



Differences in diurnal and nocturnal swimming patterns of olive ridley hatchlings in the Gulf of Fonseca, Honduras



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ABSTRACT

Sea turtle hatchlings from Honduran beaches along the Pacific coast must swim more than 30 km through the shallow, presumably predator-rich waters of the Gulf of Fonseca before reaching the open ocean. Olive ridley hatchlings from Punta Ratón, Honduras, were tracked during the first 2 h of their offshore migration to assess aquatic predation rates. No predation events were observed. The absence of rocky bottom areas and reef structures where predators can refuge, and a decline in the number of predators due to overfishing are two possible reasons for this unexpected result. Additionally, diurnal and nocturnal swimming patterns of recently emerged olive ridley hatchlings were compared with regard to their position in the water column while swimming. At night hatchlings swam near the surface 97.5% of the time, with only sporadic brief dives. During daytime, however, hatchlings spent 78% of the time swimming at depth, going back to the surface for brief periods to breathe. Due to the high turbidity of the Gulf of Fonseca waters, this daytime behavior may serve to keep hatchlings out of sight of predatory sea birds. This newly described differential swimming behavior may have adaptive significance in avoiding aerial predation in the specific conditions of the Gulf of Fonseca.

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1. Introduction

In the hours after they enter the water and swim offshore, sea turtle hatchlings can suffer high mortality from fish and avian predators (Burger and Gochfeld, 2014; Frick, 1976; Gyuris, 1994; Pilcher et al., 2000). They are therefore generally believed to swim offshore as quickly as possible (Whelan and Wyneken, 2007) and then, once in deeper offshore water, they drift passively (Bolten and Balazs, 1995; Carr, 1987). Several studies have quantified the rate of aquatic predation suffered by sea turtle hatchlings in the nearshore environment (Gyuris, 1994; Pilcher et al., 2000; Stewart and Wyneken, 2004; Whelan and Wyneken, 2007; Witherington and Salmon, 1992; Wyneken et al., 1997). Although recorded predation rates vary greatly among sites, from 4.6% for loggerhead (*Caretta caretta*) hatchlings in South Florida (Whelan and Wyneken, 2007) to 85% for green (*Chelonia mydas*) hatchlings at Heron Island, Australia (Gyuris, 1994), most authors identify nearshore waters as highly threatening for hatchling turtles. Taking into account that observation periods of these studies have typically consisted of approximately 10–15 min, even the lowest observed rates (4.6% by Whelan and Wyneken, 2007; 5% by Stewart and Wyneken, 2004; 7% by Wyneken et al., 1997) are likely to exact heavy losses if hatchlings remain in nearshore environments for long periods of time

(Whelan and Wyneken, 2007). Several factors, such as depth, bottom-structures, and release protocols have been shown to affect predation risk, which is especially high in shallow (<10 m) waters (Pilcher et al., 2000; Witherington and Salmon, 1992), and when hatchlings cross reef structures (Frick, 1976; Gyuris, 1994; Pilcher et al., 2000; Witherington and Salmon, 1992). Because high hatchling densities attract aquatic predators (Wyneken et al., 2000), hatchlings released *en masse* from hatchery sites suffer from 50% (Pilcher et al., 2000) to ten times (Wyneken et al., 2000) higher predation rates than those released from natural sites with a low density of nests. Other factors that may affect predation rates are tidal and moon phases (Gyuris, 1994; Harewood and Horrocks, 2008), water clarity, coast-specific predator assemblages, and fish movement patterns (Whelan and Wyneken, 2007).

Sea turtle hatchlings have no active defenses against predators (Gyuris, 1994; Stewart and Wyneken, 2004; Whelan and Wyneken, 2007), and thus their main options for avoiding predation are fleeing or hiding (Bolles, 1970). One general strategy used by green, loggerhead, and leatherback (*Dermochelys coriacea*) hatchlings is to leave predator-rich nearshore waters as quickly as possible, by maintaining a vigorous offshore swimming frenzy during the first 24 h (Carr, 1962; Salmon and Wyneken, 1987; Wyneken and Salmon, 1992). Conversely, hawksbill (*Eretmochelys imbricata*) hatchlings do not show a frenzy period of hyperactive swimming. Instead, they swim for only 6 h a day, employing slow, drag-based gaits, and spend most of the time floating motionless in a “tuck” position helping them remain inconspicuous to predators that

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use movement for prey detection (F. Chung et al., 2009; F.C. Chung et al., 2009). When facing attack or imminent predation threat, behavioral strategies also differ among species. A series of simulated predation experiments by Mellgren et al. (2003) demonstrated that loggerhead and hawksbill hatchlings tended to remain immobile, while green hatchlings responded by actively fleeing via vigorous swimming and diving. Field observations by Hasbún (2002) confirmed that hawksbill hatchlings fold their front flippers along the top of the carapace and remain motionless when approached or attacked by fish. Reactions to an aerial predation threat are similar for both green (Frick, 1976) and loggerhead hatchlings (Witherington and Salmon, 1992), which quickly dive in response to birds overhead.

Besides sporadic dives that usually happen in response to disturbance (Frick, 1976; Martin, 2003) or flying objects (Frick, 1976; Witherington and Salmon, 1992; Witherington et al., 1995), sea turtle hatchlings tend to swim near the water surface during their offshore migration, both during nighttime and daylight hours, likely due to their positive buoyancy (Carr, 1982; Davenport and Clough, 1986). Abe et al. (2000) and Frick (1976) followed green hatchlings during daytime and recorded them swimming at 10 and 20 cm depths, respectively. Liew and Chan (1995) tracked leatherback hatchlings with subminiature radiotransmitters for more than 30 consecutive hours, and described them swimming 5–10 cm just below the surface. Similar results were reported by Witherington et al. (1995) on loggerhead hatchlings and by Hasbún (2002) on hawksbill hatchlings.

