

# Thirty-year recovery trend in the once depleted Hawaiian green sea turtle stock

George H. Balazs<sup>a</sup>, Milani Chaloupka<sup>b,\*</sup>

<sup>a</sup>*Pacific Islands Fisheries Science Center, National Marine Fisheries Service, Honolulu, Hawaii, 96822, USA*

<sup>b</sup>*School of Economics, University of Queensland, Brisbane, Queensland, 4072, Australia*

Received 6 March 2003; received in revised form 20 August 2003; accepted 20 August 2003

## Abstract

The green sea turtle is one of the long-lived species that comprise the charismatic marine megafauna. The green turtle has a long history of human exploitation with some stocks extinct. Here we report on a 30-year study of the nesting abundance of the green turtle stock endemic to the Hawaiian Archipelago. We show that there has been a substantial long-term increase in abundance of this once seriously depleted stock following cessation of harvesting since the 1970s. This population increase has occurred in a far shorter period of time than previously thought possible. There was also a distinct 3–4 year periodicity in annual nesting abundance that might be a function of regional environmental stochasticity that synchronises breeding behaviour throughout the Archipelago. This is one of the few reliable long-term population abundance time series for a large long-lived marine species, which are needed for gaining insights into the recovery process of long-lived marine species and long-term ecological processes.

© 2003 Elsevier Ltd. All rights reserved.

*Keywords:* Green sea turtle; Abundance; Population recovery; French Frigate Shoals; Hawaii

## 1. Introduction

The green turtle (*Chelonia mydas*) has a circum-tropical distribution with distinct regional population structures (Bowen et al., 1992) and is the most abundant large marine herbivore (Bjørndal, 1997). Globally, the green turtle has been subject to a long history of human exploitation with some stocks now extinct and others in decline (Frazier, 1980; Witzell, 1994). Yet despite being recognized as globally threatened (National Research Council, 1990) there are few reliable assessments of abundance status and trend of any green turtle stock (Chaloupka and Limpus, 2001). Reliable long-term estimates of population abundance trends are needed to support recovery planning (Foin et al., 1998), model sea turtle demography (Chaloupka, 2002) and are essential for developing a better understanding of long-term ecological processes (Inchausti and Halley, 2001).

For sea turtles, such population abundance estimates are based preferably on foraging ground capture–mark–

recapture programs that can provide more detailed sex- and age-class-specific demographic information (Limpus and Chaloupka, 1997; Chaloupka and Limpus, 2001, 2002). However, capture–mark–recapture programs in the marine environment for large and highly mobile species such as sea turtles are very difficult and expensive to conduct and so are rarely undertaken (Limpus and Chaloupka, 1997; Bjørndal et al., 2000). Nearly all assessments of sea turtle population abundance have been based on trawl based catch-per-unit-effort estimation, aerial survey based density estimation or, more commonly, by monitoring the number of females that come ashore each year to nest at stock-specific rookeries (see review in Chaloupka and Limpus, 2001).

Monitoring beach nesting is by far the easiest and least expensive means to assess green turtle population abundance but short-term surveys (<10 years) are inadequate for several reasons (Chaloupka and Limpus, 2001). Most notably because green turtles are long-lived (Limpus and Chaloupka, 1997; Zug et al., 2002) and females skip several nesting seasons due to nutritional constraints (Bjørndal, 1997). Hence, long-term nesting beach surveys are essential if this form of assessment of

\* Corresponding author. Fax: +61-7-3365-7299.

E-mail address: [m.chaloupka@mailbox.uq.edu.au](mailto:m.chaloupka@mailbox.uq.edu.au) (M. Chaloupka).

green turtle population abundance and trend is to be adopted. The Hawaiian green turtle stock is one of the few sea turtle stocks that have been continuously monitored for several decades and so is suitable for population assessment using nesting beach surveys.

The Hawaiian green turtle genetic stock comprises a spatially disjunct metapopulation with numerous distinct foraging grounds within the Hawaiian Archipelago (Fig. 1). The Hawaiian stock comprises mainly the same mtDNA haplotype (Dutton, *in press*) with no difference in mtDNA stock composition between foraging ground populations and females nesting at the regional rookery (Leroux *et al.*, *in press*). In other words, both the nesters and the turtles resident in various foraging grounds throughout the Archipelago are from the same genetic stock (Leroux *et al.*, *in press*), although occasionally some turtles from the east Pacific stock that nests along the Pacific coast of Mexico are recorded in Hawaiian waters (Balazs, 1976; Dutton, *in press*). We report the results of a 30-year study of the nesting abundance of the Hawaiian green turtle stock, which suggests that this once seriously depleted stock is now well on the way to recovery. This long-term nesting abundance series provides a basis for development of meaningful recovery plans for the Hawaiian green turtle stock.

