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Comparison and review of models describing sea turtle nesting abundance

Andrea U. Whiting[1,*], Milani Chaloupka[2], Nicolas Pilcher[3], Paul Basintal[4], Colin J. Limpus[5]

[1]School of Environmental and Life Sciences, Charles Darwin University, Northern Territory 0909, Australia
[2]Ecological Modelling Services P/L, PO Box 6150, University of Queensland, St Lucia, Queensland 4067, Australia
[3]Marine Research Foundation, 136 Lorong Pokok Seraya 2, Taman Khidmat, Kota Kinabalu, Sabah 88450, Malaysia
[4]Sabah Parks, Lot 45&46, Level 1-5, Block H Signature Office, KK Times Square Coastal Highway, Kota Kinabalu, Sabah 88100, Malaysia
[5]Department of Environment and Heritage Protection, PO Box 2454, Brisbane, Queensland 4001, Australia

ABSTRACT: Count data are often used to assess relative population size and population trends with sufficient power and confidence for wildlife population studies, including those for nesting sea turtles. Although access to sea turtles while nesting is relatively simple compared to many other migratory marine animals, optimal surveys tagging every individual through the nesting season are often not feasible due to time, financial and other logistic constraints. Partial survey counts can then be used to estimate population abundance. Several models have previously been published describing the seasonal shape in abundance for nesting turtles, but none have compared different model fits using a numerical approach and all have limited general application as they describe only 1 location or 1 species. We compared 22 non-parametric and parametric modelling approaches for 9 populations of sea turtles comprising 3 different species: green sea turtles *Chelonia mydas*, loggerhead sea turtles *Caretta caretta* and leatherback sea turtles *Dermochelys coriacea*. Although models showed marked differences in the shape of their fit, all models provided reasonable estimates of annual nesting abundance, with mean errors less than 8% for 50% data coverage and mostly 8 to 10% for 20% random coverage. Of the 3 models that produced significantly lower mean absolute error, we recommend using generalized additive models to estimate annual abundance due to their ease of fitting, flexibility across populations and seasonal shapes and their good predictive ability.

KEY WORDS: Population study · Partial count · Generalized additive model · GAM · Green turtle · *Chelonia mydas* · Loggerhead · *Caretta caretta* · Leatherback · *Dermochelys coriacea*

INTRODUCTION

Count data for wildlife populations are often used in conservation research—trying to ensure the population stays within sustainable limits to ensure its survival, or to test whether populations of pest species remain below critical levels known to threaten other populations (Williams et al. 2002). Data collection for long-term monitoring of wildlife populations need to be collected consistently enough to be comparable between years and populations and precise enough to show changes in a population with sufficient confidence and power (Gerrodette 1987, Hayes & Steidl 1997, Sims et al. 2008). Where different survey methods or effort have occurred, modelling techniques may assist to standardise data. This is common with fisheries data, when the number of crew, number of bait tanks or fishing lines change, and technological

*Corresponding author: au.whiting@gmail.com

advances in vessel and catch methods mean that catch per unit effort estimates need to be adjusted between years (Hilborn & Mangel 1997, Rodríguez-Marín et al. 2003). Determining the accuracy of monitoring regimes is often more difficult, as it is often not possible to conduct a complete survey of the population to verify predicted error. Nesting sea turtles are unique in this regard, due to their easy accessibility during nesting migrations, and with adequate resources, a complete survey of the annual nesting population is sometimes possible (e.g. Limpus 1985, Boulon et al. 1996, Richardson et al. 2006, Chaloupka et al. 2008). Sea turtles also generally display strong site fidelity to their nesting area, both within a nesting season and in subsequent nesting seasons (Bjorndal et al. 1983, Limpus 1985, Girondot & Fretey 1996, Miller 1997, Limpus et al. 2003, Dethmers et al. 2006) adding to the ease of accessibility. All species of sea turtles (except for the flatback turtle *Natator depressus*) are listed as Vulnerable, Endangered or Critically Endangered on the IUCN red list (IUCN 2012), so understanding population function to efficiently monitor population size is often a priority for conservation agencies and managers.

Monitoring nesting sea turtles is often confined temporally to 1 or several periods within the nesting season (e.g. Girondot & Fretey 1996, Limpus 2009). Although tagging every individual through the nesting season is ideal for population estimates and understanding the breeding biology of sea turtles, it is often not feasible due to time, financial and other logistic constraints. Access to the animals may also prohibit a full-time tagging census ever being conducted. This occurs on nesting beaches where animal densities are either too great (e.g. arribada nesting for olive ridley turtles: Gates et al. 1996; green turtles *Chelonia mydas* nesting at Raine Island, Torres Strait: Limpus et al. 2003), beaches are very dispersed (e.g. Ningaloo region, Western Australia: Bool et al. 2009; Gabon, Equatorial West Africa: Witt et al. 2009) or access to the beach for researchers is difficult or dangerous due to remoteness or rugged coastlines (e.g. Raine Island: Limpus et al. 2003; Kimberley region of Western Australia: Whiting et al. 2008) or potential dangers to researchers from poachers or wildlife present on the nesting beach (e.g. jaguars: Autar 1994; saltwater crocodiles: Whiting & Whiting 2011). When a full-time tagging census is not feasible, a shorter count survey may be adopted.

The accuracy of estimating the annual abundance of nesting turtles from partial survey counts will depend on the monitoring regime, and may depend on the seasonal length, species of turtle and population size (Jackson et al. 2008, Sims et al. 2008, Whiting 2010). The component monitored will also impact on the total error, with higher errors associated with counts of tracks or egg counts from harvest data, than with counts of clutches or turtles. Surveys are often comprised of mid-season counts (e.g. Limpus 2009), intermittent counts throughout the season (e.g. Girondot & Fretey 1996, Bjorndal et al. 1999, Whiting et al. 2008) or a combination of the 2 methods (e.g. Bool et al. 2009). Temporal variability between studies may also occur in the monitoring regime; for example, some populations would be better suited to short frequent surveys and others are more suited to longer, less frequent surveys. Optimal survey regimes will depend on the access to the beach and resources available to each monitoring program.

