

Journal of Experimental Marine Biology and Ecology 356 (2008) 69-82

Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

www.elsevier.com/locate/jembe

The world's largest leatherback rookeries: A review of conservation-oriented research in French Guiana/Suriname and Gabon

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Abstract

The Atlantic Ocean hosts a major part of the world's leatherback population, with the largest rookeries being located in the northern part of South America (Suriname/French Guiana) and in western Central Africa (Gabon). In contrast with the dramatic decline of nesting populations in the Pacific Ocean, some Atlantic leatherback rookeries have recently been reported to be stable or even to increase. This raises the question, which particular research and conservation initiatives, past and present, may have led to such development. Here we present an overview of the historical and present research and conservation efforts in French Guiana, Suriname and Gabon and highlight current gaps in knowledge and required improvements to maintain protection for the major rookeries of this critically endangered species.

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Keywords: Atlantic ocean; Conservation; Dermochelys coriacea; Nesting; At sea ecology; Review

1. Introduction

With the dramatic decline in the nesting populations of leatherbacks (*Dermochelys coriacea* Vandelli 1761), in the Pacific Ocean during the last two decades (Chan and Liew, 1996; Sarti et al., 1996; Spotila et al., 1996, 2000; Martínez et al., 2007; Tomillo et al., 2007), the Atlantic Ocean now hosts about 70% of the world population of this critically endangered species (Troëng et al., 2004). The largest rookeries are located in the north-eastern part of South America and Trinidad (Girondot and Fretey, 1996; Eckert, 2006; Hilterman and Goverse, 2007) and in western Central Africa (Fretey and

situated in Suriname/French Guiana and Gabon.

Billes, 2000). Importantly, several Atlantic leatherback rookeries have recently been reported as stable or even on the

increase (NOAA, 2007), despite massive interactions with

human activities both on land (Verhage et al., 2006; Bal et al., 2007; Deem et al., 2007; Ordoñez et al., 2007; Chacón-Chaverri and Eckert, 2007), and at sea (Lewison et al., 2004a, 2004b). This situation encourages a review of the main research and conservation initiatives undertaken in these major Atlantic leatherback rookeries. Such review may provide a better understanding of this positive development and further allow prediction of future trends, especially in the context of global climate change and intensified human activities (Georges and Le Maho, 2003). In the following we will investigate historical and current research and conservation initiatives undertaken in the last two major leatherback rookeries that exist in the world,

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In our review, we will firstly introduce the nesting locations, then give current population trends for these rookeries, and present mathematical models, which may help to improve our understanding of leatherback population dynamics. In the second part, we will explore the main threats to leatherback rookeries and evaluate historical and recent conservation measures that were implemented at the various nesting sites.

2. Overview of the local situations

Suriname/French Guiana and Gabon are situated almost face to face on either side of the Atlantic Ocean (Fig. 1). On the eastern side, Gabon (2°N-4°S) has 950 km of seashore with a NW-SE heading and a 50-km wide continental shelf. On the western side, Suriname and French Guiana (5-6°N) have 600 km of seashore, heading in an almost NW-SE direction, with a 100-km wide continental shelf. At both sites, the seashore consists of long sandy beaches distributed patchily among mangroves and/or coastal rainforests with extensive mudflats. These sandy beaches represent a suitable landscape for sea turtles to nest, as indicated by the large numbers of leatherback, green Chelonia mydas (Linnaeus, 1758) and olive Ridley Lepidochelys olivacea (Eschscholtz, 1829) turtles (Fretey and Reichart, 1993; Mohadin, 2000; Fretey, 2005) that frequent them. In Suriname low numbers of the hawskbill turtles Eretmochelys imbricata nest as well (Fretey and Reichart, 1993; Mohadin, 2000). Both African and American littoral regions have been inhabited by human populations for a long time, so that human—sea turtle interactions reach back far in history (e.g. Fretey, 2005; Fretey et al., 2007a).

On both sides of the Atlantic, the littoral landscape is highly dynamic and, given the proximity of large rivers such as the Amazon River in South America (Gardel and Gratiot, 2005; Kelle et al., 2007; Fig. 1A), and the Congo River in Africa (Verhage et al., 2006; Fig. 1B), is dominated by the large scale coastal phenomena of seashore erosion/accretion. Consequently, the suitability of the littoral for human occupancy and for nesting turtles changed throughout time (Reichart and Fretey, 1993; Kelle et al., 2007; Hilterman et al., in press). The regular emergence of new major nesting sites makes it difficult to accurately assess population trends and implement adequate conservation measures in such dynamic areas. For example, traditional memories of native Kalina Amerindians and ancient documents do not report large numbers of leatherbacks around the Maroni/Marowijne estuary in French Guiana and Suriname before 1950 (Pritchard, 1969; Girondot et al., 2007). The discovery of great numbers of leatherbacks nesting in the Ilets Baches beaches of French Guiana, adjacent to Awala-Yalimapo village (Pritchard, 1969) paved the way for one of the longest population monitoring of sea turtles to date (e.g. Pritchard, 1973; Girondot et al., 2007). This resulted in the creation of the Amana Nature Reserve in 1998, which includes all the nesting beaches historically identified around Awala-Yalimapo beach and also includes a 30-m wide marine fringe (Fig. 1A). However, in recent years an increasing number of females have been recorded in the non-protected eastern nesting sites in French Guiana, such as around Cayenne city (Fig. 1A). These nesting sites face specific threats and a conflict of interest with local policies exists, as these

sites are considered for recreational use and undergo increasing urbanization. Such threats are currently poorly considered by local authorities. In Suriname, the first expeditions to locate nesting beaches of sea turtles were made in 1963. Since 1964, to date, staff of the Nature Reserve management organisation carries out daily nest counts. The Wia Wia Nature Reserve was implemented in 1961 (amended and enlarged in 1966 to protect sea turtles) and in 1969 the Marowijne beaches were declared a sanctuary: the Galibi Nature Reserve (Schulz, 1971) includes a protected zone of 100-m landward. In Gabon, nesting sites at the Mayumba and Gamba beaches have been discovered fairly recently. However, while they belong to a large complex of protected areas, they still remain rather isolated and barely accessible (Fretey and Girardin, 1988; Fretey and Billes, 2000; Fretey, 2001; Verhage et al., 2006; Fig. 1B). It should be noted that a large number of leatherbacks also nests on the northern beaches of the Republic of Congo located within the Conkouati-Douli National Park and monitored by the Wildlife Conservation Society. The fact that the majority of leatherback nesting beaches in Suriname/French Guiana and Gabon/Congo are situated in nature reserves or national parks is of primary importance. These reserves/parks raise awareness amongst tourists and provide protection for the rookeries through the presence of rangers and research/conservation teams on the beaches. However, reinforcement of the already existing measures and implementation of a conservation strategy able to appropriately consider the spatiotemporal dynamics of the nesting sites is still needed.