## 2. Methods

### 2.1. Study and data description

The principal rookery for the Hawaiian green turtle stock is located on sand islands at French Frigate Shoals (Fig. 1), Northwestern Hawaiian Islands, which accounts for >90% of all nesting within the Hawaiian Archipelago (Balazs, 1976). The main rookery island at the French Frigate Shoals atoll is East Island where at least 50% of all the French Frigate Shoals nesting occurs (Balazs, 1976; Niethammer *et al.*, 1997). Tagging and radio telemetry studies have shown that it is rare for a green turtle to nest on East Island in one year and then nest at another small island at French Frigate Shoals in subsequent years (Dizon and Balazs, 1982; Niethammer *et al.*, 1997). Thus there is strong island fidelity within the regional rookery, so that annual nesting trends evident at East Island are not a consequence of permanent emigration.

Annual surveys of the number of female green turtles coming ashore to nest each night have been conducted at East Island since 1973, initially by Balazs when at the Hawaii Institute of Marine Biology and from 1981 onwards as a cooperative project between the US National Marine Fisheries Service and US Fish and

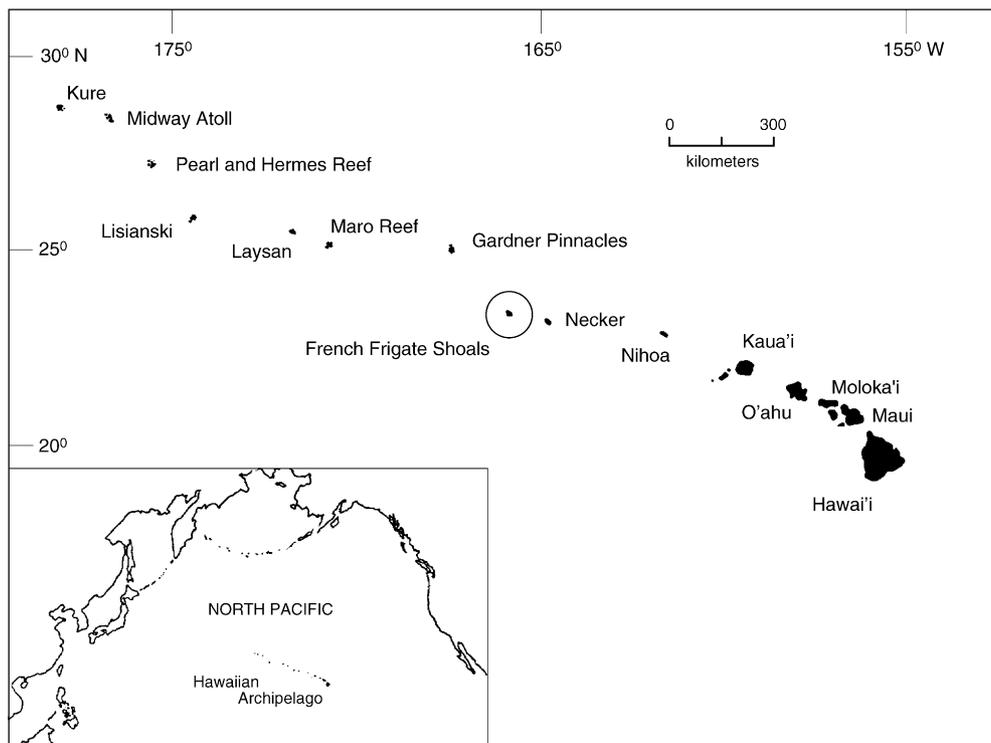


Fig. 1. Location of the Hawaiian Archipelago. The major rookery of Hawaiian green sea turtle genetic stock is at the French Frigate Shoals atoll located in the middle of the Archipelago.

Wildlife Service (Balazs, 1976; Wetherall et al., 1998). During the summer nesting season, females that emerged to nest each night were tagged and morphometric information recorded. Double-tagging with alloy tags was used prior to 1996, but double-tagging with passive integrated transponder tags has been used since to identify each individual nester uniquely. Some annual surveys were short as field personnel did not always remain on the island for the entire season due to the remoteness of French Frigate Shoals. Consequently, in some years the survey was an incomplete census of all females that emerged to nest. Therefore, a Horvitz–Thompson type estimator (see below) was used to estimate the total annual number of individual nesters since not all years provided a complete census of nesting but rather a survey with various sampling constraints.

### 2.2. Nesting abundance estimation

Briefly, the Horvitz–Thompson type estimator was derived as follows: let  $N_i = n_i/P_i$ , where  $N_i$  = estimated number of female nesters in the  $i$ th year,  $n_i$  = number of uniquely identified female nesters recorded for the  $i$ th year and  $P_i$  = probability of sighting a female that emerges ashore at the rookery and nests at least once during the  $i$ th year given various covariates such as arrival time, nesting frequency, nesting duration, and internesting interval. The sighting probability function ( $P_i$ ) was calibrated using entire nesting season census data derived from the nightly emergence probabilities for >1100 nesters recorded during a 5-year saturation tagging program conducted from 1988 to 1992. An empirical bootstrap approach was used to derive confidence intervals for each annual estimate (Wetherall et al., 1998), but the annual estimates are precise due to the substantial seasonal coverage during most seasons and so were not used here. More details are provided in Wetherall et al. (1998) and a summary of the number of tagged nesters, sighting probability, Horvitz–Thompson, and confidence interval estimates since 1973 are available from GHB on request.

