

Predicting onset and success of breeding in little penguins *Eudyptula minor* from ocean temperatures

J. M. Cullen[†], L. E. Chambers^{1,*}, P. C. Coutin², P. Dann³

¹Centre for Australian Weather and Climate Research-Bureau of Meteorology, GPO Box 1289, Melbourne, Victoria 3001, Australia

²Marine and Freshwater Fisheries Research Institute, Department of Primary Industries, PO Box 114, Queenscliff, Victoria 3225, Australia

³Research Department, Phillip Island Nature Park, PO Box 97, Cowes, Victoria 3922, Australia

ABSTRACT: As is the case for many seabirds, we found that the timing and breeding success of little penguins *Eudyptula minor* on Phillip Island, southeastern Australia, was associated with sea surface temperature (SST) variation. Using 31 yr of data (1968 to 1998), we examined the correlations between breeding variables and regional SST at different times of the year. The next 9 yr of data (1999 to 2007) were used to test the performance of our statistical predictive models. Egg-laying date, chick mass and the number of chicks fledged per pair were correlated with SST in the first 3 mo of the year prior to breeding, in slightly different ways. SST provided more accurate predictions of mean laying date (53% variance) than of chicks produced per pair (22%) or mean chick mass at fledging (16%). This model predicted an early egg-laying date, higher average chick mass at fledging and a higher number of chicks produced per breeding pair when SSTs in Bass Strait are warmer than average in March. The models presented predict that an increase in SST is likely to lead to a reversal of the trend towards later breeding and suggest improved growth of the colony of little penguins on Phillip Island, at least in the immediate future.

KEY WORDS: Little penguins · Reproduction · Climate change · Modelling · Southern Australia · Phillip Island

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INTRODUCTION

Oceanographic variation is known to affect seabirds throughout the world, particularly where upwelling and boundary currents have a major influence on local sea surface temperature (SST) and marine productivity (Boersma 1978, 1987, Ainley et al. 1988, Crawford & Jahncke 1999, Velarde et al. 2004, Congdon et al. 2007). For example, warm-water events in the Pacific have been linked to increased mortality and reduced breeding success of seabirds in the USA (Hodder & Graybill 1985), Peru (Ainley et al. 1988, Crawford & Jahncke 1999, Glantz 2001), southern Africa (La Cock 1986, Crawford & Jahncke 1999) and throughout

the Pacific basin (Ainley et al. 1988, Glantz 2001). In the Southern Ocean, rising SST has also been linked to population declines of the rockhopper penguin *Eudyptes chrysocome* at Campbell Island (Cunningham & Moors 1994) and the emperor penguin *Aptenodytes forsteri* in the Antarctic (Barbraud & Weimerskirch 2001).

Variable oceanographic conditions influence both prey density and seabird foraging (Ainley & Boekelheide 1990, Robinson et al. 2005, Congdon et al. 2007). For example, cold surface waters in the northwest Atlantic have been associated with movement patterns of migratory pelagic fish (Montevecchi & Myers 1996) and breeding failures of surface-feeding seabirds (Re

[†]Deceased

*Corresponding author. Email: l.chambers@bom.gov.au

gehr & Montevecchi 1997). Peak spawning times of capelin *Mallotus villosus* were also later and fish were smaller during a period of below-normal sea temperatures in this region (Carscadden et al. 1997).

Ocean temperatures may also influence the timing and success of breeding of seabirds (Ainley & Boekelheide 1990, Guinet et al. 1998, Inchausti et al. 2003, Irons et al. 2008). Inchausti et al. (2003) found that the breeding success of 4 seabird species foraging in Antarctic waters south of the Polar Front was negatively affected by warm SST, mainly in winter and spring.

On the southern coast of Australia, at Phillip Island, there is an internationally significant ecotourism attraction that features a colony of little penguins *Eudyptula minor*. Understanding the factors that affect their breeding success and being able to predict population trends are particularly important for providing scientific advice on management responses to climate change forecasts. Little penguins show marked annual differences in the timing and success of breeding (Reilly & Cullen 1981, Dann & Cullen 1990, Dann et al. 2000, Kemp & Dann 2001). Much of this variation is probably related to the onset of breeding because there is comparatively little variation in the conclusion of the breeding season due to the onset of moult (Reilly & Cullen 1981). The timing of breeding has important implications, as early breeding is generally more successful (Reilly & Cullen 1981).

