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Aerial and underwater surveys reveal temporal variation in cleaning-station use by sea turtles at a temperate breeding area

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ABSTRACT: Many animals invest time and energy in removing unwanted organisms from their body surface; however, the benefits of symbiotic cleaning associations to 'clients' are disputed. We used aerial (unmanned aerial vehicles, UAVs) and underwater surveys to investigate whether loggerhead sea turtles *Caretta caretta* actively or incidentally invested in using fish-cleaning stations at a temperate breeding area (Zakynthos, Greece), although they are expected to minimize movement to divert energy to egg development. If the former, we hypothesized that turtles would swim into the station (UAV surveys), visit multiple times and compete for access (underwater surveys). Underwater surveys showed that station location changed annually, ruling out usage of a long-term cognitive memory. UAV surveys showed that turtles began using the station immediately after mating activity decreased (mid-May), with use remaining high until females departed (July). Wind direction (primarily southerly) was correlated with the frequency of use (UAV and underwater surveys) and direction of movement through the station (from upwind to downwind); however, turtles swam actively (i.e. did not simply drift). Of the unique turtles photo-identified during underwater surveys, 25 and 18% of individuals were detected multiple times within and across surveys, respectively, with at least 2 turtles competing for access to cleaner fish in most surveys. UAV surveys showed that more turtles were present within 100 m of the station compared to the turtles detected by underwater surveys at the station, suggesting individuals may visit the station repeatedly through the day. We conclude that turtles might initially find a station incidentally; however, repeated visits and competition for access suggest that turtles receive direct (stress relief, epibiont removal) and/or indirect (health, fitness, migratory) benefits.

KEY WORDS: Active sampling · Competition · Foraging · Host–parasite relationship · Parasite defence grooming · Unmanned aerial vehicles · UAVs · Drone · Loggerhead · *Caretta caretta*

INTRODUCTION

For many animals, cleaning symbioses with other species (also termed interspecific reciprocal mutualism) provide an essential service to remove unwanted organisms, damaged tissues or mucus from the external body surface (Limbaugh 1961, Trivers 1971, Losey 1974). Examples of such associations exist across vertebrate and invertebrate groups and in both terrestrial and marine environments, including mites cleaning tropical bees (Biani et al. 2009), a variety of bird species cleaning ungulates (Hart 1990, Sazima 2007), albatrosses cleaning sunfish on the water surface (Abe et al. 2012) and various shrimp, crab and fish species cleaning octopuses, fishes, sea turtles, marine iguanas and

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whales (Feder 1966, Grutter 2002, Oliver et al. 2011).

Cleaning associations are expected to benefit 'clients' despite the costs associated with such an activity. Clients must usually travel to specific sites (termed 'cleaning stations') and solicit cleaners (i.e. pose for inspection) and compete with other conspecifics, whilst also reducing the time spent on other vital activities and compromising their vigilance against predators (Trivers 1971, Hart 1990, Arnal & Côté 1998, Thomson et al. 2015). In theory, the amount of time that a client spends at a cleaning station should be proportional to the net benefits that the client receives from cleaning (Poulin 1993). However, while cleaners clearly benefit by gaining access to concentrated food resources (Losey 1974, Gorlick et al. 1978, Grutter 1996a), the fitness or reproductive benefits to clients (i.e. ultimate causation or adaptive value) remain less clear (Losey 1974, 1979, Grutter 1996b, Cheney & Côté 2003, Gingins & Bshary 2015). For instance, extensive studies on tropical and temperate fish species have found that cleaners remove variable or negligible loads, with cleaning rates being dependent on the species of cleaner fish, inspection time and the abundance, body size and parasite load of clients (Hobson 1971, Grutter 1995, Arnal et al. 2000, Combes 2001, Sasal 2003, Floeter et al. 2007, Narvaez et al. 2015). Alternatively, stress relief might represent a derived benefit (Bshary et al. 2007), with clients frequenting cleaning stations as a result of receiving reinforcing positive tactile stimulus from cleaners (i.e. proximate or immediate causation mechanisms; Losey 1974, Gorlick et al. 1978). Other benefits might include disease avoidance or improved hydrodynamics (Frick & Pfaller 2013).

At least 3 sea turtle species have been documented to solicit the cleaning services of shrimp and both carnivorous and herbivorous fishes (Booth & Peters 1972, Smith 1988, Losey et al. 1994, Wicksten 1995, Sazima et al. 2004, Sazima 2007, Sazima et al. 2010, Grossman et al. 2006, Schofield et al. 2006, Maia-Nogueira et al. 2010). These cleaning associations are believed to help rid turtles of damaged tissue, barnacles, algae and propagules (e.g. barnacle cyprids, parasitic amphipods, algal spores) which, if left unchecked, could cause physiological stress by allowing the entry of pathogens through the carapace or reducing their hydrodynamic ability (Zamzow 1998, Stamper et al. 2005). Cleaning stations tend to be localised in space and/or time, and have been found in both foraging and breeding habitats. Cleaner fish would be expected to have a regular source of clientele at foraging grounds, as they tend to be used year-round (with regular inflow and outflow of different individuals; e.g. Mancini et al. 2015), with only a component of the adult population migrating to breed each year (e.g. Hays et al. 2014). In contrast, the window of opportunity for breeding is restricted to a few months of the year for most temperate and sub-tropical sea turtle populations (e.g. Dodd 1988, Hirth 1997), making the benefits to cleaner fish under such time constraints questionable. Furthermore, various studies have shown that turtles primarily rest during breeding to minimize energy expenditure and increase investment in egg development/maturation (Minamikawa et al. 2000, Houghton et al. 2002, 2008, Fossette et al. 2012), with cleaning by fish representing an energetically costly activity.

