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Impacts of recreational diving on hawksbill sea turtle (*Eretmochelys imbricata*) behaviour in a marine protected area

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ABSTRACT

The hawksbill sea turtle (*Eretmochelys imbricata*) is a critically endangered species encountered by recreational divers in marine protected areas (MPAs) circumtropically. Few studies, however, have examined the impacts of recreational diving on hawksbill behaviours. In 2014, we collected turtle sightings surveys and dive logs from 14 dive operations, and conducted in-water observations of 61 juvenile hawksbill turtles in Roatán, Honduras, to determine if differences in dive site use and diver behaviours affected sea turtle behaviours in the Roatán Marine Park. Sightings distributions did not vary with diving pressure during an 82-day study period. We found the amount of time turtles spent eating, investigating and breathing decreased when approached by divers. Our results suggest diver interactions may negatively impact sea turtle behaviours, however it is unknown if recreational diving has a cumulative effect on turtles over time. We recommend that MPA managers should implement monitoring programmes that assess the impacts of tourism on natural resources. We have established monitoring of hawksbills as representatives of the marine habitat in an MPA, which has the potential to be heavily impacted by dive tourism, and provide recommendations for continued monitoring of the resource.

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Marine ecotourism; behavioural studies; scuba diving; tourism impacts; in-water observations; coral reefs

Introduction

Within the past few decades, a new form of non-consumptive interaction with the natural world, known as ecotourism, has rapidly developed to become a multi-billion dollar industry and a critical funding source for conservation (Aylward, Allen, Echeverría, & Tosi, 1996; Davenport & Davenport, 2006; Fillion, Foley, & Jacquemot, 1994). Although often touted as an exemplary form of sustainable development in the developing world (Aylward et al., 1996; Butcher, 2006; Tisdell & Wilson, 2002), ecotourism may also cause degradation and alteration of fragile ecosystems and sensitive fauna (Boo, 1990; Krüger, 2005; Müllner, Eduard Linsenmair, & Wikelski, 2004). If the potential social, economic, and environmental impacts of ecotourism are not considered and actively managed, ecotourism industries may inadvertently destroy the natural resources they depend on (Doiron & Weissenberger, 2014; Moore & Carter, 1993). If ecotourism is to be sustainable, impacts of tourism activities on wildlife must be assessed and managed.

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Birding, for example, is a type of non-consumptive tourism which may cause unanticipated negative impacts on animal health and behaviour, including reduced foraging time (Yasué, 2005), lower survival rates (Müllner et al., 2004) and diminished breeding success (Ellenberg, Mattern, Seddon, & Jorquera, 2006). Yasué (2005) found that as tourism increased on beaches in British Columbia, Canada, semipalmated plovers' (*Charadrius semipalmatus*) swallowing rates decreased. Müllner et al. (2004) found that temporal overlap of the tourism high season with the hoatzin (*Opisthocomus hoatzin*) fledging period in the Cuyabeno Reserve, Ecuador, caused increased chick stress and mortality in tourist-exposed sites. Similarly, Ellenberg et al. (2006) found that Humboldt penguin (*Spheniscus humboldti*) breeding successes in the Damas, Choros and Chañaral islands, Chile, was significantly reduced at sites frequently visited by tourists.

Marine tourism, like birding tourism, may alter animal behaviours. Kovacs and Innes (1990) found that harp seal (*Phoca groenlandica*) pups in the Gulf of St. Lawrence, Canada, engaged in more agonistic behaviours and less resting behaviour when tourists were present. Similarly, Stafford-Bell, Scarr, and Scarpaci (2012) found that Australian fur seals (*Arctocephalus pusillus doriferus*) in Port Philip Bay, Australia, engaged in increased hauling out behaviour when human swimmers were nearby. Likewise, Vermeulen, Cammareri, and Holsbeek (2012) found that right whales (*Eubalaena australis*) in Bahía, San Antonio, Argentina, reduced social interactions and increased avoidance behaviour during encounters with whale watchers.

The detrimental effects of bird watching, whale watching and seal tourism on the behaviours of terrestrial and marine species have been well documented (Beale & Monaghan, 2004; Boyle & Samson, 1985; Vermeulen et al., 2012); however, similar studies examining the effect of recreational diving on marine animals are rare (Meadows, 2004). Similar to birding, recreational diving is usually seen as a non-consumptive activity that can promote increased awareness of marine environments (Davis & Tisdell, 1995). With the rise of international tourism, and improved safety equipment, dive tourism has grown substantially in the last 64 years, with over 1 million new recreational divers trained each year (Davenport & Davenport, 2006), and may place undue stress on rapidly diminishing coral reef ecosystems.

Recent studies indicate that in some dive locations, this increase in recreational divers is linked to increased coral mortality and spatiotemporal variability within marine protected areas (MPAs). For example, Tratalos and Austin (2001) found that diver numbers and distances from mooring buoys in the Cayman Islands were highly correlated with declines of the reef building coral, *Montastrea annularis*, and increases in dead coral coverage. Additional studies from Zakai and Chadwick-Furman (2002) in the northern Red Sea indicated that over-use of dive sites (> 30,000 dives per year) can lead to unsustainable levels of coral damage, independent of site topography. Conversely, Roupheal and Inglis (2002) found that coral degradation in the Great Barrier Reef Marine Park, Australia, was associated with variability in diver behaviour, and not primarily with dive site overuse.

In addition to causing environmental degradation, recreational swimming and diving can cause unintended behavioural changes in marine macrofauna. Constantine (2001) studied swim-with-dolphin tourism in the Bay of Islands, New Zealand, and found that large numbers of human swimmers (31 swimmers approaching one individual per year) can cause bottlenose dolphins (*Tursiops truncatus*) to become sensitized to humans and lead to reduced dolphin foraging, resting, nursing and socializing behaviour. Relatedly, Constantine, Brunton, and Dennis (2004) found that an increase in the number of dolphin-watching boats (from 49 to 60) following dolphins caused a decrease in the amount of time dolphins spent resting, which could lead to higher stress levels and a reduction in energy reserves.

Similarly, Quiros (2007) studied the impacts of recreational swimmers on whale sharks (*Rhincodon typus*) during feeding in an MPA in Donsol, Philippines, and found that small groups of recreational swimmers could alter whale shark swimming patterns through path obstruction and proximity. He also found that specific diver activities, including direct touch, close approach and flash photography, significantly increased the magnitude of the disturbance, concluding that alterations in whale shark behaviour may reduce survivability by diverting metabolic energy away from feeding and toward avoidance behaviours (Quiros, 2007).

