

**The Flatback turtle, *Natator depressus*, in Queensland:  
population size and trends**



**Colin J. Limpus, Milani Chaloupka, Janine Ferguson, Nancy N.  
FitzSimmons and C. John Parmenter**

# The Flatback turtle, *Natator depressus*, in Queensland: population size and trends

Colin J. Limpus<sup>1</sup>, Milani Chaloupka<sup>2</sup>, Janine Ferguson<sup>1</sup>, Nancy N. FitzSimmons<sup>1</sup>  
and C. John Parmenter<sup>3</sup>

<sup>1</sup>Department of Environment and Science, Ecosciences Precinct, Dutton Park, Queensland, 4102.

<sup>2</sup>Ecological Modelling Services P/L, PO Box 6150, University of Queensland, St Lucia, Queensland, 4067.

<sup>3</sup>P.O. Box 200, Tolga, Queensland, 4882.

## **This report should be cited as:**

Limpus, C. J., Chaloupka, M., Ferguson, J., FitzSimmons, N. N. and Parmenter, C. J. (2020). Flatback Turtle, *Natator depressus*, 2019-2020 Breeding Season, at Curtis, Peak and Avoid Islands. Brisbane: Department of Environment and Science, Queensland Government. Report produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program. 58 pp.

This report has been produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program. The study was undertaken under a Consultancy Agreement (CA12000291 [130032]) between Gladstone Ports Corporation and the Queensland Department of Environment and Science to monitor marine turtle nesting at Peak, Avoid and Curtis Islands.

This publication has been compiled by the Queensland Department of Environment and Science (DES).

© Gladstone Ports Corporation

## **Disclaimer:**

Except as permitted by the Copyright Act 1968, no part of the work may in any form or by any electronic, mechanical, photocopying, recording, or any other means be reproduced, stored in a retrieval system or be broadcast or transmitted without prior written permission of Gladstone Ports Corporation and/or the Ecosystem Research and Monitoring Program Advisory Panel. This document has been prepared with all due diligence and care, based on the best available information at the time of publication, with peer review, and the information contained herein is subject to change without notice. The copyright owner shall not be liable for technical or other errors or omissions contained within the document. The reader/user accepts all risks and responsibility for losses, damages, costs and other consequences resulting directly or indirectly from using this information. Any decisions made by other parties based on this document are solely the responsibility of those parties. Information contained in this document is from a number of sources and, as such, does not necessarily represent the policies of GPC or the government/department.

Enquiries about reproduction, including downloading or printing the web version, should be directed to [emp@gpcl.com.au](mailto:emp@gpcl.com.au).

## Table of Contents

Table of Contents.....	3
Table of Figures.....	5
List of Tables.....	5
Executive summary.....	6
1. Introduction.....	9
2. Methods.....	9
2.1 Environmental variables.....	10
2.2 Survival and Abundance.....	11
2.3 Statistical modelling approach.....	11
3. Results.....	12
3.1 Population abundance and survival.....	12
3.1.1 Mapoon rookery.....	12
Data summary.....	12
Exploring CJS model goodness-of-fit.....	12
Model summary.....	12
Recapture probabilities and population abundance estimates.....	12
Apparent annual survival probabilities.....	13
Nester population trend.....	13
3.1.2 Avoid Island rookery.....	13
Data summary.....	13
Exploring CJS model goodness-of-fit.....	13
Model summary.....	13
Recapture probabilities and population abundance estimates.....	13
Apparent annual survival probabilities.....	14
3.1.3 Peak Island rookery.....	14
Data summary.....	14
Exploring CJS model goodness-of-fit.....	14
Model summary.....	14
Recapture probabilities and population abundance estimates.....	14
Apparent annual survival probabilities.....	15
Nester population trend.....	15
3.1.4 Curtis Island rookery.....	15
Data summary.....	15
Exploring CJS model goodness-of-fit.....	15

Model summary.....	15
Recapture probabilities and population abundance estimates .....	16
Apparent annual survival probabilities .....	16
Nester population trend .....	16
3.1.5  Woongarra Coast rookery .....	16
Data summary.....	16
Exploring CJS model goodness-of-fit.....	16
Model summary.....	16
Recapture probabilities and population abundance estimates .....	17
Apparent annual survival probabilities .....	17
Nester population trend .....	17
3.2  Recruitment .....	17
3.2.1  Introduction .....	17
Statistical modelling approach .....	17
3.2.2  Results .....	18
Mapoon rookery .....	18
Avoid Island rookery.....	18
Peak Island rookery.....	18
Curtis Island rookery.....	19
Woongarra Coast rookery .....	19
3.3  Temporal trends in size of nesting Flatbacks .....	19
3.3.1  Introduction .....	19
Statistical modelling approach .....	20
3.3.2  Results .....	20
3.4  Remigration interval modelling.....	20
3.4.1  Introduction .....	20
Statistical modelling approach .....	21
3.4.2  Results .....	21
4.  Discussion.....	21
5.  Acknowledgements .....	24
6.  References.....	25

## Table of Figures

Figure 1: The breeding distribution of Flatback turtles, <i>Natator depressus</i> .....	32
Figure 2: Great Barrier Reef region monthly averaged time series since 1980 for (a) sea surface temperature based on the ERSST v5 and (b) bimonthly Multivariate ENSO Index. 33	33
Figure 3: Flinders Beach, Mapoon nesting numbers and recapture probability .....	34
Figure 4: Flinders Beach, Mapoon rookery population trend .....	35
Figure 5: Avoid Island rookery nesting numbers and recapture probability.....	36
Figure 6: Peak Island rookery nesting numbers and recapture probability.....	37
Figure 7: Peak Island rookery survival rate trend .....	38
Figure 8: Peak Island rookery population trend .....	39
Figure 9: Curtis Island rookery nesting numbers and recapture probability .....	40
Figure 10: Curtis Island rookery population trend .....	41
Figure 11: Woongarra Coast rookery nesting numbers and recapture probability .....	42
Figure 12: Woongarra Coast rookery population trend .....	43
Figure 13: Flinders Beach, Mapoon rookery recruitment rate .....	44
Figure 14: Peak Island rookery recruitment rate.....	45
Figure 15: Curtis Island rookery recruitment rate.....	46
Figure 16: Temporal carapace size trend at the Mapoon Flatback turtle rookery, Arafura Sea stock, since 2004. ....	47
Figure 17: Temporal carapace size trend at the Avoid Island Flatback turtle rookery, eAust stock, since 2012. ....	48
Figure 18: Temporal carapace size trend at the Peak Island Flatback turtle rookery, eAust stock, since 2008. ....	48
Figure 19: Temporal carapace size trend at the Curtis Island Flatback turtle rookery, eAust stock, since 1993. ....	49
Figure 20: Temporal carapace size trend at the Woongarra Coast Flatback turtle rookery, eAust stock, since 1968. ....	49
Figure 21: Curtis Island rookery remigration interval trends .....	50
Figure 22: Images from 1920s newspaper reporting of turtle riding and egg harvest of Flatback turtles at Peak Island (Table 2). ....	51

## List of Tables

Table 1: Rookery-specific sampling summary (rookeries arranged north to south with genetic stocks) .....	10
Table 2: Newspaper articles referring to turtle harvest and turtle riding at Peak Island prior to 1968.....	30
Table 3: Supplementary A - Avoid Island Rookery .....	52
Table 4: Supplementary A - Peak Island Rookery .....	53
Table 5: Supplementary A - Curtis Island Rookery.....	54
Table 6: Supplementary A - Woongarra Coast Rookery.....	55
Table 7: Supplementary A - Mapoon Rookery.....	56
Table 8: Supplementary B - Peak Island Rookery .....	57
Table 9: Supplementary B - Curtis Island Rookery .....	58
Table 10: Supplementary B - Mapoon Rookery.....	58

## Executive summary

- This study was commissioned by Gladstone Ports Corporation (GPC), as part of the conditions required by the Commonwealth of Australia for approvals for substantial increases in port infrastructure and associated dredging within Port Curtis in the 2010s, to monitor the Flatback turtle nesting population within and adjacent to the Port in response to these industrial developments.
- There are two independent genetic stocks of Flatback turtles, *Natator depressus*, that breed in Queensland:
  - Eastern Australian (eAust) genetic stock that breeds in eastern Australia between Bundaberg and Townsville;
  - Arafura Sea (AS) genetic stock that breeds from western Cape York Peninsula to western Arnhem Land.
- This study analyses the long term capture-tagging-recapture data for nesting Flatback turtles at four index beaches within the eAust genetic stock:
  - a) **Curtis Island** within Port Curtis: 27 yr of data, 1993-2019;
  - b) **Peak Island** adjacent to Port Curtis: 30 yr of data. 1980-2019;
  - c) **Avoid Island**, a control site well removed from coastal development: 8 yr of data, 2012-2019; and
  - d) **Woongarra Coast**, a control site at the southern limit of Flatback turtle nesting in eastern Australia: 52 yr of data, 1968-2019;and one index beach within the AS genetic stock:
  - e) **Flinders Beach** at Mapoon, a control site within a different genetic stock and well removed from industrial development: 16 yr of data, 2004-2019.
- All of these Flatback turtle nesting populations, representing two independent genetic stocks, are characterised by increasing population size since at least the early to mid 2000s.
- None of the study populations showed a decline in nester abundance during this time period.
- High mean annual survivorship of these adult female Flatback turtles was recorded at all five index study sites.
- These results are indicative of stock wide population increases in adult Flatback nesting populations across northern and eastern Australia within the last two decades.
- The mean size of the adult female Flatback turtles has been increasing at all study sites since their respective studies began.
- An examination of nester abundance, survival and recruitment estimates from the present study for Curtis Island when compared with those at Peak Island, Woongarra Coast and Avoid island, all within the eAust genetic stock, provides no indication of an anomalous population performance of the Curtis Island nesting population during or following the major dredging and infrastructure development within Port Curtis that occurred during 2011-2013.
- This study has reinforced the results of previous studies that identified a major decline in nester abundance for the largest eAust Flatback rookery at Peak Island, from 1980 to the early 2000s.
- A very minor decline in nester abundance at the Woongarra Coast rookery from the 1970s to approximately 1990 was also identified.

- Two possible contributing factors to the past population declines and subsequent population recoveries were investigated:
  - a) Unquantified harvest of eggs and turtles for human consumption and harassment of nesting females by turtle riding since the 1870s and prior to the 18 July 1968 Order in Council Queensland *Fisheries Act Amendment Act of 1962* banning the take of turtles and eggs throughout Queensland.
    - Given that Flatback turtles probably commence breeding at about 20 yr of age, the decline in nester abundance during the 1970s-1980s could have been the result, at least in part, of elevated turtle egg harvests prior to the 1968 Order in Council.
    - This was followed by an increase in nester abundance from the early 2000s until 2016.
    - These data suggest that there could have been a consequential increase in the Flatback turtle nesting population in the Keppel Bay region some 2-3 decades following the 1968 ban on the take of turtle eggs and harassment of the nesting females.
  - b) Bycatch mortality of Flatback turtles within prawn trawl fisheries across northern Australia and eastern Queensland prior to the compulsory regulated use of turtle exclusion devices (TEDs) in these prawn trawl fisheries in 2000-2002.
    - With Flatback turtles being one of the most commonly caught turtles in prawn trawl fishers in northern Australia and eastern Queensland, the decline in Flatback turtle nester abundance during the 1970s-1980s could have been the result, at least in part, of bycatch mortality in these fisheries prior to 2000.
    - The present study has demonstrated that there have been general increases in the nesting population since the early to mid 2000s at three index sites within the eAust genetic stock (Peak Island, Curtis Island and the Woongarra Coast) and one index site within the AS genetic stock (Flinders Beach, Mapoon).
    - This increase in Flatback nesting populations across two genetic stock in northern and eastern Australia within the last two decades provides strong circumstantial evidence that the compulsory use of TEDS in the northern Australian prawn trawl fisheries has been a primary contributing factor behind these increases.
- The previously identified anomalous population performances of the Flatback nesting populations at Peak Island and Wild Duck Island, the two largest rookeries within the eAust genetic stock remains unresolved:
  - a) The Peak Island Flatback rookery experienced a greater than 50% decline in nester abundance during 1980-2000 while the Wild Duck Island population remained approximately stable.
  - b) Because both these Flatback rookeries are derived from the same genetic stock and are distributed approximately uniformly throughout the same east Australian foraging range, in the absence of a decline in nester abundance at Wild Duck Island, it is reasonable to assume that the declining Peak Island nester abundance was not caused by a general problem impacting the entire foraging range of the eastern Australian Flatback management unit.
  - c) No biological issues at the islands have been identified that could account for the difference in the rookery performances.

- d) It is suggested that the problem(s) associated with the past Peak Island decline in nester abundance was operating within the adjacent inter-nesting habitat, i.e. within a few tens of kilometres of the island.
- In the absence of census monitoring of the Wild Duck Island rookery since the 2006-2007 summer, there remains no clear understanding of the underlying cause of the decline in Peak Island nester abundance.

## 1. Introduction

The Flatback turtle is the most unusual of marine turtle species, lacking an oceanic juvenile phase, laying extremely small clutches, having elevated breath holding capacity, and having a restricted geographic range (Limpus 2007). The species forages mainly in deeper sub-tidal waters across the northern Australian continental shelf and extending into waters of the southern coast of New Guinea inside of Indonesia and Papua New Guinea (Musick and Limpus 1997, Limpus 2007). Flatback turtles, as for all marine turtle species, are decades old at first breeding. Adults migrate from widely dispersed foraging areas to traditional breeding sites and are expected to breed across decades but skip years between breeding seasons (Limpus 2007). Flatback turtle breeding is restricted to northern Australia across seven genetic stocks (FitzSimmons *et al.* 2020, Figure 1A).

There is concern that the Flatback turtle is a globally threatened species due to exposure to coastal development, but its conservation status is poorly known. Reliable estimates of key demographic parameters are needed for modelling the risk of marine turtle population exposure to anthropogenic hazards and for diagnosing any trends in population abundance (Chaloupka 2003, National Research Council 2010, Bjorndal *et al.* 2011). The present study has been funded by Gladstone Ports Corporation's (GPC's) Ecosystem Research Monitoring Program (ERMP) to investigate the performance of Flatback nesting populations at Curtis Island and Peak Island adjacent to Port Curtis and Port Alma and at Avoid Island as a control study site well removed from Port activities (Figure 1B). In the context of understanding the functioning of nesting in proximity to Ports within the eAust Flatback turtle genetic stock (FitzSimmons and Limpus 2014), with Curtis, Peak and Avoid Island nesting populations being a part, additional study sites have been added into this final analysis:

- Woongarra Coast study site with 50 years of tagging census of Flatback turtle nesting is included to demonstrate population performance at the southern extremity of the breeding distribution of the eAust Stock
- Mapoon study site with a 15 year history of tagging census of a nesting Flatback turtle population on western Cape York Peninsula is included to provide comparison with population performance from a site outside the eAust stock, viz, a population from within the Arafura Sea genetic Stock (FitzSimmons *et al.* 2020); and
- Wild Duck Island is included for completeness because there are tagging census data spanning 28 years at what has been reported as the second largest nesting aggregation of breeding Flatback turtles within the eAust stock (1979-2007) (Limpus *et al.* 2013a).

## 2. Methods

In this study, capture-mark-recapture (CMR) histories are analysed for 4515 nesting turtles sampled from four Flatback rookeries located along the east Queensland coast within the eAust genetic stock and one Flatback rookery at Flinders Beach, Mapoon (western Cape York Peninsula, Arafura Sea genetic stock) ([Figure 1](#)). Estimation of the key demographic parameters and long-term abundance trends for those five Flatback nesting populations ([Table 1](#)) are reported. There is specific focus on estimating annual survival rates, annual recruitment rates, annual nester population abundance and trends in nester body size at the five rookeries. Trends in age-year-cohort specific effects for the individual turtle remigration intervals for the Curtis Island rookery were estimated.

**Table 1: Rookery-specific sampling summary (rookeries arranged north to south with genetic stocks)**

Rookery	Number of capture-mark-recapture histories	Number of turtle captures	Sample period	Genetic stock
Avoid Island 21.97710° S, 149.66430° E	260	878	2012-2019	eAust
Wild Duck Island * 22.00000° S, 149.70000° E	1265	3962	1979-2007	eAust
Peak Island 23.33330° S, 150.93330° E	2933	7275	1980-2019	eAust
Curtis Island 23.70000° S, 151.30000° E	370	2646	1993-2019	eAust
Woongarra Coast 24.78999° S, 152.43832° E	106	1170	1968-2019	eAust
Mapoon 12.22830° S, 141.72720° E	846	1712	2004-2019	AS

\* Wild Duck Island rookery reported by Limpus *et al.* (2013a) and included here for completeness but not updated to the 2019 nesting season.

## 2.1 Environmental variables

Two readily available macro-scale ocean/climate indicators as potential environmental drivers known to affect various marine turtle demographic rates were chosen for inclusion in the analyses — sea surface temperature (SST) and a multivariate ENSO metric (Chaloupka *et al.* 2008, Bjorndal *et al.* 2017, Limpus and Nicholls 2000). Spatially averaged, monthly SST data for the Great Barrier Reef region using the ERSSTv5 index (Huang *et al.* 2017) were sourced. Those monthly averaged data were annualised using a generalised additive mixed regression model (GAMM; see Gilman *et al.* 2020 for details). [Figure 2a](#) shows the monthly and expected annual SST time series since 1980 for the GBR region. The revised bimonthly Multivariate ENSO Index (MEI) data (Zhang *et al.* 2019, NOAA 2020) was annualised using the same method used to annualize the ERSST data. [Figure 2b](#) shows the monthly and expected annual MEI time series since 1980 for the GBR region. Annualised time series of the environmental metrics were necessary to match the same temporal resolution as the annual trends in expected demographic rates. For instance, all CMR models used here were based on annual sampling intervals— and so, the potential covariates or predictors also needed to be on an annual scale. These annualised series were then used as potentially informative covariates in all models used for estimating survival, recapture, and recruitment rates.

## 2.2 Survival and Abundance

Reliable estimates of key demographic parameters such as survival probabilities are needed for (1) modelling the risk of marine turtle population exposure to anthropogenic hazards, (2) for diagnosing trends in marine turtle population abundance (Chaloupka and Limpus 2001, Bjorndal *et al.* 2005) and (3) for assessment of long-term population viability and recovery planning (Chaloupka 2003, Chaloupka 2004, National Research Council 2010).

## 2.3 Statistical modelling approach

A random-effects Cormack-Jolly-Seber (CJS) statistical modelling approach that accounts for individual heterogeneity in survival and/or recapture was used to estimate key demographic parameters (Gimenez and Choquet 2010). There are no established procedures for assessing CJS random-effects model goodness-of-fit (Gimenez and Choquet 2010). Therefore, an *ad-hoc* approach based on comparison with various fixed effects CJS-type models (Lebreton *et al.* 1992) that have known goodness-of-fit metrics was used to help assess model fit. Specifically, CJS model assumptions such as transience (seen once and never again), capture heterogeneity (known as trap-dependence) and goodness-of-fit were evaluated using various test procedures (Choquet *et al.* 2009) implemented in the R2ucare package for R (Gimenez *et al.* 2017) as well as the Fletcher  $\hat{c}$  estimate of goodness-of-fit (Fletcher 2012) that has been included in program MARK recently. A time-since-marking model structure was also used to account for transient behaviour (separate survival probability estimates for newly and previously tagged turtles — Chaloupka and Limpus 2002) and the random effects model approach (Gimenez and Choquet 2010) to account for capture heterogeneity. The impact of the low incidence of tag loss within these populations was incorporated within the assessment of transient behaviour.

All random and fixed effects CJS models were fitted using the program MARK (White *et al.* 2006) via the RMark package for R (Laake 2013). Model selection was based on an information-theoretic approach with the Akaike Information Criterion corrected for sample size to determine model parsimony and support statistical inferences (Burnham *et al.* 2011). The best-fit model was used to estimate the recapture rates and apparent survival probabilities. Annual nesting population size was estimated by applying a Horwitz-Thompson-type estimator using those recapture probabilities (Chaloupka and Limpus 2001, Bjorndal *et al.* 2005) with nonparametric bootstrap-based variance estimates of the annual population size (Madon *et al.* 2013: with R code corrections by O. Gimenez). A Gompertz density-dependent population dynamics model (Anderson *et al.* 2017, Muniz Leão *et al.* 2018) was then fitted within a Bayesian state-space modelling framework with robust Student-*t* likelihood (Járez and Steel 2010) to the annual nester population size estimates using JAGS via the rjags package for R (Plummer 2015, 2016). A state-space model is a hierarchical model that enables the precision (observation component) in the annual nester abundance estimates at the Flatback rookery to be accounted for in the estimation of the long-term trend (process component). A Student-*t* likelihood is appropriate as it is robust to outliers in the observed time series (Anderson *et al.* 2017). Density-dependent demographic processes are known for marine turtle populations (Bjorndal *et al.* 2000), further supporting the use of an explicit population dynamics model to determine any long-term trend in nester abundance.

## 3. Results

### 3.1 Population abundance and survival

#### 3.1.1 Mapoon rookery

##### **Data summary**

The CMR data set comprised the capture histories for 846 individual nesting female Flatbacks tagged over the 16-year sampling period from 2004 annually to 2019. (Table 1). Many turtles were recaptured over a number of seasons with some being recaptured on up to eight seasonal occasions (Figure 3a). The number of tagged Flatbacks recorded for each season since 2004 is shown in Figure 3b, which shows a population that fluctuates significantly around a long-term mean of around 85 observed nesters each season (this estimate of course does not account for imperfect detection which is accounted for explicitly using the CJS models summarized below).

##### **Exploring CJS model goodness-of-fit**

Failure of the time dependent CJS model assumptions was assessed using variants of TESTS 2 + 3 (Choquet *et al.* 2009) in R2ucare (Gimenez *et al.* 2017), which indicated failure of TESTS 2 and 3 ( $\chi^2 = 308.8$ ,  $df = 88$ ,  $P < 0.0001$ ). More specifically, failure of particular components such as Test 2.CT is due to individual capture heterogeneity (Pradel *et al.* 2005), while failure of 3.SR could be due to transient behaviour of marked individuals just passing through the study area and never seen again (Pradel *et al.* 2005) and due to skipped breeding behaviour often found for marine turtles (Prince and Chaloupka 2012). Thus, accounting for transient behaviour and recapture heterogeneity was important. Therefore, a time-since-marking survival model was fitted to account for transients by applying a 2-ageclass model structure (separate survival probability estimates for newly and previously tagged turtles — see Chaloupka and Limpus 2002).

##### **Model summary**

The best-fit model was Model 9 (Supplementary Table A), which comprised: constant 2-ageclass-specific (time-since-marking) survival rates, time-dependent recapture probabilities that were a function of both “trap-dependence” and significant individual capture heterogeneity ( $\sigma_p = 0.96$ , 95% CI: 0.66-1.41). The Fletcher  $\hat{c}$  estimate for Model 9 was 1.006, suggesting an adequate fit to the 846 individual CMR histories. The overwhelming weight of evidence was in support of this model compared to the other eight models fitted to these CMR histories (Table Supplementary A). Model 9 accounted for ca. 77% of the weight of evidence for these data and was used to derive the survival and recapture probabilities as well as estimates of annual nester population abundance.