### 2.3. Nesting trend estimation

The long-term trend in the Horvitz–Thompson estimated annual nester series was assessed using a generalised additive model and Bayesian inference to account for any nonlinear trend and the uncertainty in the trend given the substantial interannual fluctuations in observed nester abundance. This Bayesian GAM model was fitted using BayesX with random walk smoothness priors and a Bayesian smoothing spline (Fahrmeir and Lang, 2001). A generalised additive model is particularly useful as we allow the data to define the nonlinear trend using a smoothing spline

without having to prespecify the functional form (Hastie and Tibshirani, 1990). However, there is only one time series so Bayesian inference methods are also useful here to enable an estimate of our belief of the variability around the long-term trend (Bayesian credible or probability interval) that was estimated using the smoothing spline (Fahrmeir and Lang, 2001).

Combining both features (generalised additive or nonparametric regression within a Bayesian inference framework) into a Bayesian GAM model has several other advantages over more traditional statistical methods such as linear regression (Fahrmeir and Lang, 2001). Most notably these advantages are that Bayesian confidence or credible intervals are not based on normal asymptotic approximations but are based on the data itself and provide a natural means for handling sampling uncertainty or measurement error in the annual nester population abundance estimates. Moreover, a 95% credible interval for the long-term trend in nester abundance that was used here is in fact a direct measure of the belief or probability that the trend lies within this interval. More importantly, the Bayesian regression model used here can easily incorporate (1) new annual nester abundance data as additional annual nester surveys at the French Frigate Shoals rookery are completed as well as (2) random spatial variation due to multi-site sampling within the rookery when long-term data sets for other nesting islands in the regional rookery become available (although recall that East Island accounts for >50% of nesting at the French Frigate Shoals rookery). There is increasing use of Bayesian statistical methods in ecological studies as more researchers become familiar with the advantages of this approach (Ellison, 1996; Harmon and Challenor, 1997; Saether et al., 2000; Tufto et al., 2000, and see Howson and Urbach, 1991 for a simple exposition relating to Bayesian scientific logic in general).

We further investigated the long-term trend and apparent periodicity in the Horvitz–Thompson estimated annual nester abundance using a procedure known as Seasonal and Trend decomposition using Loess or STL (Cleveland et al., 1990), which decomposes a series using nonparametric smoothing into additive frequency components of variation—(1) trend, (2) cyclical or quasi-periodic, (3) seasonal (if applicable using for instance a monthly data series) and (4) the residual or remainder. STL was used by Chaloupka (2001) to investigate spatial synchrony in egg productivity at green turtle rookeries in the Southeast Asian region. The STL remainder could reflect environmental variability (Chaloupka, 2001) so we used cross-correlation function analysis with autoregressive model based prewhitening (Vandaele, 1983) to investigate any relationship with major environmental variables such as regional sea surface temperature (see Chaloupka, 2001 for more details of the STL and

cross-correlation procedures and application within an ecological context).

### 3. Results

#### 3.1. Nesting abundance

The Horvitz–Thompson estimates of annual nester abundance at the East Island rookery are shown in Fig. 2a along with the recorded number of annual nesters. The recorded counts of nesters shows a very similar trend since the probability of sighting a female nester was very high, exceeding 0.85 in most years (Wetherall et al., 1998). The estimated trend in East

Island nester abundance shows two main features—a dramatic increase in abundance over the 30-year study and substantial fluctuations in the number of annual nesters. The substantial annual fluctuations in nester abundance for this recovering stock is a characteristic of green turtle nesting populations due to a variable proportion of females preparing to breed each year in response to strong and spatially correlated ocean-climate variability (Limpus and Nicholls, 1994; Chaloupka, 2001). Other demographic processes of green turtles such as somatic growth are also related to the same regional scale environmental variability (Limpus and Chaloupka, 1997).

#### 3.2. Abundance trends

The estimated long-term trend in the Horvitz–Thompson nester time-series (Fig. 2a, dashed curve) derived using the Bayesian GAM model is shown in Fig. 2b, which suggests that nester abundance increased rapidly during the early 1980s, levelled off during the early 1990s before again increasing rapidly during the late 1990s, and up to the present. This trend is very similar to the underlying trend in the recovery of the much larger green turtle population that nests at Tortuguero, Costa Rica (Bjorndal et al., 1999). The step-wise increase of the long-term nester trend since the mid-1980s (Fig. 3b), is suggestive but not conclusive, of a density-dependent adjustment process affecting sea turtle abundance in the foraging grounds (Bjorndal et al., 2000).

