

Original Article

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Abundance, placement and sexual identity of the epizoic barnacle *Chelonibia testudinaria* relative to the size and species of host turtles in Mabul Island, Malaysia

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Abstract

Sea turtles are partners in commensal relationships with a variety of epibionts, including barnacles. The acorn barnacle *Chelonibia testudinaria* is one species commonly found associated with sea turtles and other marine fauna throughout temperate to tropical waters including the Indo-Pacific. We conducted a study to assess the occurrence of this barnacle, relative to host life stage and species in a mixed foraging population of green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles (juvenile, sub-adult, adults (female and male)) in Mabul Island, Sabah, Malaysia (Celebes Sea). Expecting similar relative abundance by life stage, we found instead a significant effect between the combined dependent variables (abundance and size of barnacles) and the life stages of sea turtles in Mabul after controlling for the covariates of size and species of sea turtles ($F(8, 428) = 5.77, P < 0.001, \text{Pillai} = 0.19$). Among green turtles with barnacles, though adult males had larger barnacles compared with the female turtles, the mean barnacle abundance on adult females (43.4 individuals \pm 5.19 SD) was higher than all other life stages. Most of the barnacles (85.6%; $N = 1931$) were found on the plastron of the sea turtles. The highest number of barnacle reacquisition was found among the juvenile turtles. In assessing the complemental males of the barnacles, we found they were consistently attached to the shells of the larger of the hermaphrodites from each region of the host's body despite average shell-size differences with each region.

Introduction

Barnacles (subclass Cirripedia) are sessile crustaceans that are commonly found attached to natural surfaces such as rocks, shells and corals (Chan & Høeg, 2015). However, those in the superfamily Coronuloidea specialize as obligate commensals of mobile marine animals including mammals, reptiles, chelicerates and large crustaceans (Badrudeen, 2000; Cheang *et al.*, 2013; Hayashi, 2013; Hayashi *et al.*, 2013; Zardus *et al.*, 2014; Carrillo *et al.*, 2015; Buckeridge *et al.*, 2018, 2019; Dreyer *et al.*, 2020; Kim *et al.*, 2020). They live as epibionts on the exterior body of their hosts of which sea turtles carry the widest variety (Frick & Pfaller, 2013; Hayashi, 2013); therefore, in analyses of associations between sea turtles and epibionts, much attention has been given to barnacles in particular (Zardus & Balazs, 2007; Pfaller *et al.*, 2008; Frick *et al.*, 2010; Fuller *et al.*, 2010). More than 20 nominal species of barnacles from Balanomorpha (acorn barnacles) and Lepadomorpha (goose-neck barnacles) have been reported from sea turtles (Hayashi, 2009). *Chelonibia testudinaria* is the most cosmopolitan and largest acorn barnacle on sea turtles, reaching a diameter of 120 mm (Zardus & Hadfield, 2004), and associate with all seven species of sea turtles in the world's oceans including the flatback turtle (*Natator depressus*) (Monroe & Limpus, 1979); as well as the dermis-covered leatherback turtle (*Dermochelys coriacea*) (Rees & Walker, 1993). Of the four species of barnacles in the family Chelonibiidae, three have been found to be genetically identical and are synonymized under *C. testudinaria* (Zardus *et al.*, 2014). For individuals attached to sea turtles, a diagnostic trait of *C. testudinaria* (Figure 1) is its stellate shell patterning formed by open wedges at the sutures between the shell plates or compartments, sculpted along their margins with indentations (Darwin, 1854; Hayashi, 2013).

Parasitic epibionts of sea turtles, leeches for instance, which derive nutrition from the tissues of their hosts can significantly impact the health of sea turtles (Greenblatt *et al.*, 2004). In contrast, barnacles and other commensals use sea turtles primarily as a substratum or foraging platform (Frick *et al.*, 2002) with minor or equivocal impacts on the turtles' health (Stamper *et al.*, 2005; Flint *et al.*, 2010). Depending on the species of barnacle, they fasten onto the carapace and plastron, on the head, or the flippers and skin of their host turtles (Frick & Ross, 2001; Devin & Sadeghi, 2010; Ooi & Palaniappan, 2011; Nájera-Hillman *et al.*, 2012). There are two types of attachment modes across different life stages of barnacles. First, the cypris larva arrives on the substratum and secretes cypris cement from multicellular cement glands that lead to ducts on the antennules. The release of this cement triggers the metamorphosis of the cypris larva into juvenile and adult barnacles. Second, the adult secretes cement from cement glands to maintain firm attachment. Both stages secrete cement from cement glands that lead through the base (Lacombe, 1970; Walker, 1978).

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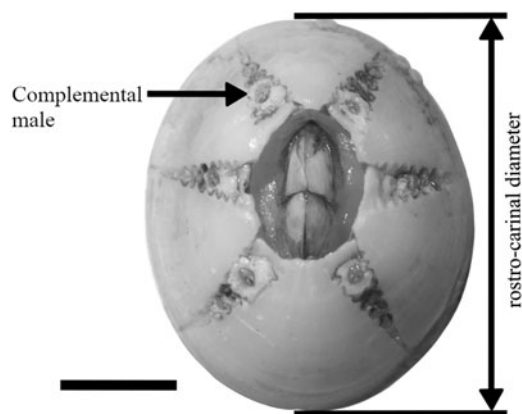


Fig. 1. A large, single hermaphroditic individual of the turtle barnacle *Chelonibia testudinaria* from a green turtle, demonstrating how size was measured (maximal rostro-carinal diameter) and the positioning of small complemental males attached to its shell (scale bar = 10 mm). Photo by Kah Kheng Lim.

How the sea turtle life cycle influences barnacle occurrence is unresolved. Most sea turtles undergo long-distance migrations to different habitats throughout their lives (Åkesson *et al.*, 2003). At hatching, newly emerged sea turtles migrate toward oceanic nursery areas then, as older juveniles, subadults and adults, return to neritic foraging grounds (Musick & Limpus, 1997; Lohmann *et al.*, 2008). A recent study by Burgett *et al.* (2018) has confirmed the ontogenetic diet shifts of green turtles (*Chelonia mydas*) in a mid-ocean developmental habitat, thus supporting the flexibility of habitat shifts between their foraging and neritic habitats (Hayashi & Nishizawa, 2015). Mature adults periodically migrate between distantly spaced breeding grounds, nesting beaches and foraging areas with a high degree of fidelity for these areas (Bjorndal, 1995; Palaniappan & Abd Hamid, 2017; Shimada *et al.*, 2020). A foraging turtle is defined as a sea turtle that resides in an area where its food source is available (Ceriani *et al.*, 2012; Cheng *et al.*, 2019) and exhibits a strong long-term fidelity to localized foraging sites whereas a resident turtle is defined as a non-migratory individual (Márquez, 1990), that after recruiting from its oceanic nursery resides predominantly at the foraging ground and thus has the probability of being recaptured throughout its resident years (Chaloupka & Limpus, 2001). Foraging turtle aggregations commonly comprise several nesting stocks (Nishizawa *et al.*, 2016). Both foraging and resident female turtles will not nest in the foraging areas. Instead, they return to their natal beach to nest due to their natal homing nature. Nesting turtles are reproductively active females that migrate from distant, long-term residence areas (hereafter, foraging grounds) to their natal nesting beaches during the breeding season (Ceriani *et al.*, 2017; Sönmez, 2019). Documenting the epibiont diversity associated with migrating sea turtles can help provide information about where epibiosis occurs and hence the migratory behaviour and habitat preferences of sea turtles (Hayashi, 2009). The findings of Robinson *et al.* (2017) suggest that sea turtle epibiont communities are more reflective of where sea turtles feed than where they nest. In addition, stable isotope analysis of barnacle shells has been used to provide insight on foraging distributions, migration distances and habitat use of nesting turtles over time (Pearson *et al.*, 2019), thus aiding in sea turtle population conservation and management.

An initial study of sea turtle epibionts for the region of Sabah, Malaysia by Ooi & Palaniappan (2011) found only one species of barnacle on sea turtles – *C. testudinaria*, occurring on both green *Chelonia mydas* (Linnaeus, 1758) and hawksbill *Eretmochelys imbricata* (Linnaeus, 1766) turtles in the waters of Mabul and Sipadan Islands. Mabul Island (Figure 2) is home to a variety of

seagrass species especially *Thalassia hemprichii* and diverse coral reef communities (Jolis & Kassem, 2011), which attracts a foraging sea turtle population dominated by green turtles, and a small number of hawksbill turtles. So far as is known, both sea turtle species are residents in Mabul Island and some have been caught repeatedly over consecutive years of sampling. Hawksbill and green turtles also share foraging grounds at neighbouring Sipadan Island (14.5 km away) (Chong, 2012; Joseph *et al.*, 2017). Only green turtles hatched in Mabul Island will travel back to their natal beach to nest during the breeding season then return to their foraging grounds, as reported by Joseph *et al.* (2017).

