

Motile homes: a comparison of the spatial distribution of epibiont communities on Mediterranean sea turtles

W.J. Fuller^{a,b,c,*}, A.C. Broderick^a, R. Enever^d, P. Thorne^e and B.J. Godley^a

^aFaculty of Agriculture Sciences and Technology, European University of Lefke, Lefke, North Cyprus, Mersin 10, Turkey; ^bCentre for Ecology and Conservation, School of Biosciences, University of Exeter, Penryn TR10 9EZ, UK; ^cSociety for the Protection of Turtles in North Cyprus, PK 42, Girne, Mersin 10, Turkey, North Cyprus; ^dCEFAS Exeter, School of Biosciences, University of Exeter, Exeter, UK; ^eSchool of Biological Sciences, University of Wales, Swansea SA2 8PP

(Received 7 September 2009; final version received 13 January 2010)

Understanding the ecological roles performed by an individual species requires knowledge from a wide range of disciplines; here we analyze the epibiont–host relationship found in marine turtles. During the study we recorded five new species of sea turtle epibiont: *Laomedea flexuosa*, *Caprella fretensis*, *Hyale nilssoni*, *Hyale schmidti*, *Parasinelobus chevreuxi*; as part of a total of nine zoological epibionts present on 35 female green turtles (*Chelonia mydas*) and 100 loggerhead turtles (*Caretta caretta*) nesting in Cyprus. The two most commonly occurring epibionts were acorn barnacles *Chelonibia testudinaria* and *Chelonibia caretta*, with larger specimens of both species recorded on loggerhead turtles. We analyzed the spatial distribution of these two barnacle species upon the carapaces of their hosts. Specimens of *C. testudinaria* situated on the anterior half of the carapace were larger than those located at the posterior. A significantly larger proportion of loggerhead turtles (52.5%) hosted epibionts in comparison to green turtles (30.3%). All non-barnacle epibionts were associated with either posterior algal mats or carapace scars.

Keywords: epibiont; spatial distribution; barnacles; *Caretta caretta*; *Chelonia mydas*

Introduction

Most hard substrata in the oceans of the world become home to a wide variety of motile and static epibionts. However, some epibionts fasten themselves to mobile structures such as ships, flotsam and jetsam, and motile marine organisms (Wahl 1989), where movement effectively creates water flow, so aiding the gathering of nutrients. Many marine vertebrates such as whales and sea turtles provide significant motile substrata for the attachment of these epibionts (Monroe and Limpus 1979; Caine 1986; Frick and Slay 2000) with some individuals supporting abundant and diverse epibiont communities. Marine epibionts represent almost every invertebrate phylum and most of these are found on marine turtles. Over 90 epibiont species were found to be associated with female loggerhead turtles (*Caretta caretta*) nesting along the coast of Georgia, USA (Frick et al. 1998).

*Corresponding author. Email: wfuller@seaturtle.org

The major phyla represented as epibionts on marine turtles are Porifera, Cnidaria, Mollusca and Arthropoda (Frick et al 1998). One of the most commonly occurring epibiont species found on sea turtles; is the turtle barnacle *Chelonibia testudinaria*. This prehistoric association has been found to exist in the fossil record as far back as 5–15 million years ago (Withers 1953; Ross 1963). Associations between epibiont and host have been used to identify host mediated genetic variation (Rawson et al. 2003) and life stage estimates (Loverich 2003). Another common epibiont is the oceanic grapsid crab, *Planus minutus*, which relies on floating substrata in order to survive (Davenport 1992), and is found to congregate around the tail and rear flippers of sea turtles, feeding on faecal material (Crane 1937; Chace 1951; Carranza et al. 2003; Frick et al. 2003). These crabs also exploit the turtle's carapace where they feed on goose barnacle spats (Davenport 1992), therefore performing a cleaning service and thus fulfilling a mutualistic role. However, not all epibionts are so benign. It could be suggested that some epibionts such as barnacles can cause a significant amount of hydrodynamic drag, requiring the individual to expend significantly more energy (Wahl 1996; Frick and Slay 2000). Indeed, it has been suggested that increased epibiont loads on marine turtles may be indicative of the host's poor health status (Herbst and Jacobson 1995). Epibionts can play an important role in the survival rates of other marine organisms, particularly during juvenile stages, where the presence of some epibiont species can lead to a greater chance of predation, whereas others can provide some form of protection (Lopez et al. 2000; Farren and Donovan 2007). This has been shown in scallop cultures where an infestation of a harmful species can cause a significant loss of income to the fisheries concerned. Additionally, epibiont encrustations on abiotic structures such as ships and oil platforms lead to increased costs through high fuel and maintenance bills. It has been estimated that barnacle encrustation alone costs the shipping industry \$2 billion per annum owing to increased fuel costs (Christie and Dalley 1987). It is therefore clear that epibiont communities play an important and diverse role in marine ecosystems.

