Is climate change affecting the population dynamics of the endangered Pacific loggerhead sea turtle?

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Abstract

The loggerhead sea turtle is an endangered species exposed to many anthropogenic hazards in the Pacific. It is widely held that pelagic longline fisheries pose the major risk for Pacific loggerheads but the effects of other risk factors such as human-induced global climate change have rarely been considered. So we used generalised additive regression modelling and autoregressive-prewhitened cross-correlation analysis to explore whether regional ocean temperatures affect the long-term nesting population dynamics for the 2 Pacific loggerhead genetic stocks (Japan. Australia). We found that both Pacific stocks have been exposed to slowly increasing trends in mean annual sea surface temperature in their respective core regional foraging habitats over the past 50 years. We show that irrespective of whether a population was decreasing or increasing that there was an inverse correlation between nesting abundance and mean annual sea surface temperature in the core foraging region during the year prior to the summer nesting season. Cooler foraging habitat ocean temperatures are presumably associated with increased ocean productivity and prey abundance and consequently increased loggerhead breeding capacity. So warming regional ocean temperatures could lead to long-term decreased food supply and reduced nesting and recruitment unless Pacific loggerheads adapt by shifting their foraging habitat to cooler regions. So the gradual warming of the Pacific Ocean over the past 50 years is a major risk factor that must be considered in any meaningful diagnosis of the long-term declines apparent for some Pacific loggerhead nesting populations.
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1. Introduction

The Pacific loggerhead comprises 2 distinct genetic stocks (Bowen et al., 1994) that are exposed to a number of hazards such as egg harvesting (Kamezaki and Matsui, 1997), egg predation (Chaloupka, 2003), turtle hunting (Gardner and Nichols, 2001), coastal development (Kamezaki et al., 2003) and incidental capture in coastal and pelagic fisheries (Poiner and Harris, 1996; Julian and Beeson, 1998; Chaloupka et al., 2004; Peckham et al., 2007). The Pacific loggerhead is an endangered species and some nesting population declines have been attributed to incidental capture in pelagic longline fisheries (Chaloupka, 2003; Lewison et al., 2004) but other risk factors such as egg predation and coastal fisheries are perhaps more

important (Chaloupka, 2003; Peckham et al., 2007). Moreover, not all Pacific loggerhead populations are in decline (foraging ground estimates in Chaloupka and Limpus, 2001; nesting estimates in Kamezaki et al., in review) despite ongoing exposure to various fisheries, which suggests that several risk factors might be implicated in any apparent nesting population declines. One major risk factor that has been neglected in the modelling of Pacific loggerhead population dynamics is the long-term affect of human-induced global climate change.

Global climate change is considered to be one of the major hazards facing the long-term future of the world's biodiversity (Root et al., 2003; Harley et al., 2006). So exploring the affect of climatic variability on ecological processes is essential for developing a better understanding of wildlife population dynamics (Hallett et al., 2004). For instance, global climate change could have a profound affect on marine turtle population dynamics through shifts in nesting phenology (Weishampel et al., 2004;

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Hawkes et al., 2007) leading to trophic mismatch (Edwards and Richardson, 2004) for the oceanic hatchling stage, increases in nesting beach temperature that determine hatchling sex ratios and incubation success (Limpus et al., 1985; Hays et al., 2003), inundation of nesting beach habitat (Fish et al., 2005), increased disease transmission (Herbst et al., 1995) and changes in migration behaviour (McMahon and Hays, 2006).

Large-scale climate indices such as the El Nino-Southern Oscillation (ENSO) or some surrogate have been used to explore marine turtle nesting population dynamics in the Pacific (Limpus and Nicholls, 2000; Chaloupka, 2001; Saba et al., 2007). Large-scale climate indices are especially needed for sea turtle studies because they forage over vast areas but then nest in a few rookeries where an index of nesting abundance can be easily monitored (Limpus et al., 1992). Moreover, such large-scale climate indices have been shown to be far better predictors of ecological processes than local weather-related variables (Hallett et al., 2004). Also the major process subsumed in the ENSO is regional sea surface temperature (SST), which is commonly used as an environmental surrogate for modelling climate variability (Edwards and Richardson, 2004; Harley et al., 2006) and is well known to be a factor affecting marine turtle nesting activity (Solow et al., 2002; Mazaris et al., 2004; Saba et al., 2007).