The STL decomposition of the 30-year time series realization of estimated green turtle nesting at East Island since 1973 is shown in Fig. 3. This shows the same series in Fig. 2a (dashed curve) but on a log scale to account for the fluctuations in the series (Fig. 3a). The STL-derived long-term trend (Fig. 3b) is very similar to the trend estimated using the Bayesian GAM model but also includes a periodic component showing a distinct quasi 3–4 year periodicity in annual nester abundance (Fig. 3c). The bottom panel in the STL plot (Fig. 3d) shows the residuals remaining after the trend and quasi-periodicity components have been fitted to the original series shown in the top panel of Fig. 3a. The remainder accounts for a substantial part of the temporal variability in nester abundance that might reflect temporal variation in sea surface temperature in the Hawaiian Archipelago. Fig. 4 shows a strong cross-correlation between sea surface temperature in the southern Hawaiian Islands (Koko Head/AVHRR MCSST series) and the STL annual nester remainder—there is in fact a significant 1-year lead and a significant 1-year lag between the two prewhitened series (see Section 2) suggesting a significant relationship between annual nesting anomalies and annual sea surface temperature anomalies.

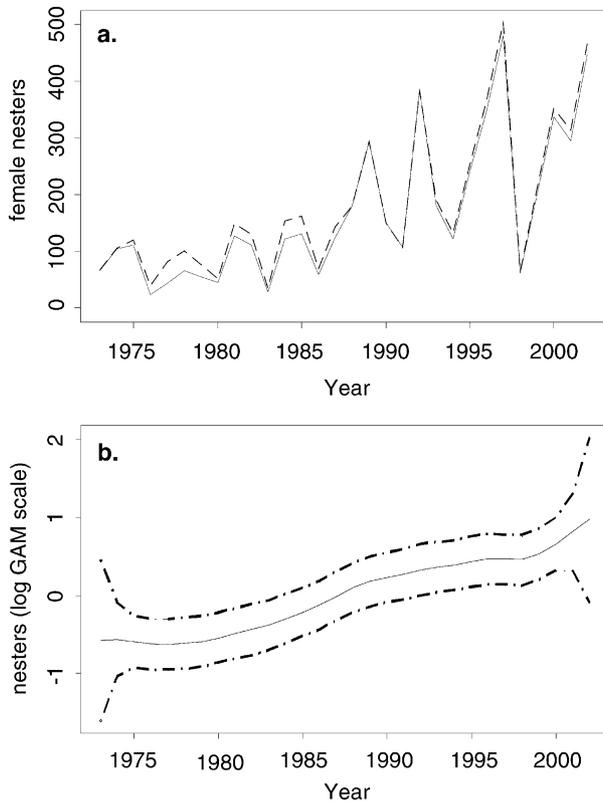


Fig. 2. Trends in nester abundance. Panel (a) shows a time series plot of number of female green turtles nesting each year at East Island (French Frigate Shoals, Northwestern Hawaiian Islands) over the 30-year period from 1973 to 2002. Solid curve shows the total number of nesters counted each year. Dashed curve shows the Horvitz–Thompson estimate of annual nester numbers conditioned on sighting probability (see Section 2). Panel (b) shows the estimated long-term trend in Horvitz–Thompson nester abundance derived using a Bayesian nonparametric regression model (Fahrmeir and Lang, 2001), which was fitted to the Horvitz–Thompson nester series shown in (a). Solid curve is the posterior mean annual nester abundance derived from the model with a Bayesian 95% credible region shown by dashed curves (posterior 2.5th–97.5th quantiles).