Few studies, however, have examined the effects of recreational diving on behaviour in any species of sea turtle. Meadows (2004) used focal-animal activity budget observations to study the impacts of recreational snorkelers on green turtle (*Chelonia mydas*) behaviour, and found that as few as 10 snorkelers making regular approaches (4 per hour) toward turtles caused a 30% increase in total bouts of swimming, eating and cleaning behaviours. Snorkeler interactions, however, tend to be short (< 5 min; Meadows, 2004) and may not accurately represent the effects of SCUBA diver interactions, which have the potential to be longer and more impactful. Moreover, Hawaiian green turtles exhibit unique behaviours due to their close proximity to humans (Balazs, 1996), making the results of Meadows' (2004) study difficult to extrapolate to other turtle species and populations.

Similarly, Kostas (2015) studied the impact of snorkeler interactions on loggerhead sea turtle (*Caretta caretta*) disturbance behaviour in Zakynthos, Greece, and concluded that adult females may seek an optimal balance between conserving energy and avoiding snorkelers. This is similar to results of Slater (2014), who found that the presence of snorkelers in Akumal Bay, Mexico, significantly reduced green sea turtle feeding behaviour. Both Kostas (2015) and Slater (2014), however, did not measure the impact of SCUBA diving on sea turtle behaviour.

Multiple studies worldwide have utilized SCUBA diving to measure sea turtle behaviours (Blumenthal, Austin, Bell, et al., 2009; Dunbar, Salinas, & Stevenson, 2008; Houghton, Callow, & Hays, 2003; Schofield, Katselidis, Dimopoulos, Pantis, & Hays, 2006; Stimmelmayer, Latchman, & Sullivan, 2010; von Brandis, Mortimer, & Reilly, 2010). However, few of these studies have taken into account the potential impacts of SCUBA diving itself, on sea turtles. If in-water observational studies are to accurately quantify sea turtle behaviour, they must take into account the potential effects of SCUBA divers.

Several recent studies have emphasized the need for additional research on the potential impacts of divers on sea turtle behaviour. Schofield et al. (2006) conducted in-water observations of male and female loggerheads (*Carreta carreta*) in Zakynthos, Greece, and concluded that existing in-water turtle watching protocols should be refined to limit tourist activities to areas where turtle behaviours are minimally impacted. Schofield et al. (2006), however, did not specifically measure the effect of human in-water activities on sea turtles. Similarly, Dunbar et al. (2008), conducted in-water observations of recently released juvenile hawksbills in Roatán, Honduras, and noted that observer proximity may have affected observed turtle behaviour. Dunbar et al. (2008), however, did not quantify the potential impacts of recreational diving on sea turtle behaviour. These studies emphasize the need for additional research on the potential effects of recreational diving on sea turtle behaviour.

The hawksbill sea turtle (*Eretmochelys imbricata*) is a circumtropically distributed, critically endangered species (McClenachan, Jackson, & Newman, 2006; Meylan, 1999; Mortimer & Donnelly, 2008). Hawksbill populations are threatened worldwide from poaching (Mortimer & Donnelly, 2008), bycatch (Lewison et al., 2013), pollution (Yender & Mearns, 2003) and climate change (Poloczanska, Limpus, & Hays, 2009), however, no studies to date have reported the effect of SCUBA diving on hawksbill behaviour or ecology. Additional studies quantifying the effects of recreational diving on hawksbill turtle behaviours are of critical importance, and will allow conservation agencies to design and implement more effective regulations for sea turtle interactions in areas heavily impacted by diving.

In the current study, our aim was to determine if differences in dive site use and diver behaviours affected hawksbill sea turtle behaviours in an MPA. Since foraging behaviour requires turtles to spend less time scanning for potential predators and more time scanning for food, we hypothesized that turtles would spend less time investigating and eating, and more time swimming in heavily used dive sites than they would in dive sites that are less heavily used. Similarly, since we expected turtles within an MPA to be accustomed to divers, we hypothesized that turtles would spend less time investigating and eating, and more time swimming when divers approached turtles than when divers were at baseline position. Results from our study will provide critical information on the impacts of SCUBA diving on sea turtles in MPAs, establish a representative monitoring programme to assess the impact of diving tourism on a natural resource and offer valuable recommendations for the continued monitoring of that resource.

Materials and methods

Study area

Roatán is a 77 km long island located approximately 52 km off the north coast of Honduras ($16^{\circ}20'24''\text{N}$, $86^{\circ}19'48''\text{W}$). The Bay Islands, of which Roatán is the largest island, form part of the Mesoamerican Barrier Reef complex, and were once one of seven major historical hawksbill nesting areas in the Caribbean, (Long, 1774; McClenachan et al., 2006; Meylan, 1999). To date, local hawksbill populations in the area are poorly understood (Dunbar & Berube, 2008). The Roatán Marine Park (RMP) is a community-based MPA covering a network of coastal coral reefs and mangrove estuaries extending approximately 13 km from the towns of West Bay, West End and Sandy Bay, as well as around the western tip of Roatán (Figure 1).

Within the RMP, the reef crest lies approximately 92 meters off shore and slopes gradually for 2.2 km before dropping off steeply (>130 m) at the reef wall (Gonzalez, 2013). Bathymetry is varied, composed primarily of hard corals from the families Faviidae, Milleporidae and Pocilloporidae; soft corals from the families Gorgoniidae and Plexauridae; sponges of Chondrillidae, Geodiidae and Petrosiidae; turtle grass (*Thalassia testudinum*); and sandy substrate (Berube, Dunbar, Rützler, & Hayes, 2012; Dunbar et al., 2008). As Roatán has grown in popularity as a scuba diving destination, the number of tourists visiting Roatán by airplane has increased annually, from 45,482 in 2010 to 82,202 in 2014 (Honduras Institute of Tourism, personal communication, December 10, 2015). Following the increase in tourism, diving within the RMP has increased substantially within the last 15 years and is concentrated in the towns of West End and West Bay (Doiron & Weissenberger, 2014). Within the RMP, there are 29 dive centres, representing 64.5% of all dive centres on the island ($n=45$). Diving tourism within the RMP is year round and typically peaks in March during the dry season between January and August (Honduras Institute of Tourism, personal communication, December 10, 2015).

