ORIGINAL ARTICLE

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Spatial distribution of turtle barnacles on the green sea turtle, *Chelonia mydas*

Abstract Distribution patterns of epibiotic barnacles on green sea turtles were investigated in waters neighboring Okinawa, Japan. A number of barnacle species were found to coexist on the turtles and were classified into three genera: *Chelonibia*, *Platylepas* and *Stomatolepas*. Attachment sites on the turtles varied among the barnacle species, suggesting that there is niche partitioning with respect to their microhabitat selection. Turtle bodies offer a ''patchy'' environment for barnacles, so we also analyzed coexistence patterns in the context of an aggregation model. Within each genus, individual barnacles showed a clumped distribution. The different genera do not have mutually exclusive distribution patterns, but instead occur on the same turtle to various degrees. However, when turtles were divided into two size classes, both the level of aggregation and the degree of interspecific overlap among the barnacles was significantly lower on large turtles. We suggest that obtaining basic information on turtle epibionts will shed light on the biology of wild turtles, which is still largely unknown.

Keywords Coexistence · Patchy environment · Turtle barnacles · Green turtle · Aggregation model

Introduction

For many animals and plants, suitable habitat occurs in restricted patches. In such situations, an aggregation model can been used to explain the coexistence of eco-logically similar forms sharing the same habitat (e.g., Shorrocks et al. 1979; Atkinson and Shorrocks 1981; Ives 1988). The aggregation model predicts that when species aggregate with their own kind in a shared habitat, intraspecific competition exceeds interspecific competition, facilitating the coexistence of potentially competitive species. The aggregation model has been used to explain community structure in closed freshwater–hydrosphere systems such as phytotelmata (e.g., Sevenster 1996). In marine ecosystems, aggregation models of intraspecific competition could also provide insights into intertidal zone habitats, where attention has typically focused on interspecific competition between barnacles and other organisms (e.g., Paine 1966; Iwasaki 1993).

Turtle barnacles are obligate commensals of sea turtles. They are widely dispersed in both tropical and temperate seas (Utinomi 1969), and multiple barnacle species are known to occur exclusively on sea turtles (e.g., Monroe and Limpus 1979). For barnacles, the sea turtle body can be viewed as a restricted or closed system, especially in contrast to the more open intertidal zone. Furthermore, turtles, as isolated patches of ''mobile sea bottom'', provide a situation quite different from phytotelmata. However, studies on community ecology of sea turtle epibionts are very few. Matsuura and Nakamura (1993) have observed the abundance of the turtle barnacle, *Chelonibia testudinaria*, on female loggerhead turtles that were landing for oviposition. These, however, are incomplete observations, as it is less likely that small barnacles attached to the turtle plastron will be found for practical reasons, i.e., female adults landing at night are very heavy, wet, and plastered with sand.

In this study, we aimed at obtaining more precise basic information on the distribution of barnacles on the green sea turtle, *Chelonia mydas*. Instead of focusing on nesting female turtles, we observed turtles that were captured by fishermen with stationary nets, enabling detailed observations of the epibionts of adult females, males, and juveniles. The distribution patterns of the barnacle assemblages observed were compared with the assumptions of the aggregation model.

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Materials and methods

Forty-seven individual green turtles (*C. mydas*) were captured by stationary nets placed near Kanna fishery port, Ginoza, Okinawa, Japan, from April 2002 to February 2003. Captured turtles were brought to the fishery port and set on their backs to limit their locomotion, enabling observation of their plastron in detail. All macroepibionts visible to the naked eye and attached anywhere on the body surfaces of the turtles were collected. The body size of each turtle was measured as the standard carapace length (SCL) and the standard width of the carapace (SCW) in centimeters.

The captured turtles were individually tagged and released. Specimens of the attached barnacles were preserved in 99% ethanol. Barnacles were classified into a number of types by their morphology, and some were identified to genus or species (for details see the "Results" section).

