RECOVERY TREND OVER 32 YEARS AT THE HAWAIIAN GREEN TURTLE ROOKERY OF FRENCH FRIGATE SHOALS

BY

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ABSTRACT

The green turtle is one of the long-lived species that comprise the charismatic marine megafauna. The species has a long history of human exploitation with some stocks extinct. Here we report on a 32-year study of the nesting abundance of the green turtles endemic to the Hawaiian Archipelago. We show that there has been a substantial long-term increase in abundance since the 1970s of this once seriously depleted stock following cessation of harvesting. 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 synchronizes 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.

INTRODUCTION

The green turtle (*Chelonia mydas*) has a circumtropical distribution with distinct regional population structures (Bowen et al., 1992) and is the most abundant large marine herbivore (Bjorndal, 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 trends of green turtle stocks (Chaloupka and Limpus, 2001). Reliable long-term estimates of population abundance trends are needed to support recovery planning (Foin et al., 1998), and to 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, 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 (Chaloupka and Limpus, 2001, 2002; Chaloupka et al., 2004; Chaloupka and Limpus, 2005). 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, so are rarely undertaken (Bjorndal et al., 2000;

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Chaloupka et al., 2004). Nearly all assessments of sea-turtle population abundance have been based on trawl-based catch-per-unit-effort estimation, aerial survey-based density and estimation or, more commonly, monitoring the number of females that come ashore each year to nest at stock-specific rookeries (see review in Chaloupka and Limpus, 2001).

Monitoring the nesting is by far the easiest and least expensive means to assess green turtle population abundance, but short-term surveys (< 10 yrs) are inadequate for several reasons (Chaloupka and Limpus, 2001). Most notably, green turtles are long-lived (Zug et al., 2002; Chaloupka et al., 2004; Balazs and Chaloupka 2004b), and females skip several nesting seasons due to nutritional constraints (Bjorndal, 1997). Hence, long-term nesting beach surveys are essential if this form of assessment of green turtle population abundance and trends is to be adopted. The Hawaiian green turtle stock is one of the few sea turtle stocks that has been continuously monitored for several decades and so is suitable for long-term 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, 2002) 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 at various foraging grounds throughout the Archipelago are from the same genetic stock (Leroux et al., 2003), although rarely turtles from the east Pacific stock that nests along the Pacific coast of Mexico are recorded in Hawaiian waters (Balazs, 1976; Dutton, 2002). We report the results of a 32-year study of the nesting abundance of the Hawaiian green turtle stock, thereby extending by two years the trend analysis presented in Balazs and Chaloupka, 2004a. We conclude 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.

