



Sampling nesting sea turtles: optimizing survey design to minimize error

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ABSTRACT: Many sea turtle studies globally use counts of nesting activities as a proxy for population abundance estimates and as an indicator of trends within the population. Often these populations are sampled temporally and spatially, but few previous studies have examined the impact of different sampling techniques on the accuracy of these estimates. We investigated temporal sampling errors using a multi-species approach, examining 10 populations comprising green, loggerhead and leatherback sea turtles. Sampling errors were investigated from random, regular and continuous sampling regimes spanning 5–80% coverage. A count approach was used rather than an individual-based capture–mark–recapture approach to broaden the scope and application of the research. Modelling showed that even low survey coverage of 5% gave reasonably accurate estimates of annual nesting activity, with estimated errors of ca. 20% (mean + 1 SD equalling 84.1% of surveys). Survey error is low relative to changes in abundance from the inter-annual variations in nesting activity that occur in sea turtle populations. Thus, annual studies are important to estimate sea turtle abundance, even if these studies have low survey coverage. An increase in survey effort may be more cost effective if spent combining estimates of total nesting activity with sampling turtles as part of a capture–mark–recapture study. This approach will provide a second estimate of annual abundance as well as an estimate of demographic parameters including clutch frequencies, remigration intervals, survivorship, immigration and emigration. This estimation of sampling errors may be useful in the design of monitoring programmes and can be used to guide management and policy decisions.

KEY WORDS: Turtle · Survey effort · Survey design · Sampling · Error · Precision · Accuracy · Population size estimation

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1. INTRODUCTION

Population ecology is an important facet of conservation research where counts of wildlife populations and robust mathematical modelling can be used to make inferences concerning biological processes

and parameters (Burnham & Anderson 2002) and identify where human impacts and extinction risks can be minimized (Williams et al. 2002). Our understanding of population dynamics, specifically the fluctuations that occur in the number of individuals in animal populations and factors controlling these

fluctuations (Isaacs et al. 1991), ultimately depends on a precise and accurate measurement index for the number of animals at a given time (Gerrodette 1987, Hayes & Steidl 1997, Sims et al. 2008, Pfaller et al. 2013). The precision, accuracy and monitoring design for monitoring wildlife populations is dependent on life history characteristics of the species, conspicuousness, density, total abundance and demographic dispersion as well as abiotic and biotic factors influencing primary population processes (Williams et al. 2002).

Sea turtles are an excellent model taxon for modelling sampling efficiency and sampling errors for migratory species due to their unique life history and availability for study. Despite the enigmatic nature of sea turtles for several life history stages that use diverse and dispersed habitats, their nesting biology is much better understood. Sea turtles generally display strong site fidelity to their nesting area (Bjørndal et al. 1983, Limpus 1985, Girondot & Fretey 1996, Miller 1997, Limpus et al. 2003, Dethmers et al. 2006), which allows identification of nesters both within a nesting season and in subsequent nesting seasons. Although behavioural plasticity has been demonstrated where some individual turtles display low fidelity to nesting sites and can nest at beaches separated by hundreds of kilometres both within and between breeding seasons, the proportion doing so is generally low (Bjørndal et al. 1983, Limpus 1985, 2009, Girondot & Fretey 1996, Limpus et al. 2003, Dethmers et al. 2006, Esteban et al. 2015). Within the nesting season, sea turtles generally nest at reasonably regular intervals of approximately 2 wk and lay on average around 2–6 clutches per season (Miller 1997, Tucker 2010). When nesting, turtles are often on the beach for at least 45 min (Miller 1997) and are readily accessible to researchers, as they have few flight or behavioural defence mechanisms while nesting, especially after mid-way through oviposition (Bustard 1972).

These characteristics make nesting sea turtles relatively easy to survey. This fact, together with the global conservation status of all species of sea turtles (except flatback turtles) as Vulnerable, Endangered or Critically Endangered in the IUCN red list (IUCN 2020), means that an abundance of information has been collected on nesting individuals compared to other life history stages of sea turtles and many other species of animals (Schroeder & Murphy 1999, National Research Council 2010, Rees et al. 2016). Hundreds of projects researching sea turtles globally have aimed to quantify abundance and trends of

nesting turtles (see Seminoff 2004, Abreu-Grobois & Plotkin 2008, Mortimer & Donnelly 2008, Wallace et al. 2013, Casale & Tucker 2017, Wibbels & Bevan 2019), as these are the ultimate variables to identify potential decline and thus enact measures to halt or reverse this decline.