Thus, here we investigated the seasonality and frequency of visitation by loggerhead sea turtles *Caretta caretta* at a breeding rookery, along with the degree of interactions with conspecifics. We aimed to use this information to determine whether use of cleaning stations was opportunistic or sustained throughout the breeding period, suggesting some benefit to turtles.

MATERIALS AND METHODS

Study area

In 2005 (Schofield et al. 2006), 2015 (Papafitsoros & Schofield 2016) and 2016, 3 fish cleaning stations (1 in each year) were opportunistically found at different locations along the NATURA 2000 submerged shallow sandbank habitats of Laganas Bay on Zakynthos Island, Greece (Fig. 1A; 37° 43′ N, 20° 52′ E) during in-water photo-identification surveys of sea turtles. The bay is 105.88 km^2 in size and contains 6 discrete loggerhead sea turtle nesting beaches, supporting 786–2018 nests (Casale & Margaritoulis 2010, Touliatou & Margaritoulis 2011) made by around 170–403 females yr^{-1}, assuming each female lays 5 clutches, or 283–670 females yr^{-1}, assuming each female lays 3 clutches (Zbinden et al. 2007, Katselidis et al. 2013, Schofield et al. 2013). This area is protected within the framework of the marine protection area of the National Marine Park of Zakynthos (Katselidis et al. 2013, 2014).

We previously described the fish species involved in cleaning turtles, along with the parts of the body that are cleaned (carapace and skin) and responses of turtles to fish cleaning activity (Schofield et al. 2006, Papafitsoros & Schofield 2016). The 2005 station was

