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PAPER



# Encouraging outlook for recovery of a once severely exploited marine megaherbivore

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## ABSTRACT

**Aim** To critically review the status of the green sea turtle (*Chelonia mydas*) using the best available scientific studies as there is a prevailing view that this species is globally endangered and its marine ecosystem functions compromised.

**Location** Ogasawara (Japan), Hawaii (USA), Great Barrier Reef (Australia), Florida (USA), Tortuguero (Costa Rica).

**Methods** We compiled seasonal nesting activity data from all reliable continuous long-term studies (> 25 years), which comprised data series for six of the world's major green turtle rookeries. We estimated the underlying time-specific trend in these six rookery-specific nester or nest abundance series using a generalized smoothing spline regression approach.

**Results** Estimated rates of nesting population increase ranged from c. 4–14% per annum over the past two to three decades. These rates varied considerably among the rookeries, reflecting the level of historical exploitation. Similar increases in nesting population were also evident for many other green turtle stocks that have been monitored for shorter durations than the long-term studies presented here.

**Main conclusions** We show that six of the major green turtle nesting populations in the world have been increasing over the past two to three decades following protection from human hazards such as exploitation of eggs and turtles. This population recovery or rebound capacity is encouraging and suggests that the green turtle is not on the brink of global extinction even though some stocks have been seriously depleted and are still below historical abundance levels. This demonstrates that relatively simple conservation strategies can have a profound effect on the recovery of once-depleted green turtle stocks and presumably the restoration of their ecological function as major marine consumers.

## Keywords

*Chelonia mydas*, conservation, green sea turtle, marine, stock recovery.

## INTRODUCTION

Human exploitation and habitat destruction have caused major declines in the abundance of marine megafauna such as leatherback sea turtles (Spotila *et al.*, 1996), Steller sea lions (Trites & Donnelly, 2003), great whales (Roman & Palumbi, 2003), pelagic sharks (Baum & Myers, 2004) and dugong (Marsh *et al.*, 2005). There is increasing concern that the widespread decline of the marine megafauna will have unexpected and grave consequences for fisheries productivity (Pauly *et al.*, 1998), the stability

of marine food web dynamics (Estes *et al.*, 1998) and the long-term viability of the world's coastal ecosystems (Jackson *et al.*, 2001). In particular, Pandolfi *et al.* (2003) found that the long-term degradation of coral reef ecosystems was always preceded by a significant loss of the large herbivores and predators that comprise the marine megafauna. However, it is believed that these degraded marine ecosystems might retain the capacity for recovery as most megafauna populations in these ecosystems still exist, although at vastly reduced levels of abundance (Jackson *et al.*, 2001; Pandolfi *et al.*, 2003).

The green turtle (*Chelonia mydas*) is one of the large long-lived vertebrate species that comprise the charismatic marine megafauna and has been subject to a long history of human exploitation for eggs, turtle meat and shell (Parsons, 1962; Horikoshi *et al.*, 1994; Frazier, 2003; Chaloupka & Balazs, 2007). Consequently, some stocks have been seriously depleted (Fig. 1a) or extirpated (Parsons, 1962). Declining stocks are of great concern because green turtle abundance is widely considered to be a key indicator of the health and resilience of seagrass and coral reef ecosystems (Jackson *et al.*, 2001; Pandolfi *et al.*, 2003).

However, green turtle conservation is severely hindered by the lack of reliable information on stock status and trends (Marine Turtle Specialist Group, 2004; Chaloupka & Balazs, 2007). Very little is known about the abundance of green turtles in the post-hatchling oceanic phase prior to recruitment as juveniles to a range of neritic or coastal and coral reef foraging habitats (Bolten, 2003). In the post-recruitment or neritic phase, green turtles from different genetic stocks can reside in the same foraging areas that are scattered over vast areas (Musick & Limpus, 1997), which also makes it extremely difficult to monitor the status and trend of any one particular stock (Chaloupka & Limpus, 2001; Bjørndal *et al.*, 2005). Fortunately, adult green turtles from a particular genetic stock that reside in various widely scattered foraging areas migrate every few years to the same stock-specific rookery that comprises one or more nesting beaches (Musick & Limpus, 1997). It is at stock-specific rookeries that it is logistically feasible to monitor the long-term abundance of green turtle nesting populations and to determine the status of various green turtle stocks.