Penguin breeding may be affected by changes in marine productivity associated with SST and driven by oceanographic processes (Middleton & Cirano 2002). However, for the little penguins at Phillip Island, the relationship between their marine environment and the timing and success of breeding is difficult to determine. SST around southeastern Australia is influenced by waters from 4 regions (Gibbs 1992). Bass Strait water around Phillip Island originates mostly from the west, flowing east across South Australia as low nutrient subtropical water from the Great Australian Bight. From the north, the East Australian Current (EAC) flows south, bringing eddies of warm nutrient-poor tropical water of the Pacific Ocean. There is mixed subtropical Central Tasman water in the east. In the south and in deep water beyond the continental shelf, cold, nutrient-rich sub-Antarctic water originates from below the Subtropical Convergence Zone and the eastward flowing Antarctic Circumpolar Current in higher latitudes. The interaction of these 4 water masses, which is influenced by the seasonal wind patterns, determines the nature of the marine environment of the little penguins and the productivity of marine ecosystems in southeastern Australia.

Mickelson et al. (1992) found that 29 and 47 % of the interannual variability in the body mass and breeding

success of the little penguin on Phillip Island was attributed, by correlation analysis, to monthly and interannual decreases in the east-west SST gradient for 2 areas in Bass Strait between the moulting and breeding periods. The mass of adult birds increased 4 mo after the decrease in SST as west winds brought cooler waters with slightly higher nutrients into Bass Strait. The authors concluded that early egg laying in September and October was associated with a decrease in the SST in July and August.

Based on that, J. M. Cullen (unpubl. data) produced statistical models to predict the mean laying date using a long-term dataset of penguin breeding parameters at Phillip Island and SST data during the 1990s. We have continued his work using a more extensive time series of data to explore the relationships between the timing of breeding, the numbers of chicks produced per pair and the mass of chicks and SST at various times prior to breeding. These relationships may help to reveal the ecological basis underlying a substantial part of the variability in breeding and could be used for predicting annual penguin productivity.

MATERIALS AND METHODS

Timing and success of little penguin breeding. Field work was conducted on the Summerland Peninsula, Phillip Island, Victoria, Australia ($38^{\circ} 30' S$, $145^{\circ} 10' E$) from 1968 to 2007. Approximately 26 000 little penguins are estimated to nest at this site (J. M. Cullen unpubl. data). Penguins nest in burrows in sandy soil and among bushy vegetation on slopes and flat ground up to 50 m above sea level; about half the birds included in this study nested in artificial burrows (nest boxes). The number and location of study sites visited and the frequency of visits to the burrows in these study sites have varied over the years. The frequency of visits to burrows in the initial study area was weekly from 1968 to 1970 and monthly from 1971 to 1984. From 1985 to 2004 it was every 2 wk during the breeding season and monthly outside the breeding season (Reilly & Cullen 1981, Dann & Cullen 1990, Dann et al. 1995). An additional 6 study sites were added between 1981 and 1984, and visited monthly until 1999, then at 2 wk intervals during breeding and infrequently at other times. On each visit, the band number(s) of the adult(s) present in the burrow, and the numbers of eggs and/or chicks were recorded. Sexes of adults were determined from bill lengths, distended cloacae in females at the time of egg laying, attendance patterns around the time of egg laying, and/or repeated cohabitation with other sexed birds (Dann & Cullen 1990, Arnould et al. 2004).

We compared 3 annual breeding parameters with monthly patterns of SST: the mean laying date of first

clutches (MLD), the mean number of chicks fledged per pair of birds that laid eggs (CPP), and the mean mass of chicks (CMass) at the age of about 6 to 8 wk when they were marked prior to fledging. Because the breeding season of the penguins overlaps the calendar year, all the data are for the period starting in March and ending in February of the following year, and are recorded as the year in which the season started. Laying dates, if not observed, were inferred retrospectively from hatching dates or the age of young chicks. For mean laying date, the integer represents the month and the decimal part represents which day of the month (e.g. 15 September is 9.5, shown in Fig. 4 with associated error bars).

Chicks were banded on the flipper prior to fledging and most breeding adults were banded from 1968 until 2000. Since 2000, most birds have been marked with implanted transponders instead of flipper bands. Chicks were deemed to have fledged if they disappeared after attaining their adult plumage and there were no indications of starvation or predation.

