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# 15 Sea Turtle Epibiosis

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## 15.1 INTRODUCTION

In the marine environment, any exposed, undefended surface will eventually be colonized by marine propagules (Wahl, 1989). Colonization of inanimate structures (e.g., dock pilings and boat hulls) is called *fouling*, while colonization of other marine organisms is called *epibiosis*. Epibiosis results in spatially close associations between two or more living organisms (Harder, 2009), in which a single host (or *basibiont*) supports one or more typically opportunistic colonizers (or *epibionts*) (Wahl and Mark, 1999). Epibiosis is the most common form of symbiosis in the marine environment and

may be classified into several types of associations (e.g., mutualism, commensalism, parasitism) depending on the interactions between a host and its epibionts (Leung and Poulin, 2008).

Sea turtles often act as hosts to a wide variety of epibionts, most of which are unspecialized organisms normally found associated with inanimate structures in the surrounding marine environment (i.e., “free living”). These types of epibiotic associations are known as *facultative commensalisms* (Wahl and Mark, 1999). That is, the host receives no direct benefit from the epibiont and the epibiont demonstrates little to no substrate specificity. For these associations to occur, the various settlement cues that facultative commensal epibionts utilize when selecting substrata must also be present on sea turtles (Zardus and Hadfield, 2004). Alternatively, there are several epibionts that are found almost exclusively on sea turtles (Frick et al., 2011a). These associations are known as *obligate commensalisms*, whereby the epibiont is dependent on the host turtle for survival, but the welfare of the host turtle is not dependent on the presence or behavior of the epibiont. While some obligate commensal epibionts are known to perform activities that might be considered beneficial to the host turtle, there are no examples of *obligate mutualisms*, in which both the host turtle and the epibiont depend on each other for survival. Future studies, however, may identify such obligate mutualisms. Most obligate (and facultative) commensal epibionts do not derive nutrients from the tissue of the host turtle and are not parasitic; instead the host turtle simply provides a foraging platform (Frick et al., 2002a). On the contrary, several sea turtle epibionts are known to derive nutrients from the tissue of the host turtle and, therefore, represent associations known as *parasitism* (Leung and Poulin, 2008). Parasitic epibionts of sea turtles are rare, but these associations may have important consequences for the health of host turtles (Greenblatt et al., 2004).

Following a rich history of anecdotal reports dating back to Darwin (1851, 1854), the study of epibiosis in sea turtles has received considerable attention in recent years. The vast majority of studies describe the diversity of epibiota, and speculate on the possible causes and effects of these associations. From these descriptive studies, we have learned a great deal with respect to the wonderful diversity of epibiotic forms found associated with sea turtles (Appendix A). Fewer studies, however, approach sea turtle epibiosis from the community perspective. These studies not only describe diversity of epibiota but also consider the structuring of epibiotic communities and the complex suite of interactions occurring on the turtle across space and time. Finally, even fewer studies attempt to quantify and understand the ecological interactions between turtles and their epibiota. These studies have allowed researchers to better understand the ecological and evolutionary implications of epibiosis, and to decipher the valuable information that can be gleaned from studying sea turtle epibionts.

Despite the antiquity of some sea turtle epibiont observations, the study of sea turtle epibiosis remains in a prolonged state of infancy when compared to the breadth of information that has recently and quickly accrued on sea turtle migrations and home ranges (largely through the deployment of satellite tags). Likewise, our understanding of sea turtle genetics and molecular phylogeny exceeds that of basic facets of sea turtle ecology—including diet, foraging behavior, and epibiotic associations. Given the documented declines of turtle populations in some areas, it has become imperative for scientists to understand how sea turtles interact with the constituents of the habitats they occupy, be it while foraging or through epibiosis. Such information allows scientists to view sea turtles within the context of a complex and ecologically rich marine environment, and it aids in modeling the potential impacts that certain natural and anthropogenic-driven events may have upon sea turtles and the habitats they utilize.

In this chapter, we begin by introducing many of the common forms of epibionts known to be associated with sea turtles. Second, we describe several common epibiotic community types, and discuss the spatial and temporal factors by which epibiotic communities are structured. Third, we propose a number of costs and benefits that may affect sea turtle–epibiont interactions and discuss the ecological inferences and implications of sea turtle epibiosis. Lastly, we outline a conceptual model of epibiosis with which researchers may apply to better understand the factors that affect their particular epibiotic systems and more easily decipher the important biological information that can be gleaned from studying epibiotic interactions.

## 15.2 COMMON FORMS

The diversity of epibionts known from sea turtles is exceptional. For example, loggerhead (*Caretta caretta*) and hawksbill turtles (*Eretmochelys imbricata*) are known to host 200+ and 150+ epibiont taxa, respectively. For this reason, we have not included an itemized list of epibionts from each turtle species. Instead, we have included a list of references that include records of epibionts from sea turtles separated by geographic region (Appendix A) and encourage investigators to examine the studies cited in this chapter.

### 15.2.1 SESSILE FORMS

Sessile forms attach directly to a substrate and do not move around freely. These forms are the most common and conspicuous epibionts of sea turtles. Most sessile forms have motile, planktonic larvae that recruit to suitable substrata, where they attach and transform into adults. For these organisms, the carapace and skin of sea turtles must possess certain settlement cues that larvae recognize, including water flow characteristics, chemical signals, and surface rugosity. Of the sessile forms documented from sea turtles, the most noticeable are barnacles (Cirripedia). Barnacles attached to the carapace of sea turtles are considered “pioneer” species that facilitate the colonization of subsequent epibiota (see Section 15.3.5; Frick et al., 2002b). Some coronuloid barnacles embed themselves in the skin and soft tissues of sea turtles (e.g., *Chelolepas cheloniae*). Through chemical mediation, these barnacles become encased in connective tissue, which aids in strengthening the shell of the barnacle while protecting the host tissue from further injury (Frick et al., 2011a). Other sessile forms include algae, foraminiferans, poriferans, cnidarians (Hydrozoa and Anthozoa), mollusks (Bivalvia), bryozoans, and tunicates. Many of these sessile forms are colonial and can reproduce asexually. As a result, some colonies are known to grow quite large and overtake much of the carapace of the host turtle. In such situations, aggregations of sessile forms provide additional surface area for the recruitment of other sessile epibiota, and create numerous crevices and spaces for the colonization of various motile epibionts (see later).