In the course of examining the sea turtles in Mabul Island, many were found hosting the barnacle *C. testudinaria* (Figure 1). In addition, many of the barnacles were found with multiple small male individuals attached to larger hermaphrodites, situated within the narrowest portions of the hermaphrodites' settlement pits as described by Zardus & Hadfield (2004) or attached randomly on the shell surface and apertural orifice (Cheang *et al.*, 2013). Barnacles in general are hermaphroditic and cross-fertilize with neighbouring individuals via the typical barnacle mode of pseudo-copulation (they deposit sperm into a partner's mantle cavity) (Murata *et al.*, 2001), though some barnacle species are capable of performing sperm casting with subsequent fertilization of the internally kept broods (Barzandeh *et al.*, 2013). Darwin (1854) was the first to describe the rare phenomenon of androdioecious reproduction in scalpellid barnacles, wherein small males fertilize larger hermaphrodites, naming the small companions as complemental males. Zardus & Hadfield (2004) found that the complemental males of *C. testudinaria* possess mature sperm and serve as sperm donors, however it is unknown if complemental males are protandrous and in time develop into full-grown hermaphrodites (Weeks *et al.*, 2006) or whether they can flexibly develop female sexual characters according to their position and partner availability (Wijayanti & Yusa, 2016).

Most sea turtle barnacle investigations have focused on barnacle abundance and diversity relative to sea turtle species (Hernández-Vázquez & Valadez-González, 1998; Pfaller *et al.*, 2006, 2008; Fuller *et al.*, 2010). This study, in addition to barnacle occurrence, presents fundamental information on the occurrence of complemental males of *C. testudinaria* as well. To date, few studies have included information on the complemental males of *C. testudinaria* from wild sea turtles. Ewers-Saucedo *et al.* (2015) studying *C. testudinaria* in the south-eastern USA, determined that complemental males were more commonly partners with hermaphrodites from loggerhead sea turtles (*Caretta caretta*) than with hermaphrodites from crabs, perhaps due to smaller group size and higher mortality rates associated with the latter hosts. The objective of the present study was to determine whether the abundance and size class distribution of the epibiotic barnacle, *C. testudinaria*, and the occurrence of its complemental males, in the foraging population of sea turtles at Mabul Island, is influenced by sea turtle species and life stage.

Materials and methods

The study was conducted on the foraging population of sea turtles at Mabul Island (4.25°N 118.63°E) located on the east coast of Sabah, Malaysia (Figure 2). Sea turtles were caught in-water from May 2015 to November 2017. Fieldwork was conducted over a period of 4–6 days once every 6 months per year (a total of 26 days spread over 6 sampling trips) to keep disturbance to the sea turtles at a minimum. The sea turtles were randomly caught by hand while scuba diving during the day at established dive sites (distance between adjacent dive sites did not exceed

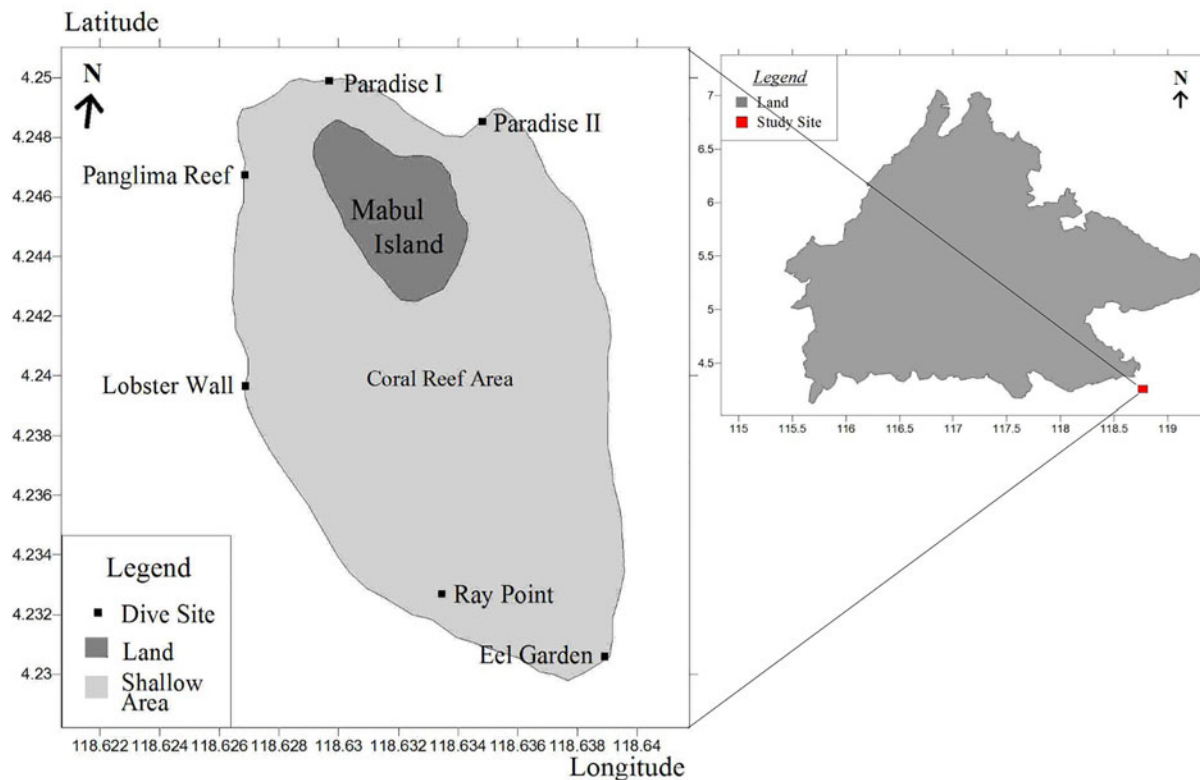


Fig. 2. Map of Mabul Island, south-eastern Sabah, Malaysia, showing established dive sites where sea turtles were captured. Map by Haziq Harith Abd Hamid.

500 m) in Mabul Island at depths not exceeding 20 m. The sea turtles were divided into three life stages based on size i.e. straight carapace length (SCL), namely juvenile, sub-adult and adult, with adults further divided into female and male following previous studies (Bresette *et al.*, 2010; Palaniappan, 2017). Sex distinctions were based on size of the tail (van Dam & Diez, 1998). The sea turtles were brought onto the research vessel to be photographed, measured and tagged. The SCL of each sea turtle was measured with 1.0 m Mitutoyo stainless Vernier callipers (accurate to 0.05 ± 0.15 mm) measuring from the anterior point at the midline (nuchal scute) to the posterior end of the supracaudal (Bolten, 1999). Inconel tags (National Band and Tag Company, Newport, Kentucky, USA) were applied to the sea turtles at the posterior edge of both front flippers.

Scaled photographs were taken of the specific locations of the barnacles found on the body of the sea turtles. For each turtle, including repeat captures, all attached barnacles larger than 5 mm were removed before release. Barnacles found on the head, carapace and plastron of the sea turtles were gently removed using a hammer and scraper. Barnacles found elsewhere on the sea turtle were not included in this study. The collected barnacle specimens (minimum size 5 mm) were kept in resealable plastic bags labelled with the turtle's ID number, date of collection and the location that they were found on the turtle's body. The barnacles were identified in the laboratory at the Borneo Marine Research Institute, Universiti Malaysia Sabah (UMS) to the lowest taxonomic level following Monroe (1981). Barnacle size was measured as maximal rostro-carinal diameter (Figure 1) with 0.3 m Mitutoyo stainless steel Vernier callipers (accurate to 0.02 ± 0.04 mm). The complementary males that were found attached on every hermaphrodite were examined and counted under a Carl Zeiss Stemi stereomicroscope. Barnacles with broken shells were excluded from the analysis.

Results and discussion

Field survey results

A total of 403 sea turtles were captured from May 2015 to November 2017 in Mabul Island, consisting of 364 green turtles and 39 hawksbill turtles. All life stage groups, as determined by SCL, were represented in the population of green turtles (77.8% juveniles, 6.0% sub-adults, 6.9% adult males, 9.3% adult females) but hawksbill turtles were mostly juveniles (94.9%) with only one sub-adult and one adult female (Table 1). The low number of sub-adult and adult hawksbill turtles suggests that juvenile hawksbill turtles eventually move to neritic habitats and utilize Mabul Island as a temporary developmental foraging ground (Pilcher, 2010; Joseph *et al.*, 2017).

