

RESEARCH ARTICLE

Contrasting impacts of environmental variability on the breeding biology of two sympatric small procellariiform seabirds in south-eastern Australia

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Abstract

Seabirds play a vital role in marine ecosystems and the long-term study of their responses to environmental variations can be used to monitor the effects of climate change on marine fauna. However, slight differences in similar seabird species result in a range of responses which complicates our understanding of the effects of environmental changes to marine ecosystems. The present study investigated inter-annual differences in the breeding biology (breeding phenology, chick growth rates and breeding success) and environmental conditions (seasonal sea surface temperatures) of important foraging areas in two sympatric small Procellariiform species, the fairy prion (*Pachyptila turtur*) and the common diving petrel (*Pelecanoides urinatrix*), over four reproductive seasons (2017–2020) in Bass Strait, south-eastern Australia. Marine heatwaves occurred during the years of 2018/19 and 2019/20 and coincided with years of delayed laying dates, slower chick growth and reduced breeding success, in both species. While fairy prions maintained a relatively high breeding success and broadly constant breeding phenology, common diving petrels delayed the start of the breeding season by up to 50 days and experienced dramatic collapses in breeding success in years of high marine heat wave occurrence. The difference in foraging ecology and physiological capacity (largely in the production of stomach oils and fasting abilities of adults and chicks) between both species are likely to influence the variability and phenology in the observed breeding seasons.

Introduction

Seabirds are top predators with a global annual consumption of 69.8 million tonnes of marine biomass [1] comprised mainly of fish, crustaceans and cephalopods [2]. Correspondingly, seabirds play a vital role in the trophodynamics of marine food-webs and are essential for maintaining ecosystem function [3]. Consequently, seabirds are recognised as marine indicator species [1, 4] and knowledge of their breeding biology and reproductive success can provide

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valuable information on ocean health. This information can be used to identify changes in oceanic conditions and highlight potential threats that seabirds face [5].

Marine ecosystems are characteristically highly spatially and temporally variable [6, 7] and seabirds have evolved to be acutely adapted in their foraging strategy to maximise prey consumption for successful breeding [8]. However, throughout the world, seabirds are currently facing substantial immediate threats. Due to such factors as direct and indirect competition from fisheries, bycatch deaths in commercial fisheries, oil and plastics pollution and loss of breeding habitat [9–13], 28% of the 346 seabird species are currently listed as threatened [1, 14]. In addition, through changes to marine productivity, significant alterations to ocean temperatures [14] and currents [15] leading to shifts in prey species distribution, abundance and availability [16, 17], the effects of global climate change are considered the most pervasive and wide-ranging of impacts, affecting 40% of threatened seabirds [1, 5].

During the breeding season, seabirds adopt a central place foraging strategy and, therefore, are restricted in their ability to range long distances in search of prey resources [18]. Consequently, they are particularly susceptible to factors impacting the local distribution of their prey [14, 19]. With rapid changes associated with climate shifts, species may not be able to adjust their timing of breeding and foraging behaviour, leading to a temporal and spatial mismatch of prey abundance to the energy requirements of chick-rearing [20–22]. As a consequence, modifications in behaviour, range, fitness and breeding success may occur when a species can no longer tolerate current food or habitat conditions [23–25].

Understanding how species may adapt to such changes can be obtained by observing their responses to environmental variability at the extent of their ranges [26–28]. More vulnerable to population decline than other seabird orders [28], Procellariiformes generally display a rigid breeding phenology [29], experience late sexual maturity, lay a single egg each season and have slow chick growth [30–32]. In particular, small Procellariiformes (< 140 g) have a more limited foraging range and are, therefore, expected to be the most affected by environmental fluctuations. Although diverse, wide-ranging, contributing to a large biomass, and threatened by environmental changes, little is known about small Procellariiformes and their adaptation capacity [33].

The fairy prion (FP, *Pachyptila turtur*) and common diving petrel (CDP, *Pelecanoides urinatrix*) are two species of small Procellariiformes ubiquitous in temperate and subantarctic regions of the Southern Hemisphere [34]. Although both planktivorous and similar sized (110–140 g), these species differ in biology and foraging strategy. Adult FP produce and feed stomach oil to chicks which enables fasting for long periods, allowing adults to have a greater foraging range during a time of increased prey dispersal [35]. Adult CDP do not produce stomach oil and, consequently, are required to feed chicks more regularly, limiting their foraging range during breeding [35, 36]. In addition, FP feed on the ocean surface while CDP may forage at depths of up to 30 m [37], potentially facilitating avoidance of interspecific competition for food [38].

Both species breed sympatrically at the northern extent of their range within Bass Strait, south-eastern Australia [39]. Bass Strait is recognised as a region of low marine productivity [40] and is expected to experience significant warming events as a result of climate change [41]. These warming events or marine heatwaves (MHW) are identified by the average local sea surface temperature (SST) being above climatological average for 5 consecutive days or more [42]. Such events lead to changes to oceanic currents [41] with potentially major impacts on the diversity, abundance and availability of prey resources [43]. In years of MHW, large-bodied cold-water euphausiids are replaced by smaller size subtropical copepods that prefer higher temperatures [43, 44]. The cold-water coastal krill (*Nyctiphanes australis*) is the main zooplankton prey for both FP and CDP [45] and with reduced abundances, birds may need to

forage farther away from the colony [46]. A longer foraging range implies that chicks will be required to fast for longer periods of time, which may have consequences for their growth and survival [47].

Considering 60% of Australian seabirds breed in Bass Strait [48], FP and CDP are especially at risk of increased interspecific competition for food in a changing ecosystem [34]. Relatively little is known of the ecology of these predominantly subantarctic species in south-eastern Australia [45, 49]. Such information is crucial for understanding how they may respond to the rapidly changing conditions in the area. Furthermore, knowledge of how current environmental variability impacts these species at the northern extent of their range is necessary for predicting how these, and other, small Procellariiformes will respond to the anticipated extreme environmental changes throughout subantarctic regions [50]. The aims of the present study, therefore, were to: 1) determine breeding phenology; 2) assess chick growth and indices of breeding success; and 3) examine inter-annual variation in environmental factors, which have the potential to influence these parameters in FP and CDP that are breeding in northern Bass Strait.

Both species are widely distributed, with different breeding phenologies throughout their respective latitudes [34, 51]. New Zealand CDP colonies breed during the winter/spring period and FP in spring/summer. Considering the latitudinal proximity to Bass Strait, both species are expected to display similar breeding phenologies [51, 52]. Due to both species exploiting the same prey resource [51, 53], CDP and FP will most likely be impacted by the local conditions of coastal krill. However, considering that each species has different physiological capacities, we hypothesise that the extent of these impacts will vary between species. For example, in New Zealand, FP have been able to maintain a high breeding success during years of extreme SST values and variation in coastal krill abundances [54].

Materials and methods

This study was conducted in accordance with the regulations of Deakin University Animal Ethics Committee (Approval B16-2017) and in accordance with the Department of Environment, Water, Land and Planning (Victoria) Wildlife Research Permit 10008452. Fieldwork was conducted over four consecutive breeding seasons (2017/18–2020/21) at Kanowna Island (39°09'S, 146°18'E) in northern Bass Strait, south-eastern Australia (Fig 1). Kanowna Island, a granite outcrop vegetated with coastal tussock grass (*Poa poiformis*), hosts ca2000 FP and ca500 CDP breeding pairs [49]. Since both species breed in subterranean burrows, the nest chamber was accessed by a short artificial tunnel and covered with a removable stone lid. This access system reduced the disturbance of the natural tunnel and facilitated rapid access to the birds [55].

Breeding phenology was designated into laying, hatching and fledging dates. Laying dates were considered as the first day the egg was found in the burrow if the burrow was checked regularly, otherwise laying dates were estimated from the observed hatching dates [51, 52]. The incubation period was denoted as the time from laying to hatching, the chick-rearing period was denoted as the time from when the chick hatched to when the chick was considered fledged [51, 52]. Fledging date was when a fully-feathered chick was no longer in the burrow. Due to logistical constraints preventing access to the island at various times, the laying and hatching dates for some CDP individuals could not be recorded in 2017 and were estimated using wing length-age relationships [52, 55, 56].

