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Oceanic survival and movements of wild and captive-reared immature green turtles (*Chelonia mydas*) in the Indian Ocean

Dominique Pelletier ^{a,*}, David Roos ^b, Stéphane Ciccione ^c

^a Lab. MAERHA, Institut Français de Recherche pour l'Exploitation de la Mer, IFREMER, BP 21105, 44311 Nantes cedex 3, France

^b IFREMER La Réunion, rue, Jean-Bertho, B.P. 60, 97822 Le Port cedex, France

^c Centre d'Etudes Des Tortues Marines (CEDTM), BP 40, 97436 St-Leu, France

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Abstract

The ability of captive-reared turtles to survive in the wild is not precisely known, nor are movements of immature turtles in the open ocean. To provide information on these issues, a satellite tracking experiment was conducted in the western Indian Ocean to monitor oceanic movements of immature green turtles. Two wild turtles and four captive-reared individuals were tracked. The latter had been displaced after birth from nesting sites to a distant rearing site. Wild turtles survived after release, but did not move far away from release site. We hypothesize that this resident behaviour may be explained by stage-specific habitat requirements. Captive-reared turtles survived after release and migrated over thousands of kilometres. Among these, the oldest immature turtles retrieved the foraging sites of their native population, with movement patterns similar to those displayed by adults. Observed movements may be linked to hydrographic conditions such as general oceanic circulation, sea temperature and thermal fronts.

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1. Introduction

Although protected sea turtle populations have critically declined over the last century, in particular due to destruction of nesting habitats, directed subsistence and commercial hunting, and harmful incidental fishing mortality (Eckert, 1995; Spotila et al., 2000). Conservation measures based on the knowledge of spatial distributions and migration patterns could help to reduce incidental catch by fisheries. Also, release of young animals caught as hatchlings and protected from predation and fishing during their first years has been envisaged as a way to enhance wild populations. However, the ability of captive-reared animals to survive release to the wild is not precisely known, nor are movements of immature turtles in the open ocean.

Sea turtles travel periodically throughout their life cycle. Mature individuals periodically migrate between breeding and foraging sites that may be thousands of kilometres apart. Immature green turtles (*Chelonia mydas*) leave the nesting

site as hatchlings and live in the open ocean at least a year, sometimes associated with algae rafts (Carr and Meylan, 1980; Carr, 1987). During this pelagic stage, they are mostly carnivorous. Between 3 and 5 years of age, they move to coastal habitats, becoming omnivorous and then herbivorous (Bjorndal, 1985). The spatial distribution and migration patterns of immature sea turtles are thought to depend upon environmental factors like oceanic fronts and gyres (Carr, 1987; Polovina et al., 2000). However, movements of immature turtles are poorly understood, as they can only be observed when they depart their place of birth, or when they are incidentally caught by offshore fisheries (Polovina et al., 2000). Mark-recapture experiments traditionally used for adult turtles (Le Gall and Hughes, 1987; Limpus et al., 1992; Miller et al., 1998) require that animals bear tags for long periods, and that the probability of recapture is large enough to get a significant number of observations. Recapturing immatures in the ocean is problematic because they are small, widely distributed and suffer intense predation; consequently there are few such experiments conducted (Limpus et al., 1992; Wood and Wood, 1993). Like mark-recapture techniques, satellite tracking requires that transmitters do not

* Corresponding author.

E-mail address: dpellet@ifremer.fr (D. Pelletier).

alter health or behaviour. To date, it has mostly been used for breeding adults to study post-nesting migrations from nesting sites to foraging sites (Balazs et al., 1994; Cheng, 2000; Godley et al., 2002; Hatase et al., 2002; Hays et al., 2001; Hughes et al., 1998; Limpus and Limpus, 2001; Limpus et al., 1992; Luschi et al., 1996, 1998; Morreale et al., 1996; Mortimer and Balazs, 2000; Nichols et al., 2000; Papi et al., 1995; Roos et al., 2001). This methodology was also used for studying movements and diving behaviour on foraging areas or nesting areas (Godley et al., 2002; Hays et al., 1991, 1999, 2000, 2001; Renaud and Carpenter, 1994; Stoneburner, 1982) and seasonal migrations (Bentivegna, 2002). As for young turtles in the pelagic environment, the only reported satellite tracking experiment concerned wild loggerhead turtles (*Caretta caretta*) in the Pacific (Polovina et al., 2000). In the neritic environment, movements of juvenile turtles have been tracked from radio or sonic transmitters for loggerheads (Gitschlag, 1996; Timko and Deblanc, 1983) and for green turtles (Brill et al., 1995).