Mabul Island consists of a mixed population of foraging, resident and nesting sea turtles. All the sea turtles caught in-water during this study were tagged upon capture. We have had no reports of these tag numbers among the green turtles that have nested in Mabul Island. Green turtles show natal homing on a very broad, regional scale well before their first reproductive migration (Allard *et al.*, 1994). When sea turtles leave the open ocean to establish coastal feeding sites, they choose foraging grounds within their general natal region, which are often a considerable distance from the natal beach (Bowen *et al.*, 2004; Bowen & Karl, 2007). A total of 2255 barnacles summed across all hosts were collected, all of a single species, *Chelonibia testudinaria*. This is consistent with previous studies of green turtles in Mabul and Sipadan Islands, Malaysia (Ooi & Palaniappan, 2011) and in the waters of Japan (Hayashi & Tsuji, 2008). Intriguingly, Dobbs & Landry (2004) did not find this barnacle species in a nesting population of Australian hawksbill turtles but did document the presence of other species of commensal coronulids, including *Chelonibia caretta* (the dominant species with 81% occurrence), *Platylepas* sp. and the burrowing barnacle *Chelolepas cheloniae*.

Table 1. Number of sea turtles (N) with and without barnacles in Mabul Island, by turtle species and life stage. Measurements shown are the straight carapace lengths (SCLs) of the turtles

Life stage	Green turtle with barnacle			Green turtle without barnacle			Hawksbill turtle with barnacle			Hawksbill turtle without barnacle		
	Mean ± SD (mm)	Range (mm)	N	Mean ± SD (mm)	Range (mm)	N	Mean ± SD (mm)	Range (mm)	N	Mean ± SD (mm)	Range (mm)	N
Juvenile	497.65 ± 81.54	351–784	164 (58.0%)	515.00 ± 88.41	369–784	119 (42.0%)	520.08 ± 79.30	381–647	20 (54.1%)	534.53 ± 71.64	426–647	17 (45.9%)
Sub-adult	807.45 ± 71.10	649–921	12 (54.5%)	818.20 ± 34.38	771–858	10 (45.5%)	763.00 ± 0.00	–	1 (100.0%)	–	–	–
Adult male	845.96 ± 35.26	775–931	14 (56.0%)	848.91 ± 34.10	799–931	11 (44.0%)	–	–	–	–	–	–
Adult female	918.39 ± 34.64	828–991	18 (52.9%)	920.31 ± 32.60	848–976	16 (47.1%)	767.00 ± 0.00	–	1 (100.0%)	–	–	–

SD, standard deviation.

Nevertheless, a recent study by Razaghian *et al.* (2019) had reported *C. testudinaria* on the nesting hawksbill turtles in Iran. The overall incidence of sea turtles carrying this barnacle was similar between the two host species with 208 green turtles (57.1%) and 22 hawksbill turtles (56.4%) hosting it. The percentage of sea turtles with *C. testudinaria* was also similar (~50%) across the host life stages present (Table 1) with no significant difference ($\chi^2(3) = 0.15$, $P > 0.05$). However, the quantity of barnacles per turtle varied with turtle size, species and sex.

Abundance and size variation of *C. testudinaria*

Overall, on sea turtles with barnacles, barnacle abundance ranged from 1–232 individuals per turtle (mean = 9.80 individuals ± 23.20 SD), across both hosts. The highest number of barnacles was found on a large adult female green turtle (SCL = 910 mm) whereas several individuals of both host species hosted only one barnacle each. In comparison between the two sea turtle species, juvenile green turtles had substantially more barnacles (mean = 6.9 individuals ± 9.34 SD) than juvenile hawksbill turtles (mean = 3.5 individuals ± 2.98 SD) (Figure 3). This could be due to the greater body surface area of green turtles which on average is larger than hawksbill turtles, a finding that is consistent with Hayashi & Tsuji (2008). There was a statistically significant difference between the sea turtle life stages on the combined dependent variables (i.e. barnacle abundance and size of barnacles) after controlling for turtle size (SCL) and turtle species ($F(8, 428) = 5.77$, $P < 0.001$, Pillai = 0.19). We found, to a lesser degree, *C. testudinaria* on the foraging population of hawksbill turtles in Mabul Island. The small sample size of adult hawksbill turtles captured in this study did not allow us to fully address the relationship between the abundance of barnacles and turtle size, therefore, no further analyses were performed.

Among green turtles, females had considerably more barnacles (mean = 43.4 individuals ± 67.96 SD) than males (mean = 12.4 individuals ± 14.39 SD), sub-adults (mean = 14.5 individuals ± 14.79 SD) and juveniles (mean = 6.9 individuals ± 9.34 SD). Few studies have compared barnacle occurrence among sea turtles in populations of mixed life stages though several have compared epibionts among mixed sea turtle species (Fuller *et al.*, 2010; Lazo-Wasem *et al.*, 2011; Ooi & Palaniappan, 2011; Robinson *et al.*, 2017). The number of barnacles per turtle varied widely in our study with the highest number (i.e. 232 individuals) collected from an adult female at Mabul Island, considered a high amount for green turtles (Bugoni *et al.*, 2001; Hayashi & Tsuji, 2008; Fuller *et al.*, 2010; Lazo-Wasem *et al.*, 2011; Nájera-Hillman *et al.*, 2012; Robinson *et al.*, 2017). Our results indicate that the number of barnacles attached to green turtles increases with turtle size, and this finding is consistent with Hayashi & Tsuji (2008) and Devin & Sadeghi (2010). The attachment area selected is due to the free space availability (Minchinton & Scheibling, 1993; Ihwan *et al.*, 2018), thus resulting in a higher abundance of barnacles in larger sea turtles.

The size of barnacles differed significantly between collecting trips as determined by one-way ANOVA ($F(5, 2249) = 15.18$, $P < 0.001$), except those collected in May of 2015 and 2016. Barnacles collected in May were larger (mean = 19.1 mm ± 8.41 SD) than those collected in November (mean = 16.7 mm ± 8.81 SD), across all sampling trips, indicative of either periodic acquisition or growth. The size frequency distribution of barnacles across the duration of the study was skewed significantly from normal as determined by the Shapiro–Wilk's test (Shapiro & Wilk, 1965) ($W = 0.95363$, $P < 0.001$). A skewness test confirmed the data were skewed to the right, driven by the presence of a few large individuals (Figure 4). However, Hartigan's dip test (Hartigan & Hartigan, 1985) for unimodality indicated our data

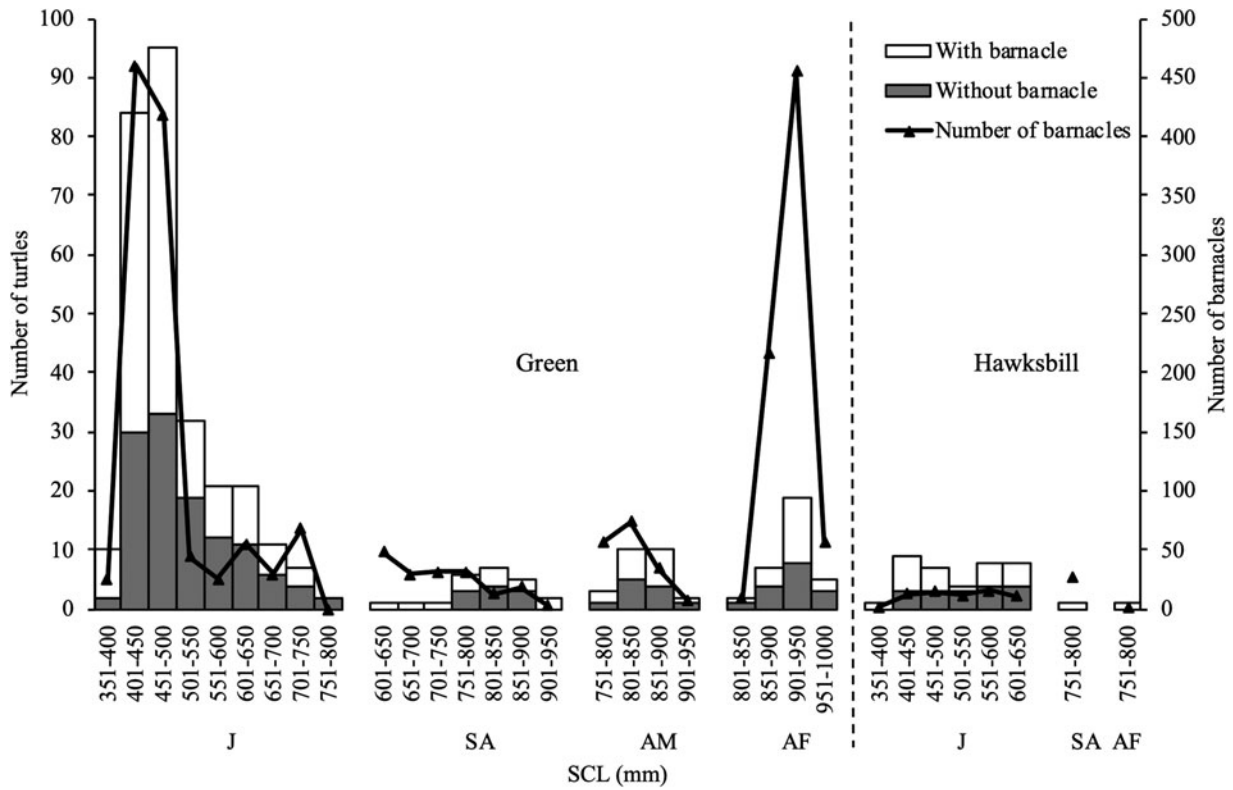


Fig. 3. Frequency distribution of Mabul Island green and hawksbill turtles, with and without barnacles, grouped by turtle straight carapace length (SCL) and life stage: juvenile (J), sub-adult (SA), adult male (AM) and adult female (AF).