Several models have previously been published describing the seasonal shape in abundance of nesting turtles (e.g. Girondot & Fretey 1996, Bjorndal et al. 1999, Godley et al. 2001, Troëng et al. 2004, Girondot et al. 2006, 2007, Gratiot et al. 2006, Whiting et al. 2008, Godgenger et al. 2009, Witt et al. 2009, Girondot 2010), but none compared different model fits using a numerical approach and all have been limited by their application to either only 1 location or 1 species. Here we compared previously published and additional non-parametric and parametric modelling approaches to describe the within-season abundance of nesting sea turtles, investigating 9 populations of sea turtles comprising 3 different species. We used a total track count approach rather than an individual based capture–mark–recapture approach to broaden the scope of the research as more data are available. Estimating annual abundance from sampled capture–mark–recapture analyses is also sensitive to changes in clutch frequencies, which may bias estimates appreciably (Hays 2000). We did not incorporate environmental parameters in the models as, even when environmental 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 between nesting abundance and tidal cycle is often not consistent between nesting populations, rookeries or sometimes even years within the same population (Caldwell 1959, Bustard 1979, Frazer 1981, 1983, Girondot & Fretey 1996, Lux et al. 2003, Girondot et al. 2006, Pike 2008). We have consequently limited our model application to those transferable between species, populations and years, and also to models that do not require substantial *a priori* information for the nesting population.

Table 1. Location, species, factor counted and seasonal range of the nightly count data used for comparing models describing seasonal nesting abundance of 3 sea turtle species

Study site	Factor counted	Season range	No. of seasons	Data reference
Green turtle *Chelonia mydas*				
Bramble Cay, Torres Strait	Turtles	Oct–Mar	1	Limpus et al. (2001); C. J. Limpus unpubl. data
Heron Island, Australia	Turtles	Oct–Mar	1	C. J. Limpus unpubl. data
Sabah Turtle Islands, Malaysia	Turtles	All year	7	N. Pilcher & L. Ali unpubl. data for 1991–1997 from Sabah Parks
Guinea-Bissau, Africa	Tracks	Jul–Dec	1	Catry et al. (2002)
Loggerhead turtle *Caretta caretta*				
Mon Repos, Australia	Turtles	Oct–Mar	7	C. J. Limpus unpubl. data
Heron Island, Australia	Turtles	Oct–Mar	1	C. J. Limpus unpubl. data
Jupiter/Carlin, Florida, USA	Nests	May–Aug	1	Davis et al. (1994)
Leatherback turtle *Dermochelys coriacea*				
Playa Grande, Costa Rica	Turtles	Oct–Feb	1	Lux et al. (2003)
Chiriqui Beach, Panama	Clutches	Mar–Jul	1	Ordonez et al. (2007)

METHODS

Data

Nightly track count data were provided by the authors and sourced from the literature for 3 species of sea turtles: green *Chelonia mydas* (n = 4 populations), loggerhead *Caretta caretta* (n = 3 populations) and leatherback *Dermochelys coriacea* (n = 2 populations) turtles (Table 1). The time-series of nightly nesting data was complete for all populations investigated, with the exception of the leatherback population nesting at Chiriqui Beach, Panama. For this population, data for 1 mo at the start of the nesting season were collected every 2 d. To generate a complete time-series for the Chiriqui Beach population, missing values were interpolated as an average of the counts for the days immediately before and after. Models were fit to data comprising the full time-series available, and data sets generated by random sampling of the nightly data to give subsets comprising 20 % and 50 % of the nightly counts. For sampled data, we used 20 replicate subsets per population per year to investigate the fit of each model.

Models

Nesting abundance for sea turtles is generally peaked and may have a multi-modal distribution (e.g. Chevalier et al. 2000, Witt et al. 2009). Models describing the shape of the nesting season using biological parameters (such as arrival and departure dates, inter-nesting intervals and clutch frequencies) are complex, rely on tagging information and are sensitive to inter-annual changes in inter-nesting intervals and clutch frequencies. As this information is often not available, we investigated models describing the overall shape of the nesting season, comparing non-parametric models with 15 parametric models (Table 2). Non-parametric models were chosen to allow the structure of the fit to be determined from the data without assuming *a priori* any particular functional form (Black et al. 2009). Non-parametric models can take any functional form, with peaked models including skewed and non-skewed forms, single or multi-modal peaks and different extents of kurtosis. Non-parametric models are sensitive to the degree of smoothing, with bandwidth selection often more important than the choice of smoothing algorithm (Wand & Jones 1995). Conversely, parametric models were investigated using assumptions about the underlying mathematical distributional form of the observed variables (Marshall & Scott 2009). Non-parametric models have fewer assumptions than parametric models, making them more robust and giving them wider applicability (Gibbons & Chakraborti 2003, Wasserman 2007). Parametric models are more constrained in their functional form, but if an appropriate model is available, then it has higher power than non-parametric models (Gibbons & Chakraborti 2003, Wasserman 2007). When a suitable parametric model is available, the higher power of parametric models means that a smaller sample size is needed than for non-parametric modelling for conclusions with the same degree of confidence. Prediction of nesting using moving averages, Lagrange interpolation, linear interpolation or kernel density

Table 2. Description of models used to describe the nesting season and estimate annual nesting abundance of sea turtles. Within the formulas, y refers to the nightly nesting abundances, x refers to time, and a to g refer to the parameters in the model. All formulae are based on those of Ratowsky (1990) unless otherwise noted