SST. SST data of $1^\circ \times 1^\circ$ spatial resolution were extracted for the period 1968 to the end of 1981 from the UK Meteorological Office Ice and Sea Surface Temperature data set (GISST, version 1.1; Parker et al. 1995). This data set was extended to June 2008 using data from the National Oceanographic and Atmospheric Administration (ftp://ftp.emc.ncep.noaa.gov/cmb/sst/oimonth_v2/) and represents mean SST values per 1° degree grid square per month, covering the whole globe (Reynolds & Smith 1994). These monthly values, 'optimum interpolation' (OI) fields, are derived by a linear interpolation of the weekly OI fields to daily fields, which are then averaged for the month. Before that analysis is computed, the satellite data were adjusted for bias due to water evaporation and checked against ground truth data when available. A description of the OI analysis can be found in Reynolds & Smith (1994). SST covering the region from 35° to 45° S and 138° to 152° E were used in the analysis because this area is influenced by the 4 water masses identified by Gibbs (1992) and represents 'local' SST.

Data analysis. Data collected from 1968 to 1998 were used to develop relationships between SSTs and penguin breeding variables. Data collected from 1999 to 2007 were used to test the predictive capacity of these relationships.

Correlations: For each of the SST grid squares that included more than 50% sea in area, and for each month of the year, the correlation coefficient was calculated between the value of each penguin variable for that year and the SST for the month in that year. The correlations were plotted for each degree square of sea (see Fig. 2) in contour form with shaded areas depicting the values statistically significant at the 5% level.

SST sub-region analysis: As the gridded SST data had very high spatial correlations ($p \leq 0.001$ for all grid points), the average of SST over a subset of the entire region was considered for all further analyses. This SST box (situated between 38° and 40° S and 143° and 145° E, Fig. 1) was selected, as water movement into Bass Strait prior to the breeding season is predominantly from the west (Gibbs 1992) and penguins from Phillip Island are known to forage within this area prior to the start of the breeding season (Collins et al. 1999). However, similar results would be obtained by taking any subset of the SST data, given the high spatial correlation in the SST. The median of the SST averages, over all months, within this box was 15.14°C (range 12.24 to 19.13°C) and, for comparison, during March was 17.73°C (range 16.42 to 19.09°C).

The monthly sub-regional averages were then used to obtain a correlation coefficient with each penguin breeding variable for each month.

Regression analysis: Using multiple linear regression, the mean monthly regionally averaged SST was used to determine the optimal model for predicting mean laying date, the mean number of chicks fledged per pair and the mean chick fledging mass. Examination of the model residuals indicated any 'unusual'

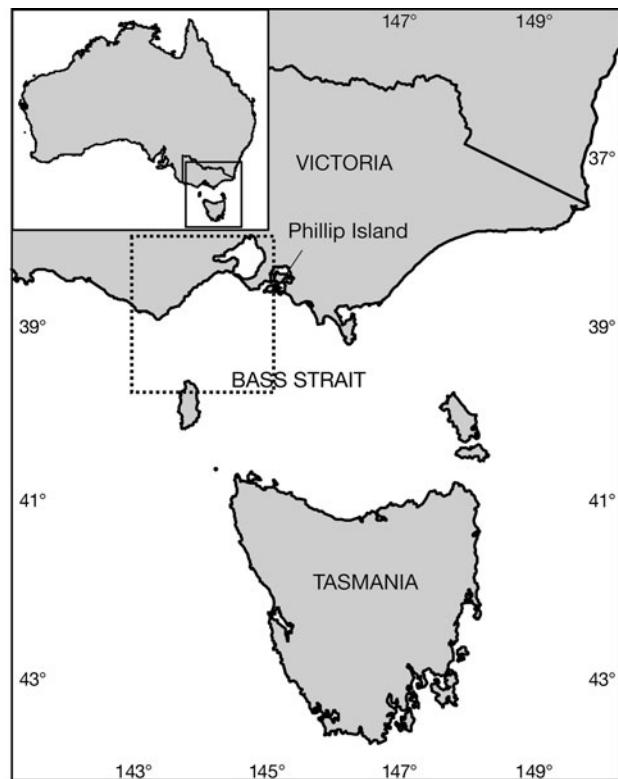


Fig. 1. Area of study showing the sea surface temperature sub-region used in the analysis (dotted line)

years. The model selected was then used in forecast mode and predictions were made of the penguin variables for the years 1999 to 2007. Comparisons between the model values and the observed values over this period give a more realistic indication of the expected model skill for future predictions. Statistically significant correlation was set at the 5% level.

RESULTS

Correlations

Correlations for each of the penguin variables were highest for the early months of the year, some time before breeding starts, with the strongest correlations generally occurring in March. The correlation coefficients between MLD and SST were generally stronger than those between SST and other variables.