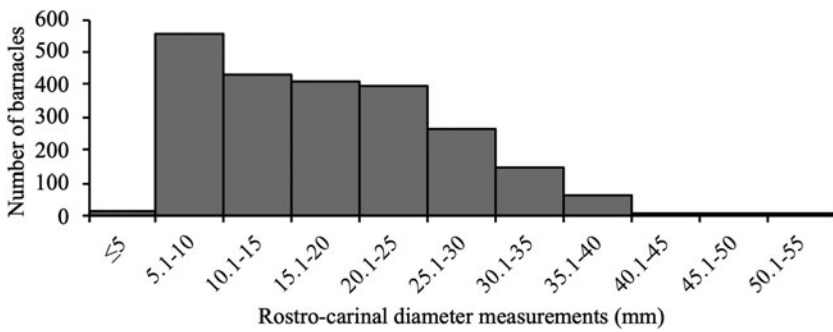


Fig. 4. Histogram showing the size frequency distribution of the turtle barnacle, *Chelonibia testudinaria* on sea turtles in Mabul Island.

had a single peak (i.e. lacked discrete size classes), at 5.1–10 mm (Figure 4). Even though we found that barnacles in Mabul Island collected in May were generally larger than those collected in November, the size frequency distribution of the barnacles was unimodal. This result is contradictory to Ewers-Saucedo *et al.* (2015) and Ten *et al.* (2019) where they detected two different age classes of *C. testudinaria* in their studies. Age estimation of barnacles as a function of their size has been examined in past studies (Ewers-Saucedo *et al.*, 2015; Doell *et al.*, 2017; Ten *et al.*, 2019). Ewers-Saucedo *et al.* (2015) suggested that the size frequency distribution of each age class in a natural population should be normally distributed and multimodal if several age classes are present. While our data were positively skewed, there was no evidence of multimodality in our data despite the presence of a few large individuals on host sea turtles. A lack of age classes in our study may be due to year-round reproduction of *C. testudinaria* in a tropical location compared with the previously mentioned studies from more seasonally influenced climates. Upon visual inspection, most of the barnacles collected in Mabul Island were in the size class of 5.1–10 mm, suggesting that these individuals were rather young. Ten *et al.* (2019) suggested that

the distribution of *C. testudinaria* in neritic waters could result from synergistic effects of its flexibility in host selection and its short planktonic phase (about 9 days).

Among the juvenile green turtles, large juveniles (501–750 mm) acquired larger barnacles (mean = 19.8 ± 9.11 SD) than the small juveniles (351–500 mm) (mean = 17.9 ± 7.09 SD) after controlling for SCL ($F(2, 158) = 4.93, P < 0.05, \text{ Pillai} = 0.06$) (Figure 5A). Such difference in barnacle size between the two juvenile groups suggests these barnacle individuals are new recruits from different locations. Post-hatchling sea turtles can travel up to 12,000 km from their natal regions to juvenile foraging sites (Hays & Scott, 2013), and might be colonized by various epibionts including barnacles along their migration pathways. The presence of bigger barnacles on larger juvenile green turtles suggests that they have acquired the barnacles prior to arrival in Mabul Island as the growth rate of the colonized barnacles is likely driven by enhanced feeding conditions caused by their host turtle’s travelling activity (Trager *et al.*, 1990; Doell *et al.*, 2017).

We conducted an ANCOVA test on barnacle size between the foraging adult male and female green turtles, with turtle body location as the covariate. While the size of barnacles found on

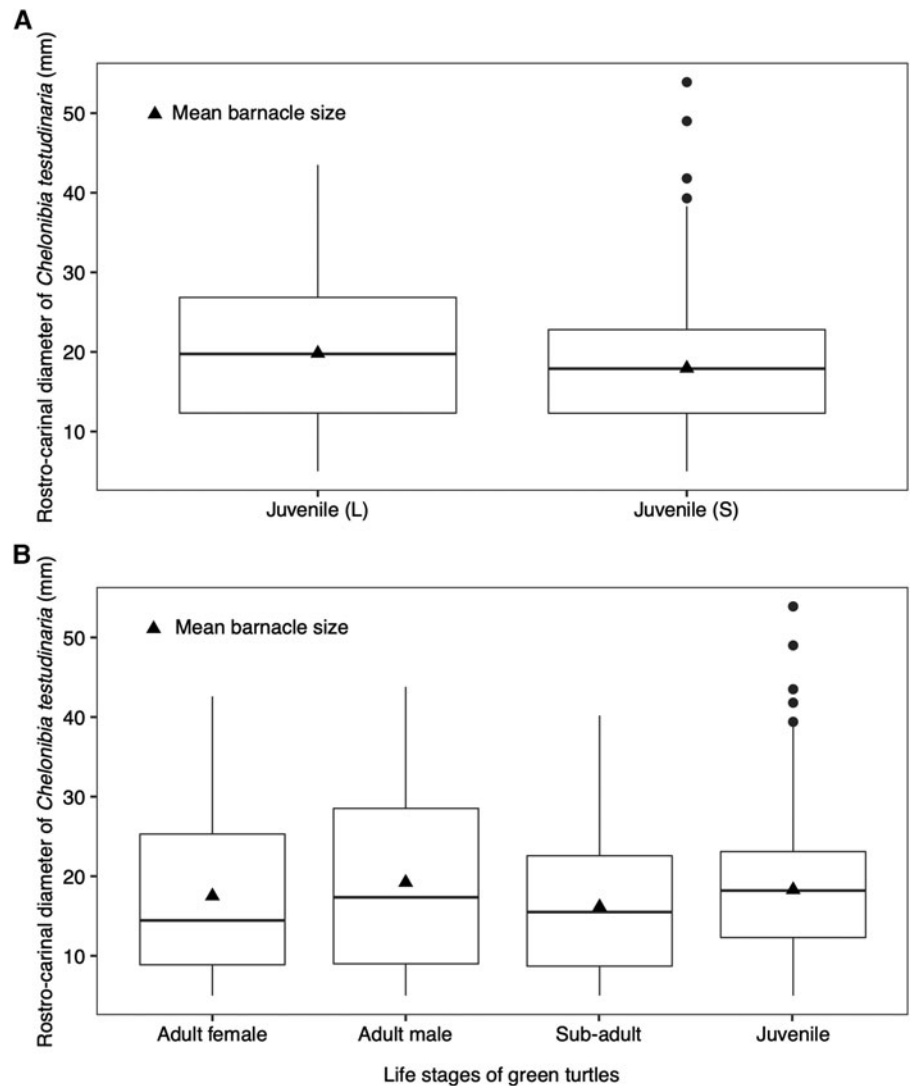


Fig. 5. Boxplots showing the distribution of rostrо-carinal diameter of *Chelonibia testudinaria* with mean barnacle size (A) between large (L; SCL: 501–750 mm) and small (S; SCL: 351–500 mm) juvenile green turtles and (B) across the green turtle life stages. Dots represent the outliers.

the plastron, carapace and head of sea turtles differed significantly ($F(3, 906) = 3.58, P < 0.05$), the interaction between the body location and the sex of sea turtles had no effect on the barnacle size ($F(1, 905) = 0.04, P > 0.05$). Nevertheless, the foraging adult males had acquired larger barnacles as compared with the foraging adult females (Figure 5B). This difference could be caused by variation in each sea turtle's historical environmental exposure (Stamper *et al.*, 2005). Male sea turtles migrate between foraging and breeding grounds more frequently (on an annual basis) compared with female sea turtles (once every 2–3 years or more) (Balazs, 1983; Hays *et al.*, 2014). The growth rate of *C. testudinaria* is attributed to food availability, which is dependent on the sea turtle's activity level, diet and feeding behaviour (Doell *et al.*, 2017). The travelling activity associated with migrating sea turtles can cause an increase in water flow and nutrient availability, providing potentially enhanced feeding conditions for barnacles (Trager *et al.*, 1990), which may promote rapid growth of barnacles on host sea turtles (Doell *et al.*, 2017). This may explain why adult male green turtles had larger barnacles as compared with females in our study.

Barnacle site selection

Enumeration of barnacles by body location for each sea turtle species of Mabul Island revealed a consistent pattern, that barnacles had a strong predisposition for the plastron (85.6%) over the carapace (13.7%) and low affinity for the head (0.6%) (Table 2).