Model	Type	Formula(e) and Reference(s)
Non-parametric models	Generalized additive model	*gam* function in library(mgcv) in R Three approaches were used: - Uniform weights - Endpoints down-weighted by factors of 10, 100 and 1000 - Endpoints up-weighted by factors of 10, 100 and 1000 (Hastie & Tibshirani 1990, Bjorndal et al. 1999, Troëng et al. 2004, Troëng & Rankin 2005, R Development Core Team 2012)
3 parameter models	Exponential	$y = \exp\left(ax^2 + bx + c\right)$
	Quadratic polynomial	$y = ax^2 + bx + c$
	Trigonometric	$y = -b\cos\left(cx + a\right)$
4 parameter model	Trigonometric	$y = \frac{a}{2}\cos\left(\frac{2\pi}{b}(x-c)\right) + \frac{a}{2} + d$ (Gratiot et al. 2006)
5 parameter models	Gompertz	$y\left[0:a\right] = a\exp\left(-\exp\left(\frac{-x+b}{c}\right)\right)$; $y\left[a:\infty\right] = a\exp\left(-\exp\left(\frac{-x+d}{e}\right)\right)$
	Logistic	$y\left[0:a\right] = \frac{a}{1+\left(\frac{x}{b}\right)^c}$; $y\left[a:\infty\right] = \frac{a}{1+\left(\frac{x}{d}\right)^e}$
	Sigmoidal	$y\left[0:a\right] = \frac{a}{1+\exp\left(\frac{-x+b}{c}\right)}$; $y\left[a:\infty\right] = \frac{a}{1+\exp\left(\frac{-x+d}{e}\right)}$
	Trigonometric-1	$y\left[0:a\right] = \frac{a}{2}\cos\left(\frac{2\pi}{b}(x-c)\right)$; $y\left[a:\infty\right] = \frac{a}{2}\cos\left(\frac{2\pi}{d}(x-e)\right)$
	Trigonometric-2	$y\left[0:a\right] = \frac{a}{2}\cos\left(\frac{2\pi}{b}(x-c)\right)+d$; $y\left[a:\infty\right] = \frac{a}{2}\cos\left(\frac{2\pi}{e}(x-c)\right)+d$
6 parameter model	Logistic	$y\left[0:a\right] = \frac{a}{1+\left(\frac{x}{b}\right)^c}+d$; $y\left[a:\infty\right] = \frac{a}{1+\left(\frac{x}{e}\right)^f}+d$
7 parameter models	Logistic	$y\left[0:a\right] = \frac{a}{\left(1+\left(\frac{x}{b}\right)^c\right)^d}$; $y\left[a:\infty\right] = \frac{a}{\left(1+\left(\frac{x}{e}\right)^f\right)^g}$
	Sigmoidal-1	$y\left[0:a\right] = \frac{a}{\left(1+\exp\left(\frac{-x+b}{c}\right)\right)^d}$; $y\left[a:\infty\right] = \frac{a}{\left(1+\exp\left(\frac{-x+e}{f}\right)\right)^g}$
	Sigmoidal-2	$y\left[0:d\right] = a\left(1+\left(2^{\exp(b)}-1\right)\exp\left(\frac{1}{c}(d-x)\right)\right)^{-1/\exp(b)}$ $y\left[d:\infty\right] = a\left(1+\left(2^{\exp(e)}-1\right)\exp\left(\frac{1}{f}(g-x)\right)\right)^{-1/\exp(e)}$ (Girondot et al. 2007)

Table 2. (continued)

Model	Type	Formula and Reference(s)
7 parameter models (continued)		
	Trigonometric-1	$y\left[0:(a+d)\right] = \frac{a}{2}\cos\left(\frac{2\pi}{b}(x-c)\right)+d;\quad y\left[(a+d):\infty\right] = \frac{a}{2}\cos\left(\frac{2\pi}{e}(x-f)\right)+g$
	Trigonometric-2	$y\left[0:b\right] = a$ $y\left[b:c\right] = \left(\frac{1+\cos\left(\pi\left(\frac{c-x}{c-b}\right)\right)}{2}\right)(g-a)+a$ $y\left[c:e\right] = g$ $y\left[e:d\right] = \left(\frac{1+\cos\left(\pi\left(\frac{x-e}{d-e}\right)\right)}{2}\right)(g-f)+f$ $y\left[d:\infty\right] = f$ (Girondot 2010)

interpolation methods were not investigated due to their limited predictive power when partial season counts are conducted.

Parametric models were selected using a minimum of 3 parameters (Table 2), to allow for changes in amplitude, position and distribution (Ratkowsky 1990). The fits of these models were compared with 2 parametric models that have previously been used to describe seasonal nesting abundances for sea turtles (Girondot et al. 2006, Gratiot et al. 2006, Girondot 2010). Parametric models investigated were restricted to models with good estimation properties (Ratkowsky 1990) and models that allowed convergence for full-season data for at least 95% of the data sets. Parametric models were fit by minimizing the sum-of-squares using the *optim* or *nls* functions in R (R Development Core Team 2012). Two sets of initial starting values were chosen for each model, 1 for the shorter season populations (3–6 mo nesting season) and 1 for nesting seasons extending over 7 mo. Initial starting values were chosen to allow convergence for data at least 95% of the time. We investigated non-parametric model fit using generalized additive models (GAMs) using a penalised regression spline approach with automatic smoothness selection via generalized cross-validation (Wood & Augustin 2002, Crawley 2007, Wood 2010). Non-parametric models were fit using the *mgcv* package in R (Wood 2010, R Development Core Team 2012) using automatic smoothing parameter selection, and the dimension of the basis used to represent the smoothing term was not specified. For non-parametric models, we compared models with 3 different weighting structures: (1) uniform weighting of all sampled data and endpoints; (2) assigning lower weights to the endpoints to account for uncertainty (Bjorndal et al. 1999); and (3) assigning higher weights to the endpoints to constrain the nesting season. Different weights were investigated with factor differences of 10, 100 and 1000. Predicted values for both parametric and non-parametric models were restricted to non-negative values.

Comparing the non-parametric and parametric models using standard model selection tools such as Akaike's information criterion (AIC) or likelihood ratio tests was not appropriate, as these tools require the log-likelihood to be computed with the same method, which does not work for GAMs that use penalised likelihood maximization rather than log-likelihood (Marx & Eilers 1998). AIC was used to compare parametric models to each other as the same fitting approach was used to calculate the log-likelihood of the function. All models were further compared using the residual sum-of-squares and mean absolute error. Goodness-of-fit between models was compared across the populations using a

