

MURDOCH RESEARCH REPOSITORY

This is the author's final version of the work, as accepted for publication following peer review but without the publisher's layout or pagination. The definitive version is available at <u>http://dx.doi.org/10.1007/s00484-013-0711-6</u>

Chambers, L.E., Dann, P., Cannell, B. and Woehler, E.J. (2013) Climate as a driver of phenological change in southern seabirds. International Journal of Biometeorology, 58 (4). pp. 603-612.

http://researchrepository.murdoch.edu.au/17894/

Copyright: © 2013 ISB.

It is posted here for your personal use. No further distribution is permitted.

Phenology - Milwaukee 2012

Climate as a driver of phenological change in southern seabirds

Lynda E. Chambers¹_, Peter Dann²_, Belinda Cannell³_ and Eric J. Woehler⁴_

- Centre for Australian Weather and Climate Research, Australian Bureau of Meteorology, GPO Box 1289, Melbourne, Victoria, 3001, Australia
- (2) Research Department, Phillip Island Nature Parks, PO Box 97, Cowes, Phillip Island, Victoria, 3991, Australia
- (3) Veterinary and Life Sciences, Murdoch University, South St, Murdoch, WA, 6150, Australia
- (4) IMAS, University of Tasmania, Sandy Bay, Tas, 7005, Australia

Abstract

Seabirds are one of the most threatened groups of birds globally and, overall, their conservation status is deteriorating rapidly. Southern hemisphere countries are over-represented in the number of species of conservation concern yet long-term phenological data on seabirds in the southern hemisphere is limited. A better understanding of the implications of changes in the marine and terrestrial environments to seabird species is required in order to improve their management and conservation status. Here we conducted a meta-analysis of the

phenological drivers and trends among southern hemisphere seabirds. Overall there was a general trend towards later phenological events over time (34 % of all data series, N=47; 67 % of all significant trends), though this varied by taxa and location. The strongest trends towards later events were for seabirds breeding in Australia, the Laridae (gulls, noddies, terns) and migratory southern polar seabirds. In contrast, earlier phenologies were more often observed for the Spheniscidae (penguins) and for other seabirds breeding in the Antarctic and subantarctic. Phenological changes were most often associated with changes in oceanographic conditions, with sea-ice playing an important role for more southerly species. For some species in some locations, such as the Little Penguin *Eudyptula minor* in south-eastern Australia, warmer oceans projected under various climate change scenarios are expected to correspond to increased seabird productivity, manifested through earlier breeding, heavier chicks, an increased chance of double brooding, at least in the short-term.

Keywords: Penguin, *Eudyptula minor*, Sea surface temperature, Southern hemisphere, Seabirds

Introduction

Seabirds are one of the most threatened of all bird groups globally and, overall, their conservation status is deteriorating rapidly (Croxall et al. *2012*). When countries are ranked according to the number of species of conservation concern, 16 of the 21 highest ranked countries are in the southern hemisphere (top 10 ranked: New Zealand, Chile, USA, Australia, South Africa, Peru, Argentina, Mexico, Namibia, French Southern Territories;

Croxall et al. 2012), emphasising the need to better understand the drivers of population change in these regions for current and future conservation and management efforts.

Within the seabird group, penguins (Spheniscidae), albatrosses (Diomedeidae) and petrels (Procellariidae) are the most threatened, the significance of this highlighted by the fact that penguins and petrels represent nearly half of all seabird species in the world (Croxall et al. *2012*).

Seabirds are recognised as potential indicators of marine environments (Woehler 2012 and references therein) and are relatively well-studied compared to other marine organisms (Croxall et al. 2012). Large- and local-scale climate processes, including El Niño-Southern Oscillation (ENSO) and sea surface temperature (SST), have been shown to influence seabird reproduction, distribution, phenology and survival in many regions of the globe. For example, breeding of seabirds in the northern Japan Sea is delayed when air and sea temperatures are lower, as a result of the influence of temperature on access to breeding sites and prey availability (Watanuki and Ito 2012), and a multivariate index of ENSO partly explained variations in tropical seabird breeding in the Seychelles (Ramos et al. 2002, 2006).

As breeding and moult require considerable amounts of energy, the timing of these activities should correspond to periods of peak prey availability and favourable environmental conditions. The timing of breeding in seabirds can influence annual breeding productivity, thereby impacting on population dynamics. The timing of breeding has been hypothesised to be the reproductive parameter most influenced by climate change (Przybylo et al. *2000*;

Ramos et al. 2002). An earlier onset to breeding often corresponds to increased seabird productivity (number of chicks raised per pair, clutch size, and chick mass on fledging) (e.g. Cullen et al. 2009; Ramos et al. 2002).

Most seabirds are migratory or dispersive during the non-breeding season and are dependent upon the availability of prey resources while on migration or away from nesting sites. During the non-breeding season many seabirds moult and may lose 50 % of their pre-moult body mass while in moult (Baduini et al. 2001; Cherubini et al. 1996; Knox 2007). The timing of moult has been shown to influence breeding timing and to be influenced by it (Paredes et al. 2002; Wolfaardt et al. 2009a).

Changes in seabird phenology, be it the timing of migration, breeding or moult, also have the potential to create a mismatch (or asynchrony) between species. This has the potential to disrupt predator-prey relationships and influence inter-species competition for resources, with subsequent changes in population abundances (Durant et al. *2007*).

In light of the conservation status of many of the world's seabirds, that a high proportion of the most threatened species are in the southern hemisphere, and that many seabirds are influenced by climatic changes in their marine and terrestrial environments (reviewed by Chambers et al. *2011*, *2013a*, *b*), this paper aims to:

1. Review published literature on the phenology of southern hemisphere seabirds, with particular emphasis on the highly threatened taxon Spheniscidae (penguins),

identifying where phenological changes have or have not been observed and possible climate drivers for any observed change(s).

