Sea surface temperature constrains wedge-tailed shearwater foraging success within breeding seasons

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ABSTRACT: Processes that underlie impacts of global warming on marine organisms at upper trophic levels are largely unknown. Long-term studies of seabirds indicate that inter-annual decreases in fledging success are correlated with El Niño years, when sea surface temperatures (SSTs) are above long-term averages. These studies propose that seasonal processes are most likely responsible. To date, no work has focused on the potential impacts of elevated SSTs on seabird reproduction at finer time scales, i.e. within a breeding season. We directly measured the influence of SST variability on foraging success in the wedge-tailed shearwater *Puffinus pacificus* within and among 3 breeding seasons at Heron Island in the southern Great Barrier Reef, Australia. We found that changes in foraging success (meal size and feed frequency) and chick growth were negatively correlated with daily variations in SST both within and among seasons. Our findings suggest that forage resource availability fluctuated daily in direct association with small-scale variation in SST. This is evidence that declines in seabird breeding success, previously coupled exclusively with large-scale El Niño conditions and processes, may also involve fine-scale mechanisms. Consequently, observed El Niño scale impacts may include season-specific outcomes of day-to-day trophic interactions that operate within all breeding seasons.

KEY WORDS: Shearwater · Sea surface temperature · SST · Seabirds · Global warming · Foraging success · Temporal-scale

INTRODUCTION

Most studies that examine the impacts of climate change on marine ecosystems do not consider the effects of day-to-day trophic interactions (Francis et al. 1998). However, defining a temporal framework over which climate change processes operate is essential for the continued development of predictive and mechanistic models (Levin 1992, Ives 1995, Stott & Kettleborough 2002).

Climate models predict that mean annual global temperature will continue to rise until the end of the 21st century (Easterling et al. 2000, Sæther 2000). Increasingly, empirical evidence is being presented that links climate change to significant impacts on both the ecological and life-history characteristics of species

(Harrington et al. 1999, Hughes 2003). Climate change is closely related to large-scale atmospheric phenomena, of which El Niño Southern Oscillation (ENSO) is best known (Cane 1983). A characteristic of El Niño events in tropical locations is the occurrence of above average sea surface temperatures (SSTs) that have been linked to coral bleaching (Hoegh-Guldberg 1999) and changes in the temporal and spatial distribution of a variety of marine organisms at lower trophic levels (eg. zooplankton, sardine and cephalopods; Nevarez-Martinez et al. 2001, Jackson & Domeier 2003, Wilson et al. 2003).

The potential impact of above average SSTs on species at higher trophic levels, such as seabirds, is unclear (Oedekoven et al. 2001, Stenseth et al. 2002). Both beneficial and detrimental long-term/seasonal

impacts on seabird breeding success have been observed in a number of temperate systems (Kitaysky & Golubova 2000, Hedd et al. 2002, Durant et al. 2003, Gjerdrum et al. 2003). These effects are thought to result from seasonal-scale changes associated with the impact of SST on productivity and prey species abundance (Stenseth et al. 2002, Durant et al. 2003, Inchausti et al. 2003). However, the relationships and mechanisms are unclear, and thought to be complex (Duffy 1993, McGowan et al. 1998, Harrington et al. 1999, Stenseth et al. 2002).

So far, only detrimental long-term/seasonal effects have been observed in tropical systems. Above average SSTs in the Central Pacific during an El Niño event in 1982–83 were associated with reproductive failure and high adult mortality in numerous seabird species (Schreiber & Schreiber 1984, Ainley et al. 1988, Schreiber 1994). Consequences included lengthened fledgling periods, lower growth rates, decreased nesting success and a reduction in the incidence of breeding (Ainley et al. 1988). More recent work in the tropics has documented similar detrimental impacts of elevated SST at the seasonal scale (Fernandez et al. 2001, Ramos et al. 2002, Schreiber 2002, Smithers et al. 2003).

Two mechanistic hypotheses can be derived from the literature. The first suggests that a change in SSTs (entrained by large-scale processes such as ENSO), cause seasonal-scale declines in productivity at lower trophic levels (Stenseth et al. 2002). Low productivity subsequently impacts on the recruitment of seabird prey species on a seasonal basis (Schreiber & Schreiber 1984, Cushing 1990, Stenseth & Mysterud 2002, Stenseth et al. 2002, Durant et al. 2003). By definition, this general model predicts that foraging success during ENSO events should be lower at the beginning of the breeding season and possibly for the duration of the breeding season.

