



Breeding success of short-tailed shearwaters following extreme environmental conditions

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ABSTRACT: Extreme weather events are increasing in frequency, causing disruption to global ecosystems. Large-scale events, such as marine heatwaves, can impact the abundance of prey species, which consequently influences the behaviour of top-level predators such as seabirds. The short-tailed shearwater *Ardenna tenuirostris* is a trans-hemispheric migrant with typically a highly synchronous breeding phenology. Here, we document short-tailed shearwater colony occupancy for the period 2011–2020, with a focussed assessment of their breeding success in the 2019/20 season, which followed a marine heatwave that occurred predominantly in the non-breeding areas in the North Pacific Ocean. The return of the birds to their breeding colonies in southeast Australia was delayed by approximately 2 wk in October 2019, and the subsequent breeding season ended with only 34 % breeding success, with nest abandonment beginning in the incubation phase. A North Pacific marine heatwave in 2019, associated with a mass mortality event of over 9000 birds ('wreck' of beach-washed birds), led to reduced adult body condition and carry-over effects causing egg and chick failures during the subsequent breeding season. Localised weather events (i.e. flooding of burrows due to heavy rainfall) also influenced breeding outcomes of the 2019/20 season. The relationship between wreck events and seabird breeding ecology is an understudied area, partly due to the difficulties around quantifying the scale of wrecks. Our study is one of few that documents poor seabird breeding success following the extreme marine conditions which have persisted in the North Pacific Ocean since 2013.

KEY WORDS: *Ardenna tenuirostris* · Mass mortality event · Migratory seabird · Phenology · Pacific marine heatwave · Short-tailed shearwater · Wreck

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1. INTRODUCTION

As top-order predators, seabirds are frequently used as sentinel organisms for monitoring marine ecosystems (Lescroël et al. 2016). However, over a third of all seabird species are currently globally threatened, raising concern for the health of the oceans and associated ecosystem functions (Dias et al. 2019). Many seabird species have been subjected to long-term monitoring programmes that have been used to calculate annual survival rates, individual

breeding success, age at first breeding and other key life-history parameters (e.g. Diamond & Devlin 2003, Pyk et al. 2013).

While breeding biology and phenology have been well-documented for seabirds, very few studies have assessed breeding in response to a range of environmental conditions, including catastrophic events, as these events are difficult to predict (Xiao et al. 2017). For seabird species that undertake trans-hemispheric or circumpolar migrations, they are exposed to a wider range of environmental conditions than

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less mobile species, increasing the probability that they will encounter extreme conditions (Newton 2007). Extreme environmental events that contribute to wildlife mortality are becoming more common, have been shown to influence species demography (Piatt et al. 2020) and are predicted to increase in severity and frequency in line with climate change (Wernberg et al. 2013, Oliver et al. 2018).

We can hypothesise that mass mortality events (hereafter 'wrecks') will increase in frequency with extreme environmental conditions; however, to assess this relationship and the subsequent impacts on populations, a reference timeline of wreck events must be established (Glencross et al. 2021). Importantly, both small- and large-scale wrecks of adult and juvenile seabirds can be difficult to quantify in marine species, as the majority of birds perish at sea (Camphuysen et al. 1999, Wiese & Jones 2001). While conditions during the non-breeding season sometimes result in rapid die-offs of adult seabirds (Piatt et al. 2020), wrecks involving breeding adults tend to be rare as birds will prioritise their own survival above that of their offspring (Navarro & Gonzalez-Solis 2007).

Extreme environmental events, which can lead to wrecks, can impact seabird demography (Tilller et al. 2000, Piatt et al. 2020). Ocean temperatures directly influence prey populations, and poor seabird breeding seasons have been linked to oceanic oscillations, including El Niño–Southern Oscillation (ENSO) (Lavers et al. 2008, Surman et al. 2012, Price et al. 2020). Marine heatwaves, such as the series of heatwaves that occurred in the North Pacific near-annually since late 2013, are often associated with seabird wrecks, potentially affecting the overall population and having cascading effects during subsequent breeding seasons (Siddon & Zador 2018, 2019, Piatt et al. 2020). Additionally, local environmental conditions can strongly influence breeding seasons. Seabird colonies, particularly of burrowing species, are vulnerable to flooding during heavy rainfalls that can collapse burrows and drown chicks, leading to breeding failure (Thompson & Furness 1991, Tilller et al. 2000).

During poor environmental conditions, breeding adults must determine whether it is viable to continue with the breeding attempt, as they will preferentially choose their own survival and lifetime breeding success over the success of one breeding attempt (Bradley et al. 2000, Weimerskirch et al. 2001, Le Bohec et al. 2007). Breeding adults will reduce their breeding effort through alterations to chick provisioning, delaying the breeding attempt, often for weeks, or abandoning the breeding attempt altogether (Schreiber 2002). Abandonment can occur

throughout the season as conditions are continually monitored by the breeding birds (Montevecchi et al. 2021). Pressures on breeding adults can be intensified by carry-over effects from the non-breeding season (Weithman et al. 2017). Extreme conditions that result in wreck events remove the individuals in poor condition from the population, but the fitness of surviving individuals is also reduced.