Moreover, composite climate indices such as ENSO have been used mainly in marine turtle studies as a surrogate for SST in the absence of accessible regional temperature data (Limpus and Nicholls, 2000; Chaloupka, 2001). However, global SST data are now readily available (Smith and Reynolds, 2004; Smith et al., in press) and so we use regional-scale SST data in our assessment of the affect of climate on the nesting population dynamics of the 2 endangered loggerhead sea turtle stocks in the Pacific. Such an assessment enables us to compare geographic variation in nesting abundance and any potential regional-specific response to climate change, which is important for developing an understanding of loggerhead population dynamics and for determining the conservation status of these stocks.

2. Materials and methods

2.1. Nesting time series

We have compiled long-term nester abundance time series for 4 Pacific loggerhead rookeries — 2 from the Japanese stock and 2 from the east Australian stock (Fig. 1). These 4 rookeries are representative of the 2 stocks in terms of temporal trends and comprise the 2 longest continuous nesting time series recorded for any loggerhead population (Kamezaki et al., 2003; Limpus and Limpus, 2003; Kamezaki et al., in review). These rookeries are also the major rookeries for the 2 Pacific loggerhead genetic stocks and have been subject to intensive multi-decadal beach monitoring programs to minimise sampling effort artefacts (Kamezaki et al., in review; Limpus and Limpus, 2003). The Kamouda rookery is located on Shikoku (Japan) and has the longest continuous nesting time series ever recorded for any loggerhead population (Kamezaki et al., in review). The Kamouda data comprises the number of landings or emergences recorded each nesting season over a 51-year
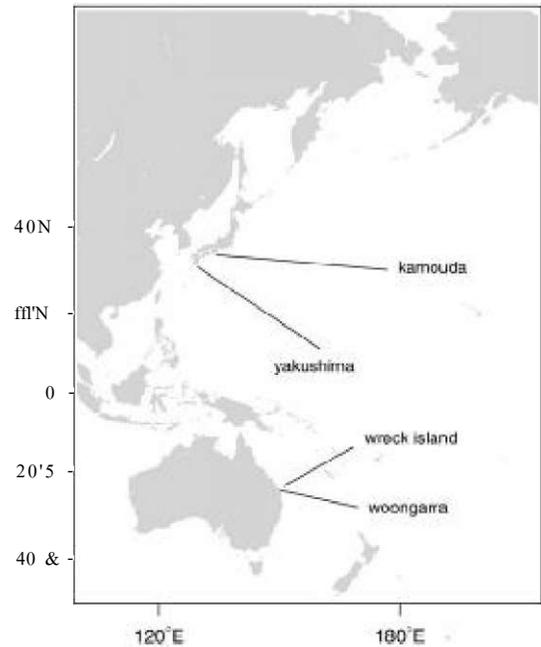

Fig. 1. Location of 2 Japanese loggerhead genetic stock rookeries at Kamouda and Yakushima and 2 Australian rookeries at Wreck Island and Woongarra coast. The Japanese and Australian loggerhead stocks are genetically distinct.