##### **Recapture probabilities and population abundance estimates**

The annual recapture probabilities derived from the best-fit model ranged from 0.09 to 0.33 and have been generally fluctuating around the long-term mean = 0.17 (Figure 3c). These recapture probability estimates were used to derive estimates of the annual Flatback nester population in the study area over the 16-year sampling period, which suggests an increasing nesting population since the 2004 spring nesting season (Figure 3d). The long-term mean nester abundance was estimated at ca. 562.

### **Apparent annual survival probabilities**

The estimated apparent annual survival probability derived from the best-fit Model 9 ([Supplementary Table A](#)) was 0.898 (95% CI: 0.87-0.92), which is consistent with other estimates for Flatback nesting populations (Pfaller *et al.* 2018).

### **Nester population trend**

The underlying long-term trend in nester abundance at the Mapoon Flatback rookery is shown in [Figure 4](#) and has been increasing over the 16-year sampling period.

## **3.1.2 Avoid Island rookery**

### **Data summary**

The CMR data set comprised the capture histories for 260 individual nesting female Flatbacks tagged over the 8-year sampling period from 2012 onwards. ([Table 1](#)). Many turtles were recaptured over a number of seasons with some being recaptured on up to five seasonal occasions ([Figure 5a](#)). The number of tagged Flatbacks recorded for each season since 2012 is shown in [Figure 5b](#), which shows a population that fluctuates significantly around a long-term mean of around 68 observed nesters each season (this estimate of course does not account for imperfect detection, associated in part with variable numbers of nights on the beach tagging the turtles, which is accounted for explicitly using the CJS models summarized below).

### **Exploring CJS model goodness-of-fit**

Failure of time-dependent CJS model assumptions was assessed using variants of TESTS 2 + 3 (Choquet *et al.* 2009) in R2ucare (Gimenez *et al.* 2017), which indicated failure of TESTS 2 and 3 ( $\chi^2 = 145.9$ ,  $df = 824P < 0.0001$ ). Failure of particular components such as Test 2.CT is due to individual capture heterogeneity (Pradel *et al.* 2005), while failure of 3.SR could be due to transient behaviour of marked individuals passing through the study area and never seen again (Pradel *et al.* 2005) or due to skipped breeding behaviour often found for marine turtles (Prince and Chaloupka 2012). So, accounting for transient behaviour and recapture heterogeneity was important. Therefore, we fitted a time-since-marking survival model to account for transients by applying a 2-ageclass model structure (separate survival probability estimates for newly and previously tagged turtles — see Chaloupka and Limpus 2002).

### **Model summary**

The best-fit model was Model 9 ([Supplementary Table A](#)), which comprised: constant 2-ageclass-specific (time-since-marking) survival rates, time-dependent recapture probabilities that were a function of both “trap-dependence” and significant individual capture heterogeneity ( $\sigma_p = 0.77$ , 95% CI: 0.45-1.32). The Fletcher  $\hat{c}$  estimate for Model 9 was 1.39, suggesting inadequate fit to the 260 individual CMR histories. The weight of evidence was in support of this model compared to the other eight models fitted ([Table Supplementary A](#)). Model 9 accounted for ca. 61% of the weight of evidence for these data and was used to derive the survival and recapture probabilities also well as estimates of annual nester population abundance.

### **Recapture probabilities and population abundance estimates**

The annual recapture probabilities derived from the best-fit model ranged from 0.07 to 0.58 and have been generally fluctuating around the long-term mean = 0.25 ([Figure 5c](#)). These recapture probability estimates were then used to derive estimates of the annual Flatback nester population in the study area over the 8-year sampling period, which suggests a relatively stable nesting population since the 2014 summer nesting season ([Figure 5d](#)). The long-term mean

nester abundance was estimated at ca. 319. The Avoid Island rookery is a medium-sized nester population relative to the other east Queensland coast Flatback rookeries ([Figure 1](#)).

### **Apparent annual survival probabilities**

The estimated apparent annual survival probability derived from the best-fit Model 9 ([Supplementary Table A](#)) was 0.98 (95% CI: 0.66-0.99), which is questionably high compared with other estimates for Flatback nesting populations (Pfaller *et al.* 2018). This rookery needs to be monitored for quite a few more seasons to support more robust estimation of demographic rates and nester population size — eight nesting seasons is simply too short a time series.

### **3.1.3 Peak Island rookery**

#### **Data summary**

The CMR data set comprised the capture histories for 2933 individual nesting female Flatbacks tagged over the 16-year sampling period from 1980 onwards ([Table 1](#)). Many turtles were recaptured over a number of seasons with some being recaptured on up to 21 seasonal occasions ([Figure 6a](#)). The number of tagged Flatbacks recorded for each season since 1980 is shown in [Figure 6b](#), which shows a population that fluctuates significantly around a long-term mean of around 197 observed nesters each season (this estimate of course does not account for imperfect detection which is accounted for explicitly using the CJS models summarized below).

#### **Exploring CJS model goodness-of-fit**

Failure of the time-dependent CJS model assumptions was assessed using variants of TESTS 2 + 3 (Choquet *et al.* 2009) in R2ucare (Gimenez *et al.* 2017), which indicated failure of TESTS 2 and 3 ( $\chi^2 = 3296.7$ ,  $df = 220$ ,  $P < 0.0001$ ). More specifically, failure of particular components such as Test 2.CT is due to individual capture heterogeneity (Pradel *et al.* 2005), while failure of 3.SR is could be due to transient behaviour of marked individuals just passing through the study area and never seen again (Pradel *et al.* 2005) and due to skipped breeding behaviour often found for marine turtles (Prince and Chaloupka 2012). So, accounting for transient behaviour and recapture heterogeneity was important. Therefore, we fitted a time-since-marking survival model to account for transients by applying a 2-ageclass model structure (separate survival probability estimates for newly and previously tagged turtles — see Chaloupka and Limpus 2002).

#### **Model summary**

The best-fit model was Model 21 ([Supplementary Table A](#)), which comprised: constant time-varying survival rates, time-dependent recapture probabilities that were a function of both “trap-dependence” and significant individual capture heterogeneity ( $\sigma_p = 0.81$ , 95% CI: 0.70-0.94). The Fletcher  $\hat{c}$  estimate for Model 21 was 1.16, suggesting an adequate fit to the 2933 individual CMR histories. The overwhelming weight of evidence was in support of this model compared to the other 27 models fitted to these CMR histories ([Table Supplementary A](#)). Model 21 accounted for >99% of the weight of evidence for these data and was used to derive the survival and recapture probabilities also well as estimates of annual nester population abundance.

#### **Recapture probabilities and population abundance estimates**

The annual recapture probabilities derived from the best-fit model ranged from 0.03 to 0.73 and have been generally fluctuating around the long-term mean = 0.39 ([Figure 6c](#)). These recapture probability estimates were used to derive estimates of the annual Flatback nester population in the study area over the 40-year sampling period, which suggests decreasing nester

abundance from 1980 to around 2000 and then a steady increasing population post-2000 ([Figure 6d](#)). The long-term mean nester abundance was estimated at ca. 537. The Peak Island rookery is one of the largest nester populations relative to other east Queensland Flatback rookeries ([Figure 1](#)).

#### **Apparent annual survival probabilities**

The estimated apparent annual survival probability derived from the best-fit Model 21 ([Supplementary Table A](#)) was time-varying and increasing in recent years since the mid-2000s ([Figure 7](#)), with a long-term mean ca. 0.87 (95% CI: 0.86-0.88), which is consistent with other estimates for Flatback nesting populations (Pfaller *et al.* 2018).

#### **Nester population trend**

The underlying long-term trend in nester abundance at the Peak Island Flatback rookery is shown in [Figure 8](#) that shows a substantially declining population prior to the early 2000s followed by an increasing trend since the early 2000s.

### **3.1.4 Curtis Island rookery**

#### **Data summary**

The CMR data set comprised the capture histories for 370 individual nesting female Flatbacks tagged over the 27-year sampling period. Many turtles were recaptured over a number of seasons with some being recaptured on up to 15 seasonal occasions ([Figure 9a](#)). The number of tagged Flatbacks recorded for each season since 1993 is shown in [Figure 9b](#), which shows a population that fluctuates significantly around a long-term mean of around 52 observed nesters each season (this estimate of course does not account for imperfect detection which is accounted for explicitly using the CJS model summarised below).

#### **Exploring CJS model goodness-of-fit**

Failure of the time-dependent CJS model assumptions was assessed using variants of TESTS 2 and 3 in U-CARE (Choquet *et al.* 2009), which indicated failure of both TESTS 2 and 3 ( $\chi^2 = 757.5$ ,  $df = 6114$ ,  $P < 0.0001$ ). Failure of particular components such as Test 2.CT is due to individual capture heterogeneity (Pradel *et al.* 2005), while failure of 3.SR is could be due to transient behaviour of marked individuals just passing through the study area and never seen again (Pradel *et al.* 2005) and due to skipped breeding behaviour often found for marine turtles (Prince and Chaloupka 2012). Failure of Test 3.Sm and Test 2 could also be due to individual survival heterogeneity. So, we fitted a time-since-marking survival model to account for transients by applying a 2-ageclass structure as for the other rookery-specific models.

#### **Model summary**

The best-fit model was Model 40 ([Supplementary Table A](#)), which comprised: constant 2-ageclass-specific (time-since-marking) survival rates, time-dependent recapture probabilities that were a function of both “trap-dependence” and significant individual capture heterogeneity ( $\sigma_p = 1.04$ , 95% CI: 0.86-1.27). The Fletcher  $\hat{c}$  estimate for Model 40 was 1.12, suggesting an adequate fit to the 370 individual CMR histories. The weight of evidence was in support of this model compared to the other 8 models fitted to these CMR histories ([Table Supplementary A](#)). Model 40 accounted for >98% of the weight of evidence for these data and was used to derive the survival and recapture probabilities and estimates of annual nester population abundance.

### **Recapture probabilities and population abundance estimates**

The annual recapture probabilities derived from the best-fit model ranged from 0.13 to 0.83 and have been generally fluctuating around the long-term mean = 0.45 ([Figure 9c](#)). These recapture probability estimates were used to derive estimates of the annual Flatback nester population in the study area over the 27-year sampling period, which suggests a stable nester abundance, or a possible very minor decline from 1993 onwards followed by a probable increase since the 2010 summer nesting season ([Figure 9d](#)). The long-term mean nester abundance was estimated at ca. 138. The Curtis Island rookery is a small sized nester population relative to other east Queensland coast rookeries ([Figure 1](#)).

### **Apparent annual survival probabilities**

The estimated apparent annual survival probability derived from the best-fit Model 40 ([Supplementary Table A](#)) was 0.949 (95% CI: 0.937-0.959), which is consistent with other estimates for Flatback nesting populations (Pfaller *et al.* 2018).

### **Nester population trend**

The underlying long-term trend in nester abundance at the Curtis Island Flatback rookery is shown in [Figure 10](#) that shows a stable population trend since 1993 but with a possible increasing trend since ca. 2010.

## **3.1.5 Woongarra Coast rookery**

### **Data summary**

The CMR data set comprised the capture histories for 106 individual nesting female Flatbacks tagged over the 52-year sampling period. Many turtles were recaptured over a number of seasons with some being recaptured on up to 17 seasonal occasions ([Figure 11a](#)). The number of tagged Flatbacks recorded for each season since 1968 is shown in [Figure 11b](#), which shows a population that fluctuates significantly around a long-term mean of around 6 observed nesters each season (this estimate of course does not account for imperfect detection which is accounted for explicitly using the CJS model summarized below).

### **Exploring CJS model goodness-of-fit**

Failure of the time-dependent CJS model assumptions was assessed using variants of TESTS 2 and 3 in U-CARE (Choquet *et al.* 2009), which indicated compliance of both TESTS 2 and 3 with the standard time-dependent CJS model ( $\chi^2 = 169.3$ ,  $df = 147$ ,  $P = 0.1$ ). Nonetheless, we fitted a time-since-marking survival model to account for transients by applying a 2-ageclass structure to be consistent with models fitted for the four other rookeries.

### **Model summary**

The best-fit model was Model 4 ([Supplementary Table A](#)), which comprised: constant 2-ageclass-specific survival rates and time-dependent recapture probabilities. Individual capture heterogeneity was not significant ( $\sigma_p = 0.0001$ , 95% CI: 0.0-0.01) so a random effects model was not necessary here. The weight of evidence was in support of this model compared to the other 3 models fitted to these CMR histories ([Table Supplementary A](#)). Model 4 accounted for ca. 89% of the weight of evidence for these data and was used to derive the survival and recapture probabilities and estimates of annual nester population abundance.

We also explored whether recapture rates might also be a nonlinear function of SST since this is a long-term time series that might reveal an environmental signal — so we estimated annual nester population size from that model as well.

### **Recapture probabilities and population abundance estimates**

The annual recapture probabilities derived from the best-fit model ranged from 0.05 to 0.59 and have been generally fluctuating around the long-term mean = 0.30 ([Figure 11c](#)). These recapture probability estimates were then used to derive estimates of the annual Flatback nester population in the study area over the 52-year sampling period, which suggests a consistently small nester abundance over half a century since 1968 ([Figure 11d](#)) for this nesting population at the southern extremity of Flatback breeding in eastern Australia. The long-term mean nester abundance was estimated at ca. 27 ([panel d](#)) with two extreme outlier estimates that are implausible or 21 ([panel e](#)) if using the model with recapture rates as a function of SST that does not display any extreme outlier estimates. The Woongarra Coast rookery is the smallest nester population relative to other east Queensland coast rookeries ([Figure 1](#)).

### **Apparent annual survival probabilities**

The estimated apparent annual survival probability derived from the best-fit Model 4 ([Supplementary Table A](#)) was 0.931 (95% CI: 0.906-0.949), which is consistent with other estimates for Flatback nesting populations (Pfaller *et al.* 2018).

### **Nester population trend**

Based on the CMR model using recapture rates as a function of regional SST, the underlying long-term trend in nester abundance at the Woongarra Coast Flatback rookeries is shown in [Figure 12](#) — which suggests a declining population trend since 1968 to about 1990, followed by a population increase until the last decade during which the population shows some stability. The population has fluctuated around a long-term mean nester abundance of ca. 21 nesters per annum.

## **3.2 Recruitment**

### **3.2.1 Introduction**

Recruitment is fundamental to understanding the population dynamics of a long-lived species such as marine turtles that are exposed to a range of anthropogenic hazards (Chaloupka 2003). There are surprisingly few estimates of age- or stage-specific recruitment for any marine turtle population (Parmenter *et al.* 1995, Chaloupka 2003, National Research Council 2010). Most attempts to estimate recruitment to the breeding component of a marine turtle population have used laparoscopy to determine whether an adult-sized female turtle had either bred in the previous season or was preparing to breed in the coming season (Limpus and Limpus 2002). Recruitment measures that are applicable to the modelling of marine turtle population dynamics (Chaloupka 2004) can be derived from a capture-mark-recapture-based sampling coupled with the reverse-time or temporal symmetry modelling approach developed originally by Pradel (1996) — see also Pradel *et al.* (1997) and Nichols *et al.* (2016). The simple recruitment metric defined here for convenience is referring to any entry into the population between marking periods of any unmarked turtles. So here recruitment measures the first time that a previously undetected or unmarked Flatback nester was estimated to have entered the Flatback rookery — also known as a per capita recruitment rate. Interestingly, if the nester population growth rate is relatively stable then the proportion of first-time nesters would be equivalent to the per capita recruitment rate.

### **Statistical modelling approach**

A range of Pradel temporal symmetry models parameterized in terms of per capita recruitment and accounting for individual capture heterogeneity (Pradel 1996, Pradel *et al.* 1997) were fitted to the capture-mark-recapture histories for each recorded Flatback nester at each of the

five rookeries. Models comprising a mixture of two hidden capture classes of unknown cause were also considered for some rookeries — in such cases a 2-class mixture is considered more than adequate for modelling detection or encounter heterogeneity (Pradel *et al.* 2009, Marescot *et al.* 2011). All models were fitted using the MARK computation back-end (White *et al.* 2006) via the RMark package for R (Laake 2013). Nonlinear covariate functional form for the two environmental predictors (SST, MEI: Figure 2) were modelled using the splines package for R via RMark. Model selection was then based on using an information-theoretic approach with the Akaike Information Criterion corrected for sample size to determine model parsimony and support statistical inferences (Burnham *et al.* 2011). It is important to note that these per capita recruitment models are a challenge to fit to these CMR data, especially for those rookeries with short sampling periods (Table 1). Therefore, any interpretation of annual recruitment and trends needs to be treated with caution.

### 3.2.2 Results

#### **Mapoon rookery**

The best-fit Pradel temporal symmetry model (Supplementary Table B) not accounting for heterogeneity comprised time-varying survival (spline with  $df = 4$ ), time-dependent detection probabilities and time-varying per capita recruitment rates (spline with  $df = 4$ ). The overwhelming weight of evidence ( $> 99\%$ ) was in support of this model compared to the one other model that could be fitted to these CMR histories. The annual recruitment rates were derived from this model and are shown in Figure 13. No meaningful recruitment estimates could be derived for this rookery using any mixture type models, to account for capture heterogeneity, and so are not considered further here. No environmental predictor was found to affect recruitment rates for this rookery given these data. The long-term mean per capita recruitment rate for this rookery fluctuated around 0.092 (or 9.2% per annum). However, the Mapoon Flatback nester trend was not stable (in fact it was increasing: Figure 3d) so the per capita recruitment rate for this rookery cannot be interpreted as an estimate of the first-time nester rate.

#### **Avoid Island rookery**

There were only eight years of CMR data for this rookery (Table 1), which is too short a time period to derive any meaningful per capita recruitment rates.

#### **Peak Island rookery**

The best-fit Pradel temporal symmetry model (Supplementary Table B) not accounting for heterogeneity comprised time-varying survival (spline with  $df = 4$ ), time-dependent detection probabilities and time-dependent per capita recruitment rates). The overwhelming weight of evidence ( $> 99\%$ ) was in support of this model compared to the other three models fitted to these CMR histories. The annual recruitment rates were derived from this model and are shown in Figure 14. No meaningful recruitment estimates could be derived for this rookery using any mixture type models, to account for capture heterogeneity, and so are not considered further here. Despite the long-term study at this rookery (see Table 1), no environmental predictor was found to affect recruitment rates given these data. The long-term mean per capita recruitment rate for this rookery fluctuated around 0.165 (or 16.5% per annum). However, the Peak Island Flatback nester trend was not stable (it was decreasing then increasing: Figure 6d). In fact, the expected population growth rate for this rookery derived from the best-fit Pradel model was  $\lambda = 1.029$  (95% CI: 0.77-1.38) reflecting an increasing population trend although with some uncertainty. Hence, the per capita recruitment

rate for this rookery cannot be interpreted as an estimate of the first-time nester rate.

### **Curtis Island rookery**

Pradel temporal symmetry models both with and without accounting for capture heterogeneity were compared. The best-fit Pradel temporal symmetry model not accounting for heterogeneity comprised constant survival, time-dependent detection probabilities and time-dependent per capita recruitment rates. The overwhelming weight of evidence (> 99%) was in support of this model compared to the other five models fitted to these CMR histories ([Supplementary Table B](#)). The annual recruitment rates were derived from this specific model and are shown in [Figure 15](#). The best-fit Pradel temporal symmetry model now accounting for heterogeneity (recapture heterogeneity mixture model) comprised constant survival, constant mixture proportion [0.67, (95% CI: 0.59-0.75)], mixture-specific time-dependent detection probabilities and also time-dependent per capita recruitment rates. The overwhelming weight of evidence (> 99%) was in support of this model compared to the other 17 models fitted to these CMR histories ([Supplementary Table B](#)). The annual recruitment rates were derived from this specific model and are also shown in [Figure 15](#). No environmental predictor was found to affect recruitment rates for this rookery given these data. The long-term mean recruitment rate across both models fluctuated around 0.113 (or 11.3% per annum) but it was apparent that estimated per capita recruitment rates prior to 2010 were lower than post-2010, irrespective of best-fit model used ([Figure 15](#)). Despite the observed decrease in the number of nesting turtles from 2013-2019 (Limpus et al. 2022), the long-term Curtis Island nester abundance trend was generally stable since the early 2000s. The population shows signs of increasing since the early 2000s ([Figure 9d](#)). The long-term mean per capita recruitment rate (0.113) also could be interpreted as an estimate of the first-time nester rate across the 27 years.

### **Woongarra Coast rookery**

The best-fit Pradel temporal symmetry model ([Supplementary Table B](#)) not accounting for heterogeneity comprised time-varying survival (spline with  $df = 4$ ), time-dependent detection probabilities and constant per capita recruitment rates. The overwhelming weight of evidence (> 99%) was in support of this model compared to the three other models that could be fitted to these fitted to these CMR histories. No meaningful recruitment estimates could be derived for this rookery using any mixture type models, to account for capture heterogeneity, and so are not considered further here. Nor was any environmental predictor found to affect recruitment rates for this rookery given these data. The estimated mean per capita recruitment rate for this rookery was 0.082 or 8.2% per annum (95% CI: 6.3-10.6%). The Woongarra Coast Flatback nester population trend was generally stable over the 52-year period from 1968-2019 ([Figure 12](#)) so the constant per capita recruitment rate estimated for this rookery can be interpreted as an estimate of the first-time nester rate.

## **3.3 Temporal trends in size of nesting Flatbacks**

### **3.3.1 Introduction**

Changing body size over time is considered to be a hallmark population-level response to climate warming but it remains unclear whether that response generally results in declining or increasing body size trends (Gardner *et al.* 2011). So comparative analyses of temporal size change for a wide range of species is needed to determine the prevalence of this phenomenon and to help develop a better understanding of the underlying mechanisms and physiological consequences of body size shifts.

### **Statistical modelling approach**

We used a Bayesian inferential procedure to fit GAMMs to the Flatback nester curved carapace length (CCL) data for each rookery. The models were fit using the Stan computation engine (Carpenter *et al.* 2017) via the brms interface for R (Bürkner 2017). The response variable is the CCL of each turtle given two predictors (nesting season, age class) while each individual turtle identity was also included as a random effect to account for any turtle-specific variability. These rookery-specific models were implemented using weakly informative regularizing priors (Lemoine 2019) with posterior samples sourced from four chains and 10k iterations after a warmup of 2000 iterations. The appropriate model likelihood (Gaussian, Student-*t*, lognormal) for these data for each rookery was determined using leave-one-out cross-validation (Vehtari *et al.* 2017). The weight of evidence in favour of one model over any other candidate models (say Gaussian vs lognormal) was also assessed using Bayesian stacking, which is the Bayesian analogue of model averaging (Yao *et al.* 2018). The estimated temporal trend for each rookery was then displayed using the ggplot2 package for R (Wickham 2016).