- 2. Explore in more detail similarities and differences in the phenologies of Little Penguins *Eudyptula minor* among various breeding locations and possible climate drivers of these, using published and unpublished data from various locations throughout their range in Australia and New Zealand.
- 3. Discuss the implications of phenological change(s) for southern seabirds.
- 4. Identify possible adaptation options to reducing any adverse effects of predicted climatic changes.

Data and methods

A literature search was used to identify seabird datasets from the southern hemisphere of at least 10 years duration and extending post-1990. In addition, known researchers of Little Penguins were contacted directly and invited to participate in this study.

Trends in the seabird datasets were obtained primarily from the literature. The exception was the case of the Little Penguin where researchers provided the time-series of the relevant phenological data. Long-term (>10 years) data were available on the timing of breeding in Little Penguins from five locations throughout their distribution (four in Australia and one in New Zealand) (Table 1). In addition, three datasets of shorter duration were available for Oamaru (two sites; 1993–1998) and Taiaroa Head (1 site; 1992–1998) on the Otago Peninsula, New Zealand (Perriman et al. 2000; Perriman and Steen 2000), which allowed some comparison of similarities in timing among colonies. Trends were calculated for the

Little Penguin datasets using generalised linear models, and raw time-series were correlated to identify potential similarities in year-to-year variability at the different sites. A number of the Little Penguin datasets are presented in this study for the first time, providing additional novel and relevant biological information on this species.

Little Penguins nest in burrows in sandy soil, under vegetation, among rocks or in nest-boxes placed throughout the colonies. On each visit to the various colonies, the tag numbers of the adult(s) present in the burrow, and the numbers of eggs and/or chicks were recorded. 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, with the frequency of visit generally ranging from twice-weekly to monthly (for further details see Cullen et al. 2009; Allen et al. 2011; Cannell et al. 2012). The mean laying dates (MLD) of first clutches were observed from field observations or inferred retrospectively from hatching dates or the age of young chicks.

The longest and most detailed study of Little Penguins is from the Summerland Peninsula, Phillip Island, Victoria, Australia (38° 30' S, 145° 10' E), since 1968. Approximately 32,000 Little Penguins are estimated to nest at this site (Sutherland and Dann 2012). At this site breeding and moult status were recorded. All the breeding 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 to allow for the breeding season of the penguins overlapping with the calendar year. We confined our moult analysis to records of the first stage of moult, and restricted the analyses to years with at least 30 observations; 1969–2012. The first stage of moult is characterised by worn plumage, swollen flippers, increased body mass and some raised old feathering (see Stahel and Gales *1987*). The first stage ends once old feathers have started to moult. Breeding and moult dates were converted to the number of days since 1 January (day of year).

Relationships between the timing of breeding and moult in Little Penguins at Phillip Island and monthly sea surface temperature (SST) data were assessed using methodology similar to that of Cullen et al. (2009). Based on known foraging regions of the birds and water movements within Bass Strait, a $2^{\circ} \times 2^{\circ}$ SST box was constructed by averaging SST data obtained on a $1^{\circ} \times 1^{\circ}$ grid from the UK Meteorological Office Ice and Sea Surface Temperature data set (GISST, version 1.1; Parker et al. *1995*; data from 1968 to end of 1981) and the National Oceanographic and Atmospheric Administration (ftp://ftp.emc.ncep.noaa. gov/cmb/sst/oimonth_v2/; Reynolds and Smith *1994*; used to extend the data to January 2012) (see Cullen et al. *2009* for further details).

Results and discussion

Overall, there was a greater number of datasets with trends towards later phenological events over time than earlier ones, but there were also many datasets that had no detectable trend over time (Tables 2, 3). Additionally, there were some differences according to taxonomic family and location. For the Procellariidae (petrels and shearwaters), no trends towards earlier phenology were observed (Table 3; four cases of later events, six of no change). Spheniscidae (penguins) were more likely to exhibit earlier phenologies or have no change (7 and 15 cases, respectively) than later timing (3 cases). For the Laridae (terns, gulls and noddies), phenology was generally delayed (eight cases) compared to earlier or no change (one and three cases, respectively). For Antarctic and subantarctic seabird species, both earlier and later phenologies were observed in almost equal proportions (seven and six cases, respectively; Table 2), whereas in Australia, the only other region to have multiple documented shifts, delayed or no shift in phenologies were more likely than advances (nine later, one earlier, nine no change).

Seabird migration phenology

Long-term information on seabird migration timing was available only for the Antarctic/subantarctic region (18 datasets, Table 2). Wilson's Storm-petrel *Oceanites oceanicus*, Southern Fulmar *Fulmarus glacialoides*, Antarctic Petrel *Thalassoica antarctica* and Cape Petrel *Daption capense* have all delayed their arrival at their breeding colonies in more recent years, while South Polar Skua *Catharacta maccormicki*, Southern Giant-Petrel *Macronectes giganteus* and Snow Petrel *Pagodroma nivea* have exhibited no consistent change in arrival timing (Barbraud and Weimerskirch 2006). Similarly, migration timing in the penguins located in the Antarctic and subantarctic has not changed significantly over time (Barbraud and Weimerskirch 2006; Crawford et al. 2006; Emmerson et al. 2011; Saraux et al. 2011) though breeding and migration timing are known to vary by latitude (Ainley 2002; Emmerson et al. 2011).

Whilst there has been no change over time in the phenology of some seabird species in the Antarctic, their phenology is influenced by environmental variability. For example, reductions in the extent of sea-ice and increases in its duration impact seabird prey abundance and availability, increasing the amount of time required for some seabirds to obtain breeding condition, thereby influencing arrival times at breeding colonies (Barbraud and Weimerskirch 2006). For penguins in East Antarctica, such environmental conditions appear to delay breeding but not their arrival timing (Barbraud and Weimerskirch 2006). However, when near-shore ice is extensive and maximum air temperatures are low, Adélie Penguins *Pygoscelis adeliae* arrive later at their breeding colonies on Béchervaise Island, East Antarctica (Emmerson et al. 2011). Although later arrival did not appear to influence breeding success, it did lead to reduced courtship and egg-laying, later clutch initiation, later parent departure for foraging trips and later chick-hatching.