To our knowledge, no previous studies on hatchling offshore swimming, in-water predation, or antipredator behavior have focused on olive ridley (*Lepidochelys olivacea*) sea turtles. In Honduras, this species nests in the eastern end of the Gulf of Fonseca, a shallow inlet of the Pacific Ocean with coast shared by El Salvador and Nicaragua (Fig. 1). Olive ridleys have been protected in Honduras since 1975, when the government established a yearly period during which commercial egg collection is forbidden and the eggs are relocated to hatcheries (Minarik,

1985). Currently there are four working hatcheries along the South coast of Honduras located on the beaches at Punta Ratón, El Venado, Boca del Río Viejo, and Cedeño. Punta Ratón (13.26570 N, 87.51228 W), the field site for this study, is the main nesting beach in the country, with an estimated 400–500 nests per season. Hatchlings released from Honduran beaches must swim across more than 30 km of shallow waters before reaching the open sea. The Gulf of Fonseca is an important fishing area for the country and several genera of fishes known to prey on sea turtle hatchlings — *Caranx* sp., *Haemulon* sp., *Lutjanus* sp., *Epinephelus* sp. (Gyuris, 1994; Stewart and Wyneken, 2004; Vose and Shank, 2003; Whelan and Wyneken, 2007; Wyneken et al., 1997) — inhabit its waters (Box and Bonilla, 2009). The Gulf of Fonseca is also home to several species of potential avian predators, such as black vultures (*Coragyps atratus*), turkey vultures (*Cathartes aura*), magnificent frigatebirds (*Frigata magnificens*), Caspian terns (*Sterna caspia*), Forster's terns (*Sterna forsteri*), laughing gulls (*Larus atricilla*), and brown pelicans (*Pelecanus occidentalis*) (Gallardo, 2014). Black and turkey vultures have been reported feeding on olive ridley hatchlings at the Ostional (Costa Rica) mass nesting beach (Burger and Gochfeld, 2014), and frigatebirds, gulls and terns are known to capture hatchlings from the water (Burger and Gochfeld, 2014; Frick, 1976; Gyuris, 1994; Martin, 2003; Stancyk, 1982).

The original goal of this study was to quantify in-water predation rates suffered by olive ridley hatchlings from Punta Ratón, Honduras, during the first hours after hatchlings are released. Taking into account that the mean depth of the Gulf of Fonseca is 15 m and the beaches in South Honduras are contiguous with several kilometers of waters less than 5 m deep, high levels of hatchling in-water predation were hypothesized.

Although abundant work has been done on tracking adult and juvenile sea turtles (Godley et al., 2008), and investigating their swimming patterns and diving behavior (Eckert et al., 1989; Hays et al., 2000; Houghton et al., 2008; Minamikawa et al., 1997), little is known about

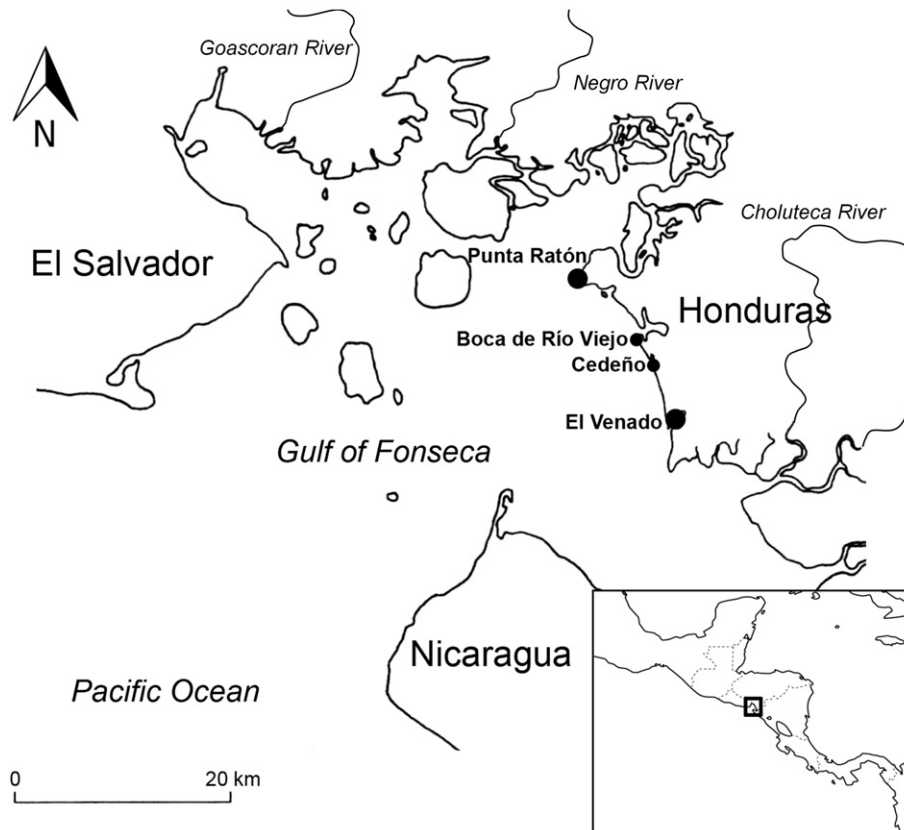


Fig. 1. The Gulf of Fonseca. Black circles indicate the four main nesting beaches for *L. olivacea* on the South coast of Honduras. Inset shows a regional view of Central America.

hatchling migration paths and swimming patterns. Laboratory experiments have yielded valuable information on hatchling orientation (Lohmann et al., 2012), and activity patterns during the frenzy swimming (Booth, 2009; Jones et al., 2007), while particle tracking models have been used to infer hatchling passive drift (Hays et al., 2010). Yet, direct observation of hatchlings migrating in their natural environment, such in the current study, may disclose previously undetected behavioral traits and their adaptive significance.