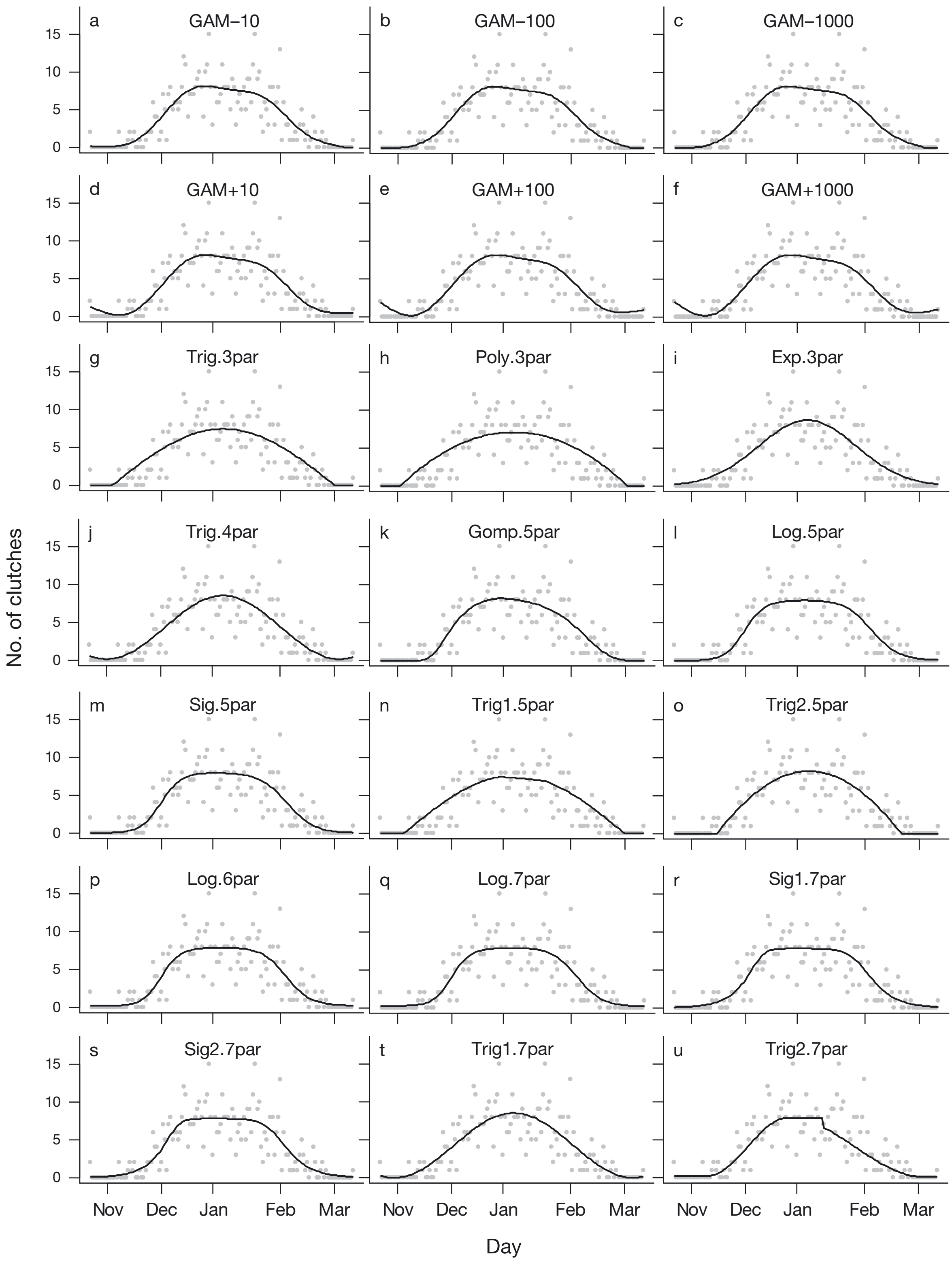

Fig. 1. Examples of model fits (solid lines) for 20 models showing data for loggerhead turtles *Caretta caretta* nesting at Mon Repos, Australia, during the 2000–2001 nesting season (points). GAM refers to generalized additive models with '–' denoting downweighting and '+' denoting upweighting for the GAM with uniform weighting, see Fig. 4f; Trig: trigonometric model; Poly: polynomial model; Exp: exponential model; Gomp: Gompertz model; Sig: sigmoidal model; par: (no. of) parameters. See Table 2 for full model descriptions

Kruskal-Wallis rank sum test, as it allows comparison between the non-parametric and parametric methods (Conover & Iman 1981) and the variation in abundance between the populations causes inflated standard deviations in model fits, rendering traditional ANOVA methods unsuitable. Post hoc analysis was conducted using the pgirmess package in R (Giraudoux 2012). To avoid pseudo-replication, we calculated means using the mean values for each population by averaging different years for the Mon Repos (Queensland, Australia) and Sabah Turtle Island (Malaysia) populations.

RESULTS

Goodness-of-fit of models

All models tested were reasonable in their description of seasonal nesting for turtles, but the functional forms of the models were different for the same data and showed slightly different peaks in the nesting season, as well as differences in kurtosis (Fig. 1). A Kruskal-Wallis rank sum test showed significant differences between the residual sum-of-squares for the models (χ^2 = 215.1, df = 21, $p < 0.001$), with all of the GAMs, Gompertz 5 parameter, Logistic 5 parameter, Sigmoidal 5 parameter, Logistic 7 parameter, Sigmoidal-1 7 parameter, Sigmoidal-2 7 parameter, Trigonometric-1 7 parameter and Trigonometric-2 7 parameter models generally showing significantly lower residual sum-of-squares than the remaining 7 models (Table 3, Fig. 2). The mean absolute error similarly showed significant differences between the models (χ^2 = 169.2, df = 21, $p < 0.001$), but highlighted different models with significant differences; specifically, the GAM with uniform weighting, Sigmoidal-1 7 parameter and Trigonometric-2 7 parameter models had significantly lower mean absolute errors than many of the other models, whereas the GAMs with ends upweighted by 100 and 1000, Exponential 3 parameter and Trigonometric 4 parameter models

Table 3. Model comparison for residual sum-of-squares, mean absolute error and Akaike's information criterion (AIC) showing significant differences (marked with an 'X') from post hoc analysis on a Kruskal-Wallis rank sum test. GAM refers to generalized additive models with '−' denoting downweighting and '+' denoting upweighting; Trig: trigonometric model; Poly: polynomial model; Exp: exponential model; Gomp: Gompertz model; Sig: sigmoidal model; par: (no. of) parameters. See Table 2 for full model descriptions

(a) Residual sum-of-squares

	GAM−10	GAM−100	GAM−1000	GAM+10	GAM+100	GAM+1000	GAM−0	Trig.3par	Poly.3par	Exp.3par	Trig.4par	Gomp.5par	Log.5par	Sig.5par	Trig1.5par	Trig2.5par	Log.6par	Log.7par	Sig1.7par	Sig2.7par	Trig1.7par
GAM−100																					
GAM−1000																					
GAM+10																					
GAM+100																					
GAM+1000																					
GAM−0																					
Trig.3par	X	X	X	X	X	X	X														
Poly.3par	X	X	X	X	X	X	X														
Exp.3par	X	X	X	X	X	X	X														
Trig.4par	X	X	X		X		X														
Gomp.5par								X	X												
Log.5par								X	X	X											
Sig.5par								X	X												
Trig1.5par	X	X	X	X	X		X														
Trig2.5par	X	X	X				X														
Log.6par	X	X	X		X		X														
Log.7par								X	X	X					X						
Sig1.7par								X	X	X					X						
Sig2.7par								X	X	X	X				X	X	X				
Trig1.7par								X	X	X					X						
Trig2.7par								X	X	X					X						