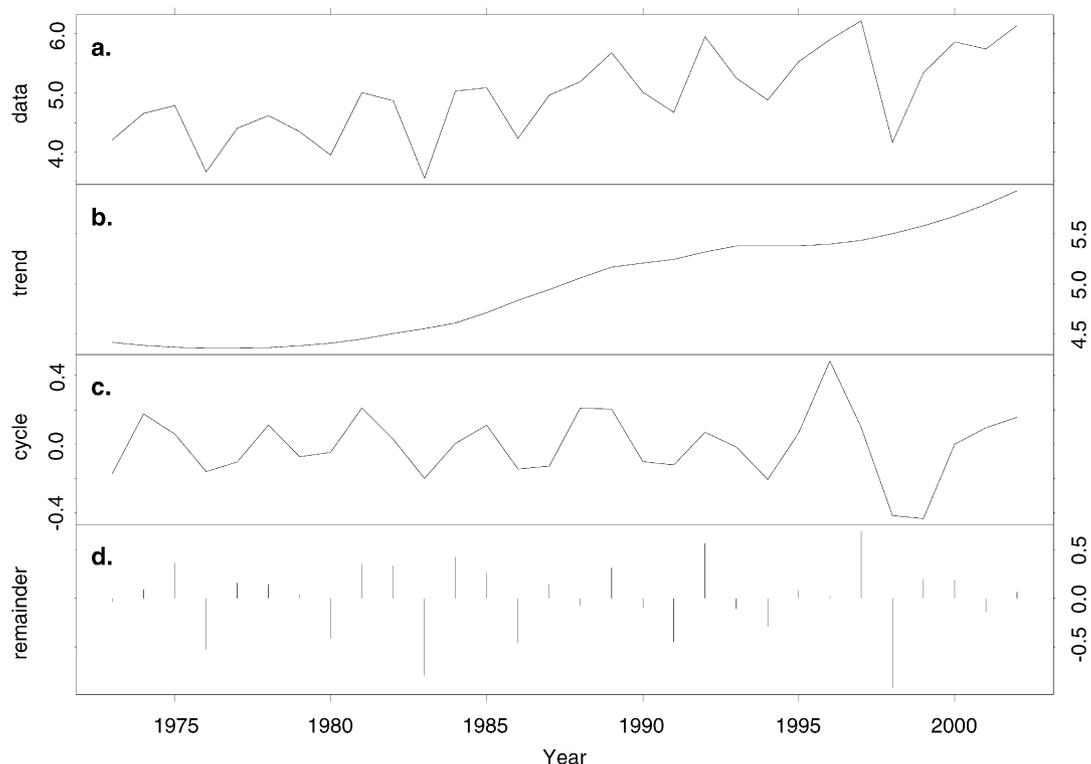


Fig. 3. STL decomposition plot of the estimated number of female green turtles nesting each year at East Island, French Frigate Shoals (1973–2002)—note the log scale. Panel (a) shows Horvitz–Thompson estimates of the annual nesting series (dashed curve in Fig. 2a). Panel (b) shows the fitted long-term trend or low-frequency variation in estimated annual number of nesters (bandwidth of trend filter = 17 years). Panel (c) shows the fitted 3–4 years quasi-periodic trend or high-frequency variation in estimated nesters (bandwidth of trend filter = 4 years). Panel (d) shows the residual component remaining after trend (b) and quasi-periodicity (c) components have been fitted to the series. The three components shown in (b–d) sum exactly to the series shown in (a). The panel scales are not the same so vertical bar at right of each panel indicates relative variation in scaling amongst the components and original data series.

#### 4. Discussion

The Hawaiian green turtle nester population has increased dramatically since protection began in 1978 under the US Endangered Species Act and could be approaching the foraging habitat carrying capacity (Fig. 2). Prior to 1974, the Hawaiian stock was subject to human exploitation such as turtle harvesting at foraging grounds from the mid-1800s, harvesting of nesters and eggs until the early 1960s, and nesting habitat destruction (Balazs, 1976; Niethammer et al., 1997). Green turtles in US waters have been protected under the US Endangered Species Act since 1978 (Witzell, 1994). Therefore, the Hawaiian stock has not been exposed to any major human hazards since. Moreover, the increase in nester abundance has occurred despite the relatively recent increase in fibropapillomatosis, a tumour-forming disease, which is prevalent in green turtles resident in some Hawaiian foraging grounds (Aguirre et al., 1998).

The increase in nester abundance is probably due to increased female nester survival since harvesting of turtles in the foraging grounds was prohibited from the mid-1970s. However, extensive nesting habitat destruction

occurred at the French Frigate Shoals rookery during the 1940s (Balazs, 1976; Niethammer et al., 1997). Moreover, the Hawaiian green turtle has about a 25–35 year generation period (Zug et al., 2002) so that it is not possible to attribute the nester increase to just protection of turtles under the US Endangered species Act since 1978. The increase is most likely a consequence of both the cessation of habitat damage at the rookery from the early 1950s onwards and also protection since the mid-1970s of turtles from harvesting in coastal waters around the main Hawaiian Islands. Moreover, the annual proportion of the recorded nesters comprising previously untagged turtles has declined to a relatively constant level around 32% as the nester population has become extensively tagged. This constant level of apparent new nester recruits suggests that the Hawaiian green turtle population might be approaching carrying capacity, which is indicative of a population well on the way to recovery.