The second goal of the study was to describe swimming patterns of the Honduran olive ridley hatchlings with regards to their position in the water column during the first hours of their offshore migration, and to assess potential differences between diurnal and nocturnal swimming patterns. Due to high turbidity of the waters in the Gulf of Fonseca, any animal swimming at depths greater than 25–30 cm cannot be seen from the air and thus, differences in swimming depth between day and night hours may suggest local strategies of predator avoidance.

2. Methods

2.1. Study site

Punta Ratón (13.26570 N, 87.51228 W) is the main nesting beach for *L. olivacea* in Honduras. This beach is located at the eastern end of the Gulf of Fonseca, a shallow 1600 km² inlet of the Pacific Ocean, 50 km wide (NE–SW) and 80 km long (NW–SE) (Fig. 1). The mean depth of the gulf is 15 m and the coastal areas are bounded by several kilometers of waters with depths less 5 m, although some channels of 10 to 12 m exist, allowing navigation by deep sea vessels. In the area near Punta Ratón the bottom is sandy or silty (Vergne et al., 1993), lacking any hard-substrate structures. During the hatching season (October–November) waters are very turbid due to the high river discharge originating from the Choluteca River.

2.2. Predation study

This study was carried out during October and November, 2011. Predation rates were assessed using 25 hatchlings from the hatchery at Punta Ratón, which were collected from the hatchery as soon as they emerged from nests, and kept in dark containers until night. Hatchlings selected for the experiments were weighed and measured. A “Witherington float” (Lorne and Salmon, 2007; Whelan and Wyneken, 2007; Witherington and Salmon, 1992) (Fig. 2A) consisting of a small black balsa wood boat (71 mm long, 16 mm high and 12 mm wide) with an embedded 3.8 cm green glowstick (GlowProducts, BC, Canada, suppliers), was attached to the animal via a 1.5 m sewing thread. The weight of the float in air (4 g) was approximately 25% of the hatchling weight. These floats may reduce swimming speed by up to 15% but do not attract predators or impede the normal swimming–diving behavior

of the hatchlings (Stewart and Wyneken, 2004). Following the usual release protocol in the hatchery at Punta Ratón, most of the observations were done at night, although three hatchlings were tracked during daytime at the end of the season. Hatchlings were released directly into the water, 5–10 m from the shore. The animals were followed using a small fishing skiff, keeping a distance of at least 10 m to avoid interfering with normal behavior, and GPS positions were recorded every 5 min. Observations continued for 2 h unless the animal was predated or lost sight of. This observation period, much longer than the 10–15 min period typical of most hatchling predation studies, was chosen because in the Gulf of Fonseca hatchlings remain in shallow, presumably predator-rich waters for several hours. After 2 h swimming away from the coast at the normal swimming speed of approximately 1.3 km/h (Salmon and Wyneken, 1987), water depth was still less than 5 m. Features used by others to identify predation events were sudden disappearance of the hatchling with submersion of the float, or recording of the float traveling faster than hatchlings are capable of swimming (Whelan and Wyneken, 2007). After each set of observations, the hatchling was recaptured, the tether and float removed, and the hatchling re-released into the water. Twenty-two trackings were performed at night, 11 during decreasing tides and 11 during increasing tides, and 3 trackings were performed during daytime. Due to the shallow depth of the Gulf, tides are extreme and large sandy areas become exposed during low tide periods. Thus, no trackings started at low tide.

2.3. Swimming pattern study

This study was undertaken during the months of October and November of 2012 and 2013. In 2012, the diurnal and nocturnal swimming patterns of 32 hatchlings were investigated through direct observations during their offshore migrations. Hatchlings were collected from the hatchery at Punta Ratón as they emerged from the nests and kept in dark containers until starting observations. The maximum retention time was 12 h. After measuring and weighting the treatment animals, a Witherington float was attached to each via a 1.5 m sewing thread. These floats were identical to the floats used for the 2011 predation study, except the glowstick was replaced with a small yellow balloon during diurnal observations (Fig. 2B). Hatchlings were released directly into the water 50 m from the shore and followed in a small fishing skiff, keeping a distance of 3–5 m. After a 5 min acclimation period, hatchlings were observed for 25 min and the time the hatchling swam near the surface and at depth was recorded. Time swimming “near the surface” was defined as the animal was swimming at the surface or just 10–20 cm below it. Although water visibility was low, hatchlings were clearly visible from the boat when they were swimming near the surface during the day, down to approximately 25–30 cm deep. Time swimming “at depth” was considered when the animal was not visible from the surface. Although the exact position of the animals was

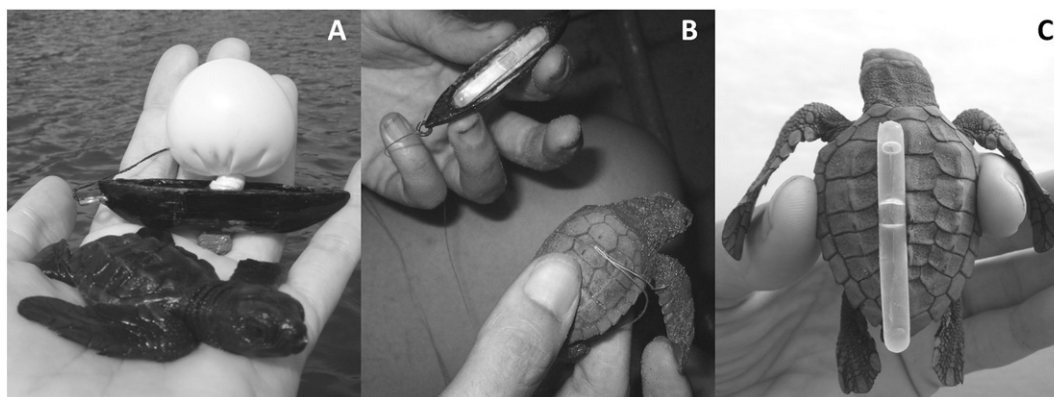


Fig. 2. Floats and identification devices. Witherington floats used for (A) diurnal, and (B) nocturnal observations. (C) Hatchling with a glowstick directly attached to its carapace, used during nocturnal and control diurnal observations.

