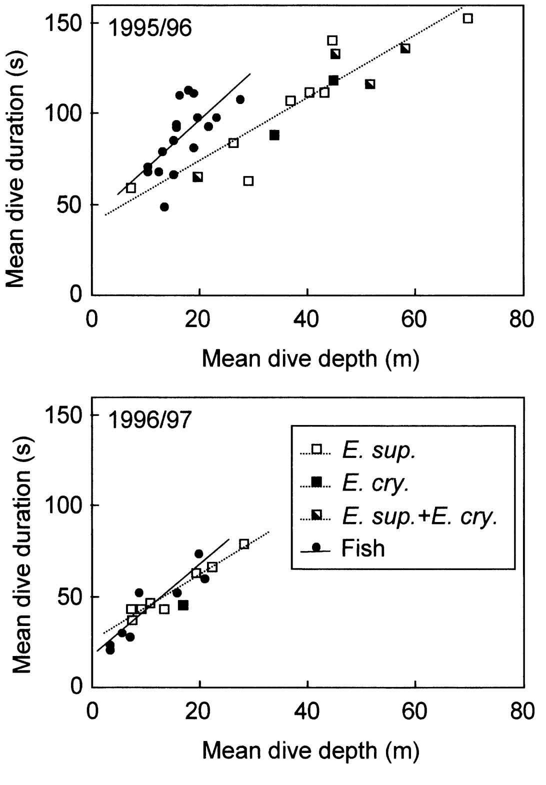

Fig. 6 Relationships between mean maximum dive depth (Dp) and mean dive duration (Dr) of krill-eating trips (*square*) and fish-eating trips (*circle*) in 1995/1996 (krill: Dr = 1.72xDp + 39.27, $r^2 = 0.83$, $P < 0.01$, fish: Dr = 2.73xDp + 42.98, $r^2 = 0.44$, $P < 0.01$) and 1996/1997 (krill: Dr = 1.82xDp + 25.85, $r^2 = 0.88$, $P < 0.01$, fish: Dr = 2.54xDp + 17.19, $r^2 = 0.84$, $P < 0.01$). *Euphausia superba* dominated (*unfilled squares*); *E. crystallorophias* dominated (*filled squares*) and mixed (*half-filled squares*) samples were found in krill-eating trips

Discussion

Effect of devices

All externally attached loggers potentially have an impact on swimming ability, reducing speed (Wilson et al. 1986) and generally increasing energy expenditure (Bannasch et al. 1994). However, these effects can be minimized by attaching small, streamlined instruments to the lower back of birds (Bannasch et al. 1994). The instruments used in this study represented < 1.0% of the Adélie penguins cross-sectional area (ca. 314 cm^2; Wilson et al. 1989), were streamlined and attached to the lower back of the bird. The meal mass, chick growth, and chick survival did not differ between parents with and without instruments in Adélie penguins breeding at Syowa and Davis (Watanuki et al. 1992, 1997). Ballard et al. (2001) reported that instrumentation (16–25 g) had no significant effect on foraging-trip duration of Adélie penguins and that no effect was evident in nesting success even for birds equipped with instruments for > 20 days. Although some birds in this study had both radio transmitter and data logger attached together, trip duration did not differ between birds with logger only and with logger and transmitter (Table 3). Therefore, foraging behavior of Adélie penguins in this study can be reliably compared between seasons and among individuals.

Comparison between seasons and years

Since the ice edge was far from the breeding colony, most penguins foraged in small areas of open water

Table 3 Trip duration of the PREY and TRACK birds in 1996/1997. Values are mean ± SD with sample size in *parentheses*