The diversity of epibionts so far described in association with marine turtles of the Mediterranean is relatively low when compared to those which inhabit the Atlantic. Gramentz (1988) found only 13 different species when studying juvenile loggerhead turtles from the western Mediterranean. Most studies on the epibiont communities of sea turtles have mainly produced taxonomic listings; however, those that have investigated the spatial distribution have concluded that *Chelonibia testudinaria* was predominantly found on the posterior portion of the carapace (Caine 1986; Matsuura and Nakamura 1993; Frick, Williams et al. 1998, Frick, Mason et al. 2003). In this study we aim to catalogue and analyze the spatial distribution of epibionts found on adult females of both species of Mediterranean marine turtles: the loggerhead turtle and the green turtle (*Chelonia mydas*) thus complementing the previous work carried out on juvenile loggerhead turtles in the region. Understanding the epibiont diversity and distribution on marine turtles will hopefully lead to a sounder understanding of the ecological roles that marine turtles perform.

Methods

During the nesting seasons of 1999–2004 (June–August) epibiont samples were collected from the external surfaces of both female Green and loggerhead turtles

during oviposition at Alagadi beach, Northern Cyprus (35°33'N, 33°48'E). Turtles were encountered during night-time beach patrols and epibionts were removed using a pocket-knife or tweezers. All carapace, flipper and head barnacles were removed and the individual scute or location from which they were taken was recorded. Samples were initially frozen and at the end of the nesting season preserved in alcohol for later identification. In the case of some small mobile epibionts (e.g., small crustacea, such as caprellids) it was only possible to sub-sample. Other data, such as curved carapace length and width, were recorded as the normal procedure followed when monitoring nesting turtles at this rookery (Broderick et al. 2002). At this site female turtles are marked using both external flipper tags and internal passive integrated transponders or indentichips (PITs). Of our study females, five green and five loggerhead turtles were sampled on more than one nesting season and to avoid pseudoreplication, only data from the first time these females were observed were included in analyses.

Carapace scutes are of variable size according to a relatively conservative plan for each species (Pritchard 1997). Individual scute areas were calculated using measurements taken from a sample of dead individuals (three loggerhead turtles and one green turtle). Each scute edge was measured appropriately and according to its basic shape, i.e. trapezium, square etc; its area was then calculated. These estimates of scute sizes are approximate, with the aim of acting as a general guide to the relative surface area among scutes.

In the laboratory, all barnacles were identified to species using Monroe and Limpus (1979); basal diameter (minimum and maximum) and height were measured using callipers (accurate to 0.1mm). An approximate basal surface area was calculated as the product of minimum and maximum basal diameters. Other epibionts were preliminarily identified to species, using Hayward et al. (1995). All samples were later cross-checked and species confirmed by Dr P.J. Hayward, University of Swansea. The position of any algal mats was noted; however, no algal samples were taken for identification.

Results

Abundance and diversity

The total number of turtles sampled possessing epibionts was 135 (35 green turtles and 100 loggerhead turtles). Nine different epibiont species were recorded (loggerhead turtles: nine species; green turtles three species) and included one species of hydrozoan (on a loggerhead turtle) and eight crustacean species (Table 1). Five of the species were new records as epibionts on marine turtles (Table 1). There was a clear difference between the two turtle species, with 52.5% of loggerhead and 30.3% of green turtles sampled hosting epibionts. The most abundant epibiont found on both species of turtle were from the class Cirripedia, the barnacles. Of these we sampled and identified 1085 specimens; for a breakdown of species and abundance, see Table 1.

Barnacles

The most abundant barnacle species present on both loggerhead and green turtles was the turtle barnacle *Chelonibia testudinaria* (loggerhead turtles: median (inter-quartile range) number per turtle 4.5 (1.25–9.0), range 1–31; green turtles: 3.5 (2–9.5), range

Table 1. Epibiont species found and the number of turtles on which they were found. The numbers in parentheses are the total number of that species sampled. Five new records for epibionts on turtles marked (#).

Species	Loggerhead turtle	Green turtle
Cnidaria		
Hydrozoa		
<i>Laomedea flexuosa</i> #	3	0
Crustacea		
Amphipoda		
<i>Caprella fretensis</i> #	12 (238)	0
<i>Hyale nilssoni</i> #	2	0
<i>Hyale schmidti</i> #	3	0
<i>Podoceridae</i> sp.	1	0
Cirripedia		
<i>Chelonibia testudinaria</i>	65 (639)	21 (179)
<i>Chelonibia caretta</i>	27 (155)	11 (48)
<i>Lepas anatifera</i>	15 (47)	6 (17)
Tanaidea		
<i>Parasinelobus chevreuxi</i> #	1	0

1–33), followed by *Chelonibia caretta* (loggerhead turtles: 5.7 (1–8.5), range 1–25; green turtles: 2.0 (1.0–8.0), range 1–15) and *Lepas anatifera* (loggerhead turtles: 1.0 (1.0–5.0), range 1–7; green turtles: 2.0 (1.0–4.75), range 1–7) respectively. There was no significant inter-specific difference between turtle species in the total number of barnacles present on those individual turtles which hosted barnacles (*Chelonibia testudinaria*: Mann–Whitney $U = 905.5$, $P = 0.81$; *Chelonibia caretta*: $U = 137$, $P = 0.49$).