### 15.2.2 SEDENTARY FORMS

Sedentary forms live a semi-sessile existence, in which motile individuals construct refugia or tubes attached to a substrate. Sea turtles host a variety of sedentary forms, including polychaete worms, amphipods, and tanaids (Frick et al., 1998, 2004b). Some sedentary forms create only small (1–2 mm long) tubes to dwell in, while others, particularly sabellariid worms and *Corophium* amphipods, will aggregate into dense communities—creating reef-like structures consisting of hundreds of individual tubes bonded together. These “worm reefs” can become quite large (up to 10 cm high) and cover the entire carapace of the host turtle (Frick et al., 2004b). These complex structures also provide suitable habitat for the colonization of small motile epibionts.

### 15.2.3 MOTILE FORMS

Motile forms do not directly attach to a substrate and are capable of free movement throughout their lives. These organisms may colonize sea turtles directly from the plankton (similar to sessile forms) or secondarily colonize turtles after initially recruiting to their primary habitat. In the latter case, colonization may occur when resting turtles contact pelagic or benthic substrata. Motile forms reported as sea turtle epibionts include protozoans, sipunculid worms, plathyelminth worms, annelid worms (hirudineans and polychaetes), mollusks (Polyplacophora and Gastropoda), dipterans (flightless marine midges), decapods (Brachyura, Anomura, Caridea), copepods, ostracods, peracarids (amphipods, isopods, and tanaids), echinoderms (Ophiuroidea and Echinoidea), and fish

(Genera *Echeneis* and *Remora*; “shark suckers”). Most motile forms are small and cryptic, and live within the gaps and sinuses provided by aggregations of sessile and sedentary epibionts. Moreover, the deposition of sediment between sessile aggregations provides habitat for small infaunal animals that live in the trapped mud layer (e.g., polychaete worms, amphipods, and clams). For these reasons, the presence of most motile forms is often dependent on the preceding colonization of other sessile and sedentary epibiota. Two exceptions are *Caprella* amphipods, which cling tightly to the host carapace via limbs with hooked dactyls, and *Planes* crabs, which hide in the inguinal notch between the carapace and tail (Chace, 1951). Not surprisingly, these are two of the more common motile epibionts of sea turtles around the world.

## 15.3 COMMUNITIES AND COMMUNITY DYNAMICS

### 15.3.1 PELAGIC/OCEANIC COMMUNITIES

All extant sea turtles, except the flatback turtle (*Natator depressus*), utilize pelagic and oceanic habitats during juvenile life stages (Bolten, 2003) and some continue to use these habitats throughout adulthood (e.g., *Dermochelys coriacea* and eastern Pacific *Lepidochelys olivacea*). Adult and subadult loggerhead turtles (*C. caretta*) are considered mostly neritic, but some individuals make occasional forays into the pelagic/oceanic environment (Frick et al., 2009; Reich et al., 2010). During pelagic/oceanic life stages, sea turtles may host communities of pelagic organisms that are typically found associated with drifting flotsam (e.g., *Sargassum*) and jetsam. These organisms primarily include pedunculate barnacles of the genera *Lepas* and *Conchoderma*, and grapsid crabs of the genus *Planes*. *Lepas* spp. and *Conchoderma* spp. are ubiquitous throughout the world’s oceanic environment and are known to colonize a variety of other nektonic hosts (e.g., Reisinger and Bester, 2010; Pfaller et al., 2012). Studies on *Planes* crabs from oceanic-stage sea turtles represent the most detailed information on sea turtle–epibiont symbiosis to date (Davenport, 1994; Dellinger et al., 1997; Frick et al., 2000a, 2003b, 2004a, 2006, 2011b; Pons et al., 2011). Other less frequent epibionts of the pelagic/oceanic community may include pelagic sea slugs (*Fiona pinnata*), sea spiders (*Endeis spinosa*), pelagic tunicates (*Diplosoma gelatinosum*), and crabs of the genera *Portunus* and *Plagusia* (Frick et al., 2003a, 2011b; Loza and López-Juado, 2004). The presence of pelagic/oceanic epibionts on sea turtles outside these areas strongly suggests that these turtles have recently migrated from the pelagic/oceanic environment, providing valuable insights into cryptic migratory behaviors and habitat preferences of sea turtles.

### 15.3.2 BENTHIC/NERITIC COMMUNITIES

After early life stages in pelagic/oceanic areas, most cheloniid sea turtles transition to more coastal and benthic habitats—presumably in search of food, and later for mates (Bjørndal, 1997). In benthic/neritic habitats, sea turtles become exposed to intense colonization pressure by marine propagules (larvae and spores) seeking to colonize submerged substrata and begin their benthic existence. The skin and especially the carapace of sea turtles provide suitable substrata for a variety of benthic/neritic organisms (Frick et al., 1998, 2000a; Schärer, 2001). As previously mentioned, the recruitment of sessile and sedentary forms (e.g., barnacles, tubicolous worms, and tunicates) facilitates the colonization of smaller motile forms (e.g., crabs, amphipods, mollusks, etc.), which inhabit the gaps and crevices between sessile aggregations. After prolonged exposure to settlement by local plants and animals in a given area, the epibiotic communities of sea turtles begin to resemble the adjacent benthic environment. For this reason, the species composition of benthic/neritic communities is largely dependent on the geographic region or habitat in which the host turtle occupies (Frick et al., 1998; Schärer, 2001). Complex benthic/neritic communities are most evident on nesting female turtles, which tend to remain relatively sedentary and localized during the nesting period (Frick et al., 2000b).

### 15.3.3 OBLIGATE COMMUNITIES

Obligate communities are composed almost entirely of organisms that are known exclusively as epibionts of sea turtles and other motile marine organisms. That is, these communities are largely independent of the habitat in which the turtle occupies (i.e., pelagic/oceanic vs. benthic/neritic). The predominant epibiont of obligate communities is the coronuloid barnacle *Chelonibia testudinaria*. This ubiquitous species is the most frequently reported epibiont of sea turtles and is also known to colonize crabs, sirenians, and crocodilians (Newman and Ross, 1976; Zardus and Hadfield, 2004; Cupul-Magaña et al., 2011; Nifong and Frick, 2011). *Chelonibia testudinaria* occurs in great numbers on some turtles and appears to function as a “pioneer” for the development of more extensive and diverse epibiotic communities (Frick et al., 2002b; Rawson et al., 2003). Aggregations of *C. testudinaria* provide refugia for other obligate epibionts, such as the ruby-eyed amphipod (*Podocerus chelonophilus*) and the robust tanaid (*Hexapleomera robusta*). However, both species will also cling directly to the skin and carapace of host turtles, and *P. chelonophilus* will also aggregate around epidermal lesions and eat necrotic tissue from the wounds of host turtles (Moore, 1995). Other obligate epibionts of sea turtles include marine red alga (*Polysiphonia carettia*), which is known only from cheloniid sea turtles (Senties et al., 1999), and several other species of coronuloid barnacles that are wholly chelonophilic (Ross and Frick, 2011). While some individual turtles are known to host strictly obligate communities (Frick et al., 2010a), most communities composed primarily of obligate epibionts also contain some facultative forms.

