

Reproductive seasonality and trend of *Chelonia mydas* in the SW Indian Ocean: a 20 yr study based on track counts

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ABSTRACT: The green turtle *Chelonia mydas* is classified as endangered because of global declines over the past few centuries due to human exploitation and habitat destruction, particularly the loss of nesting areas. We used the number of tracks as an indicator of breeding female abundance at their nesting sites to study the seasonality and trends of turtles breeding at 3 islands in the SW Indian Ocean: Europa, Tromelin and Grande Glorieuse, over 20 yr. On Tromelin, tracks were counted along the entire nesting beach, but on Europa and Grande Glorieuse counts were limited to a proportion of the island. Europa and Tromelin exhibited similar seasonal patterns, with a well-defined peak during the wet season (November–February), compared to a dry season peak for Grande Glorieuse (March–June). The main season was significantly longer on Grande Glorieuse (288 ± 43 d) than on Europa (218 ± 60 d), with Tromelin intermediate (252 ± 43 d). There was greater variation in the start of a season compared to the median and end at all sites throughout the study. Approximately 7178 ± 3053 ($n = 19$) tracks were recorded annually on the entire nesting beach on Tromelin, compared with 1480 ± 666 ($n = 19$) on 16% of nesting beaches on Grande Glorieuse and 1361 ± 903 ($n = 23$) on 26% of beaches on Europa. The number of tracks has increased significantly on Europa ($3\% \text{ yr}^{-1}$) and Grande Glorieuse ($6\% \text{ yr}^{-1}$). The increasing number of nesting turtles illustrates the effectiveness of conservation measures on sites formerly exploited by humans.

KEY WORDS: Green turtles · *Chelonia mydas* · Track count · Trend · Seasonality · Eparses Islands · Indian Ocean

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INTRODUCTION

Population assessment is based on past and present abundance of a species across its entire distributional range and for all age classes (IUCN 2004, Seminoff 2004a). However, estimation of population abundance is difficult for species with a wide spatial distribution

and cryptic life stages such as the green turtle *Chelonia mydas* (Carr & Carr 1970, Hays 2000, IUCN 2004). Assessing the population status of this species requires long-term monitoring data (Balazs & Chaloupka 2004, Troëng & Rankin 2005). In-water mark-recapture programmes crucially help to estimate the demography of a population, but these can be difficult and expensive

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to conduct (Chaloupka & Limpus 2001, Limpus et al. 2003, Balazs & Chaloupka 2004). Monitoring female nesting activity is easier, with population status based on the following proxies: numbers of nest per season, annual hatchling production, annual egg production and annual egg harvest. Track counts also can be used as an index of female abundance, assuming that the mean number of tracks per female per season remains relatively constant and that nesting success is constant (Seminoff 2004b). On a long-term basis, the number of tracks can be used to evaluate breeding seasonality and trends in the numbers of mature females at nesting sites. Most populations display a marked seasonal nesting peak, but differences exist between populations of the same region (Chaloupka 2001, Godley et al. 2002). There are several long-term data sets for green turtles nesting in Australia (Chaloupka & Limpus 2001), Hawaii (Balazs & Chaloupka 2004) and Costa Rica (Troëng & Rankin 2005), but there are few data from the western Indian Ocean (Seminoff 2004b, Troëng & Rankin 2005).

The SW Indian Ocean is an important nesting and feeding ground for green turtles (Hughes 1973, Frazier 1975, Mortimer 1984, Le Gall et al. 1986, Le Gall 1988). Over the past few centuries, over-exploitation and destruction of nesting and foraging sites have resulted in the decrease and local extinction of some populations (Frazier 1975). In this region, nesting sites are scattered over many small islands, as well as along the coasts of Madagascar and east Africa (Frazier 1975). Many sites are poorly documented and/or lack long-term data for population assessment because they are difficult to access (Hughes 1973, Frazier 1975). The Eparses Islands are 5 French islands scattered in the SW Indian Ocean around the coast of Madagascar: Europa, Bassas da India, Juan de Nova, Les Glorieuses and Tromelin. Since being discovered by Europeans in the 16th and 17th centuries, several attempts at colonization have been made, which have mainly failed due to the small size and inaccessibility of the islands, not to mention the lack of fresh water. This has not stopped their sea turtle populations from being frequently exploited by nearby islanders and temporary residents over the past few centuries (Hoareau 1993, DIREN 2003). Weather stations were built on each island in the 1950s, and in 1971 they were all declared protected areas (DIREN 2003). Three of the islands are important nesting sites for green turtles: Tromelin, Les Glorieuses and Europa (Le Gall et al. 1986, Le Gall 1988). Between 1970 and 1985, tagging studies undertaken by IFREMER (Institut Français de Recherche pour l'Exploitation de la MER) confirmed the importance of Europa and Tromelin as breeding sites for green turtles (Hughes 1973, Le Gall 1988). Females nesting at these islands were found feeding off the

coast of Madagascar and Africa (Le Gall 1988), where they are subject to illegal hunting and fisheries bycatch (Rakotonirina & Cooke 1994). IFREMER has maintained a monitoring programme at the 3 islands since the mid-1980s. The present study uses daily track counts collected over the last 20 yr as an index of the abundance of green turtles nesting on beaches of the Eparses Islands. It reports patterns of seasonality and trends in the abundance of breeding female green turtles on these islands.

MATERIALS AND METHODS

Study sites and data collection. Counts of turtle tracks have been conducted on 3 of the 5 Eparses Islands (Fig. 1). Tromelin (15° 33' S, 54° 31' E) is the smallest (1.2 km²), most isolated island of the group, and the only one outside the Mozambique Channel. It lies 560 km north of Réunion Island and 470 km east of Madagascar (Fig. 1). Most of the coast is covered with boulders, but there is 1600 m of sandy beach suitable for turtle breeding in the northwestern part. This entire stretch of coast has been checked daily for tracks since March 1986.