#### **3.3.2 Results**

A GAMM with Student-*t* likelihood was the best-fit model for the Mapoon data set and the temporal carapace size trend is shown in [Figure 16](#). A GAMM with Gaussian likelihood was the best-fit model for the Avoid Island data set and the temporal carapace size trend is shown in [Figure 17](#). A GAMM with Student-*t* likelihood was the best-fit model for the Peak Island data set and the temporal carapace size trend is shown in [Figure 18](#). A GAMM with Student-*t* likelihood was the best-fit model for the Curtis Island data set and the temporal carapace size trend is shown in [Figure 19](#). A GAMM with lognormal likelihood was the best-fit model for the Woongarra Coast data set and the temporal carapace size trend is shown in [Figure 20](#). An increasing body size trend was apparent at all five rookeries with long-term fluctuations also evident at those rookeries with long-term monitoring such as Curtis Island ([Figure 19](#)) and Woongarra Coast ([Figure 20](#)).

### **3.4 Remigration interval modelling**

#### **3.4.1 Introduction**

Any demographic process is a complex time-varying function comprising three sources of temporal variation due to age-, year- and cohort-effects (Brillinger 1986). In other words, there is natural variability in demographic processes attributable to these three factors with year-effect considered an environmental factor and cohort-effect considered a genetic or a density-dependent factor (Hagen and Quinn 1991) — and that age-year-cohort modelling approach also applies equally well to modelling of marine turtle demographics (Chaloupka and Musick 1997, Chaloupka and Limpus 1998). Here we use the so-called APC (age-period-cohort) modelling approach (Smith and Wakefield 2016, Pigeon *et al.* 2018) to help disentangle the independent effect of age, period (= year) and cohort effects on the remigration interval for the Flatback nesters at the Curtis Island rookery. The remigration interval is the number of seasons between consecutive nesting seasons. It is important to note here that most studies of nesting marine turtles use the remigration interval as a surrogate measure of the breeding rate (National Research Council 2010). This metric is a return rate only and not an informative measure of breeding rate. To be a meaningful measure of breeding rate, the remigration interval needs to be adjusted by the following: (1) survival probability for each year of the interval between consecutive nesting seasons, (2) the probability of skipped breeding and (3)

the probability of detection given that the turtle migrated that year and was detected on the beach (Chaloupka and Limpus 1998, Pilcher and Chaloupka 2013). Nonetheless, using the APC modelling approach applied to remigration data might provide useful insight into the temporal dynamics of Flatback reproductive behaviour.

### **Statistical modelling approach**

We used a Bayesian inferential procedure to fit GAMMs with Poisson or negative binomial likelihood to the 1344 (IRSP>0) Flatback nester remigration intervals for the Curtis Island rookery. The models were fit using the Stan computation engine (Carpenter *et al.* 2017) via the brms interface for R (Bürkner 2017). The response variable is the remigration interval (number of years) recorded of each turtle on each sampling occasion given four nonlinear predictors (age measured as years since first tagged, summer sampling season or year, tagging cohort and carapace size). The use of nonlinear predictor functional form helps overcome the identifiability issue with conventional age-period-cohort modelling approaches (Dobson *et al.* 2020). The individual turtle identity was also included as a random effect to account for turtle-specific variability. The models were implemented using weakly informative regularizing priors (Lemoine 2019) with posterior samples sourced from four chains and 7k iterations after a warmup of 2000 iterations. The appropriate model likelihood (Poisson, negative binomial) for these data was determined using leave-one-out cross-validation (Vehtari *et al.* 2017). The weight of evidence in favour of a Poisson likelihood or a negative binomial likelihood model was also assessed using Bayesian stacking (Yao *et al.* 2018). The estimated temporal trends for age, year, cohort, and carapace size for the Curtis Island rookery was then displayed using the ggplot2 package for R (Wickham 2016).

### **3.4.2 Results**

A GAMM with Poisson likelihood was the best-fit model for the Curtis Island data set and the estimated temporal trends for age, year, cohort, and carapace size are shown in [Figure 21](#). While there are some apparent nonlinear trends it is doubtful that any are significant. For instance, the year-effect is the strongest effect of the four effects and yet there is only a 78% probability that this effect actually exists given these data (probability of direction metric: Makowski *et al.* 2019).

## **4. Discussion**

This study was initiated to monitor the impact of extensive dredging works within Port Curtis to service the needs of three newly approved LNG processing and export terminals on the western side of Curtis Island within the Western Basin of Port Curtis. The dredging and LNG infrastructure construction commenced in 2011. The three LNG plants were operational by 2016. During the same time period, the Wiggins Island Coal Terminal, also within the Western Basin, was constructed and was operational by 2016.

Index Flatback turtle rookeries with more than 10 years of continuous census data examined in this study are characterised by generally increasing nester population abundance since at least the early to mid-2000s. This includes three index sites within the eAust genetic stock (Peak Island, Curtis Island, Woongarra Coast) and one index site within the Arafura Sea genetic stock (Flinders Beach, Mapoon). None of the study sites showed a decline in nester abundance during this time period. These results are indicative of stock wide population increases in adult Flatback nesting populations across northern and eastern Australia within

the last two decades. Although adult turtles have a slow CCL growth rate, with the high adult female survivorship recorded in this study, the increasing mean size of the adult female Flatback turtles is consistent with the increasing nester populations recorded at all the study sites.

An examination of nesting abundance, survival and recruitment estimates from the present study for Curtis Island when compared with those at Peak Island, Woongarra Coast and Avoid island, all within the eAust genetic stock, provides no indication of an anomalous population performance of the Curtis Island adult female nesting population during or following the major dredging and infrastructure development within Port Curtis that occurred during 2011-2016.

In the longer term, this study has reinforced the results of a previous study (Limpus *et al.* 2013a) that identified a major decline in nester abundance for Peak Island from 1980 to the early 2000s. The present study also has identified a very minor decline in nester abundance at the Woongarra Coast rookery from the 1970s to approximately 1990. Given that Flatback turtles probably commence breeding at about 20 yr of age (Limpus *et al.* 2013a), a decline in nester abundance during the 1970s-1980s could have been the result, at least in part, of elevated turtle egg harvests prior to the Order in Council, 18 July 1968, under the Queensland *Fisheries Act Amendment Act of 1962*. This Order in Council declared an all year closed season for turtle and egg harvest for all (marine) turtle species for all of Queensland. The harvest of Flatback turtle eggs, the less frequent harvest of nesting Flatback turtles for human consumption, and the regular disturbance of nesting turtles by turtle riding featured prominently in newspaper reports from the 1870s until 1968 ([Table 1](#); [Figure 22](#)). This egg harvest and turtle harvest at Peak Island, and more broadly in Keppel Bay, was unquantified with respect to its potential impact on population stability. The unquantified take of turtle eggs and riding of nesting turtles also occurred on the Woongarra Coast prior to 1968 (Limpus 1985). There are no comparable reports of egg harvest, turtle harvest or turtle riding at Wild Duck Island. The present study shows a decline in nester abundance in progress when the monitoring commenced at Peak Island in 1980 and which continued until the late 1990s ([Figure 8](#)). This was followed by an increase in nester abundance from the early 2000s until 2016. These data suggest that there could have been a consequential increase in the Flatback turtle nesting abundance in the Keppel Bay region some 2-3 decades following the 1968 ban on the take of turtle eggs and the harassment of the nesting females.

However, there were other long-term impacts on the northern Australian Flatback populations at the same time. Limpus (2007) reviewed the fisheries bycatch data of Flatback turtles in prawn trawl fisheries in northern and eastern Australia and identified that this species was one of the most commonly captured marine turtles in these trawl fisheries (Poiner and Harris 1996, Robins 1995, Robins and Mayer 1998). However, Flatback turtles had the lowest bycatch mortality among marine turtle species in these trawl fisheries (Poiner and Harris 1996, Robins 1995, Robins and Mayer 1998). This lower trawl bycatch mortality for Flatback turtles was consistent with their better breath holding ability demonstrated by Sperling *et al.* (2007). In contrast, there was a major decline in the eastern Australian Loggerhead turtle nesting populations during the 1970s to 2000 that was attributed to Loggerhead turtle bycatch mortality in the same prawn trawl fisheries (Limpus 2008). Limpus (2008) indicated that with a substantial reduction in trawl bycatch mortality following the compulsory use of turtle exclusion devices (TEDs) in the Northern Prawn Fishery, the Torres Strait Trawl Fishery, and the Queensland East Coast Otter Trawl Fishery during 2000-2001, there should be a slowing

of the rate of decline of the Loggerhead turtle nesting numbers detectable after one adult breeding cycle of about five years. Limpus *et al.* (2013b) identified that the eastern Australian Loggerhead nesting population shows increasing nesting numbers at all index nesting beaches since 2001.

Satellite tracking studies of eAust Flatbacks confirm their use of foraging habitat in coastal waters from at least Port Curtis in the south to Torres Strait in the north, where the trawl fisheries operate (Hamann *et al.* 2017, Shimada *et al.* 2020). The present study has demonstrated that there have been general increases in nesting population abundance since the early to mid-2000s at three index sites within the eAust genetic stock (Peak Island, Curtis Island, and the Woongarra Coast) and one index site within the Arafura Sea genetic stock (Flinders Beach Mapoon). This population increase in adult Flatback nesting populations across two genetic stock in northern and eastern Australia within the last two decades provides strong circumstantial evidence that the compulsory use of TEDs in the northern Australian prawn trawl fisheries has been a primary contributing factor behind these Flatback turtle nesting population increases.

There is still unresolved the anomalous population performances of the Flatback turtle populations at Peak Island and Wild Duck Island, the two largest nesting populations within the eAust genetic stock (Limpus *et al.* 2013a). It is generally presumed that turtle populations within the same genetic stock will function somewhat in synchrony in the absence of localised management issues. However, the Peak Island Flatback population experienced a greater than 50% decline in nester population during 1980-2000 while the Wild Duck Island population remained approximately stable (Limpus *et al.* 2013a). The nesting habitat at both islands is within National Parks on what have been substantially uninhabited Islands during this period, although a tourist resort operated intermittently since the late 1970s on Wild Duck Island. Peak Island has had no non-native predators of turtles or their eggs on the island and Wild Duck Island was similarly free of introduced predators except for a brief period in the 2000s when pigs had been introduced to the island. Limpus *et al.* (2013a) concluded that because both these Flatback nesting populations from the same genetic stock are distributed approximately uniformly throughout the same east Australian foraging range, it is reasonable to assume that the declining Peak Island nesting population had not been caused by a general problem impacting the entire foraging range of the eastern Australian Flatback management unit. If that is the case, then it would suggest the problem(s) associated with the Peak Island nesting population decline was operating within the adjacent inter-nesting habitat or at the nesting beach. No issues restricted to the islands have been identified that could account for the difference in the population performances.

The internesting home range for eAust stock Flatback turtles for this area can be expected to range out a few 10s of kilometres from the nesting beaches. Hamann *et al.* (2017), based on three years of satellite telemetry tracking of nesting Flatback turtles from Curtis Island, defined their internesting habitat use:

- Average maximum water depth used by the turtles during their 2014-2015 and 2015-2016 internesting periods was 22.3 m and the average depth was 12.3 m ( $\pm 3.9$ ).
- They spent 10% of their time in water depths less than 2 m and half of their time at depths between 10 and 20 m.

- A comparison of home range area and bathymetry indicates that the turtles spend most of their time on the bottom.
- Kernel Density Estimates of interesting home ranges based on utilisation distributions (UD) of 95%, for individual turtles ranged from 51 to 1501 km<sup>2</sup> and core home ranges (UD 50%) ranged from 6 to 458 km<sup>2</sup>.

Hamann *et al.* (2019) based on satellite telemetry tracking of nesting Flatback turtles from Avoid Island, defined their inter-nesting habitat use:

- The average interesting home range (UD 95%) was  $224.2 \pm 138.5$  km<sup>2</sup> (individual range 50 - 499 km<sup>2</sup>) and the average core home range (UD 50%) was  $46.9 \pm 33.6$  km<sup>2</sup> (individual range 11 – 113 km<sup>2</sup>).
- The turtles spent most of their time within 10 to 30 km from the nesting beach (maximum distance from Avoid was 49 km).
- They spent most of their time in waters < 12 m deep.
- Similar to the results from 2016 and 2017, most of the core home range for the tracked turtles occurred along the coastal waters from Clairview south into Broadsound.

In the absence of census monitoring of the Wild Duck Island nesting population since the 2006-07 summer, there remains no clear understanding of the underlying cause of the decline in Peak Island nester abundance. Based on the current knowledge, it is most likely that the problems occurred within the interesting habitat surrounding the Peak Island rookery and is likely to have been at least in part trawling bycatch related.

## 5. Acknowledgements

This flatback turtle projects was conducted as part of the Turtle Conservation Project of the Threatened Species Unit, Department of Environment and Science. The project was funded in part by grants from Gladstone Ports Corporation's Ecosystem Research and Monitoring Program.

The Curtis Island and Peak Island projects received logistical assistance from the Gladstone Queensland Parks and Wildlife Service staff.

The Avoid Island project was conducted as a cooperative project between the Queensland Trust for Nature (QTFN) and the Turtle Conservation Project of the Threatened Species Unit, Department of Environment and Science. Renee Rossini of QTFN provided logistic support, organised transport and organised accommodation for the field studies.

These studies could not have been completed without the assistance of the numerous Queensland Turtle Conservation volunteers, who often worked long hours in challenging conditions. The assistance of staff and volunteers is gratefully acknowledged.

## 6. References

- Anderson, S., Branch, T., Cooper, A. and Dulvy, N. (2017). Black-swan events in animal populations. *Proceedings of the National Academy of Sciences of the USA* **114**: 3252-3257.
- Bjorndal, K., Bolten, A. and Chaloupka, M. (2000). Green turtle somatic growth model: evidence for density-dependence. *Ecological Applications* **10**: 269-282.
- Bjorndal, K., Bolten, A. and Chaloupka, M. (2005). Evaluating trends in abundance of immature green turtles, *Chelonia mydas*, in the greater Caribbean. *Ecological Applications* **51**: 304-314.
- Bjorndal, K., Bowen, B., Chaloupka, M., Crowder, L., Heppell, S., Jones, C., Lutcavage, M., Policansky, D., Solow, A. and Witherington, B. (2011). Better science needed for restoration in the Gulf of Mexico. *Science* **331**: 537-538.
- Bjorndal, K., Bolten, A., Chaloupka, M. *et al.* (2017). Ecological regime shift drives declining growth rates of sea turtles throughout the West Atlantic. *Global Change Biology*. doi: 10.1111/gcb.13712.
- Brillinger, D. R. (1986). The natural variability of vital rates and associated statistics. *Biometrics* **42**: 693-734.
- Bürkner, P. (2017). brms: An R Package for Bayesian multilevel models using Stan. *Journal of Statistical Software* **81**(1): 1-28.
- Burnham, K., Anderson, D. and Huyvaert, K. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioural Ecology and Sociobiology* **65**: 23–35.
- Carpenter, B., Gelman, A., Hoffman, M., Lee, D., Goodrich, B., Betancourt M, Brubaker, M., Guo, J., Li, P. and Riddell, A. (2017). Stan: a probabilistic programming language. *Journal of Statistical Software* **76**(1): 1-32.
- Chaloupka, M. (2003). Stochastic simulation modelling of loggerhead sea turtle population dynamics given exposure to competing mortality risks in the western south Pacific. In: *Loggerhead Sea Turtles*. Eds. Bolten, A. and Witherington, B., pp 274-294, (Smithsonian Institution Press, Washington, DC).
- Chaloupka, M. (2004). Exploring the metapopulation dynamics of the southern Great Barrier Reef green turtle stock and possible consequences of sex-biased local harvesting. In: *Species Conservation and Management: Case Studies*. Eds. Akçakaya, H., Burgman, M., Kindvall, O., Wood, C., Sjogren-Gulve, P., Hattfield, J. and McCarthy M, pp. 340-354. (Oxford University Press, New York).
- Chaloupka, M. and Limpus, C. (1998). Modelling green sea turtle survivorship rates. In: Epperly SP, Braun J (eds) *Proceedings of the 17th Annual Sea Turtle Symposium*. NOAA Technical Memorandum NMFS-SEFSC-415: 24-26.
- Chaloupka, M. and Limpus, C. (2001). Trends in the abundance of sea turtles resident in southern Great Barrier Reef waters. *Biological Conservation* **102**: 235-249.
- Chaloupka, M. and Limpus, C. (2002). Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. *Marine Biology* **140**: 267-277.
- Chaloupka, M. and Musick, J. (1997). Age, growth and population dynamics. In: Chap 9, *The Biology of Sea Turtles*. Eds. Lutz, P. and Musick, J. pp. 233-276. (CRC Marine Science Series, CRC Press Inc, Boca Raton).
- Chaloupka, M., Kamezaki, N. and Limpus, C. (2008). Is climate change affecting the population dynamics of the endangered Pacific loggerhead sea turtle? *Journal of Experimental Marine Biology and Ecology* **356**: 136-143.

- Choquet, R., Lebreton, J., Gimenez, O., Reboulet, A. and Pradel, R. (2009). U-CARE: Utilities for performing goodness of fit tests and manipulating CApture-REcapture data. *Ecography* **32**: 1071-1074.
- Dobson, A., Hockey, R., Chan, H. and Mishra, G. (2020). Flexible age-period-cohort modelling illustrated using obesity prevalence data. *BMC Medical Research Methodology* **20**: 16. <https://doi.org/10.1186/s12874-020-0904-8>.
- FitzSimmons, N. N. and Limpus, C. J. (2014). Marine turtle genetic stocks of the Indo-Pacific: identifying boundaries and knowledge gaps. *Indian Ocean Turtle Newsletter* **20**, 2-18.
- FitzSimmons, N. N., Pittard, S. D., McIntyre, N., Jensen, M. P., Guinea, M., Hamann, M., Kennett, R., Leis, B., Limpus, C. J., Limpus, D. J., McCann, M. J., MacDonald, A. J., McFarlane, G., Parmenter, C. J., Pendoley, K., Prince, R. T., Scheltinga, L., Theissinger, K., Tucker, A. D., Waayers, D., Whiting, A. and Whiting, S. (2020). Phylogeography, genetic stocks, and conservation implications for an Australian endemic marine turtle. *Aquatic Conservation, Marine and Freshwater Ecosystems* **30**: 440-460.
- Fletcher, D. (2012). Estimating overdispersion when fitting a generalized linear model to sparse data. *Biometrika* **99**: 230-237.
- Gardner, J., Peters, A., Kearney, M., Joseph, L. and Heinsohn, R. (2011). Declining body size: a third universal response to warming? *Trends in Ecology and Evolution* **26**: 285-291.
- Gilman, E., Chaloupka, M., Fitchett, M., Cantrell, D. and Merrifield, M. (2020). Ecological responses to blue water MPAs. *PLoS ONE* **15**(7): e0235129. <https://doi.org/10.1371/journal.pone.0235129>.
- Gimenez, O. and Choquet, R. (2010). Individual heterogeneity in studies on marked animals using numerical integration: capture-recapture mixed models. *Ecology* **91**: 951-957.
- Gimenez, O., Lebreton, J., Choquet, R. and Pradel, R. (2017). R2ucare: Goodness-of-Fit Tests for Capture-Recapture Models. *R package version 1.0.0*.
- Hagen, P. and Quinn, T. (1991). Long-term growth dynamics of young Pacific halibut: evidence of temperature-induced variation. *Fisheries Research* **11**: 283-306.
- Hamann, M., Wildermann, N., Williams, G., Daff, K. and Limpus, C. J. (2017). Final report on inter-nesting habitat use by flatback turtles off the Curtis Island coast - 2013 to 2015. Produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program. 27 pp.
- Hamann, M., FitzSimmons, N. N., Whitchurch, R. N., Limpus, C. J., Shimada, T. and Yeates, M. (2019). Report on inter-nesting habitat use by flatback turtles off Avoid Island 2018-2019. Report produced for Eco Logical Australia.
- Huang, B., Thorne, P., Banzon, V., Boyer, T., Chepurin, G., Lawrimore, J., Menne, M., Smith, T., Vose, R. and Zhang, H. (2017). Extended Reconstructed Sea Surface Temperature, Version 5 (ERSSTv5): upgrades, validations, and intercomparisons *Journal of Climate* **30**: 8179-8205.
- Járez, M. and Steel, M. (2010). Model-based clustering of non-Gaussian panel data based on skew-*t* distributions. *Journal of Business and Economic Statistics* **28**: 52-66.
- Laake, J. (2013). RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, pp. 25. (Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Seattle).
- Lebreton, J., Burnham, K., Clobert, J. and Anderson, D. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**: 67-118.

- Lemoine, N. (2019). Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. *Oikos* **128**: 912-928.
- Limpus, C. J. (1985). A study of the loggerhead turtle, *Caretta caretta*, in eastern Australia. *PhD thesis, Zoology Department, University of Queensland*.
- Limpus, C. J. (2007) A biological review for Australian marine turtles. 5. Flatback turtle *Natator depressus* (Garman). (Queensland Environmental Protection Agency, Queensland Government, Brisbane).
- Limpus, C. J. (2008). A biological review of Australian marine turtles. 1. Loggerhead turtle *Caretta caretta* (Linnaeus). (Queensland Environmental Protection Agency: Brisbane).
- Limpus, C. and Limpus, D. (2002). The biology of the loggerhead turtle, *Caretta caretta*, in southwest Pacific Ocean foraging areas. In: The Biology and Conservation of Loggerhead Sea Turtles. Eds. Bolten, A. and Witherington, B. (Smithsonian Institution Press, Washington, DC).
- Limpus, C. and Nicholls, N. (2000). ENSO regulation of Indo-Pacific green turtle populations. In 'Applications of Seasonal Climate Forecasting in Agricultural and Natural Ecosystems.' Hammer, G., Nicholls, N. and Mitchell, C., Ed.) pp. 399-408. (Kluwer Academic Publishers: Dordrecht).
- Limpus C. J., Parmenter C. J. and Chaloupka M. (2013a). Monitoring of Coastal Sea Turtles: Gap Analysis 5. Flatback turtles, *Natator depressus*, in the Port Curtis and Port Alma Region. Brisbane: Department of Environment and Heritage Protection Report produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program. 26 pp.
- Limpus C. J., Parmenter, C. J. and Chaloupka, M. (2013b). Monitoring of Coastal Sea Turtles: Gap Analysis 1. Loggerhead turtles, *Caretta caretta*, in the Port Curtis and Port Alma Region. Department of Environment and Heritage Protection Report produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program. 31pp.
- Limpus C. J., FitzSimmons N. N., and Chaloupka M. (2022). Flatback Turtle, *Natator depressus*, Seven Year Review: 2013/14 – 2019/20 Breeding Seasons at Curtis, Peak and Avoid Islands. Brisbane: Department of Environment and Science, Queensland Government. Report produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program. 65 pp.
- Madon, B., Garrigue, C., Pradel R. and Gimenez, O. (2013). Transience in the humpback whale population of New Caledonia and implications for abundance estimation. *Marine Mammal Science* **29**: 669-678.
- Makowski, D., Ben-Shachar, M. and Lüdtke, D. (2019). bayestestR: Describing effects and their uncertainty, existence and significance within the Bayesian framework. *Journal of Open Source Software* **4**(40): 1541. <https://doi.org/10.21105/joss.01541>.
- Marescot, L., Pradel, R., Duchamp, C., Cubaynes, S., Marboutin, E., Choquet, R., Miquel, C. and Gimenez, O. (2011). Capture-recapture population growth rate as a robust tool against detection heterogeneity for population management. *Ecological Applications* **21**; 2898-2907.
- Muniz Leão, S., Pianka, E. and Pelegrin, N. (2018). Is there evidence for population regulation in amphibians and reptiles? *Journal of Herpetology* **52**: 28-33.

