

Petra Quillfeldt · Juan F. Masello · Ian J. Strange

Breeding biology of the thin-billed prion *Pachyptila belcheri* at New Island, Falkland Islands: egg desertion, breeding success and chick provisioning in the poor season 2002/2003

Received: 20 June 2003 / Accepted: 5 August 2003 / Published online: 30 September 2003
© Springer-Verlag 2003

Abstract We present data on breeding success, chick growth and chick feeding in thin-billed prions, *Pachyptila belcheri*, at New Island, Falkland Islands, in the breeding season 2002/2003. As in many populations of seabirds in the region, the overall breeding success was very low. This was mainly caused by low rate of observed burrow occupancy (60%) and hatching (57%) of thin-billed prions, while chick survival was closer to normal. Sixty-eight percent of the chicks survived to fledging. In total, a chick was successfully reared in 23% of the nests or from 38% of recorded eggs. The failed eggs were found to be incubated for 30 days, on average. The time of egg desertion coincided with the time of desertion of other seabirds at New Island, with a period of high sea-surface temperatures and low catch rates by the commercial fisheries. We describe chick growth and use repeated weighings, corrected for metabolic loss, to estimate meal sizes. Chicks were fed a mean 39.2 g in 77% of the nights. We discuss possible reasons for the observed extremely low hatching success, and compare with the breeding success of other seabirds at the Falkland Islands.

Introduction

Seabirds breeding on subantarctic islands are largely dependent directly or indirectly on the transport of plankton and minerals by the Southern Ocean, which are brought to the surface along the Antarctic convergence zone or which are transported to lower latitudes by water movements such as the Falkland current.

The cold, mineral-rich waters of the Falkland current provide food for vast breeding colonies of seabirds in the southwest Atlantic, from the Falkland Island archipelago to the Atlantic coast of Patagonia. However, the Southern Ocean and its offshoots are characterized by strong spatial and temporal variability in the availability of food. Fluctuations in the abundance of plankton have a substantial influence on the reproductive performance of predators such as seabirds, squid and seals. There are only a few series of long-term data on any level of the food chain in the Falkland Islands, and therefore our understanding about the influence of environmental variability in the Falkland current marine ecosystem is still very limited. There is also growing concern about human influence in the form of global warming on the Antarctic and related ecosystems and also in the form of fisheries. A better understanding of the variability of conditions and the impact on the various parts of the food chain is needed.

The breeding season 2001/2002 was very poor for some penguin colonies in the eastern Falkland Islands, where the number of fledglings was low, and rockhopper penguins (*Eudyptes chrysocome*) moulted a month later than usual, suggesting that they were in a poor physical condition (Falklands Conservation). The data indicate a shortage of food. In line with this, the 2001/2002 squid fishery season in the Falklands was the worst on record, with only about a tenth of the catch of other years. The squid fishing in Argentine waters was also very poor in 2001/2002 (R. Cardón, personal communication) and the situation was reported to be similarly bad in international waters. Magellanic penguins (*Spheniscus*

P. Quillfeldt (✉)
School of Biosciences,
Main Building, Museum Avenue,
P.O. Box 915, Cardiff,
CF10 3TL UK
E-mail: QuillfeldtP@Cardiff.ac.uk
Fax: +44-29-20874305

J. F. Masello
Ecology of Vision Group,
School of Biological Sciences,
University of Bristol,
Woodland Road, Bristol,
BS8 1UG UK

I. J. Strange
New Island South Conservation Trust,
The Dolphins, Stanley,
Falkland Islands

magellanicus) mainly feed on squid and juvenile fish (Pütz et al. 2001). In 2001/2002, however, they were eating large amounts of lobster krill (*Munida gregaria*) even though neither they nor their chicks can digest its shells (Thompson 1993). Corpses of starved adults were picked up at sea (Falklands Conservation). In contrast, rockhopper penguins at New Island had good breeding success in 2001/2002 and also moulted as usual. Fledgling Magellanic penguins at New Island in 2001/2002 had some of the heaviest weights recorded (I. Strange, unpublished data). Thin-billed prions, *Pachyptila belcheri*, at New Island in 2001/2002 likewise had good breeding success, when around 100 chicks fledged from 140 nests on New Island (M. Silva, personal communication). The data of the 2001/2002 breeding season indicate that, within the Falkland archipelago, there may be huge variations in productivity from area to area.