Grande Glorieuse (11° 33' S, 47° 17' E) is the largest island (7 km²) in the Les Glorieuses archipelago in the northern Mozambique Channel, 220 km from Madagascar (Fig. 1). The island is divided into 2 sampling zones: a 1500 m stretch of beach between the military base and the landing stage, and the rest of the island. The former zone has been sampled daily since the beginning of the survey in January 1987, but daily counts in the rest of the island only started in January 2001. Only data from the first zone (Zone 1) were used for the long-term trend analysis. It represents approximately 16% of suitable nesting habitat on the island, but no extrapolation to the entire island was made because of spatial heterogeneity in beach use.

Europa (22° 21' S, 40° 21' E) is the largest of the Eparses islands (38.5 km²), and is roughly circular with a 7 km diameter. It lies in the southern Mozambique Channel, 330 km from Madagascar (Fig. 1). The size of the island does not allow for all nesting beaches to be sampled. Daily counts have been made since June 1983 on a 1600 m stretch of beach, representing approximately 26% of the sandy beaches suitable for nesting turtles (Le Gall 1988).

The island staff are responsible for controlling access to the islands, cleaning beaches and participating in scientific studies such as the turtle monitoring programme. Personnel on the islands is rotated regularly, with 3 people at the weather station on Tromelin, and 15 soldiers each on Europa and Grande Glorieuse (DIREN 2003). Every morning a staff member walks the beach of each island to record the number of turtle

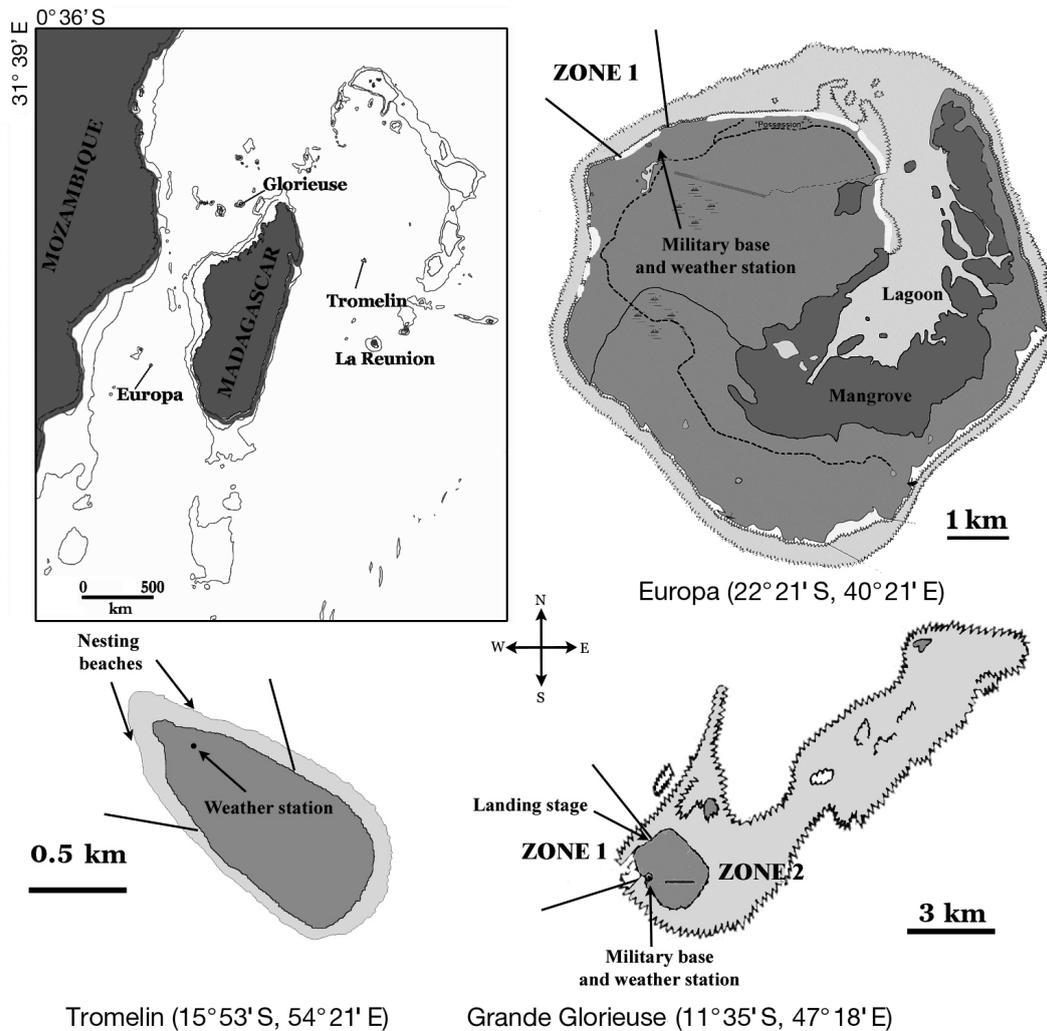


Fig. 1. Three of the 5 Eparses Islands scattered in the SW Indian Ocean: Europa, Grande Glorieuse and Tromelin. Because of the size of Europa and Grande Glorieuse, Zone 1 is the only zone of the islands that has been checked daily for tracks since the beginning of the study

tracks. Tracks are marked with a cross to avoid double-counting the next day. However, some daily counts were missed during staff changeovers, or when there were no observers on the islands due to bad weather.

Data analysis. Daily counts were grouped into three 10 d intervals per month, with the last interval of each month varying between 8 and 11 d. Pooling the data into 10 d intervals facilitates interpolation when there are missing counts. Missing counts were estimated by simple linear interpolation:

$$\text{Extrapolated no. of tracks} = \frac{\text{No. of tracks}}{\text{No. of counts}} \times 10$$

When there were no data for 10 d in a row, the total number of tracks for the 10 d interval was estimated by linear interpolation between adjacent 10 d intervals. On Europa, 4% of the 10 d intervals were estimated by interpolation, 2.5% on Tromelin and 3.5% on

Grande Glorieuse. No extrapolation was done when there were more than three 10 d intervals missing in a row, which represented 2.6% of the daily data for Europa, 5.1% for Tromelin and 1.7% for Grande Glorieuse.