Loggerhead turtles supported a significantly larger size class (maximum basal diameter) of barnacles than those found on green turtles for both types of acorn barnacles (*Chelonibia testudinaria*: $U = 29530$, $P < 0.0001$; loggerhead turtles (median, inter quartile range) 23.6, 16.5–32.6, range 5.7–55, $n = 588$; green turtles median 11.8, 8–25.4, range 3.2–48.2, $n = 178$. *Chelonibia caretta*: $U = 881$, $P < 0.0001$; loggerhead turtles median 20.0, 13.9–26.1, range 5.3–47.4, $n = 150$; green turtles median 8.5, 6.7–29.5, range 4.2–29.5, $n = 42$; Table 1 and Figures 1 and 2).

There was a lack of consistent pattern in the spatial distribution of *Chelonibia testudinaria* for either species of turtle. However, the first two central scutes in green turtles possessed a small aggregation of specimens (Figure 3a). When we looked at the size distribution of *Chelonibia testudinaria* on each species, the loggerheads showed a pattern of the larger specimens being located on the anterior half of the carapace (Figure 3b). This was not the case for green turtles. The barnacle percentage cover of each scute was greatest on the marginal scutes for both species (Figure 3c). The distribution of *Chelonibia caretta* was even less well-defined (Figure 4), with only the size of barnacle showing any sort of pattern in distribution, with larger barnacles being found at the anterior and posterior extremes of the loggerhead turtle carapaces (Figure 4b).

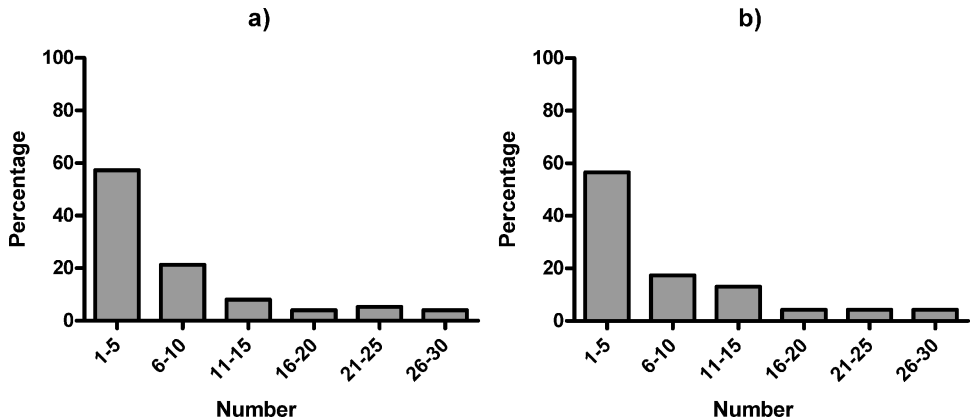


Figure 1. Relative abundance of *Chelonibia testudinaria* on (a) loggerhead and (b) green turtles. Note: 47.4% and 69.7% of loggerhead and green turtles hosted no epibionts.

Other species

All non-barnacle species (Table 1) were found to be associated with algal mats on loggerhead turtles. The algal mats were always found on the posterior third of the carapace ($n = 17$) and this was from where most amphipods were sampled. One exception was an individual with a large crack down the centre of the carapace, which provided a suitable micro-habitat for a large number of caprellids (Frick and Slay 2000). For five of these species we could locate no earlier citation of their epibiotic association with sea turtles and assumed these to be new records.

Discussion

To understand fully the ecological roles of any organism, one first has to study and identify all the interactions that species has with its environment and other species, in this study we provide a more detailed account of the epibiont host relationship found in marine turtles.

As with other similar studies the most commonly occurring epibiont species found on marine turtles were those from the class Cirripedia. The turtle barnacle *Chelonibia testudinaria* was particularly numerous (Caine 1986; Matsuura and Nakamura 1993; Frick et al. 1998; Casale 2004). Although there is a great diversity of epibionts on turtles found in the Atlantic Ocean (89 previously recorded species; Frick et al. 1998), the records found in the Mediterranean Sea are thus far depauperate (14 species, Badillo et al. 2001; 13 species, Gramentz 1988; 2 species, Sezgin et al. 2009; and 9 during this study). Kitsos et al. (2003) found nine barnacle species on dead loggerhead turtles washed up on the beaches of Greece. Some of these, however, may not naturally occur on living turtles. The possible reasons for the differences between these two oceanic basins may be the generally oligotrophic nature and high salinity of the Mediterranean Sea when compared with the Atlantic Ocean. Most of the new species of turtle epibionts found in this study are either usually associated with lower inter-tidal zones or live among marine algae (McBane and Croker 1984).