In 2002/2003, low breeding success of penguins in the Falkland Islands was observed in many colonies in different parts of the Falkland Islands. At New Island, gentoo penguins (*Pygoscelis papua*) failed completely. Black-browed albatrosses (*Diomedea melanophris*) and king cormorants (*Phalacrocorax atriceps*) likewise had extremely low breeding success (authors' observation). All king cormorants and most rockhopper penguins abandoned their nests at New Island in the days around 10 December 2002 (F. Zuñiga, personal communication). Several dead black-browed albatrosses and thin-billed prions were washed onto a beach in late December 2002 (I. Strange, personal observation). The squid fishery does not start until March 2003, after the end of the seabird breeding season. In March and April 2003, the abundance of squid around the Falkland Islands increased to near normal levels, and catches of Argentine shortfin squid (*Illex argentinus*) in the San Matías Gulf in Patagonia, Argentina, were good in this period (Rio Negro Institute of Marine Biology and Fisheries).

Thin-billed prions are small nocturnal petrels, and the absence of adults from the nest burrow during the day provides the opportunity to collect data on chick provisioning with relatively low disturbance to the birds. The life-cycle and basic biology of thin-billed prions have been described by Strange (1980). The author also provided a first growth curve for the body-mass development of chicks. More recently, studies of the biology of thin-billed prions were carried out in Kerguelen, including studies of sexual dimorphism of voice and morphology (Genevois and Bretagnolle 1995), feeding ecology (Cherel et al. 2002; Chastel and Bried 1996) and parental investment (Duriez et al. 2000; Weimerskirch et al. 1995). The aim of the present study is to: (1) examine breeding success, chick growth and provisioning of thin-billed prions on New Island, Falkland Islands in the breeding season 2002/2003, (2) compare the data with previously published data of the species, and (3) discuss the data in the context of the widespread failure of seabirds breeding in the southwest Atlantic in 2002/2003.

Materials and methods

The study was carried out on New Island, Falkland Islands, from 8 January to 4 February 2003. Thin-billed prions breed in the Falkland Islands, Isla Noir (Chile), Crozet and Kerguelen. New Island is the most important known breeding site for thin-billed prions. About 2 million pairs breed on this island (Catry et al. 2003).

Thin-billed prions show the typical procellariiform pattern of a single egg-clutch and slow chick development, with an average fledging period of 50 days (Strange 1980). Thin-billed prions are burrow-nesters, and we reached chicks in their nest chambers via short access tunnels in the roof of each burrow, capped with removable stone lids. This system facilitated rapid access to chicks, reducing overall disturbance. Nests were marked 2 years previously to the present season by M. Silva. Marked nests were monitored for eggs and hatching chicks.

When an egg was detected, length and breadth were measured to the nearest 0.1 mm with callipers, and the egg was weighed to the nearest 0.1 g using a digital balance. Egg density D was determined from egg mass M (in g), egg length L (in cm) and egg breadth B (in cm) as $D = M/\text{egg volume} = M/(L \cdot B^2 \cdot 0.507)$ according to Furness and Furness (1981).

If chicks were present on our first visit, we determined the hatching dates of chicks (to the nearest day) by calibrating wing length against wing growth in chicks of known age. Chicks were weighed daily at 0730 and 1930 hours to the nearest 1 g using a digital balance. Wing length was measured every 3 days to the nearest 1 mm with a stopped wing rule. Tarsus length was measured every 3 days to the nearest 0.1 mm using callipers.

Means are given with standard errors. Fishery data were obtained from Falkland Islands Fishery Statistics (<http://www.fis.com/falklandfish>) and SSTA data were downloaded from http://www.ingrid.ldeo.columbia.edu/SOURCES/.IGOSS/.nmc/.Reyn_SmithOiv1/.weekly.

Results

Laying success

Procellariiform seabirds are known to take "sabbatical years" in which they do not lay eggs (Chastel et al. 1993; Mougin et al. 1997; Warham 1990). In 2002/2003, 46 of 116 (40%) of nests known as active from the previous seasons remained empty.

Egg volume, hatching dates and hatching success

Measurements of 49 eggs were taken. Egg length was 47.1 ± 0.2 mm (range 44.4–51.7 mm), and egg width was 34.3 ± 0.2 mm (range 31.8–36.0 mm). The egg volume was 28.1 ± 0.3 cm³ (range 23.1–31.6 cm³).

The hatching period spanned 25 days (Fig. 1; 30 December 2002 to 23 January). The hatching period and the mean hatching date, 8 January, were later than previously reported for this colony (Strange 1980). Of 70 recorded eggs, 40 (57%) chicks hatched.