not measured when they were swimming at depth, the upper part of the 1.5 m thread connecting the turtle to the float remained tight and almost perpendicular to the surface. Therefore, hatchlings swimming at depth were thought to be located between 1 and 1.5 m deep. To see the position of the hatchlings during night observations, a 3.8 cm green glowstick was attached directly to the carapace of the hatchling (Fig. 2C). To assess if this glowstick affected hatchling swimming behavior, used glowsticks were also attached to the carapace of a group of hatchlings during daytime observations. The three experimental groups used for this study were: 13 hatchlings observed during the day with no attached glowsticks, 11 hatchlings observed at night with glowsticks attached to their carapaces, and a control group of 8 hatchlings observed during the day with attached glowsticks. Glowsticks were removed at the end of all observations and hatchlings were released directly into the water.

A repeated measures experiment was performed in 2013 using 7 hatchlings from the hatchery at Punta Ratón. Taking advantage of a study that involved following hatchlings during 12 h to assess the influence of tidal currents on their offshore migration movement (Duran and Dunbar, 2014), the swimming pattern of the same individuals was recorded during both day and night. The methods for this study were the same as in the 2012 study. The animals were attached to a Witherington float and had a glowstick attached to their carapaces during both observation periods. Each observation period was for 10 min, and time near the surface and time at depth were recorded. The first observation was done in the first hour of the tracking, and the second one between 3 and 6 h later. In all but one case, night observations were done first.

2.4. Data analysis

For the predation study, hatchling tracks were plotted in a geographic information system (GIS), superimposed on a map containing bathymetric data for the Gulf of Fonseca. Depths for the observation area were calculated. Because no predation events were observed, no calculations or further analysis were done on the frequency of predation.

For the swimming pattern study, the mean percent of time near the surface was calculated and compared among groups. Because our data were not normally distributed even after several transformations, they were analyzed with non-parametric tests. In the 2012 study with independent samples, Kruskal–Wallis was applied to compare the mean time near the surface for the three experimental groups. Subsequently, post-hoc comparisons of groups using Mann–Whitney U tests with Bonferroni correction were performed to find which group means differed significantly. In the 2013 repeated measures experiment, a Wilcoxon signed-rank test was used to compare day and night mean times near the surface. The α level was set at 0.05 for all tests.

3. Results

3.1. Predation study

A total of 461 data points on hatchling positions were collected, 90.02% (415) of which were in waters less than 5 m in depth and 79.18% (365) of which were in waters of less than 2 m in depth. Twenty-nine observation points (6.29%) were located in waters between 5 and 10 m in depth and only 17 (3.69%) were in areas deeper than 10 m (Fig. 3). Hatchling trajectories during experimental observations were mostly parallel to the coast.

The average weight for the 22 hatchlings tracked at night was 16.1 g \pm 0.3 SE (range 13–18 g), and the average curved carapace length (CCL) was 44.1 mm \pm 0.3 SE (range 40.0–46.0 mm) (Table 1). Observation times ranged from 18 to 133 min, with an average of 91.8 min \pm 8.2 SE. No predation events were observed during this study. Thirteen animals completed the 2 hour observation period and were released at the end. The remaining nine hatchlings were lost during the trial when the thread detached from the turtle or broke from the float due to friction.

Still, no evidence of predation was observed in any of these cases, such as floats quickly pulled or suddenly submerged.

The three hatchlings followed during daytime had weights ranging from 16 to 17 g and CCLs ranging from 43 to 46 mm. These hatchlings were tracked for 120, 128 and 114 min, respectively, and none of them was predated. A different swimming behavior was nevertheless observed in these three hatchlings than in those that were followed at night. During the night, the animals swam just under the surface, with a few sporadic dives, whereas the hatchlings followed during the daytime spent most of the time swimming at depth, and went up to the surface only for short periods to breathe. Because our sample size ($N = 3$) was too small to draw valid conclusions, these results were considered preliminary and no data from these animals were included in the statistical calculations for this study. Furthermore, these observations lead to a broadening of the goals for the study, with the specific investigation of the diurnal and nocturnal swimming patterns of the Honduran hatchlings during the following seasons.

