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LOW BREEDING SUCCESS OF THE ADÉLIE PENGUIN AT BÉCHERVAISE ISLAND IN THE 1998/99 SEASON

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Abstract

This paper describes the diet and foraging behaviour of Adélie penguins *(Pygoscelis adeliae)* at Béchervaise Island during 1998/99, a season of low breeding success. Fifty-six percent of nests with eggs failed during the three weeks following first hatch. A breeding success of 0.43 chicks crèched per nest was achieved, compared to previous seasons with higher annual breeding success rates ranging from 0.69 to 1.06 chicks crèched per nest. Evidence from analyses of foraging location, foraging trip duration and diet suggests that the death of chicks during the guard stage was due to an inadequate rate of food supply. In most previous seasons adults have foraged both at the continental shelf edge (particularly females) and locally (particularly males). This season male penguins carried out fewer local trips and both sexes spent longer at sea than in years of higher breeding success. Meal masses brought back to the chicks were within the normal range but extended foraging trip durations reduced feeding frequency. These findings contrast with observations made in 1994/95 (a season in which all chicks died of starvation), when smaller meals were delivered and birds foraged further offshore than in this or any other season studied. The significance to CCAMLR of these variations in foraging behaviour is discussed.

Résumé

L'auteur décrit le régime et le comportement alimentaires du manchot Adélie *(Pygoscelis adeliae)* à l'île Béchervaise en 1998/99, saison qui s'est caractérisée par son faible succès de la reproduction. Cinquante-six pour-cent des nids contenant des œufs ont échoué pendant les trois semaines qui ont suivi la première éclosion. Le nombre de jeunes arrivés en crèche correspond à 0,43 jeunes par nid alors que lors de saisons précédentes où les taux de réussite de la reproduction étaient plus élevés, il variait entre 0,69 et 1,06 oiseaux par nid. D'après l'analyse des secteurs d'alimentation, de la durée des sorties et du régime alimentaires, il semble que la mortalité des jeunes durant le stade de garde résulte d'un taux d'approvisionnement en nourriture inadéquat. Les saisons précédentes, les adultes ont recherché leur nourriture tant à la bordure du plateau continental (notamment les femelles) que localement (plus particulièrement les mâles). Cette saison, les mâles n'ont pas réalisé autant de sorties locales et les mâles et les femelles ont tous deux passé plus de temps en mer qu'ils ne l'avaient fait les années de succès reproductif plus élevé. La masse des repas rapportés aux jeunes s'inscrit dans les limites de la norme, mais la longue durée des sorties alimentaires a réduit la fréquence de ces repas. Ces résultats ne correspondent pas aux observations effectuées en 1994/95 (saison pendant laquelle tous les jeunes sont morts d'inanition), selon lesquelles des repas moins importants avaient été rapportés et les oiseaux s'alimentaient nettement plus au large que dans notre cas ou lors de toute autre saison étudiée. L'importance pour la CCAMLR de ces divers comportements alimentaires est discutée.

Резюме

В статье описываются рацион и поисковое поведение пингвинов Адели *(Pygoscelis adeliae)* на о-ве Бешервэз в сезоне 1998/99 г., характеризовавшемся низким репродуктивным успехом. Высиживание закончилось неудачей в 56% гнезд в течение трех недель после первого вылупления. Репродуктивный успех составил 0.43 птенца ясельного возраста на гнездо; для сравнения, в предыдущие сезоны годовой репродуктивный успех был более высоким и колебался между 0.69 и 1.06 птенца ясельного возраста на гнездо. Анализ районов кормления, продолжительности походов за пищей и рациона говорит о том, что смерть птенцов на стадии охраны родителями была вызвана неадекватным количеством

пищи. В большинстве предыдущих сезонов взрослые особи искали корм и на границе континентального шельфа (преимущественно самки), и локально (преимущественно самцы). В этом сезоне самцы пингвинов совершили меньше локальных походов за пищей, и оба пола провели больше времени в море, чем в годы более высокого репродуктивного успеха. Масса пищи, приносимой птенцам за один раз, была нормальной, но более длительные походы за пищей привели к сокращению частоты кормлений. Эти результаты контрастируют с наблюдениями 1994/95 г. (сезона, в котором все птенцы умерли от голода), когда масса приносимой за один раз пищи была меньше, и птицы искали корм дальше от берега, чем в любом другом изучавшемся сезоне. С позиции АНТКОМа, обсуждается значение этих изменений в поисковом поведении пингвинов Адели.

Resumen

Este trabajo describe la dieta y comportamiento de alimentación de los pingüinos adelia *(Pygoscelis adeliae)* en isla Béchervaise durante la temporada 1998/99, que se caracterizó por un bajo éxito reproductor. El 56% de los nidos con huevos fallaron en las primeras tres semanas luego de la primera eclosión. El éxito de reproducción, medido en número de polluelos por nido que alcanzaron la etapa de guardería, fue de 0,43, más bajo que en las temporadas anteriores cuando se alcanzó una tasa de reproducción anual del orden de 0,69 a 1,06. Del análisis del lugar de alimentación, la duración de los viajes en busca de alimento y la dieta se pudo determinar que la muerte de los polluelos durante la etapa de guardería se debió a la falta de alimento. En la mayoría de las temporadas anteriores las aves adultas han buscado alimento en la plataforma continental (en particular las hembras) y en el área local (en particular los machos). Esta temporada, los pingüinos machos realizaron menos viajes locales y ambos sexos pasaron más tiempo en el mar que en años de reproducción más exitosa. La porción de alimento dada a los polluelos estuvo dentro del rango normal, pero la frecuencia de la alimentación se redujo debido a la mayor duración de los viajes de alimentación. Estos resultados contrastan con las observaciones hechas en 1994/95 (temporada en la cual todos los polluelos murieron de inanición), cuando las porciones alimenticias fueron menores y las aves se alimentaron más lejos de la costa que en ninguna de las otras temporadas estudiadas. Se analiza el significado para la CCRVMA de estas variaciones en el comportamiento de alimentación.

