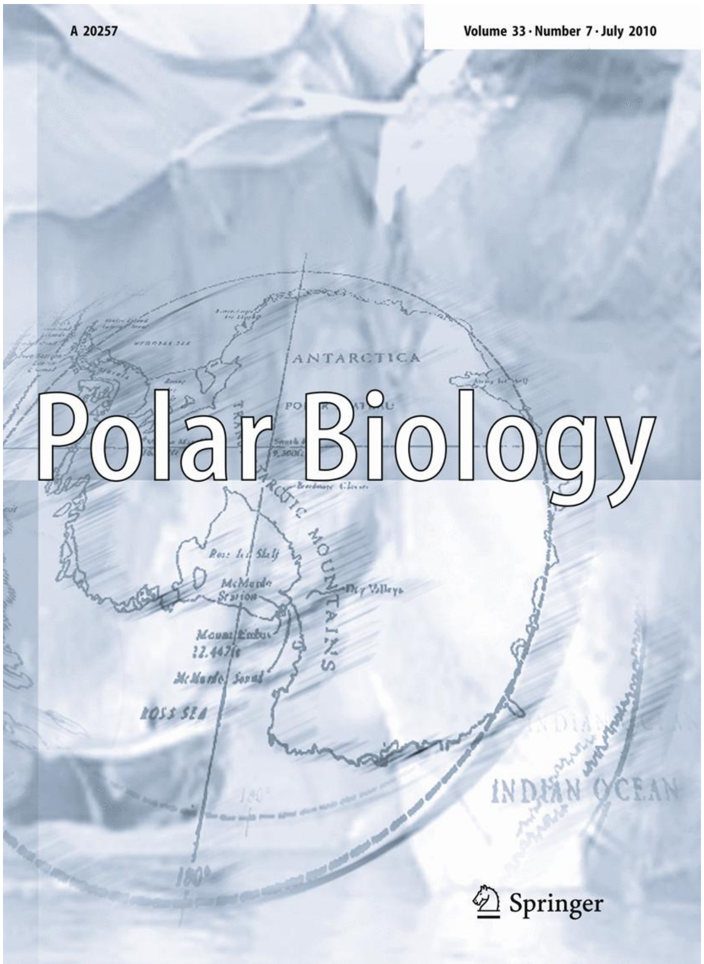
ISSN 0722-4060, Volume 33, Number 7



Polar Biol (2010) 33:969–978
DOI 10.1007/s00300-010-0775-2

ORIGINAL PAPER

Diving behaviour of chick-rearing Adélie Penguins at Edmonson Point, Ross Sea

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Received: 13 August 2009 / Revised: 22 January 2010 / Accepted: 31 January 2010 / Published online: 5 March 2010

Abstract The diving behaviour of chick-rearing Adélie penguins of Edmonson Point, Ross Sea, was analysed over two summer seasons (1994–1995 and 1995–1996). In 1994–1995, the study area was characterized by fast-ice persistency throughout season and by higher pack ice concentration than the following year, when fast-ice retreated earlier. Both females' and males' behaviour were examined, and we then compared diving characteristic between years and between guard and crèche stages of chick rearing. We found that changes in fast-ice extent influenced the transit times between colony and foraging grounds and that females conducted longer foraging trips, dived for longer periods and made more dives than males. The diving parameters were affected neither by the sex nor by the year, but differed between the breeding stages. Parents guarding chicks had longer dive and bottom phase durations than in crèche (dive duration: guard = 48 s, crèche = 42 s; bottom duration: guard = 34 s, crèche = 26 s), whilst they had shorter recovery times (e.g. post dive duration) (guard = 29 s, crèche = 32 s). Possible causes for the observed differences in diving behaviours are discussed.

Keywords Diving behaviour · Adélie penguin · Breeding stages · Sea-ice · Edmonson Point

Introduction

Sea-ice conditions in the Antarctic change annually, seasonally and locally (Lubin and Massom 2006). These changes have considerable influences on the flow of energy throughout the food chains, and changes occurring at lower levels are integrated at the upper levels. In this regard, a close examination of the foraging and breeding activities of top predators can reveal modifications in resource availability (Verity et al. 2002). In Antarctica, the Adélie penguin, *Pygoscelis adeliae*, appears as a model of top predator to study changes in resource availability as its biology is closely connected to sea-ice, spending 90% of their time at sea foraging within pack ice regions (Ainley 2002). Sea-ice condition has indeed been reported as one of the most important factors that may affect population trends of Adélie penguin (Emmerson and Southwell 2008; Jenouvrier et al. 2006). Adélie penguins mostly feed on krill, *Euphausia superba* and *E. crystallorophias,* and fish (Ainley 2002); Adélie penguins are known to adjust their diving behaviour to both environmental parameters and prey availability and distribution (Wilson 2003) in order to maximize the rate of energy gain, especially over their breeding cycle (e.g. Mori and Boyd 2004). The Adélie penguin's breeding cycle is a synchronous and coordinated event constrained by the shortness of the Antarctic summer (Trivelpiece et al. 1983). This is especially true over the chick-rearing period when adults have to supply both themselves and their chicks with sufficient food (Ainley 2002). Chick provisioning varies through the breeding season according to the increasing energetic requirements of the chick, as well as with prey availability (Williams and

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Rothery 1990). During the guard phase, parents return regularly to their nests to feed their chicks and swap over with their partners every 1–5 days until chicks move into the crèche phase. Heavier chicks in crèche are likely to modulate the foraging effort of parents. One adjustment is the simultaneous foraging of both parents during the crèche stage. However, it is also conceivable that each parent changes its own foraging and diving behaviour to respond to the increased demand of chicks in crèche. In addition, the modulation of the foraging behaviour of parents between the guard and the crèche stages may only be possible if environmental conditions allow penguins to change their behaviour (e.g. sufficient food availability in crèche).