Eggs were measured and weighed between 8 and 10 January, and from these weights we estimated the state of incubation of abandoned eggs, using the metabolic weight loss of incubated eggs (Furness and Furness 1981; Weidinger 2000). The weight of fresh eggs of thin-

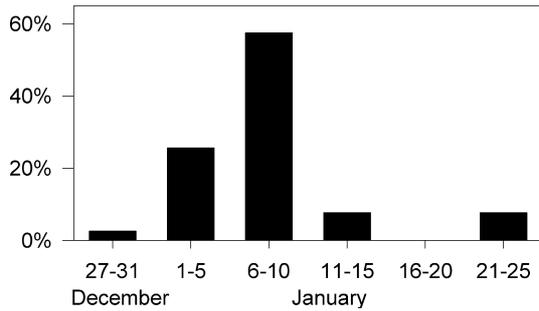


Fig. 1 Distribution of hatching dates of thin-billed prions in 2002/2003 at New Island, Falkland Islands

billed prions at New Island has been reported by Strange (1980) as 30.64 g (range 28.6–32.7 g). Given a mean volume of 28.1 cm³, the density of freshly laid eggs is $D_{\text{fresh}} = 1.09 \text{ g/cm}^3$.

The density of 12 recently pipped eggs (at the beginning of hatching) was 0.91 g/cm³. This corresponds to a loss of density of 0.18 g/cm³ in the incubation period of 47 days or $dD = 0.0038 \text{ g/cm}^3$ per day. The incubation time of abandoned eggs was calculated from the measured density D as $(D - D_{\text{fresh}})/dD$. Eggs had been incubated for a mean period of 30.6 ± 1.7 days (range 0–43 days, Fig. 2). Eight abandoned eggs were found with relatively well-preserved embryos. These embryos measured 60.8 ± 6.4 mm (range 25–80 mm), indicating that they were far developed, some very close to hatching.

Chick survival and growth

Of 40 hatched chicks, 27 (68%) of the chicks survived until the end of the observation period, and a nest control by M. Strange on 12 March suggested that they survived to fledging. In total, a chick was successfully reared in 23% of the nests or from 38% of recorded eggs. The main chick mortality was caused by starvation of very young chicks (age 1–6 days), which caused nine deaths (70% of dead chicks), while two chicks were predated by a striated caracara (*Phalacrocorax australis*), and two chicks died from nest flooding after heavy rain.

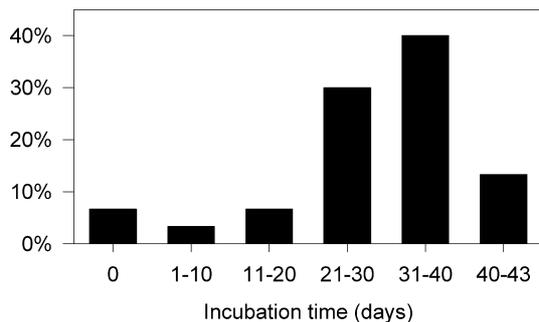


Fig. 2 Distribution of incubation times of failed eggs of thin-billed prions in 2002/2003 at New Island, Falkland Islands

The average chick growth curves showed a typical pattern for a procellariiform seabird. The growth of mass, wing and tarsus of 29 chicks that survived at least until 4 February is shown in Fig. 3. The chicks did not fledge at this time, but due to the limited duration of the field season, later data were not recorded.

Body mass increased to the age of 35 days to a mean of ca. 200 g (Fig. 3, see legend for regression equations), which equals 140% of the average adult body mass of 140 g.

Tarsus growth followed a logistic growth pattern (Fig. 3) and the maximum tarsus length was not yet reached at 35 days of age. Wing growth was well described by a logistic regression (Fig. 3) and continued after the end of our field season.