An alternative hypothesis is that fluctuating SSTs within a breeding season reduce accessibility to prey species, by affecting the vertical and/or horizontal distribution of prey. This process could be driven by numerous physiological (Yang et al. 1995), ecological (Kaplan et al. 2003, McIlwain 2003, McKinnon et al. 2003) and/or behavioural (Spear et al. 2001) factors. As a consequence, prey availability during the breeding season should track changes in SST over shorter temporal scales. Moreover, prey availability would not be depressed for the entire breeding season; instead, fluctuations should occur over the same temporal-scales as variation in SST (i.e. on a daily basis).

Wedge-tailed shearwaters *Puffinus pacificus* are tube-nosed, burrow nesting seabirds (Procellariidae) that breed on islands throughout the tropics, including coral cays of the Great Barrier Reef (GBR), Australia

(Marchant & Higgins 1990). Whilst breeding, adults forage during the day on squid (Ommastrephidae), and fish from the Carangidae and Mullidae families (Harrison et al. 1983, Marchant & Higgins 1990, D. R. Peck & B. C. Congdon unpubl. data) and return at night to feed chicks. Previously, significant decreases in provisioning rates, growth rates and fledging success have been observed on a seasonal basis in this species, in association with above average SSTs during an ENSO event (Smithers et al. 2003).

The aim of this study was to examine further the effect SST variation has on measures of foraging and breeding success in this species over a much shorter (day-to-day) time period. This was done to establish the temporal scale at which SST variation and breeding success are linked in this system, and to evaluate the relative importance of large versus small-scale temporal mechanisms so as to better understand the relationship between seabird reproductive success, prey availability and environmental change.

MATERIALS AND METHODS

This study was conducted at Heron Island (23°26′S 151°51′E), in the Capricorn Section of the GBR Marine Park, Australia. Work was undertaken during 3 breeding seasons; 2001, 2002 and 2003. A total of 27 study nests were monitored in 2001, 29 in 2002 and 26 in 2003. These sample sizes included 5 control nests for 2001, 7 for 2002 and 5 for 2003. In all 3 years, adult provisioning rates, chick growth and chick survivorship were monitored at each nest daily. Chicks were weighed twice a day at 09:00 and 16:00 h using an electronic balance (±0.1 g). Between these times, no adult visits or chick feeding were observed. Culmen and tarsus measurements were obtained for each chick every 4 d using dial callipers (±0.1 mm). At each burrow, both adults were banded for individual recognition and attendance was monitored continuously from 17:00 to 05:00 h daily. During monitoring, burrow entrances were fitted with a sliding trapdoor of clear Perspex that was triggered by adults entering the burrow. After an adult had entered a burrow and chick feeding was complete, as indicated by chicks no longer begging, the visiting adult was captured and identified. After each capture, traps were reset so that subsequent visits by the same or other adults could be detected. In 2003, chick masses were consistently obtained immediately following any adult visit to a nest (a total of 21 nests without controls). These data allowed 3 measures of adult foraging success to be calculated for each study nest during the 3 study years; adult feed frequency (F_{FREQ}), chick daily mass change (C_{MASS}) and chick survivorship, as well as per-

mitting relative meal mass (M_{MASS}) to be calculated for 2003.

Adult feed frequency (F_{FREQ}) and relative meal mass (M_{MASS}). The frequency at which adults fed chicks was evaluated for 3 breeding seasons; 2001, 2002 and 2003. An adult feeding visit was defined as an increase in chick mass between the 16:00 h weighing and the time immediately after an adult visit. The number of chicks fed each day was used to calculate the proportion fed from nests being monitored (F_{FREQ}).

Meal mass was defined as the difference in chick mass between its 16:00 h weighing and mass immediately following an adult visit. Chick ages were estimated to range between 1 and 10 d, based on a regression of tarsus length against known-age chicks ($F_{1,19}$ = 221.15, p < 0.0001, r^2 = 0.91). Therefore, to standardise for chick developmental stage, the amount of food received by chicks was divided by chick mass at 16:00 h (prior to the observed feed for that day). This gave meal mass per g of chick, or relative meal mass. The average relative meal mass (M_{MASS}) was then generated for each day of the study period. Handling caused a chick to regurgitate on 1 occasion. This data point was not included in the analysis.