Many regional subpopulations are now showing an increasing or recovering trend in population abundance (Chaloupka et al. 2008, National Research Council 2010, Mazaris et al. 2017, IUCN 2020). Population size under the IUCN red list criteria is measured as the number of mature individuals only (IUCN 2019), and sea turtle population assessments have been further limited to breeding females while they are at their nesting beach as a proxy for the number of mature individuals. Unquestionably, monitoring only one demographic life stage presents limitations on conclusions regarding the functioning of the population, as it does not consider adult males or non-breeding turtles, including sub-adults and juveniles of either sex (e.g. Bjørndal 1997, Chaloupka & Limpus 2001, 2002, 2005, Seminoff et al. 2003, Eaton et al. 2008, Blumenthal et al. 2009). Furthermore, due to the long life history of sea turtles and the high inter-annual variability in population numbers for many sea turtle populations (Broderick et al. 2001), it will take several decades of beach censuses to detect trends with reasonable power and confidence unless there are high rates of change, low inter-annual variability or high predictive power (Mazaris et al. 2017, Whiting et al. 2020). Despite these limitations, the broad extent of information on nesting sea turtle abundance makes nesting studies the most extensive global proxy for turtle abundance (National Research Council 2010, Wallace et al. 2011, Rees et al. 2016).

Monitoring nesting sea turtle populations is often further temporally limited to one or more sampling periods within the nesting season (e.g. Girondot & Fretey 1996, Limpus 2009) and requires robust and appropriate statistical analyses to estimate animal abundance (Gerrodette 1987, Bjørndal et al. 1999, Prince & Chaloupka 2012, García-Cruz et al. 2015, Piacenza et al. 2016, Kendall et al. 2019). Surveys aimed at encountering every individual throughout the nesting season have been conducted at many beaches and provide much of our understanding on nesting sea turtle biology (e.g. Limpus 1985, Boulon et al. 1996, Richardson et al. 2006, Chaloupka et al. 2008) and are used in this research to make inferences about populations where less intensive sampling occurs. Sampling errors in estimating annual abundance from nesting turtle surveys depend on the monitoring regime (Jackson et al. 2008, Sims et

al. 2008, SWOT Scientific Advisory Board 2011) and population dynamics, which may include seasonal length, species of turtle and population, and this may vary between nesting seasons (Whiting 2010). In addition to errors from temporal sampling, monitoring studies can also have observational errors from imperfect detection (Kéry et al. 2009, Pfaller et al. 2013) or the parameters measured. For example, higher errors are associated with counts of tracks or egg counts from harvest data than with counts of clutches or turtles (Whiting 2010, SWOT Scientific Advisory Board 2011). With any sampling regime, it is desirable to minimize all errors to provide the most meaningful results for the effort applied. Throughout the literature, sampling errors have rarely been calculated for abundance estimates and trend predictions, as these errors are generally unknown.

To address this knowledge gap and provide an *a priori* estimate of error for future surveys, we calculated the magnitude of sampling errors when estimating annual abundance from different sampling regimes. This was done utilising a multi-species approach, sampling several whole-season censuses of nesting green, loggerhead and leatherback turtle populations. We investigated sampling error, detailing sampling errors from random, regular and continuous sampling regimes. We use a total track count approach rather than an individual based capture-mark-recapture approach to broaden the scope and application of the research. Understanding sampling errors associated with annual abundance estimates will aid in the design of monitoring programmes and can be used to guide management and policy decisions to ensure that monitoring protocols allow accurate comparisons between years and beaches without bias from survey frequency or effort.

2. MATERIALS AND METHODS

2.1. Data

Nightly track counts were investigated for 3 species of sea turtles: green *Chelonia mydas* (n = 5 rookeries), loggerhead *Caretta caretta* (n = 3 rookeries) and leatherback *Dermochelys coriacea* (n = 2 rookeries) (Table 1; Figs. S1–S3 in the Supplement at www.int-res.com/articles/suppl/m674p257_supp.pdf). The populations investigated were chosen as we aimed to incorporate almost complete daily nesting data throughout the nesting season for the area investigated, and the data were available in the literature or from the authors. There were several limitations to the data examined, which included imperfect detection from high track densities and spatial and temporal limitations to sampling. These are discussed below.

For turtles nesting at Bramble Cay and Heron Island, each rookery is likely to host most of the spatial extent of nesting for that nesting population as these rookeries are not close to other nesting rookeries. Surveys of Bramble Cay and Heron Island were conducted over most of the nesting season so monitoring is not thought to be limited in temporal extent. The surveyed area at Mon Repos hosts most of the nesting along the mainland coast, but low-density nesting also occurs on other beaches along the Woongarra coast (Limpus 2009). Loggerhead turtles at Mon Repos show high site fidelity to the same beach both within a nesting season and in subsequent nesting seasons (Bustard 1972, Limpus 1985, 2009). The surveys at Mon Repos covered most of the nesting season temporally, with very low-density nesting reported at the start

Table 1. Location, species, factor counted and seasonal range for the nightly count data used for modelling annual abundances of sea turtles

