Elevated sea-surface temperature, reduced provisioning and reproductive failure of wedge-tailed shearwaters (*Puffinus pacificus*) in the southern Great Barrier Reef, Australia

B. V. Smithers[A], *D. R. Peck*[A], *A. K. Krockenberger*[A] *and B. C. Congdon*[A,B]

[A]School of Tropical Biology, James Cook University, Cairns, Qld 4870, Australia.
[B]Corresponding author. Email: brad.congdon@jcu.edu.au

Abstract. During the 2002 austral summer abnormally high sea-surface temperatures (SST) occurred in the southern Great Barrier Reef (GBR), Australia. This phenomenon was accompanied by reduced provisioning, decreased growth rates and reproductive failure of wedge-tailed shearwaters in the region. In 2002, adults were unable to compensate for changes in either the availability and/or accessibility of forage-fish by increasing food loads or foraging rates. This is one of few studies to explicitly correlate decreases in chick provisioning with above-average annual variation in SST and is the first to do so for a tropical seabird species in the western Pacific. It adds to an increasing number of data sets identifying the potential negative impacts of increasing SST at upper-trophic levels. As SST continue to rise with global climate change, our results predict substantial detrimental effects on seabird populations of the GBR. This finding has important implications for both seabird and coral reef ecosystem management in the region. Our results also suggest that wedge-tailed shearwaters are sensitive indicators to changes in forage-fish availability/accessibility associated with SST variation that can be used to develop models of, and monitor for, these potential impacts.

Extra keywords: El Niño–Southern Oscillation, forage-fish, seabird reproduction.

Introduction

Sea-surface temperatures (SST) in many tropical regions have increased by almost 1°C during the past 100 years, and are continuing to increase at a rate of approximately 1–2°C per century (Hoegh-Guldberg 1999). Increasing SST are related closely to various large-scale atmospheric phenomenon such as the El Niño–Southern Oscillation (ENSO) (Cane 1983).

The larger-scale impact of ENSO on seabird reproductive parameters in the central and eastern Pacific is well documented (Schreiber and Schreiber 1984; Ainley *et al.* 1988; Duffy *et al.* 1988; Cruz and Cruz 1990). A single severe ENSO event in 1982–1983 produced reproductive failure and high adult mortality in several seabird species breeding in these areas (Schreiber and Schreiber 1984; Ainley *et al.* 1988; Schreiber 1994). Detailed results correlate prevailing El Niño conditions with negative effects on many aspects of seabird breeding biology, including lengthened fledging periods, slowed growth rates, a reduced incidence of breeding and decreased nesting success (Ainley *et al.* 1988; Cruz and Cruz 1990).

Recently, several studies have directly correlated annual variation in SST with fluctuations in long-term population size (Veit *et al.* 1997; Guinet *et al.* 1998; Pinaud and Weimerskirch 2002; Ramos *et al.* 2002; Jenouvrier *et al.*

2003). Specifically, these studies suggest that, on an annual basis, SST may impact upon important demographic processes such as the timing of breeding, year-to-year recruitment, the number of breeding pairs and hatching success. Yet these studies have not documented any direct mechanism linking SST variation and fledgling survival.

Only for temperate alcids (puffins and auks) has decreased fledging success and SST variation been explicitly linked via correlated decreases in chick provisioning (Kitaysky and Golubova 2000; Hedd *et al.* 2002; Durant *et al.* 2003). For example, Durant *et al.* (2003) showed that the quality and quantity of food reaching Atlantic puffin (*Fratercula arctica*) chicks was compromised in years when SST were higher than normal, leading to significant declines in overall breeding success. The exact mechanisms by which food availability declined in their and other studies linking SST and chick provisioning remain unclear (Kitaysky and Golubova 2000; Hedd *et al.* 2002; Stenseth *et al.* 2002; Durant *et al.* 2003).

The majority of work examining the effects of SST on fledgling success has focused on species breeding in temperate climates (e.g. Guinet *et al.* 1998; Durant *et al.* 2003; Jenouvrier *et al.* 2003). Little research has examined impacts in tropical species beyond those associated with the 1982–1983 ENSO event (Schreiber and Schreiber 1984; Ainley *et al.* 1988; Cruz and Cruz 1990; Schreiber 1994), and

a recent study that documented reduced fledgling survival during abnormally high SST years in a low-latitude albatross (Fernandez *et al*. 2001).