Seasonality. Nesting season was defined from the 10 d and monthly track counts. The months with the lowest number of tracks were set as the limits of a season. The endpoints (start/end) of a season were determined as the interval including 90% of all tracks, defined as the Nesting Effort (NE) of a given season. Thus, a season started and ended after 5 and 95%, respectively, of NE had taken place. Season duration was the total number of 10 d intervals between these events. The median was defined as the 10 d interval when 50% of NE occurred. Variation in season duration between sites was tested with a 1-way ANOVA and Tukey post-hoc test. Seasonality was quantified by

numbering the 10 d intervals from January, and running into the following year if necessary. For each site and at each season, the symmetry of track counts around the median was determined with Bowley's coefficient of skewness (B; Zar 1999) and the number assigned to the 10 d intervals representing the start, median and end of a season. The relationships between B and the start of a season, duration and total NE in a season were tested using regression analysis. To compare the degree of seasonality for each island, a Seasonality Index (SI) was calculated as the ratio of highest and lowest monthly number of tracks in a season. Well-defined seasonality results in a higher SI. The variation in seasonality between each island was compared by testing SI with a 1-way ANOVA and a Tukey post-hoc test. All statistical analyses, including 1-way ANOVA and regression analysis were performed on R 2.2.0 (Ihaka & Gentleman 1996; software available online: www.r-project.org).

Rainfall and temperature data were obtained from Météo France. Average monthly minimum and maximum temperatures as well as average monthly rainfall were calculated and plotted for each site to compare environmental variations.

Trend analysis. Trends in turtle tracks were assessed up to March 2006 using the seasonal decomposition of time series by LOESS (STL; Cleveland et al. 1990). STL allows for robust statistical estimation of seasonal and trend components to limit the effect of outlying data (Chaloupka 2001). STL is a time domain filtering procedure that decomposes a series using non-parametric regression smoothing into additive frequency components of variation: data, trend, seasonal component and residuals. The trend component can be further decomposed into separate frequency components for the underlying long-term trend and non-seasonal or quasi-periodic cycles (Chaloupka 2001). A trend is obtained by applying a linear filter. Moving averages (MA) with equal weights were applied with 2 bandwidths of trend filter: 25, corresponding to an annual cycle (total number of tracks yr^{-1}) and 73, correspond-

ing to the average inter-annual cycle in green turtle nesting activity (total number of tracks per 3 yr). This multi-annual time cycle corresponds to the mean re-migration interval (period between successive nesting seasons) that has been reported to be 3 yr for several green turtle colonies (Le Gall et al. 1986, Le Gall 1988, Chaloupka 2001). All time series modeling procedures and regression analyses were implemented using R 2.2.0 (Ihaka & Gentleman 1996). Note that local smoothing such as provided by LOESS is a non-parametric method, and does not require any assumptions about the independence of observations. Unlike other time-series models (e.g. ARIMA), autocorrelation is not modelled; thus, any residual autocorrelation does not invalidate results.

RESULTS

Track counts were made on 92% of days at Europa from June 1983 to March 2006, 90% of days at Tromelin from March 1986 to February 2006 and on 91% of days at Grande Glorieuse from January 1987 to March 2006 (see Appendix 1, available at: www.int-res.com/articles/suppl/n003p217_app.pdf).

Seasonality

Turtles visit breeding beaches year round at all 3 sites, with a nesting peak during the wet season (November to February) at Europa and Tromelin, but 4 to 5 mo later during the dry season at Grande Glorieuse (March to June, Fig. 2). The nesting season was significantly longer on Grande Glorieuse (286 ± 43 d) than on Europa (218 ± 60 d, Table 1; 1-way ANOVA: $F_{2,58} = 7.83$; $p < 0.005$; post-hoc test: $p = 0.0006$), with Tromelin intermediate (252 ± 61 d) and not significantly different from the 2 other islands. Seasonality tended to be more marked on Europa (SI = 8.9 ± 5.2 with $N = 23$) than on the other islands (Tromelin: SI = 6.8 ± 3.0 with $N = 19$

Table 1. *Chelonia mydas*. Seasonality of green turtles nesting on Europa, Grande Glorieuse and Tromelin (mean \pm SD). The annual number of tracks is calculated as the average number of tracks per season. The Seasonality Index (SI) is calculated as the ratio between the month with the highest number of tracks and the month with the lowest number of tracks in a season. The average season onset/median/end is expressed here as the average mid-point of the 10 d intervals. SD is expressed as the number of 10 d intervals. Data represents tracks collected on: 26% of the total beach on Europa, 16% on Grande Glorieuse, and 100% on Tromelin

	Annual no. of tracks	Season duration (d)	SI	Onset	Season Median	End	No. of seasons
Europa	1361 \pm 903	218 \pm 60	8.9 \pm 5.2	15 Aug \pm 5.1	15 Dec \pm 1.8	15 Mar \pm 3.4	23
Tromelin	7178 \pm 3053	252 \pm 43	6.8 \pm 3.0	25 Sep \pm 4.3	25 Jan \pm 2.3	5 Jun \pm 4.4	19
Grande Glorieuse	1480 \pm 666	288 \pm 43	3.8 \pm 1.4	5 Dec \pm 4.0	25 Apr \pm 3.0	15 Sep \pm 3.2	19