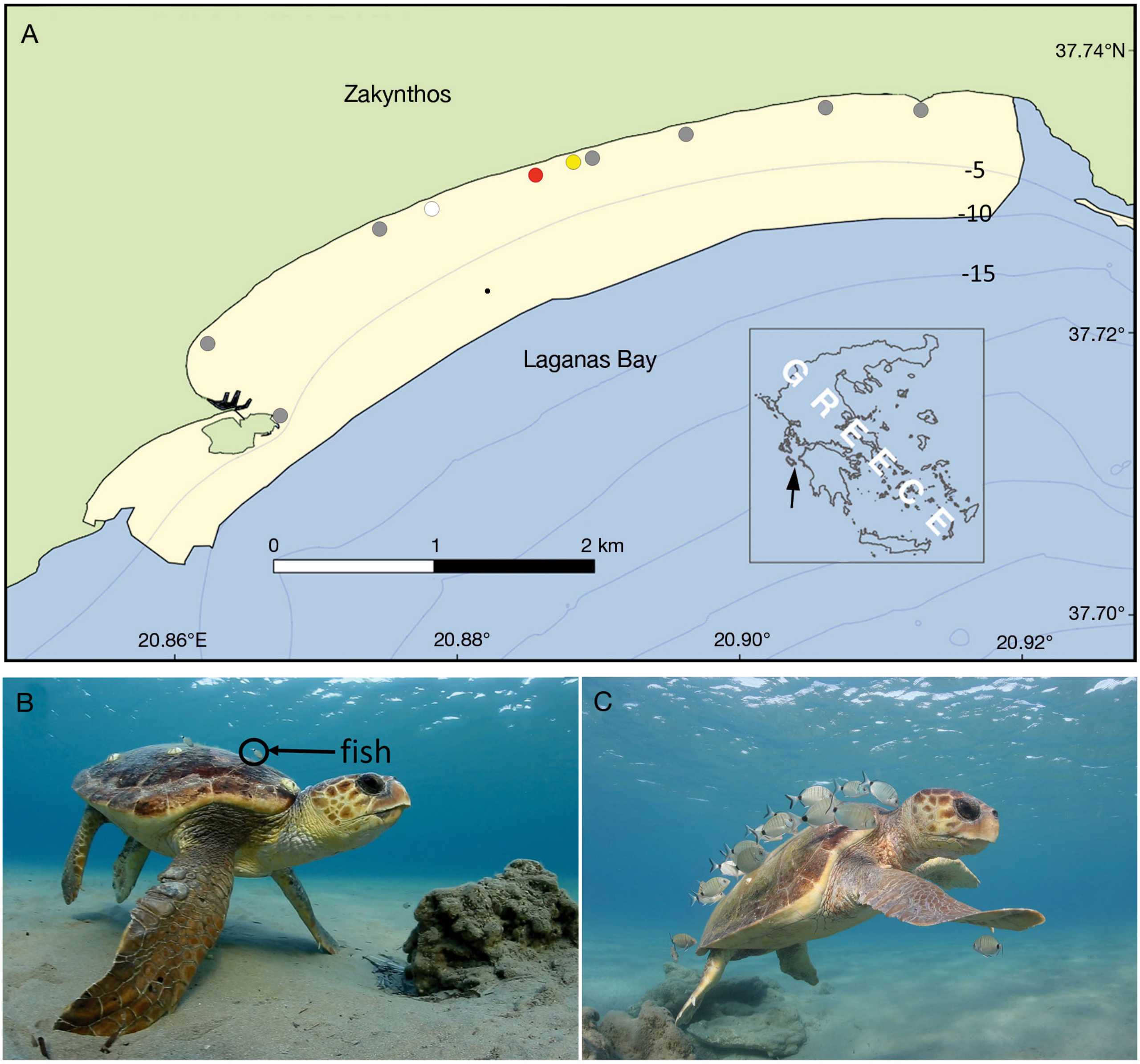

Fig. 1. (A) Study area, showing the sandbank area and the location of the cleaning station over the 3 years (2005, white circle; 2015, yellow circle; 2016, red circle). The locations of other submerged rocks detected in 2016 are shown in grey. Loggerhead turtles *Caretta caretta* being cleaned by sheepshead bream *Diplodus puntazzo* at the (B) 2015 station and (C) 2016 station, showing the difference in size of cleaner fish across years (photos by Kostas Papafitsoros)

introduced by Schofield et al. (2006), and here we present its position relative to the other stations detected in 2015 and 2016. For the 2015 station, we present our underwater observations of unique turtles from the date that the station was first detected (mid-breeding season, July). All data presented for the 2016 station (aerial and underwater) have not been previously published. This was the only station that we consistently monitored from the start to the end of the season.

In-water observations

In 2015, we primarily used still photographs (Canon 6D, Sigma 15 mm fisheye lenses) to record the turtles visiting the cleaning station, and trialled fixed underwater video cameras (GoPro Hero 4; maximum operation time 2.5 h) on a few occasions to obtain continuous footage on station use. Thus, our results for this year are restricted to presenting the number of unique turtles detected. Unique turtles were identified using photo-identification of the facial scute patterns (Schofield et al. 2008). We detected no visual signs of disturbance to turtles (i.e. departure from the station or rapid movement) by our presence when recording their behaviour underwater using the hand-held GoPros and cameras.

In 2016, we used 3 techniques to observe turtle activity at the cleaning station from 7 June to 29 July: (1) photographs (Canon 6D), (2) hand-held videos (GoPro Hero and Canon 6D) of focal turtles being cleaned and (3) fixed videos (GoPro Hero) at the station to record all turtles entering and leaving the immediate area of the rocks. Surveys were carried out for 2.5 to 5 h (i.e. duration of 1 or 2 GoPro videos) spanning between 07:00 and 20:00 h during favourable conditions (i.e. underwater visibility >1 m, low wave action). These data were assimilated to provide information on: (1) the number of unique individuals frequenting the station over the entire study period and (2) the frequency and duration of visitation within and across days.

To estimate the percentage of females observed at the cleaning station out of the total number of females that nested in 2016, we predicted the total number of females in 2016 based on estimates of about 1500 clutches according to a local newspaper (IMERA, Zakynthos, 3 Oct 2016) and assuming females lay 3 to 5 clutches in a season (Zbinden et al. 2007, Schofield et al. 2013). The number of turtles visiting the station on different days in 2015 and 2016 was compared against weather variables collected by the Zakynthos weather station (i.e. air temperature, humidity, air pressure, wind speed and direction). Details of actual cleaning behaviour were not assessed in this paper, as this information is available in previous publications (Booth & Peters 1972, Losey et al. 1994, Wicksten 1995, C. Sazima et al. 2004, I. Sazima et al. 2004, Grossman et al. 2006, Schofield et al. 2006, Maia-Nogueira et al. 2010).

The fish species that cleaned turtles were identified based on (1) their continuous presence at the station (all stations were isolated rocks in an extensive sandbank area; thus, other fish were not generally present) and (2) whether they approached turtles on arrival or waited to be solicited, and whether they remained with the turtle, foraging on the carapace and/or skin, despite turtles reacting to this activity (for further details, see Schofield et al. 2006). We estimated the length of turtles and fish by comparing their size against the known size of the camera tripod (to which we affixed the GoPro Hero) when individuals were directly beside it, and validated this measurement using turtles that had been previously measured with a tape-measure during other monitoring activities (see Schofield et al. 2013).