Relative chick daily mass change (C_{MASS}). Relative daily mass changes for individual chicks were determined for a total of 82 chicks in 3 breeding seasons (2001, 2002 and 2003) by calculating the mass change over each 24 h period (i.e. the difference between 2 consecutive 16:00 h masses). To account for the potential influence of chick developmental stage on mass change, the differences in mass were divided by the chick mass at the start of the 24 h period to obtain the mass change per g of chick (C_{MASS}). These were then averaged for all chicks for each day of the study period.

SST Data. Daily SST data were obtained from 2 primary sources: (1) mean daily values (calculated from half hour readings) obtained from the Australian Institute of Marine Science, Half-tide Rocks remote weather station (SST_{HALF}) (23° 09′ S 150° 56′ E; 125 km NE of Heron Island) and (2) observed SST at 09:00 h (SST_{HI}) obtained from the Heron Island Research Station (23° 26′ S 151° 51′ E). The 2 measures of SST were highly correlated ($F_{1,27}$ = 32.46, p < 0.0001, r^2 = 0.538) but the Half-tide Rocks data offered better instrumental resolution (0.1 vs 0.5°C) and a more representative measure of the average SST over the entire 24 h period (i.e. calculated from the mean of half-hourly readings over the previous 24 h, compared to a single daily record of the SST measured at 09:00 h). Therefore, where possible, SST at Half-tide Rocks was used in the analyses as a more representative measure of SST experienced by foraging wedge-tailed shearwaters. Half-tide Rocks data were not available for the 2002

breeding season; therefore, SST data from Heron Island had to be used for inter-annual analyses.

Relationship between daily variations in SST and foraging success. All data were tested for normality and homogeneity of variances. Linear regressions were then calculated where these assumptions were met. Measures of SST over time involve serial autocorrelation. *A priori* autocorrelation analysis of SST data indicated a significant effect at the scale of 1 day only. To account for this, we employed a conservative approach by reducing the degrees of freedom during significance testing. The dependent variables for these analyses were F_{FREQ} and M_{MASS}. SST_{HALF} was the independent variable for within season (2003) analyses, with SST_{HI} used for other (i.e. inter-annual) analyses.

Relationship between SST and annual reproductive success. To determine the influence of daily fluctuations in SST on the observed pattern of inter-annual declines in reproductive success, ANCOVA analyses were conducted with C_{MASS} and F_{FREQ} as the independent variable, year as the factor and SST_{HI} as the covariate. All statistical analyses were performed using JMP Version 4.0.2 (SAS Institute).

RESULTS

Of the 21 study chicks monitored in 2003, 19 survived until the end of the study period. Monitoring of 1 nest began on 13 February 2003, 5 d after the others. The mortality rate of 10% in this study was lower than that observed during the 2002 breeding season (50%) at the same colony, but greater than that seen during 2001 (3.4%) (χ^2 = 60.23, df = 2, p < 0.0001) (Smithers et al. 2003).

Adult feed frequency and meal mass in 2003

The proportion of chicks fed each day (F_{FREQ}) and relative meal mass (M_{MASS}), fluctuated over the 2003 study period (F_{FREQ} $F_{2,25}$ = 13.5861, p = 0.0001; M_{MASS} $F_{2,25}$ = 10.0201, p = 0.0006) (Fig. 1). Mean F_{FREQ} for the entire 2003 study period was 0.44 ± SE 0.036 (n = 28). The mean M_{MASS} for the same period was 0.142 g ± SE 0.013 (n = 28) per g of chick. Both were significantly lower during the period 19 to 26 February 2003 (inclusive). After this time, foraging success began to increase (Fig. 1).

Foraging success in relation to SST in 2003

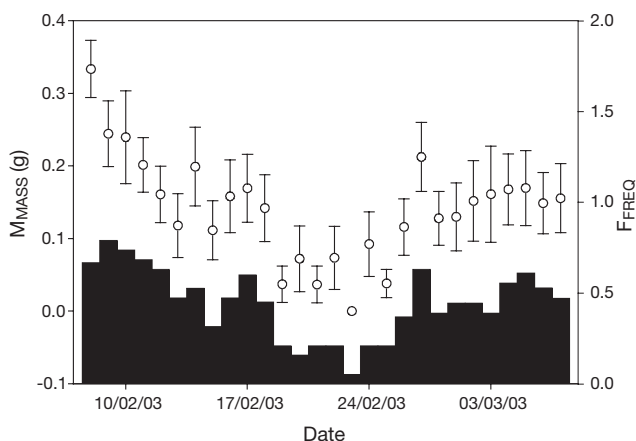Relative meal mass (M_{MASS}) was negatively correlated with SST at Half-tide Rocks (SST_{HALF}) (Fig. 2a)

