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Poorer breeding by little penguins near Perth, Western Australia is correlated with above average sea surface temperatures and a stronger Leeuwin Current

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Abstract

Using 20 years of data (1986 to 2008), we examined relationships between oceanographic variables (Fremantle sea level (FSL) – a proxy for the strength of the Leeuwin Current – and sea surface temperature (SST)) and five measures of little penguin, *Eudyptula minor*, breeding performance near Perth, Western Australia: namely (1) the laying date, (2) the number of chicks produced per pair, (3) the proportion of eggs that hatched, (4) the overall breeding success, defined as the proportion of total eggs laid that resulted in successful fledglings and (5) chick mass at fledging. The next three years of data (2009 to 2011) were used to test the performance of our statistical predictive models. FSL provided more accurate predictions of timing of laying, whereas SST provided more accurate predictions of breeding success. A later end to laying was associated with a high FSL during the

summer (December to February) before breeding. Higher SSTs in the pre-breeding period from April to May corresponded to reduced breeding success, with lower fledgling success, fewer chicks per pair and generally a lower mean mass of chicks at fledging. The models predict that future oceanographic warming is expected to reduce the breeding success of this colony of little penguins.

Additional keywords : Leeuwin Current, little penguins, Penguin Island, reproduction, sea surface temperatures, Western Australia.

Introduction

The timing and success of seabird reproduction has been linked with variability in both oceanographic conditions and prey resources. Sea surface temperatures (SSTs) higher than average, often associated with El Niño events in the Pacific Ocean (Philander 1983), have been correlated with the reduced breeding success and/or body condition of seabirds (e.g. Guinet *et al.* 1998; Boersma 1978); later breeding (e.g. Ramos *et al.* 2002); failure to breed (e.g. Valle *et al.* 1987); and reduced frequency of feeds and chick mass (e.g. Smithers *et al.* 2003; Peck *et al.* 2004; Erwin and Congdon 2007; Valle *et al.* 1987). Higher SSTs have been linked to changes in the recruitment (Cole 1999) and abundance of fish species (Barber and Chavez 1983) and not only affect the distribution and abundance of fish interannually (Nevárez-Martínez *et al.* 2001), but can affect the spatial distribution of fish within a season. Indeed, the daily feeding frequency and meal mass of wedge-tailed shearwater (*Puffinus pacificus*) and sooty tern (*Sterna fuscata*) chicks were found to be negatively correlated with daily SST (Peck *et al.* 2004; Erwin and Congdon 2007). Warm SSTs several months before the start of the breeding season have also been associated with changes in timing of breeding and participation in breeding in Lesser Noddies (*Anous tenuirostris*) (Surman and Nicholson 2009). So the breeding parameters observed in a colony of seabirds can represent both current and lag effects of ocean variables on their prey resources.

Little penguins (*Eudyptula minor*) are found along the south coast of Australia from Perth, Western Australia, to South Solitary Island, New South Wales, as well as in New Zealand (Marchant and Higgins 1990), and the location and size of their colonies appears to be limited by available nesting habitat and sufficient prey resources (Dann and Norman 2006). Colonies at different locations are likely to encounter a range of oceanographic conditions and prey resources. Such variation will undoubtedly be reflected in differences in various reproductive measures between colonies. For example, lower SST has been linked with the shorter breeding season of little penguins in Tasmania compared with Phillip Island, Victoria (Reilly and Cullen 1981). In addition, within a colony, interannual variation in SST has been shown to be associated with changes in adult mass, the length of the breeding season, and the number of chicks produced per pair (Mickelson *et al.* 1992; Cullen *et al.* 2009).

One such little penguin colony where variation in annual SST has been associated with altered breeding variables is that at Penguin Island, Western Australia, notably in 1986 and 1989. SSTs were warmer in 1989 compared with 1986, the peak of egg laying was later, a smaller proportion of birds bred and many eggs were abandoned (Wienecke *et al.* 1995). The difference in annual SST in these two years was linked to interannual variations in the strength of the Leeuwin Current (Wooller *et al.* 1991; Wienecke *et al.* 1995). This current runs southward down the Western Australian coast and brings warm tropical water, low in salinity and nutrients (Cresswell and Golding 1980; Cresswell 1990; Feng *et al.* 2003). It runs more strongly in autumn to winter, flows along the shelf break and has mesoscale features such as anti-cyclonic and cyclonic eddies (Pearce and Phillips 1988; Pearce *et al.* 2006). In the summer it flows further off-shore (Pearce *et al.* 2006). Downwellings rather than upwellings are associated with the Leeuwin Current (Pearce 1991) and the eddies are responsible for removing nutrients from the shelf (Feng *et al.* 2007). During strong Leeuwin Currents, there is more cross-shelf mixing (Pearce *et al.* 2006), and phytoplankton and zooplankton are removed from the shelf waters, thereby reducing the feeding conditions of larvae on the shelf (Gaughan 2007). Additionally, the large mesoscale eddies formed can remove large numbers of pelagic larvae (Gaughan 2007), with larvae transported up to 1000 km (Gaughan *et al.* 2001a). It is no surprise then

that peak spawning activity of small pelagic clupeid fish, such as pilchard (*Sardinops sagax*) and anchovy (*Engraulis australis*), generally occurs when offshore transport is low and larval food concentrations are high (Somarakis *et al.* 2006; Muhling *et al.* 2008a). These fish species, as well as sandy sprat (*Hyperlophus vittatus*), blue sprat (*Spratelloides robustus*) and garfish (*Hyporhamphus melanochir*), comprise the majority of the diet of the penguins from Penguin Island (Klomp and Wooller 1988a; Wienecke 1989; Wooller *et al.* 1991; Connard 1995; Bradley *et al.* 1997; Murray *et al.* 2011). During El Niño years, when the overall Leeuwin Current is weakened (Feng *et al.* 2003) and the SST along the shelf break is lower, more clupeid fish are generally caught commercially in the coastal waters of the Perth metropolitan area (Wienecke *et al.* 1995). Thus the strength of the Leeuwin Current may affect the availability of their prey and hence the breeding performance of the penguins.

Fish abundance is also potentially affected by coastal oceanographic conditions. In the summer months, the cooler, northward-flowing Capes Current strengthens and runs between the Leeuwin Current and the coast (Pearce and Pattiaratchi 1999). Localised, wind-driven upwelling associated with the Capes Current may extend northward (Pearce and Pattiaratchi 1999) and influence nutrient levels (Waite *et al.* 2007). Adjacent to the Capes Current and within ~10 km of the coast lies a band of warmer and more saline water, a result of both coastal heating and evaporation (Pearce *et al.* 2006). Therefore the offshore Leeuwin Current and the inshore air–sea exchange processes (Pearce and Pattiaratchi 1999; Pearce *et al.* 2006) impact the SST along the West Australian coast. If higher SSTs are associated with daily and seasonal shifts in the distribution and abundance of penguin prey, this could affect the timing of breeding, the duration of foraging trips and, thus, the body condition and reproductive success of the penguins.

Using data from 1986–2008 we developed relationships between SST, Leeuwin Current and little penguin breeding variables. We then assessed the predictive ability of these models using data collected from 2009–2011. If the productivity of little penguins on Penguin Island is found to be influenced by oceanographic conditions, as has been shown for other little penguin colonies (Fortescue 1999; Cullen *et al.* 2009), this will have important ramifications for the management and

long-term viability of the colony in the face of climate change, given that the SST is predicted to be 0.7–1.1°C warmer along the mid-west Australian coast by the 2030s (Feng *et al.* 2009a).

Materials and methods

Breeding data

This study was carried out on Penguin Island, Western Australia (32°18'S, 115°41'E) (Fig. 1). Penguins do not dig burrows on this island because the sandy substrate is too friable (Klomp *et al.* 1991). Rather, they nest under bushes of *Tetragonia decumbens* or *Rhagodia baccata* (Dunlop *et al.* 1988), as well as in nestboxes placed around the island in 1986 (Klomp *et al.* 1991). The nestboxes have been monitored on average every 9 ± 0.24 days (total number of visits = 740), during the breeding season from 1986–2011. The presence of adults, eggs and chicks were noted on each visit, as well as adult identity (from flipper bands or, more recently, microchips), chick identity (if it had been tagged), and mass of both adults and chicks. Microchips were read with a portable reader (Iso Max IV, scanning distance up to 30 cm; Novartis Animal Health, Sydney). Adults and chicks were weighed in a calico bag to the nearest 10 g with 2-kg \times 10-g scales (Salter Scales, Melbourne). Only limited data were available for 1992 and 1993, and none for 2004 and 2005. Because of the loss and addition of nestboxes, the number of nestboxes checked each year has varied. Between 47 and 55 nestboxes were checked from 1986–2000, 70 in 2001, 69 in 2002, and between 113 and 129 in 2006–2011.