In this study we examined, by the use of animal-borne data loggers (cf. Ropert-Coudert and Wilson 2005), the foraging behaviour of Adélie penguins over the chick-provisioning period. Study was conducted over 2 years of contrasting environmental conditions on birds from Edmonson Point, mid Victoria Land, where breeding population size was estimated around 2,000 pairs (Olmastroni et al. 2000). In this area, as well as in few others (cf. Ainley 2002; Kato et al. 2009), fast-ice often separates the colony from the open water throughout chick rearing (Olmastroni et al. 2004). As a consequence, penguins of this colony have to walk over variable extent of fast-ice to reach their feeding areas. At Edmonson Point, studies on the ecology of breeding Adélie penguins started in the austral summer 1994–1995, in the framework of the Italian-Australian Monitoring Program (Clarke et al. 1998; Olmastroni et al. 2000). Indeed, Clarke et al. (1998) investigated variation in diet components and foraging trip duration between sex, years and breeding stages, and variation in some breeding parameters, such as breeding success, was also described in Pezzo et al. (2007).

However, while diving activity during guard stage (e.g. Chappell et al. 1993a; Clarke 2001; Kato et al. 2003; Rodary et al. 2000; Yoda and Ropert-Coudert 2007) – and to a lesser extent incubation (see Kato et al. 2009) – has been well documented, few studies have provided detailed information on the diving activity at the crèche stage (Clarke et al. 1998; Wienecke et al. 2000; Wilson et al. 1991a). Thus, comparisons between guard and crèche stages are rare and they have not been yet reported for the Ross Sea. Our study will add further understanding on the foraging behaviour of the species in an area (Wood Bay) where sea-ice conditions represent unusual, though not unique, conditions.

Materials and methods

Fieldwork was conducted at Edmonson Point (74°21′S–165°10′E), a colony located in the Wood Bay, mid Victoria Land, Antarctica, from December 1994 to January 1995 and from December 1995 to January 1996 (Fig. 1).

Environmental condition at the study colony

Fast-ice extent was measured with a GIS (ArcView 3.2) as the straight line due east from the colony to the edge of fast-ice as it appeared in the cloud free available satellite picture chosen for the breeding stages. The distance between the breeding colony and the fast-ice edge was calculated on the 11th December 1994 and 8th January 1995, and on the 12th December 1995 and 23rd January 1996 for the guard and crèche stages, respectively. Satellite pictures were provided by the Italian National Antarctic Programme. The satellite image for January 1995 was obtained from Australian Antarctic Division.

Concentration of pack ice, for 1994–1995 and 1995–1996, was obtained from the NSIDC archives (http://nsidc.org). Using the GIS, we extrapolated concentration values limited to penguins' predominant foraging

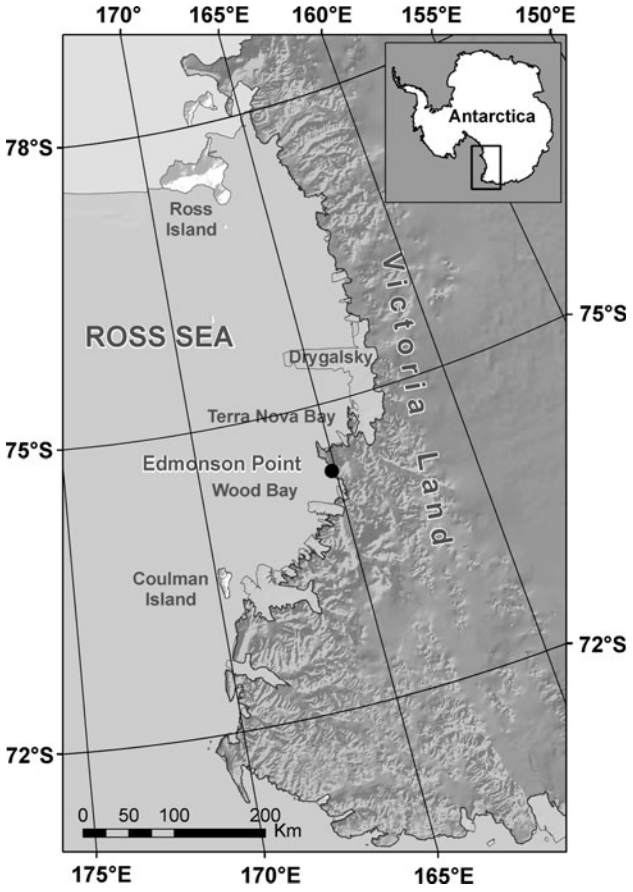

Fig. 1 Victoria Land, Western Ross Sea, Antarctica. The study area is indicated by *filled circles*

areas. These latter were inferred according to Olmastroni et al. (2000). Pack ice concentration was averaged according to guard and crèche phases for each study year, and it was expressed as percentage of sea-ice cover.