Species	Study site	Factor counted	Season range	No. of seasons	Data source
Green	Akyatan Beach, Turkey	Nests	May–Aug	1	Aureggi et al. (2000a,b)
Green	Bramble Cay, Torres Strait	Turtles laying	Oct–Mar	1	Limpus et al. (2001)
Green	Guinea-Bissau, Africa	Tracks	Jul–Dec	1	Catry et al. (2002)
Green	Heron Island, Australia	Turtles laying	Oct–Mar	1	C. J. Limpus (unpubl. data)
Green	Sabah Turtle Islands, Malaysia	Turtles laying	All year	7	Raw data for 1991–1997 from Sabah Parks provided by N. Pilcher & P. Basintal
Loggerhead	Heron Island, Australia	Turtles laying	Oct–Mar	1	C. J. Limpus (unpubl. data)
Loggerhead	Jupiter/Carlin, Florida, USA	Nests	May–Aug	1	Davis et al. (1994)
Loggerhead	Mon Repos, Australia	Turtles laying	Oct–Mar	7	C. J. Limpus (unpubl. data)
Leatherback	Chiriqui Beach, Panama	Clutches	Mar–Jul	1	Ordoñez et al. (2007)
Leatherback	Playa Grande, Costa Rica	All turtles	Oct–Feb	1	Lux et al. (2003)

and the end of the time-series (Fig. S1). The particular years of time-series of data used from Mon Repos were due to the availability of data and the temporal extent of monitoring during each of the seasons. Nesting at Selingen Island, Sabah Turtle Islands, is spatially distinct from other nesting beaches, but nesting also occurs at the other 2 Islands that constitute the Sabah Turtle Islands (Bastinal & Lakim 1993, Joseph 2017). Daily counts were conducted at the Sabah Turtle Islands throughout the entire nesting season. The different years of time-series of data from the Sabah Turtle Islands were selected due to the availability of data and temporal extent of monitoring during these seasons. At Akyatan Beach, daily track counts were available for approximately 4 km of the total 19.7 km nesting beach, representing 47% of clutches laid on the beach that year (Aureggi et al. 2000a,b). Surveys at Akyatan Beach also did not include the first ca. 1 mo of the nesting season so were temporally limited as well (Aureggi et al. 2000a,b). Nesting surveys at Guinea-Bissau are temporally estimated to cover 85% of the nesting season (Catry et al. 2002). The island monitored within Guinea-Bissau at Poilão Island is one of 4 islands within the João Vieira and Poilão Marine National Park. The extent of spatial interchange in nesting is not quantified for this population. Turtles nesting at Guinea-Bissau nest in considerably high densities such that there is likely to be error in track identification, with >200 turtles nesting in 1 night over the 2.3 km coastline (Fig. S2 and Catry et al. 2002). Nesting densities at Jupiter/Carlin are also of sufficiently high density (>50 tracks over 2.5 km) to have survey error in counts from track density (Davis et al. 1994). All other sites are much lower and likely to have low errors in double counting or missing tracks due to track densities (see Figs. S1–S3). Nesting at Jupiter/Carlin is spatially limited to 2.5 km of beach, with nesting occurring on nearby beaches within Palm Beach County and surrounding areas (Cody 2013), but the extent of nesting occurring within this section during the survey period and extent of movement between the survey area and remaining beach is not known. At Chiriqui Beach, Panama, leatherback turtle nesting data were collected every 2 d for the first month of the nesting season (Ordoñez et al. 2007). To generate a complete time-series for the Chiriqui Beach population, missing values were interpolated as an average of the counts for the immediately preceding and proceeding days, and counts were halved for the period where data were collected every 2 d. Nest-

ing surveys at Chiriqui Beach covered the entire 24 km of nesting beach aiming to record all leatherback nesting activity (Ordoñez et al. 2007). Nesting at Playa Grande was temporally limited to include the peak of the nesting season (Lux et al. 2003) but is likely to miss low-density nesting before and after the monitored period (see Fig. S3). Playa Grande is a 3.5 km long nesting beach, and 1 of 3 beaches within Parque Nacional Marino Las Baulas in Pacific northwestern Costa Rica (Nordmoe et al. 2004). There is not likely to be substantial error in spatial sampling, as leatherbacks have been shown to nest near their previous nest site (Chaves et al. 1996), and a high degree of fidelity to the area was also reported at Playa Grande (Nordmoe et al. 2004). Nesting surveys are unlikely to be biased by changes in nesting success, as all surveys (except for leatherback turtles nesting at Playa Grande, Costa Rica) counted successful clutches only so did not count multiple nesting attempts by the same turtle multiple times.

For the populations investigated, errors in track identification can make erroneous counts of turtle species, adding to survey measurement errors. For some populations analysed (Akyatan, Guinea-Bissau, Heron Island, Jupiter/Carlin, Mon Repos), several turtle species use the nesting beaches, including various combinations of green, loggerhead, hawksbill and flatback turtles. However, for all rookeries except Heron Island, the data provided are from the species that nests in the vast majority, as there are low percentages of other species (Davis et al. 1994, Aureggi et al. 2000a,b, Catry et al. 2002, Limpus 2009) which will considerably reduce the likelihood of misidentification. Although leatherback turtle tracks are unlikely to be confused with other species due to their size, misidentification can occur between some other species such as between loggerhead and hawksbill turtles, but less likely to occur between green and loggerhead turtles due to the greater differences in the appearance of tracks. All population surveys analysed were from counts from on-ground surveys rather than counts from alternative methods such as aerial surveys or use of drones (e.g. Waayers 2014, Schofield et al. 2017, Tucker et al. 2018, Dunstan et al. 2020).