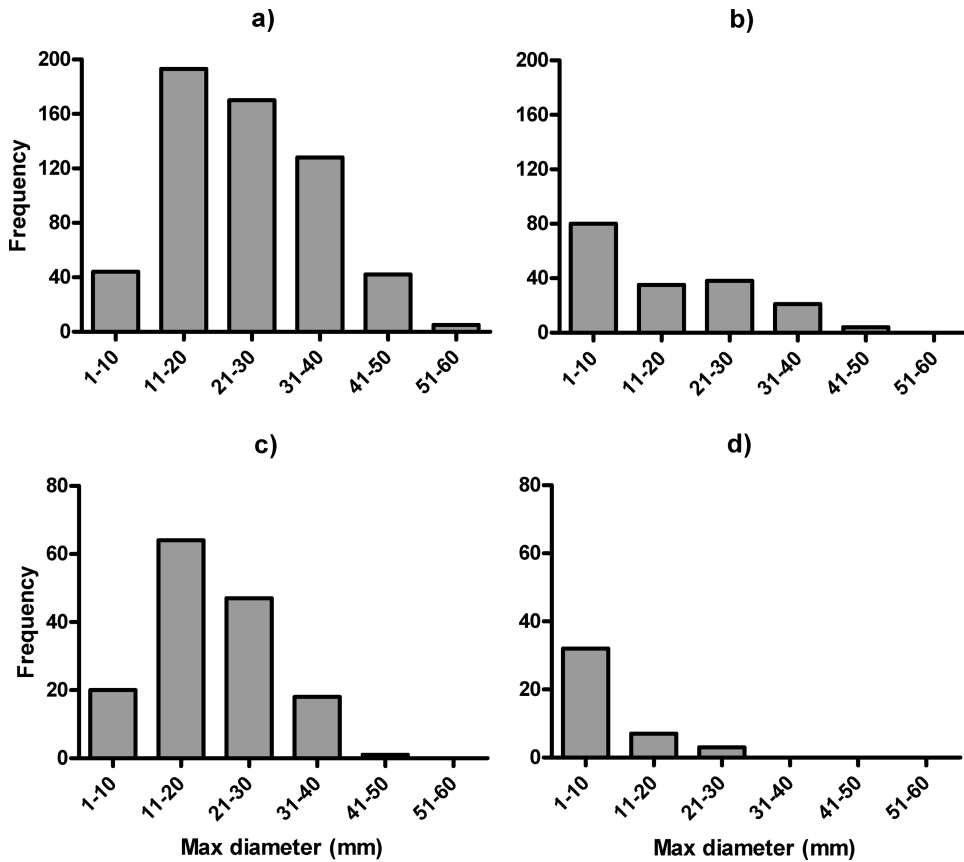


Figure 2. Frequency histogram of barnacle maximum basal diameter (mm) of *Chelonibia testudinaria* on (a) loggerhead turtles (mean = 24.9, SD \pm 10.6, range 5.7–55.0, n = 588); and (b) green turtles (mean = 16.9, SD \pm 11.1, range 3.2–48.2, n = 178); and *C. caretta* on (c) loggerhead turtles (mean = 20.7, SD \pm 8.5, range 5.3–44.5, n = 150); and (d) green turtles (mean = 10.3, SD \pm 5.6, range 4.2–29.5, n = 42).

However, there have been very few studies which have analyzed the spatial distribution of epibionts. One such study carried out in Japan by Hayashi and Tsuji (2008) found a difference in the level of aggregation and the degree of interspecific overlap among barnacles was significant on larger turtles.

Although there were no significant inter-specific differences in the numbers of barnacles found, there was a clear difference in the size of the barnacles found between the species of turtle and the proportion possessing barnacles. These differences could be associated with the differences in the foraging ecology of the two turtle species. Green turtles are primarily known as grazers of sea grasses and macroalgae (Bjorndal 1980) causing relatively little sediment disturbance, whereas loggerhead turtles are benthic foragers and have been known to feed by infaunal mining (Preen 1996) often feeding on sub-benthic organisms (Bjorndal 1997). This difference in feeding behaviour is likely to provide the barnacles present on loggerhead turtles with a greater amount of suspended organisms and particulate matter on which to