Monitoring of penguins

Penguins were previously marked by implanted passive transponders tags (Texas Instruments Remote Identification System, TIRIS, Olmastroni et al. 2000) and were automatically identified at the entrance point of the colony by an Automated Penguin Monitoring System (APMS, Kerry et al. 1993). Marked penguins entering and leaving the colony were detected *via* the APMS, and visual observations at nest with a hand-held tag reader were also conducted. Sex was determined by cloacal examination at the time of transponder implantation (Sladen 1978).

In total, 18 chick-rearing adult birds (9 individuals per year) were equipped with time-depth recorders (TDRs) before they departed to sea. Wildlife Computers MK5 (Redmond, USA), which weighed 50 g, measured 6.5 × 3.5 × 1.5 cm with a 512 Kb memory and recorded depth every 2 s with a resolution ±1 m were used. Only one member of a pair was instrumented. TDRs were glued (Loctite 401$^{\mathrm{TM}}$) to the lower back feathers to minimize the drag effect (Bannasch et al. 1994). Birds carried out 3–5 foraging trips before the devices were recovered upon the return of the penguins to their nest. Dive data were then downloaded into a laptop. Two TDRs did not record data, thus diving information were retrieved from 16 loggers (8 individuals per year: 4 during guard and 4 during crèche, Table 1). Guard periods were 20th December–5th January 1994–1995 and 22nd December–5th January 1995–1996. The studied crèche periods corresponded to 6–17 January 1995 and to 6–15 January 1996.

Effects of devices

Externally attached loggers are known to impact swimming and diving performances in diving seabirds, reducing speed and thus increasing energy expenditure (Ropert-Coudert et al. 2000, 2007; Wilson et al. 1986). The instruments used in this study were about 2.5–3.3% of the Adélie penguins cross-sectional area (CSA, ca. 525 cm^2), and they were attached to the lower back of the birds to minimize the drag (Bannasch et al. 1994). Although devices have been reported to have heavier effects in terms of chick growth and nest desertation if fitted later in the chick-rearing period (Watanuki et al. 1992), in this study, we assumed that the potential deleterious device effects were equivalent whatever the year or the breeding stage, therefore comparisons were meaningful.

Foraging trips & dive analyses

By using information gathered by APMS and visual nest monitoring, we defined foraging trip duration as the time elapsed between the departure from the colony and the return to it. Transit time between departure from the colony and the first dive (T_1 or outbound) and between the last dive and arrival at the colony (T_2 or inbound) was assumed to be travelling times to/from foraging area. Diving period was determined as the time between the first dive and last dive. Dives were analysed using IGOR software version 5.0 (WaveMetrics Inc., Lake Oswego, OR, USA). A custom-written macro calculated automatically the following parameters for each dive >2 m: maximum dive depth, dive duration (DD), post dive duration (PDD) and bottom phase duration (BD). Bottom phase started at the first time the descent rate became negative and ended at the last time the ascent rate became positive. Dive depths and durations were grouped in categories of 5 m increment and 10 s increment, respectively.

Statistical analysis

Normality of distributions of dive parameters is tested by Kolmogorov–Smirnov test and those which are not normally distributed are log transformed. To avoid pseudo-replication, dive parameters were analysed using General Linear Mixed Models (GLMM) with individual included as a random factor, whilst sex, breeding stage, year and the interaction "stage*year" as fixed factors. Since dive, bottom phase and post dive durations depend on the maximum depth reached (all $P < 0.001$), we included maximum depth as a covariate in the GLMM tests for these parameters. Normality of residuals was assessed by Kolmogorov–Smirnov test. When residuals were not normal, we used Generalized Linear Models (GzLM) with normal, gamma or Poisson in case of normal, non normal or count data, respectively. Pairwise comparisons were performed using the post hoc Bonferroni test. Statistical analyses were performed using JMP (SAS Institute Inc., USA, version 5.1.1 J) and SPSS (version 17.0 for Windows, SPSS, Chicago, IL, USA). All results are given as mean ± SE. The level of significance was set at $\alpha = 0.05$, unless stated otherwise.