Nothing is known of above-average SST effects on seabird reproductive success in the western Pacific, especially for birds nesting on the Great Barrier Reef (GBR), Australia. Similar negative impacts on breeding success may be occurring in GBR populations, particularly during events like the 1997–1998 ENSO, which was accompanied by extremely high SST and severe coral bleaching (Hoegh-Guldberg 1999; Berkelmans *et al*. 2002).

During two exceptionally warm periods in the austral summer of 2001–2002, SST in the GBR were maintained at 1.5–2°C above the long-term seasonal average of 27.5°C for up to 2 weeks (Marshall *et al*. 2002). Although this was not classified as an El Niño event, these temperatures exceeded those recorded during the 1998 El Niño and were also accompanied by extensive coral bleaching (Marshall *et al*. 2002). The previous 2000–2001 austral summer saw relatively 'normal' SST and no evidence of coral bleaching (Berkelmans 2002).

The coincident occurrence of this phenomenon with a longer-term study of the foraging ecology of the wedge-tailed shearwater (*Puffinus pacificus*) in the southern GBR provided the first opportunity to identify the potential impacts of ENSO-related SST change on breeding success in this and other associated seabird species. By comparing several wedge-tailed shearwater breeding parameters across the two breeding seasons, the first having relatively normal (2001) and the second abnormally high SST (2002), we were able to identify the potential effects of elevated SST on fledgling survival in this species.

Materials and methods

The wedge-tailed shearwater is a tube-nosed seabird (Procellariidae) that nests in burrows on islands throughout the tropics, including coral islands of the GBR (Marchant and Higgins 1990). Breeding adults rear a single chick over a relatively long 60–70-day nestling period. They forage over large distances and return to feed chicks only at night (Marchant and Higgins 1990). The present study was undertaken during February–March 2001 and 2002 at Heron Island (23°26′S, 151°51′E), a coral cay of the Capricorn Island group of the southern GBR. A total of 29 nests were monitored in 2001 and 26 in 2002. During the 2001 breeding season, SST recorded at Heron Island for the February–March study period ranged from 22.5°C to 30°C whereas they ranged from 22.5°C to 32°C for the same period in 2002 (http://www.aodc.gov.au/, accessed November 2003).

Adult provisioning rate, chick growth and chick survivorship were monitored at each nest daily. Chicks were weighed twice a day at 06:00 h and 16:00 h using an electronic balance (±0.1 g). Between these times no adult visits or chick feeding was observed. Culmen and tarsus measurements were also obtained for each chick every 4 days using dial calipers (±0.1 mm). At each burrow, both adults were banded for individual recognition and attendance was monitored continuously from 17:00 h to 05:00 h daily. During monitoring in 2001, burrow entrances were partially obstructed with markers that allowed adult visits to be detected. In 2002 a sliding trapdoor of clear Perspex, which was triggered by adults entering the burrow, replaced these markers. After adults had entered the burrow and chick feeding was complete, as indicated by chicks no longer begging, the visiting adult was captured and identified. After each capture, markers/traps were reset so that subsequent visits by the same or other adults could be detected. Chick weights were obtained immediately following any known adult visit to a nest.

Chick growth rates

Daily mass gains for each chick were determined by calculating the weight change over each 24-h period (the difference between two consecutive 16:00 h weights). The daily mass gain represents the amount a chick was fed during the previous 24 h, minus the amount used in respiration and excretion. As we were interested only in overall mass gain for comparative purposes, adjustments for mass loss owing to respiration and excretion were not required (Schreiber 1996). All else being equal, a chick's change in mass will be directly proportional to the amount of food it receives.

To control for the possibility that feed sizes may change as a season progresses, mean daily mass gains for each experimental chick were determined over 7 consecutive nights during the same 2-week period in late February–early March in both breeding seasons. To control for possible allometric differences in growth rates or metabolic demands, only chicks of similar body size were included in the comparative analyses (chick culmen length of 23–25 mm on Day 1). This provided samples of 24 chicks in 2001 and 12 in 2002. Average daily mass gains in each season were compared using Student's *t*-test. Individual chicks were used as replicates in this analysis with the data for each chick comprising the mean daily mass increase obtained over the 7-night observation period.