Based on mitochondrial DNA analyses, seven genetically different stocks of leatherbacks have been defined in the Atlantic (NOAA, 2007) among which female leatherbacks nesting in Africa between November and January are supposedly highly segregated from those nesting in the western Atlantic (Guianas [French Guiana/Suriname/Guyana] and Southern Caribbean) between March and August. In French Guiana and Suriname a limited nesting season of leatherbacks also exists between November and January (Reichart and Fretey, 1993), where a few tens of individuals nest (Chevalier et al., 1999; Ferraroli, 2004; Girondot et al., 2007). However, their numbers have been decreasing (de Thoisy, B., unpublished data). Such desynchronised phenology has also been recently reported in Papua, Indonesia (Hitipeuw et al., 2007) and certainly requires a more detailed investigation. The small nesting season reported in French Guiana probably concerns individuals that usually nest during the main season but for some reason are out of tune (Girondot et al., 2007). Knowledge of the migratory habits and the genetic profiles of these two distinct stocks may be helpful to understand the relationship between the two main Atlantic rookeries. Indeed, only a clear understanding of the interpopulation links will allow the development of a coherent global conservation strategy for these highly migratory reptiles.

3. Land based population monitoring

3.1. Individual tagging reveals population demographic parameters

For a better understanding of the ecology and demographic processes in leatherback populations, reliable estimates of

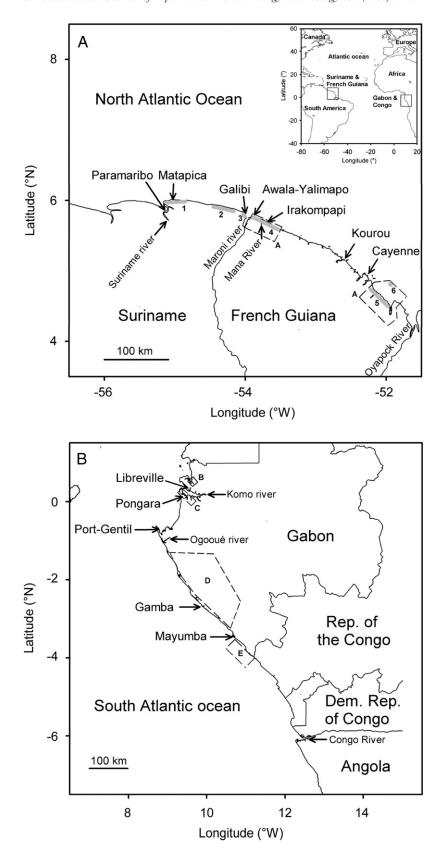


Fig. 1. Maps of (A) French Guiana and Suriname, and (B) Gabon and Congo. Bold grey lines represent coastal Nature Reserves or management areas (1: Matapica Multiple Use Management Area, 2: Wia Wia Nature Reserve, 3: Galibi Nature Reserve, 4: Amana Nature Reserve, 5: Marais de Kaw-Roura Nature Reserve, 6: Ile du Grand Connetable Nature Reserve). Dashed black boxes represent coastal National and Regional Parks (A: Natural Regional Park of French Guiana, B: Akanda National Park, C: Pongara National Park, D & E: Gamba Complex of Protected Areas including (D) Loango and Moukala Doudou National Parks and (E) Mayumba National Park).

reproductive parameters and survival probabilities are needed. Such data are based on Capture–Mark–Recapture (CMR) studies of gravid females that come ashore seasonally to nest. CMR protocols consist of identification of every individual encountered for the first time at the study site, and then controlling the site adequately in order to record every consecutive return of these identified individuals throughout their life time.

During the early years of sea turtle research in Suriname, period 1966–1973, a number of leatherback females were tagged with Monel tags (Schulz, 1975). In French Guiana, individual identification of leatherbacks has been possible through tagging, which started in 1983. Plastic tags were used originally, which were later replaced by metal flipper tags (Girondot and Fretey, 1996). Since 1994 Passive Integrated Transponder (PIT) tags have been used (McDonald and Dutton, 1996; Briane et al., 2007). In Suriname a pilot PIT tag study started in 1999 and in 2000-2005 a large scale tagging program was carried out (Hilterman and Goverse, 2007). In addition, since 2000-to date PIT tagging started on Shell Beach in Guyana. In Gabon, PIT tags were introduced in 1998 but their use was discontinued in 1999. Since 2003, PIT tags have been used in the Gamba Complex of Protected Areas only (Verhage et al., 2006). The use of metal flipper tags for leatherback identification has been shown to be unreliable (McDonald and Dutton, 1996; Rivalan et al., 2005a) as tag loss is high, leading to low survival rate estimates for nesting females (Boulon et al., 1996; Hughes, 1996). Conversely, PIT tags permit long-term monitoring and thus reliable estimates of demographic parameters for a given population (Gibbons and Andrew, 2004). Every tag database has however documented erroneous codes; errors in writing late at night or mistakes during data entry (Godfrey, 2003; Hilterman and Goverse, 2007). Even though such monitoring requires the purchase of relatively expensive PIT readers use of PIT tags in the major leatherback nesting sites seems inevitable for accurate leatherback surveys in the years to come.