Analyses of distribution patterns

We used the *J* index (Sevenster 1996) to measure the degree of intraspecific aggregation, which quantifies the increase in the average density of conspecific competitors encountered relative to a random distribution:

$$J = \left(\sum e_i/N^2\right)\left\{\sum n_i(n_i-1)/e_i\right\} - 1$$

where n_i is the number of barnacles found on turtle i, e_i is the size of turtle i, quantified by the square measure of the turtle carapace (SCL × SCW in cm^2), and N is the total number of barnacles. $J = 0$ indicates a random distribution, $J > 0$ an aggregated distribution, and $J < 0$ the tendency to a uniform distribution. Association between species was quantified by the *C* index (Sevenster 1996) as a measure of interspecific aggregation, i.e., the increase in the average density of the heterospecific competitors encountered (co-occurring on the same individual turtle) relative to a random distribution:

$$C_{xy} = \left(\sum e_i/N_xN_y\right)\left(\sum n_{xi}n_{yi}/e_i\right) - 1$$

where the subscripts x and y indicate species. $C_{xy} < 0$ indicates that the two species encounter each other, on average, less frequently than at random, and $C_{xy} > 0$ indicates more frequent encounters than at random. The expected sample variance of C_{xy} is not provided, so we used the jackknife method (Sokal and Rohlf 1994) to test the statistical significance of the deviation from independence.

Results

Morphological species and attached positions

The morphologies of the barnacles differed depending on where they adhered to the turtles. We were able to distinguish three morphological species groups. The first was *C. testudinaria*, known as the most widely distributed and conspicuous epibiont of turtles, found on carapace and plastron of turtles (Fig. 1A). The second were small barnacles with a major axis length of approximately 1 cm or less, found on soft parts of turtles, i.e., skin around the neck and around the tail, all in the genus *Platylepas* (Fig. 1B). Within this category, three species are likely to be involved (R. Hayashi, unpublished data), but they are difficult to distinguish from one another. For the present study we treat them as *Platylepas* spp. The third was *Stomatolepas transversa*, which bores into interdermal bone segments of carapace and legs (Fig. 1C).

Distribution patterns of the barnacles

Body sizes of the green turtles revealed a bimodal distribution pattern with a division between the two peaks at ca. 50–55 cm SCL (Fig. 2). Most turtles had many barnacles; for example one large individual (SCL, 90.1 cm) had 1,230 barnacles (*C. testudinaria*: 1, *Platylepas* spp.: 1,146; *S. transvesa*: 83). Some (6/47) had no barnacles attached; such barnacle-free turtles belonged

Fig. 1A–C Turtle barnacles on green turtle. **A** *Chelonibia testudinaria* on plastron, **B** *Platylepas* spp. around tail, **C** *Stomatolepas transversa* embedded in plastron sulcus

to the smallest size group collected (SCL, 40.4–46.2 cm), revealing a statistically significant positive correlation between turtle body size and the number of barnacles (Fig. 3a–d). For these reasons, we divided the turtles two size groups—large (SCL ≥ 50) and small (SCL < 50)—for subsequent analyses.

The distributional patterns of the barnacles represented by the J and the C_{xy} indices are shown in Table 1. With all turtles lumped together, each species of barnacle showed a statistically significant aggregated distribution. Additionally, a statistically significant positive association was detected between all species group pairwise combinations. However, this result varied when data were separated by turtle size class. Small-sized turtles had barnacle distributions similar to those for all turtles lumped together, though some were statistically insignificant (possibly due to the small sample size). In
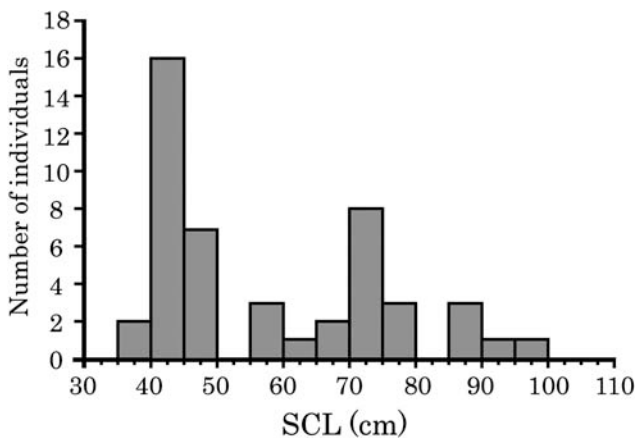
contrast, on the large turtles *C. testudinaria* showed a strongly clumped distribution, whereas *Platylepas* and *Stomatolepas transversa* were distributed more or less randomly. In addition, with the large turtles the positive interspecific associations between barnacle groups disappeared and in some combinations the C_{xy} index was even weakly negative, suggesting a negative association,