Aerial surveys

From 10 April to 28 July 2016, the 8 km stretch of nearshore submerged sandbanks in the breeding area of Laganas Bay (Zakynthos Island, Greece) was surveyed on 35 occasions primarily within 400 m of shore every 1 to 4 d using a DJI Phantom 3 Professional™ (www.dji.com), which is a relatively small, low-cost and commercially available aerial unmanned aerial vehicle (UAV, also termed drone) that can travel around 2 km from the launch point. The aircraft is controlled through the GO app from DJI™ that runs on a tablet. Each UAV battery allows for approximately 15–20 min total flight time (using the DJI TB48 battery which provides the longest flight time). This UAV model includes a camera capable of recording up to 4K quality video. In the current study, all surveys were recorded in 3840 × 2160 pixel video quality at 30 frames s^{-1}. The camera is attached to a 3-axis gimbal system that stabilizes the video in flight and allows the operator to remotely control multiple aspects of the camera angle. The aircraft has a GPS-stabilized flight control system and is stable in relatively windy conditions (up to 25 km h^{-1}). Transects were run along 4 lines at 50, 150, 250 and 350 m distance from shore, using fixed waypoints and validated through the repeated sighting of the same permanent underwater objects. During these surveys, the UAV was flown at a height of 60 m (allowing a 100 m field of view), with all turtles being visible to a seabed depth of 5 m (see Schofield et al. 2017, for validation experiments).

We reviewed the video footage collected during these surveys to detect the presence of rocks and reefs along the submerged sandbank region. All rocks and reefs were then visited and checked for the presence of fish species known to clean turtles and/or cleaning activity at 15 d intervals throughout the season (shown in Fig. 1). Using the data from the UAV surveys on all survey days, we recorded the distribution of turtles within a 100 m radius of the cleaning station (i.e. derived from 2 transect lines representing about 10 s of video data each). This information was used to detect when turtles started using the cleaning station and the frequency of use over the course of the season.

In addition, we used the 'hover' function of the UAV to fly it above the cleaning station at a height of 60 m (allowing 100 m field of view) for a period ranging from 20 min (1 battery) to 40 min (2 batteries) on 4 occasions. We used this information to investigate how turtles enter and depart the cleaning area by documenting the positions of the turtles at 30 s intervals. We also used the movement data to determine the area in which cleaning occurs (i.e. the maximum range of fish from the station), which we validated through direct observations during underwater surveys. Cleaning activity was identified from the aerial footage when turtles stopped directional swimming, surfaced regularly to breathe, and in several instances, slowly circled tightly around the station (i.e. within a 5 m radius).

Statistical analyses

For the statistical analyses, we used Student's *t*-test and Pearson's product-moment correlation to determine the relationships between our variables. We also used these tests to compare our values with the modelled general decline in the number of females in the entire breeding area (based on values extracted from the study by Schofield et al. 2015).We used the Mann-Kendall test to investigate possible monotonic trends in time. We used the Wallraff rank sum test of angular distance and Rao's spacing test and Kuiper's test to analyse circular data (i.e. wind). For all statistical analyses, we used the R program (R Development Core Team 2016).

RESULTS

In-water observations

The cleaning station was opportunistically found in 2015 during the course of in-water photo-identification surveys of turtles. Surveys were conducted on 19 favourable days between 4 July (after detection) and 1 August, totalling about 40 field hours. Around 35 juveniles (of up to 80 juveniles present) of at least 3 fish species belonging to the Mullidae and Sparidae families were observed conducting cleaning activity, including the sheepshead bream *Diplodus puntazzo*, which is an omnivore (Supplement 1; all supplements available at www.int-res.com/articles/suppl/m575p153_supp/). A total of 29 records of 13 unique turtles (12 females, 1 possible immature turtle) were obtained.

The 2016 station was surveyed on 39 favourable days between 7 June and 29 July 2016, totalling about 120 field hours. Morning surveys (between 07:00 and 12:00 h) were conducted on 7 occasions in 2016, spread at intervals across this period (9 June to 14 July); however, ≤3 turtles were detected on any of these surveys. Most turtles were detected at the station after midday. Just ~25 juvenile sheepshead bream conducted cleaning activity in 2016 (Supplement 2). The body length of the sheepshead bream was ~12–15 cm in 2016 (similar to 2005) versus ~3–5 cm in 2015 (Fig. 1B,C). In 2016, a total of 85 records of 55 unique turtles (52 females, 2 males, 1 possible immature turtle) were obtained. The recorded number of females represented 20% of females recorded in the 8 km nearshore area based on the photo-identification of 256 unique individuals in 2016 and 21.5% when using the maximum record of 242 females from drone surveys conducted in the same area during 2016 (Schofield et al. 2017). This percentage ranged from 11 to 18% based on estimates of the reproductive females in that year.

In 2016, when turtle visits to the station were assessed within surveys (i.e. within each given 2.5–5 h observation period), most turtles visited the station just once (75%), while the remainder visited 2–7 times (mean ± SD: 2.7 ± 1.2 visits). Turtles that used the station more than once in the same survey frequented the station twice as long as those that used the station just once (mean 10 versus 5 min, respectively).