Keywords: Adélie penguin, *Pygoscelis adeliae*, breeding success, prey variability, Béchervaise Island, CCAMLR

INTRODUCTION

Breeding success of predators such as seabirds can be used as an indication of the status of lower trophic levels (Furness et al., 1993; Montevecchi, 1993). Food availability is a large determinant of reproductive success and large fluctuations in prey stocks can greatly influence the reproductive performance of seabirds (Boersma et al., 1990; Croxall et al., 1999; van Heezik and Davis, 1990). Some seabird species have the ability to switch prey species successfully in times of low prey abundance (e.g. Crawford and Dyer, 1994; Croxall et al., 1999), while others that take a narrow range of prey items are prone to distress if their food source is lacking (van Heezik and Davis, 1990). Responses of specialist feeders to low prey availability include delivery of smaller meals and increased foraging trip durations (Croxall et al., 1999; Watanuki et al., 1993), both of which can result in reduced breeding success. Reduction in chick provisioning rates and meal mass result in depressed growth rates, lighter fledglings and reduced numbers of chicks reaching fledging age (Crawford and Dyer, 1994; Croxall et al., 1999; van Heezik and Davis, 1990; Watanuki et al., 1993). Knowledge of the annual variation in specific breeding parameters coupled with analyses of foraging behaviour can give real-time estimates of relative prey availability (Montevecchi, 1993).

Antarctic krill *(Euphausia superba)* is an important food source of the Adélie penguin *(Pygoscelis adeliae)* and is also the subject of a major fishery (Nicol and Endo, 1999). Any species relying predominantly on a food source which is also harvested by humans is vulnerable to prey depletion resulting from overfishing (e.g. Croxall et al., 1999). The potential for human harvesting of krill to affect the ecology of natural predators has highlighted the need for increased knowledge on the biology of krill, krill predators and the relationships between these organisms.

The CCAMLR Ecosystem Monitoring Program (CEMP) has been designed to detect changes in ecosystem performance by monitoring specific biological and environmental indicators, with the ultimate aim of determining whether any such changes are due to natural variation or the harvesting of marine living resources (Agnew, 1997). Béchervaise Island (67°35'S, 62°48'E) is the site of a CEMP program which investigates primarily predator–prey relationships between the Adélie penguin and Antarctic krill to detect fluctuations in the marine ecosystem off the Mawson coast. Annual breeding success of the Adélie penguin on Béchervaise Island has ranged from 0.05 to 1.06 chicks crèched per nest over the nine years of the program. The 1998/99 season produced 0.43 chicks per nest; a low breeding success rate in comparison to most other years. Two other years, 1994/95 and 1995/96, also experienced low breeding success rates of 0.05 and 0.35 chicks crèched per nest respectively.

In this paper we investigate the low breeding success of the 1998/99 summer and compare this to other breeding seasons. In particular, we investigate reproductive output in relation to the birds' foraging performance and comment on the potential implications of a krill fishery to penguin breeding success.

METHODS

Standard methods, as prescribed by CCAMLR, were used. These are referred to in the text as CEMP A1 to A9 (CCAMLR, 1997).

Breeding Success (CEMP A3 and A6)

Annual population counts (CEMP A3) include daily counts of arriving adults, mid-incubation count of all nests with eggs, brooded nest count during early guard, and a chick count when two thirds of the chicks were crèching.

In this paper annual breeding success has been defined as the number of chicks successfully reared to the crèche stage (measured at the time two thirds of the chicks have crèched, according to CEMP A6) divided by the number of incubated nests. Differences between annual breeding success rates were identified by a one-way ANOVA and classified into groups by the Student-Newman-Keuls method.

Sea-ice Extent

The northern edge of the Antarctic sea-ice was derived from maps obtained from passive microwave Defence Meteorological Satellite Program (DMSP) data provided by the US National Ice Center and was determined based on a 15% ice concentration threshold. The distance from the sea-ice edge to the Mawson coast was calculated from data averaged over seven days during mid-January each year at longitude 60°E.

Chick Growth (CEMP A7)

About 30 chicks were weighed throughout the guard and crèche stages during several seasons (1993/94, 1994/95, 1995/96, 1996/97, 1998/99) to determine annual growth curves. Chicks of known age were chosen at random and weighed to the nearest 25 g. The chicks were banded with Velcro™ flipper bands for individual identification; the bands were regularly loosened for flipper growth. Individuals were weighed on a five-day basis until the age of about 50 days when the flipper bands were removed to allow uninhibited fledging.

Fledglings were weighed within five-day periods according to CEMP Standard Method A7. Fifty fledglings were chosen at random each five days; a procedure carried out annually since 1990/91. One-way ANOVA was used to compare weights among seasons within each period.