In addition to the recovering nester abundance trend since the mid-1970s, there are also strong environmental forcing effects evident in the Hawaiian green turtle nesting time series. The quasi-periodicity in nester abundance (Fig. 3c) suggests that female green turtles

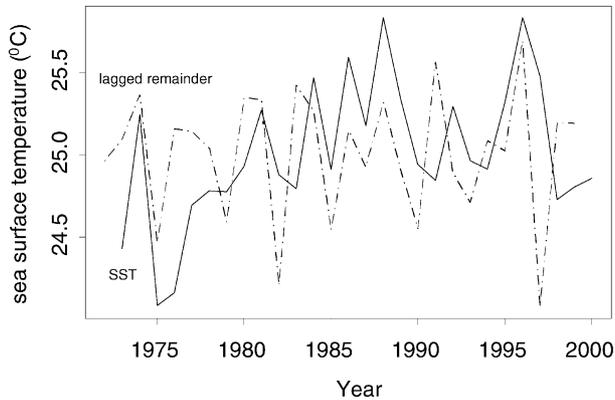


Fig. 4. Trend in mean annual sea surface temperature recorded near-shore off the southeastern coast of O'ahu, (Hawaii) and 1-year lagged STL remainder component shown in Fig. 3d. The STL remainder scale shown here has been shifted to reflect the same scale as the sea surface temperature by adding 25 (the sea surface temperature mean) to the STL remainder component (Fig. 3c) to aid visual comparison of the close association. The sea surface temperature series was a long-term data series constructed from a combination of measurements determined from near-shore surveys along the southeastern coast of O'ahu near Koko Head (Seckel and Yong, 1977) and several different satellite-based time series. The Koko Head surveys were taken approximately twice weekly from 1955 to 1992 (Seckel and Yong, 1977). From January 1992 to February 2001, the mean data were extracted from the weekly, 18 km, cloud-cleared AVHRR MCSST data set (Brown et al., 1985; McLain et al., 1985), in a 1 degree longitude by 1 degree latitude box centered on O'ahu. After February 2001, the time series is continued by extracting the same box from the 3-day composite images generated for the US National Center for Environmental Prediction. The constructed sea surface temperature series has been validated against the empirical data sets used to derive the long-term series with nominal error on each of these data sets  $<0.5$  °C (David Foley, NOAA Fisheries, pers. commun.) The composite O'ahu sea surface temperature series from 1955 onwards was provided by David Foley (National Marine Fisheries Service, Honolulu Laboratory, Hawaii).

resident in the numerous Hawaiian Archipelago foraging grounds migrate to nest at the French Frigate Shoals rookery every 3 or 4 years. The synchronizing agent for this breeding behaviour is not apparent but it might be an environmental forcing function such as a major ocean-climate anomaly, which has been shown to synchronize multi-stock nesting at Great Barrier Reef green turtle rookeries (Limpus and Nicholls, 1994) and at southeast Asian green turtle rookeries (Chaloupka, 2001). It is possible that the increased nester abundance since the late mid-1980s (Fig. 2a,b) could be due to females nesting more frequently (shorter return period between successive nesting seasons) rather than there being more nesters. This is a plausible alternative explanation but unlikely as the nesting frequency has remained constant around 3–4 years over the last 30 years with no indication of any shortening cyclicality in nesting frequency from the mid-1980s onwards as the nesting abundance increased (Fig. 3c).

In addition to the quasi-periodicity (Fig. 3c), there is also some suggestion of an aperiodic environmental effect on nesting abundance that is reflected in the sea

surface temperature anomalies (Fig. 4). Solow et al., (2002) have shown recently that sea surface temperature might be associated with annual fluctuations in the nesting of green turtles at the Tortuguero rookery on the Atlantic coast of Costa Rica. No mechanism was proposed as to why sea surface temperature would affect such nesting behaviour but a similar sea surface temperature association is shown here for the Hawaiian green turtle nesting population (Fig. 4). However, the fact that there were both 1-year lags and leads between the sea surface temperature and remainder component in Fig. 4 indicates that sea surface temperature is unlikely the causal agent but rather that anomalous nester abundance and anomalous sea surface temperature in the southern Hawaiian Archipelago are a coincidental consequence of some other long-term environmental forcing function that warrants further investigation.

It is now reasonable to conclude that the Hawaiian green turtle stock is well on the way to recovery after more than 25 years of protection of turtles and their nesting and foraging habitats in the Hawaiian Archipelago. What is also clear from our study is that a seriously depleted sea turtle stock such as the Hawaiian stock can recover following relatively simple and inexpensive policy interventions and in far less time than previously thought (National Research Council, 1990). It is widely held that a seriously depleted green turtle stock could take  $>100$  years to recover, assuming no density-dependent compensatory behaviour, when protected from exposure to anthropogenic hazards (National Research Council, 1990; Chaloupka, 2002). While speculative, the unexpected relatively rapid recovery of this stock might be due to density-dependent reproductive behaviour where the proportion of females breeding each year is higher at lower population abundance and lower at higher abundance (Chaloupka, 2003). The green turtle population that nests at Tortuguero (Costa Rica), which is the largest nesting population in the Atlantic, has also increased rapidly since the 1970s following protection of nesting turtles (Bjornald et al., 1999) while other large nesting populations with a history of habitat protection such as in the Great Barrier Reef are stable or increasing (Chaloupka and Limpus, 2001).

