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Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters

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Abstract Sex- and age-class-specific survival of a loggerhead turtle population resident in southern Great Barrier Reef waters was estimated using a long-term capture–mark–recapture (CMR) study and the Cormack–Jolly–Seber modelling approach. The CMR history profiles for 271 loggerheads tagged over 9 years (1984–1992) were classified into two age classes (adult, immature) based on somatic growth and reproductive traits. The sex and maturity status of each turtle was determined from visual examination of reproductive organs using laparoscopy. A reduced-parameter model accounting for constant survival with sex- and time-specific recapture was adequate for estimating age-class-specific survival probabilities, but inclusion of time-specific transient behaviour was informative for the immature age class. The annual fluctuations in the estimated proportion of transient immatures was not a function of sampling effort, but could be due to anomalous oceanographic conditions affecting dispersal of the immature class. There was no sex-specific difference in survival probabilities for either age class, but females were more likely to be recaptured than males, which might be related to behavioural differences such as sex-biased dispersal. The expected annual survival probability for adults was 0.875 (95% CI: 0.84–0.91). The expected annual survival probability for immatures was 0.859 (95% CI: 0.83–0.89), but when the transients were accounted for, the expected annual survival for the resident immature loggerheads was 0.918 (95% CI: 0.88–0.96). These are the first substantive estimates of annual survival probabilities for any loggerhead sea-turtle stock and provide a basis for developing a better understanding of loggerhead population dynamics.

Introduction

Age- or age-class-specific survivorship is a key demographic component of population growth and evolutionary fitness (Fox 1993). Survival data are not only needed for the development of age- (Benton and Grant 1996) or state-dependent life-history theories (McNamara and Houston 1996), but also for the modelling of demographic viability and ecological risk (Burgman et al. 1993). Despite the importance of survivorship, there is a paucity of reliable data even for well-studied vertebrate groups, such as ungulates (Loison et al. 1999), squamate reptiles (Shine and Charnov 1992) and waterfowl (Krementz et al. 1997). The lack of reliable survival data is particularly acute for turtles (Iverson 1991; Shine and Iverson 1995), although estimates for a green sea turtle population resident in southern Great Barrier Reef (sGBR) waters are now available (Chaloupka and Limpus 1998; Chaloupka 2000). We present here for the first time a detailed analysis of survivorship derived from a capture–mark–recapture sampling programme for loggerhead sea turtles resident in sGBR feeding grounds. The loggerhead (Caretta caretta) is recognised globally as one of the most endangered sea-turtle species (National Research Council 1990), with the sGBR genetic stock exposed to a very high risk of incidental capture in the otter-trawl fisheries operating in east Australian coastal waters (Slater et al. 1998). More details on sGBR loggerhead life history can be found in Limpus et al. (1994), Musick and Limpus (1997) and Chaloupka and Limpus (2001).
Materials and methods

Data set and capture-mark-recapture profiles

The data set comprised the annual capture-mark-recapture (CMR) history profiles for 271 sGBR loggerhead turtles sampled in the sGBR feeding grounds between 1984 and 1992. Capture and recapture on each of the nine sampling occasions (1984–1992) was undertaken using the turtle-rove technique, with each turtle double-marked with uniquely coded titanium tags (Limpus 1992a). Tag loss for this CMR study has been shown to be negligible (Limpus 1992a). The sampling occasions were restricted to a 4-month interval (March to June) to limit sampling overlap with the nesting season (November to February) when there is an influx of temporary breeding migrants from other feeding grounds. The 271 CMR profiles record the capture history of each turtle and include (1) size based on curved carapace length (CCL, in centimetres) at first capture and at each recapture, (2) sex and maturity status determined from visual examination of the reproductive organs using laparoscopy (Limpus et al. 1994) and (3) sex-specific ontogenetic stage or age-class classification assigned to each turtle at first capture, derived from a combination of size-specific growth functions and maturity status.

The data included CMR profiles for female and male loggerhead turtles, spanning the entire post-recruitment phase from ~69 to 120 cm CCL, with 32% of the profiles derived from sexually mature individuals. The immature age class recruit to benthic habitats in sGBR waters at ~70 cm CCL, after an unknown period of pelagic development in the south-western Pacific Ocean (Limpus 1992b). Pelagic loggerhead age-class duration is poorly known, but is estimated to be 7–10 years (Chaloupka 1998; Bjørndal et al. 2006). Age-class duration for immature sGBR loggerheads is ~12–15 years (Limpus 1992b). A demographic classification of the 271 CMR profiles used for estimation of sex- and age-class-specific survival and recapture probabilities for the sGBR foraging-ground population is shown in Table 1. More details of this CMR programme can be found in Limpus (1992a) and Limpus and Chaloupka (1997), while Chaloupka and Musick (1997) give an overview of the sampling and tagging protocols used in sea-turtle CMR programmes.

