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Sampling design and its effect on population monitoring: How much monitoring do turtles really need?

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ABSTRACT

Marine turtles are a taxon of world-wide conservation concern. Effective long-term monitoring is hampered by the fact that populations are widely dispersed except during the breeding season. Thus most monitoring programmes focus on nesting beaches, necessitating resource intensive studies, often over months, that could conceivably, be less comprehensive and focus on more parsimonious sampling. We analyse 11 years of exhaustive monitoring data for two species of Mediterranean marine turtles (*Chelonia mydas* and *Caretta caretta*). We resample using a variety of plausible sub-sampling regimens to estimate the total annual nesting population. We project our dataset into the future applying a range of population change rates to explore how adopting a monitoring programme based on sub-sampling would, for example, affect our ability to detect population decline. We show that accurate annual population estimates can be achieved with as few as 14 days of survey effort providing monitoring spans the peak of nesting. Furthermore, the modelled impact of sampling-based monitoring suggests that the duration to detect population change is not increased greatly. Our findings have implications for all marine turtle monitoring and have applicability to other animal groups. It is often considered desirable to perform exhaustive monitoring, with aversion of basing policy recommendations on partial data. However, comprehensive long-term monitoring programmes, particularly in developing nations, although presenting a number of advantages, are often impossible. Accurate total annual censuses can be achieved through a variety of sub-sampling regimens without sacrificing the ability to detect changes in the population trends over time. In this example, a solid block of at least 3 weeks sampling that encompasses the peak of the nesting season is advised.

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1. Introduction

Population census techniques are common place in ecological studies and it is rare to have complete counts for any popula-

tion. Estimates of total population can be made from sampling either spatially (Evans and Hammond, 2004) or temporally (Bjorndal et al., 1999). Any such estimate is prone to natural error – generally the more effort expended the

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more accurate and precise the estimate. There is a natural trade-off in sampling effort and minimising statistical error (Zar, 1996). However, optimising a sampling regimen involves a managerial decision that may have to take into account a wide variety of factors including money, different research agenda or impact to the habitat. Key to the conservation of some species is a requirement to retain an ability to detect a trend (usually a decline) in a population over time (Anon, 2002).

Marine turtles are subject to widespread exploitation in many countries for subsistence, as well as domestic and international trade. All species are listed on Appendix I of CITES, prohibiting international trade with or between CITES parties barring exceptional circumstances. This trade ban and the true conservation status of marine turtles, especially of the hawksbill turtle (*Eretmochelys imbricata*, L.) has been subject to extensive debate in unpublished and published fora (Brackett, 1997; Lapointe, 1997; Meylan, 1998; Mrosovsky, 1997; 1998). Effective monitoring of marine turtle population status is therefore of considerable importance.

The life cycle of marine turtles often involves movements over great spatial scales (see Musick and Limpus, 1996 for a review), with individuals generally taking decades to reach adulthood. As a result of difficulty monitoring populations at sea, and the non-random distribution of turtles in time, the technique most commonly used to assess population size and status is to count the number of clutches laid, usually inferred from tracks and nests in the sand of the nesting beaches (Schroeder and Murphy, 1999) and/or females attending nesting beaches in a season (Sims et al., 2008). However, although seemingly straightforward, this task is far from trivial when a population nests on many beaches over a wide area, and where the nesting season lasts for many months. Labour intensive surveys are required, and for this reason there are surprisingly few detailed published assessments of population size with associated ongoing monitoring of changing status. Although in recent years this is beginning to be remedied (Chaloupka et al., 2008; Lauret-Stepler et al., 2007; Marcovaldi and Chaloupka, 2007).

The challenges faced in the monitoring task broadly vary with population size. For large marine turtle nesting aggregations, the magnitude of effort required to meticulously record all nesting data is often insurmountable. Despite these challenges it is paramount to collect estimates of population data that are reliable (Shanker et al., 2004). Various methods have been used to interpolate such data, with confidence across space and time, to allow robust prediction of population size in a given year (e.g. Bjørndal et al., 1999; Girondot et al., 2002a; Godley et al., 2001; Troeng and Rankin, 2005).

Many national and regional marine turtle nesting populations are moderate to small, especially for the green (*C. mydas*, L.) and loggerhead turtle (*C. caretta*, L.) populations in the Mediterranean. For these rookeries, workers often try to exhaustively record all nesting events throughout the season. However, this is expensive in manpower and fiscal resources, such that contiguous, longitudinal monitoring data have been gathered for few sites (see Broderick et al., 2002 for a review). Exhaustive monitoring of large populations is likely impossible, and some sort of sampling is usually required (Bjørndal et al., 1999).

In the controversial case of the Caribbean hawksbill turtle, many populations are thought to be much reduced and are small (Meylan, 1999; Meylan and Donnelly, 1999). Effective management of this species in the region is hindered by the lack of reliable monitoring data at all but a few sites (Beggs et al., 2007; Garduno-Andrade et al., 1999; Kerr et al., 1999; Richardson et al., 1999). This has led to regional capacity building under the umbrella of CITES and the development of a recommended protocol for effective monitoring of nesting beaches (Anon, 2002). This protocol suggests that ideally, data be gathered on a daily basis, every other day if logistically constrained, or exceptionally 2–3 times per week. It is suggested that the complete field season should be encompassed but the minimum duration of monitoring is set at 8 weeks spanning the peak of the nesting season. Thus, for small island states, even minimum requirements represent significant amounts of manpower and resources over an extended period.

