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TASMANIA

The role of climate variability and harvest  
impacts on the short-tailed shearwater  
(*Ardenna tenuirostris*)

by

Cassandra A. Price

B.Sc. (Zoology) M.Sc. (Antarctic Marine Science) (University of Tasmania)

Institute for Marine and Antarctic Science

Submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

University of Tasmania

March 2022

*I acknowledge the Palawa People who are the Traditional Owners of the land on which the research was conducted. I pay my respects to Elders past, present and still becoming. I also pay my respects to my ancestors, the Muruwari People, who walk with me in spirit and provide strength and guidance.*

This thesis is dedicated to my grandmother, Adelaide – ‘The Little Old Lady’.

***‘Good things come in small packages.’***

## **Declaration of Originality**

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This thesis contains no material which has been accepted for a degree or diploma by the University or any other institution, except by way of background information and duly acknowledged in the thesis. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person except where due acknowledgement is made in the text of the thesis.

Cassandra Price

Date: 4 September 2021

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## Statement of Co-Authorship

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**The following people and institutions contributed to the publication of work undertaken as part of this thesis:**

**Cassandra A. Price** (University of Tasmania)

**Dr Timothy J. Emery** (Institute for Marine and Antarctic Studies, University of Tasmania)

**Dr Eric J. Woehler** (Co-Supervisor, BirdLife Tasmania and Adjunct, Institute for Marine and Antarctic Studies, University of Tasmania)

**Dr Klaas Hartmann** (Primary Supervisor Institute for Marine and Antarctic Studies, University of Tasmania)

**Dr Nils Krueck** (Institute for Marine and Antarctic Studies, University of Tasmania)

**Mr Ross Monash** (Department of Primary Industries, Parks, Water and Environment)

**Dr Clive McMahon** (Sydney Institute of Marine Science)

**Professor Mark A. Hindell** (Co-Supervisor, Institute for Marine and Antarctic Studies, University of Tasmania)

**Professor Alan M. Springer** (Institute of Marine Science, University of Alaska Fairbanks)

**Dr Gus van Vliet** (Institute of Marine Science, University of Alaska Fairbanks)

**Dr Natalie Bool** (Institute for Marine and Antarctic Studies, University of Tasmania)

**Mike Crowley** (National Parks and Wildlife Service, State Forests of NSW)

**Peter Fullagar** (Commonwealth Scientific and Industrial Research Organisation, Division of Wildlife Research)

**Mary-Anne Lea** (Institute for Marine and Antarctic Studies, University of Tasmania)

**Caitlin Vertigan** (Institute for Marine and Antarctic Studies, University of Tasmania)



## **Contribution of work by co-authors for each paper:**

### ***PAPER 1 – Located in Chapter 2: The Fisher Island Database***

Price CA, Emery TJ, Woehler EJ, Hartmann K, Hindell MA. (Intent to submit; to be published in *Scientific Data*.)

**Author contributions:** CP (95%), KH (1%), TE (1%), EW (1%), MH (2%). Collated all historical data into a database: CP; Conceived and designed research: CP, and MH; Data collection: CP and MH; Analysed the data: CP; Oversight of data analysis MH and KH; Provided Ecological insight: EW and MH; Critically reviewed the manuscript: MH, TE, EW and KH.

### ***PAPER 2 – Located in Chapter 3: Climate variability and breeding parameters of a transhemispheric migratory seabird over seven decades***

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**Author contributions:** CP (90%), TE (2%), EW (2%), KH (2%), CM (1%), MH (3%). Collated all data into a database: CP; Conceived and designed research: CP, MH, KH; Data collection: CP, MH, CM; Analysed the data: CP; Oversight of data analysis MH and KH; Provided Ecological insight: EW and MH; Critically reviewed the manuscript: MH, TE, EW, CM and KH.

### ***PAPER 3 – Located in Chapter 4: Inter-annual and inter-colony variability in breeding performance of four colonies of short-tailed shearwaters***

Price CA, Emery TJ, Woehler EJ, Hartmann K, Monash R, Hindell MA. Inter-annual and inter-colony variability in breeding performance of four colonies of short-tailed shearwaters. *Journal of Experimental Marine Biology and Ecology*. 2021 April 537:151498.

**Author contributions:** CP (90%), TE (3%), KH (2%), EW (2%), RM (1%), MH (2%). Collated all data into a database: CP; Conceived and designed research: CP, MH, EW; Data collection: CP and RM; Analysed the data: CP; Oversight of data analysis MH, TE and KH; Provided Ecological insight: EW and MH; Critically reviewed the manuscript: MH, TE, EW, and KH.

***PAPER 4 – Located in Appendix 1: Transhemispheric ecosystem disservices of pink salmon in a Pacific Ocean macrosystem***

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**Author contributions:** AMS (24%), GBV (24%), NB (20%), CP (20%), EW (4%) MC (2%), PF (2%), ML (2%), RM (1%), CV (1%). Conceived and designed research: AMS and GBV; Performed the research: all authors; Data collection: CP and RM; Formatting of data: CP, NB, AMS and GBV; Analysed the data: AMS and GBV; Provided Ecological insight: CP, NB, AMS, GBV, EW; Wrote the manuscript: AMS, GBV, CP (harvest) NB (wrecks); Critically reviewed the manuscript; CP, NB, EW, RM.

**We, the undersigned, endorse the above stated contribution of work undertaken for each of the published (or submitted) peer-reviewed manuscripts contributing to this thesis:**

Signed:

Cassandra Price

Klaas Hartmann

Catriona MacLeod

Candidate

Primary Supervisor

Head Ecology & Biodiversity  
Centre

Institute for Marine and  
Antarctic Science  
University of Tasmania

Institute for Marine and  
Antarctic Science  
University of Tasmania

Institute for Marine and  
Antarctic Science  
University of Tasmania

Date: 4 September 2021

## **Statement of Ethical Conduct**

---

The ethical guidelines of University of Tasmania Animal Ethics Committee were followed throughout this study. This research was conducted under University of Tasmania Animal Ethics Permit A14277 and the Tasmanian Department of Primary Industries, Parks, Water and Environment Scientific Research Permit FA14310.

Cassandra Price

Date: 4 September 2021

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---

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## **Preface**

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## ABSTRACT

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Environmental variations play an important role in the population dynamics of seabirds, as they influence key aspects such as survival and individual breeding success. Oscillating climatic conditions (*e.g.* the Pacific Decadal Oscillation [PDO] and the El Niño–Southern Oscillation [ENSO]) dramatically alter marine productivity, both spatially and temporally. Unpredictable environmental conditions result in prey distributions that are highly variable, patchy and unpredictable, which influences the foraging behaviour of marine predators. Small changes in oceanographic conditions can adversely affect primary productivity and therefore influence seabird foraging success, including that of the short-tailed shearwater.

The short-tailed shearwater (*Ardenna tenuirostris*, previously known as *Puffinus tenuirostris*) is a transhemispheric migratory seabird that breeds only in south-eastern Australia and migrates to the northern Pacific Ocean for the austral winter (Skira 1996). They are commonly known as the ‘mutton bird’, and their chicks are subject to annual commercial and recreational harvesting in Tasmania. The short-tailed shearwater population is fully protected and not harvested elsewhere in Australia. Currently, some short-tailed shearwater populations in south-eastern Australia are decreasing, but it is unclear what is driving this decrease. The factors influencing the population decrease may include changes to resources, in addition to, or even compounded by, the local harvesting of chicks and subsequent lower recruitment rates into the breeding population.

In this study, we investigated the breeding parameters of short-tailed shearwater from four harvested colonies (study period 2010 to 2018) and one unharvested colony (study period 1950 to 2012) within the Furneaux Islands, Tasmania, Australia. The aim was to quantify the relationship between breeding parameters and large-scale climate indices in the Northern Hemisphere (*i.e.* Northern Pacific Index and PDO) and Southern Hemisphere (*i.e.* ENSO and Southern Annular Mode [SAM]). We found that breeding parameters (*e.g.* breeding attempts and fledging rates) were influenced by large-scale climate conditions in the preceding year, and by local conditions such as rainfall. These findings demonstrate that both large-scale climate indices (*e.g.* PDO, SAM) and local environmental conditions can explain some of the variability among the breeding parameters of short-tailed shearwater within colonies in the Furneaux Island Group.

A feasibility study was also undertaken using a fisheries stock assessment package (*i.e.* C<sup>++</sup> Algorithmic Stock Assessment Laboratory [CASAL] framework) to conduct an integrated

assessment for short-tailed shearwater. We used data from a historical capture-mark-recapture program of an entire colony (100 to 200 birds) of short-tailed shearwater at Fisher Island, Furneaux Island Group, for the period 1947 to 2017, to estimate unknown population parameters and empirical data from the census (observations) to fit the model parameters (*e.g.* age frequency and abundance). We found this approach was appropriate for short-tailed shearwater. We also identified specific aspects of this approach that would require further work to enable the results to be used to inform management decisions.

The outcomes of this study address existing knowledge gaps and improve the understanding of the factors affecting short-tailed shearwater populations. The feasibility study provides a baseline for ongoing scientific management advice to improve the sustainability of the annual harvest of short-tailed shearwater, with further studies needed to conduct a fully parameterised sustainable harvest model.

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## INTRODUCTION

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Short-tailed shearwater, *Ardenna tenuirostris*

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## 1.1 Seabirds as Indicators of Ecosystems

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The importance of seabirds, particularly procellariiformes (*i.e.* albatross, petrels and shearwaters), as top-order predators in the marine environment is well known (*e.g.* Warham 1990, Weimerskirch & Cherel 1998, Connan *et al.* 2010). Seabird species are often used as indicator taxa for monitoring large-scale resource availability and environmental changes within the marine environment (McDonald *et al.* 2008). Procellariiformes have low production potential (*e.g.* low reproductive rates, single-egg clutch and delayed recruitment into the breeding population), which is an adaption to the highly variable marine productivity (Warham 1990, Weimerskirch *et al.* 2001, Meathrel & Carey 2007). Procellariiformes are typically migratory and spend the majority of their lives at sea, travelling great distances and utilising a variety of habitats during the breeding and non-breeding periods. Throughout their migration and breeding/non-breeding periods, many species of procellariiformes are exposed to a variety of weather, environmental conditions and oceanographic systems in both the Northern and Southern Hemispheres (Weimerskirch & Cherel 1998, Einoder *et al.* 2013, Yamamoto *et al.* 2015, Nishizawa *et al.* 2017).

Many high-order predators in the Southern Ocean are used as indicator species to identify shifts in the marine environment and availability of resources (McDonald *et al.* 2008). In particular, seabirds are often used because they are sensitive to changes in the oceanic environment and respond to environmental perturbations on a range of temporal and spatial scales (McDonald *et al.* 2008). For example, long-term declines in a population of seabirds may indicate a risk to the health of the marine ecosystem because changes in resource availability can affect their reproductive output and population growth (McDonald *et al.* 2008). Whereas short-term variations in the distribution of prey species (*e.g.* krill, fish and squid) due to positioning frontal systems may lead to a higher concentration of marine predations (Weimerskirch & Cherel 1998, Nishizawa *et al.* 2017). For example, the Ross Sea's Continental Shelf in the Southern Ocean is a region where mixing in the water and the oceanic frontal structures drive the primary and secondary production within the area (Ainley *et al.* 1995, Ainley *et al.* 2005, Ainley & Hyrenbach 2010). As a result, the seabird abundance is a magnitude of 10 greater than the adjacent waters (Bost *et al.* 2009).

## 1.2 The Southern Ocean

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The Southern Ocean covers approximately 10% of the world's oceans and is one of the most productive (Biuw *et al.* 2007), supporting a large biomass of high-order predators such as marine birds and mammals (Croxall 1992, Constable *et al.* 2003). The large-scale physical processes influencing the productivity of the Southern Ocean are the frontal systems within the Antarctic Circumpolar Current (ACC) and the seasonal variability in sea ice extent around the Antarctic Continent (Abrams 1985, Constable *et al.* 2003). The ACC plays a significant role in ocean circulation and is associated with many frontal systems, including the Sub-Antarctic Front (SAF), the Antarctic Polar Front (APF) and the Southern ACC Front (SACCF) (Talley 2011). The primary front in the Southern Ocean is the APF, which separates physical and biological regimes from other oceans, and divides the Southern Ocean into two distinct regions: the Sub-Antarctic and Antarctic (Abrams 1985, Constable *et al.* 2003).

Frontal systems are defined by the convergence of two water masses (Constable *et al.* 2003, Talley 2011). The different levels of freshwater, precipitation and evaporation patterns and temperature gradients contribute to the formation of distinct water masses. Water mass formation is largely controlled by temperature and salinity, which together determine density (Constable *et al.* 2003, Talley 2011). The seasonal growth and melt of sea ice extent is largely what forms the water masses in the Antarctic. There are three primary water masses in the Southern Ocean: Antarctic Bottom Water, Circumpolar Deep Water and Antarctic Surface Waters (Talley 2011). Antarctic Bottom Water is the deepest, consisting of cold dense saline water forming over the continental shelf through a process known as brine during ice production. These water masses contribute to the productivity within the Southern Ocean, through the effects of wind stress combined with the Ekman transport system, currents and bathymetry, causing upwelling, eddies and polynyas (Speer *et al.* 2000, Lumpkin & Speer 2007).

The coastal oceans of the Antarctic Continent are highly productive, and physical processes such as gyres, coastal currents and prevailing winds aid in moving this productivity offshore (Constable *et al.* 2003). Localised events such as upwelling, associated with existing bathymetric features, have also been shown to increase productivity (*e.g.* on the Kerguelen Plateau) (Constable *et al.* 2003). The spatial and temporal distributions of nutrients are influenced by interactions between bathymetry and oceanography (Biuw *et al.* 2007). Physical and oceanographic conditions can influence bottom-up processes such as primary and secondary

productivity, which in turn can influence the foraging patterns, reproductive performance and survivorship of high-order predators such as seabirds.

The Southern Ocean is a key foraging area for short-tailed shearwater (STSH) during the pre-breeding and breeding period (across oceanic regions longitude from 80°E and 160°E), feeding predominantly on myctophids (fish) and euphausiids (*E. vallentini*) (Weimerskirch & Cherel 1998, Connan *et al.* 2010, Einoder *et al.* 2013) (see Section 1.5).

### **1.3 Oceanographic Influences on Phytoplankton**

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Phytoplankton growth is predominately in the euphotic zone, where water is subject to sunlight, enabling photosynthesis. The growth and distribution of phytoplankton are influenced by changes in temperature, light and nutrient accessibility (Danovaro *et al.* 2001). Nutrients are supplied to the euphotic zone through vertical mixing of the surface layer, commonly known as the mixed layer, and through upwelling, the supply of deep nutrient-rich waters to shallow warmer layers through wind-driven processes (Danovaro *et al.* 2001). Wind conditions can affect upwelling and the depth and strength of the mixed layer, which in turn influence the availability of nutrients and light to phytoplankton (Hallegraeff 2010). Wind conditions can also influence the deposition of atmospheric dust nutrients (*e.g.* Aeolian dust deposition) such as iron from land to sea, which can also determine phytoplankton production and influence blooms (Danovaro *et al.* 2001).

Ice formation is an important process of the Southern and Northern Pacific Oceans and can provide favourable conditions for phytoplankton blooms (Hays *et al.* 2005, Boyd *et al.* 2008, Massom *et al.* 2008). Changes in sea ice conditions, such as spatial extent, thickness and duration, strongly influence primary productivity (Priddle *et al.* 1992). During ice-free conditions, surface wind stress can cause a deepening of the mixed layer, which can cause a decrease in phytoplankton production due to the critical depth limit (*i.e.* phytoplankton's ability to receive light for photosynthetic activity) (Montes-Hugo *et al.* 2009). Changes to these oceanographic conditions will have indirect and direct effects on phytoplankton growth and dynamics, thereby driving bottom-up processes and influencing higher trophic levels (Hays *et al.* 2005, Boyd *et al.* 2008). For example, in the Northern Hemisphere, the Amerasian shelf system in the northern Bering and southern Chukchi seas are highly productive marine ecosystems, supporting many top-order marine vertebrate species such as whales, seabirds and walrus (Grebmeier *et al.* 2006). This is primarily due to nutrient-rich Pacific waters flowing

northwards to the Arctic Ocean, and the seasonal sea ice dynamics contributing to high primary productivity and phytoplankton blooms (Grebmeier *et al.* 2006).

## **1.4 The Study Species: Short-Tailed Shearwater**

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The short-tailed shearwater (STSH), *Ardenna tenuirostris*, previously known as *Puffinus tenuirostris*, is a burrow-nesting medium-sized (500 to 800 g) procellariidae, also known as the Tasmanian mutton bird (Skira 1990, Berlincourt & Arnould 2015). They are a transhemispheric migratory seabird which spend the non-breeding period (approximately April to September) in the Northern Hemisphere, in the North Pacific Ocean (Carey *et al.* 2014). In September/October, STSH return to south-eastern Australia to breed (Skira 1991). Breeding adults tend to arrive in the colonies in late September and re-establish the pair bonds or find a new mate. They scratch out pre-existing burrows or dig a new burrow in preparation for mating (Serventy 1967, Serventy & Curry 1984, Wooller *et al.* 1990). Pairs copulate on land and depart for approximately 20 days at sea, before returning in November to lay (Serventy & Curry 1984).

Laying is highly synchronised, with 95% of eggs laid between 24 to 28 November; females can only lay a single egg, which is not replaced if it fails (Skira 1990). Incubation is approximately 53 days and each incubation shift is about 10 days or more; both parents alternate shifts, with the first undertaken by the male (Serventy 1967, Serventy & Curry 1984, Wooller *et al.* 1990). The chick hatches in mid-to-late January and chicks fledge in mid-April to early May (Serventy 1967, Wooller *et al.* 1990). At some colonies in Tasmanian, the chicks are subject to annual commercial and recreational harvesting known as ‘mutton birding’, which occurs between mid-March and the end of April (Skira & Wapstra 1980). After the breeding season, both adults and fledglings migrate to the North Pacific Ocean (Shaffer *et al.* 2006, Raymond *et al.* 2010, Vertigan *et al.* 2012).

## **1.5 Foraging Ecology of the Short-Tailed Shearwater**

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The diet of the STSH is highly variable across regions, seasons and years (Yamamoto *et al.* 2015, Nishizawa *et al.* 2017). Prey species include myctophids (fish), cephalopods (squid), copepods (zooplankton) and krill (euphausiids), with krill being the main component of their diet (Weimerskirch & Cherel 1998). Short-tailed shearwater feed on a variety of krill species: *Tysanoessa raschii* (Arctic krill) in the Northern Hemisphere, and *E. vallentini* (Sub-Antarctic

krill) and some reports of *E. superba* (Antarctic krill) in the Southern Hemisphere (Connan *et al.* 2010, Yamamoto *et al.* 2015, Nishizawa *et al.* 2017).

### **1.5.1 Northern Hemisphere**

During the non-breeding period (May to September), STSH forage mostly in two highly productive areas of the North Pacific Ocean: (i) the Oyashio Current and Sôya Current of Japan, and the Sea of Okhotsk and Liman Current in the Sea of Japan; and (ii) the waters around the Aleutian Islands and the southern Bering Sea (Carey *et al.* 2014). Some individuals may initially migrate to the waters off Japan, then move on later into the Bering Sea, although birds that migrate initially into the Bering Sea do not later migrate to the waters of Japan (Carey *et al.* 2014). The change in their distribution is often related to prey species, as the STSH tend to follow the primary production blooms associate with sea ice retreat. Before commencing their annual migration to breeding grounds in south-eastern Australia, individuals foraging in the Northern Pacific Ocean disperse farther north, around the Bering and Chukchi Seas, following the distribution of krill (Baduini *et al.* 2001a, Yamamoto *et al.* 2015, Nishizawa *et al.* 2017). The non-breeding period is important for building body reserves before the return migration, as a failure to adequately build sufficient reserves can impede the birds' ability to migrate and/or breed successfully in the following season (Lovvorn *et al.* 2003, Bester *et al.* 2007).

### **1.5.2 Southern Hemisphere foraging habitats**

The Southern Ocean is a key foraging area for STSH during the breeding season and for non-breeding birds. Following their migration to Australia, and before commencing breeding, STSH undertake a foraging trip to the Southern Ocean (*i.e.* honeymoon period) to restore body reserves that have been lost during the migration (Lill & Baldwin 1983). Adult STSH also forage within the Southern Ocean throughout the breeding season to maintain body reserves during the breeding period (Weimerskirch & Cherel 1998, Einoder *et al.* 2013).

STSH use a dual foraging strategy throughout the breeding season, which is employed by many species of procellariiformes (Einoder *et al.* 2011, Einoder *et al.* 2013, Berlincourt & Arnould 2015). This comprises of alternating short (local) and long (distant) foraging trips to highly productive areas, which are often characterised as physical structures such as frontal zones and shelf slopes. Shorter foraging trips are typically close to the breeding colonies (foraging ranges 200 to 240 km) and are between 1 to 3 days (Einoder *et al.* 2011, Einoder *et al.* 2013, Berlincourt & Arnould 2015). The shorter foraging trips are primarily for chick provisioning; however, these trips can result in deterioration of parental body condition as the energy reserves become

depleted (Einoder *et al.* 2011, Berlincourt & Arnould 2015). Longer foraging trips are designed to replenish adult body reserves (Weimerskirch & Cherel 1998, Einoder *et al.* 2013). These foraging trips are between 7 to 30 days and can cover over 1000 to 4000 km (Weimerskirch & Cherel 1998, Einoder *et al.* 2013, Berlincourt & Arnould 2015) to regions of the Southern Ocean characterised by physical structures such as frontal zones and shelf slopes (Woehler *et al.* 2003, Raymond *et al.* 2010).

During long trips, STSH forage predominately south of the Antarctic Polar Front (APF) in Antarctic waters in the Southern Ocean (Raymond *et al.* 2010, Berlincourt & Arnould 2015) (Woehler *et al.* 2003, Raymond *et al.* 2010). Short-tailed shearwaters have been observed over offshore waters around and to the south of the APF from 60°E to 150°E, with high densities of STSH around the APF (~140°E) (Raymond *et al.* 2010). Tracking studies confirmed STSH in the Southern Ocean 80°E and 160°E (Berlincourt & Arnould 2015). These are known to be areas of high upwelling and are driven by interaction with the ACC and large-scale bathymetric features (Raymond *et al.* 2010). South of the APF, productivity is also greater due to a number of processes, such as increased upwelling rates, iron input from the sea ice melting and shallower mixed layers (Raymond *et al.* 2010). Highly productive foraging areas are important throughout the breeding season to ensure STSH can maintain body condition, as during periods of low prey availability they may abandoned the nest or chick to preserve self-condition (Weimerskirch *et al.* 2001).

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## **1.6 Climate Variability**

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Due to the trans-equatorial migratory nature of STSH, they spend the majority of their lives at sea, travelling great distances and utilising a variety of habitats during the breeding and non-breeding periods (Weimerskirch & Cherel 1998, Einoder *et al.* 2013, Berlincourt & Arnould 2015). Consequently, STSH are exposed to a variety of weather, environmental conditions and oceanographic system. Oceanographic properties are influenced by large-scale physical forcing that alters atmospheric conditions, sea-level pressure and ocean temperature, which in turn affects bottom-up processes such as changes in primary and secondary productivity (Zador *et al.* 2013, Cushing *et al.* 2017). Therefore, environmental conditions can influence resource availability in both the non-breeding and breeding foraging grounds, which may in turn affect the breeding parameters of the STSH.

Climate variability in the Northern Hemisphere and Southern Hemisphere can be measured by large-scale climate indices. In the Northern Hemisphere, Pacific Decadal Oscillation (PDO) and

North Pacific Index (NPI) are the dominant climate drivers, and are known to influence seabird demography, abundance and distribution (Baduini *et al.* 2001a, Hunt Jr *et al.* 2002, Bond *et al.* 2011). In the Southern Hemisphere, the primary climate drivers are El Niño–Southern Oscillation (ENSO) and Southern Annular Mode (SAM) (Gaynor *et al.* 2010), which have both been linked to the breeding performance of seabirds (Duffy 1990, Clucas 2011, Humphries & Möller 2017, Pardo *et al.* 2017). These four climate indices affect marine ecosystems on temporal scales from months to years (Trathan *et al.* 2007, Sallée *et al.* 2008), which may impact the breeding parameters of the STSH.

## **1.7 History of Mutton Birding**

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Short-tailed shearwater chicks at selected colonies in Tasmania are subject to annual commercial and recreational harvest, known as ‘mutton birding’. The harvest of STSH chicks takes place in early March and continues until the end of April (Skira & Wapstra 1980). Elsewhere, STSH are a protected species in all States and Territories of Australia and are therefore not allowed to be harvested (Skira 1990, Skira 1993). They are also protected by international bilateral treaties under the Japan–Australia Migratory Bird Agreement (JAMBA), the China–Australia Migratory Bird Agreement (CAMBA), and the Republic of Korea–Australia Migratory Bird Agreement (ROKAMBA). The management of the STSH harvest is the responsibility of the Tasmanian Department of Primary Industry, Parks, Water and the Environment (DPIPWE), and recreational harvest is managed under the *Nature Conservation Act 2002* and *Wildlife Regulations 2010*, while commercial harvest is managed under the *Aboriginal Lands Act 1995*. Tasmanian Aboriginals have historically been involved in the mutton bird industry, and currently operate the commercial harvest, which is of high social and economic importance to the Aboriginal community of the Furneaux Island Group and throughout Tasmania (Skira *et al.* 1986, Skira 1990).

The commercial exploitation of STSH began in the early 1820s soon after the arrival of European settlers, with early estimates of harvest as high as one million chicks per annum (Skira 1990). In the late 1800s, as sealing declined, mutton birding became increasingly more important for the economy of the Furneaux Island Group (Skira 1993). Adult STSH were predominantly harvested for their feathers for bedding (*e.g.* mattress fill), and their meat was sold commercially, either salted or smoked, for human consumption. Similarly, the meat of the chicks was commercially harvested for human consumption, mainly sold fresh or frozen (Skira 1990, Skira 1993). The

proventricular oil of the chick was harvested for medicinal and stock use (Skira 1990). Some STSH eggs were also taken, but only used for personal consumption.

For most of the 1800s, STSH were harvested with little consideration for conservation or management of the species (Skira 1993). However, this began to change in 1891, when the first piece of legislation was introduced to regulate the industry. A restricted season was introduced, which permitted the take of STSH to only between 20 March and 20 May each year (Skira 2001). In the early 1900s, the sustainability of the industry was in question due to the continual high number of birds harvested annually, compounded by the limited knowledge of their biology (Skira 1993). This led to a number of regulations being implemented, such as a prohibition on the harvesting of eggs; licences were introduced to permit the harvesting of STSH for either personal use or commercial purposes.

In 1928, the *Animals and Birds Protection Act* was introduced to provide protection and conservation to wild animals and birds in Tasmanian, and for other purposes (Skira 1993). Under this Act, more regulations were introduced to manage the mutton bird industry, including a shortened season length and prohibiting the harvesting of STSH at night. However, the take of adult STSH was not prohibited until 1976 (Skira 2001). In 1941, the level of STSH harvest was still of great concern. A catch limit of 10,000 birds per commercial operation was proposed to protect the species from overharvesting and an over-supply to the markets. This limit was not accepted by the industry and resulted in the catch limit not being implemented (Skira & Wapstra 1980, Skira 1993). In 1947, regulations were introduced requiring commercial operators to submit a catch return showing the number of birds taken per season (Skira 2001).

A banding program at the commercial islands was introduced to determine the level of harvest and understand the biology of the species. Between 1947 and 1976, over 100,000 birds were banded, with commercial harvesters and workers required to return the bands from any harvested bird. Harvesters were apprehensive, and feared that if the bands were returned catch limits would be reduced or the industry closed (Skira 1993). Due to the lack of compliance regarding band returns, the program was ceased in 1976, and replaced with a population census (Skira 1993). A research banding study was established at Fisher Island in 1947, where the harvest of STSH was prohibited. The aim of the study was to provide biological information for the sustainable management of the STSH, and was established with the vision of being a long-term project (Bradley *et al.* 1991).



Recreational harvesting began to increase in the early 1950s, adding further harvesting pressure onto the species. By 1977, there was 7924 recreational licences issued in Tasmania, and surveys of colonies close to Hobart revealed that harvesting pressure was very high, with over 90% of chicks harvested from these areas annually (Skira 1993). This prompted a reduction in the season length, and education material was distributed to recreational participants. However, these regulatory controls had little effect on reducing the harvest. It wasn't until the late 1980s and early 1990s that regulations were introduced to reduce the daily bag limit (*e.g.* number of birds harvested per recreational licence) to those colonies that permitted recreational harvest. For example, on the islands in Bass Strait (*e.g.* Hunter Group, Furneaux Islands and King Island) bag limits were reduced from 50 to 25 birds a day, and on the west coast of Tasmania bag limits were reduced from 25 to 15 birds a day (Skira 1993).

Currently, commercial and recreational harvest rates vary annually. Between 2007 and 2017, approximately  $72,000 \pm 8800$  chicks were commercially harvested annually (Springer *et al.* 2018). For the period 2011 to 2016, an average  $884 \pm 44$  recreational licenses were sold annually, which resulted in an average annual recreational harvest of  $34,500 \pm 5300$  chicks (Springer *et al.* 2018). Since the 1980s, the commercial industry has been largely self-regulated and no quota limits are currently in place (Skira *et al.* 1986). Recreationally, bag limits have remained relatively the same over this period, at 25 birds on colonies in Bass Strait islands and 15 birds on Tasmanian mainland colonies. However, recreational licence-holders must report the number of STSH harvested each year. The population of STSH at recreational and some commercial harvested colonies are monitored annually by a population census survey (monitored by DPIPW and the Tasmanian Aboriginal Centre, retrospectively) and colonies may be closed if the bird numbers are low.

Historical surveys show that 90% or more chicks were harvested from colonies (open for harvest) in a season by recreational harvesters (Skira *et al.* 1986, Skira 1990), which would undoubtedly cause a significant reduction in the number of recruits into the breeding population. Given the long generation times ( $\sim 45$  years) of STSH (Bird *et al.* 2020), the resultant effects on colonies from intense harvesting can be delayed for many years (Skira & Wapstra 1980) and long-term series are needed to track the population trends. Exacerbating the effects of long generation times is the fact that STSH are highly philopatric and may therefore be particularly vulnerable to over-exploitation. However, little is presently known about the population structure, harvest rates and environmental conditions that may be of influence. The outcomes from this study will provide

the initial steps needed to provide ongoing support and recommendations for management strategies of the STSH.

## **1.8 History of Fisher Island Research Station**

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Fisher Island (40°13'S, 148°14'E) is a small island (0.9 ha) located within the Furneaux Group, Tasmania. Since 1947, a small colony of STSH have been monitored annually through an extensive capture-mark-recapture program (Bradley *et al.* 1991). Initially, the program was a collaborative project between the (then) Fauna Board of Tasmania and the Commonwealth Scientific and Industrial Research Organisation (CSIRO), and was led by CSIRO's ornithologist Dr Dominic Serventy (Wooller *et al.* 1985).

A previous study was undertaken by a police sergeant, Mr George Fisher (the island's namesake), to band STSH on the island from 1931 to 1935 (Skira 1993). The study fitted celluloid leg bands to the birds, but no records of any individual returning were ever made (Skira 1993). In 1947, copper leg bands were used for banding; however, they rapidly deteriorated and were replaced in 1950 with Monel bands (a nickel-copper alloy) (Wooller *et al.* 1985). As the study developed, many birds were double-banded to assess band wear and band loss (Wooller *et al.* 1985). Some bands lasted up to 30 years, while some became unreadable around 20 to 25 years later (Wooller *et al.* 1985).

In 1948, Serventy proposed the erection of a hut for field staff. The hut was built, and is used for banding to this day following renovations in 2019 (Skira 1993). The initial CSIRO study aimed to investigate the homing, duration of immaturity, pair bonding, incubation stages and longevity of the STSH (Bradley *et al.* 1991). To protect the birds from recreational harvest, Serventy suggested that heavy penalties should be applied to those interfering with the colony (Skira 1993). The monitoring of the STSH on Fisher Island continues today, through a collaboration between the DPIPWE and the Institute for Marine and Antarctic Science (IMAS), with the support of the Australian Bird and Bat Banding Scheme (ABBBS) and the Friends of Fisher Island.

## **1.9 Current Abundance and Threats to the Short-Tailed Shearwater**

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The abundance of STSH has been monitored episodically since the 1940s, with the last population estimate from the early 1980s reported the population to be approximately 23 million breeding birds in around 285 colonies in south-eastern Australia (Wooller *et al.* 1989, Skira *et*

*al.* 1996). The last survey of colonies in the late 1990s around the coast of Tasmania and the offshore islands were around 209 known colonies distributed over an estimated area of 1813 ha, with approximately 11.5 million burrows (Skira *et al.* 1996). During these surveys the percentage of burrow occupancy was not recorded, which is a limitation for estimating the overall abundance of STSH in Tasmania. Moreover, limited surveys have been conducted since earlier studies and the total population of STSH in south-eastern Australia is currently unknown.

A number of anthropogenic threats and catastrophic events have occurred since the last population estimates, which may have influenced the abundance of the STSH. During 1952 to 1991, several million STSH were killed as bycatch in salmon and squid driftnet fisheries in the northern North Pacific Ocean (Ainley *et al.* 1981, DeGange & Day 1991). However, the impact of mortality due to this bycatch on the population size and structure remains unclear.

Small plastic particles are commonly found in the stomachs of seabirds, and exposure to this threat is increasing as plastic pollution is increasing (Barnes *et al.* 2009). Studies have shown that a large number of STSH have been found with plastics in their stomachs (Skira 1986, Skira *et al.* 1996, Cousin *et al.* 2015, Puskic *et al.* 2020). For example, 96% of STSH chicks seized from an illegal harvest from a Tasmania population contained a mean plastic mass of 14.81 mg per bird (Cousin *et al.* 2015). Plastic ingestion has been a known issue for STSH since the early 1970s; however, the long-term impacts of plastic ingestion is unknown. Currently, there is no evidence demonstrating adverse physical health effects at a population level (Skira 1986, Skira *et al.* 1996, Cousin *et al.* 2015). The potential risk of toxicology from plastic ingestion by chemicals such as polybrominated diphenyl ethers (PBDE) and polychlorinated biphenyls (PCB) leaching into seabird tissues are still being investigated, and the effects of these contaminants on seabirds remain unknown (Yamashita *et al.* 2011, Cousin *et al.* 2015).

Since the 1970s, the abundance of pink salmon (*Oncorhynchus gorbuscha*) has increased in the North Pacific Ocean, potentially leading to resource competition for the STSH, as the diets of both species overlap (Springer *et al.* 2018). Resource competition has been hypothesised as a contributing factor to annual fluctuations of breeding STSH at Montague Island, as well as a contributing factor to mass mortalities (*i.e.* beach-washed ‘wrecks’) (Springer *et al.* 2018). Several wrecks in the Northern and Southern Hemispheres have also been linked to higher sea-surface temperature (SST) and reduced krill availability to STSH, resulting in death from starvation (Baduini *et al.* 2001a, Springer *et al.* 2018).

Climate change is an emerging threat to marine ecosystems and species (Chambers *et al.* 2011, Chambers *et al.* 2015). Seabirds are high-order predators and are therefore influenced by changes within the marine environment, including SST, salinity, wind speed, wind direction which influence prey distribution (Gorta *et al.* 2019). Climate change is expected to have a profound and complex effect on most species of seabirds (Chambers *et al.* 2011); however, the effects will differ between species due to the foraging techniques and ability to adapt to local environmental conditions (Chambers *et al.* 2011, Oro 2014). Higher SST can have a significant effect on the breeding success, timing and increased mortality rates of seabirds through significant changes in prey availability (Chambers *et al.* 2015).

The adverse influence of increasing SST has been demonstrated for many species of seabirds, including STSH (Baduini *et al.* 2001a, Baduini *et al.* 2001b). A widespread STSH mass mortality event occurred in the 2013 to 2014 season following the adults' return from the trans-equatorial migration (Springer *et al.* 2018) likely due to severe weather, increased SST and low prey availability (Berlincourt & Arnould 2015). South-eastern Australia has been identified as a global warming hotspot, with marine waters warming almost four times the global averages (Frusher *et al.* 2010, Chambers *et al.* 2015), which may have further implications for the STSH.

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## **1.10 Research Aims and Thesis Structure**

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Short-tailed shearwaters populations are decreasing at some colonies in south-eastern Australia (including Tasmania), but it is unclear what factors may be responsible (Vertigan 2010, Schumann *et al.* 2014). A 35% decrease in the abundance of STSH between 1978 and 1980 and between 2008 and 2011 was estimated from a survey at the islands of north-central Bass Strait (Schumann *et al.* 2014). The factors involved in the decrease remain unknown, but may include decreased productivity at the major Northern and Southern Hemisphere foraging areas and increased competition for marine prey. Climate change is likely to be implicated, or even the commercial and recreational annual harvest of fledglings, which lowers recruitment rates into the breeding population. Identifying the effects of climate variation or poor harvest management for STSH is necessary to develop enhanced policies and regulations to mitigate the effects of factors.

Therefore, the objectives of this study are to: (i) compile all of the historical data from an extensive long-term capture-mark-recapture (CMR) from a colony STSH at Fisher Island into a centralised database; (ii) investigate the annual trends in the breeding parameters of the STSH at multiple breeding colonies within the Furneaux Island Group (*i.e.* Fisher Island, Little Green

Island, Little Dog Island, Big Green Island and East Kangaroo Island), and to investigate the relationships among large-scale climate indices and local environmental conditions on the breeding parameters of the STSH at multiple colonies within the Furneaux Islands; and (iii) to examine the feasibility of using a fisheries stock assessment model to conduct an integrated assessment for the STSH population.

The thesis is structured with chapters reporting on specific studies that have been published or submitted for publication to peer-reviewed journals. Chapter 2 outlines the construction of the Fisher Island STSH database which forms the basis of the long-term (70 year) analysis. Chapter 3 investigates the breeding parameters of the STSH at Fisher Island (from 1947 to 2017) and the relationship with climate and environmental conditions in the Northern and Southern Hemispheres. Chapter 4 explores the breeding parameters of the STSH and the relationship with climate and environmental conditions at four harvested colonies (*i.e.* Little Green Island, Little Dog Island, Big Green Island and East Kangaroo Island) within the Furneaux Island Group. Chapter 5 investigates the feasibility of using a fisheries stock assessment package (CASAL) for conducting an integrated assessment for a the STSH. The General Discussion (Chapter 6) is the amalgamation of the thesis, and discusses the findings found within the study.

## CHAPTER TWO

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### THE FISHER ISLAND DATABASE

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Fisher Island

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## Abstract

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The Fisher Island database was created in 2018 to consolidate long-term field data from a colony of short-tailed shearwater (*Ardenna tenuirostris*) at Fisher Island, Tasmania, Australia. This population of birds has been monitored annually since 1947 through an extensive capture-mark-recapture (CMR) field program. The data was collated from a variety of sources, including historical banding records from the Tasmanian State Library Archives, researchers' personal handwritten notebooks and electronic banding data from the Australian Bird and Bat Banding Schemes (ABBBS). The database is comprised of records from approximately 4000 individual birds and 16,000 observations/resights. Previous studies have used this data to investigate the homing, duration of immaturity, pair bonding, incubation stages and longevity of the short-tailed shearwater, however the additional data will enable a broader spectrum of research investigations, including, but not limited to, an examination of the population-level consequences of global warming and further studies to quantify the demographic parameters of the species.

## 2.1 Introduction

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The short-tailed shearwater (STSH), commonly referred to as the 'mutton bird', or *yolla* in the language of the Palawa (Tasmanian Aboriginal) People, is a medium-sized (500 to 800 g) burrow-nesting procellariiform (Skira 1990, Berlincourt & Arnould 2015), with pronounced pan-oceanic migration. Short-tailed shearwaters are long-lived, up to 48 years (see <https://www.environment.gov.au/cgi-bin/biodiversity/abbbs/abbbs-search.pl>), and a mean age at first breeding of approximately 7 years (Wooller *et al.* 1990, Bradley *et al.* 1991).

The breeding population occurs in south-eastern Australia, with the majority of colonies located in Tasmania and many of the offshore islands (Skira 1991, Skira *et al.* 1996). Each September to October, STSH return from their non-breeding foraging areas in the North Pacific Ocean to breed in south-eastern Australia. The breeding season commences in September when their burrows are re-occupied, and in late November one egg per nest is laid. Hatching occurs from mid-to-late January (Carey 2010) and chicks fledge in mid-April to early May (Serventy 1967, Wooller *et al.* 1990).

