A Survey of the Epibiota of Hawksbill Sea Turtles (*Eretmochelys Imbricata*) of Mona Island, Puerto Rico

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A SURVEY OF THE EPIBIOTA OF HAWKSBILL SEA TURTLES (*ERETMOCHELYS IMBRICATA*) OF MONA ISLAND, PUERTO RICO

By

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Abstract

Epibiotic organisms inhabiting the surfaces of *Eretmochelys imbricata* Linnaeus are described for Mona and Monito Islands, Puerto Rico. Turtles were captured to depths of 30 m in coastal foraging areas, composed of coral reef and cliff wall habitats. Epibiont samples from 105 turtles ranging from 20 to 85 cm (straight carapace length) were collected, sorted, preserved, and identified to the lowest possible taxon. The relative frequency of each taxon was compared between habitat types. Epibiota of 12 animal and 4 algal phyla were identified, of which some groups were new findings for marine turtles, resulting in the highest phylogenetic diversity reported so far. Most epibiont fouling was located posteriorly on the carapace, plastron, and skin of the turtles. Nine taxa were significantly more frequent on turtles from coral reef and two in cliff wall habitat. Epibiota of non-nesting *E. imbricata* comprise a diverse community, which provides information about its host.

Resumen

Se describen los organismos epibioticos residentes en las superficies de *Eretmochelys imbricata* localizados en Mona y Monito, Puerto Rico. Ciento cinco tortugas entre 20 y 85 cm (medida recta de caparazón) se capturaron en dos tipos de habitat costero compuesto de arrecifes de coral y acantilados submarinos de hasta 30 m de profundidad. Se observó la localización de los epibiontes, y se tomaron muestras que luego fueron separadas, preservadas, y clasificadas. La frecuencia relativa de cada grupo taxonómico se comparó para cada taxon por tipo de hábitat. Se identificaron 12 filos animales y 4 de algas, una gran diversidad epibiotica en tortugas marinas, incluyendo nuevos hallazgos. La mayor frecuencia de estos se encontró en las superficies posteriores de las tortugas. De los habitats comparados, 9 grupos de epibiontes resultaron más frecuentes en residentes de arrecifes versus dos grupos en acantilados. La comunidad epibiótica provee información ecológica acerca de la tortuga.

Dedicated to my family and friends, who always supported me, and encouraged me to follow my marine dreams.

Especialmente a Abuela y a la memoria de Titi Bimba que saben apreciar la belleza de las garrapatas que escogí estudiar!

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Chapter 1 Introduction

1.1 Epibiota

In the marine environment, any submerged surface is susceptible to colonization by a variety of spores and larvae circulating in the water column. Epibiota, or organisms growing on the surface of a living organism, may compose a complex assemblage, also known as a fouling community. The assemblage of organisms (plant and animal) occupying the surface of another animal will be referred to as the epibiota or epibiotic community, since it occupies a discrete area with abiotic and biotic components.

Studies of marine organisms have provided information about distribution and factors affecting abundance of fouling communities. This information may provide insight about the basibiont's (substratum organism) ecology, or environmental conditions. Composition of the epibiotic community may provide clues to the physical, chemical, and biological conditions under which it has developed.

Fouling sequences in marine environments follow four major settlement steps: biochemical, bacterial, diatom, and finally larvae or spore attachment of epibiota (Wahl, 1989). Physical and biological processes influence the time for a substratum to become colonized, which can be from one to several weeks.

The natural history and environmental requirements of marine organisms, especially those from epibenthic communities, provide a complementary tool for studying the ecology of the basibiont. Factors such as seasonal influence, biogeography, ecological tolerance, and basibiont behavior will determine the composition of the epibiotic assemblage (Wahl, 1989). An assemblage is a collection of plants and animals associated with a particular environment that can be used as an indicator. A community implies that the organisms interact and they give the community a structure (Allaby, 1991). More information about interactions among organisms of epibiotic assemblages or communities, will help us understand these better, and obtain better indication of the hosts' ecology.

1.2 Marine Turtle Epibiota

Different surfaces of marine turtles provide substrata suitable for the settlement of a variety of epibiota. Many factors determine the presence or absence of epibiotic species on marine turtles including, recruitment dynamics, disturbance, competition, physical stress, and predation (Frick *et al.*, 2000b). Specific epibiota could reflect geographical range or ecological conditions where colonization on the turtle took place (Caine, 1986). According to Caine (1986) and Frazier *et al.* (1991), epibiota of marine turtles provide useful inferences about the host because their geographical ranges and environmental tolerance must coincide.

The relationship between basibiont and epibiont is a non-symbiotic facultative association (Wahl, 1989). Marine turtle epibiota and the exact nature of their relationship with the host have not been defined. Some authors refer to epibiota as commensal (Hubbs, 1977), others as parasitic associations (Clark, 1965). A turtle specific Rhodophyta (Hollenberg and Norris, 1977), and turtle specific barnacles have been reported (Monroe and Limpus, 1979), but most are still considered commensals.

In previous studies of marine turtles, epibiota were collected from nesting or stranded turtles, most commonly the loggerhead, *Caretta caretta* (Linnaeus) (Caine, 1986; Eckert and Eckert, 1988; Frazier *et al.*, 1985, 1991, 1992; Hunt and Gilchrist, 1991; Matsuura and Nakamura, 1993; Senties *et al.*, 1999; and Frick *et al.*, 1998, 2000b). Stranded individuals may lose or acquire organisms, which are not representative of natural epibiota, while long distance migrations to nesting areas could lead to changes in the epibiotic community composition.

Because marine turtles exhibit ontogenetic shifts in habitat, it is difficult to discern all aspects of their ecology (Carr, 1980). As much information as possible must be collected from wild individuals to better understand their life history stages. Epibiotic organisms have helped clarify certain aspects of sea turtle migrations (Eckert and Eckert, 1988), population dynamics (Caine, 1986), and ecology (Frazier *et al.*, 1985).

Epibiota of the more tropical hawksbill turtle, *Eretmochelys imbricata* (Linnaeus) have been described only in a few reports of stranded or nesting individuals (Monroe and Limpus, 1979; Frazier *et al.*, 1985). Adult male and immature *E. imbricata* are rarely observed in their natural habitat; therefore, the composition of the epibiotic community of these life stages was unknown.

The opportunity to study the epibiota of *E. imbricata* in Mona and Monito Islands was possible due to research conducted on this population of turtles since 1992 by Dr. Robert van Dam and Carlos Diez (Van Dam, 1997). They discovered that individual immature turtles occupy restricted areas of submarine habitat and methods devised to observe, capture, measure, tag, and release them proved feasible for long term investigations.

The findings of the current study are analyzed in lieu of the results from previous work on this assemblage of *E. imbricata*. Publications from these investigations include diving behavior (Van Dam and Diez, 1996), predation on sponges (Van Dam and Diez, 1997a), surfacing behavior (Van Dam and Diez, 1997b), morphometrics (Van Dam and Diez, 1998a), home range (Van Dam and Diez, 1998b), tag retention (1999), and genetics (Bowen, *et al.*, 1996).

Information on the population structure, dynamics, and ecology of *E. imbricata* has provided an essential understanding of the habitat requirements of this important assemblage of recruits from various Caribbean populations. Prior to this study, the epibiota of non-nesting marine turtles was only anecdotal, and the location or habitat, which the turtle occupied, was unverifiable. Given the efficient capture and release methods developed in Mona, and the amount of information collected on this assemblage, this would help support inferences made using epibiont data to understand aspects of the hosts ecology.

As much information as possible must be collected from wild populations of critically endangered marine turtles to help formulate management strategies needed to prevent decline or extinction of the species. Home range determination, diving behavior, surfacing behavior, and morphometric information available for the species will help interpret the results of this epibiota survey. For example, the repeated capture of an individual in a specific location within a habitat type indicates site residency, and has allowed the comparison of epibiota between two habitats in Mona and Monito Islands.

1.3 Study Objectives

The purposes of this research were to describe the epibiotic community of *E. imbricata* of a known habitat and geographical location and to use this information to add to the knowledge about the species. Based on the life history of epibiotic organisms this information may help to infer habitat preferences or ecological characteristics of the turtle's life history stages, and discern the nature of the association. It is possible that the wide gradient of parasitic to mutualistic relationships exists in this symbiosis.

To determine the hypothesis that the habitat of the turtle can be inferred by the community composition of turtles from different habitats, these will be analyzed statistically between two habitat types. Additionally this description will provide information of epibiota of non-nesting *E. imbricata* in different life history stages.

Specific objectives were:

- To identify the epibiota of *E. imbricata* during non-nesting life stages.
- To determine where epibiota are located on the host.
- To compare the epibiotic community of turtles from different habitats.

Chapter 2 Literature Review

2.1 Epibiota of Marine Turtles

Previous interests on sea turtle epibiota have ranged from observations taken from individual turtles to surveys of the epibiotic assemblage. Most reports on marine turtle epizoa provide a record of species occurrence, but lack information regarding host-epibiont interactions or ecological aspects. Many of these are notes of encounters and observations of one or a few turtles. However, these reports provide estimates of the distribution of epibiotic organisms worldwide. Some works have focused on specific taxonomic groups, such as cirripeds, and do not reflect the dynamics of epibiotic communities. Additionally *Eretmochelys imbricata* has only a few incidental reports of epibiota, most surveys are of *Caretta caretta.*

Witzell (1983) summarized the "commensals" of *E. imbricata* reported by different authors in a synopsis of the host species. A list of organisms associated with this species reported by various authors is presented in Table 1, with location and reference. Endoparasitic digeneans of hawksbill turtles from Puerto Rico are reviewed by Dyer *et al.* (1995).

Table 1. Incidental reports of organisms associated with *Eretmochelys imbricata*.

Group	Taxa	Location	Reference
Algae	*Cladophora* spp.	Tanzania	Frazier et al., 1985
	Enteromorpha spp.	Tanzania	Frazier et al., 1985
	Polysiphonia spp.	Tanzania	Frazier et al., 1985
	Sphacelaria furcigera	Tanzania	Frazier et al., 1985
Mollusca	*Septifer bilocularis*	Tanzania	Frazier et al., 1985
	Aeolis sp.	Unknown	Witzell, 1983
Annelida	*Ozobranchus* sp.	Tanzania	Frazier et al., 1985
Crustacea	*Chelonibia testudinaria*	Honduras	Witzell, 1983
	Chelonibia caretta	Australia	Monroe and Limpus, 1979
	Platylepas hexastylos	Australia	Monroe and Limpus, 1979
	Platylepas decorata	Australia	Monroe and Limpus, 1979
	Chelonibia sp.	Tanzania	Frazier et al., 1985
	Tubicinella cheloniae	Australia	Monroe and Limpus, 1979
	Stephanolepas muricata	Australia	Monroe and Limpus, 1979
	Lepas sp.	Australia	Monroe and Limpus, 1979
	Conchoderma sp.	Australia	Monroe and Limpus, 1979
	Eurydice sp.	‘coral reef’	Bustard, 1976
	Planes minutus	Atlantic O.	Murray, 1895
	Planes minutus	Sea of Cortez	Steinbeck, 1951
	Planes minutus	Rhode Island	Chace, 1951
	Menippe mercenaria	Sarasota, FL	Clark, 1965

2.2 Surveys

Caine (1982, 1986) reported 48 epibiotic species representing six phyla on *Caretta caretta* in South Carolina (U.S.A.). This community consisted primarily of amphipods and barnacles, with sponges, mollusks, annelids, crustaceans, tunicates and green algae being less abundant. In a survey of 138 nesting *C. caretta* from various sites in the southeastern U.S.A. Caine (1986), identified two distinct epibiotic assemblages with indicator species for each. He assumed that sessile epibionts colonized the carapace when the ranges of turtle and epibiont overlapped, therefore the territory of the turtle was reflected in the epibiotic community. Mitochondrial DNA evidence supported separate populations of *C. caretta* along the southeastern coast of U.S.A. (Bowen *et al.*, 1993). Presence of the branching coral, *Porites porites*, suggested a tropical origin for turtles from Florida. The implications of Caine's (1986) findings support the feasibility of using epibionts as a tool for the study of marine turtle populations.