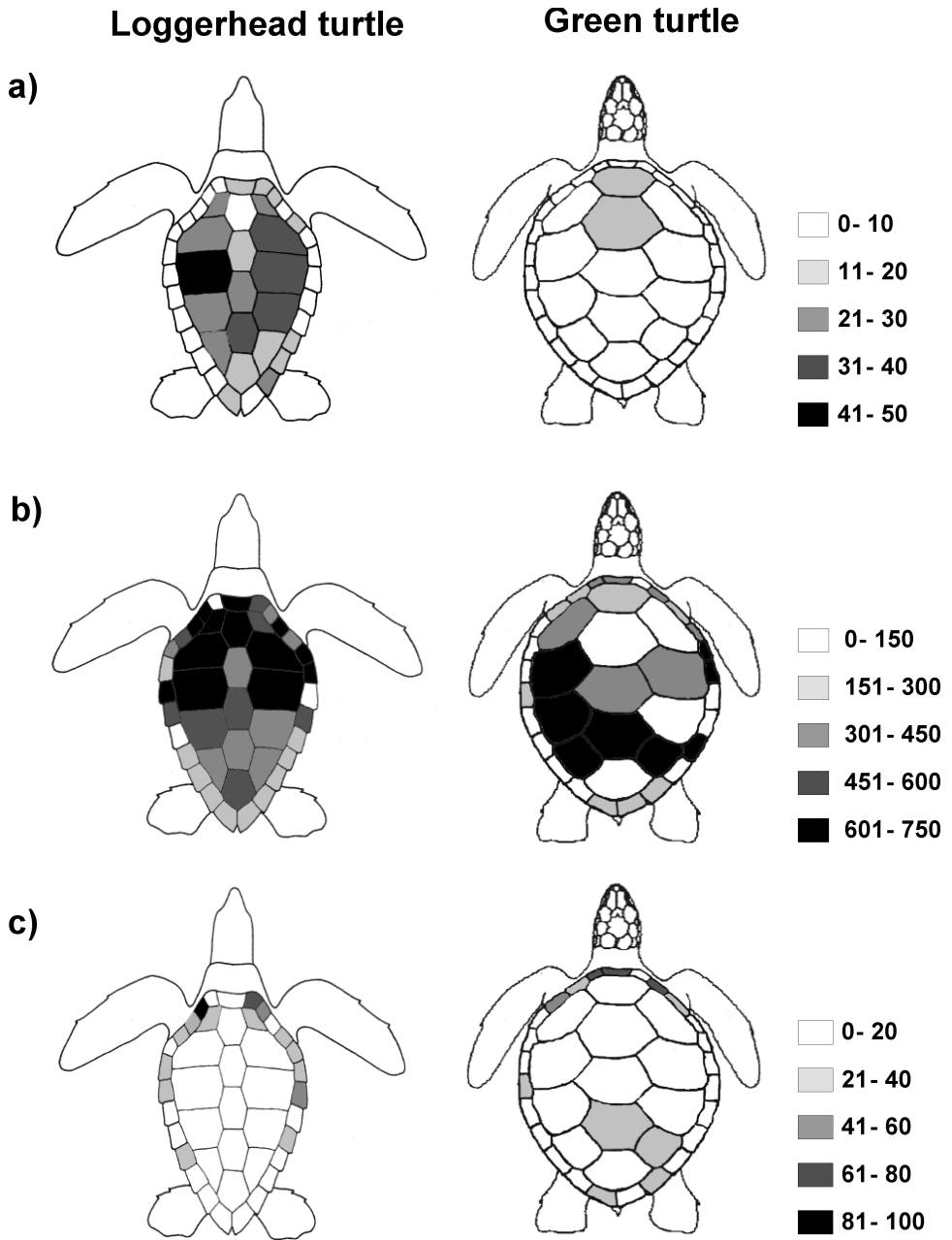


Figure 3. Diagrammatic representation of the different spatial patterns of the epibiont *Chelonibia testudinaria* found on loggerhead turtles and green turtles. (a) Total number of barnacles found for each scute; (b) mean basal area (mm²) of the barnacles for each scute; (c) percentage cover for individual scutes.

feed. This is also supported by the fact that those barnacles found on an anterior position of the carapace were substantially larger than those found in a more posterior location.