Adult provisioning rates and chick mortality

A chick was determined to have been provisioned by an adult if it gained mass during any single night, regardless of whether an adult was observed or not. Comparisons were made between the frequency of provisioning visits that occurred during each 7-night study period in 2001 and 2002, as per the mass gain experiment described above. To control for possible variation in provisioning rate associated with chick size differences, only chicks of similar body size were included in the comparative analyses, as per the chick growth rate experiment described above (chick culmen length of 23–25 mm on Day 1). Differences in both the median rate and variance of adult provisioning among the 2 years were tested using a Kolmogorov–Smirnov test for identical distributions. To determine the relationship between provisioning rate, mass gain and year, an analysis of covariance (ANCOVA) was used with provisioning rate as the covariate. Chick mortality during the entire 4-week observation period was also compared across the 2 years using a χ^2 goodness-of-fit test.

Comparison of adult self-provisioning between years

Mean empty adult mass at the end of the 4-week study period was compared between years to determine if differences in SST and/or provisioning patterns were correlated with adult mass change. To do this, between 20 and 25 adults were captured each year and weighed at dawn (04:00–05:00 h), immediately before leaving the island to begin foraging. Birds leaving on foraging trips were easily identified moving towards and queuing at known take-off points. Adults were not observed returning to feeding chicks after 04:00 h; therefore, it was assumed that birds captured between 04:00 h and 05:00 h were not carrying food to be delivered to chicks. Between-year mean empty adult mass was compared using Student's *t*-test. All statistical analyses were undertaken using SPSS 11.0.1 (SPSS 2001).

Results

Chick growth rates

Charting the daily mean mass of chicks during the 7-day observation period for each year (Fig. 1) clearly demonstrates that although both cohorts of chicks began the observation period at equivalent weights (and culmen length), in 2001 chicks gained weight considerably faster than they did in 2002. This is reflected in the overall mean mass gain for each year. Chicks gained significantly more mass per day in 2001 (4.79 g day^{-1}, s.e. = 1.23) than in 2002 (-4.36 g day^{-1}, s.e. = 2.31 or a net loss of 4.36 g day^{-1}), ($t = 4.292$, d.f. = 33, $P < 0.001$).

Adult provisioning rates and chick mortality

Chicks were fed less often in 2002 than in 2001 (Fig. 2; $Z = 3.19$, $P < 0.001$), with the median number of observed feed nights during the 7-night observation period decreasing from four in 2001 to one in 2002. There was a significant effect of feeding frequency on mean mass gain (Fig. 3; ANCOVA $F_{1,33} = 14.7$, $R^2 = 0.561$, $P = 0.001$) but no separate effect of year on mean mass gain ($F_{1,33} = 0.009$, $P = 0.925$). Thus, in both years chick mass gain per feed was equivalent, but in 2002 chicks obtained significantly fewer feeds (Figs 2 and 3). Combined, these results suggest that in both years adults provisioned chicks with an equivalent amount of food per feed, but that in 2002 they foraged for three to four times as long to obtain each feed. It is also clear that at delivery rates of below two feeds per week chicks were unable to maintain body mass (Fig. 3).

Chick mortality was significantly higher in 2002 than in 2001 ($\chi^2_{d.f.=1} = 16.6$, $P < 0.001$). Of 29 chicks monitored in 2001, one died during the 4-week observation period, whereas 13 of 26 chicks died in 2002. This gives mortality rates of 3.4% in 2001 compared with 50% in 2002. A consistent loss
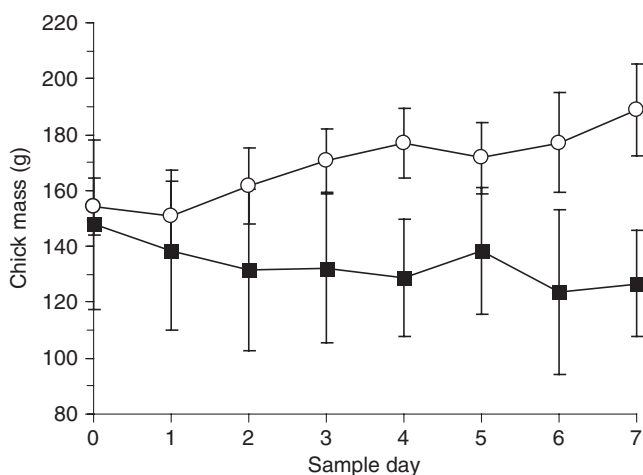
of mass in the remaining 13 chicks in 2002 further suggested that all but one individual was likely to die before fledging.