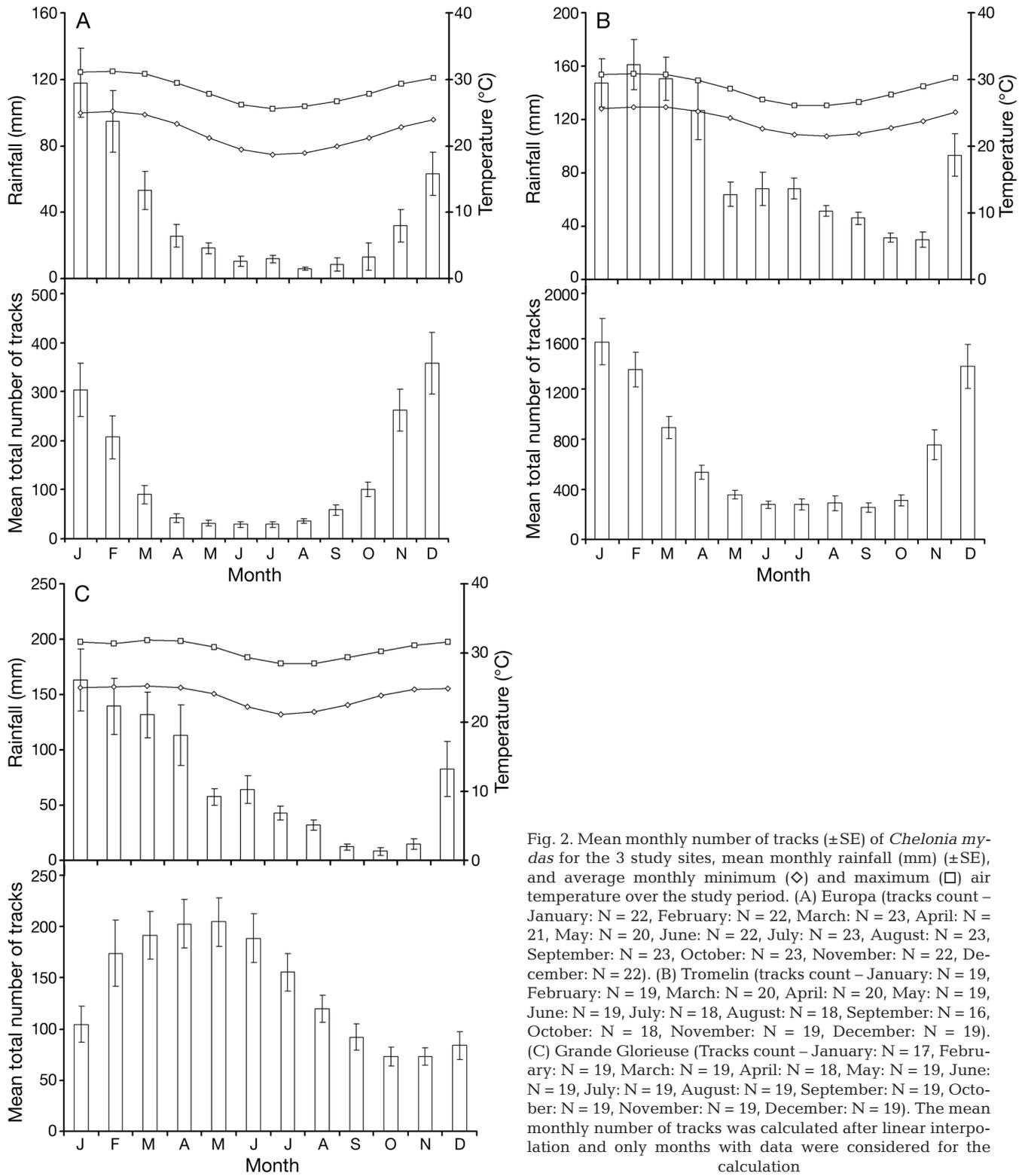


Fig. 2. Mean monthly number of tracks (\pm SE) of *Chelonia mydas* for the 3 study sites, mean monthly rainfall (mm) (\pm SE), and average monthly minimum (\diamond) and maximum (\square) air temperature over the study period. (A) Europa (tracks count – January: N = 22, February: N = 22, March: N = 23, April: N = 21, May: N = 20, June: N = 22, July: N = 23, August: N = 23, September: N = 23, October: N = 23, November: N = 22, December: N = 22). (B) Tromelin (tracks count – January: N = 19, February: N = 19, March: N = 20, April: N = 20, May: N = 19, June: N = 19, July: N = 18, August: N = 18, September: N = 16, October: N = 18, November: N = 19, December: N = 19). (C) Grande Glorieuse (Tracks count – January: N = 17, February: N = 19, March: N = 19, April: N = 18, May: N = 19, June: N = 19, July: N = 19, August: N = 19, September: N = 19, October: N = 19, November: N = 19, December: N = 19). The mean monthly number of tracks was calculated after linear interpolation and only months with data were considered for the calculation

and Grande Glorieuse: $SI = 3.8 \pm 1.4$ with $N = 19$, Table 1). SI was significantly smaller for Grande Glorieuse than for the 2 other islands (1-way ANOVA: $F_{2,58} = 9.84$; $p = 0.0002$; post-hoc test: $p < 0.05$).

The breeding peak was less marked and its timing more variable on Grande Glorieuse than on the other 2 islands (Table 1, Fig. 3). The start and end of the season were more variable on Europa (SD start = 5.1;