Fig. 1. *Puffinus pacificus*. Mean (±SE) relative daily meal mass (M_{MASS}, ○) and proportion of young fed each day (F_{FREQ}, shaded bars) for wedge-tailed shearwaters at Heron Island February–March 2003
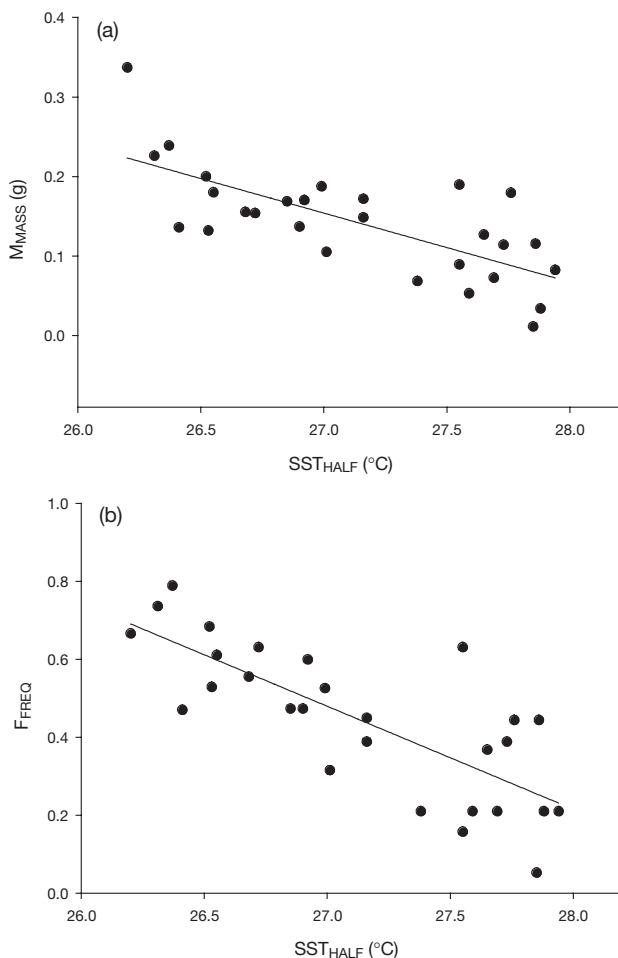

Fig. 2. *Puffinus pacificus*. Relationship between sea surface temperature at Half-tide Rocks (SST_{HALF}) and (a) relative meal mass (M_{MASS}) and (b) F_{FREQ} during the 28 d study period in 2003 ($M_{MASS} = 2.497 - 0.086\ SST_{HALF}$; $F_{FREQ} = 7.615 - 0.264\ SST_{HALF}$)

($F_{1,26} = 27.67$, $p < 0.0001$, $r^2 = 0.497$). For each 1°C increase in SST, M_{MASS} decreased by approximately 0.086 g per g chick mass (Fig. 2a). For a 100 g chick, this is equivalent to a decrease of ~8.6 g per 1°C.

Feeding frequency (F_{FREQ}) was also negatively correlated with SST at Half-tide Rocks for the 2003 study period (Fig. 2b) ($F_{1,28} = 38.233$, $p = 0.0001$, $r^2 = 0.579$). The proportion of chicks that were fed in a single night decreased by approximately 26.4 % per 1°C increase in SST between 26 and 28°C. This is equivalent to each chick being fed on average 1 night in 2 when SST = 27°C, but only 1 night in 3 when SST = 27.6°C (the long-term seasonal average temperature) and only 1 night in 5 when SST = 28°C.

Relative chick daily mass change (C_{MASS}) in 2003 and among years

The mean relative daily change in chick mass (C_{MASS}) during the 2003 study period was 0.0349 g ± 0.0102 (n = 28). Unlike M_{MASS} and F_{FREQ}, C_{MASS} was not significantly depressed during the period 19 to 26 February 2003 ($F_{2,24} = 2.46$, $p = 0.10$). However, C_{MASS} was negatively correlated with SST_{HALF} ($F_{1,25} = 5.31$, $p = 0.0297$, $r^2 = 0.175$) and shows zero or negative growth at 28°C (Fig. 3).