Adult self-provisioning between years

Mean empty adult weight in 2001 (341.18 g, $n = 25$, s.e. = 4.52) was not significantly different to that observed in 2002 (342.25 g, $n = 20$, s.e. = 5.05), ($t = -0.158$, d.f. = 43, $P = 0.8754$). This suggests that, on average, adults foraged
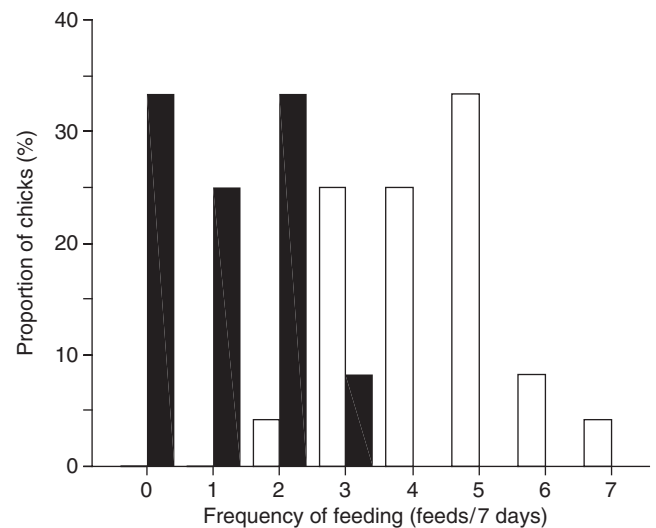

Fig. 2. The distribution of feeding frequency (feeds/7 nights) during the 7-day observation period in (□) 2001 ($n = 24$) and (■) 2002 ($n = 12$). There was a significant effect of year on the number of feeds (Kolmogorov–Smirnov $Z = 3.19$, $P < 0.001$).
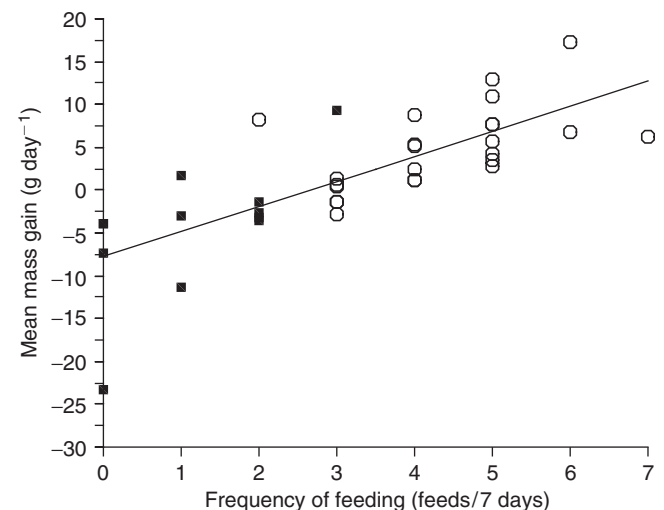

Fig. 3. The effect of feeding frequency on mean daily mass gain in (○) 2001 and (■) 2002. There was a significant effect of number of feeds on mean mass gain (ANCOVA $F_{1,33} = 14.7$, $R^2 = 0.561$, $P = 0.001$). The regression line equation is $y = 2.958x - 0.741$. The effect of year on mean mass gain was not significant (ANCOVA $F_{1,33} = 0.009$, $P = 0.925$).

Fig. 1. Mean chick mass on each day (± 2 s.e.) over the 7-day observation period in (○) 2001 and (■) 2002.

considerably longer between chick feeds in 2002 but they did not lose body condition while doing so.