METHODS

Study and Data Description

The principal rookery for the Hawaiian green turtle stock is located on the small 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 French Frigate Shoals 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 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.
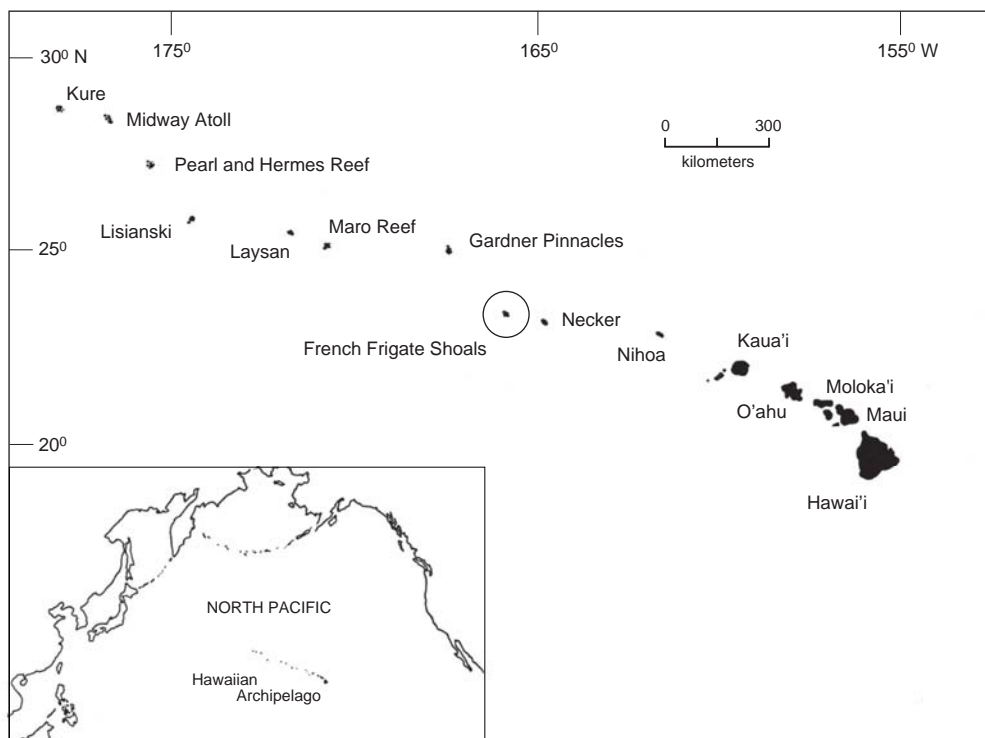
Figure 1. The Hawaiian Archipelago. The major rookery of the Hawaiian green turtle stock is at French Frigate Shoals in the Northwestern Hawaiian Islands located at the mid-point of the Archipelago.

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 the Hawaii Institute of Marine Biology (University of Hawaii) and, from 1981 onward, as a cooperative project between National Oceanic and Atmospheric Administration (NOAA)/ National Marine Fisheries Service (NMFS) and U.S. Fish and Wildlife Service (USFWS) (Balazs, 1976, 1980; Wetherall et al., 1998). During the summer nesting season, females that emerged to nest each night were tagged, and morphometric information was 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 were not always able to remain on the island for the entire nesting 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.

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 female nesters in the ith year, n_i = number of uniquely identified female nesters recorded for the ith year and p_i = probability of sighting a female that emerges ashore at the rookery and nests at least once during the ith 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 season-long 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 estimations, and confidence interval estimates since 1973 are available from the authors upon request.

Nesting Trend Estimation

We estimated the underlying time-specific trend in estimated nester abundance using a generalized smoothing spline regression approach implemented in the R package gss (Gu, 2002). This approach uses the data to determine the underlying linear or nonlinear trend without assuming any specific functional form (Gu, 2002). If the underlying trend was linear or near-linear then we estimated the linear nesting population growth rate using a parametric moving average regression, which accounts for autocorrelated error and temporal fluctuations in observed nester abundance (Chaloupka and Limpus, 2001).

We further investigated the long-term trend and apparent periodicity in the Horvitz-Thompson estimate of 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).