(b) Mean absolute error

	GAM−10	GAM−100	GAM−1000	GAM+10	GAM+100	GAM+1000	GAM−0	Trig.3par	Poly.3par	Exp.3par	Trig.4par	Gomp.5par	Log.5par	Sig.5par	Trig1.5par	Trig2.5par	Log.6par	Log.7par	Sig1.7par	Sig2.7par	Trig1.7par
GAM−100																					
GAM−1000																					
GAM+10																					
GAM+100	X	X	X																		
GAM+1000	X	X	X																		
GAM−0				X	X	X															
Trig.3par							X														
Poly.3par							X														
Exp.3par							X														
Trig.4par				X	X	X				X											
Gomp.5par																					
Log.5par																					
Sig.5par							X														
Trig1.5par							X														
Trig2.5par					X	X															
Log.6par						X															
Log.7par					X	X				X											
Sig1.7par				X	X	X		X	X	X		X		X	X						
Sig2.7par																					
Trig1.7par																			X		
Trig2.7par				X	X	X		X	X	X		X	X	X	X					X	

(c) Akaike's information criterion (AIC)

	Trig.3par	Poly.3par	Exp.3par	Trig.4par	Gomp.5par	Log.5par	Sig.5par	Trig1.5par	Trig2.5par	Log.6par	Log.7par	Sig1.7par	Sig2.7par	Trig1.7par
Poly.3par														
Exp.3par														
Trig.4par														
Gomp.5par	X	X												
Log.5par	X	X												
Sig.5par		X												
Trig1.5par					X	X								
Trig2.5par				X	X	X	X							
Log.6par						X								
Log.7par														
Sig1.7par														
Sig2.7par									X					
Trig1.7par														
Trig2.7par									X					

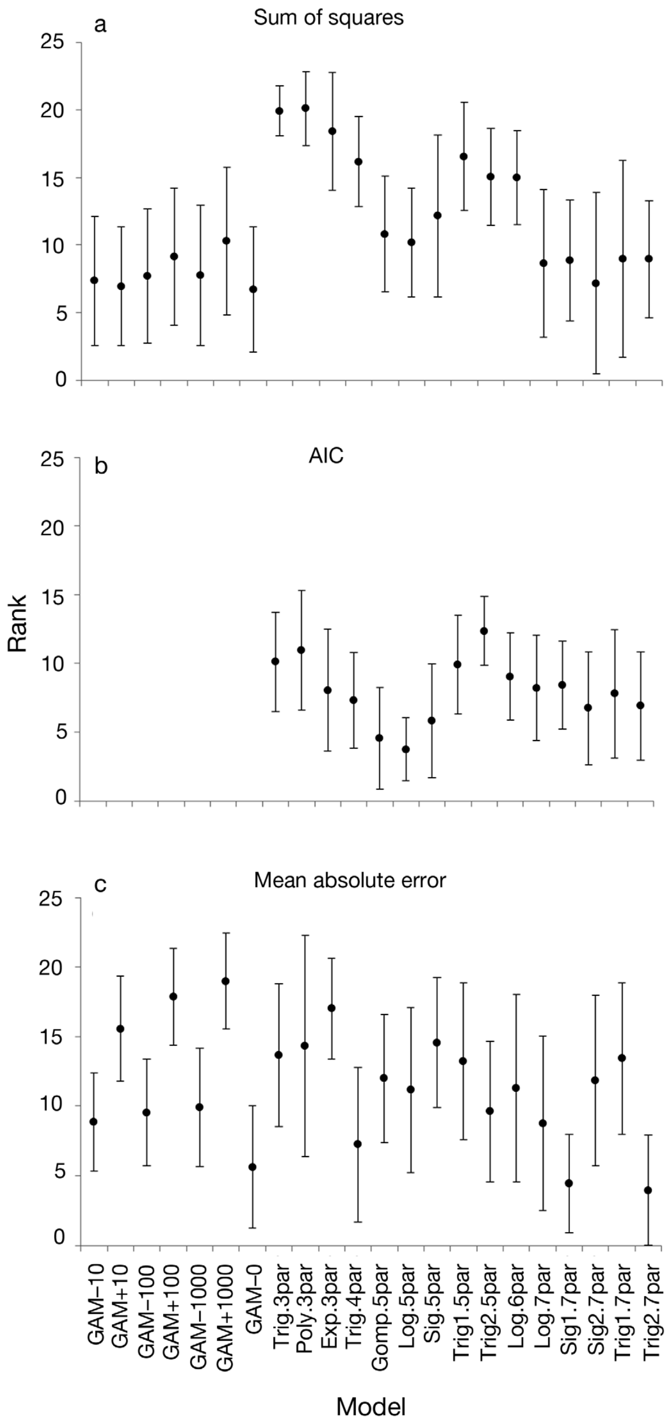

Fig. 2. Mean ± SD for model ranks, showing comparisons in (a) residual sum-of-squares, (b) Akaike's information criterion (AIC) and (c) mean absolute error. GAM refers to generalized additive models with '−' denoting downweighting and '+' denoting upweighting; Trig: trigonometric model; Poly: polynomial model; Exp: exponential model; Gomp: Gompertz model; Sig: sigmoidal model; par: (no. of) parameters. See Table 2 for full model descriptions