Results

Sea-ice condition

Sea-ice condition differed between the 2 years. In 1994–1995, the fast-ice edge was 34 and 13 km from the colony during chick guard and crèche stages, respectively. In 1995–1996, it was 11 km and not present in the respective

Table 1 Year, penguin ID, sex, breeding stage, departure weight, total number of trips per individual, mean trip duration, number of dives and hourly number of dives for 16 chick-rearing Adélie penguins of Edmonson Point colony

Year	Bird ID	Sex	Breeding stage	Date of TDR deployment	Departure weight (kg)	# of trips	Trip duration (h)	# dives	# dives/h
1994–1995	95_A	M	GUARD	21/12/1994	4.1	1	52.5	772	23.0
1994–1995	95_C	M	GUARD	20/12/1994	4.4	3	36.2	517	26
1994–1995	95_E	F	GUARD	21/12/1994	3.6	3	51.1	835	21
1994–1995	95_H	F	GUARD	21/12/1994	4.5	3	42.2	603	23
1994–1995	95_D	F	CRECHE	09/01/1995	3.9	3	62.0	1,147	23
1994–1995	95_F	M	CRECHE	09/01/1995	3.7	4	23.8	245	15
1994–1995	95_G	M	CRECHE	06/01/1995	4.4	3	16.7	171	16
1994–1995	95_I	F	CRECHE	09/01/1995	4.3	1	202.0	2,004	10
1995–1996	96_A	M	GUARD	22/12/1995	4.4	3	29.2	560	26
1995–1996	96_C	M	GUARD	22/12/1995	3.2	1	30.7	302	15
1995–1996	96_E	F	GUARD	25/12/1995	4.0	2	35.2	472	18
1995–1996	96_G	M	GUARD	27/12/1995	4.5	2	18.7	292	29
1995–1996	96_B	M	CRECHE	12/01/1996	4.1	1	54.1	836	17
1995–1996	96_D	F	CRECHE	12/01/1996	4.2	1	71.6	381	6
1995–1996	96_F	F	CRECHE	11/01/1996	3.8	2	29.1	532	22
1995–1996	96_H	M	CRECHE	11/01/1996	4.3	2	44.4	266	8

periods. Pack ice offshore from the fast-ice was also denser in the earlier summer. Accordingly, mean sea-ice concentration was greater in 1994 than in 1995 (Mean ± SE: $78.33 \pm 1.15\%$ and 57.86 ± 1.18, respectively; $F_{1,58} = 168.58$, $P < 0.001$) and in guard than in crèche (Mean ± SE: $77.24 \pm 1.07\%$ and $58.94 \pm 1.18\%$, respectively; ANOVA, stage: $F_{1,58} = 129.14$, $P < 0.001$). The interaction stage*year was significant ($F_{1,58} = 4.01$, $df = 1$, $P = 0.05$).

Body mass

The penguins' initial body mass (range = 3.2–4.5 kg, Table 1) did not vary significantly between stages (ANOVA $F_{1,12} = 0.001$, $P = 0.97$) or years (ANOVA $F_{1,12} = 0.05$, $P = 0.83$; stage*year: $F_{1,12} = 0.16$, $P = 0.69$). So that, we assumed that our results were not influenced by the effect of the bird body mass. Body mass did not either vary between sexes (ANOVA $F_{1,10} = 0.11$, $P = 0.74$; sex*stage: $F_{2,10} = 0.003$, $P = 0.99$; sex*year: $F_{2,10} = 0.04$, $P = 0.96$).

Foraging and diving performances

Overall, the 16 birds carried out 35 foraging trips, 18 during the guard and 17 during the crèche stage. Foraging trips ranged between 13.5 and 202.0 h (Table 1). Two exceptionally long trips of 131 and 202 h were performed by two females in the crèche phase of 1994–1995. A total of 19,898 dives were analysed, 10,148 and 9,750 in guard and crèche stages, respectively.

Females performed longer foraging trips and had longer diving periods than males (Table 2). Foraging trip duration did not change significantly neither between stages nor between years (Table 2). Transit time to the foraging areas (T1) was significantly longer during the guard than that in the crèche stage and it also differed between years. The interaction "stage*year" also affected T1, and the post hoc tests indicated that in 1994–95 $\mathrm{T1}_{\mathrm{guard}} > \mathrm{T1}_{\mathrm{crèche}}$ ($P < 0.001$) and in 1994–1995 $\mathrm{T1}_{\mathrm{guard/crèche}} > \mathrm{T1}_{\mathrm{guard/crèche}}$ than in 1995–1996 ($P < 0.001$). Similarly to T1, T2 significantly varied between the breeding stages but it was not different between years. During a foraging trip, the number of dives did not differ between breeding stages or between years but females made significantly more dives than males (Table 2).

If the two exceptionally long trips were removed from the analyses, foraging trip duration was still significantly different between sex ($\chi^2 = 3.85$, $df = 1$, $P = 0.05$), and so did the interaction "stage*year" ($\chi^2 = 25.87$, $df = 1$, $P < 0.001$). Differences in diving period between sexes disappeared but the interaction "stage*year" became significant ($\chi^2 = 15.81$, $df = 1$, $P < 0.001$): in 1994–1995, guard > crèche ($P = 0.03$) and $\mathrm{crèche}_{1994–1995} < \mathrm{crèche}_{1995–1996}$ ($P = 0.01$). T1 was still different between years ($\chi^2 = 18.19$, $df = 1$, $P < 0.001$), stages ($\chi^2 = 41.93$, $df = 1$, $P < 0.001$; "year*stage" $\chi^2 = 7.77$, $df = 1$, $P = 0.005$). Post hoc test indicated similar trends if those long trips were included. T2 showed no more significant differences between breeding stages ($\chi^2 = 3.53$, $df = 1$, $P = 0.14$). Total number of dives per trips became significantly greater during guard than during crèche (Wald