For the MLD, negative correlations indicated that warm SST corresponded to earlier nesting. Correlations were highest in the region between Tasmania and the mainland (including western Bass Strait), and off the southeast coast of Australia (Fig. 2), and generally lowest in the southern part of the SST region considered. The strength of the correlations increased from February to March, before declining to a level of very few significant correlations by June.

For both CPP and CMass, correlations with SST early in the year prior to the start of breeding were positive, indicating that warmer water tended to correspond to increases in both CPP and the mean CMass at fledging. For both of these variables the highest correlations were with March SST (not shown).

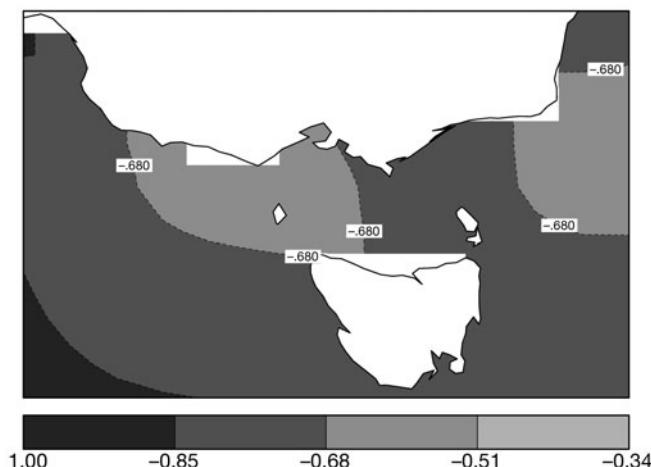


Fig. 2. Correlations between the gridded March sea surface temperature values and mean laying date of *Eudyptula minor*, 1968 to 1998. All correlations significant at the 5% level are shaded

Table 1. Correlation coefficients between little penguin *Eudyptula minor* breeding variables (mean laying date, chicks per pair and chick mass) and regionally averaged monthly sea surface temperature, 1968 to 1998. Months beyond September were not considered for mean laying date as, in some years, the breeding season has already commenced. *Correlations significant at the 5% level

Month	Mean laying date	Chicks per pair	Chick mass
January	-0.307	0.184	0.166
February	-0.498*	0.278	0.229
March	-0.736*	0.491*	0.433*
April	-0.495*	0.409*	0.342
May	-0.422*	0.348	0.279
June	-0.200	0.245	0.138
July	-0.082	0.210	0.083
August	0.068	0.317	-0.016
September	0.134	0.040	-0.106
October	-	-0.055	-0.059

SST subregion analysis

Using monthly averaged SST values, correlation coefficients with the penguin breeding variables were calculated (Table 1). Consistent with the correlations with individual SST grid boxes, the relationship between area-averaged SST and penguin breeding variables was strongest in March, particularly for MLD. Warm water during March, and to a lesser extent February and April, corresponded to an early start to egg laying. CPP and CMass were also strongly correlated with SST in the Bass Strait region, with a peak in the relationship occurring during March and decaying more rapidly than for mean laying date.

The advantage of using SST averaged over a subregion rather than SST values for individual grid squares is that there is a reduction in the number of variables describing the region, yet the basic seasonality and characteristics of the data remain intact. This was particularly useful when predictions of the breeding variables were made (see next section). Over the period 1968 to 1998, no significant temporal trend was observed in the area-averaged SST.

Regression analysis

Multiple linear regression was used to relate monthly area-averaged SST values to the penguin breeding variables. The initial regression equation fitted was of the form

$$Y_i = a + b_1 X_{m1i} + b_2 X_{m2i} + b_3 X_{m3i} \quad (1)$$

where Y_i is the penguin variable in year i , X_{m1i} is the mean monthly SST value in month $m1$ for year i , ...,

and X_{m3i} is the mean monthly SST value in month $m3$ for year i . Given that most of the higher correlations between the variables and SST occurred during the early part of the year, $m1$ to $m3$ were selected from the months January to May. Using SST information from these months also allows a useful lead time for monitoring purposes and for planning a management response to the predictions.

Assessments were then made of the relative contribution of each of the SST variables to the model fit and only those with significant contributions retained. This was achieved using best subset regression (Tabachnick & Fidell 1996).

For MLD, the model that explained a high proportion of the variance (approximately 53 %, $p \leq 0.001$), without over-fitting parameters, was

$$\text{MLD} = 23.9 - 0.77X_{\text{March}} \quad (2)$$

This model indicates that, during March, waters from the west of Bass Strait appear to influence the timing of breeding in little penguins.

