ESTIMATION OF POPULATION SIZE AND COMPARISON OF THE BENEFITS OF MID-SEASON CENSUS AND WHOLE OF BREEDING SEASON CENSUS OF FLATBACK TURTLE REPRODUCTION IN EASTERN AUSTRALIA

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Cover photographs:
Scenes from the census of flatback turtles, *Natator depressus*, in eastern Australia

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EXECUTIVE SUMMARY

This report summarises the results of monitoring the eastern Australian flatback turtle nesting population at representative index beaches (Curtis Island, Peak Island, Avoid Island) across much of the population's nesting range during the 2016-2017 breeding season:

- **Curtis Island:** Capture-mark-recapture (CMR) histories were compiled for 425 nesting flatback turtles tagged over the 22-year summer nesting period from 1995 to 2016.
- **Peak Island:** CMR histories were compiled for 722 nesting flatback turtles tagged over the 9-year summer nesting period from 2008 to 2016.
- **A *void Island:*** CMR histories were compiled for 230 nesting flatback turtles tagged over the 5-year summer nesting period from 2012 to 2016.

It is expected that about nine years of continuous capture-mark-recapture (tagging) study will be required to provide rigorous estimates of population trends and survival and recruitment probabilities.

- **Curtis Island** has changed little during 1996-2011 but is showing signs of an approximate 50% increase in the total adult female population that visits this island since 2010.
- **Peak Island** has suffered an approximate 50% decline in the total adult female population that visits this island between 1981 and 2009 (Limpus*et al*. 2013). However, the current analysis indicates that the population decline has slowed considerably during 2010 to 2016.
- **Avoid Island**: The five years of data are inadequate for providing a clear indication of trend for this population. However, there may be an increase in the population since the study began in 2012.

These data suggest that there has been some positive change in the abundance of adult female flatback turtles associated with these rookeries since about 2010.

The mean annual survival probabilities for these populations are high but with Curtis Island recording the lowest value and wider confidence limits.

Mean annual survival probability:

- **Curtis island**: 0.95 (95% CI: 0.94 – 0.96).
- **Peak Island**: 0.96 (SD = 0.015).

- **Avoid Island**: the calculated mean annual survival probability of 1.00 is considered meaningless because of the brevity of the monitoring period at this time.

Curtis Island is currently the only site for which robust long term recruitment rates can be quantified for Curtis Island:

- The mean long term annual recruitment rate has been about 0.08 across two decades of monitoring.
- The annual recruitment rate has been declining since about 2009.
- The recent recruitment rate of less than 0.05 for the Curtis Island population is of concern.

These studies demonstrate that capture-mark-recapture (tagging project) data gathered from a two-week, mid-season tagging census can produce robust estimates of total population size, annual survival probability, annual recruitment probability as well as long term trends for these significant demographic parameters.

Comparisons are made of the effectiveness of monitoring during a two-week, mid-season census for the nesting and subsequent hatching approximately 7-8 weeks later and of monitoring across and entire breeding season which was conducted at only Curtis and Avoid Islands.

While long-term total tagging census across entire breeding seasons may result similar mean results but with some reductions in the breadth of confidence limits, it is debatable whether the increased costs and logistical constraints of staffing teams on islands for 14 plus weeks of continuous monitoring could be justified for quantification these population demographic studies alone.

There are three critically important demographic parameters with respect to marine turtle population dynamics that can be quantified only by a whole of nesting season monitoring:

- Number of clutches laid for the season per female derived from tagging census,
- overall seasonal hatchling production which is derived from excavation of emerged clutches throughout the season, and
- hatchling sex ratio derived from interpretation of sand temperature data which can be monitored with the continual presence of personnel.

There were no significant differences between values derived from the two week, mid-season census and from the census across the entire breeding season at both Curtis Island and Avoid Island for the following parameters: Adult female nesting success, size of nesting females, remigration interval, incubation period to emergence, incubation success of eggs, and hatchling emergence success (Table 4).

The only parameter that showed a difference between mid-season and whole-season census was the proportion of new recruits to the nesting population at Curtis Island (12% and 27% respectively. Table 4).

While there were no differences identified for incubation period to emergence, incubation success of eggs, and hatchling emergence success during the 2016-2017 breeding season, this is not always the case. During the latter part of the flatback breeding season, there can be significant variability across years in impacts on incubating eggs and hatchlings leaving the nests. This variability depends on the frequency and intensity of cyclones with associated cooling of nests during heavy rainfall, flooding of nests with rising water tables and loss of clutches through beach erosion and storm surge flooding.

Hatchling sex ratios were predicted to be very strongly female biased from the 2016-2017 breeding season at Curtis, Peak and Avoid Islands. The majority of males would have been produced during brief periods of cool sand that occurred with periods of heavy rain (based on sand temperature data and incubation period to emergence data), or early in the season. At Avoid Island additional male hatchlings would have been produced from the limited number of clutches laid during the early nesting season or those laid in densely shaded areas of the dunes.

ESTIMATION OF POPULATION SIZE AND COMPARISON OF THE BENEFITS OF MID-SEASON CENSUS AND WHOLE OF BREEDING SEASON CENSUS OF FLATBACK TURTLE REPRODUCTION IN EASTERN AUSTRALIA.

INTRODUCTION

As demonstrated by the monitoring of Flatback turtle breeding on central Queensland nesting beaches (Limpus *et al*. 2017; Hamann *et al*. 2003; Miller and Limpus, 2003; Miller *et al.* 2003), marine turtle populations are often logistically challenging to monitor at their nesting beaches because adult turtles migrate from distant foraging areas to traditional nesting beaches to which the individual females display high fidelity within and between breeding seasons. The female does not provide maternal care for the eggs that she lays but moves off shore to prepare another clutch of eggs. Each female lays several clutches of eggs within a single breeding season at about two-week intervals, The females are not synchronised in their arrival to commence nesting within a single night and nor are they synchronised for arrival within a breeding season, with the season's new arrivals spread over several months. The adult turtles return to their respective distant foraging areas at the completion of the breeding season (Wilderman *et al*. 2017). The vast majority of the females do not breed in successive years but skip a variable number of years between breeding seasons.

With nesting beaches ranging from hundreds of metres to kilometres in length and with multiple turtles arriving at night, it requires a team of volunteers to patrol a beach to encounter, tag measure and record other data for all turtles arriving nightly. If the intention is to tag every turtle arriving for the entire season, then the team has to monitor the nesting beaches nightly for the several months duration of the nesting season. If hatchling production is to be similarly monitored, the beach will have to be monitored for at least an additional two months to examine the clutches after hatchlings emerge from the nests.

With capture-mark-recapture (CMR) studies, analysis of the data can provide estimates of the total population utilising the specific nesting beach, annual survival probability of the adult females in the population and annual recruitment of new females entering the breeding population. This is regarded as the gold standard for monitoring the size and performance of the annual nesting population (Bjorndal *et. al*. 2010). With successive years of CMR studies at the same beach, trends in these basic parameters can be determined.

It is possible to derive these same population parameter estimates by similar monitoring with nightly saturation tagging of the nesting turtles for a minimum of two weeks (one re-nesting cycle) at mid-season nesting but with wider confidence limits for the estimates (Limpus, 1985).

Additional parameters including nesting success, re-nesting interval, remigration interval, rates of clutch loss, eggs per clutch and number of eggs per clutch laid per female in a season can be measured during this monitoring and these parameters may change in value at different times of the breeding season. Perturbations may occur with these parameters when extreme weather events such as cyclones and heat waves occur during the summer nesting season.

As a consequence of concerns regarding climate change and predictions for rising sea level, increasing temperatures and more extreme weather events across decades, there is now an imperative to monitor impacts on turtle nesting populations such as reduced hatchling production and feminising of the resulting hatchlings in response to variable occurrence of cyclones, flooding rainfall and heatwaves.

As a consequence, the contract supporting the monitoring of flatback turtle, *Natator depressus*, nesting associated with Port Curtis by the Queensland Department of Environment and Heritage Protection (EHP) has required the assessment of the consequences of monitoring for only the two-week mid-season period and for the entire breeding season.

MONITORING SITES

The three monitoring sites of Curtis, Peak and Avoid Islands support marine turtle nesting dominated by flatback turtles within the eastern Australian genetic stock (eAus) nesting in summer (FitzSimmons and Limpus, 2014). These monitoring sites and the data recorded at each site are described in detail in Limpus *et al*. (2018).

CURTIS ISLAND

South End Beach, Curtis Island, 23.75°S, 151.03°E, supports a medium density nesting population of flatback turtles. This large sand island situated off the coast of Gladstone and forming part of the eastern boundary of Port Curtis extends for ~60 km to the north. South End, a small village, lies on the south-eastern tip of the island. The majority of the turtle nesting for the island occurs on the adjacent South End Beach which is approximately 5 km in length. In some years, there is occasional nesting by green turtles (*Chelonia mydas*) and/or loggerhead turtles (*Caretta caretta*). While the rookery has been monitored intermittently since 1969 (Limpus, 1971), it has been monitored annually since 1994 with support from the Gladstone Ports Corporation (Limpus 2007, Limpus *et al* 2013). Curtis Island has one of the longest histories of monitoring of flatback turtle breeding in Australia, and hence in the world.