Table 2 Partitioning of foraging of Adélie penguins

	Sex										Year					Interaction "stage × year"				
		Mean	±SE	Wald χ^2	*P*		Mean	±SE	Wald χ^2	*P*		Mean	±SE	Wald χ^2	*P*		Mean	±SE	Wald χ^2	*P*
Foraging Trip Duration (h)	♂	30.2	3.6	**5.31**	**0.02**	Guard	36.2	2.2	1.05	0.31	1994–1995	46.1	9.6	0.8	0.4	Guard 1994–1995	44.1	3.3	0.40	0.53
																Crèche 1994–1995	48.2	19.0		
	♀	57.6	11.3			Crèche	46.8	10.1			1995–1996	36.8	3.9			Guard 1995–1996	28.2	3.00		
																Crèche 1995–1996	45.5	7.1		
Diving period(h)	♂	20.6	5.2	**4.44**	**0.03**	Guard	26.0	4.9	2.73	0.09	1994–1995	36.3	8.0	0.1	0.74	Guard 1994–1995	26.0	4.9	0.12	0.73
																Crèche 1994–1995	46.6	16.1		
	♀	48.8	11.2			Crèche	43.0	10.0			1995–1996	33.0	6.9			Guard 1995–1996	26.7	6.6		
																Crèche 1995–1996	39.4	11.6		
T1 (h)	♂	4.7	0.4	0.05	0.82	Guard	7.3	0.6	**50.33**	**<0.001**	1994–1995	6.0	0.6	**17.96**	**<0.001**	Guard 1994–1995	10.1	1.2	**11.48**	**<0.001**
																Crèche 1994–1995	2.5	0.3		
	♀	4.8	0.5			Crèche	2.2	0.3			1995–1996	3.2	0.4			Guard 1995–1996	4.6	0.6		
																Crèche 1995–1996	1.9	0.6		
T2 (h)	♂	3.8	0.3	1.162	0.28	Guard	4.7	0.2	**4.69**	**0.03**	1994–1995	4.04	0.3	0.54	0.82	Guard 1994–1995	5.0	0.4	2.44	0.12
																Crèche 1994–1995	3.1	0.4		
	♀	4.4	0.5			Crèche	3.5	0.5			1995–1996	4.18	0.5			Guard 1995–1996	4.47	0.3		
																Crèche 1995–1996	4.0	0.98		
Total number of dives per trip	♂	384.1	62	**6.50**	**0.01**	Guard	624.0	73.4	0.35	0.55	1994–1995	619.96	87.48	0.29	0.59	Guard 1994–1995	665.3	79.6	0.04	0.84
																Crèche 1994–1995	574.7	117.6		
	♀	798.6	140.8			Crèche	558.7	105.5			1995–1996	562.75	91.73			Guard 1995–1996	582.7	114.5		
																Crèche 1995–1996	542.7	134.1		

Values are grand mean ± SE

Results of GzLM are given as Wald χ^2 and *P*. Degree of freedom (*df*) was always 1. Significant differences in bold. *T1* = transit time between departure from the colony and the first dive, *T2* = transit time between the last dive and arrival at the colony

$\chi^2 = 5.23$, $df = 1$, $P = 0.02$), but no differences were found between females and males anymore.

Diving pattern

Mean maximum depth did not vary between sexes, years and stages (Table 3). Around 80–90% of all dives were in the first 25 m with depth distribution being similarly skewed to the right in both stages (Fig. 2). The deepest dive occurred during the crèche stage of 1994–1995 at 82 m.

Mean dive duration was slightly but significantly longer in guard than that in crèche (Table 3). Bottom phase durations were significantly longer during guard than during crèche (Fig. 3). On the contrary, PDD was significantly longer in crèche than in guard and was positively related to dive duration in both breeding stages (guard, $\rho = 0.33$, $P < 0.001$; crèche, $\rho = 0.40$, $P < 0.001$, see Fig. 4).

The diving parameters were neither affected by the sex, the year nor by the interaction “stage*year” (Table 3).

Discussion

While the diving behaviour of Adélie penguins during the guard stage has been thoroughly documented, data are scarce or not well described on crèche-stage diving activities of this species, therefore comparisons between guard and crèche stage are rare. The present study also adds further knowledge to the temporal variation in foraging activity of Adélie penguins as sea-ice conditions vary over the breeding season (see Yoda and Ropert-Coudert 2007). This is especially true since we had the opportunity to compare diving activity during years of contrasting sea-ice conditions. In the Wood Bay, as well as in few other areas (Ainley 2002; Kato et al. 2009), fast-ice often separates the colony from the open water throughout chick rearing, forcing the penguins to walk over variable extent of fast-ice to reach their feeding grounds (Olmastroni et al. 2004). Similarly, in areas where fast-ice remains throughout the breeding season, penguins tend to cross the unprofitable zone covered by sea-ice to reach profitable feeding grounds, including small open areas/pools, polynyas, tidal cracks or open sea (Kato et al. 2003; Watanuki et al. 1993, 2002). As a matter of fact, Edmonson Point was characterized by variations in fast-ice and sea-ice conditions throughout the chick-rearing period in both study years. Considering that Adélie penguins walk on fast-ice at ca. 1.9 km h^{-1} (Watanuki et al. 1999) or 2.7 km h^{-1} if tobogganing (Wilson et al. 1991b), penguins in our study would have taken around 0–18 h (or 0–12.6 if continuously tobogganing) to reach open water 0–34 km away from the colony. These values tie nicely with our measurements that Adélie penguins started diving 0.35–17 h after they left the colony. During guard stage, outbound and inbound times were longer than in crèche stage, possibly due to the fast-ice extent decrease as the season progresses. Differences between transit times (Table 2) could be the result of different strategies. We can suppose that adults leaving the colony may linger at the ice edge as a probable consequence of predator avoidance (Muller-Schwarze 1984), while inbound time may be reduced to cope with time-constraints of chick-provisioning requirements, travelling faster and/or following straighter routes inward to the colony.