In French Guiana, the mean survival probability of gravid females was estimated at 0.91-0.93, with an average probability of re-sighting a given female of 0.58 (Rivalan et al., 2005b). In St Croix, US Virgin Islands, the estimated annual survival probability for the nesting females is also high at ca. 0.89 (95% CI: 0.87–0.92; Dutton et al., 2005). The re-sighting probability of one given individual also depends on its reproductive frequency. In French Guiana and Suriname, ~70% of the leatherback population seems to nest every second year, while ~25% nest every third year (Girondot and Fretey, 1996; Rivalan et al., 2005b, 2006b; Hilterman and Goverse, 2007). The remaining individuals nest either every year or over a longer cycle, which might be up to 6 or 7 years long (Girondot and Fretey, 1996; Rivalan et al., 2005b, 2006b; Hilterman and Goverse, 2007). Females nesting after a 3-year migration have been reported to lay more clutches than after a 2-year migration (Rivalan et al., 2005b). Such a relationship between reproductive effort and previous migration duration is consistent with the principle of capital breeders, where females cover reproductive costs from body reserves gathered during migration (Drent and Daan, 1980). However, the above relationship seems to depend on the year considered (Rivalan, 2003; Georges, J.-Y and Fossette, S., unpublished data) and has not been observed at other sites such as in Costa Rica (Price et al., 2004). It was also suggested that the reproductive effort may rather be determined by climate-driven trophic conditions in the foraging areas (Hays, 2000; Broderick et al., 2001; Price et al., 2004; Wallace et al., 2006b; Saba et al., 2007) that impact on individual body condition and reproductive potential (Wallace et al., 2006a; Georges, J.-Y and Fossette, S., unpublished data). Thus, estimating body condition in gravid females at the end of their migration (Georges and Fossette, 2006) may provide important insights into their reproductive potential during the consecutive nesting season. Furthermore, improved estimates of the metabolic rate of leatherbacks (Bradshaw et al., 2007; Wallace and Jones, 2008-this issue) and the energetic content of their prey (Doyle et al., 2007) may help to resolve what drives nesting periodicity.

Briane et al. (2007) modelled the distribution of Observed Clutch Frequency (OCF, i.e. mean number of clutches laid per female per season) and showed that two categories of females are required to better describe the observations. In their model, one of the groups has clutch frequency obtained from a fitted lognormal distribution, while the females of the other group are considered to nest only once. However, an alternative would be to use another log-normal fit for the nest distribution of the second group (Girondot, M. unpublished data). This new model was used for the 2002 Awala-Yalimapo beach dataset because observation effort and cover for that nesting season was of good quality (Fig. 2A). The model performed better with a fitted nest distribution for the one-time nesters (Fig. 2B; Akaike Information Content=82.16) than with true one-time nesters (AIC=89.33) or only one group of females (AIC=152.10; Girondot, M., unpublished data). Therefore, rather than identifying one group as "one-time nesters", it would be better to distinguish between two groups, one with a lower and one with a higher mean number of nests. Using this method gives a mean number of nests per female of 1.03 and 8.17 for the group with a lower and higher number of nests, respectively.

3.2. Direct counting reveals population trends

Population monitoring was implemented in Suriname in 1964, in French Guiana in 1977, and in 1995 in Gabon. Consequently, most of the population monitoring data presented in this review is based on work conducted in French Guiana and Suriname, and to a lesser extent in Gabon. As leatherbacks nesting in the Guianas were reported to belong to a single genetic cluster (Dutton et al., 1999), the recent Memorandum of Understanding between the three Guianas signed by all three countries in 2006 have made data sharing possible. Similarly, the first study considering data collected in French Guiana and in neighbouring Suriname together has been recently published (Girondot et al., 2007). Similar published data do not yet exist for Africa. Females nesting in Republic of the Congo and Gabon probably belong to the same assemblage. However, very little information is available for Republic of the Congo rookery and it will therefore not be further discussed in this review. The most recent population estimate for adult leatherbacks in the North Atlantic is 34,000-94,000 animals, including 20,000-56,000 adult females, almost equally

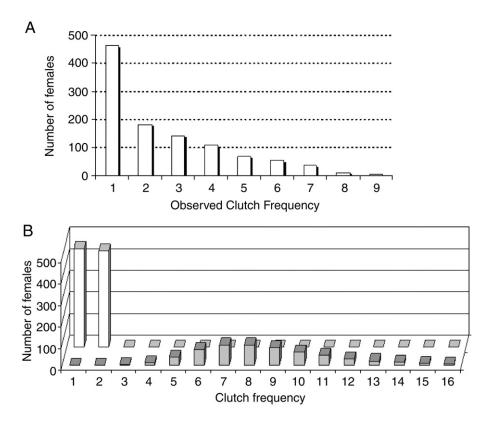


Fig. 2. (A) Distribution of observed number of nests per female (Observed Clutch Frequency) in 2002 at Awala-Yalimapo beach, French Guiana and (B) fitted distribution of the true number of nests per female for the two groups of females (low and high number of nests, respectively).

distributed between Africa and America (review in NOAA, 2007). Although the number of females is a preferred measure of population size, it is not always a directly usable figure as it requires specific and complex Capture–Mark–Recapture models that are either not available or not usable for all nesting sites. Thus, main effort should focus on the analysis of trends in the number of nests laid per year (e.g. Girondot et al., 2007).

3.2.1. Population trend of the Gabon rookery

In West Africa, the leatherback population was recently estimated to consist of 10,000–25,000 adult females (NOAA, 2007), with potentially more than half of these females nesting along the entire Gabonese coastline (Verhage et al., 2006). This estimate is based on a conservative Gabonese estimate of 30,000 nests per season, or approximately 15,000 adult females in the population, with 5 nests per female and a re-nesting interval of 2.5 years (Verhage et al., 2006). However, a precise estimate of the Gabonese leatherback population is not possible yet, due to the relatively recent start of turtle monitoring, the extended area covered by the nesting sites, and the lack of coordination and exchange of information between the different Gabonese partners in the past. However, in September 2004, a coordinated monitoring effort called "The Gabon Marine Turtle Partnership" was finally put in place. A first coherent National Status Report is expected before the end of 2008, integrating data from all five nesting beaches monitored in Gabon (Verhage, B., unpublished data).

