Dive behaviour of adult hawksbills (*Eretmochelys imbricata*, Linnaeus 1766) in the eastern Pacific Ocean highlights shallow depth use by the species

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Understanding the movement and dive behaviour of marine turtles directly informs spatial management strategies. Hawksbill turtles (*Eretmochelys imbricata*, Linnaeus 1766) are a globally endangered marine turtle species, with populations in the eastern Pacific Ocean identified as particularly threatened. To date, very little research on the dive behaviour of hawksbills has been conducted. Most studies have focused on juveniles in the Wider Caribbean region, and no dive behaviour has been described for hawksbills in the eastern Pacific. Using satellite-relayed dive loggers attached to five adult hawksbills, we analyzed dive trends and differences among individuals, movement phases and diel time periods, and compared our findings with those from hawksbills in other regions of the world. Our research indicates that adult hawksbills in the eastern Pacific predominantly use shallow waters (i.e. ≤ 10 m), with dives rarely occurring to depths > 20 m. Additionally, in contrast to previous research, we found similar dive behaviour across diel time periods, suggesting nocturnal activity may be more prevalent than previously believed. Despite some similarities in dive behaviour across individuals, individual variability was also evident. More research on adult hawksbills is urgently needed to increase our understanding of basic hawksbill ecology and behaviour, and improve management of this critically endangered species in the eastern Pacific Ocean.

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1. Introduction

Circumglobally distributed, hawksbill marine turtles (*Eretmochelys imbricata*, Linnaeus 1766) are considered critically endangered throughout their range (Mortimer and Donnelly, 2008). The species is at greatest risk in the eastern Pacific Ocean (NMFS/USFWS, 1998; Wallace et al., 2011), where precipitous declines have prompted international conservation concern (Gaos et al., 2010). Research into hawksbill movement behaviour has been identified as one of the top conservation priorities in the region (Gaos et al., 2010; ICAPO, 2008), as a more complete understanding of movement ecology is vital to effective conservation and protected area management (Blumenthal et al., 2006; Godley et al., 2008; Schofield et al., 2007; Shillinger et al., 2008).

In recent years, satellite transmitters or PTTs (platform transmitter terminals) have provided insight into the movement behaviour of a variety of marine species, including marine turtles (Block, 2005). The unique ability of satellite telemetry to remotely track marine turtles over long distances is unparalleled, and as a result, its implementation has increased exponentially over the course of the past decade (Godley et al., 2008).

In addition to surface movements, some PTTs can also relay detailed information on marine turtle diving activity (Hazan et al., 2012). Such data is particularly important considering that marine turtles spend the majority of their lives submerged (Bowen and Karl, 2007; Cuevas et al., 2008; Lutcavage and Lutz, 1997). To accurately evaluate habitat use, ecological roles, and susceptibility to anthropogenic threats, contemporaneous studies of vertical and horizontal movements performed by marine turtles are needed (Blumenthal et al., 2009; Cooke, 2008; Hindell et al., 2002; Seminoff et al., 2012).
et al., 2002). Effective management of the taxon depends on a comprehensive understanding of these movement and habitat use patterns.

Archival devices such as time depth recorders (TDR) are exceptional at generating detailed information on marine turtle dive behaviour, but have the downside of needing to be physically recovered in order to obtain data (Myers et al., 2006). PTTs equipped with sophisticated dive computers can overcome this limitation, but are constrained by the limited bandwidth available through the transmission signal relay system (Argos, 2008). There are currently two general PTT-dive logging devices available to researchers: satellite-relayed data loggers (SRDLs; Fedak et al., 2001) and satellite-linked depth recorders (SDRs; Polovina et al., 2003). SRDLs implement novel compression techniques that allow for the relay of dive profiles and other detailed dive information (see Fedak et al., 2001; Myers et al., 2006), whereas SDRs reduce the amount of information needed to be transmitted via Argos by grouping data into bins, thus relaying only summary dive information in the form of histograms (e.g. Hays et al. 1999; Hughes et al., 1998; Godley et al., 2002). Despite the reduced resolution of SDRs, these devices are cost-effective and remain a highly valuable tool in collecting dive data on marine turtles.