PEAK ISLAND

Peak Island, 23.34°S, 150.93°E, supports one of the largest populations of nesting flatback turtles in the east Australian stock (Limpus *et al*. 2013). Peak Island is a continental island in Keppel Bay and sits approximately 15 km off the mainland coast southeast of Yeppoon in eastern Australia. Tenure of the island is “National Park (Scientific)”, which is the strongest level of land management protection under the *Nature Conservation Act 1992*. Peak Island is also surrounded by a one-kilometre wide Preservation Zone within the Great Barrier Reef Coast Marine Park and the Great Barrier Reef Marine Park. The area has been managed by the Department of National Parks, Sport and Racing (NPSR) in accordance with the Keppel Bay Islands National Park (Scientific) and adjoining State Waters Management Plan. As a consequence, the turtle nesting habitat of Peak Island and immediately adjacent inter-nesting habitat are managed to provide the highest level of habitat protection available to any turtle nesting population. The island is closed to visitation by the general public and is uninhabited except by the turtle monitoring team during annual monitoring visits. There is no built structure on the island. Peak Island has one nesting beach on its north-western corner that faces westerly towards the mainland. Only 300 m of this beach provide access to sand dunes suitable for turtle nesting. The other accessible sandy beach is on the south-western side of the island, but rocks under the sand at dune level prevent successful nesting.

AVOID ISLAND

Avoid Island, 21.9744ºS, 149.6500ºE, was selected as an index beach for long-term monitoring as a control site that is not impacted by industrial or urban development. Avoid Island is a continental island located just north of Broad Sound and lying approximately 18 km from the nearest mainland shore and approximately 100 km southeast of the city of Mackay on the mainland coast of eastern Australia. The Queensland Trust for Nature (QTFN) owns the island and manages it as a designated nature refuge. Avoid Island sits within a Habitat Protection Zone of the Great Barrier Reef Coast Marine Park and the Great Barrier Reef Marine Park. The island is closed to visitation by the general public and is uninhabited except by the turtle monitoring team during annual monitoring visits, associated classes visiting for environmental education, and periodic visits by QTFN personnel for maintenance. The Island is approximately 1.6 km long and 0.4 km wide, and has undulating terrain with a rise on the northern end of the island. There are three main nesting beaches (South Beach, Middle Beach, North Beach) on the eastern side of the island that are bordered by rocky outcrops. Each beach is fronted by tidal sandy mud flats with scattered rocky shelves. These beaches are backed by dunes, providing nesting habitat on the beach slope and dunes, which are highest at South Beach. Other beaches on the island are either too narrow and rocky to provide suitable nesting habitat, though occasional nesting occurs on West Beach, the largest westerly facing beach.

METHODOLOGY FOR BEACH RELATED STUDIES

Unless otherwise stated, standard census methods were applied at all three census beaches, Curtis, Peak and Avoid Islands. Standard Queensland Turtle Conservation Project methodologies (Limpus *et al*, 1983; Limpus, 1985, 1992; Limpus *et al*. 2018) were followed for the project. These included:

- Two standard titanium tags (manufactured by Stockbrands Australia) were applied to each turtle on the beach, usually in the left and right axillary tagging positions, generally proximal to the last scute in the flipper closest to the body.
- PIT (Passive Integrated Transponder) tags (Parmenter, 1993) have been used as a second tagging method for identification of nesting females on Curtis Island since the 1997-1998 breeding season, Peak Island since the 2008-2009 season and at Avoid Island since monitoring began there in the 2007-2008 season. The PIT tags are injected usually into the upper left shoulder, below the point of the carapace, but occasionally into the right shoulder.
- Curved carapace length (CCL) has been measured from the skin/carapace junction at the anterior edge of the nuchal scale, along the midline, to the end of the carapace using a flexible fibreglass tape measure (± 0.2 cm).
- A nest tag (flagging tape ~20 cm long) with the date of laying and a tag number of the turtle (Limpus, 1985) was placed in the nest during oviposition for most clutches. The nest tag assisted in identifying the female that laid the clutch and the date laid when hatchlings emerged some two months later.

- Selected clutches of eggs were counted, eggs measured and returned to their nests within two hours of being laid and with minimum rotation to avoid movement induced mortality (Limpus *et al.* 1979).
- A clutch was assessed for incubation success and hatchling emergence success by excavating the nest site, usually 24 hr after the hatchlings have crawled from the nest. A count was made of hatched eggs, unhatched eggs with embryos, unhatched eggs with no signs of embryonic development (= undeveloped egg), eggs showing signs of predation by crabs or other animals (= predated egg), live hatchlings trapped in the nest, and dead hatchlings within the nest.

    Estimated clutch count = hatched eggs + unhatched eggs + undeveloped eggs + predated eggs

    Incubation success = (hatched eggs/estimated clutch count)*100 %;

    Emergence success = (hatched eggs – [live+dead hatchlings]/estimated clutch count)*100 %.

    Counting error, the accuracy of counting broken egg shells = estimated clutch count following hatchling emergence - clutch count made when the eggs were laid.

Sand temperatures at nest depth (50 cm) within the turtle nesting habitat are measured with Vemco Minilog II temperature data loggers deployed for a number of years at turtle nesting beaches in Queensland at 30 minute intervals. These temperature recording instruments can record temperature continuously for up to 10 years. Two data loggers have been deployed on South End Beach, Curtis Island and on South Beach, Avoid Island, and one on Peak Island.

During census nights for turtle nesting, the beaches were monitored for at least two hours before high tide to about four hours after by EHP staff and/or EHP Queensland Turtle Conservation (QTC) Volunteers. All turtles encountered were tagged, or checked for tags and measured. Clutches at risk from flooding were relocated further up the dune within two hours of being laid and their eggs counted (Pfaller *et al.* 2008). The beaches were also examined either once or twice daily depending on tides to count nesting crawls, to locate hatchling emergence and identify daylight nesters.

Any variations in methods among the study sites are defined in Limpus *et al*. (2018).

For this 2016-2017 breeding season, Curtis Island and Avoid Island were monitored on a daily basis commencing on 1 November 2016 until 15 March 2017. Peak Island was only monitored during mid-season, 24 November – 7 December 2016 and 23 January – 2 February 2017. Local QTC Volunteers provided intermittent monitoring of the beaches before and after the above continuous monitoring period.

With South End Beach, Curtis Island being 5 km long, 4x4 vehicles are used to facilitate the monitoring team patrolling the beach in a timely manner.

At South End Beach, Curtis Island, fox exclusion devices made from standard plastic garden mesh were laid horizontally at the beach surface over a series of nests to prevent foxes from digging into clutches of turtle eggs. These plastic mesh (100 mm grid size) panels were approximately 1 x 1 m square. They were placed over clutches of turtle eggs within 2 hours of the eggs being laid. Each mesh panel was held down by 25 x 25 x 400 mm timber pegs, one in each corner of the panel.

STATISTICAL ANALYSIS OF CAPTURE-MARK-RECAPTURE (CMR) DATA

Statistical modelling approach: survival and abundance estimation

A recently developed 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 for a CMR study (Gimenez and Choquet, 2010).

There are no established procedures for assessing random-effects CJS model goodness-of-fit (Gimenez and Choquet, 2010). So we used an *ad-hoc* approach based on comparison with various fixed effects CJS-type models (Lebreton *et al*. 1992) that have well-known goodness-of-fit metrics to help assess random effects CJS 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 ĉ estimate of goodness-of-fit (Fletcher, 2012) that has been included in the program MARK (White *et al*. 2006).

A time-since-marking model structure to account for transient behaviour (Chaloupka and Limpus, 2002) and the random effects model approach (Gimenez and Choquet, 2010) to account for capture heterogeneity was used. All random and fixed effects CJS models were fitted using program MARK (White *et al*. 2006) via the RMark package for R (Laake, 2013). Nonlinear effects for cohort-specific survival rates were included using the splines package for R via RMark.

Model selection was based on using an information-theoretic approach with the Akaike Information Criterion corrected for sample size (AICc) to determine model parsimony and support statistical inferences (Burnham *et al*. 2011). The best-fit model based on AICc was used to estimate apparent survival and recapture probabilities. This approach also enabled us to estimate derived parameters for the population such as annual abundance by applying a Horwitz-Thompson-type estimator using the recapture probabilities derived from the best-fit model (Chaloupka and Limpus, 2001) with nonparametric bootstrap estimates of the variance of the annual abundance estimates (Madon *et al.* 2013: including recent code corrections by O. Gimenez).

- ***Curtis Island***
  CMR histories were compiled for 425 nesting flatback turtles tagged over an approximately two weeks per year sampling session each year at Curtis Island over the 21-year summer nesting period from 1995 to 2015 plus a 4 month whole of season tagging in the final 2016 breeding season.