Foraging Trip Duration (CEMP A5)

Foraging trip durations were determined using an Automated Penguin Monitoring System (APMS) which records the dates and times on which individually identified Adélie penguins enter and leave the colony throughout each breeding season (see Kerry et al., 1993 for further details). The periods of time during which breeding penguins were absent from the colony collecting food were calculated from APMS records and validated by twice-daily nest observations. Data were collected from six seasons (1991/92, 1992/93, 1993/94, 1994/95, 1995/96 and 1998/99) during the guard stage of chick rearing. Mean trip durations were calculated for each season, and frequency histograms produced for all trips grouped into 12 hourly bins.

Mean foraging trip durations for each individual bird were calculated according to CEMP Standard Method A5. These means were used to generate

statistics based on birds, rather than trips, as sampling units, as recommended in CEMP A5. Data were normalised by log transformation, enabling the use of two-way ANOVA to compare foraging trip durations among seasons and between sexes.

Foraging Location

Satellite-tracking devices were attached to penguins during the guard phase of the 1998/99 season to determine foraging location. The devices used were Telonics (USA) platform terminal transmitters (PTTs), model ST-10, packaged by Sirtrack (New Zealand) and weighing a total of 90 g. Transmissions were detected by NOAA satellites and positions calculated through the ARGOS (France) location system.

Foraging tracks were collected from three males and four females, that conducted a total of 15 foraging trips. Following the method of Clarke et al. (1998) these foraging trips were categorised into two groups according to distance travelled from the colony. Trips restricted to within 25 km of Béchervaise Island were classified as 'local' trips and those extending beyond 80 km as 'distant' trips.

Diet (CEMP A8)

Five diet samples were collected every five days throughout the guard stage of chick rearing. All birds were breeding adults, captured at random on their return from sea. Stomach samples were collected using the water off-loading method of Wilson (1984) and multiple flushes conducted following CEMP standard methods (CCAMLR, 1997). Sex was determined by cloacal examination prior to stomach flushing.

Stomach samples were analysed according to CCAMLR (1997), and wet weights of each main dietary component determined. Samples were weighed and sorted into categories of *Euphausia superba*, *E. crystallorophias*, unidentifiable krill, fish, amphipods and squid. Fish otoliths were removed and identified. Diets of males and females were analysed separately since sex differences in foraging behaviour have been previously determined (Clarke et al., 1998).

The rate of food delivery to the chicks during the guard stage was taken to be the ratio of mean guard meal size (ascertained by stomach flushing) to mean guard foraging trip duration (measured in hours from APMS data).

RESULTS

Breeding Success

The 1998/99 breeding season extended from 18 October 1998 (first arrival) to 10 March 1999 (departure of last chick). A total of 4 063 penguins arrived on Béchervaise Island to breed, and distributed themselves amongst the 18 established colonies (Kerry et al., 1993). A total of 1 880 pairs laid eggs and of these 802 chicks crèched (CEMP A6a count; Table 1). Figure 1 provides a comparison among seasons from 1990/91 to the present. The number of nests established was similar to previous years but the number of chicks produced that reached crèche age and ultimately fledged was low.

Annual breeding success rates over the nine years were classified into four distinct groups. The 1994/95 season, a near total failure – 0.05 chicks per nest reaching crèche stage, none fledging – was identified as an outlier (Student-Newman-Keuls method: $q = 8.109$, $p < 0.001$) and was thus considered separately from the remaining dataset. All other years were classified into the following groups: low breeding success (1995/96, 1998/99), $q = 11.236$, $p < 0.001$; medium breeding success (1990/91, 1991/92, 1992/93), $q = 7.893$, $p < 0.001$; and high breeding success (1993/94, 1996/97, 1997/98), $q = 16.228$, $p < 0.001$.

Approximately 1 060 nests failed during the three-week period immediately following the start of hatching (19 December). The mid-incubation count (CEMP A3) of 1 880 nests with eggs on 2 December had dropped to 818 nests with brooded chicks by 8 January (CEMP A6c). The majority of deaths occurred when the chicks were very young: 76% died by the age of 15 days. The weather during the 1998/99 summer (October to March) was mild with just nine days of blizzard conditions over the six months. December and January, the period of early chick rearing, were both blizzard-free. The fast-ice broke away to the western side of Béchervaise Island on 9 February and blew from Kista Strait at the eastern side of the island on 20 February. This breakout was approximately three weeks later than normal.

The distance from the Mawson coast to the northern edge of the sea-ice in mid-January each

Table 1: Numbers of nests with eggs and numbers of chicks reared to crèche age (CEMP A6a count) for each breeding season. Distance from the colony to the sea-ice edge during mid-January each year is also shown.

Season	Nests with Eggs	Chicks Crèched	Distance to Ice Edge (km)
1990/91	1 791	1 345	85
1991/92	1 737	1 262	75
1992/93	1 485	1 200	85
1993/94	1 711	1 810	75
1994/95	1 736	95	175
1995/96	1 813	636	105
1996/97	1 873	1 771	85
1997/98	1 933	1 809	75
1998/99	1 880	802	125

Table 2: Mean fledgling weights (± standard deviation) within CEMP five-day periods for all seasons. Numbers of birds in each group are shown in brackets. No chicks survived to fledging age in 1994/95.