Once hatching was detected, to minimise disturbance to the nest, chicks were not handled during the brood stage (age 1–3 d and 1–10 d for FP and CDP, respectively; [51, 52]). Thereafter, chicks were monitored every 3–5 d when weather conditions allowed. To determine the

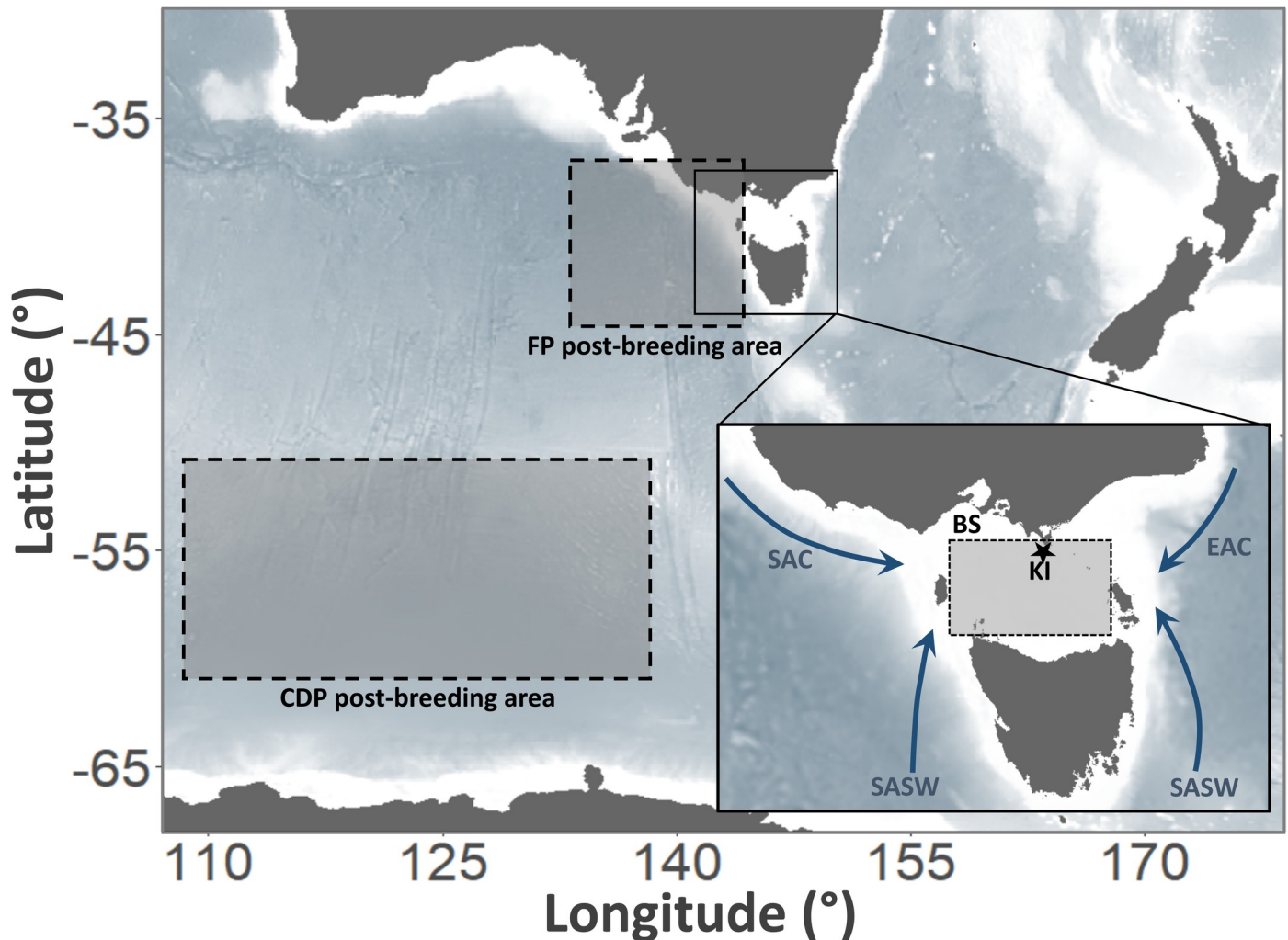


Fig 1. Study area of fairy prions (*Pachyptila turtur*) and common diving petrels (*Pelecanoides urinatrix*) from Kanowna Island, Bass Strait, south-eastern Australia. The lower right panel shows the main water masses influencing Bass Strait: Kanowna Island (KI); South Australian Current (SAC); Sub-Antarctic Surface Water (SASW); East Australian Current (EAC). The shaded rectangles describe the areas for which seasonal sea surface temperature was extracted: Bass Strait (BS; study breeding region; Fromant et al. unpublished data); post-breeding area of fairy prion (FP Post-breeding area; Fromant et al. unpublished data); post-breeding area of common diving petrels (CDP post-breeding area; [38]).

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growth rates of chicks, individuals were weighed in a cloth bag with a spring scale (± 2 g, Pesola Precision Scale, Schindellegi, Switzerland), bill and tarsus measurements were taken with Vernier callipers (± 0.1 mm) and wing length was measured with a shoulder-stopped ruler (± 1.0 mm). Mass at fledging was assumed to be the final measurement before the chick departed the burrow. Chicks no longer in the burrow that were too young to fledge were assumed to be dead if there were obvious signs of predation or if the burrow was invaded by a short-tailed shearwater (*Ardenna tenuirostris*).

Although most Procellariiform species do not show adverse effects related to repeated handling of chicks [57–59], the degree of response is likely to vary with environmental conditions and among species [59]. Therefore, the present study evaluated the potential impact of burrow disturbance and chick-handling in FP and CDP. During the 2018/19 breeding season, a group of control burrows (FP $n = 20$, and for CDP $n = 16$) was monitored monthly for each species and the hatching, fledging and breeding success were compared to those of the study burrows.

To investigate the variability in the environmental conditions experienced by the two study species, average SST data for specific periods before, during and after the breeding season were obtained for areas considered important to the study species (Fig 1). More specifically, the summer period plays a key role in the growth and reproduction of coastal krill in Bass Strait [60], the main prey of both FP and CDP [45]. Therefore, SST during the summer preceding each breeding season in Bass Strait (38–40°S, 144–148°E; Dec–Feb) was identified as a potentially important variable for both species. Additionally, during the early post-breeding period, FP occupy an area to the south of the Australian mainland, to the west of Tasmania before frequenting Bass Strait during early breeding (Fromant et al. unpublished data). Therefore, the influence of SST in this region (35–48°S, 130–152°E) in late January–early March preceding the breeding period was also assessed. Similarly, CDP from Kanowna Island have been observed to migrate during the post-breeding period to subantarctic regions [38] which may provide resources necessary for winter survival and preparation for subsequent breeding. Therefore, SST in the post-breeding area of CDP (50–60°S, 110–140°E) in December–February preceding the breeding period was chosen as an important variable. Lastly, the SST in Bass Strait (38–40°S, 144–148°E) during the early breeding period for FP (September–November) and CDP (July–September), were used as proxies to investigate potential environmental influences on breeding in both species (Fig 1). All SST data were downloaded from the Copernicus Marine Services platform [http://marine.copernicus.eu/global_analysis_forecast_phy_001_024] with a spatial resolution of 0.25 x 0.25 degrees.

All statistical analyses were conducted in the R statistical environment 4.0.0 (R Core Team 2020). Generalized linear mixed-effects models (GLMMs) were used to investigate the effect of SST on breeding success (binomial family) and phenology (Gaussian family) using the “nlme” and “lme4” packages [61]. Bird nest was fitted as random effect to account for pseudo-replication, as the majority of the nest were sampled during the all four years of the study. Models were ranked based on their Akaike’s Information Criterion (AIC) and were checked to ensure normality and homoscedasticity of residuals [62] before further statistical analysis. Data normality and homogeneity of variances were assessed with Shapiro-Wilk and Bartlett tests, respectively. Inter-annual variations in phenology (laying, hatching and fledging dates) were tested using analyses of variance (ANOVA or Welch’s ANOVA), and *post-hoc* tests were conducted using *t*-tests (parametric), or Kruskal-Wallis and Mann-Whitney *U* tests (non-parametric) depending on the data distributions. The growth curve analysis method [63] was used to investigate the potential variation in chick growth among years. Growth in body mass, wing length, tarsus length and bill length were modelled with a third-order orthogonal polynomial and fixed effects on all age terms. The model also included chick individual as a random effect. Hatching success (eggs hatched as a proportion of eggs laid), fledging success (chicks fledged as a proportion of eggs hatched) and breeding success (chicks fledged as a proportion of eggs laid) were compared between years using a Pearson’s chi-squared test.

Results

For both FP and CDP, no significant differences were found for hatching, fledging or breeding success between control and experimental groups (Pearson’s Chi-squared test, all $P > 0.4$). Therefore, for both species, data from control and study groups were pooled to investigate differences between years. For the four study years, the FP laying period occurred between 10 and 31 October (Table 1). Mean laying date varied significantly between years (Kruskal-Wallis test: $\chi^2 = 57.456$, $P < 0.001$), with eggs being laid significantly later in 2018/19 and 2019/20 than in 2017/18 and 2020/21. Correspondingly, mean hatching period was significantly delayed 2018/19 and 2019/20 compared to 2017/18 and 2020/21 (Kruskal-Wallis test: $\chi^2 =$

Table 1. Timing of laying, hatching and fledging dates (mean ± SE) of fairy prions (*Pachyptila turtur*) and common diving petrels (*Pelecanoides urinatrix*) from Kanowna Island, Bass Strait, south-eastern Australia. For each period/species, values not sharing the same superscript letter (a, b, c or d) are significantly different (Mann-Whitney *U* test: *P* < 0.05). Sample sizes are provided in parentheses.

| Species | Year | Laying | Hatching | Fledging |
|----------------------|---------|---------------------------------|---------------------------------|---------------------------------|
| Fairy prion | 2017/18 | 19 Oct ± 1 d (43) ^a | 05 Dec ± 1 d (43) ^a | * |
| | 2018/19 | 24 Oct ± 1 d (51) ^b | 10 Dec ± 1 d (48) ^b | 27 Jan ± 1 d (29) ^a |
| | 2019/20 | 22 Oct ± 1 d (56) ^b | 07 Dec ± 1 d (43) ^{ab} | 24 Jan ± 1 d (28) ^b |
| | 2020/21 | 14 Oct ± 1 d (13) ^c | 30 Nov ± 1 d (14) ^c | 16 Jan ± 1 d (12) ^c |
| Common diving petrel | 2017/18 | 27 Jul ± 1 d (61) ^{**} | 20 Sep ± 1 d (61) ^a | 14 Nov ± 1 d (61) ^a |
| | 2018/19 | 15 Sep ± 2 d (43) ^a | 07 Nov ± 2 d (33) ^b | 25 Dec ± 4 d (9) ^b |
| | 2019/20 | 05 Sep ± 2 d (35) ^b | 02 Nov ± 4 d (25) ^c | # |
| | 2020/21 | 12 Aug ± 2 d (33) ^c | 06 Oct ± 2 d (33) ^d | 19 Nov ± 10 d (33) ^c |

* fledging dates could not be obtained in this year due to logistical constraints.