We report here on the abundance trends for all green turtle nesting populations that have been the subject of extensive long-term (> 25 years) studies so that a robust assessment of the current status of these green turtle stocks can be made using the best available scientific information. Such findings might also be important for determining the recovery or rebound capacity of depleted green turtle stocks (Chaloupka & Balazs, 2007) and for developing a better understanding of the long-term effects of this megaherbivore on marine ecosystem functions (Bjørndal *et al.*, 2000; Moran & Bjørndal, 2005, 2007).

## METHODS

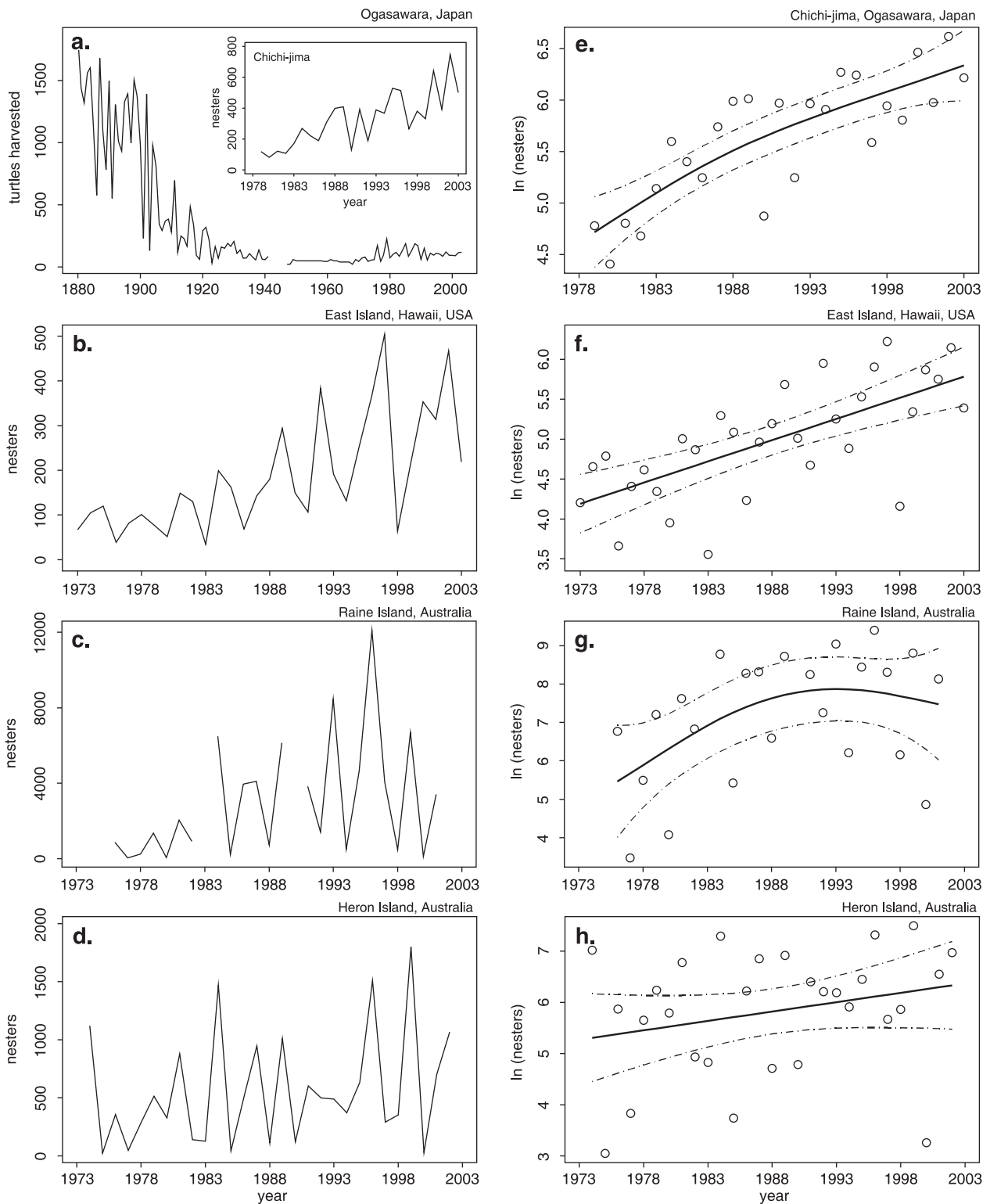
We have compiled nester abundance time series for six green turtle rookeries – four from the Pacific Ocean and two from the Atlantic Ocean. These rookeries represent six of the world's major green turtle genetic stocks (Bowen *et al.*, 1992) and are based on continuous long-term (> 25 years) research and monitoring programs. There are few long-term nesting data series for Indian Ocean green turtle rookeries but progress to derive such nesting data series is well under way (Lauret-Stepler *et al.*, 2007). The Chichi-jima rookery is in the Ogasawara Islands (southern Japan), has the longest continuous records of harvest and is one of the major rookeries of the Japanese green turtle stock (Horikoshi *et al.*, 1994; Yamaguchi *et al.*, 2005). The East Island rookery in the French Frigate Shoals, Northwestern Hawaiian Islands, is endemic to the Hawaiian Archipelago and is