Season	Mean Fledgling Weights within CEMP Five-day Periods				
	10–14 Feb	15–19 Feb	20–24 Feb	25 Feb–1 Mar	2–6 Mar
1990/91			3 079 ± 654 (50)		
1991/92			3 204 ± 488 (50)	[2]3 120 ± 565 (50)	3 067 ± 609 (50)
1992/93				3 012 ± 529 (50)	2 824 ± 507 (44)
1993/94		[1]3 411 ± 532 (50)	3 190 ± 683 (50)	3 076 ± 687 (21)	
1994/95					
1995/96	3 944 ± 605 (50)		3 359 ± 522 (23)	3 028 ± 428 (51)	
1996/97		[1]3 096 ± 473 (50)	3 076 ± 649 (50)	2 709 ± 554 (35)	
1997/98		3 279 ± 689 (8)	2 904 ±1 082 (38)	2 644 ±1 511 (14)	
1998/99			3 206 ± 587 (50)	[2]2 480 ± 790 (20)	2 797 ± 487 (15)

[1] Significant difference between 1993/94 and 1996/97 for the 15–19 Feb period ($p = 0.012$).
[2] Significant difference between 1991/92 and 1998/99 for the 25 Feb–1 Mar period ($p < 0.001$).

year is shown in Table 1. We found a negative correlation between sea-ice extent and breeding success over the nine years for which we have data (Pearson Product Moment Correlation, $R^2_{adj} = 0.794$, $p < 0.001$). This is also illustrated in Figure 1.

Chick Growth

The growth rate of the chicks was low, and up to 15 days of age was similar to that of the previous two seasons with low breeding success (1994/95 and 1995/96), a rate about half that of the seasons with higher breeding success in which known-age chicks were weighed (Figure 2). The growth rate of this season's chicks continued to be low throughout the whole of chick rearing, although the rate increased slightly when the chicks were about 25 days old, the time when both parents started to forage simultaneously. Mean fledgling weights for each CEMP five-day period are shown in Table 2. The 1998/99 season did not differ from other years except for the period from 25 February to 1 March in which birds were significantly lighter than in 1991/92 (Kruskal-Wallis One-way ANOVA on Ranks with Dunn's Pairwise Multiple Comparison Procedure, $H = 24.94$, $df = 6$, $p < 0.001$; Table 2).

Foraging Trip Duration and Location

The mean duration of all individual foraging trips carried out by breeding birds during the guard stage was longer in 1998/99 than in all previous seasons except 1994/95, averaging 45.2 hours (Table 3). This compares to an average duration of 29.8 hours in 1993/94, a season with high breeding success, and 55.3 hours in the 1994/95 season when all chicks starved. The proportion of long foraging trips during the guard stage of 1998/99 was very high, with 41% of trips being longer than 48 hours compared to 14% and 25% in 1993/94 and 1994/95, the seasons of highest and lowest breeding success respectively (Table 3).

Mean foraging trip durations for males and females (using individual birds as sampling units) are also shown in Table 3. Mean foraging trip durations in 1998/99 were greater than all years

Table 3: Mean foraging trip durations during the guard stage for male and female penguins over five seasons at Béchervaise Island. Data were collected by the Automated Penguin Monitoring System (APMS). Mean trip durations were calculated from the means of each individual bird's trip durations without weighting by the number of trips (CEMP Standard Method A5). Means of individual trips and % trips > 48 h in duration are also shown. Asterisks indicate poor seasons.

Season	Males				Females				All Birds		All Trips		
	Mean (h)	SE	*n* (birds)	*n* (trips)	Mean (h)	SE	*n* (birds)	*n* (trips)	Mean (h)	SE	Mean (h)	SE	Trips >48 h (%)
1991/92	30.0	4.5	57	344	44.8	4.3	63	449	37.4	3.1	31.4	1.3	18
1992/93	31.6	4.0	74	371	50.5	4.1	71	380	41.1	2.8	38.5	1.4	26
1993/94	27.7	4.1	71	290	37.1	3.9	76	296	32.4	2.8	29.8	0.7	14
1994/95*	42.1	4.2	67	198	91.3[2]	3.9	76	209	66.7	2.9	55.3	3.4	25
1995/96*	35.9	4.2	68	278	55.9	4.1	70	270	45.9	2.9	40.3	1.4	28
1998/99*	41.5[1]	4.3	64	163	56.8	4.5	59	152	49.1	3.1	45.2	1.8	41

[1] Significantly different from males in 1991/92 and 1993/94 ($p < 0.05$).
[2] Significantly different from females in all other seasons ($p < 0.05$).

Table 4: Details of foraging trips of penguins carrying satellite-tracked devices (PTTs) in the 1998/99 breeding season.

Sex	Trip Classification (See Figure 4)	Farthest Distance from Béchervaise Island (km)	Total Distance Travelled (km)	Trip Duration (h)
M	Local	4	22	17
M	Local	7	45	33
M	Local	15	78	25
M	Local	23	94	59
M	Distant	83	194	71
M	Distant	92	222	88
M	Distant	95	266	96
M	Distant	108	337	122
M	Distant	125	268	92
M	Distant	126	389	100
F	Local	14	53	24
F	Distant	94	267	96
F	Distant	96	347	118
F	Distant	97	291	128
F	Distant	105	332	155

Table 5: Mean meal size (obtained by stomach flushing adult birds) and mean foraging trip duration during the guard stage with the corresponding food delivery rate to the chicks and breeding success. Asterisks indicate poor seasons. Breeding success is calculated at the time when two-thirds of the chicks had crèched (CEMP A6a). The chicks that survived to crèche age in the 1994/95 season eventually died from starvation.