Little penguins on Penguin Island have been recorded laying eggs in every month from April through to December (Wooller *et al.* 1991). The eggs are incubated for 5–6 weeks and the chicks fledge at ~8 weeks of age. The penguins can lay two clutches in a year, but for this study we concentrated on measures from the first (main) breeding attempt only. We compared five measures of breeding performance with SST and the Leeuwin Current: (1) the laying dates (date of first egg, date of last egg, length of breeding season (i.e. interval between first and last eggs) and mean laying date); (2) the number of chicks produced per pair; (3) the proportion of eggs that hatched; (4) the overall breeding

success, i.e. the proportion of total eggs laid that resulted in successful fledglings; and (5) mass of chicks at fledging, when last observed in the nest. The last measure was the only one for which data from both first and second clutches were used, so as to produce a viable sample size. This was possible because there was no difference in the mass of the fledglings whether they were from the first or second clutch of eggs (two-sample $t(365) = 1.374$, $P = 0.170$). Fledgling masses were excluded from the analysis when only a small number of weights were recorded in that year (1988, 1999, 2002; 4, 3 and 3 weights recorded respectively). All fledglings used in the analysis were at least 46 days old, the approximate age at which their mass reaches an asymptote (Wienecke *et al.* 2000).

The laying dates were estimated in two ways: if the eggs did not hatch, the date on which the eggs were first seen in the nestboxes was used; if the eggs did hatch, the age of the chicks when first seen was estimated, and this age plus 35 days (the average length of incubation for little penguins, Chiaradia and Kerry 1999) was subtracted from the date when the chicks were first seen. The age of the chicks was estimated from several characteristics, including down colour, mass (particularly in first 2 weeks, when the mass : age relationship does not vary greatly between years (Wienecke *et al.* 2000)), feet colour and eyes opened or not.

Oceanographic data

Monthly values of mean Fremantle (32°3'S, 115°44'E) sea level (FSL) were obtained from the National Tidal Facility (Australian Bureau of Meteorology, South Australia). These values can be used as a proxy for the strength of the Leeuwin Current (Pearce and Phillips 1988; Feng *et al.* 2003). Low sea level values correspond to a weak Leeuwin Current and high sea level values to a strong Leeuwin Current (Pearce and Phillips 1988).

Local monthly SST data were obtained from the National Climate Data Center (<http://nomads.ncdc.noaa.gov/#climatencdc>, verified 5 October 2012 – Reynolds SST O/I v2.0), at a 15' resolution. Two SST regions were considered to have the potential to influence both the timing and success of breeding of Penguin Island penguins. Because the penguins generally forage close to their breeding colony (Penguin Island), particularly during the breeding season (B. Cannell, R.

Wooller and S. Bradley, unpubl. data – see grey area, Fig. 1), we defined SSTs averaged over the region 115°30'E to 115°45'E and 32°15'S to 32°45'S as 'Colony SST'. Primary productivity in the region is expected to be influenced by the Leeuwin Current and associated warm ocean temperatures. At the same latitude as the colony, the Leeuwin Current flows further offshore, but is closer to the coast at a higher latitude. In addition, large numbers of Clupeidae larvae have been found at a sampling station located at 31°40'47"S and 115°13'16"E (Muhling *et al.* 2008b). For these reasons a second SST region, denoted by 'Offshore SST', was defined as the average of SSTs in the region 115°00'E to 115°15'E and 31°30'S to 32°00'S (see Fig. 1 for location of these boxes with respect to Penguin Island).

Analysis

Using correlation analysis we compared monthly values of the oceanographic variables (FSL, Colony SST, Offshore SST) with the annual breeding variables, over the period 1986–2008. We used data from the previous year given there is a one year lag positive correlation between the strength of the Leeuwin Current and abundance of sandy sprat (Gaughan *et al.* 1996; Caputi *et al.* 1996). Prior to the correlation analysis, the breeding variables were assessed for possible autocorrelation, and because no evidence of autocorrelation was evident, raw values were used in further analyses. Correlations were considered significant if the probability of the observed correlation being due to chance was 5% or less. Curve-linear models were also fitted but because there was no evidence that they produced a better fit, only linear models are presented here.

Trends in the breeding parameters were assessed using simple linear regression with year as the explanatory variable. To determine the optimal model for predicting the little penguin breeding variables we used multiple linear regression (as per Cullen *et al.* 2009) using the mean monthly climate variables as predictors and data for the period 1986–2008. The selected model was then used to forecast the breeding parameters for the years 2009–2011 and comparisons performed between the modelled and observed values. This comparison provided a more realistic indication of expected model skill for future predictions.

The regression model was of the general form:

$$Y_i = a + b_1 X_{m1i} + b_2 X_{m2i} + b_3 X_{m3i}$$

where Y_i is the penguin variable in year i , X_{m1i} is the monthly climate variable in month $m1$ for year i , X_{m2i} is the monthly climate variable in month $m2$ for year i , and X_{m3i} is the monthly climate variable in month $m3$ for year i . The range of months considered for the modelling was consistent with the correlation analysis, which considered only months that would provide a useful lead time for monitoring purposes and for planning for management responses to the predictions.

Best subset regression (Tabachnick and Fidell 1996) was used to simplify the models by assessing the relative contributions of each of the climate variables to the model fit, with only significant contributions being retained. Both prediction and confidence intervals were calculated. Prediction intervals are used to predict a single response, whereas confidence intervals represent the confidence of predicting the mean response, and as a consequence, prediction intervals are always wider than confidence intervals.

All statistical analyses were performed in Minitab Release 14 (Minitab Inc., State College, PA).

Results

Using data from 1986–2008, the length of the breeding season was positively correlated with FSL for every month measured (from previous June to current July), although this relationship was generally strongest from July of the previous year through to February of the year of breeding (Fig. 2a). Longer breeding seasons were generally associated with periods of a strong Leeuwin Current (high FSL). Higher FSL in the austral summer before breeding (December–February) also corresponded to a later end to first clutches (last laying date) (Fig. 2a). Although not as strong or persistent from month to month, there were also significant correlations between the date of last clutches and SST in the same summer, both close to the colony and offshore ($r = 0.561$, $P = 0.015$ and $r = 0.566$, $P = 0.014$, respectively); warmer ocean temperatures tended to correspond to a later end to laying. There were

very few significant correlations between the oceanographic variables and the timing of the start of little penguin breeding (the exceptions being correlations of -0.591 , $P = 0.010$, for Offshore SST in March of previous year, -0.495 , $P = 0.037$, for Colony SST in same month, -0.571 , $P = 0.013$, for Offshore SST in May previous year and -0.475 , $P = 0.046$, with FSL in previous August). Thus, higher SST and FSL in the year before breeding corresponded to an earlier start to the breeding season. No significant correlations were found between mean laying date and the oceanographic variables.

Although variation in FSL was associated with variability in the timing of Little Penguin breeding at Penguin Island, it appeared to have very little influence over breeding productivity, measured by the number of chicks per pair, the percentage that hatched or fledged, and fledgling mass; no significant correlations with FSL were observed (not shown). The productivity measures were more highly correlated with SSTs (both near the colony and offshore); warmer ocean temperatures, particularly in the April and May immediately before breeding, tended to correspond to reduced productivity (e.g. Fig. 2*b*; the results for number of chicks per pair, hatching success and fledging success were similar).

Several penguin breeding variables were highly correlated with each other (Table 1). When the mean laying date (MLD) was earlier, the first laying date and, to a lesser extent, the last date of laying also tended to be earlier (Fig. 3). The interval between first and last laying dates appeared to be related mainly to when the penguins started laying rather than when they finished, with earlier laying generally corresponding to a longer laying period (Fig. 3). Fledglings tended to be heavier in years when egg laying was earlier and a lower percentage of eggs hatched when the last laying date was later (Table 1). Hatching success and fledging success were highly (positively) correlated with each other and also with the number of chicks produced per pair (Table 1).

From 1986–2008, the date on which the penguins started laying became earlier. This corresponded to a lengthening of the laying period by 3.4 days per year (Fig. 3, Table 2).

Regression analyses and predictive modelling

Using multiple regression analysis, the SST offshore in the April immediately before breeding explained the highest percentage of variance in chicks per pair and the fledgling mass (33% and 43% respectively; Table 3). However, models using SST near the colony resulted in a similar model fit (not shown). In both cases, warmer ocean temperatures corresponded to reduced breeding success (number of chicks per pair or fledgling mass). The percentage of eggs that resulted in fledged chicks was correlated with both the offshore and near colony SST in April (just before breeding) and the offshore SST in June (usually within the breeding season). The offshore April SST dominated this model, which explained 48% of variance in the percentage of fledglings, with warmer offshore SST resulting in a lower success (Table 3). No significant model could be developed for the percentage of eggs that hatched.