Discussion

Although chick feed sizes remained relatively constant between years, our results suggest overall that a reduction in average feeding rates to less than two feeds per week in 2002 led to decreases in chick mass gain and substantial increases in chick mortality. This result points to major differences in the ability of adults to successfully provision chicks between 2001 and 2002. In 2002, adults foraged on average three to four times longer for an equivalent amount of food delivered, implying they were unable to compensate for changes in either the distribution or abundance of forage-fish by increasing food loads or foraging rates. As a consequence, Heron Island shearwaters suffered an almost complete reproductive failure.

Our findings are consistent with those obtained for temperate alcids (Kitaysky and Golubova 2000; Hedd *et al.* 2002; Durant *et al.* 2003), making our study one of few to explicitly correlate decreased chick provisioning with above-average annual variation in SST, and the first to do so for a tropical species in the western Pacific. As with previous studies, the exact mechanism by which SST variation influences prey availability/accessibility remains unknown.

Wedge-tailed shearwater adults at Heron Island were not significantly lighter in 2002 despite remaining at-sea significantly longer to provision equivalent meal sizes. This suggests that the level of self-provisioning by adults did not differ significantly between years. In 2002, adults either preferentially maintained their own reserves or, alternatively, the resources accessed by adults for chick-provisioning as opposed to self-provisioning were not the same, as has been shown for many temperate procellariiforms (Weimerskirch 1998; Weimerskirch and Cherel 1998; Catard *et al.* 2000), with SST variation influencing only the availability of chick resources. Further data are required to distinguish between these alternatives.

Although it is tempting to attribute the observed differences in provisioning rate directly to variations in SST, the results of the present study are correlative across only two seasons and not replicated. They now require validation through further replication across different years and SST regimes. But, given repeated observations of similar correlated effects at different temporal scales and levels of resolution (e.g. Cruz and Cruz 1990; Guinet *et al.* 1998; Durant *et al.* 2003), the coincidental occurrence of this failure with abnormally high SST on the GBR cannot be ignored.

The implications of our results and reasons behind needing to further validate them are obvious. With SST expected to continue rising at 1–2°C per century (Hoegh-Guldberg 1999; Berkelmans *et al.* 2002), our data predict substantial detrimental effects that will significantly impact seabird populations and possibly other reef organisms at upper-trophic levels. Our findings also suggest that wedge-tailed shearwaters are sensitive indicators to spatial and temporal changes in forage-fish availability that can be effectively used to develop models of, and monitor for, these potential impacts.

References

Ainley, D. G., Carter, H. R., Anderson, D. W., Briggs, K. T., Coulter, M. C., *et al.* (1988). Effects of the 1982–83 El Niño–Southern Oscillation on Pacific Ocean bird populations. In 'Acta XIX Congressus Internationalis Ornithologici'. (Ed. H. Ouellet.) pp. 1747–1758. (University of Ottawa Press: Ottawa, Canada.)

Berkelmans, R. (2002). 'Temperature Monitoring Stations.' Available at http://www.gbrmpa.gov.au/corp_site/info_services/science/seatemp/base.html (accessed November 2003). (Great Barrier Reef Marine Parks Authority: Townsville, Australia.)

Berkelmans, R., Done, T., Goggin, L., and Harriott, V. (2002). 'Coral Bleaching and Global Climate Change.' (CRC Reef Research Centre: Townsville, Australia.)

Cane, M. A. (1983). Oceanographic events during El Niño. *Science* **222**, 1189–1202.

Catard, A., Weimerskirch, H., and Cherel, Y. (2000). Exploitation of distant Antarctic waters and close shelf-break waters by white-chinned petrels rearing chicks. *Marine Ecology Progress Series* **194**, 249–261.

Cruz, J. B., and Cruz, F. (1990). Effect of El Niño–Southern Oscillation conditions on nestling growth rate in the dark-rumped petrel. *The Condor* **92**, 160–165.

Duffy, D. C., Arntz, W. E., Serpa, H. T., Boersma, P. D., and Norton, R. L. (1988). A comparison of the effects of El Niño and the Southern Oscillation in Peru and the Atlantic Ocean. In 'Acta XIX Congressus Internationalis Ornithologici'. (Ed. H. Ouellet.) pp. 1740–1745. (University of Ottawa Press: Ottawa, Canada.)

