



Contribution to the Theme Section 'How do marine heatwaves impact seabirds?'

Marine heatwaves affect breeding, diet and population size but not body condition of a range-edge little penguin colony

B. L. Cannell^{1,2,3,*}, W. L. Kendall⁴, J. A. Tyne³, M. Bunce⁵, Y. Hetzel¹, D. Murray⁶,
B. Radford^{1,7,8}

¹Indian Ocean Marine Research Centre, University of Western Australia, Crawley, 6009 WA, Australia

²School of Biological Sciences, University of Western Australia, Crawley, 6009 WA, Australia

³College of Science, Health, Engineering and Education, Murdoch University, Murdoch, 6150 WA, Australia

⁴US Geological Survey, Colorado Cooperative Fish and Wildlife Research Unit, Colorado State University, Fort Collins, CO 80523, USA

⁵Department of Conservation, Te Papa Atawhai, Wellington 6011, New Zealand

⁶Trace and Environmental DNA Laboratory, Curtin University, Bentley, 6102 WA, Australia

⁷The Australian Institute of Marine Science, University of Western Australia, Crawley, 6009 WA, Australia

⁸School of Agriculture and Environment, University of Western Australia, Crawley, 6009 WA, Australia

ABSTRACT: Significant marine heatwaves (MHWs) developed along the Western Australian coast in 1999 and 2011. Despite ecosystem losses and the southwards occurrence of many tropical fish species during and after the extreme MHW in 2011, there have been few studies on the effects of this MHW on seabirds, and no biological impacts related to the 1999 MHW have been reported. Using data from 1986–2019, we investigated the impacts of these events on breeding outcomes, body condition, diet composition, population size and mortality of little penguins on Penguin Island, in the temperate waters off Western Australia. Breeding outcomes were negatively impacted by the MHWs but body condition was not. Diet composition changed after the MHW, with sandy sprat *Hyperlophus vittatus*, the penguins' typical major prey component, replaced by scaly mackerel *Sardinella lemuru*, a tropical fish species. Using an open robust design analysis that accounts for imperfect capture probabilities and staggered annual arrival and departure dates, we found that the population decreased by 80% following the 2011 MHW. Finally, more penguins died from starvation or from novel protozoal parasitic infections in 2011 and 2012 that were potentially introduced with the changed diet. This research highlights that the temporal and spatial influence of MHWs on seabirds depends on several factors. Furthermore, the magnitude and direction of a prey species' response can be very localised and have significant impacts on avian predators. There are no obvious ways to mediate climate effects, but perhaps measures taken to reduce any synergistic impacts on prey abundance, particularly during MHW events, could be effective.

KEY WORDS: Mark–recapture · Population decline · Seabirds · Starvation · Protozoa · SST

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1. INTRODUCTION

Marine heatwaves (MHWs) are periods of anomalously warm ocean temperatures at a particular location (Oliver et al. 2021). MHWs have increased in in-

tensity, duration and frequency globally over the past century, a trajectory that is predicted to continue in the future (Oliver et al. 2018). MHWs are discrete events that can cause rapid shifts in the ecosystem (Smale et al. 2019) but they can also have enduring

*Corresponding author: belinda.cannell@uwa.edu.au

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ecosystem impacts (Suryan et al. 2021). For example, the abundance of surface-feeding and diving seabirds declined for 5 yr after the 2014–2016 Northeast Pacific MHW. However, not all seabirds and other taxa have shown a negative trend (Suryan et al. 2021). The magnitude of these impacts depends on the cascading effects of the thermal tolerance ranges of the species within an ecosystem (Burrows et al. 2019). Moreover, thermal tolerances for species at the warm trailing edge of their distribution are more likely to be exceeded during MHWs (Smale et al. 2019, Smith et al. 2022).

An extreme MHW developed along the Western Australian coast in 2011 (Pearce et al. 2011, Hobday et al. 2018). It was associated with one of the strongest recorded La Niña events that occurred in Western Australia in 2011 (Feng et al. 2013, 2021, Benthuisen et al. 2014) and resulted in a near-record-strong Leeuwin Current in February (late austral summer) (Pearce et al. 2011, Pearce & Feng 2013), which is unusual for that time of year. At the same time, winds were also weaker than normal and there were positive atmospheric heat flux anomalies. This atypical mix of events resulted in inshore and offshore sea surface temperatures (SSTs) increasing by up to 5°C above average along the Western Australian coast (Pearce et al. 2011, Pearce & Feng 2013, Benthuisen et al. 2014). During this extreme MHW, there were noted species losses, including corals, seagrasses, kelp forests, fish and invertebrates (Thomson et al. 2011, Abdo et al. 2012, Smale & Wernberg 2012, Wernberg et al. 2016), and unusual southwards occurrences of many tropical species (Pearce et al. 2011, Wernberg et al. 2013, 2016, Lenanton et al. 2017). The only mention of the impacts of the MHW on seabirds involved the body mass of little penguins *Eudyptula minor* on Penguin Island, Western Australia (Cannell et al. 2019), a colony 50 km south of Perth, at the western and northern range edge of their distribution (Marchant & Higgins 1990). The body mass of both females and males was lighter in 2011 than in previous years (Cannell et al. 2019). Whilst not directly alluding to the MHW, Cannell et al. (2012) also noted that above-average SST and a strong Leeuwin Current in 2011 resulted in poorer hatching and fledging success, a low number of chicks per pair and a shorter breeding season of the Penguin Island penguins.

The negative influence of the elevated SSTs in 2011 on the little penguins on Penguin Island was not entirely unexpected, given that warmer oceans have been associated with poorer body condition, smaller mass of food samples collected by water offloading and a higher proportion of penguins returning to the island

with empty stomachs (Wienecke et al. 1995). Additionally, using breeding data from 1986–2008, above-average SSTs in April and May in any year corresponded to poorer breeding outcomes that year (Cannell et al. 2012). This is notable, given that little penguins on Penguin Island breed asynchronously, laying eggs in any month from April–November (Wooller et al. 1991, Cannell et al. 2012). Therefore, it is concerning that high ocean temperatures prior to or early in the breeding season were correlated with poorer breeding outcomes for that year. For penguins to breed successfully, there must be an abundance of prey fish within the 25–30 km foraging distance of the colony during chick rearing (Bradley et al. 1997, Collins et al. 1999, Chiaradia et al. 2010, Cannell 2016, 2019). It has therefore been proposed that elevated SSTs during this pre-breeding period, or other oceanographic variables related to the elevated SSTs, affect the availability of the penguins' fish prey near the colony, possibly for the entire breeding season (Cannell et al. 2012).

Little penguins are considered generalist predators (Cullen et al. 1992), but the diet composition of the penguins from Penguin Island has been found to vary with breeding stage. Prior to egg laying, when the penguins can forage further afield (Bradley et al. 1997), their diet was more diverse. It often included pilchards *Sardinops sagax*, garfish *Hyporhamphus melanochir*, anchovy *Engraulis australis*, and blue sprat *Spratelloides robustus* but few sandy sprat *Hyperlophus vittatus*, whereas sandy sprat dominated the diet during chick rearing (Klomp & Wooller 1988, Wienecke 1989, Wooller et al. 1991, Connard 1995, Bradley et al. 1997, Murray et al. 2011). The dominance of sandy sprat during chick rearing parallels their increased presence near the colony from June–November (Gaughan et al. 1996, Valesini et al. 1998). Should the presence and/or abundance of sandy sprat change, then the penguins could have poorer breeding participation or outcomes. Such a scenario occurred following widespread mortality of pilchard, one of the major components of the diets of little penguins on Phillip Island, Victoria (Chiaradia et al. 2010).

Food resources not only influence the current and future population of the penguins within the colony but also the penguins' timing of breeding and the length of time they reside within the colony; i.e. staying for shorter periods if food resources are scarce and breeding attempts are abandoned. The probability of penguins persisting in a colony, the seasonal timing of their arrival and departure, and temporal changes in the abundance of a population are among the demographic factors that can be determined using mark-recapture models (e.g. Pollock et al. 1990, Pollock 1991,

Krzystan et al. 2018, Kendall et al. 2019, English et al. 2022).

Whilst the Western Australian extreme MHW peaked in March 2011, it lasted for 66 d (Hobday et al. 2018) and above-average SSTs persisted for multiple years (Feng et al. 2021). Widescale marine ecosystem and fisheries changes were reported for multiple years following the MHW (Wernberg et al. 2013, Caputi et al. 2019), even after the waters were cooler in 2016. Previously, Western Australia experienced a severe MHW in 1999 that lasted for 132 d and peaked in July (Hobday et al. 2018), but unlike the 2011 MHW, no biological impacts related to this event have been reported (Hobday et al. 2018, Kajtar et al. 2021). As such, we do not know if any long-term impacts to the marine ecosystem were associated with this MHW. Here, we report the effects of MHWs on the little penguins of Penguin Island, thus broadening our knowledge of the im-

pacts of severe and extreme MHWs on seabirds. We hypothesised that the MHWs in both 1999 and 2011, and the persistent elevated SSTs for multiple years after 2011, impacted the body condition, breeding participation and breeding success of the penguins. Using a combination of historical regurgitant data and faecal DNA analysis, we also evaluated the hypothesis that the diet composition of the penguins changed because of the 2011 MHW and the persistent elevated SSTs. We used necropsies of penguins to determine whether the 2011 MHW was associated with changes in mortality due to starvation. Furthermore, we investigated whether a high incidence of protozoal parasites in dead penguins in 2011 and 2012 (Cannell et al. 2013, Campbell et al. 2022) was associated with ecosystem changes related to the MHW. As changes in breeding outcomes and prey abundance can influence population size, we further hypothesised that the little penguin population would decrease during the MHW. Finally, little penguins recruit to their natal colony at 2–3 yr of age (Dann & Cullen 1990) and, as chick survival influences population growth (Sandvik et al. 2012, Sydeman et al. 2021), we predicted that the population would decline not only during the MHW but for 3 yr following the event.