sampling period from 1954 to 2004 (Kamezaki et al., in review). Landings are the observed number of loggerheads that hauled out each season onto the nesting beach — a successful nesting may have occurred but that is unknown although Kamezaki et al. (in review) show that there is a very high positive correlation between landings and actual nests laid at the Japanese loggerhead rookeries where both data series are recorded. The nesting population at Kamouda has been generally declining over the past 35-40 years (Kamezaki et al., in review). The Yakushima rookery is located on Yakushima, which is a small island south of Kyushu (Japan) in the Nansei-shoto Archipelago, and accounts for ca. 48% of all loggerhead nesting in the Japanese Archipelago (Kamezaki et al., in review). The Yakushima data comprises the number of landings or emergences recorded over a 20-year period (1985-2004) for 2 nesting beaches (Inakahama, Maehama) located on northwestern Yakushima (Kamezaki et al., in review). The nesting populations on Yakushima have been generally increasing over the past 20 years (Kamezaki et al., in review). The Woongarra rookery is located on the mainland coast around Mon Repos in central Queensland (Australia) and is in close proximity to the southern Great Barrier Reef region. The Woongarra rookery is the largest remaining concentration of nesting loggerheads for the east Australian stock (Chaloupka and Limpus, 2001; Limpus and Limpus, 2003). The Woongarra data comprises the number of individual nesters recorded each season over a 38-year sampling period from 1967 to 2004 (Limpus and Limpus, 2003; recent data updates). The nesting population at Woongarra had been generally declining until the early 1990s but then appears to have been recovering ever since (Limpus and Limpus, 2003; current study). The Wreck Island rookery is located on an offshore coral cay in the southern Great Barrier
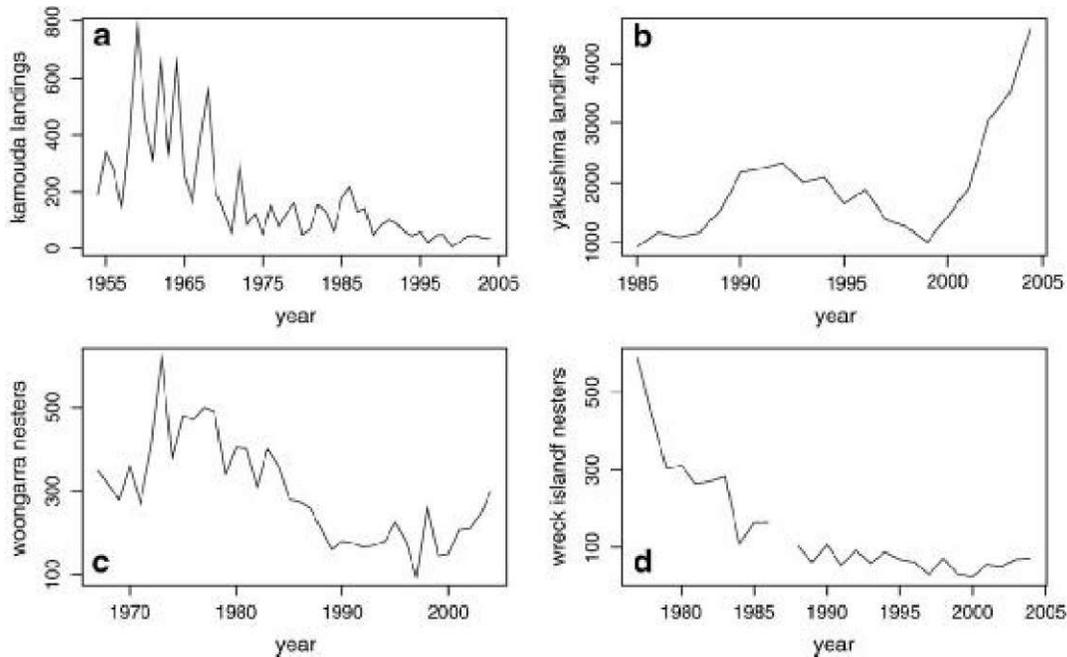
Fig. 2. Long-term nesting activity recorded at the 4 Pacific loggerhead sea turtle rookeries shown in Fig. 1: (a) Kamouda, (b) Yakushima, (c) Woongarra coast, (d) Wreck Island. Nesting activity recorded as the number of landings (emergences) for the 2 Japanese rookeries (Kamouda, Yakushima) and as the number of individual nesters for the 2 Australian rookeries (Woongarra, Wreck Island).

Reef region (Australia) and was once the largest concentrations of nesting loggerheads for the east Australian stock (Limpus and Limpus, 2003). The Wreck Island data comprises the number of individual nesters recorded during a standardised mid-season 2-week sampling protocol over the 28-year period from 1977 to 2004 (Limpus and Reimer, 1994; Limpus and Limpus, 2003). The nesting population at the Wreck Island rookery has been generally declining over the past 25 years (Limpus and Limpus, 2003).

2.2. Sea surface temperature time series

We used ERSST2 data to derive our long-term stock-specific SST time series. The ERSST2 is a validated reconstructed record of historical monthly SST with 2° global spatial resolution based on a range of in-situ and satellite-derived observations coupled

with sea-ice records (Smith and Reynolds, 2004). ERSST2 data are widely used for global climate-ocean-ecology modelling (Barton and Casey, 2005; Zhang and McPhaden, 2006; Bronnimann et al., 2007; Pascal et al., 2007) and provides similar SST series from the 1950s onwards compared to the forthcoming ERSST3 (Smith et al., in press). Specifically, we used monthly global ERSST2 data fields to derive 51-year monthly SST time series (1955-2005) for a core foraging region around the rookeries. Adult loggerheads in the Pacific forage over a wide area that can extend 100s or even 1000s of kilometers from the rookery (Limpus et al., 1992; Sakamoto et al., 1997) so we derived spatially averaged monthly series for
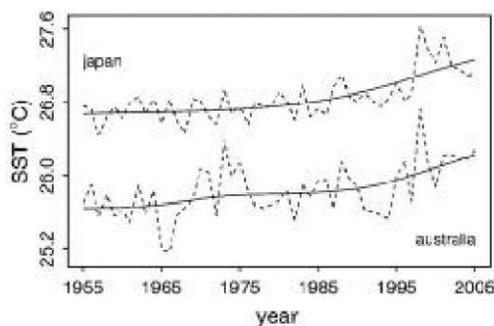