The model which explained the highest percentage of variance was that for the interval between the first and last laying date (62%). This was also the most complex model, with the FSL in the previous winter months (June, July and August) and summer months just before breeding (December and January) affecting this interval (Table 3). The models for the other timing of breeding variables, i.e. first, mean and last egg lay date also involved FSL in the previous winter and summer. In the model for first laying date (explaining 52% of the variance), warmer offshore ocean temperatures in the March of the previous year moved the laying date earlier, as did higher values of FSL in the previous August, whereas higher FSL in the January of the year of breeding tended to delay the start of breeding; the two FSL variables having the greater influence (Table 3). A slightly less complex model was that for last laying date (explaining 55% of the variance, Table 3). In this model higher FSL in the August of the year before breeding shifted laying towards earlier dates, whereas higher FSL in the February of the breeding year had the opposite effect; FSL in February having the dominant effect, with years of strong Leeuwin Current (high FSL) corresponding to a later end to first clutches. Finally, the mean laying date was earlier when the FSL in August and September of the previous year were higher and later when the February FSL was higher. This model explained 42% of the variance (Table 3).

Data from 2009–2011 were used to test the regression model's ability to predict breeding timing and productivity (Fig. 4a–h; Table 4). Although the model predicting last laying date had the second best fit for the period 1986–2008, predictions for the period 2009–2011 were generally not as good as those for the number of chicks per pair and first laying date, with only two of the prediction intervals containing the observed value. Despite having quite wide prediction intervals, the model for fledgling mass also performed relatively poorly in predictive mode, again with only two of the prediction intervals containing the observed value. The most accurate predictions were for the measures of breeding success i.e. the number of chicks per pair, the percentage of eggs that hatched and the percentage of fledglings, as well as the range of lay dates. Comparing the predictions across all five penguin variables, the least accurate predictions were for 2011.

Discussion

The timing of little penguin breeding on Penguin Island was correlated with SST and the Leeuwin Current, both in the austral winter of the year before breeding, i.e. a lag effect of one year, and in the austral summer immediately preceding breeding. The winter SST and Leeuwin Current were positively correlated with an earlier start to breeding. The timing of breeding by little penguins has been linked to an adequate supply of fish (Cullen *et al.* 1992), as well as the fat reserves of the penguins (Wienecke *et al.* 1995). Therefore, presumably these oceanographic conditions led to an enhancement of fish abundance in the local coastal marine environment. A strong summer Leeuwin Current, particularly in February, and higher summer SST were correlated with a later end to laying and probably a decrease in fish abundance.

As previously mentioned, the little penguins mainly feed on a variety of baitfish, with pilchard dominating the diet during prebreeding (Klomp and Wooller 1988a) and sandy sprat during chick rearing (Bradley *et al.* 1997). The size of all species most often taken (Klomp and Wooller 1988a; Bradley *et al.* 1997) represent the <1–2 year old age class of most species (Jones 1990; Fletcher and Blight 1996; Gaughan *et al.* 1996). Furthermore, the age classes of all these fish

species are usually found in embayments within the foraging range of the penguins (Ayvazian and Hyndes 1995; Gaughan *et al.* 1996; Valesini *et al.* 1998; Smith *et al.* 2008). Although the mechanisms underlying the interactions between the strength of the Leeuwin Current, nutrients and fish abundance in this geographical area are not clear (Gaughan 2007; Lourey *et al.* 2006; Waite *et al.* 2007; Lenanton *et al.* 2009), there is evidence to support the idea that sandy sprat abundance is enhanced the year following a strong Leeuwin Current in May to August (Gaughan *et al.* 1996; Caputi *et al.* 1996; Lenanton *et al.* 2009). During a strong winter Leeuwin Current, the already winter peak chlorophyll *a* concentrations (Koslow *et al.* 2008; Feng *et al.* 2009b) that occur from offshore to inshore (Koslow *et al.* 2008), are further increased (Feng *et al.* 2009b), thus providing better feeding conditions for fish. An increased abundance of fish would also account for the fledglings being heavier in years when breeding began earlier, because parents could return with larger meals and/or more frequently to feed their chicks. Interestingly, there has been a warming trend in the ocean off the south-west of Western Australia over the past five decades (Pearce and Feng 2007; Feng *et al.* 2009a), particularly from autumn to winter (Caputi *et al.* 2009). This is most likely to result from lower storm activity, cloud cover and thus increased solar radiation (Feng *et al.* 2009a). This may account for the overall temporal trend for egg laying to begin earlier.

In contrast, a high FSL, and hence strong Leeuwin Current in summer is very likely to transport offshore larvae southwards. Indeed, pilchards <2 years old that probably originated from the Perth region (Muhling *et al.* 2008a) have been found in Geographe Bay (Gaughan *et al.* 2001b), ~150 km south of Penguin Island. In addition, during a strong summer Leeuwin Current, the normally enhanced upwellings associated with the Capes Current in the south-west (Hanson *et al.* 2005), are likely to be less productive. This is because the nitricline, the level at which the nitrate concentration changes, is deeper in La Niña years when the Leeuwin Current is stronger, and therefore the nutrient flux will be decreased (Hanson *et al.* 2007). The ensuing poorer feeding conditions during a strong Leeuwin Current would also impact on larvae in embayments. Fewer juvenile fish, such as pilchards, in the local region will likely increase the time required by the penguins to achieve a body condition adequate to withstand breeding. This would account for penguins attempting to breed later in the year

during periods of a strong Leeuwin Current, as we found in this study. The later a first clutch is laid not only reduces the chance of the eggs hatching, but also the likelihood of laying a replacement clutch.

Higher offshore and inshore SSTs in April and May were associated with the breeding productivity of the penguins, with fewer successfully raising chicks and those chicks being lighter. One explanation for this is that when the waters are warmer in these months, the local fish stocks may move further away, as hypothesised by the Department of Fisheries (2002) to account for a reduction in locally caught pilchard stocks. If this is the case, as has been shown for pilchard distribution in South Africa (Beckley and van der Lingen 1999; and references within), then the penguins would have to increase their foraging duration and/or a reduce the meal sizes brought back to the chicks.

An increase in foraging duration was observed during a recent study in 2008 (B. Cannell unpubl. data), when water temperatures in April and May were 1–2°C above average (A. Pearce unpubl. data). Incubation shifts during 2008 extended for more than 10 days (B. Cannell unpubl. data), instead of the usual three to five days (Chiaradia and Kerry 1999; Collins *et al.* 1999). Longer foraging trips during incubation have been associated with increased abandonment of eggs (Numata *et al.* 2000; B. Cannell unpubl. data), and long incubation shifts have been associated with a reduction in the body condition of the incubating adults (Numata *et al.* 2000; Kemp and Dann 2001). This in turn could affect their ability to successfully rear chicks. If prey abundance is low during chick rearing, and the size of the meal brought back to the chick(s) is low, then chicks can take longer to develop, and will fledge at lower masses (Wienecke *et al.* 2000). Indeed, Wooller *et al.* (1991) found that penguins returned to the colony with smaller meal sizes in 1989 compared with 1986 and chick mass at fledging was lower in 1989. It is curious that SSTs two or more months before most penguins are generally feeding chicks correlated with a reduced fledgling mass. Presumably higher temperatures early in the season, or any other oceanographic factor linked with such higher temperatures, drive fish stocks further away for the whole breeding season. However, similar to the Leeuwin Current, the mechanism underlying the effect of the higher SST on the fish is not understood as yet.

As the SST of the Leeuwin Current generally increases when it is stronger, it is interesting that higher SSTs in April to May affect the number of chicks produced per pair, and the mass of the chicks at fledging, but there is no corresponding correlation with the Leeuwin Current, as measured through FSL. Feng *et al.* (2008), however, found that the SST in February to April is not only influenced by the immediate strength of the Leeuwin Current, but also by the temperature anomaly from the previous austral winter. In addition, there have been some years when there has been a decrease in the strength of the Leeuwin Current, but an increase in the SST anomaly (see fig. 22, Pearce *et al.* 2006). This highlights the very complex nature of the Leeuwin Current, SSTs and the various oceanographic factors that exist on the West Australian coast.

Model predictions and a record strong Leeuwin Current in 2011

The models performed reasonably well for 2009 and 2010, especially for the number of chicks per pair, hatching success and the range of egg laying, where the predicted and observed number were very similar. This was surprising given the large prediction intervals for these variables, which indicated that the ability of the models to forecast was slight. In contrast, most of the models for the timing of breeding, although explaining a reasonable proportion of the variance, did not perform as well in the limited number of test years (2009–2011). This highlights the necessity for continued monitoring to determine how the models perform over time and to assist in understanding the interannual variations in the effect of the Leeuwin Current and SST on the biological properties of the coast.