2. MATERIALS AND METHODS

2.1. Study species, breeding data and body condition

This study was conducted on Penguin Island, Western Australia ($32^{\circ} 18' S$, $115^{\circ} 41' E$) (Fig. 1). Little penguins *Eudyptula minor* do not dig burrows on this island, as the sandy substrate is too friable (Klomp et al. 1991). Rather, they nest under bushes of *Tetragonia decumbens* or *Rhagodia baccata* (Dunlop et al. 1988) as well as in nestboxes that were first placed around the island in 1986 (Klomp et al. 1991). Their breeding season typically occurs from April–December (Wooller et al. 1991, Cannell et al. 2012). They usually lay 2 eggs (Reilly & Cullen 1981, Wooller et al. 1991), which are incubated for 5–6 wk. Chicks are guarded for 2–3 wk after hatching and fledge at approximately 8 wk of age (Reilly & Cullen 1981, Chiaradia & Nisbet 2006). Both parents share incubation and chick-rearing duties (Reilly & Cullen 1981, Chiaradia & Nisbet 2006). During incubation, the penguins take turns foraging at sea. During the guard phase, the penguins alternate between guarding the chicks and foraging for typically 1–2 d (Collins et al. 1999, Chiaradia & Nisbet 2006, Cannell

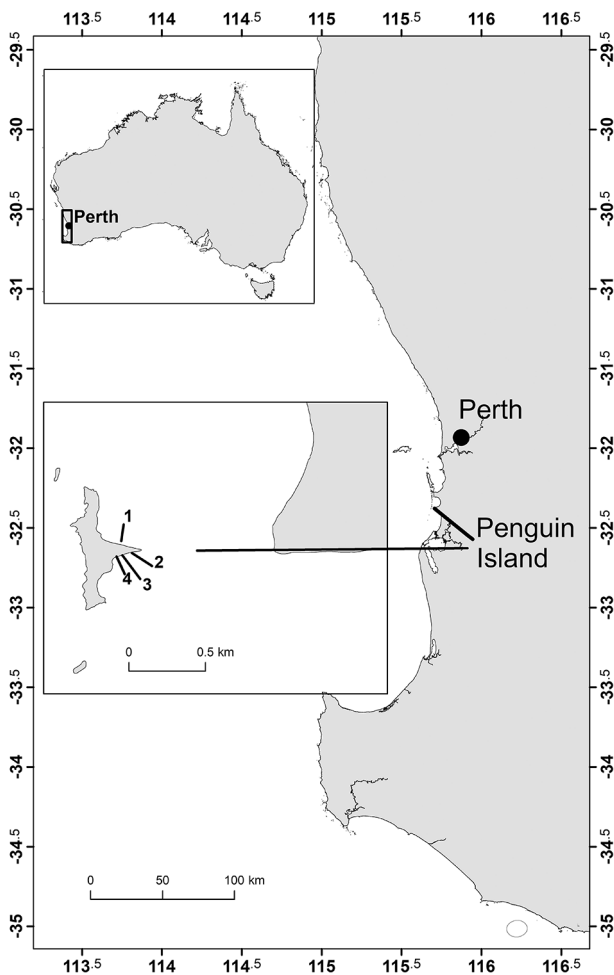


Fig. 1. Penguin Island, Western Australia ($32^{\circ} 18' S$, $115^{\circ} 41' E$) (middle inset), in relation to Perth (main map) and Australia (upper inset), showing the 4 mark–recapture sites (1–4)

2016, 2019). The penguins can lay up to 3 clutches in a breeding season, and can raise 2 clutches under favourable conditions (Reilly & Cullen 1981, Wienecke 1993). In the austral summer, the penguins undergo a complete moult. This takes 2–3 wk, during which time the penguins are not waterproof and therefore cannot forage at sea. Thus, they accumulate fat stores before moulting, often doubling their weight (Reilly & Cullen 1983).

The nestboxes on Penguin Island have been monitored regularly since their instalment in 1986, except for 1993 (when adult body condition information was collected but not breeding data), 2004 and 2005. Excluding these years, the boxes were monitored on average (\pm SD) every 8 ± 6 d (total number of visits: 1069) during the breeding season from 1986–2019. The presence of adults, eggs and chicks was noted on each visit as well as adult identity (from flipper bands or microchips on adults that were marked when first encountered), chick identity (if appropriate, with chicks marked at approximately 6 wk of age) and mass of both adults and chicks. Microchips were read with a portable reader (Iso Max IV, scanning distance up to 30 cm; Novartis Animal Health). Adults and chicks were weighed in a calico bag to the nearest 10 g with 2 kg (\pm 10 g) scales (Salter Scales). Bill length and depth (at the gonys) were obtained for all adults with known identification. Owing to the loss and addition of nestboxes, the number of nestboxes checked each year has varied (1986–2003: 47–70; 2006–2019: 92–129).

We investigated 4 measures of breeding success: (1) breeding participation (the proportion of nestboxes checked with breeding attempts and, as penguins can lay up to 3 clutches yr^{-1} , the proportion of the total number of all breeding attempts in the nestboxes checked); (2) hatching success (i.e. the percentage of eggs that hatched); (3) overall breeding success (i.e. the percentage of chicks fledged / eggs laid); and (4) the anomalies, or deviation from the mean, of the number of chicks produced per pair (CPP). As there were several consecutive years of above-average SSTs and potential long-term changes to the marine ecosystem, mean CPP was calculated from 1986–2010, excluding 1999 (MHW). We also investigated the annual peak timing of egg laying. We determined the annual body condition index of non-moulting males and females using the formula $\log_{10}(\text{mass}) / \log_{10}(\text{culmen length} \times \text{bill depth at gonys})$ (Nicholson 1994). The sex of all captured penguins was determined using bill depth measurements, with males more likely to have a bill depth of >13.0 mm (Wienecke 1993). Given that there is some

overlap in bill depth, we also used bill shape (males have a more pronounced hook) and the sex of a known partner to confirm the sex of an adult where necessary. Body condition data were not available for penguins monitored in 1987 and 1988.

2.2. Diet composition

Two methodologies have previously been used to determine the diet composition of little penguins on Penguin Island. Firstly, stomach contents (regurgitants) were collected sporadically from 1986–1997 using copper emetics or stomach flushing with saline water. Data from 1986 (February–December, $n = 212$), 1989 (April–September, $n = 108$) and 1995 (April–September, $n = 147$) were obtained from Klomp & Wooller (1988), Wienecke (1989) and Connard (1995), respectively. Data from 1996 (September–November, $n = 44$) and 1997 (February–November, $n = 94$) were obtained from Bradley et al. (1997). All regurgitant data are shown but were not used in any statistical analyses, as there are no individual data.

Faecal samples were collected for DNA analysis from little penguins in the Perth region from 2008–2012. Methods for the collection and analysis of samples from 2008–2010 were previously described and included (1) PCR amplification using universal primers with subsequent cloning and sequencing of amplicons; (2) quantitative PCR using species-specific primers and (3) High-Throughput Sequencing (HTS) or metabarcoding approaches (Murray et al. 2011). In the study by Murray et al. (2011), samples were collected from both adults and chicks on both Penguin and Garden islands from 2008–2010. Garden Island is 7 km north of Penguin Island, but as the foraging area of the birds from Garden Island is in a different embayment (Cockburn Sound) with different prey resources (B. L. Cannell unpubl. data), the resultant diet composition within the samples differs. Additionally, little penguins nesting on the NE side of Penguin Island tend to forage north of the island, whilst those on the SE and SW sides of the island forage south of the island (e.g. Cannell 2016, 2019). Therefore, we only considered samples from penguins that were likely to be foraging south of Penguin Island, and we re-analysed the diet composition accordingly. We used the methodology described by Murray et al. (2011), but only considered the results of 2 of the 3 methods: (1) PCR amplification with subsequent cloning and sequencing of amplicons, undertaken on samples collected in 2008 and 2009 only; and (2) HTS, undertaken on samples

collected in 2010–2012. Furthermore, cloning analyses were conducted only on 4 of the appropriate 8 samples collected in 2008 and are therefore not included in this re-analysis. Thus, the total number of samples and months in which they were collected each year that met our criteria were as follows: 2009: $n = 16$ (May–August); 2010: $n = 48$ (October–December); 2011: $n = 76$ (July–October); and 2012: $n = 53$ (July–December).

For both the regurgitant and DNA analyses, prey were identified to species level if possible; otherwise, to the next highest taxonomic rank. For each prey taxon within the regurgitant samples, the numerical abundance (%N) was calculated; i.e. (total number of items of a particular prey taxon / total number of all prey items found in the collected samples) $\times 100$. Additionally, for the DNA analysis samples, we determined the proportion of the 5 most prevalent species in 2009–2012 (i.e. pilchard *Sardinops sagax*, anchovy *Engraulis australis*, sandy sprat *Hyperlophus vittatus*, blue sprat *Spratelloides robustus* and scaly mackerel *Sardinella lemuru*) in each of the samples (sensu Murray et al. 2011).

2.3. Key demographic parameters

Population size was estimated for 2007, 2008, 2010, 2011, 2017 and 2019. For each year, we used mark–recapture at 4 arrival sites (Sites 1–4; Fig. 1), previously identified as having the greatest number of penguins arriving on any night. Importantly, little penguins not only land at the arrival site closest to their nest site but also display high fidelity to an arrival site (Cannell et al. 2011). The penguins were caught at Sites 1–4, one site per night for 4 consecutive nights, using an identical fence and corral setup at each site (Cannell et al. 2011). There was equal capture effort at all sites, and the captured penguins were checked for flipper bands or microchips. Each set of 4 nights is hereafter referred to as a session, and there were 4 sessions in all years except 2007, when only 3 sessions were conducted (dates are shown in Table S1 in the Supplement at www.int-res.com/articles/suppl/m737p193_supp.pdf). To obtain an island-wide population estimate, arriving penguins were counted at most available landfall sites around Penguin Island, with 4 of the sites corresponding to Sites 1–4. Royal Australian Navy night vision monoculars were used to assist in correctly observing the penguins, ensuring that each counter was able to see penguins clearly within at least a 40 m radius. The counts were conducted around the

first quarter moon phase, from sunset to 2 h after civil twilight, when the sun is at a depression angle of 6° below an ideal horizon (www.ga.gov.au/earth-monitoring/geodesy/astronomical-information/astronomical-definitions.html). We determined the proportion of penguins counted that arrived at Sites 1–4 and used this data to inflate the population estimate for the whole island (see Cannell et al. 2011 for further details of the capture methodology and formulae for determining the whole-island estimate). We also used the counts at Sites 1–4 to investigate the possibility of different impacts of the MHW on the penguins' northern or southern foraging grounds (Text S1).