### 15.3.4 COMMUNITY DISTRIBUTION

The spatial distribution of epibiont communities on host turtles may be influenced by a complex suite of factors, including recruitment dynamics, water flow patterns, differential disturbance among body regions, and inter- and intraspecific interactions (Pfaller et al., 2006). In general, studies that examine or anecdotally report on the distribution of sea turtle epibionts have found that epibiont communities tend to aggregate on the carapace, as opposed to the skin or plastron (Gramentz, 1988; Fuller et al., 2010). Extra-carapacial epibionts mostly include barnacles, parasitic leeches, and *Planes* crabs (Chace, 1951; Gramentz, 1988; Frick et al., 1998; Hayashi and Tsuji, 2008). Some barnacles occur only along the plastral sutures (e.g., *Stomatolepas transversa*) (Young, 1991), while others mostly occur along the leading edges of the front flippers (e.g., *Stephanolepas muricata*) (Frick et al., 2011a). Limb movements, unfavorable water flow patterns, and the sloughing of skin by the host turtle probably restrict the recruitment and development of extra-carapacial epibionts. Nevertheless, information on the distributions of extra-carapacial epibionts is still lacking (Frick et al., 2011a).

Most studies that examine the spatial distribution of epibiont communities on sea turtles have focused on the carapace, where the densest and most diverse communities are found (Frick et al., 1998). These studies indicate that epibiotic communities tend to be distributed in nonrandom patterns. Most studies report a tendency for epibiont communities to cluster along the vertebral scutes and across the posterior third of the carapace (Caine, 1986; Matsuura and Nakamura, 1993; Frick et al., 1998; Pfaller et al., 2006). Such nonrandom distributions are thought to reflect the preference of filter-feeding epibionts (e.g., barnacles) for elevated flow rates along the vertebral scutes and the favorable settlement conditions for other epibiota along the posterior of the carapace where flow rates are reduced (Pfaller et al., 2006). Recruitment of “pioneer” species in these areas (e.g., *Chelonibia* barnacles and *Polysiphonia* alga) will then facilitate the accumulation of more diverse epibiotic communities (Gramentz, 1988; Frick et al., 2000b; Fuller et al., 2010). Additionally, the colonization and persistence of epibionts on the anterior costal scutes may be reduced by contact from the front flippers (Caine, 1986; Dodd, 1988) and/or removal during “self-grooming” (Schofield et al., 2006; Frick and McFall, 2007). Other studies show mostly random distributions among barnacle species with some spatial structuring among different size classes of barnacles (Fuller et al., 2010).



Recently, Moriarty et al. (2008) confirmed that the obligate commensal barnacle, *Chelonibia testudinaria*, is capable of substantial (but slow) post-settlement locomotion. Individual *C. testudinaria* were shown to move across multiple scutes from areas of low water flow to areas with better filter-feeding conditions. Such movements may be triggered by differential flow rates over the carapace or/and the presence of conspecifics that disrupt flow patterns. As previously mentioned, *Chelonibia* spp. are important “pioneer” species for epibiotic communities (Frick et al., 2000) and post-settlement locomotion will certainly affect the spatial distribution of epibiotic communities. However, as the density of *C. testudinaria* and other epibiota increases, post-settlement locomotion and survival will be reduced, and the overall distribution may become more reflective of differences in recruitment patterns (Pfaller et al., 2006).

Debilitated turtles will host epibionts, especially barnacles, over their entire external surface area—including portions of the mouth regularly exposed to the outside environment. These “barnacle bill” turtles will often suffer severe deformations as a result of barnacle colonization. Current information indicates that such turtles are immunosuppressed or lethargic prior to barnacle colonization and that limited mobility by the host likely facilitates rapid and prolific colonization of barnacles (Deem et al., 2009). Nevertheless, because healthy turtles may also support massive aggregations of epibionts over much of their bodies, it is difficult to judge the health of a turtle simply by examining epibiont loads and percentage coverage (*see* Deem et al., 2009).

### 15.3.5 COMMUNITY SUCCESSION

Prior to the colonization of macroorganisms, all structures exposed to seawater initially undergo a similar sequence of events (Wahl, 1989): (1) biochemical conditioning, whereby surfaces absorb dissolved macromolecules; (2) bacterial colonization; and (3) unicellular eukaryote (e.g., yeasts, protozoa, and diatoms) colonization. To our knowledge, these critical stages in the process of epibiosis in sea turtles have never been explored.

The temporal succession of “macro”-epibiont communities on host turtles remains poorly understood, as well. To date, there is one study that examines temporal succession of epibiont communities from individual turtles over an extended period of time (Frick et al., 2002b). Using flipper-tagging data, photography, and in situ assessments, epibiont data were collected from the carapaces of nesting loggerhead turtles (*C. caretta*) in Georgia, United States, over the course of 3 months. General observations of community succession were similar to those reported for neritic, epibenthic communities (Dean, 1981). Community succession is typically initiated when hard, sessile forms like barnacles (*C. testudinaria* in Frick et al., 2002b) colonize a relatively bare carapace. These “pioneers” facilitate the subsequent colonization of other epibiota by increasing the surface area for colonization and changing water flow patterns (Pfaller et al., 2006). Secondary colonizers include other sessile forms (e.g., hydrozoans and bryozoans) and sedentary forms, which take refuge within the interstices of the barnacles (e.g., tanaisids). The accumulation of sediments among primary and secondary sessile forms then facilitates the colonization of sessile tunicates and many small, motile forms. Tunicates and other secondary sessile forms tend to overgrow and kill the barnacles beneath them. Tunicates (*Molgula manhattensis*) appear to be the climax species of the carapace epibiont community on nesting loggerheads in Georgia, United States. Aggregations of *M. manhattensis* occasionally cover the entire carapace at the end of the season, providing innumerable gaps and crevices for a diverse array of motile epibionts.