3.2.2. Population trend of rookeries in French Guiana and Suriname

For the Suriname/French Guiana region, a first population estimate for leatherbacks was made by Pritchard (1971) with an average of 15,000 nesting females and a second assessment was made by Fretey and Lescure (1979), who suggested a population of 13,966-19,596 nesting females. Less than 20 years later, Spotila et al. (1996) estimated the number of nesting females at 5100-9700, representing over 40% of the world's leatherback population. However, annual counting effort varies in time and space both in French Guiana and Suriname, depending on funding opportunities and accessibility of areas. This results in dissimilar and incomplete nest count datasets that increase the difficulty of accurately estimating regional leatherback population size and trend. Two mathematical models have recently been implemented (Girondot et al., 2006; Gratiot et al., 2006) to deal with such variable and incomplete nest count datasets. The model of Gratiot et al. (2006) provides the total number of nests laid in a season at a given site where counting effort was not complete. It suggests that a monitoring effort of 20 to 30 days per beach randomly distributed throughout the entire nesting season would be the most effective strategy to assess nesting dynamics and provide valuable information on regional leatherback population size and trend (Gratiot et al., 2006; Kelle et al., 2007). The second model from Girondot et al. (2006) provides some population size estimates and allows comparisons across nesting beach datasets that contain dissimilar spatio-temporal gaps. However, despite these modelling studies and a monitoring effort that spans more than three decades, assessing a reliable trend for the Suriname/French Guiana population is still a challenge. In the following we would like to highlight some of the reasons for this.

In addition to the irregular nature of the annual monitoring, the monitoring of nesting leatherback turtles for 20 years (1977–1999) in French Guiana focused on Awala–Yalimapo beach (Fretey and Girondot, 1987, 1988, 1989; Girondot and Fretey, 1996; Girondot et al., 2007), from which the overall nesting activity was estimated. Annual nest numbers at Awala–Yalimapo beach have been decreasing since 1992 (Fig. 3A), while interannual variability is large (Chevalier and Girondot, 1998; Rivalan, 2003). Such variability in nest numbers at a nesting site may be driven by foraging conditions linked to environmental events such as ENSO or the NAO affecting the remigration rate of individuals (Hays, 2000; Broderick et al., 2001; Rivalan et al., 2006b; Saba et al., 2007). Furthermore, since the early 1990s, several beaches suitable for nesting have become available both in eastern French Guiana (near Kourou,

Irakompapi and Cayenne) and since late 1990s in western Suriname (Samsambo and Kolukombo). Hence, the apparently observed decline at Awala–Yalimapo might reflect a displacement of females from Awala–Yalimapo to these new sites (Rivalan et al., 2006a; Briane et al., 2007). Accordingly, tagging and recent tracking data indicate that females from Awala–Yalimapo beach may travel large distances during the breeding season and even nest in Suriname (Georges et al., 2007). Thus, the observed decrease at Awala-Yalimapo may be related to natural changes of the coastline, rather than indicating a real population decline (Rivalan et al., 2006a; Kelle et al., 2007).

The most recent estimates for the annual number of leatherback nests in Suriname over the 1999–2005 nesting seasons range between 6600 and 31,000, for a minimum of 1545 to 5500 females nesting annually (Hilterman and Goverse, 2007). In French Guiana, the majority of leatherback nesting beaches are monitored since 2001 and the most recent estimates of annual nest numbers over the 1999–2002 nesting seasons range between 11,140 and 24,900 (calculated from Girondot et al., 2007) for a minimum annual number of females ranging

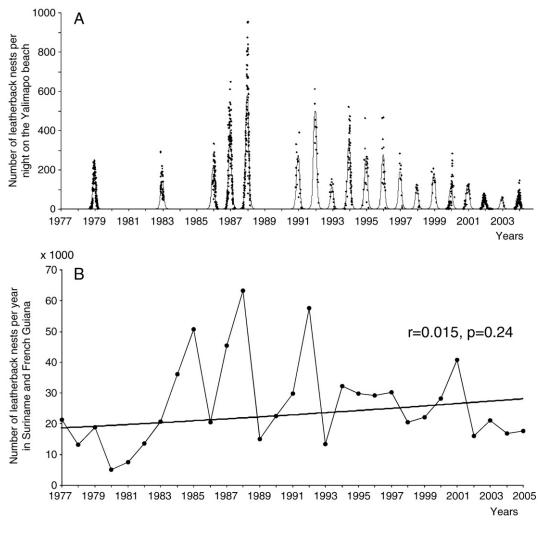


Fig. 3. (A) Number of leatherback nests per night observed in Yalimapo beach in French Guiana. The black line is the fitted model of nesting season (Girondot et al., 2006). (B) Trend of number of leatherback nests in Suriname and French Guiana. For a detailed methodology see Girondot et al. (2007). The fit is obtained using an exponential growth rate.

between 1342 and 3000 (calculated from Girondot et al., 2007; using an estimated clutch frequency of 8.3 nests per individual per year; Rivalan, 2003). This results in an estimate of 2900 to 8500 female leatherbacks nesting annually in French Guiana and Suriname compared to an estimate of 6000 females nesting annually in Gabon (Verhage et al., 2006). Data, collected between 1967 and 2002 in French Guiana and Suriname, have only been pooled recently in a modelling study that reports a low positive growth rate of 0.018 over the 36-year period investigated (Girondot et al., 2007). It has to be taken into account that the data of the high number of nests (>10,000) collected in Suriname during the 1980s and early 1990s are real underestimations (NOAA, 2007) of the true number of nests which is not corrected in the models. We added the most recent data for 2003-2005 to this database and analyzed the trend from 1977 until 2005 (Fig. 3B). We excluded data before 1977 from this analysis because the quality of survey was either very poor or unknown (Girondot et al., 2007). The trend defined as the instantaneous growth rate using an exponential growth is positive (r=0.015) but not significantly different from 0 (p=0.24). A conservative interpretation is that the leatherback population has been stable in French Guiana and Suriname during this period.

Population trend and size do not only depend on the quality of the different nesting sites (through its influence on nest and hatching success) but also on local threats to adult leatherbacks, both at sea and on land. We will discuss these aspects in the parts to follow.