Dive behaviour of adult hawksbills remains poorly understood, and to date no dive research on hawksbills has been conducted in the eastern Pacific (Table 1). As part of an ongoing, region-wide satellite tracking effort, five adult hawksbills were outfitted with SDRs at three sites in the eastern Pacific, providing rapidly generated contemporaneous information on the surface and underwater movements of the species. Here, we evaluate general trends in dive behaviour, identify differences among individuals at different movement phases and diel patterns.

### 2. Methods

Location and dive data for hawksbill turtles were collected between June 2008 and April 2010 using PTTs with SDRs. Tag models MK-10, SPLASH and SDR-T16 (Wildlife Computers Inc., Redmond, WA) were attached to five hawksbills: one adult female (Curved Carapace Length (CCL) = 73.5; ID 40652) at Quebrado Beach, Loreto Bay National Park, Mexico (25°47′N – 111°18′W); one adult female (89.0 cm; ID 79784) at San Sebastian, Bahía Jiquilisco Biosphere Reserve, El Salvador (13°11′N – 89.0 cm; ID 37623, 52670, respectively) at La Playita, Machalilla National Park, Ecuador (01°33′S – 80°50′W) (Table 2, Fig 1).

Turtles were captured in-water using tangle-nets or on beaches after having completed nesting. Turtles were tagged opportunistically as part of a region-wide, ongoing telemetry study focused principally on identifying core habitat and informing conservation planning of the species (Gaos et al., 2012a). As a result, tags were programmed with variable dive bin and temporal data capture settings. These discrepancies limited our ability to pool data across turtles and/or realize particular analyses. SDRs measured three or four dive variables, depending on tag model, including maximum dive depth (MDD), time at depth (TAD), dive duration and water temperature. Data were grouped into one 24-h or four 6-h periods and transmitted in bins. In all cases a dive was defined as any submergence > 2 m, while any dives ≤ 2 m were classified as surface time. Bathymetric values were acquired from Geophysical Data Systems (GEODAS: www.ngdc.noaa.gov/mgg/geodas) in a 1° spatial grid and converted to contour polygons. For details on tag attachment, turtle location point acquisition/filtering and track plotting, see Gaos et al. (2012a).

We analyzed differences in dive behaviour during three distinct movement phases: (1) inter-nesting, (2) migration and (3) foraging. For individuals captured in-water, these phases were determined by the activity in which the turtle was engaged when encountered (e.g. foraging). For individuals tagged on nesting beaches, we used displacement plots to identify phase shifts as turtles commenced and completed migratory movements, where inflection points distinguish among phases (Blumenthal et al., 2006; Godley et al., 2002; Seminoff et al., 2008). We analyzed daily differences in dive behaviour, with diurnal periods defined as those starting and ending between 06:00 and 14:00 and nocturnal periods defined as those starting and ending between 18:00 and 02:00 (all times local). Other time periods were excluded due to irregular overlap with crepuscular periods as a result of the variable tag settings. All dive bin comparisons discussed in this paper are descriptive in nature.

### 3. Results

#### 3.1. Turtle behaviour at surface

The five turtles were tracked for an average of 112 days (sd = 57). Among individuals, there were differences in the movement phases captured during the tracking period. Likewise, during these times, tracked individuals demonstrated a range of movement patterns. Turtles 40652 (Mexico) and 79784 (El Salvador) were tracked solely during the foraging phase and both remained in the vicinity of their original tagging sites (Fig 1(1) and 1(2)). Turtle 22130 (Ecuador) also remained close to its original tagging site, but was only tracked during the inter-nesting phase as the tag ceased transmitting prior the turtle’s departure from the nesting area. Turtles 37623 and 52670 (both in Ecuador) were tracked during all three movement phases (i.e. inter-nesting, migration and foraging) and undertook 250– km migrations from their nesting grounds to their foraging grounds (Fig 1(3)). Turtles 79784, 37623 and 52670 established foraging home ranges within shallow inshore mangrove estuaries and turtles 40652 and 22130 were tracked in nearshore, open-coast habitats.