SST accounted for less of the overall variation in CPP than for that in the timing of breeding (approximately 22 % compared to 53 %). For CPP, western Bass Strait water during March proved to be the best potential predictor. The regression model is given by

$$\text{CPP} = -4.95 + 0.33X_{\text{March}} \quad (3)$$

CMass at fledging was the least well predicted by SST of all the penguin breeding variables (percentage variance explained by the model was approximately 16 %). The best model incorporated ocean temperatures during March in the Bass Strait region using the following equation

$$\text{CMass} = 10.2 + 50.9X_{\text{March}} \quad (4)$$

Data from 1999 to 2007 were then used to test the regression models' ability to predict the observed penguin breeding variables (Fig. 3). The results are shown in Table 2. CIs for the predictions, as well as prediction intervals, are given. Prediction intervals are always wider than confidence intervals, as the latter are based on confidence in predicting the mean response, whereas the former are based on predicting a single response.

Despite a better fit to the 1968 to 1998 data, predictions of MLD from 1999 to 2007 were generally not as good as those for CPP and CMass, with only 6 of the MLD prediction intervals containing the observed value. However, the prediction intervals for CPP and CMass were quite wide and, in the case of CMass, generally covered over 93 % of the range of the 1968 to 1998 data (compared to an average of 77 % for MLD). Comparing across all 3 penguin variables, the most 'accurate' predictions were for 1999, 2000, 2004 and

2005 and the least 'accurate' for 2001, 2002, 2003 and 2006 (MLD and CMass predictions also performed poorly in 2007).

For MLD, there has also been a trend towards later breeding over time ($\sim 0.65 \text{ d yr}^{-1}$, $p = 0.021$; Fig. 4).

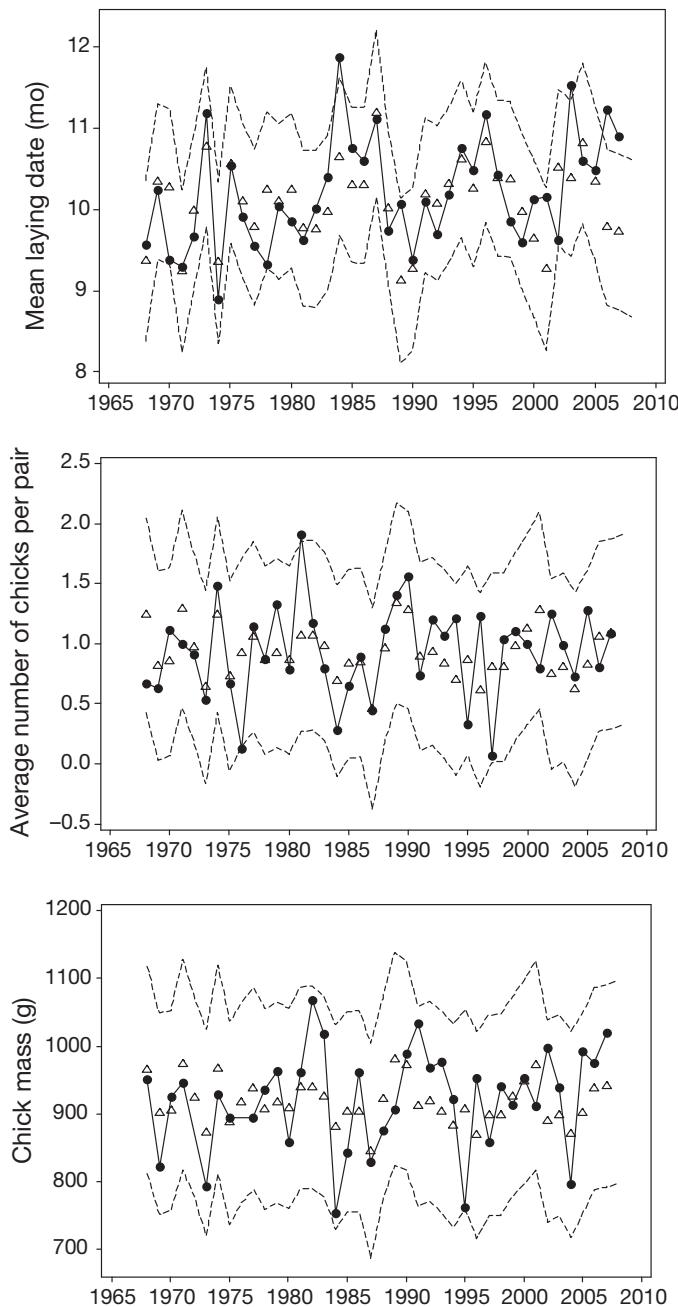


Fig. 3. *Eudyptula minor*. Observed (●) and modeled (Δ) breeding parameters, including prediction intervals (dashed lines). (a) Mean laying date; (b) chicks per pair; (c) chick mass at banding