The predictive ability of the models for each breeding variable, except hatching success, was poor in 2011. This is most likely because of a record strong La Niña and Leeuwin Current that began in the summer of 2010 and persisted throughout 2011 (Pearce *et al.* 2011). The water temperature reached $>3^{\circ}\text{C}$ above average in Warnbro Sound, the embayment directly south of Penguin Island (Pearce *et al.* 2011). Chick production was much lower than expected, and it is interesting that the last date that eggs were laid within the nestboxes was much earlier than predicted. It is likely that these lower than expected values reflect a very low abundance of fish close to Penguin Island, so that the penguins

were unable to attain the body condition necessary to undertake breeding. This was evidenced by an above average number of dead, underweight penguins in 2011 (B. Cannell, unpubl. data).

It is important to note that in Western Australia, El Niño events generally are associated with a weakening of the Leeuwin Current (Feng *et al.* 2003). This means that, unlike the eastern coast of Australia, and indeed other countries bordered by the Pacific Ocean (Philander 1983), the water temperatures along the western coast of Australia are cooler during El Niño years, and warmer during La Niña years (Feng *et al.* 2003). El Niño events elsewhere, including northern Western Australia, are typically associated with reduced breeding in seabirds (e.g. Schreiber and Schreiber 1984; Dunlop *et al.* 2002; Surman and Nicholson 2009; Surman *et al.* 2012), and they have been implicated in a lower breeding success of little penguins on Bowen Island, NSW (Fortescue 1999). For the little penguins on Penguin Island however, poorer reproductive performance is associated with La Niña events.

Potential impact of climate change on the breeding of little penguins

The possible impacts of climate change on the little penguins on Penguin Island are complicated. First, as previously noted, there has been a warming of the Indian Ocean in the south-west of Western Australia during the austral autumn and winter. Also, modelling predictions of the impacts of climate change show further decreased rainfall and continued warming of SST (Feng *et al.* 2009a). This study has shown that warmer SSTs in April and May reduced some parameters of breeding productivity in little penguins, including fledgling mass, fledging success and the number of chicks per pair, whereas increased SSTs and stronger Leeuwin Currents during December to February were associated with a later end of laying. Those penguins which lay late in the season will still be feeding chicks in November to January, when temperatures at the surface nests on Penguin Island may be high (Klomp *et al.* 1991), with possibly deleterious consequences. Terrestrial temperatures are predicted to rise by 2030, with an increase in the number of days above 35°C and the average temperatures in summer to increase by 0.9–1°C (CSIRO and Australian Bureau of Meteorology 2007). High temperatures in these months have already been associated with increased mortality of penguins (Cannell *et al.* 2011; Chambers *et al.* 2011). Accordingly, climate change is likely to adversely affect penguin prey abundance and distribution and thus this colony of little penguins, as evidenced in 2011.

Second, even though SSTs are predicted to increase, the strength of the Leeuwin Current may continue to weaken (Feng *et al.* 2009a). A strong Leeuwin Current and higher SSTs in autumn and winter correlated with earlier breeding the following year. In turn, fledgling mass was positively correlated with earlier breeding, and heavier fledglings are more likely to survive (Dann 1988; Cullen and Dann 1993). So the lag effects of a weaker Leeuwin Current in the previous austral autumn-winter are likely to be the reverse of the lag effects for higher SSTs in the same period.

Interestingly, this negative impact of climate change is in contrast to the situation for little penguins at Phillip Island, in south-eastern Australia, where egg laying was earlier when the SSTs were elevated from February to April, before breeding (Cullen *et al.* 2009). Additionally, the number of chicks per pair, and the chick mass at fledging were positively influenced by warm water in March (Cullen *et al.* 2009), and were attributed to changes in marine productivity (Cullen *et al.* 2009). If climate change is indeed likely to adversely affect the penguins on Penguin Island, the need for proactive management of any possible anthropogenic effects on fish prey availability becomes even more vital to the wellbeing of the colony. This is paramount given that the penguins on Penguin Island are not only at the western limit of the distribution of little penguins (Wienecke *et al.* 1995), but also markedly larger (Klomp and Wooller 1988b) and genetically distinct from little penguins along the east coast and indeed elsewhere in Western Australia (J. Sinclair, B. Cannell, W. Sherwin, S. Bradley and R. Wooller, unpubl. data). The models that we have developed allow predictions to be made about the timing and success of breeding well in advance, thereby enhancing management of the penguins. Perhaps more importantly, these models also indicate that the penguins are ideal sentinels of climate change.

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References

- Ayvazian, S. G., and Hyndes, G. (1995). Surf-zone fish assemblages in south-western Australia: Do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna? *Marine Biology* **122**, 527–536.
- Barber, R. T., and Chavez, F. P. (1983). Biological consequences of El Niño. *Science* **222**, 1203–1210.
- Beckley, L. E., and van der Lingen, C. D. (1999). Biology, fishery and management of sardines (*Sardinops sagax*) in southern African waters. *Marine and Freshwater Research* **50**, 955–978.
- Boersma, P. D. (1978). Breeding patterns of Galapagos penguins as an indicator of oceanographic conditions. *Science* **200**, 1481–1483.
- Bradley, J. S., Cannell, B. L., and Wooller, R.D. (1997). A radio-tracking study of the movements at sea and diet of little penguins *Eudyptula minor* breeding on Penguin Island, Western Australia. Murdoch University, Report to Bowman Bishaw Gorham. Perth.
- Cannell, B., Pollock, K., Bradley, S., Wooller, R., Sherwin, W., and Sinclair, J. (2011). Augmenting mark-recapture with beach counts to estimate the abundance of little penguins on Penguin Island, Western Australia. *Wildlife Research* **38**, 491–500.
- Caputi, N., Fletcher, W. J., Pearce, A., and Chubb, C. F. (1996). Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian coast. *Marine and Freshwater Research* **47**, 147–155.
- Caputi, N., de Lestang, S., Feng, M., and Pearce, A. (2009). Seasonal variation in the long-term warming trend in water temperature off the Western Australian coast. *Marine and Freshwater Research* **60**, 129–139.
- Chambers, L. E., Devney, C., Congdon, B. C., Dunlop, N., Woehler, E. J., and Dann, P. (2011). Observed and predicted impacts of climate on Australian seabirds. *Emu* **111**, 235–251.
- Chiaradia, A. F., and Kerry, K. R. (1999). Daily nest attendance and breeding performance in the little penguin *Eudyptula minor* at Phillip Island, Australia. *Marine Ornithology* **27**, 13–20.
- Cole, J. (1999). Environmental conditions, satellite imagery, and clupeoid recruitment in the northern Benguela upwelling system. *Fisheries Oceanography* **8**, 25–38.
- Collins, M. G., Cullen, J. M., and Dann, P. (1999). Seasonal and annual foraging movements of little penguins from Phillip Island, Victoria. *Wildlife Research* **26**, 705–721.
- Connard, M. N. (1995). Patterns of foraging by little penguins *Eudyptula minor* from Penguin Island, Western Australia. B.Sc. (Honours) Thesis, Murdoch University, Perth.
- Cresswell, G. R. (1990). The Leeuwin Current. *Corella* **14**, 113–118.