Statistical modelling approach

Maximum-likelihood estimates of the annual sex- and age-class-specific survival and recapture probabilities for the loggerhead turtle resident in sGBR feeding grounds (1984–1992) were derived from the 271 CMR profiles, using the Cormack–Jolly–Seber (CJS) modelling approach advocated by Lebreton et al. (1992). The CJS approach does not assume demographic closure and so is suitable for estimation of demographic parameters given an underlying stochastic birth, death and permanent-emigration process. The statistical assumptions and limitations of the CJS modelling for estimation of time-specific demographic probabilities are well known and have been discussed in detail elsewhere (Cormack 1989; Lebreton et al. 1992; Kendall et al. 1997; Pradel et al. 1997).

One of the major assumptions of the time-dependent survival estimators of the CJS model is homogeneity of recapture likelihood, which is addressed by including informative covariates such as sex and sampling effort in the model to account for differences in survival and/or recapture probabilities (Lebreton et al. 1992; Cormack 1993). Each age-class-specific model is referred to as the global sex- and time-dependent CJS model for this study and is the reference model to test simpler model fits (see Lebreton et al. 1992). Age was not known for the sea turtles sampled in this study, nor for any recapture study (Chaloupka and Musick 1997), so age-dependence in survivorship was not addressed directly here except within the context of the two chosen age classes.

All CJS modelling was implemented here using a combination of RELEASE (Burnham et al. 1987) and MARK (White and Burnham 1999) for goodness-of-fit testing, and SURGE (Cooch et al. 1996) and MARK for model estimation and hypothesis testing. TMSURVIV (Pradel et al. 1997) was also used to estimate survival and recapture probabilities given the presence of presumed transient loggerheads as well as the proportion of residents present in the sample. All SURGE or MARK models were based on the logistic link function (Lebreton et al. 1992) to ensure within-range parameter estimates.

Goodness-of-fit and model selection

The initial goodness-of-fit tests used here to assess compliance with the CJS model assumptions were discussed by Lebreton et al. (1992) and Pradel (1993) and implemented here using RELEASE (Burnham et al. 1987) and REL_C (Pradel et al. 1995). These tests included: (1) TEST2 + 3 to determine whether the global model (sex- and time-specific survival and recapture probabilities) fitted the data, before proceeding to other analyses (Lebreton et al. 1992); (2) the Brownie–Robson test for age/ handling effect or presumed transients (RELEASE TEST3.5R component) to diagnose any failure of global model fit (Loery et al. 1997); (3) the Peto test for specific behavioural patterns that mimic trap- dependence, such as temporary emigration or recapture heterogeneity (TEST2.CT component in some versions of RELEASE, such as REL_C) to diagnose any failure of model fit (Pradel 1993; Pradel et al. 1995) and (4) TEST1 as an omnibus test for assessing any difference in survival and recapture probabilities between demographic subgroups, such as sex or age class (Burnham et al. 1987).

Once a satisfactory age-class-specific global model was found based on the appropriate goodness-of-fit test (TEST2 + 3), then various reduced-parameter forms were fitted to find the most parsimonious model—a model that not only fitted the data well but required fewer parameters than the global CJS model or any other reduced model (Cormack 1989; Lebreton et al. 1992). Model selection and statistical inference relative to the global model was based on log-likelihood ratio tests (LRT; Lebreton et al. 1992) and the Akaike Information Criterion (AIC), which is used for rapid screening of a large number of model fits (Anderson et al. 1998). AIC is based on the number of estimable model parameters, but if inadmissible probabilities (survival or recapture probability = 1) occurred then they were discounted in the AIC calculation by subtracting the number of inadmissible values (Cooch et al. 1996). The same preferred model selections occurred here using either AIC or the more complex quasi-likelihood AIC (QAIC; Anderson et al. 1998) that is implemented in MARK and TMSURVIV. AIC was used here to be consistent with the model estimation using SURGE, which does not provide QAIC.

The goodness-of-fit of the best-fit model or most parsimonious reduced-parameter CJS model selected by AIC relative to the global model was then assessed using improved test procedures derived from the TEST2 + 3 goodness-of-fit tests and relevant likelihood-ratio tests (Meredith et al. 1995; Loery et al. 1997). The most parsimonious model selected for each age class was then used to derive maximum-likelihood estimates of the sex- and time-specific survival and recapture probabilities. Comparisons between survival probabilities derived from separate models were then assessed using a generalised chi-square test developed for testing homogeneity of demographic probabilities (Sauer and Williams 1989).

Table 1 Caretta caretta. Demographic summary of the 271 CMR profiles for the sGBR loggerhead turtle resident in sGBR feeding grounds (1984–1992). Age-class classification assigned to each turtle at first capture

<table>
<thead>
<tr>
<th>Age class</th>
<th>Sex</th>
<th>Size range</th>
<th>Female</th>
<th>Male</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults (&lt; 91 cm CCL)</td>
<td></td>
<td>25</td>
<td>62</td>
<td>87</td>
<td></td>
</tr>
<tr>
<td>Immatures (&lt; 95 cm CCL)</td>
<td></td>
<td>46</td>
<td>138</td>
<td>184</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>71</td>
<td>200</td>
<td>271</td>
<td></td>
</tr>
</tbody>
</table>