Gramentz (1988) examined *C. caretta* from Mediterranean coasts and reported the prevalent attachment sites of epibiota. He found that different epibionts showed preferences to the different kinds of surfaces, sites (dorsal, ventral), and position (anterior, posterior). Thirteen species were identified, two new to the Mediterranean, including annelids (Sedentaria), barnacles (lepadomorph and balanomorph species), *Planes minutus*, and tanaids associated with *Polysiphonia sertularioides* (a red filamentous alga). The presence of an assemblage of crustaceans (*Hexapleomera robusta, Hyale grimaldii,* and *Caprella andreae*) was dependent on the density of algae on the carapace. This suggests that interspecific interactions may be occurring within the epibiotic community.

Hunt and Gilchrist (1991) reported that the dominant commensals of *C. caretta* (3 nesting females, 1 stranded male) in southwest Florida (U.S.A.) were algae, barnacles, and amphipods. They found that the vertebral scutes were most fouled followed by the marginal and right costal scutes. From this limited sample size no correlation was found between the degree of fouling and the length and presumed age of the turtle.

Caretta caretta nesting in Georgia (U.S.A.) hosted 86 epibiotic species; four species of sponges, four hydrozoans, six anthozoans, nine gastropods, eight bivalves, two flatworms, one leech, nine polychaetes, three crabs, eight barnacles, one tanaid, ten amphipods, two isopods, four bryozoans, five tunicates and a shrimp, as well as diatoms, dinoflagellates, blue-green, green, red and brown algae (Frick *et al.*, 1998). Epibiota occurred most commonly on the posterior 1/3 of the carapace.

Frick *et al.* (2000b) reported seven previously undocumented species of epibiota on nesting *C. caretta* in Georgia (U.S.A.). The star coral (*Astrangia danae*), lunar dove snail (*Mitrella lunata*), greedy dove snail (*Costoanachis* *avara*), sea anemone (*Diadumene leucolena*), barnacle (*Balanus trigonus*), and green alga *Bryopsis plumosa* were identified. Colonies of *A. danae* were growing on the shells of barnacles, showing how microhabitats are created by sessile epibionts.

2.3 Epibiota

Algae

Algae are important components of marine habitats, and sea turtle surfaces are no exception. Various workers report algae (usually filamentous forms) on turtles, but reports are often limited to broad taxonomic groups: Chlorophyta, Rhodophyta, and Phaeophyta. Cribb (1969) identified algae from one *Eretmochelys imbricata* in northeastern Australia and for the first time reported a diverse community of various species (Table 2). The red alga *Polysiphonia carettia* (Hollenberg and Norris, 1977) may indicate a special relationship with *Caretta caretta* since it has only been reported on this species of turtle and no other substrata.

Epibiotic algae on two species of nesting marine turtles reported from the Mexican Caribbean (Quintana Roo) was comprised of 37 epibiotic species of algae on *C. caretta* and only 3 on *Chelonia mydas* (Linnaeus) (Senties *et al.*, 1999). Small macro-algae and filamentous forms of algae dominated and

Table 2. Algal species on *Eretmochelys imbricata* in Australia (Cribb, 1969).

Phylum	**Species**
Cyanophyta	*Anacystis dimidiata* (Kuetz.) Drouet & Daily
	Calothrix crustacea Thur. In Born & Thur.
	Entophysalis conferta (Kuetz.) Drouet & Daily
	Entophysalis deusta (Menegh.) Drouet & Daily
	Microcoleus lyngbyaceus (Kuetz.) Crouan
	Oscillatoria lutea C. Ag.
	Schizothrix calcicola (C. Ag.) Gom.
	Schizothrix tenerrima (Gom.) Drouet
	Spirulina subsala Oersted
Chlorophyta	*Bryopsis pennata* Lamoroux
	Cladophora crystallina (Roth) Kuetz. Prox.
	Enteromorpha clathrata (Roth) Grev.
	Ochlochaete ferox Huber
	Phaeophila dendroides (Crouan) Batters
	Pilinia sp.
	Pseudopringsheimia sp.
	Rhizoclonium implexum (Dillw.) Kuetz.
Phaeophyta	*Ectocarpus irregularis* Kuetz.
	Ectocarpus mitchellae Harv.
	Ectocarpus rhodochortonoides Boerg.
	Sphacelaria furcigera Kuetz.
	Sphacelaria novae-hollandiae Sond.
	Sphacelaria tribuloides Menegh.
Rhodophyta	*Acrochaetium catenulatum* Howe
	Acrochaetium daviesii (Dillw.) Boerg.
	Acrochaetium robustum Boerg.
	Acrochaetium sp.
	Acrochaetium sp.
	Ceramium gracillimum var. *byssoideum* (Harv.) Mazoyer
	Ceramium serpens Setch. & Gard.
	Erythrotrichia carnea (Dillw.) J. Ag.
	Fosliella sp.
	Gelidiella sp.
	Goniotrichum elegans (Chauv.) Le Jol.
	Herposiphonia tenella (C. Ag.) Ambronn
	Lophosiphonia scopulorum (Harv.) Wom.
	Melobesia sp.

are considered primary colonizers in stressful habitats (Littler and Littler, 1980). Senties *et al.* (1999) concluded that epizoic algae are not useful to infer migration paths of sea turtles because species growing on the turtles are tolerant of the range of conditions found in the Caribbean Sea and therefore persist during migration.

Zoology

Phylum Mollusca

Epibiotic bivalve and gastropod mollusks have been reported on *Caretta caretta*, *Lepidochelys olivacea*, and *E. imbricata* from all oceans (Frazier, *et al.*, 1985). At least 15 species of bivalves and 5 species of gastropods made *C. caretta* the most common host for mollusks. These infestations did not seem to affect the turtle directly, although increased drag could negatively influence smaller individuals.

Phylum Arthropoda

Epibiotic arthropods include both sessile (cirripedia) and free living (copepoda, decapoda, amphipoda, etc.) forms. These arthropods occupy the surface of the turtle directly or the microhabitats present on the turtles, such as filamentous algae. Specific reports of different groups of crustaceans are presented below.

Order Amphipoda

Thomas (1992) described a new species of amphipod (*Podocerus chelonophilus*) from *Caretta caretta* from the western Atlantic Ocean. Amphipods are mentioned in various other surveys where they seemed to be associated with the algae growing on the turtle (Murray, 1895; Caine, 1982; Matsuura and Nakamura, 1993; Davenport, 1994). Additional amphipods are reported in epibiont surveys by Caine (1986) and Frick *et al.* (1998). These organisms are direct developers, eggs are retained in a marsupium and are not expelled to the water column (Ruppert and Barnes, 1994).

Order Isopoda

Williams *et* al. (1996) summarized the occurrences of isopods on marine turtles and reported *Exocorallana acuticauda* (Corallanidae) as common on nesting *Dermochelys coriacea*. Cirolanid isopods observed on other marine turtle species are carnivorous scavengers and their association with this host may be temporary, commensal, or parasitic, as with fish hosts (Williams *et* al., 1996). Isopods seem to be associated with lesions or decaying tissues of stranded turtles, since few reports mention this group on healthy turtles (Caine, 1986 and Frick *et al.*, 1998).

Order Decapoda

Clark (1965) described a parasitic relationship of a stone crab (*Menippe mercenaria*) on a small, apparently weakened, *E. imbricata* in the Gulf of Mexico, near Sarasota, Florida (U.S.A.). This nearshore crab species was located under a partially deformed carapace, eating the flesh under the scutes.

A pelagic crab, *Planes cyaneus* was collected from *Lepidochelys olivacea* caught near San Diego, California (U.S.A) (Hubbs, 1977). *Planes minutus* (Crustacea: Brachyura) is also known as Columbus crab, because it was first recorded by his crew in 1492 (Chace, 1951). It is believed to be a pelagic species, which inhabits *Sargassum* in the Atlantic Ocean and is commonly reported on marine turtles. Chace (1951) reported a mating pair of *P. minutus*, collected from *Eretmochelys imbricata* off Block Island, Rhode Island (U.S.A.) in 1928. Steinbeck (1951) reported Columbus crabs from a 2.5 ft long *E. imbricata* captured off Baja California in the Pacific Ocean.

Davenport (1994) investigated the association between *Planes minutus* and *Caretta caretta* caught off the southern coast of Madeira, Portugal. Dissection of the crabs suggested that they were cleaning the host of other epibionts since barnacle cyprids and parasitic amphipods were found in the crab's gut. Furthermore, a comparison of the social structure of *P. minutus* from floatsam and sea turtles (*C. caretta*) exhibited different life history strategies depending on the substratum (Dellinger *et al.*, 1997). It was concluded that the crabs benefit from living on *C. caretta*, because of commensalism, or perhaps the active foraging mode of turtles somehow benefits the crabs.

Data supporting the cleaning association between crabs (*Planes minutus*) and chelonians is provided by Frick *et al.* (2000a). Results suggest that the chelonian must be associated with *Sargassum* during its early (pelagic) life history stage for the association to begin. Frick *et al.* suggest crabs and smaller turtles benefit from this symbiosis because the former may reduce epibiont colonization, and hence drag on the turtle, while obtaining food.

Class Cirripedia

There is fossil evidence that marine turtles hosted epizoic organisms since the Mesozoic era. Eocene barnacles of the chelonibiid and coronulid genera were specific to marine animals, including fish, reptiles, and mammals (Ross and Newman, 1967). Extant species of barnacles, such as *Chelonibia caretta* and *Chelonibia testudinaria*, are believed to be turtle specific, and perhaps the only example of an obligate relationship of a marine turtle epizoan. Monroe and Limpus (1979) reported three new species of barnacles, and included a key for the identification of 17 barnacle species found on five species of marine turtles.

A Japanese nesting aggregation of *Caretta caretta* hosted epibiotic algae, bivalves, amphipods, tanaids, and barnacles of which the largest sizes were attained by *Chelonibia testudinaria* (Matsuura and Nakamura, 1993). The attachment pattern of *C. testudinaria* on the carapace was predominantly axial (over vertebral scutes), and not restricted to the anterior 2/3 of the carapace as previously reported by Gramentz (1988). According to this report the dominant species of cirriped, *C. testudinaria*, differs from reports of barnacles on *C. caretta* from other geographical regions.

Pacific Ocean *Lepidochelys olivacea* hosted the barnacles *Cylindrolepas darwiniana* and *Conchoderma virgatum* (Hubbs, 1977). *Chelonia mydas* from Galápagos Islands, Ecuador hosted nine species of epizoa dominated by barnacles: *Cylindrolepas darwiniana*, *Platylepas decorata, Chelonibia testudinaria,* and *Conchoderma virgatum* (Green, 1998). Cirriped epizoa were considered common since only 3% of the turtles were free of barnacles. Other epibionts included other barnacles (*Lepas hilli, Balanus* spp.), hydrozoans, bryozoans, a gastropod, an anemone, small crabs, and only one occurrence of a remora. Infestations of *Cylindrolepas darwiniana* a boring barnacle were severe in emaciated and dead turtles, although they were not observed penetrating the body cavity. Hendrickson (1958) reported the burrowing barnacle *Stephanolepas muricata* penetrating the body cavity of *C. mydas* in Malaysia.

Commensal barnacles were used as a tool to interpret loggerhead turtle (*Caretta caretta*) movements between oceanic and brackish waters in Chesapeake Bay, Virginia (U.S.A.) (Killingley and Lutcavage, 1983). Eckert and Eckert (1988) reported epizoic cirripeds and inferred the pre-reproductive movements of leatherback turtles (*Dermochelys coriacea*) in St. Croix (U.S.V.I.), by examining temporal patterns of barnacle colonization. The presence and size of a pantropical barnacle *Conchoderma virgatum* suggested that these gravid turtles nested upon arrival from temperate waters.

Class Copepoda

Frazier (1989) commented on the absence of reports of parasitic copepods on marine turtles. It is unclear why turtles have not been observed with infestations of parasitic copepods that attach to a diversity of marine vertebrates. According to Frazier (1989), fish cleaning associations may be responsible for eliminating parasitic crustaceans of turtles, but because their associations are infrequent, another explanation is sought. Losey *et al.* (1994) describe a cleaning symbiosis where the wrasse *Thalassoma duperry* removed *Platylepas hexastylos* from the skin of *Chelonia mydas* posing to be cleaned. Furthermore, a cleaning interaction was reported between two French angelfish (*Pomacanthus paru*) and *Eretmochelys imbricata* in Grand Cayman Island, B.W.I. (Smith, 1988).