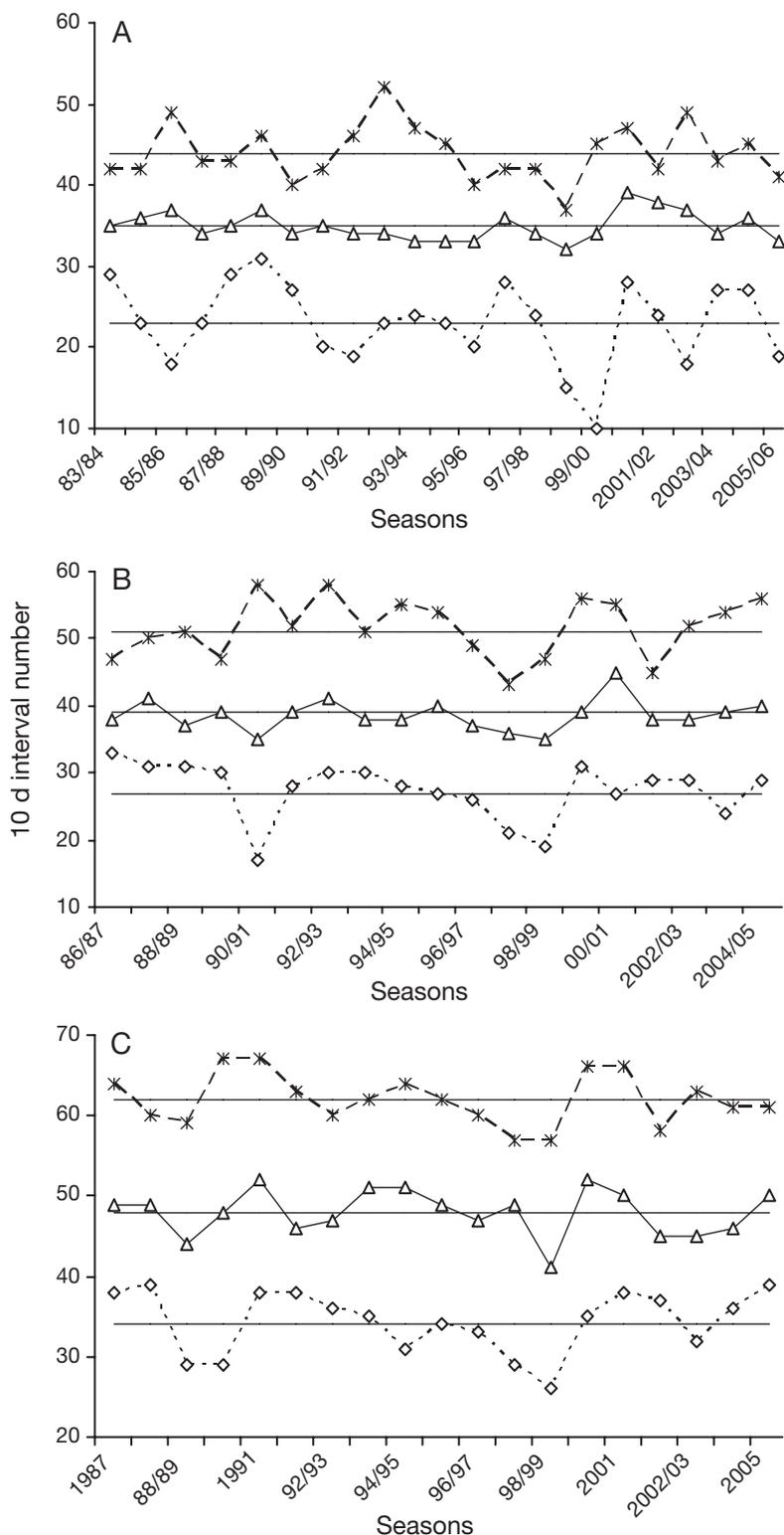


Fig. 3. Onset (◇), median (Δ) and end (✱) 10 d interval number calculated for each season over the study period for (A) Europa, (B) Tromelin and (C) Grande Glorieuse. The y-axis represents the number attributed for each 10 d interval during a year. The average 10 d interval at which the season starts and ends is also represented as a straight line for each site, so that shift and variation can be clearly seen over the study period

SD end = 3.4) and Tromelin (SD start = 4.3; SD end = 4.4) than their median dates (SD = 1.8, 2.3, respectively), whereas start, end and median points were equally variable on Grande Glorieuse (SD start = 4.0; SD end = 3.2; SD median = 3.0; Table 1). A season generally ended later when it started later than average, but there was less effect on the timing of the median date. There was a positive relationship between Bowley coefficient of skewness (B) and the start of a season at all 3 islands ($p < 0.05$), indicating that the nesting peak was largely independent of the start date. However, there were no relationships between B and NE or season duration. For all 3 islands, the mean Bowley coefficient of skewness (B) was close to zero, suggesting that the number of tracks is distributed symmetrically around the median. For Europa, the peak was right skewed (mean $B = -0.12 \pm 0.23$) compared to the other 2 islands, which were left-skewed (Tromelin: 0.07 ± 0.21 ; Grande Glorieuse: 0.02 ± 0.18).

Seasonal patterns of rainfall and temperature were similar at all 3 islands with a hot, wet season from November to April and a cooler, dry season from May to October (Fig. 2). Europa had lower average temperatures and rainfall throughout the year compared to the 2 other islands (Fig. 2). The peak nesting season started at the beginning of the wet season at Europa and Tromelin when temperatures were still high, but at the start of the dry season at Grande Glorieuse, when temperatures began to drop (Fig. 2).

Trends

On Tromelin, an estimated 7178 ± 3053 tracks per season correspond to the entire green turtle population, whereas track counts for Europa (1361 ± 903) and Grande Glorieuse (1480 ± 666) represent only the subset of females nesting on the designated sampling zones (Table 1). Time series modelling produced 2 STL decompositions at 1 yr and 3 yr cycles. As noted above, time-varying seasonal variability occurred at all 3 islands (Fig. 4). The second panel in Fig. 4A–F shows the seasonal component of the time series,

representing nesting activity variation. The third panel in each STL plot shows the fitted 1 and 3 yr trends. The trend is highly variable for all sites. Fig. 4F shows a roughly linear increasing trend for Grande Glorieuse, with less consistent trends at Tromelin and Europa (Fig. 4B,D). The trend is more linear with a 3 yr period than with 1 yr, but still not periodical compared to Grande Glorieuse. The bottom panel shows the residuals remaining once trends and cyclicity have been removed. Residual variation was greater at Europa (Fig. 4A: residual variation = 0.85; Fig. 4B: residual variation = 1.036) and Tromelin (Fig. 4C: residual variation = 0.47; Fig. 4D: residual variation = 0.60) than at Grande Glorieuse (Fig. 4E: residual variation = 0.41; Fig. 4F: residual variation = 0.59). The residual component accounts for a substantial part of the temporal variability in the number of tracks. This may be related to environmental variation. For each site, residual variation represents more than 40% of total variation (Fig. 4).

A significant increase in the total number of tracks occurred on Grande Glorieuse ($F_{1,226} = 41.8$; $p < 0.001$) and Europa ($F_{1,262} = 6.3$; $p = 0.01$) over the past 20 yr. The total number tracks increased at 6% per year on Grande Glorieuse and 3% on Europa. A slight decline (1% per year) occurred on Tromelin, but this is not significant ($F_{1,225} = 1.0$; $p = 0.3$).