Variations of the sea-ice conditions generally affect foraging behaviour in seabirds (i.e. affecting prey availability, see Quetin and Ross 2001), thus their reproductive performances (Clarke et al. 2006; Emmerson and Southwell 2008; Nicol et al. 2008). Foraging trip duration and dive duration, as well as diving depth, have been described as particularly sensitive foraging parameters to environmental fluctuations, in different Antarctic sites where different sea-ice conditions occurred (Kato et al. 2003; Rodary et al. 2000; Watanuki et al. 2002). For instance, Ainley et al. (1998) investigated the foraging effort and the diet in three different Adélies’colonies on Ross Island, finding diverse foraging trip durations (and slight differences in diet) by colonies, seasons and year, according to the proximity of the pack ice to nesting colonies. In years of early sea-ice retreat, penguins performed shorter foraging trips and had longer bottom phase duration than in years with standard timing of sea-ice retreat (Beaulieu et al. 2009).

In Lützow-Holm Bay, foraging trip duration, dive duration and dive depth were higher in those years characterized by persistent and long fast-ice extent (Watanuki et al. 1993). Likewise, Wood Bay was characterized by fast-ice extent variation, but the penguins diving behaviour was not apparently affected as suggested by the similarity in the dive durations and depths across the 2 years. The differences between the two colonies may be due to several factors: (a) fast-ice area in front of Edmonson Point colony was not used as foraging area, as penguins did not forage in ice holes around iceberg and/or in small tide cracks but beyond the fast-ice edge, in areas of open water mixed to pack ice floes (Olmastroni personal observation); (b) thus they could exploit wider feeding areas, being not limited to return to the same ice holes to breathe and by possible rapid decrease in prey availability due to depletion (Watanuki et al. 1993); (c) moreover, latitudinal difference in light condition may affect the use of depth forcing penguins of lower latitudes to forage during daylight when prey occurred at higher depths (Ainley 2002). However, a low mean meal mass and krill consumption along with low breeding success were described for the 1995–1996

Table 3 Diving parameters of Adélie penguins accordingly to sex, breeding stage, year and interaction “Stage*Year”

	Sex					Breeding stage					Year					Interaction “stage × year”				
		Mean	±SE	*F*	*P*		Mean	±SE	*F*	*P*		Mean	±SE	*F*	*P*		Mean	±SE	*F*	*P*
Maximum Depth (m)	♂	13.2	0.1	0.52	0.49	Guard	12.0	0.1	0.12	0.73	1994–1995	12.2	0.11	0.35	0.57	Guard 1994–1995	11.3	0.1	0.22	0.88
																Crèche 1994–1995	13.2	0.2		
	♀	12.0	0.1			Crèche	13.0	0.1			1995–1996	12.9	0.14			Guard 1995–1996	13.2	0.2		
																Crèche 1995–1996	12.5	0.2		
Dive duration (s)	♂	48.9	0.4	0.24	0.63	Guard	48.3	0.4	**4.61**	**0.05**	1994–1995	43.8	0.34	1.12	0.31	Guard 1994–1995	46.5	0.5	0.59	0.63
																Crèche 1994–1995	41.2	0.5		
	♀	42.8	0.3			Crèche	41.7	0.4			1995–1996	47.9	0.42			Guard 1995–1996	51.8	0.5		
																Crèche 1995–1996	43.1	0.7		
Bottom phase duration (s)	♂	32.7	0.3	0.47	0.51	Guard	34.0	0.3	**11.55**	**0.01**	1994–1995	29.3	0.24	0.68	0.43	Guard 1994–1995	33.4	0.4	1.91	0.18
																Crèche 1994–1995	25.4	0.3		
	♀	28.3	0.2			Crèche	25.9	0.2			1995–1996	31.5	0.29			Guard 1995–1996	35.1	0.4		
																Crèche 1995–1996	27.2	0.4		
Post dive duration (s)	♂	27.6	0.2	4.13	0.06	Guard	29.2	0.2	**7.33**	**0.02**	1994–1995	31.1	0.22	0.27	0.61	Guard 1994–1995	30.7	0.3	2.10	1.55
																Crèche 1994–1995	31.5	0.2		
	♀	32.1	0.2			Crèche	31.7	0.2			1995–1996	28.9	0.25			Guard 1995–1996	26.3	0.2		
																Crèche 1995–1996	32.3	0.5		