RESULTS

Nesting Abundance

The Horvitz-Thompson estimates of annual nesting turtle abundance at the East Island rookery are shown in Figure 2a. The estimated trend in East Island nester abundance shows two main features — a dramatic increase in abundance over the 32-year period and substantial fluctuations in the number of annual nesters. The substantial annual
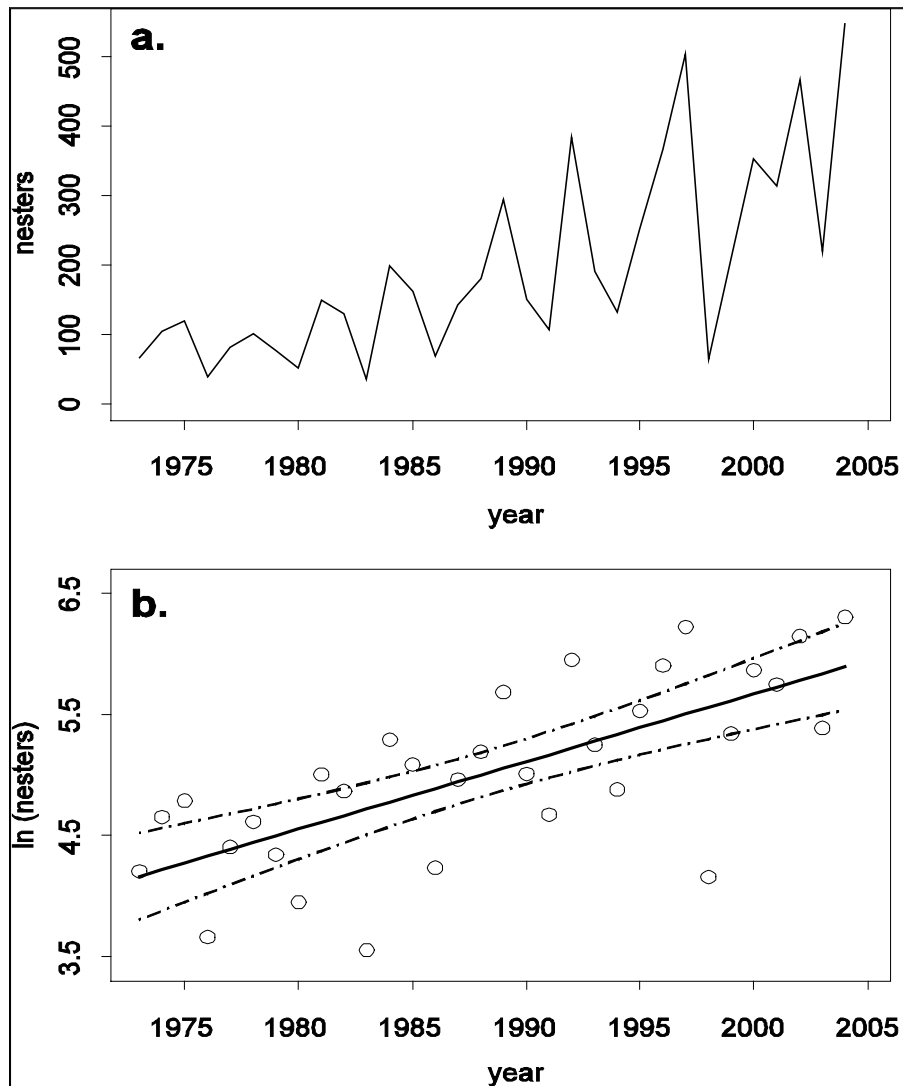
Figure 2. Trends in nester abundance. Panel (a) shows a time series plot of the Horvitz-Thompson estimate of the number of female green turtles nesting each year at the East Island rookery (French Frigate Shoals, Northwestern Hawaiian Islands) over the 32-year period from 1973 to 2004. Panel (b) shows the estimated long-term trend in nester abundance derived using a Bayesian smoothing spline regression model (Gu, 2002), 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.

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 (Chaloupka et al., 2004).

Abundance Trends

      The estimated underlying long-term trend in the annual nester series is shown in Fig. 2b where it was apparent that this rookery has experienced near-linear increasing annual nester abundance over the last 30 years or more. The underlying linear trend was estimated at ca. 5.7% pa (95% confidence interval: 5.3-6.1), which is consistent with low population growth rates expected for long-lived and late maturing species such as sea turtles (Chaloupka and Limpus, 2001) and one of the reasons why it takes decades for a green turtle population to recover following any major perturbation such as overharvesting or nesting habitat loss (Chaloupka, 2004).

      Figure 3 shows the STL decomposition for a 30-year period of the time series realization of estimated green turtle nesting at East Island from 1973-2002. This shows the same series as in Figure 2a 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 smoothing spline regression model but there is also 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) is the residuals remaining after the trend and quasi-periodicity components have been fitted to the original series shown in the top panel (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. Figure 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 Methods) suggesting a significant relationship between annual nesting anomalies and annual sea surface temperature anomalies.