The standard way to estimate the number of years monitoring required to detect a given annual decline is to use analytic power analyses (Anon, 2005). However, the impetus to explore the effect of different sub-sampling regimens on our specific baseline dataset restricts our analyses to an iterative process of re-sampling the baseline data. Marine turtles in this and other regions, typically do not lay clutches every year (Broderick et al., 2003; Miller, 1997). The relatively inconsistent remigration interval between species and individuals further complicates analysis of population growth rate for detecting change (Bjørndal et al., 1999; Taylor and Gerrodette, 1993). We discuss these points further in light of our results.

With a view to making empirically founded recommendations to help reduce the effort needed to monitor marine turtle nesting populations effectively, we use detailed and extensive baseline data collected during eleven consecutive seasons at a Mediterranean site hosting nesting populations of both green and loggerhead turtles. We seek to answer two important applied questions:

1. *How much effort is required to reliably estimate annual nest numbers?* Using the data from two species, we explore the consequences of reducing the number of days of sampling under a variety of regimens for the future monitoring at this site. The expectation being that these methods may inform the design of long-term monitoring regimes where a trade-off between monitoring effort and ability to detect trends is essential, especially relevant for the Caribbean hawksbill turtle.

2. *How many seasons of annual nest estimates are needed to reliably determine nesting trends?* There is inter-annual variation, albeit inter and intra-specifically variable, in nesting numbers in all marine turtle populations (Broderick et al., 2001). This has the capacity to mask longer-term trends in any direction. We explore a methodology which allows prediction of the minimum number of future years of sampling needed to detect a given magnitude change in the nesting level once an effective monitoring strategy is in place.

2. Methods

2.1. Study site and monitoring

We collected data on green and loggerhead turtles nesting on Alagadi Beach, Northern Cyprus (35°33'N, 33°47'E) between

1993 and 2003 (all data were gathered by field teams supervised by authors ACB, WJF, FG and BJG). The beach consists of two coves of 0.8 and 1.2 km length. We recorded the total number of nests in each year from 1993 to 2003 for both loggerhead and green turtles: this comprises our baseline dataset (Fig. 1) which we take as representative of the current status of the nesting population. For further details of monitoring methodologies see (Broderick et al., 2002, 2003). Although the magnitude of the nesting activity can vary substantially between years, the timing of the peak, and duration of the nesting season is relatively consistent between years (Fig. 2) and parallels the patterns shown elsewhere in Northern Cyprus and Turkey (Broderick et al., 2002, 2003; Kasperek et al., 2001). This predictability is exploited to generate a suite of sub-sampling regimens that have the potential to reduce survey effort required to successfully estimate the total annual nest count, whilst retaining effective monitoring capability.

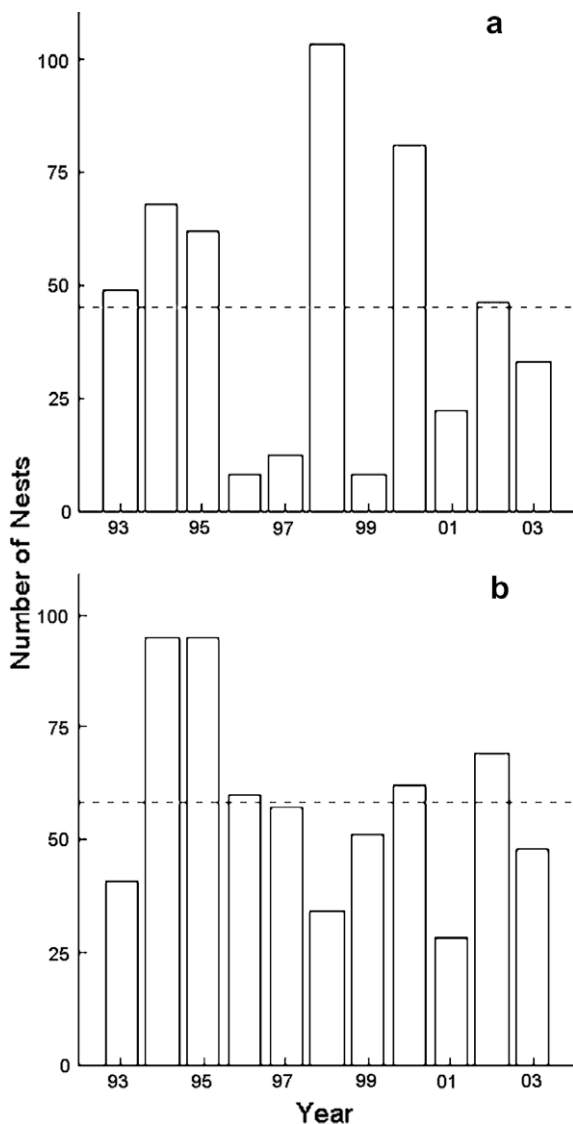


Fig. 1 – The total number of nests observed in each of the 11 years in the baseline datasets for (a) green and (b) loggerhead turtles. Horizontal dotted lines show the mean for the 11 year period.