Here we examined the breeding success of short-tailed shearwater (STSH) *Ardenna tenuirostris* from 2 colonies during the 2019/20 breeding season that followed a wreck of over 9000 STSHs on their non-breeding areas in the North Pacific Ocean (NPO) in 2019 (USFWS 2019). Specifically, we (1) compared December occupancy of breeding burrows for the years 2011–2019 and (2) assessed breeding success during the 2019/20 season.

2. MATERIALS AND METHODS

2.1. Study species and site

STSH are a migratory species of Procellariiformes, which travel approximately 15 000 km from their breeding grounds in southeast Australia to the NPO annually (Baduini et al. 2001a). They exhibit high nest site fidelity, returning to their breeding colonies each year in late September before departing on a 1 mo pre-laying exodus to the Southern Ocean. STSH exhibit highly synchronous breeding phenology, with individuals laying a single egg around 24–26 November, which is consistent among colonies and among years around southeastern Australia (Fig. 1; Marshall & Serventy 1956, Marchant & Higgins 1990). Hatching occurs around mid-January and adults depart in late March, with chicks leaving in late April to early May to undertake their first migration to the NPO (Weimerskirch & Chérel 1998).

Our study was undertaken at 2 colonies on Bruny Island in southeastern Tasmania: Whalebone Point (43.44° S, 147.23° E) and The Neck (43.27° S, 147.34° E; Fig. 2). The Whalebone Point population has remained stable since 2011 when monitoring began, at ca. 5300 breeding pairs (P. Vertigan & E. J. Woehler unpubl. data). The Neck population has been slowly increasing and is now estimated to support approximately 10 000 breeding pairs (BirdLife Tasmania unpubl. data, E. J. Woehler pers. obs.). Both sites are mixed-species colonies, also supporting nesting little penguins *Eudyptula minor*. The vegetation at the Whalebone Point colony consists largely of thick mats of *Tetragonia implexicoma* and