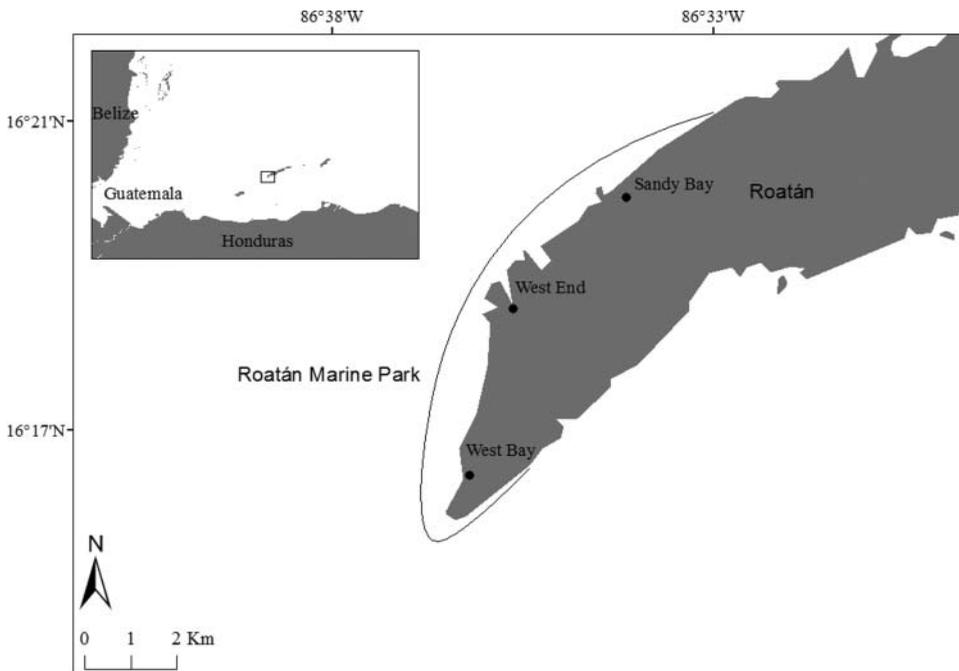


Figure 1. Map of Roatán and the Roatán Marine Park, Bay Islands, Honduras. Black line indicates the approximate area of the Roatán Marine Park. Inset shows regional location of Roatán.

Sightings and dive logs

From 9 June to 29 August 2014, we distributed weekly survey forms to 14 dive operators in the West End. On each data sheet, divers recorded the site, date, name of the diver logging the information, depth of sighting (meters), species, life stage of the turtle (adult or juvenile) and number of individuals sighted. All values that divers gave in imperial units were converted to metric. Participants were given identification sheets (in both English and Spanish) to aid in species identification and promote awareness. When species were unable to be identified, they were assigned to the “unknown” group for analysis. We collected data sheets 1–2 times per week as able, combined this data with turtle sightings from our own dives and input the information into a Microsoft Excel (2003) file for analysis. During our own dives, we estimated turtle life stage (juvenile or adult male) based on the length of the tail, with adult males having large tails extending well past the carapace and juveniles/females having small tails not extending past the carapace (Owens, 1999). Over the duration of the study period, we also collected daily dive logs from two dive centres within the West End and combined them with our own research dive logs to calculate monthly dive site use. On each dive log sheet, divers recorded date, site visited, time of day (if available) and number of divers. To avoid pseudoreplication, we only analysed the point-of-entry dive site for drift dives.

In-water observations

We conducted continuous focal and video in-water observations of hawksbills using modified methods from Dunbar et al. (2008) and von Brandis et al. (2010) during dive trips between 09:00 and 16:00 hours. We followed each individual as long as possible and recorded observed behaviours using an underwater camera (Olympus Stylus Tough-8000 12 MP with Ikelite underwater camera housing) and video camera (GoPro Hero 3+ Black Edition with underwater housing; GoPro Inc., San Mateo CA). We recorded water depth (m) using a standard wrist-worn dive computer (Leonardo; Cressi Inc., Genova, Italy), and start and stop time (to the nearest second) for all observed activities using a water resistant watch (Expedition T4005; Timex Group USA Inc., Middlebury, Connecticut). We recorded notes of observations underwater using underwater paper. To reduce the potential of recording errors, all in-water observations were conducted and recorded by the primary author. Prior to the beginning of the study, the primary author was trained in in-water observation techniques by an experienced diver and marine biologist (SGD).

All behaviours were characterized into six solitary and two social behaviour categories. The six solitary behaviour categories included swimming (active movement along the bottom, through the water column, or near the surface), resting (coming to a stationary position on the sea floor), surfacing (to breathe), investigating (active searching for food material indicated by a pause in swimming and active examination of nearby material), eating (the intentional ingestion of a substance) and scratching (on coral or object) (as per Dunbar, et al. 2008). The two social behaviour categories included reacting (physical response to diver presence) and intraspecific interacting (reacting to presence of other turtles). In addition to measuring time, we also recorded the total number of occasions a turtle engaged in each behaviour and defined this value as the number of bouts for a given activity. When visibility permitted, we counted the number of times a turtle lifted its head out of the water as a proxy for total number of breaths taken at the surface (as per Von Brandis et al. 2010).

As a control for diver interaction, we began all observations (when possible) by recording turtle behaviours for approximately 5 min with divers keeping a constant distance of approximately 3–5 m from turtles (Meadows, 2004). We defined this position as the baseline position for divers. To test if diver approach affected a change in the amount of time turtles engaged in specific behaviours, we instructed different sized groups of 1–4 divers to slowly approach and observe each turtle. We defined diver approach as the intentional movement of divers from baseline position to within 1–2 m of sea turtles. To remove user bias for choosing particular group sizes, we varied the test group size randomly on each dive. During diver–turtle interactions, we recorded all relevant diver

parameters, including the number of divers watching a turtle at the beginning and end of an interaction, the number of touches on a turtle by a diver and the closest estimated distance a diver approached a turtle. We conducted repeated in-water observations for turtles (as able) to test for turtle habituation to diver presence.

To test for repeat observations of the same turtle, we collected left, right and dorsal facial photographs of all observed turtles and analysed them with the interactive individual identification system (I³S): Pattern (Version 4.0.1; den Hartog and Reijns 2014) using methods as per Dunbar, Ito, Bahjri, Dehom, and Salinas (2014) and Baeza, Hayes, Wright, Salinas, and Dunbar (2015). After every dive, we ran photographs from each turtle encounter through I³S and assigned each individual a unique identification number.