Fig. 3. Mean annual sea surface temperature for the foraging region related to the Japanese and east Australian loggerhead rookeries for the 51-year period from 1955 to 2005. Dashed curve = ERSST2 derived mean annual SST, and solid curve = smoothing spline to highlight any underlying trend.

Table 1
Summary of rookery-specific GAM fits to nesting activity data series shown in Fig. 2

Rookery	Approximate significance of smooth terms			
	Parameter	edf	F-score	P-value
Kamouda	Year	5.5	13.27	<0.001
	SST (1 year lagged)	1.7	3.11	0.025
	Deviance explained=80%, N=51			
Yakushima	Year	2.9	38.06	<0.001
	SST (1 year lagged)	1.0	5.64	0.031
	Deviance explained=89%, N=20			
Woongarra	Year	3.8	44.80	<0.001
	SST (1 year lagged)	1.0	13.89	<0.001
	Deviance explained=86%, N=38			
Wreck island	Year	3.2	23.64	< 0.001
	SST (1 year lagged)	1.0	11.13	0.003
	Deviance explained=92%, N=27			

edf = effective degrees of freedom (1 = linear, >1 nonlinear), and N = number of years in sample. Japanese rookeries (Kamouda, Yakushima), and Australian rookeries (Woongarra, Wreck island).
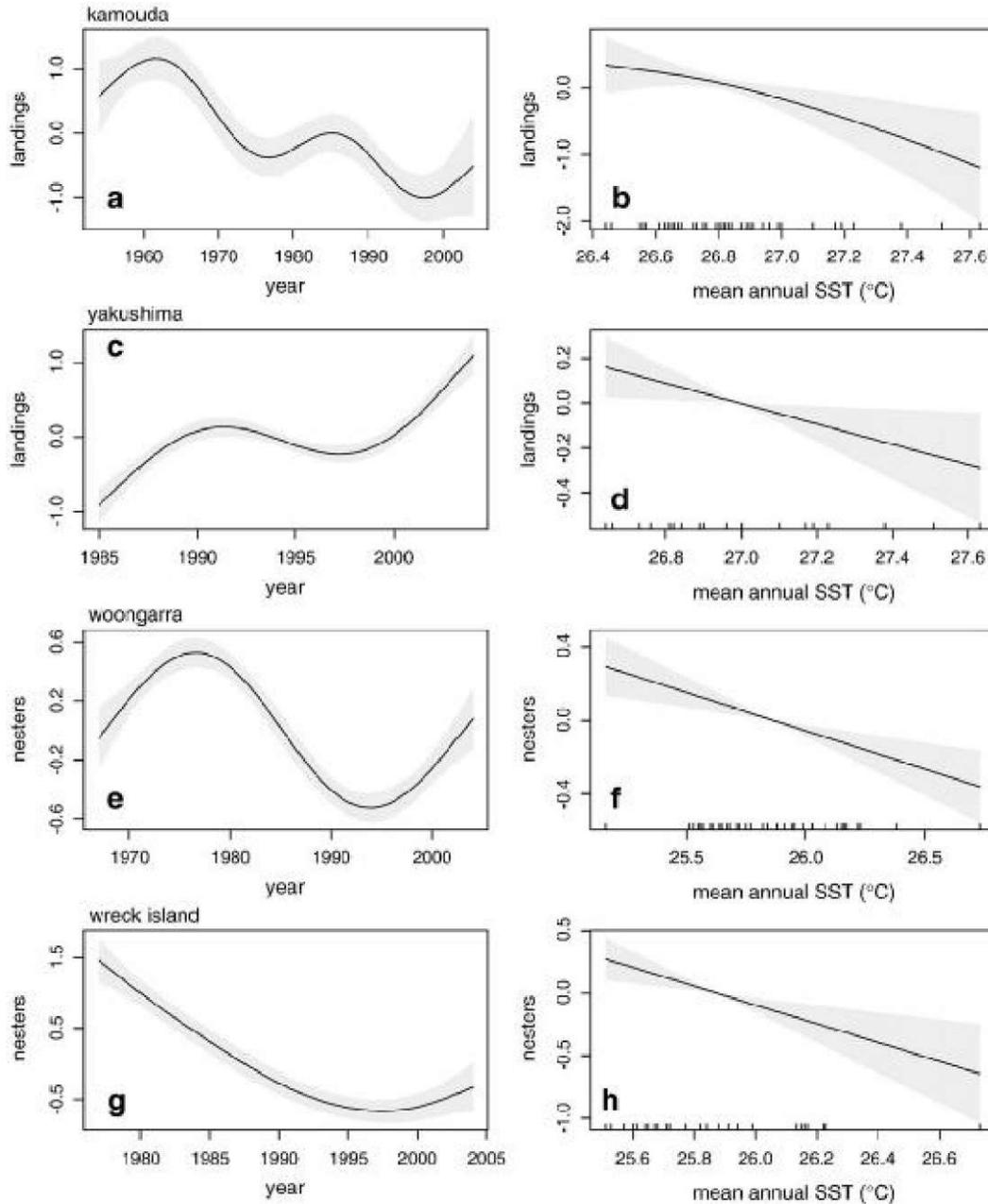
Fig. 4. GAM model fits to the nesting activity data series for the 4 loggerhead rookeries shown in Fig. 2. Data series modelled as rookery-specific nonparametric functions of year (summer nesting season) and mean annual sea surface temperature (SST) recorded for the core foraging region in the year prior to each summer nesting season. So for instance, panel (a) shows the expected Kamouda nesting activity temporal trend given the 1-year lagged mean annual SST function in (b). Solid curves = GAM model fit, shading = 95% pointwise confidence bands, and y-axis = GAM centred response on log scale. The vertical bars on the topside of the lower x-axis of the SST panels are known as a rug, which show the SST data distribution within each panel.