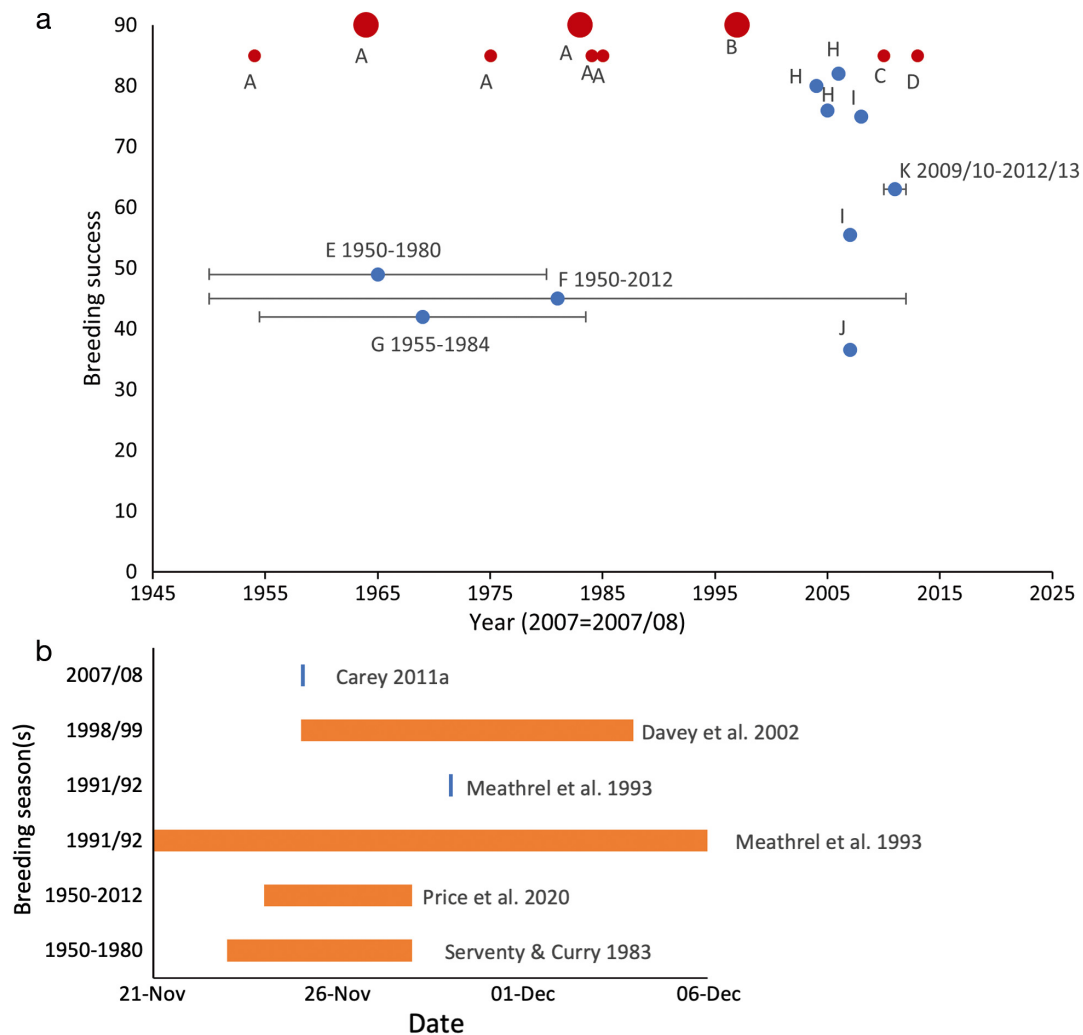


Fig. 1. (a) Records of breeding success of *Ardenna tenuirostris* in the peer-reviewed literature (blue points). Where records are averages across a range of seasons, timeframes are shown next to the corresponding point. Red points indicate when wreck events occurred. The size of a dot equates to the number of studies, with the large dots equalling 3 studies. A: Baduini et al. (2001a,b), B: Stockwell et al. (2001), C: Acampora et al. (2014), D: Totterman (2016), E: Serventy & Curry (1984), F: Price et al. (2020), G: Bradley et al. (2000), H: Einoder et al. (2013), I: Carey (2011b), J: Carey (2011a), K: Robinson et al. (2015). (b) Records of laying date ranges of *A. tenuirostris* shown in orange (n = 4). Studies reporting only a mean laying date are shown in blue (n = 2).

Carpobrotus rossii and patches of bare ground. The Neck colony contains larger patches of bare ground with native vegetation comprised primarily of *Poa* spp., *Lomandra* spp., *T. implexicoma* and *C. rossii*.

2.2. Data collection

2.2.1. Wreck events and ENSO

We reviewed the peer-reviewed literature (from January 1945 to August 2020) using the Web of Science (<https://www.webofknowledge.com>) to generate data on the severity and frequency of wrecks

involving STSH. Search terms included 'wreck', 'mortality event', 'mass mortality', 'washed up', 'beach washed', 'dead', 'stranded', 'die off' and 'mortality', as well as the common and scientific names for STSH. Since STSH were recently reclassified from the genus *Puffinus* to *Ardenna*, both binomials (i.e. *Ardenna tenuirostris* and *Puffinus tenuirostris*) were included in the searches. The Web of Science searches did not capture many wreck events reported off the coast of Japan, likely due to these reports being written predominantly in Japanese. To broaden the information gathered, we also included studies that were cited in the papers identified in our search.

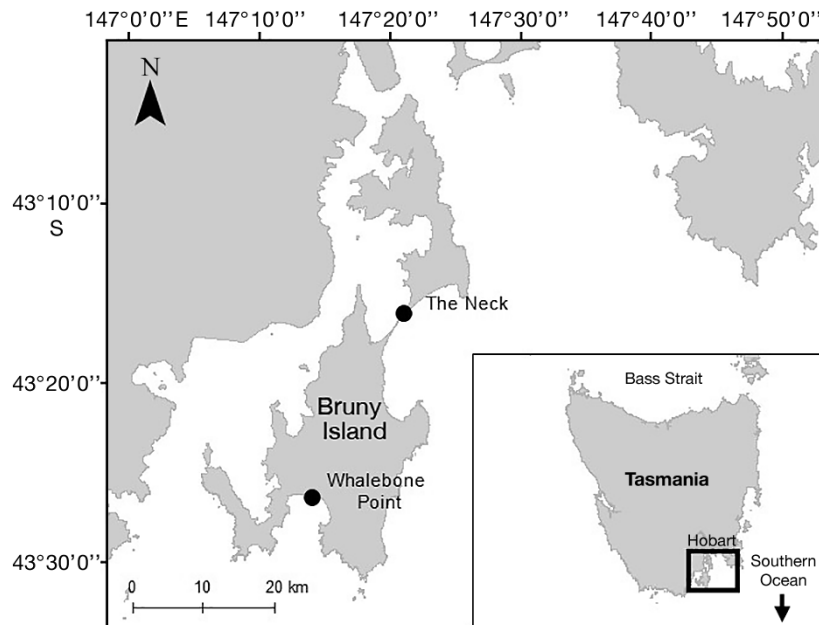


Fig. 2. Field site locations (The Neck and Whalebone Point) on Bruny Island, Tasmania, Australia

To investigate the role of ENSO on the study colonies (Price et al. 2020, Tavares et al. 2020), Southern Oscillation Indices (SOI) were obtained from the Australian Bureau of Meteorology (www.bom.gov.au/climate/enso/soi) for the years 2010–2020 to compare with colony occupancy data collected at the study sites. SOI is a measure of observed sea level pressure that corresponds with ocean temperatures. It is calculated by the difference of 2 locations divided by the long-term standard deviation of that month. Periods of SOI values below -7 indicate abnormally high ocean temperatures and suggest an El Niño episode, with the opposite (above 7) indicating a La Niña event.