Table 2. *Eudyptula minor*. Predicted and observed mean laying dates (MLD), chicks fledged per pair (CPP) and mean mass of chicks at fledgling (CMass) from 1999 to 2007, using models developed from data from 1968 to 1998. SE of the predicted values are given, as well as 95% CIs for the predictions and 95% prediction intervals (95% PI)

	Observed	Predicted	SE	95 % CI	95 % PI
MLD					
1999	9.60	9.97	0.086	(9.80,10.15)	(9.02,10.93)
2000	10.13	9.64	0.117	(9.40,9.87)	(8.67,10.60)
2001	10.16	9.27	0.168	(8.92,9.61)	(8.27,10.26)
2002	9.63	10.51	0.107	(10.30,10.73)	(9.55,11.48)
2003	11.53	10.38	0.094	(10.19,10.57)	(9.42,11.34)
2004	10.60	10.81	0.144	(10.52,11.11)	(9.83,11.80)
2005	10.48	10.34	0.090	(10.15,10.52)	(9.38,11.29)
2006	11.23	9.78	0.101	(9.57,9.99)	(8.82,10.74)
2007	10.90	9.73	0.106	(9.41,9.88)	(8.76,10.69)
CPP					
1999	1.11	0.98	0.071	(0.83,1.12)	(0.19,1.76)
2000	1.00	1.12	0.096	(0.93,1.32)	(0.33,1.92)
2001	0.80	1.28	0.138	(1.00,1.56)	(0.46,2.10)
2002	1.25	0.75	0.088	(0.57,0.93)	(0.00,1.54)
2003	0.99	0.81	0.077	(0.65,0.96)	(0.02,1.59)
2004	0.73	0.62	0.119	(0.38,0.86)	(0.00,1.43)
2005	1.28	0.82	0.074	(0.67,0.98)	(0.04,1.61)
2006	0.81	1.06	0.083	(0.89,1.23)	(0.27,1.85)
2007	1.09	1.09	0.088	(0.92,1.31)	(0.29,1.88)
CMass					
1999	914	925	13.7	(897,953)	(777,1073)
2000	953	947	18.5	(910,985)	(797,1098)
2001	911	972	26.3	(918,1026)	(817,1127)
2002	998	890	16.7	(855,924)	(740,1039)
2003	940	898	14.8	(868,929)	(750,1047)
2004	796	870	22.5	(824,916)	(717,1022)
2005	992	901	14.3	(872,931)	(753,1049)
2006	976	938	16.0	(905,971)	(789,1087)
2007	1020	942	16.9	(907,984)	(792,1091)

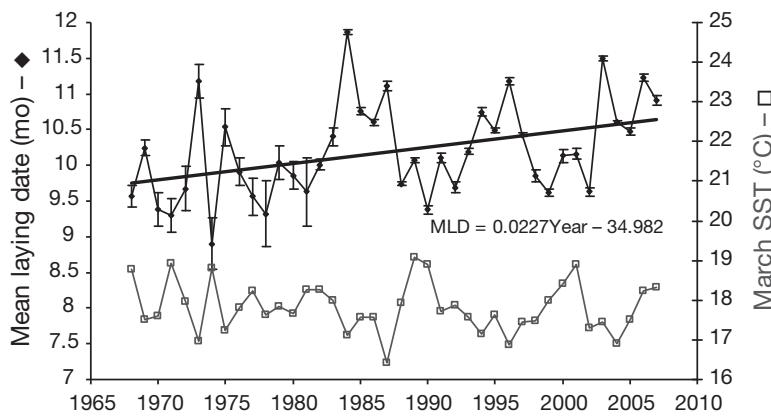


Fig. 4. *Eudyptula minor*. Temporal trend in annual timing of mean laying date of little penguins on Phillip Island (with associated standard errors). Also shown are the March sea surface temperature (SST) values for the SST sub-region of Fig. 1

DISCUSSION

The timing of egg-laying of little penguins on Phillip Island was significantly and negatively correlated with SST in southeastern Australia at some times of the year. Warmer temperatures in late summer and autumn corresponded to earlier nesting. To a lesser extent, CPP and CMass at fledging were positively correlated with SST. In years with warmer temperatures from late summer to early winter, there tended to be higher numbers of chicks and an increase in CMass.