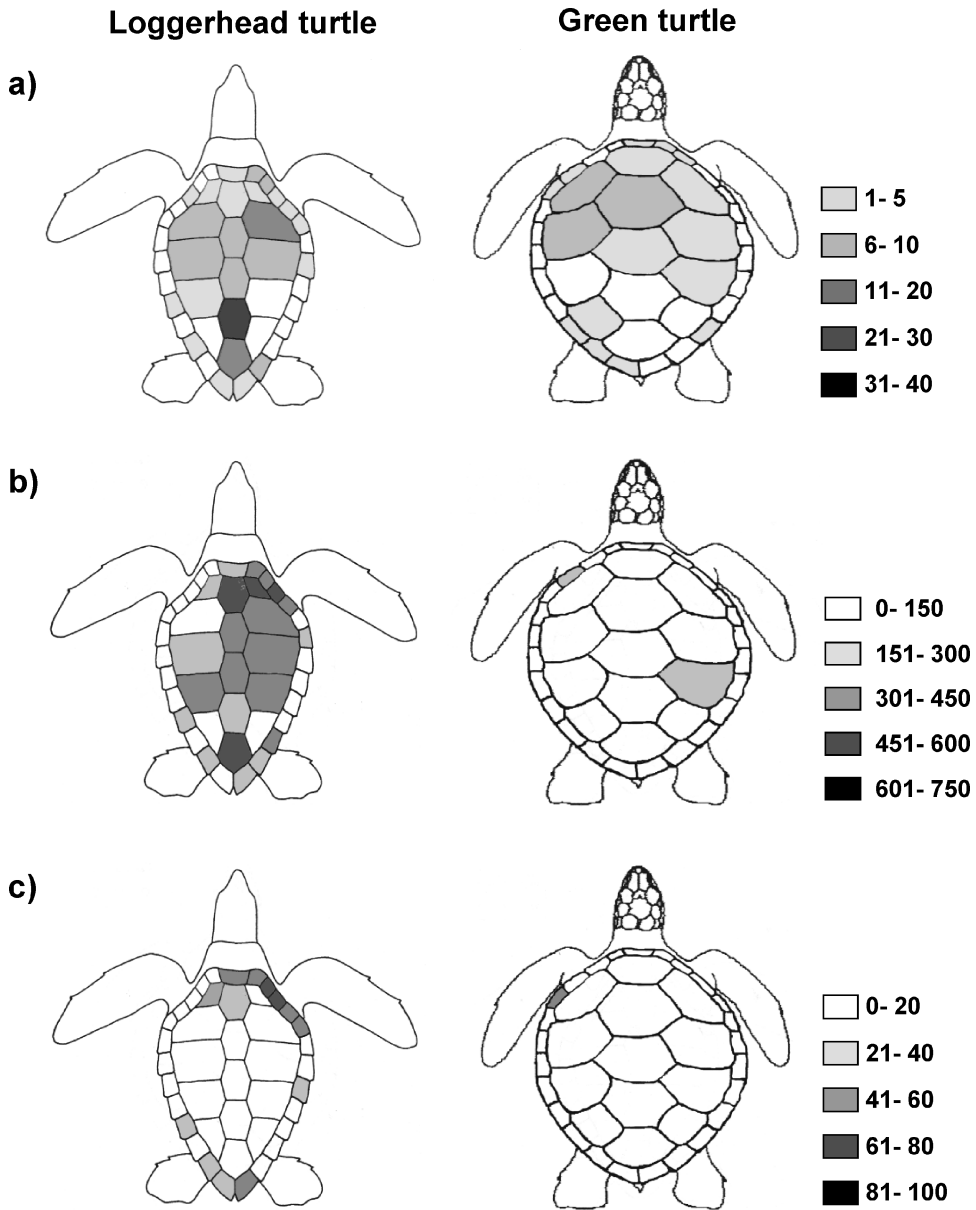


Figure 4. Diagrammatic representation of the different spatial patterns of the epibiont *Chelonibia caretta* found on loggerhead turtles and green turtles. (a) Total number of barnacles found for each scute; (b) mean basal area (mm^2) of the barnacles for each scute; (c) percentage cover for individual scutes.

There are other factors which may play a role in the size to which these barnacles develop. As reported in this study both species of acorn barnacle were significantly larger on loggerhead turtles when compared with those found on green turtles, one possible reason for this could be the variability in surface texture of scutes in that

loggerhead scutes are clearly more rugose or flaky. They maybe therefore, more prone to larval settlement (pers. obs.) and provide a greater surface area, leading to a more secure attachment. This will make the barnacle harder to dislodge during self-cleaning (Heithaus et al. 2002; Schofield et al. 2007) or when eliciting symbiotic cleaning behaviour from fish species (Balazs et al. 1994; Schofield et al. 2007).

The epibiont species diversity found on the two species of turtle was markedly different, with green turtles only supporting the three barnacle species. However, all nine species found during this study were found on nesting loggerhead turtles and all non-barnacle species were either associated with algal mats attached to the posterior region of the carapace or a scar in the carapace (Frick and Slay 2000). These abnormalities in the carapace can provide a significant niche for amphipods such as Caprellidae spp. Both the posterior region and crevices in the carapace of turtles provide a suitable area for attachment of non-barnacle epibionts, with reduced water flow and, therefore, less physical stress (Pfaller et al. 2006).

Epibionts themselves, particularly large barnacles and algae, will create new habitats as they grow and develop, increasing the overall diversity found on an individual turtle. The absence of algal mats on green turtles fundamentally reduces the diversity of epibionts found.