3.2. Swimming pattern study

The 32 hatchlings used for the first part of the study (2012) had an average weight of 15.9 g \pm 0.3 SE, and an average CCL of 44.7 mm \pm 0.3 SE (Table 1). The percentage of time spent swimming near the surface differed significantly among the three experimental groups (Kruskal–Wallis test $H = 21.103$, $df = 2$, $p < 0.001$) (Fig. 4, Table 1). Post hoc Mann–Whitney U test results showed no significant difference between the two groups of hatchlings followed during the day (without and with glowsticks attached to their carapaces), with average times swimming at the surface of 18.29% \pm 6.59 SE and 14.14% \pm 2.03 SE, respectively (Mann–Whitney $U = 51.0$, $p = 0.942$, Fig. 4). Hatchlings swimming during the night spent much more time near the surface (average 99.37% \pm 0.53 SE) than both groups observed swimming during the day (Mann–Whitney $U = 1.0$, $p < 0.001$, for comparison with hatchlings without glowstick and $U = 0.0$, $p < 0.001$, for comparison with hatchlings with attached glowstick, Fig. 4). Although the typical pattern for diurnal swimming was long periods of deep swimming separated by short periods at the surface (Fig. 5A), one hatchling observed during the day remained near the surface for 1420 out of 1500 s (95%). Because there was no difference between the two groups observed during the day, both groups were pooled (with and without glowstick). The average duration of the dives for each hatchling ranged from 20 s to 140.44 s, with a mean of 63.45 s \pm 5.59 SE. The longest recorded dive lasted 221 s. During the night, 9 out of 11 hatchlings (81.8%) swam near the surface during the whole observation time (1500 s) (Fig. 5B). For the remaining two hatchlings the average dive duration during the night was 1.75 s \pm 1.18 SE and the longest dive lasted 19 s.

The seven hatchlings used for the repeated measures experiment (2013) weighed an average of 15.3 g \pm 0.6 SE and had an average CCL of 43.7 mm \pm 0.3 SE (Table 1). Time between the two observations of each hatchling ranged between 3.00 and 5.97 h, with a mean of 5.07 h \pm 0.40 SE. Results of the Wilcoxon signed-rank test showed that hatchlings spent significantly more time swimming near the surface during the night (97.54% \pm 2.46 SE) than during the day (21.85% \pm 8.01 SE) ($Z = -2.37$, $p = 0.018$) (Table 1). These hatchlings showed diurnal and nocturnal swimming patterns similar to those shown by the hatchlings used in the independent samples 2012 experiments (Fig. 5C).

Regarding predation by birds, while no predation events or bird attacks on hatchlings were recorded during the 22.3 h of diurnal experiments (total for both studies), laughing gulls were observed attacking and capturing hatchlings from the water twice, when groups of 4–6 hatchlings were released at the end of the daily experiments. These hatchlings remained at the water surface, motionless or dog-paddling for several minutes, likely making themselves more conspicuous to the birds. On one occasion a laughing gull took one of the hatchlings,

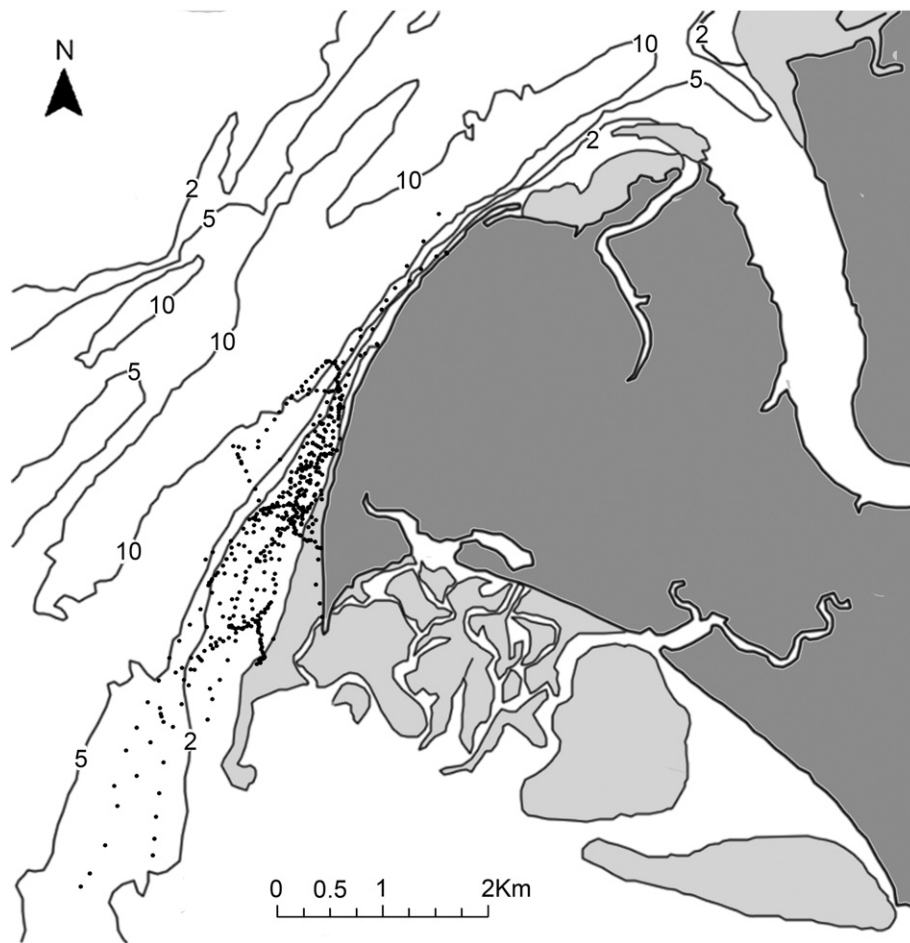


Fig. 3. Location of the observations for the predation study. Dots represent the 461 individual observation points from the 22 hatchlings tracked at night. Land area is colored dark gray, light gray zones represent very shallow areas exposed during low tide. White areas represent water, with isobaths indicating depths in meters.

which fell from its beak a few seconds later, but was not recaptured. On another occasion, several laughing gulls and terns attacked the group of hatchlings, and at least one was taken by a gull.