Values are grand mean ± SE

Results of GLMM are shown as *F* and *P* values, with significant differences in bold

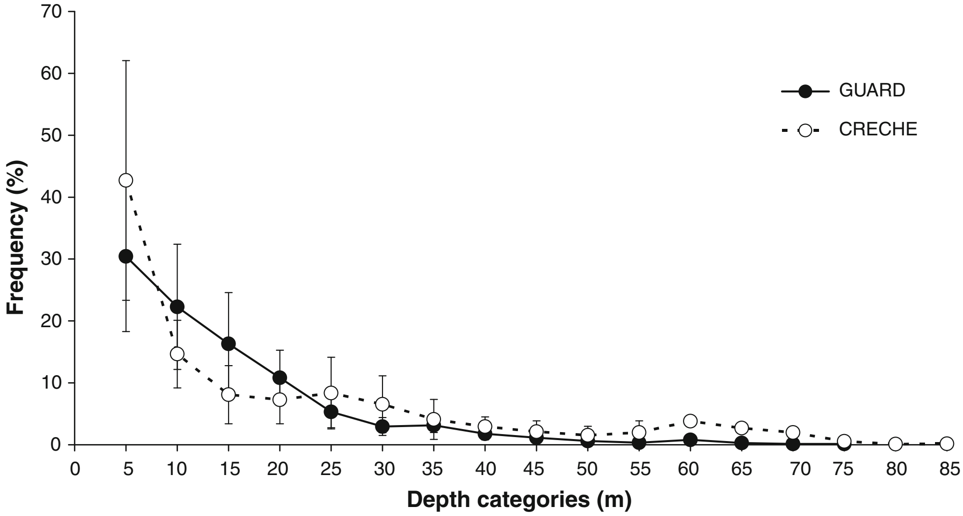

Fig. 2 Dive depth distribution (±SE) during guard and crèche periods pooled as grand means for individuals in 1994–1995 and 1995–1996 summer seasons at Edmonson Point

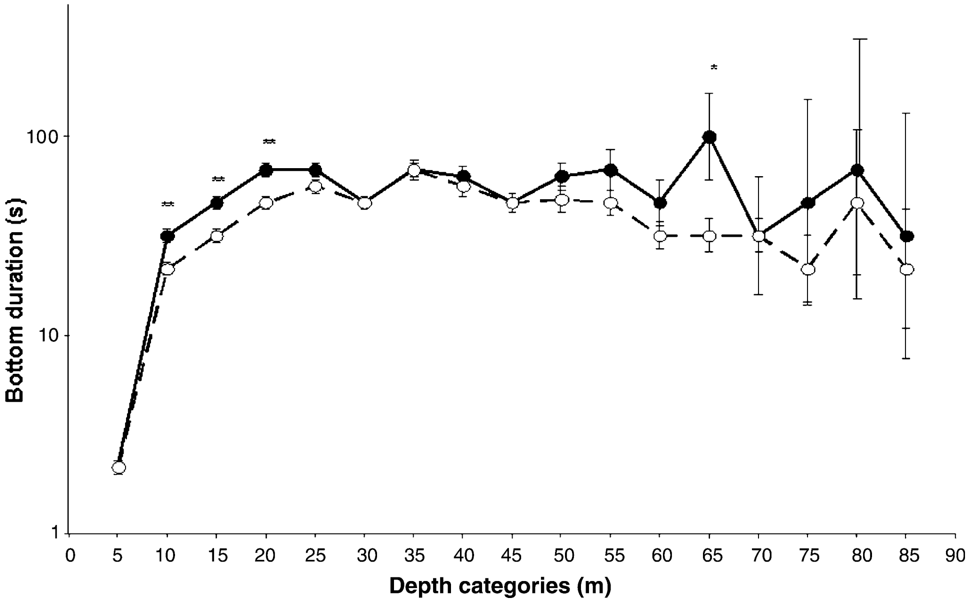

Fig. 3 Mean bottom phase duration (least square mean ± SE) in guard and in crèche stages as a function of depth categories (data pooled for 1994–1995 and 1995–1996). The differences between breeding stages are tested using simple main effect test for each depth categories. Significant differences are indicated by *($P < 0.05$) and **($P < 0.01$)

breeding season at Edmonson Point (Olmastroni et al. 2000, Pezzo et al. 2007). It is known that sea-ice concentration is directly involved in prey availability/aggregation and affect krill growth (Azzali et al. 2006; Brierley et al. 2002; Endo et al. 2002; Loeb et al. 1997; Nicol et al. 2008). Therefore, variations in diet composition (e.g. different prey availability) along with variation in breeding success suggest that sea-ice conditions caused difficulties in chick rearing and survival.

Sex differences in foraging behaviour of Adélie penguins, probably driven by different energetic requirements and possible reduction in intraspecific competition, were observed in different sites (Chappell et al. 1993a, b; Clarke et al. 1998; Clarke et al. 2006; Kato et al. 2003). Longer diving periods in females would allow them to gain more energy by spending longer in the feeding areas. Males, especially during the guard, spend more time at nest than females (Ainley 2002; Chappell et al. 1993a, b). Clarke et al. (1998) showed that, along with sex differences in dietary preference, also females from Edmonson Point travelled further and longer from the colony than did males. Although our sample size was limited only to birds carrying instruments, we found similar trend in females foraging trip.