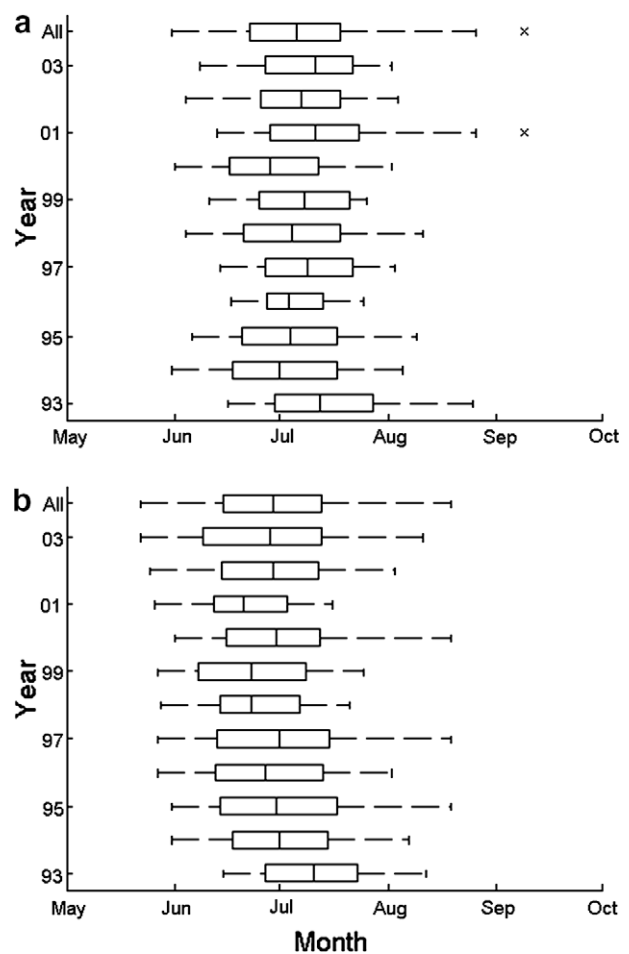


Fig. 2 – Box-whisker-plots showing the temporal distribution of nesting events during the nesting season for (a) green and (b) loggerhead turtles. The upper-most box shows the distribution for all the years pooled. Boxes show the median and inter-quartile ranges (25% and 75%), whiskers show the extent of data within 1.5 times the inter-quartile range, outliers are plotted as crosses. The upper box labelled 'All' shows the distribution when the data are pooled across all years.

2.2. Sub-sampling regimens

We developed this method by re-evaluating the baseline data recorded for both green and loggerhead turtles between the years 1993 and 2003. The range of possible sub-sampling regimens is nearly unlimited, hence we have chosen to restrict our analyses to two of the more immediately conceivable regimens: we classify these as (1) Bolus, and (2) Staccato sampling. All analyses described herein were conducted in Matlab 7.56 R2007b. All statistical equations, methods and moments described below (except Eqs. (1) and (4)) are taken from Zar (1996). In our analyses we treat green and loggerhead turtles separately but in an identical manner.

2.3. Bolus sampling

A bolus sub-sampling regimen is started on a given date and lasts for L number of days: data are recorded for every day of

the sampling regimen. We simply sample from the baseline data-set, starting on different days during the nesting season and using sub-sampling regimens of varying length to determine which regimens produce accurate estimates of total nesting activity.

2.4. Staccato sampling

A staccato sampling regimen begins on a given day in the nesting season and continues until the end of the nesting season. Staccato sampling involves sampling for a given number of days, followed by a break of no sampling, followed by a bout of sampling. We explore both 7-day and 14-day total bout lengths (i.e. days on + days off). Thus a 4/7 staccato regimen involves sampling for the first 4 days of a 7-day period and then performing no sampling for the remaining 3 days.

2.5. Estimating total annual number of nests

After sub-sampling the baseline dataset, the total number of nesting events known to have occurred for each year ($n = 11$) is regressed against the total number of nesting events during a particular sub-sampling regimen – this is repeated for all regimens for the full range of start dates. Essentially, we are asking: can we predict the total annual nesting activity from a sub-sample regimen? We use a simple linear regression of the form $Y = mX + c$; where Y is the total number of nesting activities in the whole year, X is the number of nests recorded for the sub-sampling period during that same year, m is the slope as estimated by the regression fit, and c is the estimated constant. The underlying assumption of this method is that if we then start sampling nesting activity for green turtles in Northern Cyprus on any date, in any year in the future, following one of the sub-sampling regimens we discuss here, we can predict the total annual nesting activity for that year with a statistically determined degree of confidence given the count for the sub-sampling regimen which will be known without error. We use the r^2 from these regressions as an indicator of how well the regression line predicts the total nesting activity for the year: the higher the r^2 , the lower the residual error.

2.6. Detecting population decline

Projected future datasets are generated by iteratively drawing from the baseline data using a random process, decreasing the chosen value by a given annual percentage decline and adding it onto the baseline dataset. Specifically, a projected annual nesting population value F_k is generated k years into the future by a geometric decline

$$F_k = B^*((100 - \delta)/100)^k \quad (1)$$

where, B^* is a randomly drawn value from the baseline dataset and δ is the given percentage annual decline. The projected values are then added to the end of the baseline dataset. Starting at year one ($k = 1$), we iteratively proceed into the future, one year at a time, generate a new dataset of projected future values, and test this dataset for a declining trend using simple linear regression of $\log(\text{total annual population count})$

against time until the slope is significantly less than zero at $\alpha = 0.05$.