Variation in SST has been reported to correlate with the timing and productivity of breeding in little penguins, both negatively and positively (Wooller et al. 1991, Mickelson et al. 1992, Perriman et al. 2000, Chambers 2004a,b). For example, Leeuwin Current strength affected the timing of breeding of little penguins on Penguin Island in Western Australia (Wooller et al. 1991, Wiencke et al. 1995). In contrast to our study, in years when the Leeuwin Current was strong, and consequently water temperatures were higher, little penguins in Western Australia laid much later (Wooller et al. 1991). Also in contrast to our study, Mickelson et al. (1992) found that a decrease in SST in July-August was associated with earlier egg laying, while we have shown that this is more closely associated with warm SST in March. The reason for the difference between Mickelson et al. (1992) and our study could be related to their significantly shorter time series, smaller sample sizes, fewer breeding sites and limited SST regions. However, their correlations were significant during a similar time of the year and it is possible that a computational error was responsible for the difference in sign. In New Zealand, the El Niño-

Southern Oscillation influences ocean temperatures and with cooler waters in the Pacific Ocean, the breeding of little penguin is delayed and there are fewer double breeders (Perriman et al. 2000). These regional differences in the reproductive response of little penguins to SST suggests that there is not a direct relationship with temperature and metabolic rates; rather a more complex ecological process is likely to be involved.

Our results are more consistent with an earlier study on the breeding of little penguins in southern Australia by Chambers (2004a) using a coarser spatial-resolution SST and air temperature. She found that egg laying coincided with times when local SST was rising. Warmer minimum monthly air temperature close to Phillip Island during the autumn prior to breeding corresponded to earlier breeding, as

did warmer local SST in the summer and autumn prior to breeding. These relationships were used to predict breeding success in little penguins (Chambers 2004b) but the forecast scheme differed from that presented here in that it produced categorical rather than empirical predictions.

Predictions

SST data predicted the penguin breeding variables reasonably well. As far as the predictions go, the models developed are statistically optimal. As SST values over the entire southern Australian region were highly correlated, this indicates that SST extending across all 4 water masses around the southeastern Australian coast is associated with the timing and success of breeding of little penguins on Phillip Island. Timing of breeding in other seabirds, such as Cassin's auklet *Ptychoramphus aleuticus* (Ainley & Boekelheide 1990), has also been predicted using SST prior to commencement of breeding.

Accuracy of models

The predictive equations performed relatively well on the historical data, as might be expected since these data were used to develop the model, but less well in predictive mode on post-1998 data, which were not included in the model development. The confidence and prediction intervals for MLD were much tighter than those for CPP and CMass. For CPP and CMass, the prediction intervals were quite wide and therefore almost all of the observed and predicted values fell within these intervals. Over the model testing period, 1999 to 2007, the mean laying date was relatively well predicted, with the following exceptions: 2003, 2006 and 2007. In 2003, there was a tentative start to breeding in September, when only few birds laid eggs, but most birds did not breed until November. The MLDs in 2006 and 2007 were also later than expected. With further investigation, these exceptional years may provide an indication of the ecological processes that drive these relationships.

Potential mechanisms for the effects of SST on breeding

A number of studies demonstrate a negative connection between SST and the timing and success of breeding in seabirds (e.g. Boersma 1978, Guinet et al. 1998, Smithers et al. 2003, Congdon et al. 2007), presumably due to the influence of SST or upwelling on the condi-

tion of the food web (Ainley & Boekelheide 1990). However, in the 31 yr of this study, the strongest correlations of breeding parameters with SST were positive (an earlier MLD being a positive outcome) and occurred 6 to 7 mo before breeding.

Variations in SST have been associated with recruitment, productivity and distribution of fish and other marine vertebrates in southern Australian waters (Harris et al. 1988). For example, more southern bluefin tuna *Thunnus maccoyii* were present off Maria Island in years of low SST, whereas populations of spiny rock lobster *Jasus edwardsii* were higher in years of higher SST at the same location (Harris et al. 1988). In New Zealand, increased catches of red cod *Pseudophycis bachus*, barracuda *Thyristes atun* and blue warehou *Seriola brama* occurred during the 1982 to 1983 El Niño, corresponding to a period of cooler SST in New Zealand (Basher 1998). In years of warmer ocean temperatures, larval and juvenile survival of gemfish and snapper was higher and deeper water species, such as hoki *Macruronus novaezealandiae* and silver warehou *Seriola punctata*, moved to the shallower coastal waters of the east coast of northern New Zealand (Basher 1998). Movement of fish and altered timing of peak productivity of spawning and juvenile prey species are also expected to occur in southern temperate regions of Australia as a result of changes in sea surface temperature (Congdon et al. 2007).