- ***Peak Island***
  CMR histories for 722 nesting flatback turtles tagged over a two weeks per year sampling session each year at Peak Island over the 9-year summer nesting period from 2008 to 2016 were compiled.

- ***Avoid Island***

CMR histories were compiled for 230 nesting flatback turtles tagged over a two weeks per year sampling session each year at Avoid Island over the 4-year summer nesting period from 2012 to 2015 plus a 4 month whole of season tagging in the final 2016 breeding season.

Statistical modelling approach: recruitment estimation

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 and Limpus, 1995; Chaloupka, 2003; Dobbs *et al*. 2007; National Research Council, 2010; Caillouet *et al*. 2011). Most attempts to estimate some form of 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; Dobbs *et al.* 2007).

Recruitment measures that are more applicable to the population dynamics of marine turtles can nonetheless be derived from a CMR-based sampling program like that already in place for monitoring the Curtis Island nester population coupled with the temporal symmetry modelling approach developed originally by Pradel (1996). See also Pradel *et al*. (1997), Nichols *et al*. (2000) and Nichols and Hines (2002). The recruitment metric is the per capita recruitment rate defined here as the number of adult female flatback turtles entering the Curtis Island nester population between consecutive nesting seasons per nester already in the population. Interestingly, if the nester population growth rate is stable, then the proportion of first time nesters would be equivalent to the per capita recruitment rate.

So a range of Pradel temporal symmetry models, parameterised in terms of per capita recruitment and accounting for individual capture heterogeneity, were fitted to the 425 capture histories. All models comprised a mixture of two hidden capture classes of unknown cause. A 2-class mixture is considered more than adequate for modelling detection or encountering 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 effects for possible environment effects (Bjorndal *et al*. 2017) as the Southern Oscillation Index (SOI) were included using the splines package for R via RMark. Model selection was then based on using an information-theoretic approach with the AICc corrected for sample size to determine model parsimony and support statistical inferences (Burnham *et al*. 2011). The SOI data were sourced from NOAA data repositories using the rsoi package for R (Albers, 2017).

CMR ANALYSES RESULTS

CURTIS ISLAND

Data summary

The CMR data set comprised the capture histories for 425 individual nesting female flatback turtles tagged over the 22-year sampling period from 1995 onwards. Many turtles were recaptured over a number of seasons with some being recaptured on up to 14 seasonal occasions (Figure 1a). The number of tagged flatback turtles recorded for each season since 1995 is shown in Figure

1b, which shows a population that fluctuates significantly around a long-term mean of around 55 observed nesters each season (this estimate of course does not account for imperfect detection which is accounted for explicitly using the CJS models summarised 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 (χ^2 = 697.03, df = 93, 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). Accounting for transient behaviour and recapture heterogeneity was important. So, we fitted a time-since-marking survival model to account for transients by applying a 2-ageclass structure (separate survival probability estimates for newly and previously tagged turtles (Chaloupka and Limpus, 2002).

Model summary

The best-fit model was Model 6 (Table 1), 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 (σ_p = 1.08, 95% CI: 0.88-1.32). The Fletcher $\hat{c}$ estimate for Model 6 was 1.003, suggesting an adequate fit to the 425 individual CMR histories. The overwhelming weight of evidence was in support of this model compared to the other five models fitted to these CMR histories (Table 1). Model 6 accounted for ca. 99% of the weight of evidence for these data and was used to derive the cohort-specific 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 0.25 to 0.66 and have been generally fluctuating around the long-term mean = 0.47 (Figure 1c). These recapture probability estimates were then used to derive estimates of the annual flatback nester population in the study area over the 22-year sampling period, which suggests an increasing nesting population since the 2010 summer nesting season (Figure 1d). The long-term median nester abundance was estimated at about 122.

Apparent annual survival probabilities

The estimated apparent annual survival probability derived from the best-fit Model 6 (Table 1) was 0.95 (95% CI: 0.94-0.96). The small annual numbers of nesting turtles at Curtis Island precluded the capacity for analysis of a rigorous cohort specific survival probability.

Annual recruitment probabilities

The best-fit Pradel temporal symmetry model comprised constant (fixed) survival, constant mixture proportion [0.66, (95% CI: 0.58-0.73)], mixture-specific time-varying detection probabilities and time-varying per capita recruitment rates that were a nonlinear function of the mean annual SOI for the year prior to nesting. The overwhelming weight of evidence (> 99%) was in support of this model compared to the other 21 models fitted to these CMR histories. The annual recruitment rates were derived from this model and are shown in Figure 2. The long-term mean recruitment rate was about 0.08 and that is equivalent to about six new nester recruits per annum based on the estimated nester abundance shown in Figure 1d.

Table 1. Curtis Island: Summary of six random-effects CJS models fitted to 425 flatback nester CMR histories.

Model	Model structure	np	AICc	ΔAICc	Weight	Deviance
6	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~time + td)	25	3141.87	0.00	0.990	3090.73
3	sigmaphi(~1)Phi(~1)sigmap(~1)p(~time + td)	24	3164.11	22.23	0.010	3115.05
4	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~td)	5	3176.83	34.95	0.000	3166.78
1	sigmaphi(~1)Phi(~1)sigmap(~1)p(~td)	4	3195.18	53.30	0.000	3187.15
5	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~time)	24	3778.20	636.32	0.000	2344.25
2	sigmaphi(~1)Phi(~1)sigmap(~1)p(~time)	23	3808.56	666.68	0.000	2376.70

agebin = time-since-marking (2-ageclass), time = sampling season, Phi = survival, p = recapture, td = trap-dependent effect, 1 = constant, sigmap = recapture heterogeneity, np = number of estimable parameters, ΔAICc = difference in sample size corrected AICc value compared to previous model

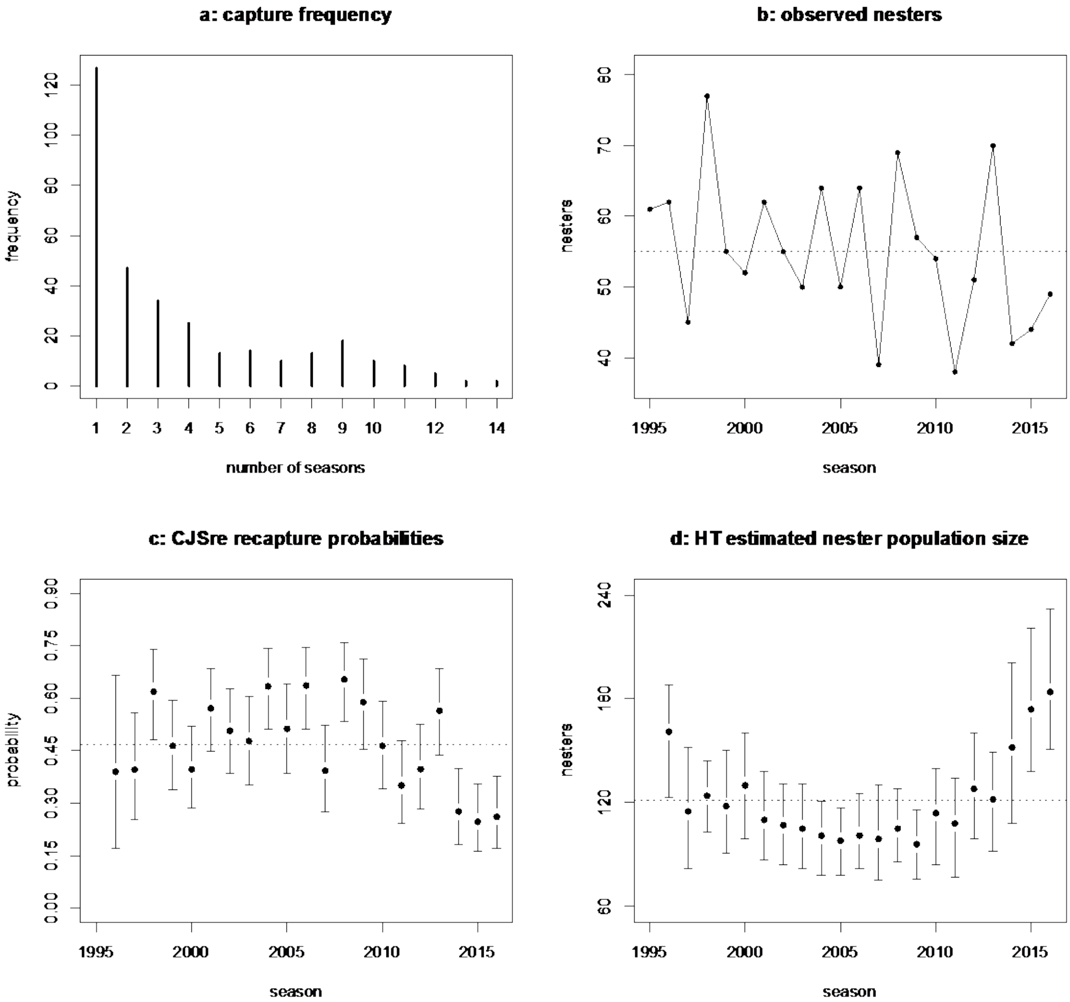


Figure 1. Curtis Island capture-mark-recapture (analysis of flatback turtle nesting since 1995 derived from the best-fit Cormack-Jolly-Seber random effects model. Dashed horizontal line in panels (b-d) shows the long-term mean value for that panel (which are 55, 0.47 and 122 respectively):