4. Nest and hatching success at the two major leatherback rookeries

Nest success at Suriname and French Guiana nesting sites is low, with only 5 to 10% of nests being successful at Awala–Yalimapo beach, French Guiana (Girondot et al., 2002) and 22 to 35% at Galibi beach, Suriname (Chevalier, J., Desbois, X., and Girondot, M., unpublished data). Additionally, hatching success is very low at Awala–Yalimapo beach (33–39%; Girondot et al., 2007) and in Suriname (10.6–56.0%; Hilterman and Goverse, 2007). By contrast, the nest success in Gabon averages 54%, with a high hatching success of 67–69% (Verhage et al., 2006; Livingstone, 2006). For comparison, hatching success has been estimated around 75% at Culebra beach, Puerto Rico and 67% at St Croix beach, Virgin Islands (review in Livingstone, 2006).

Several factors, both natural and human-induced, may influence hatching success. Among natural factors, the location of the nest relative to the highest spring tide line and the vegetation line has a strong influence on the hatching success and on the sea-finding ability of hatchlings (Kamel and Mrosovsky, 2004). Indeed, flushing by extreme high tides as well as erosion may lead to the natural destruction of egg clutches (Verhage et al., 2006). In addition, nest-site selection seems to significantly influence predation rate of eggs (Caut et al., 2006b). On nesting beaches, the high concentration of leatherback eggs attracts different predators such as dogs, raccoons, coatis, birds (e.g. *Coragyps atratus*; Bechstein, 1783), ghost crabs *Ocypode*

quadrata (Fabricius, 1787), and mole crickets (e.g. Scapteriscus didactylus; Latreille, 1804) that prey both on eggs and hatchlings (Fretey and Lescure, 1981; Maros et al., 2003; Girondot, 2006; Verhage et al., 2006; Livingstone, 2006; Hilterman and Goverse, 2007). For instance, leatherback egg predation by mole crickets is ~18% at Awala-Yalimapo beach, French Guiana (Maros et al., 2003) and ~41% at Galibi beach, Suriname (Hilterman and Goverse, 2007). In addition, at Awala-Yalimapo beach tens of nests are predated every year by feral dogs, which local authorities consider a major threat (Girondot, 2006). Hatchlings are also threatened by near-shore marine predators (catfish and sharks). The role of predation in the ecology of adult leatherbacks still needs to be explored. Indeed, in green turtles, the role of predation in driving behavioural patterns has recently been demonstrated (Heithaus et al., 2007, 2008-this issue). For instance, at Shark Bay, Australia, herbivorous green sea turtles threatened by tiger sharks (Galeocerdo cuvier; Péron and LeSueur, 1822) select microhabitats according to their body condition. This highlights that predatory pressure may modify the spatio-temporal pattern of turtle grazing and ultimately their impacts on ecosystem dynamics (Heithaus et al., 2007, 2008-this issue).

Density-dependent nest destruction has been suggested as another factor that may explain the low hatching success at the Suriname/French Guiana beaches (Girondot et al., 2002; Caut et al., 2006a). In this context, a modelling approach demonstrated that a high female density increases intraspecific nest destruction (Caut et al., 2006a). However, at Awala—Yalimapo beach, for example, the maximum number of nests recorded is two to three times lower than its predicted maximum carrying capacity (Girondot et al., 2002; Caut et al., 2006a). This would suggest that there is probably no direct link between low hatching success and density-dependent nest destruction by other nesting females.

Among human-induced factors, egg poaching still occurs at the main leatherback nesting beaches and has a strong impact on hatching success. In western Africa, marine turtles have suffered from high rates of egg poaching and killing of adults for consumption in the past (Verhage et al., 2006). Even today such behaviour continues and high poverty levels place an enormous pressure on sea turtle populations, while current protection efforts are often insufficient to significantly reduce such human pressure (Formia et al., 2003). In addition, leatherback products are also important components in traditional medicine and voodoo practices (Fretey et al., 2007a). Hence, conservation initiatives surely have to take the sociocultural aspects of turtle use in Africa into consideration. In Suriname, egg poaching is nearly 100% at unmonitored beaches (Hilterman and Goverse 2006). In 1990-1993 no sea turtle nests were protected in the Galibi Nature Reserve due to the occupation by rebellious Amerindians and these years approximately 90% of all sea turtle nests were poached, like the situation before 1967 (Schulz, 1975). Even at beaches where the local association for sea turtle conservation Foundation for Nature Conservation Suriname (STINASU) is present, it occurs fairly regularly (Mohadin, 2000; Dijn, 2001). By contrast, in French Guiana, poaching of leatherback nests is rare (less than 5% of the nests laid in French Guiana; ONCFS, pers. com.). This might be explained by local preferences for green and olive Ridley turtle eggs for consumption and animist belief. In addition, the continuous presence of people patrolling the nesting sites as part of scientific, conservation, and education programs appears to dissuade poachers from frequenting the main beaches in French Guiana but also in Suriname. This human presence also reduces other human-induced threats, such as disturbance by domestic dogs, killing of adults, beach degradation and pollution, or artificial lighting (Fretey, 2005; Girondot, 2006). Indeed, a high juvenile mortality may result from a disorientation of hatchlings due to light pollution at the nesting beaches. At Pongara beach in Gabon, 27 of 41 observed nests (66%) had significant numbers of hatchlings walking away from the ocean and towards artificial lights (Deem et al., 2007). Similarly, between 2% and 56% of the nesting females may become disoriented and walk away from the sea, rather than towards it, resulting in some mortality (Deem et al., 2007). In French Guiana, street lights are not present in Awala-Yalimapo village, while light pollution from the adjacent residential areas still poses a problem at the Cayenne nesting beaches. With respect to chemical pollution, organochloride pesticides have been detected in the sand of Awala-Yalimapo beach, French Guiana, most likely originating from pesticide use in plantations and malaria prophylaxis (Guirlet, 2005). In addition, gold mining inland results in unknown quantities of mercury-derived components being washed out by large rivers such as the Marowijne/Maroni and the Mana rivers in French Guiana and the Suriname River in Suriname. The consequences of these exposures are still unknown and require more investigation, not only for turtles, but also for the local human populations.