Among green turtles, although the foraging females had more barnacles than foraging males, the number of barnacles by body location is consistent for both sexes where higher numbers of barnacles were found on the plastron on both adult male and female turtles compared with the carapace. The occurrence of *C. testudinaria* on sea turtles is affected by the host sea turtle's behaviour (Frick & McFall, 2007), size (Hayashi & Tsuji, 2008), interactions among epibionts (Pfaller *et al.*, 2006), and tolerance to desiccation and physical trauma (Pfaller *et al.*, 2008). Swimming and resting behaviours displayed by sea turtles on hard substrates may affect the settlement of barnacles on a turtle's body (Razaghian *et al.*, 2019), while an increase in water flow could affect both settlement patterns of the larvae (Larsson & Jonsson, 2006) and further augment the feeding opportunities of the barnacles (Schärer, 2003). Sea turtles commonly visit specific cleaning stations on reefs to seek 'free' cleaning services by fishes and shrimps to get rid of inconvenient epibionts and parasites (Sazima *et al.*, 2004; Grossman *et al.*, 2006; Schofield *et al.*, 2006; Ooi & Palaniappan, 2011). Cleaning by most reef fish focuses on the carapace and skin of the sea turtles (Sazima *et al.*, 2010) while the sea turtles rest on the reef motionless with the plastron facing down. Thus, small barnacles attached on the carapace may get removed more frequently than on the plastron due to higher exposure to the cleaner organisms. The presence of distinct sea turtle cleaning stations in Sipadan Island (Ooi & Palaniappan, 2011) supports this hypothesis. Moreover, healthy sea turtles always practice self-cleaning by wedging themselves into coral

Table 2. Occurrence of barnacles on selected locations of the host body along with the frequency of complemental males for green and hawksbill turtles in Mabul Island

Site	Green		Hawksbill	
	Number of barnacles	Frequency of complemental males	Number of barnacles	Frequency of complemental males
Plastron	1861(85.3%)	39.8%	70 (94.6%)	7.1%
Carapace	309 (14.2%)	30.4%	1 (1.4%)	–
Head	11 (0.5%)	18.2%	3 (4.0%)	–
Total	2181 (100%)	–	74 (100%)	–

Table 3. Abundance of reacquired barnacles for recaptured sea turtles by turtle species and life stage

Species	Life stage	Abundance of barnacles (number of recaptured sea turtles with barnacles)			
		Recapture Event One	Recapture Event Two	Recapture Event Three	Recapture Event Four
Green	Juvenile	235 (30)	20 (4)	10 (1)	3 (1)
	Sub-adult	65 (2)			
	Adult female	3 (1)			
Hawksbill	Juvenile	14 (5)	11 (4)	3 (2)	
	Sub-adult	1 (1)			

crevices or scraping their carapace against ledges and other hard substrata to remove barnacles (Frick & McFall, 2007), which may also help explain why more barnacles were found on the plastron compared with the carapace. While there was no difference between the enumeration of barnacles by body location among the adult green turtles, this suggests that both sexes share the same cleaning behaviour in Mabul Island.

Reacquisition of barnacles on recaptured turtles

Our study is one of the few to report on reacquisition of barnacles on sea turtles. Of the 230 sea turtles with barnacles, 51 turtles were recaptured individuals (hereafter, resident sea turtles) from which all barnacles larger than 5 mm had been collected for analysis at each previous capture. Among these resident sea turtles, 39 turtles were recaptured once, eight turtles were recaptured twice, three turtles were recaptured thrice and one turtle was recaptured four times. The total quantity of reacquired barnacles was 365 (16.2% of 2255) and, among turtle life stages, was highest for juveniles for both host species (Table 3). The shortest interval for barnacle reacquisition was ~175 days (one sampling trip) whereas the longest was ~730 days (four sampling trips). The geographic localities where sea turtles are colonized by barnacles can give an understanding of the movements and habitat use by sea turtles (Ten *et al.*, 2019) and conversely, where and when barnacles accumulate on sea turtles can provide insight in barnacle life history. There were no large turtles (i.e. sub-adult, adult males and adult females) recaptured after Recapture Event One, but repeated captures after the first recapture were evident among juvenile turtles (Table 3). This could be attributed to the site-fidelity of juvenile turtles, similar to the findings of Pilcher (2010) where the author reported that young sea turtles exhibited minimal movement within their foraging areas over several recaptures in Mantanani Island (west coast of Sabah). The reacquisition of barnacles on recaptured juvenile turtles in our study verifies that Mabul Island is at least one source for barnacle larvae in the region.

Complemental males of *C. testudinaria*

Complemental males of the turtle barnacle *C. testudinaria* were encountered on 37.5% of the barnacles from the sea turtles in Mabul Island, constituting the first report of complemental males for this species in the region (Table 4). The occurrence of complemental males was greater with barnacles from green turtles (38.3%) than with barnacles from hawksbill turtles (6.8%). But, lacking larger sample sizes across other life stages of hawksbill turtles, how meaningful this difference is remains uncertain. Turtle barnacles with attached complemental males were common in this study. The complemental males of *C. testudinaria* have a unique settlement pattern among barnacles. They attach to the shells of hermaphrodite adults in the depressions between the shell plates, which are perhaps specialized for their settlement (Zardus & Hadfield, 2004), or at the margin of the orifice of the hermaphrodite (Crisp, 1983). The size of the hermaphrodites with complemental males ranged from 6.3–49.0 mm in rostro-carinal diameter (mean = 24.75 mm ± 6.86 SD) and the maximum number of complemental males arranged on a single adult hermaphrodite (25.3 mm) was 34 (mean = 3.4 individuals ± 5.93 SD). The mean size of adult hermaphrodites of *C. testudinaria* in Mabul Island was about 50% smaller than in other studies (Zardus *et al.*, 2014) while the maximum number of attached complemental males (N = 34) was a little more than 100% greater. The causative factor for this difference remains unknown. It is common for several complemental males to occur on a single hermaphrodite and for multiple complemental males to be found within a single settlement pit as described in Zardus & Hadfield (2004). The males that attach nearest to the opercular rim, where the depressions are wider and are larger, presumably have the advantage of growing larger and of having a better success rate in copulating with their 'host' hermaphrodite (Ewers-Saucedo *et al.*, 2016). Complemental males in the present study were mostly found attached away from the opercular rim within the 'settlement pits' of the adult hermaphrodite shell where they were protected from abrasion and greater risk of dislodgement (Zardus & Hadfield, 2004).

Table 4. Size of barnacle hermaphrodites with and without complementary males from selected locations on the body of host sea turtles in Mabul Island

	Rostro-carinal diameter of barnacle (mm)					
	Plastron (N = 1941)		Carapace (N = 299)		Head (N = 15)	
	Without male (N = 1185)	With male (N = 756)	Without male (N = 213)	With male (N = 86)	Without male (N = 12)	With male (N = 3)
Minimum size	5.0	6.3	5.0	14.7	7.2	15.0
Maximum size	42.5	43.8	53.9	49.0	30.1	22.1
Mean \pm SD (mm)	13.0 \pm 6.52	24.7 \pm 6.80	17.8 \pm 7.60	25.9 \pm 7.40	17.3 \pm 6.11	18.6 \pm 5.02

Measurements shown are rostro-carinal diameter of the barnacles (mm) plus or minus the standard deviation (SD) and the number sampled (N).

Hermaphrodite size was on average larger for those with complementary males than for those without, but varied by their location on the body of the sea turtles (Table 4). For instance, although hermaphrodites collected from the head were generally smaller than those of the plastron and carapace, it was the larger of the head-attached individuals that hosted complementary males. Though adult hermaphroditic barnacles appear to prefer the plastron to the carapace and head of sea turtles, there was no detectable difference in the number of complementary males associated with hermaphrodites from any body location after controlling for the effect of hermaphrodites' size, ($F(2, 841) = 1.99, P > 0.05$). Complementary males were found on hermaphrodites from all regions of the turtle body, but less frequently on the heads of sea turtles, where the overall size of adult hermaphrodites was the smallest, suggesting that substratum space availability is the key for settlement. Complementary males in androdioecious species may evolve under lower population densities (e.g. mating group size; Yamaguchi *et al.*, 2008; Dreyer *et al.*, 2018a) where hermaphrodite-hermaphrodite sperm competition is relaxed and chances of fertilizing the broods of a hermaphrodite partner become greater (Ewers-Saucedo *et al.*, 2016). In these conditions androdioecy increases opportunities for fertilization more than can be realized with two separate and autonomous sexes (Kelly & Sanford, 2010). Selection may also favour the small size of complementary males in *C. testudinaria* particularly by reducing the weight of mating units and minimizing hydrodynamic drag, thus lengthening the lives of the attached barnacles (Zardus & Hadfield, 2004). An ANOVA test verifies that the total number of complementary males increases with the size of the adult hermaphrodite ($F(1, 841) = 21.74, P < 0.001$). Our results suggest that large hermaphrodites host higher numbers of small complementary males, likely linked to space availability (Minchinton & Scheibling, 1993). Hence, we hypothesize that a larger hermaphrodite would have a larger settlement pit, thus can house more cyprids that will specifically develop into males. The settlement pits of *C. testudinaria* can be analogized with the receptacles (areas on the rim of mantle cavity; Dreyer *et al.*, 2018b) of the androdioecious barnacle *Scapellum scapellum*, where the small complementary males are exclusively attached in the receptacle area of a hermaphrodite partner and never elsewhere (Spremborg *et al.*, 2012; Høeg *et al.*, 2016). Dreyer *et al.* (2018b) found that inward curvature of the ventral transparent lamellae (a thin, cuticular membrane between the mantle rim and mantle cavity) in the receptacle area provides more space for cyprid settlement in larger species, a similar reasoning that can apply to the settlement pits of larger *C. testudinaria*. However, addressing this hypothesis requires additional measurements of the size of the pits on each hermaphrodite.