- **Panel (a): seasonal capture frequency (number of seasons that each tagged turtle was found nesting on Curtis Island).**
- **Panel (b): number of tagged nesters recorded each season on Curtis Island.**
- **Panel (c): estimated recapture probabilities from best-fit CJS model with random effects accounting for recapture heterogeneity.**
- **Panel (d): Horwitz-Thompson estimates of nester abundance (and 95% bootstrap-derived confidence intervals)**

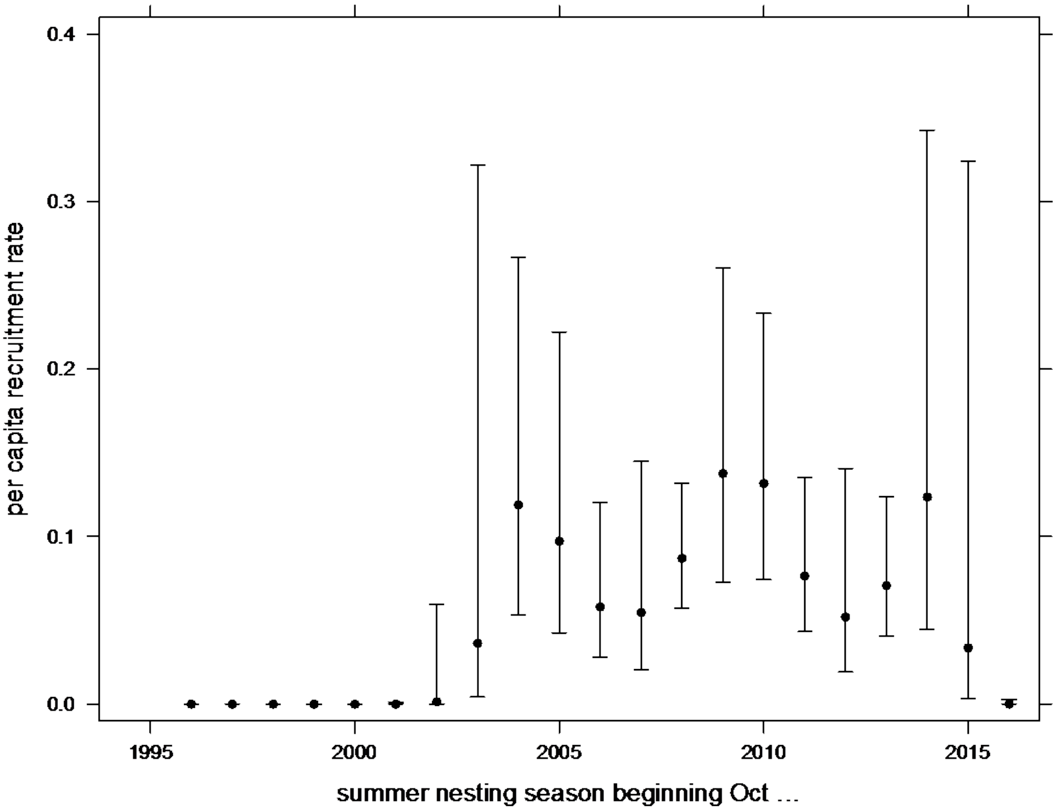


Figure 2. Curtis Island: Annual per capita recruitment rate estimates derived from best-fit Pradel robust design temporal symmetry + mixture model accounting for two distinct classes of detection heterogeneity. Recruitment was modelled explicitly as a nonlinear function of the mean annual SOI for the 12-months prior to summer nesting season. Solid dots = estimated annual per capita recruitment rate, vertical bars = 95% confidence interval.

PEAK ISLAND

Data summary

The CMR data set comprised the capture histories for 722 individual nesting female flatback turtles tagged over the 9-year sampling period from 2008 onwards. 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 flatback turtles recorded for each season since 2008 is shown in Figure 3b, which shows a population that fluctuates significantly around a long-term mean of around 201 observed nesters each season (this estimate of course does not account for imperfect detection which is accounted for explicitly using the CJS models summarised 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 ($\chi^2 = 540.8$, df = 43, $P < 0.0001$). 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). So accounting for transient behaviour and recapture heterogeneity was important. We fitted a time-since-marking survival model to account for transients by applying a 2-ageclass structure (separate survival probability estimates for newly and previously tagged turtles — see Chaloupka and Limpus, 2002) and we fitted a tagging-cohort-specific survival structure as well (in other words, separate survival rates for those nesters first tagged in 2008, or 2009 and so on).

Model summary

The best-fit model was Model 6 (Table 2), which comprised: constant tagging cohort-specific annual apparent survival rates, time-dependent recapture probabilities that were a function of "trap-dependence" and significant individual capture heterogeneity (σ_p = 0.868, 95% CI: 0.71-1.06). The Fletcher $\hat{c}$ estimate for Model 6 was about 1.2, suggesting an adequate fit to the 722 individual CMR histories. In this model, the cohort-specific annual survival rates were best fit with a nonlinear spline function. The overwhelming weight of evidence was in support of this model compared to the other 14 models fitted to these CMR histories (Table 2). The next best model was Model 5 that was similar in structure to Model 6 but here the cohort-specific effect for survival rates was not a smooth function of tagging cohort year. Model2 6 and 5 accounted for 88% of the weight of evidence for these data suggesting overwhelming support for some sort of cohort-specific structure for the survival rates. Model 6 was used to derive the cohort-specific 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 0.18 to 0.44 and have been generally fluctuating around the long-term mean = 0.26 (Figure 3c). These recapture probability estimates were then used to derive estimates of the annual flatback nester population in the study area over the 9-year sampling period, which suggests an approximately stable nesting population during 2010-2016 seasons (Figure 3d). The long-term median nester abundance was estimated at about 694 (Figure 3d).

Cohort-specific annual survival probabilities

The estimated mean annual apparent cohort-specific survival probability derived from the best-fit Model 6 (Table 2) was 0.96 (SD: ± 0.015), although there was an apparent decline in apparent annual survival rates for the more recent tagging cohorts (Figure 3e), which is consistent with a decline in nester abundance since around 2014 (Figure 3d). However, it is important to note that the lower 2014 cohort survival rate shown in Figure 3e was estimated with significant uncertainty.

Table 2. Peak Island: Summary of 15 random-effects CJS models fitted to 722 flatback turtle nester CMR histories

Model	Model structure	Np	AICc	ΔAICc	Weight	Deviance
6	sigmaphi(~1)Phi(~bs(Cohort, 4))sigmap(~1)p(~time + td)	15	4139.14	0.00	0.579	4108.83
5	sigmaphi(~1)Phi(~cohort)sigmap(~1)p(~time + td)	18	4140.61	1.47	0.277	4104.17
9	sigmaphi(~1)Phi(~1)sigmap(~1)p(~time + td)	11	4143.69	4.75	0.054	4121.73
12	sigmaphi(~1)Phi(~epoch)sigmap(~1)p(~time + td)	12	4144.14	5.00	0.047	4119.94
15	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~time + td)	12	4144.38	5.24	0.042	4120.19
2	sigmaphi(~1)Phi(~bs(Cohort, 4))sigmap(~1)p(~td)	8	4153.44	14.30	0.001	4137.35
1	sigmaphi(~1)Phi(~cohort)sigmap(~1)p(~td)	11	4155.50	16.35	0.000	4133.33
7	sigmaphi(~1)Phi(~1)sigmap(~1)p(~td)	4	4157.95	18.81	0.000	4149.93
13	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~td)	5	4158.06	18.94	0.000	4148.04
10	sigmaphi(~1)Phi(~epoch)sigmap(~1)p(~td)	5	4159.84	20.70	0.000	4149.80
4	sigmaphi(~1)Phi(~bs(Cohort, 4))sigmap(~1)p(~time)	14	4741.97	602.38	0.000	1015.83
3	sigmaphi(~1)Phi(~cohort)sigmap(~1)p(~time)	17	4747.81	608.67	0.000	1015.54
8	sigmaphi(~1)Phi(~1)sigmap(~1)p(~time)	10	4751.81	612.67	0.000	1033.80
11	sigmaphi(~1)Phi(~epoch)sigmap(~1)p(~time)	11	4753.84	614.70	0.000	1033.80
14	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~time)	11	4753.84	614.70	0.000	1033.80

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, ΔAICc = difference in sample size corrected AICc value compared to previous model, bs(x,df=4) = B-spline function to model nonlinear form for the cohort effect, epoch = 0 if prior to 2014 sampling season and 1 otherwise.