Long-term studies provide crucial understanding of how both natural variation and anthropogenic factors can influence the demographic parameters of a population (Bradley *et al.* 1991). These must be long enough to encompass rare events, such as intermittent catastrophic

events, enabling researchers to assess the frequency, context and consequences that these may have for the species. This is particularly the case for long-lived species, where the annual reproductive potential is relatively low (Bradley *et al.* 1991). Data collected over long periods of time provides a robust experimental framework for quantifying demographic parameters and trends over time, as they encompass multiple environmental cycles (Bradley *et al.* 1991). Quantifying how demographic parameters and life history strategies are affected by environmental factors or anthropogenic pressures requires long-term data. Capture-mark-recapture (CMR) methods are often used for this and can facilitate quantifying the influences on individuals and demographic parameters over time (Grosbois *et al.* 2008).

A breeding colony of STSH on Fisher Island, in eastern Bass Strait between Tasmania and mainland Australia, has been monitored annually since 1947 through an extensive CMR program (Serventy & Curry 1984, Wooller *et al.* 1990). Initially, the program was a collaborative project between the (then) Fauna Board of Tasmania and the Commonwealth Scientific and Industrial Research Organisation (CSIRO) (Wooller *et al.* 1985). The original study undertaken by the CSIRO aimed to investigate the homing, duration of immaturity, pair bonding (Bradley *et al.* 1995), incubation stages and longevity of the STSH (Serventy 1957, Bradley *et al.* 1991). The monitoring continues today, through a collaboration between the Tasmanian Department of Primary Industries, Parks, Water and Environment (DPIPWE) and the University of Tasmania's Institute for Marine and Antarctic Science (IMAS), with the support of the Australian Bird and Bat Banding Schemes (ABBBS) and the Friends of Fisher Island, a community-based group.

The objectives for the Fisher Island database were to: (i) standardise all records for the period 1947 to 2017, including metadata; (ii) compile, document and archive all data for the period 1947 to 2017; and (iii) facilitate greater access to the data within the scientific community.

## **2.2 Methods**

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### **2.2.1 Field site**

#### *2.2.1.1 Population census*

The study colony is located on Fisher Island (40°13'S, 148°14'E), a 0.9 ha island in the Furneaux Island Group, in eastern Bass Strait, between Tasmania and the Australian mainland. The methods used in this program have been constant since 1947, and are further outlined (see Serventy 1967, Serventy & Curry 1984). All burrows on the island are marked with a number, and each is checked on two complete colony censuses each season. From late November to mid-



December each year, all burrows are checked at night to locate and identify both members of each breeding pair that may be present. The only exception was the years of 2013 and 2014, when the island was not surveyed. In 2016, all unmarked burrows were marked, and burrows that were completely overgrown or washed away had labels removed. All burrows on the island were then examined again in late March and early April, and the presence or absence of chicks recorded.

#### *2.2.1.2 Banding STSH*

Since 1947, all un-banded adults and chicks captured in burrows during annual searches have been banded with a uniquely numbered stainless-steel band, and the band and burrow number recorded. Adults were banded during the November to December survey and chicks were banded during the March to April survey. Burrow and band numbers were also recorded for previously banded birds that were captured during a census. From 1973, all banding records and resights were reported to the Tasmanian Australian Bird and Bat Banding Schemes (ABBBS).

#### *2.2.1.3 Determining sex of STSH*

The sex of pair-members between 1947 and 2013 was assigned on the basis of cloacal distension at laying (see Serventy 1956). New birds to the colony were not sexed during 2014 to 2015. Between 2016 and 2017, the birds' sex was determined by CHD-1 gene amplification in blood DNA using a previously described method (Faux *et al.* 2014, De Paoli-Iseppi *et al.* 2019).

### **2.2.2 The database**

We collated and digitised the 70 years of nest monitoring data from Fisher Island, to create the longest time series of demographic data for a seabird colony in the Southern Hemisphere. There were a few challenges to overcome in developing the database and collating records, such as merging multiple data sources while maintaining data quality and consistency, removing duplicate data, and dealing with multiple band numbers for the same individual bird.

Construction of the Fisher Island database involved three steps: (i) data acquisition (assembling, recording and collating multiple datasets); (ii) consolidation (merging all datasets into a single database); and (iii) configuring and proofing (standardising data and removing duplicates). All data records/observations were entered into data tables in Microsoft Excel<sup>®</sup>, and all data manipulations were performed in R version 3.5.0 (R Development Core Team 2019).

### 2.2.3 The data sources

The data used to create the database was sourced from historical banding records from the Tasmanian State Library Archives, banding records from the ABBBS and handwritten field census data from researchers' personal notebooks. The resight data is continuous for the period 1947 to 2017, except for 2013 and 2014 when no breeding adults were recorded, and 1992 when the presence or absence of chicks was not recorded. The database is comprised of records from approximately 4000 individual birds and 16,000 observations/resights.

Each data source used in constructing the database contained census data and banding records from STSHs collated over a range of years for the duration of the monitoring program (Table 2-1). The early census data (1947 to 2003) was provided by DPWIPE in the form of handwritten index cards. The band number/s of an individual bird was recorded at the top of each card, followed by all subsequent observations (Figure 2-1). Observations recorded on the cards comprised the sex of the bird, the burrow number the bird was occupying when observed, the band number of the mate, the presence or absence of an egg (recorded only on some cards) and the presence or absence of a chick in the same burrow (Figure 2-1). Additional census data became available from the donation of handwritten research notebooks (Table 2-1). These contained similar data to the cards, although the records were not noted by individual STSH, but by breeding season.

The ABBBS provided electronic banding records from Fisher Island from 1973 (Table 2-1). The records comprised the date and band number of all newly banded adult birds and chicks. Historical banding records, including the first bird banded at Fisher Island (Table 2-1 and Figure 2-2), were obtained from the Tasmanian State Library Archive. These records comprised the date and location the bird was banded, as well as the age the bird was banded (*i.e.* adult or chick).

### 2.2.4 The data structure

The database comprises two datafiles. The first datafile, BIRD\_ID, is a unique identifier table containing all information on each individual STSH and every band number the individual has been given over its lifetime. The second datafile, RESIGHTS, contains all observations of each individual STSH (*e.g.* sex, mate pair, breeding status).

#### 2.2.4.1 Creating the unique identifier datafile: BIRD\_ID

The first step in developing the database was to create a unique identifier for each individual STSH ever recorded in the colony. This was essential, as progressive replacement of older bands meant individuals may have carried up to five different bands during their lifetime. The source

data used to create the BIRD\_ID datafiles was compiled from all banding records, cards and notebooks shown in Table 2-1.

A two-step process was used to create a unique identification number (ID) for each bird due to the difference in the recording data (*i.e.* index cards, notebooks). For the early data (1947 to 2003), based on index cards, for each individual index card a new ID was created, and the data associated with that individual was recorded on the datafile within 10 descriptive fields (see Table 2-2 and Table 2-3), to create a BIRD\_ID (1) datafile. For the later data (post 2004), based on notebooks, the ID was created using the RESIGHT datafile (see Section 2.2.4.2). All established ID from the index cards (BIRD\_ID [1]) were matched to the associated band number/s in the RESIGHT file (see Code example 1 in Appendix 2). Then all band number/s associated with an individual without an ID was given a unique number (see Code example 2 in Appendix 2). The columns *bird\_id*, *sex* and *band1* to *band5* of the RESIGHT file were used to create a second BIRD\_ID (2) datafile, which was merged with BIRD\_ID, and all duplicate records were removed (see Code example 3 in Appendix 2). After the duplicates were removed, any discrepancies were checked manually by reviewing the original data sources. For example, discrepancies were found in the sex of some individuals. This resulted in two different IDs with the same band number/s, but one record was *Male* and the other *Female*. For sex discrepancies, the sex recorded most frequently was taken as the sex of the individual.

The final step in developing the BIRD\_ID file involved combining all banding records from the multiple sources into a single file. Banding records from the Tasmanian State Library Archives were entered manually into a spreadsheet and merged with the electronic records, to create the BANDS datafile. The BIRD\_ID was compared to BANDS, to ensure all individual birds were recorded. Any individuals that were banded and recorded in the BANDS file but never sighted in the RESIGHT file were added to the BIRD\_ID datafile. This completed the BIRD\_ID datafile, which contained data on approximately 4000 individual birds recorded over the 70-year period.

#### 2.2.4.2 Creating the observation datafile: RESIGHTS

The RESIGHTS datafile was compiled from: (i) the index cards; and (ii) research notebooks (Table 2-1). A resight event was classed as every time an individual bird was seen and recorded in the colony. As not all the notebooks were available at the start of developing the database, four individual resight datafiles were created: (i) RESIGHT\_Cards; (ii) RESIGHT\_CM; (iii) RESIGHT\_IS; and (iv) RESIGHT\_CP. Each resight file comprised 30 fields that described the status of the individual at the time of observation (Table 2-4). Each individual sighted on any

one day generated a corresponding entry in the datafile. The structure of each datafile was standardised and merged to create the main datafile: RESIGHTS. Subsequently, all duplicates were removed (see Code example 4 in Appendix 2); on completion of the RESIGHT datafile there was approximately 16,000 observations/resights.

Additional observations were recorded in the RESIGHT datafiles, as several supplementary studies were undertaken at the colony. For example, a translocation program between 1960 and 1971 involved chicks being transferred from two nearby islands to Fisher Island, to see if they would adopt the colony (Serventy *et al.* 1989). A band loss/band wear study resulted in some STSH being banded on both legs (Wooller *et al.* 1985).

Discrepancies found in the RESIGHTS, such as birds recorded with the same band number, or birds recorded as dead and later recorded alive, were checked manually and compared to the original data sources. There was a substantial issue with some of the band numbers. The same band numbers were used in early 1950s and later deployed on chicks in the late 1980s. This was rectified manually by reallocating a unique BIRD\_ID to both individuals.

#### 2.2.4.3 Resight Metadata development

Documenting the resight metadata for consistency among datasets spanning 70 years was a challenging process, as observations recorded among the various sources and studies differed somewhat, and additional or less information about a particular individual bird may have been recorded during the various colony censuses. For example, the presence or absence of an egg may have been recorded on the cards as incubated egg (I) or failed egg (F), but as other researchers became involved more detailed observations were added, such as predated egg (EPr), cold egg (COE) or waterlogged/flooded egg (FLE). Despite these minor variations, the key observations on burrow number, sex, band number/s and mate band number/s were largely consistent throughout the 70 years of data collection. A comprehensive metadata code list developed for observations can be found in Table 2-4.

Most recently (2015 onwards), additional data for all new birds arriving to the Fisher Island colony were collected. For example, if an adult bird was captured with no band and subsequently banded, this individual bird was recorded as a new bird (newb). This was added to investigate immigration rates into the study colony at Fisher Island, as this had not clearly been defined throughout the study (Wooller *et al.* 1985).

## 2.3 Conclusions

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The low annual reproductive potential of STSH (as with all procellariiformes) requires long-term data to quantify their population dynamics and elucidate the effects of environmental perturbations (Bradley *et al.* 1991, Price *et al.* 2020). The Fisher Island data will contribute to future studies that look to quantify the role of environmental variability on breeding parameters, population growth and population viability at Fisher Island, and potentially elsewhere.

As STSH are hunted for commercial and recreational purposes at selected sites throughout Tasmania (Springer *et al.* 2018), the demographic parameters could be incorporated into an improved harvest model for the species, which can be used by management agencies to develop appropriate evidence-based strategies for the conservation and sustainable harvest of STSH elsewhere in Tasmania. The Fisher Island data can be further examined to investigate the causes that may be responsible for, or contributing to, the decrease in STSH at some colonies in southeast Australia. Finally, as this long-term study continues into the future and extends over multiple generations of STSH, the data can provide a valuable basis for addressing questions on broader evolutionary processes with respect to life history strategies, how lifetime reproductive success varies among individuals, and how these influence population viability and persistence.

## 2.4 Tables and Figures

Table 2-1: Dataset descriptions and sources

Period	Description	Source(s)
1947 to 1974	Tasmania Fauna Board banding records (photocopy)	Tasmanian State Library Archives
1973 to 2012	Banding records (digitised)	Australian Bird and Bat Banding Schemes (ABBBS)
1947 to 2003 <sup>^</sup>	Historical handwritten index cards (originals)	Tasmanian Department of Primary Industries, Parks, Water and Environment
1951 to 1996 <sup>+</sup>	Research notebook one (handwritten photocopies)	Dr Dom Serventy and Dr Irynej Skira
2004 to 2012 <sup>+</sup>	Research notebook two (handwritten photocopies)	Dr Cath Meathrel Notebooks
2011 to 2013 <sup>*</sup>	Research notebooks (typed) and Excel spreadsheets	Dr Cath Meathrel and Tasmanian Department of Primary Industries, Parks, Water and Environment
2014 <sup>*</sup> to 2017	Research notebook three (handwritten originals)	Cassandra Price and Dr Ricardo De Paoli-Iseppi

<sup>^</sup>1992 presence or absence of chicks not recorded; <sup>\*</sup>2013 and 2014 no breeding adults recorded;

<sup>+</sup>Notebooks became available midway through the development of the database.

Table 2-2: Metadata description for BIRD\_ID datafile

Metadata	Description
BIRD_ID	Each individual bird recorded in the database.
Sex	Sex of the bird (Male = M, Female = F, Unknown = U).
Prefix	The band serial number prefix if available.
Band1 to 5	Each individual band that an individual bird was sighted with.
Par_female	The band number of the female parent of the individual bird (if it was recorded with the sighting/s).
Par_male –	The band number of the male parent of the individual bird (if it was recorded with the sighting/s).
Pos_par –	The band number of a possible parent of the individual bird (if it was recorded with the sighting/s).
Usex_parent –	The band number of a parent with an unknown sex of the individual bird (if it was recorded with the sighting/s).

Table 2-3: An example of the file structure for the BIRD\_ID datafile

BIRD_ID	Sex	Prefix	Band1	Band2	Band3	Band4	Band5	Par_female	Par_male	Pos_par	Usex_par
1	F	162	82	8791	12378	34392	70732				
2	F	161	799	1984	12399						
3	M		808	8751	12346			3352	3369		
4	F		830	1998	12406						
5	M		836	8798	12336					77	

Table 2-4: Metadata codes for the Fisher Island data

Field	Codes	Description
bird_id		Unique identifier.
sex	M = Male F = Female U = Unknown	Sex of the individual.
prefix	162 161	The band serial number prefix if available.
band1 to 5	Band number	The band number that an individual was sighted with.
bur1 to 3	Burrow number	The burrow number that an individual bird was sighted in. This could be up to 3 burrows in a season.
colony	HR = Home rookery SR = South rookery PP = Pots Point U = Unknown	What part of the colony was the bird sighted in.
date	DD/MM/YYYY	Resight date.
status	A = Alive D = Dead	Status of the bird when sighted.
catch_loc	B = burrow S= surface	Where the bird was caught.
dead_com		Description of the dead bird (comments).
new_bird	Newb = New bird NA = Not a new bird	An adult bird that does not have a leg band and was subsequently banded.
age_class	Adult Chick	Age class.
br_status	B = Breeder NB = Non-breeder U = Unknown	Breeding Status of the bird.
mate_band1 to 5	Band number	The band number/s of the other bird found in the burrow during the breeding season.

Field	Codes	Description
mate_status	BW = Bred with A = Associated to the burrow PM = Possible mate NA= no mate pair or association recorded	The status of the other bird/s sighted in the burrow. Associated was used to describe multiple birds sighted in a burrow without an egg or not sitting on an egg. Possible mate described when there was more than one other bird associated to the burrow and was found sitting on an egg.
num_bird		How many birds that were sighted in the burrow during the breeding season.
mate_com		Comments about the mate or other associated birds in the burrow.
incub*	F = failed I = incubated U = unknown NA = not recorded	If the egg was successful (incubated) or failed.
incub_status*	NH = Not hatched Des = Deserted Rot = Rotten egg COE = Cold egg FLE = Flooded egg PrE = Predated egg	The status the egg was recorded when it failed.
egg_status*	E = Egg NE = No Egg	Egg present/absent in the burrow.
trans_col*	LGI = Little Green Island GrDog = Great Dog Island SPoint = South Point	A translocation experiment between 1960 to 1971 to investigate if banded birds adopted Fisher Island.
ch_status*	Ch = chick alive Chf = chick failed Dch = dead chick DchP = chick predated Noch = no chick NA = no status recorded	Status of chick in the burrow.
chband	xxx-band number	All live chicks were given an ABBBS band.
chweight*		Body mass of chick in burrow.
adweight*		Body mass of adult in burrow.
hlength*		Head length in millimetres.
blength*		Bill length in millimetres.
bdepth*		Bill depth in millimetres.
tenwing*		Wing length (mm).
tarsus*		Tarsus (mm).

\*Observation not recorded continuously throughout the monitoring program.



875 = 1890 = 8784 = 12262						♂
1947	Nov. Burrow	105;	brad,	mated with	1001	Ruared chick 1052
1948	"	"	105;	"	1001	" " (died)
1949	"	"	105/235;	"	1061 = 8867 = 12390	
1950	"	"	235;	"	1824 = 8820 = 12388	
1951	"	"	393;	"	12390	" (15133)
1952	"	"	393;	"	12390	
1953	"	"	393;	"	15062	
1954	"	"	393;	"	15062	
1955	"	"	393;	"	15062	
1956	"	"	106;	"	12597	
1957	"	"	106;	"	12597	
1958	"	"	106;	"	12597	
1959	"	"	106;	"	12597	
1960	"	"	106;	"	12597	
1961	"	"	106;	"	12597	
1962	"	"	159;	"	12597	

Figure 2-1: Handwritten index cards provided by Tasmanian Department of Primary Industries, Parks, Water and Environment

REGISTER OF MUTTON-BIRD BANDS

SEASON 1946-47:

- no. 1 - not used; given to Tpr. L. V. Bailey, Lady Barron, as sample.
- 1 - 100: Little Dog Is., March 18, 1947; on young birds.
- 101 - 200: Great Dog Island, March 19, 1947; on young birds.
- 201 - 330 : Great Dog Island, March 20, 1947; on young birds.
- 331 - 466: Little Green Island, March 21, 1947; on young birds, except no. 360 which was on an adult.
- 467 - 482: Fisher Island, March 22, 1947; on young birds, except no. 482 which was on an adult.
- 483 - 537: Great Dog Island, March 24, 1947; on young birds.
- 538 - 700: Mount Chappell Island, March 25, 1947; on young birds.
- 701 - 785: Fisher Island, April 10, 1947; by Tpr. L. V. Bailey on young birds.

SEASON 1947-48:

- 786 - 787: Fisher Is., November 21, 1947; adults.
- 788 - 815: Fisher Is., November 22, 1947; adults.
- 816 - 837: Fisher Is., November 23, 1947; adults.
- 838 - 868: Fisher Is., November 24, 1947; adults.
- 869 - 917: Fisher Is., November 25, 1947; adults.
- 918 - 998: Fisher Is., November 26, 1947; adults.
- 999 - 1020: Fisher Is., November 27, 1947; adults.
- 1021 - 1028: Fisher Island, November 28, 1947; adults, except no. 1022 which was lost.
- 1029 - 1035: Fisher Is., November 29, 1947; adults.
- 1036 - 1042: Fisher Is., November 30, 1947; adults.
- 1043 - 1047: Fisher Is., December 1, 1947; adults.
- 1058 - 1049: Fisher Is., December 2, 1947; adults.
- 1050         Fisher Is., December 5, 1947; adult.

Figure 2-2: The very first banding records deployed at Fisher Island from 1946 to 1947, sourced from the Tasmanian State Library Archives

Sand Rookery 1952

Burns 59- ♂ 12338  
♀ 12546

Σ<sub>21</sub>

61- ♂ 12344  
♀ 12550

Σ<sub>21</sub>

chick 18543

64- ♂ 12429  
♀ 12406

Σ<sub>21</sub>

67- ♂ 12380  
♀ 12568

Σ<sub>21</sub>

71- ♂ 12596, 12519, 15046  
♀ 12499, 12556, 15018

Σ<sub>21</sub>

75- ♂ 12599  
♀ 12515

Σ<sub>21</sub>

76- ♂ 123<sup>36</sup>  
148 ♀ 12569

Σ<sub>21</sub>

Figure 2-3: Extract of Dom Serventy research notebook

**CLIMATE VARIABILITY AND BREEDING PARAMETERS OF A  
TRANSEMISSPHERIC MIGRATORY SEABIRD OVER SEVEN  
DECADES**

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Fisher Island

📷 @melissavaroyart

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## Abstract

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Climate variability affects physical oceanographic systems and environmental conditions at multiple spatial and temporal scales. These changes can influence biological and ecological processes, from primary productivity to higher trophic levels. Short-tailed shearwaters (*Ardenna tenuirostris*) are transhemispheric migratory procellariiform seabirds that forage on secondary consumers such as fish (myctophids) and zooplankton (euphausiids). In this study we investigated the breeding parameters of the short-tailed shearwater from a colony of 100 to 200 breeding pairs at Fisher Island, Tasmania, Australia for the period 1950 to 2012, with the aim to quantify the relationship between breeding parameters with large-scale climate indices in the Northern (*i.e.* Northern Pacific Index and Pacific Decadal Oscillation) and Southern Hemispheres (*i.e.* El Niño–Southern Oscillation and Southern Annular Mode). Through the use of Generalised Linear Models, we found that breeding participation among short-tailed shearwaters was affected by climate variability with a 12-month temporal lag. Furthermore, breeding success decreased in years of increased rainfall at the colony. These findings demonstrate that both large-scale climate indices and local environmental conditions could explain some of the variability among breeding parameters of the short-tailed shearwater.

## 3.1 Introduction

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Seabirds are a higher trophic level species that is susceptible to climate variability on both a local and regional scale (Napp & Hunt 2001, Jenouvrier 2013, Zador *et al.* 2013, Cushing *et al.* 2017). Oceanographic properties are influenced by large-scale physical forcing that alters atmospheric conditions, sea-level pressure and ocean temperature, which in turn affects bottom-up processes, such as changes in primary and secondary productivity (Zador *et al.* 2013, Cushing *et al.* 2017). Variations in oceanographic and climatic conditions can influence seabird nesting habitat, foraging grounds and resource availability, which could change their distribution, abundance, reproductive output and population growth (Frederiksen *et al.* 2004, Humphries & Möller 2017).

Climate variability in the Northern Hemisphere and Southern Hemisphere can be measured by large-scale climate indices. Shifts in these indices result in changes to prevailing weather, environmental conditions and oceanographic systems, which may affect biological and ecological processes (Stenseth & Mysterud 2002, Sprogis *et al.* 2017). In the Northern Hemisphere, Pacific Decadal Oscillation (PDO) and North Pacific Index (NPI) are the dominant climate drivers, and are known to influence seabird demography, abundance and distribution



(Baduini *et al.* 2001, Hunt Jr *et al.* 2002, Bond *et al.* 2011). The PDO operates on a quasi-decadal scale lasting 15 to 30 years (Humphries & Möller 2017), while NPI measures the strength of the Aleutian Low, an indicator of climate forcing in the Bering Sea (Trenberth & Hurrell 1994). In the Southern Hemisphere, the primary climate drivers are El Niño–Southern Oscillation (ENSO) and Southern Annular Mode (SAM) (Bindoff 2010), which have both been linked to the breeding performance of seabirds (Duffy 1990, Clucas 2011, Humphries & Möller 2017, Pardo *et al.* 2017). ENSO is a dominant climate index that fluctuates between three phases – neutral, warm (*i.e.* El Niño) and cool (*i.e.* La Niña) and affects global climate, sea-surface temperature (SST) and rainfall, while SAM is the primary driver for climate variability in the Southern Hemisphere (Lovenduski & Gruber 2005, Stammerjohn *et al.* 2008, Sprogis *et al.* 2017) and is characterised by the movement of the westerly wind belt that circles Antarctica.

These four climate indices affect marine ecosystems on temporal scales from months to years (Trathan *et al.* 2007, Sallée *et al.* 2008). Low trophic order species can be rapidly affected by environmental changes; however, the effect on a predator population can take place months or even years later, as the changes in primary productivity propagate through the food web (Humphries & Möller 2017, Cox *et al.* 2018). Numerous studies have shown that the foraging success of seabirds affects their breeding performance, both directly during the breeding season (Pinaud & Weimerskirch 2002, Jenouvrier *et al.* 2018) and indirectly through carry-over effects during the non-breeding season (Shoji *et al.* 2015, Jenouvrier *et al.* 2018).

Procellariiformes (albatross, petrels and shearwaters) are seabirds with low production potential (*e.g.* low reproductive rates, single-egg clutch and delayed recruitment into the breeding population) (Warham 1990, Weimerskirch *et al.* 2001, Meathrel & Carey 2007). They are a trans-equatorial migratory seabird and spend the majority of their lives at sea, travelling great distances utilising a variety of habitats during the breeding and non-breeding periods. Consequently, they are exposed to a variety of weather, environmental conditions and oceanographic systems in both the Northern and Southern Hemispheres (Weimerskirch & Cherel 1998, Einoder *et al.* 2013, Yamamoto *et al.* 2015, Nishizawa *et al.* 2017).

One of the longest ecological studies (from 1947 to the present) of a procellariiformes is that of the short-tailed shearwater (STSH) at Fisher Island, Tasmania, Australia. This population of birds has been monitored annually since 1947 through an extensive capture-mark-recapture (CMR) program (Serventy & Curry 1984, Wooller *et al.* 1990) that we use to investigate the breeding parameters of the STSH from Fisher Island and their relationship with large-scale climate indices from both the Northern and Southern Hemispheres. More specifically, we aim

to: (i) investigate the annual trends in the breeding parameters of the STSH at Fisher Island; (ii) determine which climate indices have the most influence on breeding parameters; and (iii) identify any local environmental conditions that may also affect breeding success.

## **3.2 Materials and Methods**

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### **3.2.1 Study species**

The STSH is a medium sized (500 to 800 g) burrow-nesting procellariiform (Skira 1990, Berlincourt & Arnould 2015), with pronounced pan-oceanic migration. Each September to October, they return from their non-breeding grounds in the Northern Hemisphere to south-eastern Australia to breed (Skira 1991). During the breeding season, shearwaters alternate short (local) and long foraging trips (Southern Ocean, across oceanic regions longitude from 80°E and 160°E) (Woehler *et al.* 2003, Raymond *et al.* 2010). The breeding season of the STSH begins in November, where one egg per successful breeding pair is laid. Laying is highly synchronised, with 95% of the eggs laid between 24th and 28th November. A breeding pair will not replace the single egg if it fails (Skira 1990). Hatching occurs from mid-to-late January (Carey 2010) and chicks fledge in mid-April to early May (Serventy 1967, Wooller *et al.* 1990). After the breeding season, adults and fledglings return to the North Pacific during the austral winter (Shaffer *et al.* 2006, Raymond *et al.* 2010, Vertigan *et al.* 2012).

### **3.2.2 Field site**

The study colony is located on Fisher Island (40°13'S, 148°14'E), a 0.9 ha island in the Furneaux Island Group, Tasmania, Australia. All burrows on the island have been marked with a number. Each year of the study, all new individuals captured in burrows during searches, including chicks, were banded with a uniquely numbered stainless-steel band, and the band and burrow number was recorded. If the bird was already banded, the band and burrow number was recorded. The methods used in the program to identify individuals and reproductive performance have been constant since 1947, and are further outlined in previous studies (Serventy 1967, Serventy & Curry 1984).

### **3.2.3 Shearwater breeding parameters**

#### *3.2.3.1 Breeding birds and chick numbers*

From late November to mid-December each season, all burrows on the island were checked at least twice every 10 days to locate and identify both members of each breeding pair. Non-breeding (prospecting) birds generally only make short nocturnal visits to the island during the incubation and chick-rearing periods (Bradley *et al.* 1999), and tend to explore unoccupied burrows without taking up residency. While non-breeding birds constitute the majority of birds found on the surface within the colony (Serventy 1967), searching burrows minimises the likelihood of detecting a non-breeding bird. All burrows were checked again in late March to early April the following year and the presence or absence of chicks recorded, with all new chicks banded. This study dataset is continuous since 1947, with the exception of 2013 and 2014 when no breeding adults were recorded, and 1992 when the presence or absence of chicks was not recorded. In the first three years of the study there is a rapid increase in the number of breeding pairs, which could be attributed to initial difficulties in the establishment of the banding program. Consequently, we chose to remove the first three years of data, from 1947 to 1949. We also chose to remove all data after 2012 due to the data gaps for breeding adults, to maintain consistency. Therefore, the time series used in this study is from 1950 to 2012.

#### *3.2.3.2 Breeding success*

Breeding success was calculated as the number of chicks in March divided by the number of burrows occupied by birds in December of the previous year. The number of eggs was not used to determine breeding or hatching success, as the detection of eggs in burrows on Fisher Island was relatively low due to a lack of experience among observers, and the lengths and intricacies of the burrows themselves (Serventy & Curry 1984).

### **3.2.4 Breeding periods**

To quantify the influence of climate on the breeding parameters of the STSH, three breeding periods were chosen in this study: (i) the pre-breeding/migration period (May to October), when the birds are building their body lipid reserves in the North Pacific Ocean in preparation for their return migration to south-eastern Australia and subsequent breeding attempt (Yamamoto *et al.* 2015, Nishizawa *et al.* 2017); (ii) the early-breeding period (September to November), used to examine environmental variabilities that could affect adult condition and reproduction; and (iii) the chick-rearing period (December to March), where parental conditions/investment could be



affected by environmental variabilities, which in turn could impact on chick body condition and survival (Fay *et al.* 2015).

### **3.2.5 Temporal lags**

Additionally, three temporal lags were chosen for each breeding period and incorporated into the analysis (Table 3-1). Temporal lag one (3 to 4 months) was chosen, to account for variation in spatial-temporal scales of oceanographic conditions, which may impact local resources (see Cox *et al.* 2018), and the direct effects of local environmental conditions such as poor weather conditions (Genovart *et al.* 2013; Fagundes *et al.* 2016) (Table 3-1). Temporal lag two (6 to 7 months) and three (12 months) were chosen, as climate fluctuations, irradiation and wind stress can influence primary productivity (Sharples *et al.* 2006; Cox *et al.* 2018) and the propagation of lower trophic consumers, such as fish (myctophids) and zooplankton (euphausiids), which are a large component of the diet of STSH (Nishizawa *et al.* 2017) (Table 3-1).

### **3.2.6 Environmental data**

We used the PDO and NPI as indicators of Northern Hemisphere climatic conditions, and ENSO and SAM as indicators of Southern Hemisphere climatic conditions during the breeding periods. Monthly PDO values for the period 1949 to 2012 were obtained from the National Oceanic and Atmospheric Administration (NOAA) at <https://www.ncdc.noaa.gov/teleconnections/pdo/>. The PDO index is calculated from the principal component of monthly SST anomalies in the North Pacific poleward of 20°N (Mantua & Hare 2002). The PDO values consist of persistent positive or negative temperature anomalies, classified as warm (positive value) or cool (negative value), which have been shown to impact marine ecosystems through changes in the species composition, distribution and abundance (Mantua & Hare 2002, Becker *et al.* 2007).

Monthly NPI means for the period 1949 to 2012 were obtained from the NOAA at [https://www.esrl.noaa.gov/psd/gcos\\_wgsp/Timeseries/Data/np.long.data](https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/Data/np.long.data) (Hurrell 2017). The NPI is the mean sea-level pressure over the North Pacific Ocean 30°N to 65°N and 160°E to 140°W (Trenberth & Hurrell 1994). NPI measures the strength of the Aleutian Low in the atmosphere and is an indicator of climate forcing in the Bering Sea (Trenberth & Hurrell 1994, Zador *et al.* 2013). NPI has been linked to changes in physical ocean properties, such as sea ice retreat (Zador *et al.* 2013), which can influence bottom-up processes, such as phytoplankton blooms.

Monthly Southern Oscillation (SOI) Index values for 1949 to 2012, were obtained from the Australian Bureau of Meteorology (BOM) at <http://www.bom.gov.au/climate/current/soi2.shtml>. The SOI measures the difference in surface-air pressure between Tahiti and Darwin (Trenberth 1997). It is also a key atmospheric index for ENSO and determines the strength of El Niño and La Niña events. El Niño events are sustained values of the index (lower than -8) and are associated with a warming of the central and eastern tropical Pacific Ocean, whereas La Niña events are sustained values of the index (higher than +8) and are associated with oceanic cooling within these same areas (Trenberth 1997).

The SAM is the dominant mode of atmospheric variability at mid and high latitudes in the Southern Hemisphere. Monthly SAM data for 1957 to 2012 were extracted from the Natural Environment Research Council British Antarctic Survey at <http://www.nerc-bas.ac.uk/icd/gjma/sam.html> (Marshall 2003). The SAM consists of both positive and negative states. During a positive SAM state, a strong westerly wind belt contracts toward Antarctica, causing high-pressure atmospheric systems over southern Australia that can result in either stable or dry conditions. Negative SAM values reflect the expansion of the strong westerly winds towards the equator, with low atmospheric pressure systems over southern Australia that can increase storm and rain events. These westerly winds are responsible for driving the circulation within the Southern Ocean (Lovenduski & Gruber 2005). Changes in wind patterns can affect the stirring of the water column, which can alter the depth in the mixed layer, impacting nutrient availability in the upper ocean, with follow-on consequences for biological production (Lovenduski & Gruber 2005).

Finally, we included monthly rainfall during the chick-rearing period (December to March), as localised rain events have been shown to influence the breeding parameters of burrowing seabirds (Serventy & Curry 1984, Bester *et al.* 2007). Monthly rainfall for the chick-rearing period between 1949 to 2012 were obtained from the Lady Barron station (< 1 km from Fisher Island) from the Australian BOM at [http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p\\_nccObsCode=136&p\\_display\\_type=dailyDataFile&p\\_startYear=&p\\_c=&p\\_stn\\_num=099002](http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=136&p_display_type=dailyDataFile&p_startYear=&p_c=&p_stn_num=099002).

### **3.2.7 Statistical analysis**

Prior to model selection, a nonparametric measure of rank correlation (Spearman's  $\rho$ ) was used to investigate correlation among the variables. Breeding success and the annual number of chicks were highly correlated, therefore the annual number of chicks was removed from the analysis

(S3-1). Correlations were found between several of the climate indices at each temporal lag (S3-2, S3-3). For model parsimony, temporal lag two was excluded from the analysis based on rank correlation, as the relationship for each climate indices (*e.g.* SAM) was strong ( $> 0.75$  correlation) between temporal lag one and/or three (S3-2). Removing temporal lag two also limits the number of model parameters, as constructing all possible models for each climate variable and temporal lag would create an unmanageable number of models. Additionally, PDO for the duration of pre-breeding/migration with temporal lag one (PDO PB<sup>0</sup>) and PDO with temporal lag three (PDO PB<sup>-1</sup>) was highly correlated, thus only PDO PB<sup>-1</sup> was used in the analysis (S3-2). Additionally, SOI during the early-breeding period with temporal lag one (SOI EB<sup>0</sup>) and SOI with temporal lag three (SOI EB<sup>-1</sup>) during the early-breeding period was correlated, therefore SOI EB<sup>-1</sup> was used in the analysis. PDO PB<sup>-1</sup> and SOI EB<sup>-1</sup> were chosen, as productivity lags can occur throughout the trophic levels, and over a 12-month period the distribution and abundance of fish and krill may be affected (Jenouvrier 2013, Zador *et al.* 2013, Saba *et al.* 2014).

Generalised Linear Models were fitted to the data using the R *glm* package in R version 3.5.0 (R Development Core Team 2019). The assumption of normality of residuals was checked using standard graphical methods (Zuur *et al.* 2010). Two models were subsequently used to investigate the relationship between breeding parameters and large-scale climate indices.

#### 3.2.7.1 Model 1 – number of breeding shearwaters

The first model related the number of breeding birds arriving at Fisher Island to the suite of environmental covariates. Climatic variables based on the appropriate breeding period included in the full model were: (i) NPI during the pre-breeding/migration period with temporal lag one (NPI PB<sup>0</sup>); (ii) NPI during the pre-breeding/migration period with temporal lag three (NPI PB<sup>-1</sup>); (iii) PDO PB<sup>-1</sup>; (iv) SOI EB<sup>-1</sup>; (v) SAM during the early-breeding period with temporal lag one (SAM EB<sup>0</sup>); and (vi) SAM during the early-breeding period with temporal lag three (SAM EB<sup>-1</sup>). SAM EB<sup>0</sup> was not significant and was removed from the analysis to limit the number of parameters within the model.

#### 3.2.7.2 Model 2 – breeding success of shearwaters

The second model related breeding success to a number of climate variables in the Southern Hemisphere. Climatic and environmental variables based on the chick-rearing period included in the full model were: (i) SAM during the chick-rearing period with temporal lag one (SAM CR<sup>0</sup>); (ii) SAM during the chick-rearing period with temporal lag three (SAM CR<sup>-1</sup>); (iii) rainfall

during the chick-rearing period with temporal lag one (Rainfall  $CR^0$ ); (iv) SOI during the chick-rearing period with temporal lag one (SOI  $CR^0$ ); and (v) SOI during the chick-rearing period with temporal lag three (SOI  $CR^{-1}$ ).

Model selection was conducted through the comparison of Akaike's Information Criterion (AIC), Akaike weights ( $w_i$ ) and Akaike's Information Criterion differences ( $\Delta_i$ ). Akaike weights ( $w_i$ ) were calculated to provide a measure of strength for each model (Anderson & Burnham 2004). Models with an AIC  $\Delta_i \leq 2$  were considered to have equivalent support. To assess the most important covariate, in these cases, we used model averaging to provide a final model (Anderson & Burnham 2004). Model averaging was calculated as a sum of the Akaike weights ( $w_i$ ) over the number of models where the covariate appears (Anderson & Burnham 2004).

### 3.3 Results

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There was considerable variability over the time period in both reproductive parameters (Figure 3-1a and Figure 3-1b). There were  $98 \pm 29$  breeding pairs per year when averaged across the entire time period. However, from the start of the survey period in 1950, there was a gradual decline in the number of breeding pairs, reaching 58 pairs in 1971 and 1973 (Figure 3-1a). From the mid-1980s, the number of breeding pairs increased until 2007, when 160 breeding pairs were recorded (Figure 3-1a). From 2007 to 2012, there was slight variation in the annual number of breeding pairs. Breeding success fluctuated annually, with an average of  $45 \pm 20\%$  across the entire time period. The lowest breeding success was recorded in 2004 and 2006 (less than 1%) (Figure 3-1b). The most successful breeding season was in 1961, where there was a 92% success rate (Figure 3-1b).

#### 3.3.1 Climatic variability and the number of breeding shearwaters

There were six models with an AIC  $\Delta_i \leq 2$ , containing all covariates (Table 3-2, S3-4). After model averaging, SAM  $EB^{-1}$  explained the most variation (Table 3-3), with the number of birds arriving to the breeding colony increasing in years of positive SAM (Figure 3-2). Furthermore, there was a negative relationship between the number of birds arriving at Fisher Island and NPI  $PB^0$  and PDO  $PB^{-1}$  (Figure 3-2). Lastly, the contribution of NPI  $PB^{-1}$  and SOI  $EB^{-1}$  to explain any variability within the model was marginal (Table 3-3).

### 3.3.2 Effects of climate variability and environmental conditions on shearwater breeding success

The full model, which contained all variables considered to be important, presented 10 models with an  $AIC \Delta_i \leq 2$ , with all covariates included in these models (Table 3-4, S3-5). After model averaging, the covariate that explained the greatest amount of variability of breeding success was localised rainfall, with years of higher rainfall associated with reductions in breeding success (Table 3-5, Figure 3-3). SOI  $CR^{-1}$  conditions demonstrated a positive relationship with breeding success. In contrast, as SOI  $CR^0$  values increased, this led to a decrease in breeding success (Figure 3-3). The contribution of SAM  $CR^{-1}$  and SAM  $CR^0$  was negligible (Table 3-5).

## 3.4 Discussion

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This 63-year study has demonstrated that breeding performance of the STSH was influenced by climate indices, local weather and environmental conditions. The annual number of breeding birds arriving at Fisher Island was influenced by climate indices in both the Northern and Southern Hemispheres, while breeding success at Fisher Island was affected by local weather conditions (*i.e.* rainfall). Moreover, the breeding parameters within this study were affected by climate indices with a 12-month temporal lag more so than climate indices lagged over the associated breeding period.