We recorded interactions between turtles on 8 and 33 occasions during the 2015 and 2016 surveys, respectively, when more than 1 turtle (usually 2, but sometimes 3) entered the station area at the same time, leading to different types of interactions between turtles. When a turtle entered the station area where a turtle was already being cleaned, some or all fish immediately switched turtles, but did not necessarily remain on the new client. However, in the 41 instances when more than 1 turtle was present, 2 distinct behaviours were detected between the turtle being cleaned and the turtle entering the station: no contact (n = 25) versus physical contact (n = 16). In the instances with no contact, the entering turtle approached the station, either maintaining a distance of several metres from the turtle being cleaned or passing and circling within 1 m of the other turtle, but not touching (Fig. 2A; Supplement 3), with fish remaining with the same turtle, permanently transferring to the new turtle, or cleaning both turtles at the same time on similar numbers of observed occasions. In the instances with physical contact, the entering turtle directly approached the turtle being cleaned, nudging at its flippers or nudging the side of its body (Fig. 2B,C; Supplement 4), with fish permanently transferring to the new turtle on 50% of observed occasions. However, none of the physical contacts

Fig. 2. Examples from observations, showing (A) fish switching from one loggerhead turtle *Caretta caretta* to another, with no physical contact between the turtles; (B) turtle approaching, physically nudging and successfully displacing another turtle being cleaned; (C) turtle approaching, nudging its hind flippers and failing to displace a turtle being cleaned (see Supplements at www.int-res.com/articles/suppl/m575p153_supp/ for full series of slides and example videos). Cleaning activity occurred over the rock and within a 5 m radius from the rock; thus, not all images contain the rock (see Fig. 3B; photos by Kostas Papafitsoros)

escalated into full-scale aggressive interactions (see Schofield et al. 2007 for a schematic of the escalation in agonistic behaviour between turtles). In both instances, if the fish did not transfer to the entering turtle, the turtle would circle the station (remaining in view of the observer) and approach the rock again. On some occasions, the larger turtle (based on measuring the relative size of the turtles from photographs with fish) was selected, but not consistently (Supplement 3c).

During the 2015 survey, 1 turtle was observed using the station on 7 consecutive days, while 6 other turtles were sighted returning to the station between 1 and 2 times at intervals of 7 ± 4 d (range: 2–12 d). During the 2016 survey, 15 turtles were sighted returning to the station between 1 and 5 times after intervals of mean 11 ± 9 d (range: 1–37 d), with 5 turtles being repeatedly (3–5 times) recorded over 30–40 d periods. Two turtles (1 female and 1 possible immature turtle) were observed at the respective cleaning stations in both 2015 and 2016.

Aerial surveys

UAV transect surveys showed that 8 possible submerged rocky features were present within 400 m of shore along the 8 km submerged sandbank area, of which we observed only one being used by turtles for cleaning in 2016 (Figs. 1 & 3). This station was first confirmed by direct observation to be used for cleaning activity on 6 June (at the start of the nesting period). The rocks at the station covered an area of about 2 × 2.5 m and were located 116 m directly offshore from the beach at about 2 m seabed depth. The 2015 station was located 350 m east of the 2016 station, and was almost completely submerged in sand by 2016. The 2015 station was not used by turtles in 2016. The 2015 station was of a similar size to the 2016 station, at a similar seabed depth and a similar distance offshore (about 100 m) to the 2016 station. Out of the 7 other submerged rocky features, only 3 were inhabited by the known cleaner fish species, but none were visited by sea turtles during 2016.

From 6 May 2016 onwards, we detected >100 turtles in each transect survey along the 8 km submerged nearshore sandbank area, with only one mating pair being detected within 100 m radius of the station before 16 May 2016 (Fig. 4). From 16 May to 28 July 2016, 2 to 14 turtles (n = 85 turtles counted in total for all transect surveys) were detected at distances of mean 27 m (SD ± 19.14) from the station.

We hovered the UAV over the cleaning station for a total of 120 min (40 min on 2 occasions, 20 min on