2.2. Models

We used 2 modelling approaches to estimate annual nesting abundance. Firstly, we used a generalised additive model with uniform weighting

using the 'mgcv' package in R version 3.3.1 (R Core Team 2016) to predict nesting abundance throughout the season. A generalised additive model was chosen because of its goodness-of-fit and flexibility across different species and populations (Whiting et al. 2014). This non-parametric approach did not force the data to conform to a predefined shape and allowed for skewed and multi-modal seasonal shapes. Secondly, we used linear regression models to extrapolate from sampled data to full-season counts without predicting the time-series (as described by Jackson et al. 2008, Limpus et al. 2008, Whiting 2008, Limpus 2009). Regular, random and mid-season samples were plotted against full-season counts with the relationship described by the linear form $y = ax + b$ where y is the estimated annual nesting activities, x is the sum of the sampled counts of nesting activities, and a and b are variables describing the slope and position of the line. For linear regression models to be accurate in estimating population size, they assume that if sampling occurs in the same manner and with the same effort each year, then the annual population size can be estimated with a given degree of certainty irrespective of the inter-annual changes in nesting abundance. The goodness of fit between data points and the predicted line was evaluated using the r^2 value as a measure of dispersion of the data: the higher the r^2 value, the lower the error in estimating annual nesting abundance. The use of linear regression models to predict nesting abundance was restricted to 1 population of green turtles and 1 population of loggerhead turtles, as several seasons of data were required to develop these models.

2.3. Sampling design

Monitoring regimes investigated included: monitoring intermittently throughout the season and monitoring once during the peak of the season as different populations often have different optimal survey methodologies (e.g. Girondot & Fretey 1996, Bjorndal et al. 1999, Whiting et al. 2008, Bool et al. 2009, Limpus 2009). Temporal coverage was investigated for a proportion of the total nesting season and varied from 5 to 100% coverage of the nesting season. Intermittent monitoring through the season was investigated for both random and regular monitoring regimes. To investigate the impacts of random selection in monitoring days, we generated 1000 replicate sampled datasets using a random number generator in the pro-

gram R version 3.3.1 to create each dataset (R Core Team 2016). Annual abundance was estimated for each data subset using the statistical models, and error was calculated for each sample using the absolute difference in actual and predicted nesting abundances. The mean errors were then calculated from the replicate datasets for each sampling combination values to give an indication of the precision of the annual estimates. Mean errors and standard deviations are presented throughout. We also conducted auto-correlation function analyses for within-season time-series data for all species, with data detrended using the generalised additive model smoothing. For regular monitoring intermittently throughout the season, monitoring was investigated for each combination of days with that monitoring regime to increase the power of the analysis. For example, for monitoring 2 days per week, we investigated samples starting on Days 1, 2, 3, 4, 5 and 6 to give all combinations of 2 d per week of sampling.

3. RESULTS

Generalised additive models and linear regression models both provided good estimation of annual nesting abundance for all populations and species studied. Given the same survey effort, survey error was considerably lower when monitoring occurred randomly throughout the season (Fig. 1) rather than at regular intervals (Fig. 2). There were no apparent differences in error between the 2 populations with several years of monitoring and other populations for each species, so each season was included as a distinct sample to estimate errors. Although limited by having one population available with multiple seasons of data for each of green and loggerhead turtles, mid-season surveys showed similar magnitudes of errors in abundance estimates to random survey coverage given the same survey coverage (cf. Figs. 1 & 3). There was significant auto-correlation in nesting activity, with positive lags grouped between 1 and 3 d, and negative lags grouped between 5 and 9 d (Table 2). This means, for example, that if nesting numbers are low on Day 1, then it is more likely that they are also low on the next day and 3 d later, and more likely that they are higher 5 and 9 d later.

Using sampling regimes with lowest error per unit effort, survey errors (estimated using mean error plus 1 SD) of less than 20, 10 and 5% required survey coverage of 5, 25 and 60%, respectively, for green