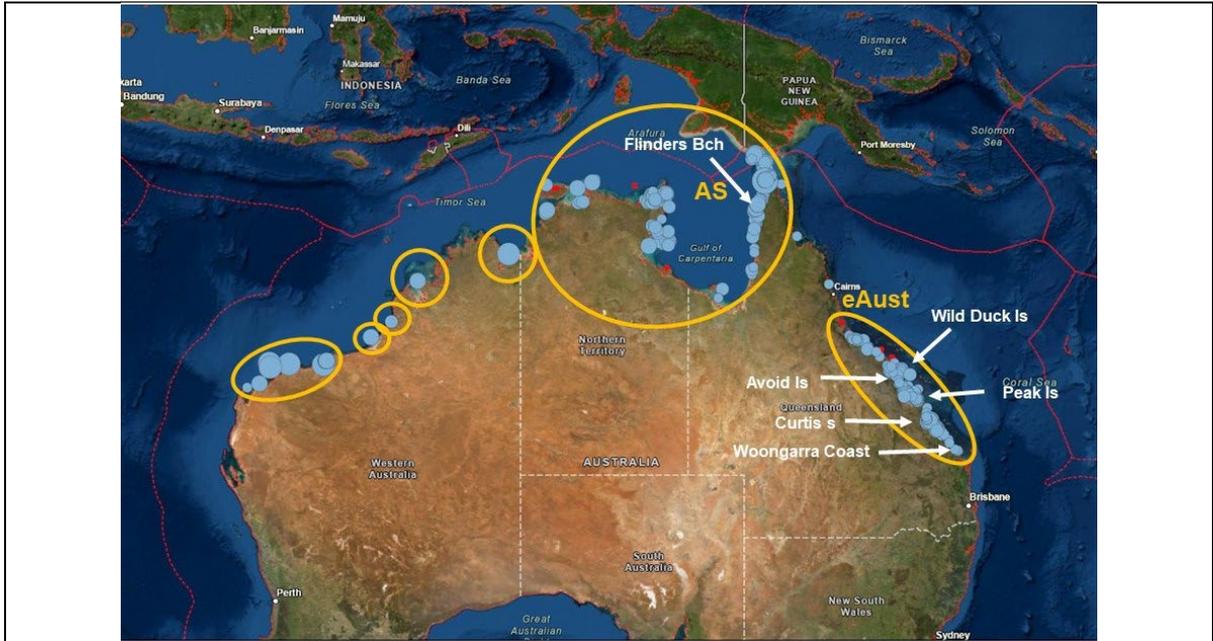
- Musick, J. and Limpus, C. J. (1997) Habitat utilization and migration in juvenile sea turtles. In: The Biology of Sea Turtles. Eds. Lutz, P and Musick, J., pp. 137-163. (CRC Marine Science Series, CRC Press. Inc, Boca Raton).
- National Research Council (2010). Sea Turtle Status and Trends: Integrating Demography and Abundance. (National Academies Press, Washington DC).
- Nichols, J. (2016). And the first one now will later be last: time-reversal in Cormack–Jolly–Seber models. *Statistical Science* **31**: 175-190.
- NOAA (2020) Multivariate ENSO Index Version 2. [www.esrl.noaa.gov/psd/enso/mei/](http://www.esrl.noaa.gov/psd/enso/mei/). (Physical Sciences Division, ESRL, Boulder).
- Parmenter, C. and Limpus, C. (1995). Female recruitment, reproductive longevity and inferred hatchling survivorship for the Flatback turtle (*Natator depressus*) at a major eastern Australian rookery. *Copeia* **2**: 474-477.
- Pedersen, M., Berg, C., Thygesen, U. A., Nielsen, A. and Madsen, H. (2011). Estimation methods for nonlinear state-space models in ecology. *Ecological Modelling* **222**: 1394-1400.
- Pfaller, J., Chaloupka, M., Bolten, A. and Bjorndal, K. (2018). Phylogeny, biogeography and methodology: a meta-analytic perspective on heterogeneity in adult marine turtle survival rates. *Scientific Reports* **8**: 5852. doi:10.1038/s41598-018-24262-w
- Pigeon, G., Loe, L., Albon, S., Bonenfant, C., Elston, D., Justin Irvine, R., Ropstad, E., Veiberg, V. and Stien, A. (2018). Biased estimation of trends in cohort effects: the problems with age-period-cohort models in ecology. *Ecology* **99**: 2675-2680.
- Pilcher, N. and Chaloupka, M. (2013). Using community-based monitoring to estimate demographic parameters for a remote nesting population of the Critically Endangered leatherback turtle. *Endangered Species Research* **20**: 49-57.
- Plummer, M. (2015). JAGS version 4 user manual. [https://sourceforge.net/projects/mcmc-jags/files/Manuals/4.x/jags\\_user\\_manual.pdf/download](https://sourceforge.net/projects/mcmc-jags/files/Manuals/4.x/jags_user_manual.pdf/download).
- Plummer, M. (2016). rjags: Bayesian Graphical Models using MCMC. *R package version 4-6*. <https://CRAN.R-project.org/package=rjags>.
- Poiner, I. R. and Harris, A. N. M. (1996). Incidental capture, direct mortality and delayed mortality of sea turtles in Australia's Northern Prawn Fishery. *Marine Biology* **125**: 81-825.
- Pradel, R. (1996). Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* **52**: 371-377.
- Pradel, R., Johnson, A., Viallefont, A., Nager, R. and Cezilly, F. (1997). Local recruitment in the greater flamingo: a new approach using capture–mark–recapture data. *Ecology* **78**: 1431-1445.
- Pradel, R., Gimenez, O. and Lebreton, J. (2005). Principles and interest of GOF tests for multistate capture-recapture models. *Animal Biodiversity Conservation* **28**:189-204.
- Pradel, R., Choquet, R., Lima, M., Merritt, J. and Crespín, L. (2009). Estimating population growth rate from capture-recapture data in presence of capture heterogeneity. *Journal of Agricultural, Biological, and Environmental Statistics* **15**: 248-258.
- Prince, R. and Chaloupka, M. (2012). Estimating demographic parameters for a critically endangered marine species with frequent reproductive omission: hawksbill turtles nesting at Varanus Island, Western Australia. *Marine Biology* **159**: 355-363.
- Robins, J. B. (1995). Estimated catch and mortality of sea turtles from the east coast otter trawl fishery of Queensland, Australia. *Biological Conservation* **74**: 157-167.
- Robins, J. B. and Mayer, D. G. (1998). Monitoring the impact of trawling on sea turtle populations of the Queensland East Coast. *DPI Project Report Series Q098012*: 1-59.

- Shimada, T., Thums, M., Hamann, M., Limpus, C. J., Hays, G. C., FitzSimmons, N. N., Wildermann, N. E., Duarte, C. M., and Meekan, M. G. (2020). Optimising sample sizes for animal distribution analysis using tracking data. *Methods in Ecology and Evolution* **12**: 288-297.
- Smith, T. and Wakefield, J. (2016). A review and comparison of age–period–cohort models for cancer incidence. *Statistical Science* **31**: 591-610.
- Sperling, J. B., Grigg, G. C., Beard, L. A., and Limpus, C. J. (2007). Respiratory properties of blood in flatback turtles ( *Natator depressus*). *Journal of Comparative Physiology B* **177**: 779-786.
- Vehtari, A., Gelman, A. and Gabry, J. (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* **27**: 1413-1432.
- White, G. and Cooch, E. (2017). Population abundance estimation with heterogeneous encounter probabilities using numerical integration. *Journal of Wildlife Manage* **81**: 322-336.
- White, G., Kendall, W. and Barker, R. (2006). Multistate survival models and their extension in Program MARK. *Journal of Wildlife Management* **70**: 1521-1529.
- Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. 2nd Edition. (Springer-Verlag, New York, USA).
- Yao, Y. and Vehtari, A., Simpson, D. and Gelman, A. (2018). Using stacking to average Bayesian predictive distributions (with Discussion). *Bayesian Analysis* **13**: 917-1003.
- Zhang, T., Hoell, A., Perlwitz, J., Eischeid, J., Murray, D., Hoerling, M. and Hamill, T. (2019). Towards probabilistic multivariate ENSO monitoring. *Physical Research Letters* **46**: DOI: 10.1029/2019GL08394.

**Table 2: Newspaper articles referring to turtle harvest and turtle riding at Peak Island prior to 1968.**

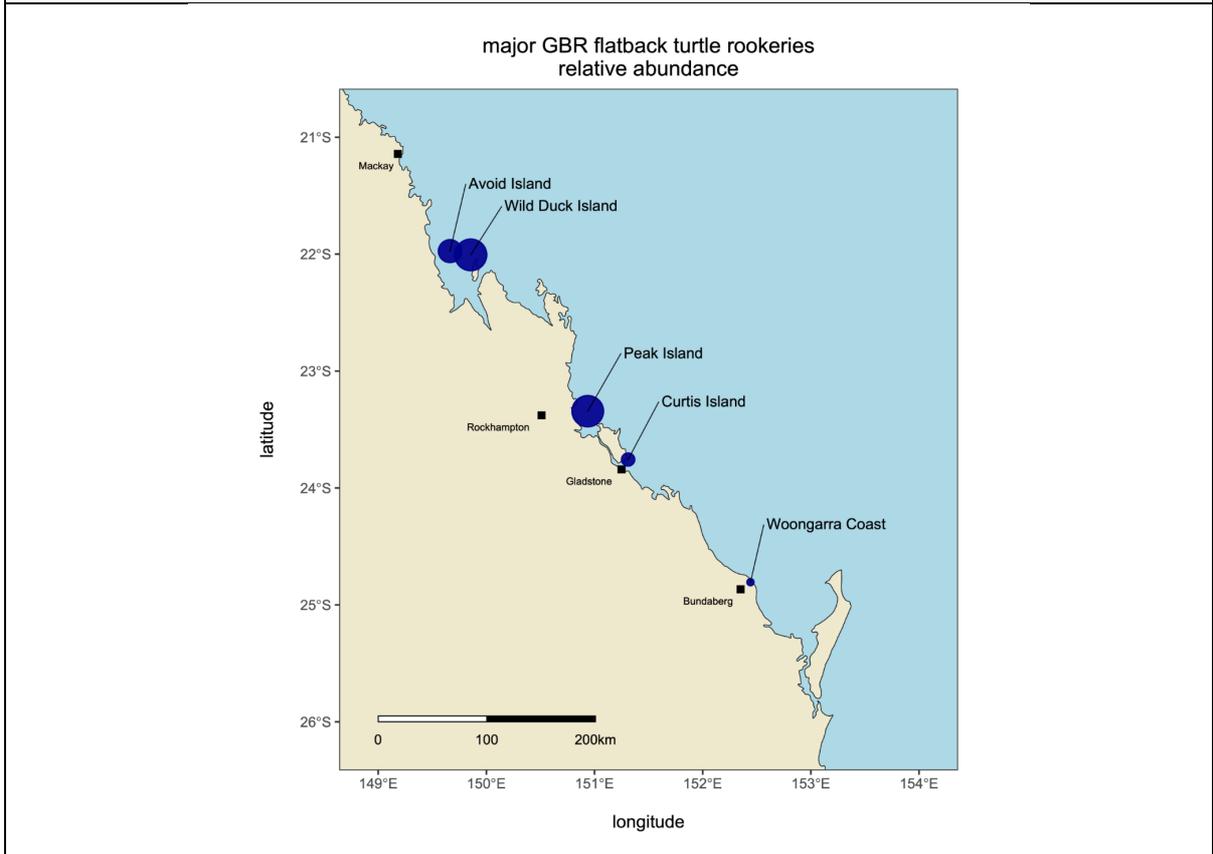
Observation date	Observations	Reference
Dec 1872	<p>The turtle trade is attaining significant progress. A week or two since the two small vessels engaged in the trade have returned to Lake's Creek with 122 green turtles.</p> <p>17 specimens of the hawksbill turtle have also been brought to town from the 'Lump' but they are not suitable for preserving or edible purpose.</p> <p>[CJL note: species ID error; "Lump" was named by Mathew Flinders in 1800 and now is called Peak Island].</p>	<p><i>Rockhampton Bulletin</i>, 22 Dec 1872, P.5</p>
Nov 1894	<p>Peak Island: Cutter, MV Dolphin sailed down Fitzroy for some turtle hunting at Peak Island; camp fire got out of control and burnt out the island. Three nesting turtles turned on back at night and taken off by boat the next day and distributed to Emu Park Hotels; 3 clutches of eggs collected and sent to Rockhampton and distributed among the community.</p> <p>The clutches contained 60, 60, 66 eggs; "The eggs were about the size of a duck egg, but round, with soft but tough shells, not easily broken."</p>	<p><i>Morning Bulletin</i>, (Rockhampton), 19 Nov 1894, P.3</p>
7 Dec 1912	<p>"The turtle season is now on.....a party of visitors went in Mr. Bolderson's boat to Peak Island for the week-end. They report that Peak Island was infested with loggerhead turtles and hundreds of these creatures were seen coming out of the sea and depositing their eggs in the sands of the foreshore. The trippers brought home sugar-bags full if turtle steak and dozens of eggs."</p> <p>CJL note: misidentification of species.</p>	<p><i>Capricornian</i>, 14 Dec 1912, P.30</p>
Photos from before WWI	<p>Book of photographs prepared by Great War service men while in England as a gift to Miss Beta Richardson in appreciation of kindness of her mother to the service men while in England – "the most interesting .... Views of the doing of a party of Rockhampton and Mount Morgan residents catching and riding turtles on Peak Island , off Emu Park."</p>	<p><i>Morning Bulletin</i>, 27 Jul 1920, P.8</p>
10 Jan 1922	<p>THE NOVEL SPORT OF TURTLE-RIDING</p> <p>.. Peak Island ... 3 miles in circumference .... one small beach on the western side... where the turtles come to lay their eggs .....it is the only one &lt;island&gt; which the turtles visit in any numbers, although there are several other islands not far away. ... generally somewhere about 9 o'clock when they begin to show up. [Followed by a reasonable description of nesting behaviour] ...laid her 79 eggs in the short space of 15 minutes....[photos of flatback turtle; people riding turtles; pyramid of eggs] ...No turtle was interfered with until it had finished laying its eggs, when the presence of these was marked, and the turtle was secured as it made its way back to the sea. .... Some thirty were obtained .... And all those that came afterwards were allowed to lay and return again to the sea. .. The next day ... the first thing was to collect the turtles together by passing ropes around their shells and pulling them along the beach to a central position where the "horsemen" could congregate ....[Followed by a description of how to ride a turtle into the sea].... Another form of amusement was races on the beach. .... The laying period ... is from October to December.... These turtles are of no use commercially. It is the species known as the green turtle that is used in the manufacture of turtle soup.</p>	<p><i>Sydney Mail</i>, 25 Jan 1922, P.13</p>
? date	<p>Photos of girls astride turtles at Peak Island by Colin MacDonald: published July 30, P.20.</p>	<p><i>Daily Mail</i> (Brisbane), 20 Aug 1922, P.9</p>

? date	On one occasion a party of Rockhampton Motor-boatmen went over to North Keppel and there found that another party had captured quite a number of green turtles. They had turtles them on their backs and cut the throats of several. When questioned they admitted that they had done this for fun and expressed the intention of treating the remainder similarly. They got quite a shock when severely rated by one of the new-comers, for their wantonness. .... Some of the injured turtles were righted and ridden down the beach..... [one turtle was cut open and contained "fully sixty eggs"] CJL: note mis-ID species.	<i>Capricornian</i> , 19 Jan 1924, P.34
? date	<b>Turtle Riding at Peak Island by W. S. Buzacott:</b> Emu Park: "No fewer than 26 islands are visible, set in a sea of ultramarine blue. .... One island, The Peak, is the hatching ground of the great sea turtle, Peak Island lies nine miles south-east of emu park, is easily accessible, .... It is about 10 acres an extent, with short broken beaches on the leeward side, and has been the incubating resort od turtles in the Keppel Bay area for centuaries. <b>From middle October till late December each year from 20 to 100 turtles crawl out of the sea each night and deposit from 60 to 80 eggs</b> in a specially-prepared cache. ... on a bright moon-light night it is possible to watch the whole procedure. And very interesting does it prove. Boating parties are made up at Emu Park to suit the occasion, so there is no lack of opportunity. [followed by a description of turtle nesting behaviour and hatchling emergence]. .... If the visitor is so inclined, turtle races can be arranged, the turtles being mounted and ridden into the water, where they soon rid of their riders by diving to the bottom. Turtle eggs are nourishing and make good cakes, abut as the whites do not set they are not in much favour. The flesh is rich and tender if allowed to hang for the night after killing. It is said o be very nutritious, but the writer always notices a fishy flavour about it – either real or imagined.	<i>Sydney Mail</i> (NSW), 8 May 1929, P.14
23 Nov 1937	"One enthusiastic party spent last weekend at Peak Island, there to witness the unique sight of turtles laying eggs and to experience the thrill of turtle-riding. Their efforts were well rewarded for during the night over 20 turtles made their appearance, 16 of them were turned over in readiness for the great race the next morning. This event was very spectacular with the ladies of the party providing the bigger thrill with their adept handling of the speedsters."	<i>Morning Bulletin</i> , 30 Nov 1937, P.14;  <i>Central Queensland Herald</i> , 2 Dec 1937, P.64
5 Nov 1938	"...Mr C. Morris of Emu Park to a party from Mt. Morgan to Peak Island, where they had a delightful time riding turtles. It is understood that each member of the party had two turtles to his credit, and the supply of eggs left at the Oyster Saloon testifies to the success of the party."	<i>Morning Bulletin</i> , 9 Nov 1938, P.15;  <i>Central Queensland Herald</i> , 10 Nov 1938, P.50
Jan 1956	"Mr R. McDougall's launch, <i>Pacificque</i> , has continued to take fishing parties out almost daily, and the most popular trip was the moonlight run to Peak Island to watch the turtles. Residents are looking forward to more of these trips."	<i>Central Queensland Herald</i> , 12 Jan 1956, P.23



**1.A. Nesting distribution of Flatback turtles with approximate boundaries of the genetic stocks identified by FitzSimmons *et al.* 2020.**

The two genetic stocks sampled in the present study were the AS and eAust stocks, with index beaches identified.

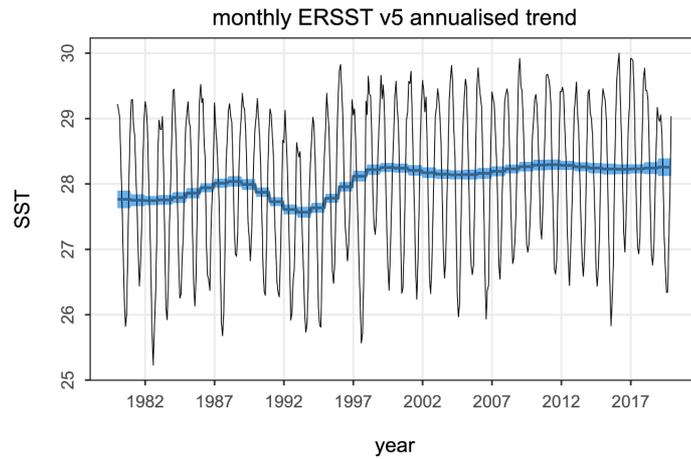


**1.B. Flatback rookeries sampled from within the eAust genetic stock along the southern Great Barrier Reef (see Table 1).**

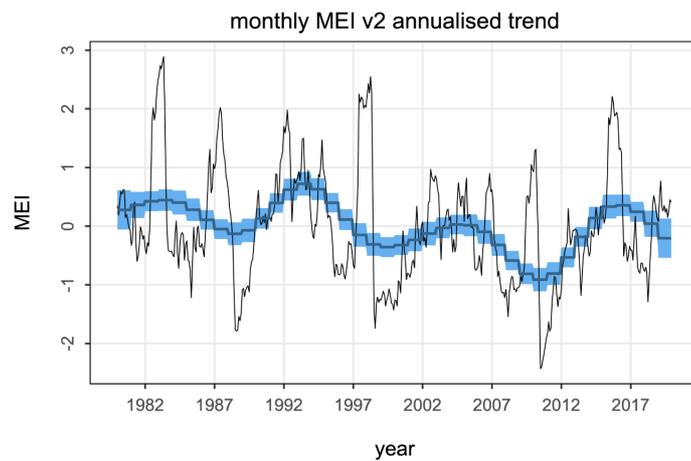
- Dot size is proportional to nester abundance at the Peak Island rookery (present study).
- Wild Duck Island rookery abundance estimate sourced from Limpus *et al.* 2013a.