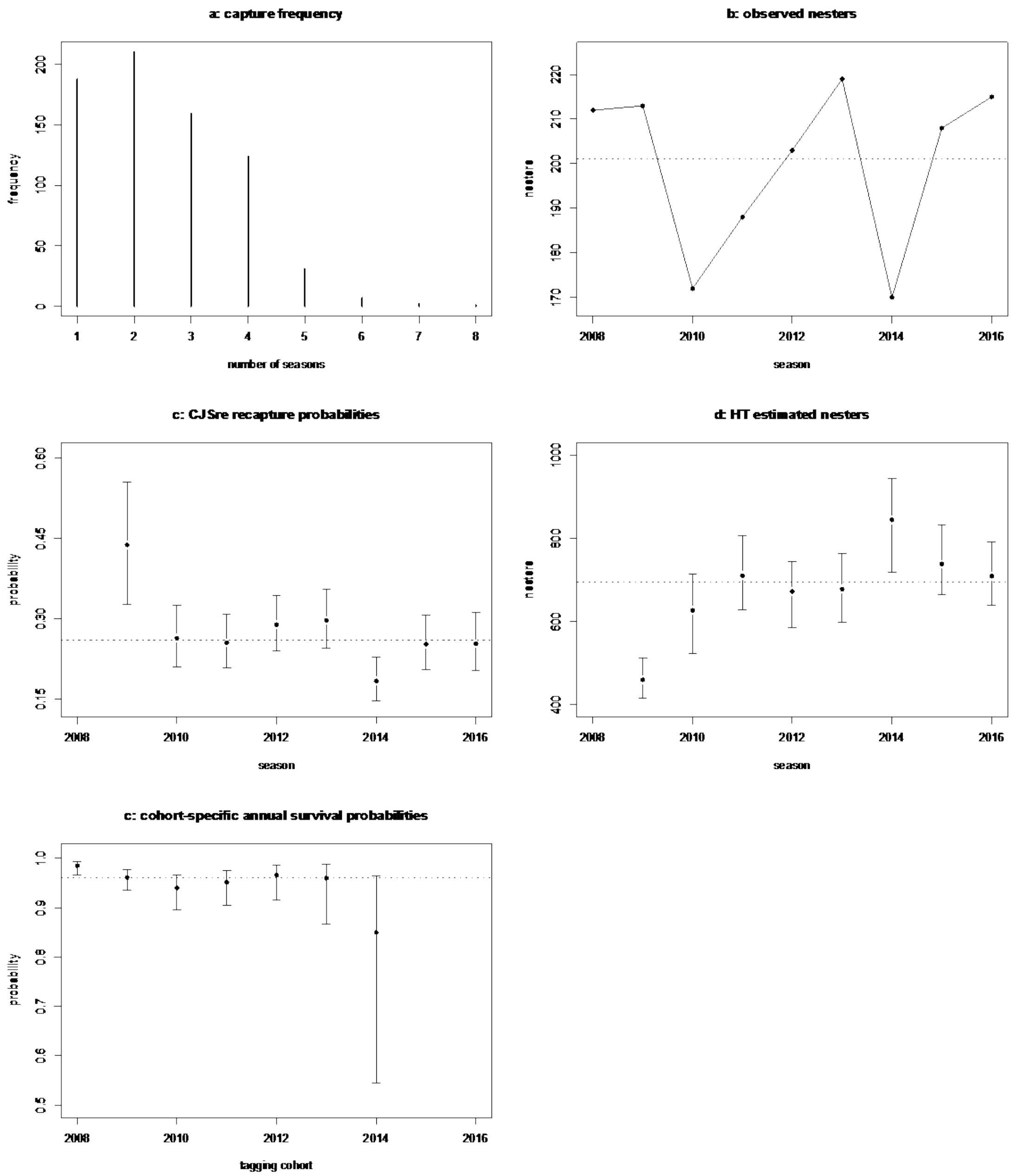


Figure 3. **Peak Island capture-mark-recapture analysis of flatback nesting since 2008 derived from the best-fit Cormack-Jolly-Ssber random effects model. Dashed horizontal line in panels (b-e) shows the long-term mean value for that panel (which are 201, 0.26, 694 and 0.96 respectively). There are insufficient data to estimate the 2015 and 2016 tagging cohort survival rates:**

- **Panel (a): seasonal capture frequency (number of seasons that each tagged turtle was found nesting on Peak Island).**
- **Panel (b): number of tagged nesters recorded each season on Peak Island.**
- **Panel (c): estimated recapture probabilities from best-fit CJS model with random effects accounting for recapture heterogeneity.**
- **Panel (d): Horwitz-Thompson estimates of nester abundance (and 95% bootstrap-derived confidence intervals) of flatback nesting on Peak Island since 2009 derived from the best-fit CJS random effects model.**
- **Panel (e): the tagging cohort-specific apparent annual survival probabilities derived from best-fit random effects CJS model.**

Avoid Island

Data summary

The CMR data set comprised the capture histories for 230 individual nesting female flatback turtles tagged over the 5-year sampling period from 2012 onwards. Many turtles were recaptured over a number of seasons with some being recaptured on up to four seasonal occasions (Figure 4a). The number of tagged flatback turtles recorded for each season since 2012 is shown in Figure 4b, which shows a population that fluctuates significantly around a long-term mean of approximately 76 observed nesters each season (this estimate of course does not account for imperfect detection which is accounted for explicitly using the CJS models summarised 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 ($\chi^2 = 71.82$, df = 8, $P < 0.0001$). More specifically, failure of particular components such as Test 2.CT is due to individual capture heterogeneity (Pradel *et al*. 2005). 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). So accounting for transient behaviour and recapture heterogeneity was important. We fitted a time-since-marking survival model to account for transients by applying a 2-ageclass structure (separate survival probability estimates for newly and previously tagged turtles).

Model summary

The best-fit model was Model 3 (Table 3), 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 (σ_p = 1.49, 95% CI: 1.05-2.13). The Fletcher $\hat{c}$ estimate for Model 3 was about 3.9, suggesting an inadequate fit to the 230 individual CMR histories. The overwhelming weight of evidence was in support of this model compared to the other 5 models fitted to these CMR histories (Table 3). Model 3 accounted for about 74% 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. Note that this model (nor any other model) was not a good fit to this short-term study.

Recapture probabilities and population abundance estimates

The annual recapture probabilities derived from the best-fit model ranged from 0.15 to 0.50 and have been generally fluctuating around the long-term mean = 0.28 (Figure 4c). These recapture probability estimates were then used to derive estimates of the annual flatback nester population in the study area over the 5-year sampling period, which suggests an increased nesting population since the 2013 summer nesting season (Figure 4d). The long-term median nester abundance was estimated at about 329.

Apparent annual survival probabilities

The estimated apparent annual survival probability derived from the best-fit Model 3 (Table 3) was 1.00 (95% CI: 0.999-1.00), which is meaningless and a consequence of too short a study (only five seasons). A similar problem exists for estimation of recruitment rates. It is expected that about nine years of continuous capture-mark-recapture (tagging) study will be required to provide rigorous estimates of survival and recruitment probabilities.

Table 3. Avoid Island: Summary of six random-effects CJS models fitted to 231 flatback nester CMR histories.

Model	Model structure	Np	AICc	ΔAICc	Weight	Deviance
3	sigmaphi(~1)Phi(~1)sigmap(~1)p(~time + td)	7	623.47	0.00	0.735	609.09
6	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~time + td)	8	625.58	2.10	0.256	609.08
1	sigmaphi(~1)Phi(~1)sigmap(~1)p(~td)	4	632.98	9.51	0.006	624.86
4	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~td)	5	635.05	11.58	0.002	624.85
2	sigmaphi(~1)Phi(~1)sigmap(~1)p(~time)	6	708.61	85.14	0.000	118.37
5	sigmaphi(~1)Phi(~agebin)sigmap(~1)p(~time)	7	710.70	87.23	0.000	118.38

agebin = time-since-marking (2-ageclass), time = sampling season, Phi = survival, p = recapture, td = trap-dependent effect, 1 = constant, sigmap = recapture heterogeneity, np = number of estimable parameters, ΔAICc = difference in sample size corrected AICc value compared to previous model.