- Cresswell, G. R., and Golding, T. J. (1980). Observations of a south-flowing current in the southeastern Indian Ocean. *Deep-Sea Research Part A* **27**, 449–466.
- CSIRO and Australian Bureau of Meteorology (2007). Climate change in Australia. Technical Report 2007. Available at http://www.climatechangeinaustralia.gov.au/technical_report.php [Verified 5 October 2012].
- Cullen, M., and Dann, P. (1993). A study of the impact of tourism on penguins at Bowen Island, Jervis Bay National Park. Report to the Australian Nature Conservation Agency, Canberra.
- Cullen, J. M., Montague, T. L., and Hull, C. (1992). Food of little penguins *Eudyptula minor* in Victoria: comparison of three localities between 1985 and 1988. *Emu* **91**, 318–341.
- Cullen, J. M., Chambers, L. E., Coutin, P. C., and Dann, P. (2009). Predicting onset and success of breeding in little penguins *Eudyptula minor* from ocean temperatures. *Marine Ecology Progress Series* **378**, 269–278.
- Dann, P. (1988). Research Annual Report 1997–98. Phillip Island Penguin Reserve, Melbourne.
- Dann, P., and Norman, F. I. (2006). Population regulation in Little Penguins (*Eudyptula minor*): the role of intraspecific competition for nesting sites and food during breeding. *Emu* **106**, 289–296.
- Department of Fisheries (2002). State of the Fisheries Report 2001/2002. Department of Fisheries, Perth.
- Dunlop, J. N., Klomp, N. I., and Wooller, R. D. (1988). Penguin Island, Shoalwater Bay, Western Australia. *Corella* **188**, 93–98.
- Dunlop, J. N., Long, P., Stejskal, I., and Surman, C. A. (2002). Inter-annual variations in breeding participation at four Western Australian colonies of the Wedge-Tailed Shearwater *Puffinus pacificus*. *Marine Ornithology* **30**, 13–18.
- Erwin, C., and Congdon, B. C. (2007). Day-to-day variation in sea-surface temperature reduces sooty tern *Sterna fuscata* foraging success on the Great Barrier Reef, Australia. *Marine Ecology Progress Series* **331**, 255–266.
- Feng, M., Meyers, G., Pearce, A., and Wijffels, S. (2003). Annual and interannual variations of the Leeuwin Current at 32°S. *Journal of Geophysical Research* **108**, 3355.
- Feng, M., Majewski, L. J., Fandry, C. B., and Waite, A. M. (2007). Characteristics of two counter-rotating eddies in the Leeuwin Current system off the Western Australian coast. *Deep-sea Research. Part II, Topical Studies in Oceanography* **54**, 961–980.
- Feng, M., Biastoch, A., Böning, C., Caputi, N., and Meyers, G. (2008). Seasonal and interannual variations of upper ocean heat balance off the west coast of Australia. *Journal of Geophysical Research* **115**, C12505.
- Feng, M., Weller, E., and Hill, K. (2009a). The Leeuwin Current. In ‘A Marine Climate Change Impacts and Adaptation Report Card for Australia 2009’. (Eds E. S. Poloczanska, A. J. Hobday and A. J. Richardson.) NCCARF Publication 05/09. Available at http://www.oceanclimatechange.org.au/content/index.php/site/report_card_extended_2/category/leeuwin_current/ [Verified 5 October 2012].
- Feng, M., Waite, A. M., and Thompson, P. A. (2009b). Climate variability and ocean production in the Leeuwin Current system off the west coast of Western Australia. *Journal of the Royal Society of Western Australia* **92**, 67–81.

- Fletcher, W. J., and Blight, S. J. (1996). Validity of using translucent zones of otoliths to age the pilchard *Sardinops sagax neopilchardus* from Albany, Western Australia. *Marine and Freshwater Research* **47**, 617–624.
- Fortescue, M. (1999). Temporal and spatial variation in breeding success of the Little Penguin *Eudyptula minor* on the east coast of Australia. *Marine Ornithology* **27**, 21–28.
- Gaughan, D. J. (2007). Potential mechanisms of influence of the Leeuwin Current eddy system on teleost recruitment to the Western Australian continental shelf. *Deep-sea Research. Part II, Topical Studies in Oceanography* **54**, 1129–1140.
- Gaughan, D. J., Fletcher, W. J., Tregonning, R. J., and Goh, J. (1996). Aspects of the biology and stock assessment of the whitebait, *Hyperlophus vittatus*, in south western Australia. Report No. 108, Department of Fisheries, Perth, Western Australia.
- Gaughan, D. J., White, K. V., and Fletcher, W. J. (2001a). The links between functionally distinct adult assemblages of *Sardinops sagax*: larval advection across management boundaries. *ICES Journal of Marine Science* **58**, 597–606.
- Gaughan, D. J., Baudains, G. A., Mitchell, R. W. D., and Leary, T. I. (2001b). Pilchard (*Sardinops sagax*) nursery areas and recruitment process assessment between different regions in southern Western Australia. Report No. 131, Department of Fisheries, Perth, Western Australia.
- Guinet, C., Chastel, O., Koudil, M., Durbuc, J. P., and Jouventin, P. (1998). Effects of warm sea surface temperature anomalies on the blue petrel at Kerguelen Islands. *Proceedings: Biological Sciences* **265**, 1001–1006.
- Hanson, C. E., Pattiaratchi, C. B., and Waite, A. M. (2005). Seasonal production regimes off southwestern Australia: influence of the Capes and Leeuwin Currents on phytoplankton dynamics. *Marine and Freshwater Research* **56**, 1011–1026.
- Hanson, C. E., Pesant, S., Waite, A. M., and Pattiaratchi, C. B. (2007). Assessing the magnitude and significance of the deep chlorophyll maxima of the coastal eastern Indian Ocean. *Deep-sea Research. Part II, Topical Studies in Oceanography* **54**, 884–901.
- Jones, G. K. (1990). Growth and mortality in a lightly fished population of garfish (*Hyporhamphus melanochir*), in Baird Bay, South Australia. *Transactions of the Royal Society of South Australia* **114**, 37–45.
- Kemp, A., and Dann, P. (2001). Egg size, incubation periods and hatching success of Little Penguins, *Eudyptula minor*. *Emu* **101**, 249–253.
- Klomp, N. I., and Wooller, R. D. (1988a). Diet of little penguins *Eudyptula minor* from Penguin Island, Western Australia. *Australian Journal of Marine and Freshwater Research* **39**, 633–640.
- Klomp, N. I., and Wooller, R. D. (1988b). The size of little penguins *Eudyptula minor* on Penguin Island, Western Australia. *Records of the Western Australian Museum* **114**, 211–216.
- Klomp, N. I., Meathrel, C. E., Wienecke, B. C., and Wooller, R. D. (1991). Surface nesting by little penguins on Penguin Island, Western Australia. *Emu* **91**, 190–193.
- Koslow, J. A., Pesant, S., Feng, M., Pearce, A., Fearn, P., Moore, T., Matear, R., and Waite, A. (2008). The effect of the Leeuwin Current on phytoplankton biomass and production off Southwestern Australia. *Journal of Geophysical Research* **113**, C07050.
- Lenanton, R. C., Caputi, N., Kangas, M., and Craine, M. (2009). The ongoing influence of the Leeuwin Current on economically important fish and invertebrates off temperate Western Australia-has it changed? *Journal of the Royal Society of Western Australia* **92**, 111–127.

- Lourey, M. J., Dunn, J. R., and Waring, J. (2006). A mixed-layer nutrient climatology of Leeuwin Current and Western Australian shelf waters: Seasonal nutrient dynamics and biomass. *Journal of Marine Systems* **59**, 25–51.
- Marchant, S., and Higgins, P. J. (1990). 'Handbook of Australian, New Zealand and Antarctic Birds. Vol. 1: Ratites to Ducks, Vol 1.' (Oxford University Press: Melbourne.)
- Mickelson, M. J., Dann, P., and Cullen, J. M. (1992). Sea temperature in Bass Strait and breeding success of the Little Penguin *Eudyptula minor* at Phillip Island, south-eastern Australia. *Emu* **91**, 355–368.
- Muhling, B. A., Beckley, L. E., Gaughan, D. J., Jones, C. M., Miskiewicz, A. G., and Hesp, S. A. (2008a). Spawning, larval abundance and growth rate of *Sardinops sagax* off southwestern Australia: influence of an anomalous eastern boundary current. *Marine Ecology Progress Series* **364**, 157–167.
- Muhling, B. A., Beckley, L. E., Koslow, J. A., and Pearce, A. F. (2008b). Larval fish assemblages and water mass structure off the oligotrophic south-western Australian coast. *Fisheries Oceanography* **17**, 16–31.
- Murray, D. C., Bunce, M., Cannell, B. L., Oliver, R., Houston, J., White, N. E., Barrero, R. A., Bellgard, M. I., and Haile, J. (2011). DNA-based faecal analysis: A comparison of qPCR and high throughput sequencing approaches. *PLoS ONE* **6**, e25776.
- Nevárez-Martínez, M. O., Lluch-Belda, D., Cisneros-Mata, M. A., Santos-Molina, J. P., Martínez-Zavala, M. D., and Lluch-Cota, S. E. (2001). Distribution and abundance of the Pacific sardine (*Sardinops sagax*) in the Gulf of California and their relation with the environment. *Progress in Oceanography* **49**, 565–580.
- Numata, M., Davis, L. S., and Renner, M. (2000). Prolonged foraging trips and egg desertion in little penguins (*Eudyptula minor*). *New Zealand Journal of Zoology* **27**, 277–289.
- Pearce, A. F. (1991). Eastern boundary currents of the southern hemisphere. *Journal of the Royal Society of Western Australia* **74**, 35–45.
- Pearce, A., and Feng, M. (2007). Observations of warming on the Western Australian continental shelf. *Marine and Freshwater Research* **58**, 914–920.
- Pearce, A., and Pattiaratchi, C. (1999). The Capes Current: a summer countercurrent flowing past Cape Leeuwin and Cape Naturaliste, Western Australia. *Continental Shelf Research* **19**, 401–420.
- Pearce, A. F., and Phillips, B. F. (1988). ENSO events, the Leeuwin Current, and larval recruitment of the western rock lobster. *Journal du Conseil* **45**, 13–21.
- Pearce, A. F., Lynch, M. J., and Hanson, C. E. (2006). The Hillary's Transect (1): Seasonal and cross-shelf variability of physical and chemical water properties off Perth, Western Australia, 1996–98. *Continental Shelf Research* **26**, 1689–1729.
- Pearce, A., Lenanton, R., Jackson, G., Moore, J., Feng, M., and Gaughan, D. (2011). The “marine heat wave” off Western Australia during the summer of 2010/11. Fisheries Research Report No. 222. Fisheries Research Division, Perth, Western Australia.
- Peck, D. R., Smithers, B. V., Krockenberger, A. K., and Congdon, B. C. (2004). Sea surface temperature constrains wedge-tailed shearwater foraging success within breeding seasons. *Marine Ecology Progress Series* **281**, 259–266.
- Philander, S. G. H. (1983). El Niño Southern Oscillation phenomena. *Nature* **302**, 295–301.
- Ramos, J. A., Maul, A. M., Ayrton, V., Bullock, I., Hunter, J., Bowler, J., Castle, G., Mileto, 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.