The procedure employed assumes that sampling is sufficiently comprehensive that there is perfect knowledge about the nesting population size in the future dataset. We can relax this restrictive assumption: incorporating uncertainty about an estimated annual population derived from using a specific sub-sampling regime is a straight forward process. Any additional predicted total population value ($\hat{Y}$) calculated from a count resulting from a sub-sampling regimen (X_i) has an associated standard error of the estimate given by

$$(S_{\hat{Y}})_1 = \sqrt{S_{Y.X}^2 \left[1 + \frac{1}{n} + \frac{(X_i - \bar{X})^2}{\sum x^2} \right]} \quad (2)$$

where, n = the number of samples in the regression, $\sum x^2$ is the sum of squares of the x -values in the regression, and $\bar{X}$ = mean of the x -values in the regression and $S_{Y.X}$ = the standard error of the estimated $\hat{Y}$ value (standard error of the regression) given by

$$S_{Y.X} = S_Y \sqrt{(1 - r^2)(n - 1)/n - 2} \quad (3)$$

where, S_Y is the standard error of the Y values in the regression (since the Y values are the total number of nesting activities in the baseline dataset, S_Y remains constant for each of the species throughout our analyses). This variation around the estimated total annual nesting numbers is included by randomly drawing a sub-sample from a particular set (in our example this is a 21 day bolus sample starting on July 25), reducing it by a given percentage, applying the appropriate regression equation, and incorporating the added variation associated with this estimate. This is achieved by modifying Eq. (1) to

$$F_k = m(X_i^*((100 - \delta)/100)^k) + c + \varepsilon \quad (4)$$

$$\varepsilon \sim N(0, (S_{\hat{Y}})_1)$$

where, X_i^* is a randomly drawn value from the set of sub-sampling nesting values associated with the defined sampling regimen, m and c are the parameter estimates derived from the regression for that regimen, and ε is a number drawn randomly from a normal distribution with mean = 0 and standard deviation $(S_{\hat{Y}})_1$ from Eq. (2). Any F_k values which may take a negative value due solely to the addition of the random error term are set to zero. This $(S_{\hat{Y}})_1$ value is the key input for adding uncertainty in our analyses – from Eqs. (3 and 4), it is dependent on the variation in the sub-sampling counts (X values) and the r^2 value derived from the sub-sampling regression equation. By way of an example, the 95% confidence intervals for a single estimated total annual count given a particular sub-sampling count are included on the regression model in Fig. 3. We again iteratively proceed into the future and apply the same linear regression of $\log(\text{total annual nesting count})$ against time until the slope is significantly less than zero. Specifically we have run our simulations to explore two specific cases of using a bolus sub-sampling regimen: one starting on June 17 and lasting 7 days (poor-fit regimen), the other starting June 25 lasting 21 days (good-fit regimen): for the green turtles these regimen yield $r^2 = [0.71, 0.98]$ respectively, and for loggerhead turtles they yield $r^2 = [0.37, 0.83]$. Because the procedure we describe is a stochastic process, we

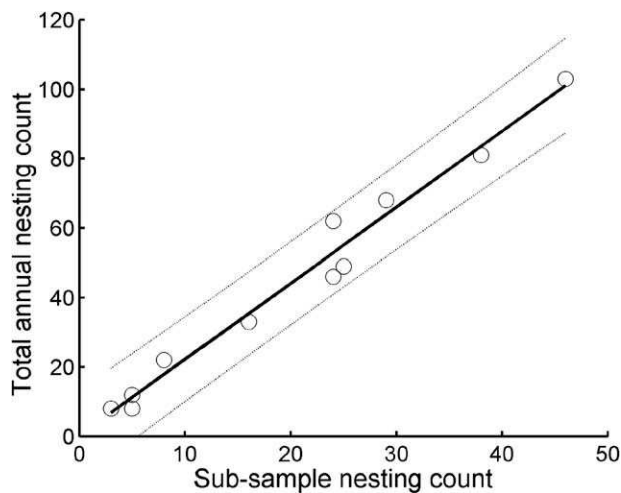


Fig. 3 – Example regression for a single sample regimen for green turtles. Start-date = June 25th, sampling duration (L) = 21 days. Regression statistics: Slope = 2.19, constant = 0.33, $r^2 = 0.98$, $p < 0.001$. The dotted lines shows the 95% confidence intervals for the error associated with estimating total annual nesting count from a single observed sub-sampling count.

have performed 2000 repetitions for each percentage annual decline (δ) analysed. We present the median number of years (and the spread of 95% of the data, i.e. the 2.5 and 97.5 percentiles) of future sampling required to detect a change in population size for each value of percentage annual decline δ .

3. Results

3.1. Estimating total annual number of nests

The temporally consistent nesting season of both the green and loggerhead turtles (Fig. 2) allows us to propose much more efficient sampling regimens despite the relatively large degree of inter-annual variation in nesting numbers (Fig. 1). Sub-samples from both the bolus and staccato regimens are treated identically in our analyses, however, for the purposes of an example we will focus only on the bolus approach. Purely in terms of detecting a trend, the particular choice of regimen does not matter, rather the error associated with estimating nest numbers is key. Fig. 3 shows an example regression of a particular bolus sub-sample of nesting activity for green turtles against the total nesting activity for each year ($n = 11$), for a regimen starting on June 25 sampling every day for 21 days. The data represented in Fig. 3 were generated as follows: starting on June 25 for each of the 11 years in the baseline dataset we added up the number of nesting activities that occurred during the 21 day period (June 15–July 15) – this gives us the sub-sample estimate (X). We then plotted the known total number of nesting activities that occurred in each year (y -axis) against these sub-samples (x -axis) and fitted a linear regression. Thus, if we undertook a sub-sampling regimen of nesting activity for green turtles in Northern Cyprus on June 25 in any year in the future, and continued sampling every day for 21 days to yield a particular sub-sample

nesting activity (X_i), then we could apply the equation derived from the baseline data to derive the estimate of total nesting activity (Y_i), i.e. $Y_i = 2.19(X_i) + 0.33$.