In addition to fishing and hunting mortality, immature turtles are subject to intense predation from birds and crustaceans at nesting sites, and from pelagic species in the ocean. In many countries, projects have been undertaken to enhance natural populations by growing hatchlings in captivity and releasing them into the wild (see review in Mortimer, 1995). Many projects were evaluated ineffectively, partly because methods to monitor released animals were lacking (but see Wood and Wood 1993). Furthermore, whether captivity affects the ability of turtles to survive in the ocean and to resume a natural migratory behaviour remains unknown (Mortimer, 1995).

In this paper, we report the findings of a satellite tracking experiment that is innovative in two respects: (i) it is the first reported experiment carried out on immature green turtles; and (ii) it is the first time turtles reared in captivity since their birth were released and monitored through satellite telemetry. The objectives of the experiment are to (i) evaluate the ability of turtles displaced from their birth place as hatchlings and reared in captivity to survive in their native environment; and (ii) study the movements of immature green turtles in the pelagic environment.

2. Materials and methods

2.1. Selection of captive-reared turtles

Hatchling green turtles were caught on Tromelin (15° 33 S and 54° 31 E, Fig. 1) during summer, from 1989 to 1992, and transferred to the laboratory in La Reunion (21° S, 55° E), i.e. hundreds of kilometres away from their nesting site. They were placed in 20 m³ tanks and fed with floating granules (Biomar, Inc., France) for 5 years. Twenty healthy animals were selected for the experiment, and their ability to feed on natural food was first tested. They were fed various live or dead fish (*Oreochromis mossambicus*) weighing from 35 to 350 g each, squid (*Loligo*), small crabs (*Grapsus*) and land

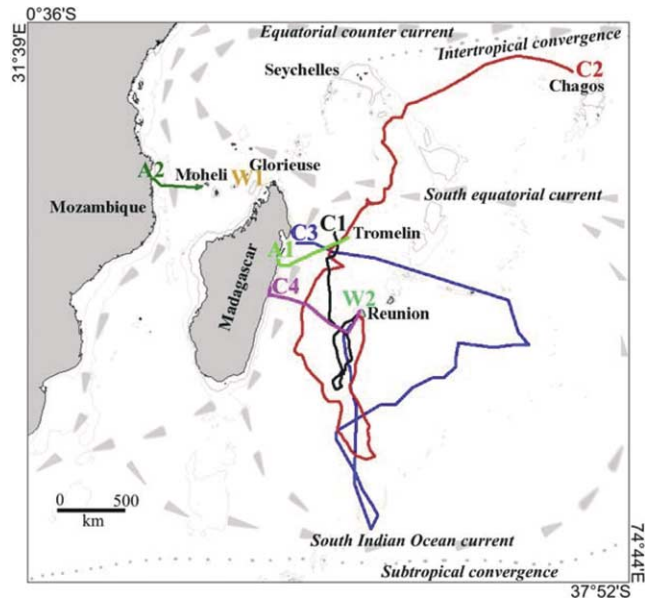


Fig. 1. Trajectories of tracked turtles (see Table 1 for details about turtles). Large-scale oceanic currents and convergence areas are also reported (gray arrows and dots, respectively) after Humbert-Droz and Jullien (1983).

vegetable (*Scovea taccata*). Four turtles could not feed on this food. After 6 or 7 weeks, they became motionless and stayed apart from other individuals. However, they were still reactive to human stimuli, and they did not lose weight. They resumed feeding when they were offered floating granules. We assumed these turtles would not be able to survive in the ocean. Note that these were the only individuals older than 8 years. In contrast, 16 individuals could be fed on natural food, and after 6 months, they were healthy with a weight either stable or increasing. In a final step aimed at dissociating human presence from feeding, these turtles were placed in individual tanks for 3 weeks with no other food than live fish. After this experiment, turtles were no longer attracted by human presence near their tank. We assumed they were ready to return to sea where they would hunt to eat.