** duration dates estimated based on mean common diving petrel incubation duration.

all study nests failed in 2019/20 so no fledging data was available.

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51.939, *P* < 0.001), as well as fledging (Table 1; Kruskal-Wallis test: $\chi^2 = 47.28$, *P* < 0.001). The average duration of the incubation and chick-rearing periods for FP were consistent between years at, 47 ± 1 d and 50 ± 1 d, respectively.

The breeding phenology in CDP was also significantly delayed in 2018/19 and 2019/20 compared to 2017/18 and 2020/21, though to a much greater degree than in FP (Fig 2). Mean

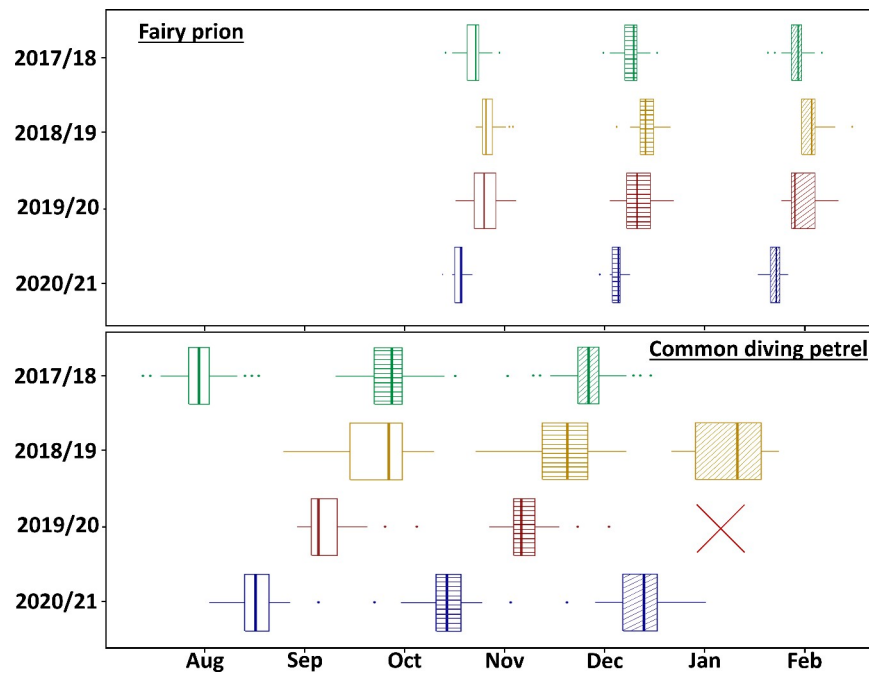


Fig 2. Inter-annual variation in the breeding phenology of fairy prions (*Pachyptila turtur*) and common diving petrels (*Pelecanoides urinatrix*) from Kanowna Island, Bass Strait, south-eastern Australia. Laying date = open boxplots; hatching date = horizontal dashed boxplots; fledging date = diagonal dashed boxplot. Laying date of CDP in 2017/18 was estimated based on mean incubation duration. Fledging date of FP in 2017/18 was estimated based on mean chick-rearing duration. Fledging date for CDP in 2019/20 was not determined because all study nests failed so no fledging data was available (red cross).

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laying date were 50 d in 2018/19 and 40 d in 2019/20 later than in 2017/18 (Table 1; Kruskal-Wallis test: $\chi^2 = 112.75$, $P < 0.001$). Correspondingly, the hatching dates were 48 d and 43 d later in 2018/19 and 2019/20, respectively, than in 2017/18 (Kruskal-Wallis test: $\chi^2 = 89.26$, $P < 0.001$), and fledging date was 41 d later in 2018/19 than in 2017/18 (t -test: $t_{9,097} = -11.092$, $P < 0.001$; no study nests fledged in 2019/20). Intermediate phenology was observed in 2020/21, with the mean laying date being delayed 16 d compared to 2017/18 (Table 1). The duration of incubation was longer in 2018/19 and 2019/20 compared to 2020/21 (56 ± 1 d, 57 ± 1 d and 55 ± 1 , respectively; Kruskal-Wallis test: $\chi^2 = 15.289$, $P < 0.001$; no data available in 2017/18). Conversely, the duration of the chick-rearing period was not different between years (54 ± 1 d in 2017/18, 55 ± 1 d in 2018/19 and 55 ± 1 d in 2020/21, respectively; Kruskal-Wallis test: $\chi^2 = 2.081$, $P = 0.353$; no study nests fledged in 2019/20).

Hatching success for FP was not significantly different between years (Pearson's Chi-squared test, $\chi^2 = 3.627$, $P = 0.305$) (Table 2). Due to logistical constraints, no data were available for fledging and breeding success in 2017/18. However, the study nests were monitored during the early chick-rearing period (up to age 12 d) and the proportion of chicks surviving during this time was not significantly different between years (93% in 2017/18, 83% in 2018/19, 88% in 2019/20 and 91% in 2020/21; Pearson's Chi-squared test, $\chi^2 = 1.795$, $P = 0.616$). Fledging success (Pearson's Chi-squared test, $\chi^2 = 4.688$, $P = 0.096$) and breeding success (Pearson's Chi-squared test, $\chi^2 = 3.713$, $P = 0.156$) did not vary significantly between years.

Hatching success for CDP was significantly higher in 2017/18 and 2020/21 than in 2018/19 and 2019/20 (Pearson's Chi-squared test, $\chi^2 = 46.291$, $P < 0.001$) (Table 2). Similarly, fledging success varied significantly between years (Pearson's Chi-squared test, $\chi^2 = 90.391$, $P < 0.001$), fluctuating from 0% in 2019/20 to 91% in 2020/21. Correspondingly, breeding success in 2017/18 (69%) and 2020/21 (84%) was significantly higher than in 2018/19 (6%) and 2019/20 (0%) (Pearson's Chi-squared test, $\chi^2 = 127.73$, $P < 0.001$).

For both species, growth parameters (body mass, wing, tarsus and bill lengths) varied significantly among years (Fig 3, Table 3). There was a significant effect of year on both the intercept and quadratic terms, highlighting that growth rates decreased from 2017/18 to 2019/20. For FP, measurements of 12 d old chicks were significantly greater in 2017/18 and 2020/21 than in 2018/19 and 2019/20 (Fig 3). The difference was particularly pronounced between 2017/18 and 2019/20 for the wing length (t -test: $t_{24,58} = 5.803$, $P < 0.001$) and tarsus length (t -test: $t_{21,694} = 2.337$, $P = 0.029$). Additionally, body mass of FP fledging chicks was lower in 2019/20 than in 2018/19 (t -test: $t_{29,333} = 3.129$, $P = 0.004$), similarly to wing length t -test: $t_{35,965} = 3.592$, $P < 0.001$) and tarsus length (t -test: $t_{32,699} = 2.728$, $P = 0.010$). For CDP, body mass at fledging

Table 2. Hatching, fledging and breeding success (mean \pm SE) of fairy prions (*Pachyptila turtur*) and common diving petrels (*Pelecanoides urinatrix*) from Kanowna Island, Bass Strait, south-eastern Australia. Sample sizes are provided in parentheses.

| Species | Year | Hatching success | Fledging success | Breeding success |
|----------------------|---------|------------------|------------------|------------------|
| Fairy prion | 2017/18 | 88% (18) | # | # |
| | 2018/19 | 65% (37) | 62% (47) | 38% (37) |
| | 2019/20 | 68% (63) | 67% (43) | 46% (63) |
| | 2020/21 | 70% (33) | 86% (23) | 61% (33) |
| Common diving petrel | 2017/18 | 81% (16) | 90% (32) | 69% (16) |
| | 2018/19 | 36% (66) | 17% (24) | 6% (66) |
| | 2019/20 | 41% (63) | 0% (26) | 0% (63) |
| | 2020/21 | 92% (50) | 91% (46) | 84% (50) |

Fledging and breeding success for fairy prion in 2017/18 was not determined due to logistic constraints.