#### 3.2. Turtle behaviour at depth

The five SDRs successfully relayed an average of 576.0 h (sd = 194.8) of dive depth data, 594.0 h (sd = 191.2) of time at depth data, 502.8 h (sd = 178.8) of dive duration data and 577.5 h (sd = 110.9) of time at temperature data. Results were pooled when feasible.
Nearly all recorded dives were to maximum dive depths (i.e. MDD) of \(\leq 10\) m (mean = 84.7%, sd = 12.8%, Fig. 2A). MDDs for tags 52670 and 22130, the only turtles with SDR’s programmed to record in successive 5 m increments, indicated a large proportion of their dives were actually to depths \(\leq 5\) m. Furthermore, dives of these two turtles rarely exceeded 20 m in depth, doing so only on 11 occasions, representing \(<0.3\%\) of their total records (nine dives to the 21–25 m and once each to the 31–35 m and 36–40 m).

Turtles also spent nearly all their time at depth (i.e. TAD) in the depth strata of \(\leq 10\) m (mean = 89.4%, sd = 10.2%, Fig. 2B). An average of 2.7% of their time was spent on the water’s surface and this value varied little across individuals (sd = 1.2%). Turtle 22130 spent the highest percentage (28.7%) of time at depths >10 m, but had only a slight increase in the rate of MDDs to depths >10 m when compared to three other turtles (Fig. 2B), indicating its visits to deeper areas were brief.

Dive duration for all but one turtle (79784) was bimodal, with dives either lasting \(\leq 5\) min (mean = 32.1%, sd = 20.2%) or lasting >20 min (mean = 46.8%, sd = 21.5) (Fig. 2C). Information on the duration of dives in this second mode (>20 min) was only available for turtle 22130 and suggests that at least some hawksbills can dive for 41–90 min (29.2%) and even >2 h (2.1%).

The TDR data also revealed a temperature association for hawksbills, e.g. the tracked individuals spent 91.6% (sd = 6.6%) of their time in waters between 25 °C and 30 °C, although here, too, there was evidence of individual variability. Three turtles, 52670, 37623 and 22130, registered some proportion of their time (8.2%, 6.0% and

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**Fig. 1.** Argos location data of the five hawksbill turtles outfitted with SDRs. Box 1 = foraging locations for turtle 40652 in Mexico; Box 2 = foraging locations for turtle 79784 in El Salvador; Box 3 = all foraging locations for turtles 22130, 52670 and 37623 in Ecuador, with inset 3a showing inter-nesting phase locations for all three turtles and inset 3b showing foraging phase locations for turtles 52670 and 37623. Star indicates turtle release sites.

**Fig. 2.** Maximum dive depth (m), time at depth (m) and dive duration (min) for the five turtles tracked in this study.
15.5%, respectively) in slightly cooler waters, i.e. 19–24 °C. Only one turtle, 52670, was found to spend some time (2.9%) in substantially colder waters, i.e. 16–18 °C.

The sea floor depth of location points ranged from 0 to 70 m, with 85.8% (sd = 9.8%) of tag transmissions coming from areas ranging from 0 to 20 m in depth and 72.0% (sd = 17.9%) occurring over bathymetric values of ≤ 5 m.

3.2.1. Dive behaviour among movement phases

The two turtles (37623 and 52670) tracked for all three movement phases (i.e. inter-nesting, migration and foraging) were tagged during the same season at the same nesting site in Ecuador. These turtles exhibited similar post-nesting migration routes and settled in adjacent foraging areas (Fig. 1(1)).

During the inter-nesting phase, data for both turtles showed that the highest frequency of MDDs were to depths ≤ 5 m (Fig. 3A). Nonetheless, there were individual differences in all dive categories during this phase, most notably in the time at depth, during which turtle 52670 spent a greater amount of time in the deeper depth ranges (Fig. 3D).