- Reilly, P. N., and Cullen, J. M. (1981). The Little Penguin *Eudyptula minor* in Victoria Australia II. Breeding. *Emu* **81**, 1–19.
- Schreiber, R. W., and Schreiber, E. A. (1984). Central Pacific seabirds and the El Niño Southern Oscillation: 1982 to 1983 Perspectives. *Science* **225**, 713–716.
- Smith, K., Brown, J., Hammond, M., and Nardi, A. (2008). Development of cost-effective indices to monitor the nearshore fish communities of the Swan Region. Final report to the Swan Catchment Council. Department of Fisheries, Western Australia.
- Smithers, B. V., Peck, D. R., Krockenberger, A. K., and Congdon, B. C. (2003). Elevated sea-surface temperature, reduced provisioning and reproductive failure of wedge-tailed shearwaters (*Puffinus pacificus*) in the southern Great Barrier Reef, Australia. *Marine and Freshwater Research* **54**, 973–977.
- Somarakis, S., Ganias, K., Siapatis, A., Koutsikopoulos, C., Machias, A., and Papaconstantinou, C. (2006). Spawning habitat and daily egg production of sardine (*Sardina pilchardus*) in the eastern Mediterranean. *Fisheries Oceanography* **15**, 281–292.
- Surman, C. A., and Nicholson, L. W. (2009). The good, the bad and the ugly: ENSO-driven oceanographic variability and its influence on seabird diet and reproductive performance at the Houtman Abrolhos, Eastern Indian Ocean. *Marine Ornithology* **37**, 129–138.
- Surman, C. A., Nicholson, L. W., and Santora, J. A. (2012). Effects of climate variability on breeding phenology and performance of tropical seabirds in the eastern Indian Ocean. *Marine Ecology Progress Series* **454**, 147–157.
- Tabachnick, B. G., and Fidell, L. S. (1996). 'Using multivariate statistics.' 3rd edn. (Harper Collins College Publishers: New York.)
- Valesini, F. J., Potter, I. C., Hyndes, G. A., and Platell, M. E. (1998). The fish faunas in the vicinity of the proposed Port Kennedy marina development, with particular reference to the sandy sprat (*Hyperlophus vittatus*) and blue sprat (*Spratelloides robustus*). Murdoch University, Report to Bowman, Bishaw and Gorham, Perth.
- Valle, C. A., Cruz, F., Cruz, J. B., Merlen, G., and Coulter, M. C. (1987). The impact of the 1982–1983 El Niño-Southern Oscillation on seabirds in the Galapagos Islands, Ecuador. *Journal of Geophysical Research C* **92**, 14 437–14 444.
- Waite, A. M., Thompson, P. A., Pesant, S., Feng, M., Beckley, L. E., Domingues, C. M., Gaughan, D., Hanson, C. E., Holl, C. M., Koslow, T., Meuleners, M., Montoya, J. P., Moore, T., Muhling, B. A., Paterson, H., Rennie, S., Strzelecki, J., and Twomey, L. (2007). The Leeuwin Current and its eddies: An introductory overview. *Deep-sea Research. Part II, Topical Studies in Oceanography* **54**, 789–796.
- Wienecke, B. C. (1989). The breeding patterns of little penguins on Penguin Island, Western Australia, in relation to dietary and oceanographic factors. B.Sc. (Honours) Thesis, Murdoch University, Perth.
- Wienecke, B. C., Wooller, R. D., and Klomp, N. I. (1995). The ecology and management of little penguins on Penguin Island, Western Australia. In 'The Penguins'. (Eds P. Dann, I. Norman, P. Reilly.) pp. 440–467. (Beatty and Sons: Surrey, England.)
- Wienecke, B. C., Bradley, J. S., and Wooller, R. D. (2000). Annual and seasonal variation in the growth rates of young little penguins *Eudyptula minor* in Western Australia. *Emu* **100**, 139–147.
- Wooller, R. D., Dunlop, J. N., Klomp, N. I., Meathrel, C. E., and Wienecke, B. C. (1991). Seabird abundance, distribution and breeding patterns in relation to the Leeuwin Current. *Journal of the Royal Society of Western Australia* **74**, 129–132.

Fig. 1. The location of Penguin Island in relation to Perth, Western Australia, with an enlarged map of Penguin Island. The grey area represents the general foraging area of the penguins during chick rearing in Warnbro Sound and Comet Bay (from B. Cannell, R. Wooller and S. Bradley, unpubl. data). O – the grids for which Offshore SSTs were obtained, C – the grids for which Colony SSTs were obtained.

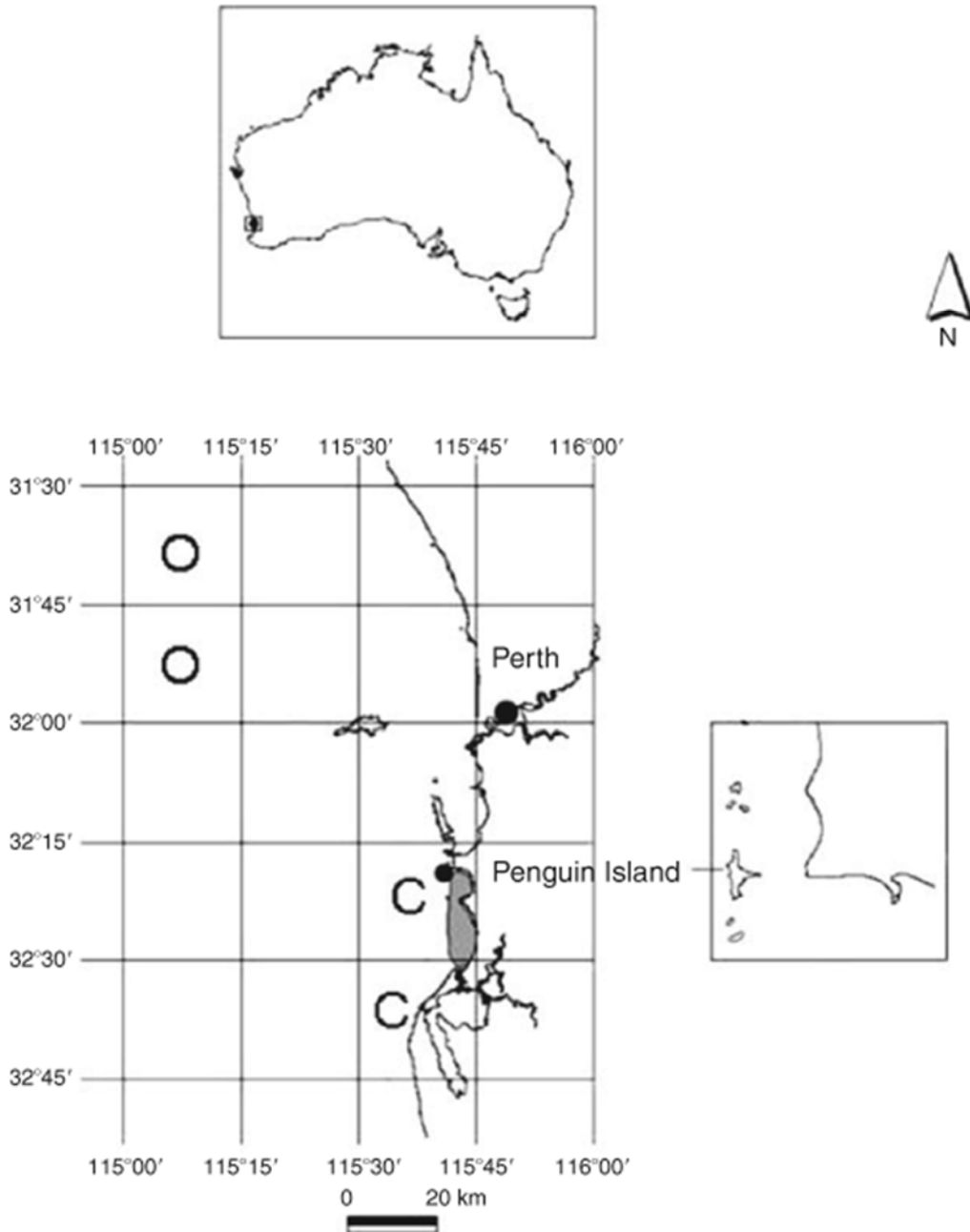


Fig. 2. (a) Temporal pattern of correlation of monthly FSL with last laying date (■) and length of breeding season (●). Correlations significant at the 5% level appear above the horizontal line. (b) Temporal pattern of correlation of Colony SST with chick mass at fledging. Correlations significant at the 5% level appear below the horizontal line. A similar pattern of correlations was found for Offshore SST.