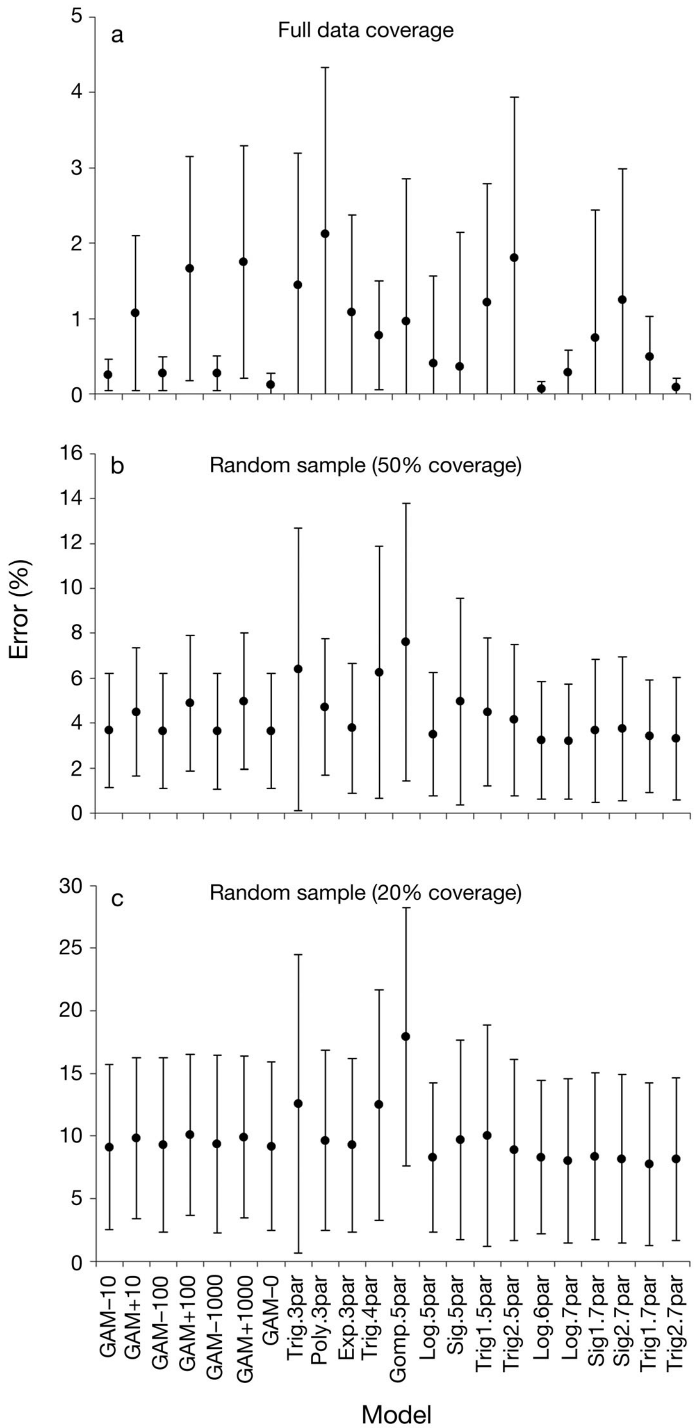

Fig. 3. Mean ± SD for error in predicting annual nesting abundance, showing comparisons using (a) full-season data, (b) random samples using 50% of the annual nightly counts and (c) random samples using 20% of the annual nightly counts. GAM refers to generalized additive models with '−' denoting downweighting and '+' denoting upweighting; Trig: trigonometric model; Poly: polynomial model; Exp: exponential model; Gomp: Gompertz model; Sig: sigmoidal model; par: (no. of) parameters. See Table 2 for full model descriptions

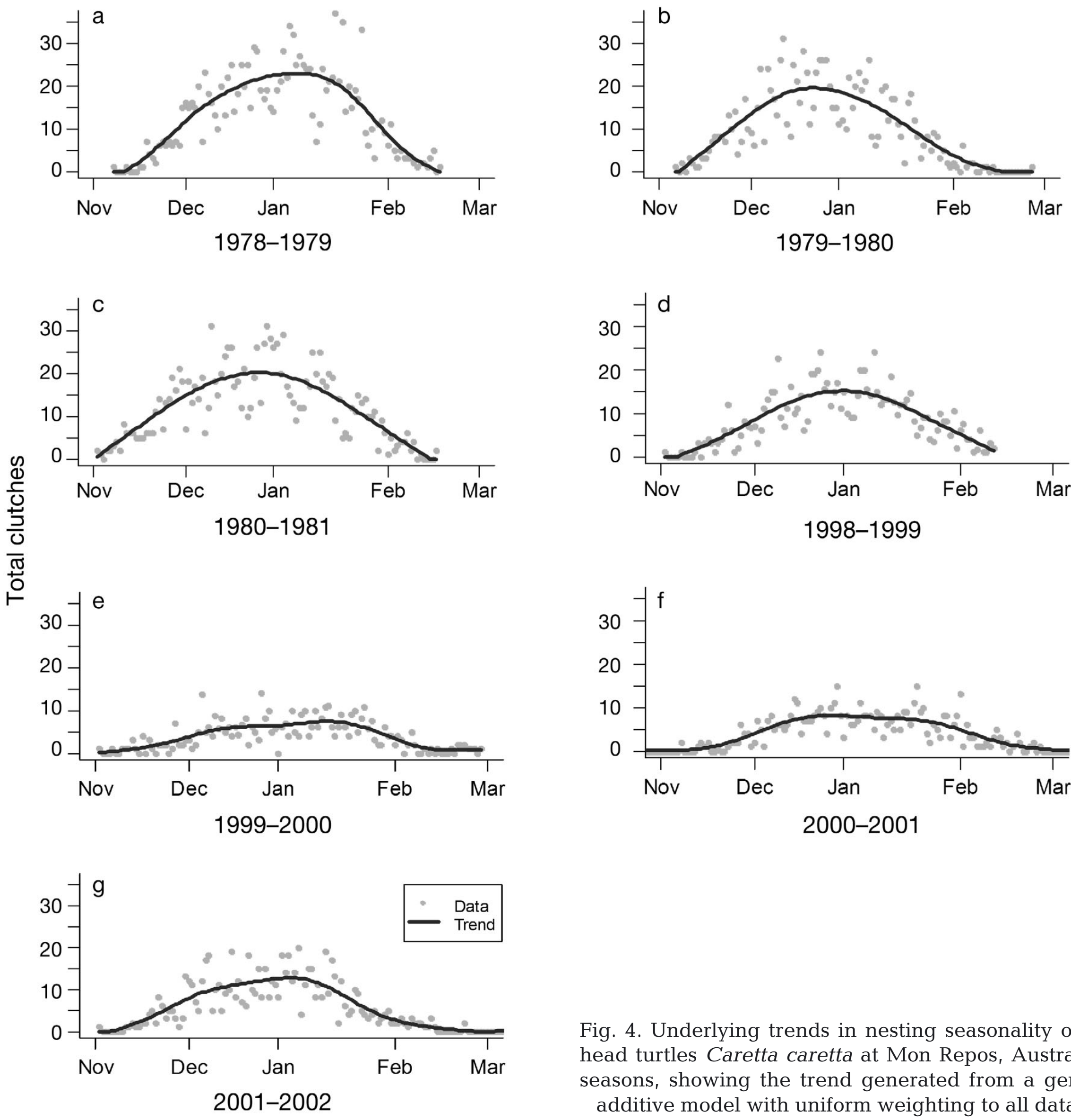

Fig. 4. Underlying trends in nesting seasonality of loggerhead turtles *Caretta caretta* at Mon Repos, Australia, for 7 seasons, showing the trend generated from a generalized additive model with uniform weighting to all data points