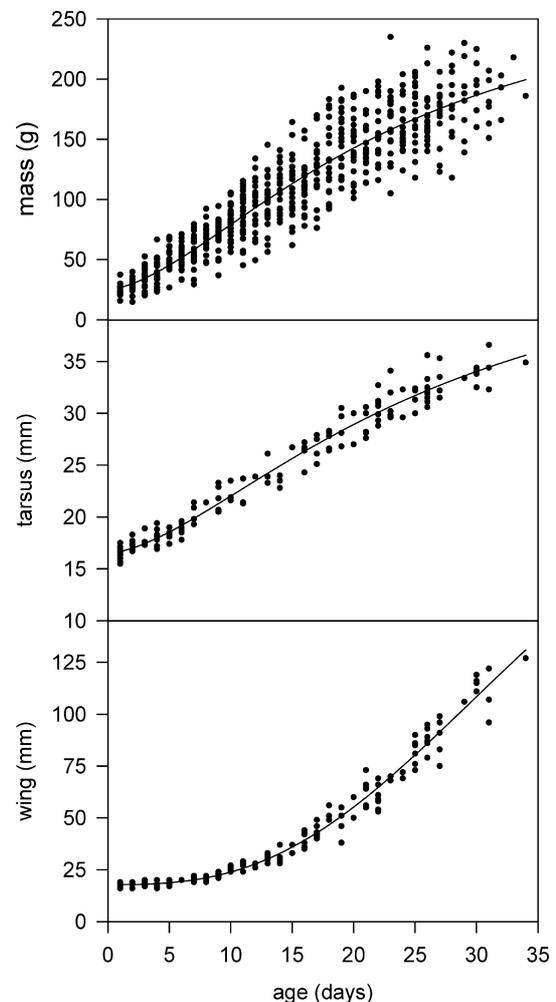


Fig. 3 Chick growth in thin-billed prions in 2003 at New Island, Falkland Islands, until the age of 35 days ($n = 29$). The body-mass development (top) was described by the logistic regression: $m(\text{g}) = 25.3 + 268.6 / (1 + (\text{age}/23.4)^{-1.6})$ ($R^2 = 0.86$, $df = 602$, $F = 1188$, $P < 0.001$), where age is measured in days from hatching. The tarsus growth (middle) and the wing growth (bottom) followed logistic regressions: $\text{tarsus (mm)} = 16.5 + 31.7 / (1 + (\text{age}/26.3)^{-1.6})$ ($R^2 = 0.97$, $df = 134$, $F = 1338$, $P < 0.001$) and $\text{wing (mm)} = 17.9 + 278.1 / (1 + (\text{age}/38.9)^{-2.8})$ ($R^2 = 0.99$, $df = 163$, $F = 2299$, $P < 0.001$)

Chick feeding

Meal sizes and feeding frequencies were estimated from the evening and morning weights, by correcting the mass differences for metabolic mass loss (e.g. Quillfeldt and Peter 2000). We calculated weight-loss data for loss before and after a feeding event. The mass loss before and after a feeding event depended on the weight of the chick at the beginning of the interval. The mass loss was greater in 12-h periods after a feeding event. The metabolic mass loss dm (g/h) can be described by the following linear regressions: $dm(\text{before feeding}) = -0.004 \text{ g/h} \cdot m + 0.050 \text{ g/h}$ ($R=0.71$, $F=46.7$, df 1,45, $P<0.001$), and $dm(\text{after feeding}) = 0.112 \text{ g/h} \cdot m + 0.109 \text{ g/h}$ ($R=0.78$, $F=269.8$, df 1,179, $P<0.001$), where m is the mass of chicks at the beginning of the interval. Using these mass-loss equations, we analysed data from evening and morning weighings for 363 chick nights of chicks older than 5 days. We first determined whether chicks had been fed or not. We calculated the mass loss over 12 h without a feeding event for each chick night according to the mass of the chick, using the regression equation from intervals before feeding. For a total of 41 chick nights, the observed overnight mass change (calculated from evening and morning measurements) was larger than the estimated metabolic mass loss, indicating that these chicks were not fed and lost more than the average weight over the 12-h night period. We assume that there was the same number of chicks that were not fed and lost less than the average amount of mass, giving a total of 82 chicks (22.6%) that were not fed. For the other 77.4% of chick nights, in which feedings occurred, we calculated the daily mass loss using the regression equation for the mass loss after feeding, starting with the evening weight. Meal sizes were calculated as the sum of the observed mass change overnight and the estimated metabolic mass loss.

Using this method, the estimated sizes of nightly meals were between 10.2 and 104.2 g (Fig. 3), with a mean of 39.2 ± 16.9 g. Meal sizes were defined to represent one feeding for meal sizes up to 50 g and two feedings for meal sizes larger than 50 g (about half of the maximum food delivered by two parents). Using this definition, the mean meal size for a single feeding was 32.6 ± 6.6 g ($n=223$, range 10.2–49.9 g). There was a total of 58 double feedings, with a mean size of 64.7 g (range 50.5–104.2 g), corresponding to a mean of 32.4 g per parent. This value was very close to that found for single feedings. The maximum value of a double feeding was registered at 104.2 g, corresponding to 52.1 g per parent. This value was very close to the maximum value for a single feeding using the present definition. However, two meals of the smallest recorded mass (10.2 g) would weigh considerably less than the presumed lowest mass of a double meal (50 g), and in this case the analysis would underestimate the proportion of double meals (Fig. 4).