Season	Guard Stage Meal Size			Mean Foraging Trip Duration (h)	Provisioning Rate (g/h)	Annual Breeding Success (chicks/nest)
	Mean Meal Mass (g)	*n*	SD			
1991/92	279	25	189	31.4	8.9	0.73
1992/93	269	32	167	38.5	7.0	0.81
1993/94	405	31	220	29.8	13.6	1.06
1994/95*	218	20	187	55.3	3.9	0.05
1995/96*	259	14	139	40.3	6.4	0.35
1996/97	507	20	173	na		0.95
1997/98	na			na		0.94
1998/99*	329	17	110	45.2	7.3	0.43

except 1994/95 for both males and females. Two-way ANOVA following normalisation of the data by log transformation demonstrated significant differences in foraging trip durations among seasons ($F = 8.419$, $p < 0.001$) and between sexes ($F = 112.696$, $p < 0.001$), as well as a significant interaction between season and sex ($F = 2.795$, $p < 0.02$). The mean male foraging trip duration was significantly greater in 1998/99 than in two of the years with higher breeding success ($p < 0.05$), and the mean female foraging trip duration was significantly greater in 1994/95 than in all other years ($p < 0.05$) (Table 3). No other seasons differed significantly among males; for females the only other significant difference found was between 1995/96 and 1993/94 ($p = 0.05$).

Frequency histograms of foraging trip duration during the 1998/99 guard stage showed a bi-modal distribution for both males and females (Figure 3), indicating that local and distant trips were conducted at this time by both sexes, as demonstrated by Clarke et al. (1998) in previous seasons. Satellite tracks of penguins carrying PTTs showed a similar trend with local and offshore foraging trips for both males and females (Figure 4, Table 4). Six out of 10 male trips and four out of five female trips extended to the continental shelf zone. These birds carrying satellite trackers took an average of 32 h (range 17–59 h) to carry out local trips and 107 h (range 71–155 h) to undertake trips to the shelf edge (Table 4).

Diet

The mean meal size delivered to the chicks during the guard stage was 329 g. This mass was greater than in both the 1990/91 and 1992/93 seasons when the breeding success was nearly twice that of the 1998/99 season (Table 5). This meal size is also larger than that of the previous seasons with low breeding success (1994/95 and 1995/96). None of these differences are, however, statistically significant (one-way ANOVA within ranks).

Annual breeding success was positively correlated to chick provisioning rate but not to chick meal size (Pearson Product Moment Correlation, $R^2_{adj} = 0.724$, $p = 0.02$; $R^2_{adj} = 0.428$, $p = 0.066$ respectively).

The diet biomass composition, by percentage, varied slightly throughout chick rearing with the diet consisting of 44% krill (*E. superba* and *E. crystallorophias*) and 56% fish and amphipods during the guard stage and 54% krill and 45% fish and amphipods during crèching. Females had a larger, although not statistically significant (z-test), proportion of krill in their diet during the crèche stage (71%) than during the guard stage (44%). The male diet remained constant throughout chick rearing, 43% krill and 57% fish and amphipods during both guard and crèche stages. An analysis of otoliths from the fish component of the diet showed that birds were feeding predominantly on *Pleuragramma antarcticum*, with smaller amounts of *Electrona antarctica* present. *E. superba* was the predominant krill species present.

DISCUSSION AND CONCLUSIONS

The breeding success of 0.43 chicks crèched per nest in the 1998/99 season was low in comparison to other seasons. This corresponds to the third poorest year, in terms of breeding success, since the inception of the Australian CEMP program in 1990. The foraging behaviour of Adélie penguins in 1998/99 indicates that the high chick mortality was brought about by starvation due to the increased interval between chick feeds during the guard stage. Most of the chicks died when they were young, the time at which frequent energy acquisition is essential for survival.

The mean foraging trip duration of the birds during the 1998/99 guard stage was greater than in all seasons with higher breeding success. Males in particular undertook foraging trips that were longer than those conducted in years of higher breeding success (Table 3). This pronounced increase was due to a higher proportion of trips to distant feeding grounds (trips to the continental shelf), illustrated by the bimodal distribution of the duration of these foraging trips (Figure 3). This type of distribution is common among the Béchervaise Island females during the guard stage and both sexes during the crèche stage (Clarke et al., 1998). However, it is unusual among males in the guard stage, which in previous seasons have concentrated on local foraging grounds (Clarke et al., 1998). This change in foraging behaviour suggests that prey availability (abundance and/or accessibility) inshore was low early in the season, causing the males to forage further afield. The result of these offshore trips is an increase in the time spent at sea, with the consequence of reducing the chick feeding frequency.

The females exhibited normal foraging behaviour, i.e. regular trips out to the continental shelf to acquire krill, but their foraging trip durations were

also longer (although not significantly so) than those during seasons of higher breeding success. Investigation of satellite tracks (Figure 4) showed that females were spending long time periods at their feeding grounds rather than on their way to them, indicating that prey abundance offshore may have been limited also.

The mean meal size of the 1998/99 guard stage was comparable to that in seasons with nearly twice the breeding success. The difference between this season and those of higher breeding success was the frequency of chick feeds which, coupled with meal size, determines the total amount of food delivered to the chicks. Chick growth was low during guard and the late fledglings were lighter than in some previous seasons, indicating that the chicks were not receiving sufficient food for normal growth. Most of the chicks (76%) starved before the age of 15 days indicating that food supplies were insufficient during the guard phase. The guard phase is the most vulnerable time for the chicks as one parent must always be attending the nest, leaving only one adult to forage. At this time, the chicks are weak and incapable of thermoregulation (Bucher et al., 1990), and they require frequent meals for energy acquisition.