As little penguins breed asynchronously, the birds coming ashore during the mark–recapture sessions could be pre-breeding adults involved in courtship or pre-laying attendance, partners of penguins incubating eggs or guarding chicks, or have post-guard-phase chicks. As the beach captures coincided with breeding and encompassed approximately a 6 wk block, we were likely to catch penguins that were involved in 2 or 3 of these breeding stages. In addition to breeding birds, both juveniles and non-breeding adults could be caught (Dann & Cullen 1990, Sutherland & Dann 2012). However, as only a few chicks are marked at fledging and juveniles are similar in appearance to adults, it is not possible to identify any unmarked bird as either a juvenile (1–2 yr old) or an adult (≥ 3 yr old). Thus, the population sampled during the mark–recapture is composed of breeding adults, potential breeders and sexually immature penguins.

2.4. Penguin necropsies

We conducted necropsies on penguins to investigate annual differences in the number of birds considered to have died either from starvation, as determined by poor body condition, lack of ingesta, absence of lesions and/or low adult body weight (Cannell et al. 2016), or from protozoal parasites (see Text S2 for a detailed description of the collection and necropsy procedure).

2.5. Data analyses

2.5.1. Environmental covariates

The covariates for potential inclusion in models were chosen based on their immediate or lagged

potential influence on fish production or that had been previously reported to influence little penguin breeding (Cannell et al. 2012) (Table S2). These included SST, the Southern Oscillation Index (SOI), winter and annual rainfall, the Fremantle Sea Level (FSL; a proxy for the strength of the Leeuwin Current), the north–south component of the wind (a proxy for the strength of the Capes Current) and the number of summer days when the southerly winds were $>7 \text{ m s}^{-1}$. We also included the catch per unit effort of commercially caught baitfish as an index of fish abundance (Table S2).

2.5.2. Breeding data and body condition

We investigated differences in breeding outcomes for periods before the MHW (1986–2010 but not including 1999, the year of a severe MHW) and after (2011–2019, including 1999) using independent sample *t*-tests (or Welch's *t*-test if the variances between groups were unequal), with a logit transformation for proportion/percentage data. We conducted this analysis using the function 't.test' in R version 4.0.5 (R Core Team 2021). We used a univariate random forest (RF) regression model to determine the variables that influenced breeding participation, overall breeding success and the body condition of the adult penguins, as well as the relative contributions of each variable. RFs use all available variables in the construction of the response variable and can identify a number of different patterns, including step-wise and curvilinear relationships (Breiman 2001). Each tree is generated with a bootstrapped subset of the samples. We used 70% of the data to generate the tree, and 30% was left out for validation with out-of-bag prediction. We optimised all models using the function 'tuneRF' in the package 'randomForest' (Liaw & Wiener 2002) to set the 'mtry' argument (i.e. the number of variables to try at each split) and ensured the errors had stabilised with the number of trees used in the model. We then used the function 'rfe' in the package 'caret' (Kuhn 2021) in the optimised model to backwards-select the top predictors, based on predictor importance ranking, that capture most of the model variance. To assess which variables had the greatest influence on the dependent variables, we determined the variable importance (% increased mean square error) of each independent variable. This measures the performance of the model with and without the variable in it (Ishwaran et al. 2021).

Partial dependence plots of the top predictors were then constructed. For the breeding participation and breeding success models, we used 24 environmental variables (Table S2) and the year in which the breeding occurred. We generated 1000 trees, and 4 and 5 variables were used at each split (for breeding participation and breeding success models, respectively). We used a binary response variable; i.e. breeding participation (eggs laid or not) or breeding success (chicks successfully raised or not). For the body condition model, we used sex of the penguin, date the body condition was measured and 26 environmental variables as the predictor variables (Table S2). We generated 500 trees, and 7 variables were used at each split.

2.5.3. Diet composition

We used a multivariate RF regression model to determine the environmental variables that influenced diet composition in 2009–2012 and their relative importance. We used 20 environmental variables as predictors (Table S2) but substituted the north–south wind component (a proxy of the Capes Current) with the monthly mean along-shore volume transport inshore of the continental shelf break ($\text{m}^3 \text{ s}^{-1}$, derived from the OzROMS ocean circulation hindcast; Wijeratne et al. 2018), with positive values representing the wind-driven northward flow of the Capes Current (Pearce & Pattiaratchi 1999). This was because the along-shore volume transport data were only available for a limited time period, including 2009–2012. The response variables were the proportions of each of the 5 major fish prey in each sample. We used the function 'rfsrc' in the package 'randomForestSRC' (Ishwaran & Kogalur 2022). We ran models using 500 trees, with 2 environmental variables considered at each split, and a minimum terminal node was set to $n = 5$. The models were checked for convergence by plotting the number of trees incrementally against model error to make sure that the plot asymptotes.

2.5.4. Model performance

To evaluate the performance of all the RF models, we either obtained an out-of-bag explained variance value for continuous variables or a confusion matrix, accuracy and Kappa values for ordinal and nominal variables. We used the package 'caret' to obtain the

confusion matrix, which details the model's accuracy, measured as the percent of correct classification, and Cohen's Kappa statistic, K (Cohen 1960), a measure of the agreement between predicted and observed values.

2.5.5. Key demographic parameters

To estimate abundance for the beaches where captures were conducted, we used an open robust design analysis that accounts for imperfect capture probabilities and staggered arrival and departure dates (Kendall et al. 2019) for each breeding season to determine the population estimate each year. This was necessary for the determination of the island-wide population estimate, as we found the fraction of penguins using arrival Sites 1–4 varied between years. Given that penguins have high fidelity to an arrival site, this means that the number of penguins returning to specific areas of the island varied between years. The modelled parameters included the probability of entering the colony for the first time in a given session ($pent$), the probability of capture (p) for those that are present in a given session and the probability of persisting at the colony from one session to another (φ). We included models in which p was constant between sessions or varied with time (when both $pent$ and p were session-dependent, we set $p_1 = p_2$ because p_1 cannot be estimated separately; Schwarz & Arnason 1996). The $pent$ either varied with time or was the same for each session. As it takes approximately 13 wk from egg lay to chick fledge, we assumed that once a penguin had been captured in the colony it is reasonable to expect it will be caught again, unless it is not a breeding penguin. However, given the asynchronous nature of the penguins' breeding, the probability of a penguin being captured within all sessions is dependent on when its clutch was laid. Therefore, we modelled φ to be constant over all the sessions, to vary over time or to be dependent on when it arrived (e.g. a penguin will be less likely to depart shortly after its egg is laid than shortly before its chick fledges). We also considered models in which there were arrivals but no departures, only departures but no arrivals or no arrivals or departures (i.e. the population was closed) over all sampling sessions.

In addition to the population estimate, the model derived parameters of (1) intensity of availability (the probability that an individual in year t is present and available for detection in capture session j); (2) mean

residence time; and (3) expected arrival and departure times.

Model selection was based on the Akaike information criterion corrected for small sample sizes (AIC_c) (Burnham & Anderson 2004), and model averaging was used to address model selection uncertainty. We used the median c -hat procedure in Program MARK (White & Burnham 1999) to estimate the overdispersion parameter, c , for the global model. When $c > 1$, the median c -hat estimate was used to adjust the AIC model selection metric (and report $QAIC_c$). Model assumptions were homogeneity of detection of individuals that are present, no effect of tagging on the penguins, tags are not lost and mortality does not occur among mark–recapture sessions. The models were constructed and run in program MARK v.6.2 (White & Burnham 1999).

As the island-wide abundances were based on a combination of marked individuals and the fraction of the population sampled by the mark–recapture study, to determine the change in the population each year, we used:

$$\lambda = N_{(t+1)} / N_{(t)}$$

where $N_{(t+1)}$ = the population estimate at time $t + 1$ and $N_{(t)}$ is the population estimate at time t . The variance of the estimator was derived using the delta method.

We determined the difference in the percentage of penguins arriving at each of the 4 mark–recapture sites using 2-sample t -tests (or Welch's t -test if the variances between groups were unequal), with a logit transformation for proportion/percentage data. We used the function 't.test' in R (R Core Team 2021).

3. RESULTS

3.1. Breeding data and body condition

The lowest participation in breeding by little penguins occurred in 2011 (extreme MHW) and 2019, with breeding attempts in only 18 and 13% of the nestboxes, respectively (Fig. 2). Before the 2011 MHW, below-average breeding participation occurred in 1986 (first year the nestboxes were introduced on the island), 1999 (severe MHW) and 2002. The average proportion of breeding attempts by the penguins was significantly greater before the 2011 MHW, with $54 \pm 11\%$ from 1986–2010 (not including 1999, as it was an MHW year) compared to $28 \pm 8\%$ after the MHW (including 1999) ($t_{28} = 6.2543$, $p < 0.001$). The optimal RF model for breeding partic-

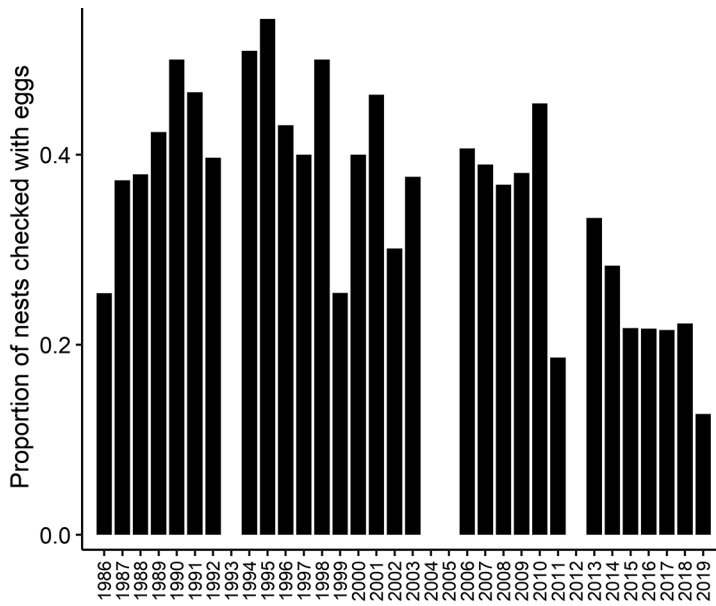


Fig. 2. Breeding participation of little penguins on Penguin Island, Western Australia, each year from 1986 to 2019 (no data for 1993, 2004, 2005 and 2012). As the number of nestboxes available to be checked varied in some years, the participation is the proportion of the number of nestboxes checked in which breeding occurred