Statistical analysis

We consolidated turtle sightings and dive log data into an 82-day database for 9 June 9–29 August, and used linear regression to test for a relationship between number of sightings and sighting survey effort. To test for relationships between recreational diving pressure and sighting rate, we ran a Spearman's correlation (r_s) for hawksbill sightings rate (number of hawksbill sightings/number of dives) and the number of divers per logged visit. Using ArcGIS for Desktop (Version 10.2; ESRI 2013), we mapped fixed kernel density (1 km) estimates of hawksbill sightings rates against the total number of divers logged at each site for 46 dive sites in the RMP.

For analyses of turtle behaviour, we only analysed behaviours from the first interaction with each individual turtle to avoid pseudoreplication. To maximize sample size and test for the overall effect of diver presence on turtle behaviour, we pooled all diver group size categories (1–4) together and calculated the total mean time for each turtle behaviour. To test for association of turtle behaviours with dive site use, we ran Spearman's correlations comparing the total number of divers per visit to the total amount of time turtles engaged in each behaviour. Similarly, to test for an association between the duration of surface intervals and the number of breaths turtles took at the surface, we ran a Spearman's correlation comparing total breathing time to total number of breaths. We also ran Spearman's correlations to test for associations between the mean time turtles engaged in each activity and the mean number of behaviour bouts for each observed behaviour. Separate Spearman's correlations were run for each observed behaviour before and during diver approach.

We ran paired *T*-tests and nonparametric Wilcoxon signed ranks tests comparing the total number of bouts and time for each behaviour that turtles engaged in before and after divers approached. We also ran repeated measures analysis of covariance (ANCOVAs), adjusting for total baseline and diver approach time covariates, comparing the total time turtles engaged in each behaviour before and after divers approached turtles. When necessary, we normalized the data using square root transformations and back transformed the adjusted means, as specified in the results. Means are reported with ± 1.0 standard error and sample range, and medians are reported with interquartile range (IQR). Effect size for repeated measures ANCOVAs are reported as β estimates. We used IBM SPSS Statistics (Version 13; IBM Corporation 1989–2004) and SAS (Proc Mixed, Version 9.4; SAS Institute Inc. 2013) for all statistical analyses. Alpha level was set at 0.05 for all analyses.

Results

Sightings and dive logs

We collected turtle sightings information from 14 dive centres in the West End. Dive centres recorded 701 dives at 46 sites between 9 June and 29 August 2014. Ten survey entries did not specify either the dive site or date, and were excluded from analysis. On the majority of occasions ($n = 445$), one turtle was seen, and 26 dives recorded no turtle sightings. A total of 666 hawksbill sightings, 420 green sightings (*Chelonia mydas*), four loggerhead sightings (*Caretta caretta*) and 22 unknown turtle

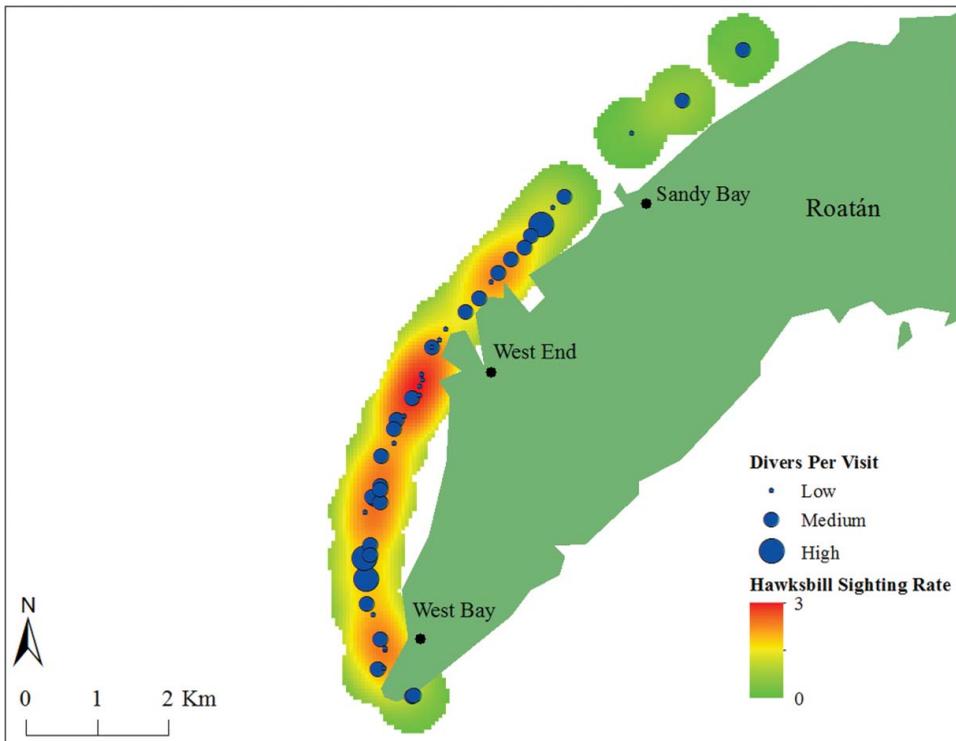


Figure 2. Hawksbill sightings rate and diver density for 46 dive sites in the Roatán Marine Park. Size of dots indicates mean number of divers per visit from two dive operations to each site over an 82-day period. Gradation indicates fixed kernel density (1 km) estimate of hawksbill sightings rates from 14 dive operations. Hawksbill sightings rates are associated with dive site coordinates.

sightings were reported during the study. Of the hawksbills reported, 393 (59%) were reported as adults and 273 (41%) as juveniles. Of the greens reported, 282 were reported as adults and 138 as juveniles.

We compiled 648 dive logs involving 3092 divers between 9 June and 29 August. Mean number of divers per dive was 5.0 ± 0.3 SE and mean hawksbill sightings rate per dive was 1.0 ± 0.1 SE. Spearman's correlations indicated there was no relationship between hawksbill sighting rate and the number of divers per visit ($n = 46$, $r_s = 0.07$, $p = 0.67$), the total number of divers ($n = 46$, $r_s = -0.12$, $p = 0.44$) or the total number of dives at each site ($n = 46$, $r_s = -0.110$, $p = 0.47$). Spatial distribution of sightings and divers indicated that divers tended to make more sightings between West End and West Bay and fewer between West End and Sandy Bay (Figure 2).

Sightings survey effort was unevenly distributed over the three months, with peak intensity occurring in July. This distribution significantly correlated with total turtle sightings ($n = 46$, $r_s = 1.00$, $p < 0.01$).