### 3.4.1 Lags in productivity transfer to breeding parameters of shearwaters

Lags in productivity transfer may occur throughout the food web, and have been associated with changes in breeding success, distribution, abundance and demographic parameters of several seabird species (Jenouvrier 2013), which is consistent with our findings in this study. Climatic variability influences environmental conditions, which can alter primary productivity and influence aspects of secondary production, such as the recruitment of fish and krill (Zador *et al.* 2013, Saba *et al.* 2014), which are both prey for STSH. For example, in Antarctica, a one-year lag was found between primary production and the recruitment of Antarctic Krill (*E. superba*) (Saba *et al.* 2014), which can influence food availability to higher trophic species. Due to the delay in energy transfer through the food chain (Sandvik *et al.* 2007, Sandvik & Einar Erikstad 2008), these effects are not observed immediately (Zador *et al.* 2013, Cox *et al.* 2018). Similarly, in the North Atlantic, breeding success of 13 species of seabirds were influenced by lagged variables of the North Atlantic Oscillation (NAO) and SST (Sandvik *et al.* 2007, Sandvik & Einar Erikstad 2008). During negative NAO, values with a one-year lag and low SST with a two-year lag resulted in higher breeding success (Sandvik *et al.* 2007, Sandvik & Einar Erikstad

2008). Similarly, lower reproductivity in diving seabirds (*e.g.* murres and cormorants) have been demonstrated one to two years after warmer SST in the Bering Sea (Zador *et al.* 2013).

### **3.4.2 Climatic variability and its influence on the number of breeding shearwaters**

The low production potential of shearwaters requires long-term data, to be able to assess their population dynamics and elucidate the effects of environmental perturbations on their abundance (Bradley *et al.* 1991). Environmental conditions can influence resource availability in both the non-breeding and breeding foraging grounds, which will in turn affect breeding participation of STSH at Fisher Island, as body condition is an important determinant in the decision of whether to breed (Weimerskirch *et al.* 2001). The main reason for birds to skip a breeding event is a shortage in resource availability, which prevents them from acquiring sufficient food reserves to invest in reproduction (Chastel *et al.* 1995, Coulson 2008). Furthermore, resource acquisition and foraging behaviour during the non-breeding periods may have carry-over effects into the breeding season, as diminished body reserves can impact their ability to breed (Lovvorn *et al.* 2003, Bester *et al.* 2007).

#### *3.4.2.1 Influence of Northern Hemisphere climate indices on the number of breeding shearwaters*

Foraging grounds during the non-breeding period are important areas for birds to accumulate body lipid reserves before migration (Lovvorn *et al.* 2003, Bester *et al.* 2007). Over the last 50 years, the climate in the Northern Hemisphere has experienced an increase in the intensity of the winter NAO, which has affected survival of the adult northern fulmar (*Fulmarus glacialis*) due to changes in resource availability (Grosbois & Thompson 2005). It is likely that similar effects have been felt among adult STSH at Fisher Island, as demonstrated by fluctuations in the number of breeding participants. For example, the number of birds breeding at Fisher Island decreased one year after warm phases of the PDO (positive index) and slightly increased with lower NPI values (*i.e.* stronger Aleutian Low) during the pre-breeding period. NPI is an indicator of the strength of the Aleutian Low and PDO has shown to influence SST (Bond *et al.* 2011, Springer *et al.* 2018). Both climate patterns influence primary production and prey availability in the North Pacific through changes in ocean properties and sea ice dynamics. For example, a stronger Aleutian Low is linked to larger phytoplankton spring blooms in the Bering Sea (Iida & Saitoh 2007, Bond *et al.* 2011). Prior to migrating southwards, STSH foraging in the Northern Pacific Ocean move further north, around the Bering and Chukchi Seas, as the distribution of krill shifts (Baduini *et al.* 2001, Yamamoto *et al.* 2015, Nishizawa *et al.* 2017). Consequently, any changes

in bottom-up processes that influence krill abundance and availability will impact STSH populations prior to their migration south.

Furthermore, warm phases of the PDO (positive index), influence oceanographic properties and environmental conditions, which in turn affects the availability of zooplankton biomass in the surface waters (Jin *et al.* 2009, Bond *et al.* 2011). For example, high SST in the Bering Sea in 1997 redistributed the vertical distribution of euphausiids (*i.e.* krill) to deeper waters (Baduini *et al.* 2001). In the northern Gulf of Alaska during warm phases of the PDO, there was a decrease in the availability of euphausiids and capelin (*Mallotus villosus*), which led to starvation of murre (*Uria* spp.) and decreased reproductive output of kittiwakes (*Rissa* spp.) (Hatch 2013). However, during cool phases of the PDO (negative index) the opposite occurred, resources increased having a positive impact on both species, respectively (Hatch 2013). Therefore, it is highly likely that during a cool phase of the PDO, resource availability increased, which would improve foraging success among STSH prior to their migration south. Concurrently, this may have facilitated the accumulation of body lipid reserves and contributed to an increase in the number of breeding participants at Fisher Island.

#### 3.4.2.2 *Influence of Southern Hemisphere climate indices on the number of breeding shearwaters*

In the Southern Hemisphere, the Southern Ocean is a key foraging area for STSH during the pre-breeding and breeding period, which is highly influenced by SAM. The number of breeding participants at Fisher Island increased under positive SAM conditions. When SAM is positive, winds intensify which causes stronger mixing of the water column and a deeper mixed layer. This combined with increased up-welling, may influence nutrient availability within surface waters (Lefebvre *et al.* 2004). This may increase productivity, which would have flow-on effects throughout the food web. For example, early recruitment into a population of wandering albatross (*Diomedea exulans*) has been linked to positive SAM, thought to be due to increases of resource availability (Fay *et al.* 2017). Therefore, during a positive SAM event, ocean productivity may increase, having a positive influence on STSH abundance the following year.

SAM can affect the strength of the Antarctic Circumpolar Current (ACC) and the seasonal extent of sea ice around the Antarctic Continent, both of which have been shown to influence the productivity of the Southern Ocean (Constable *et al.* 2003, Lefebvre *et al.* 2004). Over the past 20 years, SAM has been increasing, leading to changes in wind direction and intensity (Stammerjohn *et al.* 2008), with cooling waters shifting out from Antarctica and influencing the extent of sea ice (Stammerjohn *et al.* 2008). Changes in the timing of sea ice formation and

retreat, along with temperature, determine the intensity and location of phytoplankton spring blooms, affecting the availability and abundance of primary and secondary consumers (Nishizawa *et al.* 2017). These changes during positive SAM may be influencing productivity in the Southern Ocean (Lefebvre *et al.* 2004), leading to greater prey availability for seabirds such as STSH in the following year (Nishizawa *et al.* 2017), resulting in higher breeding participation at Fisher Island.

Prior to breeding, STSH undertake a foraging trip to the Southern Ocean (*i.e.* honeymoon period) to rebuild their body condition, which deteriorates during the long migration from the Northern Hemisphere (Lill & Baldwin 1983, Weimerskirch & Cherel 1998, Vertigan *et al.* 2012). Additional long foraging trips to the Southern Ocean are also undertaken by STSH throughout the incubation period (Weimerskirch & Cherel 1998, Einoder *et al.* 2013, Berlincourt & Arnould 2015). These long foraging trips (1000 km to 4000 km) are designed to replenish adult body condition that deteriorates during the incubation period (Weimerskirch & Cherel 1998, Einoder *et al.* 2013). Short-tailed shearwaters forage across different oceanic regions within the Southern Ocean, including south of the Polar Front (PF), the Sub-Antarctic Front (SAF) and Antarctic waters (Woehler *et al.* 2003, Raymond *et al.* 2010, Berlincourt & Arnould 2015), feeding predominantly on myctophids (fish) and euphausiids (*E. vallentini*) (Weimerskirch & Cherel 1998, Connan *et al.* 2010, Einoder *et al.* 2013). When resources are low, breeding procellariiform species may skip breeding if it poses a risk to their own survival (Chastel *et al.* 1995, Weimerskirch *et al.* 2001). Therefore, breeding decisions of STSH are likely to also be influenced by the resource availability and successful foraging within the Southern Ocean.

### **3.4.3 Influence of environmental conditions on the breeding success of shearwaters**

Localised rainfall and ENSO were found to influence the breeding success of STSH at Fisher Island, with rainfall having the greatest influence. Burrowing procellariiformes are adversely affected by heavy rainfall due to burrow flooding, which causes chick mortality and egg failure (Serventy & Curry 1984, Warham 1996, Bester *et al.* 2007, Fagundes *et al.* 2016). For example, young providence petrel (*Pterodroma solandri*) chicks were more vulnerable to rainfall conditions than older chicks (Bester *et al.* 2007), probably because their down is not water repellent, resulting in them becoming waterlogged and unable to maintain core body temperature (Warham 1996). During this study, the mortality rate between eggs and chicks were not recorded, therefore we were unable to determine at which stage of development rainfall had the greatest impact.



ENSO is a significant contributor to Australia's climate, altering environmental conditions that influence seabird ecology (Bindoff 2010, Chambers *et al.* 2011). Nonetheless, the effects of ENSO in south-eastern Australia on seabird populations are not well established (Chambers *et al.* 2011, Litzow *et al.* 2015). In our study, breeding success was influenced by ENSO; however, the nature of the relationship varied depending on the temporal lag. Breeding success decreased with negative values of SOI lagged over a 12-month period, while breeding success increased with negative values of SOI lagged over three months, during the chick-rearing period. This may suggest the environmental conditions one year prior to STSH breeding affects prey availability. Therefore, in the case of negative SOI values, this may lead to lower resource availability. On the west coast of Australia, studies have highlighted the adverse effects of El Niño (*i.e.* sustained values of SOI lower than -8). For example, warm surface waters caused by El Niño events can block nutrient upwelling, influencing primary production, which in turn affects the distribution and abundance of zooplankton, fish and higher trophic predators (Jenouvrier 2013). These El Niño events have been linked to delays in breeding and reduced breeding success for the wedge-tailed shearwater (*Ardenna pacifica*).

However, there are a few possibilities to explain the contrasting results during the chick-rearing period for SOI. Local environmental conditions, such as wind, humidity and temperature, are influenced by ENSO, which may have impacted burrow conditions of the STSH during chick rearing. For example, local environmental conditions have been shown to influence the microclimate of the burrows of the Macaronesian shearwater (*Puffinus lherminieri baroli*), which can impact chicks and influence breeding success (Fagundes *et al.* 2016). Therefore, the local environmental conditions during negative SOI values may have been advantageous for chick development, leading to an increase in breeding success. Secondly, STSH are able to mitigate unfavourable environmental conditions due to their flexible foraging strategies. They frequent more distant foraging areas when resources are low (Berlincourt & Arnould 2015), providing a buffer during adverse conditions. Finally, only individuals of high fitness may be choosing to return to Fisher Island to breed more frequently (Bradley *et al.* 2000), therefore enabling them to successfully breed during negative SOI values. These possibilities require further exploration, to unravel the relationship between ENSO and breeding success and to understand the ecological processes at play.

There are several other, non-resource, factors that may have contributed to some of the variability in breeding success at Fisher Island. For example, predation on STSH eggs occurred at Fisher Island during the 1980s from native water rats (*Hydromys chrysogaster*) (Bradley *et al.* 2000).

While these effects have not been quantified, on Big Dog Island, within the Furneaux Island Group, approximately 8% of the STSH eggs laid were lost to two species of predators: water rats and the blotched blue-tongue lizard (*Tiliqua nigrolutea*) (Carey 2010). Furthermore, breeding success in STSH is also influenced by the experience and quality of the pair-bonds, which if lacking, may result in the abandonment of eggs and breeding failure (Wooller *et al.* 1990, Bradley *et al.* 1999, Meathrel & Carey 2007). This effect was not accounted for in the study.

#### **3.4.4 Final considerations**

Long-lived seabirds integrate the variabilities in their marine environments in various manifestations – from foraging trip durations to demographic parameters. In many cases, these signals are direct – prey species' abundances during ENSO events in the Galapagos result in catastrophic breeding failures (Schreiber 1989, Boersma 1998), while long-term changes in SST altering the distributions and abundances of prey species over decades result in population decreases of 90% of Rockhopper Penguins at Sub-Antarctic Campbell Island (Moors 1986).

Temporal and/or spatial correlates and lags between the environmental drivers and biological responses range from days to decades (Stommel 1963, Haury *et al.* 1978) and disentangling short-term from long-term responses using seabirds such as STSH requires long-term time series, as most species of long-lived seabirds do not recruit into breeding populations until they are several years old. Short-tailed shearwaters commence breeding by a mean age of 7 years (Wooller *et al.* 1990, Bradley *et al.* 1991), providing an extended temporal window for environmental drivers to influence demographic parameters, often through resource availability (Ainley *et al.* 1995, Bost *et al.* 2015, Fay *et al.* 2015, Fay *et al.* 2017). This may also be the situation for the Fisher Island STSH breeding population and further investigation is required to unravel further long-term population responses to environmental pressures.

Another key aspect of the bird's life history that will be affected by environmental factors is age specific survival. For example, an early-life demographic study of the wandering albatross showed that juvenile females had a higher survival rate compared to males; however, in adult wandering albatross this was reversed, thus environmental and trophic conditions may impact on survival different depending on age (Fay *et al.* 2015, Fay *et al.* 2017). There are mark-recapture data available for each year of this long-term dataset, and an analysis of these data will be the focus of future studies. However, because the breeding population on Fisher Island is quite small (20 to 80 chicks produced per year), this results in a dataset in which annual resight data is relatively sparse. Also, given that recapture/resight effort was varied considerably among

years, this further complicates the issue, making interannual survival comparisons difficult (Desprez *et al.* 2013). Finally, imperfect detections further limit our ability to conduct a survival analysis, especially across the entire 70-year time series. Devising techniques that can tease relationships out of the considerable uncertainty that is a product of these small samples is beyond the scope of the present study.

The findings of this study highlight the importance of long-term monitoring to assess large-scale climate indices and local environmental conditions affecting seabirds' breeding parameters. Ecological lags are also an important factor to consider when identifying climate-induced effects, as any impact to bottom-up processes (*i.e.* nutrient upwellings in the ocean) need time to filter through to the higher trophic levels. Given that ecosystem processes are complex and often difficult to quantify, other intrinsic and extrinsic factors not considered in the study may also contribute to the variability of breeding parameters of the STSH (*e.g.* breeding experience, inadequate pair-bond, and predation). To further understand impacts at the population level, demographic studies are needed to investigate the long-term impact on the STSH population in south-eastern Australia.

### 3.5 Tables and Figures

Table 3-1: *Breeding periods and temporal lags used in the Generalised Linear Models to determine the influence of climate on breeding parameters of the short-tailed shearwater*

Breeding Period	Temporal Lag One <sup>(0)</sup>	Temporal Lag Two <sup>(-0.5)</sup>	Temporal Lag Three <sup>(-1)</sup>
<b>Pre-breeding/Migration (PB)</b> <i>May to October</i>	May to August* (PB <sup>0</sup> )	February to August,* the same year as the pre-breeding season (PB <sup>-0.5</sup> )	November to October (PB <sup>-1</sup> )
<b>Early Breeding (EB)</b> <i>September to November</i>	September to November (EB <sup>0</sup> )	June to November the same year as the pre-breeding season (EB <sup>-0.5</sup> )	December to November (EB <sup>-1</sup> )
<b>Chick Rearing (CR)</b> <i>December to March</i>	December to March (CR <sup>0</sup> )	September to March, the same year as the pre-breeding season (CR <sup>-0.5</sup> )	April to March (CR <sup>-1</sup> )

\*Most short-tailed shearwaters migrate around September to October, so we did not include these months in this time period.

Table 3-2: Akaike information criteria (AIC) ranked model selection results to explain the effects of temporal lag one ( $t^0$ ) and temporal lag three ( $t^1$ ) climate indices NPI, SOI, SAM, PDO on the number of birds arriving to breed at Fisher Island

Model No.	Intercept	NPI PB <sup>0</sup>	NPI PB <sup>-1</sup>	SAM EB <sup>-1</sup>	SOI EB <sup>-1</sup>	PDO PB <sup>-1</sup>	df	logLik	AICc	delta	weight
<b>5</b>	<b>94.632</b>	<b>NA</b>	<b>NA</b>	<b>10.952</b>	<b>NA</b>	<b>NA</b>	<b>3</b>	<b>-257.671</b>	<b>521.813</b>	<b>0.000</b>	<b>0.116</b>
<b>6</b>	<b>6899.754</b>	<b>-6.697</b>	<b>NA</b>	<b>12.412</b>	<b>NA</b>	<b>NA</b>	<b>4</b>	<b>-256.793</b>	<b>522.386</b>	<b>0.574</b>	<b>0.087</b>
<b>21</b>	<b>92.841</b>	<b>NA</b>	<b>NA</b>	<b>10.261</b>	<b>NA</b>	<b>-6.028</b>	<b>4</b>	<b>-256.816</b>	<b>522.432</b>	<b>0.618</b>	<b>0.085</b>
<b>22</b>	<b>7338.209</b>	<b>-7.131</b>	<b>NA</b>	<b>11.769</b>	<b>NA</b>	<b>-6.427</b>	<b>5</b>	<b>-255.790</b>	<b>522.805</b>	<b>0.992</b>	<b>0.071</b>
<b>23</b>	<b>7196.822</b>	<b>NA</b>	<b>-7.018</b>	<b>9.367</b>	<b>NA</b>	<b>-11.986</b>	<b>5</b>	<b>-255.824</b>	<b>522.872</b>	<b>1.059</b>	<b>0.068</b>
<b>19</b>	<b>8317.722</b>	<b>NA</b>	<b>-8.126</b>	<b>NA</b>	<b>NA</b>	<b>-13.752</b>	<b>4</b>	<b>-257.446</b>	<b>523.693</b>	<b>1.879</b>	<b>0.045</b>
<b>1</b>	<b>94.091</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>2</b>	<b>-259.780</b>	<b>523.791</b>	<b>1.978</b>	<b>0.043</b>
17	92.066	NA	NA	NA	NA	-6.946	3	-258.713	523.897	2.083	0.041
24	12254.749	-6.066	-5.927	10.789	NA	-11.399	6	-255.083	523.916	2.103	0.041
13	94.667	NA	NA	10.865	0.090	NA	4	-257.657	524.113	2.300	0.037

Models selected for model averaging with AIC  $\Delta_i \leq 2$  are in **bold**. Only the top 10 models are displayed.

Table 3-3: Models with an AIC  $\leq 2$  relative importance values of each climate indices for temporal lag one ( $t^0$ ) and temporal lag three ( $t^1$ ) on the number of breeding birds arriving to breed at Fisher Island

Indices	SAM EB <sup>-1</sup>	PDO PB <sup>-1</sup>	NPI PB <sup>0</sup>	NPI PB <sup>-1</sup>	SOI EB <sup>-1</sup>
<b>Importance</b>	0.83	0.52	0.31	0.22	0.00
<b>No. containing models</b>	5	4	2	2	0

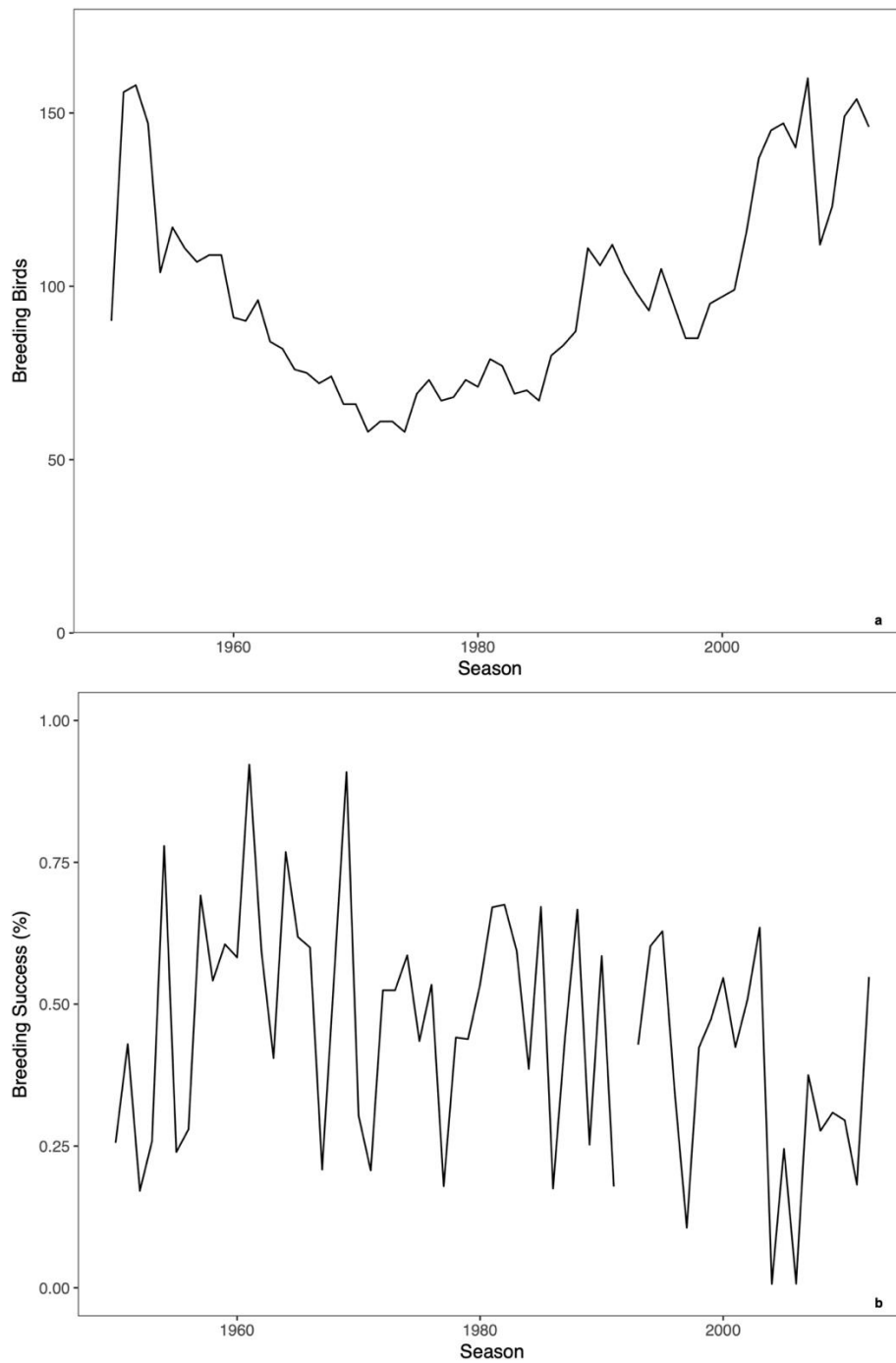
Table 3-4: Akaike information criteria (AIC) ranked model selection results to explain the effects of temporal lag one ( $^0$ ) and temporal lag three ( $^1$ ) for climate indices SOI, SAM, and rainfall on breeding success at Fisher Island

Model No.	Intercept	Rainfall CR <sup>0</sup>	SAM CR <sup>0</sup>	SAM CR <sup>-1</sup>	SOI CR <sup>0</sup>	SOI CR <sup>-1</sup>	df	logLik	AICc	delta	weight
<b>10</b>	<b>0.619</b>	<b>-0.003</b>	<b>NA</b>	<b>NA</b>	<b>-0.005</b>	<b>NA</b>	<b>4</b>	<b>13.171</b>	<b>-17.491</b>	<b>0.000</b>	<b>0.163</b>
<b>2</b>	<b>0.632</b>	<b>-0.004</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>3</b>	<b>11.590</b>	<b>-16.682</b>	<b>0.810</b>	<b>0.109</b>
<b>18</b>	<b>0.639</b>	<b>-0.004</b>	<b>NA</b>	<b>NA</b>	<b>NA</b>	<b>0.005</b>	<b>4</b>	<b>12.544</b>	<b>-16.237</b>	<b>1.255</b>	<b>0.087</b>
<b>26</b>	<b>0.626</b>	<b>-0.003</b>	<b>NA</b>	<b>NA</b>	<b>-0.004</b>	<b>0.003</b>	<b>5</b>	<b>13.685</b>	<b>-16.066</b>	<b>1.426</b>	<b>0.080</b>
4	0.634	-0.004	-0.022	NA	NA	NA	4	12.077	-15.303	2.188	0.055
9	0.454	NA	NA	NA	-0.006	NA	3	10.848	-15.197	2.296	0.052
12	0.621	-0.003	-0.008	NA	-0.005	NA	5	13.235	-15.164	2.327	0.051
14	0.621	-0.003	NA	-0.005	-0.005	NA	5	13.181	-15.058	2.434	0.048
6	0.638	-0.004	NA	-0.019	NA	NA	4	11.728	-14.6051	2.887	0.038
20	0.640	-0.004	-0.017	NA	NA	0.004	5	12.849	-14.394	3.098	0.035

Models selected for model averaging with AIC  $\Delta_i \leq 2$  are in **bold**. Only the top 10 models are displayed.

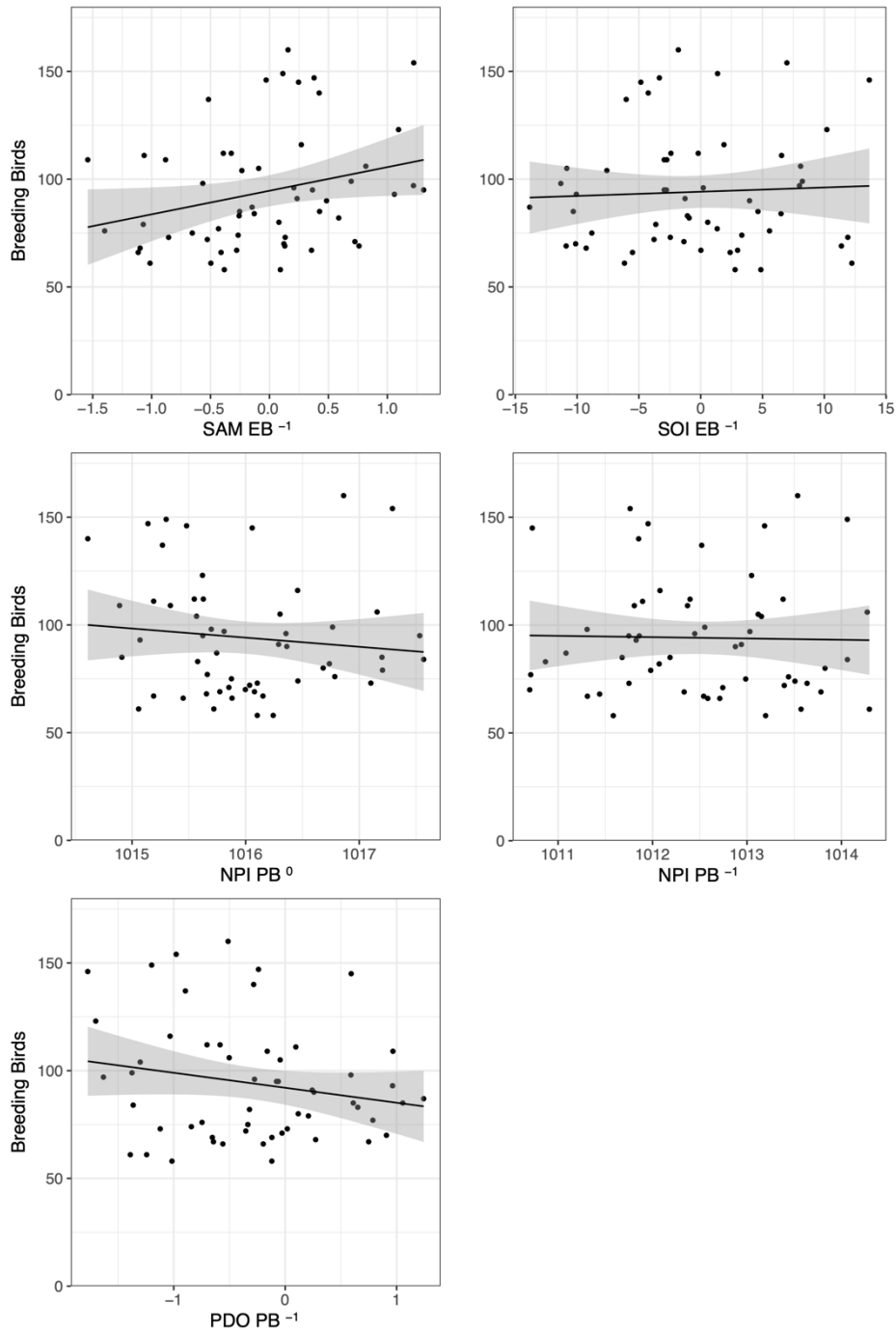
Table 3-5: Models with an AIC  $\leq 2$  relative importance values of each climate indices and rainfall for temporal lag one ( $^0$ ) and temporal lag three ( $^1$ ) on breeding success at Fisher Island

Indices	Rainfall CR <sup>0</sup>	SOI CR <sup>0</sup>	SOI CR <sup>-1</sup>
<b>Importance</b>	1.00	0.55	0.38
<b>No. containing models</b>	4	2	2



*Figure 3-1: The time series (1950 to 2012) of STSH breeding at Fisher Island*

(3-1a) The annual number of breeding participants arriving to Fisher Island; (3-1b) The annual variation of breeding success at Fisher Island.

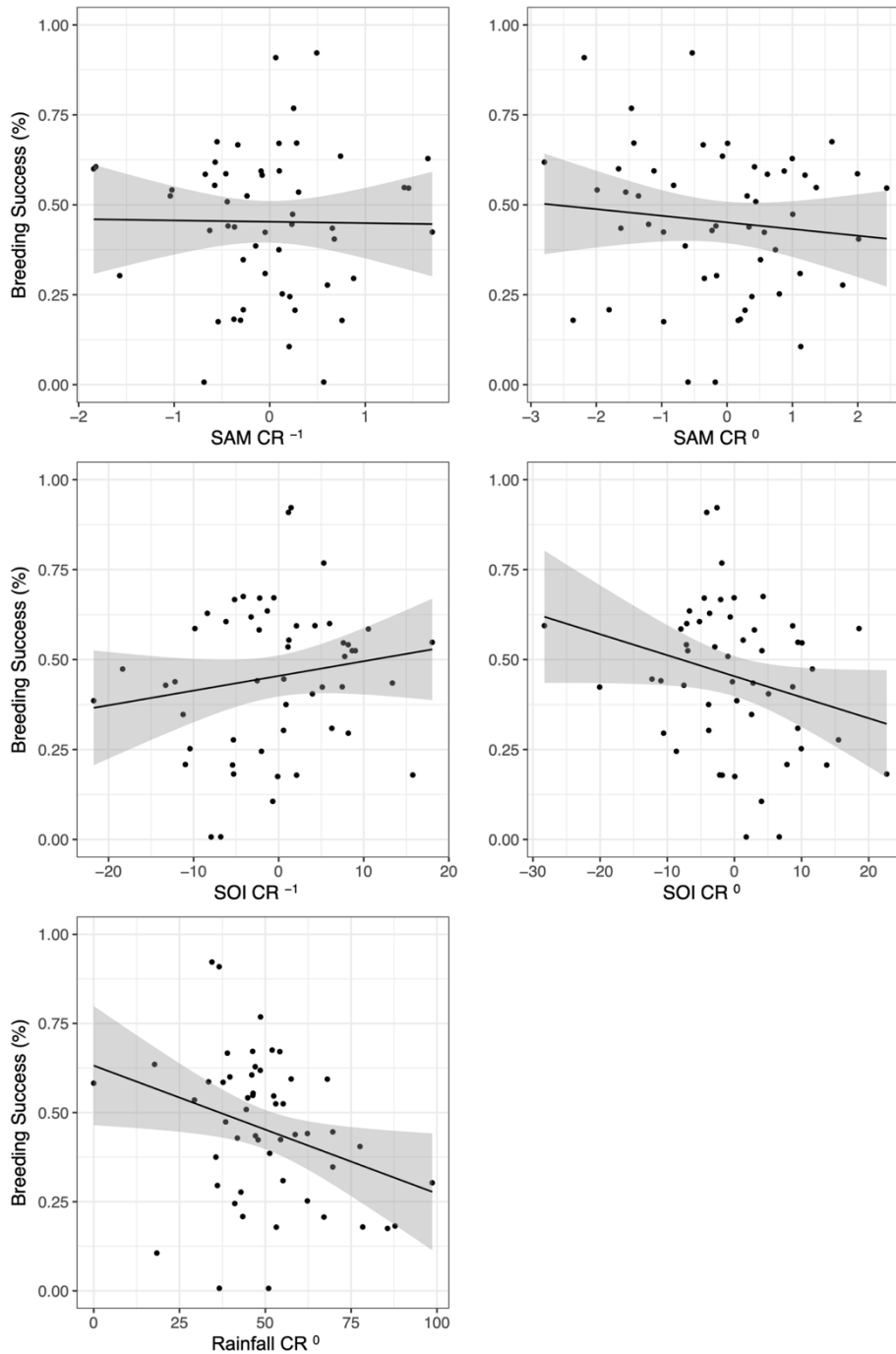


*Figure 3-2: Relationship between the number of breeding participants arriving at Fisher Island and climate indices in the Southern and Northern Hemisphere*

Climate Indices: Southern Annual Mode = SAM, Southern Oscillation Index = SOI, Northern Pacific Index = NPI, Pacific Decadal Oscillation = PDO. Temporal lag one: climate indices average between May to August ( $PB^0$ ), climate indices average between September to November ( $EB^0$ ); temporal lag three = climate indices average between November to October ( $PB^{-1}$ ), climate indices average between December to November ( $EB^{-1}$ ).

SAM  $EB^{-1}$  = SAM during the early-breeding period with temporal lag three; SOI  $EB^{-1}$  = SOI during the early-breeding period with temporal lag three; NPI  $PB^0$  = NPI during the pre-breeding/migration period with temporal lag one; NPI  $PB^{-1}$  = NPI during the pre-breeding/migration period with temporal lag three; PDO  $PB^{-1}$  = PDO during the pre-breeding/migration period with temporal lag three.





*Figure 3-3: Relationship between breeding success at Fisher Island and Southern Hemisphere climate indices and local weather conditions*

Climate Indices: Southern Oscillation Index = SOI, Southern Annual Mode = SAM. SAM CR<sup>-1</sup> = SAM averaged between April the previous year to March the same year as the chick-rearing period; SAM CR<sup>0</sup> = SAM averaged between December to March during the chick-rearing period; SOI CR<sup>-1</sup> = SOI averaged April the previous year to March, the same year as the chick-rearing period; SOI CR<sup>0</sup> = SOI averaged between December to March during the chick-rearing period; Rainfall CR<sup>0</sup> = Precipitation (mm) averaged between December to March during the chick-rearing period.

### 3.6 Supplementary Material

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S3-1: *Spearman's  $\rho$  correlation matrix for breeding parameters*

	<b>BB</b>	<b>Ch</b>	<b>BS</b>
<b>BB</b>	1.00	0.21	-0.28
<b>Ch</b>	0.21	1.00	<b>0.83</b>
<b>BS</b>	-0.28	<b>0.83</b>	1.00

BB = Number of breeding birds; Ch = Number of chicks;  
BS = Breeding success. Values in **bold** represent correlated relationships.

S3-2: *Spearman's  $\rho$  correlation matrix for climate indices affecting the breeding birds arriving to Fisher Island*

	PDO PB <sup>-1</sup>	SOI EB <sup>-1</sup>	NPI PB <sup>-1</sup>	SAM EB <sup>-1</sup>	PDO <sup>0</sup>	NPI PB <sup>0</sup>	SOI EB <sup>0</sup>	SAM PB <sup>0</sup>	PDO PB <sup>-0.5</sup>	NPI PB <sup>-0.5</sup>	SOI EB <sup>-0.5</sup>	SAM EB <sup>-0.5</sup>
PDO PB <sup>-1</sup>	1.000	-0.540	-0.685	-0.018	<b>0.891</b>	-0.062	-0.344	0.184	0.966	-0.477	-0.321	0.153
SOI EB <sup>-1</sup>	-0.540	1.000	0.378	0.049	-0.515	0.232	<b>0.783</b>	-0.128	-0.548	0.262	<b>0.809</b>	-0.166
NPI PB <sup>-1</sup>	-0.685	0.378	1.000	-0.054	-0.589	0.146	0.086	-0.201	-0.736	<b>0.753</b>	0.079	-0.108
SAM EB <sup>-1</sup>	-0.018	0.049	-0.054	1.000	-0.025	0.193	0.129	0.339	0.012	0.030	0.018	0.601
PDO PB <sup>0</sup>	<b>0.891</b>	-0.515	-0.589	-0.025	1.000	-0.235	-0.373	0.098	<b>0.928</b>	-0.484	-0.348	0.063
NPI PB <sup>0</sup>	-0.062	0.232	0.146	0.193	-0.235	1.000	0.249	0.074	-0.087	0.366	0.274	0.103
SOI EB <sup>0</sup>	-0.344	<b>0.783</b>	0.086	0.129	-0.373	0.249	1.000	0.009	-0.308	-0.017	<b>0.946</b>	-0.021
SAM EB <sup>0</sup>	0.184	-0.128	-0.201	0.339	0.098	0.074	0.009	1.000	0.173	0.029	-0.074	<b>0.756</b>
PDO PB <sup>-0.5</sup>	<b>0.966</b>	-0.548	-0.736	0.012	<b>0.928</b>	-0.087	-0.308	0.173	1.000	-0.569	-0.290	<b>0.756</b>
NPI PB <sup>-0.5</sup>	-0.477	0.262	<b>0.753</b>	0.030	-0.484	0.366	-0.017	0.029	-0.569	1.000	-0.023	-0.015
SOI EB <sup>-0.5</sup>	-0.321	<b>0.809</b>	-0.201	0.339	-0.348	0.074	0.009	-0.074	-0.290	0.029	1.000	<b>0.756</b>
SAM EB <sup>-0.5</sup>	0.153	-0.166	-0.108	0.601	0.063	0.103	-0.021	<b>0.756</b>	0.119	-0.015	-0.133	1.000

Breeding Periods: Pre-breeding/migration = PB, Early-breeding = EB. Climate Indices: Pacific Decal Oscillation = PDO, Northern Pacific Index = NPI, Southern Oscillation Index = SOI, Southern Annual Mode = SAM. Temporal lag one: climate indices average between May to August (PB<sup>0</sup>), climate indices average between September to November (EB<sup>0</sup>); temporal lag two: climate indices average between February to August (PB<sup>-0.5</sup>), climate indices average between June to November (EB<sup>-0.5</sup>); temporal lag three = climate indices average between November to October (PB<sup>-1</sup>), climate indices average between December to November (EB<sup>-1</sup>). Values in **bold** represent correlated relationships (greater than > 0.75).

S3-3: *Spearman's  $\rho$  correlation matrix for climate indices affecting breeding success at Fisher Island*

	Rainfall CR <sup>0</sup>	SOI CR <sup>0</sup>	SAM CR <sup>0</sup>	SOI CR <sup>-0.5</sup>	SAM CR <sup>-0.5</sup>	SOI CR <sup>-1</sup>	SAM CR <sup>-1</sup>
Rainfall CR <sup>0</sup>	1.000	0.156	-0.046	0.027	-0.179	0.047	-0.161
SOI CR <sup>0</sup>	0.156	1.000	0.297	-0.145	0.144	-0.214	0.196
SAM CR <sup>0</sup>	-0.046	0.297	1.000	-0.068	0.245	-0.131	0.238
SOI CR <sup>-0.5</sup>	0.027	-0.145	-0.068	1.000	0.287	<b>0.944</b>	0.220
SAM CR <sup>-0.5</sup>	-0.179	0.144	0.245	0.287	1.000	0.212	<b>0.843</b>
SOI CR <sup>-1</sup>	0.047	-0.214	-0.131	<b>0.944</b>	0.212	1.000	0.127
SAM CR <sup>-1</sup>	-0.161	0.196	0.238	0.220	<b>0.843</b>	0.127	1.000

Climate Indices: Pacific Decadal Oscillation = PDO, Northern Pacific Index = NPI, Southern Oscillation Index = SOI, Southern Annual Mode = SAM. Temporal lags: Temporal lag one = 3 to 4 months <sup>(0)</sup>, temporal lag two = 6 to 7 months <sup>(-0.5)</sup>, temporal lag three = 12 months <sup>(-1)</sup>. Rainfall CR<sup>0</sup> = rainfall averaged between December to March during the chick-rearing period; SOI CR<sup>0</sup> = SOI averaged between December to March during the chick-rearing period; SAM CR<sup>0</sup> = SAM averaged between December to March during the chick-rearing period; SOI CR<sup>-0.5</sup> = SOI averaged between September to March, the same year as the chick-rearing period; SAM CR<sup>-0.5</sup> = SAM averaged between September to March, the same year as the chick-rearing period; SOI CR<sup>-1</sup> = SOI averaged April the previous year to March, the same year as the chick-rearing period; SAM CR<sup>-1</sup> = SAM averaged between April the previous year to March the same year as the chick-rearing period. Values in **bold** represent correlated relationships.