We then similarly interrogated our baseline dataset for different sampling regimens and regress this estimate against the known value for each year, as per the example described in Fig. 3. The resultant r^2 values for green and loggerhead turtles for a set of bolus and staccato regimens beginning on dates 15 May–31 July are shown in Figs. 4 and 5 respectively. Intuitively, accuracy of the sub-sampling regimens increases with the number of days sampling performed: as we look down the rows of the panels in Figs. 4 and 5 so the number of days sampling increases, and so too the r^2 values indicating increasing fit of the regression to the data. Furthermore, accuracy increases when the peak of nesting activity in the season is included in the sub-sampling regimen (mid-June to mid-July); this is evident from both the bolus and staccato regimens. Sampling accuracy falls away rapidly as sub-sampling regimens are started after July (Figs. 4 and 5). Both bolus and staccato sub-sampling regimens are capable of predicting total annual nesting activity with high degrees of accuracy – as determined from r^2 values ($r^2 > 0.8$ are achievable in both cases). Whereas the bolus sampling tends to produce a smooth trend in r^2 values, the staccato sampling is sensitive to inter-diel variations in start-date, displaying marked sinusoidal patterns in model fit that vary in frequency with particular regimen.

Each datum represented in Figs. 4a and b and 5a and b has an associated value derived from the regression for the slope, constant and standard error of the estimate. Therefore, it is possible to sample in the future using a sub-sampling regimen starting on any date (some are better than others) and then, using the resultant parameters for the regression, generate an accurate estimate of the total nesting activity for that year. The associated standard error of the estimate can then be used in the later analysis described below, which incorporates the added variation resulting from the regression analysis into the estimation of minimum number of years of sampling required to detect a change in nesting populations status.

3.2. Detecting population decline

We have demonstrated that sub-sampling regimens can predict the total nesting activity for a year with confidence. However, the added uncertainty of this estimate will likely reduce our ability to detect population declines (or indeed increases). The number of years of sampling that must be undertaken, henceforth can be estimated by projecting the baseline data into the future, and subjecting it to an annual percentage decline until a statistically significant declining trend is detected. For the current set-up, where the annual nesting is determined through exhaustive monitoring (effectively $r^2 = 1$), and when the percentage annual decline is small ($\delta = 1\%$ per annum), the number of future years monitoring needed is large (Fig. 6a and b), approximately 52 years for green, and 25 for loggerhead turtles. Although Fig. 6 shows results specifically for bolus sampling regimens, choosing a staccato regimen equal r^2 values would produce an identical set of graphs. As the percentage annual decline becomes greater, the number of years monitoring required falls

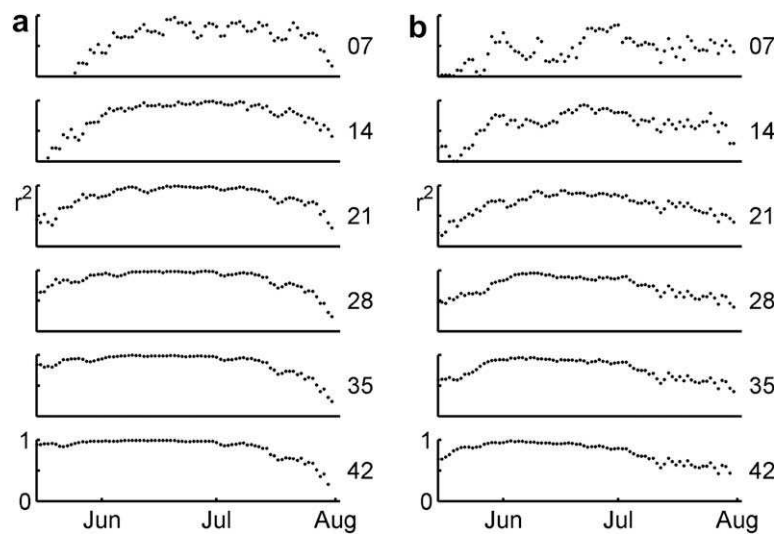


Fig. 4 – Resultant r^2 values for different sub-sampling regimens for green (a) and loggerhead (b) turtles. Each row in the panel describes a different length bolus sampling in days (as defined to the right of each panel: $L = [07, 14, 21, 28, 35, 42]$ days) and the x-axis of each panel shows the start date of a given sub-sampling regimen. Note, only the lowest y-axis is labelled for clarity.