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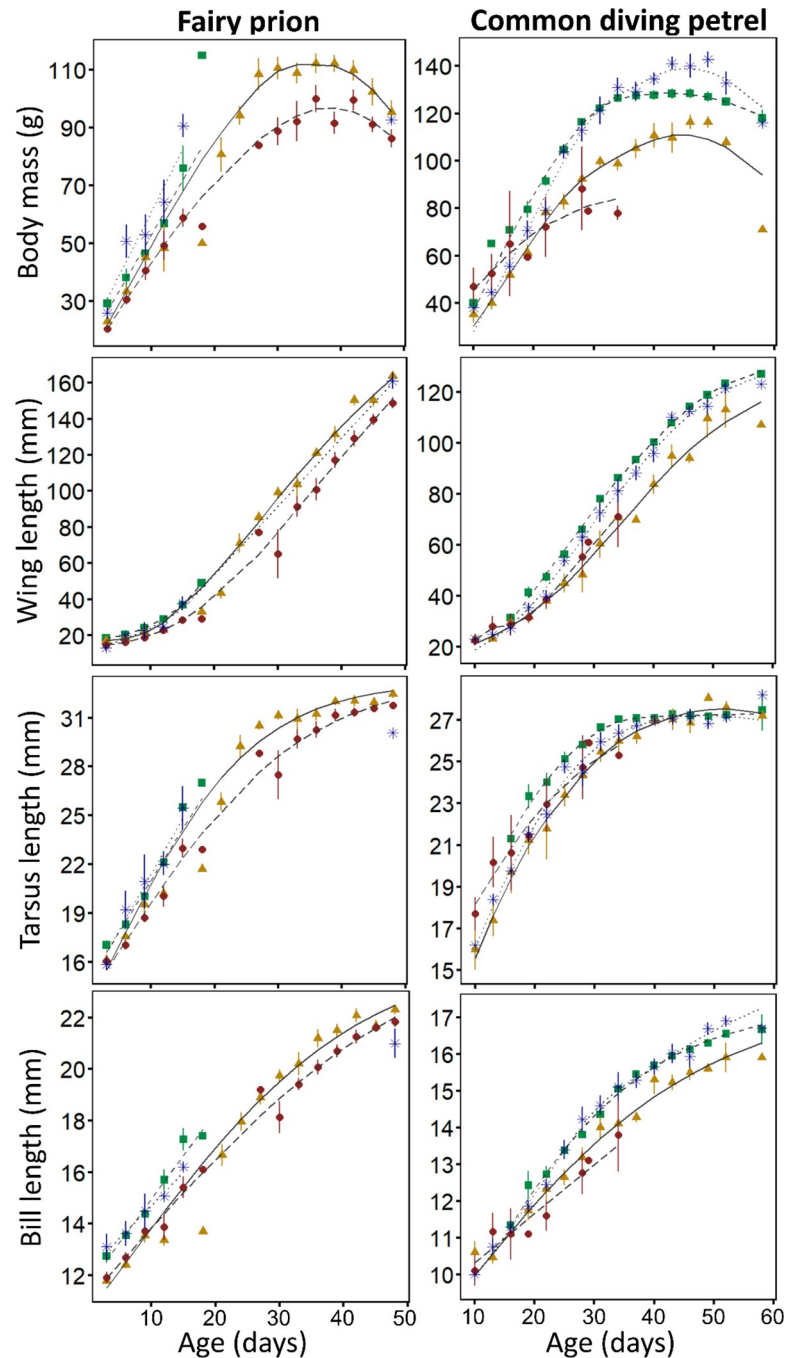


Fig 3. Growth curves of chick fairy prions (*Pachyptila turtur*) and common diving petrels (*Pelecanoides urinatrix*) from Kanowna Island in 2017/18 (green squares), 2018/19 (orange triangles), 2019/20 (red circles) and 2020/21 (blue stars).

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was significantly higher in 2017/18 and 2020/21 than in 2018/19 (Table 3; t -test: $P < 0.03$), as was wing length between 2017/18 and 2018/19 (t -test: $t_{4,269} = 2.924$, $P = 0.039$) but not in bill length (t -test: $P > 0.161$) or tarsus length (t -test: $P > 0.323$). In 2019/20, chick body mass growth rate decreased rapidly and lead to the death of all chicks during the first half of the chick-rearing period (mean age of chicks when found dead was 17.6 ± 8.2 d).

Table 3. Body mass, wing length, tarsus length, and bill length (mean \pm SE) of fairy prion (*Pachyptila turtur*) and common diving petrel (*Pelecanoides urinatrix*) fledglings from Kanowna Island, Bass Strait, south-eastern Australia. For each period/species, values not sharing the same superscript letter (a, b, or c) are significantly different (Mann-Whitney U test: $P < 0.05$). Sample sizes are provided in parentheses.

| Species | Year | Body mass (g) | Wing length (mm) | Tarsus length (mm) | Bill length (mm) |
|----------------------|--------------|--------------------------|--------------------------|-----------------------------|-----------------------------|
| Fairy prion | 2017/18 (0) | # | # | # | # |
| | 2018/19 (23) | 99 \pm 4 ^a | 161 \pm 2 ^a | 32.4 \pm 0.1 ^a | 22.2 \pm 0.1 ^a |
| | 2019/20 (18) | 86 \pm 2 ^b | 142 \pm 3 ^b | 31.6 \pm 0.2 ^a | 21.8 \pm 0.2 ^a |
| | 2020/21 (2)* | 92 \pm 2 | 164 \pm 6 | 30.1 \pm 0.1 | 21.4 \pm 0.7 |
| Common diving petrel | 2017/18 (40) | 126 \pm 2 ^a | 122 \pm 1 ^a | 27.3 \pm 0.1 ^a | 16.4 \pm 0.1 ^a |
| | 2018/19 (6) | 103 \pm 8 ^b | 113 \pm 3 ^b | 27.6 \pm 0.3 ^a | 16.2 \pm 0.2 ^a |
| | 2019/20 (0) | ## | ## | ## | ## |
| | 2020/21(21) | 139 \pm 5 ^c | 118 \pm 2 ^b | 27.2 \pm 0.2 ^a | 16.6 \pm 0.1 ^a |

fledging and breeding success for fairy prion in 2017/18 was not determined due to logistic constraints.

all common diving petrel study nests failed in 2019/20 so no fledging data was available.

* the low sample size of fairy prions in 2020/21 impeded statistical comparison.

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The SST in Bass Strait during summer preceding the breeding season of FP and CDP varied significantly between years (Dec-Feb; ANOVA: $F_{10,976} = 94.321$, $P < 0.001$) and in the post-breeding migration area of CDP (Fig 4; ANOVA: $F_{3,792} = 18.803$, $P = 0.011$). In Bass Strait, SST in the summers preceding the 2018/19 and 2019/20 breeding seasons was 2–4°C warmer than prior to the 2017/18 and 2020/21 breeding seasons. During this period, SST in Bass Strait was $>1^\circ\text{C}$ above the climatologic average for 95 consecutive days in 2018/19, and 68 consecutive days in 2019/20, while it was only four consecutive days above the average in 2017/18 and 0 in 2020/21, delineating 2018/19 and 2019/20 as years of MHW. Accordingly, the GLMM results indicated a strong negative effect of SST on the phenology for FP (S1-S3 Tables in S1 File) and both breeding success and phenology for CDP (S4-S6 Tables in S1 File).

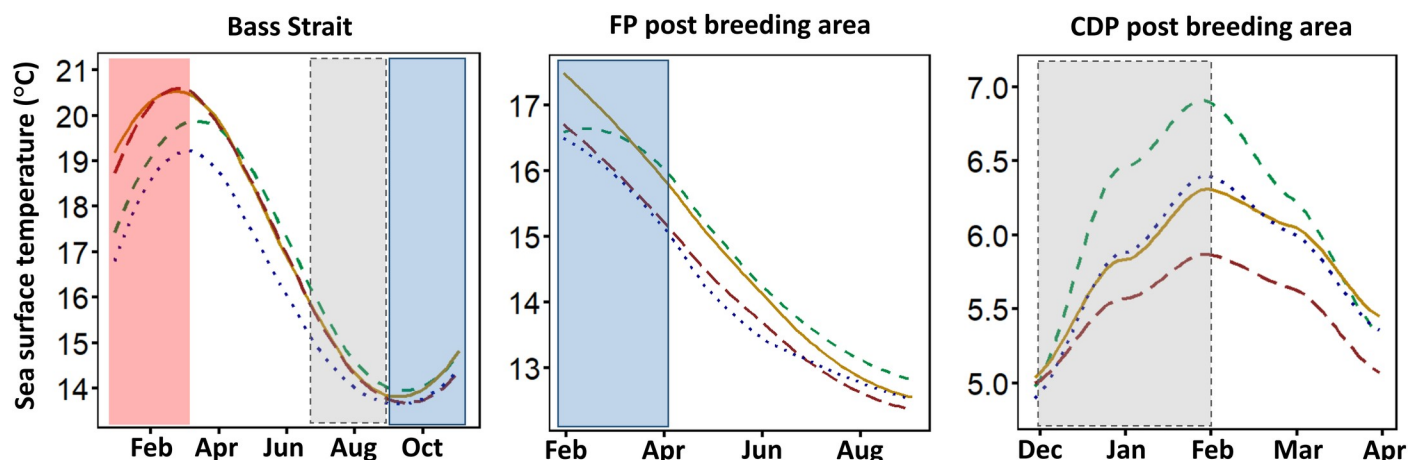


Fig 4. Inter-annual variation of sea surface temperature in three areas of importance to FP and CDP. The lines represent the conditions in the year preceding the 2017/18 breeding season (green dashed line); 2018/19 breeding season (orange line); 2019/20 breeding season (red dashed line); the 2020/21 breeding season (blue dotted line). Post-breeding migration area refers to the core area used by fairy prion and common diving petrels from Kanowna Island during their post-breeding migration (see Fig 1). Shaded columns refer to the period of time regarded as important for coastal krill (red; Bass Strait = December–February), FP (blue; Bass Strait early breeding = September–November; Post breeding area = mid-January–mid-March) and CDP (grey; Bass Strait early breeding = July–September; Post breeding area = December–February).