Phylum Ectoprocta

Bryozoans, classified as rare marine turtle epibionts by Frazier *et* al. (1992), appear to provide no benefit for the host, yet the dispersion potential of migratory turtles may give the bryozoans a rafting advantage. Frazier *et al.* (1992) commented on the unexpected absence of reports of bryozoans from *Eretmochelys imbricata* especially since it is one of the most sedentary of the marine turtles.

Subphylum Urochordata

Frazier *et al.* (1991) reported tunicates from marine turtles. Two *Caretta caretta* (one dead and one nesting) from Georgia (U.S.A.) hosted simple ascidia of the genus *Molgula* as well as barnacles, oysters, crabs, amphipods, mollusks, polychaetes, hydroids, octocorals, bryozoans, and red algae (Frazier *et al.*, 1991). They concluded that the presence of tunicates on marine turtles is casual, and it is unlikely that any mutualistic relationship exists between them.

2.4 Basibiont Life History

Eretmochelys imbricata is a medium sized (90 cm maximum carapace length, weight to about 80 kg), tropical species found in all oceans (Pritchard and Mortimer, 1999), and considered Critically Endangered (Meylan and Donnelly, 1999). The life history of *E. imbricata* is not fully understood due to the lack of data on immature life stages, and the difficulty of observing adults in the marine realm. It is believed that this tropical species spends the first years of life in pelagic "nursery" habitats (i.e. *Sargassum* rafts) at the surface of the ocean (Meylan and Donnelly, 1999). Juveniles settle in benthic developmental habitats (i.e. coral reefs and mangrove estuaries) where they feed on sponges (Meylan, 1988; Van Dam and Diez, 1997a) and other benthic invertebrates. Turtles in Mona inhabit the upper few meters (2-7) of the sublittoral zone where abundant food and shelter is available (Van Dam and Diez, 1998a).

Eretmochelys imbricata has been labeled as non-migratory or sedentary in the past (Witzell, 1983), but long-range migrations between feeding grounds and nesting beaches have been documented for female adults (Boulon, 1984; Meylan, 1999). Migrations covering up to thousands of kilometers have been confirmed by tag recoveries (Nietschmann, 1981; Meylan, 1999), and satellite telemetry (R. van Dam and C. Diez, pers. comm.).

Immature *E. imbricata* have demonstrated site fidelity (Limpus, 1992) and juvenile home range less than 1 km^2 (Van Dam and Diez, 1998a; León and Diez, 1999) have been observed in some hawksbill assemblages. Nonetheless, long distance migrations by sub-adults have been reported (Kamezaki, 1987: Boulon, 1984), including one from Atol das Rocas, Northeast Brazil across the Atlantic Ocean to West Africa (Marcovaldi and

Filippini, 1991). If immature *E. imbricata* remain in a specific coastal area for several years, they will be exposed to epibionts present in that region or habitat, and hosts may transport epizoic organisms during migrations.

Chapter 3 Methodology

3.1 Study Site

Mona Island and satellite Monito Island are located in the south central Mona Passage midway between Hispaniola and Puerto Rico, 40 nautical miles (72 km) west of Puerto Rico, between 18° 00' N and 18° 13' N and 67° 01' W and 67° 48' W (Figure 1). Mona Island's southern coast is surrounded by coral reef formations and sandy beaches, which are nesting habitat for marine turtles (*C. mydas, D. coriacea, E. imbricata*). Cliff walls make up the northern coast of Mona and surround Monito Island. During the year 1999-2000, water temperatures around Mona and Monito ranged between 25.5° and 29.5° C with the highest temperatures occurring in September (Van Dam, unpublished data). Trade winds and surface currents prevail from the east and southeast. Clear oceanic waters surrounding both islands provided optimal conditions to capture hawksbill turtles underwater.

The submarine habitats around Mona and Monito can be divided into two broad types, coral reefs and submarine cliff walls. For this study, areas where hermatypic or soft corals dominated the benthic fauna were considered coral reef habitat. This habitat type ranges in depth from 1 to 40 m on the southern insular shelf of Mona Island. Spur and groove, fringing, and patch reef formations are interspersed by sand, and hard bottom areas. Hard

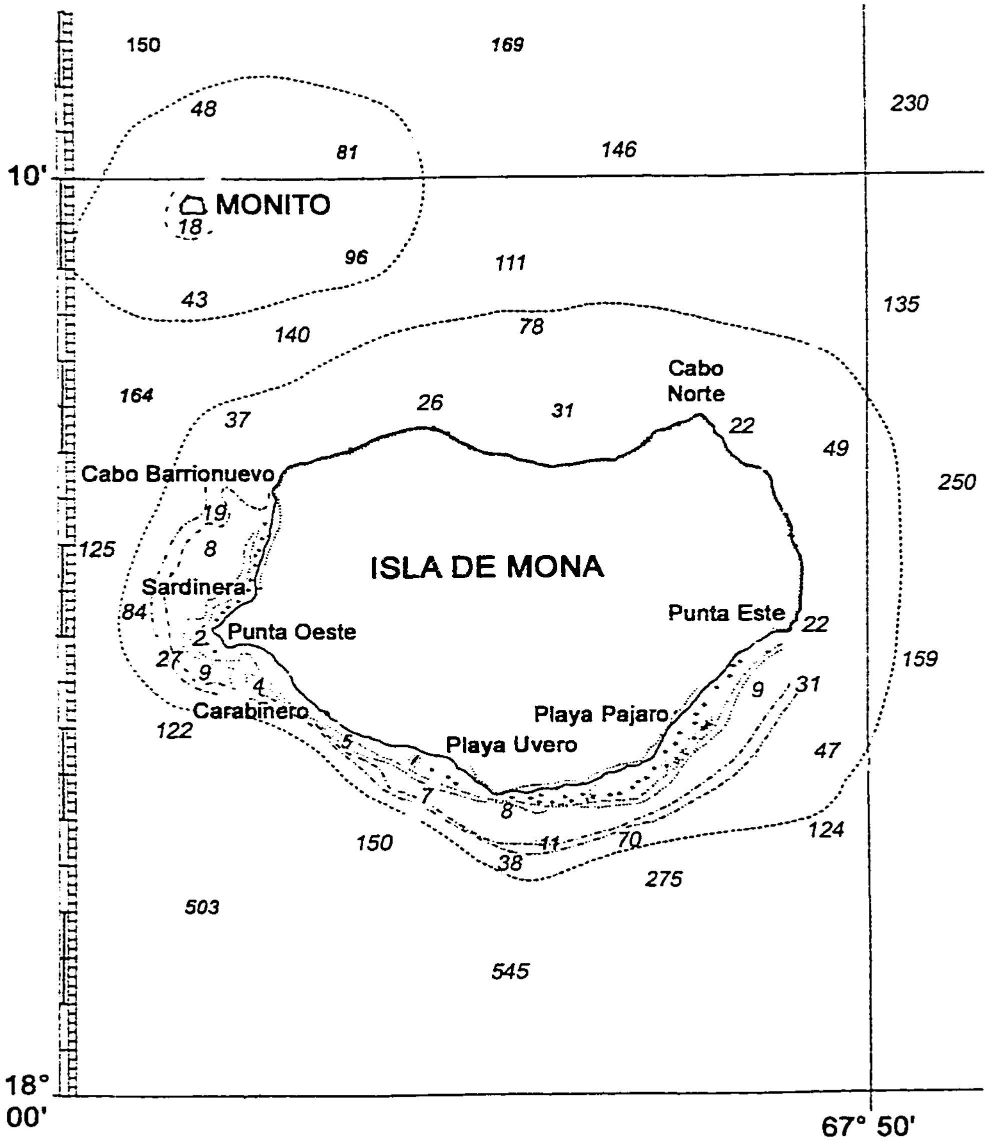

Figure 1. Location and bathymetry (fathoms) of Mona and Monito Islands, shaded area indicates coral reef habitat (modified from Kaye, 1959).

bottom epifauna include diverse macro-algae, hydrocorals, scleractinian corals (*Diploria* spp., *Montastrea* spp., *Siderastrea* spp., *Acropora* spp., *Dendrogyra cylindrus, Colpophyllia natans, Eusmylia fastigata* and others), plexaurids, gorgonians, and sponges (*Aplysina* sp., *Tethya* sp. and *Xestospongia muta* are common) (Van Dam and Diez, 1997a). Coral reef habitat includes a contiguous area from Punta Este in the East, along the south to Cabo Barrionuevo (Figure 1).

Monito Island and the northern coast of Mona are composed of nearly vertical cliff walls rising to 60 m above sea level. An upward sloping hard bottom meets the base of cliff walls at 20 to 30 m depths. For this research, areas surrounding Monito and the northern coast of Mona were considered cliff wall habitat. This habitat provides a generally darker environment because sand is found deeper, and there is less reflection of light from the bottom. These habitats are less prone to sediment re-suspension during strong wave conditions due to increased depths, compared to coral reef habitat. Submerged rock walls are colonized by encrusting sponges, calcareous and phaeophytic algae, hydrozoans and other invertebrates (Van Dam and Diez, 1997a).

3.2 Methods

During July and August 1999, four divers hand captured hawksbill turtles by free diving or with the aid of SCUBA. Turtles were brought to a 17-ft fiberglass boat for data collection. Straight carapace length (SCL) was measured with a Haglof tree caliper, from the nuchal notch to the posterior most tip of each (right and left) posterior marginal (post-central) scute (Figure 2). Turtles were tagged with passive internal transponders (PIT) and Inconel metal or colored plastic tags, following protocol by Van Dam and Diez (1999). Individuals were classified into size classes according to Table 3, using the longest SCL measurement. Turtles of size classes 1 through 3 are considered juveniles, those between 4 and 5 are considered sub-adults, and size classes 6 and 7 are considered adults, even though the size to age relation of the turtle is confounded by variable growth rates in this species. In Mona, the smallest observed adult male (sexual dimorphism in tail size) was 68.2 cm SCL (Van Dam and Diez, 1998a).

The location of the epibiotic community of *E. imbricata* on the carapace, plastron and skin of each turtle was noted on water-resistant data sheets having schematic diagrams of the turtle surfaces. Epibionts were collected from the carapace (over and under scutes), plastron, and skin of each turtle. Where epibiota were visible a sample of epibiotic community was removed with a metal spatula or knife and placed in individual, labeled plastic jars, half