Seabird breeding phenology

There was a significant difference among the seabird families and observed changes in breeding timing (Chi-square = 14.11, df = 4, P = 0.007). Laridae were more likely to have shifted to later breeding over time (eight later, one earlier, two no change), while Spheniscidae are generally breeding earlier over time (seven earlier, three later, ten no change). The Procellariidae showed little shift in phenological timing (none earlier, one later, four no change).

Observed changes in phenology also differed significantly according to location, though only Australia and the Antarctic/subantarctic region had sufficient information for a formal test to be applied (Chi-square = 9.04, df = 2, P = 0.011). Seabirds breeding in the Antarctic/subantarctic were slightly more likely to breed earlier over time (seven earlier, two later, six no change), while those in the Australian region were more likely to breed later (one earlier, nine later, eight no change). Earlier breeding for Adélie and Emperor Penguins Aptenodytes forsteri in East Antarctica occurred in years of higher sea ice extent; however, only Adélie Penguins showed a significant trend towards later breeding over time (Barbraud and Weimerskirch 2006). In Emmerson et al.'s (2011) study of Adélie Penguins in East Antarctica, there was no change in laying dates over time; however, the laying dates were correlated with the Southern Annular Mode (SAM), a broad-scale climate index of north-south movement of a westerly wind belt around the higher latitudes of the southern hemisphere (positive SAM was linked to later laying), and wind direction (southerly winds corresponding to later laying). For the birds in their study, later hatching dates but not later fledging dates were associated with later arrival to the colony. For three penguin species in the Western Antarctic Peninsula (Adélie, Chinstrap P. antarctica and Gentoo P. papua) earlier laying dates were linked with higher air temperatures before laying, with warmer temperatures leading to an earlier appearance of snow-free areas necessary for breeding in these species (Lynch et al. 2012). However, response rates varied among the species; Gentoo Penguins advanced their laying at a higher rate than the other two species, potentially increasing competition for nesting space in mixedspecies colonies.

For Royal Penguins *Eudyptes schlegeli* nesting on Macquarie Island, laying dates during the 1990s were on average 3 days earlier than during the 1960s (Hindell et al. 2012). Breeding timing in this species was associated with the SAM; years of lower values of the SAM, and associated reduced food availability, resulting in a delayed start to breeding.

In East Antarctica, variations in laying dates in Snow Petrels and South Polar Skuas were not linked to sea ice extent, and only South Polar Skuas had a noticeable shift in breeding timing (earlier egg laying; Barbraud and Weimerskirch 2006). In contrast, breeding timing in the Cape Petrel was related negatively to sea ice extent, with breeding occurring later over time. The observed reduction in sea ice extent in East Antarctica has been linked to reduced prey availability for many Antarctic seabirds (Barbraud and Weimerskirch 2006).

For some species, such as the migratory Wedge-tailed Shearwater *Ardenna pacifica*, breeding is highly synchronous with very little inter-annual variability and, perhaps as a consequence, its breeding phenology had not shifted over time and did not appear to be influenced by climatic variables, such as ocean temperatures (Surman et al. 2012). In contrast, there has been a shift towards later breeding for other seabird species breeding in Western Australia, including at the same location in Houtman Abrolhos (Dunlop and Surman 2012; Surman et al. 2012). Over the last two decades, breeding participation in three species, Lesser Noddy *Anous tenuirostris*, Brown Noddy *A. stolidus* and Sooty Tern *Onychoprion fuscata*, was lower in years of later breeding, though the resident Lesser Noddies appeared to be more resilient than the two migratory species (Surman et al. 2012). There is some evidence that ENSO influences the timing of breeding in Western Australian Laridae, with potentially new (but as yet unknown) complicating factors appearing in more recent years, resulting in reduced reproductive performance in both ENSO and non-ENSO years (Surman and Nicholson 2009b; Chambers et al. 2011).

Relationships between breeding phenology and environmental variability are not always static. For example, Mills et al. (2008) found breeding in New Zealand Red-billed Gulls was earlier and productivity increased when the population was at its maximum; food availability being higher during La Niña conditions. Later, when the population began to decrease, laying

dates became later, even when prey availability was high. Links between the timing of breeding and colony size have also been reported for African Penguins *Spheniscus demersus* (Wolfaardt et al. 2009a), with nest density suggested as having a greater influence on nesting synchrony than wide-scale seasonal effects.

The Little Penguin is one of the better studied seabirds in the Australian/New Zealand region and, accordingly, various aspects of its phenology are well documented, and the species is considered separately to other species herein.

Little penguin phenology: breeding

Little Penguins generally start breeding when they are 2 or 3 years old (Dann and Cullen *1990*). The timing of breeding and moult in this species varies by location (Table 4); however, the same general annual pattern of moult following breeding by 1–2 months is observed. Adult Little Penguins do not migrate although there are pronounced local movements and dispersion of the penguins breeding on Phillip Island in winter (McCutcheon et al. *2011*). Little Penguins remain ashore for up to 3 weeks during moult (Reilly and Cullen*1983*), making them vulnerable to extreme heat and rainfall events (Cannell et al. *2011*; Dann and Chambers *2013*), predation and human disturbance.

There was considerable inter-annual variability in the breeding timing of Little Penguins at each of the colony sites (Table 4). Interestingly, the timing of breeding was generally not highly correlated among colonies (notable exceptions being the New Zealand sites surveyed by Perriman et al. 2000). No significant temporal trends in the mean laying dates were observed across all Little Penguin breeding colonies.