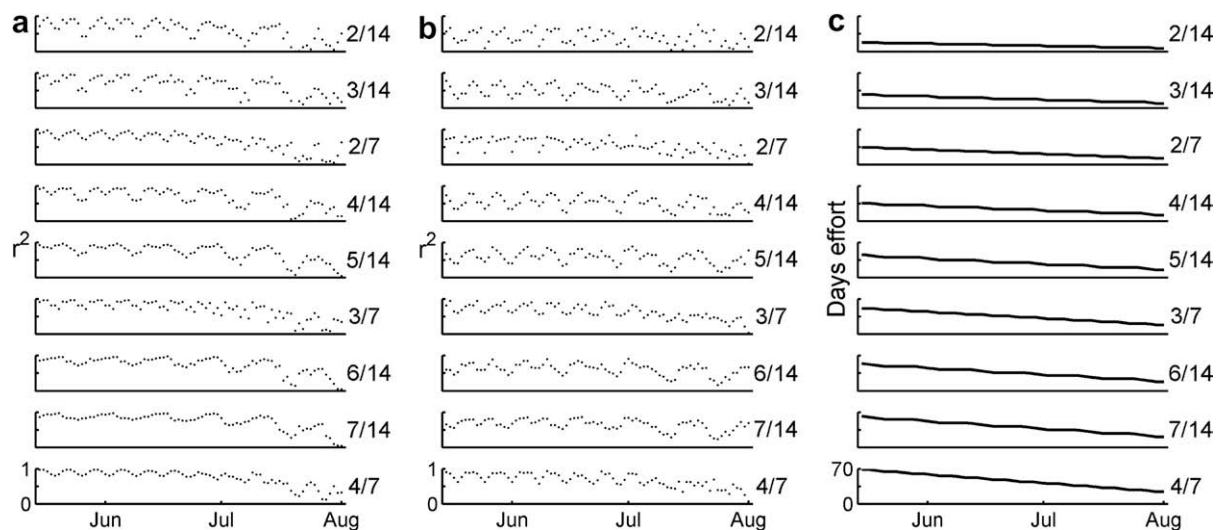


Fig. 5 – Resultant r^2 values for different staccato sub-sampling regimens for (a) green and (b) loggerhead turtles. The total number of days sampling effort for a given staccato regimen is given in (c). Each row in the panel describes a different staccato regimen as defined (to the right of each panel): i.e. 2/7 equates to sampling for 2 days out of 7 (2 days sampling, 5 days off). The x-axis of each panel shows the start date of a given sub-sampling regimen. Note, only the lowest y-axis is labelled for clarity.

exponentially such that a $\delta = 10\%$ per annum decline can be detected in, on average, 12 years for green and 5 years for loggerheads. The error associated with this ability is largest for small rates of decline and decreases towards negligible deviation as the rate of decline becomes more rapid. The very large deviations of approximately ± 35 years (95% confidence intervals) associated with a $\delta = 1\%$ per annum decline for green turtles gives way to smaller 95% confidence intervals of $+4, -6$ years when $\delta = 10\%$. The deviations are smaller for the loggerhead turtles with a maximum of approximately ± 20 years when $\delta = 1\%$ falling to 95% confidence intervals of $+4, -3$ years when $\delta = 10\%$.

As expected, when the variation of estimating annual nesting activity through sub-sampling is considered, we find that the median number of years of sampling required increases, and so too does the variance about this estimate. Surprisingly, although consistently larger, this increase is trivial for the regimens that yield high r^2 values (>0.8) and all but disappears as the rate of population decline increases: red region in Fig. 6. Intuitively, sub-sampling regimens that yield much lower r^2 values reduce our ability to detect population decline to a much greater extent (blue regions), taking more years of monitoring to detect the same rate of population decline. Unlike the better-fit regimen ($r^2 > 0.9$), these poorer ones do not

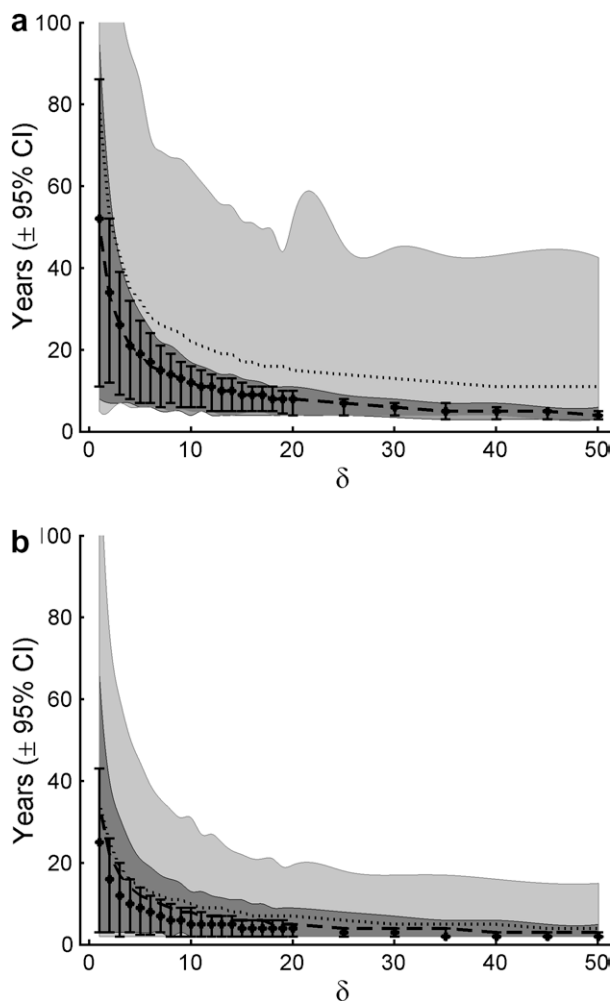


Fig. 6 – The minimum number of years sampling required to detect a given annual percentage decline in population size (δ) in the baseline datasets (Fig. 1) for a) green and b) loggerhead turtles. The errorbars show the median number of years (and the location of 95% of the data) for the case of exhaustive sampling in the future (perfect knowledge of annual nesting numbers). The dark grey shaded area and associated dashed line shows how a 21 day bolus sub-sampling regimen started on June 25th affects this estimate, which yields $r^2 = 0.98$ for green – i.e. from Fig. 3 (a), and $r^2 = 0.83$ for loggerhead (b) turtles. The central dashed line shows the median number of years and the shaded band shows the extent of 95% of the data. The light grey shaded area and associated dotted line show the case for a much less accurate sub-sampling regimen comprising a 7 day bolus sample initiated on June 17th, which yields $r^2 = 0.71$ for green (a), and $r^2 = 0.37$ for loggerhead (b) turtles.