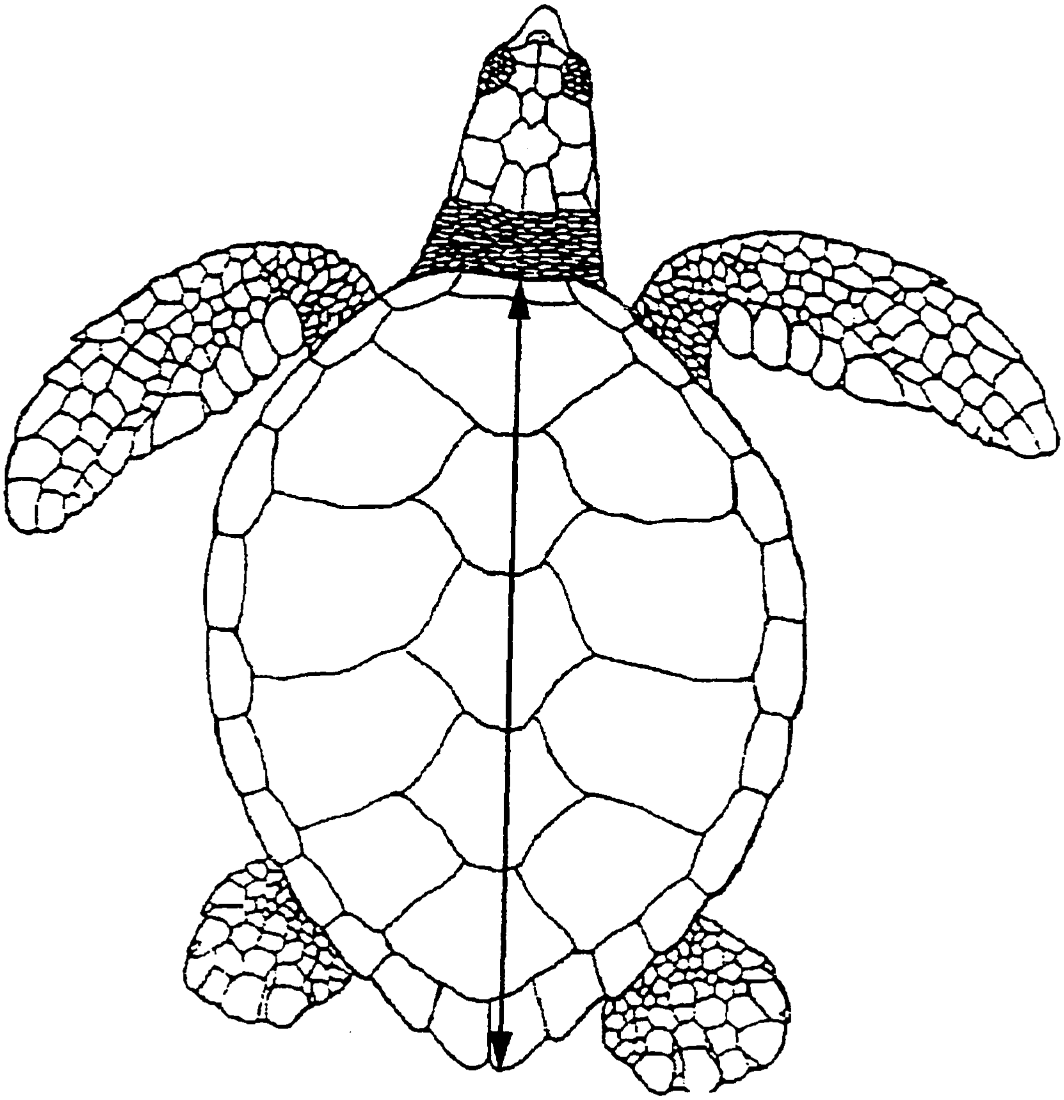

Figure 2. Straight carapace length (SCL) measurement of *Eretmochelys. imbricata* (modified from Pritchard and Mortimer, 1999).

Table 3. *Eretmochelys imbricata* size classes used in this study determined by straight carapace length (SCL).

Size Class	SCL (cm)
1	≤ 29.9
2	30.0 – 39.9
3	40.0 – 49.9
4	50.0 – 59.9
5	60.0 – 69.9
6	70.0 – 79.9
7	≥ 80.0

full of seawater. The presence or absence of sediments within samples was noted. After sorting samples, a few representatives of each organism were collected for identification. Animals were preserved in 70% ethyl alcohol, and algae were placed in 10% formalin in 4 dram (or less) labeled glass vials with plastic screw tops.

After data and sample collection, turtles were released as close as possible to the initial location by navigating to coordinates recorded upon capture by a hand-held GPS (Garmin model 12 XL). Epibiotic organisms were identified to the lowest taxonomic level possible following Gosner (1971), Carson (1976), Monroe and Limpus (1979), Gittings *et al.* (1986), Williams (1984), Ruppert and Barnes (1994), and other marine invertebrate keys. Algae were classified into functional groups (calcareous encrusting, calcareous erect, filamentous and foliose macroalgae) that reflect ecological traits (Littler and Littler, 1984).

3.3 Analysis

To describe the epibiotic community of *E. imbricata,* epibiotic organisms were identified, their attachment site noted and the prevalence of each taxon (or functional group) reported. The presence of epibiotic taxa was tested statistically between turtles captured in different habitats. By analyzing the life history of each epibiont taxon, some inferences could be made about the host.

After identification the relative frequency (expressed as percent occurrence) of each taxa was calculated by dividing the number of turtles with that particular epibiotic taxon, by the total number of turtles sampled. No attempt was made to quantify the abundances of epibiotic taxa on individual turtles, but carapace drawings were employed to calculate the relative frequency of scutes overgrown by epibiota.

To test the hypothesis that epibiota reflect habitat characteristics, presence of each taxon was compared between assemblages of turtles captured from coral reef and cliff wall habitats. Chi squared (X^2) contingency tables (Sokal and Rohlf, 1995) were performed for each epibiotic taxon (Appendix 1). The columns represented presence or absence of the epibiotic component, and the rows compared coral reef or cliff wall habitat.

Chapter 4 Results

Samples of epibiota from 105 turtles were collected. The size class distribution of turtles sampled from coral reef (n=39) and cliff wall (n=66) habitats is presented in Figure 3. Fifty-five turtles (52.4%) sampled had been tagged in previous years dating to 1992. All turtles captured appeared to be in good health and none possessed external tumors, although 2 individuals were missing a hind flipper.

The number of different epibiotic taxa found in each sample averaged 9.25 organisms per turtle, and ranged from 0 to 20 (n=105). Two size class 1 turtle had zero epibionts upon capture (one from reef, one from wall habitat). A taxonomic list of epibionts collected is presented in Appendix 2. At least 93 different epibiotic organisms, which can also be referred to as operational taxonomic units (OTU), were collected throughout the survey, yet this could represent over 100 species once identifications to species level are complete.

4.1 Location of Epibiota

The percent occurrence of epibiota on each scute is presented in Figure 4. Epibiota were most frequently attached to the posterior dorsal and ventral 1/3 of the turtles. The epibiotic community was located both on the surface and underneath the scutes where space was available. Overlapping

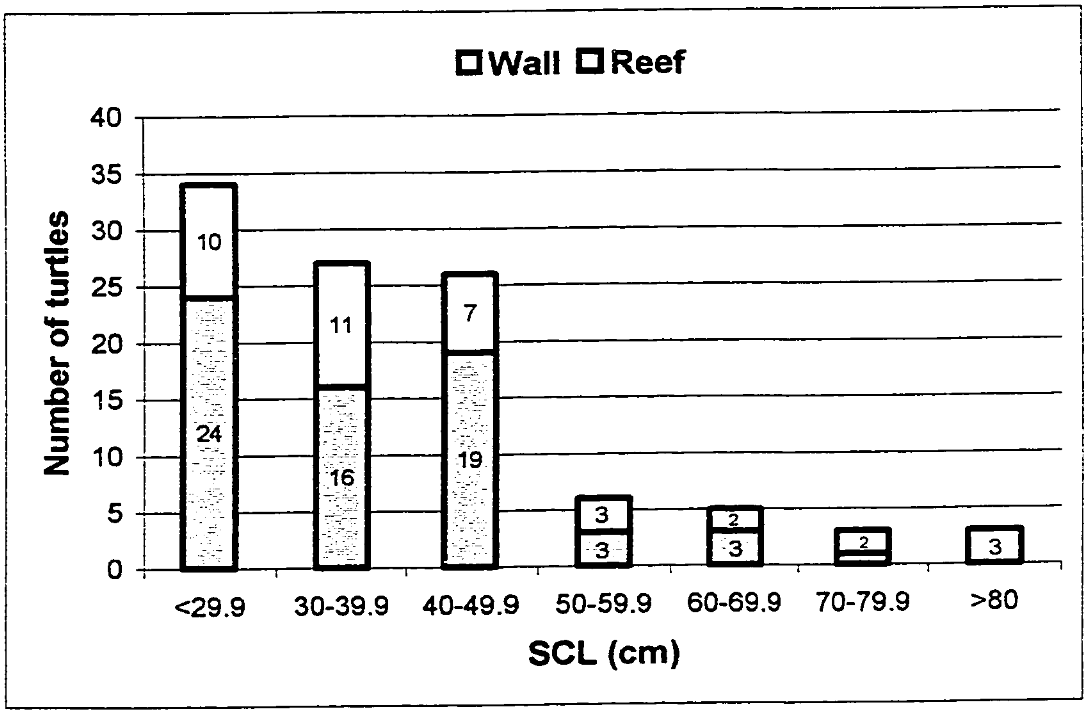

Figure 3. Size distribution of straight carapace length (SCL) in cm of *Eretmochelys imbricata* sampled from coral reef and cliff wall habitats (n=105).

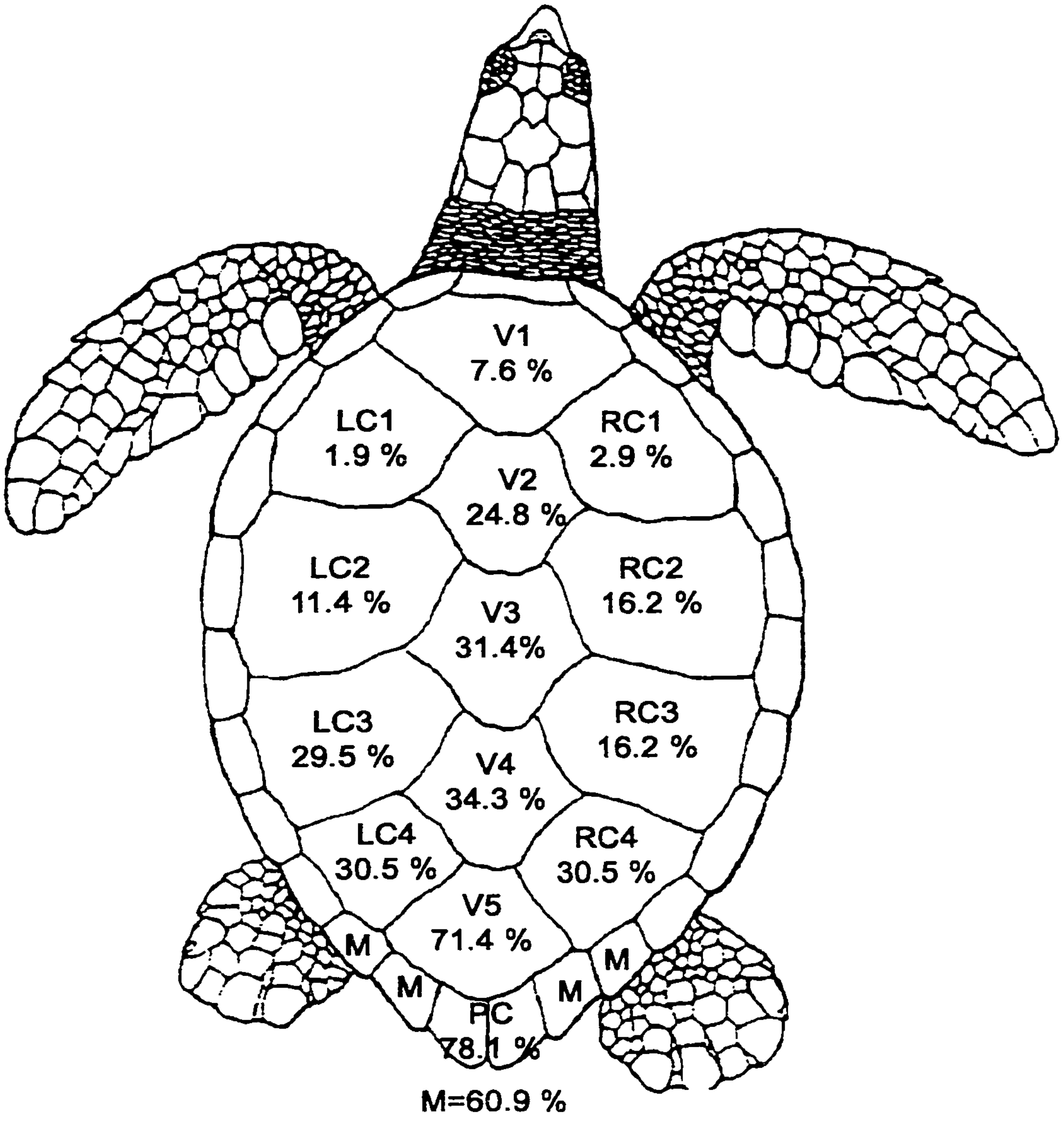

Figure 4. Percent occurrence of epibiota on each carapace scute of *Eretmochelys imbricata*. Scutes: V=Vertebral, LC=Left costal, RC=Right costal, PC=Post-central, M=Marginal (modified from Pritchard and Mortimer, 1999).

carapace scutes, found in juvenile and subadult turtles, provided areas for epibiotic colonization between the underside of the more anterior and dorsum of the following scute. Adult turtles provided limited space under scutes, unless they were uplifted due to deformity or barnacle colonies.