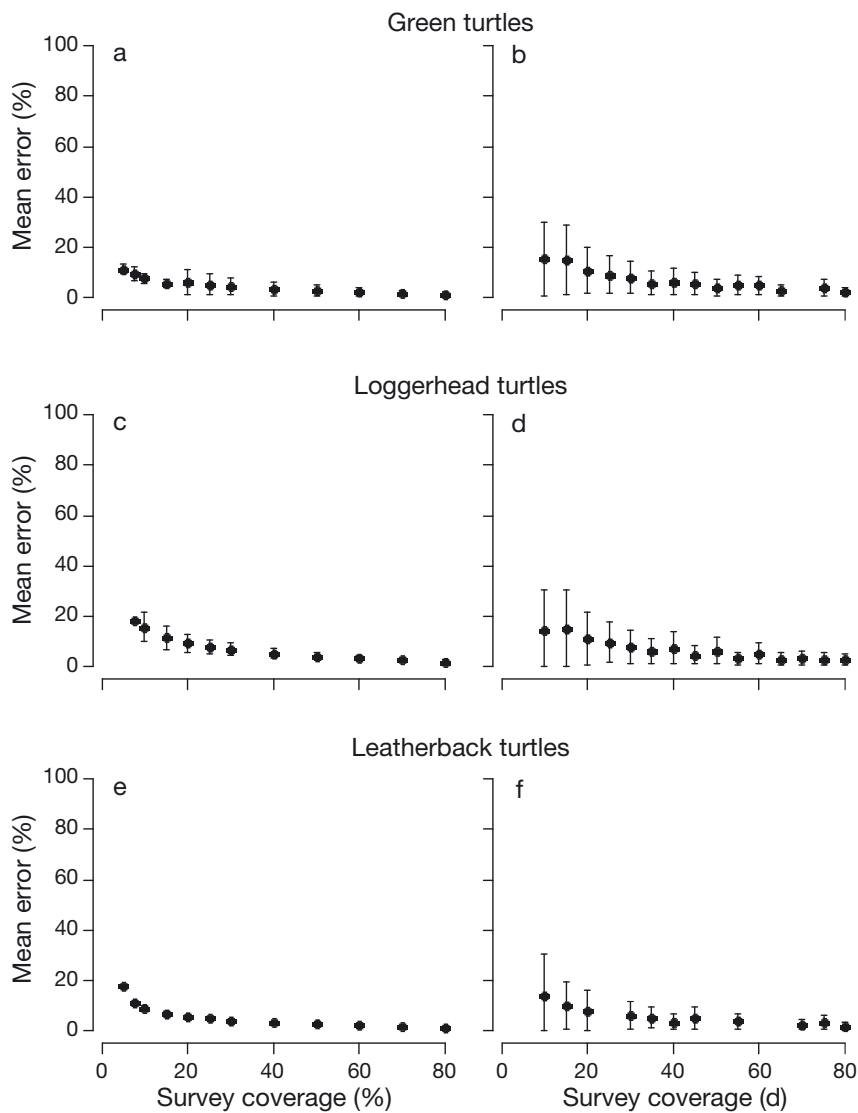


Fig. 1. Mean errors in estimating annual abundance of nesting turtles when conducting surveys randomly throughout the nesting season for (a,b) green turtles ($n = 5$ populations), (c,d) loggerhead turtles ($n = 4$ populations) and (e,f) leatherback turtles ($n = 2$ populations). Error bars indicate SD

turtles; survey coverage of 15, 30 and 60%, respectively, for loggerhead turtles; and survey coverage of 5, 10 and 30%, respectively, for leatherback turtles (Fig. 1).

3.1. Surveys with random monitoring

Error in estimating abundance from random survey coverage throughout the nesting season decreased exponentially with increasing survey coverage (Fig. 1). The greatest decrease in errors for green, loggerhead and leatherback turtles occurred until

survey coverage reached ca. 40%, corresponding to a mean error of less than 5% (Fig. 1).

For green turtles nesting year-round at the Sabah Turtle Islands, linear regression analyses showed that all random survey samples were significantly correlated with annual abundance when survey coverage was over 20% ($p < 0.05$), correlating with an r^2 of over 0.9 (Fig. 4). Survey coverage of 5, 10 and 15% had significant correlations with annual abundance 82.7, 96.6 and 99.8% of the time, respectively. For loggerhead turtles nesting during a distinct nesting season of less than 6 mo at Mon Repos, all survey samples were significantly correlated with annual abundance when survey coverage was over 30% ($p < 0.05$), correlating with an r^2 of over 0.9 (Fig. 4). Survey coverage of 5, 10, 15, 20 and 25% had significant correlations with annual abundance 55.1, 85.7, 96.0, 99.7 and 99.7% of the time, respectively.

3.2. Surveys with regular monitoring

Error in estimating abundance from regular survey coverage throughout the nesting season also decreased exponentially with increasing survey coverage (Fig. 2); mean error (grouped by the number of days of surveys) = $70.73 \times \exp(-0.041 \times \text{survey coverage in days})$, $r^2 = 0.90$; mean

error (not grouped by survey days) = $52.12 \times \exp(-0.037x)$, $r^2 = 0.54$.

Errors in abundance estimates were significantly dependent on the survey coverage as a percentage of the season ($F_{1,3152} = 878.5$, $p < 0.001$) and survey duration in days ($F_{1,3152} = 884.2$, $p < 0.001$). However, it was not possible to differentiate factors that were correlated with mean errors in estimating nesting abundance, due to the lack of independence between the factors. Survey coverage (as a percentage or the number of days) was significantly correlated with the species, population, seasonal length, frequency of surveys and the number of consecutive