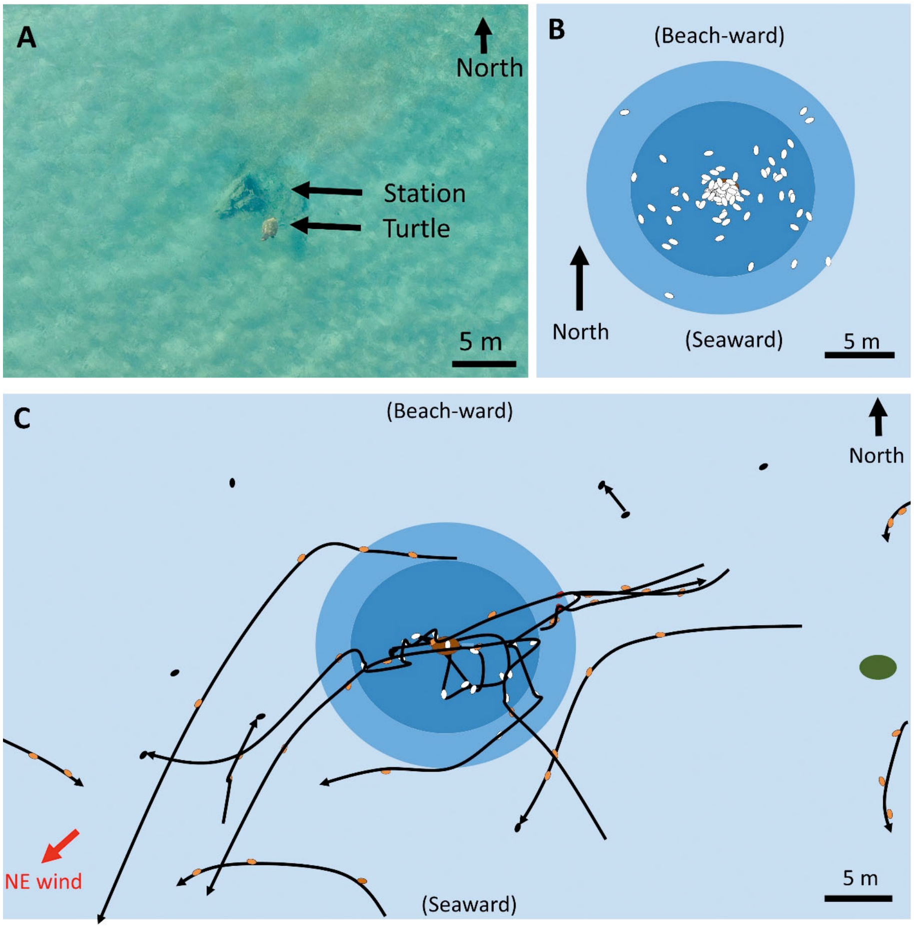

Fig. 3. (A) Zoomed-in view of the cleaning station and a loggerhead turtle *Caretta caretta* being cleaned. (B) Locations of turtles at 30 s intervals when cleaning was documented in the 120 min unmanned aerial vehicle (UAV) footage, validated by underwater video and direct observations. (C) Breakdown of movement of 9 turtles over a 40 min period on 20 June 2016 (see Supplement 5 for UAV footage at 8× speed for part of this observation). Arrows show the direction of movement of individual turtles linking the 30 s positions. Some lines are short, as the turtles were resting. White ovals indicate turtles being cleaned; brown ovals are moving turtles; black ovals are resting turtles

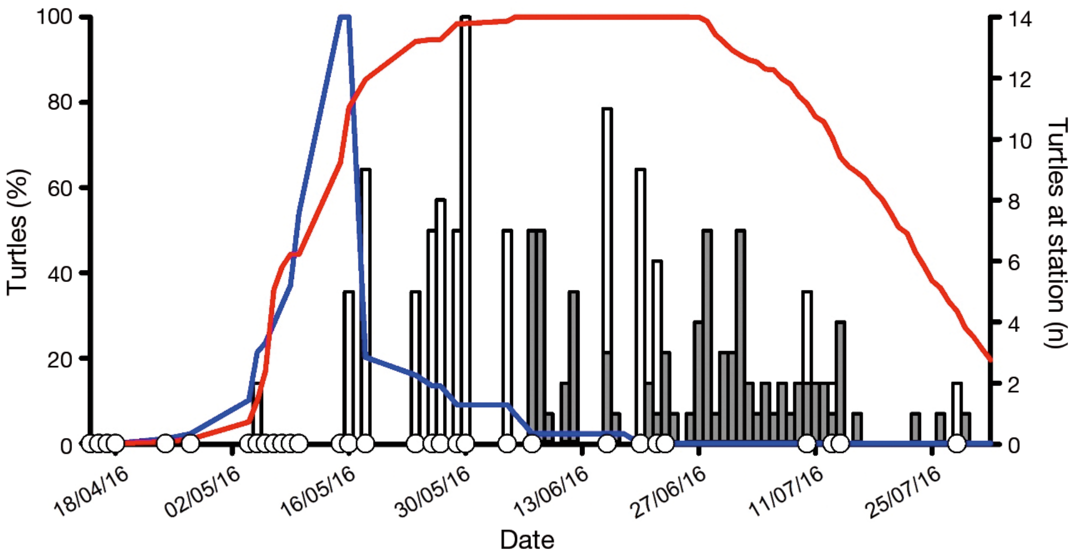

Fig. 4. Number of loggerhead turtles *Caretta caretta* detected within 100 m radius of the cleaning station by the unmanned aerial vehicle (UAV; white bars) and during direct underwater observation surveys (dark grey bars) from 10 April to 1 August 2016 in relation to the change in the percentage of mating pairs (blue line) and females in the survey area (red line) (maximum number of pairs or individuals was allocated as 100%). The white dots indicate the days on which aerial surveys were conducted. The 2 turtles detected by the UAV within 100 m of the station on 5 May were mating. Numbers of mating pairs and numbers of females were derived from UAV surveys (see Schofield et al. 2015, 2017)

2 occasions), with the activity of 9, 6 and 2 turtles being recorded, respectively (Fig. 3A; Supplement 5). The data showed that most cleaning activity occurred within a 5 m radius of the rock (maximum 7 m; Fig. 3B), which was confirmed by direct underwater observations; thus, cleaning activity was conducted over the rock and on the sandbank area up to 5 m from the rock. All turtles were recorded actively swimming (not drifting), with most entering from upwind and leaving downwind, appearing to pass through the station in the same direction as the wind (Fig. 3C).