S3-4: *Coefficient values of each climate indices for the response variable number of breeding birds arriving to Fisher Island*

	Estimate	SE	t value	Pr (> t )
<b>Intercept</b>	11907.927	6817.288	1.747	0.087
<b>NPI PB<sup>0</sup></b>	-5.356	5.370	-0.997	0.323
<b>SAM EB<sup>-1</sup></b>	10.738	5.477	1.961	0.055
<b>NPI PB<sup>-1</sup></b>	-6.297	5.268	-1.195	0.237
<b>PDO PB<sup>-1</sup></b>	-13.671	7.532	-1.815	0.075
<b>SOI EB<sup>-1</sup></b>	-0.389	0.674	-0.577	0.566

NPI PB<sup>0</sup> = North Pacific Index averaged from November to October during the pre-breeding/migration period; SOI EB<sup>-1</sup> = Southern Oscillation Index averaged from December the previous year to November the same year as the early-breeding period; SAM EB<sup>-1</sup> = SAM averaged between December the previous year to November the same year as the early-breeding period; NPI PB<sup>-1</sup> = North Pacific Index averaged from November the previous year to October the same year as the pre-breeding/migration period; and PDO PB<sup>-1</sup> = Pacific Decadal Oscillation averaged from November the previous year to October the same year as the pre-breeding/migration period.

S3-5: *Coefficient values of each climate indices for the response variable breeding success at Fisher Island*

	Estimate	SE	t value	Pr (> t )
<b>Intercept</b>	0.632	0.085	7.396	2.33e-09
<b>SOI CR<sup>0</sup></b>	-0.004	0.003	-1.116	0.250
<b>SAM CR<sup>0</sup></b>	-0.005	0.025	-0.198	0.844
<b>SOI CR<sup>-1</sup></b>	0.003	0.003	0.982	0.331
<b>SAM CR<sup>-1</sup></b>	-0.012	0.040	-0.313	0.755
<b>Rainfall CR<sup>0</sup></b>	-0.003	0.002	-2.00	0.033

Rainfall CR<sup>0</sup> = rainfall averaged between December to March (the chick-rearing period); SOI CR<sup>0</sup> = SOI averaged between December to March (the chick-rearing period); SAM CR<sup>0</sup> = SAM averaged between December to March (the chick-rearing period); SOI CR<sup>-1</sup> = SOI averaged April the previous year to March the same year as the chick-rearing period; SAM CR<sup>-1</sup> = SAM averaged between April the previous year to March the same year as the chick-rearing period. Significant < 0.05 are in **bold**.

**INTER-ANNUAL AND INTER-COLONY VARIABILITY IN  
BREEDING PERFORMANCE OF FOUR COLONIES OF SHORT-  
TAILED SHEARWATERS**

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Little Green Island

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## Abstract

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Biotic responses to large-scale climate processes are scale-dependant and can influence population trajectories of highly migratory species such as short-tailed shearwaters (*Ardenna tenuirostris*). In this study, we quantified changes in climate, measured through large-scale climate indices (*i.e.* Northern Pacific Index, Pacific Decadal Oscillation, El Niño–Southern Oscillation and Southern Annular Mode) and local weather conditions (*i.e.* rainfall) on the breeding performance of short-tailed shearwaters at four of their breeding colonies within the Furneaux Island Group, Tasmania, Australia, from 2010 to 2018. There was inter-colony variability in adult body mass and breeding participation, which were influenced by climate conditions in the preceding year. In contrast, breeding success was influenced by climate conditions in the preceding three to four months and by local weather conditions at the time of breeding. These findings demonstrate that variation in the breeding performance of short-tailed shearwaters is explained both by large-scale climate indices and local environmental conditions. The outcomes of this study provide a better understanding of the environmental factors affecting short-tailed shearwaters.

## 4.1 Introduction

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The marine environment is heterogeneous, with resources patchily distributed both in space and time (Stommel 1963, Haury *et al.* 1978). Large-scale climate processes influence physical oceanographic and atmospheric characteristics (*e.g.* wind, temperature and air pressure) (Jenouvrier 2013, Cushing *et al.* 2017). These affect bottom-up processes, such as nutrient upwellings, which in turn, influence the abundance and availability of resources to higher tropic level species, such as seabirds (Pace *et al.* 1999, Polis *et al.* 2000, Ainley & Hyrenbach 2010). Small changes in physical oceanographic conditions that alter primary productivity can also influence seabird foraging behaviour and distribution (*e.g.* Humphries & Möller 2017, Jenouvrier *et al.* 2018). For example, krill is an important component of the diet of short-tailed shearwaters (STSH) and their movements have been shown to follow the distribution of krill (Yamamoto *et al.* 2015, Nishizawa *et al.* 2017), whose abundance in places such as the Bering Sea and in the Antarctic has been linked to sea ice dynamics, increases in sea-surface temperature (SST), and the timing of the phytoplankton blooms (Shaffer *et al.* 2006, Stafford *et al.* 2010, Stabeno *et al.* 2012, Saba *et al.* 2014, Nishizawa *et al.* 2017).

The STSH is a trans-equatorial migratory seabird that spends the majority of its life at sea, travelling great distances and utilising a variety of habitats during the breeding and non-breeding periods. They are meso-predators in marine ecosystems that can travel long distances from breeding colonies to exploit food resources (Weimerskirch 2007, Fagundes *et al.* 2016). For example, during the breeding season, STSH use a dual foraging strategy, characterised by either short (100 to 200 km) or long (1000 to 4000 km) foraging trips (Weimerskirch & Cherel 1998, Einoder *et al.* 2013, Berlincourt & Arnould 2015). Consequently, STSH are exposed to a variety of weather, environmental conditions and oceanographic systems (Weimerskirch & Cherel 1998, Einoder *et al.* 2013, Yamamoto *et al.* 2015, Nishizawa *et al.* 2017).

Inter-annual and inter-colony variations in foraging behaviour have been identified in procellariiformes, and reflect many factors, including intrinsic parameters (*i.e.* gender, age and experience), climate variability and prey availability (Quillfeldt & Peter 2000, Darren & Bradley 2005). For example, both inter-annual and inter-colony differences in the diet of STSH were found across three regions in Bass Strait southeast Australia (Fromant *et al.* 2020). However, due to flexible foraging strategies, STSH are able to seek out prey in a changing marine environment (Berlincourt & Arnould 2015). Other factors, such as age-related foraging (*i.e.* senescence), can impact the bird's ability to forage efficiently. For example, young individuals may be too inexperienced to seek out high-quality resources, or may be excluded from the best foraging areas by older and/or more experienced individuals (Clutton-Brock 1988, Weimerskirch 1992, Cam & Monnat 2000). Both age effects and environmental variations can affect demographic parameters (*i.e.* survival, recruitment) and influence the population dynamics (Pardo *et al.* 2013).

Each September to October, STSH return from their non-breeding grounds in the Northern Hemisphere to southeast Australia to breed (Skira 1991). The breeding season of the STSH begins in November when one egg per successful breeding pair is laid, which is not replaced if it fails. Chicks hatch from mid-to-late January and fledge mid-April to early May (Serventy 1967, Skira 1990, Wooller *et al.* 1990). At some STSH colonies in Tasmania, the chicks are subject to annual commercial and recreational harvesting efforts known as 'mutton birding' (Skira & Wapstra 1980). After the breeding season, adults return to the North Pacific for the boreal summer (Vertigan *et al.* 2012, Carey *et al.* 2014).

In the Northern Hemisphere, two main climate indices – the Pacific Decadal Oscillation (PDO) and the North Pacific Index (NPI) – reflect the oceanographic and atmospheric conditions in the non-breeding areas used by STSH (Trenberth & Hurrell 1994, Humphries & Möller 2017). In



the Southern Hemisphere, the El Niño–Southern Oscillation (ENSO) and the Southern Annual Mode (SAM) are the predominant climate drivers influencing the prevailing oceanographic and atmospheric conditions, affecting the breeding and foraging areas of the STSH (Price *et al.* 2020). These climate indices have been connected to changes in the marine ecosystems and have been demonstrated to influence the breeding success of seabirds in both the Northern and Southern Hemispheres (Devney *et al.* 2009, Clucas 2011, Bond & Lavers 2014).

A previous study of an unharvested colony of STSH (Fisher Island, 40°13'S, 148°14'E) from Tasmania demonstrated that breeding parameters were affected by both climate variability with a 12-month temporal lag, and also that local environmental conditions influenced breeding success (Price *et al.* 2020). In this study, we investigated how these large-scale climate indices (*i.e.* PDO, NPI, ENSO and SAM) and local weather conditions (*i.e.* rainfall) influenced the breeding performance of STSH at four harvested breeding colonies within the Furneaux Island Group, Tasmania, Australia, from 2010 to 2018.

Our study aimed to quantify the influence of climate variation on STSH colonies within the Furneaux Island Group, a region subject to an annual chick harvest. We investigated: (i) how large-scale climate indices influence the breeding parameter of STSH; (ii) whether there is inter-colony variability among breeding parameters in the Furneaux Island Group; and (iii) whether local environmental conditions (*i.e.* rainfall) influence STSH breeding. The findings from this study will address existing knowledge gaps, allowing an improved understanding of the environmental factors affecting STSH throughout their transhemispheric range.

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## **4.2 Materials and Methods**

### **4.2.1 Field sites**

The study was undertaken from 2010 to 2018 on four islands in the Furneaux Island Group, Bass Strait, Tasmania: Little Green (40°13'S, 148°15'E), Little Dog (40°15'S, 148°12'E), Big Green (40°11'S, 147°59'E) and East Kangaroo (40°18'S, 147°54'E). The islands are up to 32 km apart but are likely to be exposed to similar local weather conditions. The commercial and recreational harvesting activities on these islands are managed by the Tasmanian Department of Primary Industries, Parks, Water and Environment (DPIPWE). The four study islands were open to recreational harvest of STSH intermittently during of the study period, and livestock grazing was also permitted on some of the islands during the study period (Table 4-1).

#### 4.2.2 Annual life cycle periods

Three periods were defined to investigate the relationship among environmental conditions and STSH breeding parameters: (i) the migration/overwintering period, from May to October, which encompasses the post-breeding time, followed by their migration north and overwintering in the North Pacific Ocean. During this time, environmental conditions may influence their ability to build body reserves for their migration north and for the return to southeast Australia for the onset of breeding (Yamamoto *et al.* 2015, Nishizawa *et al.* 2017); (ii) the pre/early-breeding period, from September to November, which corresponds to the time STSH are in southeast Australia. During this time, environmental conditions may potentially influence adult condition and breeding effort; and (iii) the incubation and chick-rearing period, from December to the end of March, when adult STSH are in southeast Australia. During this time, environmental conditions and local weather (in particular, rainfall) may impact on parental conditions and investment in chick rearing (Fay *et al.* 2015).

#### 4.2.3 Temporal lags

Two temporal lags were chosen for each breeding period and incorporated into the analyses to account for variation in spatial-temporal scales of oceanographic conditions, which may impact resource availability to STSH (Cox *et al.* 2018, Price *et al.* 2020). The first temporal lag (denoted <sup>0</sup>) of approximately 3 to 4 months duration (Table 4-2), was chosen to account for potential influences on local resources, either on-shore, through changes in local weather conditions acting directly on the colony (*e.g.* flooding burrows), or offshore, through fluctuations in local oceanographic conditions that influenced prey distribution and abundance (Genovart *et al.* 2013, Fagundes *et al.* 2016). The second temporal lag (denoted <sup>-1</sup>) of 12 months duration (Table 4-2) was selected as climate may influence the strength of irradiation and wind stress, resulting in variations in primary productivity (Sharples *et al.* 2006, Cox *et al.* 2018). Changes in the availability and distribution of primary production can influence the propagation and distribution of lower trophic consumers, such as fish (myctophids) and zooplankton (euphausiids), which constitute a large portion of the STSH diet (Nishizawa *et al.* 2017, Fromant *et al.* 2020).

#### 4.2.4 Shearwater breeding parameters

##### 4.2.4.1 Breeding participation and chick occupancy

There are six permanent monitoring transects on Little Green and Little Dog Islands, and 10 on Big Green and East Kangaroo Islands (DPIPWE 2010). All transect start and end points were located with GPS, and a measuring tape was rolled out between these points to locate the

transects for burrow inspections. The transects are 100 m in length, and all burrows within 1 m either side of the transect were examined for the presence or absence of STSH. Burrows were searched using a thin wooden stick (approximately 60 cm), with the observer laying on the ground in order to get their whole arm into the burrow. A burrow is classified as occupied if the observer feels any sharp pecking on the stick (or arm) from a resident STSH while gently probing the burrow.

Censuses of all STSH colonies occurred twice per year during the breeding season (November to March). The first census, to assess breeding participation, was in late November/early December at the start of the breeding period at the onset of incubation. The second census was in late March, to assess the number of chicks just before fledging. During the second census, only half of the permanent monitoring transects (three on Little Green and Little Dog Islands, and five on Big Green and East Kangaroo Islands), were checked before the annual recreational harvest commenced; this constraint was due to the established management regime for these islands. Observers were constant during the season. Adult and chick occupancy rates were calculated for each island as the number of occupied burrows divided by the total number of burrows on both sides of the transect line. A breeding season in this study is defined as the year in which the chick fledged (*e.g.* breeding season 2009/10 is hereafter referred to as the 2010 season), and includes the adult survey count from the preceding year.

#### *4.2.4.2 Breeding success*

An index of abundance was calculated to determine breeding success. This was calculated as the number of chicks present per transect in late March, divided by the number of occupied burrows in late November/early December in that same transect.

#### *4.2.4.3 Body mass of adults and chicks*

We used body mass as an indicator of body condition. The body mass of adults and chicks were measured using a Pesola spring balance ( $1000 \pm 5$  g). Adults ( $n = 1052$ , over the entire study period) were weighed in late November to early December, and chicks ( $n = 510$ , over the entire study period) were weighed in late March before fledging. Individual adults and chicks were selected at random along each transect for weighing. Adult body mass was not recorded for the 2010 season.

#### 4.2.5 Environmental variables

We included the PDO and NPI to represent climatic conditions in the Northern Hemisphere. In the Southern Hemisphere, ENSO and SAM were included as indicators of climate conditions. Rainfall was included as local environmental conditions have been shown to influence breeding parameters of seabirds (Fagundes *et al.* 2016, Price *et al.* 2020). PDO monthly means for the period of January 2009 to December 2018 were obtained from the US National Oceanic and Atmospheric Administration (NOAA 2018, from <https://www.ncdc.noaa.gov/teleconnections/pdo/>). The PDO index is calculated from the Principal Component of monthly SST anomalies in the North Pacific Ocean poleward of 20°N (Mantua & Hare 2002, Clucas 2011). PDO has been categorised into either warm phases (positive values) or cool phases (negative values) depending on the patterns of SST, surface wind and sea-level pressure in the northeast and tropical Pacific Ocean (Mantua & Hare 2002, Becker *et al.* 2007).

Monthly NPI means for the same period were obtained from NOAA at [https://www.esrl.noaa.gov/psd/gcos\\_wgsp/Timeseries/Data/np.long.data](https://www.esrl.noaa.gov/psd/gcos_wgsp/Timeseries/Data/np.long.data) (Hurrell 2017). The NPI is the mean sea-level pressure over the North Pacific Ocean between 30°N and 65°N and between 160°E and 140°W (Trenberth & Hurrell 1994), which measures the strength of the Aleutian Low (AL) pressure system (*i.e.* NPI decreases as the low-pressure system intensifies) (Beamish *et al.* 1997). PDO and NPI have been linked to changes in SST and sea ice dynamics (Trenberth & Hurrell 1994), resulting in changes in the North Pacific Ocean marine ecosystem (Mantua & Hare 2002, Becker *et al.* 2007).

ENSO and SAM are the key drivers influencing the climate and weather conditions across southeast Australia (Gaynor *et al.* 2010), and both have been linked to changes in the marine environment, such as variations in the survival, breeding success and reproductive output of seabirds (Chambers *et al.* 2015). The Southern Oscillation Index (SOI) was used as a proxy for ENSO, measuring the difference in surface air pressure between Tahiti and Darwin (Trenberth & Hurrell 1994). There are two main phases of the ENSO, El Niño (*i.e.* a sustained SOI lower than 8) and La Niña (*i.e.* a sustained SOI higher than 8), which strongly influence environmental conditions such as rainfall and temperature in southeast Australia. SOI monthly means for the study period were obtained from the Australian Bureau of Meteorology (BOM) at <http://www.bom.gov.au/climate/current/soi2.shtml>.

SAM is the leading cause of atmospheric variability at mid and high latitudes in the Southern Hemisphere (Lovenduski & Gruber 2005). For the study period, monthly SAM data was obtained from the Natural Environment Research Council (NERC) at <http://www.nerc-bas.ac.uk/icd/gjma/sam.html>. SAM exists in one of two states, positive and negative, which can influence the westerly wind belt and atmospheric pressures over southern Australia. The westerly winds are responsible for driving the circumpolar circulation of the Southern Ocean (Lovenduski & Gruber 2005).

Monthly rainfall data for the chick-rearing period over the study period were obtained for Badgers Corner, station number 099025 (40°23'S, 148°19'E, < 20 km from East Kangaroo Island), from BOM at <http://www.bom.gov.au/climate/data/>.

#### 4.2.6 Statistical analysis

Before model selection, a nonparametric measure of rank correlation (Spearman's  $\rho$ ) was performed to investigate correlation among the variables. Breeding success and chick occupancy were highly correlated, so chick occupancy was removed from subsequent analyses (S4-1). During the migration/overwintering and early-breeding periods, a correlation was identified between PDO during the migration/overwintering with temporal lag one (PDO  $M^0$ ) and PDO during the migration/overwintering period with temporal lag two (PDO  $M^{-1}$ ) (> 0.75 correlation), so PDO  $M^0$  was removed from subsequent analyses. Moreover, a correlation was found between SOI during the early-breeding period with temporal lag one (SOI  $EB^{-0}$ ) and SOI during the early-breeding period with temporal lag two (SOI  $EB^{-1}$ ) (> 0.75 correlation), so SOI  $EB^0$  was removed from subsequent analyses. No correlations were identified for any other variables in this study (S4-2 and S4-3).

We constructed Generalised Linear Models (GLMs) using the *glm* function in R version 3.5.0 (R Development Core Team 2019). The *MuMIn* package was used to generate the model selection tables (Bartoń 2018). The assumption of normality of residuals was checked using standard graphical methods (Zuur *et al.* 2010). Initial analyses were used to determine if the date on which an adult shearwater was weighed affected their mass. The initial analyses indicated that the day of the year (DOY) (based on the Julian date format) was not significant, therefore DOY was removed from the analyses (see S4-4 and S4-5). Preliminary univariate analyses were performed to select significant variables to be included in the multivariate models, as constructing all possible models for each climate variable and potential interactions would be

unmanageable. Four models were subsequently used to investigate the relationship between inter-colony variability, breeding parameters and large-scale climate indices.

#### 4.2.6.1 *Model 1 – inter-colony variability and climate on adult body mass*

The first model examined the effect of island and climate indices (as covariates) on the body mass of adult STSH. Relevant climatic variables included in the model were: (i) NPI during the migration/overwintering period with temporal lag one ( $\text{NPI } M^0$ ); (ii) NPI during the migration/overwintering period with temporal lag two ( $\text{NPI } M^{-1}$ ); (iii) PDO  $M^{-1}$ ; (iv) SOI during SOI  $EB^{-1}$ ; and (v) SAM during the early-breeding period with temporal lag two ( $\text{SAM } EB^{-1}$ ). A *post hoc* test was performed to assess the inter-colony difference in body mass.

#### 4.2.6.2 *Model 2 – inter-colony variability and climate on breeding participation*

The second model examined the effect of island and climate indices (as covariates) on the burrow occupancy of breeding STSH. Relevant climatic variables included in the model were: (i)  $\text{NPI } M^{-1}$ ; (ii) PDO  $M^{-1}$ ; and (iii) SOI  $EB^{-1}$ . A *post hoc* test was performed to assess the inter-colony difference in breeding participation.

#### 4.2.6.3 *Model 3 – inter-colony variability and climate on chick body mass*

The third model examined the effect of island, climate indices and localised weather (as covariates) on the body mass of STSH chicks. Relevant climatic variables included in the model were: (i) SOI during the chick-rearing period with temporal lag two ( $\text{SOI } CR^{-1}$ ); (ii) SAM during the chick-rearing period with temporal lag one ( $\text{SAM } CR^0$ ); and (iii) SAM during the chick-rearing period with temporal lag two ( $\text{SAM } CR^{-1}$ ). A *Tukey post hoc* test was performed to assess the inter-colony difference in chick body mass.

#### 4.2.6.4 *Model 4 – inter-colony variability and climate on breeding success*

The fourth model examined the effect of adult body mass, island, climate indices and localised weather (as covariates) on the breeding success of STSH. Relevant climatic indices included in the model were: (i) adult body mass; (ii) rainfall during the chick-rearing period with temporal lag one ( $\text{Rainfall } CR^0$ ); (iii) SOI during the chick-rearing period with temporal lag one ( $\text{SOI } CR^0$ ); and (iv)  $\text{SAM } CR^0$ .

Model selection was informed through the comparison of Akaike's Information Criterion (AIC), Akaike weights ( $w_i$ ) and Akaike's Information Criterion differences ( $\Delta_i$ ). Akaike weights ( $w_i$ ) were calculated to provide a measure of strength for each model (Burnham & Anderson 2002). We considered the best model to have the lowest AIC, and models with an AIC  $\Delta_i \leq 2.0$  were

considered to have equivalent support (Burnham & Anderson 2002). Furthermore, models with an AIC  $\Delta_i \leq 4.0$  were not considered, as 4.0 is the cut-off point for reasonable modes (Burnham & Anderson 2002).

## 4.3 Results

During the study period (2010 to 2018), large-scale climate indices were found to influence the body mass and breeding participation of STSH at the Furneaux Island Group, Australia. Inter-colony differences were found for breeding participation and body mass, but not breeding success. Local environmental conditions, such as rainfall, impacted breeding success more than large-scale meteorological and oceanographic processes.

### 4.3.1 Model 1 – inter-colony variability and climate on adult body mass

The best-fitting model to describe the annual variation in adult body mass comprised: *Island*, NPI  $M^{-1}$ , NPI  $M^0$ , PDO  $M^{-1}$ , SAM  $EB^{-1}$  and SOI  $EB^{-1}$  (S4-6). The large-scale climate indices PDO  $M^{-1}$  and SOI  $EB^{-1}$  had the strongest influence on adult body mass (Figure 4-1 and S4-7). A negative relationship was found for PDO  $M^{-1}$ , with decreases in adult body mass evident under positive PDO values. In contrast, increasing NPI  $M^0$  and NPI  $M^{-1}$  values led to increases in adult body mass. Positive SOI  $EB^{-1}$  also led to increases in adult body mass, while positive SAM  $EB^{-1}$  led to a slight decrease in adult body mass (Figure 4-1 and S4-7).

During the study period, the overall STSH adult mean body mass across all colonies was  $589 \pm 64$  g. Short-tailed shearwater body mass varied across each colony – Big Green ( $599 \pm 71$  g), East Kangaroo ( $595 \pm 61$  g), Little Dog ( $595 \pm 45$  g) and Little Green ( $572 \pm 61$  g) – which was supported by a *post hoc* test. Significant difference was found between Big Green and Little Dog (z ratio = 3.13,  $p = < 0.001$ ), Big Green and Little Green (z ratio = 5.29,  $p = < 0.0001$ ), and East Kangaroo and Little Green (z ratio = 4.62,  $p = < 0.0001$ ). On average, adult STSH were the heaviest in the 2012 season, at  $649 \pm 59$  g, and lightest in the 2014 season, at  $562 \pm 61$  g (Figure 4-2a).

### 4.3.2 Model 2 – inter-colony variability and climate on breeding participation

The model that described the annual variation in breeding participation included *Island*, NPI  $M^{-1}$ , PDO  $M^{-1}$  and SOI  $EB^{-1}$  (S4-8). PDO  $M^{-1}$  and SOI  $EB^{-1}$  conditions had the strongest influence on breeding participation (Figure 4-3 and S4-9). The number of breeding participants increased

when PDO was positive and decreased under positive SOI values. Breeding participants decreased slightly when NPI  $M^{-1}$  values increased (Figure 4-3 and S4-9).

Overall, average breeding participation for the study period was  $57 \pm 16\%$ , which varied between colonies: East Kangaroo ( $61 \pm 16\%$ ), Big Green ( $60 \pm 14\%$ ), Little Dog ( $54 \pm 16\%$ ) and Little Green ( $50 \pm 16\%$ ). The difference was confirmed by a *post hoc* test, which showed significant differences between Big Green and Little Green ( $z$  ratio = 3.90,  $p = < 0.001$ ), and East Kangaroo and Little Green ( $z$  ratio = 4.20,  $p = < 0.001$ ). The mean annual breeding participation across all colonies was lowest ( $33 \pm 12\%$ ) in the 2014 season and highest in the 2015 season, at  $73 \pm 7\%$  (Figure 4-2b).

#### **4.3.3 Model 3 – inter-colony variability and climate on chick body mass**

The best-fitting model to describe the variation in chick body mass comprised SAM  $CR^0$ , SAM  $CR^{-1}$  and an *Island* \*  $SOI^{-1}$  interaction term (S4-10).  $SOI$   $CR^{-1}$  had the greatest influence on chick body mass; under positive values of SOI, chicks were lighter (S4-11, S4-12). SAM  $CR^0$  and SAM  $CR^{-1}$  both had a slight positive effect on chick body mass, with chicks being heavier when SAM was positive (S4-11, S4-12).

For the duration of the study, overall average chick mean body mass was  $565 \pm 131$  g; however, no inter-colony variation was found for chick body mass: East Kangaroo ( $579 \pm 144$  g), Little Dog ( $577 \pm 143$  g), Big Green ( $552 \pm 120$  g) and Little Green ( $555 \pm 119$  g). The mean annual chick body mass across all colonies was lowest in the 2010 season, at  $562 \pm 61$  g, and highest in the 2014 season, at  $629 \pm 165$  g (Figure 4-2c).

#### **4.3.4 Model 4 – inter-colony variability and climate on breeding success**

The model that explained the greatest variation in the breeding success of STSH comprised adult body mass, Rainfall  $CR^0$ , SAM  $CR^0$  and  $SOI$   $CR^0$  (S4-13). Adult body mass was correlated with breeding success; breeding success increased with heavier breeding adult STSHs (Figure 4-4 and S4-14). Breeding success strongly decreased with higher local rainfall, and with positive SOI values (Figure 4-4 and S4-14). Breeding success was higher under positive SAM (Figure 4-4 and S4-14).

The overall average annual breeding success of STSH during the study period was  $56 \pm 27\%$  among colonies. There was no inter-colony variation found for STSH breeding success: East Kangaroo ( $81 \pm 56\%$ ), Little Dog ( $68 \pm 58\%$ ), Big Green ( $65 \pm 40\%$ ) and Little Green ( $69 \pm$



36%). Breeding success among colonies was lowest in the 2014 season, at  $29 \pm 15\%$ , and highest in the 2012 season, at  $89 \pm 37\%$  (Figure 4-2d).

## 4.4 Discussion

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Seabird condition, breeding performance and foraging success are strongly linked to resource availability and abundance (*e.g.* Frederiksen *et al.* 2004, Durant *et al.* 2006, Price *et al.* 2020). There was inter-colony variability in body mass and breeding participation among the four colonies. Breeding parameters of STSH at the Furneaux Island Group were influenced by large-scale (ocean-basin) oceanographic and atmospheric processes in both hemispheres; however, the strength and nature of the relationships varied among the parameters investigated. Local environmental conditions (*i.e.* rainfall) were also an important factor in breeding success.

In our study, climate indices that were lagged by 12 months influenced body mass (both adult and chick) and breeding participation to a greater extent than climate indices lagged over three to four months. Lags in productivity transfer can occur due to climate-induced effects on oceanographic properties that affect bottom-up processes, which take time to propagate through the food chain (Sandvik *et al.* 2007, Sandvik & Einar Erikstad 2008). This result suggests that climate in the previous year may be influencing the resource availability of STSH throughout their range during their breeding season, affecting their body condition. Nevertheless, climate indices lagged over a 3 to 4 month period had a greater influence on breeding success, which could suggest that local weather conditions (*i.e.* storms, rainfall and temperatures) are influencing breeding success more than offshore effects (*i.e.* resource availability).

### 4.4.1 Climate and inter-colony variability – adult STSH

#### 4.4.1.1 Northern Hemisphere climate indices

The non-breeding period in the North Pacific Ocean is a critical period for STSH to build body reserves before the return migration to their colonies in southeast Australia. Failure to build sufficient reserves can impede the birds' ability to migrate and/or breed successfully (Lovvorn *et al.* 2003, Bester *et al.* 2007). Adult STSH arriving at the Furneaux Island Group were heavier when the AL was weaker and during a cool phase (negative) PDO one year before migration. Adult STSH were also heavier when the AL was weaker during the migration/pre-breeding season lagged over a three-month period. Heavier breeding adults were more likely to have greater breeding success (see below). The relationship between breeding participation and

climate indices AL, PDO and SOI lagged over a 12-month period varied depending on the strength or phase of the indices.

During the boreal summer, STSH forage in the North Pacific Ocean, where the NPI and PDO are the climate drivers that influence atmospheric and local weather conditions (Beamish *et al.* 1997, Sugimoto & Hanawa 2009), and oceanographic properties (*e.g.* sea ice dynamics and variations in SST) (Bond *et al.* 2011). In the Bering Sea, a stronger AL influences local physical oceanography and light conditions (Sambrotto *et al.* 1986), which alter the input of nutrients through vertical mixing and stratification of the water column. A stronger AL is also accompanied by higher wind intensity, which leads to increased wave action (Bond *et al.* 2011). This can reduce the abundance of zooplankton in the surface waters, limiting their availability to surface predators (Wroblewski & Richman 1987, Bond *et al.* 2011). Similarly, the different phases of PDO (*i.e.* warm and cool phase) are strongly linked to variations in SST, which have also been shown to influence the distribution of zooplankton in the water column (Baduini *et al.* 2001, Coyle *et al.* 2008, Jin *et al.* 2009, Bond *et al.* 2011). This could potentially influence prey availability to STSH, resulting in annual variations in the body mass and breeding participation of migrating birds arriving at the Furneaux Island Group.

As body mass is linked to breeding participation and ultimately success (Weimerskirch 1998, Weimerskirch *et al.* 2001), breeding participation should increase during periods of higher resource availability. The relationship between the AL and breeding participation of STSH found in this study are consistent with an earlier study of STSH at Fisher Island, also within the Furneaux Island Group (between 1 and 30 km from the colonies within the study) (Price *et al.* 2020). However, the relationship found between PDO and breeding participation at Fisher Island are inconsistent with that study. In this study, breeding participation increased during the warm phase (positive), while the opposite relationship occurred at Fisher Island (Price *et al.* 2020). Our result is confounding, as the warm phase (positive) PDO has been linked to a number of negative effects for several species of seabirds (*e.g.* decreased reproduction, starvation and delayed breeding) (Hunt Jr *et al.* 2002, Bond *et al.* 2011). A possible explanation is that the times series in this study (9 years) may be too brief to detect a similar pattern to that on Fisher Island (63 years) (Price *et al.* 2020). Other possible factors include the persistence of PDO events over 20 to 30 years, and the longevity of STSH, with some individuals living over 48 years (see <https://www.environment.gov.au/cgi-bin/biodiversity/abbbs/abbbs-search.pl>).

#### 4.4.1.2 Southern Hemisphere climate indices

In the Southern Hemisphere, SAM and ENSO affect the climate and environmental conditions where STSH breed and forage, and influence the success of the STSH foraging trips to the Southern Ocean, which they make to restore body reserves (Lill & Baldwin 1983). In this study, ENSO had the strongest association with adult body mass and breeding participation, which may suggest that the changes in oceanography and climate conditions driven by ENSO are influencing resource availability.

In the tropical Pacific marine system, the adverse consequences of El Niño on seabirds have been studied (*e.g.* Valle *et al.* 1987, Anderson 1989, Tershy *et al.* 1991), however there are limited studies on the effects of La Niña events (*e.g.* Schreiber & Schreiber 1984). The trade winds weaken during ENSO, and warm surface water suppresses the thermocline and nutrient upwelling, decreasing primary production, with repercussions throughout the food chain (Schreiber & Schreiber 1984, Jenouvrier 2013). During these events, adult seabirds may face starvation as food resources become scarce and there is a reduced capacity to replenish body reserves (Schreiber & Schreiber 1984, Baduini *et al.* 2001).

The results for STSH adult body mass reported here demonstrate that under increasing positive SOI conditions, one year before the breeding season, STSH body mass increases, which may be due to an increase in resources (Chambers *et al.* 2011). However, due to the limited number of years of this study and the cyclic nature of ENSO, the exact relationship is unclear, although it is indicative that under La Niña conditions STSH body mass increases.

The relationship between ENSO and breeding participation in this study were inconsistent with the literature in that breeding participation increased during periods of negative SOI values (*i.e.* El Niño), and decreased during positive SOI values (*i.e.* La Niña). We hypothesised that breeding participation would decrease during periods with negative SOI values, due to poor resource availability among seabirds as previously described (see Schreiber & Schreiber 1984). For example, in 1997 during an El Niño event on the west coast of Australia, breeding participation dramatically decreased in wedge-tailed shearwaters (*Ardenna pacifica*) due to limited food resources resulting from changes to the strength of the Leeuwin Current (Dunlop *et al.* 2002). A possible explanation for the results obtained in this study is that, under La Niña conditions in the Southern Ocean, lower SST temperatures are present, which may increase sea ice extent (Yuan 2004, Stammerjohn *et al.* 2008). Increasing sea ice extent may influence resource availability for STSH, as sea ice dynamics is linked to primary production and krill abundance (Nicol *et al.* 2000, Woehler *et al.* 2010). Therefore, changes in sea ice extent in the Southern Ocean may have

offshore (distant) effects on breeding participation of STSH. Further studies are necessary to investigate the implication of ENSO on distant foraging areas of the STSH.

#### *4.4.1.3 Inter-colony difference – adult body mass and breeding participation*

At a finer spatial scale, there were differences in mean annual body mass and breeding participation among the four colonies. We also found a strong relationship between mean annual body mass and breeding participation, which is consistent with Weimerskirch 1992 and Weimerskirch *et al.* 2001, and reflects greater energy gains by adults before their annual breeding effort.

Harvest rates influence survival and recruitment into a population (Juillet *et al.* 2012). Recreational harvest in the Furneaux Group varied inter-annually and among the islands during the study period (Table 4-1), with the lowest level of harvest occurring on East Kangaroo and Big Green Islands. Harvester preference for heavier chicks was observed in a study of sooty shearwater (*Ardenna grisea*) (Hunter & Caswell 2005). This may also be the case for STSH, leaving reduced quality (smaller) chicks surviving (Weimerskirch *et al.* 2001). It is possible that recreational and commercial harvesting may influence breeding performance through specific chick selection, which can subsequently alter the population dynamics of the colony through adverse impacts on survival. In light of the emerging evidence for this, albeit limited, further investigations are warranted as to the potential for harvesting to influence population demographics in other shearwaters.

Heterogeneity in survival over time can lead to a disparity in demographic parameters (*e.g.* age or experience) at the population level (Newton 1989, Cam & Monnat 2000). Variation in annual harvesting levels among the islands may have altered local age structures, resulting in individuals that have different levels of reproductive and foraging efficiency, which may explain the variability of body condition and breeding participation between islands (Bradley *et al.* 1989, Bradley & Wooller 1991). However, the effects of harvest may be compounded by the influence of climate, as lower-quality individuals and younger or older birds (*i.e.* senescent individuals) are more sensitive to climatic and environmental perturbations (Lescroël *et al.* 2009). Our findings warrant further investigation, as they highlight the significant role that individual life history traits play in lifetime reproductive success (Newton 1989).

#### **4.4.2 Climate and inter-colony variability in breeding success and chick mass**

Environmental conditions during the breeding season investigated in this study were associated with fluctuations in chick body mass and breeding success. Chick growth can fluctuate

depending on the availability of local resources; growth will be slower during years of low resource availability and higher during years of increased resource availability (Fagundes *et al.* 2016). Moreover, adult STSH undertake long foraging trips to the Southern Ocean to replenish body condition lost while attending to chicks (Einoder *et al.* 2013, Berlincourt & Arnould 2015). During periods of low prey availability, procellariiformes may skip breeding or even abandon their chick to preserve self-condition, reducing breeding success (Weimerskirch *et al.* 2001). Consequently, chick body mass and breeding success of STSH are likely to be influenced by distant factors (*i.e.* the Southern Ocean), and local (*i.e.* within 200 km of breeding colony) foraging areas (Weimerskirch & Cherel 1998, Einoder *et al.* 2013, Berlincourt & Arnould 2015).

#### 4.4.2.1 Southern Hemisphere climate indices

There was a negative relationship between ENSO, chick mass ( $\text{SOI CR}^0$ ) and breeding success ( $\text{SOI CR}^{-1}$ ). As with breeding participation, chick mass and breeding success may have been indirectly influenced through resource availability. Chicks were lighter during positive SOI in the preceding year, which may reflect poor local resources available for provisioning. Moreover, La Niña events may reduce resource availability in the Southern Ocean as a result of increased sea ice extent (Yuan 2004, Massom *et al.* 2008, Stammerjohn *et al.* 2008). This may have consequences for chicks, as limited resources may lead to adults abandoning the nest early, reducing breeding success (Jenouvrier *et al.* 2009, Genovart *et al.* 2013).

The relationship between ENSO and chick body mass was dissimilar to the results found for adult body mass. This may be attributed to their contrasting life stages, as the effect of climate variability can affect adults and juveniles differently (Fay *et al.* 2017). Contrasting results for adults and chicks to climatic conditions have also been reported for little penguin (*Eudyptula minor*), where higher SST around southeast Australia contributed to higher survival rates and heavier chicks, whereas the opposite effect was shown for adult survival (Cullen *et al.* 2009).

The productivity of the Southern Ocean foraging areas of STSH are strongly influenced by SAM (Price *et al.* 2020). Over the last 20 years, SAM has been increasingly positive, resulting in changes to wind direction and intensity (Stammerjohn *et al.* 2008). We found that chick body mass and breeding participation of STSH increased with increasing SAM. During a positive SAM phase, stronger winds result in a deeper mixed layer that increases primary productivity through elevated nutrient availability in the upper layers of the ocean, which improve foraging conditions for adult STSH. Modification of wind patterns and strength can also result in energetically favourable conditions for STSH (Raymond *et al.* 2010). The body mass of southern

rockhopper penguins (*Eudyptes chrysocome*) increased during a positive SAM, as the conditions associated with a positive SAM (*i.e.* lower SST and increased westerly winds) resulted in higher primary productivity and better foraging conditions (Dehnhard *et al.* 2015).

#### 4.4.2.2 *Local rainfall and breeding success*

Short-tailed shearwaters are negatively affected by heavy rainfall, which can cause burrow flooding, and egg and chick losses (Serventy & Curry 1984, Tiller *et al.* 2000, Price *et al.* 2020). Increased rainfall led to a decrease in breeding success in all four colonies during the study period, which is similar to other studies within the Furneaux Island Groups (Serventy & Curry 1984, Price *et al.* 2020). The result is also consistent with a study at Montague Island, which demonstrated catastrophic breeding failures were associated with high rainfall for a mixed colony of STSH and wedge tailed shearwater (Tiller *et al.* 2000). During heavy rainfall, eggs are often abandoned by the parents (Bester *et al.* 2007), and young chicks die from hypothermia as their feathers are not developed enough to provide waterproofing (Warham 1996).