extensive geographic areas for the Japanese (10-30°N, 120-140°E) and east Australian (10-30°S, 150-170°E) foraging stocks. We then derived the mean annual SST series from the monthly ERSST2 data for each of these 2 core foraging regions.

2.3. Statistical modelling approach

We estimated the temporal trend and mean annual SST-effect in the rookery-specific annual nesting abundance series using the generalised additive regression modelling approach implemented

in the *mgcv* package for R (Wood, 2006). This GAM or nonparametric regression approach uses the data to determine the underlying linear or nonlinear trend and covariate functional form without having to assume any specific functional form. Each rookery-specific GAM used a log link with quasi-likelihood error structure and thin plate regression splines to model nonlinear covariate function form with smoothness parameters estimated simultaneously using generalised cross-validation (Wood, 2006). Other error structures are possible including low order auto-correlated error and so we explored these alternatives using a

generalised additive mixed (GAMM) regression approach (Wood, 2006). We also explored lagged SST-effects on nesting abundance such as mean annual SST in the core foraging region over the previous 1, 2 or 3 years prior to the current nesting season. This GAM(M) regression modelling approach enabled us to explore the affect of foraging habitat SST on nesting ecology while controlling for rookery-specific differences in nesting trends. We also used a simple cross-correlation function analysis with autoregressive-prewhitened data series to test for the possibility of any spurious correlations between nesting activity and SST and also to assess whether there was any evidence for 2- or 3 -year or higher order lags — see Chaloupka (2001) for details relevant to sea turtle data series.

3. Results

The long-term time-specific data series compiled for the 4 Pacific loggerhead sea turtle nesting populations or rookeries (Fig. 1) are shown in Fig. 2(a-d). The 51 -year mean annual S ST time series derived from ERSST2 data for the Japan and east Australian core foraging regions are shown in Fig. 3 where it is apparent that region-specific SST has been increasing slowly since the 1950s. This finding of slowly increasing regional SST is consistent with a general warming of the oceans due to human-induced global climate change (Barnett et al., 2005), and especially so in the Northwest Pacific near to our Japan core foraging region (Casey and Cornillon, 2001).