4. Discussion

The absence of predation by fish during the initial phase of the offshore migration of olive ridley hatchlings in the Gulf of Fonseca diverges from the findings of previous studies on other sea turtle species in different regions, which always found predation, although in variable rates (60–76% in Gyuris (1994); 40.7–61.9% in Pilcher et al. (2000); 5% in Stewart and Wyneken (2004); 1–9% in Whelan and Wyneken (2007); 6.8% in Witherington and Salmon (1992); and 7–34% in Wyneken et al. (1997)). Due to the shallow depth of the Gulf waters even as far as several kilometers away from the beach, high losses from in-water predation were originally expected, using calculations from Whelan and Wyneken (2007). Still, none of the 25 hatchlings in the predation

study were taken by fish during the experiments, likewise none of the 39 hatchlings in the swimming pattern study were predated over the period of our observations. Although the sample sizes in this study were lower than sample sizes in other predation studies, the observation time (2 h) exceeded most (10 min by Gyuris, 1994; 15 min by Wyneken et al. 1997, Stewart and Wyneken, 2004, and Whelan and Wyneken, 2007). The total observation time in the current study was 33 h for the predation study and 15 h for the swimming pattern study. The fact that no predation events were recorded during the 48 h of observation suggests that predation rates in the Gulf of Fonseca may be extremely low. Several factors may contribute to these findings. First, high hatchling predation rates tend to be associated with shallow waters, but also with the presence of reef or reef-like structures (Gyuris, 1994; Witherington and Salmon, 1992), which are typical shelters for predatory fish (Gyuris, 1994). These two factors characterize many sea turtle nesting sites, yet on the Honduran coast at Punta Ratón, although depth is low, the bottom is sandy and silty and hatchlings do not cross over rocky areas or reef

Table 1

Overview of hatchling measurements and results for all three studies.

Study	Mean weight (g)	Mean CCL (mm)	Mean % surface time DAY	Mean % surface time NIGHT
Night predation study (N = 22)	16.1 ± 0.3	44.1 ± 0.3	–	–
Independent samples swimming study (N = 32)	15.9 ± 0.3	44.7 ± 0.3	18.29 ± 6.59 ^a 14.14 ± 2.03 ^b	99.3 ± 0.53 ^c
Repeated measures swimming study (N = 7)	15.3 ± 0.6	43.7 ± 0.3	21.85 ± 8.01	97.54 ± 2.46

^a Hatchlings with no glowstick attached to their carapaces (N = 13).

^b Control hatchlings with glowstick attached to their carapaces (N = 11).

^c Hatchlings observed at night (N = 8).

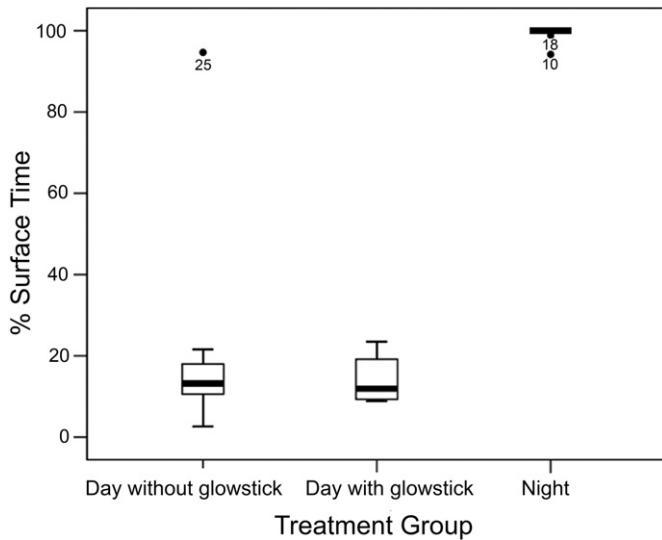


Fig. 4. Box and whisker plots comparing the average percent time swimming near the surface by the three experimental groups. Thick lines represent mean values for each group. Bars represent standard errors.

structures. According to the observations from the current study, the type of bottom structures present in shallow waters may be more important in determining predation rates than depth alone. Results from the study of Whelan and Wyneken (2007) on loggerhead hatchlings from South Florida support this idea. They assessed hatchling predation by fish in three different beaches and found very low rates (1%) in one of them, the beach at Naples. The characteristics of this beach are quite similar to those present in the Gulf of Fonseca; turbid waters with visibility lower than 0.5 m, and sandy bottom. Only one species of predatory fish was recorded in snorkeling surveys in that study and the authors suggested that the absence of bottom structures that allow fish to congregate could explain the low predation rates. Second, it is possible that, for some reason, fish from the Gulf of Fonseca do not feed on olive ridley hatchlings. The Gulf of Fonseca contains fish assemblages known to feed on sea turtle hatchlings in other regions yet to date there is no actual evidence of Gulf fishes feeding on olive ridley hatchlings. During the three years of this study we interacted regularly with the fishermen from Punta Ratón, who never reported finding sea turtle hatchling remains when eviscerating captured fish. On only one occasion was a fish observed feeding on a hatchling, which was dead prior to the incident. In that case a hatchling carcass attached to a Witherington float was

being used as a control experiment for a study on the influence of tidal currents on hatchling offshore migration (Duran and Dunbar, 2013), when the hatchling was taken by a large unidentified fish. Finally, predation rates may have been higher in the past, but may now have decreased to minimum levels due to a decline in predator numbers. In a study on the fishing activity at the Gulf of Fonseca from 2004 to 2010, Soto (2012) suggested that fish populations in the Gulf have been threatened by recent fishing efforts. Over-fishing and declining fishing stocks are global trends (Jackson et al., 2001; Pauly et al., 2002) that have previously been suggested as one explanation for a decrease in nearshore predation pressure on sea turtle hatchlings (Whelan and Wyneken, 2007). It is likely that such declines in the Gulf of Fonseca may also contribute to low predation risks to hatchlings in this area.