DISCUSSION

      The Hawaiian green turtle nesting population has increased dramatically since protection began in 1978 under the U.S. Endangered Species Act (ESA) and could be approaching the foraging habitat carrying capacity at some locations (Balazs and Chaloupka, 2004b). 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 United States waters have been protected under the ESA since 1978 (Witzell, 1994). Therefore, the Hawaiian stock has not been exposed to any major human hazards since that time. Moreover, the increase in the abundance of nesting turtles has occurred despite the relatively recent increase in fibropapillomatosis, a tumor-forming disease, which is prevalent in green turtles resident in some Hawaiian foraging grounds (Aguirre et al., 1998; Chaloupka and Balazs, 2005).

      The increase in nesting abundance (ca. 5.7% pa) 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).
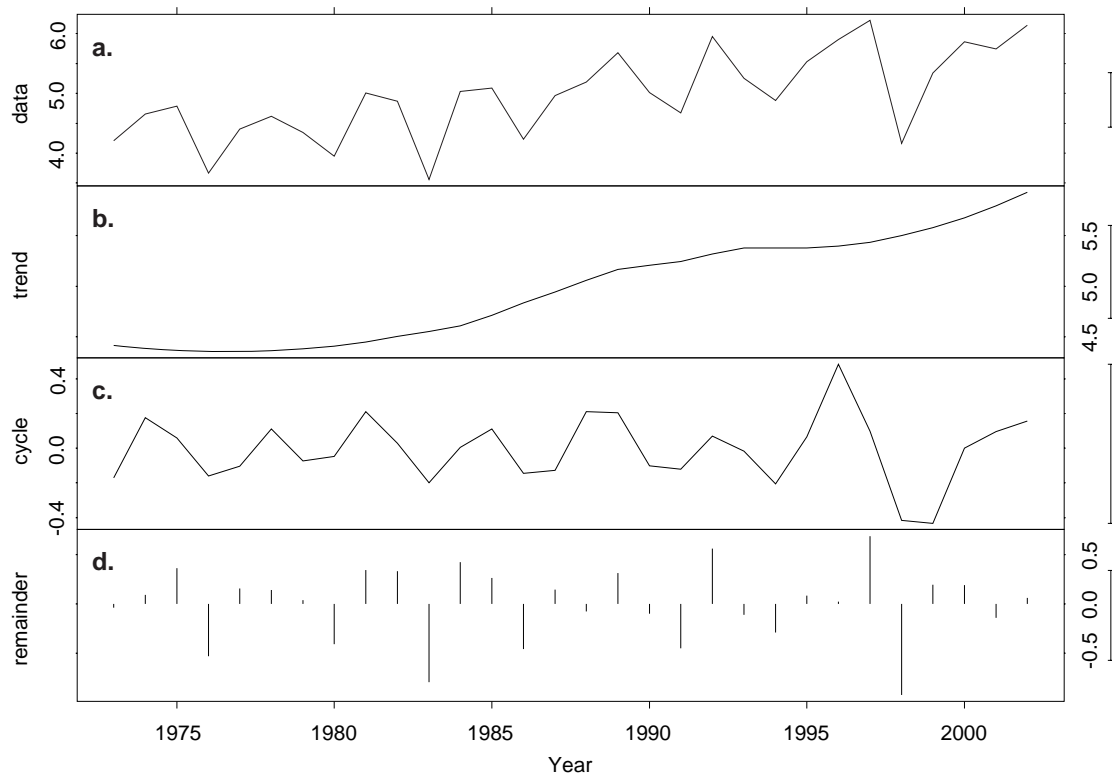
Figure 3. STL decomposition plot of the estimated number of female green turtles nesting each year at East Island, French Frigate Shoals over a 30-year period (1973-2002) — note the log scale. Panel (a), Horvitz-Thompson estimates of the annual nesting series. Panel (b), the fitted long-term trend or low-frequency variation in estimated annual number of nesters (bandwidth of trend filter = 17 yr). Panel (c), the fitted 3-4 yr quasi-periodic trend or high-frequency variation in estimated nesters (bandwidth of trend filter = 4 yr). Panel (d), 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 among the components and original data series.