5. Artificial hatcheries and sex-ratio manipulation

The use of artificial hatcheries, using either the natural environment or incubators, may increase hatching success. Both methods were used widely in the past and, to a lesser extent, even in the present, with varying success (e.g Pritchard, 1980; Dutton and Whitmore, 1983; Girondot et al., 1998, Hoekert et al., 1998). At Awala-Yalimapo, French Guiana, artificial hatcheries in incubators were active between 1981 and 1993. These hatcheries incubated up to 7247 eggs per year but the hatching success never exceeded 50% (Fretey et al., 1986). Relocation of eggs to an open-air hatchery on the beach also occurred at Awala-Yalimapo beach but resulted in significantly lower hatching success rates than when eggs were left undisturbed at the beach (Caut et al., 2006a). At Cayenne, a similar project was operating between 2000 and 2003, during which time a total of 80 nests of both olive Ridley and leatherback turtles were relocated. Hatching success was high for olive Ridleys (67%) but low for leatherbacks (40%) (de Thoisy, B., unpublished data). Consequently, it was suggested that the best way to increase hatching success in turtles would be to focus on natural nests and stop translocation of nests to hatchery. In Gabon, an open-air hatchery was introduced in 2004 in an attempt to protect nests. Still, during the 2004/2005

season, hatching success for the hatchery nests (46%) was significantly lower than for the in-situ nests (83%) (Verhage et al., 2006) which might be explained by the method used to translocate eggs from the beach to the hatchery. However, during the 2005/2006 season, a different translocation technique was used to move the nests to the hatchery, which was much less intrusive and involved less direct handling of the eggs (Livingstone, 2006). Consequently, the hatching success within the hatchery (n=15 nests) was increased to 69%, which was similar to the success of the in-situ nests (Verhage et al., 2006). As a consequence of this trial, it was recommended that translocated nests should be dug deeper and regularly filled with clean sand from the beach, in order to maximise their hatching success. Thus, in Gabon, open-air hatcheries seem to be very effective in keeping out predators and also in keeping the nests safe from the other threats present at the beach. They therefore help to increase hatchling production, while also raising awareness for turtle protection amongst school children and tourists visiting the infrastructures. A recent study supports this conclusion, highlighting the increase of a Caribbean nesting population (Ste Croix, US Virgin Island) because of an intensive program for beach protection and egg relocation carried out over a long period (>20 years) (Dutton et al., 2005).

Leatherbacks, like all marine turtles, exhibit temperaturedependent sex determination (TSD). A pivotal temperature for sex determination (theoretical temperature that produces the same proportions of males and females hatchlings) of 29.5 °C was first determined for leatherback turtles by experiments on artificially incubated nests at Awala—Yalimapo beach (Rimblot et al., 1985; Rimblot-Baly et al., 1986). Because of TSD, the sex ratio of the hatchlings changes during the nesting season in tropical nesting sites. During the wetter, cooler months in the middle of the nesting season more males are produced, while more females hatch during the drier, warmer months at the start and end of the season (Mrosovsky et al., 1984). Such seasonal pattern in the production of male/female hatchlings may have important implications for sea turtle conservation programs that involve manipulation or harvesting of eggs. Furthermore, given TSD, global climate change will likely bias turtle reproduction in favour of females, even if mean nest temperatures will only increase by a few tenths of a degree. Godfrey et al. (1996) reported that 69.4% of the hatchlings produced at Matapica beach, Suriname, in 1993 were females, while this percentage was only ~59% in 1982 (Mrosovsky and Provancha, 1989). Although such pattern could be driven by global climate change, sex-ratio estimates also vary considerably between years (Godfrey et al., 1996; Davenport, 1997; Hawkes et al., 2007).

Still, there have been several attempts to enhance sea turtle populations by manipulating the sex ratio to highly feminized populations, using high incubation temperatures (review in Girondot et al., 1998) or estrogenic treatment (e.g. Desvages et al., 1993). However, introducing a strongly female-biased sex ratio in a natural population for a long period may favour masculinizing alleles and have unexpected long-term effects. Indeed, when the manipulation is stopped, the primary sex ratio as well as the adult sex ratio become male-biased and ultimately

result in the decrease in population size (Girondot et al., 1998). Additionally, estrogenic treatment of embryos has been shown to produce females that might be unable to evacuate eggs from the oviduct due to morphological changes (Girondot et al., 1998). For these reasons, it has been suggested that conservation actions should rather focus on the adult population and natural nesting sites to improve adult survival and incubation conditions at these sites. Despite the implementation of significant management measures at nesting sites for several years and even decades now, further improvement is still needed to mitigate the impact of tourism, beach pollution and predation. Such measures include beach patrols, nest protection reinforcement, and the wide diffusion of information towards local inhabitants and tourists. However, the success of conservation measures at nesting beaches also depends on adult mortality rates at sea. For example, egg protection measures at the rookery in Terengganu, Malaysia may have been ineffective due to high adult mortality from coastal fisheries (Chan et al., 1988).

6. At-sea based monitoring

6.1. Incidental capture in fisheries

Accidental catches of sea turtles by fisheries in coastal and shelf waters have recently been identified as a rapidly emerging threat, particularly for leatherbacks (FAO, 2004; James et al., 2005; Parnell et al., 2007). In the Gulf of Guinea, hundreds of leatherbacks are thought to be caught by traditional and commercial fisheries. In Gabon for instance, industrial trawlers and illegal small fishing vessels are commonly reported within Mayumba National Park (in Georges et al., 2007). These illegal fishing boats use long nets deployed very close and parallel to the shore, forming a barrier, which prevents turtles from coming ashore to nest (Parnell et al., 2007). Studies evaluating bycatch are slowly getting underway in some countries of this region.