At or before reaching terminal succession, epibiont communities may be partially or catastrophically disturbed by various biotic and abiotic factors. Turtles that accumulate benthic/neritic communities may immigrate to different, less favorable habitats, causing the less tolerant epibionts to die and slough off. In some cases, this may completely clear the carapace of epibiota. Moreover, community succession may be disrupted when host turtles “groom” themselves by actively rubbing against submerged structures to remove epibiota (Heithaus et al., 2002;

Schofield et al., 2006; Frick and McFall, 2007). Evidence of such behaviors is often present in the form of longitudinal scratch marks on the carapace (Caine, 1986; Frick and McFall, 2007). Lastly, predatory epibionts (e.g., *Planes* crabs and several gastropods) and fish may systematically clean/remove certain epibionts (Davenport, 1994; Losey et al., 1994; Frick et al., 2000a, 2011b; Pfaller et al., 2008; Sazima et al., 2010). These factors may lead to partial or complete turnover of the epibiotic communities of sea turtles.

## 15.4 ECOLOGICAL INTERACTIONS

### 15.4.1 EFFECTS ON EPIBIONTS

Epibionts may benefit from epibiosis through reduced competition and predation. These are major factors affecting the ability of marine propagules to successfully colonize a substratum (Enderlein and Wahl, 2004). Thus, when risk of predation is high or when settlement area is limited—whether by high population densities (e.g., on benthic structures) or by low substrata availability (e.g., on pelagic flotsam)—epibiosis of sea turtles may be beneficial for the survival of marine propagules (Wahl, 1989; Pfaller et al., 2012). Some “burrowing” barnacles may avoid predation by encasing themselves within the tissue of host turtles via chemical mediation (Frick et al., 2011b). Epibionts may also benefit from improved energetic positioning. Filter-feeding epibionts, such as barnacles, may benefit from favorable feeding currents on host turtles (Pfaller et al., 2006), while photosynthetic epibionts, such as algae, may benefit from increased oxygen and light availability (Shine et al., 2010). Furthermore, epibionts may benefit through range expansion and increased genetic mixing by hitchhiking on migratory turtles (termed *phoresis*). Researchers have hypothesized that sea turtles may act as long-distance dispersal vectors for benthic marine invertebrates (Schärer and Epler, 2007; Harding et al., 2011).

Epibiosis may be costly to epibionts when turtle behaviors cause physical disturbance and unfavorable fluctuations in physiological conditions (Wahl, 1989). Contact between turtles during mating, or between turtles and submerged structures (e.g., rock or coral ledges), may physically damage epibionts, especially those with fragile, erect body forms (e.g., leafy bryozoans and soft corals). As previously mentioned, sea turtles are also known to actively remove epibionts by scraping against submerged structures (Heithaus et al., 2002; Schofield et al., 2006; Frick and McFall, 2007). Moreover, epibionts that are sensitive to desiccation may die when turtles emerge to nest or bask at the surface (Caine, 1986; Bjorndal, 2003). Similarly, epibionts that are sensitive to fluctuations in temperature, salinity, or pressure may not survive when turtles migrate and/or dive. Another cost for certain epibionts might be reduced access to food resources and mates, which would ultimately cause reduced longevity and reproductive capacity. These costs might favor epibionts capable of asexual reproduction and dietary versatility.

### 15.4.2 EFFECTS ON HOST TURTLES

Epibiosis may be costly to host turtles when epibionts cause increased weight and drag. In extreme cases, epibiotic loads have been reported that effectively double the mass and volume of juvenile sea turtles (Bolten unpubl. data *in* Bjorndal, 2003). Epibionts attached to the carapace may increase drag by disrupting the laminar flow over the carapace (Logan and Morreale, 1994) and those embedded in the leading edge of the front flippers may increase drag while swimming (Wyneken, 1997; Frick et al., 2011a). The energetic costs of hosting epibionts are likely greatest when turtles undertake long-distance migrations and least when turtles remain relatively sedentary (e.g., females during internesting periods). Because otherwise healthy turtles will often support massive epibiont aggregations (Deem et al., 2009), turtles are apparently capable of overcoming the costs associated with “epibiotic drag” and should not be judged as healthy or unhealthy simply by examining epibiotic loads (see Deem et al., 2009). Furthermore, the aforementioned

“barnacle bill” turtles tend to accumulate their prolific barnacle loads after (not before) becoming lethargic at the surface.

Epibiosis may also be costly to host turtles when certain epibionts detrimentally affect the health of host turtles. A number of common epibionts of sea turtles (e.g., platyhelminth worms, annelid worms and barnacles) are thought to be the cause of or related to infections of sea turtles (George, 1997; Alfaro, 2008). Tissue damage caused by burrowing epibionts may increase the vulnerability of host turtles to pathogens (George, 1997). Some coronuloid barnacles (e.g., *C. cheloniae*, *S. muricata*, and *Cylindrolepas darwiniana*) become embedded within hard and soft tissues of host turtles causing deep-tissue wounds that can sometimes leave impressions on the underlying bone (Hendrickson, 1958; Green, 1998; Frick and Zardus, 2010; Frick et al., 2010a). *Platylepas decorata* have also been found imbedded in the beaks of host turtles causing severe beak deformation, which may lead to reduced foraging capacity and death of the host turtle (see Green, 1998; Frick and Zardus, 2010). Other non-barnacle forms may act as disease vectors of pathogens. Parasitic marine turtle leeches (*Ozobranchus* sp.) not only consume host tissue but also are believed to act as disease vectors for the dispersal of the fibropapilloma-associated herpes virus found in latent tumors that often cover, deform, and debilitate host turtles (Greenblatt et al., 2004). Commensal gastropods of sea turtles may act as intermediate hosts for spirorchiid blood flukes (Frazier et al., 1985), which can have devastating effects on host turtles (George, 1997).

Host turtles may benefit from epibiosis through improved optical, chemical, or electrical camouflage. Predators may not recognize hosts as potential prey items if epibiotic communities visually or chemically resemble the surrounding benthic communities (Rathbun, 1925; Fishlyn and Phillips, 1980; Feifarek, 1987; Frazier et al., 1991). Moreover, dense epibiotic communities may disrupt electric fields produced by hosts, allowing hosts to avoid predation by predators that utilize electrolocation when searching for prey (e.g., sharks) (Ruxton, 2009). Hosts may also benefit from epibiosis through associational defense and cleaning. Epibionts with chemical or structural defenses (e.g., toxins, sharp projections, or hard outer coverings) may deter predation on host turtles (Wahl and Mark, 1999; Bjorndal, 2003). Predatory epibionts may provide a cleaning benefit by consuming other epibionts—some of which may be harmful—from the surface of host turtles (Davenport, 1994; Sazima et al., 2010).