#### 4.4.2.3 *Inter-colony variability – chick body mass and breeding success*

Breeding success and chick body mass varied annually; however, there was no significant inter-colony differences found. There was an *Island* and SOI<sup>-1</sup> interaction with chick body mass, which may be due to the different vegetation on the study islands, or other factors not considered here, such as density dependence and foraging competition (Oro 2014). As the vegetation is vastly different on each of the study islands, environmental and climate conditions may influence the burrow conditions through microclimate of the burrows (*i.e.* temperature and relative humidity), which may influence chick condition and survival (Bester *et al.* 2007, Fagundes *et al.* 2016). To understand the complex interaction between ENSO and chick body mass, further investigations are required.

In this study, chick body mass was greatest during the 2014 season; however, breeding success was at its lowest during this season, which corresponded to a La Niña event. Concurrently, a widespread STSH mass mortality event was reported during this season in southeast Australia, following the adults' return from the trans-equatorial migration (Springer *et al.* 2018), thought to be due to severe weather and low prey availability (Berlincourt & Arnould 2015). During the same breeding season, STSH colonies at Gabo Island (37°33'S, 149°54'E < 350 km from study sites) and Griffith Island (38°22'S, 142°13'E < 540 km from study site) also showed a decrease in breeding parameters (Berlincourt & Arnould 2015).

## 4.5 Conclusion

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This study demonstrates the complexity of the interaction between climate, physical oceanographic conditions and resource availability, which greatly influences the breeding condition (body mass), breeding participation and breeding success of STSH. Other elements may influence breeding performance at each colony, such as site-specific intrinsic parameters (*i.e.* age-specific foraging and survival) or biological processes (*i.e.* density dependence) (Oro 2014, Fay *et al.* 2017, Pardo *et al.* 2017), and warrant further investigation. The mean age of first breeding of STSH is 7 years (Wooller *et al.* 1990, Bradley *et al.* 1991), which provides a prolonged period for environmental conditions to impact the demographic parameters (*i.e.* survival and recruitment to the breeding population), through limiting or increasing resource availability (Ainley *et al.* 1995, Bost *et al.* 2015, Fay *et al.* 2015, Fay *et al.* 2017). To understand fully the long-term effects of climate and other environmental influences on STSH and other long-lived species, decadal-scale is are required to deconstruct the complex ecological interactions. The broad ranges of the temporal and spatial scales influencing STSH populations (individuals can live for more than 45 years) present challenges that can only be addressed with longitudinal time series data.

## 4.6 Tables and Figures

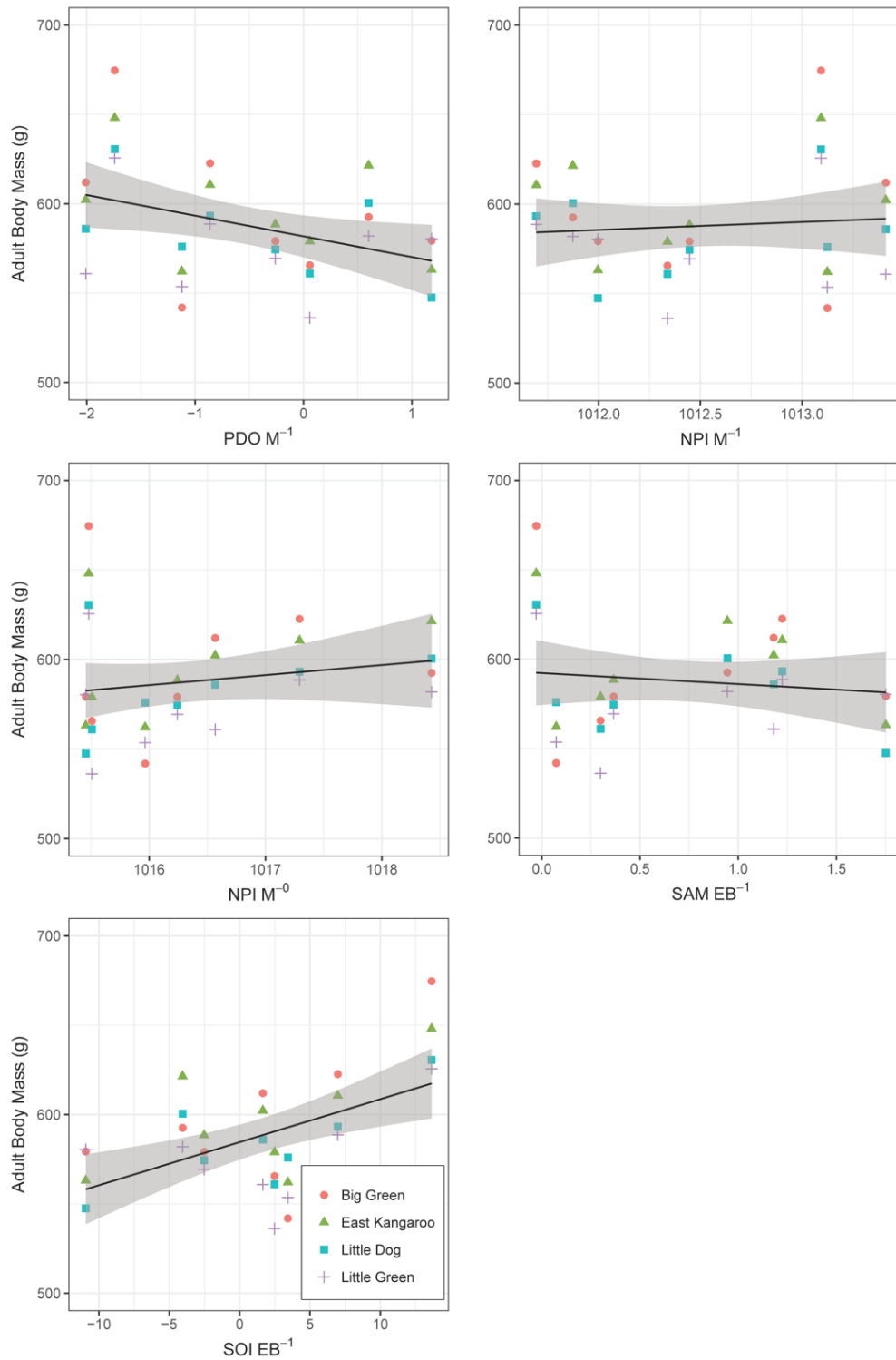
Table 4-1: Detailed description of the management and STSH colony size for four islands within the Furneaux Island Group

Island	Description and size	STSH colony size	Harvest	Vegetation	Land management	Grazing
Little Green (40°13'S, 148°15'E)	A low-lying island, 87 ha in size.	138,000 ( $\pm 16,000$ ) STSH burrows are within the 30 ha colony on the island (Skira <i>et al.</i> 1996).	The island was accessed annually for recreational harvest of STSH chicks throughout the study period.	Granitic outcrops and deep sandy soils vegetated with Tussock grass ( <i>Poa poiformis</i> ).	23 ha of the island is freehold, and the remaining (64 ha) is zoned Conservation Area.	Historically grazed with low numbers of sheep ( $< 5$ ).
Little Dog (40°15'S, 148°12'E)	A flat granitic island, 83 ha in size.	184,000 ( $\pm 32,000$ ) STSH burrows are within the 40 ha colony on the island (Skira <i>et al.</i> 1996).	The island was accessed annually for recreational harvests of STSH chicks throughout the study period.	Deep sandy soils vegetated with Tussock grass and Tick bush ( <i>Poa poiformis</i> and <i>Kunzea ambigua</i> , respectively).	Two-thirds of the island is zoned Game Reserve and the remainder is Leasehold.	Since 2015, between 2 to 3 cows have been present on the island, causing significant vegetation damage around the outskirts of the island.
Big Green (40°11'S, 147°59'E)	An island composed of granite with large outcrops of dolerite and limestone, 122 ha in size.	20,500 ( $\pm 7000$ ) STSH burrows are within the 5 ha colony on the island (Skira <i>et al.</i> 1996).	The island was closed for harvest in 2011, 2014 and 2015.	Due to high grazing pressure, the entire island has associated weeds and small patches of African boxthorn ( <i>Lycium ferocissimum</i> ).	Nature Reserve, although leased for sheep grazing.	Heavy grazing occurring before and throughout the study period.
East Kangaroo (40°18'S, 147°54'E)	An island dominated by limestone, granitic outcrops and dolerite dykes, 156.9 ha in size.	24,000 ( $\pm 9000$ ) STSH burrows are within the 10 ha colony on the island (Skira <i>et al.</i> 1996).	The island was opened for harvest from 2015.	Introduced African boxthorn ( <i>L. ferocissimum</i> ) and the native species, including Spear grass ( <i>Stipa spp</i> ) and Bower spinach ( <i>Tetragonia implexicoma</i> ).	Nature Reserve, although leased for sheep grazing.	Grazing ceased in the 1990s, before recommencing in 2010. In 2016, sheep were removed from the island, however during the March 2017 survey, sheep were observed on the island.



Table 4-2: Annual life cycle periods and temporal lags used in the Generalised Linear Models to determine the influence of climate on breeding parameters of the STSH

Annual life cycle period	Temporal lag one <sup>(0)</sup>	Temporal lag two <sup>(-1)</sup>
<b>Migration/overwintering (M)</b> <i>May to October</i>	May to August (M <sup>0</sup> )	November to October (M <sup>-1</sup> )
<b>Pre/early-breeding (EB)</b> <i>September to November</i>	September to November (EB <sup>0</sup> )	December to November (EB <sup>-1</sup> )
<b>Incubation/chick rearing (CR)</b> <i>December to March</i>	December to March (CR <sup>0</sup> )	April to March (CR <sup>-1</sup> )



*Figure 4-1: Relationship between STSH adult body mass at the Furneaux Islands and climate indices in the Northern and Southern Hemisphere*

Climate Indices: Pacific Decal Oscillation = PDO, Northern Pacific Index = NPI, Southern Annual Mode = SAM, Southern Oscillation Index = SOI. PDO  $M^{-1}$  = PDO during the migration/overwintering period with temporal lag two; NPI  $M^{-1}$  = NPI during the migration/overwintering period with temporal lag two; NPI  $M^0$  = NPI during the migration/overwintering period with temporal lag one; SAM  $EB^{-1}$  = SAM during the early-breeding period with temporal lag two; SOI  $EB^{-1}$  = SOI during the early-breeding period with temporal lag two.

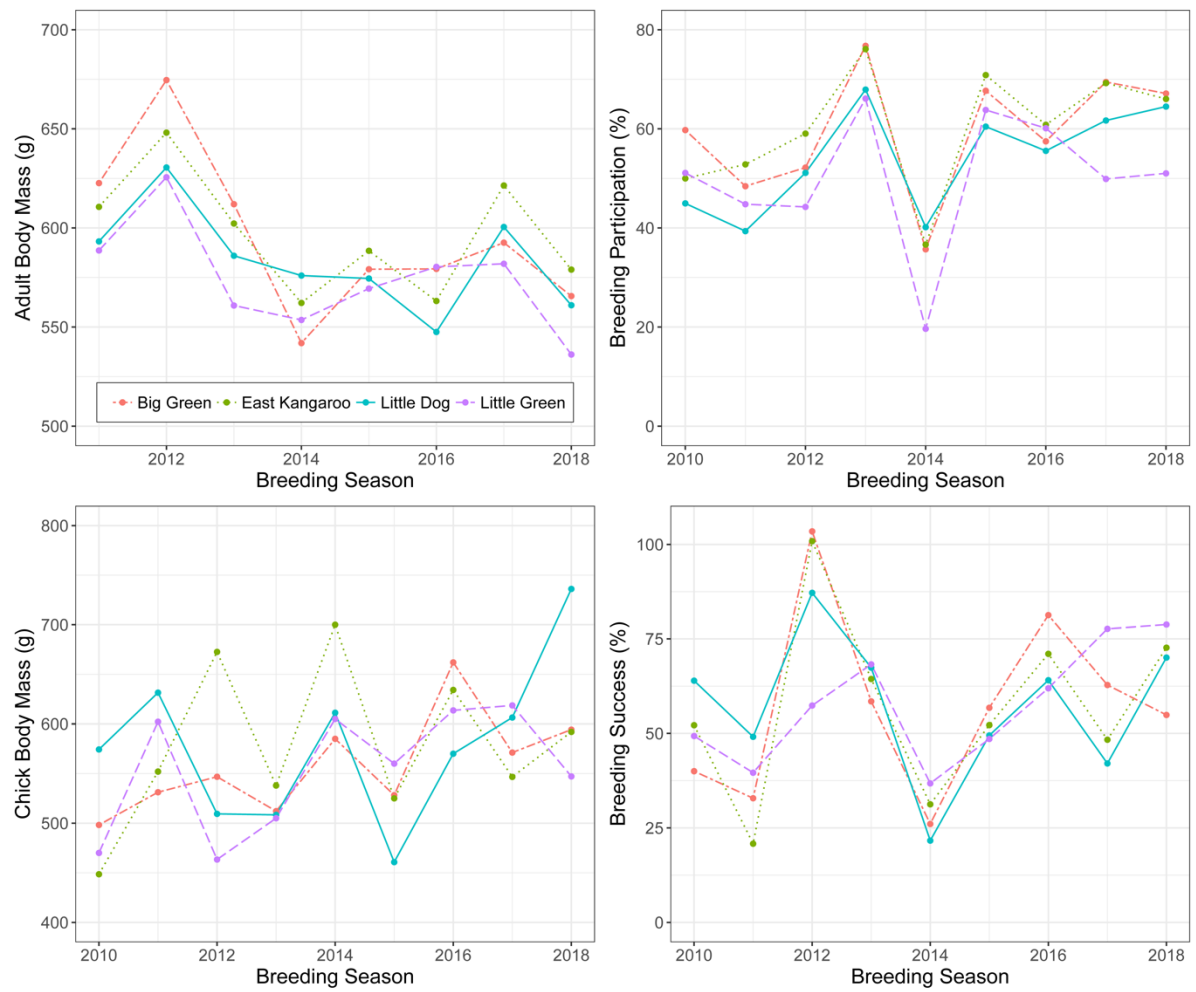
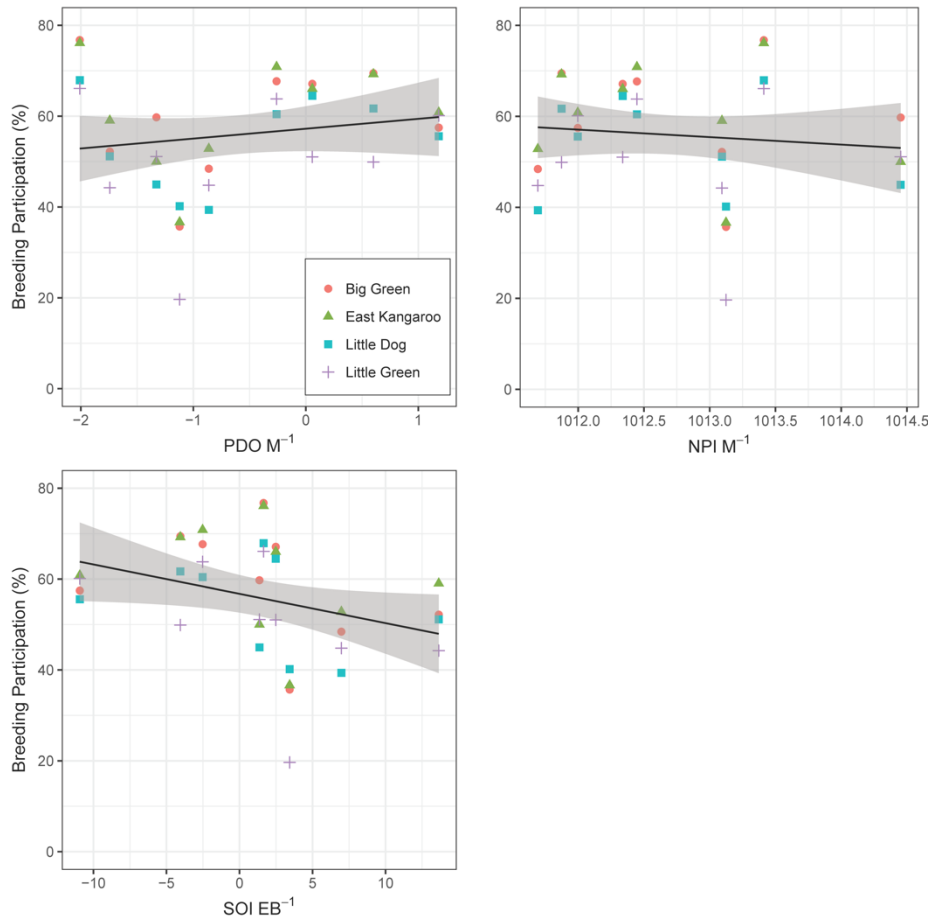


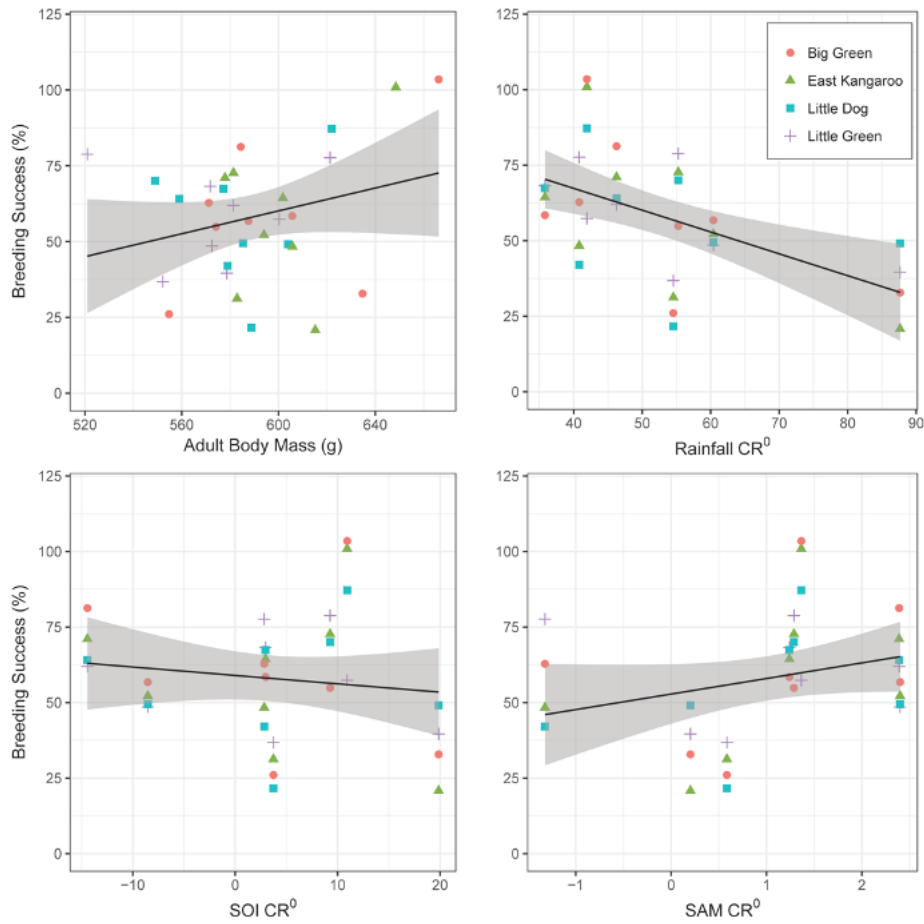
Figure 4-2: The time series (2010 to 2018) of STSH breeding parameters at the Furneaux Islands

(4-2a) The annual number of breeding participants arriving at the Furneaux Islands; (4-2b) The annual variation of breeding success at the Furneaux Islands; (4-2c) The annual variation of adult body mass at the Furneaux Islands; (4-2d) The annual variation of chick body mass at the Furneaux Islands.



*Figure 4-3: Relationship between the number of breeding participants arriving at the Furneaux Islands and climate indices in the Northern and Southern Hemisphere*

Climate Indices: Pacific Decadal Oscillation = PDO, Northern Pacific Index = NPI, Southern Oscillation Index = SOI.  $\text{PDO M}^{-1}$  = PDO during the migration/overwintering period with temporal lag two;  $\text{SOI EB}^{-1}$  = SOI during the early-breeding period with temporal lag two;  $\text{NPI M}^{-1}$  = NPI during the migration/overwintering period with temporal lag two.



*Figure 4-4: Relationship between breeding success at the Furneaux Islands and Southern Hemisphere climate indices and local weather conditions*

Climate Indices: Southern Oscillation Index = SOI, Southern Annual Mode = SAM. Adult Body Mass (g); Rainfall CR<sup>0</sup> = Precipitation (mm) averaged between December to March during the chick-rearing period; SOI CR<sup>0</sup> = SOI averaged between December to March during the chick-rearing period; SAM CR<sup>0</sup> = SAM averaged between December to March during the chick-rearing period.

## 4.7 Supplementary Material

S4-1: *Spearman's  $\rho$  correlation matrix for breeding parameters*

	BS	BP	Ch
BS	1.00	0.40	<b>0.90</b>
BP	0.40	1.00	0.69
Ch	<b>0.90</b>	0.69	1.00

BP = Breeding participation, occupancy of breeding birds; Ch = Occupancy of chicks; BS = Breeding success. Values in **bold** represent correlated relationships (greater than  $> 0.75$ ).

S4-2: *Spearman's  $\rho$  correlation matrix for climate indices affecting breeding participation at the Furneaux Islands*

	PDO M <sup>-1</sup>	SOI EB <sup>-1</sup>	NPI M <sup>-1</sup>	SAM EB <sup>-1</sup>	PDO <sup>0</sup>	NPI M <sup>0</sup>	SOI EB <sup>0</sup>	SAM EB <sup>0</sup>
PDO M <sup>-1</sup>	1.00	-0.53	-0.68	-0.01	<b>0.86</b>	-0.03	-0.29	0.19
SOI EB <sup>-1</sup>	-0.53	1.00	0.33	0.05	-0.51	0.23	<b>0.78</b>	-0.13
NPI M <sup>-1</sup>	-0.68	0.33	1.00	-0.05	-0.55	0.13	0.04	-0.22
SAM EB <sup>-1</sup>	-0.01	0.05	-0.05	1.00	-0.03	0.19	0.13	0.34
PDO <sup>0</sup>	<b>0.86</b>	-0.51	-0.55	-0.03	1.00	-0.24	-0.37	0.10
NPI M <sup>0</sup>	-0.03	0.23	0.13	0.19	-0.24	1.00	0.25	0.07
SOI EB <sup>0</sup>	-0.29	<b>0.78</b>	0.04	0.13	-0.37	0.25	1.00	0.01
SAM EB <sup>0</sup>	0.19	-0.13	-0.22	0.34	0.10	0.07	0.01	1.00

Annual life cycle periods: Migration/overwintering = M, Early-breeding = EB. Climate Indices: Pacific Decadal Oscillation = PDO, Northern Pacific Index = NPI, Southern Oscillation Index = SOI, Southern Annual Mode = SAM. Temporal lag one: climate indices average between May to August (M<sup>0</sup>), climate indices average between September to November (EB<sup>0</sup>); temporal lag two = climate indices average between November to October (M<sup>-1</sup>), climate indices average between December to November (EB<sup>-1</sup>). Values in **bold** represent correlated relationships (greater than  $> 0.75$ ).

S4-3: *Spearman's  $\rho$  correlation matrix for climate indices affecting breeding success at the Furneaux Islands*

	<b>Rainfall CR<sup>0</sup></b>	<b>SOI CR<sup>0</sup></b>	<b>SAM CR<sup>0</sup></b>	<b>SOI CR<sup>-1</sup></b>	<b>SAM CR<sup>-1</sup></b>
<b>Rainfall CR<sup>0</sup></b>	1.00	-0.03	0.21	-0.42	-0.50
<b>SOI CR<sup>0</sup></b>	-0.03	1.00	-0.26	0.09	-0.32
<b>SAM CR<sup>0</sup></b>	0.21	-0.26	1.00	0.33	-0.20
<b>SOI CR<sup>-1</sup></b>	-0.42	0.09	0.33	1.00	0.02
<b>SAM CR<sup>-1</sup></b>	-0.50	-0.32	-0.20	0.02	1.00

Annual life cycle periods: Chick-rearing period. Climate Indices: Southern Oscillation Index = SOI, Southern Annual Mode = SAM. Rainfall CR<sup>0</sup> = rainfall averaged between December to March during the chick-rearing period; SOI CR<sup>0</sup> = SOI averaged between December to March during the chick-rearing period; SAM CR<sup>0</sup> = SAM averaged between December to March during the chick-rearing period; SOI CR<sup>-1</sup> = SOI averaged April the previous year to March, the same year as the chick-rearing period; SAM CR<sup>-1</sup> = SAM averaged between April the previous year to March the same year as the chick-rearing period.

S4-4: *Coefficient values of day of year for the response variable adult body mass*

	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>Intercept</b>	671.16	1791.34	0.38	0.71
<b>DOY</b>	-0.23	5.06	-0.05	0.96

DOY = Day of year based on the Julian date format

S4-5: *Coefficient values of day of year for the response variable chick body mass*

	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>Intercept</b>	675.64	112.17	6.02	3.13E-09
<b>DOY</b>	-1.41	1.43	-0.99	3.24E-01

DOY = Day of year based on the Julian date format

S4-6: *Adult body mass of the STSH at the Furneaux Islands*

Model No.	Intercept	Island	NPI M <sup>0</sup>	NPI M <sup>-1</sup>	SAM EB <sup>-1</sup>	SOI EB <sup>-1</sup>	PDO M <sup>-1</sup>	df	logLik	AICc	$\Delta_i$	Weight
<b>64</b>	<b>-40514.55</b>	+	<b>11.34</b>	<b>29.21</b>	<b>26.39</b>	<b>5.75</b>	<b>23.34</b>	<b>10</b>	<b>-5793.28</b>	<b>11606.76</b>	<b>0.00</b>	<b>0.84</b>
28	-5996.77	+	6.48		14.77	3.33		8	-5797.65	11611.44	4.68	0.08
60	-5960.63	+	6.44		15.86	3.69	2.52	9	-5797.22	11612.62	5.85	0.04
32	-6406.98	+	6.54	0.34	14.78	3.32		9	-5797.65	11613.47	6.70	0.03
26	581.59	+			18.38	3.43		7	-5802.47	11619.04	12.28	0.00
58	581.76	+			19.52	3.82	2.68	8	-5801.99	11620.12	13.35	0.00
30	3429.67	+		-2.81	17.96	3.51		8	-5802.14	11620.41	13.64	0.00
20	-8072.71	+	8.53			2.55		7	-5803.89	11621.89	15.13	0.00
62	-684.05	+		1.25	20.09	3.91	3.57	9	-5801.98	11622.13	15.36	0.00
52	-8063.16	+	8.52			2.53	-0.20	8	-5803.89	11623.92	17.15	0.00

Akaike information criteria (AIC) ranked model selection results to explain the effects of temporal lag one (<sup>0</sup>) and temporal lag two (<sup>-1</sup>) climate indices North Pacific Index (NPI), Pacific Decal Oscillation (PDO), Southern Oscillation Index (SOI) and Southern Annular Mode (SAM) on the adult body mass of the STSH at the Furneaux Islands. Models with an AIC  $\Delta_i <$  are in **bold**. Only the top 10 models are displayed.



S4-7: *Coefficient values of each climate indices for the response variable adult body mass at the Furneaux Islands*

	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>Intercept</b>	-40510.00	12510.00	-3.24	1.24E-03
<b>SOI EB<sup>-1</sup></b>	5.76	0.91	6.34	3.53E-10
<b>NPI M<sup>-1</sup></b>	29.21	10.42	2.80	5.16E-03
<b>PDO M<sup>-1</sup></b>	23.34	7.91	2.95	3.25E-03
<b>NPI M<sup>0</sup></b>	11.34	2.72	4.17	3.29E-05
<b>SAM EB<sup>-1</sup></b>	26.39	5.73	4.60	4.69E-06
<b>East Kangaroo Island</b>	-3.31	4.82	-0.69	4.93E-01
<b>Little Dog Island</b>	-16.91	5.40	-3.13	1.78E-03
<b>Little Green Island</b>	-27.62	5.23	-5.29	1.52E-07

Annual life cycle periods: Migration/overwintering = M, Early-breeding = EB. Climate Indices: Pacific Decal Oscillation = PDO, Northern Pacific Index = NPI, Southern Oscillation Index = SOI, Southern Annual Mode = SAM. Temporal lag one: climate indices averaged between May to August (M<sup>0</sup>), climate indices averaged between September to November (EB<sup>0</sup>); temporal lag two = climate indices averaged between November to October (M<sup>-1</sup>), climate indices.

S4-8: *Breeding participation of the STSH at the Furneaux Islands*

Model No.	Intercept	Island	NPI M <sup>-1</sup>	SOI EB <sup>-1</sup>	PDO M <sup>-1</sup>	df	logLik	AICc	$\Delta_i$	Weight
<b>16</b>	<b>4340.00</b>	+	<b>-4.23</b>	<b>-1.25</b>	<b>-6.61</b>	<b>8</b>	<b>-1156.45</b>	<b>2329.40</b>	<b>0.00</b>	<b>0.86</b>
14	59.55	+		-0.93	-2.65	7	-1159.762	2333.90	4.50	0.09
6	60.72	+		-0.61		6	-1161.752	2335.80	6.37	0.04
8	209.80	+	-0.15	-0.60		7	-1161.74	2337.90	8.46	0.01
15	4357.00		-4.25	-1.25	-6.59	5	-1168.11	2346.40	17.00	0.00
13	56.80			-0.92	-2.61	4	-1171.19	2350.50	21.08	0.00
10	61.08	+			1.92	6	-1169.55	2351.40	21.96	0.00
5	57.96			-0.61		3	-1172.96	2352.00	22.58	0.00
12	-175.90	+	0.23		2.06	7	-1169.54	2353.50	24.04	0.00
7	241.80		-0.18	-0.61		4	-1172.95	2354.00	24.61	0.00

Akaike information criteria (AIC) ranked model selection results to explain the effects of temporal lag one (<sup>0</sup>) and temporal lag two (<sup>-1</sup>) climate indices North Pacific Index (NPI), Pacific Decadal Oscillation (PDO), Southern Oscillation Index (SOI) and Southern Annular Mode (SAM) and breeding participation at the Furneaux Islands. Models with an AIC  $\Delta_i <$  are in **bold**. Only the top 10 models are displayed.

S4-9: *Coefficient values of each climate indices for the response variable breeding participation at the Furneaux Islands*

	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>Intercept</b>	4339.73	1675.21	2.59	1.01E-02
<b>SOI EB<sup>-1</sup></b>	-1.25	0.24	-5.17	4.50E-07
<b>PDO M<sup>-1</sup></b>	-6.61	2.04	-3.24	1.33E-03
<b>NPI M<sup>-1</sup></b>	-4.23	1.66	-2.56	1.12E-02
<b>East Kangaroo Island</b>	0.77	2.20	0.35	7.25E-01
<b>Little Dog Island</b>	-6.05	2.54	-2.38	1.78E-02
<b>Little Green Island</b>	-9.83	2.52	-3.90	1.22E-04

Annual life cycle periods: Migration/overwintering = M, Early-breeding = EB. Climate Indices: Pacific Decal Oscillation = PDO, Northern Pacific Index = NPI, Southern Oscillation Index = SOI, Southern Annual Mode = SAM. Temporal lag two = climate indices averaged between November to October (M<sup>-1</sup>), climate indices averaged between December to November (EB<sup>-1</sup>).

S4-10: Chick body mass of the STSH at the Furneaux Islands

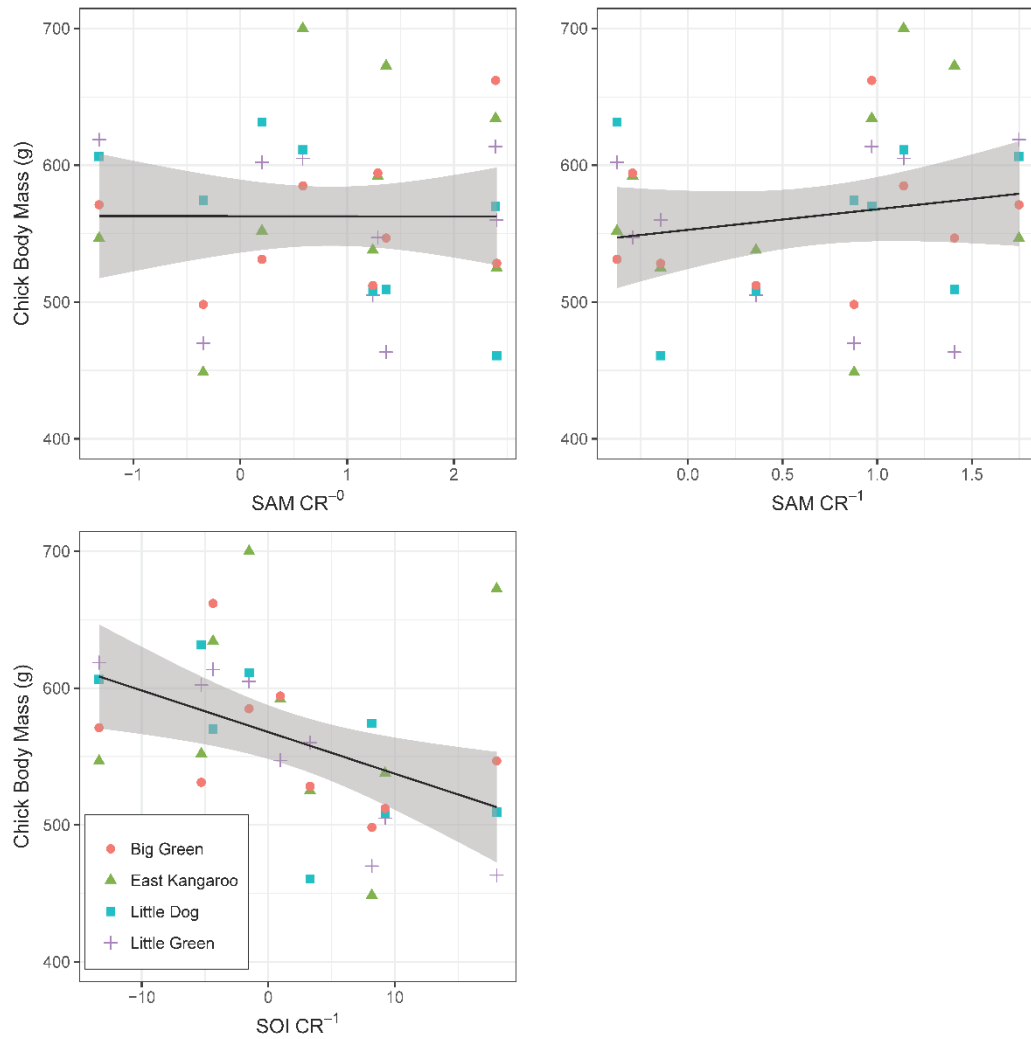
Model No.	Intercept	Island	SAM CR <sup>0</sup>	SAM CR <sup>-1</sup>	SOI CR <sup>-1</sup>	*SOI CR <sup>0</sup>	df	logLik	AICc	$\Delta_i$	Weight
<b>32</b>	<b>533.00</b>	+	<b>17.63</b>	<b>17.48</b>	<b>-2.77</b>	+	<b>11</b>	<b>-3454.16</b>	<b>6930.80</b>	<b>0.00</b>	<b>0.683</b>
28	548.10	+	10.46		-2.35	+	10	-3456.55	6933.50	2.69	0.177
26	553.70	+			-1.60	+	9	-3458.27	6934.90	4.07	0.089
30	549.60	+		6.53	-1.56	+	10	-3457.83	6936.10	5.25	0.049
15	544.40		18.81	18.25	-3.10		5	-3467.64	6945.40	14.58	0.00
16	531.90	+	18.59	18.93	-3.14		8	-3464.65	6945.60	14.76	0.00
11	560.90		11.38		-2.66		4	-3470.15	6948.40	17.57	0.00
12	548.20	+	10.82		-2.69		7	-3467.35	6948.90	18.09	0.00
9	568.10				-1.89		3	-3472.11	6950.30	19.46	0.00
10	554.10	+			-1.96		6	-3469.12	6950.40	19.60	0.00

Akaike information criteria (AIC) ranked model selection results to explain the effects of temporal lag one (<sup>0</sup>) and temporal lag two (<sup>-1</sup>) for climate indices Southern Oscillation Index (SOI) and Southern Annular Mode (SAM) on chick body mass at the Furneaux Islands. Models with an AIC  $\Delta_i <$  are in **bold**. Only the top 10 models are displayed.

*S4-11: Coefficient values of each climate indices for the response variable chick body mass at the Furneaux Islands*

	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>Intercept</b>	533.04	11.82	45.10	2.00E-16
<b>SOI CR<sup>-1</sup></b>	-2.77	1.03	-2.68	7.51E-03
<b>East Kangaroo</b>	21.08	13.92	1.52	1.30E-01
<b>Little Dog</b>	28.80	15.46	1.86	6.30E-02
<b>Little Green</b>	5.21	16.49	0.32	7.52E-01
<b>SAM CR<sup>0</sup></b>	17.63	6.55	2.69	7.30E-03
<b>SAM CR<sup>-1</sup></b>	17.48	8.06	2.17	3.04E-02
<b>SOI * East Kangaroo Island</b>	3.21	1.43	2.25	2.48E-02
<b>SOI * Little Dog Island</b>	-2.61	1.61	-1.62	1.06E-01
<b>SOI * Little Green Island</b>	-3.85	1.61	-2.39	1.72E-02

Chick-rearing period. Climate Indices: Southern Oscillation Index = SOI, Southern Annual Mode = SAM. Rainfall CR<sup>0</sup> = rainfall averaged between December to March during the chick-rearing period; SOI CR<sup>0</sup> = SOI averaged between December to March during the chick-rearing period; SAM CR<sup>0</sup> = SAM averaged between December to March during the chick-rearing period; SOI CR<sup>-1</sup> = SOI averaged April the previous year to March the same year as the chick-rearing period; SAM CR<sup>-1</sup> = SAM averaged between April the previous year to March the same year as the chick-rearing period.



*S4-12: Relationship between STSH chick body mass at the Furneaux Islands and Southern Hemisphere climate indices and local weather conditions*

Climate Indices: Southern Oscillation Index = SOI, Southern Annual Mode = SAM. SAM CR<sup>-1</sup> = SAM averaged between April the previous year to March the same year as the chick-rearing period; SAM CR<sup>0</sup> = SAM averaged between December to March during the chick-rearing period; SOI CR<sup>-1</sup> = SOI averaged April the previous year to March, the same year as the chick-rearing period; SOI CR<sup>0</sup> = SOI averaged between December to March during the chick-rearing period; Rainfall CR<sup>0</sup> = Precipitation (mm) averaged between December to March during the chick-rearing period.

S4-13: *Breeding success of the STSH at the Furneaux Islands*

Model No.	Intercept	Island	Adult body mass	Rainfall	SAM CR <sup>0</sup>	SOI CR <sup>0</sup>	df	logLik	AICc	$\Delta_i$	Weight
<b>30</b>	<b>0.20</b>		<b>0.00</b>	<b>-0.01</b>	<b>0.09</b>	<b>0.01</b>	<b>6</b>	<b>1.26</b>	<b>10.30</b>	<b>0.00</b>	<b>6.44E-01</b>
14	-0.03		0.00	-0.01	0.06		5	-1.01	12.60	2.30	2.04E-01
29	0.98			-0.01	0.09	0.01	5	-1.69	13.95	3.65	1.04E-01
32	0.22	+	0.00	-0.01	0.09	0.01	9	1.41	16.97	6.67	2.29E-02
16	-0.02	+	0.00	-0.01	0.06		8	-0.90	19.23	8.93	7.40E-03
13	0.92			-0.01	0.06		4	-5.65	19.69	9.38	5.91E-03
31	1.00	+		-0.01	0.06	0.01	8	-1.37	20.17	9.87	4.63E-03
6	0.09		0.00	-0.01			4	-6.01	20.40	10.10	4.14E-03
22	0.11		0.00	-0.01		0.00	5	-5.99	22.56	12.25	1.41E-03
5	0.93			-0.01			3	-9.77	25.76	15.46	2.83E-04

Akaike information criteria (AIC) ranked model selection results to explain the effects of temporal lag one (<sup>0</sup>) and temporal lag two (<sup>-1</sup>) for climate indices Southern Oscillation Index (SOI) and Southern Annular Mode (SAM) and rainfall on breeding success at the Furneaux Islands. Models with an AIC  $\Delta_i <$  are in **bold**. Only the top 10 models are displayed.