Within-season patterns in station use

When combining all aerial and underwater sightings of turtles at the cleaning stations, turtle presence at the cleaning stations showed a strong negative trend over time (Mann-Kendall tau = −0.345, $p < 0.01$), which was strongly correlated with the predicted decline in females in the breeding area (Pearson's correlation, $t = 3.74$, df = 30, $p < 0.01$; Fig. 4). We found no significant difference in the density of turtles recorded during UAV surveys versus underwater surveys ($t = 2.7383$, df = 29.163, $p < 0.05$). The decline in visits to the stations was similar in July of both 2015 and 2016 (Mann-Kendall tau = −0.4 and −0.476 respectively, $p < 0.05$), and turtle visiting was strongly correlated for these 2 months (Pearson's correlation, $t = 2.7351$, df = 12, $p < 0.05$). We found no significant difference in the wind direction recorded by the UAV and the airport weather station when using a Wallraff rank sum test of angular distance (Kruskal-Wallis chi-squared = 1.64, $p > 0.1$). When combining all aerial and underwater sightings of turtles at the cleaning stations, the wind direction was highly directional (Rao's spacing test statistic = 228.7209, critical value = 155.49; Kuiper's test statistic = 2.7447, critical value = 1.747), of which 52% of sightings occurred when the wind was in a predominantly southeast direction, and 76% of sightings occurred when the wind was in a southeast to south-southwest wind direction.

DISCUSSION

Our results show that turtles visited the cleaning stations throughout the breeding period, when they should, theoretically, be minimizing movement and energy expenditure. Movement into a station appeared to be correlated with the wind, suggesting that turtles might initially detect cleaning stations incidentally when actively (i.e. swimming, not drifting) responding to changes in wind direction during the early part of the season (Schofield et al. 2009); however, several turtles repeatedly used the station within and across surveys, suggesting intentional use. Furthermore, 2 or more turtles were simultaneously using the station in most surveys, and exhibiting behaviours to attract fish or displace the turtle being cleaned. While physical contact was made in some instances, these interactions never escalated to agonistic interactions (Schofield et al. 2007) and did not seem to enhance the ability of turtles to attract fish. There was also a clear change in station use over the course of the breeding season, beginning immediately following the completion of mating (May) and ending after the completion of nesting (July), with numbers also varying in relation to wind direction. Overall, the repeated use of the stations by turtles and competition for access to fish suggest that the turtles experience some benefit to cleaning activity.

At our study site, we have previously shown that turtles actively shift (i.e. by swimming, not drifting) their position in the nearshore waters each day in response to prevailing wind conditions, aggregating in warmer downwind waters along the 8 km stretch of submerged sandbanks during the early part of the breeding season (i.e. until early to mid-June) when the ambient water temperature is suboptimal (Schofield et al. 2009, 2013, Fossette et al. 2012). This activity allows females to locate the optimal (warmest) spots to mature their eggs before depositing them in nests, with cooler sea temperatures delaying this process by several days (Hays et al. 2002). Our current study also showed that turtles passed through the stations in the same direction as the wind (upwind to downwind), suggesting that they do not locate cleaning stations using olfactory cues (Lohmann et al. 2008). Thus, it is possible that, each year, as female turtles locate the optimal spots to mature their eggs in the nearshore waters (Schofield et al. 2009), they find rocks containing the appropriate cleaner fish species by accident, but return on subsequent occasions within the season using memory (e.g. cognitive map, Benhamou 2007, 2014, Schick et al. 2008). Previous studies have shown that animals actively explore their environment (termed active sampling) when information is lacking or limited, due to biological constraints associated with perception or learning (e.g. Lima & Zollner 1996, Bartumeus et al. 2016).

Females might only use the station once peak mating activity has ceased, as using the station when males are in high abundance might place females at a disadvantage, leading to unwanted sexual advances (Lee & Hays 2004, Schofield et al. 2006, Fossette et al. 2012) as a result of lowered vigilance and reduced active evasion (Trivers 1971, Hart 1990, Arnal & Côté 1998). Using accelerometers, Fossette et al. (2012) showed that the activity of females clearly declined as sea temperature increased and interactions with males ceased, suggesting that energy was preferentially devoted to egg maturation, in parallel with a reduction in unnecessary locomotory activity, even though some turtles at this site explored adjacent sites up to 100 km away (Schofield et al. 2010). However, the energetic costs of grooming are also considered to be high (Iwata et al. 2013), with accelerometry combined with time-activity budgets potentially providing a way to quantify relative energy expenditure accurately (Jeanniard-du-Dot et al. 2017). Thus, trade-offs might exist in the investment of different types of activities.