Another explanation for the absence of predation found in our study is that such absence is actually an artifact of the study methods, because the presence of the boat, or the sound of its engine, could have caused fight reactions in fish predators. Following hatchlings with a kayak from an approximate distance of 10 m is the usual method for studies on hatchling nearshore predation (Stewart and Wyneken, 2004; Whelan and Wyneken, 2007). In this study an engine boat was required for safety reasons because of the substantial currents and the sudden, violent electrical storms common in the area. Still, it is unlikely that the use of the engine distorted the results of the study, for two reasons. First, the engine remained turned off most of the time and was turned on for short periods of time to approach the hatchling when it had moved too far away to be observed. Second, the boat used was a local fishing skiff, similar to most boats that work in the Gulf of Fonseca during both night and day. Thus, fishes in the Gulf of Fonseca are likely accustomed to the presence of these types of boats and their sounds, which constitute a common disturbance in their environment. Only when in close proximity to the engine were behavioral changes observed in the hatchlings tracked at night, which tended to dive when they approached the engine of the boat. Frick (1976) reported a similar behavior in Costa Rican green turtle hatchlings, whose dives were sometimes caused by the approach of a boat. Some recent studies have avoided the use of a boat when tracking sea turtle hatchlings in nearshore waters, by equipping the hatchlings with miniature acoustic-coded transmitters, and deploying an array of receivers in the surf zone (Thums et al., 2013). Although very useful, this technique does not allow continuous monitoring or direct observations of each individual hatchling, and thus, visual tracking was preferred for the current study.

We are aware of no research studies to date that have focused on assessing rates of bird predation on sea turtle hatchlings once they have reached the water. Although not a primary goal of the current

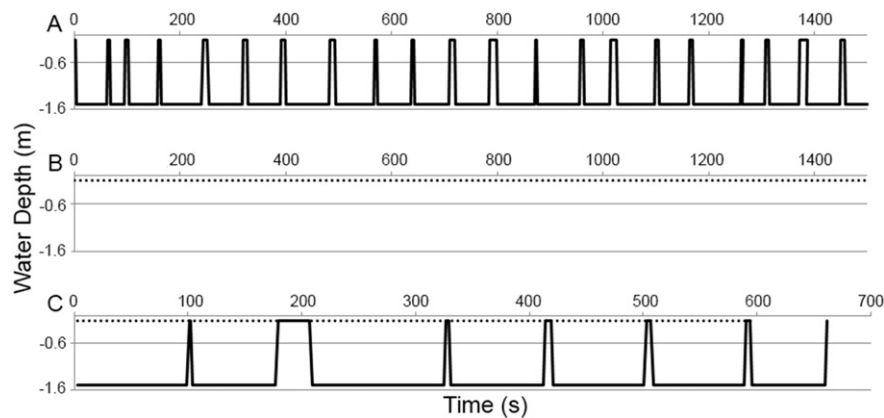


Fig. 5. Swimming profiles. A shows the swimming profile of hatchling H12, representative of the typical diurnal swimming profile for olive ridley hatchlings at Punta Ratón. B shows the most common nocturnal profile, displayed by 9 out of 11 hatchlings, which remained near the surface during the entire observation time. C shows the nocturnal and diurnal profiles of hatchling H107 during the repeated measures experiment. The upper horizontal line represents the water surface. Solid black lines represent diurnal profiles, dotted lines represent nocturnal profiles. X axis represents time in seconds, and Y axis represents water depth in meters. We did not record actual dive profiles, the swimming depth when the hatchling was not visible from the surface was assumed to be approximately the length of the tether (1.5 m).

investigation, this study on diurnal and nocturnal swimming patterns provided some insights regarding bird predation pressure on sea turtle hatchlings in the Gulf of Fonseca waters, as well as about potential anti-predator strategies employed by hatchlings.

In many sites, the risk of aerial predation on sea turtle hatchlings is relatively low. Hatchlings usually emerge soon after dusk in response to cooling surface sand (Hays et al., 1992), implying that the initial phase of their migration tends to be at night when most seabirds remain inactive. After several hours of swimming offshore and as daylight approaches, hatchlings are usually far enough from land to be out of reach of most birds. In southern Honduras, however, this is not the case. Sea birds are abundant in the Gulf of Fonseca. During the day, magnificent frigatebirds, brown pelicans, terns, and gulls are frequently observed over the entire Gulf. To reach open water, olive ridley hatchlings from Punta Ratón must swim more than 30 km across the Gulf waters, and thus are exposed to attacks by sea birds. These hatchlings swim at an average speed of 1.2 km/h (Duran and Dunbar, 2014), which is a normal swimming speed for hatchlings during the frenzy period. Loggerhead hatchlings are known to swim at 1.10 to 1.37 km/h (Salmon and Wyneken, 1987) and green hatchlings reach speeds of up to 1.62 km/h (Abe et al., 2000; Frick, 1976). Swimming continuously at 1.2 km/h in a straight line from Punta Ratón would require more than 25 h for the hatchlings to reach the mouth of the Gulf of Fonseca, yet the actual time they spend may be much longer. The observation of hatchling trajectories being parallel to the coast rather than directly offshore, along with recent data from Duran and Dunbar (2013, in preparation) suggest that these hatchlings are being pulled back and forth by tidal currents during their offshore migration, potentially extending their stay in the Gulf, along with their exposure to bird predation, for up to several days.