There was a significant negative effect of SST_{HI} on C_{MASS} for all years (Fig. 4a) ($F_{5,66} = 6.09$, $r^2 = 0.264$, $p = 0.0001$). There was also an effect of year on C_{MASS} ($F_{1,66} = 8.438$, $p = 0.0005$); however, the slopes of the regression lines for each year were not significantly different from each other ($F_{1,66} = 0.0186$, $p = 0.9816$). Thus, in all 3 yr, chick mass change declined at the same rate with increasing SST, but in 2002 the average amount of chick growth per g of chick was less at any given SST (Fig. 4a).

As with mean relative mass change, F_{FREQ} was also significantly correlated with SST_{HI} among years (Fig. 4b, $F_{5,62} = 10.92$, $p < 0.0001$, $r^2 = 0.425$), with a significant effect of year on mean mass change ($F_{1,2} = 13.696$, $p < 0.0001$) but with no difference among the slopes of the regression lines for each year (Fig. 4b, $F_{1,2} = 0.5805$, $p = 0.5626$). Results suggest that among years, SST affected feeding frequency in the same way that it affected chick mass changes; feeding decreased at the same rate in all 3 seasons, except that during 2002, feed frequency for a given SST was consistently lower.

We observed autocorrelation in our SST data at the scale of 1 d. This effectively reduces the number of independent data points in our analyses by 1 and so requires a similar reduction in the associated degrees of freedom. On testing the robustness of our results, we found that the significance of all regression analyses, except SST versus C_{MASS}, did not change when
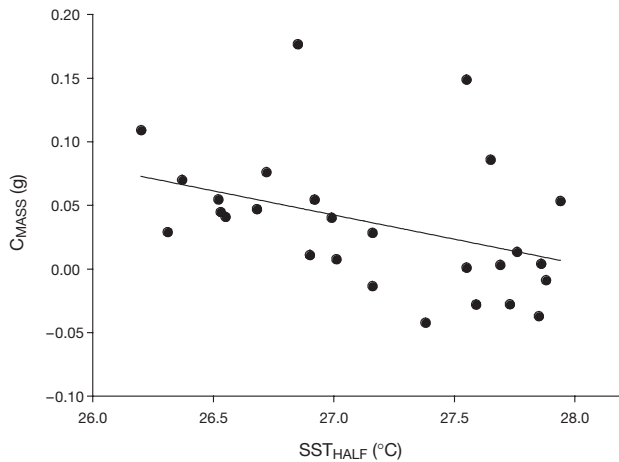
Fig. 3. *Puffinus pacificus*. Relationship between relative daily change in chick mass (C_{MASS}) and SST_{HALF} during the 2003 study period ($C_{MASS} = 1.128 - 0.040 \, SST_{HALF}$)

degrees of freedom were reduced by up to 14. The SST versus C_{MASS} regression remained significant with a reduction of up to 4 degrees of freedom. Therefore, since only a 1 degree reduction is required for the level of autocorrelation observed, we are confident that our findings are not affected by this phenomenon.

DISCUSSION

Both the frequency at which Heron Island wedge-tailed shearwater chicks were fed and the meal mass delivered by adults were highly variable during the 2003 study period with a marked decrease during the period 18 to 27 February 2003 (Fig. 1). This decrease was followed by a steady increase (Fig. 1) and indicates that prey species available to adults feeding chicks were depressed during the period 18 to 27 February 2003. Also, in 2003 both feeding frequency and chick meal mass were strongly negatively correlated with daily variation in SST_{HALF} (Fig. 2). Chick growth was also correlated with SST_{HALF} (Fig. 3). Furthermore, feed frequency and chick growth were correlated with SST_{HI} on a daily basis in all 3 breeding seasons (Fig. 4). Therefore, small-scale daily fluctuations in SST significantly and consistently impacted both the foraging success and chick growth of wedge-tailed shearwaters both within and among breeding seasons at Heron Island.