coalesce with the case of exhaustive sampling (errorbars), and for much of the range of rates of decline they remain substantially insensitive to detecting this change. Very apparent though is the inflation in the error around the ability to detect a decline. For green turtles monitored with an accurate sub-sampling regimen (Fig. 6 dark grey region) the increase in error is negligible. In contrast however, when a poorer sub-sampling regimen is used (Fig. 6 light grey region), the error

remains high (the interval is 10 times that of the error associated with exhaustive sampling) even at large rates of decline with a minimum error of -10 and $+25$ years. A similar trend is seen in the loggerhead turtles although increase in error interval is consistently between 2 and 5 times that associated with exhaustive sampling. There is marked difference between our ability to detect a population decline between the two species even with exhaustive sampling – it takes longer to detect a given rate of decline for green turtles, although this discrepancy lessens with increasing rate of decline (δ). These species specific effects are most likely driven by the marked differences in the inter-annual variation in baseline data between the two species (Fig. 1).

4. Discussion

It is clear from our analysis that there are ways that the monitoring efforts of even the smallest of populations can be more parsimonious by adopting sampling-based protocols. Using our example in Cyprus, accuracy of predicting the total annual nesting population from a sub-sample is increased with days of effort and furthermore increased when the peak nesting period is included (June–July). Bolus sampling for a block period of several days is preferable to a staccato regimen in terms of both maximising the accuracy of prediction, minimising days effort and avoiding complications arising from non-trivial fluctuations arising from slight differences in choice of start-date. Specifically, any bolus sampling regimen begun in early June and lasting longer than 21 days provides a high degree of accuracy with regard prediction of total nesting activity for both loggerhead and green turtles (certainly 28 days is more than sufficient). Given that data recording can be exhaustive with surveys every other day, when accurate nest counts are still possible by reading tracks on the nesting beach, this means as few as 10 days effort.

Detecting the sensitivity of monitoring to decline in population size is possible by forward projecting the baseline data into the future and applying a nominal annual decline to the simulated data. Detecting a very small percentage annual decline (1% per annum) by this method would require decades of future sampling. Intuitively, this trend declines asymptotically as a function of annual decline at a high rate such that a 10% annual decline would be detected in, on average, 12 years for the green turtles and 5 years for the loggerheads. Sims et al. (2008) report similar figures for a study on an Antiguan population of hawksbill turtles, where exhaustive monitoring can detect a 3% annual trend in 14 years, increasing to 21 years with 21 days of monitoring.

Application of population growth is also possible using this framework, however, the nesting numbers will naturally move outside the maximum range of observed values in our baseline dataset and the application of the derived regression equations for estimating total counts from sub-sample counts will become rapidly error-prone and potentially unsuitable. For this reason we have not shown this data, needless to say that should a welcome population increase be suspected, then it would be very worthwhile investing in exhaustive monitoring to re-assess the sub-sampling protocol. Additionally, our method for forecasting future population values is a

simplification of the biology of turtles. The complex life cycle of marine turtles and the existence of time-lag effects relating to environmental factors means that observing nesting numbers may not necessarily translate directly into a population measure. A full matrix model could be used, but parameterising this would be difficult and prone to non-trivial uncertainties. It is possible that with future datasets, such a model could be built but for now, simplicity should prevail.

Incorporating the resultant uncertainty arising from sub-sampling into our methodology intuitively increases the number of years of future sampling required to detect a given annual decline. However, this increase is generally small (negligible for the 21 day bolus sampling for green turtles), and for an annual decline of 5% per annum requires on average, only an additional 0 and 3 years sampling for green and loggerhead turtles, respectively when a 21 day bolus regiment commencing 25th June is employed. Indeed, the fact that increased uncertainty of the regression estimate from sub-sampling does not adversely affect our ability to detect a change through this method suggests that we may be able to consider sub-sampling regimens with r^2 values lower than 0.9. A further complication however, is that smaller rates of decline are more likely to be hidden by the stochasticity of the population projection process, and also more importantly from the error associated with adopting less accurate sub-sampling regimens. As the accuracy of the sub-sampling regimen decreases so this error becomes larger to the point that sub-sampling error can completely mask any population decline thereby rendering it impossible to conduct a meaningful monitoring programme. Expansion of the dataset to include many more years of data into a temporally autocorrelated model of inter-annual population variation would remove some of the error but that associated with sub-sampling will always remain. As it stands, our population projection algorithm (Eq. (1)) does not include variation in remigration intervals, mortality and fecundity which are all likely to be related to varying environmental conditions (Solow et al., 2002). With more years of data, a fuller more accurate model could be constructed, but until then the extra uncertainty in these parameters for this population would render the model far more complicated to interpret than it needs to be.

A balance must be struck between sampling effort and goodness-of-fit (r^2), which will affect the number of years sampling needed to detect a change: choosing a cut-off r^2 does however, remain a somewhat arbitrary decision. This decision should be tailored to the demands of specific populations where human or fiscal resources may be more or less limiting in some cases compared to others. Indeed, our example from Cyprus shows that there may be conflict between desired monitoring regimen for different species. This methodology does, however, allow the trade-off between monitoring effort and ability to detect a trend to be quantified and hence an informed decision can be made on a case-by-case basis.