### 15.4.3 ECOLOGICAL INFERENCES

Studies of epibiosis have helped elucidate cryptic life history attributes of sea turtles and informed the implementation of conservation measures. While such studies will not and should not supplant the use of tag-return data, satellite telemetry, stable-isotope analyses, or population genetics, studying epibiosis can provide a time- and cost-effective alternative to elucidate the geographic ranges, habitat preferences, and migratory corridors of sea turtles. Using primarily examples from the well-studied epibiont community of loggerhead turtles in the northwestern Atlantic Ocean, we illustrate the types of ecological inferences that can be gained by studying the epibionts of sea turtles.

Epibiont data have been used to elucidate the foraging locations of loggerhead turtles nesting along the Atlantic coast of Florida, United States. These turtles occasionally host epibionts that are geographically restricted to far southern Florida, the Bahamas, and the Caribbean (Caine, 1986; Pfaller et al., 2008). Such associations suggest that these nesting turtles had recently migrated from more southerly areas where their range overlapped with free-living populations of the epibionts. Data from flipper-tag returns, satellite telemetry, and stable-isotope analyses have confirmed that turtles nesting in Florida frequently utilize these more southerly, tropical waters during nonbreeding seasons (Meylan, 1983; Foley et al., 2008; Pajuelo et al., 2012). Caine (1986) further extrapolated these epibiont data to suggest the presence of two discrete nesting assemblages along the southeastern United States, one to the north and one to the south of Daytona Beach, Florida (approximately 29° N latitude). Several years later this hypothesis was rather precisely confirmed by



molecular data (Bowen et al., 1993; Encalada et al., 1998) and now these two nesting assemblages receive markedly different conservation status (Turtle Expert Working Group, 2009).

In another example from nesting loggerhead turtles in Florida, United States, Reich et al. (2010) supplemented stable-isotope data with epibiont community data to suggest a bimodal foraging strategy by female loggerheads prior to their arrival at breeding grounds. Because isotopic signatures (depleted vs. enriched  $\delta^{13}\text{C}$ ) can vary along multiple environmental continua, the incorporation of epibiont data in this study provided additional support for an oceanic versus neritic dichotomy, as opposed to dietary or latitudinal gradients. These results have important implications for role of adult loggerhead turtles in the oceanic environment and the management policies that serve to protect them.

Epibiont data have also been used to assess the foraging migrations of juvenile and subadult loggerhead turtles. Killingley and Lutcavage (1983) used dual isotopic profiles ( $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$ ) from the shells of *C. testudinaria* to reconstruct the movements of subadult loggerheads between oceanic habitats in the northwest Atlantic and estuarine habitats in the Chesapeake Bay (Maryland and Virginia). Moreover, Limpus and Limpus (2003) used the presence of particular epibionts (*Planes* sp. and *S. muricata*) and morphological features to identify which juvenile turtles caught in neritic habitats in the southwest Pacific Ocean had recently recruited from the open ocean. In both studies, epibiont data provided valuable insights in to cryptic host movements that otherwise would have been very difficult to obtain.

Lastly, in another interesting application of epibiont data, Eckert and Eckert (1988) measured the size distribution of epibiotic barnacles (*Conchoderma virgatum*) on nesting leatherback turtles to extrapolate the time of arrival to the tropical nesting region. Because reproduction in these barnacles is typically restricted to tropical regions, their colonization of turtles is limited to the period when turtles also occupy tropical waters. Based on reproductive periodicity and established growth rates of barnacles (Eckert and Eckert, 1987), the authors determined that turtles do not arrive from temperate latitudes until just prior to nesting and orient directly toward their preferred nesting beach (Eckert and Eckert, 1988). These data have provided important information on the cryptic migratory behavior of leatherback turtles and have better informed the implementation of conservation measures.

#### 15.4.4 ECOLOGICAL IMPLICATIONS

The ecological implications of sea turtle epibiosis remain one of the most poorly understood aspects of this nascent field. Aside from many of the direct effects of epibiosis on host turtles and epibionts discussed earlier (Sections 15.4.1 and 15.4.2), sea turtle epibiosis may have other less obvious, indirect effects on the marine communities and habitats that sea turtles inhabit.

Several authors have discussed the potential role of sea turtles as dispersal vectors for a diverse array of marine invertebrates over broad geographic regions (Bjorndal and Jackson, 2003; Schärer and Epler, 2007; Harding et al., 2011; Lezama et al., 2012). Hitchhiking on highly mobile hosts may facilitate genetic mixing and/or range expansion for epibionts capable of reproducing on turtles or after arriving in distant locations (Rawson et al., 2003). These factors may be particularly important for invertebrate taxa with limited dispersal capacities (Schärer and Epler, 2007). Turtle-mediated genetic mixing may aid in maintaining the genetic diversity and homogeneity of marine invertebrate populations (Rawson et al., 2003), but may also inhibit biological diversification by impeding local adaptation or random divergence. Moreover, turtle-mediated range expansion may promote biological diversification if newly established populations subsequently remain isolated from their source populations, or disrupt ecosystem functioning when invaders compete with or consume resident species.

A recent study has drawn attention to the potential for turtle-mediated introductions of nonindigenous and potentially invasive species. Harding et al. (2011) report the first records of the nonindigenous veined rapa whelk (*Rapana venosa*) as an epibiont of loggerhead turtles in Virginia

and Georgia. *R. venosa* is a generalist shellfish predator native to Asia that has recently been introduced in to the Chesapeake Bay (Harding and Mann, 1999). However, the size and stage of the epibiotic individuals on turtles in Georgia indicate the presence of an extra-Chesapeake breeding population of this invasive species. The authors suggest that turtle-mediated dispersal is currently the only compelling explanation for the occurrence of *R. venosa* on turtles in Georgia. These findings have important implications for the future management of invasive marine invertebrates.

Sea turtles are known to modify the physical structure of their habitat in a number of ways (Bjorndal and Jackson, 2003). Thus, another unexplored ecological implication of sea turtle epibiosis might be the extent to which turtles modify hard-bottom habitats when actively removing epibiota. This behavior involves turtles pushing their carapace against the underside of rock ledges and vigorously scrapping against the rock to remove epibiota, particularly barnacles (Frick and McFall, 2007). The rock ledges often erode during such behaviors, leaving behind scours or arched ledges, which turtles may return to for subsequent “self-grooming.” The extent to which these habitat modifications affect the surrounding reef or hard-bottom communities remains unknown.