the most important green turtle rookery in the Central Pacific (Balazs & Chaloupka, 2004). The Raine Island rookery in the northern Great Barrier Reef region (Australia) is the largest nesting concentration of green turtles in the world and the major rookery for the northern Great Barrier Reef genetic stock (Limpus *et al.*, 2003). The Heron Island rookery in the southern Great Barrier Reef region (Australia) is one of the most important rookeries for the southern Great Barrier Reef genetic stock and fluctuates in synchrony with the Raine Island rookery (Limpus *et al.*, 2003) even though both rookeries comprise distinct genetic stocks (Dethmers *et al.*, 2006). The Archie Carr National Wildlife Refuge rookery on the central east coast of Florida (USA) is one of the more important concentrations of nesting green turtles in the Atlantic and accounts for at least 50% of all green turtles nesting in Florida (Ehrhart & Bagley, 1999; Weishampel *et al.*, 2003). The Tortuguero rookery on the Caribbean coast of Costa Rica is the largest green turtle rookery in the Atlantic and has the second largest concentration of nesting green turtles in the world (Troëng & Rankin, 2005). These six nesting populations comprise nearly 20% of the green turtle nesting populations for which at least some (mainly anecdotal) nesting data have been recorded (Marine Turtle Specialist Group, 2004).

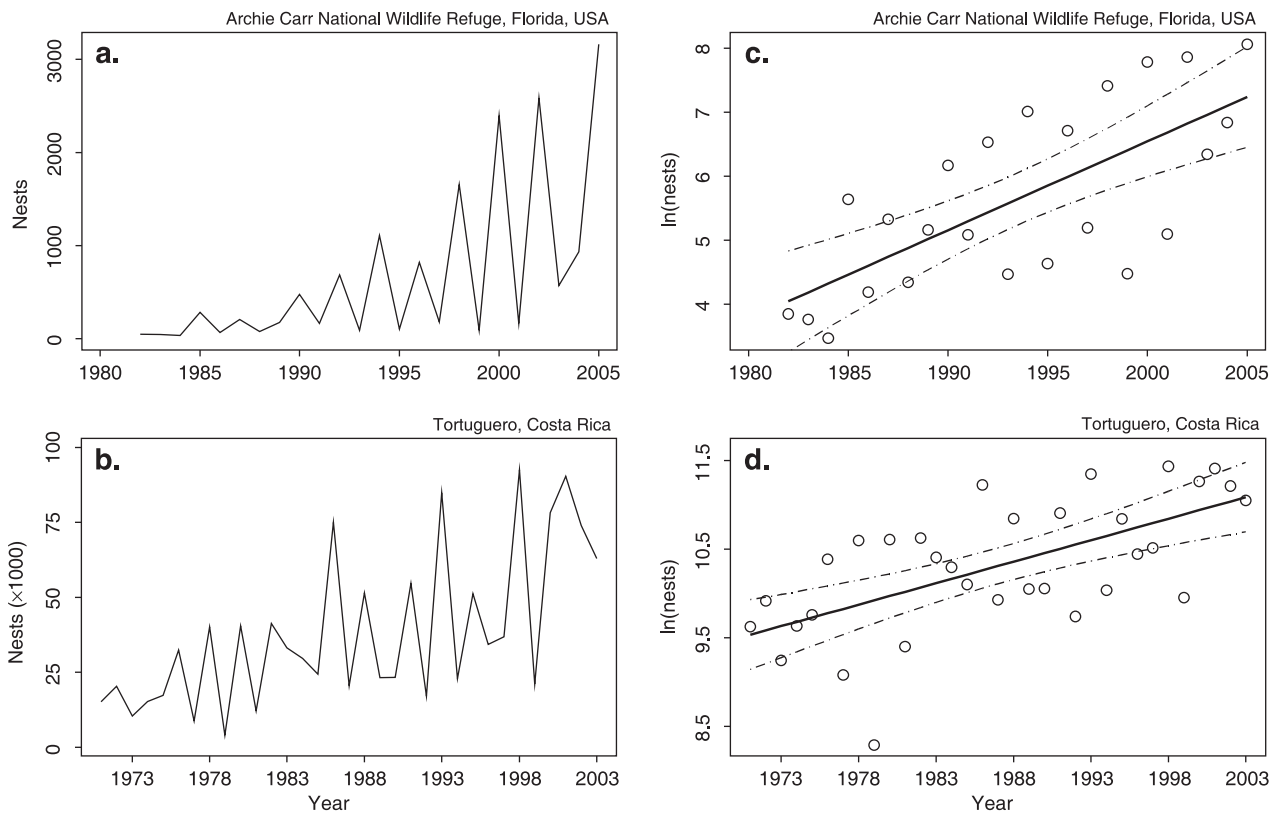
We estimated the underlying time-specific trend in these rookery-specific nester or nesting abundance series using a generalized smoothing spline regression approach implemented in the *gss* library for R (Gu, 2002). This nonparametric approach uses the data to determine the underlying linear or nonlinear trend without assuming any specific functional form. If the underlying trends indicated by the smoothing splines were linear, then we matched these linear trends using a parametric time-series regression (either first-order autoregressive or first-order moving average) that accounts for autocorrelated error and the temporal fluctuations in observed nester or nest abundance (Chaloupka & Limpus, 2001). This latter parametric approach enables robust estimation of the linear nesting population growth rate (Chaloupka & Limpus, 2001). The response variable (nesters or nests) was in natural log form so that the parameter estimate for the independent variable, which was nesting season or 'year', was then interpretable as a constant annual growth rate of the nesting population.

## RESULTS

The long-term time-specific data compiled for the four Pacific Ocean green turtle nesting populations or rookeries are shown in Fig. 1(a–d) with all populations reflecting the significant inter-annual fluctuations considered characteristic of green turtles (Bjørndal *et al.*, 1999; Chaloupka, 2001). The estimated underlying trend for each of these rookeries is shown in Fig. 1(e–h) to better highlight any long-term linear trend that is not necessarily apparent in the nesting data shown in Fig. 1(a–d). It is apparent that all Pacific rookeries except for Raine Island experienced approximately linearly increasing nester abundance over the last 25 years or more. The Raine Island nesting population also increased, but at a decreasing rate of increase in more recent



**Figure 1** Time-series plots of the annual nester abundance for four Pacific Ocean green turtle rookeries. Panel (a) shows harvest of green turtles since 1880 from the Ogasawara Islands in southern Japan while inset shows nester abundance since 1979 at the Ogasawara rookery on Chichi-jima. Panel (b) shows nester abundance since 1973 at East Island, Northwestern Hawaiian Islands, USA. Panel (c) shows nester abundance since 1976 at Raine Island, northern Great Barrier Reef, Australia. Panel (d) shows nester abundance since 1974 at Heron Island, southern Great Barrier Reef, Australia. Panels (e–h) show the estimated underlying trend in nester or nest abundance corresponding to each rookery shown in (a–d). Open circles, recorded nester or nest abundance; solid curve, smoothing spline regression fit to time-specific nester abundance trend; dashed curves, 95% Bayesian confidence interval for the estimated underlying smoothing spline trend.