During the migration phase, MDD and TAD were most evenly distributed between the ≤ 5 m and ≤ 10 m depth bins (Fig. 3B and E). The majority of dives tended to last > 20 min during this phase, including nearly all dives for turtle 52670 (Fig. 3H). Overall, turtles also spent the greatest amount of time at the water's surface during the migration phase (Fig. 3E).

The foraging phase was characterized by longer dives and reduced surface times, with the majority of dives for both turtles lasting > 20 min (Fig. 3I) and time spent at the water’s surface lower than for any other phase (Fig. 3F). However, the greatest proportion of MDDs and TADs occurred in depths ≤ 5 m for turtle 52670 and at depths > 5 m for turtle 37623 (Fig. 3C and F).

3.2.2. Diel dive behaviour

Three tags (22130, 79784 and 40652) had 6-hour intervals that allowed us to analyze diel dive behaviour (Fig. 4). As a general trend, turtles tended to reach similar depth bins and have similar dive durations during both diurnal and nocturnal time periods. There were similarities in the dive behaviour of two of these three turtles (22130 and 40652), both of which inhabited nearshore open-coast habitats; these two turtles used a greater range of depths, had deeper MDDs and undertook longer dives during the day. The majority of dives for these turtles were to depths ≤ 5 m and ≤ 6 m, respectively, for each time period. The third turtle (79784), in contrast, inhabited an inshore estuary (Gaos et al., 2012a, 2012b) and undertook longer dives at night although the range of depths were similar between diel periods (Fig. 4A–I). No nocturnal dives and only 10.5% of diurnal dives were to depths ≤ 5 m for turtle 79784. The shortest duration dives (i.e. those lasting ≤ 10 min) for turtle 79784 occurred solely at night (Fig. 4H).

4. Discussion

The SDR data suggests adult hawksbills in the eastern Pacific are nearly always found in the top 10 m of the water column regardless of individual, site, movement phase or diel time period. Although hawksbills did dive deeper than 10 m, these dive events were relatively rare and only 34 of 13,710 total dives (0.2%) were recorded to depths > 20 m. The hawksbills tracked here spent the greatest proportion of their time at depths ≤ 10 m, a finding supported by several
published studies on juvenile and adult conspecifics in other ocean regions (e.g. Bell and Parmenter, 2008; Blumenthal et al., 2008; Houghton et al., 2008; Witt et al., 2010). Our data provide additional evidence that suggest hawksbill turtles of all life stages and among ocean regions concentrate activities at these depths, and rarely dive deeper than 20 m (but see Blumenthal et al., 2009; van Dam and Diez, 1996).

The virtually exclusive shallow diving by hawksbills contrasts the frequent deeper diving exhibited by several other marine turtle species (e.g. Georges et al., 2006; Hatase et al., 2007; Hays et al., 2004; Houghton et al., 2008; McMahon et al., 2007; Polovina et al., 2004; Rice and Balazs, 2008). These differences may be associated with dietary preferences. For example, loggerhead turtles can often dive to depths >50 m in pursuit of prey items such as demersal fish (Hatase and Sakamoto, 2004; Peckham et al., 2011), while leatherback turtles are known to commonly dive to depths >100 m in search of gelatinous zooplankton (Fossette et al., 2010; Hays et al., 2004). Hawksbill turtles often feed on sponges and macroalgae, which are typically found at highest densities in shallow water (Huston, 1985; Leon and Bjorndal, 2002; Meylan, 1988). Similarly, green turtles, which also feed predominantly on light dependent organisms (e.g. sea grass and macroalgae), generally also remain at shallow depths (Hays et al., 2002; Hazel et al., 2009; Seminoff et al., 2006).