**Figure 1: The breeding distribution of Flatback turtles, *Natator depressus*.**

(A)

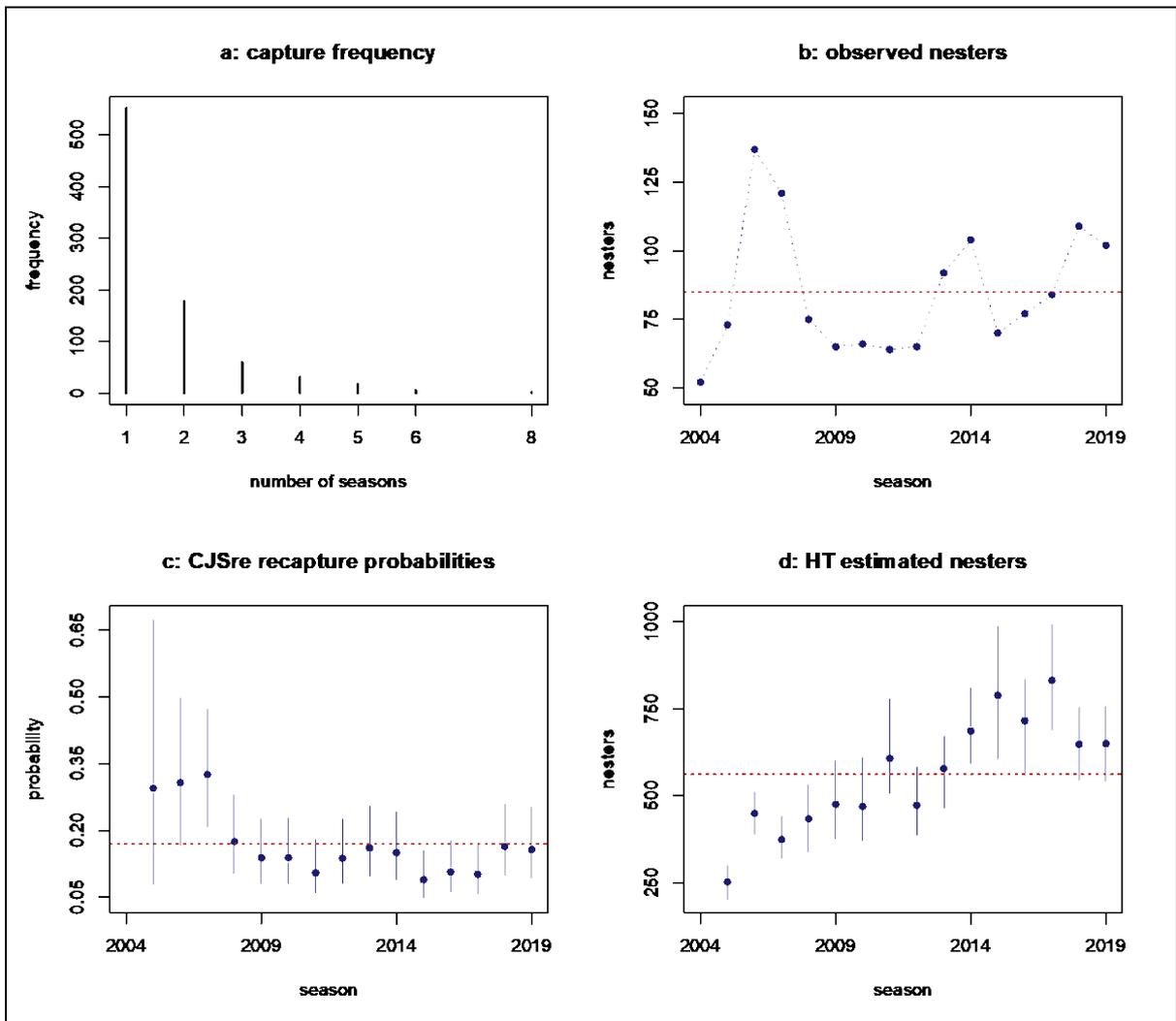


(B)



**Figure 2: Great Barrier Reef region monthly averaged time series since 1980 for (a) sea surface temperature based on the ERSST v5 and (b) bimonthly Multivariate ENSO Index.**

- Thin black line in each panel shows the monthly averaged values.
- The blue curve shows a GAMM smooth curve (and 95% confidence band) superimposed to highlight the underlying long-term trend to derive the annualized estimates.



**Figure 3: Flinders Beach, Mapoon nesting numbers and recapture probability**

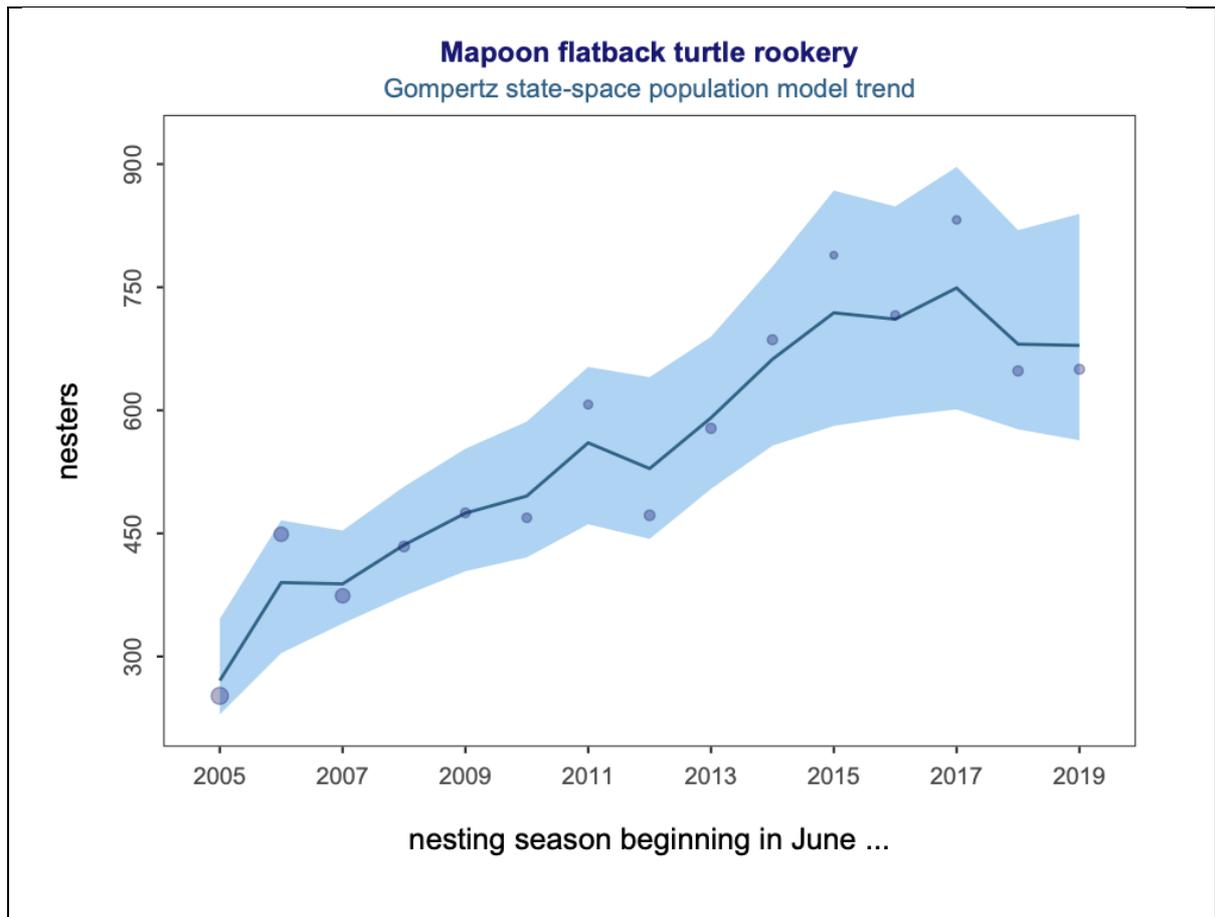
Panel (a): seasonal capture frequency (number of seasons that each tagged turtle was found nesting at the Mapoon rookery).

Panel (b): number of tagged nesters recorded each season at Mapoon.

Panel (c): estimated recapture probabilities from the best-fit CJS model with random effects accounting for both survival and recapture heterogeneity.

Panel (d): Horwitz-Thompson estimates of nester abundance (and 95% bootstrapped-based confidence intervals) of Flatback turtle nesting at Mapoon since 2004 derived from the best-fit CJS random effects model.

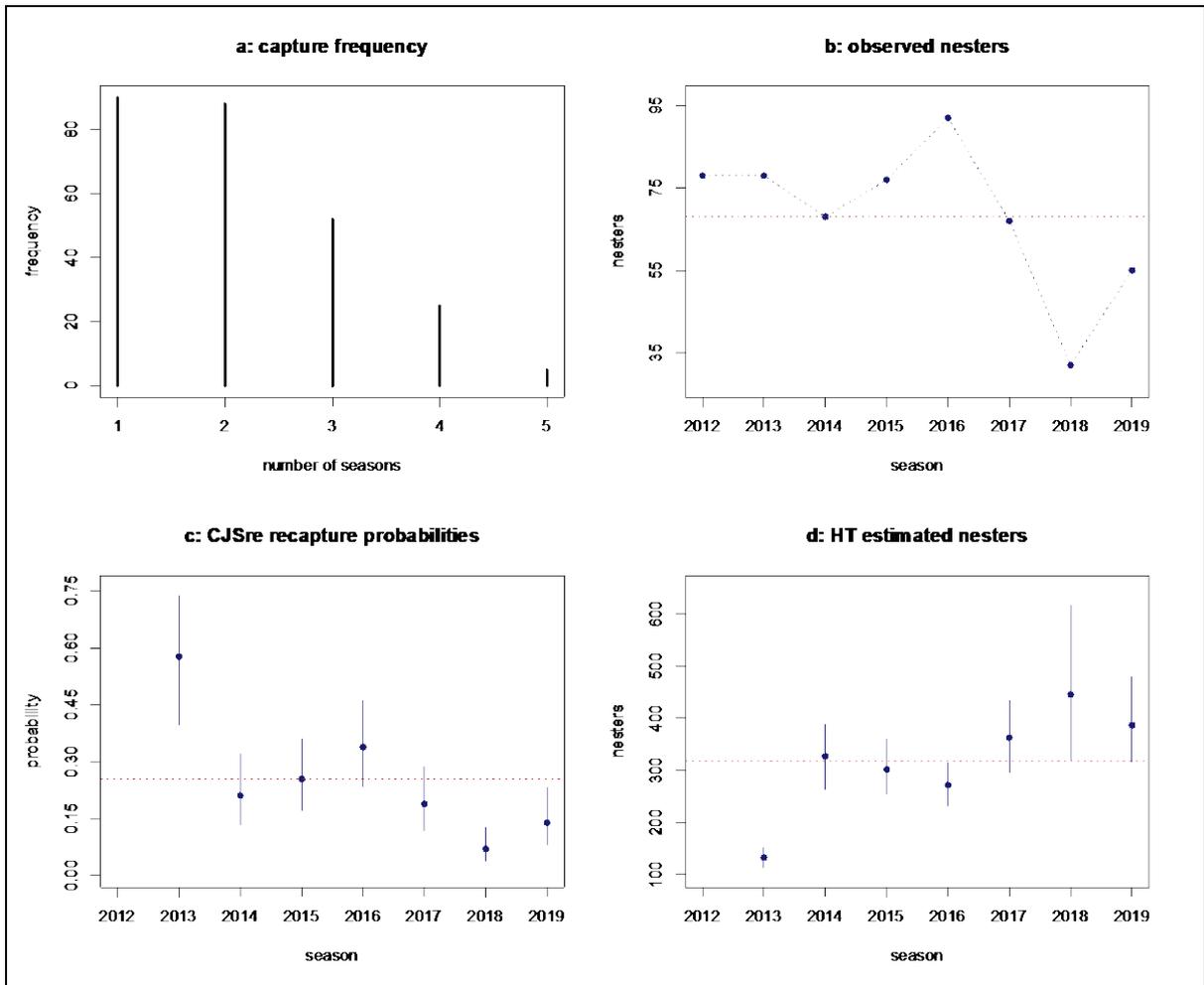
- Dashed horizontal line in panels (b-d) shows the long-term mean value for that panel (which are 85, 0.17 and 562 respectively).



**Figure 4: Flinders Beach, Mapoon rookery population trend**

Estimated nester population trend at the Mapoon Flatback rookery derived using an inverse-precision weighted density-dependent Gompertz population dynamics model (Anderson *et al.* 2017) fitted within a Bayesian state-space modelling framework (Pedersen *et al.* 2011) using JAGS (Plummer 2015, 2016).

- Solid dots are the annual nester counts derived from the estimated annual nester abundance (Fig 3d) with the dot size proportional to precision of those estimates (Fig 3d).
- Solid curve shows the expected model trend fitted to those annual estimates and weighted by the precision of those estimates.
- Shaded polygon shows the 95% credible region for that trend.



**Figure 5: Avoid Island rookery nesting numbers and recapture probability**

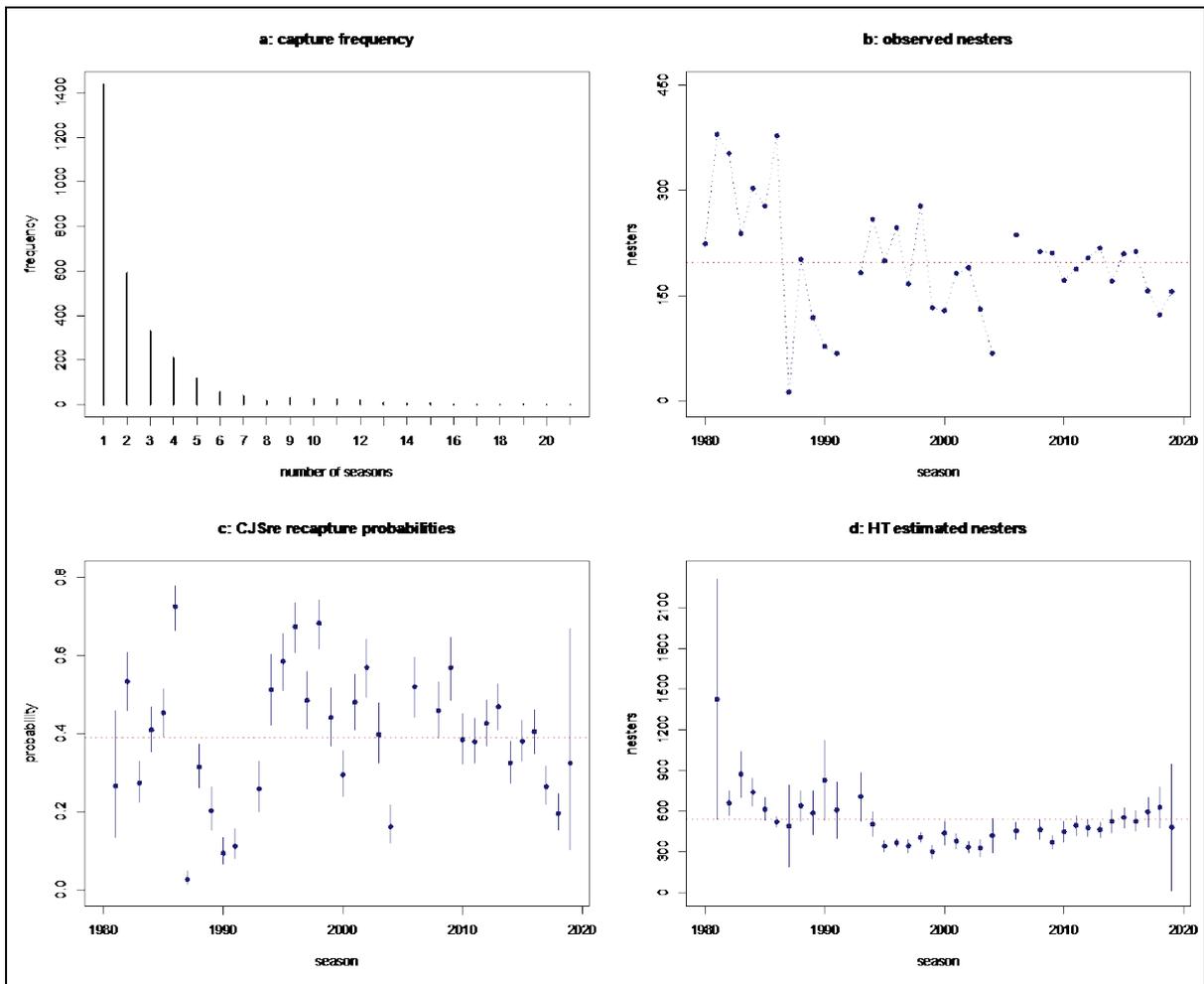
Panel (a): seasonal capture frequency (number of seasons that each tagged turtle was found nesting at the Avoid Island rookery).

Panel (b): number of tagged nesters recorded each season at the Avoid Island rookery.

Panel (c): estimated recapture probabilities from the best-fit CJS model with random effects accounting for both survival and recapture heterogeneity.

Panel (d): Horwitz-Thompson estimates of nester abundance (and 95% bootstrapped-based confidence intervals) of Flatback turtle nesting at Avoid Island since 2012 derived from the best-fit CJS random effects model.

- Dashed horizontal line in panels (b-d) shows the long-term mean value for that panel (which are 68, 0.25 and 319 respectively).



**Figure 6: Peak Island rookery nesting numbers and recapture probability**

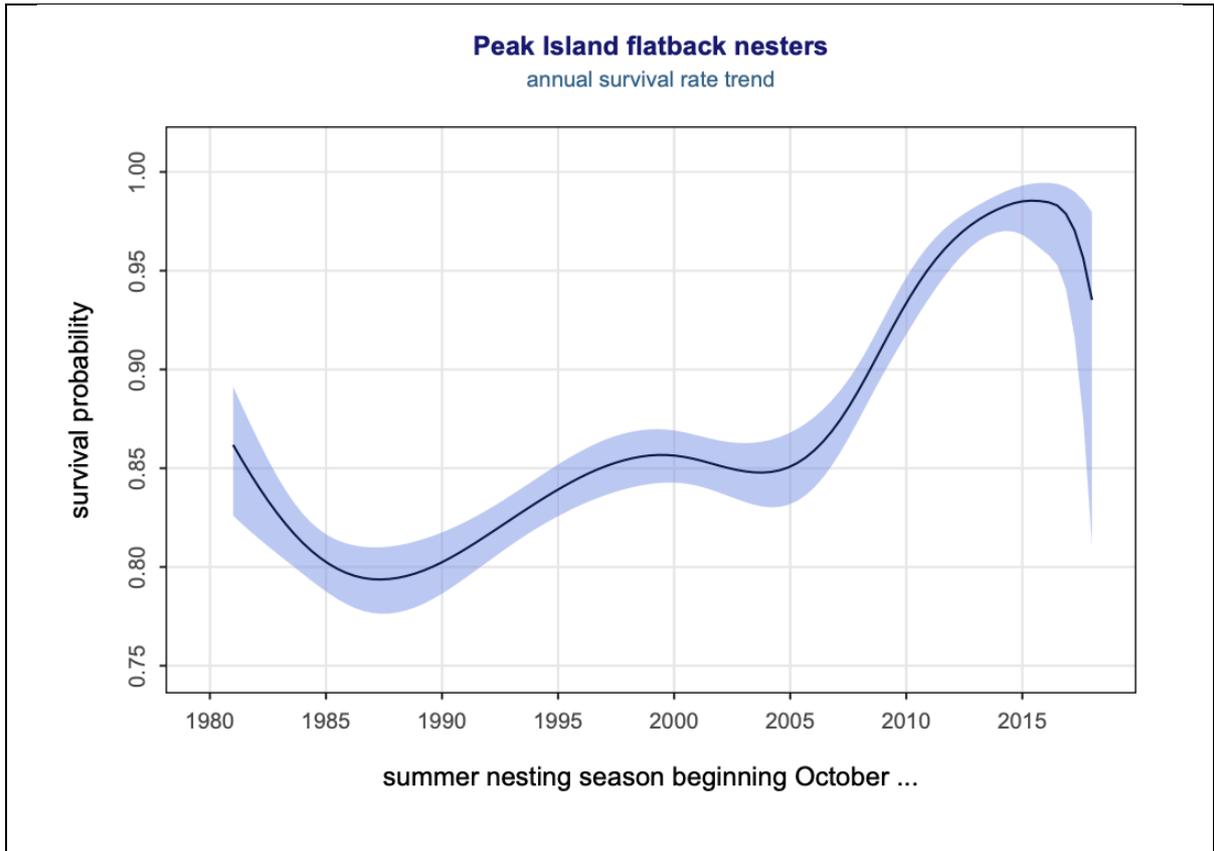
Panel (a): seasonal capture frequency (number of seasons that each tagged turtle was found nesting at the Peak Island rookery).

Panel (b): number of tagged nesters recorded each season at the Peak Island rookery.

Panel (c): estimated recapture probabilities from the best-fit CJS model with random effects accounting for both survival and recapture heterogeneity.

Panel (d): Horwitz-Thompson estimates of nester abundance (and 95% bootstrapped-based confidence intervals) of Flatback turtle nesting at Peak Island since 1980 derived from the best-fit CJS random effects model.

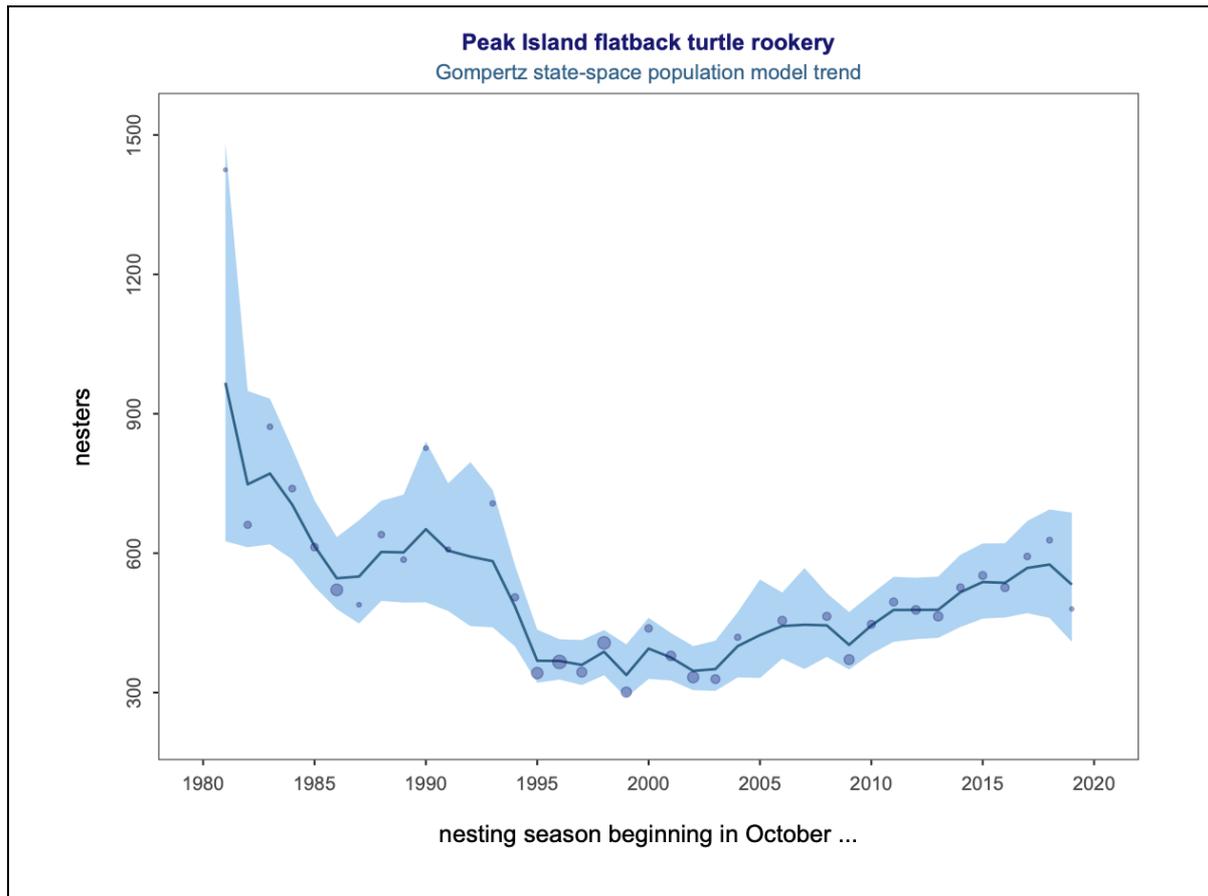
- Dashed horizontal line in panels (b-d) shows the long-term mean value for that panel (which are 197, 0.39 and 537 respectively).



**Figure 7: Peak Island rookery survival rate trend**

Time-varying survival rate trend for Peak Island nesting Flatback turtles.