DISCUSSION

Seasonality

Nesting seasonality on the Eparses Islands is similar to that of the majority of green turtles colonies studied worldwide. Green turtles nest all year round, but typically exhibit a distinct nesting peak (Bjørndal et al. 1999, Chaloupka 2001, Godley et al. 2001, Limpus et al. 2001, 2003). Our study illustrates variability in seasonality among colonies in the same region. In the northern Mozambique Channel, on Grande Glorieuse, nesting occurs at the start of the dry season and lasts longer with a more variable peak than at Europa in the southern Mozambique Channel, where nesting occurs during the wet season. Outside the Mozambique Channel, on Tromelin, the nesting season is somewhat intermediate between the other 2 islands (Fig. 2).

It is not uncommon for colonies in the same region to have different patterns of seasonality. Shifts in the nesting peak have been reported at some southeast Asian and Australian colonies (Chaloupka 2001, Limpus et al. 2001). Many of the southeast Asian colonies are characterised by year round nesting with a distinct dry season nesting peak (Chaloupka 2001). Not all Australian colonies nest all year round (Limpus et al.

2001). However most of them are characterised by a wet season peak, except for the Gulf of Carpentaria colonies, which have a dry season peak similar to the southeast Asian colonies, to which they are genetically closer (Chaloupka 2001, Limpus et al. 2001). In some instances, seasonal variability between colonies may be genetically determined. Bourjea et al. (2007) found that green turtles nesting on the Eparses Islands belong to 2 separate genetic stocks: the South Mozambique Channel (SMC) and the North Mozambique Channel (NMC). The SMC, including Europa, is genetically closer to the Atlantic stock, while the NMC including Tromelin, Grande Glorieuse and adjacent islands like Mohéli, Mayotte, Nosy Iranja and the Seychelles is genetically closer to the larger Indo-Pacific stock. The specific oceanic conditions experienced in the Mozambique Channel (Quartly & Srokosz 2004) are thought to be responsible for this genetic structuring (Bourjea et al. 2007). However, if genetic differences were responsible for seasonal differences in our study, we would expect Europa to differ from the other 2 islands, whereas Grande Glorieuse was most distinctive. This suggests that environmental factors at the breeding and feeding sites are most likely responsible for inter-colony differences in seasonality (Limpus & Nicholls 1988, Hays et al. 1999, Godley et al. 2002, Wibbels 2003).

Development and sex determination in sea turtle hatchlings is largely dependent on temperature, with optimal embryonic development at sand temperatures above 27°C (Wibbels 2003). Godley et al. (2002) showed a correlation between sand temperature and the number of turtles coming to nest, confirming the importance of environmental factors in determining turtle breeding seasons (Wibbels 2003). The choice of breeding season is not related to the warmest time of the year, but to that providing the best sand temperatures for incubation, sex ratio, hatchling dispersal and survival (Godley et al. 2002). El Niño has been found to influence the number of females that breed each year, but not seasonality or migration patterns of nesting (Limpus & Nicholls 1988). Sea surface temperatures (SST) may also influence breeding seasonality, with seasons starting earlier with warming SST (Weishampel et al. 2004). Environmental conditions at the feeding sites also play an important role in migration patterns to nesting sites (Limpus & Nicholls 1988). Changes in climate can alter the abundance, quality and distribution of food, thus influencing nutritional pathways (Hamann et al. 2002). Little is known about the migration routes and foraging sites of female turtles nesting on Grande Glorieuse. This information could add substantially to the factors underlying the variability in the peak season at this site. Equatorial colonies with year round nesting can receive females