*S4-14: Coefficient values of each climate indices for the response variable breeding success at the Furneaux Islands*

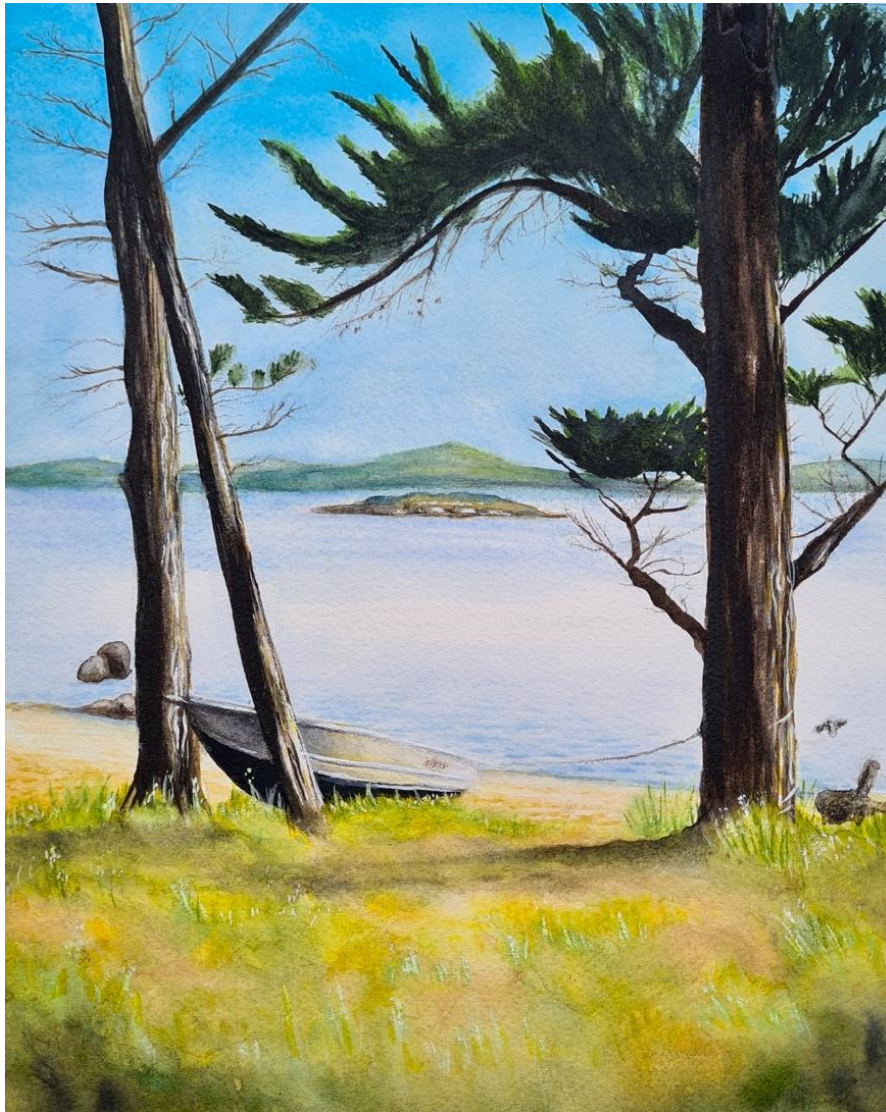
	<b>Estimate</b>	<b>Std. Error</b>	<b>t value</b>	<b>Pr(&gt; t )</b>
<b>Intercept</b>	0.22	0.35	0.63	5.28E-01
<b>Adult body mass</b>	0.00	0.00	2.30	2.33E-02
<b>SOI CR<sup>0</sup></b>	0.01	0.00	2.10	3.86E-02
<b>SAM CR<sup>0</sup></b>	0.09	0.02	3.79	2.55E-04
<b>Rainfall</b>	-0.01	0.00	-5.68	1.26E-07
<b>East Kangaroo Island</b>	-0.01	0.06	-0.17	8.64E-01
<b>Little Dog Island</b>	0.00	0.07	0.01	9.93E-01
<b>Little Green Island</b>	-0.04	0.07	-0.50	6.15E-01

Annual life cycle periods: Chick-rearing period. Climate Indices: Southern Oscillation Index = SOI, Southern Annual Mode = SAM. Rainfall CR<sup>0</sup> = rainfall averaged between December to March during the chick-rearing period; SOI CR<sup>0</sup> = SOI averaged between December to March during the chick-rearing period; SAM CR<sup>0</sup> = SAM averaged between December to March during the chick-rearing period.



**INTEGRATED ASSESSMENT MODEL FOR THE SHORT-TAILED  
SHEARWATERS USING A FISH STOCK ASSESSMENT  
PACKAGE, CASAL**

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Fisher Island from the shores of Lady

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## Abstract

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Where resources permit, management of fish and invertebrate stocks worldwide is mostly based on integrated stock assessment models. In fisheries science there are many pre-existing stock assessment packages, which provide a foundation to develop a model that can have a wider acceptance of the results as the methods are from a pre-established model. However, these assessment packages have not been widely used to manage the harvest of wildlife such as seabirds. One commonly used stock assessment framework is CASAL (C++ Algorithmic Stock Assessment Laboratory), which is widely used for fisheries assessments. In this study, we investigated the feasibility of using the CASAL framework for an integrated assessment model of the short-tailed shearwater (*Ardenna tenuirostris*), which are subject to an annual harvest in Tasmania. Short-tailed shearwaters are transhemispheric migratory procellariiformes that breed only in southern Australia. We used data from a long-term capture-mark-recapture data from a well-studied colony (100 to 200 birds) of short-tailed shearwater at Fisher Island, Furneaux Island Group, for the period 1947 to 2017. We used CASAL to estimate key population parameters using empirical data from the annual census (observations). This study demonstrates that the available data is sufficient and appropriate to use as an integrated stock assessment model. Moreover, as adult mortality has a strong effect on population growth, further studies may include environmental determinates associated with individual survival. This study also highlights that for future works, a key benefit of using this type of modelling is the ability to incorporate known annual harvest, which could be used to explore the consequences of different management scenarios.

## 5.1 Introduction

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Management of fish and invertebrate stocks, where resources permit, is mostly based on integrated stock assessment models (Punt *et al.* 2020). Integrated analysis (integrated population modelling) is used for conducting stock assessments and provide a basis to use for management of fish and invertebrate species (Punt *et al.* 2020). The integrated assessment model uses three model components: (i) a population model, which incorporates measured population parameters (*e.g.* mortality and reproduction); (ii) an observation model, which creates predictions from the population model (*e.g.* abundance, age structure); and (iii) a statistical model, which compares the data predictions to the observed data from the population and observation model to fit the data (see [www.fisheries.noaa.gov](http://www.fisheries.noaa.gov)). These provide an estimate of stock status that can be used in

the decision-making processes, as the assessment model can be used to investigate alternative scenarios to inform different management strategies (e.g. Punt *et al.* 2020).

Using assessment packages can be advantageous as many are readily available and avoid the need to implement a model from scratch, and are less likely to contain errors as they have been rigorously tested (Privitera-Johnson & Punt 2020, Punt *et al.* 2020). Several generic assessment packages are well documented, and have been well tested using simulation (Dichmont *et al.* 2016). The availability of training, manuals and example datasets for stock assessment packages can provide a strong foundation to understand the use and functionality of the assessment package (Dichmont *et al.* 2016, Punt *et al.* 2020), particularly in a management setting.

The majority of these packages have been used for fisheries stock assessments, and not widely used to manage the harvest of wildlife such as seabirds. Adopting and using the packages for stock assessment of harvested bird species such as waterfowl (*Anseriformes*) (Kingsford *et al.* 2020), short-tailed shearwaters (STSH) (*Ardenna tenuirostris*) (Springer *et al.* 2018), sooty shearwaters (*A. grisea*) (Clucas 2011) and puffins (*Fratercula arctica*) (Stempniewicz & Jensen 2007) may provide a robust framework for management decision-making, and reduce the cost and time. CASAL (C++ Algorithmic Stock Assessment Laboratory) (Bull *et al.* 2012) is one such framework that allows implementation of generalised age or size structured stock assessment models. CASAL is designed for flexibility, and can be used for a single fishery or multiple stocks, areas and/or fishing methods, and is adaptable in specifying the population dynamics, parameter estimation and model outputs (Bull *et al.* 2012). The CASAL framework can also be used for qualitative assessments of marine populations, including fish, invertebrates, marine mammals and seabirds (Bull *et al.* 2012).

The STSH is a transhemispheric migratory seabird that breeds only in southern Australia migrating to the North Pacific Ocean for the austral winter. Chicks at selected colonies in Tasmania are subject to annual commercial and recreational harvest, known as ‘mutton birding’. Between 2007 and 2017,  $72,000 \pm 8,800$  chicks were commercially harvested annually (Springer *et al.* 2018). Between 2011 and 2016, an average of  $884 \pm 44$  recreational licenses were sold annually, which resulted in an average annual recreational harvest of  $34,500 \pm 5,300$  chicks (Springer *et al.* 2018). The management of the STSH is the responsibility of the Tasmanian Department of Primary Industry, Parks, Water and the Environment (DPIPWE), and the recreational harvest is managed under the *Nature Conservation Act 2002* and *Wildlife Regulations 2010*, while commercial harvest is managed under the *Aboriginal Lands Act 1995*. Tasmanian Aboriginals have historically been involved in the mutton bird industry and currently

operate the commercial harvest, which is of high social and economic importance to the Aboriginal community of the Furneaux Island Group and throughout Tasmania (Skira *et al.* 1986, Skira 1990).

The commercial exploitation of STSH began in the early 1820s soon after the arrival of European settlers (Skira 1990), while recreational harvesting began to increase in the early 1950s (Skira 1993). Over the years, a number of input and output controls have been implemented to regulate the harvest and maintain sustainability for current regulations (see [www.dpipwe.tas.gov.au](http://www.dpipwe.tas.gov.au)). Currently, only STSH chicks are harvested, with the season commencing in early March and continuing until the end of April (Skira & Wapstra 1980). Recreationally, bag limits are 25 birds per day per person at the Bass Strait islands colonies and 15 birds per day at the Tasmanian mainland colonies.

Recreational licence-holders must report the number of STSH harvested each year. Since the 1980s, the commercial industry has been largely self-regulated and with no quota limits (Skira *et al.* 1986). The population of STSH at recreational and some commercial harvested colonies are monitored annually prior to harvest (monitored by DPIPWE and the Tasmanian Aboriginal Centre, retrospectively). Recreationally harvested colonies may be closed if the bird numbers are low, while the commercial industry may choose to close if harvesting will not be economically viable.

This study tests the feasibility of using a fisheries stock assessment package (*i.e.* CASAL framework) to develop an integrated assessment model for the STSH. The outcomes from this study will provided the initial steps, explore the suitability of using a stock assessment package and identify datasets that are needed to provide ongoing support and recommendations for management strategies of the STSH.

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## **5.2 Materials and Methods**

### **5.2.1 Species**

Short-tailed shearwaters are commonly referred to as the Tasmanian mutton bird, or *yolla* in Tasmanian Aboriginal language. It is a medium-sized (500 to 800 g) burrow-nesting procellariiform (Skira 1990, Berlincourt & Arnould 2015), which are long-lived, up to 48 years (see <https://www.environment.gov.au/cgi-bin/biodiversity/abbbs/abbbs-search.pl>), with an annual pan-oceanic transhemispheric migration.

Every September and October, approximately 18 million STSH arrive in Tasmania and re-occupy over 200 colonies, primarily located around Tasmania and the offshore islands (Skira *et al.* 1996). The breeding season begins in November, when one egg per breeding pair is laid. Laying is highly synchronised, with 95% of the eggs laid between 24 and 28 November. A breeding pair will not replace the single egg if it fails (Skira 1990). Hatching occurs from mid-to-late January (Carey 2010) and chicks fledge in mid-April to early May (Serventy 1967, Wooller *et al.* 1990). After the breeding season, adults and fledglings return to the North Pacific for the austral winter (Shaffer *et al.* 2006, Raymond *et al.* 2010, Vertigan *et al.* 2012).

The STSH exhibits a high degree of nest fidelity (Vertigan 2010), and often returns to the island to their natal colony for one or more years (prospecting) before they breed for the first time at age 4 to 15 (Wooller *et al.* 1989). The mean age at first breeding is approximately 7 years, and the mean age of prospecting birds is approximately 4 years (Bradley *et al.* 1989, Wooller *et al.* 1990, Bradley *et al.* 1991). Prospecting behaviour consists of nocturnal visits during the incubation and chick-rearing periods; sometimes birds will visit unoccupied burrows without taking up residency (Bradley *et al.* 1989). Not all individuals breed annually once they start breeding (Bradley *et al.* 1989).

## **5.2.2 Field site**

### *5.2.2.1 Fisher Island banding program and census*

Since 1947, the entire population (100 to 200 birds) of the STSH colony at Fisher Island (40°13'S, 148°14'E), Furneaux Island Group, has been monitored continuously through a capture-mark-recapture (CMR) field research program. All burrows on the island have been marked with a single burrow number. Annually, all new individual birds (including chicks) captured in burrows during the census have been banded with a uniquely numbered stainless steel band, and the band and burrow number was recorded. If the bird was already banded, the band and burrow number were recorded. Birds that were banded as chicks and later resighted on the island are classed as known-aged birds, and adult birds that were banded on the island are classed as unknown-aged birds.

From late November to mid-December each season, all burrows on the island were checked at least twice every 10 days to locate and identify both members of each breeding pair. Searching the burrows minimises the likelihood of detecting a non-breeding (prospecting) bird, and encompasses the majority of birds found on the surface within the colony (Serventy 1967). All burrows were checked again the following late March to early April and the presence or absence

of chicks recorded, with all new chicks banded. Many of the chicks banded on Fisher Island returned to the island to breed and have provided up to half of the breeding population (Serventy & Curry 1984, Bradley *et al.* 1989), and a comparable number of un-banded birds (immigrants) are recruited into the Fisher Island breeding population (Serventy & Curry 1984).

The data is continuous from 1947, with the exception of 2013 and 2014 when no searches for breeding adults were made, and in 1992 when the presence or absence of chicks was not recorded. The methods used in the program have been constant since 1947, and are further outlined in previous studies (Serventy 1967, Serventy & Curry 1984, Price *et al.* 2020).

### 5.2.3 Model structure

The STSH population was modelled using CASAL v2.30 (Bull *et al.* 2012). The data from the unharvested colony of STSH on Fisher Island was used to estimate unknown population parameters, such as selectivity and maturity (see Section 5.2.3.2), independent of the CASAL model. These population parameters were combined with census data to obtain model estimates of annual biomass and age structure. The census data produced the following information to which the model was fit:

- Relative abundance of adults breeding at the colony from annual census data,
- Relative abundance of chicks (recruitment) at the colony from annual census data, and
- Annual age-frequency distributions (from the CMR field research program).

#### 5.2.3.1 Population model

The population of STSH was modelled as an age-structured population, with 35 age groups from 1 to 35 years, with the last group being a ‘plus’ group that allowed for older birds to be included in the model. The model was a single-area model, modelling a single population (*i.e.* the one research colony). Two time-steps were included to represent the breeding and non-breeding season. We included male and female birds and presumed the sex ratio to be equal (1:1), as is the norm for procellariiform seabirds (Genovart *et al.* 2005, Lawrence *et al.* 2008, Medeiros *et al.* 2012). We modelled the population with combined males and females. Abundance indices, recorded as numbers of birds rather than biomass, was modelled. We used two abundance indices, adults and chicks, which were represented in CASAL by defining a separate ‘fishery’ for each with an appropriate selectivity curve. The population has remained at high levels, resulting in high burrow occupancy, with burrows being a limited resource. Consequently,

recruitment was assumed to be a stationary process and that future recruitment could be estimated on the basis of historic values.

#### 5.2.3.2 *Selectivity and maturity*

In fisheries modelling, selectivity refers to the relative probability of animals of different sizes/ages being caught by the commercial or scientific sampling equipment. Adult birds sighted in the burrows during the November to December census were assumed to be breeding birds, therefore we considered selectivity and maturity for the adult abundance index to be equal. For the selectivity of adult birds, a logistic function was fitted to the age at which the birds were first resighted, which was based on known-aged birds only. Selectivity for chicks was based on the first year of age only, as chicks are banded and not resighted until several years later (Bradley *et al.* 1989).

#### 5.2.3.3 *Mortality/survival*

For the first seven years of life, natural mortality for STSH was considered as a single net mortality value based on the probability of a bird fledged at the colony ever being resighted. This is appropriate as birds are not resighted between fledging and subsequently returning to the colony to breed (see Section 5.2.2.1).

Following the first seven years, natural mortality was based on empirical data. We assumed the age of last resight of an individual to be its age of mortality. Annual survival rates were observed to decrease consistently. A linear regression on empirical year-to-year survival gave a good fit. The high frequency of resights and observation provides a higher understanding of annual mortality and survival compared to model estimates generated for fisheries. It was assumed that a STSH that was not resighted at Fisher Island was dead and not breeding elsewhere (see Section 5.4).

#### 5.2.3.4 *Relative abundance of adults and chicks*

For the study period of 1947 to 2017, adult relative abundance was defined as the number of breeding adults recorded at the colony during the November to December census. The methods for the census have been previously described in detail (Serventy 1967, Serventy & Curry 1984, Price *et al.* 2020).

The relative abundance of chicks was calculated as the number of chicks sighted during the census in the March to April period, approximately four months after the adult census. All chicks

were banded with a uniquely numbered stainless steel band, and the band and burrow number was recorded (see Serventy & Curry 1984, Price *et al.* 2020).

#### 5.2.3.5 Age frequency

To generate age-frequencies, birds that were banded as chicks and resighted were classed as known-aged birds. For these birds, the age was simply calculated from their banding year. For birds that were first sighted at the colony as an adult (*i.e.* birds classed as unknown-aged) from either immigration or missed in the previous census year (*i.e.* 1992, 2013 and 2014), a mean age at first breeding of seven years was assumed. The ages of birds banded as adults was calculated as seven, plus the elapsed time since the first sighting/banding. This was based on a previous study, where the age of first breeding was between 4 and 15 years of age, with a mean breeding age of 7.2 years (Bradley *et al.* 1991). Age data between 1947 to 1963 was excluded from the age structure parameter of the model to ensure a high proportion of birds were known-aged, as required by CASAL.

#### 5.2.3.6 Model fits – Coefficient of variation

In order to investigate the sensitivity of predictions of age structure, the Coefficient of Variation (CV) parameter was varied under three alternative assumptions for adult and chick abundance indices. These were: (i) the CV was set to 0.01 and to 0.06 for adult and chick abundances, respectively; (ii) the CV was set to 0.25 and 0.03; and (iii) the CV was set to 0.5 and to 0.01.

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## 5.3 Results

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### 5.3.1 Selectivity and maturity

The cumulative proportions of the first resights of breeding STSH show that 43% of individuals had returned to breed by 6 years of age, by 8 years of age 91% of individuals returned to breed, and all birds had started breeding by 16 years of age (Figure 5-1).

### 5.3.2 Mortality/survival

For the first seven years of life the mortality rate (natural mortality) was approximately 23% per annum for the population over the study period (see Section 5.2). This mortality rate equates to a net survival of 20% over the first seven years of life. A high proportion of known-aged birds were last resighted at the colony between 5 to 10 years of age, and annual resights became fewer with increasing age (Figure 5-2). Survival rates of breeding STSH decreased with increasing age (Figure 5-3a). For example, birds aged 18 years had a higher annual survival rate (84%)



compared to birds aged 30 (67%) (Figure 5-3a). Survival from age seven was calculated as shown in Figure 5-3b, with 50% of birds surviving to age 16.

### **5.3.3 Relative abundance of adults and chicks**

There was considerable inter-annual variability in both adult and chick abundance in the colony (Figure 5-4a and Figure 5-4b), with an average of  $96 \pm 29$  SE breeding pairs per season for the entire study period of 1947 to 2017 (Figure 5-4a). The number of breeding pairs gradually decreased from the year 1942, reaching 58 pairs in 1971 and 1973 (Figure 5-4a). The number of breeding pairs increased from the mid-1980s until 2007, where 160 breeding pairs were recorded (Figure 5-4a). In 2015 there was a steep decrease, when only 63 breeding pairs were recorded. However, as there is no available data for 2013 and 2014, this decrease could have occurred during these years (Figure 5-4a).

One hundred chicks were banded at the start of the study period in 1947, and chick abundance fluctuated annually, with no temporal trend evident (Figure 5-4b). On average, there were  $41 \pm 22$  chicks banded per season for the study period (Figure 5-4b). Apart from the first year of the study, the greatest number of chicks banded at Fisher Island was 87 in 2003, and the least was one in 2004 and 2006 (Figure 5-4b).

### **5.3.4 Age frequency/age structure**

The age structure of the population changed during the study period (1947 to 2017) (Figure 5-5). The median age of birds at the colony became younger towards the end of the study, and fluctuated by about 11.4 years ( $n = 27$ ) between 1989 and 2017 (Figure 5-5).

### **5.3.5 Model fits**

The relative weight that the model placed on fitting the adult and the chick data was varied by manipulating the CV parameter for these indices (see Section 5.2). Under all three scenarios, the biomass of the population fluctuated annually, and the population oscillated around an unharvested biomass (*i.e.* value 1). Depending on the relative weight placed on the two time series, the model would switch from fitting adult abundance well but not chick abundance (Figure 5-6), to fitting chick abundance well but not adult abundance (Figure 5-8). The challenge was finding a balance where the model could fit both time series reasonably well. Figure 5-7 shows the best model that was achieved; however, given the difficulties in fitting both time series there are some fundamental inconsistencies between them. The chick abundance index may not be very informative due the possibility of high interannual variability in survival rates. This

indicates that models should place a greater emphasis on adult abundance, and/or not use a chick abundance index at all.

## **5.4 Discussion**

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The CASAL framework is widely used for fisheries assessments, including a number of New Zealand's fish stocks (Bull *et al.* 2012, Stacy *et al.* 2020). The CASAL package is capable of integrating various sources of information and explicitly modelling spatio-temporal stock structures and dynamics (Stacy *et al.* 2020). In this study, we demonstrate that the CASAL package is suitable for an integrated assessment model for a seabird species – the STSH.

Before running the CASAL model, historical CMR and census data (observations) were used to estimate some population parameters, calculate age frequency and produce annual abundance indices. The CMR data comprised records from approximately 4000 individual birds and 16,000 observations/resights over the 1947 to 2017 study period. Forty three percent of STSH returning to breed were age 6 years and older and all birds returned to the island to breed by 16 years of age, a result that is consistent with previous studies, based on a shorter subset of the Fisher Island data (Bradley *et al.* 1989, Bradley *et al.* 1999, Bradley *et al.* 2000). Known-aged birds were predominately last sighted between ages 5 to 10 years, and annual resights and survival rates of breeding STSH decreased with increasing age. This result is similar to other studies that found STSH that were breeding for the first time between 5 to 10 years had a higher mortality rate compared to other ages, and survival rates decreased with increasing age (Bradley *et al.* 1990).

### **5.4.1 Model structure and validity**

The CV parameters for the CASAL applications were varied under three alternative scenarios to fit the predicted abundances of STSH adults and chicks. As expected for an unharvested population, no scenarios showed signs of depletion. The scenario with a smaller CV (*i.e.* 0.01) for adult abundance fitted the observed data for adult abundances well over the study period. However, the model was unable to fit both parameters (adult and chick abundances) simultaneously, suggesting that the adult and chick abundances were not compatible for simultaneous predictions by CASAL.

The chick abundance index proved to be an uninformative measure for the model, which may suggest that chick abundance does not have a large impact on the subsequent recruitment into the adult population. A possible explanation is that high interannual variability in survival affected by external parameters outside the colony, such as environmental drivers (*e.g.* rainfall

and large-scale climate variability) (see Price *et al.* 2020, Price *et al.* 2021), may dampen any signal in chick abundance. For further modelling work, a greater emphasis on adult abundance will be required. This will create a model with the greatest capacity to produce STSH reproductive potential (in fisheries terms, this relates to the spawning stock biomass). Similar findings were observed for the sooty shearwater in New Zealand, which showed that adult mortality had a greater effect on the population growth rate compared to chick mortality (Hunter *et al.* 2000, Hunter & Caswell 2005). Therefore, factors that may affect mortality (environmental or anthropogenic factors such as bycatch or harvest) of the adults will need to be considered in future studies, as small changes in adult survival (from natural or anthropogenic pressures) may have a larger impact than previously thought, and estimates of uncertainty associated with these measures will be more important for quantitative evaluations for future management strategies of the population.

The long STSH generation time ( $> 45$  years) (Bird *et al.* 2020), coupled with the delayed recruitment into the breeding population (breeding by a mean age of 7 years) (Wooller *et al.* 1990, Bradley *et al.* 1991), provide an extensive timeframe during which environmental drivers can influence demographic parameters, typically (but not exclusively) through resource availability (Bost *et al.* 2015, Fay *et al.* 2017, Price *et al.* 2020, Price *et al.* 2021). Analyses drawing on inter-annual recruitment and environmental variability may provide the necessary insights to further unravel the underlying mechanisms involved that failed to provide any relationship to chick abundances (Springer *et al.* 2018, Price *et al.* 2020, Price *et al.* 2021).

#### **5.4.2 STSH reproduction**

Reproductive performance is related to the total cumulative breeding experience of an individual, in which reproductive success increases over multiple attempts, thereby increasing with age (Bradley *et al.* 1989, Bradley *et al.* 1991). Incorporating reproductive parameters in the model may improve the relationship between the predicted abundances of adults and abundance of chick in the model. Additional aspects of reproductive performance are also related to breeding experience with a particular partner (improved breeding success associated with the length of the pair-bond). In a previous study at Fisher Island, reproductive success increased in consecutive years as a pair remained together, except in older birds whose breeding success was already high (Bradley *et al.* 1989, Bradley *et al.* 1991). These complex interactions (*i.e.* reproductive performance, reproductive success by age and duration of pair bonds) have not been considered in this model and could be incorporated into future models to generate a more refined

assessment of the population over time, as these elements are particularly important for recruitment and growth of the population.

Not all STSH breed annually (*i.e.* skipping a season). In our model, we considered that the effect of skipping was equal for all age classes; in future models, this should be investigated further, as mortality rates in the model are likely to be affected when a STSH is recorded absent after the last sighting in a season but may be alive. Absence from the breeding colony tends to be higher in early reproductive years and a skipped breeding event has also been linked to resource availability (Chastel *et al.* 1995, Weimerskirch *et al.* 2001). For example, during periods of low prey availability, procellariiformes may skip breeding or even abandon their chick to ensure their own survival rather than putting energy into breeding (Chastel *et al.* 1995, Weimerskirch *et al.* 2001, Coulson 2008).

Seabirds are archetypal *k*-selected species and are subject to density dependent regulation. Density dependent competition for resources may limit the abundance of STSH during a breeding season (Wooller *et al.* 1992); however, we did not consider density dependence in this study. While density dependence can be added to the CASAL framework for future studies, there is a risk of over-parameterisation in a model, and the additional parameters may not be relevant or essential for assessing/setting management strategies. Moreover, previous studies of the sooty shearwater population indicate that incorporating density dependence in the model structure is unnecessary for setting alternative management strategies (Hunter *et al.* 2000), although may be useful for answering research questions such as the influence of density dependence on non-breeders, breeders and immigrants in the population.

#### **5.4.3 Parameter estimations**

A limitation of this model is that a bias may be introduced into survival rates, such as if the bird ceased to visit the island but continued to survive without breeding on the island for several years (*i.e.* skipping for several seasons) or emigrated to another colony. Data on the emigration rates of STSH from Fisher Island is relatively poor. Previous studies have resighted birds banded from Fisher Island (*i.e.* known-aged and unknown-aged birds) on a nearby island, although no evidence has been found of them breeding there (Bradley *et al.* 1989). It has been suggested that any interchange (of breeding birds) occurs before the first breeding attempt (Bradley *et al.* 1989). Like many long-term studies of procellariiformes, information is limited for survival of immature/pre-breeding birds, and the processes (*i.e.* environmental or biological) that influence recruitment are poorly understood. For future studies, a Cormack-Jolly-Seber Model could also

be used to obtain a more accurate estimate; however, given the high resight probability this would provide minimal improvement in mortality estimates.

#### **5.4.4 Age structure and population**

The age structure of a population is a key component of this type of modelling, and the age-related parameters of animals are key inputs to many demographic studies (Klomp & Furness 1992). The age structure of the STSH colony at Fisher Island varied over the study period, with the median age of birds at the colony becoming younger towards the end of the study, so will need to be parameterised in future studies. The use of age-related parameters provides a tool to calculate life tables for a population, which form the basis of a population viability assessment. Estimates of age can also be used to understand reproductive potential, developmental processes and the aspects influencing survival and reproductive success (Polanowski *et al.* 2014).

One of the potential limitations of applying the CASAL model to other bird species is that the age structure of the population is a key data requirement. Non-invasive techniques for ageing birds can be calculated with similar methods used in this study (*i.e.* capture-mark-recapture methods), but are costly for long-lived species or inappropriate for nomadic species (*e.g.* some waterfowl). Other methods, such as identifying age through difference in plumage, colouration of soft parts or morphometrics, can be used; however, these techniques are typically limited in their utility (*i.e.* can only identify juvenile or adult) and cannot provide a chronological age (Jannett 1983, Klomp & Furness 1992). Recent advancements in the development of non-invasive age determination techniques, such as molecular ageing for birds (see Polanowski *et al.* 2014, De Paoli-Iseppi *et al.* 2019), may be able to obtain age frequency data for birds in the future.

Another limitation of this study is that it is based on a very small proportion of the global population – just 4000 individuals from a global population of approximately 18 million (Skira *et al.* 1996). The use of multiple study sites would provide a more robust understanding of the population. Previous studies have demonstrated inter-colony differences in reproductive success, breeding parameters and age structure over decadal scales (Springer *et al.* 2018, Price *et al.* 2020, Price *et al.* 2021). However, there are significant logistical challenges to collecting basic demographic rates in a seabird population, and establishing a new banding study at multiple islands would be time-consuming, with any results not being seen for at least 20 years due to the long generation times of STSH (Bird *et al.* 2020). The use of census data from other breeding islands and sensitivity/elasticity analyses using varying demographic parameters based on the

Fisher Island population may allow for further predictions for an integrated stock assessment model.

#### **5.4.5 Environmental considerations**

As a migratory species, the environmental conditions in both the breeding and non-breeding grounds contribute to the survival of STSH adults, and incorporating small- and large-scale processes will be an important factor in assessing the sustainability of the population. As adult mortality has a strong effect on the population growth rate, future studies may benefit from including environmental determinants of individual survival, as seabirds are susceptible to climate variability both at local and regional scales (Napp & Hunt 2001, Jenouvrier 2013, Zador *et al.* 2013, Cushing *et al.* 2017). Short-tailed shearwater breeding parameters are also affected by large-scale climate indices (*e.g.* El Niño–Southern Oscillation and the Southern Annular Mode) and local weather conditions such as rainfall (Springer *et al.* 2018, Price *et al.* 2020, Price *et al.* 2021). Future studies will need to consider the implications of environmental conditions and stochastic events on the demographics and population trends of STSH.

#### **5.4.6 Harvest modelling considerations**

A key benefit of using an integrated stock assessment model is the ability to incorporate a known annual harvest, but this was beyond the scope of this pilot study. The annual recreational and commercial STSH harvests almost certainly influence the population, as has been shown elsewhere for other shearwaters (Hunter & Caswell 2005, Juillet *et al.* 2012). Historical surveys show that 90% or more chicks were harvested in a season by recreational harvesters at permitted colonies (Skira *et al.* 1986, Skira 1990); such harvesting would undoubtedly cause a significant local reduction in the number of recruits into the breeding population and likely be unsustainable. For colonies of harvested populations, the biomass may have been depleted to the point where it has affected future recruitment, and consequently a stock recruitment relationship should be explored.

Given the longevity of STSH (Bird *et al.* 2020), the resultant impacts to colonies from intense harvesting can be delayed for many years (Skira & Wapstra 1980), and any impacts may not manifest for decades. The low turnover rate of long-lived species may mask the long-term trends in the population caused by harvesting (or bycatch), resource availability or long-term cycles in climate and other environmental parameters. Long-lived species such as STSH provide remarkable opportunities for research into marine systems at multiple time and space scales.

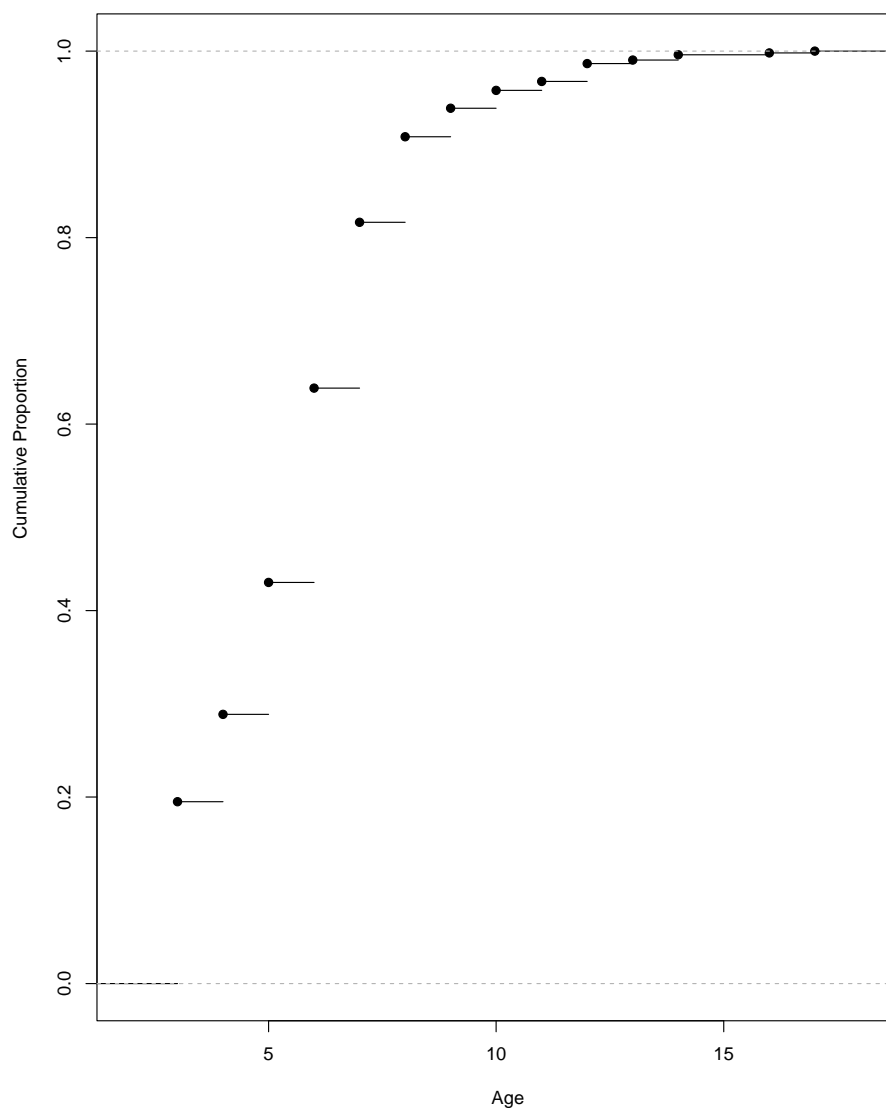
## 5.5 Conclusion

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As previously discussed, there are many improvements that can be made to future models, which include incorporating multiple study sites, environmental or anthropogenic factors, complex intrinsic interactions (*i.e.* reproductive performance, reproductive success by age and duration of pair bonds) and density dependence. Survival rates may also be improved by using a Cormack-Jolly-Seber Model to obtain a more accurate estimate. Moreover, for future models a greater emphasis on adult abundance will be required, as chick abundance index proved to be uninformative. Even though there is a risk of over-parameterisation of a model, it will be necessary to determine which parameters are vital for assessing/setting management strategies.

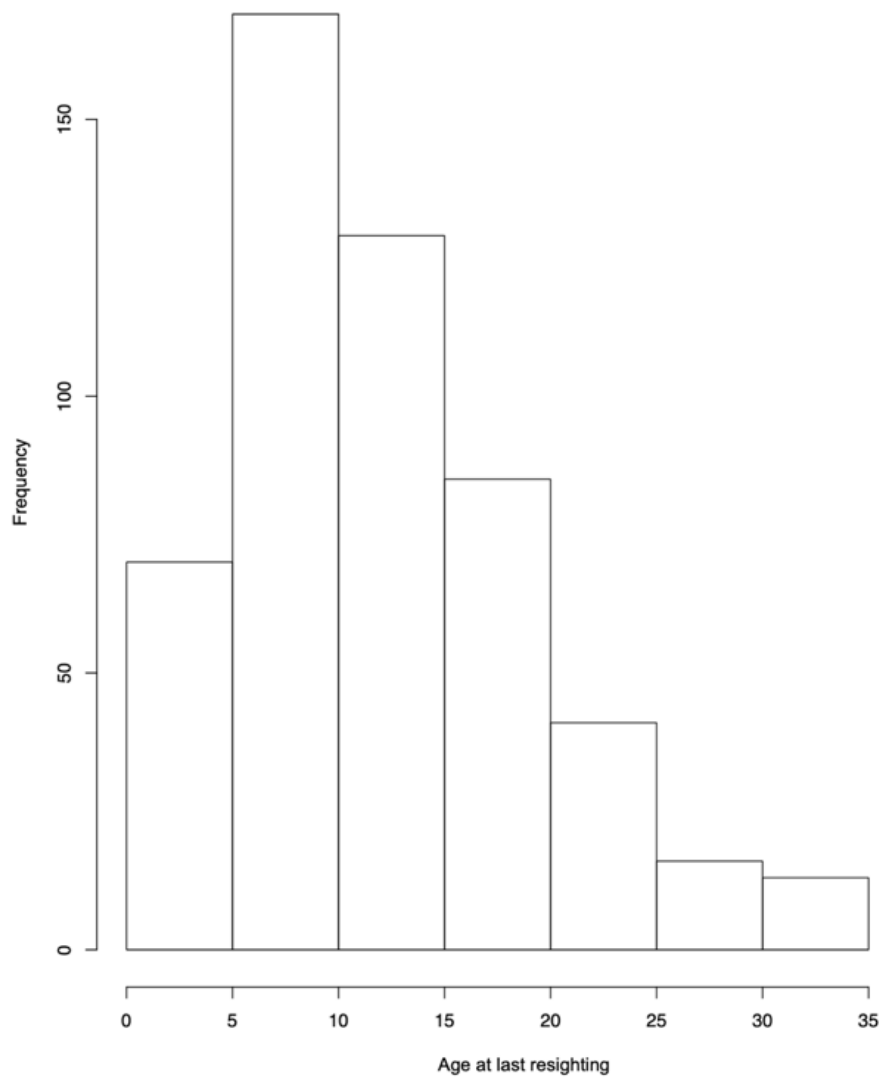
While this study applied the CASAL package to a non-harvested STSH population, adding harvest rates to the model would be an easy next step. Adopting and using pre-existing packages for stock assessment can be advantageous as it may reduce the cost, time and effort involved in conducting assessments, and provide a robust framework for management decision-making for seabirds. The development of well documented and validated software tools such as CASAL for fish and seabird population assessment reduces the need to develop complex models from scratch. This allows for easier training of staff to create population models with a lower programming skill requirement, and can allow for easy replication and updating of assessments, both of which may have great benefits to scientist and managers for setting a wildlife harvesting framework for STSH.