Annual or decadal variation in SST have often been correlated with fluctuations in seabird reproductive success (Francis et al. 1998) and have generally been framed in the context of large-scale (both spatial and temporal) atmospheric processes such as ENSO (in the Pacific Ocean) or NAO (in the North Atlantic Ocean)
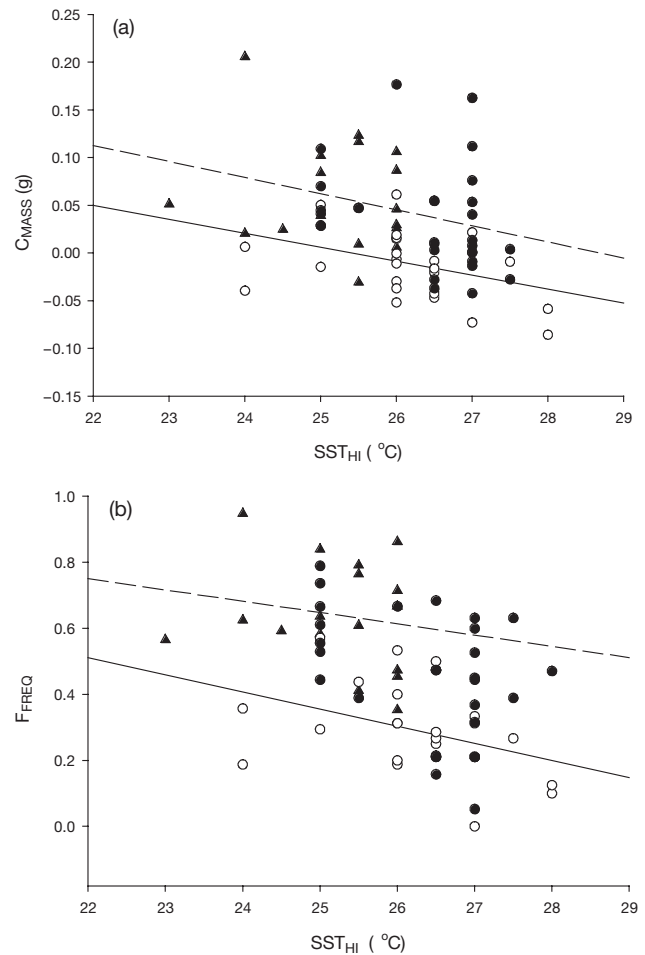

Fig. 4. *Puffinus pacificus*. (a) Effect of sea surface temperature at Heron Island (SST_{HI}) on C_{MASS} in 2001 (▲), 2002 (○) and 2003(●). There was a significant effect of SST_{HI} on C_{MASS} among years ($C_{MASS} = 0.533 - 0.0195 \, SST_{HI}$). The effect of year on C_{MASS} was also significant. There was no effect of year on SST_{HI}. (b) The effect of SST_{HI} on F_{FREQ} in 2001 (▲), 2002 (○) and 2003(●). There was a significant effect of SST_{HI} on F_{FREQ} among years ($F_{FREQ} = 2.856 - 0.092 \, SST_{HI}$). The effect of year on F_{FREQ} was also significant. There was no effect of year on SST_{HI}. In both graphs, the dashed line represents the 2001/2003 regression. 2002 regressions are represented by a solid line

(Cushing 1990, Ainley et al. 1995, Ramos et al. 2002, Durant et al. 2003). It is thought that unfavourable SSTs, in some cases, can disrupt or block nutrient rich up-welling zones, thereby disrupting phytoplankton distribution and abundance (McGowan et al. 1998, Kaplan et al. 2003, Wilson et al. 2003). This in turn causes decreased productivity at higher trophic levels (Sanchez-Velaso et al. 2000, Stenseth et al. 2002). Work in temperate systems has expanded this model by showing that SSTs during the spawning and/or juvenile life-history stages of prey species can impact seabird breeding success via phenological 'mismatches' be-

tween prey recruitment and the chick rearing period (Cushing 1990, Stenseth & Mysterud 2002).