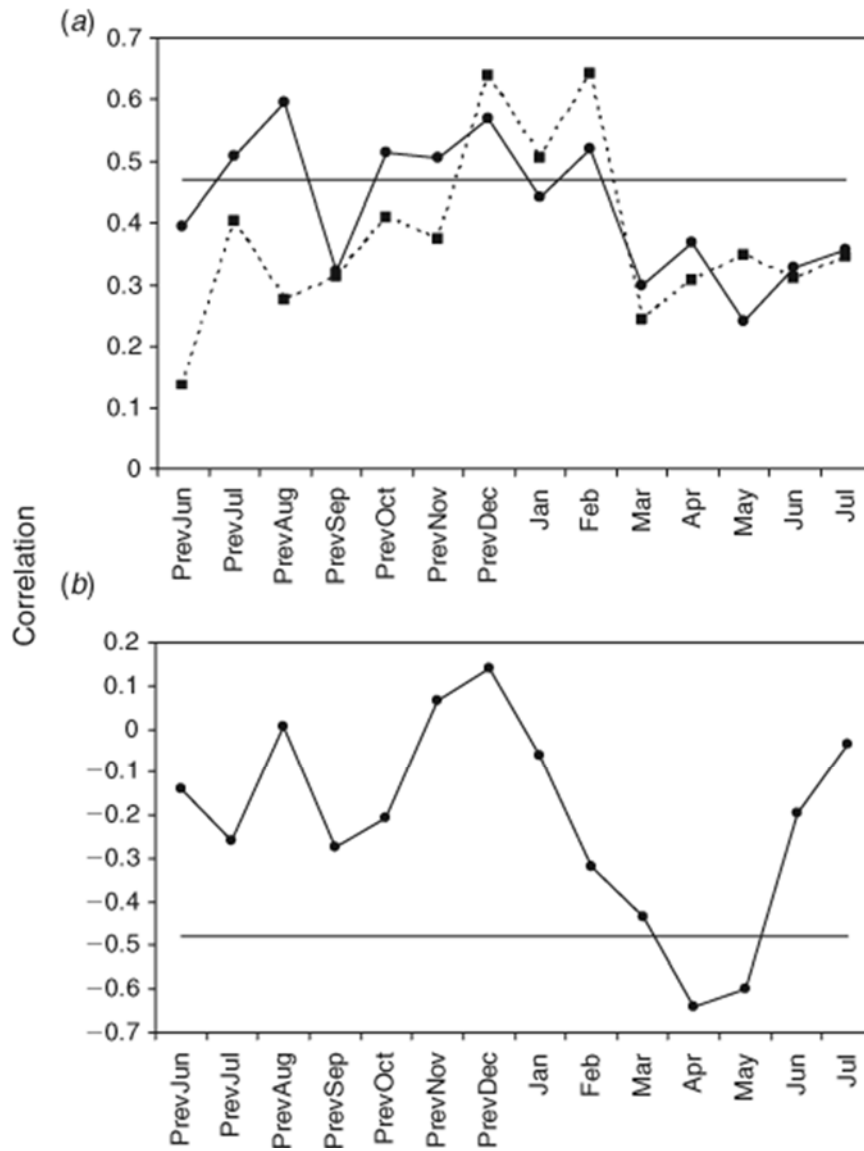


Fig. 3. The dates of the first (■), and last (▲) clutches, and mean lay date (•) for first clutches each year. LOWESS smoothing has been applied.

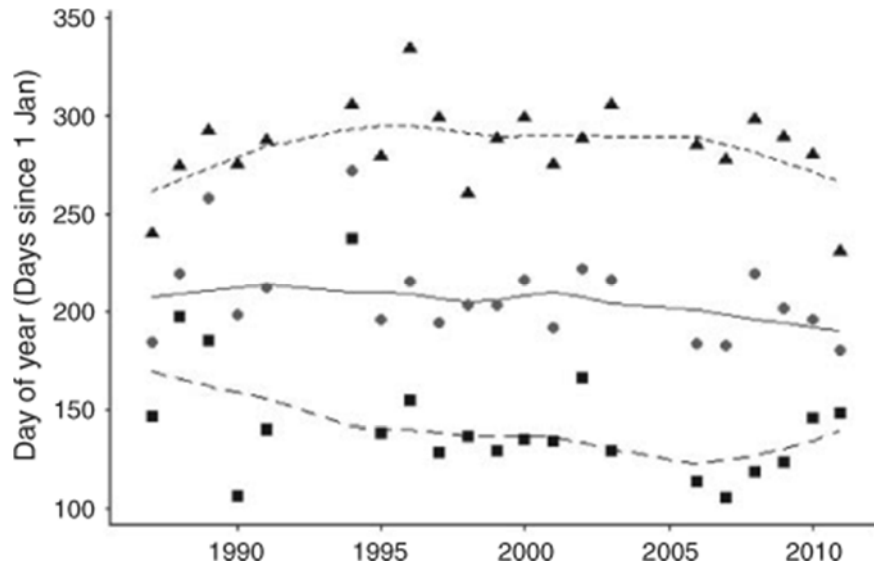


Fig. 4. Observed (\bullet) and modelled (\triangle) breeding parameters, including prediction intervals (dashed lines). (a) Average number of chicks per pair; (b) chick mass at fledging; (c) first laying date; (d) mean laying date; (e) last laying date; (f) length of breeding season; (g) hatching success; (h) fledging success. Above average FSL (stronger Leeuwin Current) was observed in 1988, 1989, 1996, 1999, 2000, 2008, 2009 and 2011.