Chicks were fed in 77% of the nights ($n=363$). Single meals were fed on 223 nights (61% of all nights); 2

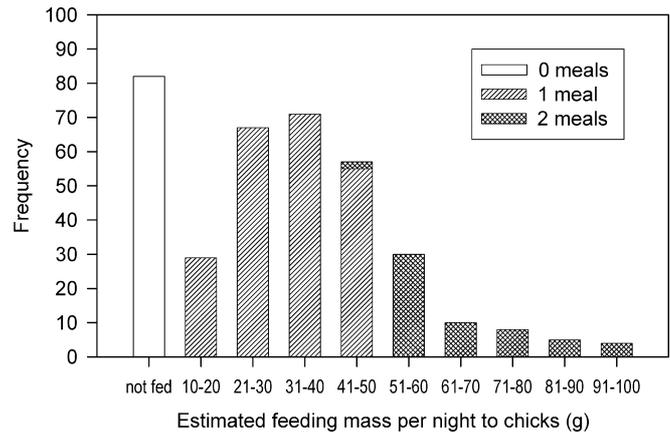


Fig. 4 Distribution of feeding rates of chicks of thin-billed prions in 2003 at New Island, Falkland Islands (grams of food received per chick and night) over 363 chick nights and feeding events defined to represent no feedings, single and double meals

adults fed on 58 (16%) nights. Over 363 nights, chicks thus received 339 feedings, averaging 0.93 feedings per night. Assuming equal feeding behaviour between pair partners, each parent fed on 47% of nights.

The feeding rate was correlated to chick age ($R=0.224$, df 362, $P<0.001$) and date ($R=0.191$, df 362, $P<0.001$). The feeding rate of older chicks was increased (Fig. 5). This was mainly due to an increase in feeding frequencies, while the meal size did not show seasonal effects for chicks older than 5 days (Fig. 5).

Discussion

Thin-billed prions at New Island experienced a late and poor season, with a high rate of egg desertion. The main time of egg desertion was 30 days after laying, in the first half of December. This coincided with observed desertion of breeding attempts by cormorants and rockhopper penguins at New Island. There have been suggestions that Harmful Algal Blooms (HAB or “red tide”) might have been responsible for the desertion of seabirds (Falklands Conservation). However, no evidence for this could be found (M. Bingham, personal communication). Samples of dead penguins have not shown any evidence of toxic poisoning from HAB. Moreover, virtually all the dead penguins had empty stomachs, which is not consistent with HAB poisoning, as HAB poisons typically act within 15–60 min and poison victims have remains of the food in their stomachs. HAB affects mostly shellfish, and there is no record of penguins ever having been affected by HAB, even in areas where red tide is prevalent, as penguins do not eat shellfish.

The desertion of thin-billed prions and other seabirds thus suggests that there was a general food shortage. Thin-billed prions feed predominantly on amphipods (Cherel et al. 2002; Strange 1980), which are also a minor component of the diet of rockhopper penguins (Pütz et al. 2001). However, in a year of low food

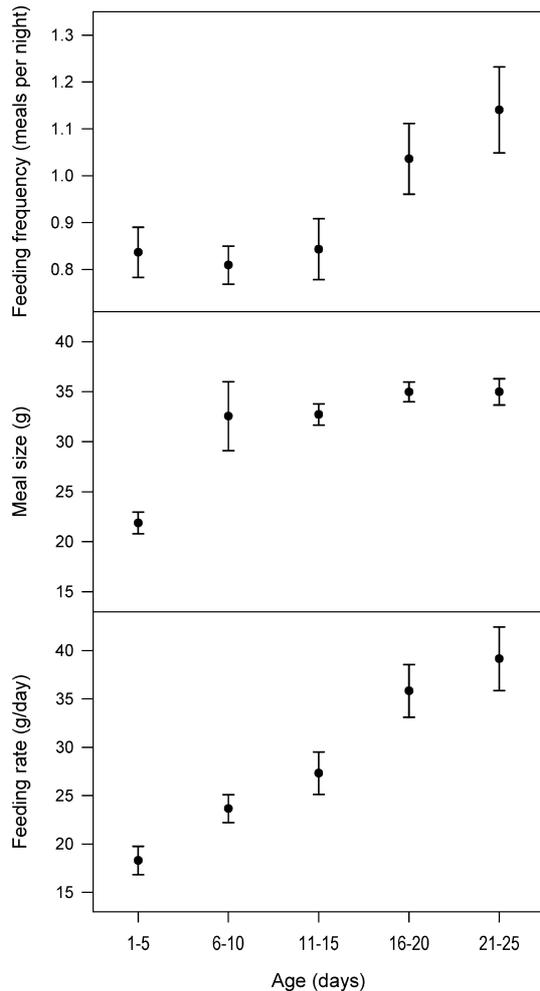


Fig. 5 Changes of feeding frequencies and meal sizes with age (1–25 days) of chicks of thin-billed prions in 2003 at New Island