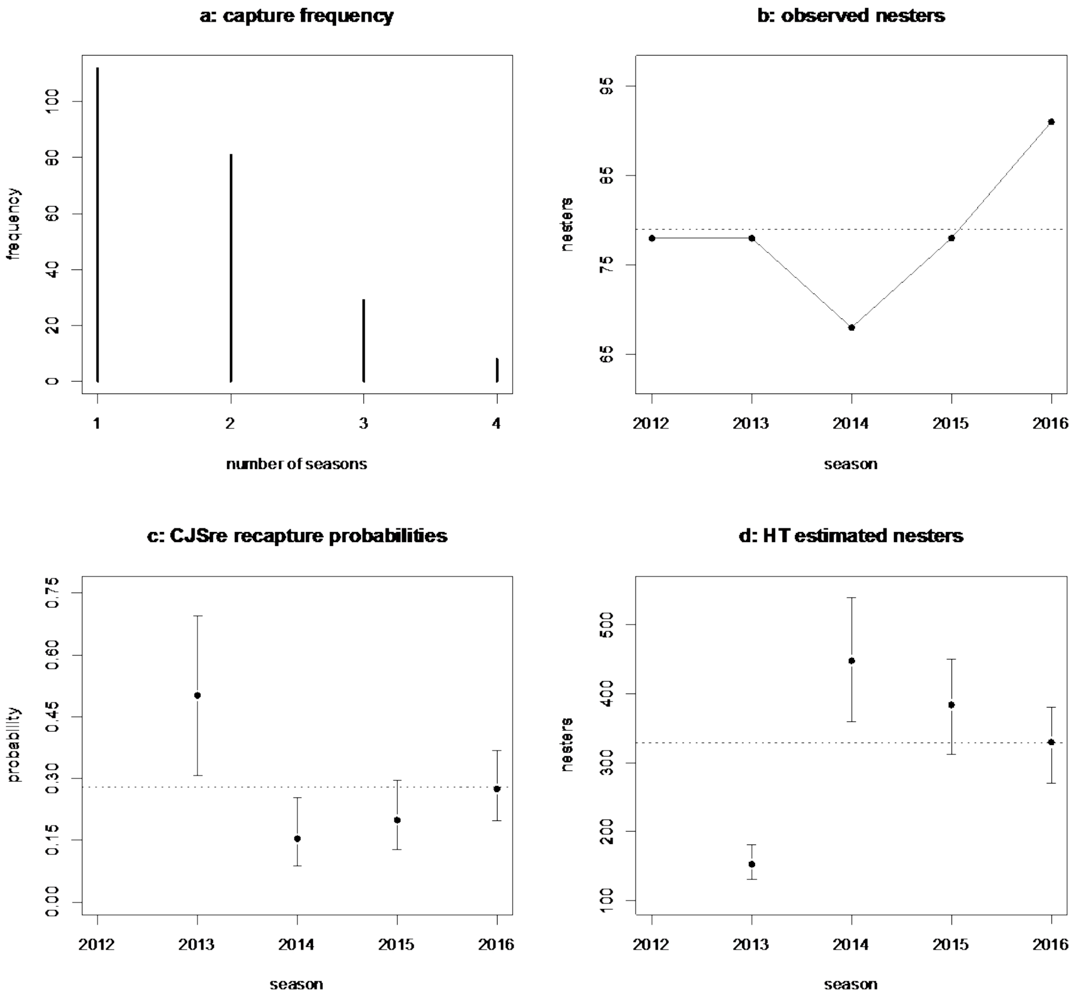


Figure 4. Avoid Island capture-mark-recapture analysis of flatback turtle nesting since 2012 derived from the best-fit CJS random effects model. Dashed horizontal line in panels (b-d) shows the long-term mean value for that panel (which are 79, 0.28 and 329 respectively).

- **Panel (a): seasonal capture frequency (number of seasons that each tagged turtle was found nesting on Avoid Island).**
- **Panel (b): number of tagged nesters recorded each season on Avoid Island.**
- **Panel (c): estimated recapture probabilities from best-fit CJS model with random effects accounting for recapture heterogeneity.**
- **Panel (d): Horwitz-Thompson estimates of nester abundance (and 95% bootstrap-derived confidence intervals) of flatback nesting on Avoid Island since 2012 derived from the best-fit CJS random effects model.**

CMR ANALYSES CONCLUSIONS

The CMR analyses for Curtis and Peak Islands in the present studies are an extension of initial studies for flatback turtle nesting populations at these islands reported by Limpus, Parmenter and Chaloupka (2013). The current Curtis Island analysis extends that previous analysis by another five years. The majority of the original CMR data for Peak Island was not available for the present study which only presents analysis from the last nine seasons, 2008 to 2016. Results from both studies are considered when drawing conclusions regarding the behaviour of the Peak Island population. The present study provides the commencement of CMR analysis for defining the behaviour of the nesting population at Avoid Island.

These studies demonstrate that CMR data gathered from a two-week, mid-season tagging census can produce robust analysis for estimation of total population size, annual survival probability, annual recruitment probability as well as long term trends for these significant demographic parameters. This is to be expected because a high proportion of the annual nesting population comes ashore to nest during this mid-season period with populations that breed over only a few months per year, in contrast with populations with year round nesting (Limpus *et al*. 2001; Miller *et al*. 2007). During the 2016-2017 breeding season at Curtis Island and Avoid Island, 84 ± 10% and 82 ± 8% respectively of the turtles recorded during the entire season of monitoring were recorded during the standard two-week mid-season census period. A critical issue with respect to providing reliable data for species such as marine turtles that do not breed annually and hence have low recapture probabilities is that the studies need to run consecutively across a number of years. For nesting flatback turtles, a minimum of nine consecutive years is about the minimum duration of a study to produce reliable data for all parameters.

The trends in the size of these three flatback nesting populations have not been consistent across the rookeries.
Estimated population size:

- Curtis Island: this population which had changed little during 1996-2011 is showing signs of an approximate 50% increase in the total adult female population that visits this island since 2010.
- Peak Island: This population had suffered an approximate 50% decline in the total adult female population that visits this island between 1981 and 2009 (Limpus*et al*. 2013). However, the current analysis indicates that the population decline has slowed considerably during 2010 to 2016.
- Avoid Island: The five years of data are inadequate for providing a clear indication of trend for this population. However, there may be an increase in the population since the study began in 2012.

Collectively these data suggest that there has been some positive change in the abundance of adult female flatback turtles associated with these rookeries since about 2010.

In contrast, the mean annual survival probabilities for these populations are high but with Curtis Island recording the lowest value and wider confidence limits.
Mean annual survival probability:

- Curtis island: 0.95 (95% CI: 0.94 – 0.96).
- Peak Island: 0.96 (SD = 0.015).
- Avoid Island: the calculated mean annual survival probability of 1.00 is considered meaningless because of the brevity of the monitoring period at this time.

These high survivorship values indicate that mortality of the adult females within their dispersed foraging areas and migratory corridors is unlikely to be a threat to these populations. The beach monitoring studies have detected negligible mortality of these nesting females on the nesting beaches across recent decades.

There is currently only long term recruitment rates quantified for Curtis Island: While the mean long term annual recruitment rate has been about 0.08 across two decades of monitoring, the annual recruitment rate has been declining since about 2009. The recent recruitment rate of less than 0.05 for the Curtis Island population is of concern.

CONCLUSIONS FROM OTHER ASPECTS OF THE MONITORING

While long-term total tagging census across entire breeding seasons may result in some reductions in the breadth of confidence limits, it is debatable whether the increased costs and logistical constraints of staffing teams on islands for 14 plus weeks of continuous monitoring could be justified for quantification these population demographic studies alone.

The data for the comparison of mid-season and whole of nesting season census during the 2016-2017 breeding season at Curtis Island and Avoid Island are summarised in Table 4 and have been reported in detail by Limpus *et al*. (2018). Additional data for comparison have been included in Table 4 from other flatback populations monitored during the 2016-2017 breeding season: Peak Island (monitored only for mid-season census; Limpus *et al*. 2018) and the Woongarra Coast (monitored for the entire season, Limpus e*t al*. 2017).

Table 4. Comparative data from the census of flatback turtle nesting populations in central and south Queensland during the 2016-2017 breeding season. See Limpus *et al*. 2017, 2018 for a full description of these parameters and related analyses.