**Figure 2** Time-series plots of the annual nest abundance for two Atlantic Ocean green turtle rookeries. Panel (a) shows nest abundance recorded since 1982 at the Archie Carr National Wildlife Refuge, FL, USA. Panel (b) shows nest abundance recorded since 1971 at Tortuguero, Costa Rica. Panels (c) and (d) show the estimated underlying trend in nest abundance corresponding to each rookery shown in (a) and (b). Open circles, recorded nest abundance; solid curve, smoothing spline regression fit; dashed curves, 95% Bayesian confidence interval.

**Table 1** Estimated annual population growth rates for the three Pacific rookeries (Fig. 1) and the two Atlantic rookeries (Fig. 2) displaying approximately linear increase over the past 25 years or more. ACNWR, Archie Carr National Wildlife Refuge; AR(1), first-order autoregression linear regression model; MA(1), first-order moving average linear regression model.

Rookery	Annual growth rate (%)	95% confidence interval	Model
ACNWR (Florida)	13.9	11.8–16.1	AR(1)
Chichi-jima (Japan)	6.8	4.8–8.8	MA(1)
East Island (Hawaii)	5.7	5.3–6.1	MA(1)
Tortuguero (Costa Rica)	4.9	4.1–5.9	MA(1)
Heron Island (Australia)	3.8	3.3–4.3	MA(1)

years (Fig. 1g). The long-term time-specific data compiled for the two Atlantic Ocean green turtle nesting populations are shown in Fig. 2(a,b) with the estimated underlying trend for each rookery shown in Fig. 2(c,d). It is apparent that the Atlantic rookeries experienced approximately linearly increasing nest abundance over the last 25 years or more.

The estimated linear nester population growth rates varied considerably among the rookeries (Table 1), perhaps reflecting the level of historical exploitation experienced by each rookery and the subsequent recovery rate assuming density-dependent demographic behaviour apparent for some green turtle populations (Bjorndal *et al.*, 2000; Chaloupka & Balazs, 2007). A linear trend estimate was not applicable for the Raine Island data as the underlying functional form was intrinsically nonlinear, although there was significant uncertainty in the estimation of the underlying trend (Fig. 1g). The estimated growth rate for the Heron Island rookery in Australia was significantly lower than the four other rookeries, probably because it had not been subject to as extensive human exploitation (Limpus *et al.*, 1994). The Archie Carr National Wildlife Refuge rookery in east central Florida increased at *c.* 14% per annum from 1982 on, which was significantly higher than at other rookeries (Table 1) and perhaps reflected a strong density-dependent rebound effect given just how seriously depleted the Florida green turtle stock was.

## DISCUSSION

The status and trend of sea turtle stocks is best based on ageclass- and sex-specific abundance estimates of sea turtles in the foraging habitat but such capture–mark–recapture estimates are only

available for two small green turtle populations (Chaloupka & Limpus, 2001; Bjørndal *et al.*, 2005). Most measures of sea turtle abundance are based on monitoring of the number of nesters observed or nests laid each season on a beach (Chaloupka & Limpus, 2001). Long-term data series with a duration of at least 20–25 years are needed to provide a reliable indication of trends in sea turtle nesting abundance (Bjørndal *et al.*, 2005), primarily because of the large annual variation in nesting numbers that has been attributed to environmental variability (Chaloupka 2001; Limpus *et al.*, 2003).

Using such long-term data series, we found that six major populations of green turtles have shown significant increases in nester or nest abundance over the past 25 years or more. It is important to note that the trends in nesting activity shown here for the six populations (Figs 1 & 2) reflect the nesting female proportion of each stock, which only accounts for a very small fraction of a green turtle stock (Chaloupka, 2002). Consequently, given the current estimated nesting activity (Figs 1 & 2), these six stocks probably comprise tens of millions of green turtles.