availability, rockhopper penguins may change their diet composition and take up to 100% crustaceans, including amphipods. The synchronous desertion of thin-billed prions and rockhopper penguins suggests that sufficient crustaceans were not available to sustain the breeding colonies of these birds. This is not the first time starvation led to heavy mortality of seabirds in the Falklands. Keymer et al. (2001) reported heavy mortality of rockhopper penguins during the 1985–1986 breeding season. Starvation was diagnosed as the primary cause of death, possibly caused by a shortage of crustaceans due to unusual meteorological conditions. No conclusive evidence of infectious disease or toxicosis was found.

Thin-billed prions, preying mainly on amphipods, are at the same trophic level as most commercially caught fish and squid in the Falkland islands, and data from the fishery may thus give some insight into variations of resource availability. The southern blue whiting (*Micromesistius a. australis*) is a highly commercially exploited mid-water pelagic gadiform fish, occurring between 38°S and 62°S. The southern blue whiting invades shelf waters during summer in order to feed on amphipods and euphausiids, and it is thus

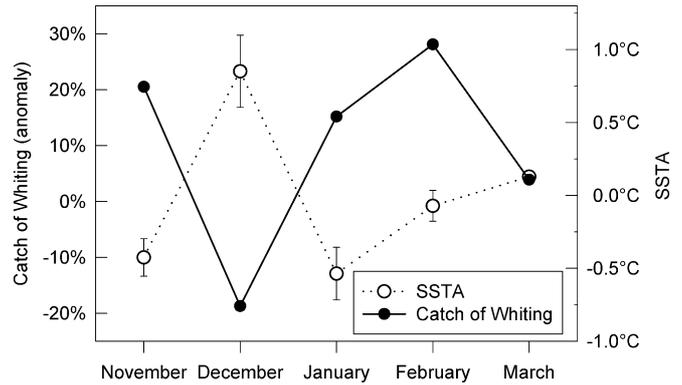


Fig. 6 Catch of southern blue whiting (*Micromesistius australis*) (relative to mean monthly catch rates) and monthly sea-surface temperature anomaly (SSTA) in the area 50–52°S, 61–63°W

potentially suitable for assessing amphipod and euphausiid abundance. The time of egg desertion of thin-billed prions at New Island coincided with a period of high sea-surface water temperatures and low catch rates of southern blue whiting by the commercial fisheries (Fig. 6). Later in the breeding season, both the feeding rate of thin-billed prions and the catch rates by the commercial fisheries (Fig. 6) increased.

The surface oceanography of the southwest Atlantic is characterized by the presence of the Atlantic Circumpolar Current (ACC), its extension, the Falkland (Malvinas) current and opposing flow, the subtropical Brazil current. The Falkland current originates in the northern flow of the ACC. The current's main flow carries water of Antarctic origin, from the APFZ, north along the Patagonian Shelf edge to its confluence with the subtropical Brazil current at approximately 38°S. When meeting the Patagonian shelf break front, found along the 200-m isobath, the waters generate a zone of increased productivity. More minor subsurface flows carry cool, nutrient-rich Antarctic water over the continental shelf to the west of the Falkland Islands as the inner branch of the Falkland current. An increase in water temperature such as observed in December 2002 indicates that the influx of the Falkland current was weakened during the period, and the transport of nutrients and zooplankton was slowed down.

Thin-billed prions had a relatively much higher breeding success than penguins and cormorants breeding at New Island during 2002/2003. Thin-billed prions had an average breeding success in 2001/2002, when around 100 chicks fledged from 140 nests on New Island (M. Silva, personal communication), while many species of seabirds failed in the Falklands. The most likely reason for the relative success of thin-billed prions is their diet composition. By relying nearly exclusively on small amphipods, thin-billed prions are not in direct competition with the fishery. Thus, they are not affected by the fishery-related decreases in breeding success that have led to a dramatic decline in population size in rockhopper penguins and Magellanic penguins in the