A. Nesting females

Parameter and rookery	Census method		Significant Difference
	Mid-season	Whole season	
Adult female nesting success			
• Curtis Is	63.9%, CI = 12.1%	73.1%, CI = 5.8%	No
• Peak Is	53.1%, CI = 4.9%	-	-
• Avoid Is	68.3%, CI = 4.6%	70.5%, CI = 8.5%	No
Proportion 1st time tagged turtles in the adult nesting population = presumed new recruits to breeding			
• Curtis Is	12%, CI = 10%	27%, CI = 12%	Marginal
• Peak Is	12.6%, CI = 4.4%	-	-
• Avoid Is	18.4%, CI = 8.7%	23.9%, CI = 8.7%	No
Size of nesting females (cm)			
• Curtis Is	94.0, SD = 2.55	93.9, SD = 2.5; n = 46	No
• Peak Is	93.1, SD = 2.7; n = 203	-	-
• Avoid Is	93.3, SD = 1.7; n = 76	93.6, SD = 2.5; n = 76	No
• Woongarra Coast	-	94.5, SD =2.8; n = 10	-
Remigration interval (yr)			
• Curtis Is,	-	3.66, SD = 1.55; n = 35	-
• Peak Is	3.0, SD = 1.4; n = 184	-	-
• Avoid Is	2.4, SD = 0.9, = 63	2.32, SD = 0.9; n = 69	No
• Woongarra Coast	-	3.43, SD = 1.27; n = 7	-

Table 4 (continued)
B. Eggs

Rookery and parameter	Census method		Significant difference
	Mid-season	Whole season	
Clutches laid per female per season			
• Curtis Is	Not measurable	2.65, SD = 0.92; n = 40	-
• Peak Is	Not measurable	-	-
• Avoid Is	Not measurable	2.73, SD = 1.0; n = 92	-
• Woongarra Coast	Not measurable	3.3, SD = 0.68; n = 10	-
Incubation period to emergence (d)			
• Curtis Is	47.4, SD =2.16; n = 29	48.1, SD = 2.64; n = 122	No
• Peak Is	52.7, SD = 3.82; n = 21	-	-
• Avoid Is	50.2, SD = 2.67; = 60	49.6, SD = 2.53; n = 172	No
• Woongarra Coast	-	50.0, SD = 3.26; n = 27	-
Incubation success of eggs			
• Curtis Is	89.0%, SD = 15.8%; n = 37	83.4%, SD = 20.7%; n = 151	No
• Peak Is	88.4%, SD = 8.78% n = 36	-	-
• Avoid Is	73.7%, SD = 31.06% n = 80	74.8%, SD = 28.98%; n = 325	No
• Woongarra Coast	-	67.7%, SD = 22.48%; n = 30	-
Hatchling emergence success			
• Curtis Is	85.7%, SD = 15.87%	80.2%, SD = 21.20%	No
• Peak Is	86.7%, SD = 11.47% n = 36	-	-
• Avoid Is	71.4%, SD = 32.10% n = 80	74.8%, SD = 28.98% n = 325	No
• Woongarra Coast	-	56.1%, SD = 23.91% n = 30	-

One critically important demographic parameter with respect to marine turtle population dynamics, number of clutches laid for the season per female, can be quantified only by a whole of nesting season tagging census.

There were no major differences between values derived from the two-week mid-season census and from census across the entire breeding season at both Curtis Island and Avoid Island for the following parameters (Table 4):

- Adult female nesting success,
- Size of nesting females,
- Remigration interval,
- Incubation period to emergence,
- Incubation success of eggs, and
- Hatchling emergence success.

The greatest difference in magnitude of a parameter between the two census methods occurred with the proportion of first-time tagged turtles in the adult nesting population (presumed new recruits to breeding). This is not unexpected since the late arrivals for the breeding season have a higher proportion of untagged turtles (unpublished data from 50 yr census of the Woongarra Coast population). Although the mid-season census can provide an index of trends across years in the proportion of newly recruiting females, entire season monitoring is needed to provide an accurate estimate.

Caution needs to be exercised in applying the results (Table 4) beyond the current breeding season. The 2016-2017 was a season with no cyclonic disturbances during the breeding season. Cyclones typically occur in the mid to late summer, i.e. after the mid breeding season for eastern Australian flatback turtles. Hence, during the latter part of the flatback season, there can be significant variability across years in impacts on incubating eggs and hatchlings leaving the nests. This variability depends on the frequency and intensity of cyclones with associated cooling of nests during heavy rainfall, flooding of nests with rising water tables and loss of clutches through beach erosion and storm surge flooding. These factors can create seasonal stochasticity in late season values of multiple parameters, including:

- Incubation period to emergence.
- Hatchling sex ratio:
    - Increased male production in cool sands and increased female production in warm sands.
- Proportion of the season clutches failing to hatch and
- Incubation success of eggs and hatchling emergence success in surviving clutches.

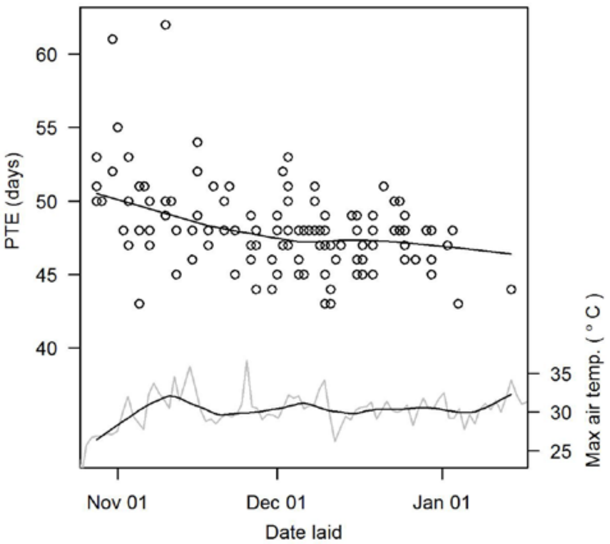
In addition, during the 2016-2017 breeding season we were confronted with an entirely new phenomenon, an extreme heat wave accompanied by extremely reduced rainfall in late January and extending into February. We were unprepared for this type of impact that resulted in increased death of hatchlings and eggs within the nests and feminised hatchlings.

The data collected from incubated clutches of flatback turtle eggs on South End Beach, Curtis Island during the 2016-2017 breeding season were analysed for trends in these parameters with respect to date laid or hatchlings emerged (Figure 5).

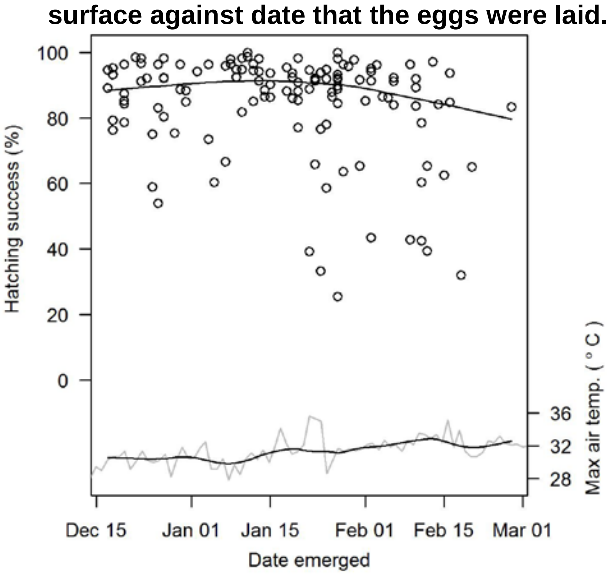
In the absence of sand temperature data from different habitats on South End Beach, Curtis Island, the effects of air temperature on the incubation parameters were visually examined using the maximum daily air temperature observed at Gladstone Airport as a proxy to sand temperature. The air temperature data were obtained from the Bureau of Meteorology (http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=122&p_display_type=dailyDataFile&p_startYear=&p_c=&p_stn_num=039326). Lowess smoothing was used to fit a trend line to the incubation data and maximum air temperature data. Air temperature increased through November to March (Figure 5). Prolonged heat waves (>35 °C for three days) were observed from 19 to 21 of January 2017 and elevated temperatures continued for the following weeks (Figure 5bc). In general:

- Incubation duration until hatchling emergence from the nest became shorter as the summer progressed with warmer temperatures (Figure 5a).

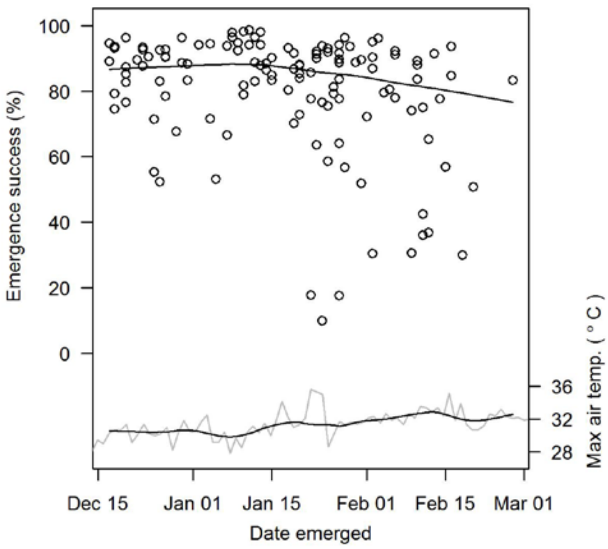
- Incubation and emergence success decreased after mid January, which coincided with the late January heat wave events (Figure 5bc).



a. Period to hatchling emergence to the beach surface against date that the eggs were laid.



b. Hatching success of eggs with respect to date that the hatchlings emerged from the nest.



c. Emergence success of hatchlings with respect to date that the hatchlings emerged from the nest.

Figure 5. Incubation parameters analysed with respect to date laid or date of hatchling emergence for flatback turtle clutches laid on South End Beach, Curtis Island, during the 2016-2017 breeding season. Trend lines were fitted with Lowess smoothing of the incubation data and the maximum air temperature recorded at Gladstone Airport.