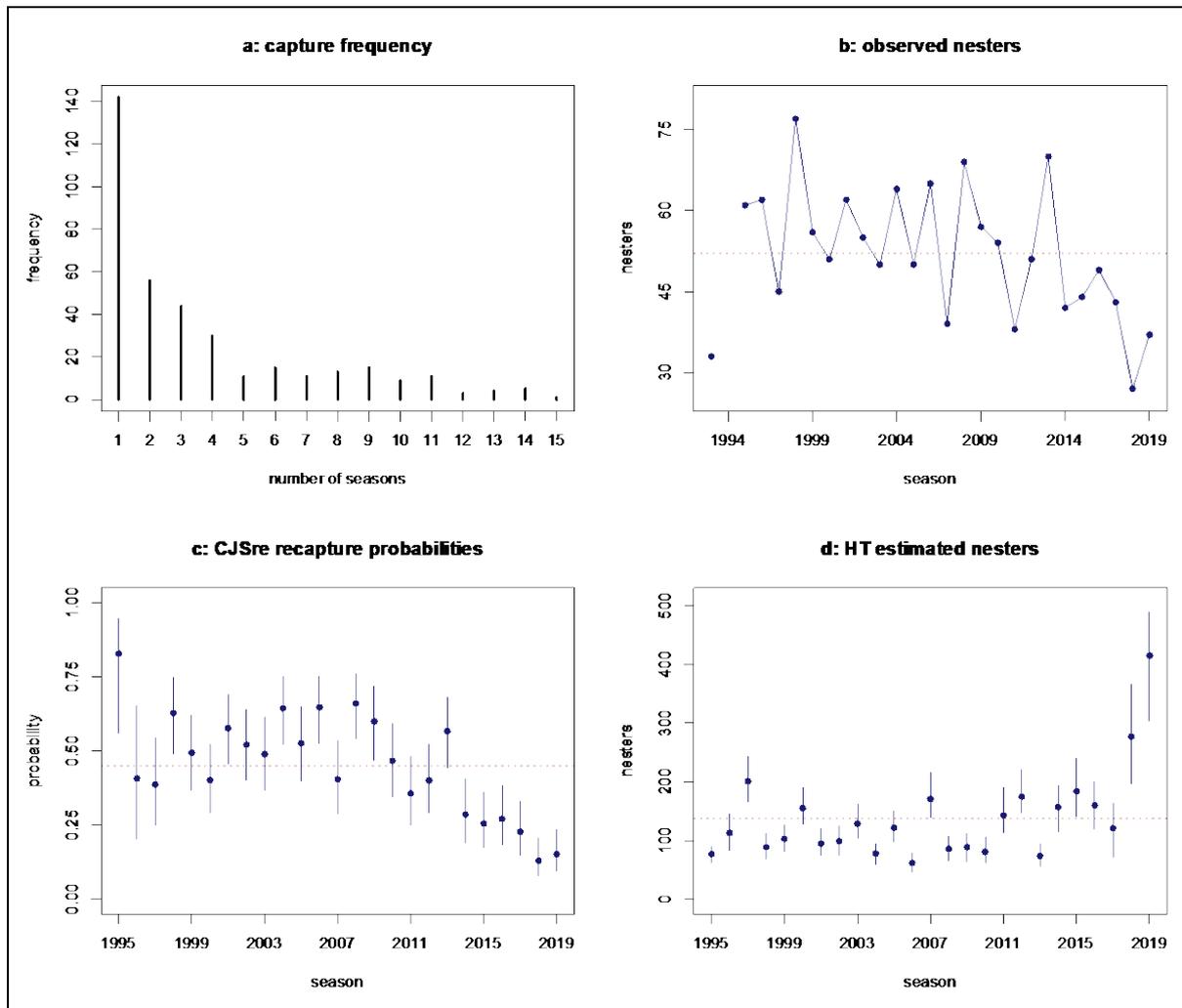
- Solid curve = mean estimate
- Shaded polygon = 95% confidence interval.



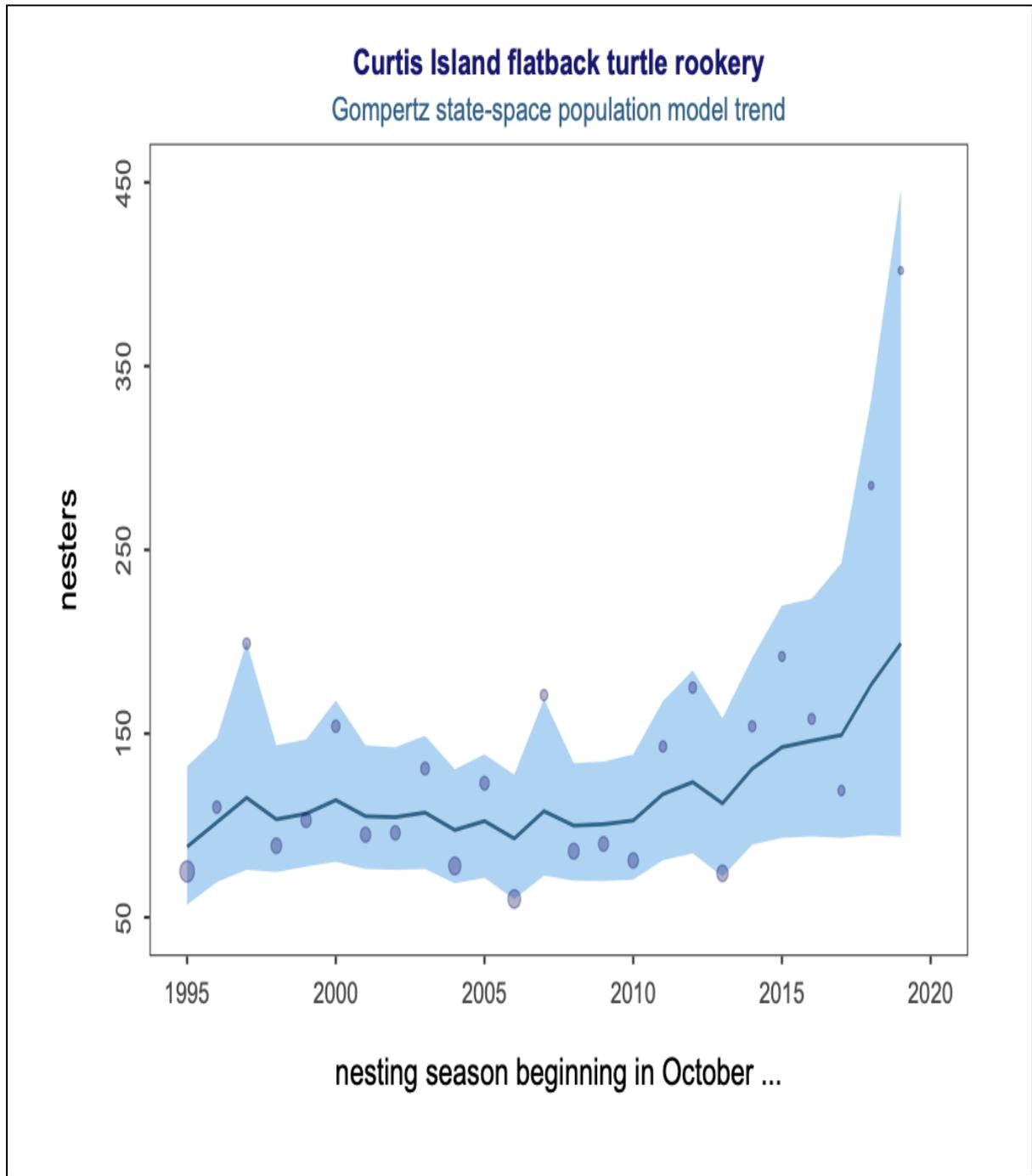
**Figure 8: Peak Island rookery population trend**

Estimated nester population trend at the Peak Island Flatback turtle rookery derived using an inverse-precision weighted density-dependent Gompertz population dynamics model (Anderson *et al.* 2017) fitted within a Bayesian state-space modelling framework (Pedersen *et al.* 2011) using JAGS (Plummer 2015, 2016).

- Solid dots are the annual nester counts derived from the estimated annual nester abundance (Fig 6d) with the dot size proportional to precision of those estimates (Fig 6d);
- Solid curve shows the expected model trend fitted to those annual estimates and weighted by the precision of those estimates
- Shaded polygon shows the 95% credible region for that trend.



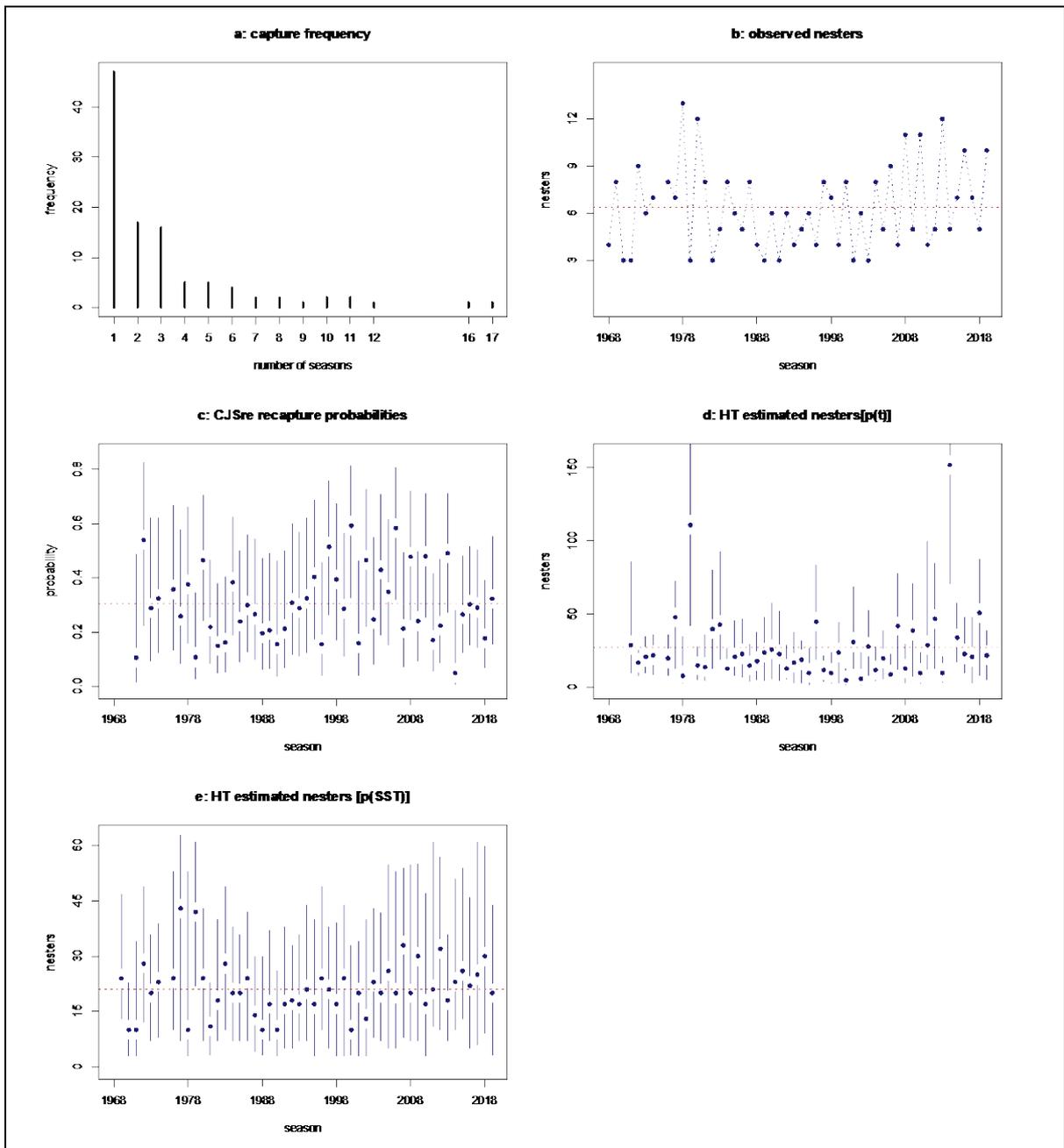
**Figure 9: Curtis Island rookery nesting numbers and recapture probability**  
 Panel (a): seasonal capture frequency (number of seasons that each tagged turtle was found nesting at the Curtis Island rookery).  
 Panel (b): number of tagged nesters recorded each season at the Curtis Island rookery.  
 Panel (c): estimated recapture probabilities from the best-fit CJS model with random effects accounting for both survival and recapture heterogeneity.  
 Panel (d): Horwitz-Thompson estimates of nester abundance (and 95% bootstrapped-based confidence intervals) of Flatback turtle nesting at Curtis Island since 1993 derived from the best-fit CJS random effects model.  
 Dashed horizontal line in panels (b-d) shows the long-term mean value for that panel (which are 52, 0.45 and 138 respectively).



**Figure 10: Curtis Island rookery population trend**

Estimated nester population trend at the Curtis Island Flatback turtle rookery derived using an inverse-precision weighted density-dependent Gompertz population dynamics model (Anderson *et al.* 2017) fitted within a Bayesian state-space modelling framework (Pedersen *et al.* 2011) using JAGS (Plummer 2015, 2016).

- Solid dots are the annual nester counts derived from the estimated annual nester abundance (Fig 9d) with the dot size proportional to precision of those estimates (Fig 9d).
- Solid curve shows the expected model trend fitted to those annual estimates and weighted by the precision of those estimates.
- Shaded polygon shows the 95% credible region for that trend.



**Figure 11: Woongarra Coast rookery nesting numbers and recapture probability**

Panel (a): seasonal capture frequency (number of seasons that each tagged turtle was found nesting at the Woongarra Coast rookery).

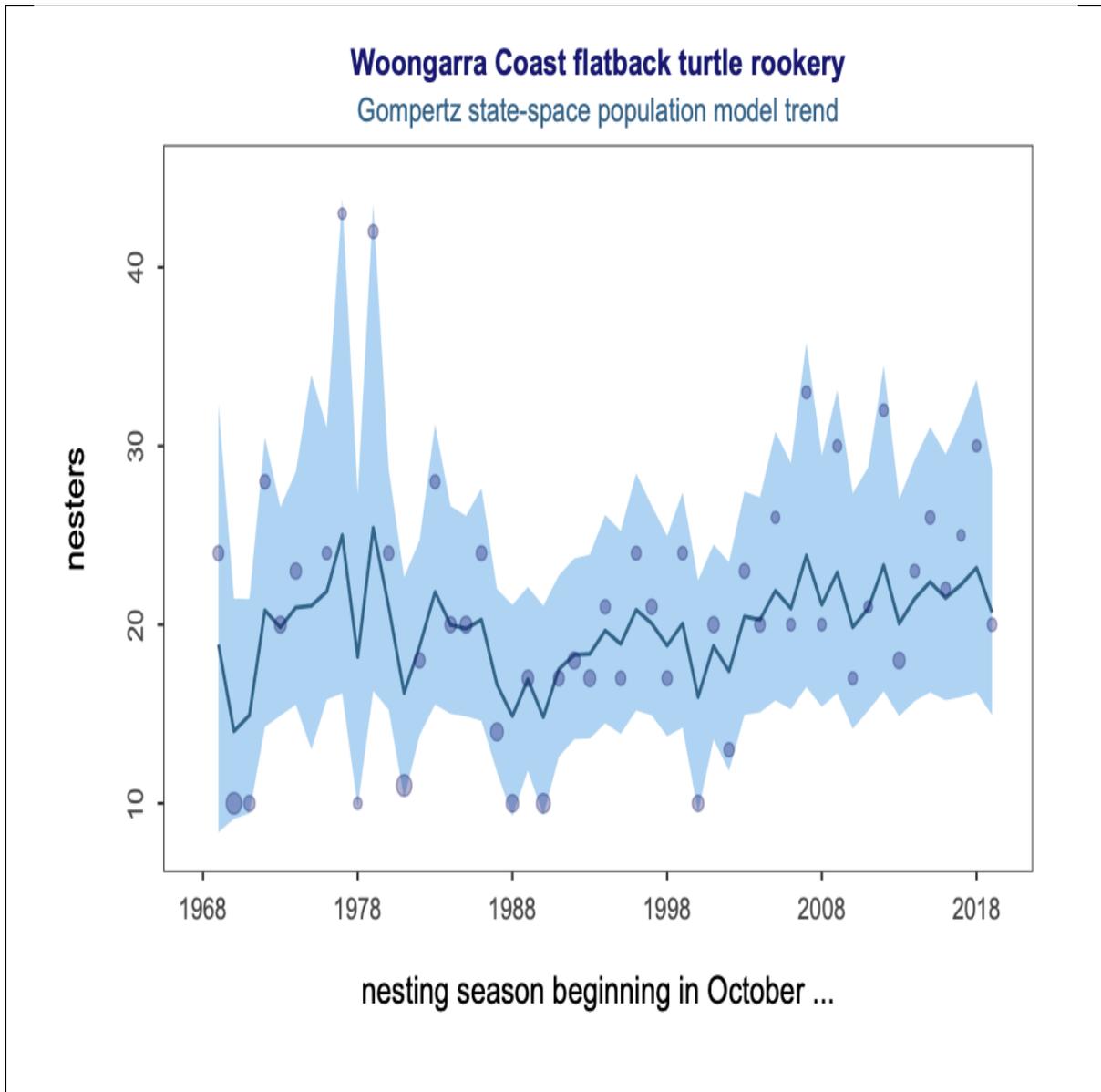
Panel (b): number of tagged nesters recorded each season at the Woongarra Coast.

Panel (c): estimated recapture probabilities from the best-fit CJS model with random effects accounting for both survival and recapture heterogeneity.

Panel (d): Horwitz-Thompson estimates of nester abundance (and 95% bootstrapped-based confidence intervals) of Flatback turtle nesting at the Woongarra Coast rookery since 1968 derived from the best-fit CJS random effects model with time-dependent recapture rates.

- Panel (e): Horwitz-Thompson estimates of nester abundance (and 95% bootstrapped-based confidence intervals) of Flatback turtle nesting at the Woongarra Coast rookery since 1968 derived from a CJS random effects model with recapture rates that are a function of regional SST.

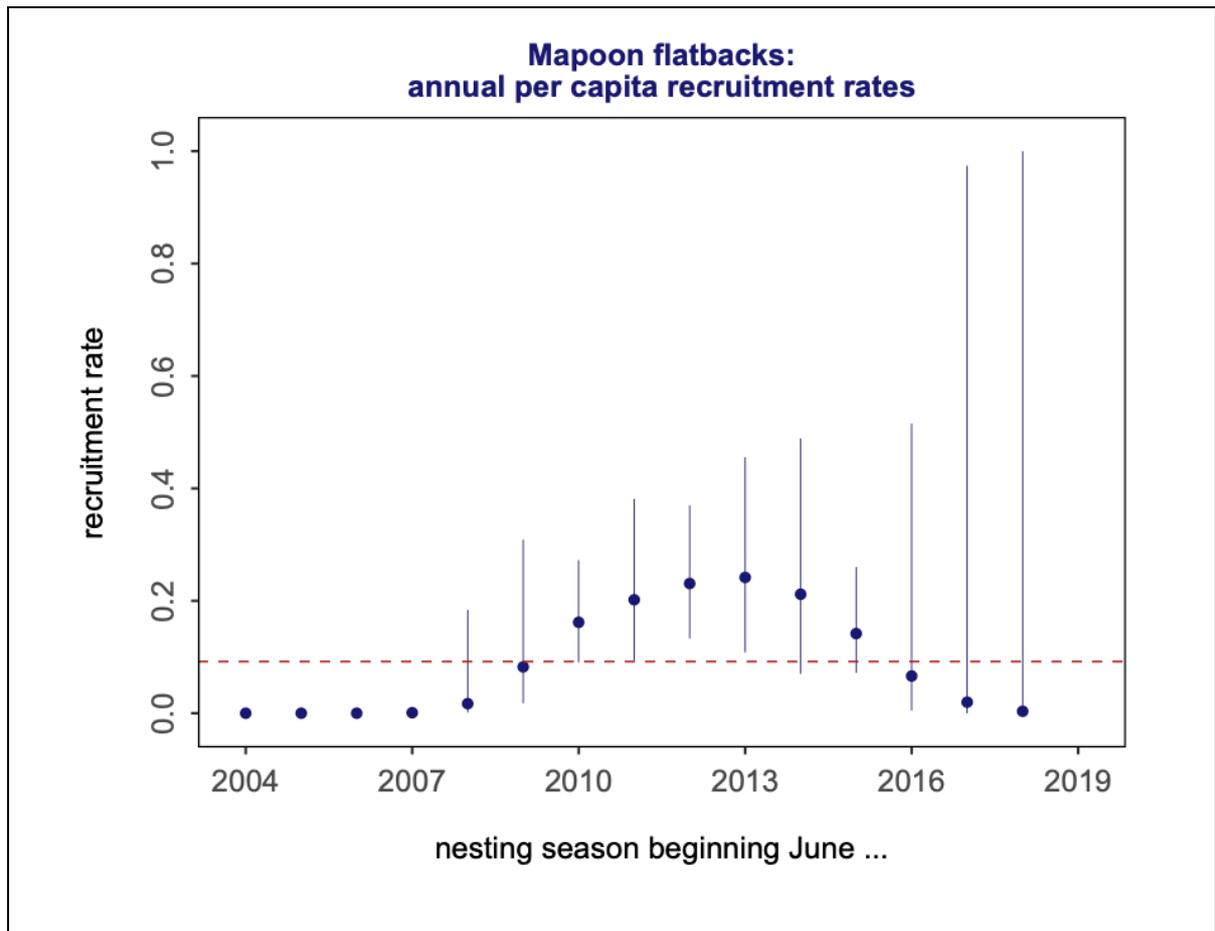
- Dashed horizontal line in panels (b-e) shows the long-term mean value for that panel (which are 6.4, 0.30 and either 27 (d) or 21 (e)).



**Figure 12: Woongarra Coast rookery population trend**

Estimated nester population trend at the Woongarra Coast Flatback turtle rookery derived using an inverse-precision weighted density-dependent Gompertz population dynamics model (Anderson *et al.* 2017) fitted within a Bayesian state-space modelling framework (Pedersen *et al.* 2011) using JAGS (Plummer 2015, 2016).