The timing of Little Penguin breeding appears to be related to ocean temperatures before the start of the breeding season. For example, in Western Australia Cannell et al. (2012) found that laying occurred later when local sea level, an indicator of the strength of the Leeuwin Current and, therefore, ocean temperatures, was higher before breeding. In New Zealand and on Phillip Island in eastern Australia, higher ocean temperatures lead to earlier laying (Perriman et al. 2000; Cullen et al. 2009). Earlier laying corresponded to improved breeding success in this species, with heavier chicks and an increased chance of double breeding in a season (Perriman et al. 2000; Cullen et al. 2009; Cannell et al. 2012). A number of mechanisms have been proposed to explain the relationship between ocean temperature and breeding productivity including SST affecting recruitment, productivity and the distribution of prey and warmer water earlier in the year which may result in more prey close to the colony at the time of breeding (Cullen et al. 2009). Projected increases in ocean temperature under climate change are expected to improve breeding success for some colonies, at least in the short term (Cullen et al. 2009; Dann and Chambers 2013).

Little penguin phenology: moult

Although all seabirds moult, very few studies in the Southern Hemisphere have investigated changes in moult phenology over long periods of time. A notable exception is for the Little Penguin at Phillip Island (1969–2012). Moult timing appears to be less variable interannually than the timing of breeding (mean laying date day 278.4 ± 3.1 days; mean moult date 67.5 ± 1.5 days). Greater synchrony for moult compared to breeding was also observed in African Penguins breeding at Dassen Island, South Africa (Wolfaardt et al.2009a). Two alternative hypotheses have been proposed for why the timing of moult in penguins is more constrained than breeding timing; the timing of breeding activities determines when moult can occur or, alternatively, moult drives the annual cycle and is the priority activity (Paredes et al. 2002; Wolfaardt et al.2009a).

For the Little Penguins of Phillip Island, the timing of moult did not appear to be related to timing of breeding, at least not based on mean laying date of first clutch (r = -0.11, P = 0.587) nor to any measure of breeding productivity (number of chicks raised per pair or chick mass at fledging, P > 0.1) and has not changed significantly over the available time-series (trend = -0.20 days per year, P = 0.116). Wolfaardt et al. (2009a) found that the timing of breeding did not determine moult timing and suggested that other environmental or biological variables may be involved. For example, the timing of moult may be constrained by availability of food resources (e.g. Paredes et al. 2002; Wolfaardt et al. 2009a), potentially more so than breeding as it is more energetically expensive. Unlike breeding, once the moult process is started it can not be brought to a premature end (Wolfaardt et al. 2009a).

As was the case for mean laying date, the timing of moult at Phillip Island appeared to be predictable from ocean temperatures, with higher ocean temperatures in October (Spring) leading to an early start to moult in the subsequent summer (-7.38 days per °C, P = 0.016), possibly indicating relatively more abundant prey resources during the pre-moult fattening period.

Projected warming of land surface temperatures is expected to have a negative impact on breeding and moult in Little Penguins (Dann and Chambers 2013) with temperatures above 35 °C leading to increased heat stress (Cannell et al. 2011; Dann and Chambers 2013). As warmer (ocean) conditions are expected to shift moult and breeding towards earlier (cooler) periods of the year, at least for the colonies in south-eastern Australia and New Zealand, there is some potential to offset the negative impacts of increased land surface temperatures. Additional ways to reduce heat stress and related mortality are discussed below.

Management-based adaptation options

Adaptation options for southern hemisphere seabirds under projected climate change scenarios have been considered most highly for Australian seabirds (e.g. Chambers et al. 2011), in particular for the Little Penguins of Phillip Island (e.g. Dann and Chambers 2013). Most suggested adaptation options designed to allow managers to buffer seabirds against changing climatic or oceanographic conditions are land-based, with few developed around the marine environment. Therefore, increasing the resilience of seabirds by managing non-climatic effects, including reducing fisheries competition and predator control, becomes increasingly important. Two examples of adaptation options that have the potential to directly buffer seabirds against environmental change are given below.

Heat stress in Little Penguins is a significant issue, particularly as air surface temperatures are projected to rise (Dann and Chambers 2013). There are a number of simple adaptation options that can be used to reduce heat exposure by the penguins. Little Penguins readily use artificial structures for nesting (and moult) and it is possible to design artificial burrows to

reduce heat exposure (e.g. Ropert-Couder et al. 2004). Other options include the provision of shade through appropriate vegetation and other structures (such as boardwalks) and active management during forecast heat events (e.g. cooling heat-stressed birds) (Fig. 1). Various management agencies in Australia and New Zealand are presently trialling these adaptation options under local management regimes to assess their efficacy.

For some species, alternative breeding sites may be sought by individuals as sea level and SST rise. New breeding sites may include artificial habitats, such as artificial islands, breakwaters (e.g. Little Penguin, in St Kilda, Australia) and navigation structures (e.g. Australasian Gannet *Morus serrator*, Port Phillip Bay, Australia), providing an opportunity for managers to directly buffer seabirds against changing oceanographic conditions.

Conclusions

Seabirds are a highly threatened group globally; however, long-term phenological data on seabirds in the southern hemisphere are limited to a few regions and species. Although there was a general trend towards later phenological events over time, this varied by both taxa and location. The strongest trends were towards later events occurring in Australia for Laridae (gulls, noddies, terns) and migratory southern polar seabirds. In contrast, earlier phenologies were more often observed for breeding seabirds in the Antarctic and subantarctic and for Spheniscidae (penguins).

Proposed climate drivers for southern hemisphere seabird phenology vary, but are generally related to oceanographic conditions, with sea-ice playing an important role for the more

southerly species. For some species in some locations, such as the Little Penguin in southeastern Australia, warmer oceans projected under various climate change scenarios are expected to correspond to increased productivity, manifested through earlier breeding, heavier chicks and an increased chance of double breeding, at least in the short-term (Dann and Chambers 2013). For other species, productivity has the potential to be reduced as higher temperatures bring greater competition for nesting sites (Lynch et al. 2012).

The conservation status of many southern hemisphere seabird species highlights the importance of obtaining a better understanding of the implications of changes in the marine and terrestrial environments to seabird species, including on their phenology, in order to improve their management and conservation status.