The nonparametric regression models (GAMs) that accounted for nonlinear temporal and 1-year lagged SST-effects fitted the rookery-specific data series well with the proportion of deviance explained ranging from 80% for the Kamouda data series to 92% for the Wreck Island data (Table 1). There were no 2- or 3-year lag functional relationships apparent in rookery-specific GAM models, which is consistent with the cross-correlation analysis for the Kamouda data series (see below). The GAM-estimated underlying trend for each rookery accounting for the effect of regional SST during the year prior to each nesting season is shown in Fig. 4. The underlying long-term trend for each rookery was significantly nonlinear (Table 1) with an oscillating downward trend apparent for Kamouda (Fig. 4a), an oscillating upward trend apparent for Yakushima (Fig. 4c), an oscillating but stationary trend apparent for Woongarra (Fig. 4e) and a downward trend that might have levelled off by the late 1990s apparent for Wreck Island (Fig. 4g).

It is also apparent from Fig. 4 that nesting abundance for all rookeries was an inverse and generally linear function of SST — higher SST during the previous year in the core foraging region results in lower summer season nesting at all 4 rookeries (Fig. 4b,d,f,h). The inclusion of AR1 error structures in the GAMs did not improve model fit and so we report only using the GAM results rather than from the various GAMMs also fitted. Only the 51-year Kamouda data series was sufficiently long enough to use the prewhitened cross-correlation approach (Fig. 5), which showed a significant 1-year lag between the Kamouda nesting activity and the core Japanese foraging region SST (Fig. 5c). So then at least for the Kamouda rookery, 2 alternative forms of time series analysis suggest a significant inverse relationship between summer nesting season activity and SST in the foraging region over the previous 12 months.
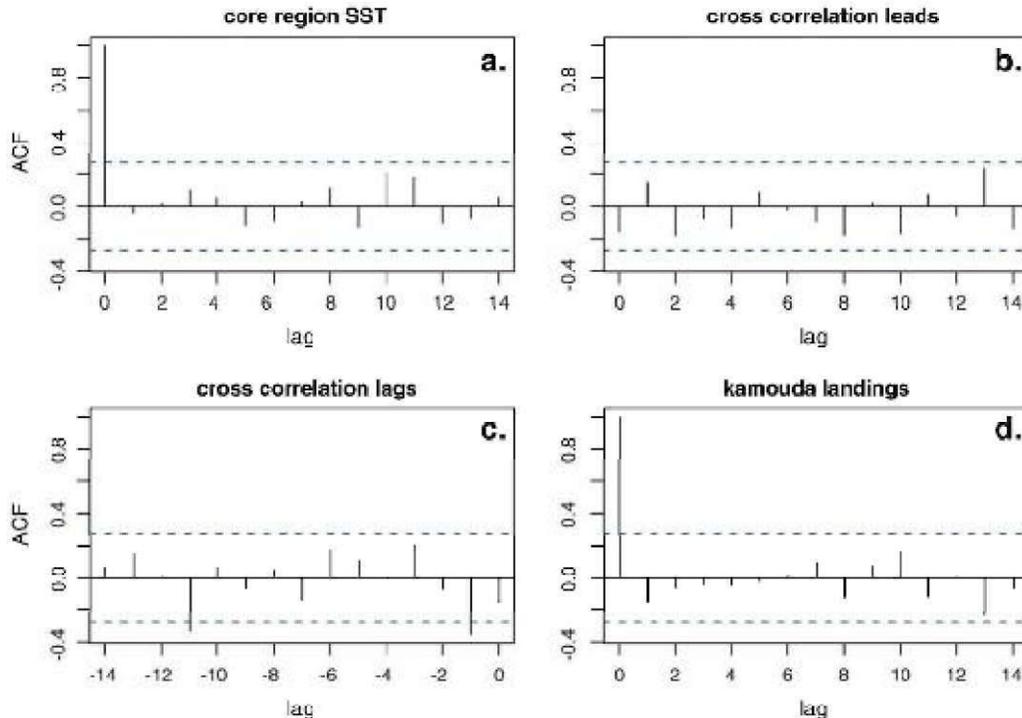

Fig. 5. Autocorrelation (a,c) and cross-correlation (b,c) functions for assessing any lagged relationship between Kamouda annual nesting activity (landings) and the core foraging region mean annual SST. Approximate 95% confidence intervals shown by dotted lines. Functions derived from autoregressive prewhitening of the two 51 -year data series (Kamouda nesting, regional SST).