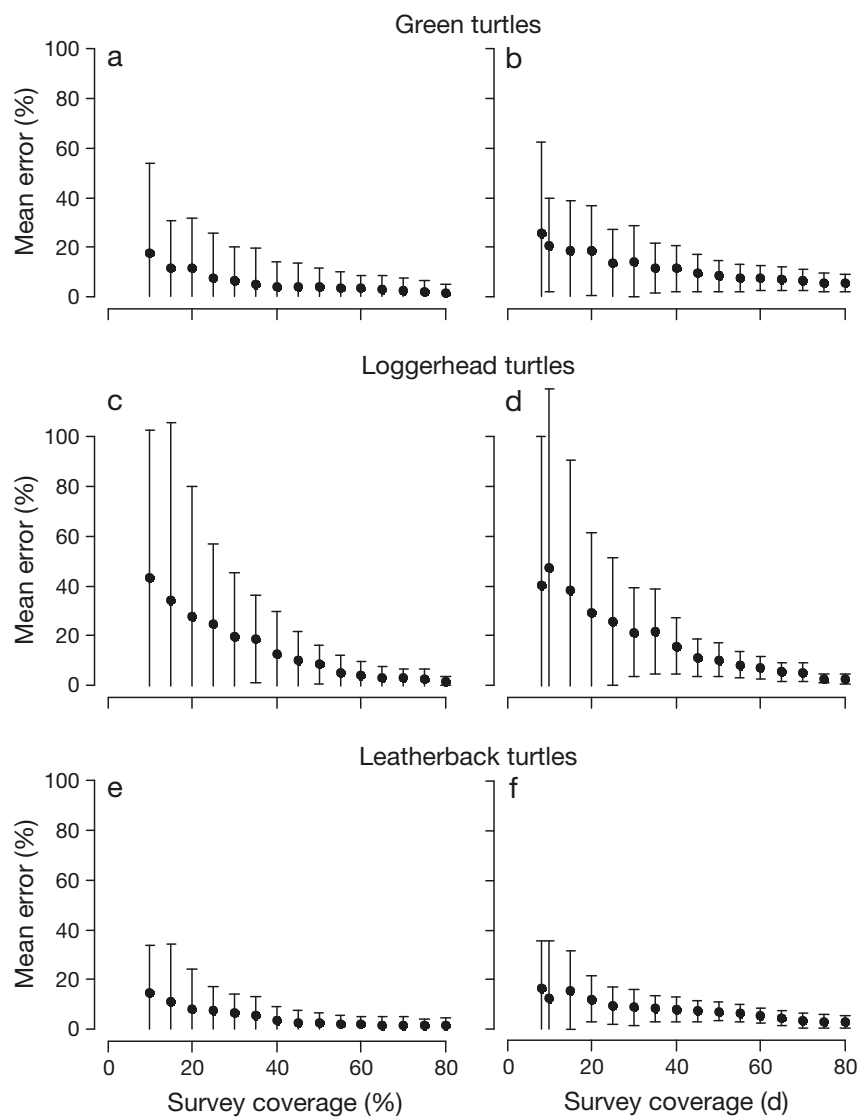


Fig. 2. Mean errors in estimating annual abundance of nesting turtles when conducting surveys at regular intervals throughout the nesting season. Details as in Fig. 1

days of surveys ($p < 0.001$). The number of consecutive days of surveys was also significantly correlated with the frequency of surveys and the species of turtle ($p < 0.001$).

3.3. Surveys conducted continuously during the peak nesting period

Comparing survey efforts between 10 and 80% in increments of 10%, the mean error in estimating annual nesting abundance was lower for mid-season surveys of green turtles than for regular sampling ($t = 3.8$, $p < 0.01$), but not statistically different

from random sampling of green turtles ($t = 1.6$, $p = 0.16$). Error in abundance estimates for mid-season surveys of loggerhead turtles was not statistically different from random ($t = 1.4$, $p = 0.18$) or regular ($t = 1.9$, $p = 0.10$) sampling.

4. DISCUSSION

The models and sampling techniques presented here show good model fits for relatively low data input, giving expected errors for 84.1% of cases of less than 20% with survey coverage of 5% or more for green and leatherback turtles, and 15% or more for loggerhead turtles when using the most accurate monitoring timings. This is considerably lower than the monitoring of 3 d wk^{-1} (43% coverage) throughout the nesting season recommended by the State of the World of Turtles Minimum Data Standards for Nesting Beach Monitoring (SWOT Scientific Advisory Board 2011) to obtain a mean error within 20% of annual nesting abundance. The relatively high expected error reported by SWOT Scientific Advisory Board (2011) may have been attributable to auto-correlation in data series investigated, an artefact of the modelling or sampling design or functional differences in populations investigated. In contrast, our study showed monitoring of 2 d wk^{-1} , irrespective of when those days were monitored, had a mean error of $< 20\%$ for all populations and species investigated.