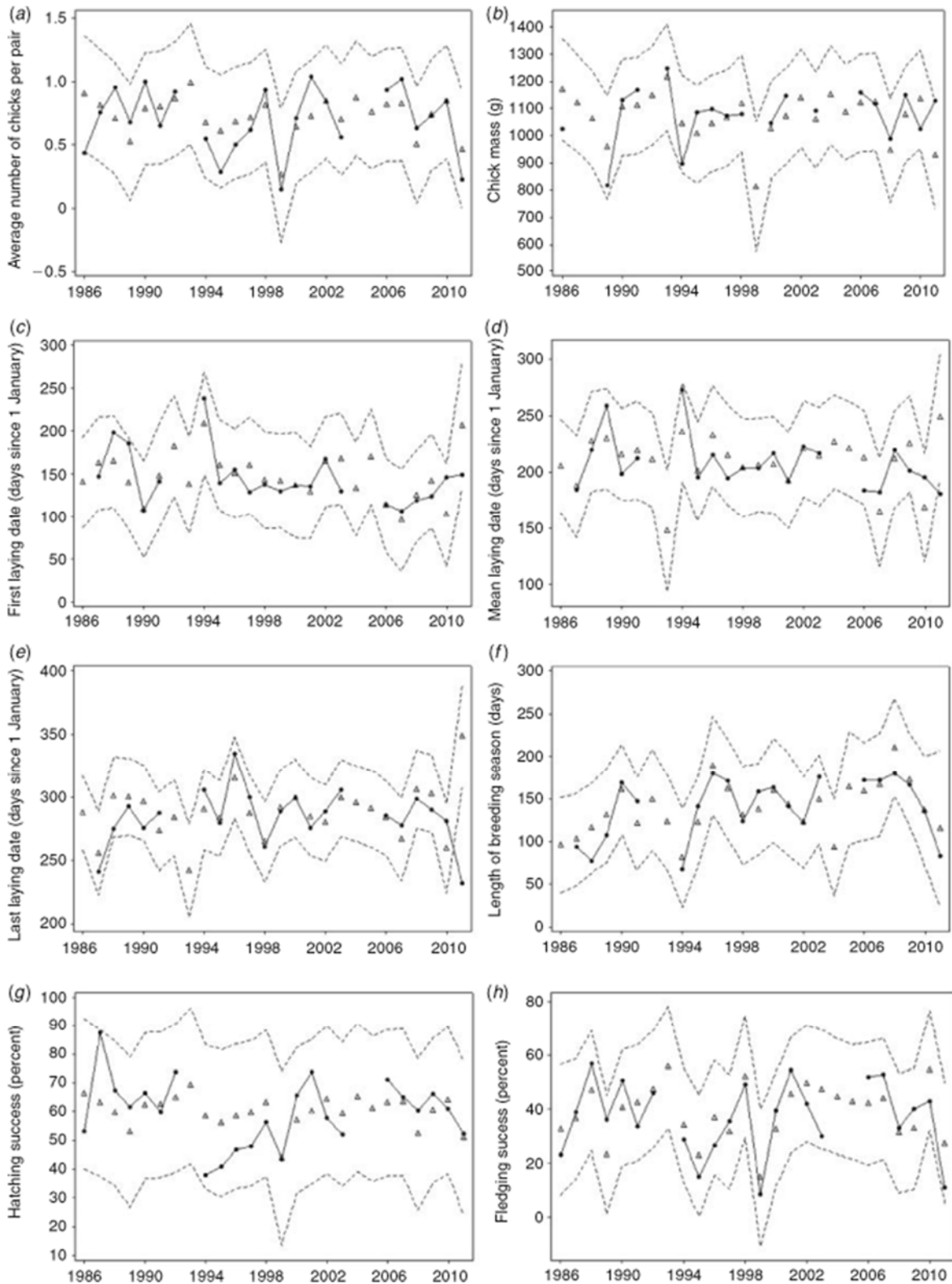


Table 1. Correlations between the little penguin breeding variables (using data from 1986–2008)

CPP – average number of chicks per pair; LD – laying date; LBS – length of breeding season from first to last eggs; % Hatch (fledge) is the percentage of eggs that resulted in successful hatching (fledglings). **, $P < 0.01$; *, $0.01 < P < 0.05$

	CPP	Fledgling mass	Mean LD	First LD	Last LD	LBS	% Hatch
Fledgling mass	0.350						
Mean LD	-0.254	-0.863**					
First LD	-0.144	-0.724**	0.810**				
Last LD	-0.433	-0.259	0.463	0.175			
LBS	-0.107	0.623*	-0.499*	-0.837**	0.393		
% Hatch	0.724**	0.339	-0.424	-0.273	-0.627**	-0.093	
% Fledge	0.988**	0.355	-0.250	-0.111	-0.411	-0.125	0.709**

Table 2. Temporal trends in the little penguin breeding variables and oceanographic variables over 1986–2008

CPP – average number of chicks per pair; LD – laying date; LBS – length of breeding season from first to last eggs; % Hatch (fledge) – the percentage of eggs that resulted in successful hatching (fledglings); FSL – Fremantle sea level; SST (Offshore) – SST averaged over the region 115°00'E–115°15'E and 31°30'S–32°00'S; SST (inshore) – SST averaged over the region 115°30'E–115°45'E and 32°15'S–32°45'S

	Trend	s.e.	<i>P</i> -value	% Variance explained	Data range
CPP	0.004 chicks year ⁻¹	0.009	0.628	<0.1	0.15–1.04 chicks
Fledgling mass	2.975 g year ⁻¹	4.147	0.485	<0.1	819–1248 g
Mean LD	–0.934 days year ⁻¹	0.882	0.296	1.0	Day 183–273
First LD	–2.519 days year ⁻¹	1.116	0.038	19.4	Day 106–238
Last LD	0.852 days year ⁻¹	0.733	0.262	2.0	Day 241–335
LBS	3.371 days year ⁻¹	1.083	0.007	33.8	68–180 days
% Hatch	–0.174% year ⁻¹	0.435	0.693	<0.1	38–88%
% Fledge	–0.215% year ⁻¹	0.457	0.643	<0.1	9–57%
FSL	0.004 m year ⁻¹	0.001	<0.001	6.8	0.51–1.07 m year ⁻¹
SST (Offshore)	0.016°C year ⁻¹	0.013	0.208	0.2	17.93–25.39°C
SST (Colony)	0.012°C year ⁻¹	0.014	0.403	<0.1	17.05–24.10°C

Table 3. Optimal models for period 1986–2008

SST (°C), FSL (m). CPP – average number of chicks per pair; LD – laying date, LBS – length of breeding season from first to last eggs; % Hatch (fledge) is the percentage of eggs that resulted in successful hatching (fledglings)

	Model	<i>P</i> -value	% Variance explained
CPP	$4.658 - 0.173 \text{ SST (Offshore)}_{\text{Apr}}$	0.005	33.2
Fledgling mass	$3257.1 - 96.3 \text{ SST (Offshore)}_{\text{Apr}}$	0.004	42.5
First LD	$946.8 - 28.1 \text{ SST (Offshore)}_{\text{PrevMar}} - 502.5 \text{ FSL}_{\text{PrevAug}} + 314.3 \text{ FSL}_{\text{Jan}}$	0.004	51.5
Mean LD	$322.2 - 541.9 \text{ FSL}_{\text{PrevAug}} + 193.9 \text{ FSL}_{\text{PrevSep}} + 218.8 \text{ FSL}_{\text{Feb}}$	0.014	41.5
Last LD	$287.1 - 227.0 \text{ FSL}_{\text{PrevAug}} + 237.5 \text{ FSL}_{\text{Feb}}$	0.001	54.6
LBS	$-291.1 - 418.6 \text{ FSL}_{\text{PrevJun}} + 573.8 \text{ FSL}_{\text{PrevJul}} + 684.6 \text{ FSL}_{\text{PrevAug}} + 356.1 \text{ FSL}_{\text{PrevDec}} - 624.1 \text{ FSL}_{\text{Jan}}$	0.004	61.7
% Hatch	$198.0 - 6.1 \text{ SST (Offshore)}_{\text{Apr}}$	0.065	13.1
% Fledge	$88.3 - 51.0 \text{ SST (Offshore)}_{\text{Apr}} + 11.0 \text{ SST (Offshore)}_{\text{Jun}} + 40.2 \text{ SST (Colony)}_{\text{Apr}}$	0.004	48.0

Table 4. Predicted and observed chicks per pair (CPP), mean mass at fledging (Fmass), first laying date (FLD), last laying date (LLD), length of breeding season (LBS), percentage of eggs that resulted in successful hatching (% Hatch) or fledglings (% Fledge) from 2009–2011, using models developed from the data from 1986–2008

CI, confidence interval; PI, prediction intervals. Bold indicates that the value contains observed value (see Table 3 for model details)

	Observed	Predicted	SE	95% CI	95% PI
CPP					
2009	0.73	0.74	0.046	(0.64, 0.83)	(0.30, 1.18)
2010	0.85	0.84	0.061	(0.71, 0.97)	(0.39, 1.27)
2011	0.23	0.46	0.088	(0.28, 0.65)	(0.00, 0.93)
Fmass					
2009	1149	1078	20.0	(1036, 1121)	(902, 1255)
2010	1025	1135	26.5	(1078, 1192)	(955, 1315)
2011	1128	927	46.7	(827, 1027)	(729, 1125)
FLD					
2009	124	141	10.0	(120, 163)	(87, 196)
2010	146	102	15.7	(67, 136)	(42, 163)
2011	149	206	25.6	(151, 261)	(131, 280)
MLD					
2009	202	225	7.6	(209, 241)	(183, 268)
2010	196	169	13.0	(141, 196)	(121, 217)
2011	181	249	18.3	(210, 288)	(193, 305)
LLD					
2009	290	303	4.9	(293, 313)	(272, 334)
2010	281	259	9.5	(239, 280)	(224, 295)
2011	232	348	13.2	(320, 377)	(308, 389)
LBS					
2009	166	172	10.8	(149, 196)	(118, 226)
2010	135	136	19.4	(94, 178)	(72, 200)
2011	83	115	35.6	(37, 192)	(23, 206)
% Hatch					
2009	66	61	2.7	(55, 66)	(35, 86)
2010	61	64	3.5	(57, 71)	(38, 90)
2011	52	51	5.1	(40, 62)	(24, 78)
% Fledge					
2009	40	33	4.5	(23, 42)	(11, 55)
2010	43	54	4.5	(45, 64)	(32, 77)
2011	11	27	4.3	(18, 36)	(5, 49)