Yearly chick provisioning rate was positively correlated to annual breeding success, indicating that breeding success is strongly influenced by fluctuations in food availability. Food availability will, by simple definition, influence the breeding success of any animal species. This relationship has been reported in numerous seabirds, including both penguins and flying seabirds (Boersma et al., 1990; Crawford and Dyer, 1994; Croxall et al., 1999; Watanuki et al., 1993). In times of prey deficiency seabirds respond by either capturing smaller meals or increasing their foraging time to maintain meal size. In previous studies, Adélie penguins and grey-headed *(Diomedea chrysostoma)* and black-browed albatrosses *(D. melanophris)* have been found to increase their foraging trip duration in times of low food availability, while macaroni penguins (*Eudyptes chrysolophus*) and gentoo penguins (*Pygoscelis papua*) have been seen to acquire smaller meals (Croxall et al., 1999; Watanuki et al., 1993).

Sex differences in feeding strategies have been described in Clarke et al. (1998) with males conducting predominantly short-duration local trips and females undertaking longer trips to the continental shelf. The short-duration male foraging trips have been attributed to nest defence (Clarke et al., 1998) and replenishment of body reserves after the long fasting period (Chappell et al., 1993). It is possible that these sex differences are also partly due to the energy requirements of the chicks during guard. Long-duration feeding trips to the shelf edge may be intentionally alternated with short-duration foraging trips within the neritic zone, to fulfil the chicks' regular energy requirements during the guard stage, their most vulnerable time. This has been noted for several seabird species (e.g. Clarke, in prep; Weimerskirch et al., 1994; Weimerskirch et al., 1997).

We conclude from this study that the low breeding success in the 1998/99 season was brought about by starvation due to a low chick-provisioning rate during the guard stage. Although the individual meal sizes of Adélie penguins were substantial during this time, they were maintained at the expense of longer foraging trip durations, particularly of the males which foraged offshore rather than in the local area.

Causes of Increased Foraging Trip Duration

The reasons for the prey deficiency in the penguins' normal foraging range are unclear. Natural phenomena rather than human activities are causing the fluctuations in food availability since there has been no krill fishery in the Mawson area since 1988 (CCAMLR, 1998; CCAMLR, 2000). It is well known that natural fluctuations in the physical environment, in such factors as sea-ice distribution, temperature and salinity, directly affect the biological environment (Daly and Macaulay, 1988; Hosie and Cochran, 1994; Loeb et al., 1997).

The sea-ice around Mawson persisted until late in the 1998/99 breeding season. In the 1994/95 season, late breakout of the fast-ice around Béchervaise Island and persistence of pack-ice also coincided with chick starvation, suggesting that there is a relationship between sea-ice extent in summer and low Adélie breeding success in the Mawson region. Ainley and LeResche (1973) also found this relationship at Ross Island, the low breeding success being attributed to the extra energy required for the adults to walk across the ice to their feeding grounds. The relationship at Béchervaise Island does not seem as simple. The adults had access to local feeding grounds (personal observations) but were instead foraging offshore. Satellite tracks of distant trips showed long periods at sea once the penguins had reached their foraging grounds. Low usage of local feeding grounds

Table 6: Five scenarios of foraging behaviour associated with different prey availability.

	Scenario	Likely Cause
1	Males forage at the shelf break instead of locally during guard.	Lack of inshore food, or food inaccessible.
2	Birds return from the shelf break with smaller meals.	Decreased availability of krill and fish at the shelf break.
3	Birds spend longer at the shelf break and return with normal-sized meals.	Decreased availability of krill and fish at the shelf break.
4	Birds travel north beyond the shelf break and return with food.	Krill and/or fish available, but out of normal range.
5	Birds travel north beyond the shelf break and return empty.	Virtual absence of krill, fish and local food.

implies that there was a prey shortage in the local area. The extended foraging time of the adults in distant feeding grounds indicates that there was a prey shortage offshore as well. Thus it appears that there was a general prey deficiency in the Mawson region. Fast-ice persistence may contribute to longer foraging trips by increasing the time spent travelling to foraging grounds or by reducing access to local prey, but observations suggest that the presence of ice is not the sole cause. Sea-ice persistence and chick starvation appear to be coincidental rather than directly linked, although the observed correlation between mid-January sea-ice extent and breeding success suggests that there may be a common cause for these events. The physical conditions preventing the fast-ice from breaking out also may be responsible for redistributing prey away from the normal feeding grounds of the penguins.

Significance for CCAMLR

The results of this study suggest that the established foraging patterns of males and females combine in a way that maximises the nourishment of their chicks. In some seasons the predominantly near-shore feeding of males is able to provide food at sufficient frequency for small chicks to survive. In the event of a depletion of food in the inshore zone both males and females may be able to feed offshore in turn and still provide sufficient food. However if food availability is also decreased at the shelf break, then the mortality rate of young chicks will increase and those that survive to the crèche stage are likely to be underweight.

It follows that if a fishery makes krill unavailable by removal or dispersion, then changes in the foraging behaviour of penguins may be observed. If these effects occur during the guard stage then one of the five scenarios described in Table 6 may arise. This table relates to penguins breeding along the Mawson coastline where the shelf break is located 100 to 120 km offshore. The differences between scenarios 2 and 3 may depend on the distribution of prey, rather than the absolute amount present.