The good estimation of annual abundance for track count data means it is not a major limiting factor in confidence in trend detection and comparison between populations with relatively low-intensity monitoring regimes contributing little to changes in power of trend detection (see Whiting et al. 2020). Low-intensity surveys of ca. 2 wk yr^{-1} have been successful in identifying trends of some turtle populations (National Research Council 1990, Limpus et al. 2013, Mortimer et al. 2020). Increases in survey effort might therefore give better outcomes by coupling

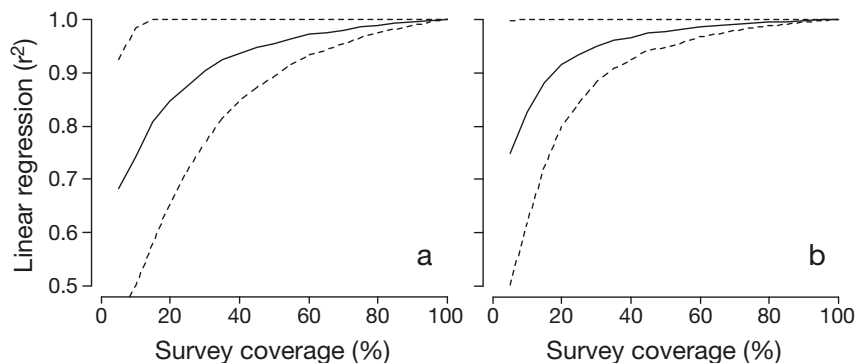


Fig. 4. Linear regression r^2 for correlations between random partial survey counts and full-season counts for survey coverage ranging from 5 to 100%. Data are shown for (a) loggerhead turtles nesting at Mon Repos, Australia, and (b) green turtles nesting at the Sabah Turtle Islands, Malaysia. Dashed lines indicate 95% confidence intervals

corresponds with the range in semidiurnal tidal cycles. The causes of nightly variation in the number of nesting turtles are not well understood or able to be predicted for any species of turtle. Positive autocorrelation lags also occurred for 3 populations of green turtles at approximately 2 wk intervals, but the prevalence amongst days was lower than for loggerhead turtles. A similar situation was seen for green and loggerhead turtles in the Mediterranean, where Jackson et al. (2008) found a periodicity in the r^2 values associated with start date for correlations between full season counts and partial counts when surveys were conducted every week or 2 wk.

For all studies of sea turtles and especially when conducting surveys intermittently throughout the nesting season, observation error and imperfect detection also needs to be addressed to avoid erroneous conclusions about abundance or trends (Kéry et al. 2009, Pfaller et al. 2013). Imperfect detection is when individuals present during the sampling period are double counted, misidentified or overlooked (Kéry et al. 2009). Observation error was not included in analyses within this manuscript, as it varies between monitoring programmes based on the survey methodology used. There are several ways in which observation error can confound abundance estimates. For instance, track counts have higher error in estimating annual abundance of turtles than counts of clutches or counts of turtles; if tracks are monitored during the morning, the characteristics of the nesting beach and the weather will impact whether the previous night's nesting activities can be differentiated from older nesting activities. The ability to detect a track can be affected by tide, rain, wind and human or animal activity which may obliterate tracks, and tidal heights which may

indicate recent or older nesting activities (Schroeder & Murphy 1999). Observer error may also occur from misidentification of the species of turtle if several turtle species are nesting on the same beach. Tracks can be double counted or overlooked if tracks overlap, such as from high-density nesting; from double counting activity from the previous night of nesting without marking tracks sufficiently; or from other human observation, recording or transcription errors. When surveys are conducted by drone or from the air rather than on the ground (e.g. Waayers 2014, Schofield et al. 2017, Tucker et al. 2018, Dunstan et al.

2020), observational errors may be higher. All sampling regimes investigated assume that an accurate count of 1 night of nesting activity can be obtained and may require an additional survey day preceding the counts to cross old tracks so that the previous night of nesting activity can be differentiated from nesting that occurred before this. Further investigations of observer error specific to each nesting beach are recommended to encompass all potential survey errors in estimating nesting abundance.

Analyses presented herein did not show any consistent difference between continuous and intermittent monitoring given the same survey effort. The type of sampling regime, i.e. whether sampling is conducted intermittently throughout the nesting season, during an intensive survey period at the peak of the nesting season or a combination of the 2 regimes, should therefore depend on the cost and resources available for monitoring. Preferred monitoring regimes will vary between nesting populations; for example, at remote locations where cost is substantial in reaching the nesting beach (e.g. Limpus et al. 2001, 2003, Guinea et al. 2005), it is probably preferable to visit less often but for a longer period of time during each visit. However, for beaches closer to towns which rely on volunteers to monitor nesting activities (e.g. Ningaloo Reef, Western Australia; Carter et al. 2004, Bool et al. 2009), monitoring intermittently throughout the nesting season may be preferable, as this could be done during weekends. As long as an appropriate modelling methodology is used, either method is suitable for monitoring turtle nesting events and can provide estimates with relatively low sampling errors.

Previous studies that have recommended one particular type of sampling appear biased by their meth-

ods of analyses used to estimate survey error. Jackson et al. (2008) recommend a solid block of 3 wk of sampling and used linear regression to extrapolate between sampled and full-season counts, and mid-season monitoring corresponded to the time where the greatest proportion of the population can be encountered. In contrast, Gratiot et al. (2006) recommend that sampling should be conducted throughout the season. However, they used a sinusoidal model which is sensitive to estimates of the timing of the beginning, end and peak of the nesting season. The median error for sampling during block periods shown by Gratiot et al. (2006) was substantially greater than the mean error for continuous sampling shown herein using linear regression analysis. Even though the error is for different populations of turtles, the large difference indicates that linear regression models may be more suitable analysis tools for block monitoring than parametric models which force a shape of the season or non-parametric models that require enough data throughout the season to show the seasonal shape (see Whiting et al. 2014 for a review of models).