2.2. Selection of wild turtles

We also tracked two wild immatures for comparison with captive-reared turtles. Turtle W1 was caught close to a nesting beach on Glorieuse (Fig. 1). It was uninjured and could be released a few hours after being caught. Turtle W2 was incidentally injured and caught by fishermen offshore from La Reunion. It was healed in an individual tank at the laboratory for 6 months, being fed with live fish and dead squid.

2.3. Tracking experiment

Satellite transmitters manufactured by Telonics, Inc., (Mesa, Arizona, USA) were attached to four immatures out of the 16 captive-reared turtles, and two wild immatures (Table 1).

Each satellite transmitter was attached on the dorsal carapace with fibre-glass cloth and resin following the technique

Table 1

Turtles released and corresponding transmitters. Transmitters were manufactured by Telonics, Inc. (Mesa, Arizona, USA). Duration of the monitoring period mostly depends on duty cycle. For instance, due to on-continuously duty cycle, turtle C1 was precisely tracked, but only for 55 d. Turtle W2 was monitored only for 56 d because it was recaptured by fishermen and brought back to the laboratory for treatment. Transmitter weights are 200 g for ST-18, 325 g for ST-6, and 350 g for ST-10 transmitters. This corresponds to a proportion of body weight of 2.5% for W2, and at most 0.8% for the others. Adults are only reported for comparison with immatures. They were equipped with a transmitter after they laid eggs at nesting sites

Turtle	Birth place	Age (years)	Curved carapace	Weight (kg)	Transmitter type	Duty cycle
			Length (cm)			
C1	Tromelin	5	70	45.5	ST-10	Continuous
C2	Tromelin	6	77	52.8	ST-10	6 h on, 6 h off
C3	Tromelin	9	69	45.0	ST-18	6 h on, 30 h off
C4	Tromelin	9	75	42.0	ST-18	6 h on, 30 h off
W1	Unknown (wild turtle)	4–5	56	Not measured	ST-18	6 h on, 30 h off
W2	Unknown (wild turtle)	3–4	44	7.7	ST-18	6 h on, 30 h off
A1	Probably Tromelin	Mature female	–	Not measured	ST-6	Continuous
A2	Probably Moheli	Mature female	–	Not measured	ST-18	6 h on, 30 h off

Table 2

Characteristics of trajectories followed by tracked turtles. The standard deviation of average speed is reported between parentheses, with the number of points (*n*) from which the average and standard deviation were calculated

Turtle	Deployment date	Days monitored	Minimum distance traveled (km)	Average speed (km h ⁻¹)	
C1	25th March 1998	55	2485	2.44 (1.65) (<i>n</i> = 176)	
C2	10th October 1998	158	6884	2.95 (1.72) (<i>n</i> = 531)	
C3	1st August 2000	154	5833	1.70 (0.60) (<i>n</i> = 20)	
W1	15th June 2000	156	11	0.02 (0.013) (<i>n</i> = 4)	
W2	11th December 2000	56	94	0.85 (1.67) (<i>n</i> = 21) ^a	
C4	11th December 2000	82	1017	In open sea	3.14 (1.91) (<i>n</i> = 35)
				On sea grass beds	0.37 (0.43) (<i>n</i> = 7)
A1	7th April 1998	30	1120	On nesting site	0.17 (<i>n</i> = 1)
				In open sea	2.90 (0.37) (<i>n</i> = 9)
				On sea grass beds	0.29 (<i>n</i> = 1)
				On nesting site	0.23 (0.28) (<i>n</i> = 12)
A2	10th May 2001	113	608	In open sea	0.68 (0.75) (<i>n</i> = 5)
				On sea grass beds	0.10 (0.04) (<i>n</i> = 4)