## 15.5 CONCEPTUAL MODEL OF EPIBIOSIS

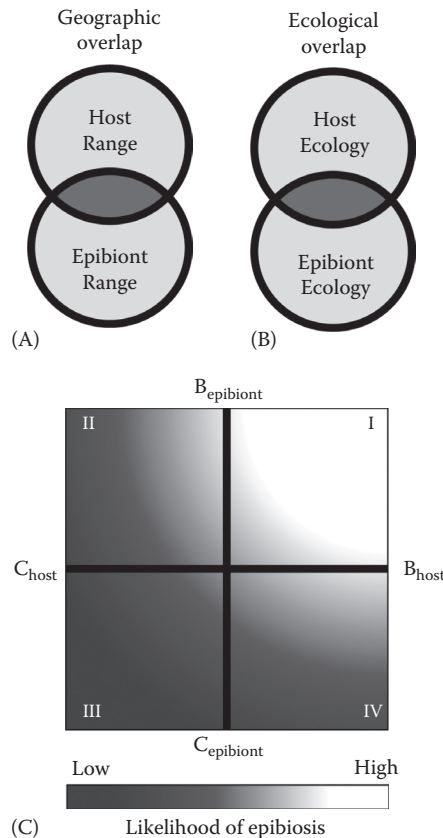
As we accumulate studies of epibiotic diversity in sea turtles, we have begun to formulate a conceptual framework to better understand and learn from these epibiotic interactions. While there have been several broad reviews on epibiosis (see Wahl, 1989; Wahl and Mark, 1999; Harder, 2009; Wahl, 2009), there has been no attempt to construct a conceptual framework to explain such associations. The conceptual model of epibiosis depicted in [Figure 15.1](#) outlines three hierarchical factors inherent to epibiotic interactions: (1) geographic overlap ([Figure 15.1A](#)), (2) ecological overlap ([Figure 15.1B](#)), and (3) the balance of costs and benefits to hosts and epibionts that dictate the likelihood of epibiosis once in close proximity ([Figure 15.1C](#)). Because the factors that affect epibiotic interactions—as displayed in this conceptual model—are inherent to the biology of the species involved, we can learn about the ecology and evolution of these species by studying epibiosis. Such a conceptual framework will hopefully allow researchers to better understand the factors that affect their particular epibiotic systems and more easily decipher the important biological information that can be gleaned from studying epibiosis in sea turtles.

### 15.5.1 GEOGRAPHIC OVERLAP

A necessary prerequisite for epibiosis is geographic overlap between the range of the host turtle and the range of the epibiont ([Figure 15.1A](#)). Logically, without geographic overlap, epibiosis between a host turtle and any potential epibiont would never occur. This is an obvious criterion for epibiosis. However, because the host turtles are highly mobile, the occurrence of particular epibiont taxa with more limited distributions can reveal information about cryptic host movements. Studies of sea turtle epibionts have provided important information on the migratory behavior of loggerhead and leatherback turtles (Caine, 1986; Eckert and Eckert, 1988), and subsequently informed the implementation of conservation measures.

### 15.5.2 ECOLOGICAL OVERLAP

Where geographic ranges overlap, epibiosis will then depend on the spatial and temporal overlap in ecology of the host turtles and potential epibionts ([Figure 15.1B](#)). Local geographic areas are typically heterogeneous mosaics of different habitats, each characterized by different ecological communities of plants and animals (e.g., saltmarshes, coral reefs, pelagic areas). The species composition of local communities may also vary through time, especially for seasonal differences



**FIGURE 15.1** Conceptual model of epibiosis. (A,B) Venn diagrams showing the geographic and ecological overlap between hosts and epibionts, respectively. (C) Graph showing the likelihood of epibiosis based on the balance of cost and benefits to hosts and epibionts ( $B_{\text{epibiont}}$ , benefit to the epibiont;  $B_{\text{host}}$ , benefit to the host;  $C_{\text{host}}$ , cost to the host;  $C_{\text{epibiont}}$ , cost to the epibiont).

in recruitment of larval propagules. Host turtles may utilize many different habitats or may show preferences for certain habitats during different behaviors (e.g., foraging, resting, and mating) or life stages, or at different times of the year. In order for epibiosis to occur, the host turtles must occupy the same habitat at the same time as free-living populations of potential epibionts. Thus, the epibionts associated with a given host turtle should reflect the assemblage of plants and animals that occupy the habitats where the hosts spend time. For example, sea turtles that tend to inhabit benthic/neritic habitats tend to host different epibionts than turtles that tend to inhabit pelagic/oceanic habitats (Limpus and Limpus, 2003; Reich et al., 2010). Such information can be used to assess interspecific and intraspecific differences in habitat use, which is critical for the implementation of effective conservation strategies.

### 15.5.3 BALANCE OF COSTS AND BENEFITS

Once in close proximity, there is a complex balance of costs and benefits for host turtles and potential epibionts that ultimately determine the likelihood of epibiosis. Figure 15.1 displays a 2D likelihood surface in which each axis represents a continuum from high benefit to high cost. The various positions of different hosts and epibionts along these cost-benefit axes depend on the net cost or benefit experienced during epibiosis. Because the relative costs and benefits are

different for different turtle–epibiont pairs, some associations are more likely and therefore more frequent than others. Epibiotic interactions in which both species experience a net benefit would have a high likelihood of occurring and therefore would be more frequent (quadrant I). Such mutually beneficial associations would favor mechanisms for active attraction and may develop into obligate associations over evolutionary time. On the other end of the continua, interactions in which both species suffer high costs would have a low likelihood and would effectively never occur (quadrant III). Interactions in which one species incurs a high cost while the other receives minimal benefit would also have a low likelihood (bottom left of quadrants II and IV), as the former species would actively avoid such interactions and the latter would gain very little by exploiting the former. Conversely, if one species receives a high benefit at a high cost to the other species (top left of quadrant II and bottom right of quadrant IV), then such associations might exhibit patterns similar to that of parasitic interactions (top left of quadrant II only). Lastly, interactions in which one species receives a high benefit while the other incurs little or no cost would have a higher likelihood and would be relatively frequent (top left of quadrants II and IV). This last scenario characterizes many of the interactions between sea turtles and their epibiota, and is typically referred to as commensalism (Leung and Poulin, 2008).