## 5.6 Tables and Figures



*Figure 5-1: The cumulative proportions of recruitment into the breeding population of known-age STSH at Fisher Island*





*Figure 5-2: The ages of STSH (breeders) at the time of the last resighting on Fisher Island, 1947 to 2017*

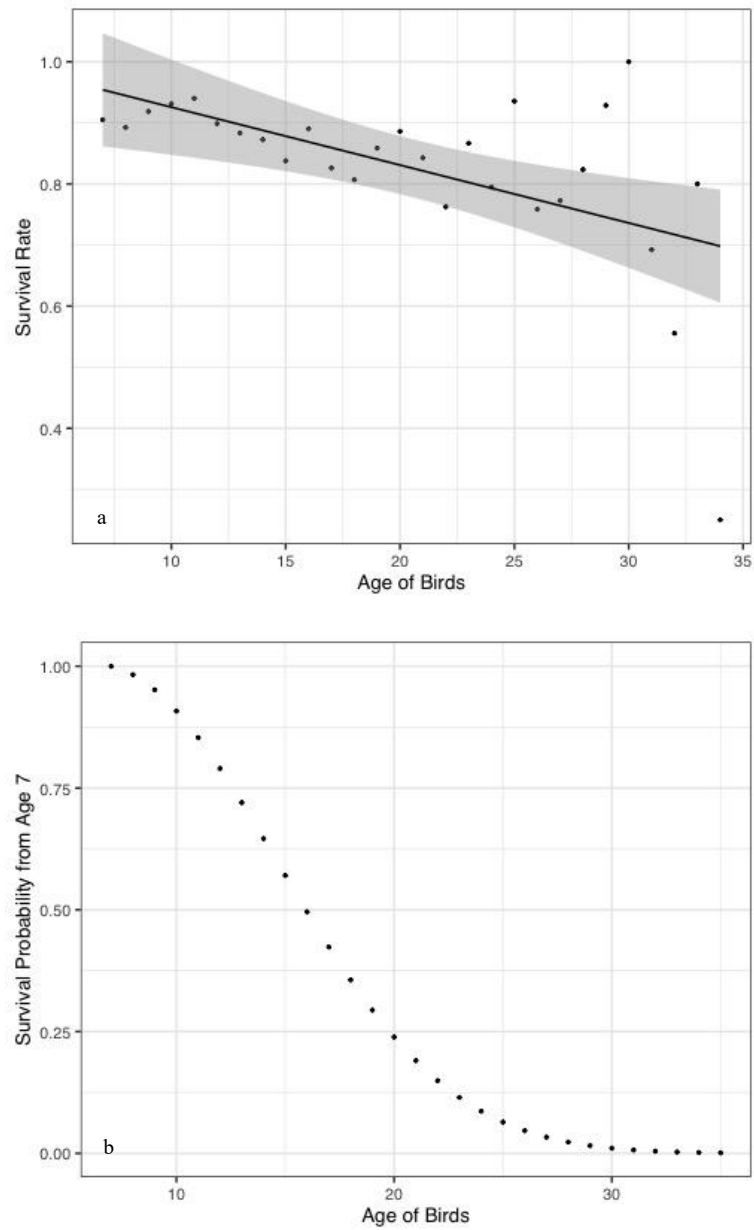


Figure 5-3: Annual survival probability of STSH

(5-3a) From age 7 breeding at Fisher Island, 1947 to 2017, assuming the last year of sighted was the last year alive; (5-3b) From age 7 to any given age.

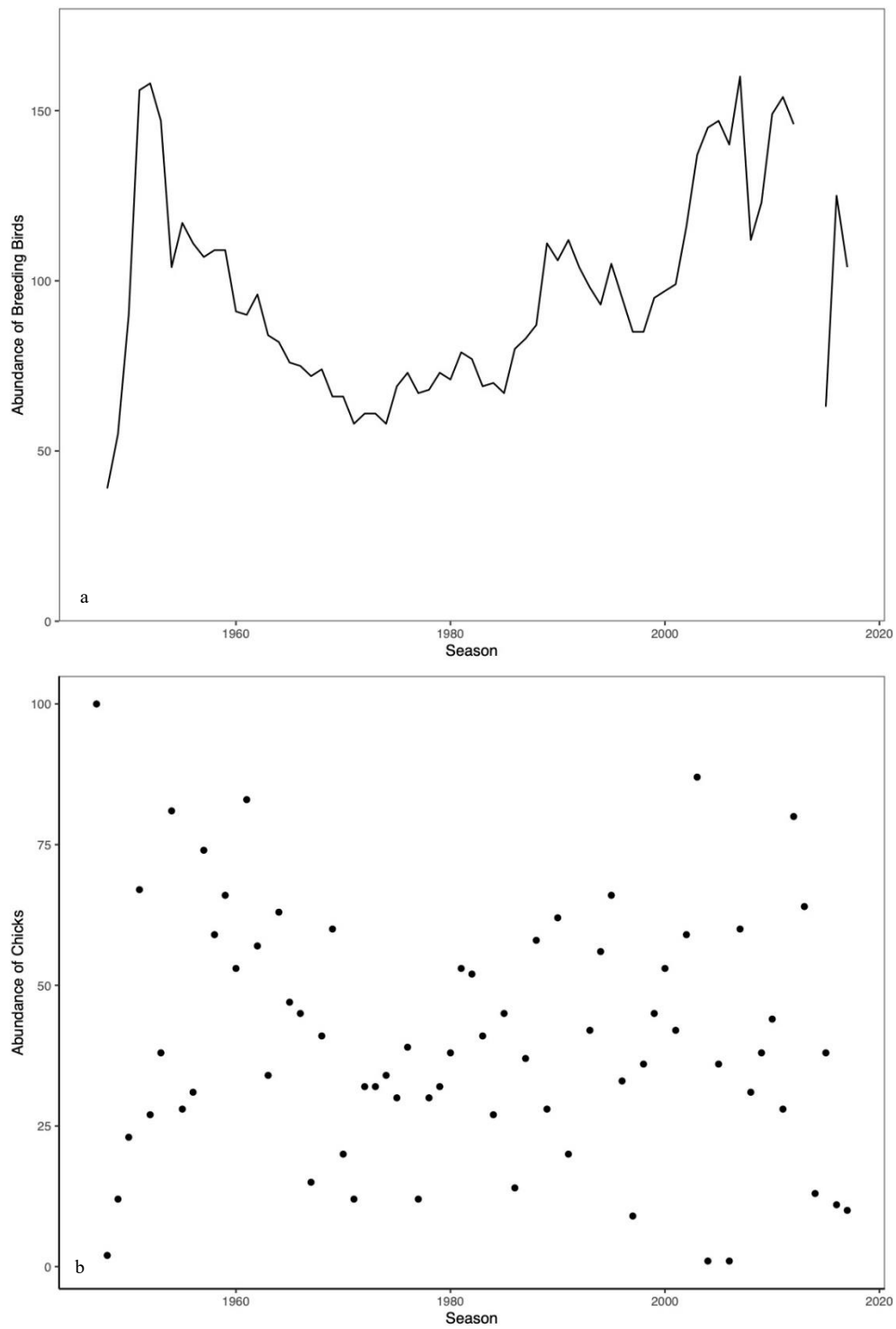


Figure 5-4: Abundance of adults and chicks at the Fisher Island colony, 1947 to 2017

(5-4a) Observed adult abundance (breeding pairs); (5-4b) Observed chick abundance.

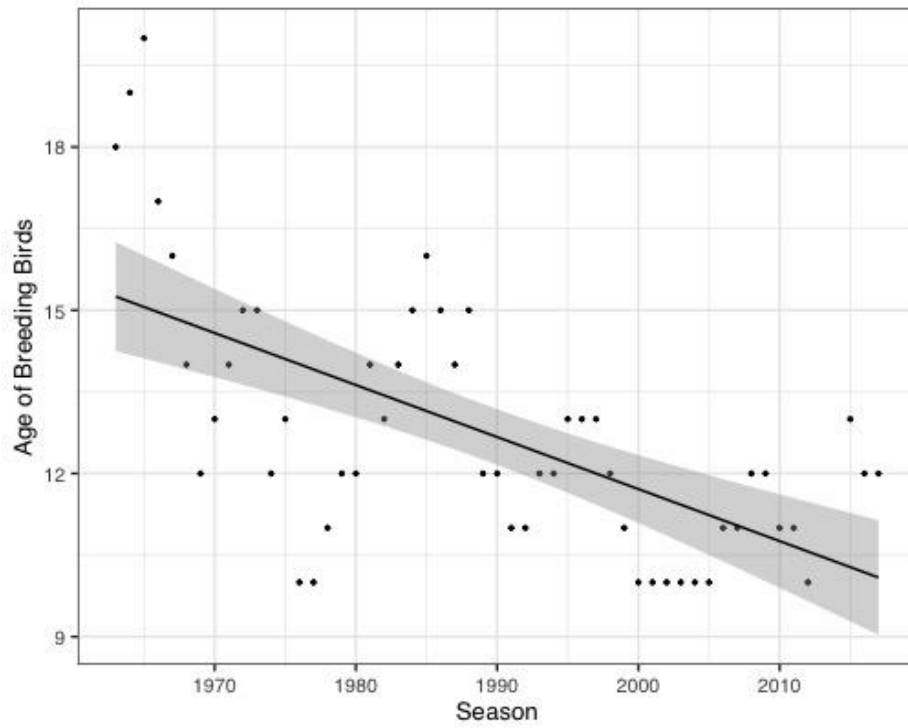


Figure 5-5: The median age structure of the short-tailed shearwater at Fisher Island between 1967 and 2017

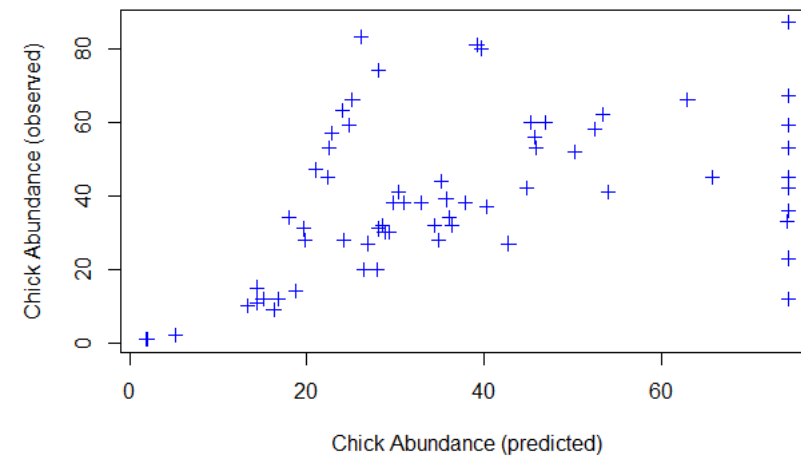
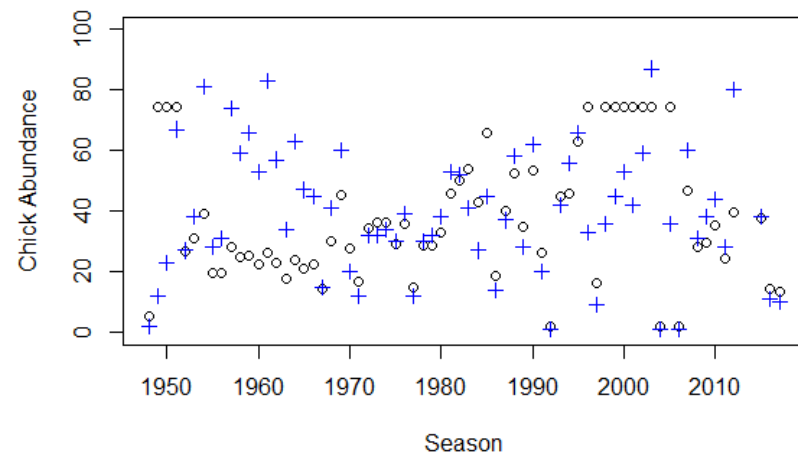
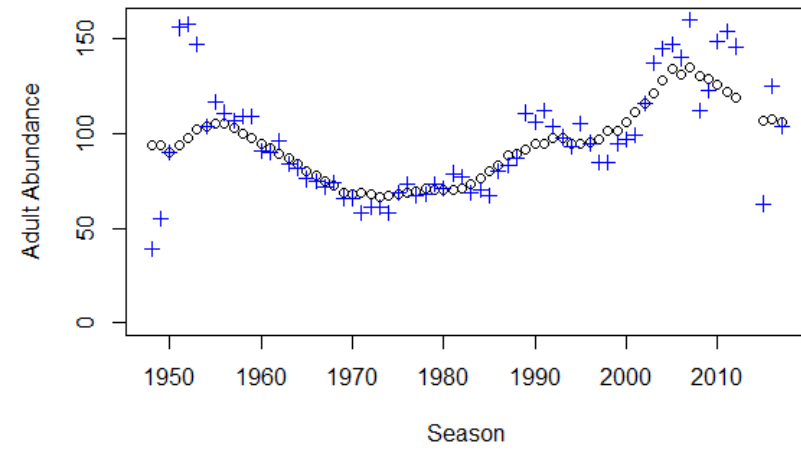
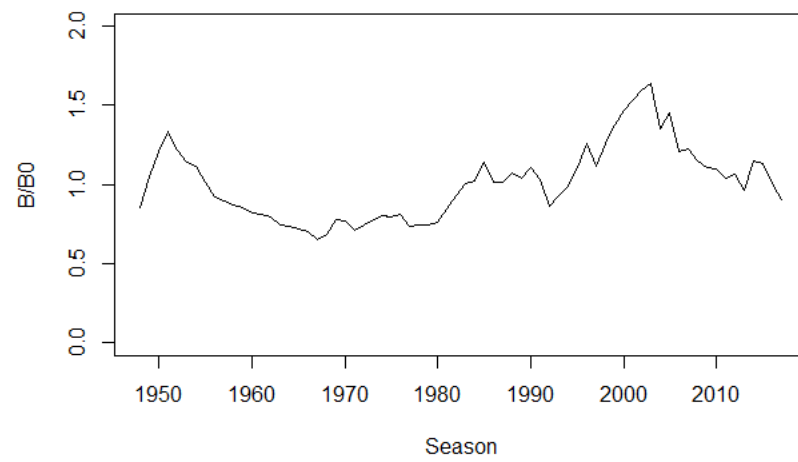


Figure 5-6: The Coefficient of Variation (CV) parameter, scenario 1: Adults C.V. 0.01 Chick C.V. 0.06

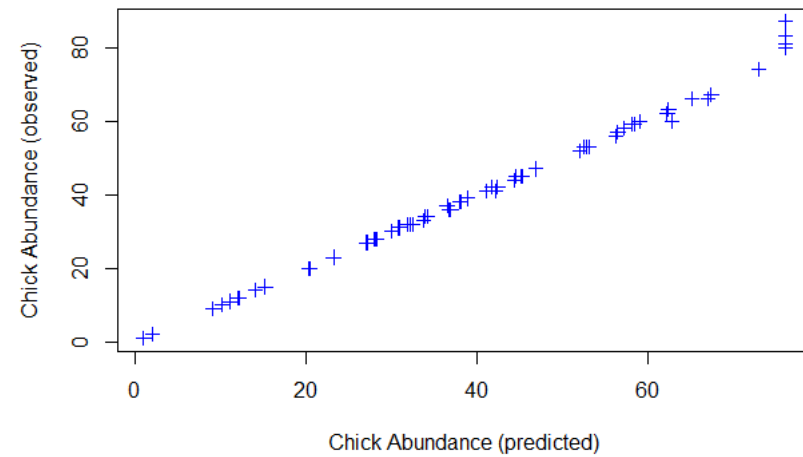
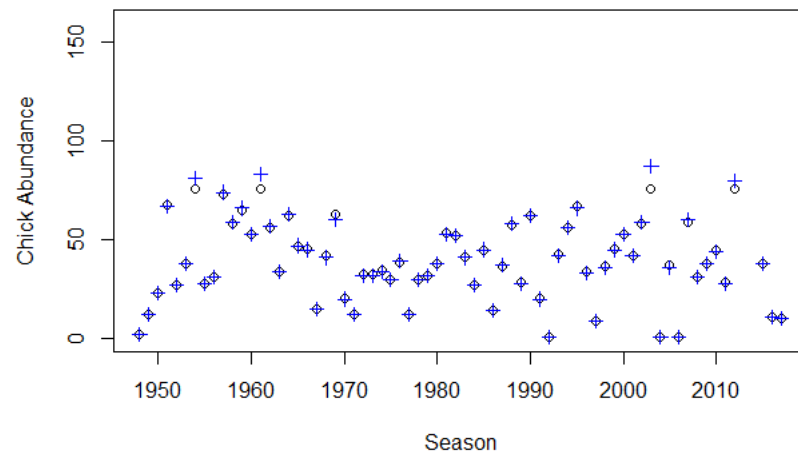
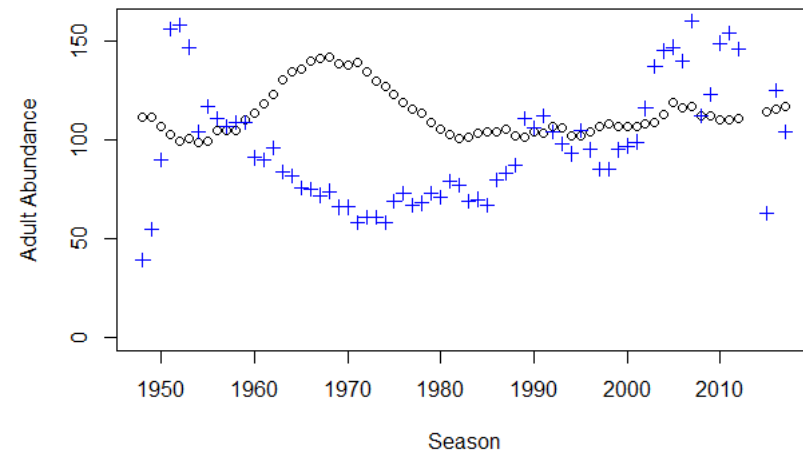
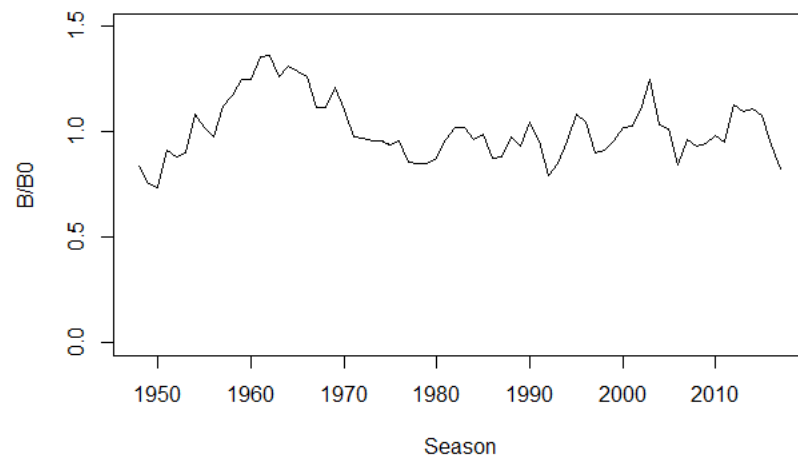


Figure 5-7: The Coefficient of Variation (CV) parameter, scenario 2: Adults C.V. 0.5 C.V. Chick 0.01

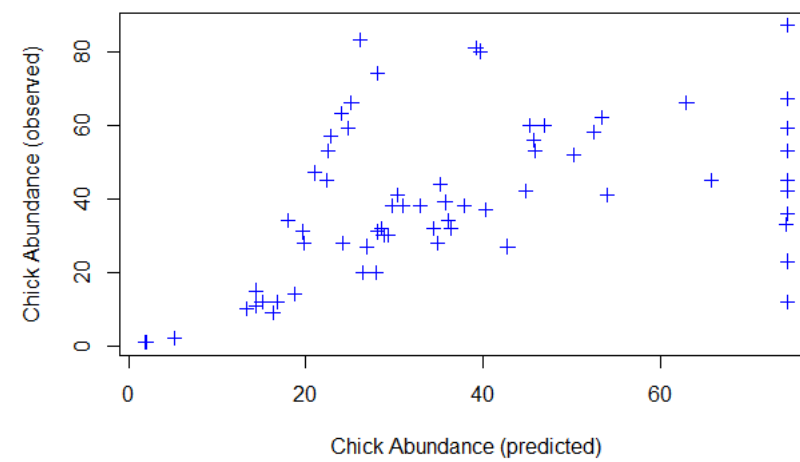
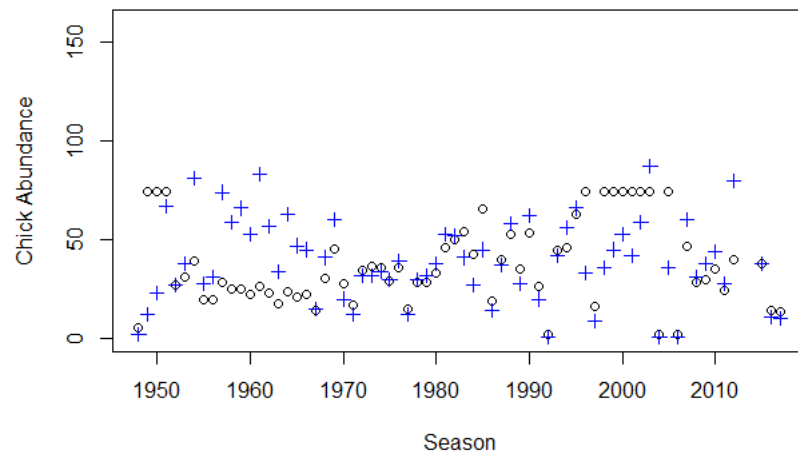
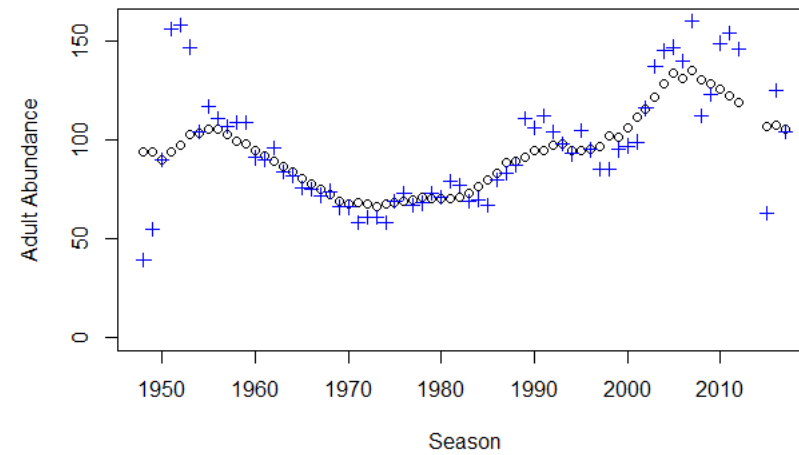
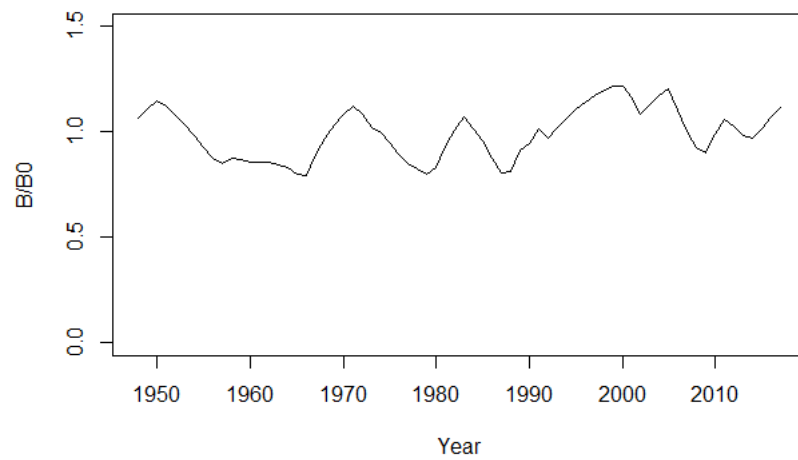


Figure 5-8: The Coefficient of Variation (CV) parameter, scenario 3: Adults C.V. 0.25 C.V. Chick 0.03

**GENERAL DISCUSSION**

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East Kangaroo Island

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## 6.1 Synthesis and Conclusion

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### 6.1.1 Introduction

The first objective of this study was to compile all the historical data from an extensive long-term capture-mark-recapture (CMR) research project from the unharvested Fisher Island colony of banded short-tailed shearwater (STSH), to create one of the longest continuous demographic time series (from 1947 to present) of a seabird species in the Southern Hemisphere. Beyond the needs of the current study, this dataset offers a number of benefits to the broader ecological research, and provides the basis for a broad suite of ecological and applied management investigations to be undertaken on a species that has cultural and economic value to the community.

The second objective was to (i) investigate annual trends in the breeding parameters of the STSH at multiple breeding colonies at the Furneaux Island Group, and (ii) investigate the relationship among large-scale climate indices and local environmental conditions on the breeding parameters of the STSH at multiple colonies within the Furneaux Islands off the northeast coast of Tasmania, Australia. This objective sought to gain insights into inter-annual variabilities in breeding effort and success. The inclusion of one unharvested colony, Fisher Island (the study colony for the period 1950 to 2012), and four harvested colonies, Little Green, Little Dog, Big Green and East Kangaroo Islands (study period 2010 to 2018), provided the opportunity to compare and contrast population trends between harvested and unharvested populations subjected to the same environmental drivers.

The final objective was to examine the feasibility of using a fisheries stock assessment model to conduct an integrated assessment for the STSH population. This objective investigated whether pre-packaged modelling frameworks provide a viable alternative to dataset, species-specific models.

The data from the study colonies at the Furneaux Islands was also incorporated into an ocean-basin, transhemispheric study examining drivers of population-level responses to prey availability for STSH in the North Pacific Ocean (Springer *et al.* 2018) (see Appendix 1). While not initially part of this thesis, the collaborative study reinforced and highlighted the complex ecosystem dynamics involved in regulating STSH populations. Short-tailed shearwaters are long-lived birds, with some living well into their 40s, and food limitations in their wintering

areas in the North Pacific are clearly linked with the broad-scale environmental drivers investigated for Objective 2 and contribute to population dynamics investigated for Objective 3.

The results for each objective were discussed in their own particular context at the end of each chapter; this discussion provides an overall synthesis of the findings of the study and preliminary indications for future work.

### **6.1.2 Climate, environmental conditions and breeding parameters**

Large-scale climate indices such as the El Niño–Southern Oscillation (ENSO) and Southern Annular Mode (SAM) in the Southern Hemisphere, and the Pacific Decadal Oscillation (PDO) and the North Pacific Index (NPI) in the Northern Hemisphere can strongly influence marine productivity on temporal scales, from weeks to years (Trenberth & Hurrell 1994, Humphries & Möller 2017). Large-scale climate processes can influence primary production, affecting the composition, distribution, abundance and timing of secondary production that feed into higher trophic level species, such as seabirds and marine mammals, including STSH (Sarmiento *et al.* 2004, Iida & Saitoh 2007, Bond *et al.* 2011).

Chapters 3 and 4 examined the relationship between STSH breeding parameters and climate, using large-scale climate indices (*i.e.* NPI, PDO, ENSO and SAM) and local weather conditions (*i.e.* rainfall). Over the course of the 63-year study (1947 to 2010) at Fisher Island, breeding participation among STSH was affected by climate variability with a 12-month temporal lag (Chapter 3). Similarly, for the study period 2010 to 2018 at the Furneaux Islands colonies (harvested populations), both adult body mass and breeding participation were influenced by climate conditions in the preceding year. Additionally, inter-colony variability was demonstrated for adult body mass and breeding participation among the Furneaux Islands colonies. In both studies (*e.g.* Furneaux Island and Fisher Island colonies) breeding success was influenced by large-scale and local climate conditions; however, local rainfall had the greatest impact: breeding success decreased in years of increased rainfall. These findings demonstrate that both large-scale climate indices and local environmental conditions contribute towards explaining some of the variability among breeding parameters of STSH.

Not all interactions between large-scale climate indices and STSH breeding parameters showed the same relationship (Price *et al.* 2020, Price *et al.* 2021), suggesting further studies are required to elicit the linkages involved. Between the two studies (differing in the datasets' time scales), the relationship between the PDO and breeding participation were inconsistent; breeding participation at the Fisher Island study colony increased during cool phases, which was the opposite of the

findings for other Furneaux Island colonies investigated in this study (*i.e.* Little Green, Little Dog, Big Green and East Kangaroo Islands). At present, the relationship between PDO phases and STSH populations remains open for further investigation; it is possible that the disparate results obtained herein are an artefact of the datasets.

Further research is required to give a clearer understanding of the roles and influences that climate and environmental conditions have on STSH breeding success at different colonies in the same breeding season. It is likely that the climate indices investigated in this study are influencing the prey resource availability for STSH throughout their annual range, which is reflected in their subsequent breeding performance at different stages as a consequence of differing ecological linkages.

The overall relationship between climate, environmental drivers and STSH breeding parameters identified in this study are broadly similar to those for other seabird species. Breeding success of red-faced cormorants (*Phalacrocorax urile*) and common murrelets (*Uria aalge*) decreased 1 to 2 years after increases in Bering Sea sea-surface temperature (Zador *et al.* 2013). The warmer waters lower primary productivity, leading to a reduction in abundance of pollock (*Theragra chalcogramma*), an important prey species for Bering Sea seabirds. Decreased breeding participation by whiskered and crested auklets (*Aethia pygmaea* and *A. cristatella*, respectively) in the Aleutian Islands, Alaska, was thought to be driven by stronger manifestations of the Aleutian Low, which affects bottom-up processes, leading to a change in the composition and quality of prey resources (Bond *et al.* 2011). These changes in oceanographic conditions during different Aleutian Low states may contribute to the variability found for STSH breeding parameters in this study.

### **6.1.3 Feasibility of using an existing stock assessment package**

Chapter 5 assessed the feasibility of using a fisheries stock assessment package (*i.e.* CASAL framework) for the STSH population on Fisher Island. The commercial exploitation of STSH began in the early 1820s soon after the arrival of European settlers (Skira 1990), while recreational harvesting has increased since the early 1950s (Skira 1993). Only STSH chicks are currently harvested in the annual season that commences in early March and continues until the end of April (Skira & Wapstra 1980). Daily bag limits depend on colony-specific harvest limits, and ranges between 15 to 25 birds per day for each recreational licence holder (see [www.dpipwe.tas.gov.au](http://www.dpipwe.tas.gov.au)), while the Aboriginal commercial industry is largely self-regulated (Skira *et al.* 1986).

The CASAL (C<sup>++</sup> Algorithmic Stock Assessment Laboratory) framework allows for the production and parameterisation of generalised age- or size-structured stock assessment models. CASAL is designed for flexibility, and can be used for a single fishery or multiple stocks areas and/or fishing methods, and is adaptable in specifying the population dynamics, parameter estimation and model outputs (Bull *et al.* 2012). While it is desirable for management decisions to be based on quantitative assessments of available data, this is not always possible (Punt *et al.* 2020), particularly for harvested wildlife such as birds.

The study demonstrated that the CASAL framework was an appropriate modelling tool for investigating the STSH population at Fisher Island. The data from the unharvested colony of STSH on Fisher Island allowed the study to estimate unknown population parameters such as maturity and selectivity (*i.e.* relative probability of animals of different sizes/ages being caught by the commercial or scientific sampling equipment), and census data from the colony was also used to fit model parameters (*e.g.* age frequency and abundance), to provide estimates of annual recruitment deviations.

A key strength of this study was access to the 70-year CMR data, which provided a unique opportunity to utilise the age structure (frequency) in the CASAL framework. However, this also highlights the limitations of applying this type of modelling to other bird species, as relatively few bird populations have a known age structure, and age frequency data is a key requirement for use of the CASAL framework. Age frequency data is essential to estimate demographic parameters confidently (Klomp & Furness 1992). Recent advances in the development of non-invasive age determination techniques such as molecular ageing (*e.g.* De Paoli-Iseppi *et al.* 2019) may make this possible. Expansion of the model to a larger proportion of the population by including additional colonies would be the next step in creating a model representative of the harvested population.

The sensitivity of the age structure predictions was investigated by varying the Coefficient of Variation (CV) parameter under three alternative scenarios for adult and chick abundance indices. However, the challenge was finding a balance when the model could fit both indices reasonably well. This suggests there are some fundamental inconsistencies between the two, and suggests that chick abundance index was uninformative, possibly due to the interannual variability in survival. A population model for a closely related species that is also harvested, sooty shearwaters (*Ardenna grisea*) in New Zealand, showed that adult sooty shearwater mortalities had a greater effect on population dynamics than did chick mortalities (Hunter *et al.* 2000, Hunter & Caswell 2005). This may be similar to the STSH, indicating that future models

should place a greater emphasis on adult abundance, and/or not use the chick abundance index.

This study identified a number of additional parameters that would improve the CASAL model. In particular, age-related reproductive performance, reproductive success and the duration of pair bonds could be incorporated to reflect a more accurate assessment of the population parameters in the wild, as these elements are of particular importance for recruitment and growth of seabird populations (*e.g.* Bradley *et al.* 1989, Bradley *et al.* 1991). Density-dependent parameters could also be incorporated into a future CASAL model to investigate additional aspects of the study population, such as the role of resource constraints on offspring survival (Hunter *et al.* 2000).

A key benefit of using the CASAL framework is the ability to incorporate a known annual harvest parameter. One aim of fish population modelling in a stock assessment context is to quantify the effect of fisheries on fish populations, and thereby inform management of the fishery. As STSH are a harvested species, future integrated stock assessment modelling incorporating both annual and recreational harvest numbers of STSH into a CASAL framework would be the next recommended step. The further development of a harvest model could provide results that assist management agencies (*i.e.* DPIPWE) and Aboriginal communities to refine existing strategies for management and harvesting of STSH.

#### **6.1.4 Climate and environmental considerations**

Since commercial harvest began in the 1820s, numerous management controls have been implemented to regulate the harvest of STSH, following the limited controls that were in place when commercial harvesting began (Skira 1990). These controls have been adjusted in response to the annual harvesting pressure on the species. However, in more recent times environmental pressures and extreme climate events are also affecting STSH and other bird species in Australia (*i.e.* waterfowl) (Kingsford *et al.* 2020). It is predicted that extreme environmental events (*e.g.* marine heatwaves, storm events), that contribute to wildlife mortality will increase in severity and frequency due to climate change (Wernberg *et al.* 2013, Oliver *et al.* 2018). Therefore, it is highly likely that mass mortality events (*i.e.* wrecks) will increase in frequency (Glencross *et al.* in press-a, Glencross *et al.* in press-b). For example, during the 2013 to 2014 breeding season, a widespread STSH mass mortality event was reported in southeast Australia following the adults' return from the trans-equatorial migration (Springer *et al.* 2018) (see Appendix 1), thought to be due to severe weather and low prey availability (Berlincourt & Arnould 2015).

Under extreme circumstances, the increased intensity and frequency of storm events may contribute additional pressures on the STSH population. In the North Atlantic, La Niña events are connected to extreme climate events and storms conditions, including increased frequency of hurricanes. These events were shown to significantly decrease the survival of adult Cory's shearwater (*Calonectris diomedea*) (Jenouvrier *et al.* 2009, Genovart *et al.* 2013). In the Southern Hemisphere, storm events increase under La Niña conditions (Yuan 2004, Stammerjohn *et al.* 2008), which may negatively influence STSH survival and breeding parameters. Currently, there is limited information on the impacts of storms in the Southern Ocean where STSH forage during the breeding season, which needs to be investigated further (Glencross *et al.* in press-b). As STSH undertake transhemispheric migration and long foraging trips (Carey *et al.* 2014), they are exposed to a variety of environmental conditions, which may increase the probability of encountering extreme conditions (Newton 2007). Understanding the impacts of extreme environmental events for STSH is vital, as mass mortality events can impact seabird demography (Piatt *et al.* 2020).

#### **6.1.5 Harvest management**

The effects of harvest on STSH populations may be exacerbated by local conditions and the impacts of climate change. The harvest rates of sooty shearwaters in New Zealand were linked to climate indices; the harvest increased (or decreased) one year before positive Southern Oscillation Index (SOI) values (or negative SOI values). This was believed to be due to differences in prey availability in response to climate and oceanographic conditions (Clucas 2011). Lescroël *et al.* (2009) also showed that lower-quality individuals and younger or older birds (*i.e.* senescent individuals) were more sensitive to climatic and environmental perturbations. These findings highlight the importance of considering environmental and climate parameters in a sustainable harvest model for STSH.

STSH are highly philopatric (Bradley *et al.* 1990, Warham 1996), and colonies may be vulnerable to depletion from localised over-harvesting. In light of our currently limited understanding of emigration and immigration between and among colonies, little is known about the impact of recreational and commercial harvesting on the population as a whole. As harvesting can influence recruitment into the population, further investigation is required to understand long-term population responses to harvesting pressures. Inter-annual variations in harvesting may alter age structures of colonies (Juillet *et al.* 2012), potentially resulting in individuals that have different levels of reproductive efficiency and capacity. Integrated stock assessment modelling incorporating local and large-scale environmental conditions is necessary to explore

alternative management strategies for effective decision-making and sustainability for the species.

#### **6.1.6 Conclusion**

This study highlights the importance of climate to breeding performance, measured through large-scale climate indices (*i.e.* NPI, PDO, ENSO and SAM) and local weather conditions (*i.e.* rainfall), and the critical importance of long-term datasets to monitoring populations of long-lived species. The low production potential of STSH (in terms of only laying a single egg per year at most) and the longevity of individuals (over 45 years) requires long-term, decadal-scale data to investigate population dynamics, and to elucidate the effects of environmental perturbations on population dynamics and trends (Bradley *et al.* 1991).

Ecosystem processes and trophic linkages to top-order predators are complex, and often difficult to quantify (*e.g.* Springer *et al.* 2018). Other intrinsic and extrinsic factors not considered in the current study may also contribute to the inter-annual variability of STSH breeding parameters, such as breeding experience and pair bond duration. Additional demographic studies incorporating census data and other breeding parameters from other colonies throughout their range are needed to investigate STSH population at a continental scale. Incorporating the impact of harvesting will be critical for future modelling studies.

The temporal and/or spatial lags between the numerous oceanographic and environmental drivers, and the corresponding biological responses, range from days to decades (Stommel 1963, Haury *et al.* 1978). To further understand the impacts at the population level, demographic studies are needed to investigate the long-term impact on STSH populations in southeast Australia. The findings of this study clearly reinforce the importance of long-term monitoring to assess the influence of large-scale climate indices and local environmental conditions as drivers affecting seabirds' breeding parameters.

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Sunset over Cape Barron Island from Fisher Island

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## APPENDICES

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Short-tailed shearwater, *Ardenna tenuirostris*

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**TRANSEMISSPHERIC ECOSYSTEM DISSERVICES OF PINK  
SALMON IN A PACIFIC OCEAN MACROSYSTEM**

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# Transhemispheric ecosystem disservices of pink salmon in a Pacific Ocean macrosystem

Alan M. Springer<sup>a,1</sup>, Gus B. van Vliet<sup>b,2</sup>, Natalie Bool<sup>c</sup>, Mike Crowley<sup>d,2</sup>, Peter Fullagar<sup>e,2</sup>, Mary-Anne Lea<sup>c,f</sup>, Ross Monash<sup>g</sup>, Cassandra Price<sup>c</sup>, Caitlin Vertigan<sup>c</sup>, and Eric J. Woehler<sup>c,h</sup>

<sup>a</sup>Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, AK 99775; <sup>b</sup>Private address, Auke Bay, AK 99821; <sup>c</sup>Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7000, Australia; <sup>d</sup>South Coast Region, State Forests of NSW, Australia, Moruya Heads, NSW 2537, Australia; <sup>e</sup>Commonwealth Scientific and Industrial Research Organization, Division of Wildlife Research, Australia, Belconnen, ACT 2617, Australia; <sup>f</sup>Antarctic Climate and Ecosystems CRC, Hobart, TAS 7000, Australia; <sup>g</sup>Marine Conservation Program, Department of Primary Industries, Parks, Water and Environment, Hobart, TAS 7001, Australia; and <sup>h</sup>BirdLife Tasmania, Hobart, TAS 7001, Australia

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**Pink salmon (*Oncorhynchus gorbuscha*) in the North Pacific Ocean have flourished since the 1970s, with growth in wild populations augmented by rising hatchery production. As their abundance has grown, so too has evidence that they are having important effects on other species and on ocean ecosystems. In alternating years of high abundance, they can initiate pelagic trophic cascades in the northern North Pacific Ocean and Bering Sea and depress the availability of common prey resources of other species of salmon, resident seabirds, and other pelagic species. We now propose that the geographic scale of ecosystem disservices of pink salmon is far greater due to a 15,000-kilometer transhemispheric teleconnection in a Pacific Ocean macrosystem maintained by short-tailed shearwaters (*Ardenna tenuirostris*), seabirds that migrate annually between their nesting grounds in the South Pacific Ocean and wintering grounds in the North Pacific Ocean. Over this century, the frequency and magnitude of mass mortalities of shearwaters as they arrive in Australia, and their abundance and productivity, have been related to the abundance of pink salmon. This has influenced human social, economic, and cultural traditions there, and has the potential to alter the role shearwaters play in insular terrestrial ecology. We can view the unique biennial pulses of pink salmon as a large, replicated, natural experiment that offers basin-scale opportunities to better learn how these ecosystems function. By exploring trophic interaction chains driven by pink salmon, we may achieve a deeper conservation conscientiousness for these northern open oceans.**

teleconnection | short-tailed shearwater | carryover effect | interaction chain | ecosystem management

Linkages between ecosystems and the importance to animal and plant populations, production processes, and community characteristics within and between them are known from a variety of examples at regional geographic scales (e.g., refs. 1–4). On larger scales, linkages, or teleconnections, across broadly separated regions of Earth have been described in numerous fields, including atmospheric sciences, marine and terrestrial ecology, social-ecological systems, and economic markets (e.g., refs. 5–15), and are a foundational element of the emerging subdiscipline of macrosystem ecology (e.g., refs. 16–17, and references therein). Macrosystem ecology draws attention to interactions spanning spatially distant regions that, taken together, have ecosystem characteristics, and indirectly addresses the difficulty in defining ecosystem space. Here we describe a remarkable example of a transhemispheric macrosystem that integrates processes at five geographic scales and six trophic levels spanning some 15,000 km of the Pacific Ocean, with links between meteorology and marine climate in the Northern Hemisphere; the abundance of pink salmon (*Oncorhynchus gorbuscha*) and marine ecology in the northern North Pacific Ocean and Bering Sea (NP/BS); the ecology of a transhemispheric migrant seabird, the short-tailed shearwater (*Ardenna tenuirostris*); and terrestrial ecology and social systems in the Tasman Sea in the South Pacific Ocean (SP/TS). Interesting in its own right, this

macrosystem is important because it further exposes concern over the growing abundance of wild and hatchery produced salmon, competition for finite common prey resource pools in the NP/BS, and international management and conservation responsibilities for these little-known pelagic ecosystems.