In conclusion, the turtle barnacle *C. testudinaria* was found in abundance on the foraging populations of sea turtles in Mabul Island. The highest number of barnacles found on an individual

sea turtle was 232 and barnacle abundance was slightly affected by turtle size only for green turtles. Colonization of this barnacle species was the highest among adult female turtles with SCL of 828–991 mm. The majority of hawksbill turtles that were captured in the current study were juveniles, suggesting that Mabul Island serves as a temporary developmental foraging ground for this species. The repeated captures of juvenile turtles over several sampling trips, together with the abundant small-sized barnacles found among the smaller juvenile green turtles, suggest that barnacle larvae were present in Mabul Island. Among the adult green turtles, adult males had larger barnacles compared with the adult females. It is generally known that the adult males travel more frequently than females during the breeding seasons. Such intensive travelling activity may directly enhance barnacle feeding conditions, thus leading to an increase in the growth rate of barnacles on the adult male turtles particularly. Although the overall sizes of barnacles collected in May were larger than those collected in November, we were unable to relate this to seasonality due to the limited duration of sampling. The size frequency distribution of *C. testudinaria* in the current study was unimodal and not normally distributed. Barnacles were found to recolonize the same sea turtles several times, but the factor that drove the temporal succession of barnacles on these turtles is unclear. The highest abundance of *C. testudinaria* was found on the plastron (85.6%), followed by the carapace (13.7%) and the least on the head (0.6%) of sea turtles. Reacquisition of barnacles on recaptured turtles and the presence of complementary males of *C. testudinaria* were recorded for the first time on the foraging population of sea turtles in Mabul Island. More complementary males were found on the larger hermaphrodites, suggesting that substratum space availability is a factor in complementary male recruitment. This is supported in scalpellid barnacles, where the size and shape of the male-housing receptacle area on the scutal shell plates are positively correlated with the number of males attached (Dreyer *et al.*, 2018b). Future insights on the aggregation pattern of complementary males on adult hermaphrodites could be done by using a zonal model to determine settlement behaviour and survival of barnacles in relation to distance of the nearest conspecific from a given individual. Future studies should consider barnacle shell isotopes to trace movements and residence time of sea turtles in each habitat, such as has been done for inferring ancient whale migration routes and patterns (Buckeridge *et al.*, 2018; Taylor *et al.*, 2019).

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References

- Åkesson S, Broderick C, Glen F, Godley BJ, Luschi P, Papi F and Hays GC (2003) Navigation by green turtles: which strategy do displaced adults use to find Ascension Island? *OIKOS* **103**, 363–371.
- Allard MW, Miyamoto MM, Bjørndal KA, Bolten AB and Bowen B (1994) Support for natal homing in green turtles from mitochondrial DNA sequences. *Copeia* **1**, 34–41.
- Badrudeen M (2000) On the occurrence of the cirriped barnacle, *Chelonibia patula* (Ranzani) on the sea snake, *Hydrophis cyanocinctus* (Daudin). Marine Fisheries Information Service. Technical and Extension Series, vol. 164. Cochin: Central Marine Fisheries Research Institute.
- Balazs GH (1983) Recovery records of adult green turtles observed or originally tagged at French Frigate Shoals, Northwestern Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Memo, NMFS, NOAA-TM-NMFS-SWFC-36, 42 pp.
- Barazandeh M, Davis CS, Neufeld CJ, Coltman DW and Palmer AR (2013) Something Darwin didn't know about barnacles: spermcast mating in a common stalked species. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20122919.
- Bjørndal KA (1995) *Biology and Conservation of Sea Turtles*. Washington, DC: Smithsonian Institution Press, pp. 199–209.
- Bolten AB (1999) Techniques for measuring sea turtles. In Ecker KL, Bjørndal KA, Abreu-Gobrois FA and Donnelly M (eds), *Research and Management Techniques for the Conservation of Sea Turtles*. Washington, DC: IUCN/SSC Marine Turtle Specialist Group, pp. 110–114.
- Bowen BW and Karl SA (2007) Population genetics and phylogeography of sea turtles. *Molecular Ecology* **16**, 4886–4907.
- Bowen BW, Bass AL, Chow S-M, Bostrom M, Bjørndal KA, Bolten AB, Okuyama T, Bolker BM, Epperly S, Lacasella E, Shaver D, Dodd M, Hopkins-Murphy SR, Musick JA, Swingle M, Rankin-Baransky K, Teas W, Witzell WN and Dutton PH (2004) Natal homing in juvenile loggerhead turtles (*Caretta caretta*). *Molecular Ecology* **13**, 3797–3808.
- Bresette MJ, Witherington BE, Herren RM, Bagley DA, Gorham JC, Traxler SL, Crady CK and Hardy R (2010) Size-class partitioning and herding in a foraging group of green turtles *Chelonia mydas*. *Endangered Species Research* **9**, 105–116.
- Buckeridge JS, Chan BKK and Lee SW (2018) Accumulations of fossils of the whale barnacle *Coronula bifida* Bronn, 1831 (Thoracica: Coronulidae) provides evidence of a late Pliocene cetacean migration route through the Straits of Taiwan. *Zoological Studies* **57**, 54.
- Buckeridge JS, Chan BKK and Lin JP (2019) Paleontological studies of whale barnacles in Taiwan reveal new cetacean migration routes in the western Pacific since the Miocene. *Zoological Studies* **58**, 39.
- Bugoni L, Krause L, de Almeida AO and de Pádua Bueno AA (2001) Commensal barnacles of sea turtles in Brazil. *Marine Turtle Newsletter* **94**, 7–9.
- Burgett CM, Burkholder DA, Coastes KA, Fourqurean VL, Kenworthy WJ, Manuel SA, Outerbridge ME and Fourqurean JW (2018) Ontogenetic diet shifts of green sea turtles (*Chelonia mydas*) in a mid-ocean developmental habitat. *Marine Biology* **165**, 33.
- Carrillo JM, Overstreet RM, Raga JA and Aznar FJ (2015) Living on the edge: settlement patterns by the symbiotic barnacle *Xenobalanus globicipitis* on small cetaceans. *PLoS ONE* **10**, e0127367.
- Ceriani SA, Roth JD, Evans DR, Weishampel JF and Ehrhart LM (2012) Inferring foraging areas of nesting loggerhead turtles using satellite telemetry and stable isotopes. *PLoS ONE* **7**, e45335.
- Ceriani SA, Weishampel JF, Ehrhart LM, Mansfield KL and Wunder MB (2017) Foraging and recruitment hotspot dynamics for the largest Atlantic loggerhead turtle rookery. *Scientific Reports* **7**, 16894.
- Chaloupka M and Limpus C (2001) Trends in the abundance of sea turtles resident in southern Great Barrier Reef waters. *Biological Conservation* **102**, 235–249.
- Chan BKK and Hoeg JT (2015) Diversity of lifestyles, sexual systems, and larval development patterns in sessile crustaceans. In Thiel M and Watling L (eds), *The Natural History of the Crustacea: Lifestyles and Feeding Biology*. New York, NY: Oxford University Press, pp. 14–34.
- Cheang CC, Tsang LM, Chu KH, Cheng I-J and Chan BKK (2013) Host-specific phenotypic plasticity of the turtle barnacle *Chelonibia testudinaria*: a widespread generalist rather than a specialist. *PLoS ONE* **8**, 1–12.
- Cheng WH, Chan YT, Hong H, Johnson B and Cheng IJ (2019) Using programming languages and geographic information system to determine spatial and temporal variability in a green turtle foraging population on Liuchiu Island, Taiwan. *Zoological Studies* **58**, 18.
- Chong YK (2012) Determination of natal origins of green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles at feeding grounds in Malaysian waters. Master of Science thesis. Universiti Malaysia Terengganu.
- Crisp DJ (1983) *Chelonibia patula* (Ranzani), a pointer to the evolution of the complemental male. *Marine Biology Letters* **4**, 281–294.
- Darwin CR (1854) *A Monograph on the Sub-Class Cirripedia, with Figures of All the Species*, vol. 2. The Balanidae, (or Sessile Cirripedes); the Verrucidae, etc., etc., etc. London: The Ray Society, 684 pp.
- Devin ML and Sadeghi P (2010) Barnacles on hawksbill sea turtles, *Eretmochelys imbricata*, in Hormoz Island, Iran: (Reptilia: Cheloniidae). *Zoology in the Middle East* **49**, 45–48.
- Dobbs KA and Landry AM (2004) Commensals on nesting hawksbill turtles (*Eretmochelys imbricata*), Milman Island, northern Great Barrier Reef, Australia. *Memoirs – Queensland Museum* **49**, 674–699.
- Doell SA, Connolly RM, Limpus CJ, Pearson RM and van de Merwe JP (2017) Using growth rates to estimate age of the sea turtle barnacle *Chelonibia testudinaria*. *Marine Biology* **164**, 222.
- Dreyer N, Sørensen S, Yusa Y, Sawada K, Nash DR, Svennevig N and Hoeg JT (2018a) Sex allocation and maintenance of androdioecy in the pedunculate barnacle *Scalpellum scalpellum* (Crustacea: Cirripedia: Thoracica). *Biological Journal of the Linnean Society* **124**, 776–788.
- Dreyer N, Yusa Y, Gale A, Melzer RR, Yamato S and Hoeg JT (2018b) In the footsteps of Darwin: dwarf male attachment sites in scalpellid barnacles (Crustacea: Cirripedia: Thoracica) – implications for phylogeny and the evolution of sexual systems. *Zoological Journal of the Linnean Society* **184**, 999–1023.
- Dreyer N, Zardus JD, Hoeg JT, Olesen J, Yu MC and Chan BKK (2020) How whale and dolphin barnacles attach to their hosts and the paradox of remarkably versatile attachment structures in cypris larvae. *Organisms Diversity & Evolution* **20**, 233–249.
- Ewers-Saucedo C, Arendt MD, Wares JP and Rittschof D (2015) Growth, mortality, and mating group size of an androdioecious barnacle: implications for the evolution of dwarf males. *Journal of Crustacean Biology* **35**, 166–176.
- Ewers-Saucedo C, Hope NB and Wares JP (2016) The unexpected mating system of the androdioecious barnacle *Chelonibia testudinaria* (Linnaeus 1758). *Molecular Ecology* **25**, 2081–2092.
- Flint M, Morton JM, Limpus CJ, Patterson-Kane JC, Murray PJ and Mills PC (2010) Development and application of biochemical and haematological reference intervals to identify unhealthy green sea turtles (*Chelonia mydas*). *The Veterinary Journal* **185**, 299–304.
- Frick MG and Ross A (2001) Will the real *Chelonibia testudinaria* please come forward: an appeal. *Marine Turtle Newsletter* **94**, 16–17.
- Frick MG and McFall G (2007) Self-grooming by loggerhead turtles in Georgia, USA. *Marine Turtle Newsletter* **118**, 15.
- Frick MG and Pfaller JB (2013) Sea turtle epibiosis. In Wyneken J, Lohmann KJ and Musick JA (eds), *The Biology of Sea Turtles*, Vol. III. Boca Raton, FL: CRC Press, pp. 399–426.
- Frick MG, Williams KL and Veljacic DC (2002) New records of epibionts from loggerhead sea turtles *Caretta caretta* (L.). *Bulletin of Marine Science* **70**, 953–956.
- Frick MG, Zardus JD and Lazo-Wasem EA (2010) A new stomatolepas barnacle species (Cirripedia: Balanomorpha: Coronuloidea) from leatherback sea turtles. *Bulletin of the Peabody Museum of Natural History* **51**, 123–136.
- Fuller WJ, Broderick AC, Enever R, Thorne P and Godley BJ (2010) Motile homes: a comparison of the spatial distribution of epibiont communities on Mediterranean Sea turtles. *Journal of Natural History* **44**, 1743–1753.
- Greenblatt RJ, Work TM, Balazs GH, Sutton CA, Casey RN and Casey JW (2004) The *Ozobranchus* leech is a candidate mechanical vector for the