We found that the majority (72.0%) hawksbill location points occurred over bathymetric values of ≤5 m. The shallow maximum dive depth exhibited by hawksbills in this study is likely influenced by these local bathymetric constraints, which are characteristic of the inshore estuaries predominantly inhabited by the species in the eastern Pacific (Gaos et al., 2012b). Hawksbills have been documented undertaking prolonged bouts on the seafloor with few mid-water dives in other ocean regions (Houghton et al., 2008; Okuyama et al., 2010) and our findings suggest the hawksbills tracked here also spent considerable time near the sea floor.

The shallow dive behaviour and highly neritic habitats used by hawksbills in this study have implications on hawksbill persistence as it may make them more susceptible to natural predators (von Brandis et al., 2010) and vessel strikes (Hazel et al., 2007), the latter a particular concern in coastal areas where fishing and/or recreational boat traffic is high. Furthermore, the specialized use of shallow, neritic areas may put these turtles at greater risk from catastrophic environmental shifts (McMahon et al., 2007). Associations with shallow coastal waters may also, however, convey benefits to hawksbills, including increased access to food, suitable habitat structures that facilitate resting via buoyancy control, and stable temperatures (Blumenthal et al., 2009; Houghton et al., 2003, 2008; van Dam and Diez, 1996). Their shallow and coastal horizontal and vertical movements may also be a boon to hawksbill conservation along coastlines in the eastern Pacific Ocean, i.e. associations with coastal habitats may facilitate research and targeted conservation actions in neritic waters.

Hawksbills occupied water temperatures between 25 and 30 °C across sites. These warm temperatures and the general use of shallow, coastal areas, which are typically warmer than those offshore, may confer a thermal advantage by facilitating food digestion and the build-up of fat stores (Krawchuk and Brooks, 1998; Snell and Fritts, 1983). The lowest temperature ranges were registered for the three turtles in Ecuador, which is the latitudinal margin of the species’ breeding range (Alfaro-Shigueto et al., 2010; Quiñones et al., 2011), and may be a result of the Humboldt Current consistently bringing colder waters into coastal areas in the region (Penven and Echevin, 2005).
It is noteworthy that the lowest water temperatures were recorded during the turtles’ inter-nesting and migration phases, whereas all warmer temperatures were registered during the foraging phase, suggesting that turtles may tolerate lower than ideal temperatures/conditions during their inter-nesting phase in order to complete this crucial life history stage. The SDRs recorded several diverges \(n = 22\) as lasting longer than 2 h, representing the longest recorded dive time for this species. These dives all occurred during the inter-nesting phase and at the coldest temperatures \((16–24 \, ^\circ\text{C})\). A slower metabolic rate induced by the coldest periods would alleviate the need for frequent surfacing, thus facilitating the prolonged dives \((\text{Southwood et al., 2003})\). Despite their duration, these dives were likely aerobic, particularly considering the ability of sea turtles to conserve oxygen at low temperatures \((\text{Hochscheid et al., 2004, 2005})\). Extended dives are often used to infer resting \((\text{van Dam and Diez, 1996; Wallace et al., 2005})\). Increased resting periods during the inter-nesting phase is congruous with the behaviours turtles are known to exhibit during this phase \((\text{Fossette et al., 2012})\), i.e. between nesting events, turtles typically only forage opportunistically, often resting to direct energy to egg production and nesting \((\text{Hays et al., 2000; Owens, 1980; Wallace et al., 2005})\).

There were similarities in the patterns of dive depths across diel time periods, indicating that vertical movement occurs both diurnally and nocturnally. For diurnal time periods, it is likely that dive behaviour is related to foraging and feeding, activities that occur almost exclusively during the day \((\text{Blumenthal et al., 2009; Okuyama et al., 2010; Storch et al., 2005; van Dam and Diez, 1997})\). Surface times have been found to be longer between feeding bouts as turtles recover from extended foraging dives \((\text{Blumenthal et al., 2009})\). Our data did not fully conform to this pattern as we found increased surface times during diurnal periods for two turtles and less for one.