Although this paper refers to daily counts of nesting activity, it is important to note that if nesting tracks persist between surveys and nesting densities are low enough to allow an accurate count of all tracks, the total number of nesting events since the last survey could be counted. Counting the total number of nesting activities would substantially reduce sampling error in annual abundance estimates and would not require mathematical models to estimate abundance. Sources of uncertainty in abundance estimates would still include other observation and measurement errors, including errors from determining what proportion of tracks resulted in successful nest deposition and errors in estimating the annual number of turtles from differences in clutch frequencies.

4.2. Influence of breeding biology

Given the relatively low number of populations per species investigated, it is not possible to ascertain whether the apparent differences in sampling errors between species are due to the species of turtle examined or to other aspects of the populations investigated, such as differences in reproductive output, nest site fidelity, length of the nesting season or spatial distribution of nesting and extent of movement between sampled and non-sampled nesting beaches. Additional analyses of nesting data from

populations across all species are required to ascertain any species-specific differences in sampling errors. Theoretical population models indicate that the amount of monitoring required to obtain the same accuracy in population estimates increases with increasing seasonal length with a similar percentage of the nesting season required to gain similar accuracies between short and protracted nesting seasons (Whiting et al. 2013). However, due to the low replication of populations with different seasonal lengths and other potentially confounding factors, this was not ascertained within the current study.

The impact of varying breeding behaviours, specifically different numbers of clutches laid per turtle per season (clutch frequencies) and remigration intervals of nesting females, have the potential to significantly bias estimates of nesting females (Hays 2000, Tucker 2010, Esteban et al. 2017). Significant variations in clutch frequencies occur from sampling techniques, with observed clutch frequencies from beach patrols often underestimating clutch frequencies (National Research Council 2010, Tucker 2010, Esteban et al. 2017), or from annual variation in observed clutch frequencies (e.g. Frazer & Richardson 1985, Rivalan et al. 2006). Annual variability in observed clutch frequencies may be confounded by sampling errors (National Research Council 2010), so the true extent of annual changes is not well understood. This adds appreciable error in estimating the number of females nesting annually, and suggests that even with a full-time census of counts there may exist substantial error in estimating abundances and trends. Estimates of clutch frequency could be ascertained using satellite telemetry or intensive capture–mark–recapture studies (National Research Council 2010, Tucker 2010, Esteban et al. 2017), but both methods require considerable cost or effort or the combination of both to gain sufficient samples within and between seasons. Capture–mark–recapture studies, although not as accurate in assessing clutch frequencies (National Research Council 2010, Tucker 2010, Esteban et al. 2017), can also provide demographic parameters such as survivorship and recruitment, which can provide an additional estimate of population function and abundance (e.g. Prince & Chaloupka 2012, García-Cruz et al. 2015, Piacenza et al. 2016, Kendall et al. 2019).

4.3. Influence from environmental factors

Environmental parameters were not incorporated in the models presented herein, as even when envi-

ronmental parameters such as moon phase or tidal height are shown to have a significant relationship, the predictive power is low (Pike 2008). Furthermore, the influence is often not consistent between nesting populations or rookeries (e.g. Girondot & Fretey 1996, Lux et al. 2003, Girondot et al. 2006). Substantial *a priori* information from a full-time survey would therefore be required. Because such intensive surveys are often not practical, the modelling techniques presented herein are aimed to be transferable between populations without needing a full-time survey of that particular nesting population.

4.4. Conservation and management implications

Complex mathematical modelling tools can be difficult to implement on-ground, especially when *a priori* information is needed to produce models specific to different nesting populations. Models presented within this manuscript are straightforward enough to be implemented with Microsoft Excel or other spreadsheet software and can be applied across nesting populations without prior information about the nesting behaviour at that nesting beach. Sampling techniques are also sufficiently broad to be implemented across nesting populations.

As intensive surveys such as the ones presented throughout are often not feasible, sampling studies can estimate the accuracy of their techniques using the error estimates reported here. To test the accuracy of models in predicting annual nesting abundance where full-season nightly surveys are not feasible, a combination of intermittent and intensive surveys could be conducted to gain 2 estimates of nesting abundance and give an indication of the accuracy of survey techniques. This will provide a feedback response to managers on the effectiveness of their monitoring regimes. Furthermore, a combination of intermittent surveys and intensive surveys will highlight different changes in the shape and peak of the nesting season (from intermittent surveys) and can also monitor additional key demographic parameters of the population such as inter-nesting intervals (from intensive surveys). Climate change has the potential to bias estimates from mid-season counts as changes in climate may impact the shape and peak of the nesting season. Using a combination of nest counts and capture-mark-recapture monitoring methods would be optimal to determine any potential changes in nesting seasonality and long-term trends in abundance.

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