2.2.2. December occupancy

BirdLife Tasmania established 3 transects at Whalebone Point in 2011 (total length 375 m), and 5 transects at The Neck in 2013 (total length 935 m). Burrow occupancy surveys were conducted over 2 or 3 d at approximately the same time each year in December, following egg laying and close to the onset of incubation. Burrows within 1 m either side of the transect were inspected using a probe to establish occupancy. Probes consisted of a flexible wire with a plastic tab at the end and are approximately 1 m long (Scoleri et al. 2020). Birds readily responded to the probe by pecking and vocalising. Where there

was uncertainty as to the specific identity of the burrow, a burrowscope (DeWalt DCT410D1-XE) was used to confirm identity of the species. Burrows were classified into 4 categories: occupied by STSH, occupied by little penguins, empty, and too long/indefinite. Burrow occupancy was calculated by dividing the number of burrows occupied by STSH by the total number of surveyed burrows. We also calculated occupancy per search effort (occupancy m^{-2}) by dividing burrow occupancy by the annual search area.

2.2.3. Breeding success and burrow collapses

During 2019/20, additional surveys were conducted throughout the season to monitor burrow parameters. We marked 50 occupied burrows at each colony during December. Burrows were chosen along transects that were least likely to be disturbed by the public (i.e. away from the public viewing area at The Neck colony). On 27 January 2020, we inspected these burrows to assess hatching success, which was calculated as the proportion of eggs laid that successfully hatched. We returned on 27 March 2020 to assess the overall breeding success, i.e. the proportion of eggs that yielded a chick. Chicks that were present at the end of March were expected to fledge.

In cases where we had previously misidentified a burrow as empty in January but a chick was found in March, burrows were reclassified to contain a chick ($n = 11$ of 100 burrows originally inspected). In some instances, we could not determine whether the responding adult was attending an egg or chick, so these burrows were conservatively classified as having an adult and egg present ($n = 13$ of 91 burrows inspected in both colonies). Overall breeding success was calculated as the number of chicks present in burrows in the March 2020 visit as a proportion of the eggs present in burrows in the December 2019 visit. No birds were handled during this project, and visits to the colony were kept to a minimum to diminish the risk of disturbance on breeding success (Carey 2009, 2011a).

We monitored the number of intact burrows throughout the season and recorded collapsed burrows. Local rainfall is a known factor that influences burrow stability and breeding failure, so rainfall data

for Adventure Bay, Bruny Island, were obtained from the Australian Bureau of Meteorology (www.bom.gov.au).

2.3. Statistical analyses

Statistical analyses were conducted in R version 4.0.0 (R Core Team 2020). All results are presented as mean \pm 1 SE. To evaluate annual differences in occupancy between colonies and among years, a fixed effect model was fitted with an interaction assuming data were consistent with a binomial distribution with a logit link function. As occupancy was over-dispersed with respect to the binomial distribution, we fitted the data assuming a quasi-binomial likelihood. We used a one-way ANOVA with a post hoc test to compare occupancy m^{-2} between wreck and non-wreck years that were identified during our literature search.

3. RESULTS

3.1. Wreck events and ENSO

We found published records of wreck events in 10 years between 1945 and 2019 (Fig. 1; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m672p193_supp.pdf). Only 3 reports referred to

events at the STSH breeding grounds in Australia. The majority of the studies reported on wrecks before 2000 ($n = 8$), with the most recent wreck reported occurring in 2019 (USFWS 2019). Of the wreck event reports, one occurred during the period when occupancy surveys were conducted on Bruny Island. The 2013 wreck occurred during the breeding season along the east coast of Australia, and we have also included the 2019 wreck in the non-breeding season in the Bering Sea that prompted this study.

El Niño and La Niña events occur in a cyclic pattern on average every 2–7 yr. Abnormally high ocean temperatures occur during El Niño when the SOI is below -7 (Fig. 3). The opposite occurs during La Niña, when the SOI exceeds 7 and water temperatures are lower than the long-term average. Between 2010 and 2020, the strongest La Niña took place in December 2010 when the SOI was 27.1 and the strongest El Niño occurred 6 yr later when the SOI was -22 .