4. Discussion

Some loggerhead nesting populations in the Pacific have declined while others have remained stable or are increasing (Kamezaki et al., in review; our Fig. 4). The North Pacific or Japanese stock is listed as threatened under the US Endangered Species Act while the South Pacific or east Australian stock is listed as endangered under the Australian Endangered Species legislation. All Pacific loggerhead population declines have previously been attributed to pelagic fisheries interactions (Chaloupka, 2003; Lewison et al., 2004) but it is apparent that other risk factors such as egg predation and exposure to coastal fisheries are also implicated (Chaloupka, 2003; Peckham et al., 2007). Using long-term data series, we found that both the Japanese and east Australian loggerhead stocks have been exposed to slowly increasing trends in mean annual sea surface temperature in their core regional foraging habitats over the past 50 years or more (Fig. 3). We show that irrespective of whether a population was decreasing or increasing (or otherwise) that there was a significant inverse correlation between nesting abundance and mean annual sea surface temperature in the core foraging region during the year prior to the summer nesting season (Fig. 4). Female marine turtles generally require at least 1 year to acquire sufficient body fat deposits for vitellogenesis to occur in the foraging grounds let alone the energy requirements needed for migration to distant rookeries (Kwan, 1994; Miller, 1997). Hence there is a physiologic basis for the consistent pattern of a 1-year lagged foraging ground SST function apparent in our study of 4 nesting populations for 2 genetic stocks in 2 different hemispheres of the Pacific. Moreover, our study comprised long-term data series subject to 2 alternative forms of time series analysis to avoid as far as possible spurious correlations that continue to plague time series analyses of ecology-climate data (Stenseth et al., 2003).

Cooler foraging habitat ocean temperatures are presumably associated with increased western Pacific Ocean productivity and prey abundance and consequently increased loggerhead breeding capacity. Regional SST affects decadal changes in pelagic fish recruitment and abundance in the Kuroshio Current region, which is an area similar to our core Japanese loggerhead foraging region. For instance, variation in abundance of the Pacific saury has been shown to be a consequence of oceanic-climatic variability rather than commercial fishing effort with strong winter-spawning saury cohorts and juvenile survival associated with cool-phase ENSO events in the northwestern Pacific (Tian et al., 2004). The Pacific saury is also one of the major summer prey species for northwest Pacific minke whales (Tian et al., 2004). So warming regional ocean temperatures apparent in our study could also lead to long-term decreased loggerhead food supply and reduced nesting and recruitment unless Pacific loggerheads adapt by shifting their foraging habitat to cooler regions. Furthermore, loggerheads are ectothermic, so it is probable that individual metabolic rates will also increase with warmer SSTs in the foraging grounds, which might act in combination with reduced food availability to reduce nesting numbers in the subsequent year (see Wallace and Jones, 2008-this issue). Consequently, the gradual long-term warming of the western Pacific Ocean over the past 50 years is a major risk factor that should be considered in any meaningful and comprehensive diagnosis of the long-term declines apparent for some Pacific loggerhead nesting populations.

It is becoming increasingly apparent that sea temperature in the foraging habitats is an important factor affecting the inter-seasonal nesting population dynamics of marine turtles such as green turtles (Limpus and Nicholls, 2000; Chaloupka, 2001; Solow et al., 2002), leatherbacks (Saba et al., 2007) and loggerheads (our study). An inverse sea surface temperature response is also apparent for Pacific green turtle nesting populations (Limpus and Nicholls, 2000; Chaloupka, 2001) as well as for the Pacific leatherback (Saba et al., 2007). So the temperature-dependent breeding ecology affect in the Pacific is apparent irrespective of species-specific feeding ecology since the green turtle is herbivorous while the leatherback and loggerhead are carnivores (Bjorndal, 1997). However the extent of inter-annual variability in nesting numbers seems to vary with trophic status across sea turtles, being highest in green turtles and lower, for example, in loggerhead turtles (Broderick et al., 2001). This presumably reflects a different degree of coupling between environmental conditions and the abundance of food for green turtles (seagrass, macroalgae) versus the abundance of food for loggerhead turtles (various invertebrates). Moreover, during the winter it is possible that loggerheads in certain areas may show prolonged winter quiescence (Hochscheid et al., 2007) and so the role of changing water temperatures in driving this behaviour and its wider impact on reproductive success needs to be considered in terms of climate change scenarios for the species.