Acknowledgements

We wish to acknowledge countless students and volunteers who have helped to monitor the various Little Penguin colonies over the years and whose dedication has greatly enhanced our knowledge of this species. These include members of the Penguin Study Group (Phillip Island) and Earthcare St Kilda Inc. We are grateful to two anonymous reviewers for comments and suggestions on an earlier version of this manuscript.

References

Ainley DG (2002) Adélie penguin bellwether of climate change. Columbia University Press, New York

- Allen WJ, Helps FW, Molles LE (2011) Factors affecting breeding success of the Flea Bay white-flippered penguin (*Eudyptula minor albosignata*) colony. N Z J Ecol 35:199–208
- Baduini CL, Hyrenbach KD, Coyle KO, Pinchuk A, Mendenhall V, Hunt GL (2001) Mass mortality of shorttailed shearwaters in the south-eastern Bering Sea during summer 1997. Fish Oceanogr 10:117–130

- Barbraud C, Weimerskirch H (2006) Antarctic birds breed later in response to climate change. Proc Natl Acad Sci USA 103:6248–6251
- Barlow ML, Dowding JE (2002) Breeding biology of Caspian terns (*Sterna caspia*) at a colony near Invercargill, New Zealand. Notornis 49(2):79–90
- Baylis AMM, Zuur AF, Brickle P, Pistorius PA (2012) Climate as a driver of population variability in breeding Gentoo Penguins *Pygoscelis papua* at the Falkland Islands. Ibis 154:30–41
- Boersma PD, Rebstock GA (2009) Intraclutch egg-size dimorphism in Magellanic Penguins (*Spheniscus magellanicus*): adaptation, constraint, or noise? Auk 126(2):335–340
- Cannell B, Pollock K, Bradley S, Wooller R, Sherwin W, Sinclair J (2011) Augmenting mark-recapture with beach counts to estimate the abundance of little penguins on Penguin Island, Western Australia. Wildl Res 38:491–500. doi:10.1071/WR11042
- Cannell BL, Chambers LE, Wooller RD, Bradley JS (2012) Poorer breeding by Little Penguins near Perth, Western Australia is correlated with above average sea surface temperatures and a stronger Leeuwin Current. Mar Freshw Res 63(10):914–925. doi: 10.1071/MF12139
- Chambers LE, Devney CA, Congdon BC, Dunlop N, Woehler EJ, Dann P (2011) Observed and predicted effects of climate on Australian seabirds. Emu 111:235–251
- Chambers LE, Keatley MR, Woehler EJ, Bergstrom DM (2013a) Antarctica. In: Schwartz MD (ed) Phenology: an integrative environmental science. Springer, Berlin
- Chambers LE, Altwegg R, Barbraud C, Barnard P, Beaumont L, Crawford R, Durrant JM, Hughes L, Keatley MR, Low M, Morellato LPC, Poloczanska E, Ruoppolo V, Vansteels R, Woehler E, Wolfaardt A (2013b) Changes in Southern Hemisphere phenology. PLOS One (in press)
- Cherubini G, Serra L, Baccetti N (1996) Primary moult, body mass and moult migration of Little Tern *Sterna albifrons* in northeast Italy. Ardea 84:99–114
- Crawford RJM, Dyer BM, Cooper J, Underhill LG (2006) Breeding numbers and success of *Eudyptes* penguins at Marion Island, and the influence of mass and time of arrival of adults. CCAMLR Sci 13:175–190
- Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. Bird Conserv Int 22:1–34
- Cullen JM, Chambers LE, Coutin PC, Dann P (2009) Predicting the onset and success of breeding of Little Penguins, *Eudyptula minor*, on Phillip Island from ocean temperatures off south east Australia. Mar Ecol Prog Ser 378:269–278
- Dann P, Chambers LE (2013) Ecological effects of climate change on Little Penguins *Eudyptula minor* and the potential economic impact on tourism. Clim Res (in press)
- Dann P, Cullen JM (1990) Chapter 3. Survival, patterns of reproduction and lifetime reproductive success in little blue penguins (*Eudyptula minor*) in Victoria, Australia. In: Davis L, Darby J (eds) Penguin biology. Academic, San Diego, pp 63–84
- Dunlop JN, Surman CA (2012) The role of foraging ecology in the contrasting responses of two dark terns to a changing ocean climate. Mar Ornithol 40:105–110
- Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271–283