In this study, penguins altered their diving behaviour in response to their breeding stages (i.e. different dive, bottom and post dive durations). In particular, it has been shown that 75% of prey is caught by Adélie penguins during the bottom phase (Ropert-Coudert et al. 2001), that is considered as a sensitive dive component whose temporal variation may reflect a change in foraging condition or foraging strategy. According to Chappell et al. (1993b), Adélie

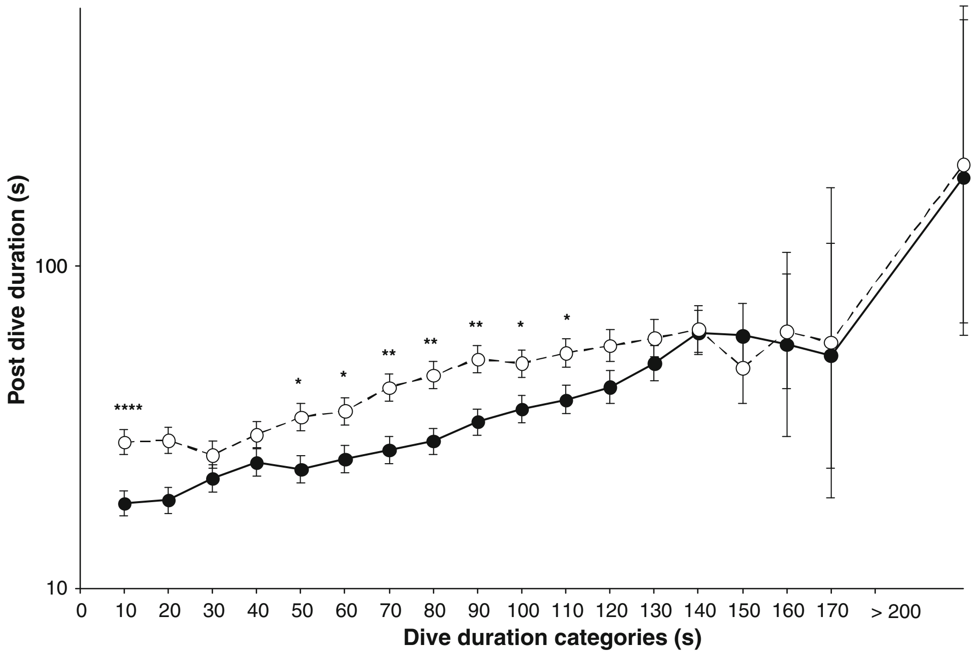

Fig. 4 Mean post dive durations (least square mean ± SE) in guard and in crèche stages (data pooled for 1994–1995 and 1995–1996) as a function of dive duration categories. The differences between breeding stages are tested using simple main effect test for each depth categories. Significant differences are indicated by *($P < 0.05$) and **($P < 0.01$)

penguins would increase the percentage of bottom time from incubation to crèche and that prey capture would be mainly limited by their ability to find krill swarms, but not by pursuit and handling time. Indeed, during the guard phase, the fast-ice edge forced penguins to forage further from the colony, feeding mainly on fish (Clarke et al. 1998; Olmastroni et al. 2004). In our case, differences in dive and bottom phase durations may reflect prey switching between guard and crèche, suggesting longer capturing and handling time when penguins preyed on fish. Changes in diving behaviour between breeding stages may be thus induced by prey type and/or seasonal distribution and habitat availability, in fact as the breeding season progresses, at Edmonson Point both fast-ice extent and pack ice concentration tended to diminish from guard to crèche phase, likely offering different foraging scenarios to adult penguins.

Moreover, we should keep in mind also the constraints imposed by the life history factors, as adult condition and chick provisioning vary through the breeding season according to the increasing energetic requirements of the offspring (Chappell et al. 1993b, Culik 1995). In particular, during the guard stage, parents return regularly to their nests to feed their chicks and swap over with their partners. The apparent increase in dive duration along with decrease in post dive duration in guard may be a response to the chick requirements. In this phase, adult Adélie penguins may have reduced the recovery times (e.g. post dive duration) in order to face the need of the chicks to be fed frequently and protected by predation (Ainley 2002). In contrast, during crèche, chicks form groups and parents can forage simultaneously, having the potential to sustain the increasing chicks demand.

Future investigation on possible linkage between adult body condition, diet, chick growth and diving characteristics (e.g. dive bout) throughout the chick-rearing period may give additional highlights on the complex dynamics of the diving behaviour.

Acknowledgments This project has been funded by the Italian National Programme on Antarctic Research (PNRA) and Ministry of University and Research (MIUR). Australian Antarctic Division provided the APMS. We are grateful to the Australian and Italian researchers who contributed to the data collection in the field and to V. Volpi for GIS and sea-ice data elaboration. Erasmus Placement programme funded I.N. scientific training at IPHC-DEPE CNRS, France. We would like to thank Roger James Kirkwood and the other anonymous reviewers that made valuable comments that contributed to improve this manuscript.

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