Right and left posterior marginal (post-central) scutes of the carapace were the most frequently fouled region both on the dorsal and ventral surfaces. The posterior (5th vertebral) scute was the next most frequently fouled, and was colonized dorsally and ventrally within hollow cavities where epibionts were protected. Marginal scutes surrounding the posterior scute were also frequently colonized by epibiota.

Ventrally, the caudal 1/3 of the plastron was most frequently (37.1%) fouled by epibiota on all turtles sampled. No fouling of the anterior plastron was observed. The underside of these individuals was covered by a layer of filamentous turf algae and calcareous encrusting algae. The turf was usually dark red in color when compared to the algae from the carapace, and the only animals found ventrally were harpacticoid copepods, and sessile polychaetes (Family Serpulidae).

Besides the hard keratin shell, softer skin regions such as the tail (53.3%), neck (40.0%), hind flippers (33.3%), and front flippers (17.1%) were colonized by algae and small barnacles (*Platylepas* spp.). Thin algal turfs of filamentous algae occurred on both surfaces of all four flippers and the head.

Calcareous encrusting algae were observed on the side of the head of one adult individual.

4.2 Epibiota

Abiotic Component

The epibiotic community of 30.5% of the turtles contained sand. Sand grains were white and pink carbonate material, probably of coral skeletal and coralline algal origin, and also contained fragments or tests of mollusks, foraminiferans, ostracods, and other organisms. Sediments were associated with filamentous algae, which entrapped and grew over the sand layer reaching 1 cm thickness. The occurrence of sand was significantly ($x = 70.34$, $p < 0.001$) higher in coral reef habitat versus cliff wall.

Algal Component

Filamentous forms of algae were present in 94.3% of the epibiotic communities sampled. Various species composed the turf that colonized dorsal and ventral regions of the host. Calcareous encrusting forms of Rhodophyta (Family Corallinaceae) were observed on 82.9% of turtles. This form of algae occupied the dorsal and ventral surfaces of scutes on the carapace and plastron. Calcareous erect forms of Rhodophyta (Family Corallinacea) grew on 57.1% of turtles studied, and were significantly ($x = 9.9$, $p < 0.001$) more common on turtles from coral reef habitat. Calcareous erect algae were located under overlapping scutes or within cavities formed under scutes.

Finally, foliose macroalgae were collected from 25.7% of the epibiotic communities, commonly on the carapace, under scutes. *Lobophora variegata* (Lamoroux) Womersley (9.5%), *Dictyota* spp. (2.9%), and *Neomeris annularis* Dickie (1%) are new records of epizoic algae on marine turltes. *Anadyomene stellata* (Wulfen) C. Agardh was previously reported on *Caretta caretta* by Sentíes *et* al. (1999) and is a new record for *Eretmochelys imbricata*. Further identification of algae will undoubtedly provide new records and perhaps new species for the Caribbean.

Zoological Component

The relative frequency of animal taxa found as epibionts is summarized in Table 4. Sessile and motile animals of 12 phyla were identified to the lowest possible taxon. Due to the diversity of organisms collected, the complexity of taxonomic characters and lack of complete tropical species descriptions, classification to species is only available for a few groups.

Phylum Rhizopoda

Order Foraminiferida was represented in the epibiotic community by three different forms dominated by *Amphistegina* sp. (35.3 %). Foraminiferans were found attached to algal filaments and within the sediment grains. The

Table 4. Relative frequency expressed as percent occurrence (% O) of zoological component of *Eretmochelys imbricata* epibiota, ranked from most to least frequent (n=105).

Taxon	% O
Phylum Annelida	85.7
Class Cirripeda	80.0
Phylum Ectoprocta	53.3
Class Copepoda	51.4
Order Foraminiferida	40.0
Phylum Porifera	33.3
Order Amphipoda	26.7
Phylum Mollusca	22.0
Phylum Nematoda	21.0
Phylum Sipunculida	21.0
Order Diptera	16.2
Subphylum Urochordata	14.3
Order Tanaidacea	12.4
Class Hydrozoa	5.7
Class Ostracoda	5.7
Order Decapoda	5.7
Phylum Echinodermata	5.7
Class Anthozoa	4.8
Class Osteichythyes	1.9
Phylum Platyhelminthes	0.9

presence of foraminiferans was significantly higher ($x = 18.4$, $p < 0.001$) in the epibiotic assemblages of turtles captured in coral reef habitat.

Phylum Porifera

At least six forms of sponges were detected based on color and texture of samples. They were most commonly located under the posterior scute (V5) of the carapace. Poriferans provided attachment sites for other epibiota such as annelids and crustaceans. Sponges were significantly ($x = 9.0$, $p < 0.005$) more frequent on turtles from cliff wall habitat.

Phylum Cnidaria

Classes Hydrozoa and Anthozoa were represented in the samples. A solitary hydrozoan was present on 4 turtles (3.81 %), and two colonial forms of thecate hydrozoa were collected from two turtles of size class one, from cliff wall habitat. Anemones of the Class Anthozoa were collected from three turtles from cliff wall habitat. Other cnidarians included two octocorals (*Pseudoptergorgia* sp. and *Gorgonia* sp.) on two turtles captured in coral reef habitat.

Phylum Platyhelminthes

A flatworm was collected once from a size class one individual from cliff wall habitat.

Phylum Nematoda

Three types of unsegmented worms were collected more frequently in coral reef than cliff wall habitats ($x = 15.1$, $p < 0.001$). Nematodes were found within the algae and sediment samples collected from the carapace. It seems these are free-living forms associated with turf algae and sediments.

Phylum Annelida

Segmented worms were present in high frequency (85.7%), and included oligochaetes and polychaetes of at least 12 families. The most frequent (65.7 %) annelids were, filter feeding, orange worms located inside secreted white calcareous tubes (Family Serpulidae). Other families identified included: Cirratulidae, Onuphidae, Spirorbidae, Amphinomidae, Eunicidae, Nereidae, Syllidae, Terebellidae, Dorvilleidae, and Glyceridae. Annelids were common in both habitats and were distributed in the algae, sediments, and sponges or directly on scutes, usually within protected areas.

Phylum Sipunculida

Sipunculids were present on 21 % of turtles sampled. *Phascolosoma* sp. was most common (13.3 %) and other unidentified sipunculids were present on 8.6 % of turtles. Sipunculids were significantly ($x = 8.38$, $p < 0.005$) more common on turtles from coral reef habitat and individuals were usually found within sediments in protected areas of carapace scutes.

Phylum Mollusca

Various forms of mollusks were present as epibiota including motile and sessile forms. Gastropods (six forms including *Dendropoma* sp., *Litiopa* sp., and *Fissurella* sp.), bivalves (*Pinna* sp., *Isognomon* sp., and *Chama* sp.), opisthobranchs (including *Aplysia dactylomela*), and a chiton (*Tonicia* sp.) were collected from turtle carapaces. Most individuals were small and located underneath the overlapping scutes. Those that were attached were found underneath the posterior scute. Mollusks were more prevalent in coral reef ($x = 4.74$, $p < 0.05$) than cliff wall habitat.

Phylum Arthropoda

Diverse groups of sessile and motile crustaceans were present on *Eretmochelys imbricata*. Amphipods were located on the carapace, usually among algae or sediments. Amphipods were significantly ($x = 6.5$, $p < 0.025$) more common on turtles from coral reef habitat. Tanaids such as *Leptognathus* sp. and *Heterotanais* spp. were significantly ($x = 14.3$, $p < 0.001$) more common in coral reef habitat. Tanaids were most commonly found in the sediment within tubes constructed with sand grains, and ovigerous females were observed.

Ostracods were collected from the carapaces of turtles from all habitats, and were usually among the algae or sediment of samples. Copepods from the Order Harpacticoida were collected from 51.4 % of turtles. These non-parasitic copepods were usually associated with the filamentous algal turfs found on the carapace and plastron of basibionts, and various ovigerous copepods were observed. Harpacticoid copepods are abundant in benthic habitats (Dr. Juan González, pers. comm.).

Crab and shrimp epibionts of the Order Decapoda were present in epibiotic samples. A male and female pair of *Planes minutus* was collected from a size class one (26.3 cm SCL) turtle under the posterior carapace just above the tail. The male and female crabs measured 9 mm and 12 mm carapace length respectively. Ovigerous *P. minutus* were observed on two additional occasions from small juvenile *E. imbricata*. Other crabs of the Family Xanthidae were collected among algae growing under the posterior scute. Snapping shrimp of the Family Alpheidae (*Alpheus* sp.) were occasional (3.8 %) within the epibiotic community and were located under overlapping scutes of four turtles. Decapods were significantly ($x = 5.8$, $p< 0.025$) more common on turtles from coral reef habitat.

Barnacles of Order Thoracica (Class Cirripeda) were present on 80 % of the turtles. Gooseneck barnacles *Lepas anatifera* grew on the carapace scutes of two small turtles (21.7 cm and 26.3 cm SCL). In both cases, the gooseneck barnacles were attached to the marginal scutes of the posterior carapace, or under overlapping scutes of the carapace.

The most common barnacle species was *Platylepas decorata* attached to the epidermis on all regions of the turtle as well as on postcentral scutes and scute unions of the carapace. *Chelonibia caretta* was observed attached to the surface of anterior scutes of five adult (SCL >75.0 cm) turtles. The number of *Chelonibia caretta* barnacles on these turtles was1,1, 6, 11, and 39. The congener *Chelonibia testudinaria* was present on two subadult (SCL < 70) individuals from cliff wall habitat.

Larval forms of marine insects, *Clunio* sp. and *Pontomyia* sp. (Family Chironomidae: Order Diptera) were identified. *Pontomyia* sp. spends 90% of their life as larvae and was found within algae and sediments. Small flightless midges mate on the oceans surface minutes after emergence from pupa (Armitage *et* al., 1995). Chironomids were significantly (x = 22.7, $p< 0.001$) more common on turtles from coral reef habitat but were nonetheless present on 2 turtles from cliff wall habitat.

Phylum Ectoprocta

Bryozoans were common on turtles from both habitats, although significantly (x = 7.6, $p< 0.01$) more common in the cliff wall habitat. Nine different forms of encrusting and erect bryozoa were collected from carapace scutes. These were substrata to other organisms such as algae and annelids.

Phylum Echinodermata

Echinoderms were collected on two occasions. One pencil urchin (*Eucidaris tribuloides*) was located under the posterior scute of a turtle from cliff wall habitat. Ophiuroid brittle stars were collected from four turtles (3 cliff, 1 reef habitat). One specimen of the Family Ophiactidae was observed on a turtle captured in the cliff wall habitat.

Subphylum Urochordata

Tunicates of solitary (11.4%) and colonial (3.8%) forms were collected from the carapace, under overlapping scutes. The solitary tunicate *Microcosmus* sp. and other unidentified species were present. Compound tunicates such as *Trididemnum solidum* were identified by spicules within the test. One colony of *T. solidum* contained several larvae within the tunic.

Subphylum Vertebrata

On two occasions, fishes were collected from *Eretmochelys imbricata*. A remora (*Echeneis naucrates*) was attached to the plastron of a small (26.3 cm SCL) turtle in cliff wall habitat. Secondly, an unidentified larval fish was collected under the posterior scute of a 29.4 cm SCL turtle from cliff wall habitat.

Finally, unidentified organisms occurred in 7.62% of the samples collected. Unidentified specimens were collected more frequently from coral reef habitat.

4.3 Habitat Comparison

The percent occurrence of epibiotic taxa from turtles captured in the two different habitats is presented in Table 5, with Chi squared values of contingency tables. Foraminiferans, nematodes, sipunculids, mollusks, amphipods, decapods, tanaids, and dipterans were significantly more common in coral reef habitats. The presence of sand and erect forms of calcareous algae was also significantly higher in reefs. Sponges and bryozoans were more frequent on turtles of cliff wall habitat although sometimes present on turtles from coral reef habitat.