- Durant JM, Crawford RJM, Wolfaardt AC, Agenbag CJ, Visagie J, Upfold L, Stenseth NC (2010) Influence of feeding conditions on breeding of African penguins—importance of adequate local food supplies. Mar Ecol Prog Ser 420:263–271
- Emmerson L, Pike R, Southwell C (2011) Reproductive consequences of environment-driven variation in Adélie penguin breeding phenology. Mar Ecol Prog Ser 440:203–216
- Fortescue M (1998) The marine and terrestrial ecology of a northern population of the Little Penguin, *Eudyptula minor*, from Bowen Island, Jervis Bay. PhD Thesis, University of Canberra
- Hindell MA, Bradshaw CA, Brook BW, Fordham DA, Knowles K, Hull C, McMahon CR (2012) Long-term breeding phenology shift in royal penguins. Ecol Evol 2:1563–1571
- Imber M, West JA, Cooper WJ (2003) Cook's petrel (*Pterodroma cookii*): historic distribution, breeding biology and effects of predators. Notornis 50:221–230
- Knox GA (2007) Biology of the southern ocean, 2nd edn. CRC, Boca Raton
- Lynch HJ, Fagan WF, Naveen R, Trivelpiece SG, Trivelpiece WZ (2009) Timing of clutch initiation in *Pygoscelis* penguins on the Antarctic Peninsula: towards an improved understanding of off-peak census correction factors. CCAMLR Sci 16:149–165
- Lynch HJ, Fagan WF, Naveen R, Trivelpiece SG, Trivelpiece WZ (2012) Differential advancement of breeding phenology in response to climate may alter staggered breeding among sympatric pygoscelid penguins. Mar Ecol Prog Ser 454:135–145
- McCutcheon C, Dann P, Salton M, Renwick L, Gormley A, Arnould J (2011) Foraging range of Little Penguins during winter. Emu 111:321–329
- McMahon C, Hindell MA (2009) Royal penguin phenology: Changes in the timing of egg-laying of a Sub-Antarctic predator in response to a changing marine environment. In: Stienin E, Ratcliffe N, Seys J, Jürgen T, Mees J, Dobbelaere I (eds) Seabird Group 10th International Conference VLIZ Special Publication 42. Communications of the Research Institute for Nature and Forest. Research Institute for Nature and Forest (INBM), Brussels, Belgium. Flanders Marine Institute (VLIZ) Oostende, Belgium, p 45
- Mills JA, Yarrall JW, Bradford-Grieve JM, Uddstrom MJ, Renwick JA, Merilä J (2008) The impact of climate fluctuation on food availability and reproductive performance on the planktivorous red-billed gull *Larus novaehollandiae scopulinus*. J Anim Ecol 77:1129–1142
- Paredes R, Zavalaga CB, Boness DJ (2002) Patterns of egg laying and breeding success in Humboldt penguins (*Spheniscus humboldti*) at Punta San Juan, Peru. Auk 119:244–250
- Parker DE, Folland CK, Bevan AC, Ward MN, Jackson M, Maskerll K (1995) Marine surface data for analysis of climatic fluctuations on interannual-to-century time scales. In: Climate Research Committee (ed) National climate variability on decade-to-century time scales. National Academy Press, Washington DC, pp 241–252
- Peacock L, Paulin M, Darby J (2000) Investigations into climate influence on population dynamics of yelloweyed penguins *Megadyptes antipodes*. N Z J Zool 27:317–325
- Perriman L, Steen H (2000) Blue penguin (*Eudyptula minor*) nest distribution and breeding success on Otago Peninsula, 1992 to 1998. N Z J Zool 27:269–275
- Perriman L, Houston D, Steen H, Johannesen E (2000) Climate fluctuation effects on breeding of blue penguins (*Eudyptula minor*). N Z J Zool 27:261–267

- Przybylo R, Sheldon BC, Merila J (2000) Climatic effects on breeding and morphology: evidence for phenotypic plasticity. J Anim Ecol 69:395–403
- Ramos JA, Maul AM, Ayrton V, Bullock I, Hunter J, Bowler J, Castle G, Mileto R, Pacheco C (2002) Influence of local and large-scale weather events and timing of breeding on tropical roseate tern reproductive parameters. Mar Ecol Prog Ser 243:271–279
- Ramos JA, Maul AM, Bowler J, Wood L, Threadgold R, Johnson S, Birch D, Walker S (2006) Annual variation in laying date and breeding success of Brown Noddies on Aride Island, Seychelles. Emu 106:81–86
- Reilly PN, Cullen JM (1983) The Little Penguin Eudyptula minor in Victoria, IV: the moult. Emu 83:94-98
- Reynolds RW, Smith TM (1994) Improved global sea surface temperature analysis using optimum interpolation. J Clim 7:929–948
- Ropert-Couder Y, Cannell B, Kato A (2004) Temperature inside nest boxes of little penguins. Wildl Soc Bull 32:177–182
- Sagar P, Miskelly C, Sagar J, Tennyson AJD (2003) Population size, breeding, and annual cycle of the New Zealand Antarctic tern (*Sterna vittata bethunei*) at the Snares Islands. Notornis 50:36–42
- Saraux C, Le Bohec C, Durant JM, Viblanc VA, Gauthier-Clerc M, Beaune D, Park Y-H, Yoccoz NG, Stenseth NC, Le Maho Y (2011) Reliability of flipper-banded penguins as indicators of climate change. Nature 469:203–208
- Stahel C, Gales R (1987) Little penguins: Fairy penguins in Australia. New South Wales University Press, Kensington
- Surman CA, Nicholson LW (2009a) El Niño Southern Oscillation and the Leeuwin Current influence on seabird reproductive performance and diet at the Houtman Abrolhos. J R Soc West Aust 92:155–163
- Surman CA, Nicholson LW (2009b) 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. Mar Ornithol 37:129–138
- Surman CA, Nicholson LW, Santora JA (2012) Effects of climate variability on breeding phenology and performance of tropical seabirds in the eastern Indian Ocean. Mar Ecol Prog Ser 454:147–157
- Sutherland DR, Dann P (2012) Improving the accuracy of population size estimates for burrowing seabirds. Ibis 154:488–498
- Underhill L, Crawford R (1999) Season of moult of African penguins at Robben Island, South Africa, and its variation, 1988–1998. S Afr J Mar Sci 21:437–441
- Watanuki Y, Ito M (2012) Climatic effects on breeding seabirds of the northern Japan Sea. Mar Ecol Prog Ser 454:105–307
- Woehler EJ (2012) What do signals from seabirds tell us about the marine environment? In: Heuttmann F (ed) Protection of the three poles. Springer, Berlin, pp 218–225
- Wolfaardt AC, Underhill LG, Visagie J (2009a) Breeding and moult phenology of African Penguins *Spheniscus demersus* at Dassen Island. Afr J Mar Sci 31:119–132
- Wolfaardt A, Underhill L, Crawford R (2009b) Comparison of moult phenology of African penguins *Spheniscus demersus* at Robben and Dassen islands. Afr J Mar Sci 31:19–29