In this study, warm water that occurred up to 6 mo prior to the onset of the breeding season was associated with an earlier-than-average start to breeding and improved the breeding success of little penguins on Phillip Island. Although there is considerable inter-annual variability, it appears that waters to the east and west of Bass Strait are influenced by mixing of continental shelf waters, which bring higher concentrations of nutrients in winter (Gibbs 1992). The concentration of nitrates in Bass Strait water declines seasonally from a peak in July/August to low levels in December (Norman 1992). Penguin breeding may be affected by changes in marine productivity associated with SST and driven by oceanographic processes (Middleton & Cirano 2002).

At the time of breeding, SST appeared to have weaker association with the success of breeding. There are at least 2 possible explanations for the association between warmer water and more successful breeding that warrant further investigation: (1) a longer breeding season and (2) greater availability and quality of food.

Longer breeding season

Our results have shown that CPP increases during years when SST is warmer and that this is related to

early egg laying, which increases the length of the breeding season. A longer breeding season allows more time for replacement clutches and second clutches (Reilly & Cullen 1981), since there is little annual variation in the date when egg laying ceases.

Availability and quality of food

Breeding success in little penguins has been linked to adult weight and the availability and quality of food may determine the onset of laying (Cullen et al. 1992, Robinson et al. 2005). Alternatively, the warmer water earlier in the year (i.e. March to April) may improve breeding success by resulting in more prey (or higher quality food) being available closer to the breeding colony. Better nutrition for chicks during warm years would increase chick masses, which increases both fledging success and post-fledging survival rates (Reilly & Cullen 1981, Dann 1988, Dann & Cullen 1990, Chiaradia & Nisbet 2006).

Little penguins eat fish and squid, but their diet consists mostly of small clupeiform fish, particularly anchovy *Engraulis australis* and pilchard *Sardinops sagax*, that are less than 10 cm long and less than 2 yr old (Cullen et al. 1992, Chiaradia et al. 2004). When feeding their chicks, penguins usually forage within 30 km of Phillip Island but may travel greater distances in some years when food is apparently less abundant (Weavers 1992, Collins et al. 1999, Dann & Norman 2006). SST could influence the local abundance of these small pelagic fishes in several ways. Interannual differences in temperature may directly or indirectly effect the distribution, recruitment, growth and mortality of prey species in the 6 mo leading up to and during breeding (Harris et al. 1988, Basher 1998). Fluctuations in anchovy and pilchard stocks have also been attributed to changes in water temperature (Hoedt et al. 1996). So it is possible that similar ecological mechanisms are forcing the breeding dynamics of the little penguin colony at Phillip Island.

Implications for predicting climate change effects

More information is needed on the potential impact of climate change on the future trends in the productivity of Australian marine ecosystems. Climate change projections are for warming of waters in the region and a strengthening of the EAC (IPCC 2007), bringing warmer waters further south. This is expected to have flow-on effects on marine biota, productivity and the local abundance of the prey for little penguins. Long-term biological data sets, such as those recorded at Phillip Island, are uncommon and of high scientific

value for anticipating climate change impacts. The models presented here, based on the water temperatures experienced over the last 30 yr, predict that increased SST, at least in the immediate future, is likely to lead to a reversal of the trend towards later breeding; the models also suggest improved growth of the colony of little penguins on Phillip Island in Victoria, provided no currently unknown detrimental temperature-dependent marine productivity thresholds are breached or that temperature changes are not too rapid (Irons et al 2008).

Although there were no significant trends in SST during the January to June prior to the breeding season, the onset of breeding of little penguins on Phillip Island became later over time (Fig. 4), but with considerable year-to-year variability in MLD. Previous studies have shown that the cessation of breeding each year varies little with time (Reilly & Cullen 1981), which could be related to photoperiod, as has been observed in other seabird species (Ainley & Boekelheide 1990). The environmental factors and stimulus for the onset of breeding in little penguins are still unknown, but our modelling demonstrates that breeding timing and success can be predicted by water temperatures in the western Bass Strait region during March.

Validation of the predictions and improvement of the models are warranted to account for the lower performance of the models in predicting the mean laying date in 2003, 2006 and 2007. It is also important to determine the ecological mechanisms driving these relationships in Victoria and in other locations, given the opposite effect of SST on reproduction of little penguins in Western Australia and differences in the breeding season of little penguin colonies in South Australia.

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