^a These values mostly rely on two large speeds observed immediately after release, the turtle swimming away quite rapidly. When these values are excluded, the average speed falls down to 0.25 with a standard deviation of 0.46.

described by Balazs et al. (1996). Transmitter weight ranges from 200 to 350 g, depending on transmitter type (Table 1). The western Indian Ocean is covered by NOAA satellites NOAA-11, NOAA-12 and NOAA-14. Transmitter data were received and collected by the Argos CLS¹ system, which classifies signal locations in six location classes (LC): 3, 2, 1, 0, A and B. For LC greater or equal to 1, accuracy is less than 1000 m in latitude and longitude, namely <150 m for LC 3, <350 m for LC 2, and <1 km for LC 1. No accuracy limit is available for LC 0. Locations in LC A and B are based on a lesser number of signals, and were thus excluded from results. Only fixes in classes 0, 1, 2 and 3 were retained for computing distances travelled and swim speeds. We did not distinguish signals received during day time from those received at night. In addition to transmitters, a Monel tag, and a passive integrated transponder were fixed on the right anterior flipper of each individual to identify turtles upon recapture after the transmitter stopped operating.

Six immature turtles were released from March 1998 to December 2000 (see Tables 1 and 2 for details). Turtles grown in captivity (C1–C4) were released from La Reunion at different times of the year to examine their movements in response to environmental variables. Their age is perfectly known (Table 1) since they were caught as hatchlings. Although C1–C4 were approximately of the same size, C3 and C4 were close to sexual maturity. The wild turtle W2 was released the same day as C4 to compare their behaviour. Apart from W2, each turtle was kept in a tank for 2 d to check that behaviour was not perturbed by the transmitter. Although this was apparently not the case, we cannot formally exclude the possibility of perturbations of movement energetics and turtle's maneuverability (Watson and Granger, 1998).

In addition to immatures, we here report results from another tracking experiment on two nesting females (A1 and A2) undertaking their post-nesting migration from nesting sites (Tromelin and Moheli) to foraging sites (Fig. 1). These results will be used for comparison with the oldest immature turtles C3 and C4.

¹ Argos CLS, 2002. User's manual. http://www.cls.fr/manuel_fr/

2.4. Computation of distances and speeds

The distance travelled between two successive signal locations 1 and 2 was estimated from the classical equation:

$$d(x_1, x_2) = \text{Radius } a \cos(\sin(\text{lat}_1) \sin(\text{lat}_2) + \cos(\text{lat}_1) \cos(\text{lat}_2) \cos(\text{lon}_1 - \text{lon}_2))$$

where *Radius* is earth radius, and lat_i and lon_i are latitude and longitude of signal location i . This distance is the minimum distance travelled between 1 and 2, since it assumes a straight trajectory. For each turtle, total distance travelled is obtained by summing distances between two successive valid signal locations over the tracking period.

Average speed between two successive signal locations is $d(x_1, x_2)/(t_1 - t_2)$ where t_1 and t_2 are GMT times corresponding to emissions of signals 1 and 2. Due to inaccuracy in signal location, very close locations may result in unrealistic speed estimates. Speed values larger than 10 km h^{-1} were thus excluded. Average speed over the tracking period is the mean of average speeds between two successive signal locations. The trajectory of each turtle was established considering only the most precise location of each tracking day.

Note that distances and speeds are calculated with respect to ground, thereby including local currents.

3. Results and discussion

3.1. Captive-reared turtles

They immediately swam toward the ocean and steadily travelled long distances (average speed in open sea ranging from 1.7 to 3.14 km h^{-1}) over the monitoring period (from 2 to 5 months). They first migrated southwards in the same direction as the southern bifurcation of the South Equatorial Current (Fig. 1). C1, C2 and C3 travelled for 1 month in water temperatures of 27 – $28 \text{ }^\circ\text{C}$ before turning back northwards. In each case, the turn back coincides with the northwards progression of thermal fronts, local temperatures dropping 2 – $3 \text{ }^\circ\text{C}$ in the following days. During several days, C1 closely followed a thermal discontinuity separating water at $28 \text{ }^\circ\text{C}$ from water at $29 \text{ }^\circ\text{C}$ (Fig. 2), before returning northwards.