It could be suggested that the epibiont communities found on Mediterranean turtles are non-successional, as the epibiont community does not appear to develop into a climax community (Frick and Slay 2000). It is clear that marine turtles play numerous ecological roles within the marine and terrestrial environment, nutrient transporters (Bouchard and Bjorndal 2000), predators (Iverson et al. 1986), possibly even keystone species (Bjorndal 1997). Their importance in providing an ecological niche for other invertebrate species is little understood. The fact that five new species of epibionts for turtles were found on the nesting females at one breeding site highlights the need for further research.

Acknowledgements

This work is part of the doctoral thesis of WJF, begun at the University of Wales, Swansea, and completed at the University of Exeter, part-funded by a University Scholarship. The authors thank all the student volunteers who assisted with fieldwork as part of the Marine Turtle Conservation Project 1999–2004, a collaboration between the Marine Turtle Research Group, The Society for the Protection of Turtles in North Cyprus and the Department of Environmental Protection. Sponsors included British Chelonia Group, British High Commission, and the Royal Society. The authors would also like to thank Dr P.J. Hayward for his confirmation of the non-barnacle species and Mike Frick for his advice and confirmation of the five new turtle epibiont records. BJG and ACB were funded by grants from the Darwin Initiative, European Social Fund and NERC. This manuscript was improved by comments from reviewers.

References

- Badillo FJ, Aznar FJ, Tomas J, Raga JA. 2001. Epibiont fauna of *Caretta caretta* in the Spanish Mediterranean. In: D. Margaritoulis and A. Demetropolous, editors Proceedings, first Mediterranean conference on marine turtles, Rome. Nicosia: Barcelona Convention - Bern Convention - Bonn Convention (CMS).

- Balazs GH, Miya RK, Finn MA. 1994. Aspects of green turtles in their feeding, resting, and cleaning areas off Waikiki Beach. In: Schroeder BA Witherington BE, compilers. Proceedings, 13th annual symposium sea turtle biology and conservation, NOAA Tech. Memo. NMFS-SEFSC-341. Miami (FL): US Department of Commerce. p. 15–18.
- Bjorndal KA. 1980. Nutrition and grazing behaviour of the green turtle. *Mar Biol.* 56:147–154.
- Bjorndal KA. 1997. Foraging ecology and nutrition of sea turtles. In: Lutz PL, Musick JA, editors. *The biology of sea turtles*. Boca Raton (FL): CRC Press. p. 199–231.
- Bouchard SS, Bjorndal KA. 2000. Sea turtles as biology transporters of nutrients and energy from marine to terrestrial ecosystems. *Ecology* 81(8):2305–2313.
- Broderick AC, Glen F, Godley BJ, Hays GC. 2002. Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. *Oryx* 36:227–235.
- Caine EA. 1986. Carapace epibionts of nesting loggerhead sea turtles: Atlantic coast of USA. *J Exp Mar Biol Ecol.* 95:15–26.
- Carranza A, Domingo A, Verdi A, Forselledo R, Estrades A. 2003. First report of an association between *Planes cyaneus* (Decapoda: Grapsidae) and loggerhead sea turtles in the southwestern Atlantic Ocean. *Mar Turt Newsl.* 102:5–7.
- Casale P, Feggi D, Basso R, Argano R. 2004. Epibiotic barnacles and crabs as indicators of *Caretta caretta* distribution and movements in the Mediterranean Sea. *J Mar Biol Assoc, UK.* 84:1005–1006.
- Chace FA. Jr. 1951. The oceanic crabs of the genera *Planes* and *Pachygrapsus*. *Proc US Natl Mus.* 101(3272):65–103.
- Crane J. 1937. The Templeton Crocker Expedition. III. Branchygnathous crabs from the Gulf of California and the west coast of Lower California. *Zoologica* 22:47–48.
- Christie AO, Dalley R. 1987. Barnacle fouling and its prevention. In: Southward AJ, editor. *Crustacea issues 5. Barnacle biology*. Boca Raton (FL): CRC Press. p. 419–420.
- Davenport J. 1992. Observations on the ecology, behaviour, swimming mechanism and energetics of the neustonic grapsid crab, *Planes minutus*. *J Mar Biol Assoc, UK.* 72:611–620.
- Frick MG, Mason PA, Williams KA, Andrews K, Gerstung H. 2003. Epibionts of hawksbill turtles in a caribbean nesting ground: a potentially unique association with snapping shrimp (Crustacea: Alpheidae). *Mar Turt Newsl.* 99:8–11.
- Frick MG, Slay CK. 2000. *Caretta caretta* (loggerhead sea turtle) Epizoans. *Herpetol Rev.* 31(2):102–103.
- Frick MG, Williams KL, Robinson M. 1998. Epibionts associated with nesting Loggerhead sea turtles (*Caretta caretta*) in Georgia, USA. *Herpetol Rev.* 29(4):211–214.
- Gramentz D. 1988. Prevalent epibiotic sites on *Caretta caretta* in the Mediterranean Sea. *Naturalista Sicil. Ser. 4,* 12(1–2):33–46.
- Farren H, Donovan D. 2007. Effects of sponge and barnacle encrustation on survival of the scallop *Chlamys hastate*. *Hydrobiologia* 592(1):225–234.
- Hayashi R, Tsuji K. 2008. Spatial distribution of turtle barnacles on the green sea turtle, *Chelonia mydas*. *Ecol Res.* 23:121–125.
- Hayward PJ, Isaac MJ, Makings P, Moyle J, Naylor E, Smaldon G. 1995. Crustaceans. In: Hayward PJ, Ryland JS, editors. *The handbook of marine fauna of the north-west Europe*. Oxford (UK): Oxford University Press. p. 289–483.
- Herbst LH, Jacobson ER. 1995. Diseases of marine turtles. In: Bjorndal KA, editor. *Biology and conservation of sea turtles*. Revised ed. Washington (DC): Smithsonian Institution Press. p. 593–596.
- Heithaus MR, McLash JJ, Frid A, Dill LM, Marshall GJ. 2002. Novel insight into green sea turtle behaviour using animal-borne video cameras. *J Mar Biol Assoc, UK.* 82:1049–1050.
- Iverson ES, Jory DE, Bannerot SP. 1986. Predation of queen conchs, *Strombus gigas*, in the Bahamas. *Bull Mar Sci.* 39:61–75.