- fibropapilloma-associated turtle herpesvirus found latently infecting skin tumors on Hawaiian green turtles (*Chelonia mydas*). *Virology* **321**, 101–110.
- Grossman A, Sazima C, Bellini C and Sazima I** (2006) Cleaning symbiosis between hawksbill turtles and reef fishes at Fernando de Noronha Archipelago, off Northeast Brazil. *Chelonian Conservation and Biology* **5**, 284–288.
- Hartigan JA and Hartigan PM** (1985) The dip test of unimodality. *Annals of Statistics* **13**, 70–84.
- Hayashi R** (2009) New host records of the turtle barnacle, *Cylindrolepas sinica*: a case study of sea turtles' behaviour and their epibionts. *Marine Biology Records* **2**, E165.
- Hayashi R** (2013) A checklist of turtle and whale barnacle (Cirripedia: Thoracica: Coronuloidea). *Journal of the Marine Biological Association of the United Kingdom* **93**, 143–182.
- Hayashi R and Tsuji K** (2008) Spatial distribution of turtle barnacles on the green sea turtle, *Chelonia mydas*. *Ecological Research* **23**, 121–125.
- Hayashi R and Nishizawa H** (2015) Body size distribution demonstrates flexible habitat shift of green turtle (*Chelonia mydas*). *Global Ecology and Conservation* **3**, 115–120.
- Hayashi R, Chan BKK, Simon-Blecher N, Watanabe H, Guy-Haim T, Yonezawa T, Levy Y, Shuto T and Achituv Y** (2013) Phylogenetic position and evolutionary history of the turtle and whale barnacles (Cirripedia: Balanomorpha: Coronuloidea). *Molecular Phylogenetics and Evolution* **67**, 9–14.
- Hays GC and Scott R** (2013) Global patterns for upper ceilings on migration distance in sea turtles and comparisons with fish, birds and mammals. *Functional Ecology* **27**, 748–756.
- Hays GC, Mazaris AD and Schofield G** (2014) Different male vs female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Frontiers in Marine Science* **1**, 1–9.
- Hernández-Vázquez S and Valdez-González C** (1998) Observations of the epizoa found on the turtle *Lepidochelys olivacea* at La Gloria, Jalisco, Mexico. *Ciencias Marinas* **24**, 119–125.
- Hoeg JT, Yusa Y and Dreyer N** (2016) Sex determination in the androdioecious barnacle *Scalpellum scalpellum* (Crustacea: Cirripedia). *Biological Journal of the Linnean Society* **118**, 359–368.
- Ihwan MZ, Joseph J, Jamaan AS, Wahidah W and Marina H** (2018) Occurrence of epibiont barnacles *Chelonibia testudinaria* on green turtle *Chelonia mydas* at Brunei Bay. *International Journal of Zoological Research* **14**, 43–48.
- Jolis G and Kassem K** (2011) *Marine Turtle status in Northeast Semporna Priority Conservation Area*. Kota Kinabalu, Malaysia: WWF-Malaysia. Available at http://awsassets.wwf.org.my/downloads/marinerturtlestatusreportofsempornapca_final_pdf
- Joseph J, Nishizawa H, Hassan M, Zakariah MI, Jaaman SA and Zhang X** (2017) Utilization of Brunei Bay (Malaysia) as a developmental and foraging habitat for hawksbill turtle (*Eretmochelys imbricata*). *Regional Studies in Marine Science* **16**, 304–307.
- Kelly MW and Sanford E** (2010) The evolution of mating systems in barnacles. *Journal of Experimental Marine Biology and Ecology* **392**, 37–45.
- Kim HK, Chan BKK, Kang CB, Kim HY and Kim W** (2020) How do whale barnacles live on their hosts? Functional morphology and mating-group sizes of *Coronula diadema* (Linnaeus, 1767) and *Conchoderma auritum* (Linnaeus, 1767) (Cirripedia: Thoracalcareia). *Journal of Crustacean Biology*, ruaa075. <https://doi.org/10.1093/jcabi/ruaa075>
- Lacombe D** (1970) A comparative study of the cement glands in some balanid barnacles (Cirripedia, Balanidae). *Biology Bulletin* **139**, 164–179.
- Larsson AI and Jonsson PR** (2006) Barnacle larvae actively select flow environments supporting post-settlement growth and survival. *Ecology* **87**, 1960–1966.
- Lazo-Wasem EA, Pinou T, Peña de Niz A and Feuerstein A** (2011) Epibionts associated with the nesting marine turtles *Lepidochelys olivacea* and *Chelonia mydas* in Jalisco, Mexico: a review and field guide. *Bulletin of the Peabody Museum of Natural History* **52**, 221–240.
- Lohmann KJ, Putman NF and Lohmann CMF** (2008) Geomagnetic imprinting: a unifying hypothesis of long-distance natal homing in salmon and sea turtles. *Proceedings of the National Academy of Sciences USA* **105**, 19096–19101.
- Márquez MR** (1990) *FAO Species Catalogue. Sea Turtles of the world. An Annotated and Illustrated Catalogue of Sea Turtle Species Known to Date*. FAO Fisheries Synopsis, no. 125, vol. 11, Rome: FAO, 81 pp.
- Minchinton TE and Scheibling RE** (1993) Free space availability and larval substratum selection as determinants of barnacle population structure in a developing rocky intertidal community. *Marine Ecology Progress Series* **95**, 233–244.
- Monroe R** (1981) Studies in the Coronulidae (Cirripedia): shell morphology, growth, and function, and their bearing on subfamily classification. *Memoirs of the Queensland Museum* **20**, 237–251.
- Monroe R and Limpus CJ** (1979) Barnacles on turtles in Queensland waters with descriptions of three new species. *Memoirs – Queensland Museum* **19**, 197–223.
- Murata A, Imafuku M and Abe N** (2001) Copulation by the barnacle *Tetraclita japonica* under natural conditions. *Journal of Zoology* **253**, 275–280.
- Musick JA and Limpus CJ** (1997) Habitat utilization and migration in juvenile sea turtles. In Lutz PL and Musick JA (eds), *The Biology of Sea Turtles*. Boca Raton, FL: CRC Press, pp. 137–163.
- Nájera-Hillman E, Bass JB and Buckham S** (2012) Distribution patterns of the barnacle, *Chelonibia testudinaria*, on juvenile green turtles (*Chelonia mydas*) in Bahía Magdalena, Mexico. *Revista Mexicana de Biodiversidad* **83**, 1171–1179.
- Nishizawa H, Joseph J and Chong YK** (2016) Spatio-temporal patterns of mitochondrial DNA variation in hawksbill turtles (*Eretmochelys imbricata*) in Southeast Asia. *Journal of Experimental Marine Biology and Ecology* **474**, 164–170.
- Ooi SL and Palaniappan PM** (2011) Silent turtle dwellers: barnacles on resident green (*Chelonia mydas*) and hawksbill turtles (*Eretmochelys imbricata*) of Mabul and Sipadan Islands. *Borneo Science* **28**, 66–72.
- Palaniappan P** (2017) Morphometric analysis of resident green sea turtles (*Chelonia mydas*) in Mabul Island, Sabah, Malaysia. *International Journal of Fisheries and Aquatic Studies* **5**, 174–178.
- Palaniappan P and Abd Hamid HH** (2017) Spatial site fidelity of sea turtles at a foraging ground in Mabul Island, Sabah, Malaysia. *International Journal of Fisheries and Aquatic Studies* **5**, 140–144.
- Pearson RM, van de Merwe JP, Gagan MK, Limpus CJ and Connolly RM** (2019) Distinguishing between sea turtle foraging areas using stable isotopes from commensal barnacle shells. *Scientific Reports* **9**, 6565.
- Pfaller JB, Bjørndal KA, Reich KJ, Williams KL and Frick MG** (2006) Distribution patterns of epibionts on the carapace of loggerhead turtles, *Caretta caretta*. *Journal of the Marine Biological Association of the United Kingdom Biodiversity Records* **5381**, 1–4.
- Pfaller JB, Frick MG, Reich KJ, Williams KL and Bjørndal KA** (2008) Carapace epibionts of loggerhead turtles (*Caretta caretta*) nesting at Canaveral National Seashore, Florida. *Journal of Natural History* **42**, 13–14.
- Pilcher N** (2010) Population structure and growth of immature green turtles at Mantanani, Sabah, Malaysia. *Journal of Herpetology* **44**, 168–171.
- Razaghian H, Esfandabad BS, Hesni MA, Shoushtari RV, Toranjzar H and Miller J** (2019) Distribution patterns of epibiotic barnacles on the hawksbill turtle, *Eretmochelys imbricata*, nesting in Iran. *Regional Studies in Marine Science* **27**, 1–6.
- Rees EIS and Walker G** (1993) A record of the turtle barnacles *Chelonibia* in the Irish Sea. *Porcupine Newsletter* **5**, 189.
- Robinson NJ, Lazo-Wasem EA, Paladino FV, Zardus J and Pinou T** (2017) Assortative epibiosis of leatherback, olive ridley and green sea turtles in the Eastern Tropical Pacific. *Journal of the Marine Biological Association of the United Kingdom* **97**, 1233–1240.
- Sazima I, Grossman A and Sazima C** (2004) Hawksbill turtles visit moustached barbers: cleaning symbiosis between *Eretmochelys imbricata* and the shrimp *Stenopus hispidus*. *Biota Neotropica* **4**, 1–6.
- Sazima C, Grossman A and Sazima I** (2010) Turtle cleaners: reef fishes foraging on epibionts of sea turtles in the tropical Southwestern Atlantic, with a summary of this association type. *Neotropical Ichthyology* **8**, 187–192.
- Schärer MT** (2003) A survey of the epibiota of *Eretmochelys imbricata* (Testudines: Cheloniida) of Mona Island, Puerto Rico. *Revista de Biología Tropical* **51**, 87–90.
- Schofield G, Katselidis KA, Dimopoulos P, Pantis JD and Hays GC** (2006) Behavioural analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. *Endangered Species Research* **2**, 71–79.
- Shapiro SS and Wilk MB** (1965) An analysis of variance test for normality (complete samples). *Biometrika* **52**, 591–611.
- Shimada T, Limpus CJ, Hamann M, Bell I, Esteban N, Groom R and Hays GC** (2020) Fidelity to foraging sites after long migrations. *Journal of Animal Ecology* **89**, 1008–1016.
- Sönmez B** (2019) Morphological variations in the green turtle (*Chelonia mydas*): a field study on Eastern Mediterranean nesting population. *Zoological Studies* **58**, 16.