One of the goals of any recovery plan is to revise the risk status of endangered or threatened stocks when there is substantive evidence that an at-risk population or stock fulfils a set of recovery criteria (Foin et al., 1998). The recovery plan for the US Pacific populations of green turtles (National Marine Fisheries Service and US Fish and Wildlife Service, 1998) states that one of the recovery criteria for stocks in US Pacific waters should be a nesting population that is stable or increasing over a 25-year monitoring period. Our 30-year study finds that the Hawaiian green turtle stock now meets this specific recovery criterion and that the at-risk status

of this stock warrants reconsideration in accordance with the procedures specified in the US recovery plan (National Marine Fisheries Service and US Fish and Wildlife Service, 1998).

## Acknowledgements

We thank Shawn KK Murakawa and Jerry Wetherall (National Marine Fisheries Service, Honolulu Laboratory) and staff from the US Fish and Wildlife Service for extensive support with this long-term and ongoing ecological study of Hawaiian green turtles. We are especially grateful to David Foley (National Marine Fisheries Service, Honolulu Laboratory) for extensive advice and access to the sea surface temperature data series with the AVHRR MCSST data courtesy of the Physical Oceanography Distributed Active Archive Center at the California Institute of Technology and NASA Jet Propulsion Laboratory and the Koko Head data provided by Patrick Caldwell (National Marine Fisheries Service, Honolulu Laboratory). We thank Alberto Abreu, Bud Antonelis, Karen Bjorndal, Paul Dalzell, Judy Kendig, Mike Laurs, Colin Limpus, Jack Musick, Denise Parker, Jeff Polovina and Jerry Wetherall for helpful comments on the manuscript. This work was supported by NOAA Fisheries Contract No. AB133F02SE0905 to the second author.

## References

- Aguirre, A.A., Spraker, T.R., Balazs, G.H., Zimmerman, B., 1998. Spirorchidiasis and fibropapillomatosis in green turtles of the Hawaiian Islands. *Journal of Wildlife Diseases* 34, 91–98.
- Balazs, G.H., 1976. Green turtle migrations in the Hawaiian Archipelago. *Biological Conservation* 9, 125–140.
- Bjorndal, K.A., 1997. Foraging ecology and nutrition of sea turtles. In: Lutz, P.J., Musick, J.A. (Eds.), *The Biology of Sea Turtles*. CRC Marine Science Series. CRC Press Inc, Boca Raton, pp. 199–231.
- Bjorndal, K.A., Bolten, A.B., Chaloupka, M.Y., 2000. Green turtle somatic growth model: evidence for density-dependence. *Ecological Applications* 10, 269–282.
- Bjorndal, K.A., Wetherall, J.A., Bolten, A.B., Mortimer, J.A., 1999. Twenty-six years of green turtle nesting at Tortuguero, Costa Rica, an encouraging trend. *Conservation Biology* 13, 126–134.
- Bowen, B.W., Meylan, A.B., Ross, J.P., Limpus, C.J., Balazs, G.H., Avise, J.C., 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. *Evolution* 46, 865–881.
- Brown, O.B., Brown, J.W., Evans, R.H., 1985. Calibration of advanced very high resolution radiometer infrared observations. *Journal of Geophysical Research* 90, 11667–11677.
- Chaloupka, M., 2001. Historical trends, seasonality and spatial synchrony in green turtle egg production. *Biological Conservation* 101, 263–279.
- Chaloupka, M., 2002. Stochastic simulation modelling of southern Great Barrier Reef green turtle population dynamics. *Ecological Modelling* 148, 79–109.
- Chaloupka, M., 2003. Exploring the metapopulation dynamics of the southern Great Barrier Reef green sea turtle genetic stock using RAMAS/Metapop. In: Akçakaya, H., Burgman, M., Kindvall, O., Wood, C., Sjogren-Gulve, P., Hattfield, J., McCarthy, M. (Eds.), *Species Conservation and Management: Case Studies*. Oxford University Press, New York.
- Chaloupka, M., Limpus, C., 2001. Trends in the abundance of sea turtles resident in southern Great Barrier Reef waters. *Biological Conservation* 102, 235–249.
- Chaloupka, M., Limpus, C., 2002. Estimates of survival probabilities for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. *Marine Biology* 140, 267–277.
- Cleveland, R.B., Cleveland, W.S., McRae, J.E., Terpenning, P., 1990. STL: a seasonal-trend decomposition procedure based on Loess. *Journal of Official Statistics* 6, 3–73.
- Dizon, A.E., Balazs, G.H., 1982. Radio telemetry of Hawaiian green turtles at their breeding colony. *Marine Fisheries Review* 44, 13–20.
- Dutton, P.H., in press. Molecular ecology of the eastern Pacific green turtle. *Proceedings of the 22nd Annual Symposium on Sea Turtle Biology and Conservation*. NOAA Technical Memorandum, NMFS-SEFSC.
- Ellison, A.M., 1996. An introduction to Bayesian inference for ecological research and environmental decision making. *Ecological Applications* 6, 1036–1046.
- Foin, T.C., Riley, S.P.D., Pawley, A.L., Ayres, D.R., Carlsen, T.M., Hodum, P.J., Switzer, P.V., 1998. Improving recovery planning for threatened and endangered species. *Bioscience* 48, 177–184.
- Fahrmeir, L., Lang, S., 2001. Bayesian inference for generalised additive mixed models based on Markov random field priors. *Applied Statistics* 50, 201–220.
- Frazier, J., 1980. Exploitation of marine turtles in the Indian Ocean. *Human Ecology* 8, 329–370.
- Harmon, R., Challenor, P., 1997. A Markov chain Monte Carlo method for estimation and assimilation into models. *Ecological Modelling* 101, 41–59.
- Hastie, T.J., Tibshirani, R.J., 1990. *Generalized Additive Models*. Monographs on Statistics and Applied Probability 43. Chapman and Hall, London.
- Howson, C., Urbach, P., 1991. Bayesian reasoning in science. *Nature* 350, 371–374.
- Inchausti, P., Halley, J., 2001. Investigating long-term ecological variability using the population dynamics database. *Science* 293, 655–657.
- Leroux, R.A., Balazs, G.H., Dutton, P.H., in press. Genetic stock composition of foraging green turtles off the southern coast of Molokai, Hawaii. *Proceedings of the 22nd Annual Symposium on Sea Turtle Biology and Conservation*. NOAA Technical Memorandum, NMFS-SEFSC.
- Limpus, C.J., Chaloupka, M., 1997. Nonparametric regression modelling of green sea turtle growth rates (southern Great Barrier Reef). *Marine Ecology Progress Series* 149, 23–34.
- Limpus, C.J., Nicholls, N., 1994. Progress report on the study of the interaction of the El Niño—Southern Oscillation on annual *Chelonia mydas* at the southern Great Barrier Reef rookeries. In: James, R. (Ed.), *Proceedings of the Marine Turtle Conservation Workshop*. Australian National Parks and Wildlife Service, Canberra, pp. 73–78.
- McLain, E.P., Pichel, W.G., Walker, C.C., 1985. Comparative performance of AVHRR-based multichannel sea surface temperatures. *Journal of Geophysical Research* 90, 11587–11601.
- National Research Council, 1990. *Decline of Sea Turtles: Causes and Prevention*. National Academy Press, Washington DC.
- National Marine Fisheries Service and US Fish and Wildlife Service, 1998. *Recovery Plan for US Pacific Populations of the Green Turtle (Chelonia mydas)*. National Marine Fisheries Service, Silver Spring, Maryland, USA.
- Niethammer, K.R., Balazs, G.H., Hatfield, J.S., Nakai, G.L., Megyesi, J.L., 1997. Reproductive biology of the green turtle