3.2. December burrow occupancy 2011/12–2019/20

The model fit to the data suggested an interaction between year and colony (likelihood ratio test; $G_4 = 56.2$, $p < 0.05$). Compared to The Neck, burrow occupancy was significantly different at Whalebone Point in 2016/17 and 2017/18 ($t = 2.49$, $p < 0.05$ and $t = 3.80$,

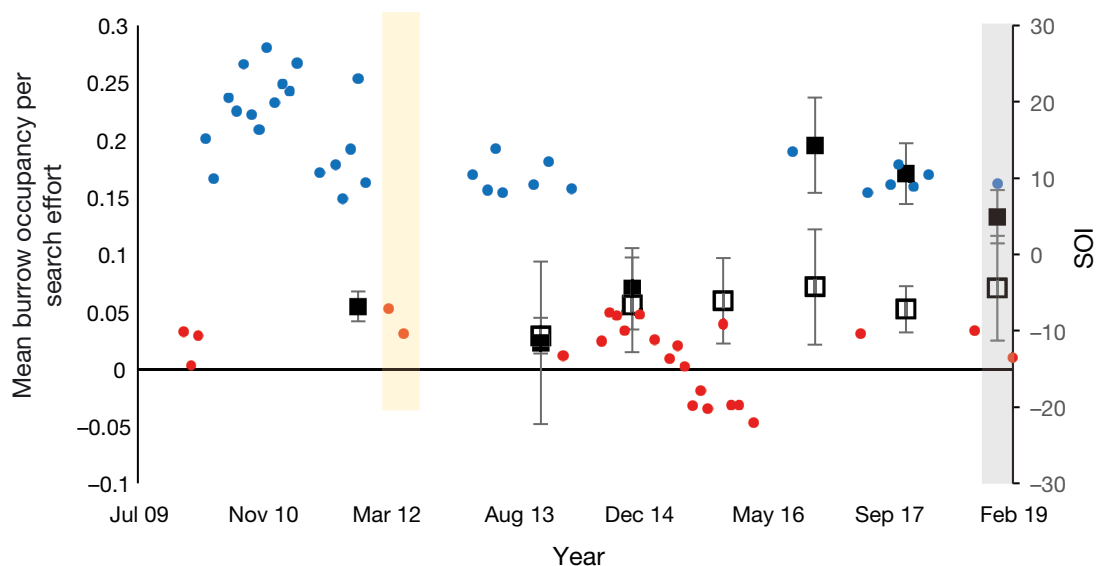


Fig. 3. Mean (\pm SE) burrow occupancy per search effort of short-tailed shearwater colonies during December surveys at The Neck \square and Whalebone Point \blacksquare , Bruny Island, Tasmania 2011/12–2019/20. Coloured bars highlight years where wrecks occurred (yellow: 2013 wreck in Australia during the breeding season, grey: 2019 wreck in the North Pacific during the non-breeding season). Monthly Southern Oscillation Index (SOI) values are presented as blue and red dots that indicate La Niña and El Niño events, respectively

$p < 0.01$). Occupancy m^{-2} did not vary significantly depending on whether a wreck occurred that year (ANOVA, $F_{2,11} = 1.60$, $p = 0.25$). The 2013/14 breeding season had the lowest occupancy m^{-2} but it was not significantly different from non-wreck years (Fig. 3; Tukey test, $p = 0.26$).

3.3. Phenology 2019/20

The 2019/20 arrival of STSH to their colonies in southeast Tasmania was approximately 2 wk later than normal (approximately 9 October rather than around 25 September). The late arrival was consistent with observations at colonies elsewhere in southeast Australia (Phillip Island Nature Parks 2019). Despite their delayed return, the Tasmanian populations of STSH resumed their typical breeding phenology (Fig. 1, Table S2), returning to their burrows from their pre-laying exodus in late November and then laid their eggs (approximately 25 November), with burrow occupancy approaching 40% at the onset of incubation.

3.4. Breeding success 2019/20

During the January 2020 (hatching) survey, burrows were recorded at disparate stages of the breeding cycle: unattended eggs, adults with an egg, adults with a chick and unattended chicks (Fig. 4). Hatching success was $41.3 \pm 7.0\%$ at The Neck and $28.9 \pm 6.6\%$ at Whalebone Point ($n = 50$ and 49 , respectively). Nest abandonment was highest in

December 2019 and January 2020 (Fig. 4, $n = 35$). Abandonment in study burrows increased by 12 burrows in March 2020. Overall breeding success at The Neck was $33.3 \pm 6.8\%$ ($n = 49$). Chick survival estimates at Whalebone Point in March were similar to egg hatching rates (overall breeding success $35.1 \pm 7.3\%$, $n = 44$).

In January 2020, 8% of burrows at each colony had collapsed (Fig. 4). Burrow collapses occurred after dry weather periods that were followed by heavy rainfall (Fig. 5). In both study colonies, the areas that experienced more collapses were less densely vegetated. By March 2020, the substrate at The Neck had become unstable in the less densely vegetated areas, and subsidence and localised erosion were evident, increasing the number of collapsed study burrows to 26%, compared to 14% at Whalebone Point. Monthly rainfall during December 2019 to April 2020 was close to the long-term average, except in March when more than 70 mm over the long-term average was recorded (Fig. 5b). Finer-scale rainfall data showed that before the January and March visits, colonies experienced dry weather followed by single heavy rainfall events (Fig. 5a).