In French Guiana and Suriname, leatherback turtles regularly become entangled in coastal gillnets. Gillnet entanglement was first reported in 1979 and was recently confirmed to occur frequently within the Maroni estuary (Chevalier, 2001), most likely as a consequence of the increasing illegal fishing pressure (Ferraroli et al., 2003; Kelle, L., unpublished data). Fishermen mainly use nets with a large mesh size that are several kilometres long and which are deployed throughout the leatherback nesting season (Blanchard, F., IFREMER, pers. com.), putting turtles under substantial threat (Ferraroli et al., 2003). For instance, the accidental capture rate of leatherbacks linked to coastal fisheries during the nesting season in the Maroni estuary was estimated to vary from one turtle per day (Chevalier et al., 1998; Chevalier, 2001) to 10% of the nesting population in some years (Georges et al., 2007). A study based on interviews with fishermen estimated that leatherbacks represent 70-85% of the marine turtles incidentally captured by coastal gill-netters in French Guiana (Delamare, 2005). This percentage is similar to the proportion of nesting leatherbacks in the overall nesting population of sea turtles in this region, suggesting that bycatch does not specifically affect leatherbacks in terms of survival. Injuries potentially related to interactions with fisheries (i.e. scars on shoulders, presence of a

hook or a piece of net) have been recorded in 8% to 18% of the nesting females at sites in French Guiana and Suriname (NOAA, 2007; Hilterman and Goverse, 2007). It should be noted that these injuries represent the sum of injuries, accumulated during the lifetime of females. In addition, it is important to point out that new oil or gas stocks have recently been discovered in Gabon and also in French Guiana and Suriname, which may increase threats to areas used by marine turtles for nesting, foraging, and migration (Weir, 2007).

For international oceanic waters, it has been shown that industrial fishing fleets, such as the long-line fishery for pelagic predatory fish, aggregate in the same areas as leatherback turtles (Ferraroli et al., 2004), thereby increasing the probability of incidental catch (Carranza et al., 2006). Indeed, it has recently been shown that bycatch of turtles in the long-line fishery is substantial and may be equally high as in gillnets and trawl fisheries (Lewison et al., 2004a, 2004b; Carranza et al., 2006; Lewison and Crowder, 2007).

6.2. Stranding events

In Suriname, between 6 and 43 dead leatherbacks washed ashore every year during the nesting seasons 2000-2005 (Hilterman and Goverse, 2007). In French Guiana, stranding events are also frequent and highly variable between years (Chevalier, 2001). At Cayenne, between three and five leatherbacks typically wash ashore every year (de Thoisy, B., unpublished data). However, at Awala-Yalimapo beach, 54 dead leatherbacks were recorded in 2001 (Chevalier, 2001). In Gabon, 19 dead leatherbacks were found at a beach within Mayumba National Park during the 2006 and 2007 nesting seasons (Parnell et al., 2007). Most of the stranded turtles were injured, most likely a consequence of incidental fisheries capture or accidents with boat propellers (Spotila et al., 1996, 2000; George, 1997; Lutcavage et al., 1997). It should be noted that the number of stranding events is relatively small, given the potentially high risk for accidental capture. This may be due to the fact that either the majority of dead animals do not wash ashore at the monitored beaches or that females manage to avoid fishing nets. Dead leatherbacks are however observed, during aerial surveys on the mudflats in remote areas.

Consequently, before implementing conservation strategies in an attempt to limit turtle bycatch, the first step is to clearly identify areas where leatherbacks may gather, and to detail their vertical and horizontal movements, so that a better understanding of their potential interactions with fisheries can be achieved (Hays et al., 2004; Ferraroli et al., 2004; James et al., 2005; Eckert, 2006; Georges et al., 2007; Zbinden et al., 2007). With the emergence of new technologies (e.g. satellite telemetry), this challenging task is now achievable.

6.3. At-sea tracking

At-sea movements of marine turtles were historically studied through the opportunistic recovery of flipper tags (e.g. for leatherbacks see Pritchard, 1973, 1976; Fretey and Girondot, 1996; Girondot and Fretey, 1996). Such approach illustrated the

great mobility of leatherback turtles, since tags attached to leatherback turtles nesting in French Guiana and Suriname were recovered around the Atlantic Ocean, in the USA, Mexico, Venezuela, Spain, France, Marocco, Canada, and Ghana (review in Girondot and Fretey, 1996). In 1987, the first leatherback turtle was satellite-tracked for 3 weeks, following her departure from French Guiana (Duron-Dufrenne, 1987). Since this first deployment, tracking technology has evolved steadily, currently enabling us to track leatherbacks for up to 2 years (e.g. Eckert, 2006; Hays et al., 2006).

During the nesting season in French Guiana, Suriname and Gabon, satellite-tracked leatherbacks were shown to disperse across the continental shelf—from the coastal zone to the shelf break—and move extensively over hundreds of kilometres, crossing national boundaries (Suriname and Republic of the Congo respectively; Fossette et al., 2007; Georges et al., 2007; Fig. 4). For instance, leatherbacks spend between 40% and 70% of their time at sea at the border between French Guiana and Suriname in waters <20 m deep where they intend to forage (Fig. 4; Fossette et al., 2007, in press, submitted for publication; Georges et al., 2007). It is worth noting that in French Guiana and Suriname tracking of gravid leatherbacks was only conducted with animals from nesting sites around the Maroni estuary, while nesting events have been recorded along the entire shore. This probably biases the recorded distribution of leatherbacks during the nesting season and emphasises the need for deployment of satellite transmitters at other nesting sites.

Once the distribution area has been identified, one option to mitigate interactions with fisheries is to implement marine protected zones (Morreale et al., 1996; Hyrenbach et al., 2000). In Suriname, a "no-fishing zone" is in place every year during

the leatherback turtle's main nesting season (Mohadin, 2000). These fishing restrictions have been endorsed by the Suriname State following the request from the Galibi Amerindian community. However, at the regional scale, implementation of such protected areas is questionable. In Guyana, a similar "nofishing zone" was experimentally introduced (Pritchard, 2001) but did not lead to a consensus to maintain fisheries restrictions on an annual basis. In French Guiana, the Amana Nature Reserve includes a 30-m wide "no-fishing zone" (Fig. 1A) which is not sufficient given the leatherback's distribution during the nesting season. In addition, the way some coastal nature reserves within inhabited regions were created (i.e. without local consultation of inhabitants) led to misunderstandings with local communities (Collomb and Girondot, 2006). The result of such actions is often a real distrust in any kind of protected status for particular areas that might be required for turtles.