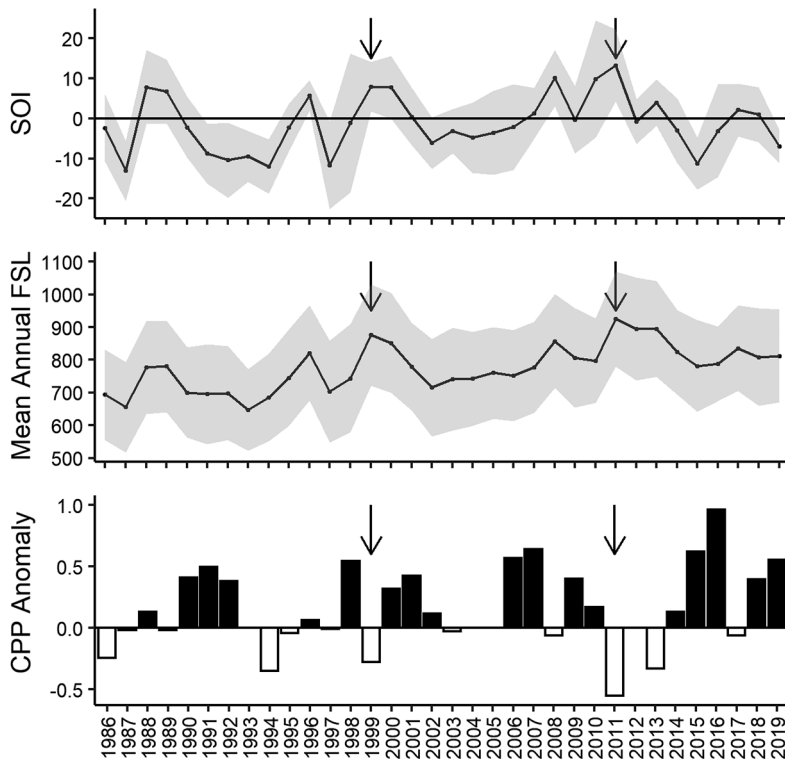


Fig. 3. Annual Southern Oscillation Index (SOI); Fremantle Sea Level (FSL) anomaly, which has been linearly detrended to remove the long-term sea level rise; and the number of chicks per pair (CPP) relative to the long term mean (1986–2010, i.e. prior to the extreme marine heat wave [MHW] in 2011 and excluding the severe MHW in 1999) for little penguins on Penguin Island, Western Australia, from 1986–2019. Shading around the SOI and FSL anomaly indicates ± 1 SD. There are no CPP anomaly data for 1993, 2004, 2005 and 2012. Arrows: years of the MHW in 1999 and 2011

icipation had an overall accuracy of 0.62 (95% CI = 0.58–0.65) and a K statistic of 0.24. More penguins participated in breeding as the baitfish caught in the SW region increased, the mean annual FSL < 825 mm, when winter rainfall the previous year was >400 mm and the mean winter FSL was 800–875 mm (Figs. S1 & S2).

The lowest CPP occurred during the MHW in 2011 (0.23) and the greatest was in 2016 (1.74). The CPP was below average in the MHW years, i.e. 1999 and 2011, as well as in 1994 and 2013 (there are no breeding data for 1993, 2004, 2005 and 2012). All 4 of these years coincided with elevated FSL (Fig. 3) and above-average SST over most of the year (Fig. 4) but only 3 coincided with positive SOI (Fig. 3). Conversely, the CPP was above average in 9 of the 13 years in which the SST was lower than average (Figs. 3 & 4). However, not all years of positive SOI or above-average SST had below-average CPP (Figs. 3 & 4).

Furthermore, the years of the lowest CPP and overall breeding success did not always coincide with the lowest percentage of eggs that hatched. For example, a greater percentage of eggs hatched during the MHW in 2011 (51%) than in both 1997 (41%) and 2017 (43%) (Fig. 5) and yet the CPP in 1997 and 2017 was just below average and much greater than the CPP for 2011 (Fig. 3). Conversely, years with a higher percentage of eggs hatching did not always have high overall breeding success; e.g. the percentage of eggs that hatched in 2014, 2015 and 2016 was equivalent but overall breeding success varied from 40% in 2014, 50% in 2015 and 67% in 2016 (Fig. 5). There was no difference in either the percentage of eggs that hatched or the overall breeding success before and after the MHW ($t_{11.04} = -0.707$, $p = 0.494$; $t_{9.36} = 0.291$, $p = 0.777$, respectively). This was despite the hatching and overall breeding success during the MHWs in 1999 and 2011 either being the lowest, or amongst the lowest, recorded (Fig. 5).

The peak month of egg laying varied annually, as it occurred in any month from May to September, with

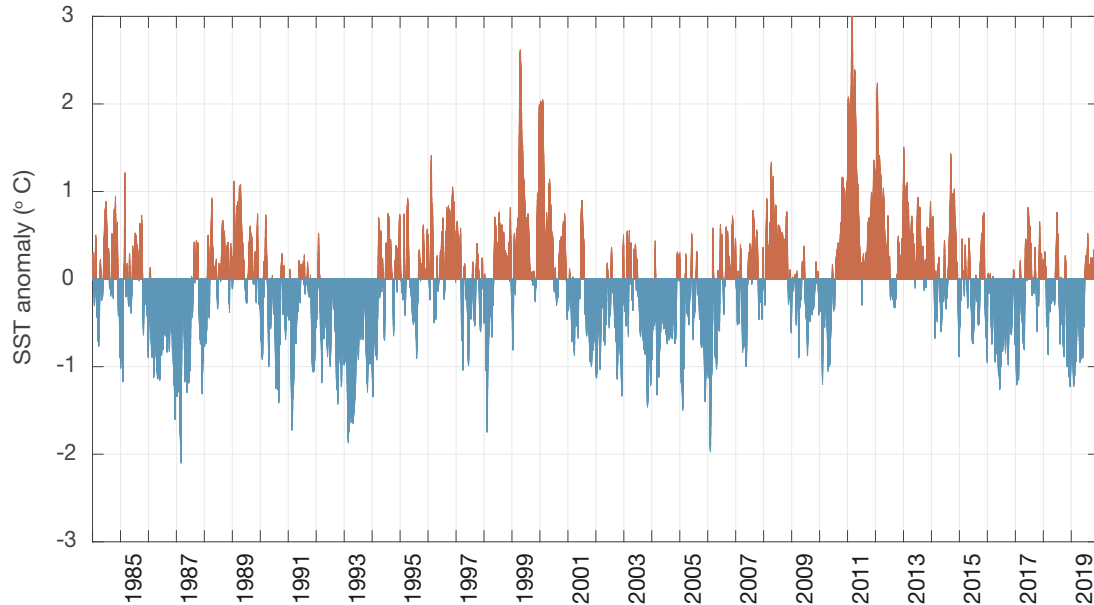


Fig. 4. Sea surface temperature (SST) anomaly for a box bounded by 115° – $115^{\circ}15'E$, $32^{\circ}30'$ – $31^{\circ}30'S$ for 1984–2019. Daily SST anomalies were calculated against a 1993–2016 climatology using 5 km gridded daily European State Agency CCI v.2 SST data (Merchant et al. 2019). These were then averaged over the entire box and smoothed using a 10 d running mean. Data were retrieved from the Copernicus Climate Data Store (<https://doi.org/10.24381/cds.cf608234>)

peak egg laying in June or July being most common (i.e. in 16 of the 29 years; Fig. S3). For a detailed description of the timing of peak egg laying and breeding success as well as the influence of the 2011 MHW on peak egg laying, see Text S3.

The optimal RF model for breeding success had an overall accuracy of 0.58 (95 % CI = 0.52–0.63) and a K statistic of 0.15. The breeding success was greater when the mean SST in April was $<22.5^{\circ}\text{C}$, mean winter FSL was <875 mm, there was greater variance in the SOI and less variance in the April SST (Figs. S4 & S5).

The best RF model for annual variation in the body condition of the non-moulting penguins did not perform well, with an out-of-bag explained variance of 27%. The top 5 variables, in decreasing order of variable importance, were sex, date when the adult was measured, mean FSL during the moult period (i.e. from December in the preceding year to February of the year the adult was measured), mean FSL during the pre-breeding period of the year the adult was measured (i.e. from March–May) and strength of the Capes Current in January the year the adult was measured (Fig. S6). The body condition of the non-moulting females was better than the males and, for both sexes, their body condition was only slightly improved between 2006 and 2010 (Figs. 6 & S7). The other 3 variables showed little variation despite being in the top 5 predictors (Fig. S7).

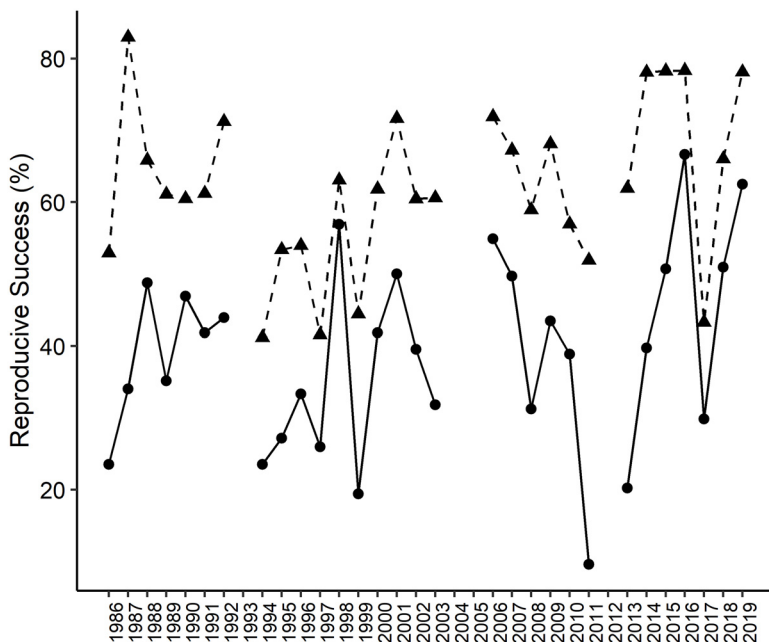


Fig. 5. Annual percentage of little penguin eggs that hatched (\blacktriangle) and overall breeding success (i.e. [percentage of chicks fledged]/[eggs laid]; \bullet) of little penguins on Penguin Island, Western Australia, from 1986–2019. There are no data for 1993, 2004, 2005 and 2012