Falkland Islands during the 1980s and early 1990s. These declines did not occur in coastal South America, and therefore the suspected cause of decline is a reduction of fish and squid due to large-scale commercial fishing around the Falklands (Bingham 2002). Sixty percent of the biomass of fish and squid are commercially removed every year, causing widespread breeding failure even in years of good natural-food abundance. This is especially obvious in Magellanic penguins. Diet analysis showed that Magellanic penguins have a greater reliance on squid and fish species being taken commercially (Pütz et al. 2001) than the other species of penguins. While rockhopper and gentoo populations had a stable period during years of good natural-food abundance in 1995 and 2000, albeit at a much lower level than before commercial fishing began (Bingham 2002), Magellanic penguins continued declining in the Falklands even during the good years 1995–2000 (Bingham 2002). In Chile and Argentina (where no-fishing zones are in place to protect the penguin colonies), Magellanic penguin chicks get fed over twice the amount of food than in the Falkland Islands, and chick survival is higher (1.4 chicks per nest vs 0.6 chicks per nest in the Falklands; Bingham 2002). The surviving chicks, furthermore, fledge with an average weight of 3.6 and 3.4 kg in Chile and Argentina, while in the Falklands, it is much lower at 2.7 kg. Very few of the chicks that fledge in the Falklands will survive their 1st year as juveniles.

In years of poor natural-food abundance, such as 2001/2002 and 2002/2003, the breeding colonies cannot sustain themselves, and adults that are already in poor condition either abandon their breeding attempts (e.g. Chastel et al. 1995; Chaurand and Weimerskirch 1994) or starve. Diet change may additionally lead to increased competition among the top predators. In rockhopper penguins, squid gradually disappeared from the diet over the period 1990–1999 (Pütz et al. 2001). Rockhopper penguins take large amounts of crustaceans (Pütz et al. 2001), and therefore potentially have considerable dietary overlap with thin-billed prions. They may have distinct foraging zones and foraging depths, provided there is sufficient abundance of food.

A larger foraging range of thin-billed prions, compared with penguins and cormorants, may be a further factor for the normally robust breeding success (M. Silva, personal communication). Closely related dove prions (*Pachyptila desolata*) have an estimated foraging range of 300 km during a feeding trip of 1–2 days (Croxall and Prince 1980; Croxall et al. 1984), much higher than penguins breeding at New Island: gentoo penguins < 25 km, Magellanic penguins < 90 km, rockhopper penguins < 35 km (Boersma et al. 2002). Moreover, thin-billed prions can leave their egg unattended in the nest burrow for periods of 1 to several days during the incubation time. This gives them an even more flexible foraging range during incubation. During chick-feeding, thin-billed prions in Kerguelen have been found to alternate between short and long trips, lasting for up to 8 days (Weimerskirch et al. 1995). During this

time, they can cover large distances, and the foraging range may be substantially enlarged. At New Island, rockhopper penguins have been shown to use a similar strategy (Boersma et al. 2002), although on a smaller spatial scale than thin-billed prions. All rockhoppers tracked during incubation, and several of those tracked during chick-rearing, took long foraging trips more than 100 km in southerly and westerly directions from the colony, in some cases more than 300 km (Boersma et al. 2002).

In the present study, chick mortality was initially high, but chicks that survived the 1st week had a very good chance of fledging. However, compared with the results of Strange (1980), the average weight of 200 g at 35 days was low. Strange (1980, see Fig. 11) reported that thin-billed prions reached peak masses of 240 g at 34 days of age. Feeding frequencies increased only slowly with age (Fig. 5), while other species of small petrels show a very rapid increase (e.g. Quillfeldt and Peter 2000). The low mass of chicks and the low feeding frequencies during the first weeks of chick-feeding can be explained by two, not mutually exclusive, hypotheses. Either the food availability was still relatively low in January 2003 (but Fig. 5 suggests it was increasing), or provisioning adults still had low body conditions following the food shortage in December, and were recovering by undertaking long foraging trips.

The range of meal sizes observed here was similar to meal sizes reported for thin-billed prions breeding in Kerguelen (Cherel et al. 2002), with a maximum of about 100 g/night delivered by two parents. The maximum meal size that can be carried depends on the body mass and wing size of the bird, and is not dependent on food abundance or the distance to the foraging area. When the meal sizes are thus limited, adults can only increase feeding rates by increasing feeding frequencies.

Compared with feeding frequencies reported for thin-billed prions breeding in Kerguelen (Cherel et al. 2002; Weimerskirch et al. 1995), the feeding frequencies reported here were high. Adults in Kerguelen made only 50% short trips (1–4 days), and long trips lasted for up to 8 days (Weimerskirch et al. 1995). This resulted in an average feeding rate of only 0.41 feedings per night, compared with 0.93 feedings per night reported here. Cherel et al. (2002) observed similarly low feeding rates: in three seasons on Kerguelen, 53, 52 and 45% of chicks were fed, compared with 77% in the present study. Although the thin-billed prions of the present study had masses below those previously reported for New Island (Strange 1980), none of the older chicks showed signs of starvation, and the comparison with the feeding rates of the same species in Kerguelen suggests that they were relatively well fed.