Table 1 Distribution patterns of the barnacles represented by the J and C indices of Sevenster (1996)

J	
Small turtles	
Chelonibia testudinaia	3.63
Platylepas spp.	4.29*
Stomatolepas transversa.	3.79*
Large turtles	
C. testudinaria	17.88**
Platylepas spp.	0.98
S. transversa.	0.92
All turtles	
C. testudinaria	6.87**
Platylepas spp.	1.78**
S. transversa	1.21*
C_{xy}	
Small turtles	
C. testudinaria vs. *Platylepas*	2.34
C. testudinaria vs. *S. transversa*	2.42
Platylepas vs. *S. tansversa*	3.46*
Large turtles	
C. testudinaria vs. *Platylepas*	−0.30
C. testudinaria vs. *S. transversa*	0.43
Platylepas vs. *S. tansversa*	−0.07
All turtles	
C. testudinaria vs. *Platylepas*	1.15**
C. testudinaria vs. *S. transversa*	0.47**
Platylepas vs. *S. tansversa*	0.30*

*$P < 0.05$, **$P < 0.01$ by t-test after jackknife estimation of SE

Fig. 2 Frequency distribution of turtle by body size

Fig. 3a–d Relationship between turtle body size (cm^2) and individual density of each of three different barnacle taxa; **a** *C. testudinaria*; **b** *Platylepas* spp.; **c** *S. transversa*. **d** Total number of barnacles
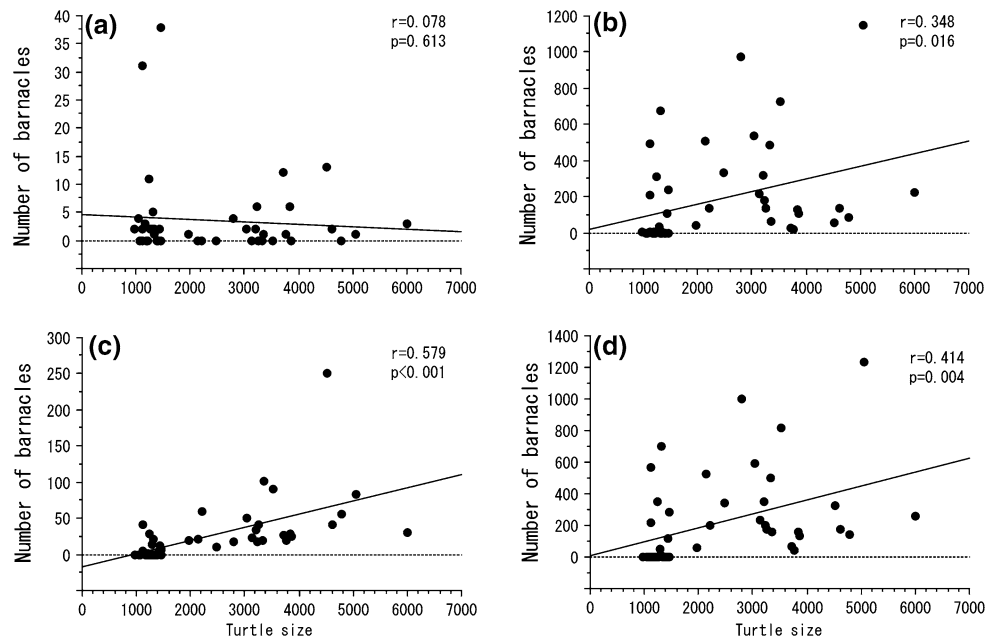
though the difference from a random association was statistically insignificant.

Discussion

Our study confirms that various barnacle species coexist on the body surface of the green turtle and that turtle body size positively correlates with the number of barnacles attached. The barnacles encountered can be classified into three species groups according to their morphology and where they attach to the turtle. Individuals from each barnacle species group were found to aggregate when data from all turtles were combined, and slightly positive pairwise associations between the three species groups were also found.

Niche partitioning is the most likely explanation for the coexistence of the three species groups of barnacles, because the attachment sites had different microhabitats, i.e., *C. testudinaria* was found on the surface of the carapace and the plastron, whereas *Platylepas* attached to the soft parts of turtles, and *S. transversa* bored into interdermal bone segments of the carapace and legs. The aggregation model was not well supported, as all pairs of the barnacle species groups showed a positive association, though individuals were distributed in aggregations within each species group.