The low breeding success in the 1998/99 season appeared to be due to scenarios one and three, whereas the total failure of the 1994/95 season was caused by scenario five (Kerry et al., 1995). The low breeding success in 1995/96 at first sight would appear to fit scenario two. However, although meal sizes tended to be small, there was no statistical difference between this season and 1998/99. In addition, the foraging trips tended to be long (although not significantly different from other years) and slightly bimodal for both sexes, indicating that this year also fits scenario three. The three seasons of low breeding success appear to have been influenced by various different events that resulted in changes in the foraging behaviour of the adults and ultimately led to high chick mortality.

We suggest that in years when sea-ice persists along the coast it may be more difficult for parent birds to find food for the chicks. Food resources may be lacking in the local region or offshore in the shelf break zone, or alternatively, in both of these areas. If prey resources offshore are diminished by fishing activity there may be a consequential deleterious effect on penguin breeding success.

The degree to which the presence of a krill fishery could affect chick mortality rates in the Mawson region presently remains undetermined. Ultimately the effects of a fishery will be superimposed upon natural variations in prey abundance and distribution. The latter are two factors for which insufficient temporal data

presently exist in the Mawson region and which require further directed research in concert with existing predator monitoring programs.

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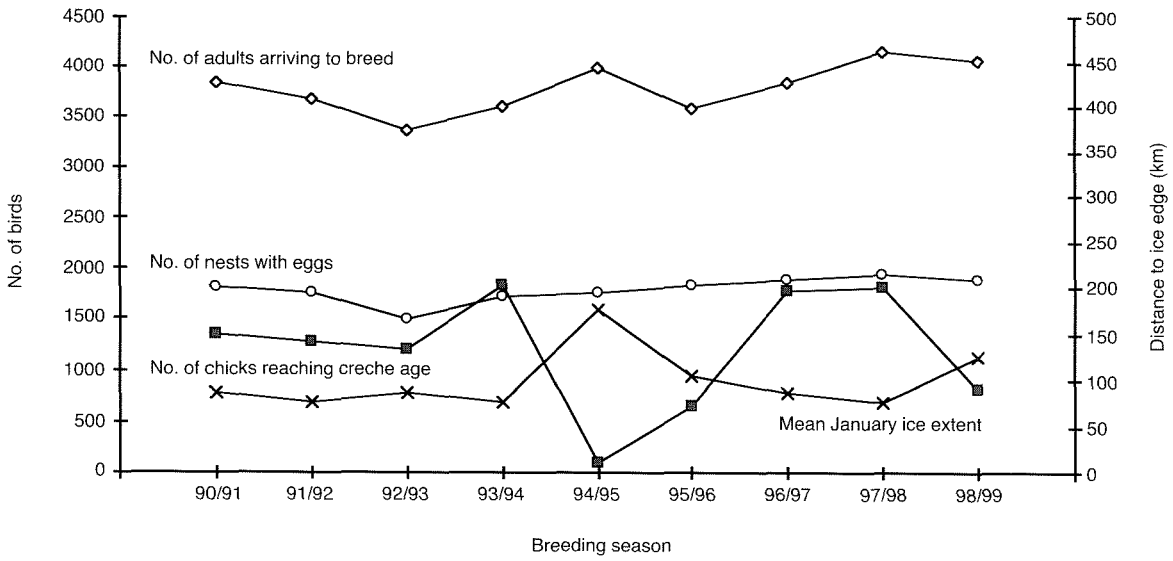


Figure 1: Annual breeding population and breeding success of Adélie penguins at Béchervaise Island. Northern sea-ice extent during mid-January is also shown.