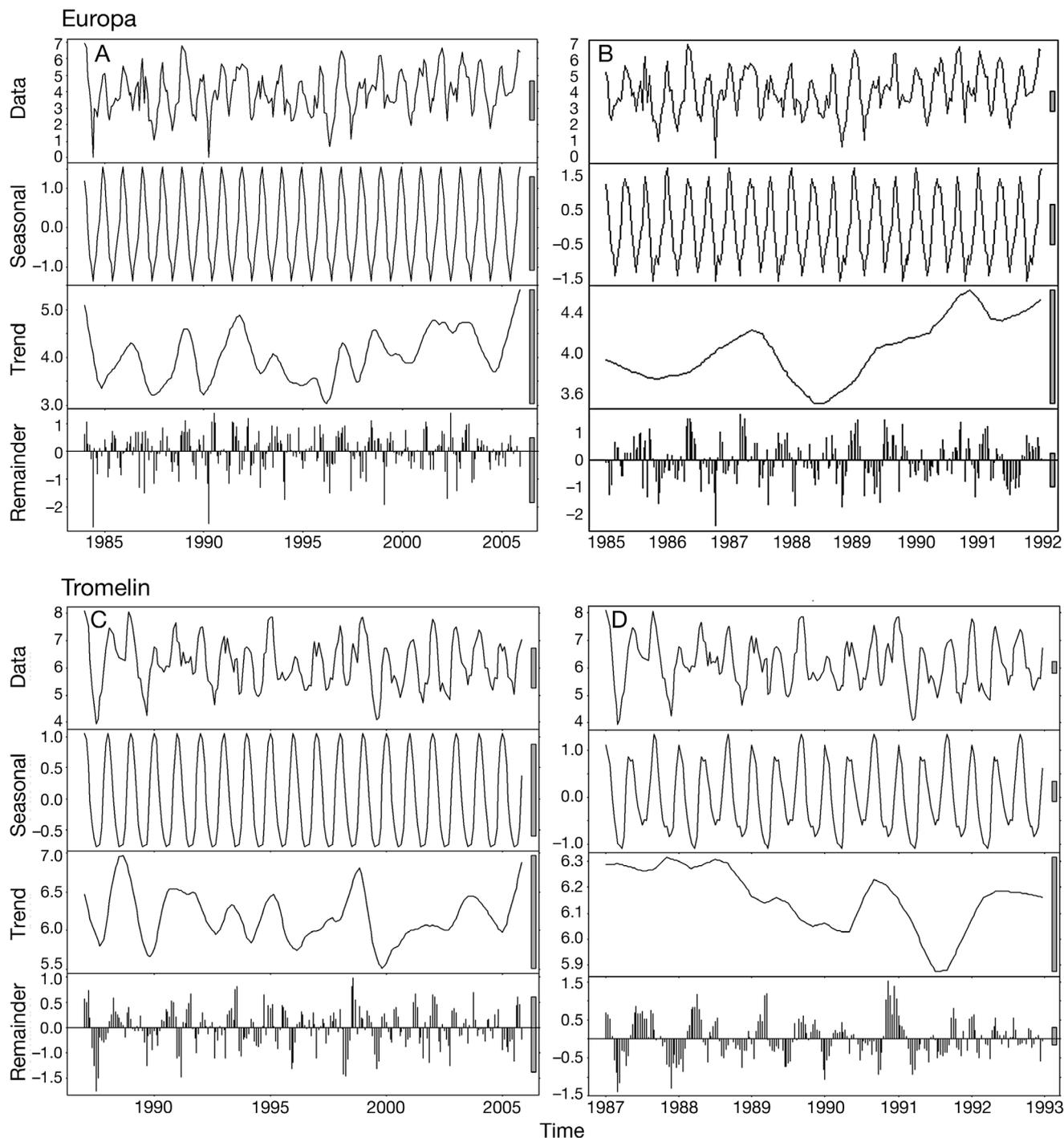
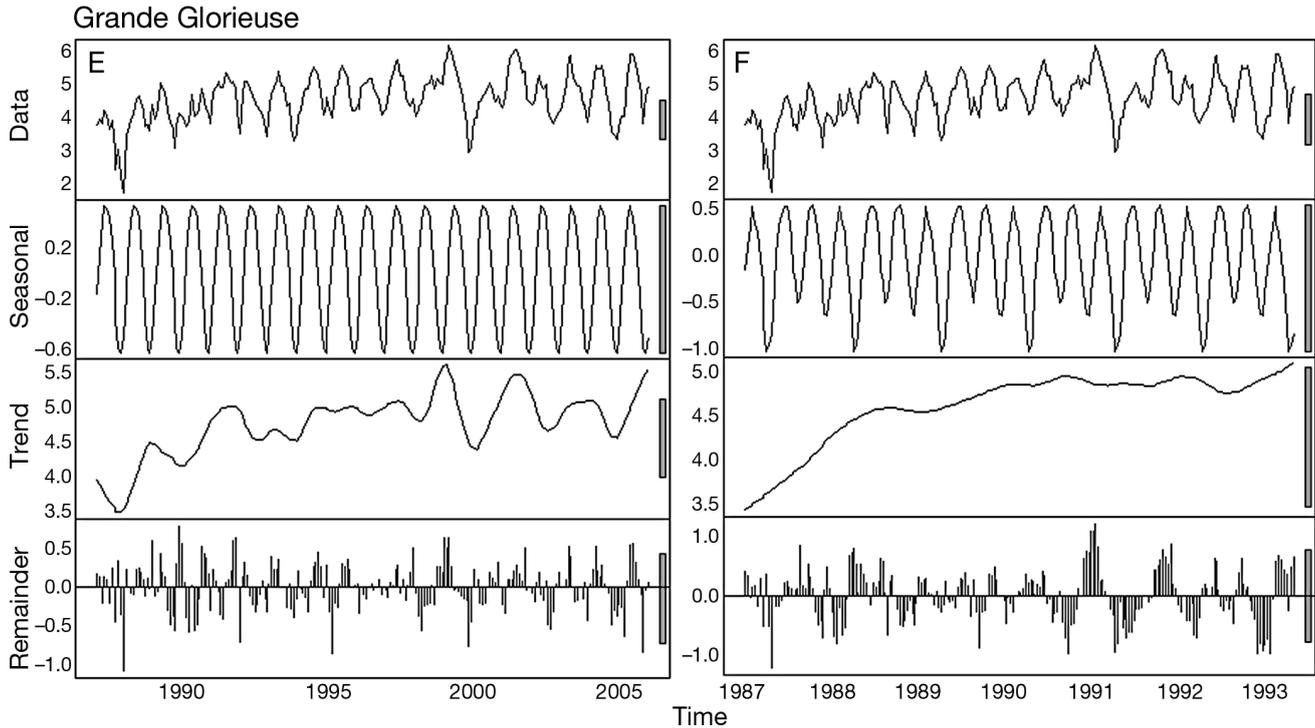


Fig. 4. *Chelonia mydas*. Long-term trend in number of tracks for (A,B) Europa, (C,D) Tromelin, and (E,F) Grande Glorieuse. (A) Annual frequency of log(number of tracks) from January 1984 to December 2005, (B) 3 yr frequency trend from January 1985 to December 2005), (C) annual frequency from January 1987 to December 2005, (D) 3 yr frequency trend from January 1987 to December 2004, (E) annual frequency from January 1987 to December 2005, (F) 3 yr frequency trend from January 1987 to December 2004. (B,D,F) Time scale represents a season of 3 yr. (A–F) Data: monthly track count series (raw data; log(monthly number of tracks)); seasonal: seasonal component; trend: fitted long-term trend; remainder: residuals component remaining after the trend. For Europa: (A) residual variation (0.85) represents 46.2% of the total variation; (B) residual variation (1.04) represents 57.5% of the total variation. For Tromelin: (C) residual variation (0.47) represents 39.1% of the total variation; (D) residual variation (0.60) represents 46.8% of the total variation. For Grande Glorieuse: (E) residual variation (0.41) represents 43% of the total variation; (F) the residual variation represents 62.3% of the total variations. (A–F) Grey bar at the right of each panel represents the scale relative to each component



(Fig. 4 continued)

from foraging areas in both hemispheres (Hamann et al. 2002). Thus, regional climatic difference and oceanographic patterns can have an impact on the variability of the nesting peak season (Hamann et al. 2002). However, it is possible that females nesting at Grande Glorieuse do not share the same feeding ground as those nesting at Europa and Tromelin, which could explain the difference in seasonality between Eparses islands. These hypotheses need to be further investigated through additional tagging studies and satellite tracking of individuals to their foraging sites, data on sand and sea temperatures. SST is highly variable in the SW Indian Ocean, depending on the season and the region (Piton et al. 1981), and could be correlated to nesting seasonality of turtles breeding on the Eparses Islands.