Acknowledgements We are grateful to the New Island South Conservation Trust for permission to work on the island. We wish to thank Monica Silva for the excavation and marking of nests during her fieldwork and Maria Strange for her support of this work. This study was funded by a grant provided by the German Science Foundation DFG (Qu 148/1).

References

- Bingham M (2002) The decline of Falkland Islands penguins in the presence of a commercial fishing industry. *Rev Chil Hist Nat* 75:805–818
- Boersma PD, Stokes DL, Strange IJ (2002) Applying ecology to conservation: tracking breeding penguins at New Island South reserve, Falkland Islands. *Aquat Conserv Mar Freshwater Ecosyst* 12:63–74
- Catry P, Campos A, Segurado P, Silva MC, Strange IJ (2003) Population census and nesting habitat selection of thin-billed prion *Pachyptila belcheri* on New Island, Falkland Islands. *Polar Biol* 26:202–207
- Chastel O, Bried J (1996) Diving ability of blue petrels and thin-billed prions. *Condor* 98:627–629
- Chastel O, Weimerskirch H, Jouventin P (1993) High annual variability in reproductive success and survival of an Antarctic seabird, the snow petrel *Pagodroma nivea*. *Oecologia* 94:278–285
- Chastel O, Weimerskirch H, Jouventin P (1995) Influence of body condition on reproductive decision and reproductive success in the blue petrel. *Auk* 112:964–972
- Chaurand T, Weimerskirch H (1994) Incubation routine, body mass regulation and egg neglect in the blue petrel *Halobaena caerulea*. *Ibis* 136:285–290
- Cherel Y, Bocher P, De Broyer C, Hobson KA (2002) Food and feeding ecology of the sympatric thin-billed *Pachyptila belcheri* and Antarctic *P. desolata* prions at Iles Kerguelen, Southern Indian Ocean. *Mar Ecol Prog Ser* 228:263–281
- Croxall JP, Prince PA (1980) Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol J Linn Soc* 14:103–131
- Croxall JP, Ricketts C, Prince PA (1984) Impact of seabirds on marine resources, especially krill, of South Georgian waters. In: Wittow GC, Rahn H (eds) *Seabird energetics*. Plenum, New York, pp 285–317
- Duriez O, Weimerskirch H, Fritz H (2000) Regulation of chick provisioning in the thin-billed prion: an interannual comparison and manipulation of parents. *Can J Zool* 78:1275–1283
- Furness RW, Furness BL (1981) A technique for estimating the hatching dates of eggs of unknown laying date. *Ibis* 123:98–102
- Genevois F, Bretagnolle V (1995) Sexual dimorphism of voice and morphology in the thin-billed prion *Pachyptila belcheri*. *Notornis* 42:1–10
- Keymer IF, Malcolm HM, Hunt A, Horsley DT (2001) Health evaluation of penguins following mortality in the Falklands. *Dis Aquat Organism* 45:159–169
- Mougin J-L, Jouanin C, Roux F (1997) Intermittent breeding in Cory's shearwater *Calonectris diomedea* on Selvagem Grande, North Atlantic. *Ibis* 139:40–44
- Pütz K, Ingham RJ, Smith JG, Croxall JP (2001) Populations trends, breeding success and diet composition of gentoo *Pygoscelis papua*, magellanic *Spheniscus magellanicus* and rock-hopper *Eudyptes chrysocome* penguins in the Falkland Islands. *Polar Biol* 24:793–807
- Quillfeldt P, Peter H-U (2000) Provisioning and growth in chicks of Wilson's storm-petrels (*Oceanites oceanicus*) on King George Island, South Shetland Islands. *Polar Biol* 23:817–824
- Strange I (1980) The thin-billed prion, *Pachyptila belcheri*, at New Island, Falkland Islands. *Gerfaut* 70:411–445
- Thompson KR (1993) Variation in Magellanic penguin diet in the Falkland Islands. *Mar Ornithol* 21:57–67
- Warham J (1990) *The petrels. Their ecology and breeding systems*. Academic, London
- Weidinger K (2000) Incubation mass loss in Cape petrel *Daption capense* eggs. *Folia Zool* 49:27–31
- Weimerskirch H, Chastel O, Ackermann L (1995) Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the thin-billed prion *Pachyptila belcheri*. *Behav Ecol Sociobiol* 36:11–16