In this scenario, to adopt an antipredator strategy specific for birds may have adaptive significance for Honduran olive ridley hatchlings. The diurnal swimming pattern observed in this study has not been previously described in the literature, suggesting it may be a localized behavior of this population. Previous studies have recorded differences in the nocturnal activity of loggerhead hatchlings from different populations (Scott et al., 2014; Wyneken et al., 2008), suggesting that local oceanic conditions drive the evolution of innate swimming behaviors (Scott et al., 2014). Wyneken et al. (2008) showed that hatchlings from SE Florida beaches, much closer to their target current than those of SW Florida beaches, were more inactive at night after the first 24 h of frenzy swimming. Scott et al. (2014) found a similar result studying hatchlings from Cape Verde, which by the third night were essentially inactive. He suggested that this behavior helps hatchlings to minimize predation risks from crepuscular and nocturnal aquatic predators. In the case of Honduran olive ridley hatchlings, no difference was found in the amount of nocturnal swimming activity, but instead in diurnal swimming depth. In both cases, the observed differences may be adaptations to improve effectiveness of the offshore migration behavior under specific local conditions. Given the high turbidity of the Gulf of Fonseca waters, swimming at depth during the daytime may serve as an antipredatory strategy to reduce detection of hatchlings by aerial predators. Observations of sporadic birds attacking and capturing hatchlings that remained conspicuous at the water surface during day time support the effectiveness of swimming at depth as an antipredatory measure.

In the Gulf of Fonseca, due to its abundance of sea birds and very turbid waters, it is clearly advantageous for the hatchlings to swim at depth as much of the time as possible during the day, but this strategy may represent high energetic costs for the animals. Swimming 10–20 cm from the water surface, with only occasional dives, is the normal behavior for sea turtle hatchlings (Abe et al., 2000; Davenport et al., 1984; Frick, 1976; Hasbún, 2002; Liew and Chan, 1995; Witherington et al., 1995), and appears to be the most efficient form of swimming. Swimming just at the water surface, or very close to it, reduces performance due to the creation and propagation of surface

waves (Webb et al., 1991). Total drag due to these types of waves becomes minimal at a depth of at least 2.5–3 times the animal's body thickness (Hertel, 1966, 1969), coinciding with the approximate depth at which sea turtle hatchlings (Martin, 2003), as well as sea turtle adults (Hays et al., 2001), swim.

While drag avoidance may be the reason why sea turtle hatchlings do not swim at the water surface, it does little to explain why they do not usually swim deeper than 20 cm. One likely reason is that swimming at depth would imply spending more time moving to and from the surface for breathing. Hatchlings swimming at depth would spend excess time and energy in vertical movements when they should maximize horizontal offshore movements. An additional important reason is that hatchlings are positively buoyant (Carr, 1982; Davenport and Clough, 1986). Studies on loggerhead and green turtles showed that the diving abilities of hatchlings are poor until they are several months old, because buoyancy control is undeveloped (Davenport and Clough, 1986; Davenport et al., 1984; Milsom, 1975). Still, several studies have shown that hatchlings are able to dive down to depths of more than 1 m, yet do so only sporadically (Abe et al., 2000; Davenport and Clough, 1986; Hasbún, 2002; Martin, 2003; Witherington et al., 1995). These dives usually happen when hatchlings are disturbed (Frick, 1976; Martin, 2003), or in response to a bird or other object appearing overhead (Frick, 1976; Witherington and Salmon, 1992; Witherington et al., 1995). When hatchlings are threatened from the air they dive almost vertically, and remain underwater for up to two minutes (Frick, 1976; Witherington and Salmon, 1992). To keep themselves at depth implies a great effort on the part of the hatchlings. Davenport and Clough (1986) observed that loggerhead hatchlings beat their foreflippers vigorously in order to dive down to 1 m, and rapidly bobbed to the surface as soon as they stopped swimming. To remain submerged, hatchlings needed to counteract the tendency to float by holding the body 45° to the horizontal plain with the head down and performing specific flipper movements.

At night hatchlings from the Gulf of Fonseca, typically swim near the surface with only a few deep dives, however, during the day, their swimming pattern was the opposite. Swimming at depth during the daytime did not appear to be a reaction to overhead disturbances, but instead appeared to be the normal behavior for these hatchlings. After spending a few seconds at the surface, Honduran hatchlings went straight down from the surface and continued swimming at 1–1.5 m deep for more than one minute, after which they returned to the surface to breathe. This cycle was repeated uninterruptedly during our diurnal observations. Because of the energy investment required, an animal with low energy reserves could not perform deep dives for long. This could explain the inconsistent behavior of hatchling number 25, which spent 95% of the time at the surface during the day time. This hatchling happened to be one of the smallest hatchlings in the study, with a weight of only 14 g.

Results of this study suggest that the diurnal diving behavior shown by olive ridley hatchlings in the Gulf of Fonseca has adaptive significance in avoiding aerial predation in the specific conditions of the site, where turbid waters obscure hatchlings swimming more than 25 cm from the surface. Although there are no specific studies on the swimming and diving abilities of olive ridley hatchlings, it is likely that, similarly to the hatchlings of other sea turtle species, they are positively buoyant and thus, this behavior implies an energetic investment that is compensated by the advantages it confers on hatchlings. This diurnal strategy of deep swimming appears to be successful, since no aerial predation events or bird attacks were observed on hatchlings employing this swimming pattern.

Further research is needed to determine whether this behavior is characteristic of olive ridley sea turtles in other areas or if it is a local adaptation for enhancing survival under the specific conditions of the Gulf of Fonseca. In any case, it would be of interest to perform laboratory studies to assess the actual energy investment this behavior requires of the animals, and compare it with the amount of energy used by

hatchlings of other species normally swimming near the surface and during diving in response to the presence of aerial threats. In the case that this behavior appears to exist only in the Honduran population of the Gulf of Fonseca, it would be worth investigating whether hatchlings of other sea turtle species nesting in the area, such as hawksbill and green turtles, also show a similar behavior during offshore migration from beaches of Pacific Honduras.

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