Trends

The increasing number of turtle tracks on Grande Glorieuse confirms that protection of nesting sites can have a positive impact on nesting populations, as has been observed at other colonies (Chaloupka & Limpus 2001, Balazs & Chaloupka 2004, Troëng & Rankin 2005). Historical records indicate that Grande Glorieuse used to be an important nesting site for green turtles (Frazier 1975), but compared to Tromelin and Europa, it has been the most affected by human activi-

ties, with harvests of eggs and meat (Hoareau 1993). The SW Indian Ocean region comprises many islands scattered across millions of square kilometres, on which thousands of sea turtles used to nest (Frazier 1975). Overexploitation of green turtles in the Seychelles led to a severe decline in the population during the first two-thirds of the 20th century (Mortimer 1985, 1988). In the 1970s, green turtle catches reached approximately 400 to 500 yr^{-1} on Aldabra Island (Frazier 1975), causing a severe decline in the population. However, since the ban on killing turtles in 1968, the number of females has increased significantly. There are no reliable records on the number of green turtles exploited on Grande Glorieuse (Frazier 1975), and it is difficult to test whether the increase is due to recovery from past exploitation. For instance, Frazier (1975) reported very little nesting activity on Grande Glorieuse in the early 1970s, with only an estimated 250 nesters visiting the island per year. In addition, nesting success on this island (and possible changes over time) is not known. Indeed, nesting success may vary with environmental and temporal factors, e.g. between beaches and between seasons, as illustrated by Le Gall (1988), Godley et al. (2001) and Limpus et al. (2003). Without additional information on nesting success, our results may not be interpreted in terms of nester abundance. Track counts can be still used as a relative index of abundance of nesters in order to monitor the effectiveness of conservation measures on colonies,

where intensive field surveys to assess the total population of nesting sea turtles is impossible.

The effectiveness of protecting nesting sites is shown by the sustainability of the population nesting on Tromelin. The number of tracks on Tromelin has remained constant over the study period. Population growth rate in terms of nester or nest abundance was found to range between 4 and 14% per annum in 6 major green turtle colonies located through the Pacific and the Atlantic, after conservation measures were introduced and enforced (Chaloupka & Limpus 2001, Balazs & Chaloupka 2004, Troëng & Rankin 2005, M. Chaloupka et al. unpubl. data). Europa and Grande Glorieuse displayed positive growth rates (3 and 6% yr⁻¹, respectively). However, these growth rates were calculated for a small proportion of the nesting population. The variability and intensity of growth rate estimated for these colonies may be influenced by a number of factors, such as the extent to which the nesting population has been exploited, distance between feeding and nesting grounds and adult mortality at sea (Broderick et al. 2006, M. Chaloupka et al. unpubl. data). Females nesting on Europa and Tromelin were probably exploited less than the females nesting on Grande Glorieuse (Hoareau 1993), which explains the stable and low growth rates estimated on the former sites. However, females nesting on Europa and Tromelin are known to migrate great distances and therefore do not return to breed as frequently as females nesting in Florida (Le Gall et al. 1986, LeGall 1988, M. Chaloupka et al. unpubl. data). Feeding grounds of females nesting on Grande Glorieuse are unknown, unlike the population of Ascension Island in the central Atlantic Ocean, which forage in Brazilian coastal waters, where conservation measures have been implemented to reduce bycatch (Broderick et al. 2006). However, this conclusion should be interpreted with caution because the trend analysis was performed on track counts and not on abundance of nesters.

Trends in the numbers of tracks at Europa and Tromelin display high inter-annual variability. As shown in other studies (Le Gall 1988, Hays 2000, Solow et al. 2002), this high variability in track numbers can complicate the interpretation of trends at different sites. Variability in re-migration intervals and weak synchrony in re-migration behaviour can account for inter-annual variability in the number of individuals attending a colony (Solow et al. 2002). Environmental factors such as cyclones and El Niño Southern Oscillation associated with warmer sea surface temperatures were found to influence the number of individuals migrating to their nesting sites (Limpus & Nicholls 1988, Solow et al. 2002, Ross 2005). On Europa and Grande Glorieuse, movements between breeding

beaches may also influence inter-annual variability (Le Gall et al. 1986, Le Gall 1988). The effect of such environmental factors on the Eparses Islands population needs to be further investigated.

Perspectives

For green turtles and other species of sea turtles, conservation measures are most effective when they ensure long-term nesting success, hatchling survival and protection from overuse (Chaloupka & Limpus 2001, Balazs & Chaloupka 2004, Troëng & Rankin 2005). To date, conservation efforts for many populations have been concentrated on the protection of nesting sites. However, the condition and status of green turtles at their feeding sites are also important, as they spend a major part of their life there preparing for migration and breeding. The coast of Madagascar appears to be the main feeding ground for turtles nesting on Europa and Tromelin, but despite official protection, poaching and illegal trade still occur (Rakatonirina & Cooke 1994). It would thus be important to monitor and protect sea turtles on their feeding grounds as well as on their nesting grounds.

A key issue in the conservation of green turtles is the time lag at which the impact of conservation measures may be detected, due to the slow demography of the species (Seminoff 2004a); this reinforces the case for collecting long-term data on sea turtles, as well as data on other life stages of each species, since reproductive females represent only one component of the population. More emphasis is needed on protecting sea turtles at their feeding grounds and on pelagic stages at sea in order to complement protection at nesting sites.

Acknowledgements. This project was supported by Région Réunion. Counts of turtle tracks were conducted by Les Forces Armées de la Zone Océan Indien (FAZOI) and the Gendarmerie Nationale and Météo France. We also thank Le Préfet from Réunion Island and Le Préfet des Terres Australes et Antartiques Françaises (TAAF), who allowed us to work on these protected areas. We are grateful to George Hughes, who started studying the green turtle populations breeding on Eparses Islands, to Jean Yves Le Gall, who initiated the sea turtle monitoring programme on Eparses Islands in the 1980s, and to Julie Frappier for her help with statistical analyses. We thank 4 anonymous reviewers for their useful comments on the manuscript.

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Editorial responsibility: Brendan Godley (Editor-in-Chief), University of Exeter, Cornwall Campus, UK

Submitted: November 27, 2006; Accepted: May 14, 2007
Proofs received from author(s): August 7, 2007