Durant, J. M., Anker-Nilssen, T., and Stenseth, N. C. (2003). Trophic interactions under climate change fluctuations: the Atlantic puffin as an example. *Proceedings of the Royal Society B* **270**, 1461–1466.

Fernandez, P., Anderson, D. J., Sievert, P. R., and Huyvaert, K. P. (2001). Foraging destinations of three low-latitude albatross. *Journal of Zoology* **254**, 391–404. doi:10.1017/S0952836901000899

Guinet, C., Chastel, O., Koudil, M., Durbec, J. P., and Jouventin, P. (1998). Effects of warm sea surface temperature anomalies on the blue petrel at the Kerguelen Islands. *Proceedings of the Royal Society B* **265**, 1001–1006.

Hedd, A., Ryder, J. L., Cowen, L. L., and Bertram, D. F. (2002). Inter-annual variation in the diet, provisioning and growth of Cassin's auklet at Triangle Island, British Columbia: responses to variation in ocean climate. *Marine Ecology Progress Series* **229**, 221–232.

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* **50**, 839–866.

Jenouvrier, S., Barbraud, C., and Weimerskirch, H. (2003). Effects of climate variability on the temporal population dynamics of southern fulmars. *Journal of Animal Ecology* **72**, 576–587. doi:10.1046/J.1365-2656.2003.00727.X

Kitaysky, A. S., and Golubova, E. G. (2000). Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. *Journal of Animal Ecology* **69**, 248–262. doi:10.1046/J.1365-2656.2000.00392.X

Marchant, S., and Higgins, P. J. (1990). 'Handbook of Australian, New Zealand and Antarctic Birds.' (Oxford University Press: Melbourne, Australia.)

Marshall, P., Hoey, J., and Berkelmans, R. (2002). 'Report on the Mass Bleaching Event on the Great Barrier Reef in 2002.' http://www.gbrmpa.gov.au/corp_site/bleaching/final_report/. (Great Barrier Reef Marine Park Association: Townsville, Australia.)

Pinaud, D., and Weimerskirch, H. (2002). Ultimate and proximate factors affecting the breeding performance of a marine top-predator. *Oikos* **99**, 141–150. doi:10.1034/J.1600-0706.2002.990114.X

Ramos, J. A., Maul, A. M., Ayrton, V., Bullock, I., Hunter, J., Bowler, J., Castle, G., Mile, R., and Pacheco, C. (2002). Influence of local and large-scale weather events and timing of breeding on tropical roseate tern reproductive parameters. *Marine Ecology Progress Series* **243**, 271–279.

Schreiber, E. A. (1994). El Niño–Southern Oscillation effects on provisioning and growth in red-tailed tropicbirds. *Colonial Waterbirds* **17**, 105–215.

Schreiber, E. A. (1996). Experimental manipulation of feeding in red-tailed tropicbird chicks. *Colonial Waterbirds* **19**, 45–55.

Schreiber, R. W., and Schreiber, E. A. (1984). Central Pacific seabirds and the El Niño Southern Oscillation, 1982–1983 perspectives. *Science* **225**, 713–716.

SPSS. (2001). 'SPSS for Windows.' (SPSS Inc.: Chicago, IL, USA.)

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K. S., and Lima, M. (2002). Ecological effects of climate fluctuations. *Science* **297**(5585), 1292–1296. doi:10.1126/SCIENCE.1071281

Veit, R. R., McGowan, J. A., Ainley, D. G., Wahl, T. R., and Pyle, P. (1997). Apex marine predator declines ninety per cent in association with changing oceanic climate. *Global Change Biology* **3**, 23–28. doi:10.1046/J.1365-2486.1997.D01-130.X

Weimerskirch, H. (1998). How can a pelagic seabird provision its chick when relying on a distant food source? Cyclic attendance, foraging decision and body condition in sooty shearwaters. *Journal of Animal Ecology* **67**, 99–109. doi:10.1046/J.1365-2656.1998.00180.X

Weimerskirch, H., and Cherel, Y. (1998). Feeding ecology of short-tailed shearwaters: breeding in Tasmania and foraging in the Antarctic? *Marine Ecology Progress Series* **167**, 261–274.