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Conversely, SST in the area used by CDP during the post-breeding migration exhibited an opposite trend, with mean December to February values prior to the 2017/18 breeding season higher than in 2018/19, 2019/20 and 2020/21 (Fig 4; ANOVA: $F_{3,792} = 18.803$, $P = 0.011$).

Discussion

The present study documented inter-annual variations in the breeding phenology over four consecutive breeding seasons, chick growth and breeding success of FP and CDP breeding in northern Bass Strait, south-eastern Australia. In support of our hypothesis, these variations, which are likely to be related to shifts in food availability [64], differed between the species despite their consumption of similar prey [45]. The findings suggest potential differences in foraging areas and/or constraints on their breeding biology. Such observations, from the northern extent of their range, may provide insights into how these two ubiquitous species of the Southern Ocean may respond to anticipated effects of climate change in more southerly latitudes.

Inter-annual variation in breeding biology

During the study period, both FP and CDP exhibited delayed phenology and low breeding performance in two consecutive years (2018/19 and 2019/20). Overlap between timing of reproduction and the peak of prey availability is crucial for seabird breeding success [65], with the timing of laying having been shown to be influenced by oceanographic conditions and, ultimately, food availability [66]. In the present study, the late start of the breeding season for both species in 2018/19 and 2019/20 was followed by substantial incubation failure, lower chick growth and/or lower fledging success and, for CDP in 2019/20, complete breeding failure. This suggests both species may have faced significant prey shortages during the two consecutive breeding seasons [67]. Additionally, for CDP, the rapid acceleration of breeding failure during the first few weeks post hatching suggests an energetic trade-off induced by a lack of food. With an exceptionally low prey availability, adults might not have been able to both self-maintain and feed their chick [68], leading to the extremely low breeding success [69]. As well as low food availability, low breeding success can be triggered by extreme environmental events such as intense rain [70], or infectious diseases [71]. However, the sequence of delayed phenology, low hatching success, low chick growth and low fledging success support a scenario of reduced availability of important prey [72].

In south-eastern Australia, coastal krill plays a key role in the marine ecosystem with abundances observed to vary substantially between years, heavily affecting fish recruitment, seabird distribution and breeding success [73–76]. The optimal temperature for this large cold-water euphausiid ranges from 12–18°C [77] and a major factor influencing the survival and growth of coastal krill is ocean temperatures exceeding this range [75, 78]. During recent decades, this optimal temperature has been disrupted in the region by MHW [79, 80] which profoundly impact local zooplanktonic communities [43]. The MHW recorded in Bass Strait during the summers preceding the 2018/19 and 2019/20 breeding seasons, therefore, are likely to have affected the abundance of the main prey for both FP and CDP, inducing changes in their breeding biology. Additionally, the lowest SST recorded in the summer preceding the 2020/21 breeding season coincided with the highest recorded breeding success for both species and with CDP chicks reaching the highest maximum mass towards the end of fledging.

Variations in peripheral upwellings and currents around Bass Strait influence local oceanographic conditions, yet relatively little is known of the mechanisms involved. Warmer waters in Bass Strait can be the result of a lower influence of the northward cool Sub-Antarctic Surface Waters (SASW) and/or an increased eastward warm South Australian Current (SAC) and southward East Australian Current (EAC) [81]. Specifically, over recent decades, the

strengthening of the EAC has resulted in a large influx of warm subtropical water southward [82, 83], inducing a replacement of large cool water zooplanktonic communities (including coastal krill) by smaller sub-tropical species [44]. Additionally, the strength and duration of the numerous upwelling systems on the edges of Bass Strait vary seasonally and annually [84], and their effect on the inner part of the strait depend on the confounding effects of the currents cited above [81].

Similarly, low food availability during the non-breeding period can induce low breeding performances through carry-over effects [85]. This period is critical for both study species, as adults need to restore their body reserves and, more importantly, undertake the energetically costly renewal of their plumage [38, 86]. In the post-breeding area of CDP in the Southern Ocean, zooplanktonic communities can be affected by warmer SST [87] impacting the body condition and survival of planktivorous seabird species [88]. As shown in Fig 4, the highest SST in the CDP post-breeding area corresponds to a year with a successful subsequent breeding season, while the lowest SST in the same area corresponds to the year of subsequent complete breeding failure. This suggests that the post-breeding area may not impose carry-over effects on the breeding season if local conditions are poor. In the present study, the link between zooplanktonic abundance and oceanographic variables remains unclear. While SST was selected as one of the most influential parameters of productivity in important foraging areas, many other environmental variables could also influence levels of productivity. Large-scale oceanographic indices such as the Southern Oscillation Index (SOI) and the Indian Ocean Dipole (IOD) have also been used to investigate the impact of temperature on the variation in planktonic productivity [89]. Observations in the present study suggest that MHW occurring in the years preceding each breeding season influences breeding biology, yet, the mechanisms causing these lags are unknown. Environmental variation may impact seabird species differently and further research exploring these mechanisms will provide knowledge about the responses of small seabird species that are in areas exposed to extreme oceanographic changes, like the Southern Ocean [25, 90].

Different responses to environmental variability

In the present study, the impact of environmental variability differed greatly between the two study species. In contrast to FP, CDP exhibited inter-annual variations in breeding biology unexpectedly large for a subantarctic/temperate species [69]. The observed variation in phenology of 40–50 d far exceeds what has previously been reported in Procellariiformes and is highly unusual for temperate/subpolar species [91, 92]. Throughout their range, CDP have been shown to display variation in breeding phenology, with subantarctic populations laying in the mid-spring (October–November) [56, 93] while some populations have bred successfully during winter in Australia and New Zealand [52, 53]. Temporal shifts in breeding may affect the availability of food and nesting habitat as well as having implications for interspecific competition.

Additionally, there was no overlap between the chick rearing periods of both species during the years of high breeding success. In 2017/18 and 2020/21, the average CDP fledging date was 11–20 days before the average FP hatching date, reducing the possibility of interspecific competition for the same prey species in Bass Strait during the most energetically expensive period of breeding. In contrast, the chick-rearing period in both species overlapped by 15 days in 2018/19 and the mean death/failure date of CDP in 2019/20 was 18 days before the FP hatching date such that there was no overlap in chick-rearing. Although uncommon at the most northern extent of their range [51, 52], FP and CDP display full temporal overlap in breeding season throughout their subantarctic range [69, 94]. Avoiding an overlap in breeding season is

a niche segregation mechanism for reducing interspecific competition in species that rely on similar prey. The temporal segregation in breeding season of CDP and FP observed in Bass Strait may enable both species to acquire local prey resources for chick-rearing without having to compete with each other. Therefore, when conditions lead to a delayed breeding season for CDP in Bass Strait, it could lead to increased difficulty for both species.

During years of low productivity, often associated with higher than average SST [95], Procellariiformes can demonstrate various techniques to help maintain offspring survival [96]. During such years, species like the yellow-nosed albatross (*Diomedea chlororhynchos*) increase their foraging duration to adequately provision chicks [97]. Similarly, both the thin-billed prion (*Pachiptila belcheri*) and Antarctic prion (*Pachiptila desolata*) maintain a relatively stable breeding success in years of high SST anomaly by increasing their foraging effort through prey-switching [98, 99]. However, these strategies rely on the ability of chicks to survive longer durations without adult provisioning.

While FP and CDP feed mainly on the same prey during the breeding season [45, 69], their physiological and ecological differences may explain the contrasting impacts of environmental variability on these species. Provisioning chicks with highly concentrated stomach oil [100], FP chicks are able to regulate energy and water supply as well as allowing both adult and chick to endure long periods of fasting [100]. Being the only Procellariiformes to not produce stomach oil [35, 91], diving petrels chicks are subsequently required to be fed twice as frequently as other Procellariiformes [35]. Compared to CDP, the physiological characteristics of other small Procellariiformes are likely to provide better tools to cope with a decrease in prey availability in Bass Strait. In addition to the absence of stomach oil, the high wing load of CDP might be detrimental to their capacity to extend their foraging range and trip duration. Indeed, while CDP are restricted to short trips in both incubation and chick-rearing (< 200 km; 1–2 days; [69, 101, 102], FP are able to extend their range and trip duration to access distant foraging areas (600 km; 1–7 days) (Fromant et al. unpublished data).