Taxa, which occurred equally frequently in both habitats, include the most common groups, such as annelida, copepoda, cirripeda, ascidia, filamentous, calcareous encrusting, and foliose algae. Some of these frequent groups were also very abundant on the turtle surfaces like annelida, copepoda, and cirripeda. Less frequent groups such as hydrozoa, anthozoa, platyhelminthes, ostracoda, echinodermata, and chordata were not significantly different in both habitats.

Table 5. Percent occurrence (% O) of epibiotic taxa on *Eretmochelys imbricata* from coral reef (n=39) and cliff wall (n=66) habitats. Chi square value for contingency tables and (p) indicated when significant at α=0.05.

Group	Coral Reef	Cliff Wall	*x* (p)
Order Foraminiferida	66.7	24.2	18.4 (< .001)
Phylum Porifera	15.4	43.9	9.0 (< .005)
Class Hydrozoa	2.6	7.6	1.1
Class Anthozoa	5.1	4.6	0.0
Phylum Platyhelminthes	0	1.5	0.6
Phylum Nematoda	41.0	9.1	15.1 (< .001)
Phylum Annelida	82.1	87.9	0.68
Phylum Sipunculida	25.9	12.1	8.4 (<.005)
Phylum Mollusca	33.3	15.2	4.7 (<.05)
Order Amphipoda	41.0	18.2	6.5 (<.025)
Class Ostracoda	10.3	3.0	2.4
Class Copepoda	48.7	53.0	0.2
Order Decapoda	12.8	1.5	5.8 (<.025)
Order Tanaidacea	28.2	3.0	14.3 (<.001)
Class Cirripeda	87.2	75.8	2.0
Order Diptera	38.5	3.0	22.7 (<.001)
Phylum Ectoprocta	35.9	63.6	7.6 (<.01)
Phylum Echinodermata	2.6	7.6	1.1
Subphylum Urochordata	15.4	13.6	0.06
Class Osteichythyes	0	3.0	1.2
Filamentous Algae (Turf)	97.4	92.4	1.1
Calcareous Encrusting	74.4	87.9	3.2
Calcareous Erect Algae	76.9	45.5	9.9 (<.001)
Macroalgae	28.2	24.2	0.2
Sand	79.5	1.5	70.34 (<.001)

Chapter 5 Discussion

5.1 Location of Epibiota

Epibiota were most frequent on the posterior 1/3 of *Eretmochelys imbricata* dorsally and ventrally as reported by Caine (1986), Gramentz (1988), Hunt and Gilchrist (1991), and Frick *et al.* (1998) for *Caretta caretta*. Posterior carapace fouling may be due to hydrodynamics and basibiont behavior during swimming and resting. Hubbs (1977) noted an increase in algae colonization when turtles were confined and movement was restricted.

Water flow patterns created by the shape of the carapace deter colonization of the anterior body regions according to Logan and Morreale (1994). Turbulence caused behind overlapping scutes may favor larvae and spore colonization in posterior regions where there is less drag. Additionally, postcentral and marginal scutes extend horizontally around the carapace and retain sediments and other small particles more effectively. Colonization of some species may be limited to the underside of overlapping scutes due to increased drag forces elsewhere.

Caine (1986) suggested that the turtle's habit of placing front flippers over the carapace, wedging into crevices, mating, and sand accumulations while nesting influenced the location of epibiota. Flipper movements of

Eretmochelys imbricata impede the colonization of the anterior marginals, first and second costal scutes of the carapace because these sometimes touch during swimming. Turtles have been observed resting with front flippers placed on top of the anterior portion of the carapace. This would probably dislodge settling larvae and spores from anterior dorsal and lateral portions of the carapace. *Eretmochelys imbricata* usually feed and rest in caves, crevices, and under coral ledges against which the turtles' carapace and plastron are abraded. Swimming and resting on the sea floor, coral, rocks, or sand, would remove epibiota from the plastron due to abrasion.

Finally, some turtles have been observed scraping against live coral, apparently to remove epibiota. Adult turtles with very little epibiotic colonization possessed various longitudinal scrape marks on all portions of the carapace. Scraped carapaces were also observed for *Caretta caretta* in Georgia and Florida (Caine, 1986). Therefore, scraping against hard substrates actively reduces the area covered by epibiota. Epibiota located under overlapping scutes are protected from the hosts anti-fouling behavior.

Other factors reported influencing the location of epibiota could be related to desiccation (Caine, 1986). Gramentz (1988) suggested that exposure to air limited the occurrence of algae to posterior regions. Every time turtles surface for air the anterior portion of the carapace is exposed for a brief period. Exposure time will affect epibiota differently depending on their tolerance to emersion. Van Dam and Diez (1997b) measured surface intervals less than one minute (mean coral reef = 50.5 sec, mean cliff wall = 32.9 sec) for *Eretmochelys imbricata*. Nesting turtles will expose epibiota for hours and sand may bury epibionts during nest excavation. Although this usually occurs at night, delicate organisms would perish due to burying or desiccation.

Scute flaking has been proposed by Caine (1986) as an epibiont removal mechanism in *Caretta caretta*. During my observations the only time scutes were lifted from their normal position was when barnacle colonies caused uplifting of the overlapping scute, but based on my observations it is probably not very frequent. Areas on the scutes colonized by barnacles did seem to be thicker than the rest of the scute, demonstrating some reaction of underlying tissue to the epibiont, although there was no perforation of the keratin scute in the cases I observed.

Predation pressures may influence the location or composition of the epibiotic community. I observed a Blue tang (*Acanthurus coeruleus*) feeding on the turf growing on post-central scutes while a juvenile *Eretmochelys imbricata* swam on. Another observation included two banded coral shrimp (*Stenopus hispidus*) which were picking epibiota on the carapace of an adult female *E. imbricata* resting in a cave. Smith's (1988) observation of a similar interaction by a group of angelfish (*Pomacanthus paru*) supports the possibility of a mutualistic interaction. A cleaning symbiosis between *Chelonia mydas* and the wrasse *Thalassoma duperry* occurs in Hawaii, where skin barnacles (*Platylepas* spp.) are removed from posing turtles (Losey *et al.*, 1994).

Hawksbills were colonized by *Platylepas decorata* mostly on the epidermis and the tissue between scutes of the carapace and the plastron. This barnacle genus has been reported from the skin of other marine vertebrates including turtles, manatees, and dugongs (Monroe and Limpus, 1979). In the cases observed, barnacles caused no bleeding, although upon removal, the skin appeared red, probably due to increased vascularization. In a few cases, thickened epidermis covered with *P. decorata* was shed while the turtle scraped against the floor of the boat during data collection. Shedding of epidermis may be categorized as an antifouling mechanism analogous to scute flaking, since the underlying skin was free of barnacles.

5.2 Epibiota

Abiotic Component

Sediment found in the epibiotic communities of *Eretmochelys imbricata* were commonly held in place by filamentous algae. Sediment settles on turtle surfaces and algal turfs collect and incorporate particles into basal layers, covering the attachment site of algal filaments. Eventually sand accumulation may prevent photosynthesis of the basal layers of algae, making detachment of turf easier as it grows and causes drag. Thick turf and sediment layers may become anoxic, facilitating detachment, although 1cm thick turf and sand accumulations were observed firmly attached on the post central scutes of juvenile turtles.

Eretmochelys imbricata most commonly utilize depths less than 10 m (Van Dam and Diez, 1996) for foraging and resting. The seabed containing unconsolidated sediments in coral reef habitats ranges from 1 to 40 m, but is found at depths greater than 20 m in cliff wall habitats. Sediments were most common in the epibiotic communities of turtles from coral reef habitat, probably due to these bathymetric differences. Turtles in coral reef habitat occupy depths where benthic sediments are re-suspended more often than in deeper habitats. Sand collected from hawksbill epibiotic communities of other locations (i.e. Desecheo Island, Puerto Rico) was very different in size and color of grains from Mona Island. From a geological perspective, the analysis of grain composition and foraminiferan tests may be used to differentiate geographical regions (H. Santos, pers. comm.) where the turtle has been.

Algal Component

Algal turfs were abundant on turtles from both habitats. Turf algae were filamentous and represented opportunistic and primary colonizers (Steneck and Dethier, 1994; Littler and Littler, 1984). Only six turtles were free of turf colonization, and all were from size class one. This could reflect their recent arrival from habitats where larval spores are less abundant (pelagic habitat). Lack of filamentous algae is an important clue that may indicate recent establishment in neritic habitats as suggested by Meylan and Carr (1982).

Calcareous encrusting forms of algae were common on turtles of cliff wall habitat, but erect forms of calcareous algae were significantly less frequent. In cliff wall habitat the turtles carapace is frequently abraded by rocky surfaces during feeding and resting in crevices. Continued disturbance by strong surge in cliff walls may inhibit the establishment of erect forms of calcareous algae, while encrusting forms tolerate disturbances (Steneck and Dethier, 1994). Lack of spores from a nearby population of erect calcareous algae may be another reason for the observed differences. To confirm this hypothesis further work is needed to compare the algal species composition of both habitats.

Foliose macro algae were less frequent (26.7%), although commonly found within the posterior scute or on the surface of the carapace within accumulated sediments. These algae may benefit from growing on a turtle occupying shallow sublittoral zones, but on the other hand, they will be subject to changes in drag, depth, temperature, and light regimes. The turtles probably acquire these algae from fragments and spores released by local populations of macroalgae in both habitats, and are capable of introducing species to new areas during migrations.

Zoological Component

Eretmochelys imbicata hosts the greatest phylogenetic diversity of epibiotic animal taxa that has been reported for any marine turtle. Twelve phyla comprise the zoological component of the epibiotic community of *E. imbricata* (Table 4). Reports of marine turtle epibiota have previously documented up to 8 phyla of animals in *Caretta caretta* (Frick *et al.*, 1998). Foraminiferans, nematodes, sipunculids, ostracods, dipterans, and echinoderms reported here are newly documented taxa of marine turtle epibiota. The biodiversity supported by the surfaces of hawksbill turtles in Mona and Monito Islands may be a result of several factors including the morphology, behavior, habitat, and tropical range of the host species. This finding suggests that the surfaces of *E. imbricata* serve as an important ecological niche that supports a diverse community previously ignored in studies of marine benthic ecology.

Phylum Rhizopoda

Foraminiferans are reported as a marine turtle epibiont for the first time, although they may have been previously overlooked. Foraminiferans are abundant in sandy intertidal habitats and their identification could lead to geographical information about the host. The difference in percent occurrence between the coral reef and cliff wall habitats may be attributed to the bathymetric range utilized by the host and the presence of re-suspended particles.

Phylum Porifera

Sponges are reported for the first time as epibiotic on *Eretmochelys imbricata*, although previously reported for *Caretta caretta* in Georgia (Frick *et al.*, 1998). Sponges are abundant in both reef and wall habitats, and may attach to turtles by fragmentation or larval settlement, especially while in direct contact with the benthos such as when feeding or resting in caves and wall crevices. Encrusting sponges cover cliff walls in which turtles feed and rest, which increases the probability of colonization. Sponges provided a suitable microhabitat for other epibiota (annelids, alpheids) perhaps due to increased water circulation or sharing of protected microhabitats.

Phylum Cnidaria

Cnidarians were previously reported as epibiotic only on *Caretta caretta* (Caine, 1986; Frick *et al.*, 1998). The sea plume *Pseudopterogorgia* sp. and the sea fan *Gorgonia* sp. are sessile tropical species that share the range of *Eretmochelys imbricata*. Anemones may associate with turtles if they remain in a protected area, are not scraped off, buried, or exposed to air. This association is rather uncommon probably because of the drag and scraping actions on the carapace.

Phylum Nematoda

Nematodes are newly documented marine turtle epibionts and may be associated with the sediment and turf component of the epibiotic community. Hence, they are not directly dependent on the turtle, but are living within the microhabitat present on the carapace. Nonetheless, they are an important component of the epibiotic community as available prey to other organisms.

Phylum Annelida

Annelids were the most frequent and apparently abundant epibiotic species of *Eretmochelys imbricata.* Sessile, filter-feeding tubeworms of Family Serpulidae and Spirorbidae were growing directly on the host's carapace and within microhabitats available on the turtle. The larvae and epitokes of most polychaetes are planktonic and probably colonize turtles as post-larvae. Motile polychaetes appear to be associated with the sediment and turf microhabitats, and provide predatory as well as prey functions within the community.