In-water observations

From 12 June to 2 September, 2014, we conducted 6092.0 min of in-water surveys at 23 sites in the Roatán Marine Park. We devoted 1027.3 min (16.9% of total survey time) to conducting in-water observations of 61 juvenile hawksbills. The average number of hawksbills observed per dive was 0.7 ± 0.1 . We obtained repeated observations of 11 turtles, with nine individuals observed twice and two individuals observed three times. Total initial observation time was 823.9 min. and total time for

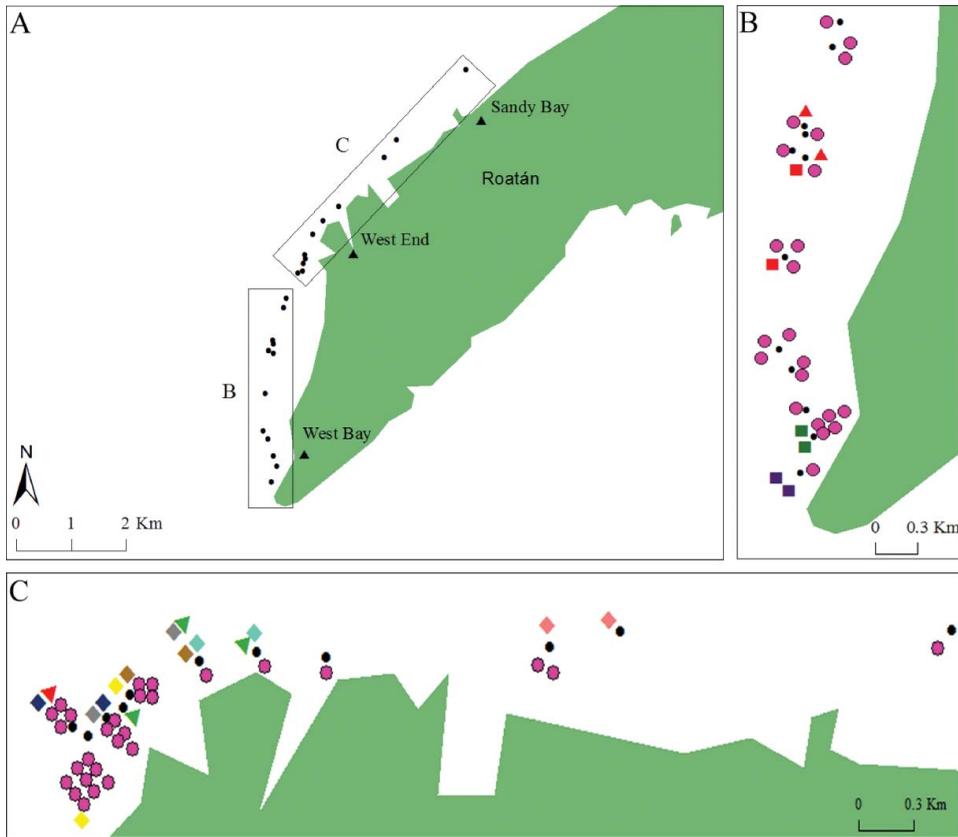


Figure 3. (A) In-water observation locations from 61 hawksbills in the Roatán Marine Park between. (B) West Bay to West End ($n = 30$). (C) West End to Sandy Bay ($n = 31$). Small dots: dive sites ($n = 23$). Large circles: single observations of individuals ($n = 50$). Squares: individuals observed twice ($n = 18$). Triangles: individuals observed three times ($n = 6$). All observations are associated with the geographic coordinates of the closest dive site.

repeated observation (not including initial observation time) was 203.4 min. All re-observed turtles were found within five sites of their initial observation location (Figure 3).

Mean turtle observation depth ($n = 61$) was 14.3 ± 1.0 m (range 4.6–39.6 m). Mean observation time per turtle was 13.3 ± 7.5 min (1.2–36.0 min). During 823.9 min of observations, swimming was the most commonly observed behaviour. Mean turtle swimming time was 7.8 ± 0.7 min (0.0–25.5), and represented 57.9% of all observation time (Table 1). Turtles spent a mean of 0.5 ± 0.1 min breathing (0–3.6 min) and took a mean of 3.3 ± 0.1 breaths ($n = 203$, 0–12) at the surface. Mean number of divers ($n = 183$) observing turtles was 3.0 ± 0.2 (1–8). Our sample size of dives ($n = 2$) with large dive groups (> 4 divers), was too small for statistical comparison to dives ($n = 59$) with small dive groups (≤ 4 divers), so that criteria was excluded from the analysis.

On three occasions, we observed intraspecific interactions between hawksbills. Twice, two hawksbills approached each other, circled for several seconds and then swam away, and once, two individuals pressed their left ventral postocular and tympanic scales flat against each other, circled around each other for 26.0 seconds, and then swam in different directions.

Spearman's correlations indicated that the time turtles spent in each of the three most common behaviour categories was independent of the numbers of divers per site ($r_s < 0.25$, $p > 0.05$), and that total number of breaths was highly correlated with total breathing time ($r_s = 0.92$, $p < 0.0001$). Spearman's correlations also indicated that the mean proportion of time turtles ($n = 61$) engaged

Table 1. Behaviour categories, mean time (min) displaying behaviour, time range of each activity and proportion of total observation time of each activity for 61 hawksbills in the Roatán Marine Park. Total observation time: 823.9 min.

Behaviour	Mean time of each activity \pm S.E.	Range (min)	Proportion of observation time
Swimming	7.8 \pm 0.7	0.0 – 25.5	57.9
Eating	2.2 \pm 0.5	0.0 – 15.9	16.5
Investigating	2.2 \pm 0.4	0.0 – 12.8	16.3
Breathing	0.5 \pm 0.1	0.0 – 3.6	4
Reacting	0.5 \pm 0.2	0.0 – 7.0	3.4
Interacting	0.2 \pm 0.1	0.0 – 5.8	1.4
Resting	0.1 \pm 0.1	0.0 – 3.0	0.4
Scratching	0.1 \pm 0.1	0.0 – 0.5	0.1

in eating, investigating and breathing behaviours correlated with the total number of turtle behavioural bouts for each behaviour ($r_s > 0.80$, $p < 0.0001$).