4. DISCUSSION

4.1. Wreck events

We found no reports in the literature of breeding success that correspond with wreck events, highlighting the need for studies such as this one. Only 3 published studies mentioned wreck events that occurred in Australia, one of which collected carcasses for measurements rather than reporting on the wreck event itself (Table S1; Totterman 2016). More wrecks were reported from the NPO; this could be due to the fact that wreck reporting in peer-reviewed literature is less common in Australia where reports in the grey literature are more frequent (e.g. Pearl 2013, Sunshine Coast Council 2019).

We also found no reports of wrecks on coasts between Japan and Australia, likely due to the oceanic migration routes of STSH. Most reports were of events before 2000; however, we suggest that wreck events have not decreased in frequency but that lags in publishing have resulted in

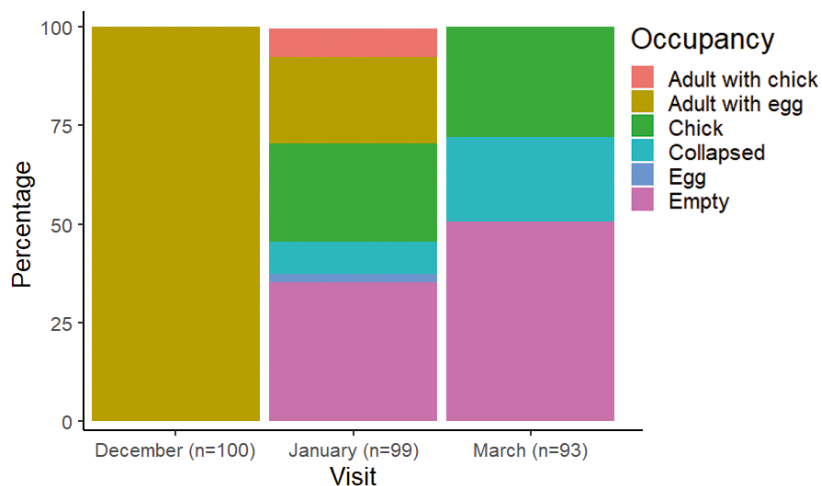


Fig. 4. Short-tailed shearwater burrow contents at initially occupied burrows on 3 visits to The Neck and Whalebone Point colonies on Bruny Island, Tasmania, during the 2019/20 breeding season