Nocturnal periods are thought to be largely a time when marine turtles rest on the bottom, indicated by longer dive durations and decreased variability in depth use \((\text{Fossette et al., 2012; Houghton et al., 2008; Okuyama et al., 2010; van Dam and Diez, 1996, 1997; Witt et al., 2010})\). The similar dive behaviour and transmissions received during diel time periods in our data does not fully support nocturnal resting and thus we cannot exclude the possibility that adult hawksbills may alternate between foraging and resting during both nocturnal and diurnal time periods. Previous research has documented juvenile hawksbills alternating between these behaviours during the day \((\text{Houghton et al., 2003})\), but not at night. The restricted home ranges demonstrated by adult hawksbill turtles in the eastern Pacific \((\text{Gaos et al., 2012a})\) may indicate that resting and foraging areas overlap \((\text{Houghton et al., 2003})\), which would facilitate switching between these activities. The use of TDRs or SRDLs to provide dive profile information would help clarify nocturnal activity of adult hawksbills in the region \((\text{Houghton et al., 2003})\).

The inter-individual variability in dive behaviour may indicate vertical and/or temporal (diel) partitioning of habitat to decrease intraspecific competition \((\text{Blumenthal et al., 2008})\). In addition to being used by conspecifics of various life stages, most of our study sites are also inhabited by other marine turtle species \((\text{Wallace et al., 2011})\), which suggests there may be further benefits to resource partitioning.

We also found some differences in dive behaviour among the three movement phases. Surface times were longest during the migration phase, which may be associated with increased basking/resting at water’s surface between prolonged bouts of travel \((\text{see Storch, 2003})\). However, the inability of tags to distinguish dives at depths \(\leq 2\) m may mean that much of this ‘surface time’ during migration was actually spent just below the water’s surface.

Previous research on adult hawksbills has found that dive behaviour during the foraging phase is very regular and uniform compared to that undertaken during the inter-nesting phase \((\text{Storch, 2003})\). However, we did not find substantial differences in the dive behaviour between these two phases, with dives predominantly remaining at \(\leq 10\) m during both.

Dive patterns have been shown to be influenced by a complex interaction of physiological and environmental factors \((\text{Blumenthal et al., 2008})\). Because the eastern Pacific Ocean is an area with complex topography and substantial spatiotemporal variability in oceanographic characteristics \((\text{Seminoff et al., 2008})\), some differences in dive behaviour among individual turtles in this region are not surprising. Indeed, individual hawksbills in the Caribbean have also been documented exhibiting substantially different diving behaviour \((\text{Blumenthal et al., 2009})\). The variable bin settings of the tags used in this study, as well as the limited depth use demonstrated by turtles, may have hindered our ability to differentiate more detailed behaviours and trends among individuals. Additional dive research, including the use of devices that generate dive profiles, is needed to more fully understand dive behaviour of adult hawksbill turtles. Future efforts should focus on increasing sample size per nesting colony and tagging individuals over multiple seasons. Increased understanding of hawksbill dive behaviour will facilitate the management and conservation of this imperilled species. Direct in-water observations may also play an important role in this respect, providing context for remotely gathered data \((\text{Blumenthal et al., 2009; Schofield et al., 2006})\). Juvenile hawksbill turtles have been considered particularly suitable for in-water studies due to their use of accessible neritic habitats and restricted home ranges \((\text{von Brandis et al., 2010})\). Likewise, our results indicate that adult hawksbills in the eastern Pacific are also good candidates for directed in-water monitoring.

The vertical habitat use patterns for adult hawksbills in the eastern Pacific identified here highlight frequent use of shallow waters for this species, particularly the top \(10\) m of the water column. Dive behaviour was similar across diel time periods, suggesting nocturnal activity may be more prevalent than previously believed. While dive behaviour did vary among movement phases, differences were minimal, further demonstrating dependence on shallow areas for the adult age class. These findings provide unique insights into adult hawksbill biology in the eastern Pacific. Nonetheless, a paucity of information continues to inhibit our understanding of hawksbill dive behaviour, particularly for adults, and data gaps will persist until further research is conducted. Effective national and international management and conservation efforts rely on the collection of more data on this endangered species.

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