Diver approach did not impact the median number of bouts that hawksbills ($n = 42$) engaged in swimming, eating, investigating and breathing behaviour (Wilcoxon signed rank: $S < 41$; $p > 0.05$). Similarly, Paired T -tests and Wilcoxon signed rank tests indicated that diver approach did not alter the median time that turtles ($n = 45$) engaged in swimming, eating and investigating behaviour (swimming: $t_{(DF)} = 0.97_{(44)}$, $p = 0.34$; eating: $S = -55.5$, $p = 0.21$; investigating: $S = -4$, $p = 0.94$). Conversely, turtle ($n = 45$) median breathing time was significantly less during diver approach (Median = 0.00, IQR = [0.00, 0.00]) than when divers were at baseline position (Median = 0.00, IQR = [0.00, 30.00]) (Wilcoxon signed rank: $S = -38.5$, $p = 0.01$).

To normalize time variables, we square root transformed the mean time turtles spent eating and investigating and back transformed the adjusted means. Repeated measures ANCOVAs, adjusted for total baseline time and diver approach time, indicated that diver approach did not impact the mean time turtles ($n = 53$) spent swimming (Figure 4(A); $F_{(1, 43)} = 0.33$, $p = 0.57$, β estimate = -15.00). Conversely, the mean time turtles ($n = 53$) spent eating and investigating was significantly lower during diver approach than when divers were at baseline position (Figure 4(B); eating: $F_{(1, 43)} = 4.31$, $p = 0.044$, β estimate = -1.79 ; investigating: $F_{(1, 43)} = 5.12$, $p = 0.029$, β estimate = -2.48).

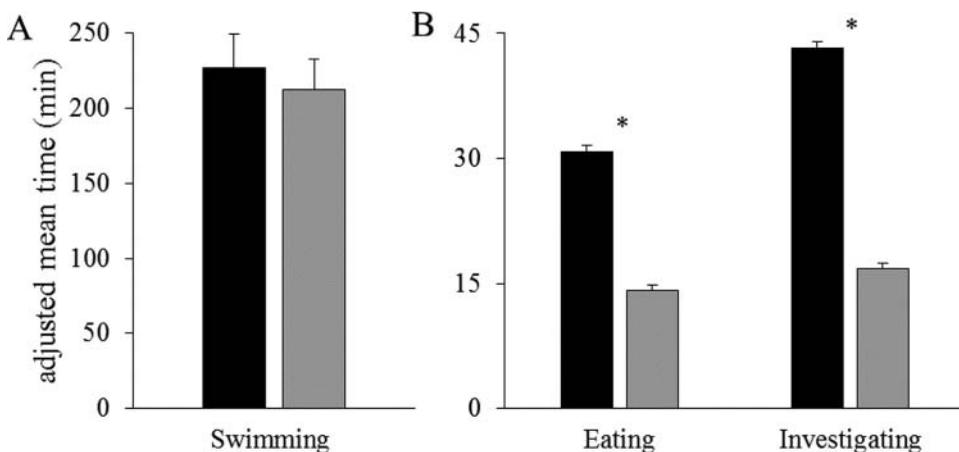


Figure 4. Adjusted mean time (min) + 1 SE that turtles ($n = 53$) engaged in (A) swimming behaviour, and (B) eating and investigating behaviour when divers were at baseline position (black bar) and during diver approach (grey bar). Time values are adjusted by the total time when divers were at baseline position (285.5 min) and the total time during diver approach (538.4 min). Asterisk (*) indicates $p < 0.05$.

Discussion

Sightings and dive logs

Our study is among the first to quantify the impacts of recreational diving on sea turtle sightings rates. Turtle sightings distributions throughout the RMP did not vary with the total number of divers per visit at each site over the 82-day period, suggesting that hawksbill abundance in the RMP is independent of current diving pressure. Similarly, Bell et al. (2009) studied recreational diving in the Cayman Islands and found that the most heavily dived area in the Cayman Islands, Bloody Bay Marine Park in Little Cayman, had hawksbill sightings comparable to less frequently dived areas. We also found that turtle eating, swimming and breathing behaviour did not differ with dive site use, suggesting that turtle behaviour is independent of diving pressure within the RMP. These results are supported by Slater (2014) who found that green turtle (*Chelonia mydas*) foraging behaviour was not correlated with tourist abundance. However, because our sightings and dive log survey results are limited to a single time period (June–August, 2014), our results may represent seasonal trends in turtle sightings and diving pressure.

In-water observations

The behaviour of juvenile hawksbills in local foraging grounds has been previously described at Mona Island, Puerto Rico (van Dam & Diez, 1996, 1997a, 1997b), at D'Arros Island, Republic of Seychelles (von Brandis et al., 2010), at St. Kitts, Lesser Antilles (Stimmelmayer et al., 2010), and in Roatán, Honduras (Dunbar et al., 2008). However, the current study is the first to measure effects of recreational diving on hawksbill behaviour.

Similar to Dunbar et al. (2008), we found that swimming was the most commonly observed behaviour in hawksbills (57.9% of total observation time). However, unlike Dunbar et al. (2008), we found that eating was the second most commonly observed behaviour (16.5%). Whereas Dunbar et al. (2008) conducted observations in an area outside the RMP, where sea turtle protection is not enforced, our study was conducted within the RMP, where daily patrols regulate sea turtle poaching and harassment. Studies of state-dependent risk-taking in green turtles by Heithaus et al. (2007) in Shark Bay, Western Australia, indicated that turtles preferentially foraged closer to bank edges in safer, yet lower foraging quality micro-habitats, when tiger shark (*Galeocerdo cuvier*) populations are high, and move farther from bank edges into areas with better foraging quality when shark population levels are reduced. If foraging behaviour in hawksbills is similar to predation-dependent foraging behaviour in green sea turtles, it is possible that turtles within the RMP spend a larger proportion of time eating than turtles outside the RMP due to reduced predation and harassment risk within the RMP. However, it is important to note that we observed the behaviours of turtles that had never been captured, whereas Dunbar et al. (2008) observed the behaviours of recently released hawksbills that may have exhibited atypical behaviour. Consequently, care must be taken when comparing results from the two studies.

In support of our original hypothesis and the findings of Slater (2014), we found that hawksbills within the RMP spent less time eating, investigating and breathing during diver approach. However, contrary to Meadows (2004) and our original hypothesis, we found that human approach had no significant effect on hawksbill behaviour bouts. In his study, Meadows (2004) concluded that the frequency change in the number of behaviour bouts was likely a consequence of turtles switching rapidly between behaviours to avoid snorkeler attempts to chase, touch or ride them. Unlike Meadows (2004), however, we did not observe any attempts by recreational divers to chase, touch or ride turtles. Thus, we suggest that turtles in our study were affected differently by human approach because divers followed strictly enforced policies prohibiting the harassment of sea turtles. Instead, we hypothesize that hawksbills within the RMP are habituated to diver presence and interested in diver activity, leading them to engage in less investigating, eating and breathing behaviour when divers are present.