	Trip duration (h)		
	Late Dec.	Early Jan.	Mid-/late Jan.
TRACK	15.7 ± 4.1 (6)	28.3 ± 21.8 (5)	21.0 ± 11.4 (5)
PREY	18.1 ± 5.3 (9)	14.1 ± 6.4 (9)	36.3 ± 44.3 (3)

along the shore or around icebergs and islets within 5 km of the colony (see also Watanuki et al. 1993, 1999). In December, available areas of small open water were restricted along the shore. As sea ice melted later in the season, more open-water sites became available over a larger area. Hence, birds were able to forage farther afield later in the season, which might reduce the intraspecific competition for food. It is also possible that inshore prey stocks became depleted, forcing birds to forage farther away (Watanuki et al. 1999). Furthermore, food demand from growing chicks and for molting adults increased later in the breeding season (Williams and Rothery 1990). In order to comply with increased energy demand, birds would increase their foraging effort. Richer, more profitable, food sources might exist far from the colony and, as the chicks got older, may have been able to withstand longer trips while their parents foraged in more distant but more productive areas.

Foraging sites spread over a wider range in 1996/1997 than in 1995/1996. Because sea ice was thinner along the coast from the beginning of the season in 1996/1997, more small open-water sites existed and more foraging sites were thus available. Foraging sites were more restricted by the sea-ice distribution in 1995/1996 than in 1996/1997. However, mean travel distance to foraging sites and food mass did not differ between years. Trip duration, meal delivery rate, and chick growth were also similar in these 2 years (Watanuki et al. 2002). This suggests that under variable environmental conditions, parents modified their behavior to maintain chick growth.

E. superba is known to be an important prey of Adélie penguins in this region (Watanuki et al. 1994). In this study, fish (*Pagothenia borchgrevinki*) also appeared as a main dietary item. Dive depth of seabirds is known to be influenced by prey distribution (Barrett and Furness 1990). Penguins might have explored zones just below the sea ice where young *Pagothenia borchgrevinki* are distributed (Andriashev 1970), with shallow dives <5 m (Fig. 3). Ropert-Coudert et al. (2002) reported only slight differences in the diving patterns of Adélie penguins feeding on krill and fish in open waters. However, dive depth was different between krill- and fish-eating trips in 1995/1996 but not in 1996/1997 in our study (Table 2), though penguins ate the same species of krill and fish in both years. The size of *E. superba* eaten by penguins was smaller in 1996/1997 than 1995/1996 (Endo et al. 2002), and penguins that dove deeper are known to have eaten larger *E. superba* in 1995/1996 (Endo et al. 2000). Hence, deep-diving krill-eating trips in 1995/1996 suggest that a substantial number of large krill were distributed in deeper water, while a smaller number of small krill were distributed in shallow waters in 1995/1996 than in 1996/1997. Depth distribution of fish also seemed to be different between years and this possibly relates to size difference in fish. These depth differences in prey distribution affected foraging depth in Adélie penguins. Takahashi (2000) also reported that Adélie penguins dove deeper in 1995/1996 than in 1996/1997 at the same colony using a different data set. Dive-depth difference between years was found in PREY birds but not in TRACK birds. This was due to the shallow dive depth of TRACK birds in 1995/1996. The dive depth of fish-feeding trips was shallower than that of krill-eating trips in this year. There might have been a bias towards the fish-eating TRACK birds, though we could not confirm it because of the lack of diet samples from these birds. The difference in the tracking method between years, i.e., different individuals used for each stage in 1995/1996 and the same individuals used throughout 1996/1997, may also account for these discrepancies.

Adélie penguins are opportunistic feeders, seeking various type of prey using various diving patterns that change according to environmental conditions, such as sea-ice distribution and prey availability. Such plasticity in their behavior enabled them to breed in extreme environments such as fast sea-ice areas.

Individual foraging behavior

Foraging-site fidelity has been noted in some seabird species (Weimerskirch et al. 1993; Irons 1998; Kato et al. 1998; Grémillet et al. 1999; Mehlum et al. 2001). For such a foraging strategy to be successful, prey must have some degree of spatial and temporal predictability (Irons 1998). Foraging sites of Adélie penguins are small areas of open water in fast sea ice and are highly predictable. Consequently, individuals in our study showed a certain degree of fidelity in the direction of foraging trips. Since the birds are required to walk to their foraging sites, their range of exploration appears limited. Birds could only extend their foraging range by walking to new foraging sites farther from the known sites as more open water appeared later in the season.

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