Phenological trends broken down by species and location. Data type: *B* breeding dates(*B* laying, *B1* first laying, *B2* mean lay, *B3* last lay, *B4* hatching, *B5* creching, *B6* fledging),*Mi* migration (*A* arrival: *A1* first; *D* departure), *Mo* moult

| Species | Location | Years | Data Type | Trend direction | Reference | | | | | |
|-----------------------------------|----------------------|-----------|--------------|-----------------|--|--|--|--|--|--|
| Australia | | | | | | | | | | |
| Little Penguin Eudyptula minor | Phillip Island, Vic | 1968–2007 | B2 | Later | Cullen et al. (2009) | | | | | |
| Little Penguin | Phillip Island, Vic | 1968–2011 | В2 | No change | L.E.C. and P.D. (unpublished) | | | | | |
| Little Penguin | Phillip Island, Vic | 1969–2012 | Мо | No change | L.E.C, and P.D. (unpublished) | | | | | |
| Little Penguin | St Kilda, Vic | 1986–2011 | B1 | No change | Zoe Hogg, Earthcare St Kilda (unpublished) | | | | | |
| Little Penguin | Penguin Island, WA | 1986–2011 | B2 | No change | Cannell et al. (2012) | | | | | |
| Little Penguin | Penguin Island, WA | 1986–2011 | B1 | Earlier | Cannell et al. (2012) | | | | | |
| Little Penguin | Penguin Island, WA | 1986–2011 | В3 | No change | Cannell et al. (2012) | | | | | |
| Little Penguin | Bowen Island, NSW | 1987–1997 | B2 | No change | Fortescue (1998) | | | | | |
| Sooty Tern Onychoprion fuscata | Houtman Abrolhos, WA | 1993–2007 | B1 | Later | Surman and Nicholson (2009b) | | | | | |
| Sooty Tern | Houtman Abrolhos, WA | 1991–2010 | B1 | Later | Surman et al. (2012) | | | | | |
| Sooty Tern | Houtman Abrolhos, WA | 1991–2010 | B2 | Later | Surman et al. (2012) | | | | | |
| Bridled Tern O. anaethetus | Penguin Island, WA | 1986–2011 | B1 | Later | Dunlop and Surman (2012) | | | | | |
| Brown Noddy Anous stolidus | Lancelin Island, WA | 1994–2011 | B1 | No change | Dunlop and Surman (2012) | | | | | |
| Brown Noddy | Houtman Abrolhos, WA | 1993–2007 | B1 | Later | Surman and Nicholson (2009b) | | | | | |
| Brown Noddy | Houtman Abrolhos, WA | 1991–2010 | B1 | Later | Surman et al. (2012) | | | | | |
| Brown Noddy | Houtman Abrolhos, WA | 1991–2010 | B2 | Later | Surman et al. (2012) | | | | | |
| Lesser Noddy A. tenuirostris | Houtman Abrolhos, WA | 1991–2007 | B1 | Later | Surman and Nicholson (2009b) | | | | | |

| Lesser Noddy | Houtman Abrolhos, WA | 1991–2010 | B1 | Later | Surman et al. (2012) |
|--|--------------------------------|-----------|------|--------------|--|
| Lesser Noddy | Houtman Abrolhos, WA | 1991–2010 | B2 | No change | Surman et al. (2012) |
| Wedge-tailed ShearwaterArdenna pacifica | Houtman Abrolhos, WA | 1991–2007 | B1 | No change | Surman and Nicholson (2009b) |
| Wedge-tailed Shearwater | Houtman Abrolhos, WA | 1991–2010 | B1 | No change | Surman et al. (2012) |
| Wedge-tailed Shearwater | Houtman Abrolhos, WA | 1991-2010 | В2 | No change | Surman et al. (2012) |
| New Zealand | | | | | |
| Little Penguin | Flea Bay | 1996–2009 | B2 | No change | (unpublished data) from study described in Allen et al. (2011) |
| Caspian Tern <i>Hydroprogne caspia</i> | Invercargill | 1964–1993 | B1 | No change | Barlow and Dowding (2002) |
| Argentina | | | | | |
| Magellanic Penguin Spheniscus magellanicus | Punta Tombo | 1983–2006 | B2 | Later | Boersma and Rebstock (2009) |
| Antarctica - subantarctic | | | | | |
| Adelie Penguin Pygoscelis adeliae | Dumont d'Urville Station | 1950–2004 | MiA1 | No change | Barbraud and Weimerskirch (2006) |
| Adelie Penguin | Dumont d'Urville Station | 1950–2004 | B1 | Later | Barbraud and Weimerskirch (2006) |
| Adelie Penguin | Béchervaise Island | 1995–2008 | MiA | No change | Emmerson et al. (2011) |
| Adelie Penguin | Béchervaise Island | 1990-2003 | В | No change | Emmerson et al. (2011) |
| Adelie Penguin | Béchervaise Island | 1990-2005 | MiD | No change | Emmerson et al. (2011) |
| Adelie Penguin | Béchervaise Island | 1990-2005 | MiD | No change | Emmerson et al. (2011) |
| Adelie Penguin | Béchervaise Island | 1990–2005 | B4 | No change | Emmerson et al. (2011) |
| Adelie Penguin | Béchervaise Island | 1990–2005 | В5 | No change | Emmerson et al. (2011) |
| Adelie Penguin | Béchervaise Island | 1990–2005 | B6 | No change | Emmerson et al. (2011) |
| Adelie Penguin | Western Antarctic Peninsula | 1991-2007 | В | Earlier | Lynch et al. (2012) |
| Gentoo Penguin P. papua | Western Antarctic Peninsula | 1991–2007 | В | Earlier | Lynch et al. (2012) |
| Chinstrap Penguin P. antarctica | Western Antarctic Peninsula | 1991–2007 | В | Earlier | Lynch et al. (2012) |
| Pygoscelid penguins | Western Antarctic Peninsula | 1991–2007 | В | Earlier | Lynch et al. (2012) |
| Emperor Penguin Aptenodytes forsteri | Dumont d'Urville Station | 1950–2004 | MiA1 | No change | Barbraud and Weimerskirch (2006) |