Phylum Sipunculida

Sipunculids are reported as marine turtle epibionts for the first time. Some species are known to bore into coral rock and are commonly found within sand grains of intertidal areas. On turtles, it appears that sipunculids are associated with turf and sediment microhabitats. Their settlement mechanism may be similar to that of the polychaetes, since sipunculid larvae were observed within the epibiotic community.

Phylum Mollusca

Bivalves seem to favor the hard substratum provided by the turtle carapace. Motile gastropods and nudibranchs appear associated with turf microhabitats on the surface of the turtle. No obvious added benefits to either basibiont or epibiont are obvious, besides the aforementioned increased food supply, protection, and dispersion possibilities to the epibionts. Bivalves may affect carapace scutes as they attain large sizes. This was observed once where *Isognomon* sp. was tightly attached to the underside of the posterior scute, and its growth could eventually deform the overlying scutes.

Phylum Arthropoda

Non-sessile crustaceans inhabiting the surfaces of marine turtles are probably associated with microhabitats available on the turtle. Amphipods, tanaids, alpheid shrimp, crabs, ostracods, dipterans, and perhaps copepods may be exploiting a productive habitat, which simply happens to be on the surface of a turtle. Because some of these species are direct developers, they have limited dispersion range, which may be greatly expanded if they are transported by the turtle with a food source (algae in the case of amphipods).

The presence of a pair of *Planes minutus* crabs on a small (26.3 cm SCL) turtle may indicate previous floating behavior or pelagic habitat (*Sargassum* sp.). According to Davenport (1994) and Dellinger *et* al. (1997), *P. minutus* are associated with floating substrata (floatsam and *C. caretta*). In this study most *P. minutus* occurred in mating pairs or with ovigerous females on juvenile *Eretmochelys imbricata*, contrary to Gramentz (1988), who reported single crab associations on *C. caretta* in Malta. Dellinger *et al.* (1997) observed mostly pairs of *P. minutus* on *Caretta caretta* in Madeira, and Michael Bresette (pers. comm.) observed ovigerous crabs on small loggerhead turtles in Florida. The presence of *P. minutus* may indicate recent arrival from the Sargasso Sea, where Carr (1980) and others believe post-hatchlings spend the first years of development. Based on these and the observations of Frick *et al.* (2000a), *Sargassum* habitats must be considered essential for sea turtle development and should be considered a priority in conservation strategies.

Cirriped species such as *Lepas anatifera* are found on floating objects throughout temperate and tropical regions of the world (Scheltema and Carlton, 1984). Their presence on turtles less than 29.9 cm SCL indicates that these individuals probably were floating on surface layers of the ocean, where *Lepas* sp. are most abundant. This epibiont could be utilized as an indicator of basibiont floating behavior, habitat, and health condition. *Lepas* sp. barnacles were also found in stomach contents of juvenile turtles and were considered indicators of oceanic, surface, or pelagic habitat (Van Dam and Diez, 1997a).

In the present study, unstalked barnacles such as *Platylepas* spp. and *Chelonibia* spp. were observed on the skin and carapace respectively. The exact mechanism of larval attachment, substrate recognition, and settlement remains a mystery. Chemotaxis, rheotaxis, or pressure cues may induce larvae to settle specifically on turtles, although other marine animals (alligators, manatees, and whales) are colonized by some of these species as well (Frick, pers. comm.).

Chelonibia caretta seems to be the most frequent barnacle colonizing the carapace of *Eretmochelys imbricata* in this region of the Caribbean based on observations of over 300 turtles. Other reports indicated *Chelonibia testudinaria* as the most common barnacle on *C. caretta* (Caine, 1986; Gramentz, 1988; Matsuura and Nakamura, 1993; Frick *et al.*, 1998) in more temperate regions. Water temperatures may limit the larval range of *Chelonibia caretta* to coincide more with the distribution of *E. imbricata.*

Barnacles of the genus *Chelonibia* which settle on the carapace of *Eretmochelys imbricata* appear on larger sized (>50 cm SCL) turtles, as observed by Gramentz (1988) on *Caretta caretta*. More information on the settlement, growth rates, and life expectancy of barnacles may provide clues to determine basibiont age or residence time (Eckert and Eckert, 1987).

Gregarious settlement of cyprid larvae may cause aggregated barnacle colonies on the carapace and plastron, although predation of cyprid larvae by epibiotic crabs (*Planes minutus*) and antifouling behavior of the host may further influence distribution on the carapace.

Large encrustations of barnacles on the carapace produce drag and may reduce the swimming efficiency of turtles (Logan and Morreale, 1994). The occurrence of barnacle colonies on the anterior 1/3 of the turtle seems to cause the greatest influence on the hydrodynamics of the host, and reducing efficiency of migrating animals may provide a significant negative effect to nesting turtles. Barnacles on the other hand may benefit from the increased water flow over the carapace to catch prey throughout the surface layers of the water column.

Phylum Ectoprocta

The presence of bryozoa on *Eretmochelys imbricata* seems to be related to the hard substratum provided by the carapace. Identification of bryozoan species is necessary to determine the significance of their association, as some species are restricted to *Sargassum* habitats. Since they were observed as substrata for sponges, sessile annelids, and turf algae, it is possible that they are primary colonizers of turtle surfaces.

Phylum Echinodermata

Echinoderms are probably associated with the hard substratum and protected microhabitats available on the carapace. The echinoderms collected were small juveniles, therefore they may have settled on the turtle from larval stages. Urchins and sea stars could crawl onto a turtle from adjacent substrata while the host is resting near the benthos. Echinoderms were rare epibionts, although they may function as grazers and predators of the epibiotic community.

Phylum Chordata

Tunicates settling under overlapping scutes of the carapace receive protection and benefit from this association. The hosts vertical movement through the water column could increase nutrient availability to filter feeding sessile tunicates on the carapace. The colonial ascidian *Trididemnum solidum* is common on Caribbean coral reefs and has limited larval dispersion. Larva bearing colonies of *T. solidum* observed on hawksbill turtles may aid the dispersion of tunicates beyond their usual geographical limits.

Subphylum Vertebrata

Vertebrates associated with *Eretmochelys imbricata* are probably not as fixed as other epibiota. A juvenile remora *Echeneis naucrates* was attached to a small turtle, which recently arrived from a pelagic habitat as inferred by the presence of *Planes minutus* and *Lepas anatifera*. I have only observed two other occasions of remora or pilot fish associated with adult *E. imbricata* in Mona and Monito, although *E. naucrates* are associated with *Chelonia mydas* in Culebra Island, east of Puerto Rico. A fish larva collected from the posterior scute cavity of a turtle may have settled there because of recruitment behavior of larva seeking dark, protected spaces in the benthos.

5.3 Symbiosis

The term symbiosis involves the close association of two different organisms. The associations have various combinations of benefits and costs to each. Mutualism, also known as protocooperation is the association that is beneficial to both organisms (Allaby, 1991). Commensalism is the case in which one organism is benefited and the other is unaffected. Parasitism is beneficial for one because it lives off the other, which may or may not be harmed.

Living on a turtle may benefit epibiotic species (food, illumination, water flow, migrations, etc.) while the host is unaffected. The epibiota of *Eretmochelys imbricata* may be considered commensals, where the symbiosis seems to be facultative or random and the epibiont simply takes advantage of an available hard substratum with associated microhabitats for settlement. Additionally, epibiota may receive an abundant food source, protection from predators, escape from unfavorable surroundings, and a dispersal advantage.

The only advantage to the basibiont may be camouflage on the seafloor, by the turf assemblage on the posterior carapace in the case of juvenile turtles.

The evolutionary significance of commensalism in which epibiota is favored may be due to four factors (Armitage *et* al., 1995). First, a commensal may experience better feeding opportunities by constant supply of algae or detritus due to the hosts' behavior or morphology. Second, there is increased mobility with a 'living' substratum, which may provide optimum living conditions. Finally, protection from predators and escape from adverse conditions is possible because the host provides better locomotion.

Another hypothesis involves the increased dispersal potential of epibiota living on migrating hosts. Long distance migrations may influence biodiversity of marine ecosystems and biogeography of species with limited dispersal (i.e. amphipods, alpheids, tanaids, and tunicates).

Phoresy is a dispersal method where one animal clings to the body of another, much larger animal of another species and is carried some distance before releasing its grip and falling (Allaby, 1991). This may be occurring in the association of *Eretmochelys imbricata* and *Planes minutus*, which hide under the carapace above the tail, and move around the surface of the turtle by grabbing on to it. The coloration of the crabs resembles the carapace scutes of *E. imbricata*, and may help camouflage it. This relationship seems phoretic since the crabs were clinging on a small turtle, but were not seen on larger turtles, indicating that they are temporarily on the turtles.

Studying the epibiota of hawksbill turtles in foraging habitats has demonstrated the possibility of successional stages and trophic interactions within the epibiotic community. Suitable substratum colonized by sessile epibiota (algae, sponge, barnacle, bryozoan, etc.) provides a microhabitat for a variety of benthic detritivores and herbivores (cnidarians, annelids, mollusks, amphipods, tanaids, dipterans, sipunculids, polychaetes, echinoderms, fish, etc.). The prey species in this microhabitat provide a foraging area for predatory crustaceans or vertebrates, which, in some cases, benefit the host by reducing epibiota.

Some cases provide a mutualistic relationship in which epibiont and basibiont benefit from the association. The natural actions of herbivores (fish) or carnivores (*P. minutus*) may be considered beneficial by reducing the fouling communities, which cause drag and reduce swimming efficiency of the turtle. These cases were rare, and usually, turtles were colonized by a diverse epibiotic community, although limited to the posterior portion of the turtle. Epibiota must be analyzed in the context of attachment mode, feeding strategy, and habitat preferences to determine its relation to the host. After this has been determined, the type of symbiosis may be classified. Quantitative data may be helpful in determining the drag created by the epibiotic community and hence the degree of negative effect. It is difficult to determine if epibiotic colonization is a cause or result of lethargic individuals in order to infer health or physical condition, although increased colonization may reflect the duration of this condition.

Infestations of large barnacles (*Chelonibia caretta*, *C. testudinaria*) negatively affect the host by increasing drag. Boring barnacles (Hendrickson, 1958) and ship boring, teredo mollusks (T. Razak, pers. comm.) have been observed embedded in the carapace of *Chelonia mydas*. I observed one case of an unidentifiable boring organism within a vertebral bone of a dead adult female *Eretmochelys imbricata*, although this was not the cause of death. An indirect negative effect of barnacle encrustation was reported for *E. imbricata* in Australia (Lance Ferris, pers. comm.), where a *C. testudinaria* colony had sealed the gap under scutes, and infection (*Pseudomonas, Aeromonas*, and *Streptococcus*) had accumulated gas, which interfered with the diving ability of the juvenile host.

5.4 Habitat Comparison

Coral reefs and associated ecosystems provide a diversity of microhabitats (heterogeneity) in which a great diversity of species occupy various niches. Warm tropical waters and the heterogeneous substrata provided by the surface of hawksbill turtles may help explain the high biodiversity found for this species of sea turtle. Tropical marine ecosystems are known to harbor greater diversity than temperate coasts. Pielou (1975) defined the substrata patchiness effect as a mosaic of different microhabitats which lead to different species segregating into different habitat patches.

In the case of the epibiota of *Eretmochelys imbricata,* the organisms colonizing the skin are different from those on the carapace. At the same time, a nook and cranny effect (Smith, 1972) predicts that protection from predators in certain patches of habitat allows the community to sustain various species, maintaining high diversity. Niches created by protected spaces under overgrowing scutes of the carapace favor the development of a complex epibiotic community.

Chi squared comparisons yielded significant differences in percent occurrence between habitats for half of the epibiotic taxa identified (Table 5). The power of this statistical method may be compromised because of the collection method. Due to time restraints, the whole community of epibionts on each turtle could not be collected, and perhaps organisms were missed causing artificial absences. However, an effort was made to standardize the collection of samples to avoid differences in the experimental error among turtles.