Moreover, the Hawaiian green turtle has an approximate 25-35-year generation period (Zug et al., 2002; Balazs and Chaloupka, 2004b) so that it is not possible to attribute the nester increase to just protection of turtles under the ESA since 1978. The increase is most likely a consequence of both the cessation of habitat damage at the French Frigate Shoals rookery from the early 1950s onward, 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.
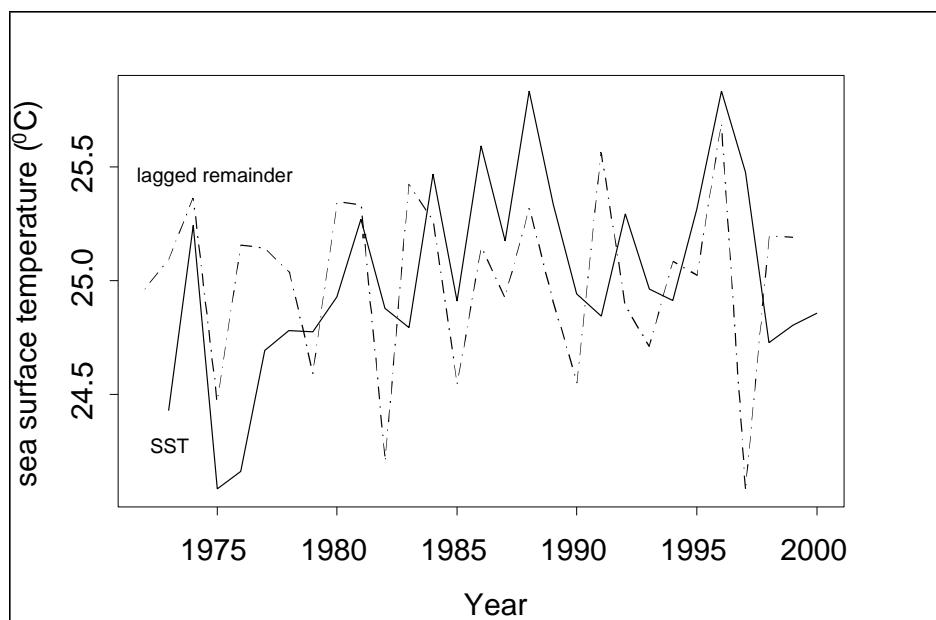
Figure 4. Trend in mean annual sea surface temperature recorded near-shore off the southeastern coast of Oahu, (Hawaii) and 1-year lagged STL remainder component shown in Figure 3d. The STL remainder scale shown here has been shifted to reflect the same scale as the sea surface temperature by adding 25 (the sea surface temperature mean) to the STL remainder component (Fig. 3c). 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 Oahu near Koko Head (Seckel and Yong, 1977) and several different satellite-based time series.