Although FP appeared to respond better to environmental variations than CDP in the present study, they still experienced slower growth and poorer body condition of fledglings during breeding seasons following MHW. Such reduced fledging size and condition could lead to reduced first year survival [103]. Therefore, while the eco-physiological flexibility of FP may mitigate the apparent intensity and ecological impact of environmental variability [104], the long-term effects remain to be explored. Since CDP and FP share breeding periods during the austral summer throughout their subantarctic range, a delay in the breeding season further challenges breeding outcomes as winter snow and ice impact nesting and foraging options. Therefore, gathering long-term ecological and demographic knowledge about small Procellariiformes is particularly important to observe and understand the evolutionary response of Southern Ocean communities facing climate change.

Supporting information

S1 File. Information explaining the effect of inter-annual variation of Sea Surface Temperature (SST) on breeding parameters for fairy prions and common diving petrels. This file contains all the supporting tables.
(PDF)

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References

1. Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, et al. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*. 2012; 22(1):1–34. <https://doi.org/10.1017/S0959270912000020> WOS:000301298900001.
2. Crawford RJM, Ryan PG, Williams AJ. Seabird consumption and production in the Benguela and Western Agulhas ecosystems. *South African Journal of Marine Science*. 1991; 11(1):357–75.
3. Schreiber EA, Burger J. *Biology of Marine Birds*: CRC Press; 2001.
4. Frederiksen M, Mavor RA, Wanless S. Seabirds as environmental indicators: the advantages of combining data sets. *Marine Ecology Progress Series*. 2008; 352:205–11.
5. Dias MP, Opper S, Bond AL, Carneiro APB, Cuthbert RJ, González-Solís J, et al. Using globally threatened pelagic birds to identify priority sites for marine conservation in the South Atlantic Ocean. *Biological Conservation*. 2017; 211:76–84. <https://doi.org/10.1016/j.biocon.2017.05.009>
6. Armbrrecht LH, Schaeffer A, Roughan M, Armand LK. Interactions between seasonality and oceanic forcing drive the phytoplankton variability in the tropical-temperate transition zone (~30°S) of Eastern Australia. *J Mar Syst*. 2015; 144:92–106. <https://doi.org/10.1016/j.jmarsys.2014.11.008>.
7. Southward A, Hawkins S, Burrows M. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology*. 1995; 20(1–2):127–55.
8. Ramos JA, Rodrigues I, Melo T, Geraldés P, Paiva VH. Variation in ocean conditions affects chick growth, trophic ecology, and foraging range in Cape Verde Shearwater. *The Condor*. 2018; 120(2):283–90. <https://doi.org/10.1650/condor-17-220.1>
9. Boersma PD, Parrish JK. Limiting abuse: marine protected areas, a limited solution. *Ecological Economics*. 1999; 31:287–304.
10. Barbraud C, Rolland V, Jenouvrier S, Nevoux M, Delord K, Weimerskirch H. Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review. *Marine Ecology Progress Series*. 2012; 454:285–307. <https://doi.org/10.3354/meps09616> WOS:000304605500023.

11. Lewison R, Oro D, Godley B, Underhill L, Bearhop S, Wilson RP, et al. Research priorities for seabirds: improving conservation and management in the 21st century. *Endangered Species Research*. 2012; 17(2):93–121. <https://doi.org/10.3354/esr00419> BCI:BCI201200456398.
12. Oppel S, Bolton M, Carneiro APB, Dias MP, Green JA, Masello JF, et al. Spatial scales of marine conservation management for breeding seabirds. *Marine Policy*. 2018; 98:37–46. <https://doi.org/10.1016/j.marpol.2018.08.024> WOS:000454467100005.
13. Fromant A, Carravieri A, Bustamante P, Labadie P, Budzinski H, Peluhet L, et al. Wide range of metallic and organic contaminants in various tissues of the Antarctic prion, a planktonophagous seabird from the Southern Ocean. *Sci Total Environ*. 2016; 544:754–64. <https://doi.org/10.1016/j.scitotenv.2015.11.114> WOS:000369491500081. PMID: 26674704
14. Constable AJ, Melbourne-Thomas J, Corney SP, Arrigo KR, Barbraud C, Barnes DKA, et al. Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Global Change Biology*. 2014; 20(10):3004–25. <https://doi.org/10.1111/gcb.12623> WOS:000342168500002. PMID: 24802817
15. Feng M, Meyers G, Pearce A, Wijffels S. Annual and interannual variations of the Leeuwin Current at 32 degrees S. *Journal of Geophysical Research: Oceans*. 2003; 108(C11). <https://doi.org/10.1029/2002jc001763> WOS:000186899100004.
16. Bost CA, Cotte C, Terray P, Barbraud C, Bon C, Delord K, et al. Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nature Communications*. 2015; 6:8220. Epub 28/10/2015. <https://doi.org/10.1038/ncomms9220> PMID: 26506134; PubMed Central PMCID: PMC4639794.
17. Boyd C, Grunbaum D, Hunt GL, Punt AE, Weimerskirch H, Bertrand S. Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers. *Journal of Applied Ecology*. 2017; 54(5):1362–72. <https://doi.org/10.1111/1365-2664.12832> WOS:000410678700009.
18. Orians GH, Pearson NE. In: Horn D.J., Stairs G.R., Mitchell R.D. (Eds.) *On the Central Place Foraging*. Ohio State University Press. 1979:155–77
19. Chambers LE, Devney CA, Congdon BC, Dunlop N, Woehler EJ, Dann P. Observed and predicted effects of climate on Australian seabirds. *Emu—Austral Ornithology*. 2016; 111(3):235–51. <https://doi.org/10.1071/mu10033>
20. Both C, Visser ME. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*. 2001; 411:296–8. <https://doi.org/10.1038/35077063> PMID: 11357129
21. Durant J, Hjermann D, Ottersen G, Stenseth NC. Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*. 2007; 33:271–83.
22. Watanuki Y, Ito M, Deguchi T, Minobe S. Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. *Marine Ecology Progress Series*. 2009; 393:259–71. <https://doi.org/10.3354/meps08264> WOS:000272187800022.
23. Ecological Parmesan C. and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*. 2006; 37(1):637–69. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
24. Burke CM, Montevicchi WA. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. *Journal of Zoology*. 2009; 278(4):354–61. <https://doi.org/10.1111/j.1469-7998.2009.00584.x> WOS:000268222100012.
25. Gaglio D, Cook TR, McInnes A, Sherley RB, Ryan PG. Foraging plasticity in seabirds: A non-invasive study of the diet of greater crested terns breeding in the Benguela region. *PLoS ONE*. 2018; 13(1): e0190444. Epub 2018/02/01. <https://doi.org/10.1371/journal.pone.0190444> PMID: 29385167; PubMed Central PMCID: PMC5791960.
26. Crick H, Dudley C, Glue DE, Thomson DL. UK birds are laying eggs earlier. *Nature*. 1997; 38:538.
27. Nussey D, Postma E, Gienapp EP, Visser ME. Selection on a heritable phenotypic plasticity in a wild bird population. *Science*. 2005;310.
28. Chevin L, Lande R, Mace G. Adaptation, plasticity, and extinction in a changing environment towards a predictive theory. *PLoS Biol*. 2010; 8(4):1–8.
29. Chambers LE, Dann P, Cannell B, Woehler EJ. Climate as a driver of phenological change in southern seabirds. *International Journal of Biometeorology*. 2014; 58(4):603–12. <https://doi.org/10.1007/s00484-013-0711-6> WOS:000336329300017. PMID: 23934162
30. Dobson FS, Jouventin P. How slow breeding can be selected in seabirds: testing Lack's hypothesis. *Proc R Soc B*. 2007; 274:275–9. Epub 2006/12/07. <https://doi.org/10.1098/rspb.2006.3724> PMID: 17148257; PubMed Central PMCID: PMC1685855.