These results, as well as multiple other examples, suggest that diver habituation may negatively impact marine macrofaunal behaviour. On multiple occasions, we observed groupers (Epinephelinae) alter their normal foraging behaviours and follow spear-hunting divers, in order to take advantage of speared fish as an accessible food resource. Similarly, we were informed by multiple dive centres that divers will feed groupers at certain dive sites, causing large numbers of groupers to periodically abandon regular foraging behaviours and form large aggregations at those sites (Baumbach, personal observation). Moreover, Titus, Daly, and Exton (2015) found that cleaning behaviour of reef fish on a heavily dived reef in Utila, Honduras was suppressed >50% when divers were nearby, and concluded that diver presence could reduce the fitness and lifespan of coral reef fish communities. These studies suggest that habituation of marine fauna to recreational divers can cause unintended behavioural changes over time.

It remains unknown, however, if recreational diving may have a cumulative effect on turtles over time. If long-term changes in behaviour are energetically expensive for turtles, divers may negatively impact sea turtle growth and fecundity, as suggested by Meadows (2004), and may cause changes to short- and long-term fitness levels (Amo, López, & Martín, 2006). For example, Amo et al. (2006) found that common wall lizards (*Podarcis muralis*) inhabiting areas of higher tourism in the Guadarrama mountains, Spain, had a higher infestation of ticks and poorer body condition at the end of the breeding season compared with lizards inhabiting areas of lower tourism. Counterintuitively, lizards in high tourism areas did not alter approach and flight-initiation distance behaviours in response to potential human threat (Amo et al., 2006). Similarly, Ellenberg et al. (2006) found that Humboldt penguin heart rates significantly increased during human approaches, and recovery to baseline heart rate required up to half an hour. Ellenberg et al. (2006) concluded that the long recovery phase following human approach was likely associated with significant energetic costs to penguins. Implications of these studies suggest that a similar phenomenon may be taking place in MPAs, and that divers may negatively impact sea turtle physiology without causing sea turtles to visibly alter their behaviour patterns.

In addition to having potential physiological effects, diver interactions with sea turtles could have long-term population effects. Long-term studies (13.5 years) by Bejder, Samuels, Whitehead, Gales, et al. (2006) of *T. truncatus* in Shark Bay, Australia, indicated that increases in dolphin-watching tourism led to a significant decline in local dolphin populations over time. In a similar study, Bejder, Samuels, Whitehead, and Gales (2006) found that dolphins in regions of low dolphin-watching vessel traffic exhibited longer lasting behavioural changes than dolphins in regions of high vessel traffic. Bejder, Samuels, Whitehead, and Gales (2006) concluded that individual dolphins sensitive to dolphin-watching tourism departed the study area, whereas dolphins less sensitive to tourism remained in Shark Bay. It follows that individual hawksbills within the RMP may be differentially susceptible to recreational diving tourism. As recreational diving tourism continues to increase in the RMP (Doiron & Weissenberger, 2014), hawksbills that are more susceptible to recreational tourism may move into foraging areas outside the RMP, where diving pressure is lower, although poaching pressure is much higher. This alteration in foraging behaviour may result in increased numbers of hawksbills being captured and killed.

Diver interactions with turtles may also have indirect effects on other species within reef ecosystems. Studies of behaviourally mediated indirect interactions (BMIs) with dugongs (*Dugong dugon*), tiger sharks (*Galeocerdo cuvier*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, by Heithaus and Dill (2002) and Heithaus, Dill, Marshall, and Buhleier (2002) suggest that the presence of dugongs in seagrass habitats can increase shark predatory behaviour which, in turn, can cause dolphins to reduce foraging behaviour. It follows that changes in sea turtle foraging behaviour may initiate a behavioural cascade, analogous to a trophic cascade, altering the behaviour of multiple reef species down the food chain (Dill, Heithaus, & Walters, 2003). Current predictive models, however, fail to integrate anthropogenic BMIs, and consequently may fail to accurately predict if the effects of diving tourism on marine ecosystems are sustainable (Dill et al., 2003).

The potential long-term impacts of diving tourism on turtles and reef ecosystems support the need for sustainable tourism frameworks that minimize disturbance in MPAs and satisfy the needs of tourists and key stakeholders (Landry & Taggart, 2009). Sustainable tourism, as defined by the World Commission on Environment and Development, must meet the needs of the present generation without depleting the ability of future generations to meet their own needs (WCED, 1987), and is directly connected to sustainable development, since tourism may operate by transforming environmental resources into products to sell in consumer markets (Garrod & Fyall, 1998). However, in many cost benefit analysis models used for tourism management, monetary valuations for natural resources are rarely determined, and tourism suppliers tend to view these resources as free goods (Garrod & Fyall, 1998). As a result, natural resources may be drastically degraded and overused during tourism production. This prioritization toward immediate, profit-driven returns often places the tourism industry in direct conflict with the protection of dwindling natural resources, so that the industry is actually destroying the resources it is trying to promote (Berno & Bricker, 2001). It is entirely possible that the environmental impacts of tourism are ignored by tourism practitioners because these impacts are outside of decision-making processes that are primarily focused on monetary value.

Doiron and Weissenberger (2014) studied diving tourism in Roatán and concluded that current practices were unsustainable because management strategies prioritized short term economic growth over the long-term health of coral ecosystems. These results suggest a growing need to account for natural resources used in tourism sectors, and to establish regular monitoring of natural resources to observe and mitigate resource changes in response to tourism pressure.

Our study used multiple methods to delineate the impacts of recreational diving on hawksbill sea turtles. However, several caveats must be noted. Following the observations of Bell et al. (2009) and Williams, Pierce, Fuentes, and Hamann (2015), positive sighting bias may have been a problem. Divemasters tended to record dive sightings only when a turtle was observed during a dive, and did not fill in forms when no turtles were sighted. Additionally, we had little control over preventing divers from recording multiple sightings of the same individual on the same dive, which may have positively skewed turtle sightings. Moreover, because hawksbills in Roatán exhibit high fidelity to local foraging areas (Berube et al., 2012), we could not determine whether turtle sightings from divemasters comprised unique records of multiple individuals or repeated sightings of single individuals.