Nonetheless, the underlying trend for the largest rookery in the world at Raine Island was nonlinear, showing an increasing trend from the mid-1970s that levelled off by the mid-1990s (Fig. 1h). The lack of increase in nesters at this rookery in recent years could be due to increasing sea surface temperature that affects breeding behaviour of this stock (Chaloupka, 2001; Limpus *et al.*, 2003), decreasing reproductive output as the stock approaches carrying capacity (Troëng & Chaloupka, 2007), turtle harvesting in northern Australian and New Guinean waters (Limpus *et al.*, 2003) or rising groundwater that floods the egg chambers leading to recent recruitment failures (Limpus *et al.*, 2003). We believe that more detailed study of this particular rookery is warranted to better diagnose any trends in nester abundance of the northern Great Barrier Reef genetic stock.

The estimated long-term abundance trends for most of the six rookeries reflect relatively low population growth rates (Table 1) as would be expected for such a long-lived, slow-growing and late-maturing species (Bjørndal *et al.*, 2000; Chaloupka *et al.*, 2004). This relatively low population growth rate is one of the reasons why it can take decades for some green turtle populations to recover following major perturbations such as over-harvesting or loss of nesting habitat (Troëng & Rankin, 2005; Chaloupka & Balazs, 2007). These low recovery or population growth rates are consistent with estimates for other long-lived and slow-growing marine or maritime species such as large coastal sharks (Smith *et al.*, 1998), manatees (Craig & Reynolds, 2004), humpback whales (Chaloupka *et al.*, 1999), blue whales (Branch *et al.*, 2004), bowhead whales (Gerber *et al.*, 2007) and sea birds (Russell, 1999) but significantly lower than estimates for the short-lived fast-growing marine species like small coastal or oceanic sharks (Smith *et al.*, 1998), marine teleost fishes (Musick *et al.*, 2000) or sea otters (Estes *et al.*, 2003).

On the other hand, the estimated rate of increase in nest abundance at the Archie Carr National Wildlife Refuge rookery is greater than that found for any other green turtle rookery subject to long-term protection, which could be due to a number of factors. For instance, it might be an artifact of changing nester

behaviour as more turtles relocate to nest in the refuge due to increasing coastal development and other forms of disruptive human activity at nearby east Florida beaches (Witherington & Koeppel, 2000). It could also be because Florida green turtles reside year-round much closer to the regional rookery than other stocks and so have shorter reproductive migrations and subsequently reproduce far more frequently (Troëng *et al.*, 2005), which is a demographic process that has a significant effect on green turtle population growth rates (Chaloupka, 2002).

The long-term increase in green turtle nester or nest abundance shown here for the four Pacific (Fig. 1) and two Atlantic rookeries (Fig. 2) is due mainly to protection over recent decades from human exploitation (Ehrhart & Bagley, 1999; Limpus *et al.*, 2003; Weishampel *et al.* 2003; Balazs & Chaloupka, 2004; Troëng & Rankin, 2005; Yamaguchi *et al.*, 2005). Importantly, the Chichi-jima (Japan), East Island (Hawaii), Archie Carr National Wildlife Refuge (Florida) and Tortuguero (Costa Rica) rookeries are all from green turtle stocks recovering from serious depletion due to over-harvesting of eggs and turtles during and prior to the 20th century (Parsons, 1962; Horikoshi *et al.*, 1994; Ehrhart & Bagley, 1999; Troëng & Rankin, 2005; Chaloupka & Balazs, 2007). In fact the Florida green turtle nesting populations were probably close to extinction in the early 1980s (Fig. 2a) before undergoing a dramatic reversal in nesting abundance in the Archie Carr National Wildlife Refuge (Fig. 2c).