had significantly higher mean absolute error than many other models (Table 3, Fig. 2). For parametric models, there were significant differences in the rank of AIC ($\chi^2 = 84.8$, df = 14, $p < 0.001$), with the Logistic 5 parameter, Sigmoidal 5 parameter and Gompertz 5 parameter modes showing significantly lower AIC rank than several other models, while the Trigonometric-2 5 parameter model showed a significantly higher AIC rank than several other models (Table 3, Fig. 2).

Mean error in estimating annual abundance was low for all models (<3%; Fig. 3a) when using all nightly counts. Error in estimating annual nesting was still reasonably low for all models when using 20% and 50% samples of data throughout the nesting season; 50% samples had a mean error of <8% (Fig. 3b), and 20% samples gave a mean error of 8 to 10% for all but 3 models (Fig. 3c). There was no significant difference between any of the models in their estimate of annual nesting abundance when using random samples comprising of 20% or 50% of the nightly counts ($p > 0.05$).

Intra-seasonal variability

Intra-seasonal trends in abundance were similar between nesting seasons at each of the Mon Repos and the Sabah Turtle Island populations (see Figs. 4 & 5). The largest variation was shown for 1 year

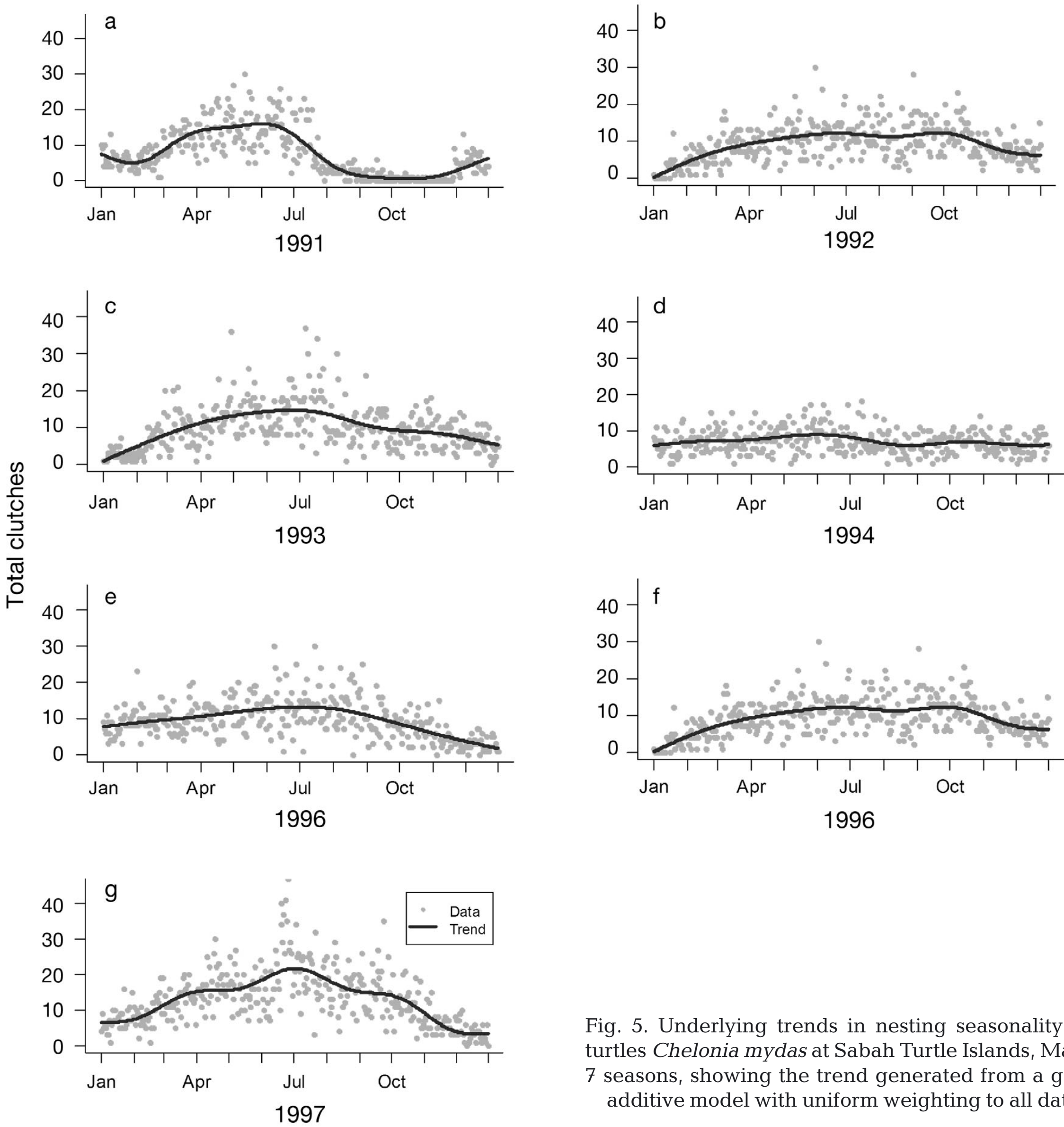

Fig. 5. Underlying trends in nesting seasonality for green turtles *Chelonia mydas* at Sabah Turtle Islands, Malaysia, for 7 seasons, showing the trend generated from a generalized additive model with uniform weighting to all data points

Table 4. Annual variation in seasonal shape for green turtles *Chelonia mydas* nesting on the Sabah Turtle Islands, Malaysia (n = 7 yr) and loggerhead turtles *Caretta caretta* nesting at Mon Repos, Australia (n = 7 yr). The kurtosis value was calculated by the peak value divided by total annual abundance. A low kurtosis value refers to a broad peak (platykurtic) and a high kurtosis value refers to an acute peak (leptokurtic)

Species	Peak			Kurtosis value		
	Mean	SD	Range	Mean	SD	Range
Green	18 Jul	50.3 d	2 Jun – 27 Sep	0.0039	0.0008	0.0027–0.0049
Loggerhead	29 Dec	7.8 d	11 Dec – 26 Jan	0.017	0.001	0.015–0.018

(1991) at the Sabah Turtle Islands, where the season had an unusually abrupt end with very low nesting during a 3 mo period (see Fig. 5a). Inter-seasonal changes in the kurtosis of the nesting season were low. Larger differences were seen between the populations than between seasons within the 1 population (see Table 4). The peak in nesting abundance varied by 117 d for green turtles nesting on the Sabah Turtle Islands and by 23 d for loggerhead turtles nesting at Mon Repos (Table 4).