Secondly, the leatherback turtle nesting distribution in the region is highly heterogeneous in space and time (Kelle et al., 2007; Hilterman et al., in press). In Suriname, the Wia Wia Nature Reserve (Fig. 1A) was implemented in 1961 to protect major nesting sites. Despite an enlargement of the reserve in 1966, it no longer hosted any nesting leatherback turtles in 1974, as sandy beaches moved westward, outside the nature reserve's boundaries (Reichart and Fretey, 1993). Similar limitations might apply for marine protected areas expected to cover the overall marine range of leatherback turtles in the region. It is unlikely that terrestrial and marine protected areas could cover large enough areas to ensure the long-term survival of the leatherback turtle in French Guiana/Suriname. Thus, it is important to continue working with the different fishing communities, to investigate alternative fishing techniques. Ideally,

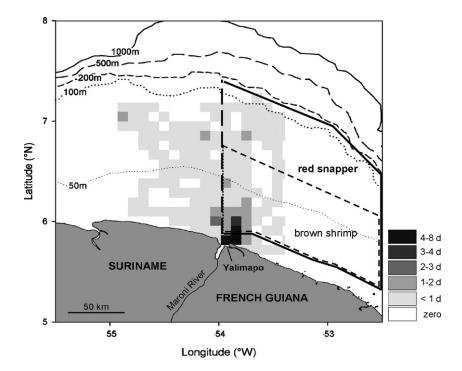


Fig. 4. Topographic representation of space use by 10 tracked leatherback turtles during inter-nesting movements off French Guiana in 2004, in relation to bathymetry and local fisheries targeting red snapper $Lutjanus\ purpureus$ (solid bold line) and brown shrimp $Penaeus\ subtilis$ (dashed fine line). Grey shading denotes total time turtles spent in each $0.1 \times 0.1^{\circ}$ square. Modified from Georges et al. (2007).

these techniques should maintain high catch rates for targeted species, while mitigating any kind of bycatch, as has been achieved with the long-line fishery in the Pacific Ocean (Gilman et al., 2006), or with the shrimp trawlers in French Guiana and Suriname.

During their long distance, post-nesting movements, leatherback turtles from French Guiana, Suriname and the Caribbean disperse widely throughout the North Atlantic Ocean, following variable patterns (e.g. Ferraroli et al., 2004; Hays et al., 2004, 2006; Eckert, 2006). However, they spend a great amount of time in a few hotspots (e.g. the Azores, the Gulf Stream area, or the Cape Verde islands; Eckert et al., 2006; Eckert, 2006), where they meet pelagic long-line fisheries (Ferraroli et al., 2004; Lewison et al., 2004a, b). Leatherbacks nesting in Gabon may move across the Atlantic to South American waters off Argentina and Brazil (Transatlantic migration; Billes et al., 2006). They may also undertake a trans-African migration towards the southern end of the African continent (Fretey et al., 2007b). At both sites, turtles might be caught accidentally, particularly in the highly exploited Benguela system. Leatherback hotspots are mainly critical deep sea habitats (Eckert et al., 2006), where conservation efforts should be reinforced (Ferraroli et al., 2004; Eckert et al., 2006; Eckert, 2006). Pelagic protected areas may be a solution but to be effective, they will require dynamic boundaries (since pelagic habitats are not fixed), wide dimensions, and international scheme management (Hyrenbach et al., 2000). Consequently, establishment of such protected areas may require further enforcement, research, and monitoring programmes before effective boundaries can be determined. Indeed, novel data analysis procedures and ever expanding sample sizes will allow identification of important foraging habitats for turtles at sea with improved accuracy (Jonsen et al., 2006; Gaspar et al., 2006; Kobayashi et al., 2008this issue). It has to be stressed, however, that due to global climate change the foraging range of leatherbacks might change and the demographic implications of this will need to be considered (McMahon and Hays, 2006).

In short, the most urgent conservation needs would appear to be changes in fishing practices in some defined priority areas that are particularly sensitive. This would require onboard observers for the fishery, so that the impact of bycatch in both coastal and oceanic areas can be reliably evaluated and the appropriate measures for mitigation can be determined (Parnell et al., 2007). However such an ambitious observer program is still largely absent both at the regional and international levels.

7. Conclusions

While the leatherback turtle is protected by many international agreements and classified as a critically endangered species by the IUCN (2007), some concrete measures are still needed at the local, national and regional scales to reinforce current conservation initiatives. In this context, research activities can play an important role in guiding conservation projects, once they are implemented in collaboration with key partners and when research initiatives demonstrate a conserva-

tion-driven objective. For instance, a national plan of recovery for marine turtle populations in French Guiana has recently been validated by the French administration. The aim is mainly to reduce human-induced threats by (1) assessing capture and mortality rates by fisheries to reduce bycatch, (2) controlling legal/illegal fisheries and their practices, (3) reducing poaching of eggs and killing of adults, (4) maintaining beach monitoring and demographic studies, (5) expanding research into the effects of environmentally driven changes on reproductive parameters, such as clutch frequency and remigration intervals, to improve the interpretation of nesting beach trends, (6) reducing habitat damage and artificial light pollution, (7) raising awareness amongst the native human population and tourists, and (8) reinforcing regional cooperation between neighbouring countries. Lastly, another important conservation aspect for marine turtle populations would be the focus on the survivorship of juveniles and subadults, which are identified as one of the main factors driving population dynamics (Heppell, 1998) but also on the life-history of males which is almost unknown.

We conclude that solutions to the numerous threats that leatherback turtles face do exist. However, conservation measures have to be implemented urgently and/or rigorously applied at both the regional and international level, if we want to maintain the apparently positive trend that currently exists for the last major leatherback rookeries.

Acknowledgments

We thank GC Hays for inviting us to submit this review, F Blanchard, IFREMER, and E. Hansen, ONCFS for personal communications and M Enstipp for correcting the English. The preparation of this review was supported by a studentship from the French Ministry of Research to S. F. [SS]

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