- Kitsos MS, Christodoulou M, Kalpakis S, Noidou M, Koukouras S. 2003. *Cirripedia thoracica* associated with *Caretta caretta* (Linnaeus, 1758) in the northern Aegean Sea. *Crustaceana* 76(4):403–409.
- Lopez DA, Riquelme VA, Gonzalez ML. 2000. The effect of epibionts and predators on the growth and mortality rates of *Argopecten purpuratus* cultures in southern Chile. *Aquac Int.* 8:431–442.
- Loverich GA, Calcagno JA, Smith BD. 2003. The barnacle *Notokalanus flosculus* as an indicator of the intermolt period of the male lithodid crab *Paralomis granulosa*. *Mar Biol.* 143(1):143–156.
- McBane CD, Croker RA. 1984. Some observations on the life history of the Amphipod crustacean, *Hyale nilssoni* (Rathke), in New Hampshire. *Estuaries* 7(4):541–545.
- Matsuura I, Nakamura K. 1993. Attachment pattern of the turtle barnacle *Chelonibia testudinaria* on carapace of nesting loggerhead turtle *Caretta caretta*. *Nippon Suisan Gakkaishi* 59(10):1083.
- Monroe R, Limpus CJ. 1979. Barnacles on turtles in Queensland waters with descriptions of three new species. *Mem Qld Mus.* 19(3):197–223.
- Pfaller JB, Bjørndal KA, Reich KJ, Williams KL, Frick MJ. 2006. Distribution patterns of epibionts on the carapace of loggerhead turtles, *Caretta caretta*. *JMBA 2 - Biodiversity Records* <<http://www.mba.ac.uk/jmba/pdf/5381.pdf>>
- Preen AR. 1996. Infaunal mining: a novel foraging method of loggerhead turtles. *J Herpetol.* 30(1):94–96.
- Pritchard PCH. 1997. Evolution, phylogeny and current status. In: Lutz PL, Musick JA, editors. *The biology of sea turtles*. Boca Raton (FL): CRC Press. p. 1–28.
- Rawson PD, MacNamee R, Frick MG, Williams KL. 2003. Phylogeography of the coronulid barnacle, *Chelonibia testudinaria*, from loggerhead sea turtles, *Caretta caretta*. *Mol Ecol.* 12:2697–2706.
- Ross A. 1963. *Chelonibia* in the Neogene of Florida. *Q J Fla Acad Sci.* 26:221–233.
- Sezgin M, Ates AS, Katagan T, Bakir K, Yalcinozdilek S. 2009. Notes on the amphipods *Caprella andreae* Mayer, 1890 and *Podocerus chelonophilus* (Chevreux and Guerne, 1888) collected from the loggerhead sea turtle, *Caretta caretta*, off the Mediterranean and the Aegean coasts of Turkey. *Turk J Zool.* 33:1–5.
- Schofield G, Katselidis KA, Pantis JD, Dimopoulos D, Hays GC. 2007. Female–female aggression: structure of interaction and outcome in loggerhead sea turtles. *Mar Ecol Prog Ser.* 336:267–274.
- Wahl M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. *Mar Ecol Prog Ser.* 58:175–189.
- Wahl M. 1996. Fouled snails in flow: potential of epibionts on *Littorina littorea* to increase drag and reduce snail growth rates. *Mar Ecol Prog Ser.* 138:157–168.
- Withers TH. 1953. *Catalogue of fossil Cirripedia in the department of geology*. Vol. 3, Tertiary. London: British Museum of Natural History. p. 396.