However, phenological 'mismatches' involve within-season time lags between shifting SSTs and the availability of prey species to seabirds (Stenseth & Mysterud 2002, Durant et al. 2003). Moreover, this mechanism predicts that food availability should be consistently lower and/or delayed during the beginning of the breeding season when a reliable food source is needed for young chicks. We observed fluctuating foraging success on a daily basis (Fig. 1) and no time lag within seasons (Fig. 4), indicating that other factors were operating within the system over much shorter temporal-scales. This is evidence that decreases in seabird breeding success, previously correlated with elevated SSTs at the seasonal/yearly scale (Schreiber & Schreiber 1984, Guinet et al. 1998, Ramos et al. 2002, Smithers et al. 2003), may not exclusively involve large-scale, inter-annual processes such as ENSO. Instead, these impacts may involve cumulative effects of day-to-day trophic interactions that operate within each breeding season. If so, long-term decreases in breeding success that have been linked to ENSO may also involve mechanisms operating on much shorter temporal-scales than previously thought (e.g. Cruz & Cruz 1990, Veit et al. 1997, Guinet et al. 1998, Ramos et al. 2002).

Nevertheless, during the 2002 season, when substantially greater chick mortality was observed (50%), feeding rates and chick growth were lower than during the other seasons, even when taking into account the daily effect of SST (Fig. 4). This indicates that a seasonal-scale process may also be operating to depress foraging success and growth rates, in addition to the observed within-season effect of SST (Fig. 4). We, therefore, suggest that while the general large-scale seasonal model described above may still be the primary mechanism driving seabird mortality events, it can be significantly enhanced by the addition of possible 'day-to-day' mechanisms.

To our knowledge, there are 2 previously described trophic mechanisms that may influence forage-resource availability on a 'day-to-day' basis. The first incorporates the physiological requirements of seabird prey species. The distribution of seabird prey species is known to change in accordance with temperature-dependent physiological requirements (Castillo et al. 1996, Waluda et al. 2001). This can occur in both vertical and/or horizontal space and affects the accessibility of prey to foraging seabirds (Le Corre 2001, Spear et al. 2001). However, this mechanism has previously been viewed as a link to seabird breeding success (via SST change) only at seasonal scales (Maravelias 1997, Kitaysky & Golubova 2000, Navarez-Martinez et al. 2001, Takahashi et al. 2001). This is despite work in the Southern Ocean showing that seabird/prey abundance

is strongly associated with SSTs measured on a daily basis (Pakhomov & McQuaid 1996) and data linking short-term (weekly) fluctuations in prey availability with chick provisioning and growth rates (Suryan et al. 2002). Therefore, if prey species prefer specific temperature regimes, it is reasonable to assume that rapid movement in vertical and/or horizontal space to preferred temperatures could decrease their accessibility to aerial predators. In general, the impact on prey species of short-term SST changes is unknown. Our results suggest that they may be considerable and need to be incorporated into mechanistic models defining ENSO related decreases in seabird breeding success at tropical locales.

A second possible 'day-to-day' mechanism is that SST directly influences the abundance of subsurface predators (Le Corre 2001, Ramos et al. 2002). These predators drive prey to the surface, making them available to seabirds (Brown 1980, Shealer 1996, Balance & Pitman 1999). The most important predators associated with this behaviour in the tropical Pacific Ocean are tuna *Thunnus* spp. (Ashmole & Ashmole 1967, Harrison & Seki 1987). Extensive work has documented a close relationship between foraging seabirds and tuna (Harrison & Seki 1987, Balance et al. 1997), and it is generally accepted that oceanographic conditions (such as SST) are important to the ecology of this group (Lehodey et al. 1997, Lu et al. 2001, Brill et al. 2002). However, the complex relationships among tuna and oceanographic variation remains poorly understood (Harrison & Seki 1987, Lehodey et al. 1997, Lu et al. 2001). Consequently, the applicability of this mechanism to wedge-tailed shearwaters remains unclear, but warrants further research.

In conclusion, it has been known for some time that ENSO/NAO driven inter-annual fluctuations in SST can have significant negative impacts on reproductive characteristics of tropical seabirds (Schreiber & Schreiber 1984, Cruz & Cruz 1990, Guinet et al. 1998, Ramos et al. 2002, Schreiber 2002). However, to date, studies have considered this to be due solely to productivity decreases and phenological 'mismatches' at the seasonal scale. Our study demonstrates the importance of daily fluctuations in SST on the foraging success of a seabird species, indicating that important processes may also act at finer temporal scales. Our findings imply that to fully understand the potential impact of elevated SSTs on seabird reproduction, work is also needed that identifies the effects of short-term variation in SST on breeding success within and between seasons. In addition, our findings expand research for underlying mechanisms to include within-season SST effects on prey distribution and abundance, as well as correlated variation in commensal predatory fish distributions.

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