C1 and C2 continued travelling northwards into the South Equatorial Current (Fig. 1) and passed very close to their birth place, Tromelin. Unfortunately, turtle's C1 transmitter stopped emitting for unknown reasons around this period. C2 finally reached the Chagos archipelago after travelling 6884 km . During the last (eastwards) leg of the trajectory (9 d), its speed increased to an average of 4.97 km h^{-1} ($\pm 1.01 \text{ km h}^{-1}$, $n = 22$), travelling being facilitated by the Equatorial Countercurrent. On its way north and west, turtle C3 was swimming in the South Equatorial Current. C3 and C4 headed for Madagascar at the same time and at the same latitude (Fig. 1). They swam straight to sea grass beds, which are the main foraging sites for adult green turtles born in Tromelin as

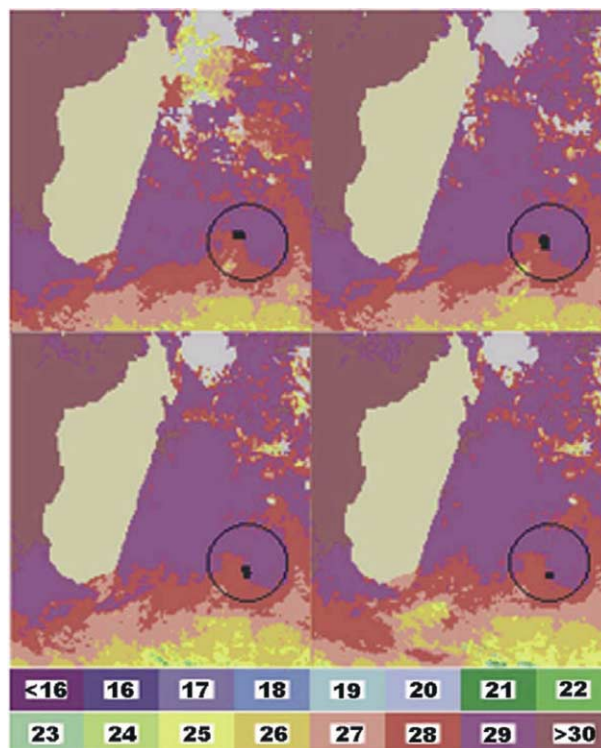


Fig. 2. Movements of turtle C1 and sea surface temperature (SST) between 4 and 8 April 1998 (top to bottom, then left to right). Turtle's locations are represented by black dots within a black circle. There are several locations per day due to on-continuously duty cycle of the transmitter. Sea Surface Temperature (SST) images were obtained from Advanced Very High Resolution Radiometer (AVHRR) transmitted NOAA satellites, and were provided by IRD La Reunion. The spatial resolution of the maps is approximately 2 km at the equator. In order to eliminate clouds and gaps left by satellites' trajectories, SST data are usually averaged over several days, 5 d in the present case. Although based on averages, SST maps reflect well short-term variations (Petit et al., 1994).

shown by mark-recapture (Le Gall and Hughes, 1987) and satellite tracking (e.g. turtle A1 on Fig. 1) experiments. After 3 weeks of directed movement, turtle C4 wandered on foraging sites for 2 months. Unlike the other turtles of the experiment, C3 and C4 were close to sexual maturity (Lutz and Musick, 1997), which may explain why their behaviour is similar to that of an adult. For comparison, adults A1 and A2 swam within a few days from their nesting site (Tromelin and Moheli) to their foraging site (Madagascar and Mozambique), where they remained for at least 2 and 8 weeks, respectively.