Significant differences in the occurrence of epibiont taxa may be dependent on diverse factors or interactions occurring in each habitat or at the microhabitat level. This argument is based on the life history of organisms that were significantly different which may include larval dispersal, ecology, behavior, and foraging strategies that are more efficient in certain microhabitats. Causes of present distribution of epibiota could be influenced by larval supply, differential settlement, or post-settlement mortality, which would result in the most adapted species recruiting successfully in a given area (Hadfield, 1986). Epibiotic species must resist drag forces during host movement, tolerate a range of depths (pressure, irradiance, and temperature), and survive scraping against other surfaces (antifouling).

Sand on the carapace of some turtles probably increases the diversity of the epibiotic community because it provides additional microhabitat for sediment-adapted species. Turtles from cliff wall habitat usually do not have sand on the carapace, providing better conditions for attachment of filter feeding invertebrates, such as sponges, tunicates, and ectoprocts, which would otherwise be buried by sediments. The absence of sand may be due to the depth of the sea floor (which exceeds the host's depth range), lack of re-suspended sediments, and vertical orientation of the benthos where turtles feed and rest. Sediment accumulations are habitat for sipunculids, nematodes, mollusks, amphipods, tanaids, decapods, motile polychaetes, and perhaps dipterans. Sediment accumulation on the surface of hosts is promoted in the shallower coral reef areas where re-suspension is common and turtles orient horizontally on the benthos.

The diversity of microhabitats available on the surface of the turtle and the growth of these substrates through the life of the turtle provide an interesting micro-ecosystem that may reflect environmental conditions surrounding the host. Studying the ecological relationships of this community may shed light on other processes, such as disturbances, or provide an index of environmental quality (bioindicators). Increased epibiotic loads may be an indicator of turtle condition related to swimming speed. Slower turtles will promote fouling due to the lack of drag, and this in turn will slow the turtle further, therefore the epibiotic overgrowth on all surfaces of the turtle may indicate health problems as is seen in emaciated or lethargic turtles. Additionally, I have observed increased colonization of calcareous algae on portions of the carapace, above the area of a missing limb. This could be due to reduced speed while swimming (less drag) or the inability to scrape that region against hard substrata.

Epibiota should be studied on turtles of distant localities to determine population characteristics of epi- and basibiont. I assume that the epibiotic community of turtles of the wider Caribbean is composed of similar organisms since the environmental conditions are similar throughout the range of the species, but differences in habitats at each location must be assessed. Unfortunately, the larval ecology and distribution of many intertidal species is unknown, and their presence may be random through space and time. Problems with taxonomy and lack of records from every epibiotic group throughout the region inhibit conclusions about the correlation of ranges of epi- and basibiont. Direct developers, such as tanaids, amphipods, alpheids, and tunicates are probably widespread throughout the Caribbean, because turtles may bridge the gap of oceanic barriers of distances, currents, or depth.

Epibiotic surveys are probably uncommon in ecological studies due to the difficulty of capturing healthy individuals in their natural habitat and difficulty of properly identifying the epibiota. Operational taxonomic units or functional groups seem to be helpful in qualitative studies such as this, although the cooperation of various marine taxonomy professionals is essential to resolve species identifications. Nevertheless, the taxonomic groupings provide a clear picture of what is occurring at the microhabitat level. A complex community with different microhabitats can be identified on the surface of juvenile *E. imbricata* for this Caribbean region.

Conclusions

The results of this investigation demonstrate that there is high phylogenetic diversity within the epibiota of non-nesting hawksbill turtles, which is helpful in understanding aspects of their ecology. The absence of epibionts may indicate recent recruitment to the neritic habitat from the pelagic one. Indicator species, such as those found on floating objects provide a clue to the turtle's swimming behavior, which may indicate physical condition. This information helps understand the ecology of juvenile turtles and non-nesting stages of *Eretmochelys imbricata*, contrary to epibiota of adult nesting or stranded individuals, which may reflect a different composition of epibiota (due to slower swimming, increased sedimentation, lower salinity, emersion, etc).

The posterior location of the epibiotic community suggests that the morphology of the turtle, hydrodynamics, and scraping against hard surfaces affect this community. This information is useful to detect abnormal morphology, behavior, or lethargy if epibionts grow on other areas besides the posterior regions. It also sheds light on the different factors influencing settlement of larvae and spores. The availability of spaces under the overlapping scutes is characteristic for *Eretmochelys imbricata* due to the growth form of keratin scutes. Epibiotic diversity may be influenced by the availability of theses spaces, absent in other species of marine turtles.

In this investigation, the presence of sand on the carapace of the turtle appeared to influence the type of epibiotic fauna on turtles from different habitats. Therefore, the difference between epibiotic communities may be influenced by other factors that depend on sea bottom characteristics, which may correlate with differences in habitat. These considerations are important to understand the critical habitats of marine turtles that can lead to better management of these endangered species.

The description of a migrating benthic habitat should be given special consideration in marine ecology, biogeography, and evolutionary studies. Biodiversity of marine benthic ecosystems may be maintained by the constant supply of genetic variability of organisms that are adapted to survive on migrating turtles. Other ecological information about epibiotic species may be extracted from this available substratum which moves through the water column, and across ocean basins.

Recommendations

Further classification of epibiotic organisms is necessary to determine how many new species are associated with *Eretmochelys imbricata*. Species lists will provide information on the biodiversity of epibiota, and their distribution. Surveys should be performed on larger geographical scales to determine if there are indicator species of specific regions or habitats.

Community level studies could also help clarify questions such as residence time of epibiota on the turtle, species turnover information, and trophic interactions, which may benefit the host. Turtle-specific barnacles should be researched further to determine attachment cues, and larval distribution patterns. This information could help understand the differences in colonization by barnacles.

Quantitative data on epibiota may reflect differences between turtle assemblages, populations, or habitats more clearly, although confounding factors should be considered. Perhaps some organisms are better indicators and these should be investigated further. This qualitative description provides a baseline for further ecological experimentation with a phylogenetically diverse community, composed of a diversity of microhabitats.

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Appendices

Appendix 1. Chi^2 two-way contingency table used to determine habitat association of epibiotic taxa.

	Yes	**No**	Σ
Reef	a	b	**a + b**
Wall	c	d	**c + d**
Σ	**a + c**	**b + d**	**n**

Formula to determine X^2 value: $X^2 = (ad-bc)^2 n / (a+b)(c+d)(a+c)(b+d)$

Appendix 2. Epibiotic organisms collected from *Eretmochelys imbricata* from Mona and Monito Islands, Puerto Rico. Relative frequency of each epibiont is expressed as percent occurrence (% O), and number of occurrences (# O) (n=105).

Epibiota	**% O**	**# O**
Foraminiferan 1 - *Amphistegina* sp.	35.24%	37
Foraminiferan 2 - (nautilus)	8.57%	9
Foraminiferan 3 - (grid)	1.90%	2
Poriferan 1 - (stiff brown)	0.95%	1
Poriferan 2 - (orange)	16.19%	17
Poriferan 3 - (clear triaxon spicules)	14.29%	15
Poriferan 4 - (white)	7.62%	8
Poriferan 5 - (yellow)	4.76%	5
Poriferan 6 - (purple)	2.86%	3
Hydrozoan 1 - (Solitary) Order Athecata	3.81%	4
Hydrozoan 2 - (Compound) Order Thecata	0.95%	1
Hydrozoan 3 - *Cnidoscyphus marginatus*	0.95%	1
Cnidarian 1 – *Gorgonia* sp.	0.95%	1
Cnidarian 2 - *Pseudopterogorgia* sp.	0.95%	1
Cnidarian 3 – Class Anthozoa	2.86%	3
Flatworm - unidentified	0.95%	1
Nematode 1 (thin blunt end)	10.48%	11
Nematode 2 (thin pointy ends)	1.90%	2
Nematode 3 (red dot)	10.48%	11
Oligochaete - unidentified	2.86%	3

Epibiota	% O	# O
Polychaete 1 - Family Cirratulidae	1.90%	2
Polychaete 2 - Family Onuphidae	1.90%	2
Polychaete 3 - Family Spirorbidae	1.90%	2
Polychaete 4 - Family Amphinomidae	5.71%	6
Polychaete 5 - Family Eunicidae	12.38%	13
Polychaete 6 - Family Serpulidae	65.71%	69
Polychaete 7 - Family Nereidae	23.81%	25
Polychaete 8 - Family Syllidae	20.95%	22
Polychaete 9 - Family Terebellidae	7.62%	8
Polychaete 10 - Family Dorvilleidae	0.95%	1
Polychaete 11 - Family Glyceridae	0.95%	1
Polychaete 12 - unidentified	25.71%	27
Sipunculid 1 - *Phascolosoma scolops*	13.33%	14
Sipunculid 2 - unidentified	8.57%	9
Gastropod 1- Family Fissurellidae	0.95%	1
Gastropod 2 – Conical Shell (red)	0.95%	1
Gastropod 3 – Conical Shell (white and brown)	7.62%	8
Gastropod 4 - *Dendropoma annulatus*	6.67%	7
Gastropod 5 - *Litiopa melanostoma*	0.95%	1
Gastropod 6 - unidentified	1.90%	2
Opisthobranch 1 - unidentified	0.95%	1
Opisthobranch 2 - *Aplysia dactylomela*	0.95%	1
Bivalve 1 - *Pinna* sp.	0.95%	1
Bivalve 2 - *Chama* sp.	1.90%	2

Epibiota	**% O**	**# O**
Bivalve 3 - *Isognomon alatus*	2.86%	3
Chiton - *Tonicia schrammi*	0.95%	1
Amphipod 1 - Sub Order Gammaridea	5.71%	6
Amphipod 2 - Sub Order Gammaridea	19.05%	20
Amphipod 3 - Sub Order Gammaridea	4.76%	5
Amphipod 4 - Sub Order Gammaridea	0.95%	1
Amphipod 5 - unidentified	0.95%	1
Ostracod 1 - (Clear Shell)	4.76%	5
Ostracod 2 - (White Hairy Shell)	0.95%	1
Copepods -Order Harpacticoida	51.43%	54
Decapod 1 - *Planes minutus*	0.95%	1
Decapod 2 - Family Xanthidae	1.90%	2
Decapod 3- Family Alpheidae	3.81%	4
Tanaid 1 - *Leptognathus* sp.	0.95%	1
Tanaid 2 - *Heterotanais dubia*	9.52%	10
Tanaid 3 - *Heterotanais savignyi*	1.90%	2
Tanaid 4 - unidentified	0.95%	1
Cirriped 1 - *Platylepas decorata*	77.14%	81
Cirriped 2 - *Lepas anatifera*	1.90%	2
Cirriped 3 - *Chelonibia caretta*	4.76%	5
Cirriped 4 - *Chelonibia testudinaria*	1.90%	2
Dipteran - Family Chironomidae	16.19%	17
Bryozoan 1 - (Thick gray encrusting)	5.71%	6
Bryozoan 2 - (White thin sheet)	4.76%	5

Epibiota	% O	# O
Bryozoan 3 - (Red Encrusting)	31.43%	33
Bryozoan 4 - (White Round Encrusting)	23.81%	25
Bryozoan 5 - (Square Zooids)	3.81%	4
Bryozoan 6 - (Y-colony)	2.86%	3
Bryozoan 7 - (Tube forming)	1.90%	2
Bryozoan 8 - Family Hippothoidae	0.95%	1
Bryozoan 9 - (Brown Encrusting)	0.95%	1
Echinoderm 1 - Class Ophiuroidea	3.81%	4
Echinoderm 2 - Family Ophiactidae	0.95%	1
Echinoderm 3 - Eucidaris tribuloides	0.95%	1
Tunicate 1 - (Compound) *Trididemnum solidum*	3.81%	4
Tunicate 2 - (Solitary) *Microcosmus* sp.	1.90%	2
Tunicate 3 - (Solitary) unidentified	9.52%	10
Remora - *Echeneis naucrates*	0.95%	1
Fish larva - unidentified	0.95%	1
Other unidentified animal	7.62%	8
Filamentous or turf algae	94.29%	99
Calcareous encrusting algae	82.86%	87
Calcareous erect algae	57.14%	60
Foliose algae 1 - unidentified	12.38%	13
Foliose algae 2 - *Lobophora variegata*	9.52%	10
Foliose algae 3 - *Dictyota* sp.	2.86%	3
Foliose algae 4 - *Neomeris annulata*	0.95%	1
Foliose algae 5 - *Anadyomene stellata*	0.95%	1