However, it is still possible that some mechanisms underlying the aggregation model may account for the coexistence of epibionts on turtles. When we focused on large turtles, the three barnacle species groups showed more or less random or even negative associations (Table 1), supporting the aggregation model. If the positive associations between species are caused by outliers (i.e., small turtles with no barnacles; see later), the data from large turtles may represent the correct sample for studying barnacle distribution patterns. Within *Platylepas*, if individual barnacles were to be identified to the species level, a distribution pattern that more strongly supports the aggregation model of coexistence might be found. Many epibionts other than the barnacles, for example crabs (Davenport 1994), amphipods (Moore 1995), marine leeches (Choy et al. 1989) and others (Kitsos et al. 2005), are known to exist on turtles. Coexistence patterns may differ when we take into account potential positive and negative associations involving these other organisms. It was not feasible in the present study to count all epibiotic organisms because many were likely to have been detached before the turtles were removed from the setnets. The validity of the aggregation model for coexistence patterns among turtle barnacles needs further testing and investigation; in particular a more precise taxonomy is required for the barnacles.

However, interpreting this system using the aggregation model should be done with caution. Aggregation models (e.g., Shorrocks et al. 1979; Atkinson and Shorrocks 1981; Ives 1988) usually assume environments with a short temporal lifespan. Sea turtles are long-lived,

reaching their first breeding at about 30–50 years (Van Buskirk and Crowder 1994), whereas barnacle lifespans are far shorter (possibly a maximum of three years in *C. testudinaria*; Fujimi Fukuhara, personal communication). Thus, a sea turtle body is a more or less permanent environment for the barnacles. However, the long lives of turtles need not necessarily mean that a turtle body is always available to barnacles. There can be a time constraint; for example the larvae might only be able to attach to a turtle during a relatively short window of time, when the turtle enters the area where the barnacle's larvae occur.

Why does the *C* index show a positive association in small turtles but not in large turtles?

Values of the *C* index suggest no interspecific associations of barnacles living on large turtles (Table 1), while positive associations were detected with small turtles. There are at least three possible reasons for this. First, there could be direct interspecific competition. Hence, on large turtles, barnacles have experienced a long history of direct competition for attachment space that resulted in decreased interspecific association on large turtles. Second, the decreased positive association could be due to indirect effects through turtle mortality. Large numbers of barnacles may cause overall stress in sea turtles (Kinne 1985) and might increase the host's mortality, especially in old turtles, which may lead to the reduction of distributional overlap. Last, each species distributes independently, as the aggregation model assumes, but the pattern of positive interspecific associations (as well as the strong aggregation within species) is caused by an analytical artifact due to outliers. The outliers we mean here are the small turtles that have no barnacles. Later we discuss possible biological reasons for this. Evaluating the relative importance of the above mechanisms is currently a difficult task.

Our study suggests that the body surface of the sea turtle is an excellent system for the study of species coexistence, except that longitudinal tracking of individuals is less feasible.

Why do the barnacles show aggregated distributions on turtles?

Individual differences in physical, and/or behavioral properties of turtles may account for the variations in the density of attached barnacles. Turtles might have a substance that repel barnacles, which might differ in the quality and in the amount produced between individuals. Alternatively, turtles moving about in an area with a higher density of barnacle larvae may simply host more barnacles. One way to separate these possibilities in the future is to focus on turtles kept in a preserve in which all turtles experience a similar environment. Even in such a situation, if barnacles aggregate, individual

differences in physical properties among turtles may account for barnacle distributions. Alternatively, if the barnacles attach randomly, a behavioral explanation is more likely.

Information about sea turtles in the wild, from hatchling to subadult, SCL ca. 5–30 cm, is scarce (Hirate and Kimura 1996). This period is called the "lost age" for turtles. Interestingly, the barnacle-free turtles belonged the smallest size class (around SCL 40 cm) in this study. This might suggest that turtles experience a time during the "lost age" in which any barnacle species does not access or adhere easily to them. We suggest that by examining the epibionts one can obtain new information about the life history of sea turtles in the ocean.

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