Wild pink salmon stocks began to increase in the 1970s across much of their range in the North Pacific Ocean in association with a shift in the mean state of the Aleutian Low pressure system, the dominant meteorological feature affecting ocean climate over this broad region (e.g., ref. 18). The ensuing regime was favorable for pink salmon (19, 20), and despite subsequent meteorological state shifts (21), their abundance continued to grow. Two other species of Pacific salmon also increased during this time, sockeye (*Oncorhynchus nerka*) and chum (*Oncorhynchus keta*), but to far lesser degrees (22). These increasing trends contrast with widespread declines in the abundance of coho salmon (*Oncorhynchus kisutch*) and the iconic Chinook, or king, salmon (*Oncorhynchus tshawytscha*) that are of great concern in many ways (e.g., refs. 22–25).

Returns of wild stocks of pink salmon have been augmented 10–20% by hatchery production since the 1980s, primarily in Russia and the United States (22). Pink salmon now constitute ~70% of the total of all species of Pacific salmon combined and have annual returns in recent years of up to  $650 \times 10^6$  fish (22).

## Significance

Ecological processes at regional geographic scales can be connected to those in far distant locations by teleconnections, or interactions between species and systems far removed from one another. Macrosystem ecology views such interactions as elements of much larger ecosystems than either component. We have identified a remarkable example of a transhemispheric macrosystem spanning 15,000 kilometers of the Pacific Ocean maintained by a migratory species of seabird that nests in the South Pacific and winters in the North Pacific. It highlights another example in a growing list of ecosystem disservices of an abundant species of North Pacific salmon, and the need to include ecosystem processes at such geographic scales in conservation and management considerations for this northern open ocean.

Author contributions: A.M.S. and G.B.v.v. designed research; A.M.S., G.B.v.v., N.B., M.C., P.F., M.-A.L., R.M., C.P., C.V., and E.J.W. performed research; A.M.S. analyzed data; and A.M.S. wrote the paper.

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<sup>1</sup>To whom correspondence should be addressed. Email: amspringer@alaska.edu.

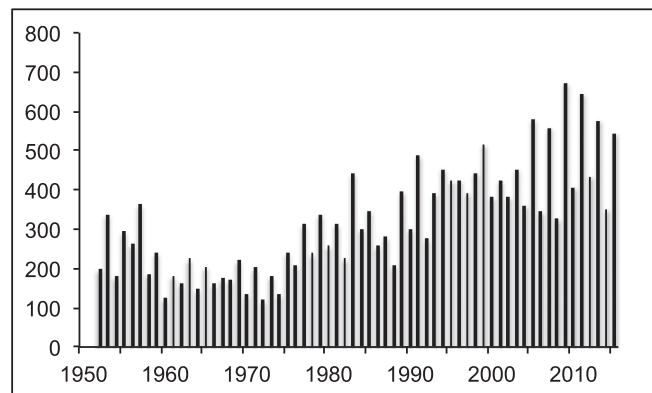
<sup>2</sup>Retired.

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The mechanisms linking pink salmon population dynamics to meteorology and ocean climate are not fully known, but the principal hypotheses focus on early marine survival that is determined in large measure by seawater temperature, the abundance of zooplanktonic prey, and the abundance of piscine predators (e.g., refs. 26 and 27).

Among the Pacific salmon, pink salmon have a unique 2-y life cycle between egg and spawning adult, and most stocks alternate in abundance between years; the majority are much more abundant in odd years than in even years (22, 28). Overall, odd-year stocks are now over twice as abundant as they were in the 1970s (22, 29). It has been argued since the mid-1990s that pink salmon have been having important negative effects on other resident species in the NP/BS through exploitative competition for common prey resources, on the structure of pelagic food webs, and on ecosystem function (30–39).

Pink salmon also have been reported to be an important factor in the ecology of short-tailed shearwaters, seabirds that breed in the SP/TS, specifically southeastern Australia, Bass Strait, and Tasmania (*SI Appendix*, Fig. S1), and spend the austral winter primarily in the NP/BS, although some continue north into the Chukchi Sea (Fig. 1). Roughly  $23 \times 10^6$  short-tailed shearwaters (45), one of the most abundant species of seabirds in the world, undertake annual migrations of some 30,000-km round trip between the Southern and Northern Hemispheres. Short-tailed



**Fig. 2.** Returns (catch plus escapement, millions) of pink salmon in the North Pacific Ocean, 1952–2015. Data from ref. 22.

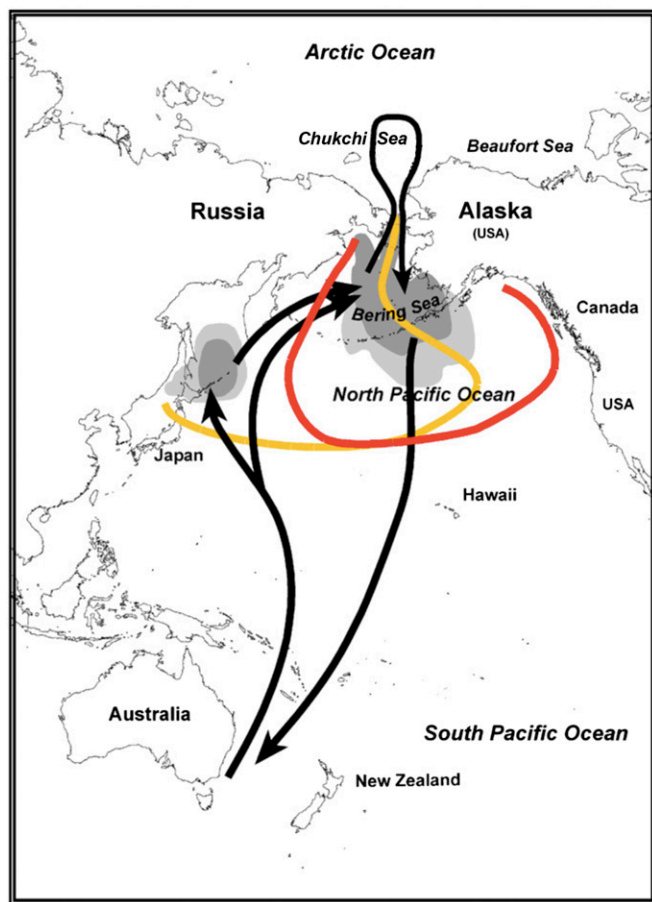
shearwaters were shown to be in poorer physical condition and to succumb in greater numbers in the northwestern North Pacific Ocean and central Bering Sea in odd years than in even years (46, 47). Numbers of dead shearwaters encountered on St. Paul Island (Pribilof Islands, eastern Bering Sea) were more than an order-of-magnitude greater in odd years than in even years between 2006 and 2010: odd-year average of 0.57 versus even-year average of 0.022 birds per standardized beach survey (from data reported in ref. 48). Diets of pink salmon and short-tailed shearwaters overlap (49–54), and the biennial pattern in shearwater body condition has been linked to competition with pink salmon for common prey (47). These patterns are distinct from occasional mass mortalities (wrecks), which are comprised primarily of immature birds that occur off Japan in spring as they arrive from the Southern Hemisphere (55), and in the Bering Sea, where wrecks have occurred at least twice in late summer, in 1983 and 1997 (56, 57). Both years were odd years but were further beset by strong El Niño conditions. Birds found in wrecks off Japan and in the Bering Sea appeared to have starved to death. The return migration from the NP/BS to the SP/TS takes about 18 d in September to October (42), and is fueled by fat stores accumulated on the wintering grounds. Because both fall and spring migrations are nonstop, short-tailed shearwaters would not be a factor in, or be affected by, food web processes in the intervening ocean.

## Results

**Trends in Pink Salmon Abundance.** The overall abundance of pink salmon varied over a comparatively small, low range from the early 1950s to the mid-1970s, then increased markedly through about 1990 (Fig. 2). That increase was followed by a second period of relative stability to about 2004. Beginning in 2005, odd-year stocks increased substantially, whereas even-year stocks remained about the same as in the previous interval: the odd-year mean in 2005–2015 increased by 35% over the odd-year mean for 1990–2004 (from  $440 \times 10^6$  to  $595 \times 10^6$  fish,  $P = 0.0001$ ), with odd-year stocks averaging 60% greater than even year stocks ( $595 \times 10^6$  fish vs.  $372 \times 10^6$  fish,  $P = 0.0001$ ).

Long-term trends in abundance of the four groups of salmon we used in our analyses (*Methods*) were generally similar (*SI Appendix*, Fig. S2). The greatest difference from the overall pattern was for salmon from the Western Kamchatka Peninsula.

**Trends in Shearwater Abundance.** The abundance of short-tailed shearwaters at Montagu Island fell by about 50% during the 1980s (Fig. 3 and *SI Appendix*); Montagu Island is one of the longest systematic annual monitoring sites for the species. There was no trend in the interval 1990–2016 ( $R^2 = 0.043$ ,  $P = 0.86$ ),



**Fig. 1.** Generalized open ocean ranges of pink salmon from Japan and Russia (yellow) and Alaska (red) as depicted by refs. 40 and 41, and generalized migration routes of short-tailed shearwaters (arrows) and distribution in the northern North Pacific Ocean, Bering Sea, and Chukchi Sea (after refs. 42 and 43, and information presented in ref. 44). Shearwater distribution depicted in gray, with higher concentrations in darker shades.





**Table 2. Mean and median values of short-tailed shearwater abundance at the Furneaux Islands in even years and odd years (eggs per 100 burrows)**

Interval	Mean ( $\pm$ SE) even	Mean ( $\pm$ SE) odd	<i>P</i>	Median even	Median odd	Mean ratio	Median ratio
1997–2015	61.7 (3.1)	58.1 (4.9)	0.55	66.4	58.0	1.06	1.14
2005–2015	58.9 (4.4)	50.1 (8.9)	0.41	60.1	51.6	1.16	1.16

Environmental conditions in the broader marine region of the Tasman Sea as the birds return from the Northern Hemisphere may at times be responsible: for example, anomalously warm sea surface temperatures in October 2000 may have reduced the availability of important prey at a critical time that caused a major wreck that year (59).

However, beginning in 2007 and coinciding with the increasing abundance of odd-year pink salmon, wrecks occurred in every odd year to at least 2013. The wreck in 2013 was extreme, when very high numbers of birds were stranded in Australia and Tasmania, and even in New Zealand, where they do not nest (60), and corresponded with extremely high abundances of pink salmon returning to United States waters (ref. 22 and [www.npafc.org/new/science\\_statistics.html](http://www.npafc.org/new/science_statistics.html)). Birds in those wrecks also were emaciated, suggesting that they failed to accumulate sufficient fat before departure on their southward migration to sustain them until they could refuel upon their return. Because the wrecks have been occurring in odd years, pink salmon may be implicated as the cause. Negative carryover effects of poor nutrition, apparently due to competition with pink salmon in odd years, also have been seen in resident seabirds that nest in the Aleutian Islands and Bering Sea (37).

## Discussion

Short-tailed shearwaters depart their wintering areas beginning in mid to late September (42, 43), about 1 to 2 mo after the peak spawning runs of pink salmon (61, 62). However, their distributions broadly overlap during the time in summer when salmon are feeding voraciously and growing rapidly as they return to their spawning rivers. We believe correlations between the abundance of short-tailed shearwaters and pink salmon in this study provide strong support for the hypothesis that exploitative competition by the fish is having negative effects on the birds, with carryover effects on them at their nesting colonies in the SP/TS. The evidence includes observations of poor physical condition and elevated mortality in the western and eastern Bering Sea in odd years that have been noted previously and that we report here, and in recent years: (i) the wrecks in odd years in southeastern Australia as birds return to their nesting grounds; (ii) the tendency for greater numbers of shearwaters to nest in even years than in odd years, with the biennial difference growing as pink salmon abundance has increased in odd years; (iii) the negative trends in shearwater abundance at Montagu Island and the Furneaux Islands; and (iv) after accounting for the important effect of rainfall, the strong inverse relationship between the abundance of nesting shearwaters at Montagu Island and the abundance of Alaska pink salmon in all five time intervals we examined. That Alaska pink salmon, and not Asian pink salmon, explained most of the variability in shearwater abundance at Montagu Island is perhaps not surprising, since the range of Alaska pink salmon at sea appears to overlap most with the wintering range of the birds. We do not know why Eastern Kamchatka Peninsula salmon were positively related to shearwater abundance at Montagu Island in

the full model, but the strength of the relationship was weak or absent after removing Japan + Sea of Okhotsk and Western Kamchatka Peninsula from our analysis. Moreover, there was no evidence of a relationship of the birds to Eastern Kamchatka Peninsula pink salmon in the latter four time intervals when only those fish were considered.

Nor do we know why correlations between pink salmon and shearwaters nesting at the Furneaux Islands and Wedge Island were not identified in our analysis, and refrain here from speculating about possible reasons. However, we believe that this does not materially controvert our hypothesis, based on the totality of evidence, that competition by pink salmon leads to negative effects on overwintering and nesting short-tailed shearwaters.

Our hypothesis is bolstered by compelling correlations between pink salmon abundance and the phenologies, productivity, and diets of several species of resident seabirds in the Bering Sea (37). The weaker strength of correlations between shearwaters and salmon compared with resident seabirds and salmon may be explained by the broad distribution of shearwaters during their nonbreeding season and the smaller spatial, and briefer temporal, overlap with foraging areas occupied by pink salmon. Interannual variability in shearwater distribution in the Bering Sea due to changing sea ice conditions (63) may further mask the appearance of relationships to pink salmon.

The proposed role of pink salmon in the ecology of short-tailed shearwaters does not preclude other negative or positive impacts on the abundance or productivity of the birds that may derive from seasonal or annual vagaries in ocean climate or longer-term changes in the marine environment of the Tasman Sea or the Southern Ocean due to ocean warming or other causes (e.g., refs. 64–66).

**Shearwaters and Terrestrial Ecology.** The putative negative effects of pink salmon on short-tailed shearwaters carry beyond just the birds. Many species of seabirds can be important to terrestrial ecology on islands where they nest, chiefly by the transport of marine-derived nitrogen and phosphorus that fertilize soils and streams, and by bioturbation by burrowing species, such as shearwaters, which mixes and aerates soils, all of which alter the composition and productivity of floral communities (e.g., refs. 3 and 67–69). The effects of guano deposition and bioturbation by short-tailed shearwaters on physical and chemical soil properties and on terrestrial vegetation are well documented, as they are for two closely related species, wedge-tailed shearwaters (*Ardenna pacifica*) in Western Australia and sooty shearwaters (*Ardenna grisea*) in New Zealand, and are important influences on island ecology (69–73). At Bruny Island, for example, changes in abundances of short-tailed shearwaters between 1977 and 1992 led to marked changes in the composition of the floral community (71).

**Shearwaters and Society.** Short-tailed shearwaters also are important to cultural, social, and economic systems in Tasmania, as are other species of shearwaters and petrels there and in New

**Table 3. Mean and median abundances of short-tailed shearwaters at Wedge Island in even years and odd years (adults)**

Interval	Mean ( $\pm$ SE) even	Mean ( $\pm$ SE) odd	<i>P</i>	Median even	Median odd	Mean ratio	Median ratio
2004–2015	25,154 (2,462)	21,903 (2,008)	0.33	26,498	20,074	1.15	1.32

**Table 4. Results of multiple regression analysis of short-tailed shearwater abundance at Montagu Island versus summer (December to February) rainfall at Montagu Island and pink salmon abundance in four regions of the North Pacific Ocean**

Interval	Adjusted $R^2$ ( $P$ )	December to February rain, $t$ ( $P$ )	A*, $t$ ( $P$ )	B <sup>†</sup> , $t$ ( $P$ )	C <sup>‡</sup> , $t$ ( $P$ )	D <sup>§</sup> , $t$ ( $P$ )
1967–2016	0.61 (<0.0001)	−5.5 (<0.0001)	−1.2 (0.24)	−1.3 (0.21)	0.63 (0.53)	−5.1 (<0.0001)
1980–2016	0.50 (0.0001)	−3.7 (0.001)	−1.4 (0.17)	−0.77 (0.44)	1.2 (0.24)	−3.7 (0.0009)
1990–2016	0.65 (0.0001)	−5.6 (<0.0001)	−1.8 (0.08)	0.028 (0.98)	2.8 (0.013)	−4.2 (0.0006)
2000–2016	0.33 (0.11)	−1.6 (0.14)	−1.5 (0.15)	0.28 (0.79)	2.1 (0.064)	−2.2 (0.053)
2005–2016	0.73 (0.031)	−1.7 (0.14)	−1.4 (0.21)	2.0 (0.10)	3.5 (0.017)	−2.9 (0.033)

\*Japan + Sea of Okhotsk, excluding Western Kamchatka Peninsula.

<sup>†</sup>Western Kamchatka Peninsula.<sup>‡</sup>Eastern Kamchatka Peninsula.

<sup>§</sup> Alaska.

Zealand (74, 75). A commercial harvest of short-tailed shearwater chicks by Aboriginal residents averaged about  $72,000 \pm 8,800$  birds each season in 2007–2017 (76). Chicks also are harvested under recreational licenses available to the public: for example, an average of  $884 \pm 44$  licenses were sold annually in 2011–2016 that resulted in an average annual harvest of about  $34,500 \pm 5,300$  chicks (77).

As a consequence of the massive wreck in 2013 and the dramatic drop in abundance of nesting adults, only 3,300 chicks were taken in the commercial harvest and only 10,913 in the recreational harvest during the ensuing season in 2014 (76, 77).

**Teleconnections.** The conceptual model of the macrosystem we propose integrates processes at five geographic scales: local, regional, basin, hemispheric, and transhemispheric. At local scales, individual stocks of pink salmon prosper or not depending on factors that influence early marine survival: that is, prey and predator fields that are in turn determined by local and regional ocean climate (26, 27). At basin scales, atmospheric forcing sets up regional and local ocean climate conditions (78) that influence trends in pink salmon abundance (79) and the effect salmon have on basin-scale prey fields as they mature and migrate in a consumer front back to their spawning rivers. At hemispheric scales, teleconnections between atmospheric systems over the Pacific Ocean, North America, and the Arctic drive basin-scale physical forcing in the NP/BS that condition local-, regional-, and basin-scale ocean climate (refs. 18 and 80, and references therein). At transhemispheric scales, shearwaters migrate 15,000 km from wintering grounds in the NP/BS to nesting colonies in the SP/TS, where in odd years they arrive in poorer physical condition, may experience wrecks, and tend to nest in fewer numbers than in even years. And back to local and regional scales, where wrecks and an apparent decline in shearwater abundance is of concern to Aboriginal residents in regard to their subsistence economy, cultural identity, and recreational and commercial harvests, and stand to impact ecosystem services in the form of soil fertilization

and aeration that are important to vegetation community structure on islands where they nest.

The model also integrates interactions across at least six trophic levels in the NP/BS and three in the SP/TS. In the NP/BS pink salmon apparently can initiate pelagic trophic cascades by depleting the abundance of herbivorous zooplankton that leads to elevated standing stocks of phytoplankton. In the other trophic direction, reductions of zooplankton stocks impact predatory micronekton and mesonekton, including other species of salmon that prey upon them. Many species of zooplankton and micronekton are important prey of resident NP/BS seabirds and migratory short-tailed shearwaters. In the SP/TS, shearwaters are important in several ways to indigenous residents and to terrestrial vegetation patterns and ecology.

**Conservation of Ecosystems.** Competition among wild pink salmon and numerous other species for finite, common prey resources in the NP/BS appears to have been increasing as salmon abundance has grown. The addition of hatchery-produced salmon that are further filling the ocean is becoming a particular cause for concern; for example, since 1990 in the order of  $1.2\text{--}1.5 \times 10^9$  juvenile pink salmon have been released annually into the northern North Pacific Ocean (22). In 2016  $\sim 0.64 \times 10^9$  smolts were released into Prince William Sound, Alaska alone, where they appear to be having negative impacts on wild pink salmon, sockeye salmon (*O. nerka*), and Pacific herring (*Clupea pallasii*) (81–83). In 2013 an estimated  $103 \times 10^6$  adult pink salmon returned to Prince William Sound, of which  $\sim 30\%$  were wild and  $70\%$  were hatchery fish (84).

Salmon and seabirds are conspicuous and have high ecological, economic, cultural, and societal values, thus a great amount of research is devoted to them. But there are other crucial species in the oceanic ecosystems of the NP/BS, including mesopelagic squids, myctophids (Myctophidae), and deep-sea smelts (Bathylagidae) that also compete for the same prey (85–89). They are of particular ecological value in a variety of ways, from sustaining numerous species of salmon, seabirds, and marine mammals (90–96), to being important engines in the oceanic

**Table 5. Results of multiple regression analysis of short-tailed shearwater abundance at Montagu Island versus summer (December to February) rainfall at Montagu Island and pink salmon abundance in two regions of the North Pacific Ocean**

Interval	Adjusted $R^2$ ( $P$ )	December to February rain, $t$ ( $P$ )	$C^*$ , $t$ ( $P$ )	$D^+$ , $t$ ( $P$ )
1967–2016	0.60 (<0.0001)	−5.6 (<0.0001)	0.76 (0.45)	−6.3 (<0.0001)
1980–2016	0.50 (<0.0001)	−4.2 (0.0002)	1.2 (0.23)	−4.4 (0.0001)
1990–2016	0.62 (<0.0001)	−5.4 (<0.0001)	2.5 (0.019)	−4.1 (0.0005)
2000–2016	0.29 (0.069)	−1.7 (0.10)	1.7 (0.11)	−2.9 (0.012)
2005–2016	0.53 (0.040)	−1.5 (0.18)	1.9 (0.10)	−3.8 (0.007)

\*Eastern Kamchatka Peninsula.

<sup>†</sup>Alaska.

biological pump as vertically migrating predators (97). The biomass of myctophids and bathylagids in the eastern Bering Sea basin alone has been placed in the order of  $1\text{--}8 \times 10^6$  tons each (97, 98), but nothing is known about trends in abundance and other fundamental elements of their ecology because they have no direct economic value.

The desire to continue to raise production levels of wild and hatchery salmon is understandable; the overall annual multinational economic value of Pacific salmon is in the order of  $10^9$  US \$ and the industry employs tens of thousands of people (99). But it is now time to take stock of the consequences—the ecosystem disservices of salmon—of doing so on other economic, social, cultural, and ecological values in the NP/BS (100, 101) and, because of the teleconnection described here, in the SP/TS as well.

The short-tailed shearwater is not a species in peril, but the apparent response of these birds, as well as responses of humans, resident NP/BS seabirds, other salmon, herring, and likely species yet to be identified, to ecological forcing by pink salmon suggests that pink salmon are altering the distribution of wealth stored in this macrosystem (in the sense of ref. 102). Together, these responses emphasize that we must develop a deeper conservation conscientiousness for this entire oceanic system and more informed approaches for the management of the whole.

This large, replicated, natural experiment is not strictly a replicated natural experiment, since conditions in the NP/BS vary on annual and multiyear timescales for reasons other than pink salmon, for example weather and climate have large influences over patterns of annual production, including those of pink salmon. However, it is perhaps as near as we can come to experimental replication at ocean basin scales, and we should therefore use this unique opportunity to delve into trophic interaction chains driven by pink salmon and help remedy the conspicuous and unfortunate lack of knowledge about marine ecology in these important realms.

## Methods

**Shearwater Abundance.** The abundance of adult shearwaters arriving at the nesting colonies and the numbers that lay eggs are most meaningful to address correlations with pink salmon abundance. However, this information is very difficult to acquire and is lacking for most sites. Thus, we used proxies of abundance for Montagu Island, the Furneaux Islands, and Bruny Island (*SI Appendix, Fig. S1*). The proxy at Montagu Island (1967–2016) was the density of chicks on three representative study plots in late March, just before fledging of chicks, as reported by refs. 103–107 for 1967–2003, and by ref. 108 for 2004–2015; P.F. provided data for 2016. Single annual values were derived by summing the numbers of chicks on the plots, calculating the density by dividing that number by the total area of the three plots (1,014 m<sup>2</sup>), and converting that value to chicks per hectare. Burrow searches were thorough and counts were made only once each year to reduce disturbance and the possibility of desertion by adults.

The proxy of abundance at the Furneaux Islands (1997–2015) was the mean number of eggs per 100 burrows on standardized survey transects on four islands in the island group (East Kangaroo, Little Green, Little Dog, and Big Green) provided by R.M. Counts were made in all but 1 y at East Kangaroo and Big Green, and in 14 of 19 y at Little Green and Little Dog. The proxy at Bruny Island was the number of burrows occupied by nesting birds per total number of burrows examined. Data from 2011 were provided by B. Edwards, Bruny Island, Parks and Wildlife Service, Hobart, Tasmania, Australia; data from 2012 and 2013 were provided by N.B.; and data from 2015 were provided by P. Vertigan, BirdLife Tasmania, Hobart, Tasmania, Australia. We used the actual number of breeding pairs on Wedge Island (2004–2015) as reported by (109) for 2004–2010 and provided by N.B. for 2011–2015. All census data used here for the Furneaux Islands, Wedge Island, and Bruny Island were collected in December. As at Montagu Island, burrow searches at those locations were thorough and were made only once each year.

We compared shearwater abundance between even years and odd years at Montagu Island during five intervals: (i) 1967–2016, (ii) 1980–2016, (iii)

1990–2016, (iv) 2000–2016, and (v) 2005–2016. The intervals correspond to: (i) the full sampling interval, (ii) the approximate beginning of the decline in abundance in 1980, (iii) the approximate end of the decline in 1990 and ensuing period of markedly higher salmon abundance, (iv) a period of relative stability in shearwater abundance following a partial recovery during the 1990s, and (v) an interval of very high salmon abundance (Fig. 3 and *SI Appendix, Fig. S2*). Near or total nesting failures occurred in 1971 and 1999 due to heavy rainfall (107), so we did not use those years in intervals one to three. We used the intervals 1997–2015 and 2005–2015 at the Furneaux Islands and the single interval 2004–2015 at Wedge Island. The time series at Bruny Island was too short for these analyses.

**Shearwater Abundance Versus Pink Salmon Abundance.** We used annual catch plus escapement data reported by ref. 22 for the estimate of pink salmon abundance. These data do not have confidence intervals associated with them, as the methods used to derive the values do not lend themselves to variance statistics.

We compared the abundance of shearwaters at Montagu Island, the Furneaux Islands, and Wedge Island in the same intervals to summer rainfall and the abundance of four groups of pink salmon that were aggregated based on the winter ranges and return spawning migration corridors of stocks, as depicted by refs. 40 and 41. We included rainfall data because it has been shown to be important to chick survival at Montagu Island (107). Rainfall data for Montagu Island came from the Montagu Island Lighthouse, for the Furneaux Islands from the Flinders Island airport, and for Wedge Island from Tarana, Tasmania. All rainfall data are available at [www.bom.gov.au/climate/data/index.shtml?bookmark=136](http://www.bom.gov.au/climate/data/index.shtml?bookmark=136). The pink salmon groups were: (i) Japan + Sea of Okhotsk, excluding Western Kamchatka Peninsula; (ii) Western Kamchatka Peninsula; (iii) Eastern Kamchatka Peninsula; and (iv) Alaska. British Columbia and Washington pink salmon were not included in the models because their at-sea range overlaps little with the winter distribution of the majority of short-tailed shearwaters. Although the winter distribution of pink salmon from Western Kamchatka Peninsula generally overlaps those of fish from Japan and elsewhere in the Sea of Okhotsk, they are predominantly even-year dominant stocks so were considered separately from the other stocks in the northwestern Pacific Ocean that are predominantly odd-year dominant. Also, their trend in abundance generally differs from trends of the other groups (*SI Appendix, Fig. S2*). Again, there were too few years for this analysis at Bruny Island.

**Data Analysis.** Mean values of shearwater abundances in even and odd years were compared using Student's *t* test. Shearwater annual abundance data were natural log-transformed to calculate trends in abundance using linear regression.

We compared the abundance of shearwaters to rainfall and the abundance of pink salmon using multiple linear regression. We first assessed the extent of collinearity among the salmon groups, but found little evidence for it, as variance inflation factors for all groups were  $\leq 2.4$ . We used summer (December–February) rainfall as a fifth independent variable in the model for Montagu Island because chicks were counted there in March, and used only December rainfall in models for the Furneaux Islands and Wedge Island because census counts at those locations were made in December.

We compared shearwater chick counts at Montagu Island in March to pink salmon abundance values from the previous calendar year. Shearwater counts at the Furneaux Islands and Wedge Island were made in the same calendar year as salmon abundance estimates.

We did not select an *a priori* strict threshold for statistical significance. Instead, all correlation coefficients and significance values are presented and considered, along with temporal patterns in change and values of group means and medians, to make biological inferences.

**Research Permits.** BirdLife Tasmania holds all animal research and scientific permits required by law to undertake the surveys and research described in the study. All surveys were approved by the Animal Ethics Committee of the Department of Primary Industries, Parks, Water, and Environment. The University of Tasmania Animal Ethics Committee also approved research at Wedge Island and Fisher Island.

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# Supplementary Information for

Transhemispheric ecosystem disservices of pink salmon in a Pacific Ocean macrosystem

Alan M. Springer (University of Alaska Fairbanks)

Gus B. van Vliet (PO Box 210442, Auke Bay AK)

Natalie Bool (University of Tasmania)

Mike Crowley (Formerly: State Forests of NSW, Australia)

Peter Fullagar (Formerly: CSIRO Division of Wildlife Research, Australia)

Mary-Anne Lea (University of Tasmania)

Ross Monash (Marine Conservation Program, Department of Primary Industries, Parks, Water and Environment, Hobart, Tasmania)

Cassandra Price (University of Tasmania)

Caitlin Vertigan (University of Tasmania)

Eric J. Woehler (University of Tasmania)

Alan M. Springer

[amspringer@alaska.edu](mailto:amspringer@alaska.edu)

## **This PDF file includes:**

Supplementary text

Figs. S1 to S2

References for SI reference citations

## Supplementary Information

### *Long-term change in shearwater abundance*

Short-tailed shearwater abundance has not been monitored systematically at most colonies, thus estimates of the total population size and trends in abundance are imprecise. Overall abundance is thought to have increased considerably after the 1940s and 1950s and then stabilized through the 1970s (1, 2). However, in a region of north central Bass Strait, where about  $1.3 \times 10^6$  pairs were recorded in 1978-1980 (3), abundance had declined by some 35% to about  $0.75 \times 10^6$  pairs by 2011 (4). That pattern appears to be similar in timing to the decline in the 1980s at Montagu Island.

As many as one million short-tailed shearwater chicks were harvested annually in Australia and Tasmania during the 19<sup>th</sup> and early 20<sup>th</sup> Centuries, and harvests remained at high levels through the 1980s (5 – in 6, and 6). Millions of shearwaters also were killed on their wintering grounds as bycatch in salmon and squid driftnet fisheries that operated between 1952-1991 in the northern North Pacific Ocean, most of which were immature birds as they are in the occasional wrecks off Japan (7-10). Uhlmann et al. (11) subsequently estimated that 2.9–16.6 (95% CI) million short-tailed shearwaters were killed in total in the driftnet fisheries between 1952 and 1977, and between 4.6 and 21.2 (95% CI) million overall between 1952 and 2001.

The effect those losses had on the abundance of shearwaters is not known, but such extensive and sustained mortality might have caused, or contributed to, the population declines observed in Bass Strait and at Montagu Island. However, in the case of the sooty shearwater (*Ardenna grisea*), a closely related species in New Zealand that also migrates to the North Pacific Ocean in the austral winter, also was caught in great numbers in the drift net fisheries, and also is in decline, (11) stressed that for various reasons it is not possible to infer the cause or causes of the recent decreases. That reasoning also can be applied to short-tailed shearwaters. Yet, the declines of short-tailed shearwaters in Bass Strait sometime after the early 1980s, at Montagu Island in the 1980s, and to some extent at Montagu Island and the Furneaux Islands in this century, and declines of sooty shearwaters in New Zealand all coincided with the growth in abundance of North Pacific salmon since the 1970s, and thus it could be hypothesized that competition with salmon in the North Pacific Ocean and Bering Sea was a contributing factor.

## References

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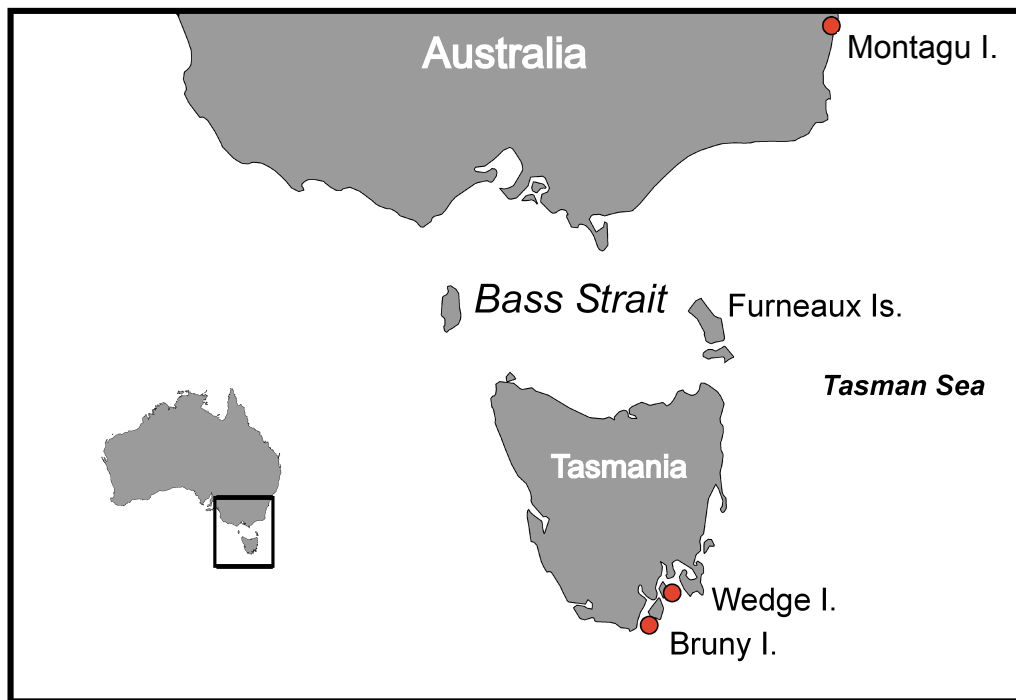


Fig. S1. Locations of Montagu Island, the Furneaux Islands, Wedge Island, Bruny Island, and other locations mentioned in the text.

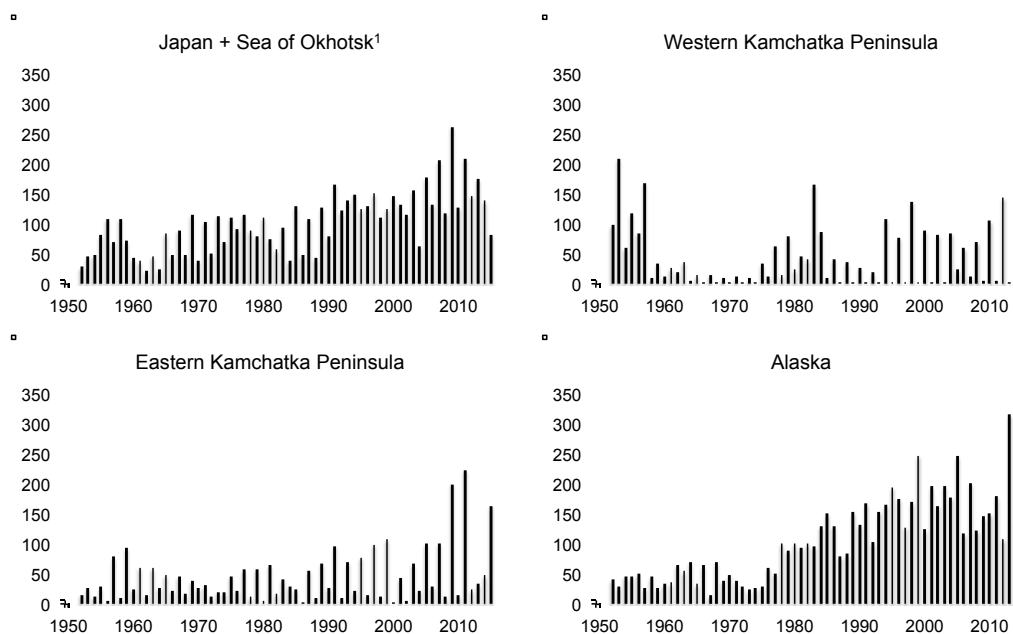


Fig. S2. Trends in the abundance of pink salmon (millions of fish) from four geographic regions of the North Pacific Ocean. <sup>1</sup>Excludes the Western Kamchatka Peninsula.

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## CODE EXAMPLES

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*Code example 1: Adding unique identifiers from the BIRD\_ID to RESIGHT datafile*

```
for(i in 1: nrow(sb)){
  print(i)
  rr <- sb[i,]
  xx <- which(c$band1==rr$band1 | c$band2==rr$band1 |
    c$band1==rr$band2 | c$band2==rr$band2 |
    c$band1==rr$band3 | c$band2==rr$band3 |
    c$band1==rr$band4 | c$band2==rr$band4 |
    c$band1==rr$band5 | c$band2==rr$band5)
  if(length(xx) !=0) c$bird_id[xx] <- rr$bird_id
}
```

*Code example 2: Adding new ID to RESIGHT datafile*

```
newID <- 201299
```

```
c1 <- c[is.na(c$bird_id),]
c2 <- c[!is.na(c$bird_id),]
c1$bird_id <- seq(newID, newID+(nrow(c1)-1))
```

*Code example 3: Merging and removing duplicates from the BIRD\_ID file*

```
c3 <- rbind(c2, c1)

dlist <- c3[which(duplicated(c3$bird_id)), "bird_id"]
d <- c3[c3$bird_id %in% dlist,]
d <- d[order(d$bird_id, d$sex),]

c4 <- c3[!duplicated(c3$bird_id),] ##drop duplicates
```

*Code example 4: Standardising, merging and removing duplicates from the main RESIGHT file*

```
nb7$bird_id <- NA
nb7$band3 <- NA
nb7$band4 <- NA
nb7$band5 <- NA
nb7$par_fem <- NA
nb7$par_male <- NA
nb7$com <- NA

rb <- rbind(a, nb7)
rb1 <- rb[order(rb$bird_id,rb$bird_id),]

dups <- rb1[duplicated(rb1$bird_id), c("bird_id")]
reps <- rb1[rb1$bird_id %in% dups,]
```