Our results suggest that green turtles grown in captivity are able to survive in the open ocean for months and travel long distances if they are released before they become sexually mature. During the feeding experiment at the laboratory, turtles that refused natural food stopped swimming after 6–7 weeks. The steady swimming activity displayed by tracked turtles throughout their oceanic travel demonstrates that they could feed at sea. In this respect, released turtles apparently show good adaptation to the oceanic environment. In another study, a loggerhead turtle maintained in captivity for 10 years

was able to survive and travel for 1 year after release (Nichols et al., 2000).

Several of the movements we observed may be related to hydrological stimuli like ocean currents and thermal fronts. In the Pacific Ocean, young loggerhead turtles preferentially migrate between the subarctic and the subtropical gyres, in a zone spanned by a series of fronts (Polovina et al., 2000). Primary production in the western tropical Indian Ocean is generally low (Humbert-Droz and Jullien, 1983), but food for marine animals accumulates along thermal fronts, convergence and divergence areas (Yoder et al., 1994). These zones also concentrate various floating objects, algae (Carr, 1987) and debris (Nichols et al., 2000), which provide shelter for marine animals. More generally, high abundances of large pelagic species are often associated to hydrological discontinuities in the ocean, like fronts, eddies and upwellings (Fonteneau et al., 2000; Herron et al., 1989; Olson and Polovina, 1999; Power and May, 1991).

Our results also suggest that turtles grown in captivity and displaced from their birth place are able to retrieve the foraging sites of their native population. Furthermore, their route toward these sites is straight, and their movements once on foraging sites are quite similar to those of wild adults. Fidelity of marine turtles to foraging areas has already been demonstrated in several studies (Godley et al., 2002; Limpus and Limpus, 2001). It is thus likely that these turtles did not land by chance on these foraging areas. However, we could not identify climatic or hydrological conditions that explain why the oldest immature turtles we tracked moved toward foraging sites at the same time. Other external stimuli could help them to recognize the foraging sites of their population.

Based on these results and others (Lohmann and Lohmann, 1996; Morreale et al., 1996; Polovina et al., 2000), we hypothesize that sea turtles utilize several types of environmental cues for navigating in the ocean, including hydrological conditions. The specific hydrological characteristics of oceanic basins would then favour the geographic segregation of populations in each basin. In the western Indian Ocean, genetic analyses indeed distinguished only two populations, respectively east and west of Madagascar (Broderick, 2001). Under this hypothesis, a displaced turtle would be able to recover foraging and breeding sites of its population only if it is released in its native basin.

3.2. *Wild immature turtles*

In contrast to captive-reared turtles, the wild immatures remained close to the release site during monitoring, never travelling further than 9 km per day and at low speed (<0.9 km h⁻¹). Turtle W1 wandered around Glorieuse (3 km long) for 5 months and turtle W2 remained less than 2 km away from the release beach. These two turtles were smaller than the other turtles studied. In the Indian Ocean, small immature green turtles (<30 – 40 cm CCL) are rarely seen on adult foraging sites (Musick and Limpus, 1997), but are frequently observed around islands like Reunion (Sauvignet et al., 2000), Comoros (Frazier, 1985), or the Seychelles (Frazier,

1984). These results indicate that these young immatures may reside for several months, possibly in association with coral reefs (Ogden, 1980). They corroborate the hypothesis that the reefs of such islands and nearby sea grass beds may constitute suitable habitats, allowing immature turtles to become omnivorous and eventually herbivorous, while providing relative shelter from oceanic predators (Musick and Limpus, 1997).

4. Conclusion

Young turtles grown in captivity are apparently perfectly able to survive and migrate in the ocean after release. However, their ability to retrieve breeding sites and reproduce successfully remains uncertain until recaptures on nesting sites are observed (Balazs et al., 2002).

In this experiment, the behaviour of these captive-reared immatures seemed unaltered after several years in captivity. Therefore, these observations shed light on the oceanic movements of immature green turtles in general. They appear capable of long-range movements in their pelagic environment. The oldest immature turtles join foraging areas and reside there like adults. The knowledge of movement trajectories together with additional information on diving behaviour and depth preferences should help to design appropriate conservation measures through reduction of incidental fishing mortality.

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