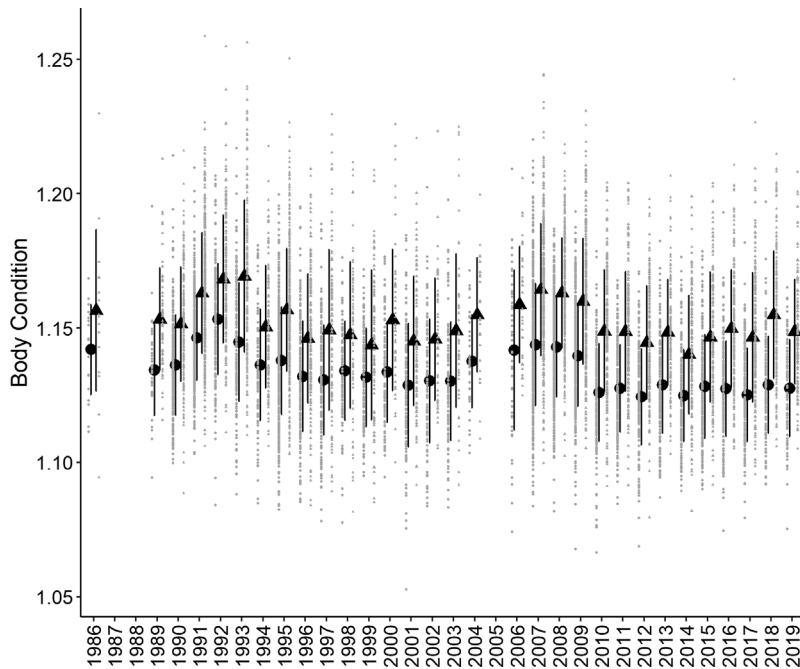


Fig. 6. Non-moulting mean body condition index (\pm SD) of male (●) and female (▲) little penguins on Penguin Island, Western Australia, from 1986 to 2019, overlaid on the data points for individual birds each year. There are no data for 1987, 1988 and 2005

3.2. Diet composition

A total of 30 fish taxa, 3 cephalopods and 5 crustaceans were identified from the regurgitant and faecal samples (Table S3). Sandy sprat *Hyperlophus vittatus* only comprised a small proportion of the diet in 1989, and were not observed at all in 2011. Garfish *Hyporhamphus melanochir* were not observed in any samples collected after 1997. Pilchard *Sardinops sagax* and anchovy *Engraulis australis* were observed in all years; however, the contribution of pilchard to the diet during only the breeding season (1996, 2009–2012) was greater after the MHW (Table S3, Fig. 7). Scaly mackerel *Sardinella lemuru* were rarely observed in the diet before the MHW (Table S3, Fig. 7), and tropical species such as fivespot herring *Hilsa kelee* and western striped grunters *Pelates octolineatus* were only observed following the MHW in 2011 and in 2012 (Table S3, Fig. 7).

Of the samples collected for DNA analysis, sufficient DNA (and prey species) were recovered from 88% of the samples collected in 2009 (using the cloning approach) and in 50, 55 and 38% of the samples collected in 2010, 2011 and 2012, respectively (using metabarcoding). The out-of-bag explained variance of the full RF model of the diet composition in 2009–2012 was 49%. The environmental variables

that most influenced the diet composition differed for each of the 5 fish species (Fig. 8). The proportion of sandy sprat in the diet was lower with increased rainfall, higher mean winter FSL, a higher SOI in the previous year and when the variance in the SST from May–November (i.e. when the little penguins on Penguin Island typically breed) was higher (Fig. S8). Conversely, the proportion of scaly mackerel increased with a higher SOI in the previous year and when the variance in the SST during the breeding months was higher (Fig. S9). The proportion of blue sprat was positively influenced by a stronger Capes Current, more rainfall in the previous year and lower mean SST from May–November (Fig. S10).

3.3. Key demographic parameters

The numbers of penguins caught at each of the 4 arrival sites varied within and between years, but there was an

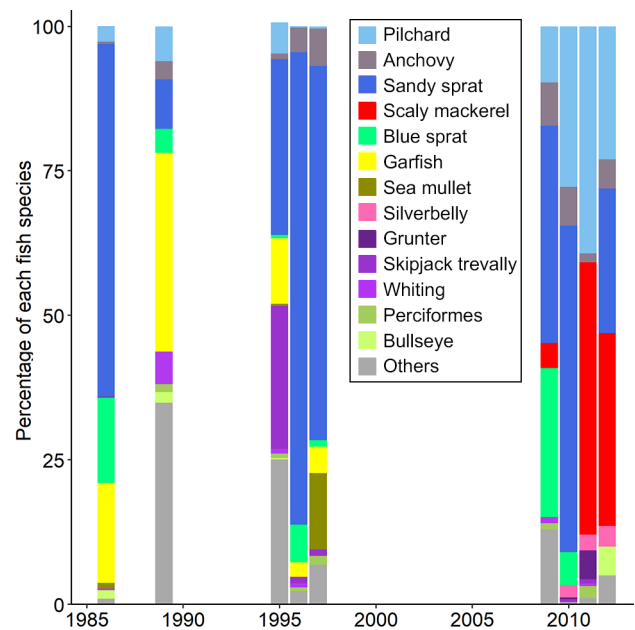


Fig. 7. Percentage of each fish species within all samples collected from little penguins on Penguin Island, Western Australia, obtained from regurgitants (pre 2008) and molecular analyses of faeces (post 2008). The samples collected in 1986, 1989, 1995 and 1997 represent the diet during pre-breeding and breeding; those collected in 1996 and 2009–2012 represent the diet during breeding only

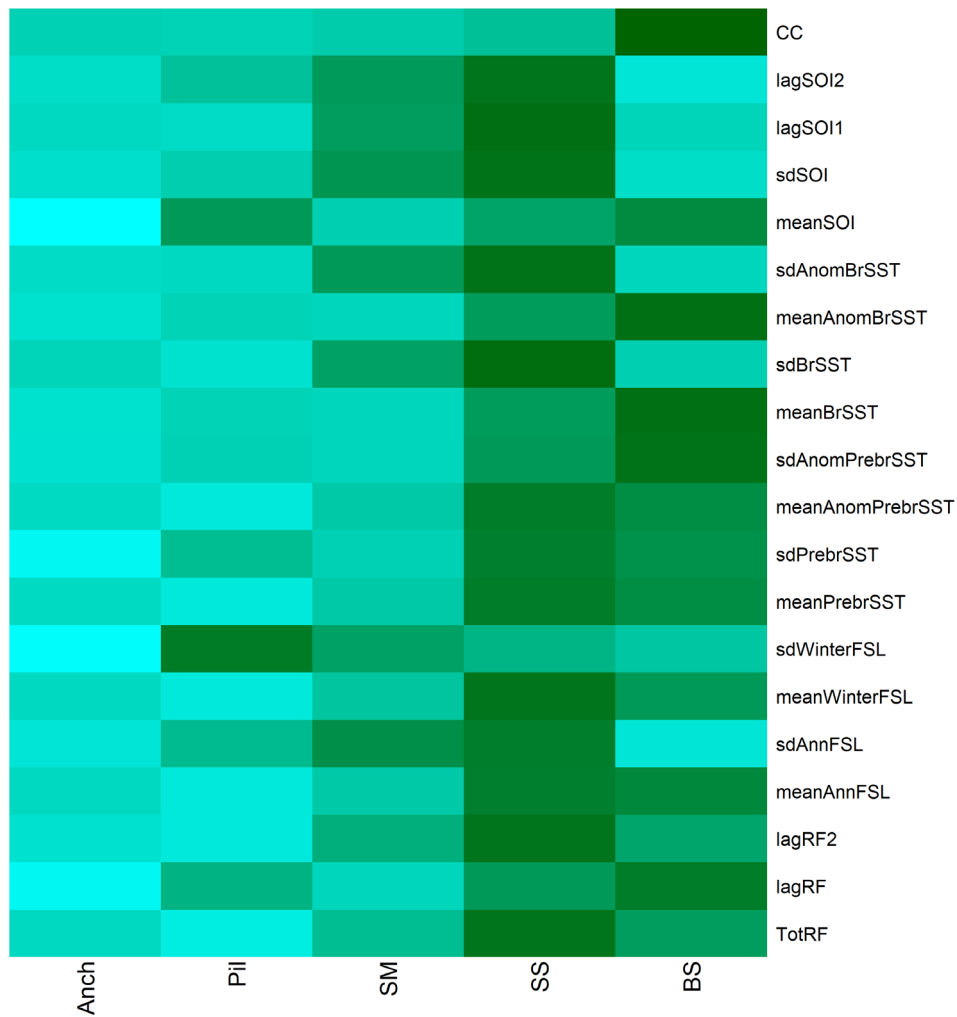


Fig. 8. Variable importance scores from a full multivariate random forest analysis exploring the influence of 20 environmental variables on the proportion of pilchard (Pil), anchovy (Anch), scaly mackerel (SM), sandy sprat (SS) and blue sprat (BS) in the diet of little penguins on Penguin Island, Western Australia, from 2009 to 2012. Diet composition was obtained from molecular analysis. The darker the green within each row, the more influence the environmental variable had on the presence of that fish species. Abbreviated environmental variables are Capes Current (CC); total annual rainfall and 1 and 2 yr lags (TotRF, lagRF, lagRF2); mean and SD of annual and winter Fremantle Sea Level (meanAnnFSL, sdAnnFSL, meanWinterFSL, sdWinterFSL); mean and SD of the annual Southern Oscillation Index (SOI) and mean SOI with 1 and 2 yr lags (meanSOI, sdSOI, lagSOI1, lagSOI2); mean and SD sea surface temperatures during pre-breeding and breeding (meanPrebrSST, sdPrebrSST, meanBrSST, sdBrSST) and mean and SD anomalies of SSTs during pre-breeding and breeding (meanAnomPrebrSST, sdAnomPrebrSST, meanAnomBrSST, sdAnomBrSST)

overall decline from 2011–2019 (Fig. 9). Prior to the 2011 MHW, a similar percentage of penguins was caught at Sites 1 and 4, but the overall percentage of penguins caught at Site 1 more than doubled that at Site 4 after the MHW (Fig. 9, Table 1). Additionally, the proportion of penguins caught at Site 1 was significantly greater from 2011 onwards and the proportion of penguins caught at Sites 2, 3 and 4 was significantly lower (Fig. 9, Table 1).