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 resident in the numerous foraging grounds of the Hawaiian Archipelago 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 multistock 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 mid-1980s (Figs. 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 32 years with no indication of any shortening (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 Figure 4 indicates that sea-surface temperature is unlikely the causal agent but rather that anomalous nester abundance and anomalous sea surface temperature in the Archipelago's main (southern) Hawaiian Islands 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 29 years of protection. What is also clear from our study is that a seriously depleted sea turtle population, 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 unexpectedly rapid recovery of the Hawaiian 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, 2004). The green turtle population that nests at Tortuguero (Costa Rica), which is the largest nesting population in the Atlantic, also has increased rapidly since the 1970s following protection of nesting turtles (Bjorndal 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 U.S. Pacific populations of green turtles (NMFS and USFWS, 1998) states that one of the recovery criteria for stocks in U.S. Pacific waters should be a nesting population that is stable or increasing over a 25-year monitoring period. Our 32-year study indicates 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 U.S. recovery plan (NMFS and USFWS, 1998).
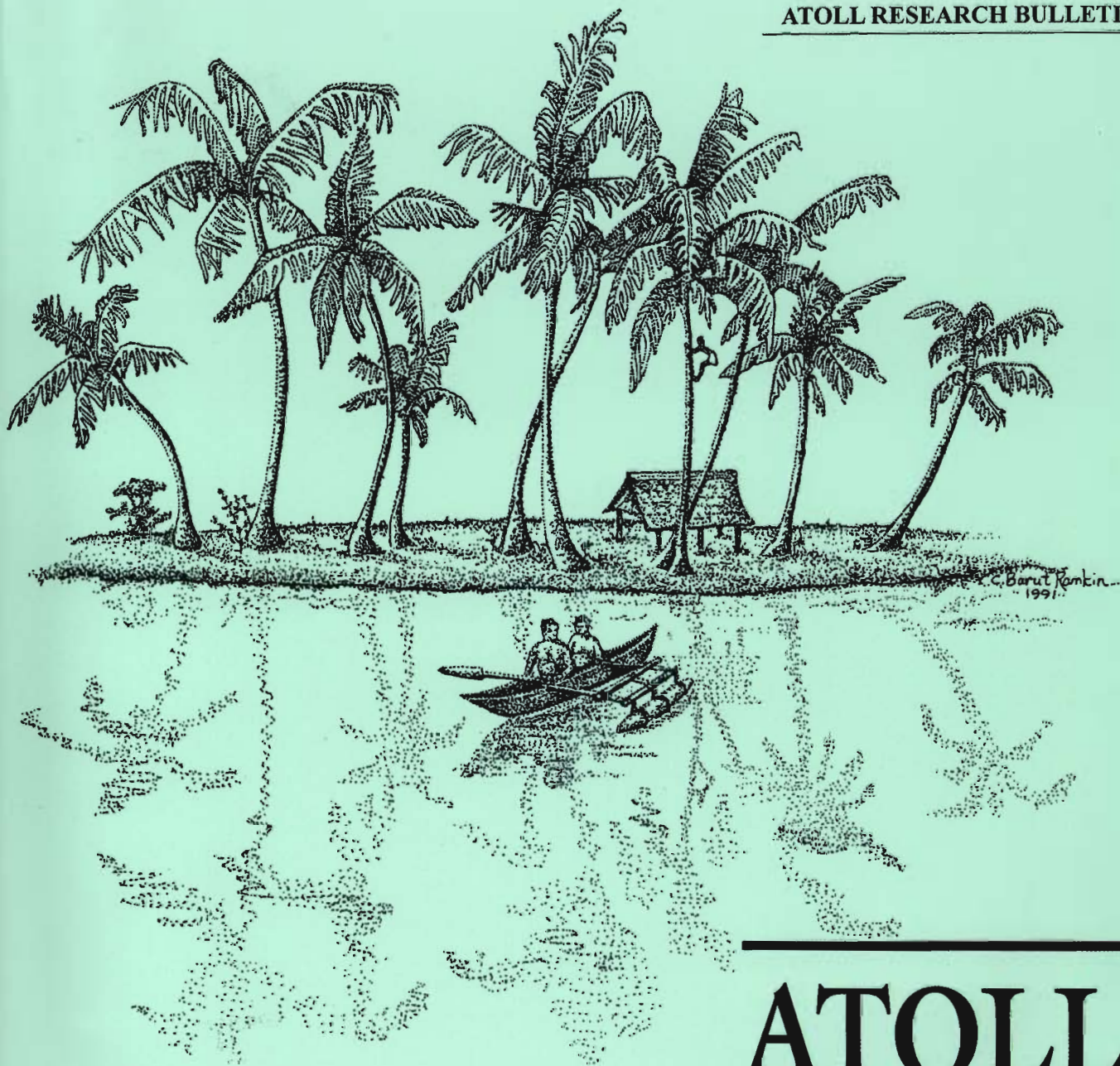
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