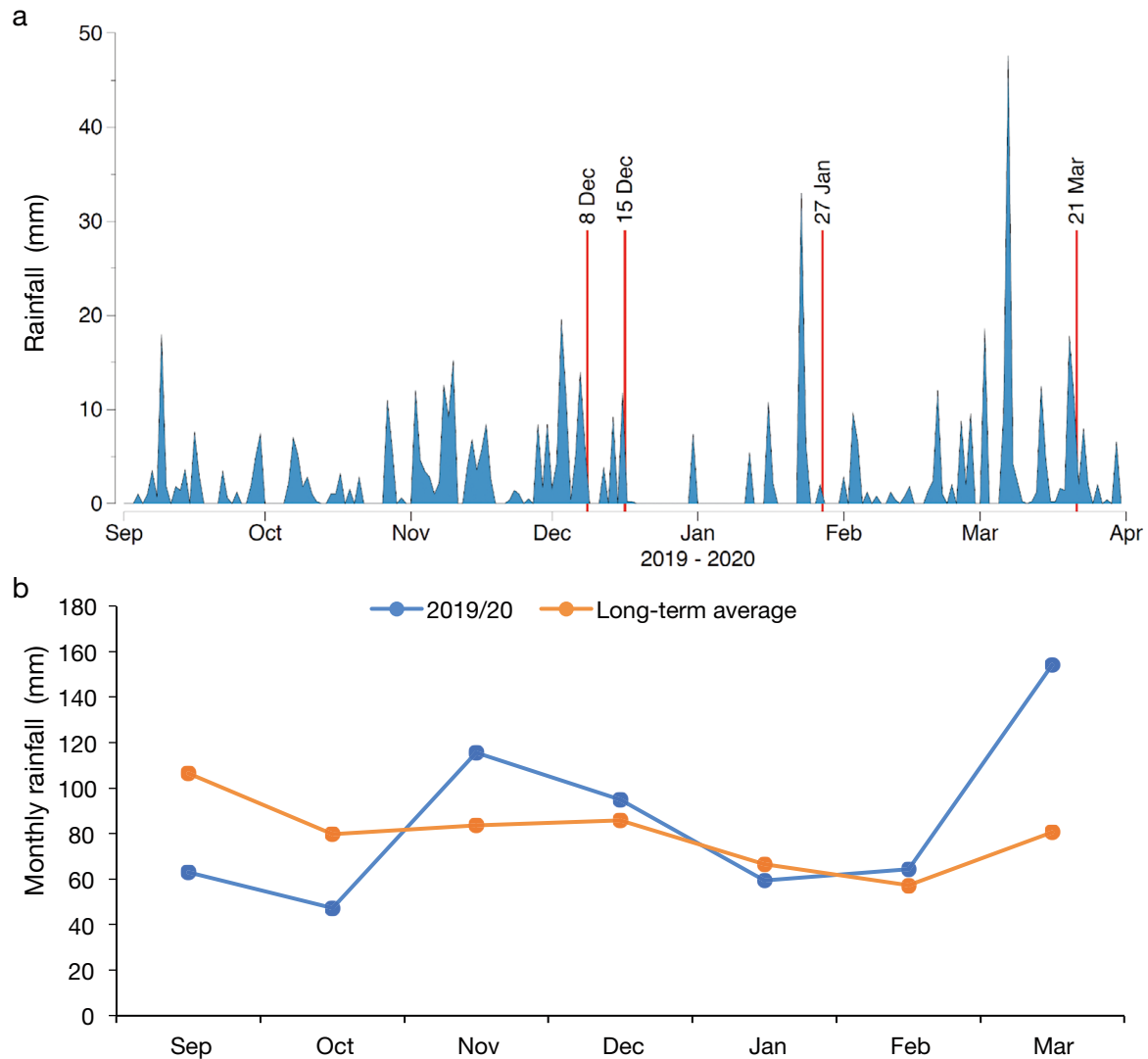


Fig. 5. Rainfall (mm) at Adventure Bay, Bruny Island, Tasmania, for the 2019/20 study period. (a) Daily rainfall. Red lines indicate dates of data collection. (b) Monthly rainfall during the 2019/20 short-tailed shearwater breeding season and the long-term average. Rainfall data obtained from www.bom.gov.au/climate/data/

recent events being under-represented in the peer-reviewed literature. Our search was limited to peer-reviewed literature and therefore we did not obtain alternative sources such as government reports and grey literature, which are often published more promptly (e.g. Siddon & Zador 2018, 2019).

4.2. Occupancy 2011/12–2019/20

Burrow occupancy m^{-2} increased at Whalebone Point following the 2015/16 season, while it remained low at The Neck. Occupancy m^{-2} was lowest at both colonies during the 2013 wreck (Fig. 3). Occupancy was higher at Whalebone Point com-

pared to The Neck during the 2016/17 and 2017/18 seasons ($p < 0.05$ for both). Wreck events were reported in the NPO during these years, but STSH were not common among beach-washed birds in the NPO (Coastal Observation and Seabird Survey Team 2016–2018, <http://explore.coasst.org:3838/Explore-data/>).

During the 2019/20 season, we documented what appeared to be a 'normal' year in terms of occupancy rates in December, but was followed by poor breeding success (see Section 4.3.2). This decrease in occupancy over the season illustrates the challenges in gauging the breeding success of a season based on single snapshots, and highlights the importance of regular monitoring throughout breeding seasons.

4.3. The anomalous 2019/20 STSH breeding season

4.3.1. Phenology

This study is the first to document a significant phenological shift in the return of STSH to their colonies, in contrast with the species' previously well-documented, highly-synchronised breeding timetable (Serventy & Curry 1984, Marchant & Higgins 1990, Price et al. 2020). Elevated ocean temperatures in the NPO coincide with a northward shift in STSH foraging areas (Kuletz et al. 2020). If STSH foraged farther north during their non-breeding season to obtain sufficient food, this would extend their southward migration to their breeding colonies and likely contributed to their delayed arrival in 2019.

Following their late arrival to breeding colonies in the second week of October 2019, STSH laid their eggs in late November at the normal laying time. The observed change in arrival date suggests that while STSH are typically very synchronous in their phenology, they have greater behavioural plasticity in their breeding phenology than previously recognised. During the 2019/20 season, breeding STSH demonstrated an ability to 'catch up' to return to their normal breeding phenology in terms of egg production and laying, despite their late return to colonies.

In addition, occupancy m^{-2} at the onset of incubation was similar to previous years despite the significant delay in their arrival of ≥ 2 wk at other Australian colonies. Although egg laying and occupancy m^{-2} were similar to previous years, the pre-laying exodus to the Southern Ocean was briefer due to their late arrival. This shorter foraging period reduced the capacity of adults to build sufficient reserves in preparation for the breeding season, and increased the likelihood of nesting failure.

Asynchrony of arrival in seabirds can contribute to higher rates of 'divorce' in breeding pairs, adversely impacting breeding success, since newly formed pairs tend to have a lower success than well-established breeding pairs (Johnston & Ryder 1987, Naves et al. 2006, 2007, Ismar et al. 2010). The extreme environmental conditions led to less synchrony in the 2019/20 STSH breeding phenology that resulted in poor overall breeding success and recruitment to the population.