Our sub-sampling methodology is simpler than those previously described in the literature, which have used combinations of various mathematical functions to recreate sinusoidal curves describing the temporal distribution of nesting events during a season (Bjørndal et al., 1999; Girondot et al., 2002a,b, 2006). Although these methods have proved

successful at interpolating these curves over a season from fragmentary data, our approach, which seeks only to estimate the total annual nesting numbers (the most important information), performs equally well in terms of error around this estimate. Annual nesting numbers are important from a population monitoring point of view. Predicting annual nesting numbers as in our method does preclude the estimation of temporally specific events such as density dependent nest disturbance (Girondot et al., 2002a): something that the other methods can allow, although the fine detail of inter-dial variation in nesting activity will still be lost to an interpolative method. Furthermore, our method performs best when a single period of intensive (daily) monitoring is performed, rather than the methods described by Gratiot et al. (2006) and Girondot et al. (2002b), where the greatest accuracy is achieved when monitoring is distributed evenly (or randomly) across the entire season. Bjørndal et al. (1999) explore how sampling interval (akin to our staccato sampling) affected estimates of hatchling emergences over a season. Their use of cubic-spline interpolations and integration under the resultant curve produced more accurate and less biased estimates when survey interval was small. Their method is probably better suited to their system where emergence rate was high enough to minimise zero-counts on given days. In our system, we often observed low annual nesting numbers, with highly over-dispersed data containing several zero-counts. Such a characteristic will lead to a general over-estimation of the total count when integration is performed over a smoothed curve. Whether a bolus or staccato sampling regimen suits a particular population is likely to be a highly site-specific feature. The choice of established and successful methods described in the literature is welcome and will allow those tasked with monitoring to select the best tool for the particular job.

We have presented one possible model for predicting a total count from a sub-sample. The regression approach suited our data as we had 11 years of full counts and we were able to produce a model with good explanatory power. However, different situations may favour alternative approaches such as use of cubic-splines to interpolate between missed days (as employed by Bjørndal et al., 1999), use of binomial estimators when both p and n are unknown (DasGupta and Rubin, 2005) or a simple change to poisson regression (Sims et al., 2008). Whatever method is employed, the error associated with the estimated value is key when trying to monitor population trends. Researchers could replace our model with their own as necessary.

Of course, researchers perform sampling or monitoring for reasons other than to simply count the number of nesting females. Many programmes serve additional purposes of increasing awareness, promoting reproductive success through nest relocation and screening and may have the intended or unintended effect of reducing threats such as illegal take of adults and eggs. Protocols will therefore be constrained by the requirements of a particular expedition and may well vary between years. Our method is entirely insensitive to such wishes, as the estimated values and its associated error can be generated for any imaginable sampling regimen. We also chose not to optimise the sampling regimen according to some arbitrary cost-benefit function such as variance in the estimate per total days of effort for this very reason:

the decision will likely often remain a managerial call. Indeed one could choose to monitor tracks or emergences, which may be particularly suitable for large populations (Sims et al., 2008), and adjust the model accordingly, but for small populations we are always likely to be left with nest counts as the only viable survey method (Bell et al., 2007; McClenachan et al., 2006; McGowan et al., 2008).

Our methodology requires that both the shape and temporal location of the distribution of nesting events remains similar between seasons. Our baseline data comprising 11 years for two species suggest that both these assumptions are appropriate, at least at present. Although seasonality of green turtles and loggerhead turtles has been demonstrated to be largely conservative (Godley et al., 2002; Hawkes et al., 2005) the possible impact of global climate change on marine turtle phenology must be taken into consideration. Some authors have suggested that loggerhead turtle nesting has the potential to shift earlier as a result of high sea temperatures; a trend that may continue under current climate change (Hawkes et al., 2007; Weishampel et al., 2004). It would therefore be prudent to perform more exhaustive sampling periodically in order to re-assess the temporal distribution of nesting events in any population monitored through a sampling protocol. Any apparent shift in the sampled data (either bolus, staccato or other derived) should alert researchers to a possible temporal shift in the nesting season. Detecting such a shift would require enough data around the peak, something that a staccato regimen may offer with fewer days sampling than bolus – although the inter-diel variability of the staccato's performance may again hinder detection of a temporal trend rather than simply a change in nesting magnitude. Centring the data around the peak, rather than basing it on date, may offer a solution to this issue.

Importantly, the marked inter-specific difference in the duration of monitoring needed to detect similar levels of change highlights the fact that inter-annual variation in levels of nesting is likely to be the prime driver in the number of monitoring seasons that are required to detect a given trend, with green turtles requiring significantly longer. Some caution must be used when considering a population new to monitoring, that is apparently stable and has high inter-annual variation in nesting numbers, as slight declines in such populations may be masked for long periods of time. Many green turtle populations have these characteristics (Broderick et al., 2001) and we would suggest performing as much sampling effort as required to yield regression r^2 values approaching 0.9 in these cases to avoid missing potentially detrimental population declines. In summary, using sub-sampling regimens to generate reliable annual estimates hold promise for resource-limited marine turtle monitoring in that they are valid for rigorous population trend analysis. We agree with Gratiot et al. (2006) that direct comparisons of all the available methods would be a useful contribution to the literature.

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