Species identification accuracy could not be confirmed for individual sightings, and although participating divers were given ID sheets and instructed on species identification, incorrect identifications may still have occurred. Widespread misidentification of sea turtle species is a common problem in sea turtle sightings surveys. Hickerson (2000) found that divers in the Gulf of Mexico will disagree on correct species identification of an individual turtle observed by multiple divers on the same dive. Similarly, Humeau (2007) found that divers in French Guadeloupe commonly misidentified sea turtle species. Studies from Bell et al. (2009) in the Cayman Islands noted that divers, when identifying species, may fail to take into account differences in weather conditions, which may impact sighting ease and identification. Similarly, Williams et al. (2015) found that divers at Tofo Beach, Mozambique, tended to misidentify green turtles, particularly juveniles, as hawksbills.

One potential mechanism to reduce replication error and species misidentification in volunteer-based surveys is to utilize sea turtle photo identification methods. Both Hickerson (2000) and Williams et al. (2015) recommend the use of photographic surveys, and multiple studies indicate that photo identification systems are an effective method to identify sea turtle species and individuals (Baeza et al., 2015; Dunbar et al., 2014; Jean, Ciccione, Talma, Ballorain, & Bourjea, 2010; Reisser, Proietti, Kinas, & Sazima, 2008; Schofield, Katselidis, Dimopoulos, & Pantis, 2008). Dunbar et al. (2014) used I³S spot to re-identify hawksbills that had lost their flipper tags, illustrating the viability of using photo-identification software for long-term identification. Similarly, Baeza et al. (2015) used I³S pattern to successfully re-identify nine hawksbills observed on multiple occasions. We concluded that photographic identification software systems may offer a useful method to re-identify specific individuals, reduce replication error and allow for long-term studies of individual turtles.

In addition to potentially misidentifying species and repeat individuals, divers may also have misidentified turtle life stages. Divers were not specifically trained to estimate sea turtle carapace length underwater or determine life stages, and may have failed to take into account the magnification effect of water, potentially positively skewing sea turtle size estimates. Additionally, divers did not record how far away turtles were from observers during sightings or quantify water quality variability, which may introduce inaccuracy in size estimation and species identification (Bell et al., 2009). Williams et al. (2015) compared local sightings logs to dedicated sea turtle sightings surveys intended for scientific use, and found that divers made biologically implausible overestimates of sea turtle carapace length in 11.7% of survey records ($n = 22$). These studies combined with the results of our current study suggest that divers in the RMP require additional training in sea turtle identification and data recording methods prior to beginning future turtle sightings surveys.

Care must be taken when interpreting dive logs, as differences in sample sizes and recording frequencies can skew comparisons of dive logs and turtle sightings. There is a negative bias in our dive log survey data, because we were only able to collect monthly dive logs from two dive centres within the West End. However, during the study, dive centres within the West End tended to frequent the same sites each month (Hayes, personal observation), suggesting that dive logs from a small number of dive centres may accurately estimate relative diving pressure at different sites.

During the current study, we observed the impacts of small groups (1–4) of volunteer divers that may not have exhibited the same behaviours as larger dive groups from local dive operations. Unlike large dive groups, which tend to proceed slowly and explore within 1–2 dive sites of the original buoy, our group swam rapidly, specifically focused on finding turtles, and covered more area (1–4 dive sites). Moreover, unlike many commercial dive groups, which consist of both experienced and inexperienced divers, most of our volunteers had several months of diving experience. Multiple studies of diver impacts on marine ecosystems suggest that inexperienced divers have greater impacts on coral reef ecosystems than experienced divers (Chung, Au, & Qiu, 2013; Thapa, Graefe, & Meyer, 2006; Worachananant, Carter, Hockings, & Reopanichkul, 2008). Worachananant et al. (2008) found a negative correlation between diver experience and the number of diver contacts with coral in Thailand. Likewise, Thapa et al. (2006) found a correlation between diver experience level and environmentally responsible behaviours of divers in southwest Florida. If the behaviour of inexperienced divers (i.e. contact with coral, harassment of local biota, mixing of seafloor sediment) is detrimental to coral reef health, it follows that inexperienced diver behaviour may also negatively impact the behaviour and health of animals, including sea turtles, that live in coral reef ecosystems. However, to date, few studies have examined whether inexperienced divers negatively impact marine macrofauna.

It is also important to note that we conducted our study between June and August during peak diving season in Roatán which lasts from January to August (Honduras Institute of Tourism, personal communication, 10 December 2015). Diving pressure within the RMP is lower during the rainy season from August to December, and it is possible that turtle–diver interactions during the off season are fewer and have different effects on sea turtle behaviours. Long-term annual studies of diving tourism within the RMP, however, are currently not available.

Conclusions

Our results suggest that small groups of intermediate to experienced divers (1–4 divers) in MPAs can significantly reduce the amount of time hawksbills spend foraging and breathing. Conversely, we found that current levels of recreational diving within the RMP do not significantly impact hawksbill abundance.

Based on these findings, we make the following recommendations. First, in-water observations should be conducted in conjunction with time depth recorder studies (similar to Blumenthal et al. 2009 and Francke et al. 2013) to form a comprehensive overview of recreational diving impacts on sea turtle behaviours. Specifically, foraging and flight response behaviours of turtles within and

outside MPAs should be compared to quantify the effect of recreational diving policy on sea turtle behaviours.

Second, additional long-term sightings and dive log surveys should be conducted in MPAs, particularly in areas heavily impacted by diving. These surveys should be combined with habitat assessments of local sea turtle foraging grounds to evaluate if recreational diving pressure indirectly impacts sea turtle population levels through the degradation of foraging habitats.

Third, long-term sea turtle photo-identification surveys using computer-assisted software systems should be implemented in MPAs to facilitate accurate species identification and long-term studies of individual turtles. If implemented over an entire MPA, long-term photo-identification surveys may enable resource managers to estimate sea turtle population numbers, monitor changes in sea turtle populations over multiple years and re-identify resident and migrating individuals.

Finally, MPA managers should collaborate with key stakeholders and researchers to implement monitoring programmes that assess the impacts of tourism on natural resources. The current study has been an initial effort toward meeting this objective. We established monitoring of hawksbill sea turtles as representatives of a marine habitat which has the potential to be heavily impacted by dive tourism in Roatán, and provided recommendations for continued monitoring of the resource. If diving tourism is to continue as a long-term tourist attraction in MPAs, managers must be able to evaluate the environmental costs of tourism on sea turtles and coral reef ecosystems, and ensure that current management policies do not endanger marine resources in the future.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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