31. Weimerskirch H, Louzao M, de Grissac S, ne Del K. Changes in wind pattern alter albatross Distribution and Life-history Traits. *Science*. 2012; 335:211–4. <https://doi.org/10.1126/science.1210270> PMID: 22246774
32. Velarde E, Ezcurra E. Are seabirds' life history traits maladaptive under present oceanographic variability? The case of Heermann's Gull (*Larus heermanni*). *The Condor*. 2018; 120(2):388–401. <https://doi.org/10.1650/condor-17-5.1>
33. Rodriguez A, Arcos JM, Bretagnolle V, Dias MP, Holmes ND, Louzao M, et al. Future directions in conservation research on Petrels and Shearwaters. *Frontiers in Marine Science*. 2019; 6. <https://doi.org/10.3389/fmars.2019.00094>. WOS:000462726300001.
34. Marchant S, Higgins PJ. *Handbook of Australian, New Zealand and Antarctic Birds*. Melbourne, Australia: Oxford University Press; 1990.
35. Roby DD, Place AR. Significance of stomach oil for reproduction in seabirds: An interspecies cross-fostering experiment. *The Auk*. 1997; 114(4):725–36. <https://doi.org/10.2307/4089292> WOS: A1997YA45100019.
36. Roby DD, Ricklefs RE. Energy Expenditure in Adult Least Auklets and Diving Petrels during the Chick-Rearing Period. *Physiological Zoology*. 1986; 59(6):661–78. <https://doi.org/10.1086/physzool.59.6.30158613> WOS:A1986F425200008.
37. Bocher P, Labidoire B, Cherel Y. Maximum dive depths of common diving petrels (*Pelecanoides urinatrix*) during the annual cycle at Mayes Island, Kerguelen. *Journal of Zoology*. 2000; 251:517–24. <https://doi.org/10.1111/j.1469-7998.2000.tb00807.x>. WOS:000089506700011.
38. Fromant A, Bost CA, Bustamante P, Carravieri A, Cherel Y, Delord K, et al. Temporal and spatial differences in the post-breeding behaviour of a ubiquitous Southern Hemisphere seabird, the common diving petrel. *Roy Soc Open Sci*. 2020; 7(11). ARTN 200670 WOS:000595464300001. <https://doi.org/10.1098/rsos.200670> PMID: 33391785
39. Schumann N, Dann P, Hoskins AJ, Arnould JPY. Optimising survey effort for burrow-nesting seabirds. *Association of field Ornithologists*. 2013; 84(1):69–85. <https://doi.org/10.1111/jofo>
40. Gibbs CF, Tomczak M, Longmore AR. The Nutrient Regime of Bass Strait. *Australian Journal of Marine and Freshwater Research*. 1986; 37(4):451–66. WOS:A1986D778900003.
41. Hoegh-Guldberg O, Jacob D, Taylor M, Guillén Bolaños T, Bindi M, Brown S, et al. The human imperative of stabilizing global climate change at 1.5°C. *Science*. 2019; 365(6459):1–11. <https://doi.org/10.1126/science.aaw6974> PMID: 31604209
42. Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver ECJ, et al. A hierarchical approach to defining marine heatwaves. *Prog Oceanogr*. 2016; 141:227–38. <https://doi.org/10.1016/j.pocean.2015.12.014>
43. Harley CDG, Randall Hughes A, Hultgren KM, Miner BG, Sorte CJB, Thornber CS, et al. The impacts of climate change in coastal marine systems. 2006; 9(2):228–41. <https://doi.org/10.1111/j.1461-0248.2005.00871.x> PMID: 16958887
44. Evans R, Lea M-A, Hindell M, Swadling K. Significant shifts in coastal zooplankton populations through the 2015/16 Tasman Sea marine heatwave. *Estuarine, Coastal and Shelf Science*. 2020; 235:106538.
45. Fromant A, Schumann N, Dann P, Cherel Y, Arnould JPY. Trophic niches of a seabird assemblage in Bass Strait, south-eastern Australia. *Peerj*. 2020; 8. ARTN e8700 WOS:000518941800003. <https://doi.org/10.7717/peerj.8700> PMID: 32201643
46. Harding AMA, Welcker J, Steen H, Hamer KC, Kitaysky AS, Fort J, et al. Adverse foraging conditions may impact body mass and survival of a high Arctic seabird. *Oecologia*. 2011; 167(1):49–59. <https://doi.org/10.1007/s00442-011-1971-7> PMID: 21445685
47. Boersma D, Wheelwright N. Egg neglect in the Procellariiformes Reproductive Adaptation in the Fork-tailed Storm Petrel. Oxford University Press. 1979; 81(2):157–65.
48. Ross GJB, Burbidge AA, Brothers N, Canty P, Dann P, Fuller PJ, et al. The status of Australia's seabirds. The state of the marine environment report for Australia technical annex: 1 the marine environment Ocean Rescue 2000 Department of the Environment, Sport and Territories, Canberra Zann LP, Kailola P, eds.; 2001.
49. Schumann N, Dann P, Arnould JPY. The significance of northern-central Bass Strait in south-eastern Australia as habitat for burrowing seabirds. *Emu—Austral Ornithology*. 2014; 114(3):234–40. <https://doi.org/10.1071/mu13048> WOS:000340594800006.
50. Boyd PW, Doney SC, Strzepek R, Dusenberry J, Lindsay K, Fung I. Climate-mediated changes to mixed-layer properties in the Southern Ocean: assessing the phytoplankton response. *Biogeosciences*. 2008; 5(3):847–64. <https://doi.org/10.5194/bg-5-847-2008> WOS:000257303400016.
51. Harper PC. Breeding biology of the fairy prion (*Pachyptila turtur*) at the Poor Knights Islands, New Zealand. *New Zeal J Zool*. 1976; 3(4):351–71. <https://doi.org/10.1080/03014223.1976.9517925>

52. Thoresen AC. Observations on the breeding behaviour of the diving petrel (*Pelecanoides u. urinatrix*) (Gmelin). *Notornis*. 1969; 16(4):241–60. BCI:BCI197006069547.
53. Schumann N, Arnould JPY, & Dann P. Diet of Common Diving-Petrels in Southeastern Australia during Chick rearing. *Waterbirds: The International Journal of Waterbird Biology*. 2008; 31(4):620–4.
54. Manno K, Loh G, Van Heezik Y. Buffering against food availability? The physical environment has little influence on breeding performance of fairy prions (*Pachyptila turtur*). *Austral Ecol*. 2014; 39(5):548–59. <https://doi.org/10.1111/aec.12115>. WOS:000339421000007.
55. Fromant A, Miskelly CM, Arnould JPY, Bost CA. Artificial burrows as a tool for long-term studies of diving petrels. *Polar Biology*. 2020; 43(5):435–42. <https://doi.org/10.1007/s00300-020-02645-y> WOS:000521007900001.
56. Payne MR, Prince PA. Identification and breeding biology of the diving petrels (*Pelecanoides georgicus*) and (*P. urinatrix exsul*) at South Georgia. *New Zeal J Zool*. 1979; 6(2):299–318. <https://doi.org/10.1080/03014223.1979.10428368>. WOS:A1979HE80100009.
57. Saffer VM, Bradley JS, Wooller RD, Meathrel CE. The effect of human activity on the growth rates of Short-tailed Shearwater (*Puffinus tenuirostris*) chicks. *Emu—Austral Ornithology*. 2000; 100(1):49–53. <https://doi.org/10.1071/MU9712>
58. Sagar RL, Cockrem J, Rayner MJ, Stanley MC, Welch J, Dunphy BJ. Regular handling reduces corticosterone stress responses to handling but not condition of semi-precocial mottled petrel (*Pterodroma inexpectata*) chicks. *Gen Comp Endocrinol*. 2019; 272:1–8. Epub 2018/11/13. <https://doi.org/10.1016/j.ygcen.2018.11.004> PMID: 30419229.
59. Dupont SM, Barbraud C, Chastel O, Delord K, Parenteau C, Ribout C, et al. Do repeated captures and handling affect phenotype and survival of growing Snow Petrel (*Pagodroma nivea*)? *Polar Biology*. 2020; 43(6):637–46. <https://doi.org/10.1007/s00300-020-02666-7>
60. Hobday D. Abundance and distribution of Pilchard and Australian anchovy as prey species for the Little Penguin (*Eudyptula minor*) at Phillip Island, Victoria. *Emu—Austral Ornithology*. 1991; 91(5):342–54. <https://doi.org/10.1071/MU9910342>.
61. Pinheiro J, Bates D, DebRoy S, Sarkar DJNI, models nme. R development core team. 2013:3.1–113.
62. Zuur AF, Ieno EN, Elphick CS. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*. 2010; 1(1):3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>. WOS:000288913700002.
63. Mirman D, editor Growth curve analysis: A hands-on tutorial on using multilevel regression to analyze time course data. *Proceedings of the Annual Meeting of the Cognitive Science Society*; 2014.
64. Seress G, Sándor K, Evans KL, Liker A. Food availability limits avian reproduction in the city: An experimental study on great tits (*Parus major*). *Journal of Animal Ecology*. 2020; 89(7):1570–80. <https://doi.org/10.1111/1365-2656.13211>.
65. Regehr HM, Montevecchi WA. Interactive effects of food shortage and predation on breeding failure of black-legged kittiwakes: indirect effects of fisheries activities and implications for indicator species. *Marine Ecology Progress Series*. 1997; 155:249–60.
66. Frederiksen M, Harris MP, Daunt F, Rothery P, Wanless S. Scale-dependent climate signals drive breeding phenology of three seabird species. *Global Change Biology*. 2004; 10(7):1214–21. <https://doi.org/10.1111/j.1529-8817.2003.00794.x>. WOS:000222206300015.
67. Barbraud C, Weimerskirch H. Antarctic birds breed later in response to climate change. *PNAS*. 2006; 103(16):6248–51. <https://doi.org/10.1073/pnas.0510397103> PMID: 16601100
68. Ponchon A, Grémillet D, Christensen-Dalsgaard S, Erikstad KE, Barrett RT, Reiertsen TK, et al. When things go wrong: intra-season dynamics of breeding failure in a seabird. *Ecosphere*. 2014; 5(1):art4. <https://doi.org/10.1890/ES13-00233.1>.
69. Chastel O, Weimerskirch H, Jouventin P. Body condition and seabird reproductive performance: a study of three petrel species. *Ecology*. 1995; 76(7):2240–6.
70. Ropert-Coudert Y, Kato A, Meyer X, Pellé M, MacIntosh A, Angelier F, et al. A complete breeding failure in an Adélie penguin colony correlates with unusual and extreme environmental events. *Ecography*. 2014; 38. <https://doi.org/10.1111/ecog.01182>
71. Jaeger A, Lebarbenchon C, Bourret V, Bastien M, Lagadec E, Thiebot J-B, et al. Avian cholera outbreaks threaten seabird species on Amsterdam Island. *PLoS One*. 2018; 13(5):e0197291. <https://doi.org/10.1371/journal.pone.0197291> PMID: 29847561
72. Chambers LE, Altwegg R, Barbraud C, Barnard P, Beaumont LJ, Crawford RJM, et al. Phenological Changes in the Southern Hemisphere. *PLoS ONE*. 2013; 8(10):e75514. <https://doi.org/10.1371/journal.pone.0075514> PMID: 24098389