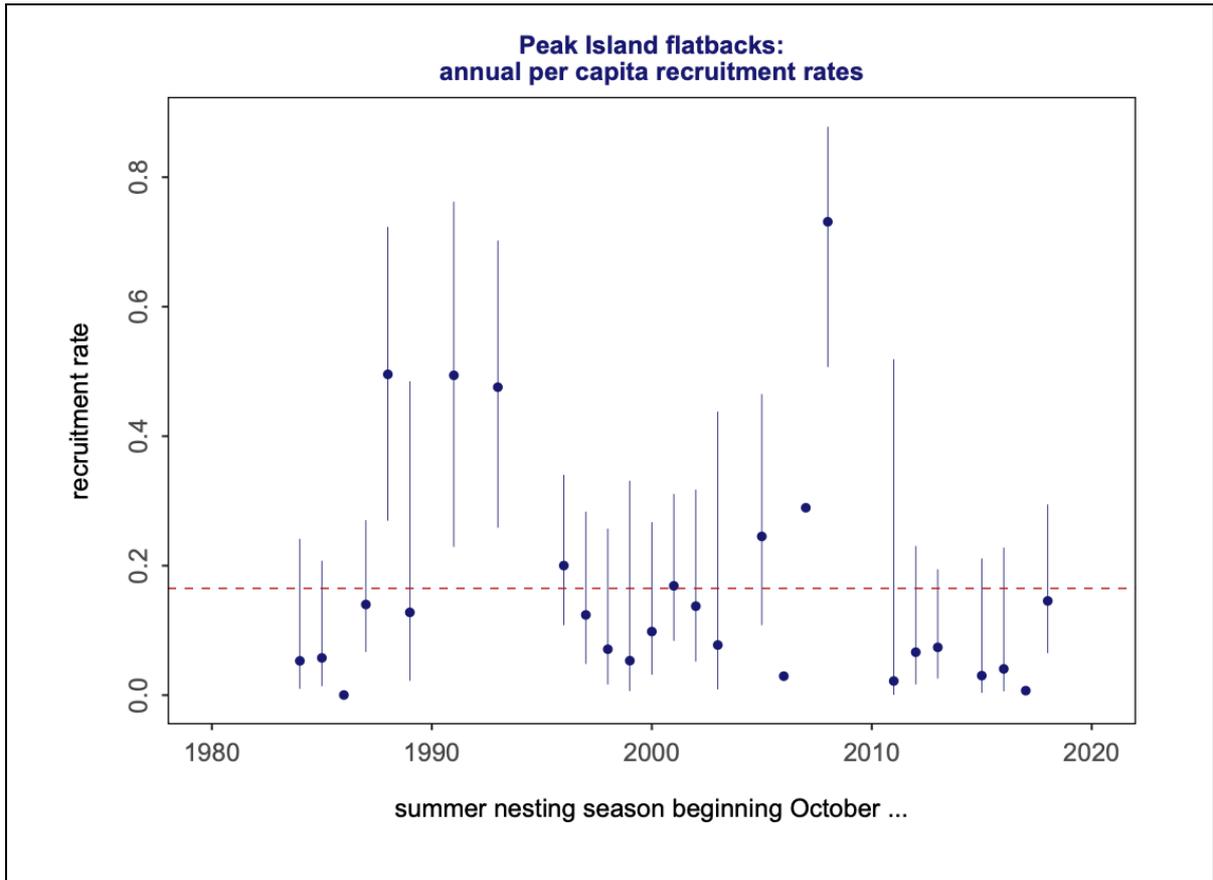
- Solid dots are the annual nester counts derived from the estimated annual nester abundance (Fig 11e) with the dot size proportional to precision of those estimates (Fig 11e).
- Solid curve shows the expected model trend fitted to those annual estimates and weighted by the precision of those estimates.
- Shaded polygon shows the 95% credible region for that trend.



**Figure 13: Flinders Beach, Mapoon rookery recruitment rate**

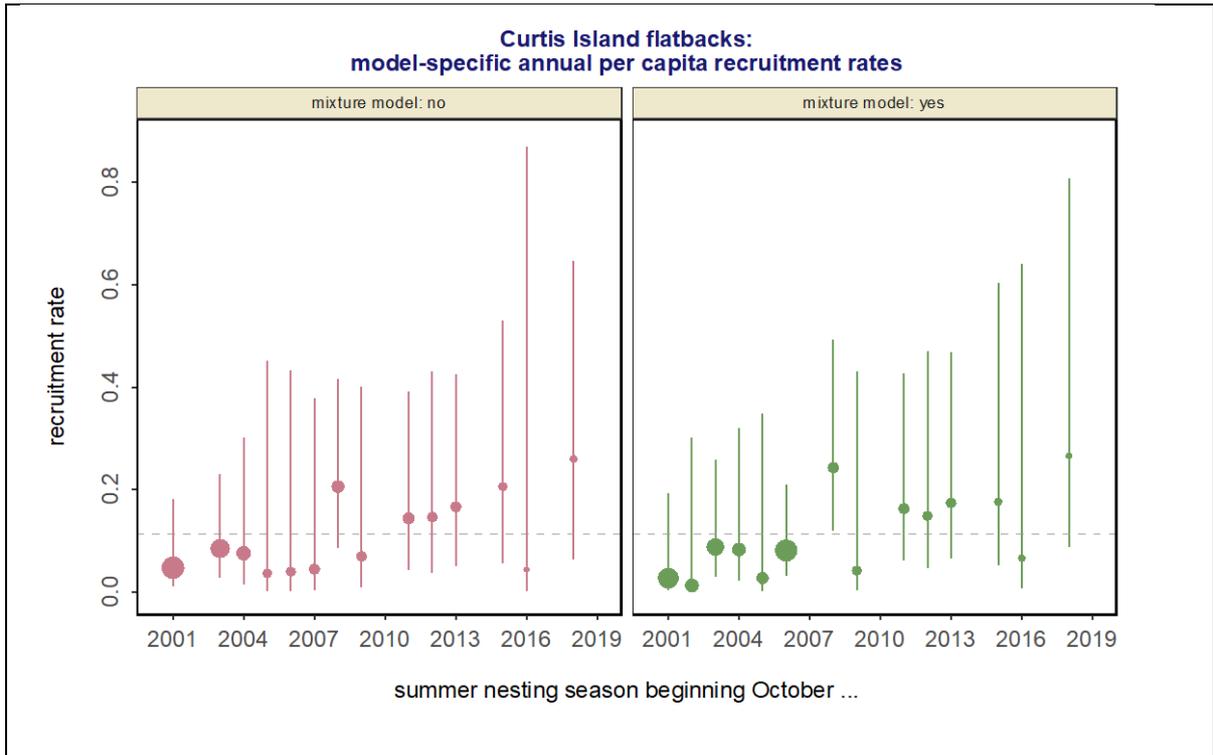
Annual per capita recruitment rates derived from best-fit Pradel robust design temporal symmetry model with time-dependent recruitment fitted to the CMR histories for 846 Flatback turtles nesting at the Mapoon rookery.

- Solid dots = estimated annual per capita recruitment rate.
- Vertical bars = 95% confidence interval.
- Dashed horizontal line = mean per capita rate (ca. 0.092).



**Figure 14: Peak Island rookery recruitment rate**

Annual per capita recruitment rates derived from best-fit Pradel robust design temporal symmetry model with time-dependent recruitment fitted to the capture-mark-recapture histories for 2933 Flatback turtles nesting at the Peak Island rookery: Solid dots = estimated annual per capita recruitment rate, vertical bars = 95% confidence interval, dashed horizontal line = mean per capita rate (ca. 0.165).



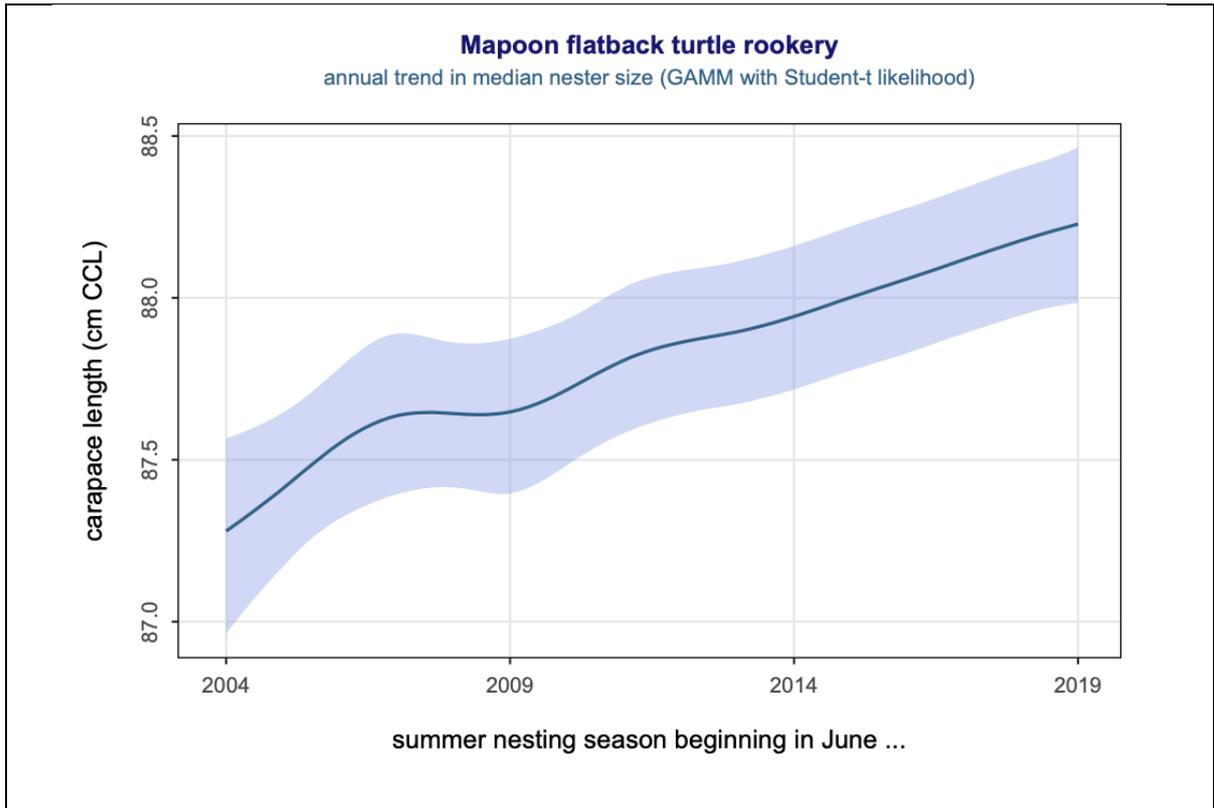
**Figure 15: Curtis Island rookery recruitment rate**

Annual per capita recruitment rates derived from best-fit Pradel robust design temporal symmetry models with time-dependent recruitment fitted to the capture-mark-recapture histories for 370 Flatback turtles nesting at the Curtis Island rookery:

*Left panel* shows model estimates with no accounting for recapture heterogeneity.

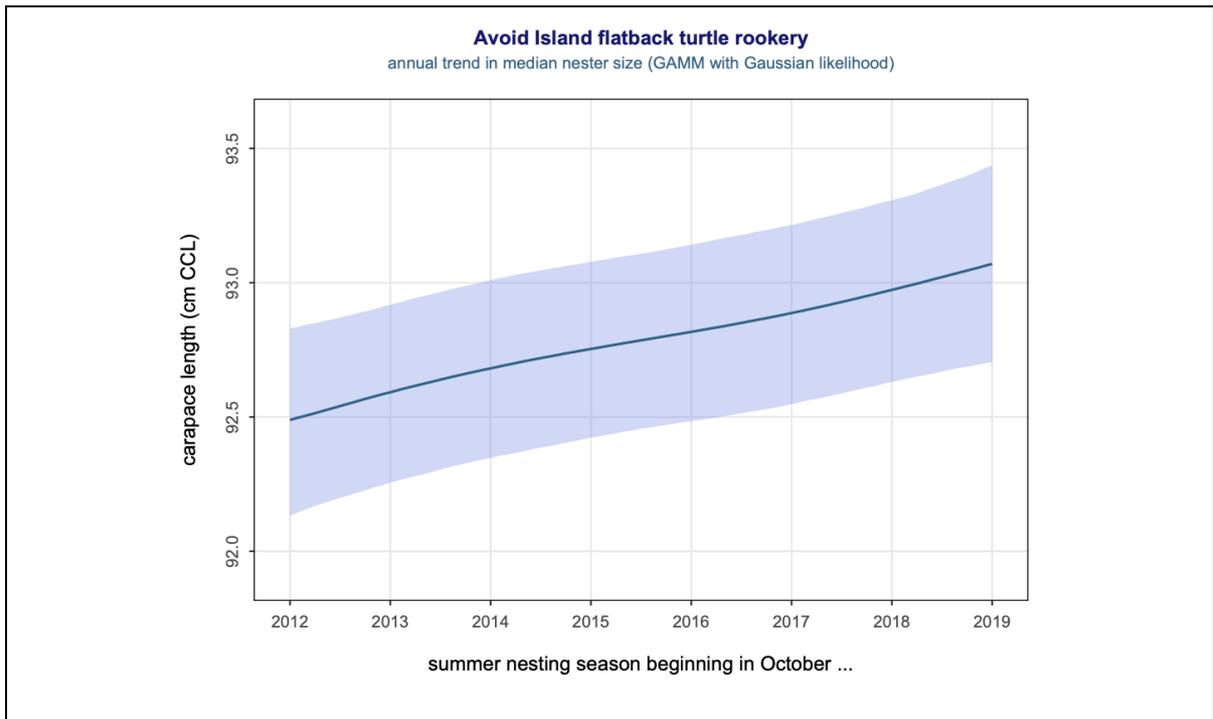
*Right panel* shows model with a mixture component accounting for two distinct classes of detection heterogeneity.

- Solid dots = estimated annual per capita recruitment rate.
- Vertical bars = 95% confidence interval, size of dot is proportional to precision of the annual recruitment rate estimate.
- Dashed horizontal line = mean per capita rate ca. 0.113).



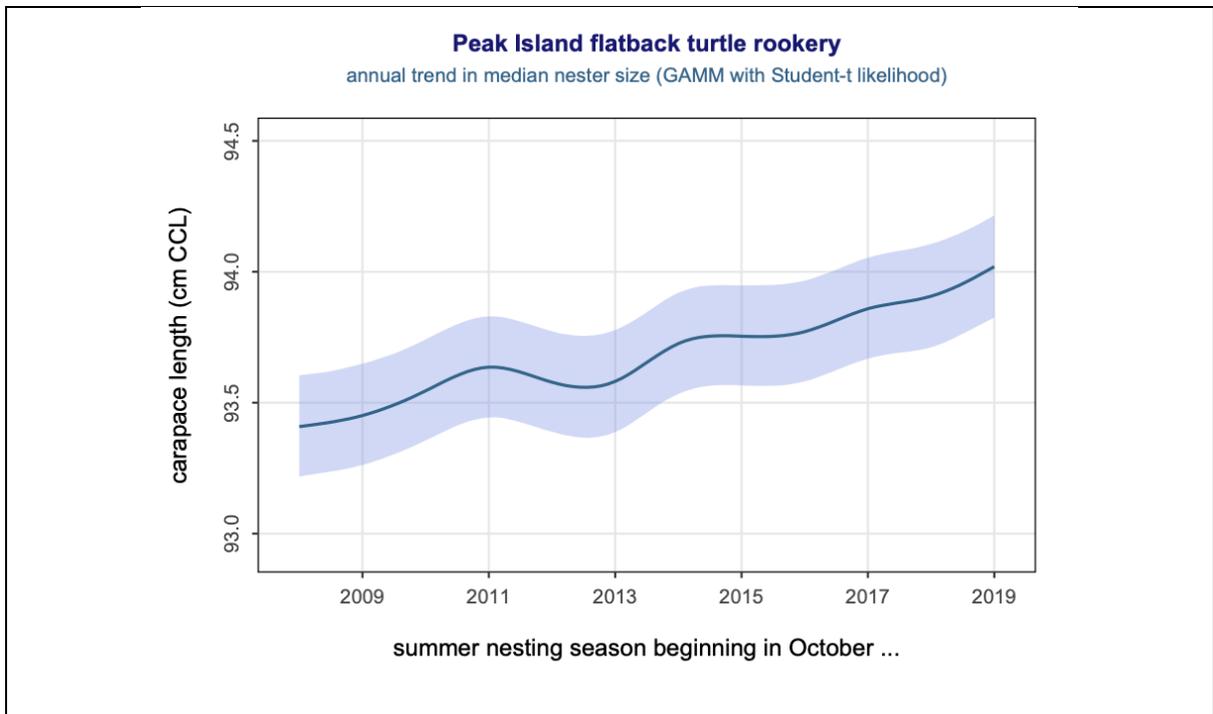
**Figure 16: Temporal carapace size trend at the Mapoon Flatback turtle rookery, Arafura Sea stock, since 2004.**

- Solid curve shows the median trend.
- Shaded polygon shows the 95% credible or uncertainty interval.



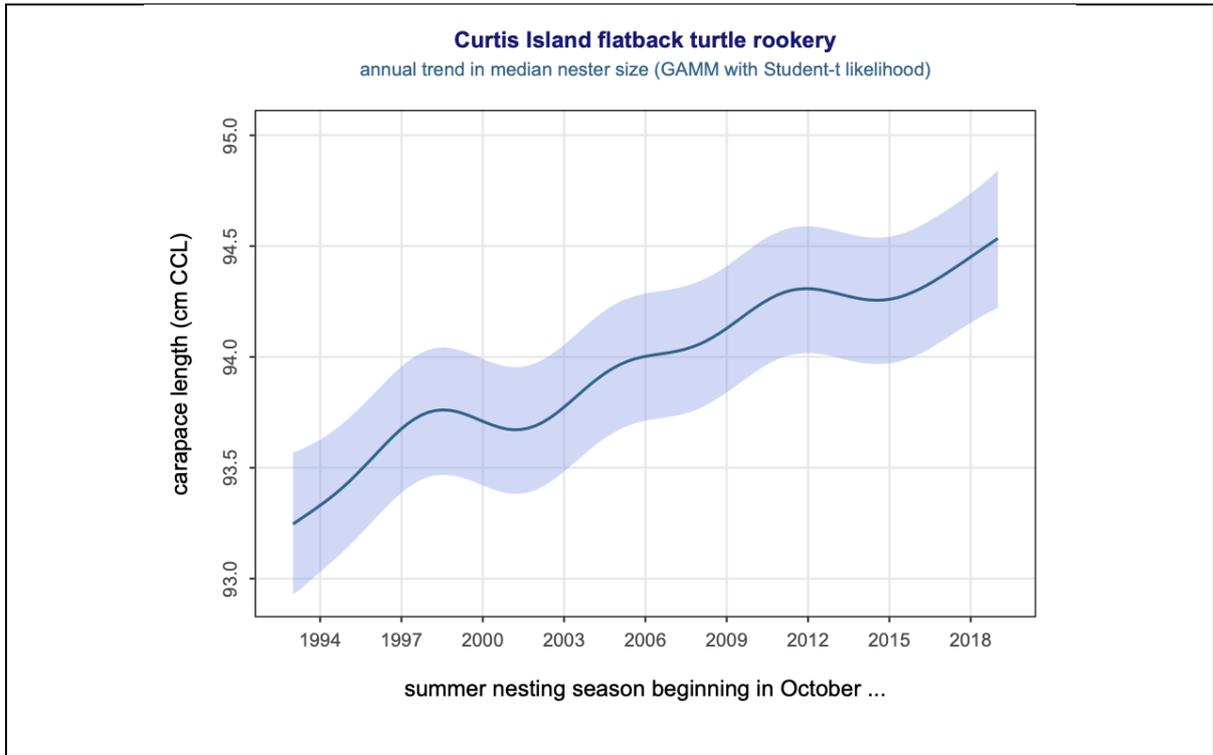
**Figure 17: Temporal carapace size trend at the Avoid Island Flatback turtle rookery, eAust stock, since 2012.**

- Solid curve shows median trend.
- Shaded polygon shows the 95% credible or uncertainty interval.



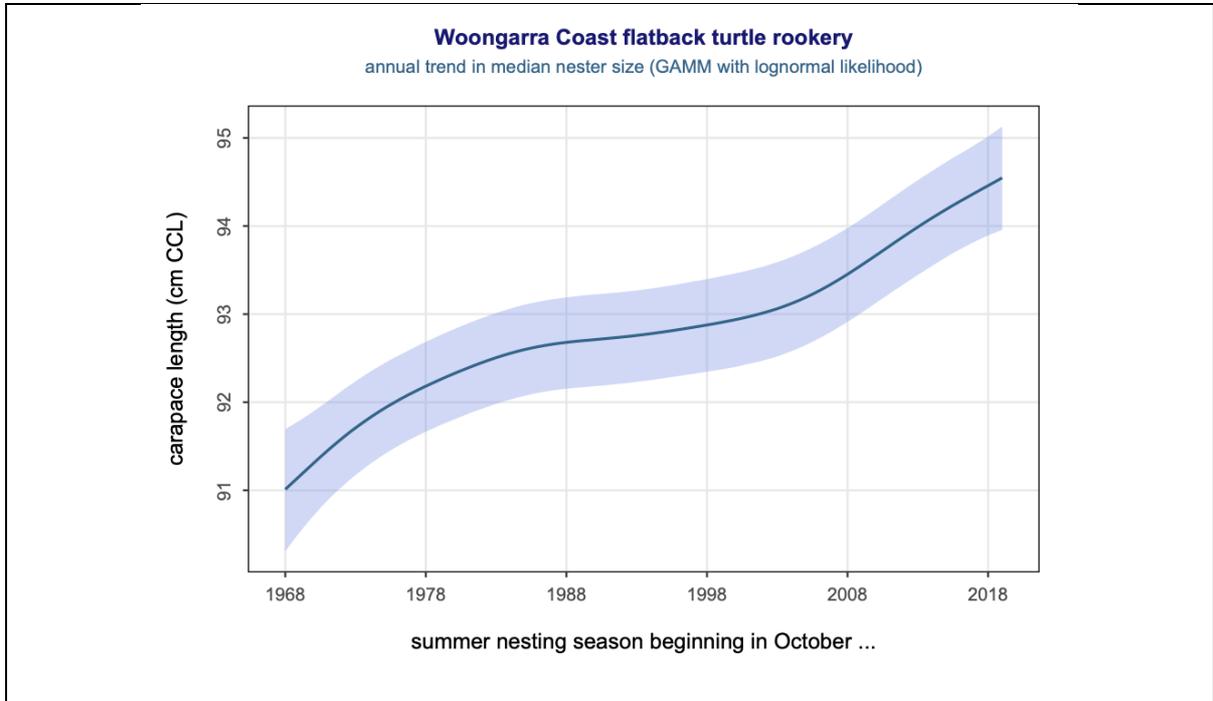
**Figure 18: Temporal carapace size trend at the Peak Island Flatback turtle rookery, eAust stock, since 2008.**

- Solid curve shows median trend.
- Shaded polygon shows the 95% credible or uncertainty interval.