For the annual population estimates, the model with the highest AIC_c weight was not consistent in all years, but for 4 of the years (2008, 2011, 2017 and

Table 1. Percentage of little penguins caught at each of the 4 arrival sites ([total no. of penguins caught at an arrival site / total caught across all arrival sites] \times 100) on Penguin Island, Western Australia, before and after the 2011 marine heat wave (MHW), with a 2-sample *t*-test or Wilcoxon test (Site 2) comparing before and after capture values

Arrival site	Before MHW	After MHW	Test statistic	df	p
1	29	54	-6.064	17.91	<0.005
2	17	9	122		<0.005
3	20	14	3.227	17.18	<0.005
4	34	24	2.371	20.96	<0.05

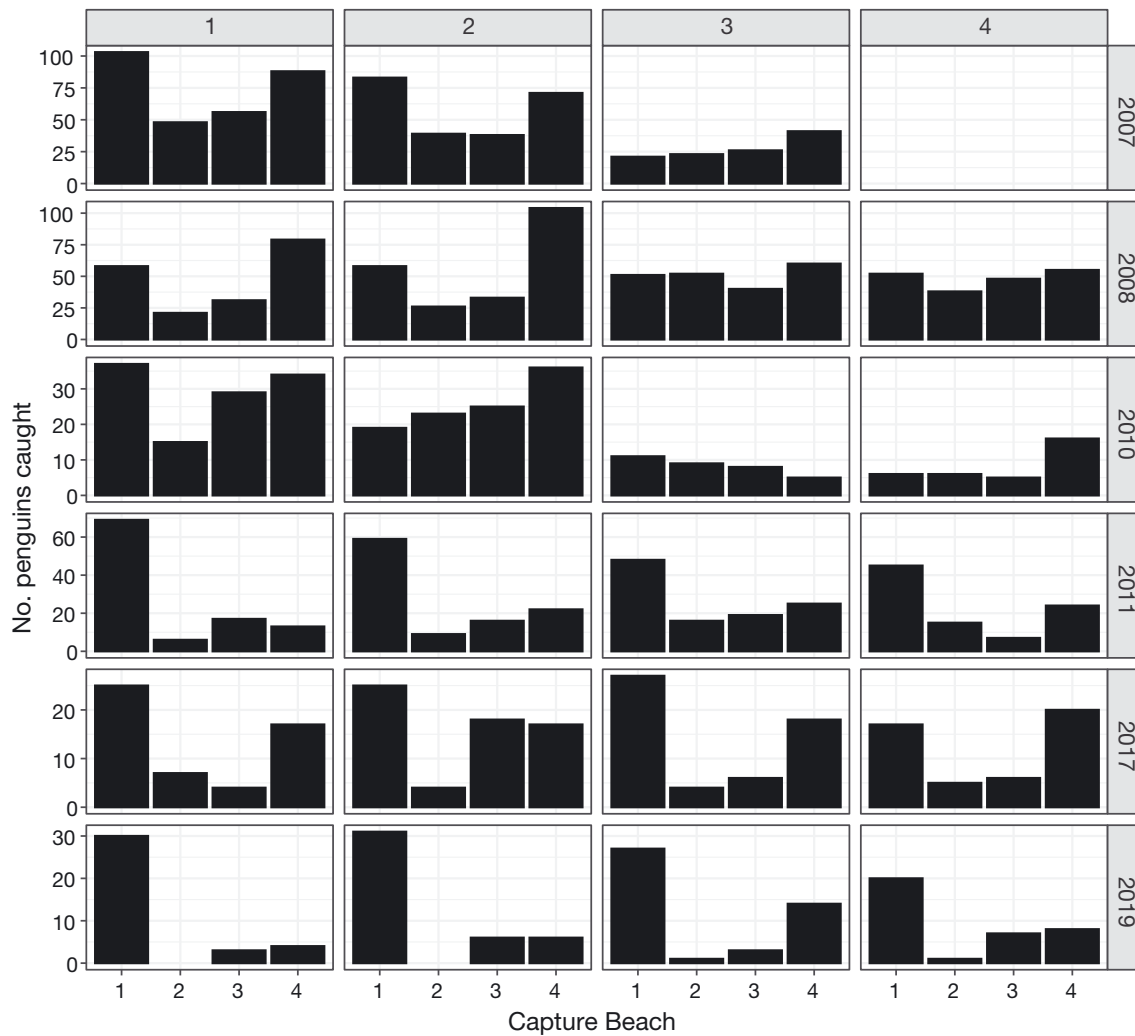


Fig. 9. Number of little penguins caught at each of 4 arrival beaches during each mark–recapture session at Penguin Island, Western Australia, in 2007, 2008, 2010, 2011, 2017 and 2019. Note that 4 sessions were undertaken each year except in 2007, when only 3 sessions were undertaken

2019) the top model included a constant recapture rate, a time-variant *pent* and a constant φ within the colony (Tables S4–S9). The probability of recapture was lowest in the third mark–recapture session in 2007 (the top model for 2007 had a *p* that changed over time) and across all sessions in both 2011 and 2017 (2007: 0.21 ± 0.07 , 95% CI = 0.11–0.37; 2011: 0.23 ± 0.05 , 95% CI = 0.14–0.35; 2017: 0.22 ± 0.06 , 95% CI = 0.12–0.37) (Table 2). The MHW did not affect the probability of new birds entering the colony for the first time in each session (i.e. *pent*), with *pent* declining between sessions in most years (Table 2). The only exceptions were in 2019, where *pent* remained similar between the second and third session, and in 2007, which had a constant *pent* of 33% between sessions. The probability of persistence, i.e. remaining in the colony, was the lowest between sessions 1 and 2 in 2010 (0.36 ± 0.08 , 95%

CI = 0.23–0.52), meaning that 64% of penguins left the colony between these sessions. Penguins were more likely to remain in the colony after the MHW, with only 22–25% of penguins leaving the colony between sessions (Table 2).

The annual probability that an individual is present and available for detection in a capture session of that year was typically higher after the MHW than before the MHW. The residency time of the penguins was lowest in 2008 and 2010 (Table S10). The average departure time was after session 3 in 2008, 2011, 2017 and 2019, i.e. early to mid-October, and after session 2 in 2007 and 2010, i.e. early to mid-November (Table S10).

Over the 6 yr of the mark–recapture study, the island-wide population of penguins peaked in 2008 at 1857 (95% CI = 1667–2069) in September–October (Fig. 10). The population has declined by

Table 2. Estimated rates (\pm SE) of the probability of recapture (p); the probability of entering the colony for the first time in a given session ($pent$) and the probability of persisting at the colony from one session to another (φ) for little penguins on Penguin Island, Western Australia. The data are from the top model each year; 95% CI are given in square brackets. Note that if the top model included a constant structure for $pent$, then the SE for that parameter is 0 and the CI is equal to the constant value. NA: not available

Parameter	2007	2008	2010	2011	2017	2019
p (session 1)	0.83 (0.16) [0.34–0.98]	0.37 (0.04) [0.30–0.45]	0.66 (0.13) [0.39–0.85]	0.23 (0.05) [0.14–0.35]	0.22 (0.06) [0.12–0.37]	0.41 (0.08) [0.26–0.57]
p (session 2)	0.49 (0.12) [0.27–0.72]	0.37 (0.04) [0.30–0.45]	0.66 (0.13) [0.39–0.85]	0.23 (0.05) [0.14–0.35]	0.22 (0.06) [0.12–0.37]	0.41 (0.08) [0.26–0.57]
p (session 3)	0.21 (0.07) [0.11–0.37]	0.37 (0.04) [0.30–0.45]	0.34 (0.12) [0.15–0.59]	0.23 (0.05) [0.14–0.35]	0.22 (0.06) [0.12–0.37]	0.41 (0.08) [0.26–0.57]
p (session 4)	NA	0.37 (0.04) [0.30–0.45]	0.34 (0.12) [0.15–0.59]	0.23 (0.05) [0.14–0.35]	0.22 (0.06) [0.12–0.37]	0.41 (0.08) [0.26–0.57]
$pent$ (session 1)	0.33 (0.00) [0.33–0.33]	0.51 (0.05) [0.42–0.61]	0.55 (0.08) [0.40–0.69]	0.61 (0.12) [0.36–0.81]	0.57 (0.015) [0.29–0.81]	0.59 (0.13) [0.33–0.81]
$pent$ (session 2)	0.33 (0.00) [0.33–0.33]	0.23 (0.04) [0.16–0.32]	0.30 (0.05) [0.21–0.41]	0.16 (0.08) [0.05–0.39]	0.26 (0.09) [0.12–0.47]	0.18 (0.10) [0.05–0.47]
$pent$ (session 3)	NA	0.14 (0.04) [0.08–0.23]	0.04 (0.05) [0.004–0.37]	0.11 (0.08) [0.03–0.36]	0.10 (0.10) [0.01–0.51]	0.21 (0.09) [0.08–0.44]
φ (session 1–2)	0.44 (0.10) [0.26–0.64]	0.71 (0.05) [0.62–0.79]	0.36 (0.08) [0.23–0.52]	0.76 (0.10) [0.52–0.90]	0.73 (0.13) [0.43–0.91]	0.79 (0.09) [0.55–0.92]
φ (session 2–3)	0.44 (0.10) [0.26–0.64]	0.71 (0.05) [0.62–0.79]	0.73 (0.22) [0.22–0.96]	0.76 (0.10) [0.52–0.90]	0.73 (0.13) [0.43–0.91]	0.79 (0.09) [0.55–0.92]
φ (session 3–4)	NA	0.71 (0.05) [0.62–0.79]	0.92 (0.16) [0.11–0.99]	0.76 (0.10) [0.52–0.90]	0.73 (0.13) [0.43–0.91]	0.79 (0.09) [0.55–0.92]

80% since the MHW in 2011, with an estimated 309 penguins (95% CI = 251–381) present in September–November 2019 (Fig. 10). The 2010 data are aberrant compared to the data for 2007, 2008 and 2011, owing to a large proportion of penguins completing their

breeding before the capture sessions (which unavoidably began in late October or early November; Table 1, Figs. S3 & S11) and a very low hatching or overall breeding success of those eggs laid in September and October (Fig. S12).