- (*Chelonia mydas*) at Tern Island, French Frigate Shoals, Hawaii. *Pacific Science* 51, 36–47.
- Saether, B.E., Tufto, J., Engen, S., Jerstad, K., Rostad, O.W., Skatan, J.E., 2000. Population dynamical consequences of climate change for a small temperate songbird. *Science* 287, 854–856.
- Seckel, G.R., Yong, M.Y.Y., 1977. Koko Head, O'ahu, sea surface temperature and salinity, 1956–1973, and Christmas Island sea surface temperature, 1954–1973. *Fishery Bulletin* 75, 767–787.
- Solow, A.R., Bjorndal, K.A., Bolten, A.B., 2002. Annual variation in nesting numbers of marine turtles: the effect of sea surface temperature on re-migration intervals. *Ecology Letters* 5, 742–746.
- Tufto, J., Saether, B.E., Engen, S., Arcese, P., Jerstad, K., Rostad, O.W., Smith, J.N.M., 2000. Bayesian meta-analysis of demographic parameters in three small temperate passerines. *Oikos* 88, 273–281.
- Vandaele, W., 1983. *Applied Time Series and Box-Jenkins Models*. Academic Press, Orlando.
- Wetherall, J.A., Balazs, G.H., Yong, M.Y.Y., 1998. Statistical methods for green turtle nesting surveys in the Hawaiian Islands. In: Epperly, S.P., Braun, J. (Eds.), *Proceedings of the 17th Annual Symposium on Sea Turtle Biology and Conservation*. NOAA Technical Memorandum, NMFS-SEFSC-415, pp. 278–280.
- Witzell, W.N., 1994. The origin, evolution and demise of the US sea turtle fisheries. *Marine Fisheries Review* 56, 8–23.
- Zug, G.R., Balazs, G.H., Wetherall, J.A., Parker, D.M., Murakawa, S.K.K., 2002. Age and growth in Hawaiian green seaturtles (*Chelonia mydas*): an analysis based on skeletochronology. *Fishery Bulletin* 100, 117–127.