As previously mentioned, epibionts may benefit from epibiosis through reduced spatial competition and predation (Wahl, 1989; Enderlein and Wahl, 2004; Pfaller et al., 2012), improved energetic positioning (Pfaller et al., 2006; Shine et al., 2010), and range expansion (Schärer and Epler, 2007; Harding et al., 2011), while coping with costs associated with physical disturbance (Wahl, 1989; Schofield et al., 2006; Frick and McFall, 2007), transport to unfavorable physiological environments (Caine, 1986; Bjorndal, 2003), and reduced access to food resources and mates. Host turtles may benefit from epibionts through optical, chemical, or electrical camouflage (Rathbun, 1925; Fishlyn and Phillips, 1980; Feifarek, 1987; Frazier et al., 1991; Ruxton, 2009) and associational defense and cleaning (Davenport, 1994; Wahl and Mark, 1999; Bjorndal, 2003), while coping with costs associated with increased weight and drag (Logan and Morreale, 1994; Bjorndal, 2003), and tissue damage and associated susceptibility to pathogens (George, 1997; Greenblatt et al., 2004). The balance of costs and benefits to host turtles and epibionts will ultimately determine the likelihood—and therefore the frequency—of epibiosis for most turtle–epibiont associations.

## 15.6 CONSIDERATIONS

Studies that seek to elucidate the relationships that exist between sea turtles and other marine organisms require investigators to adopt an interdisciplinary approach to data collections and analyses. Knowledge of the standard measurements and preservation methods employed by taxon specialists is important to properly report and archive marine algae and invertebrate specimens (Lazo-Wasem et al., 2011). A familiarity with the life histories and general biology of the marine organisms that utilize the habitats occupied by sea turtles is essential for identifying situations that bring sea turtles into contact with the marine organisms they consume and those that attach to them. An understanding of the major systematic characters that define the major family-groups of local marine flora and fauna is helpful for identification, and to adequately ascertain evolutionary relationships between sea turtles and other marine organisms.

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## 15.A APPENDIX A: ANNOTATED BIBLIOGRAPHY OF SELECTED SEA TURTLE EPIBIONT STUDIES AND REPORTS LISTED BY GEOGRAPHIC REGION

### 15.A.1 CARIBBEAN–WESTERN ATLANTIC

Bacon, 1976 (Trinidad); Bugoni et al., 2001 (Rio Grande do Sul: Brazil); Cardenas-Palomo and Maldonado-Gasca, 2005 (Yucatan: Mexico); Caine, 1986 (South Carolina, Florida); Farrapeira-Assunção, 1991 (Brazil); Frazier et al., 1985 (Georgia, Florida); Frazier et al., 1991 (Georgia); Frazier et al., 1992 (Georgia; Rio Grande do Sul: Brazil); Frick et al., 1998 (Georgia); Frick and Slay, 2000 (Georgia); Frick and Zardus, 2010 (Panama, Georgia, and Florida); Frick et al., 2000a, 2000b (Georgia); Frick et al., 2002a,b (Georgia); Frick et al., 2003a (Jumby Bay: Antigua); Frick et al., 2004b (Georgia); Frick et al., 2006 (Florida); Frick et al., 2010a (Nova Scotia, Georgia); Frick et al., 2010b (Georgia and Florida); Gruvel, 1905 (Antilles Sea); Henry, 1954 (Florida, Texas); Hunt, 1995 (Florida); Ives, 1891 (Yucatan: Mexico); Killingley and Lutcavage, 1983 (Virginia); Lutcavage and Musick, 1985 (Virginia); Nilsson-Cantell, 1921 (Florida); Nilsson-Cantell, 1939 (Bay of Chacopata: Venezuela); Pereira et al., 2006 (Almofala: Brazil); Pilsbry, 1916 (Cape Frio: Brazil; Delaware, Florida, New Jersey; Point Patuca: Honduras; West Indies); Plotkin, 1996 (Texas); Richards, 1930 (New Jersey); Rudloe et al., 1991 (Florida); Schwartz, 1960 (Maryland); Walker, 1978 (North Carolina); Wass, 1963 (Virginia); Wells, 1966 (Florida); Weltner, 1897 (Florida; Cuba; Bahia: Brazil); Young, 1991 (Brazil); Zavodnik, 1997 (Rovinj: Croatia); Zullo and Bleakney, 1966 (Massachusetts; Nova Scotia: Canada); Zullo and Lang, 1978 (South Carolina).

### 15.A.2 MEDITERRANEAN–EASTERN ATLANTIC

Badillo-Amador, 2007 (Mediterranean Sea); Barnard, 1924 (Table Bay: South Africa); Broch, 1924 (Baie du Levrier: Mauretania; Gambia); Broch, 1927 (Rabat: Morocco); Carriol and Vader, 2002 (Finmark: Norway); Caziot, 1921 (Nice: France); Chevereaux and de Guerne, 1893 (between Algeria and Balaeres); Darwin, 1854 (Africa; Mediterranean Sea); Davenport, 1994 (Madeira); Frazier et al., 1985 (Peloponnesus, Zakynthos Island: Greece); Frick et al., 2010a (Gabon: Africa); Gauld, 1957 (Accra: Ghana); Geldiay et al., 1995 (Koycegiz-Dalyankoy: Turkey); Gramentz, 1988 (Malta, Zacharo, Zakynthos: Greece; Lampedusa: Italy); Gruvel, 1903 (Palermo: Italy; Alexandria: Egypt); Gruvel, 1931 (Gulf of Alexandrette); Haelters and Kerckhof, 1999 (DeHaan: Belgium); Haelters and Kerckhof, 2001 (Oostende: Belgium); Holothuis, 1952 (Ouddorp: the Netherlands); Holothuis, 1969 (Ameland Island: the Netherlands); Kitsos et al., 2005 (Aegean Sea); Kolosvary, 1939 (Rovigno, d'Istria: Croatia); Kolosvary, 1943 (Alexandria: Egypt; Palermo, Sicily: Italy); Kolosvary, 1951 (Mediterranean Sea); Koukouras and Matsa, 1998 (Aegean Sea; Levantine Basin); Lanfranco, 1979 (St. Julian's: Malta); Lucas, 1968 (Mediterranean Sea); Margaritoulis, 1985 (Zakynthos: Greece); Nilsson-Cantell, 1921 (Bibundi: Cameroon); Nilsson-Cantell, 1931 (Mediterranean Sea); O'Riordan, 1979 (Dingle: Ireland); O'Riordan and Holmes, 1978 (Ventry Harbor: Ireland); Pilsbry, 1916 (Taranto: Italy; Cape of Good Hope: South Africa); Quigley and Flannery, 1993 (Dingle Bay: Ireland); Relini, 1968 (Gulf of Trieste: Italy); Relini, 1969 (Adriatic Sea); Relini, 1980 (Adriatic Sea); Sezgin et al., 2009 (Turkey); Smaldon and Lyster, 1976 (Skarvoy: Norway; Crail, Kirkcudbrightshire: Scotland; Cornwall: England); Stubbings, 1965 (Hann, Saloum River: Senegal); Stubbings, 1967 (Goree, Hann: Senegal); Utinomi, 1959 (Banyuls-sur-Mer: France); Zakhama-Sraieb et al., 2010 (Gulf of Gabès: Mediterranean Sea).