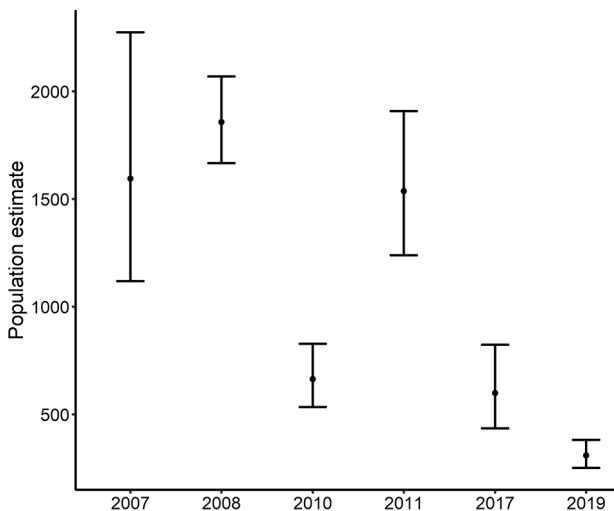


Fig. 10. Island-wide population estimates (\pm 95% CI) of little penguins on Penguin Island, Western Australia, in 2007, 2008, 2010, 2011, 2017 and 2019

3.4. Mortality of penguins from starvation or protozoal parasites

More malnourished penguins were found dead in 2011 and 2012 than any other year since necropsies began in 2003 (Fig. 11). Unusually, the penguins were mainly found during winter–spring 2011 (after the 2011 MHW) (Fig. 11). The only other year in which malnourished penguins were found across winter–spring was in 2017 (Fig. 11). Whilst dead birds were often found in December and January, which coincides with the penguins' annual moult, in 2012 they were found between January and April (Fig. 11). The number of penguins that died from either starvation or protozoal parasitic infections peaked in 2011 and 2012 (Fig. 11), with the latter cases found in the austral spring months in 2011 and in most months of 2012 (Fig. 11). Protozoal parasites

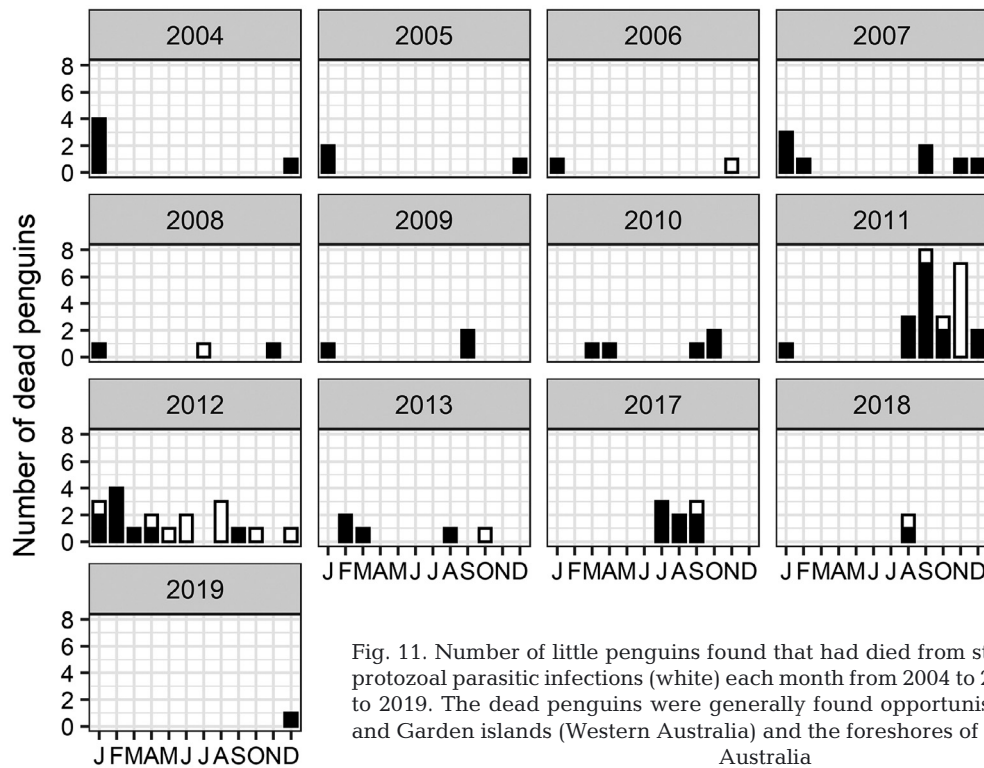


Fig. 11. Number of little penguins found that had died from starvation (black) or protozoal parasitic infections (white) each month from 2004 to 2013 and from 2017 to 2019. The dead penguins were generally found opportunistically on Penguin and Garden islands (Western Australia) and the foreshores of southwest Western Australia

were only found sporadically before the MHW and after 2012 (Fig. 11).

4. DISCUSSION

We have used multiple lines of evidence to show that the MHWs in 1999 and 2011 negatively impacted little penguins on Penguin Island, Western Australia. We found that the penguins' breeding participation over the past 3 decades was the lowest during the extreme MHW in 2011 and amongst the lowest in 1999. Hatching success, overall breeding success and CPP were also either the lowest or amongst the lowest recorded in 1999 and 2011. Diet composition was substantially different in 2011 and 2012 (following the 2011 MHW) compared to that in the other 7 yr in which diet samples were collected. Following the 2011 MHW, there was a shift in the distribution of penguins on the island, the population estimate over the austral spring period declined by 80% and more penguins were found to have died from starvation or infections with protozoal parasites in 2011 and 2012 than in any other year. We believe that our paper is the first to describe prolonged impacts of the extreme MHW in 2011 on seabirds in Western Australia. Moreover, it is the first to identify biological impacts of the severe MHW in 1999 on any

marine flora or fauna in Western Australia. Our findings reinforce the negative influence that MHWs can have on seabirds (Piatt et al. 2020, Suryan et al. 2021, Tate et al. 2021)

4.1. Influence of MHWs on breeding parameters, body condition and diet composition

4.1.1. Breeding participation and success

The MHWs in 1999 and 2011 clearly impacted the breeding parameters of the little penguins but breeding performance of the penguins was also poor in other years. For example, fewer penguins participated in breeding after the 2011 MHW and they were less likely to lay eggs when there was a reduction in baitfish availability in the southwest region of Australia. This region has been identified as foraging habitat for the penguins nesting on the SE, SW and W side of Penguin Island during pre-breeding (B. L. Cannell unpubl. data) and during incubation (Cannell 2016, 2019). Furthermore, participation and breeding success were negatively influenced by higher FSL, i.e. a stronger Leeuwin Current. The breeding success of penguins, as with other seabirds, is associated with prey availability (Jenouvrier et al. 2005, Piatt et al. 2020), and whilst the strength of

the Leeuwin Current influences fish assemblages (Gaughan et al. 1996, Gaughan 2007, Lenanton et al. 2009), the relationships are complex (Lenanton et al. 2009). For example, a stronger Leeuwin Current the previous year has been associated with improved commercial catches of sandy sprat *Hyperlophus vittatus* in coastal waters from Perth to the southwest region (Gaughan et al. 1996, Lenanton et al. 2009), likely by improving spawning success and/or larval and juvenile retention in this area as well as their survival (Gaughan 2007, Lenanton et al. 2009). However, the relationship has weakened with the addition of more data, intimating that other factors are influencing the presence and abundance of this patchily distributed species (Lenanton et al. 2009). The complex relationship with rainfall and sandy sprat abundance, which are location-specific (Paerl et al. 1990, Gaughan et al. 1996, Rivers et al. 2022), also affected penguin diet and thus breeding success. Our research showed that penguins consumed fewer sandy sprats when faced with higher average winter FSL when combined with greater rainfall in the same year. This is surprising, as fewer penguins participated in breeding when rainfall in the previous year was lower. A similar pattern was observed with the presence of blue sprat in the penguins' diet, suggesting that the effects of rainfall on baitfish abundance and proportional consumption by penguins is not clear.

Penguins and baitfish are both affected by SSTs and MHWs, which are increasing with climate change. Decreased rainfall and more extreme rain events are also predicted with climate change, which will likely influence the penguins' diet. But to what extent and when the effects will be negative or positive is unclear. Unpredictable access to food following adverse combinations of SSTs, MHWs and change in rainfall has the potential to have detrimental effects on penguin populations by adversely impacting breeding participation and success.

4.1.2. Body condition

Prey availability is intrinsically linked with the body condition of little penguins, which influences when (or if) they breed (Wienecke et al. 1995), and their body condition improves from non-breeding to breeding (Robinson et al. 2005). Contrary to what we predicted, the non-moult body condition of those adults that were present on the island was not significantly lower in 1999 or 2011 relative to many of the other years. As experienced little penguin breeders

are also better foragers (Saraux & Chiaradia 2022), it is likely that those birds that attempt to breed in years when there is less prey are better foragers and hence will be in better body condition. It is also likely that the penguins will protect their own condition and ability to breed in the future, even if this means deserting a mate, egg or chick, leaving a chick poorly fed, or not breeding at all. Interestingly, females were consistently in better body condition, which contrasts with that found for little penguins in New Zealand (Numata et al. 2000) and at Phillip Island (McCutcheon et al. 2011). This could be an artefact of the condition estimate that was used, caused by the beak dimensions of males being larger than that of the females. However, the Penguin Island colony is also genetically differentiated from that at Phillip Island (Burrige et al. 2015), and whether this confers advantages in body condition for the females requires further investigation.