It has also been shown that the timing of loggerhead nesting within a season is also a SST-dependent function. For instance, Pike et al. (2006) found that warmer summer SSTs were associated with earlier but shorter summer nesting seasons for the loggerhead population that nests along the Atlantic coast of central Florida, USA. Meanwhile, Hawkes et al. (2007) found that warmer summer SSTs were associated with earlier but longer summer nesting seasons for the loggerhead population that nests along the Atlantic coast of North Carolina (USA). So a variety of intra-season nesting duration responses are apparent for the loggerhead populations that nest along the Atlantic coast of the USA. The reason for earlier SST-dependent nesting is possibly due to accelerated vitellogenesis in the foraging grounds (Limpus et al., 1994) and then faster egg development following mating nearby the rookery (Hawkes et al., 2007). A consequence of shorter nesting seasons could perhaps be reduced hatchling production and recruitment but this is still speculative (Pike et al., 2006). Nonetheless, a plausible consequence of increased Pacific Ocean warming for Pacific loggerhead population dynamics is lower recruitment due to a combination of (1) fewer females undergoing vitellogenesis and migrating to the rookeries each summer to mate and nest because of reduced foraging ground food stocks (our study) and (2) for those females that do migrate then perhaps reduced per capita fecundity due to shorter nesting seasons (Pike et al., 2006). Lower recruitment due to these 2 processes will result in reduced Pacific loggerhead abundance and increase the

extinction risk (Chaloupka, 2003). Meanwhile, it is also worth noting that Pacific warming might increase sand temperatures in the nests, which would lead to an increasing probability of hatching failure as temperatures approach lethal temperatures >34 °C (Limpus et al., 1985; Matsuzawa et al., 2002).

Loggerheads have 4 basic means for responding to increased ocean warming due to global climate change: (1) shift timing of the nesting season to cooler seasons, (2) shift nesting areas poleward to cooler beaches, (3) shift foraging habitats to cooler and more productive waters or (4) become regionally extinct. There is recent evidence of phenologic changes with nesting season shifts for Atlantic loggerheads (Weishampel et al., 2004; Pike etal., 2006; Hawkes etal., 2007). Reece etal. (2005) provide phylogeographic and population genetic evidence that geographic range shifts in loggerhead nesting habitats might have occurred in the Atlantic during the Pleistocene due to climatic and sea level fluctuations. Indeed, poleward shifts in nesting habitat are geographically feasible for loggerheads nesting along the east coast USA (Ehrhart et al., 2003), Brazil (Marcovaldi and Chaloupka, 2007), east coast Australia (Limpus and Limpus, 2003), east coast Japan (Kamezaki et al., 2003), west coast Australia (Baldwin et al., 2003) and east coast South Africa (Baldwin et al., 2003). However, poleward shifts in nesting habitat would be infeasible for geographically constrained populations such as in the Mediterranean sea (Margaritoulis et al., 2003). In fact Mediterranean nesting populations may have become regionally extinct during the Pleistocene due to cooling with subsequently recolonisation from Pleistocene refugia in more tropical regions such as Florida and Mexico (Reece et al., 2005).

Our simple statistical model identified a pressing need for climatic variables such as SST (Fig. 4) to be included in any process-based model of loggerhead population dynamics. However, our analysis was limited to considering only density independent climate affects on abundance but it has been shown that marine turtle demography is also density dependent (Bjorndal et al., 2000; Chaloupka and Balazs, 2007). The competing risks stochastic simulation modelling framework developed to account for the sex- and ageclass-specific population dynamics of the south Pacific loggerhead can be readily extended to explore the interaction between both effects (Chaloupka, 2003). Importantly, climate-driven breeding behaviour and its implication for the commonly monitored remigration or inter-seasonal breeding interval (Hays, 2000) could also be modelled explicitly using this extended simulation modelling approach. This is a particularly important issue since the low frequency oscillations apparent in Pacific loggerhead nesting abundance (Figs. 1 and 4) could also be a consequence of SST-induced breeding behaviour leading to increasing remigration intervals as SST increases in the foraging grounds (Hays, 2000). If so then reduced nesting abundance does not necessarily reflect abundance in the foraging grounds where loggerheads spend most of their lives. Therefore, comprehensive assessments of the conservation status of loggerheads depend on contemporaneous estimates of abundance in the foraging grounds and on the nesting beaches as was shown for the east Australian loggerhead stock (Chaloupka and Limpus, 2001) and for a Caribbean green turtle stock (Bjorndal et al., 2005).

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