73. Evans R, Lea MA, Hindell M. Predicting the distribution of foraging seabirds during a period of heightened environmental variability. *Ecol Appl*. 2021:e2343. <https://doi.org/10.1002/eap.2343> PMID: 33817895
74. Mills JA, Yarrall JW, Bradford-Grieve JM, Uddstrom MJ, Renwick JA, Merila J. The impact of climate fluctuation on food availability and reproductive performance of the planktivorous red-billed gull (*Larus novaehollandiae scopulinus*). *Journal of Animal Ecology*. 2008; 77(6):1129–42. <https://doi.org/10.1111/j.1365-2656.2008.01383.x>. WOS:000260052400008.
75. Young JW, Jordan AR, Bobbi C, Johannes RE, Haskard K, Pullen G. Seasonal and interannual variability in krill (*Nyctiphanes australis*) stocks and their relationship to the fishery for jack mackerel (*Trachurus declivis*) off eastern Tasmania, Australia. *Marine Biology*. 1993; 116(1):9–18. <https://doi.org/10.1007/bf00350726>. WOS:A1993LG62800002.
76. Fromant A, Eizenberg YH, Jessop R, Lec'hvien A, Geeson JJ, Arnould. Colony relocation of Greater Crested Terns (*Thalasseus bergii*) in Bass Strait, south-eastern Australia. 2020; 37:166–71.
77. Sheard K. Taxonomy, distribution and development of the Euphausiacea (Crustacea). BANZ Antarctic Research Expedition Reports, Series B (Zoology and Botany). 1953; 8(1):72.
78. Cochrane K, De Young C, Soto D, Bahri T. Climate change implications for fisheries and aquaculture. 2009.
79. Oliver ECJ, Benthuisen JA, Bindoff NL, Hobday AJ, Holbrook NJ, Mundy CN, et al. The unprecedented 2015/16 Tasman Sea marine heatwave. *Nature Communications*. 2017; 8(1):16101. <https://doi.org/10.1038/ncomms16101> PMID: 28706247
80. Perkins-Kirkpatrick S, King A, Coughon E, Grose M, Oliver E, Holbrook N, et al. The role of natural variability and anthropogenic climate change in the 2017/18 Tasman Sea marine heatwave. *Bulletin of the American Meteorological Society*. 2019; 100(1):105–10.
81. Sandery PA, Kämpf J. Transport timescales for identifying seasonal variation in Bass Strait, south-eastern Australia. *Estuarine, Coastal and Shelf Science*. 2007; 74(4):684–96. <https://doi.org/10.1016/j.ecss.2007.05.011>
82. Ridgway K. Seasonal circulation around Tasmania: an interface between eastern and western boundary dynamics. *Journal of Geophysical Research: Oceans*. 2007; 112(C10).
83. Cresswell G. Currents of the continental shelf and upper slope of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*. 2000; 133(3):21–30.
84. Huang Z, Wang XH. Mapping the spatial and temporal variability of the upwelling systems of the Australian south-eastern coast using 14-year of MODIS data. *Remote sensing of environment*. 2019; 227:90–109.
85. Marra PP, Hobson KA, Holmes RT. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. *Science*. 1998; 282(5395):1884–6. <https://doi.org/10.1126/science.282.5395.1884> PMID: 9836637
86. Jones CW, Phillips RA, Grecian WJ, Ryan PG. Ecological segregation of two superabundant, morphologically similar, sister seabird taxa breeding in sympatry. *Marine Biology*. 2020; 167(4). <https://doi.org/10.1007/s00227-020-3645-7>. WOS:000519214400007.
87. Pakhomov E, McQuaid C. Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biology*. 1996; 16(4):271–86.
88. Barbraud C, Weimerskirch H. Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society B-Biological Sciences*. 2003; 270(1529):2111–6. WOS:000186067000004. <https://doi.org/10.1098/rspb.2003.2488> PMID: 14561273
89. Catry T, Ramos JA, Catry I, Monticelli D, Granadeiro JP. Inter-annual variability in the breeding performance of six tropical seabird species: influence of life-history traits and relationship with oceanographic parameters. *Marine Biology*. 2013; 160(5):1189–201.
90. Camprasse ECM, Sutton GJ, Berlincourt M, Arnould JPY. Changing with the times: little penguins exhibit flexibility in foraging behaviour and low behavioural consistency. *Marine Biology*. 2017; 164(8).
91. Warham J. The petrels: their ecology and breeding systems. London: Academic Press; 1990.
92. Roby DD. Chick feeding in the diving petrels (*Pelecanoides georgicus*) and (*P. urinatrix exsul*). *Antarctic Science*. 1989; 1(4):337–42.
93. Brothers NP. Breeding, Distribution and status of burrow nesting Petrels at Maquarie Island. *Australian Wildlife Research*. 1984; 11(1):113–31.
94. Prince PA, Copestake PG. Diet and Aspects of Fairy Prions Breeding at South Georgia. *Nortornis*. 1990; 37:59–69.

95. Inchausti P, Guinet C, Koudil M, Durbec JP, Barbraud C, Weimerskirch H, et al. Inter-annual variability in the breeding performance of seabirds in relation to oceanographic anomalies that affect the Crozet and the Kerguelen sectors of the Southern Ocean. 2003; 34(2):170–6.
96. Waugh SM, Weimerskirch H, Chereil Y, Prince PA. Contrasting strategies of provisioning and chick growth in two sympatrically breeding albatrosses at Campbell Island, New Zealand. 2000; 102(4):804–13.
97. Weimerskirch H, Zimmermann L, Prince PA. Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. Behavioral Ecology. 2001; 12(1):22–30.
98. Liddle GM. Interannual variation in the breeding biology of the Antarctic prion (*Pachyptila desolata*) at Bird Island, South Georgia. 1994; 234(1):125–39.
99. Chereil Y, Bocher P, De Broyer C, Hobson KA. Food and feeding ecology of the sympatric thin-billed *Pachyptila belcheri* and Antarctic *P. desolata* prions at Iles Kerguelen, Southern Indian Ocean. Marine Ecology Progress Series. 2002; 228:263–81. <https://doi.org/10.3354/meps228263> WOS:000174655000022.
100. Warham J, Watts R, Dainty R. The composition, energy content and function of the stomach oils of petrels (order, Procellariiformes). J Exp Mar Biol Ecol. 1976; 23(1):1–13.
101. Navarro J, Votier SC, Aguzzi J, Chiesa JJ, Forero MG, Phillips RA. Ecological segregation in space, time and trophic niche of sympatric planktivorous Petrels. PLoS ONE. 2013; 8(4): e62897. WOS:000319077300109. <https://doi.org/10.1371/journal.pone.0062897> PMID: 23646155
102. Zhang J, Rayner M, Vickers S, Landers T, Sagar R, Stewart J, et al. GPS telemetry for small seabirds: using hidden Markov models to infer foraging behaviour of Common Diving Petrels (*Pelecanoides urinatrix urinatrix*). Emu—Austral Ornithology. 2019; 119(2):126–37. <https://doi.org/10.1080/01584197.2018.1558997>. WOS:000465179500004.
103. Lindström J. Early development and fitness in birds and mammals. Trends in Ecology & Evolution. 1999; 14(9):343–8. [https://doi.org/10.1016/s0169-5347\(99\)01639-0](https://doi.org/10.1016/s0169-5347(99)01639-0) PMID: 10441307
104. Grémillet D, Welcker J, Karnovsky NJ, Walkusz W, Hall ME, Fort J, et al. Little auks buffer the impact of current Arctic climate change. Marine Ecology Progress Series. 2012; 454:197–206. <https://doi.org/10.3354/meps09590>