4.1.3. Changes in diet composition

While the extension of tropical and sub-tropical fish species into temperate communities as a result of MHWs has been well documented (e.g. Pearce et al. 2011, Smale & Wernberg 2012, Wernberg et al. 2013, 2016), we found that this had consequences for the penguins. We failed to detect either sandy sprat or blue sprat *Spratelloides robustus* in the penguins' diet during the MHW in 2011. Both of these species had been regularly detected in diet samples in previous years, except for a much lower proportion of sandy sprat in 1989 (another year of elevated SST) and no blue sprat in 1995. The lack of blue sprat in 1995 may be attributed to the increased abundance of presumably dead or dying pilchards *Sardinops sagax* in the diet during the mass mortality of pilchards from a herpesvirus in autumn (Connard 1995, Fletcher et al. 1997). In contrast, the tropical scaly mackerel *Sardinella lemuru* had rarely been found in diet samples before the MHW in 2011 but comprised a large proportion of the penguin diet during the typical breeding months in 2011 and 2012, as did pilchard. The larger proportion of pilchard was also unusual, as pilchards were previously predominantly found in penguin diet in the austral autumn and winter (Klomp & Wooller 1988, Connard 1995). Whilst these findings could be an artefact of the different methodologies used to determine the diet composition, they are mirrored in the faecal DNA analysis before and after the MHW. We found that high variability in

the SST during the breeding season (May–November) positively influenced the proportion of scaly mackerel in the diet but negatively influenced that of sandy sprat. Higher SST during the breeding season also negatively influenced the proportion of blue sprat, as did a reduced strength of the Capes Current, which is generally associated with cooler water, stronger southerly winds and more nutrients. Whilst the blue sprat has not contributed a significant component to the penguins' diet, unlike the sandy sprat, this may be due to differences in the timing of recruitment and spawning of both species in local waters. Large numbers of age-0+ sandy sprat were found in nearshore waters 7 km south of Penguin Island from September–December, whereas large numbers of age-0+ blue sprat were found in the same area from January–May (Valesini et al. 1998). Thus, sandy sprat were more likely to be available during the incubation and early chick-rearing stages, predominantly May–October. However, breeding success also decreased with elevated SST in April, prior to breeding. This relationship was identified by Cannell et al. (2012) and has persisted with additional data. It is possible that elevated SSTs in April are a barrier to sandy sprat returning to spawn in the local coastal waters. With the increasing likelihood of climate change impacts on sandy sprat in the inner shelf within foraging range of the penguins, the question remains as to which species could shift into the role as important food resource for the penguins on Penguin Island. Here, we show that whilst scaly mackerel comprised a greater proportion of the diet after the 2011 MHW, breeding outcomes were poorer in 2011, and a greater number of dead and malnourished penguins were found in 2011 and 2012. It is unlikely that scaly mackerel are of lower quality than sandy sprat, given that they are a source of fish oil supplements, and <1 yr old fish are similar size to adult sandy sprat. Therefore, it is likely that the scaly mackerel were not available within the foraging range of the penguins, especially during the chick-rearing stage when the penguins are constrained to forage within 30 km of the colony (Collins et al. 1999, Berlincourt & Arnould 2015, Cannell 2016, 2019, Carroll et al. 2016). Unfortunately, we were unable to determine whether there was a similar change in diet composition during the MHW in 1999. Given the reduced breeding participation and breeding success, however, it is likely that the elevated SST associated with the MHW impacted the presence and abundance of baitfish near the colony.

4.1.4. Timing of peak egg laying and its relationships with breeding success and SST

The timing of egg laying by the penguins did not markedly change before and after the MHW. Peak egg laying in June–July was associated with above-average CPP before the extreme MHW but below average after it. We suspect that there has been a temporary regime shift in the coastal ecosystem south of Penguin Island since the extreme MHW. Furthermore, the ecosystem likely reverted during the cold spells on the west coast in 2015–2016, when phytoplankton production in the Leeuwin Current was enhanced (Feng et al. 2021) and CPP was well above average (See Text S4 for detailed description).

4.2. Influence of MHW on demographic parameters

There were some notable changes in the demographic parameters of the little penguins following the MHW. Firstly, and ignoring the aberrant data from 2010 (as detailed in Section 3.3, and possibly influenced by unusually warm conditions from October 2010–January 2011; Kajtar et al. 2021), many fewer penguins were caught on all beaches. Additionally, the proportion of penguins caught at Site 1 increased relative to the other 3 sites. Penguins that inhabit the NE side of the island (and arrive at Site 1) typically forage north of the island, while penguins nesting on the other sides of the island typically forage south of the island (e.g. Cannell 2016, 2019). It is surmised that the greater proportion of penguins caught at Site 1 reflects a more consistent prey resource north of the island since the MHW (as evidenced by better breeding outcome for penguins from Garden Island that forage in the same area; B. L. Cannell unpubl. data). If this difference in prey resources north and south of the colony continues, it could result in a shift in the proportion of penguins nesting in different areas on the island. However, given their high site fidelity to an arrival beach (Cannell et al. 2012) and nesting area (chicks return to within 50 m of where they were raised; Nicholson 1994), it is unlikely that the shift is due to penguins changing nesting areas on the island, but rather better breeding outcomes for those penguins nesting on the NE side.

Secondly, the residency time of the penguins in the colony was approximately 1–2 wk longer after the MHW than in 2008 and 2010. This is interesting, especially given the low rate of chick production in

2011 and the low number of hatched eggs and successfully fledged chicks in 2017, especially for those eggs laid from July onwards. It is possible that limited prey resources meant that the parents were provisioning chicks for a longer than normal period of time if the size of the meals they were bringing back to the chicks was smaller. Indeed, chick growth has been found to be slower in years that coincided with overall lower breeding success and proposed lower prey availability (Wienecke et al. 2000). Additionally, the low recapture rates of the penguins but high persistence in 2011 and 2017 could indicate that the individuals were feeding for longer at sea before returning to the island, and thus were not available for capture.

Thirdly, the population on the island declined, but not immediately. Although adult survival is important for population growth in seabirds, chick production was deemed more important during a study of 378 populations of North Atlantic seabirds comprising 29 different species (Sandvik et al. 2012). Since the MHW, chick production was well above average in 2015, 2016, 2018 and 2019, yet the population on Penguin Island during the austral spring has declined by approximately 80% from 2011 to 2019 and breeding participation has generally been lower than before the MHW. As little penguins are philopatric, recruitment into the colony is influenced by the proportion of penguins breeding, their breeding success and the survival of the juveniles. So even though breeding success has improved, fewer pairs produced offspring. In conjunction, the first-year survival rate of little penguins is lower than that of adults (Sidhu et al. 2007, Agnew et al. 2015), suggesting that very few chicks would be available to recruit back into the colony. Climate effects on a seabird population operate at a lag equivalent to the species' age at first breeding (Sandvik et al. 2012), which is 2–3 yr for little penguins. However, the annual commercial catch of sandy sprat was correlated with a 1 yr lag of the FSL (Gaughan et al. 1996). Thus, it is likely that climate effects on the survival of chicks operate in the year of fledging as well as at lags of 1–3 yr due to indirect effects through prey. Indeed, the first-year survival of little penguins at Phillip Island, Victoria, decreased as east–west sea-temperature gradients increased (Sidhu et al. 2012). Furthermore, the survival of the juveniles may be even more compromised if food resources are scarce, as fledgling little penguins initially have poorer foraging skills than adults (Cannell 1994). Therefore, although chick production in 2016 was the highest recorded since monitoring began, adverse climate

conditions in 2017 likely influenced the survival of the first-year birds as well as breeding success in 2017. It is, therefore, not surprising that the population continued to decline to lows in 2019. Little penguins have a relatively short lifespan compared to other seabirds; thus, they are vulnerable to demographic collapse if food becomes scarce and reproductive rates are negatively impacted.

Finally, even though the population of penguins using the island during September–November in 2011 was not lower than in 2007 and 2008, many more malnourished penguins were found dead in 2011. Unlike any other year except 2017, the malnourished penguins were found in the late austral winter and early austral spring. In conjunction with the poor breeding parameters, this signifies that prey resources for the penguins within their home range were scarce. Furthermore, the reduction in fish availability continued in 2012, with malnourished penguins uncommonly found in February–April, which coincided with the post-moult exodus from the colony before their pre-breeding return in April–May. It is important to note that it is not unusual to find malnourished penguins in December–January, which coincides with the 2–3 wk moult period that the penguins undergo annually, and during which they cannot forage. Thus, malnourished penguins during these months represent those penguins who were not able to gain enough fat reserves before moulting. We also found that many penguins had died from protozoal parasitic infections in 2011 and 2012, with only sporadic cases observed before and after these years. The protozoal parasites were identified in many of the cases, using PCR, as *Toxoplasma gondii* (Campbell et al. 2022) and/or *Haemoproteus* spp. (Cannell et al. 2013). As part of the *T. gondii* lifecycle only occurs in cats, and there are no cats on Penguin Island (or nearby Garden Island), this suggests that *T. gondii* oocysts from cat faeces can contaminate water bodies (Campbell et al. 2022). Indeed, pilchards can filter *T. gondii* oocysts from seawater and these oocysts remain infectious (Massie et al. 2010). Pilchards are consistently found in the diet of the little penguins, but there was a greater percentage of pilchards in their diet from 2010–2012. Also, the sudden and short-lived increase in the number of penguins found with these parasites coincided with the appearance and great proportion of scaly mackerel in the diet. Further research is necessary to determine if indeed scaly mackerel can harbour the oocysts and where the oocysts may be entering the marine system.

4.3. Future research

This paper has highlighted data deficits that, if rectified, would improve model outputs. Additionally, changes in the penguin distribution raises issues for more impacts on the penguins from multiple developments within Cockburn Sound. These areas of future research are developed in the Supplement (Text S5).

5. CONCLUSIONS

MHWs on the west coast of Australia impacted the breeding participation, breeding success, diet composition, population size, nesting distribution, mortality due to starvation and presence of a novel protozoal parasite (potentially introduced in the changed diet) of the little penguins on Penguin Island. Since the MHW in 2011, warmer SST anomalies persisted in the area in 2012, 2013 and late 2014. A strong El Niño in 2015–2016 resulted in marine cold spells (Feng et al. 2021), and the reproductive success of the penguins did improve with the cooler periods. Despite this improvement, the population using the island in the austral spring declined by 80%. It is likely that the poor breeding outcomes for multiple years resulted in low recruitment into the colony and, ultimately, an aging population of breeding penguins.

The little penguin colony on Penguin Island is at the warm trailing-edge of their range. As such, their thermal niches and critical thresholds are more likely to be exceeded, especially for the time that they must spend on land during breeding and moulting. Interestingly, both the onset of breeding and breeding success of little penguins on Phillip Island, Victoria, improved with warmer SST (Cullen et al. 2009). This highlights the localised influence of climatic variables on primary productivity, the distribution of prey and, ultimately, predators such as seabirds. As such, the magnitude and direction of a species' response is due to very localised oceanographic and trophic conditions (Sandvik et al. 2012, Santora et al. 2020). Recently, Sydeman et al. (2021) identified that changes in breeding productivity for seabirds in the Southern Hemisphere were not as significant as in the Northern Hemisphere and suggested that there was the possibility to implement timely changes that improved the foraging opportunities for seabirds. Given the impacts of MHWs observed in this little penguin colony and the predicted future increase of such events, measures that improve baitfish abun-

dance in the local coastal waters are warranted. This is especially important in areas where there will be cumulative impacts on fish resources, such as in Cockburn Sound. Without such informed management, we will very likely lose this genetically important, range-edge population of little penguins. Importantly, this paper demonstrates how a seabird population at the limits of its possible distribution can be negatively impacted by a warming ocean and highlights the value of long-term monitoring studies to detect such change.

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