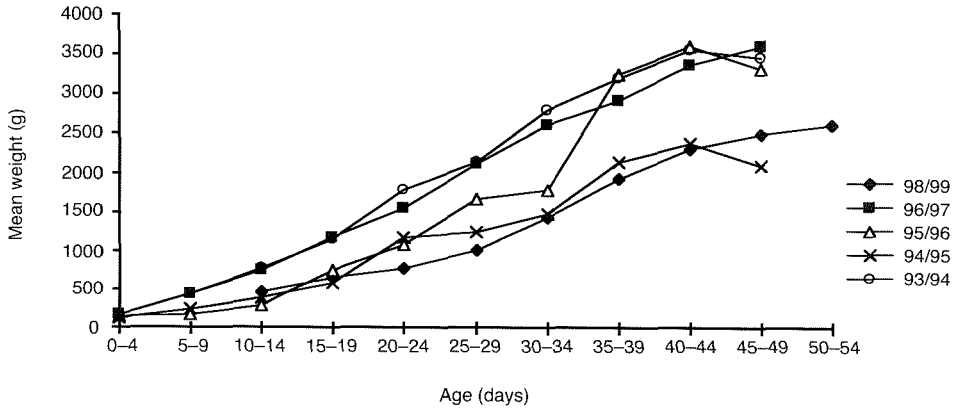
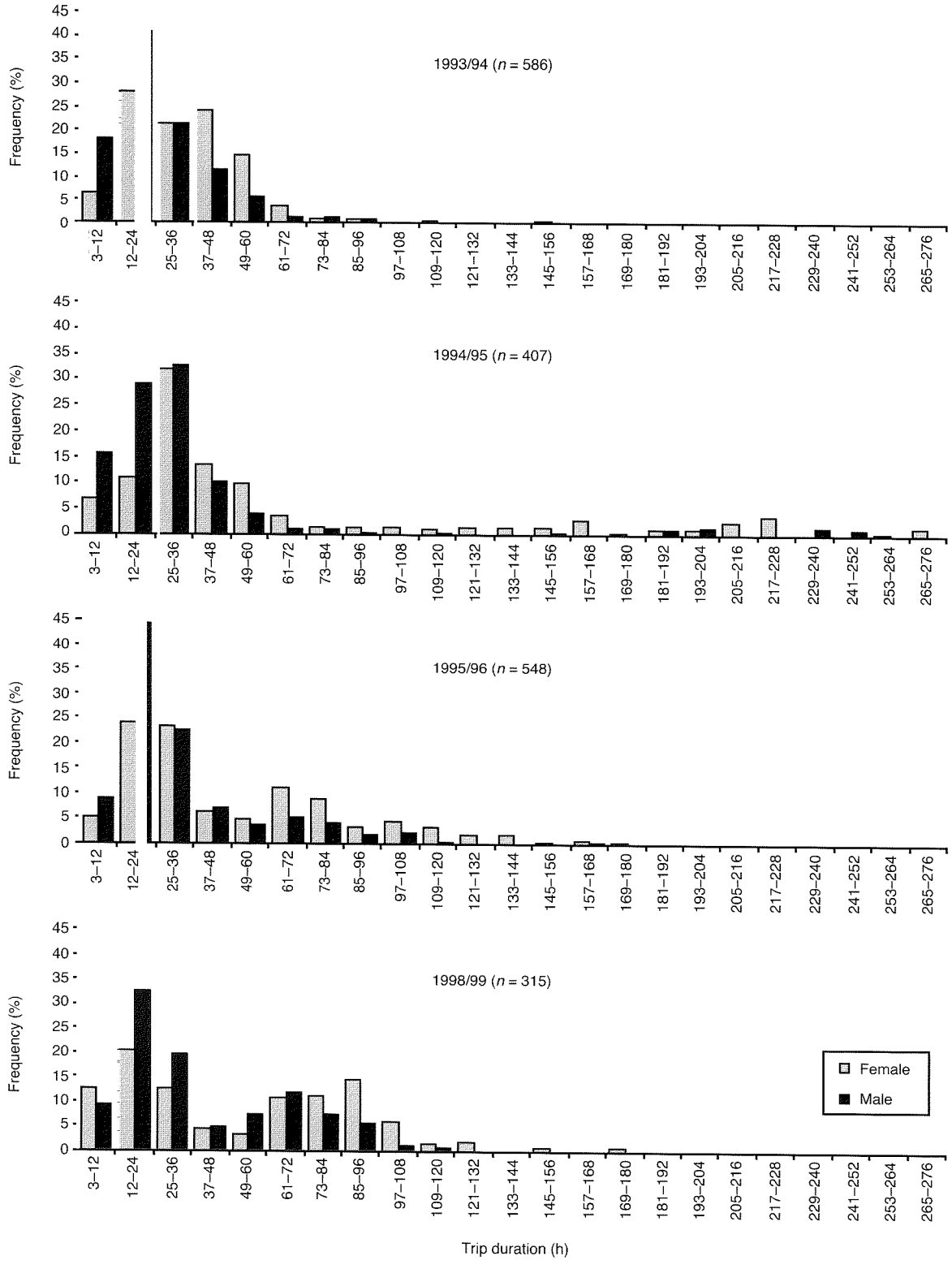


Figure 2: Chick growth curves for the 1994–1999 breeding seasons obtained from manual weighing of the chicks. These curves are derived from chicks taken at random from the colony and the weights averaged within five-day age classes. No account is taken of chicks that died subsequent to a particular weighing.



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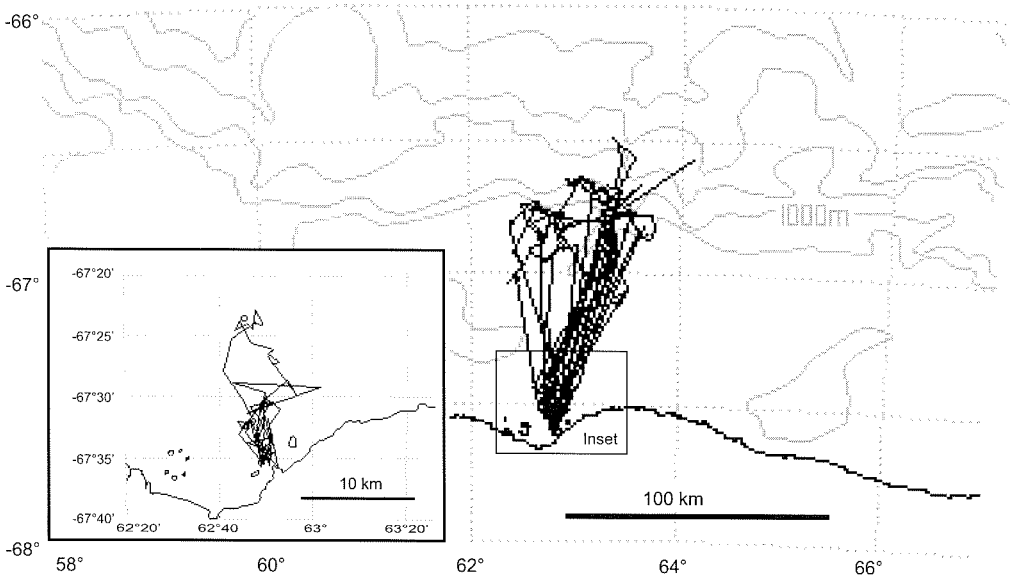

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