4.3.2. Breeding success

Poor environmental conditions, such as the near-annual heatwaves that have been present in the NPO

since 2013, can adversely affect adult body condition, directly influencing the success of breeding attempts and individual health (Meathrel et al. 1993, Chastel et al. 1995, Bradley et al. 2000). While we cannot directly link the NPO marine heatwave to the asynchronous STSH breeding season in southeast Australia during 2019/20, the anomalous conditions experienced by wintering STSH in the NPO likely contributed to their delayed arrival and subsequent poor breeding season observed during this study (Springer et al. 2018, Price et al. 2020). Nest abandonment started during the incubation phase and continued until the end of the breeding season in the 2 study colonies. The low breeding success in the study colonies in 2019/20 is believed to have been influenced by decreased prey availability in the STSH foraging areas in the Gulf of Alaska, likely the result of anomalous oceanic temperatures (Stabeno et al. 2019, Litzow et al. 2020).

Burrow occupancy decreased by 44% in January 2020 in the 2 study colonies, further highlighting the anomalous nature of the 2019/20 STSH breeding season in Tasmania. As with egg laying, hatching also occurs during a brief period of approximately 10 d. Of the 11 eggs found in January, only 2 yielded chicks, while the remaining burrows were either found collapsed, empty, or the marker was missing (see Section 4.3.3). The variation in chick development in January was likely an indication of burrows that would fail due to low provisioning rates by adults, rather than a high level of asynchrony in laying.

Occupancy in March 2020 was 26% lower than January (hatching), resulting in an overall mean breeding success of 33% in the 2 study colonies for 2019/20. The breeding success of STSH typically ranges between 50 and 75% (Fig. 1; Serventy & Curry 1984, Carey 2011b, Robinson et al. 2015), but the maximum range is 35–82% (Table S2). As breeding success was only calculated at our 2 study colonies for the 2019/20 season, we cannot directly compare the results of this season to previous seasons that were unaffected by wrecks. The anomalous conditions in the NPO almost certainly affected the entire population of STSH, and it is expected that other STSH colonies also experienced poor breeding success in the 2019/20 season. Breeding failures in seabirds often follow wreck events (e.g. Harris & Wanless 1996, Piatt & van Pelt 1997). Wide-spread breeding failure in common murre *Uria aalge* colonies in Alaska, Oregon and California (USA) occurred during and for 2 yr following a wreck recorded in 2015/16 along the coasts of the Gulf of Alaska (Piatt et al. 2020).

Occupancy decreased most rapidly early in the incubation period of the 2019/20 season, potentially indicating carry-over effect(s) from poor foraging conditions in the NPO before the return migration (Springer et al. 2018, Piatt et al. 2020). It is possible that the STSH returned to their colonies late and with insufficient energy reserves to undertake their extended breeding season of approximately 160 d. Had occupancy decreased towards the end of the breeding season (e.g. March), it would have indicated poor foraging conditions in the Southern Ocean later in the breeding season (Price et al. 2020). Poor environmental conditions before or during the breeding season can also have long-term adverse effects on the chicks produced that year (Jenouvrier et al. 2008). Thus it is possible that the poor 2019/20 STSH breeding season could extend into the future through poor cohort recruitment to the population.

ENSO, and sea surface temperature (SST) in general, have been linked to changes in seabird prey species availability, such as krill and juvenile fish, and has been shown to impact STSH breeding success and survival (Price et al. 2020). We found no clear pattern between occupancy m^{-2} and the SOI in this study. Despite being a neutral year with regards to ENSO, very high global mean SSTs in 2013 likely resulted in reduced feeding of STSH, leading to the 2013 wreck (Einoder et al. 2013, NOAA 2014).

4.3.3. Burrow collapse

Conditions within the colony also contributed to the relatively low chick survival in 2019/20. By the end of the 2019/20 breeding season, approximately 20% of burrows in the 2 study colonies had collapsed. Other studies have previously reported between 7 and 42% burrow collapse, so the rates observed at these colonies were within the reported range (Norman 1970, Tiller et al. 2000). Two common causes of burrow collapse for seabirds are heavy rainfall and human disturbance.

Monthly rainfall in 2019/20 was similar to the long-term average in December–February, except in March, when more than 70 mm above the long-term average was recorded (Fig. 5b). The unusually high March rainfall likely contributed to the subsequent increase in burrow collapses late in the season. Catastrophic breeding failure has been reported for STSH and wedge-tailed shearwaters *Ardenna pacifica* following periods of heavy rainfall that flooded burrows, killing the eggs and drowning the chicks (Tiller et al. 2000). Rainfall results in adults aban-

doning eggs, or the reduced temperatures killing the developing embryo (DPIPWE 2019). The Neck colony had a higher proportion of burrow collapses in 2019/20, likely due to the extensive areas of exposed (unvegetated) ground.

4.4. Conclusion

The 2019/20 STSH breeding season ended in very low breeding success, likely the consequences of elevated SSTs and a wreck in the non-breeding grounds during the northern summer of 2019, which was followed by a high proportion of burrow collapses throughout the breeding season. We also document the first report of a significant phenological shift in the return of STSH to their colonies following their trans-hemispheric migration. Our study highlights the need for reporting seabird phenologies and reproductive success in the context of anomalous and extreme events, particularly in association with wrecks. Such studies can identify mechanisms affecting population trends that are increasingly important in the rapidly changing climate.

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