In 2016, we only observed about 11–18.5% of unique females in the breeding population at the station, of which 75–82% of individuals were detected just once (across and within surveys, respectively), leading to our continuously identifying new individuals (i.e. we did not reach a plateau). Similar numbers of turtles were detected within a 100 m radius of the station from UAV surveys as within 5 m radius of the station from underwater surveys, indicating that turtles frequenting the station on a given day rest on the seabed in the surrounding area, with turtle movement into and out of the station during hovering UAV transect surveys supporting this suggestion (see Fig. 3). Thus, it is likely that more turtles visit the station throughout the day than we were able to detect during the short (2–3 h) periods of our underwater surveys. Furthermore, other turtles might have frequented stations in other parts of the breeding area, which encompasses an area of 105.88 km^2. These suggestions are supported by the fact that out of 202 females that were uniquely identified in 2016, 70% had <15 barnacles, while 40% had evidence of recent recruitment of barnacles (e.g. smaller than 0.5 cm, Frick et al. 2002), with these percentages being reflected in the 55 unique turtles recorded using the station. Thus, more turtles were likely investing in cleaning activity (to maintain low barnacle loads) than were detected by our study alone.

Turtles likely receive both health and locomotory benefits that are not directly measurable. For instance, Frick et al. (2002) showed that the recruitment of epibionts is high during breeding, with barnacle loads increasing within the 14 d interval between the first 2 nesting events by loggerheads in Georgia (USA), and loads steadily increasing over the course of the nesting season (42 d period). This observation reflects the timeframe for the larvae (cyprids) of the barnacle *Chelonibia testudinaria*, an obligate commensal of sea turtles, to develop and recruit onto turtles at temperatures of 25°C (Zardus & Hadfield 2004). Thus, in our study, the regular visits by turtles to the cleaning stations (i.e. of the turtles that returned, 75% did so within 10 d intervals) might help to mitigate the establishment of epibionts. Unregulated recruitment of larvae could result in barnacle loads that cause health issues (damage to carapace, disease etc.) or reduce hydrodynamic ability (Stamper et al. 2005). While high barnacle loads might not impact breeding success, after completing breeding, the turtles must migrate back to foraging grounds located at distances of ~1000 km away on depleted reserves following several months without eating, as they are capital breeders (e.g. Hays et al. 2002, Schofield et al. 2013). Thus, maintaining external body condition through regular cleaning activity might directly benefit fitness and survival after the completion of breeding, providing ultimate causation or adaptive value (Losey 1974, Gorlick et al. 1978, Stamper et al. 2005).

It is possible that turtles target isolated rocks (i.e. stations) within the submerged sandbank area because the fish remain within a certain distance of the rock (in our case 5–7 m), and so are dependent on food resources at the rock, or resources that 'visit' the rock (e.g. turtles). Thus, compared to fish occupying extensive reefs with broad resources, those at the station might clean turtles with greater efficiency (e.g. Grutter & Poulin 1998). We assumed the fish were cleaning damaged tissue and propagules (e.g. barnacle cyprids, parasitic amphipods and algal spores; Wicksten 1995, C. Sazima et al. 2004, I. Sazima et al. 2004, Maia-Nogueira et al. 2010), as the fish were too small to remove fully formed barnacles like wrasse do in Hawaii (Losey et al. 1994). Our surveys showed that the turtles only frequented the station for 2–3 mo (i.e. June and July, the breeding period), with 2 or more turtles being present on many occasions. The fish appeared to primarily feed on the hard body surfaces (carapace and plastron), but also the soft surfaces (skin), which resulted in negative reactions (see also Schofield et al. 2006), causing turtles to swipe or bite their own fins or depart the station and return again a short time later (within 1 to 3 h). The targeting of healthy skin by fish is considered 'cheating' (Côté 2000, Bshary & Grutter 2005), while the movement of turtles in and out of the station area might represent a way of regulating this unfavourable activity. Our observations indicated that the fish decided which turtle to clean (sometimes both); however, it was unclear whether this was regulated by turtle size or other parameters that we were unable to measure, such as barnacle cyprid load. Regular turtle movement in and out of the station might also have been a form of cheating, as this triggered fish to check the turtle again. In addition, some turtles obtained the fish by approaching and nudging the turtle already being cleaned, triggering fish to switch and/or causing the other turtle to depart. Yet, even though encounters between turtles escalate to physical aggression at this breeding site (Schofield et al. 2006, 2007), particularly between females during the early part of the season, we never recorded aggressive interactions between turtles at the cleaning station (Schofield et al. 2006, Papafitsoros & Schofield 2016). The lack of aggression might be attributed to the fact that fish selected which turtle to clean. Alternatively, because there was a steady flow of turtles passing through the station, aggression might have become energetically detrimental to the instigator.

In conclusion, the use of a combination of aerial and underwater surveys showed that many turtles frequent cleaning stations by actively swimming into the area, and compete with one another to gain access to cleaners. Thus, we suggest that cleaning by fish (i.e. removal of larvae and spores) provides both immediate and adaptive benefits to turtles that might not be directly measurable, including relief from stress, reduction of negative health impacts (e.g. disease) and reduced drag (lowering energetic costs) during locomotion, which might enhance survival, particularly during long-distance migration back to the foraging grounds (Frick & Pfaller 2013). Because the location of cleaning stations is not constant across years at our breeding site, further studies on how turtles detect these microscale features and the precision with which they are able to relocate them over the course of a season could facilitate future studies on memory and navigation in this group of animals.

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