While of shorter survey duration, many other studies have also found increasing nesting populations of green turtles following protection from human exploitation such as at three Southeast Asian rookeries (Chaloupka, 2001), the Aldabra Atoll (Mortimer, 1988), Europa (Lauret-Stepler *et al.*, 2007), Grand Glorieuse (Lauret-Stepler *et al.*, 2007) and Mayotte (Bourjea *et al.*, 2007) rookeries in the south-west Indian Ocean, and at the Ascension Island rookery (Broderick *et al.*, 2006), which is one of the largest green turtle rookeries in the Atlantic. So these eight rookeries combined with the six rookeries in our study represent c. 44% of the 32 index populations compiled in a recent global assessment for green turtles (Marine Turtle Specialist Group, 2004). Moreover, these 14 rookeries comprise the world's largest green turtle rookeries such as Raine Island in the northern Great Barrier Reef (Fig. 1c), Tortuguero in Costa Rica (Fig. 2b) and Ascension Island in the mid-Atlantic (Broderick *et al.*, 2006).

It is apparent then that depleted green turtle populations can respond positively to relatively simple conservation strategies, which has also been shown for other sea turtle species at specific rookeries such as the olive ridley, *Lepidochelys olivacea* (Oaxaca, Pacific Mexico; Márquez *et al.*, 1998), the giant leatherback, *Dermodochelys coriacea* (St Croix, US Virgin Islands; Dutton *et al.*, 2005), the Kemp's ridley, *Lepidochelys kempii* (Rancho Nuevo, Atlantic Mexico, Márquez *et al.*, 1998; Padre Island, Texas; Shaver, 2005) and the loggerhead, *Caretta caretta* (Brazil; Marcovaldi & Chaloupka, 2007).

Despite serious depletion, many of the world's major green turtle stocks have maintained the capacity to recover if adequate protection measures are put in place (Chaloupka & Balazs, 2007). The upward abundance trends shown here for six of the major green turtle populations support the premise (Jackson

*et al.*, 2001; Pandolfi *et al.*, 2003) that marine ecosystems are still recoverable, because most species, including the megafauna, are still extant and their ecosystem functions can be restored. The importance of the green turtle for maintenance of seagrass and algal ecosystems (including detrital pathways and nutrient recycling) has been well documented using ecosystem mass-balance simulation models (Thayer *et al.*, 1982; Polovina, 1984) and by manipulative field experiments (Moran & Bjorndal, 2005, 2007). This optimism that the ecological role of the green turtle can be restored following recovering stocks is further supported by recent findings that seriously depleted green turtle stocks such as the east Pacific stock (Seminoff *et al.*, 2003) have not suffered any significant loss of genetic diversity (Chassin-Noria, *et al.* 2004), perhaps because the long generation time of green turtles (Bjorndal *et al.*, 2000; Chaloupka *et al.*, 2004) acts as a buffer against loss of genetic diversity (Hailer *et al.*, 2006). Furthermore, disease epidemics such as the tumour-forming disease fibropapillomatosis, do not appear to have hindered the recovery of some green turtle stocks such as the Hawaiian stock (Chaloupka & Balazs, 2005), which is now approaching full recovery (Chaloupka & Balazs, 2007).

Nonetheless, while our results suggest an optimistic outlook, some green turtle populations were more abundant historically than today and some have been extirpated (Parsons, 1962; Frazier, 2003; Marine Turtle Specialist Group, 2004; see also Fig. 1a). So the encouraging trends in green turtle nesting abundance reported here (Figs 1 & 2) need to be set in an appropriate historical context to avoid the 'shifting baseline syndrome' or use of a narrow temporal perspective to assess population trends (Pauly, 1995). However, historical baselines are difficult to set because several of these green turtle stocks (Japan, Hawaii, Florida, Costa Rica) were exposed to significant human exploitation over the past 200 years or more and so were already seriously depleted before our nesting beach studies began more than 25 years ago. Moreover, ongoing exposure to local harvesting still occurs for the Raine Island (Limpus *et al.*, 2003) and the Tortuguero green turtle stocks (Campbell & Lagueux, 2005), which could threaten the long-term recovery of both stocks. Therefore, some of these globally important nesting populations are probably still below their historical abundance and will require ongoing protective management to ensure full recovery of any depleted stocks.

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