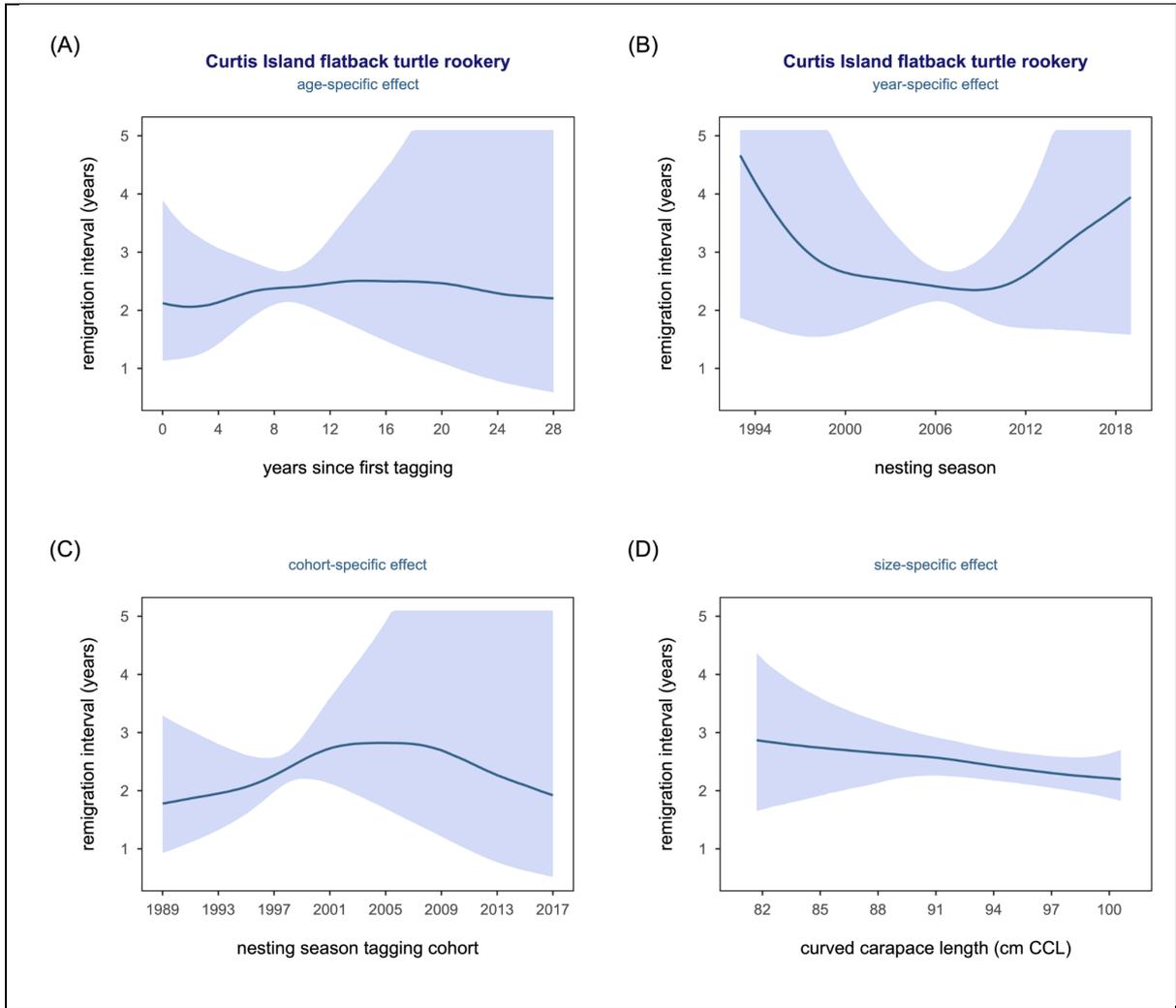
**Figure 19: Temporal carapace size trend at the Curtis Island Flatback turtle rookery, eAust stock, since 1993.**

- Solid curve shows median trend.
- Shaded polygon shows the 95% credible or uncertainty interval.



**Figure 20: Temporal carapace size trend at the Woongarra Coast Flatback turtle rookery, eAust stock, since 1968.**

- Solid curve shows median trend.
- Shaded polygon shows the 95% credible or uncertainty interval.

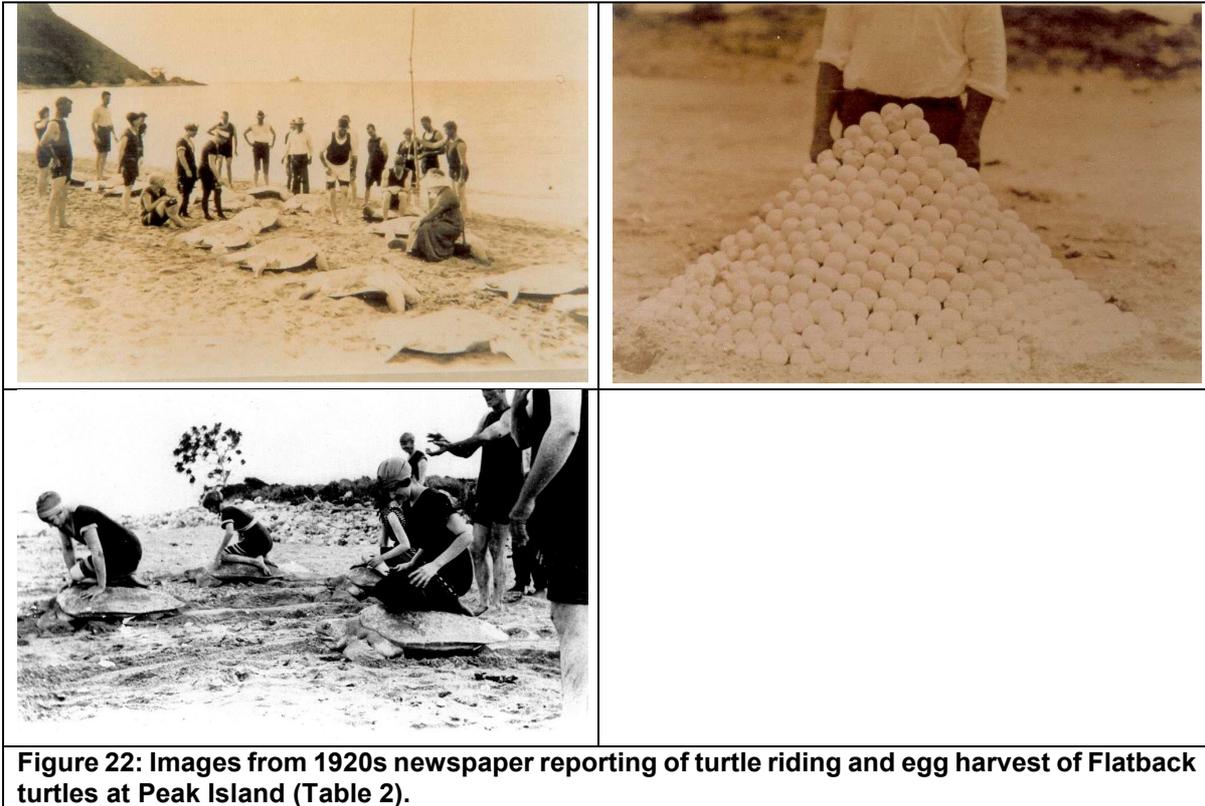


**Figure 21: Curtis Island rookery remigration interval trends**

Solid curve in each panel shows the median trend while the shaded polygon shows the 95% credible or uncertainty interval.

Panels A-C: Nonlinear age-year-cohort specific effects summary for the Curtis Island remigration interval data.

Panel D: Carapace size was also included as a predictor along with the three predictors shown in (a-c).



**Figure 22: Images from 1920s newspaper reporting of turtle riding and egg harvest of Flatback turtles at Peak Island (Table 2).**

### Supplementary Table A

Summary of rookery-specific CJS random effects models to estimate survival and recapture rates.

- *agebin* = time-since-marking (2-ageclass), *time* = sampling season,
- *Phi*=survival,
- *p*=recapture,
- *td* = trap-dependent effect,
- 1 = constant,
- *sigmap* = recapture heterogeneity,
- *Cohort* = tagging cohort as a continuous variable,
- *cohort* = tagging cohort as a discrete factor variable,
- *np* = number of estimable parameters,
- $\square$ AICc = difference in sample size corrected
- $\Delta$ AICc value compared to previous model,
- *bs(x,df=4)* = B-spline function to model nonlinear form for the cohort effect

**Table 3: Supplementary A - Avoid Island Rookery**

model	model structure	np	$\square$ AICc	$\Delta$ AICc	weight	Deviance
9	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>agebin</i> ) <i>sigmap</i> (~1) <i>p</i> (~ <i>time</i> + <i>td</i> )	10	1213.30	0.00	6.023701e-01	1192.84
3	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~ <i>time</i> + <i>td</i> )	10	1214.88	1.57	2.741491e-01	1194.42
6	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> ( <i>Time</i> , <i>df</i> = 4)) <i>sigmap</i> (~1) <i>p</i> (~ <i>time</i> + <i>td</i> )	12	1216.47	3.16	1.234806e-01	1191.82
4	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> ( <i>Time</i> , <i>df</i> = 4)) <i>sigmap</i> (~1) <i>p</i> (~ <i>td</i> )	7	1243.15	29.84	1.986452e-07	1228.92
7	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>agebin</i> ) <i>sigmap</i> (~1) <i>p</i> (~ <i>td</i> )	4	1276.58	63.27	095631e-14	1268.49
1	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~ <i>td</i> )	4	1278.73	65.43	3.730401e-15	1270.65
2	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~ <i>time</i> )	7	1360.06	146.76	0.000000e+00	284.12
5	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> ( <i>Time</i> , <i>df</i> = 4)) <i>sigmap</i> (~1) <i>p</i> (~ <i>time</i> )	8	1361.90	148.59	0.000000e+00	283.89
8	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>agebin</i> ) <i>sigmap</i> (~1) <i>p</i> (~ <i>time</i> )	8	1361.90	148.59	0.000000e+00	283.89

**Table 4: Supplementary A - Peak Island Rookery**

model	model structure	np	□AICc	ΔAICc	weight	Deviance
21	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Time, df = 6)) <i>sigmap</i> (~1) <i>p</i> (~time + td)	45	19555	37	0.00	19464.78
7	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Cohort, 6)) <i>sigmap</i> (~1) <i>p</i> (~time + td)	45	19709	22	153.84	19618.63
14	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~time + td)	39	19978.91	423.53	0	19900.46
28	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>agebin</i> ) <i>sigmap</i> (~1) <i>p</i> (~time + td)	39	20137.81	582.43	0	20059.36
19	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Time, df = 6)) <i>sigmap</i> (~1) <i>p</i> (~td)	10	20464.48	909.11	0	20444.45
5	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Cohort, 6)) <i>sigmap</i> (~1) <i>p</i> (~td)	10	20713.72	1158.34	0	20693.69
26	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>agebin</i> ) <i>sigmap</i> (~1) <i>p</i> (~td)	5	20758.94	1203.56	0	20748.92
12	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~td)	4	20946.60	1391.23	0	20938.59
20	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Time, df = 6)) <i>sigmap</i> (~1) <i>p</i> (~time)	43	22327.22	2771.85	0	9756.64
16	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Time, df = 6)) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sst) + time)	44	22330.69	2775.31	0	9758.08
18	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Time, df = 6)) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sstl) + time)	46	22333.30	2777.92	0	9756.64
2	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Cohort, 6)) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sst) + time)	44	22520.49	2965.11	0	9947.88
4	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Cohort, 6)) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sstl) + time)	44	22520.49	2965.11	0	9947.88
6	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Cohort, 6)) <i>sigmap</i> (~1) <i>p</i> (~time)	44	22520.49	2965.11	0	9947.88
23	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>agebin</i> ) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sst) + time)	38	22615.89	3060.51	0	10055.43
25	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>agebin</i> ) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sstl) + time)	38	22615.89	3060.51	0	10055.43
27	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>agebin</i> ) <i>sigmap</i> (~1) <i>p</i> (~time)	38	22615.89	3060.51	0	10055.43
9	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sst) + time)	38	22827.59	3272.22	0	10267.13
11	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sstl) + time)	38	22827.59	3272.22	0	10267.13
13	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~time)	38	22827.59	3272.22	0	10267.13
15	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Time, df = 6)) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sst))	12	23047.81	3492.43	0	10539.72
17	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Time, df = 6)) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sstl))	12	23153.39	3598.01	0	10645.30
1	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Cohort, 6)) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sst))	12	23270.24	3714.86	0	10762.15
3	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>bs</i> (Cohort, 6)) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sstl))	12	23317.31	3761.94	0	10809.22
22	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>agebin</i> ) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sst))	6	23362.26	3806.89	0	10866.21
24	<i>sigmaphi</i> (~1) <i>Phi</i> (~ <i>agebin</i> ) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sstl))	6	23422.58	3867.20	0	10926.52
8	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sst))	6	23573.89	4018.52	0	11077.84
10	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~ <i>bs</i> (sstl))	6	23679.22	4123.85	0	11183.17

**Table 5: Supplementary A - Curtis Island Rookery**

model	model structure	np	□AICc	ΔAICc	weight	Deviance
40	<i>sigmaphi</i> (~1) <i>Phi</i> (~agebin) <i>sigmap</i> (~1) <i>p</i> (~time + td)	29	3650.81	0.00	9.825459e-01	3591.46
32	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Time, df = 4)) <i>sigmap</i> (~1) <i>p</i> (~time + td)	29	3658.88	8.06	1.743381e-02	3593.23
24	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~time + td)	28	3672.67	21.85	1.766819e-05	3615.40
16	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Cohort, 4)) <i>sigmap</i> (~1) <i>p</i> (~time + td)	32	3677.06	26.24	1.963771e-06	3611.41
29	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Time, df = 4)) <i>sigmap</i> (~1) <i>p</i> (~bs(sst1) + td)	11	3679.22	28.40	6.687734e-07	3657.01
15	<i>sigmaphi</i> (~1) <i>Phi</i> (~cohort) <i>sigmap</i> (~1) <i>p</i> (~time + td)	48	3690.18	39.36	2.777883e-09	3590.46
37	<i>sigmaphi</i> (~1) <i>Phi</i> (~agebin) <i>sigmap</i> (~1) <i>p</i> (~bs(sst1) + td)	8	3709.26	58.44	2.000497e-13	3693.15
30	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Time, df = 4)) <i>sigmap</i> (~1) <i>p</i> (~td)	8	3719.15	68.33	1.427202e-15	3703.04
10	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Cohort, 4)) <i>sigmap</i> (~1) <i>p</i> (~bs(sst1) + td)	11	3722.98	72.16	0	3700.77
21	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~bs(sst1) + td)	7	3723.43	72.61	0	3709.34
9	<i>sigmaphi</i> (~1) <i>Phi</i> (~cohort) <i>sigmap</i> (~1) <i>p</i> (~bs(sst1) + td)	30	3740.44	89.62	0	3678.99
38	<i>sigmaphi</i> (~1) <i>Phi</i> (~agebin) <i>sigmap</i> (~1) <i>p</i> (~td)	5	3743.89	93.07	0	3733.84
12	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Cohort, 4)) <i>sigmap</i> (~1) <i>p</i> (~td)	8	3751.60	100.78	0	3735.49
22	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~td)	4	3753.84	103.02	0	3745.80
11	<i>sigmaphi</i> (~1) <i>Phi</i> (~cohort) <i>sigmap</i> (~1) <i>p</i> (~td)	27	3769.02	118.20	0	3713.84
39	<i>sigmaphi</i> (~1) <i>Phi</i> (~agebin) <i>sigmap</i> (~1) <i>p</i> (~time)	28	4332.33	681.51	0	2766.31
31	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Time, df = 4)) <i>sigmap</i> (~1) <i>p</i> (~time)	30	4338.73	687.91	0	2768.52
23	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~time)	27	4363.78	712.96	0	2799.85
14	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Cohort, 4)) <i>sigmap</i> (~1) <i>p</i> (~time)	31	4368.24	717.42	0	2795.94
13	<i>sigmaphi</i> (~1) <i>Phi</i> (~cohort) <i>sigmap</i> (~1) <i>p</i> (~time)	48	4380.03	729.21	0	2771.56
36	<i>sigmaphi</i> (~1) <i>Phi</i> (~agebin) <i>sigmap</i> (~1) <i>p</i> (~bs(sst1))	7	4387.09	736.27	0	2864.25
28	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Time, df = 4)) <i>sigmap</i> (~1) <i>p</i> (~bs(sst1))	10	4388.23	737.41	0	2859.30
20	<i>sigmaphi</i> (~1) <i>Phi</i> (~1) <i>sigmap</i> (~1) <i>p</i> (~bs(sst1))	6	4419.94	769.12	0	2899.12
8	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Cohort, 4)) <i>sigmap</i> (~1) <i>p</i> (~bs(sst1))	10	4422.14	771.32	0	2893.22
35	<i>sigmaphi</i> (~1) <i>Phi</i> (~agebin) <i>sigmap</i> (~1) <i>p</i> (~bs(sst))	7	4430.72	779.90	0	2907.88
7	<i>sigmaphi</i> (~1) <i>Phi</i> (~cohort) <i>sigmap</i> (~1) <i>p</i> (~bs(sst1))	28	4432.73	781.91	0	2866.72
27	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Time, df = 4)) <i>sigmap</i> (~1) <i>p</i> (~bs(sst))	10	4436.59	785.77	0	2907.67
25	<i>sigmaphi</i> (~1) <i>Phi</i> (~bs(Time, df = 4)) <i>sigmap</i> (~1) <i>p</i> (~bs(wei))	10	4438.44	787.62	0	2909.52

**Table 5: Supplementary A - Curtis Island Rookery continued...**

model	model structure	np	□AICc	ΔAICc	weight	Deviance
33	<i>sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~bs(meil))</i>	7	4439.01	788.19	0	2916.17
34	34 <i>sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~bs(meil1))</i>	7	4441.07	790.25	0	2918.23
26	<i>sigmaphi(~1)Phi(~bs(Time, df = 4))sigmap(~1)p(~bs(meil1))</i>	10	4447.43	796.61	0	2918.51
6	<i>sigmaphi(~1)Phi(~bs(Cohort, 4))sigmap(~1)p(~bs(sst))</i>	10	4455.88	805.06	0	2926.95
19	<i>sigmaphi(~1)Phi(~1)sigmap(~1)p(~bs(sst))</i>	6	4456.62	805.80	0	2935.80
2	<i>sigmaphi(~1)Phi(~bs(Cohort, 4))sigmap(~1)p(~bs(meil))</i>	10	4460.63	809.81	0	2931.71
17	<i>sigmaphi(~1)Phi(~1)sigmap(~1)p(~bs(meil))</i>	6	4464.24	813.42	0	2943.42
4	<i>sigmaphi(~1)Phi(~bs(Cohort, 4))sigmap(~1)p(~bs(meil1))</i>	10	4465.72	814.90	0	2936.80
18	<i>sigmaphi(~1)Phi(~1)sigmap(~1)p(~bs(meil1))</i>	6	4467.56	816.74	0	2946.74
5	<i>sigmaphi(~1)Phi(~cohort)sigmap(~1)p(~bs(sst))</i>	29	4469.19	818.38	0	2901.09
1	<i>sigmaphi(~1)Phi(~cohort)sigmap(~1)p(~bs(meil))</i>	29	4474.43	823.61	0	2906.32
3	<i>sigmaphi(~1)Phi(~cohort)sigmap(~1)p(~bs(meil1))</i>	29	4479.54	828.72	0	2911.44

**Table 6: Supplementary A - Woongarra Coast Rookery**

model	model structure	np	□AICc	ΔAICc	weight	Deviance
4	<i>sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~time)</i>	50	1193.67	0.00	0.8914	900.29
3	<i>sigmaphi(~1)Phi(~bs(Time, 6))sigmap(~1)p(~time)</i>	55	1198.58	4.90	0.0768	890.71
2	<i>sigmaphi(~1)Phi(~1)sigmap(~1)p(~time)</i>	49	1200.49	6.81	0.0295	909.94
1	<i>sigmaphi(~1)Phi(~bs(Cohort, 6))sigmap(~1)p(~time)</i>	55	1205.65	11.97	0.0022	897.78

**Table 7: Supplementary A - Mapoon Rookery**

model	model structure	np	$\square$ AICc	$\Delta$ AICc	weight	Deviance
9	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~time + td)	19	3234.00	0.00	7.660694e-01	3195.38
3	sigmaphi(~1)Phi(~bs(Cohort, 4))sigmap(~1)p(~time + td)	22	3237.19	3.18	1.554566e-01	3192.37
6	sigmaphi(~1)Phi(~bs(Time, df = 4))sigmap(~1)p(~time + td)	22	3238.56	4.56	7.808644e-02	3193.74
4	sigmaphi(~1)Phi(~bs(Time, df = 4))sigmap(~1)p(~td)	7	3249.26	15.25	3.721979e-04	3235.17
7	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~td)	5	3255.90	21.89	1.346281e-05	3245.85
1	sigmaphi(~1)Phi(~bs(Cohort, 4))sigmap(~1)p(~td)	8	3259.76	25.75	1.953140e-06	3243.64
5	sigmaphi(~1)Phi(~bs(Time, df = 4))sigmap(~1)p(~time)	20	3474.74	240.73	0.000000e+00	1043.62
8	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~time)	18	3475.01	241.01	0.000000e+00	1048.01
2	sigmaphi(~1)Phi(~bs(Cohort, 4))sigmap(~1)p(~time)	21	3477.53	243.52	0.000000e+00	1044.34

### Supplementary Table B:

Summary of rookery-specific Pradel temporal symmetry models to estimate per capita recruitment.

- *time* = sampling season,
- *Phi* = survival, *p*=recapture,
- *f* = recruitment,
- *1* = constant,
- *np* = number of estimable parameters,
- $\square$  *AICc* = difference in sample size correcte,
- *AICc* value compared to previous model,
- *bs(x,df=6)* = B-spline function to model nonlinear form for that effect,
- *mei* = Multivariate ENSO Index,
- *meil1* = Multivariate ENSO Index lagged one year,
- *sst* = sea surface temperature,
- *sstl1* = sea surface temperature lagged one year

**Table 8: Supplementary B - Peak Island Rookery**

model	model structure	np	$\square$ <b>AICc</b>	$\Delta$ AICc	weight	Deviance
4	Phi(~bs(Time, df = 6))p(~time)f(~time)	6	41772.09	0.00	1.00	9847.34
2	Phi(~time)p(~time)f(~time)	115	41828.73	56.63	5.028317e-13	9809.59
1	Phi(~time)p(~time)f(~1)	77	42200.06	427.96	0	10258.98
3	Phi(~bs(Time, df = 6))p(~time)f(~1)	44	42210.62	438.52	0	10336.66

**Table 9: Supplementary B - Curtis Island Rookery**

model	model structure	np	□AICc	ΔAICc	weight	Deviance
6	Phi(~1)p(~time)f(~time)	42	6615.088	0.00	9.999970e-01	2828.11
2	Phi(~1)p(~time)f(~bs(meil))	29	6640.539	25.45	2.974421e-06	2881.01
3	Phi(~1)p(~time)f(~bs(meil1))	30	6954.291	339.20	0	3192.67
5	Phi(~1)p(~time)f(~bs(sst1))	30	6967.302	352.21	0	3205.68
1	Phi(~1)p(~time)f(~1)	27	6971.343	356.25	0	3215.99
4	Phi(~1)p(~time)f(~bs(sst))	30	6971.837	356.74	0	3210.21

**Table 10: Supplementary B - Mapoon Rookery**

model	model structure	np	□AICc	ΔAICc	weight	Deviance
2	Phi(~bs(Time, 4))p(~time)f(~bs(Time, 4))	26	8075.050	0.00	0.995591174	1076.52
1	Phi(~bs(Time, 4))p(~time)f(~1)	22	8085.889	10.83	0.004408826	1095.65