### 15.A.3 INDO–WEST PACIFIC

Annandale, 1906 (Rameswaram Island: India; Gulf of Manaar); Balazs, 1978 (Hawaii); Balazs, 1980 (Hawaii); Balazs et al., 1987 (Hawaii); Borradaile, 1903 (Minikoi Island: India); Broch, 1916 (Broome: Australia); Broch, 1931 (Gulf of Thailand; Nagasaki: Japan); Broch, 1947 (Ream: Cambodia; Indochina); Bustard, 1976 (Great Barrier Reef: Australia); Daniel, 1956 (Tuticorin, Drusadai Islands, Royapuram Coast, Madras Coast: India); Daniel, 1962 (Little Andaman



Island: India); Darwin, 1854 (Low Archipelago: French Polynesia; Australia); Dawydoff, 1952 (Pulo Condore: Vietnam; Ream: Cambodia); Deraniyagala, 1939 (Bentota: Ceylon); Dobbs and Landry, 2004 (Great Barrier Reef: Australia); Fernando, 1978 (Porto Novo: India); Glazebrook and Campbell, 1990 (Torres Strait: Australia); Fischer, 1886 (Pulo Condor: Vietnam); Foster, 1978 (North Island: New Zealand); Frazier, 1971 (Aldabra Atoll); Frazier et al., 1985 (Orissa: India; Tanzania: Africa); Frazier, 1989 (Dwarka Island: India); Frazier et al., 1992 (Orissa, Gujarat: India; Karachi, Pakistan); Gordon, 1970 (Hawaii); Gruvel, 1903 (Seychelles; Mallicolo: Vanuatu; Djibouti; Sandwich Island; Cochinchina: Vietnam); Gruvel, 1907 (Andaman Islands: India); Gruvel, 1912 (Tuamotu Archipelago: French Polynesia); Hayashi and Tsuji, 2008 (Okinawa: Japan); Hendrickson, 1958 (Johor, Sarawak: Malaysia); Hiro, 1936 (Wakayama Prefecture, Aichi Prefecture: Japan); Hiro, 1937a (Baberudaobu Island: Palau); Hiro, 1939 (Toyama Bay: Japan); Jones, 1990 (Australia); Jones et al., 1990 (Tasmania; Australia); Jones et al., 2000 (summary of distribution); Kruger, 1911b (Sagami Bay: Japan); Kruger, 1912 (Timor Sea); Lanchester, 1902 (Kota Bharu: Malaysia); Limpus et al., 1983a (Campbell Island: Australia); Limpus et al., 1983b (Crab Island: Australia); Limpus et al., 2005 (Raine Island: Australia); Loop et al., 1995 (Milman Island: Australia); Losey et al., 1994 (Hawaii); Matsuura and Nakamura, 1993 (Kagoshima Prefecture: Japan); McCann, 1969 (North Island: New Zealand); Monroe and Limpus, 1979 (Queensland: Australia); Mustaquim and Javed, 1993 (Sandspit Beach: Pakistan); Newman et al., 1969 (Hawaii); Newman and Abbott, 1980 (California); Nilsson-Cantell, 1921 (Western Australia: Australia); Nilsson-Cantell, 1930a (Enoe Island: Malaysia); Nilsson-Cantell, 1932 (Bentota: Sri Lanka); Nilsson-Cantell, 1937 (Singapore); Nilsson-Cantell, 1938 (Maldives; Kilakarai, Andaman Islands, River Hooghly, mouth of Ganges: India); Pillai, 1958 (Quilon: India); Pilsbry, 1916 (Hawaii; Caroline Islands; Ana: Japan; Saigon: Vietnam); Pilsbry, 1927 (Hawaii); Ren, 1980 (Xisha Islands); Ren, 1987 (China); Ross, 1981 (Oman); Smaldon and Lyster, 1976 (Kuala Lumpur: Malaysia); Tachikawa, 1995 (Japan); Utinomi, 1949 (Hakata Bay: Japan); Utinomi, 1958 (Sagami Bay: Japan); Utinomi, 1966 (Amakusa: Japan); Utinomi, 1969 (Kharg: Iran); Utinomi, 1950 (Tanabe Bay: Japan); Utinomi, 1970 (Hakui, Cape Kyoga-misaki, Kamo, Nezugaseki, Sado Island: Japan); Wagh and Bal, 1974 (Bombay: India); Weltner, 1897 (Massaua: New Guinea; Torres Strait); Weltner, 1910 (Ile Europa); Zann and Harker, 1978 (Queensland: Australia); Zardus and Balazs, 2007 (Hawaii).

#### 15.A.4 EASTERN PACIFIC

Angulo-Lozano et al., 2007 (Sinaloa: Mexico); Beaumont et al., 2007 (Galapagos Islands: Ecuador); Brown and Brown, 1995 (Peru); Darwin, 1854 (Mexico; Galapagos Islands: Ecuador); Frazier et al., 1985 (Galapagos Islands: Ecuador); Frazier et al., 1992 (Santa Rosa: Ecuador); Frick et al., 2011a,b (Baja California: Mexico; Eastern Tropical Pacific; Galapagos: Ecuador); Green, 1998 (Galapagos Islands: Ecuador); Henry, 1941 (La Paz: Mexico); Henry, 1960 (Gulf of California, Guaymas: Mexico); Hernandez-Vasquez and Valadez-Gonzalez, 1998 (Jalisco: Mexico); Hubbs, 1977 (California); Kolosvary, 1943 (San Jose: Guatemala); Lazo-Wasem et al., 2011 (Jalisco: Mexico); MacDonald, 1929 (Cocos Island: Costa Rica); Newman et al., 1969 (Baja California: Mexico; Eastern Pacific); Pilsbry, 1916 (Baja California: Mexico; Galapagos Islands: Ecuador); Ross and Newman, 1967 (Baja California: Mexico); Stinson, 1984 (California); Vivaldo et al., 2006 (Michoacan, Oaxaca: Mexico); Weltner, 1897 (western Mexico; California; Valparaiso: Chile); Young and Ross, 2000 (Sonora: Mexico); Zullo, 1986 (Galapagos Islands: Ecuador); Zullo, 1991 (Galapagos Islands: Ecuador).

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