- Spremborg U, Høeg JT, Buhl-Mortensen L and Yusa Y** (2012) Cypris settlement and dwarf male formation in the barnacle *Scalpellum scalpellum*: a model for an androdioecious reproductive system. *Journal of Experimental Marine Biology and Ecology* **422–423**, 39–47.
- Stamper MA, Harms C, Epperly SP, Braun-McNeill J and Stoskopf MK** (2005) Relationship between barnacle epibiotic load and hematologic parameters in loggerhead sea turtle (*Caretta caretta*), a comparison between migratory and residential animals in Pamlico Sound, North Carolina. *Journal of Zoo and Wildlife Medicine* **36**, 635–641.
- Taylor LD, O’Dea A, Bralower TJ and Finnegan S** (2019) Isotopes from fossil coronulid barnacle shells record evidence of migration in multiple Pleistocene whale populations. *Proceedings of the National Academy of Sciences USA* **116**, 7377–7381.
- Ten S, Pascual L, Pérez-Gabaldón MI, Tomás J, Domènech F and Aznar FJ** (2019) Epibiotic barnacles of sea turtles as indicators of habitat use and fishery interactions: an analysis of juvenile loggerhead sea turtles, *Caretta caretta*, in the western Mediterranean. *Ecological Indicators* **107**, 105672.
- Trager GC, Hwang J-S and Strickler JR** (1990) Barnacle suspension-feeding in variable flow. *Marine Biology* **105**, 117–127.
- van Dam RP and Diez CE** (1998) Caribbean hawksbill turtle morphometrics. *Bulletin of Marine Science* **62**, 145–155.
- Walker G** (1978) A cytological study on the cement apparatus of the barnacle, *Chelonibia testudinaria* Linnaeus, an epizoite on turtles. *Bulletin of Marine Science* **28**, 205–209.
- Weeks SC, Benvenuto C and Reed SK** (2006) When males and hermaphrodites coexist: a review of androdioecy in animals. *Integrative and Comparative Biology* **46**, 449–464.
- Wijayanti H and Yusa Y** (2016) Plastic sexual expression in the androdioecious barnacle *Octolasmis warwickii* (Cirripedia: Pedunculata). *Biological Bulletin* **230**, 51–55.
- Yamaguchi S, Yusa Y, Yamato S, Urano S and Takahashi S** (2008) Mating group size and evolutionarily stable pattern of sexuality in barnacles. *Journal of Theoretical Biology* **253**, 61–73.
- Zardus JD and Hadfield MG** (2004) Larval development and complemental males in *Chelonibia testudinaria*, a barnacle commensal with sea turtles. *Journal of Crustacean Biology* **24**, 409–421.
- Zardus JD and Balazs GH** (2007) Two previously unreported barnacles commensal with the green sea turtle, *Chelonia mydas* (Linnaeus, 1758), in Hawaii and a comparison of their attachment modes. *Crustaceana* **80**, 1303–1315.
- Zardus JD, Lake DT, Frick MG and Rawson PD** (2014) Deconstructing an assemblage of “turtle” barnacles: species assignments and fickle fidelity in *Chelonibia*. *Marine Biology* **161**, 45–59.