DISCUSSION

It is not surprising that most of the models tested showed a reasonable fit to the data, given the large variation in nesting abundance between successive nights for all populations investigated and the simple functional form of the models investigated, with parametric models following a peaked pattern with both a skewed or symmetrical shape and non-parametric models having sufficient smoothing to depict the general form of nesting. It is also probable that moving averages, Lagrange interpolation, linear interpolation or kernel density interpolation methods would also give good fits to the data, but they would not be as suitable for partial season counts. Using residual sum-of-squares for model comparison, 15 models were highlighted as having significantly better model fits than the other 7 models. Of these 15 models, a further 3 models showed significantly lower mean absolute error than the other models: the GAM with uniform weighting, Sigmoidal-1 7 parameter and Trigonometric-2 7 parameter models.

The major differences in the 3 best-fit models are that the GAM is a non-parametric model which is not constrained in its functional form, whereas Sigmoidal-1 7 parameter and Trigonometric-2 7 parameter models are parametric models. The non-parametric model is more flexible in its application across species, populations and seasons, as it is more flexible in its constraints, does not require initial parameter estimates and will not substantially overestimate or underestimate nesting activity where no data are available. Conversely, the parametric models are constrained to a single peak, so would not be suitable for multi-modal seasonal data (e.g. Figs. 4 & 5; Chevalier et al. 2000, Witt et al. 2009). Furthermore, if data are not collected throughout the season, the model may substantially overestimate nesting abundance (Gratiot et al. 2006) unless the values are constrained to force the peak to occur within a certain period. This is a major limitation for nesting populations where access to the beach is a major logistic constraint. Furthermore, to increase the goodness-of-fit of the parametric models while minimizing survey effort, the SWOT (State of the World's Sea Turtles) Scientific Advisory Board (2011) recommended greater effort in sampling during the peripheries of the nesting season when fewer turtles are encountered. Monitoring more at the peripheries of the nesting season may be less effective if a capture–mark–recapture program is running alongside the track count surveys as it would increase the error for capture–mark–recapture population estimates as a smaller proportion of the population is seen. Given that mark–recapture data can produce important demographic data required by managers, we would not recommend moving more on-ground effort to the peripheries of the nesting season for marginal increases in precision for track count abundance estimates.

Due to the variable shapes of the nesting seasons between years (Figs. 4 & 5), all of the models investigated will show increased error when extrapolating outside the sampled timeframe. Where sampling occurs during 1 or 2 block periods during the nesting season, linear regression models may be preferred to estimate annual nesting abundance with lower error. Linear regression models have been used previously to estimate annual nesting abundance from mid-season counts and have generally shown consistently good correlations between years for counts of 2 wk or more (Kerr et al. 1999, Jackson et al. 2008, Limpus et al. 2008, Limpus 2009). The variable phenology in nesting may impact on the best-fit of the GAMs. When using nightly data from the full season, GAMs had a better fit when data points had uniform weighting. Up-weighting the endpoints may be favourable when an intermittent survey is conducted that is skewed to either the beginning or the end of the nesting season, or a mid-season count is conducted.

Although model fit can sometimes be optimized using environmental parameters such as moon phase and tidal height (Girondot et al. 2006), these impacts are not consistent between populations or years (Caldwell 1959, Bustard 1979, Frazer 1981, 1983, Girondot & Fretey 1996, Dobbs et al. 1999, Lux et al. 2003, Girondot et al. 2006, Pike 2008), which indicates that a more refined model would not be superior for use between populations, seasons or species. A more complex model is also limited in its application by requiring significant *a priori* information for the nesting population investigated.

The seasonal trend models described within this paper only investigated error in estimating the annual abundance of the nesting activities or number of tracks. Additional potential sources of error in the data collected include error in identifying species from tracks, error in assessing nesting success from tracks, missing tracks caused by survey error or by wind or tides removing signs of tracks, and errors in recording and transcription. For example, assessing nesting success by visually assessing tracks in the sand has a much higher error and more impact from the ability of the observer than assessing nesting success from watching turtles or digging in the sand to confirm the presence of eggs (see Schroeder & Murphy 1999 for discussion). Furthermore, assessing annual nesting numbers using count data would not detect potential changes in the population from changes in reproductive effort per female within the year (e.g. Broderick et al. 2003) or changes in remigration intervals (e.g. Hays 2000), and limits abundance estimates to 1 demographic state. Use of capture–mark–recapture methods on the nesting beach and in in-water studies would therefore be desirable to more accurately estimate the number of nesting females (e.g. Pfaller et al. 2013), adult males (e.g. Hays et al. 2010) and juveniles (e.g. Chaloupka & Limpus 2001) in the population.

As there was no significant difference between any of the models in estimating annual nesting abundance, any of the models investigated could be applied to random sampling with at least 20% coverage of the nesting season to provide an annual estimate with reasonable accuracy. Of the 3 models that had the lowest mean absolute error, we recommend using GAMs to estimate annual abundance due to their ease of fitting, flexibility across populations and seasonal shapes and their good predictive ability. GAMs are easily applied to partial-season data and allow the beginning and end of the season to be fixed via weighting end-points. They also do not create potential problems in fitting (as highlighted by Gratiot et al. 2006), where data may be substantially over- or underestimated unless specific parameter restrictions are applied. As with all models investigated within this paper, GAMs will provide a better estimate of annual abundance if data are collected at several different times throughout the season than only 1 point source, as this minimizes the length of time of extrapolation.

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