Hatchling sex ratios were predicted from the 2016-2017 breeding season's monitoring (Limpus *et al*. 2018):

- Curtis Island: A very strongly female biased hatchling cohort is expected to have been produced. The majority of males would have been produced during three brief periods of cool sand that occurred with periods of heavy rain (based on sand temperature data and incubation period to emergence data), or early in the season.

- Peak Island: A strongly female biased hatchling cohort is expected to have been produced. The majority of males should have been produced from the early season clutches (based on incubation period to emergence data).
- Avoid Island: A strongly female biased sex ratio should have been produced. Any male hatchlings produced at this island during the 2016-2017 breeding season would have come from the limited number of clutches laid during the early nesting season or those laid in densely shaded areas of the dunes (based on incubation period to emergence data and sand temperatures at 50 cm depth (Limpus *et al*. 2017a).

Absolute identification of the sex of a hatchling requires the death of the hatchling and histological examination of its gonads. However, hatchling sex ratio can be predicted with reasonable confidence from sand temperatures at nest depth measured across the entire breeding season from representative locations on the beach. Sand temperature can be measured using temperature data loggers whose stored data can be down loaded when convenient. They do not require daily attendance at the beach. The downside with temperature data loggers that are not regularly checked is that they can be lost when beaches erode, when nesting turtles dig them up or when there is instrument failure. In addition, temperatures cease to be representative for the general clutch when nesting turtles or other disturbances alter the sand depth above the data logger. In general however, use of sand temperature data loggers offers cost effective means of understanding the variable sand temperature of a beach and the probable sex ratio of the hatchlings produced. These results can be enhanced when there are clutches with known dates of laying and hatching that provide quantified incubation duration. This parameter can also be used to predict the probable sex ratio of hatchlings from the respective nests. However, this latter method requires that clutches are marked for identification as they are laid throughout the breeding season and recorded on the day that the hatchlings leave the nests some two months later.

Based on these considerations, it needs to be acknowledged that it is not possible to predict hatchling sex ratios and seasonal hatchling production for the entire breeding season without sampling across the entire breeding season, where data on incubation duration can be included in the estimates. The placement of additional temperature loggers at each rookery should be a priority to guard against some of the problems that have occurred with the temperature loggers and to obtain data from a wider range of nesting habitats.

While monitoring of the breeding biology of the adult females appears to be adequately addressed with a mid-season census, consideration could be given to an alternate sampling regime for assessing sex ratio and hatchling production without daily monitoring of the beach during the hatching season. These parameters can be addressed in the context of a whole of nesting season monitoring required for quantifying the number of clutches laid per season for each female.

REFERENCES

Albers, S. (2017). rsoi: El Nino/Southern Oscillation (ENSO) Index. R package version 0.2.1. https://CRAN.R-project.org/package=rsoi.

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.

Bjorndal, K. A., Bowen, B. W., Chaloupka, M., Crowder, L. B., Heppell, S. S., Jones, C. M., Lutcavage, M. E., Solow, A. R., and Witherington, B. E. (2010). Assessment of sea-turtle status and trends. Integrating demography and abundance. (The National Academies Press: Washington, D.C.)

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.

Caillouet, C., Shaver, D., Landry, A., Owens, D. and Pritchard, P. (2011). Kemp's ridley sea turtle (*Lepidochelys kempii*): age at first nesting. *Chelonian Conservation and Biology* **10**: 288-293.

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. (2003). Stochastic simulation modelling of loggerhead sea turtle population dynamics given exposure to competing mortality risks in the western south Pacific. p 274-294, In: Bolten, A. and Witherington, B. (Eds) Loggerhead Sea Turtles. (Smithsonian Institution Press, Washington, DC, USA)

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.

Dobbs, K., Miller, J. and Landry, A. (2007). Laparoscopy of Nesting Hawksbill Turtles, *Eretmochelys imbricata*, at Milman Island, Northern Great Barrier Reef, Australia. *Chelonian Conservation and Biology* **6**: 270-274.

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.

Fletcher, D. (2012) Estimating overdispersion when fitting a generalized linear model to sparse data. *Biometrika* **99**: 230-237.

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. https://CRAN.R project.org/package=R2ucare.

Hamann, M., Limpus, C. J., and Owens, D. W. (2003). Reproductive cycles of males and females. In 'The Biology of Sea Turtles. Volume II'. (P. L. Lutz, J. A. Muzick, and J. WynekenEds.) pp. 135-161. (CRC Press: Boca Raton.)

Laake, J. (2013). RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

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.

Limpus, C. J. (1971). The flatback turtle, *Chelonia depressa* Garman in southeast Queensland, Australia. *Herpetologica* **27**, 431-436.

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. (1992). Estimation of tag loss in marine turtle research. *Wildlife Research* **19**, 457-469.
Limpus, C. J. (2007). A biological review of Australian marine turtles: 5. Flatback turtle, (*Natator depressus*) (Garman). (State of Queensland, Environmental Protection Agency.) ISBN 978-0-9803613-2-2.
Limpus, C. J., Baker, V., and Miller, J. D (1979). Movement induced mortality of loggerhead eggs. *Herpetologica* **35**, 335-338.
Limpus, C. J., Carter, D., and Hamann, M. (2001). The green turtle, *Chelonia mydas*, in Queensland: the Bramble Cay rookery in the 1979-1980 breeding season. *Chelonian Conservation and Biology* **4**, 34-46.
Limpus, C. J., Ferguson, J., Gatley, C., and D. Limpus (2017). Queensland Turtle Conservation Project: Woongarra Coast Flatback Turtles, 2016-2017 breeding season. (Department of Environment and Heritage Protection, Queensland Government: Brisbane.).
Limpus, C. J., FitzSimmons, N. N., Sergeev, J. M., Ferguson, J., Hoffmann, F., Phillot, A., Pople, L., Rose, A., Tompkins, B. Turner, T. and Wenk, L. (2018). Marine turtle nesting populations, Flatback turtle, Natator depressus, 2016-2017 breeding season, (Department of Environment and Heritage Protection, Queensland Government: Brisbane). Report produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program 76 pp.
Limpus, C. and Limpus, D. (2002). The biology of the loggerhead turtle, *Caretta caretta*, in southwest Pacific Ocean foraging areas. In: Bolten, A. and Witherington, B. (eds) The Biology and Conservation of Loggerhead Sea Turtles. (Smithsonian Institution Press, Washington, DC, USA).
Limpus, C. J., Parmenter, C. J., Baker, V. and Fleay, A. (1983). The Crab Island sea turtle rookery in northeastern Gulf of Carpentaria. *Australian Wildlife Research* **10**, 173-184.
Limpus C. J., Parmenter C.J., and Chaloupka M. (2013). 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.
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.
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.
Miller, J. D. and Limpus, C. J. (2003). Ontogeny of marine turtle gonads. In 'The Biology of Sea Turtles. Volume II'. (P. L. Lutz, J. A. Muzick, and J. WynekenEds.) pp. 199-224. (CRC Press: Boca Raton.)
Miller, J. D., Limpus, C. J., and Bell, I. P. (2008). The nesting biology of *Eretmochelys imbricata* in the northern Great Barrier Reef. In "Australian hawksbill turtle population dynamics project." (Eds. Limpus, C. J. and Miller, J. D.) Pp. 41-93. (Queensland Environmental Protection Agency: Brisbane).

Miller, J. D., Limpus, C. J., and Godfrey, M. H. Nest site selection, oviposition, eggs, development, hatching, and emergence of loggerhead turtles. Bolten, A. B. and Witherington, B. E. Biology and Conservation of Loggerhead Turtles. 125-143. 2003. Washington, D. C., Smithsonian Institution Press.

National Research Council (2010). Assessment of Sea-Turtle Status and Trends: Integrating Demography and Abundance. (National Academies Press, Washington, DC.)

Nichols, J. and Hines, J. (2002). Approaches to the direct estimation of χ, and demographic contributions to σ, using capture-recapture data. *Journal of Applied Statistics* **29**: 539-568.

Nichols, J., Hines, J., Lebreton, J. D. and Pradel, R. (2000). Estimation of contributions to population growth: reverse-time capture-recapture approach. *Ecology* **81**: 3362-3376.

Parmenter, C. J. (1993). A preliminary evaluation of the performance of passive integrated Transponders and metal tags in a population study of the flatback sea turtle (*Natator depressus*). *Wildlife Research* **20**, 375-381.

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.

Pfaller, J. B., Limpus, C. J., and Bjorndal, K. A. (2008). Nest-site selection in individual loggerhead turtles and consequences of doomed-egg relocation. *Conservation Biology* **23**, 72-80.

Pradel, R. (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometrics* **52**: 371-377.

Pradel, R., Choquet, R., Lima, M., Merritt, J., and Crespin, 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.

Pradel, R., Gimenez, O., and Lebreton, J. (2005). Principles and interest of GOF tests for multistate capture-recapture models. *Animal Biodiversity and Conservation* **28**:189-204.

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.

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.

White, G., Kendall, W. and Barker, R. (2006). Multistate survival models and their extension in Program MARK. *Journal of Wildlife Management* **70**:1521-1529.