| Emperor Penguin | Dumont d'Urville Station | 1950–2004 | B1 | No change | Barbraud and Weimerskirch (20 |
|--|--------------------------|-----------|------|--------------|-----------------------------------|
| Royal Penguin <i>Eudyptes</i> schlegeli | Macquarie Island | 1964–1999 | B2 | Earlier | Hindell et al. (2012) |
| Southern Giant Petrel <i>Macronectes</i> giganteus | Dumont d'Urville Station | 1960–2004 | MiA1 | No change | Barbraud and Weimerskirch (20 |
| Southern Fulmar Fulmarus glacialoides | Dumont d'Urville Station | 1950–2004 | MiA1 | Later | Barbraud and Weimerskirch (20 |
| Antarctic Petrel Thalassoica antarctica | Dumont d'Urville Station | 1980–2004 | MiA1 | Later | Barbraud and Weimerskirch (20 |
| Cape Petrel Daption capense | Dumont d'Urville Station | 1950–2004 | MiA1 | Later | Barbraud and Weimerskirch (20 |
| Cape Petrel | Dumont d'Urville Station | 1950–2004 | B1 | Later | Barbraud and Weimerskirch (20 |
| Snow Petrel Pagodroma nivea | Dumont d'Urville Station | 1970–2004 | MiA1 | Later | Barbraud and Weimerskirch (20 |
| Snow Petrel | Dumont d'Urville Station | 1950–2004 | B1 | No change | Barbraud and Weimerskirch (200 |
| Wilson's Storm Petrel Oceanites oceanicus | Dumont d'Urville Station | 1959–2004 | MiA1 | No change | Barbraud and Weimerskirch (20 |
| South Polar Skua Stercorarius maccormicki | Dumont d'Urville Station | 1950–2004 | MiA1 | Later | Barbraud and Weimerskirch (20 |
| South Polar Skua | Dumont d'Urville Station | 1960–2004 | B1 | Earlier | Barbraud and Weimerskirch (20 |
| South Africa | | | | | |
| African Penguin S. demersus | Dassen Island | 1995–2008 | В | Earlier | Durant et al. (20 |

Summary statistics. Number of studies by species and region and data type (no long-term data ending post 1990 was found for any other regions). Note only 48 of the 83 datasets had reported trends over time in the phenological variables^a

| | | | N | | Phenological type | | Trend of | over time | | |
|----------------------------|----|------------------|----------------|--|-------------------|-----------|----------|-----------|-------|------|
| Region | N | No. locations | No. species | No. years data: median (min, max) | Breeding | Migration | Moult | Earlier | Later | n.s. |
| Antarctic/ subantarctic | 41 | 9 | 15 | 16 (10–55) | 23 | 18 | 0 | 7 | 6 | 14 |
| Argentina | 1 | 1 | 1 | 24 | 1 | 0 | 0 | 0 | 1 | 0 |
| Australia | 21 | 5 | 7 | 20 (10-40) | 20 | 0 | 1 | 1 | 9 | 9 |
| New Zealand | 14 | 7 | 6 | 16 (11–28) | 14 | 0 | 0 | 0 | 0 | 1 |
| South Africa | 7 | 2 | 1 | 13 (13–23) | 1 | 0 | 6 | 0 | 0 | 0 |
| Total | 84 | 24 | 30 | 19 (10–55) | 59 | 18 | 7 | 8 | 16 | 24 |

^aData sources: Antarctic/subantarctic (Barbraud and Weimerskirch 2006; Crawford et al. 2006; Emmerson et al. 2011; Hindell et al. 2012; Lynch et al. 2009; Lynch et al. 2012; McMahon and Hindell 2009; Saraux et al. 2011; Baylis et al. 2012), Argentina (Boersma and Rebstock 2009), Australia (Cannell et al. 2012; Cullen et al. 2009; Fortescue 1998; Surman and Nicholson 2009a, b; Surman et al. 2012; unpublished (St Kilda Earthcare; Dann and Chambers)), New Zealand (Allen et al. 2011; Barlow and Dowding 2002; Imber et al. 2003; Mills et al. 2008; Peacock et al. 2000; Sagar et al. 2003), South Africa (Underhill and Crawford 1999; Wolfaardt et al. 2009a, b)

Summary statistics. Number of studies by family and data type (N is the number of datasets within this family and may include the same species more than once). Data sources as in Table 1

| | | Phenologica | al type | | | | |
|----------------|----|-------------|-----------|-------|---------|-------|------|
| Family | Ν | Breeding | Migration | Moult | Earlier | Later | n.s. |
| Hydrobatidae | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| Laridae | 17 | 16 | 1 | 0 | 1 | 8 | 3 |
| Procellariidae | 16 | 11 | 5 | 0 | 0 | 4 | 6 |
| Spheniscidae | 50 | 32 | 11 | 7 | 7 | 3 | 15 |
| Total | 84 | 59 | 18 | 7 | 8 | 16 | 24 |

Summary of Little Penguin breeding timing information. Timing is measured in mean laying date (MLD; day of year), except in the case of St Kilda where date first eggs are seen is used

| Colony | Latitude (° S) | Period of data | Ν | Mean timing | S.E. |
|--------------------------------------|----------------|----------------|----|-------------|------|
| Penguin Island, Western Australia | 32.3 | 1986–2011 | 22 | 209 | 4.9 |
| Bowen Island, New South Wales | 35.12 | 1987–1997 | 10 | 246 | 4.2 |
| St Kilda (Melbourne), Victoria | 37.86 | 1986–2010 | 25 | 187* | 7.9 |
| Phillip Island, Victoria | 38.52 | 1968–2011 | 43 | 279 | 3.1 |
| Flea Bay (New Zealand) | 43.87 | 1996–2007 | 12 | 275 | 2.7 |
| Oamaru (NZ) (Site 1) | 45.12 | 1993–1998 | 6 | 257 | 7.9 |
| Oamaru (NZ) (Site 2) | 45.12 | 1993–1998 | 6 | 267 | 6.3 |
| Taiaroa Head (NZ) | 45.83 | 1992–1998 | 7 | 265 | 8.6 |

Fig. 1

Artificial burrows of Little Penguins can be designed to reduce the chance of heat stress during extreme heat events. Additional gains can be made through providing shade either through man-made structures (*left*) or vegetation (*right*). Images L.E.C.



