

# Hitchhikers reveal cryptic host behavior: new insights from the association between *Planes major* and sea turtles in the Pacific Ocean

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**Abstract** Studies that incorporate information from habitat-specific ecological interactions (e.g., epibiotic associations) can reveal valuable insights into the cryptic habitat-use patterns and behavior of marine vertebrates. Sea turtles, like other large, highly mobile marine vertebrates, are inherently difficult to study, and such information can inform the implementation of conservation measures. The presence of epipelagic epibionts, such as the flotsam crab *Planes major*, on sea turtles strongly suggests that neritic turtles have recently occupied epipelagic habitats (upper 200 m in areas with >200 m depth) and that epipelagic turtles spend time at or near the surface. We quantified the

effects of turtle species, turtle size, and habitat (neritic or epipelagic) on the frequency of epibiosis ( $F_0$ ) by *P. major* on sea turtles in the Pacific Ocean. In neritic habitats, we found that loggerhead ( $F_0 = 27.6\%$ ) and olive ridley turtles ( $F_0 = 26.2\%$ ) host crabs frequently across a wide range of body sizes, and green turtles almost never host crabs ( $F_0 = 0.7\%$ ). These results suggest that loggerheads and olive ridleys display variable/flexible epipelagic-neritic transitions, while green turtles tend to transition unidirectionally at small body sizes. In epipelagic habitats, we found that loggerheads host crabs ( $F_0 = 92.9\%$ ) more frequently than olive ridleys ( $F_0 = 50\%$ ) and green turtles ( $F_0 = 38.5\%$ ). These results suggest that epipelagic loggerheads tend to spend more time at or near the surface than epipelagic olive ridleys and green turtles. Results of this study reveal new insights into habitat-use patterns and behavior of sea turtles and display how epibiont data can

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supplement data from more advanced technologies to gain a better understanding of the ecology of marine vertebrates during cryptic life stages.

## Introduction

Large, highly mobile marine vertebrates are inherently difficult to study and monitor, which makes them vulnerable to overexploitation (Heppell et al. 1999). Long life spans, delayed sexual maturity, and wide spatiotemporal habitat-use patterns prevent direct monitoring of individuals during most life stages, especially as juveniles. An interdisciplinary approach is needed to better understand the ecology of marine vertebrates during cryptic life stages (Jones and Seminoff 2013). New advances in molecular and satellite-tracking technologies have helped reveal critical information on migratory behavior and habitat-use patterns of these elusive and often threatened organisms (Graham et al. 2012; Saba 2013). However, such tools remain expensive and, in the case of satellite tracking, the small number of transmitters that are deployed and the short duration of deployment relative to life span limit our ability to infer population-wide and long-term patterns. Studies that incorporate information from habitat-specific ecological interactions (e.g., with predators, prey, parasites, and commensals) can reveal valuable insights into the habitat-use patterns and behavior of marine vertebrates and help inform the implementation of conservation measures.

The external surfaces of marine vertebrates are often colonized by a variety of marine plants and animals. This phenomenon, termed “epibiosis,” results when a host supports one or more colonizers, called epibionts (Wahl and Mark 1999). Most epibionts are unspecialized organisms normally found associated with inanimate structures in the surrounding marine environment (i.e., “free living”). Epibiosis necessitates spatial overlap between the geographic ranges and habitats of the hosts and free-living populations of potential epibionts (Frick and Pfaller 2013). Thus, the epibionts associated with a given host should reflect the characteristic assemblage of plants and animals that occupy the regions and habitats where the host spends time. Because marine vertebrates often use different geographic regions and habitat types during different behaviors or life stages, the presence of particular epibiont taxa with more limited distributions can reveal information about cryptic host behavior (Frick and Pfaller 2013).

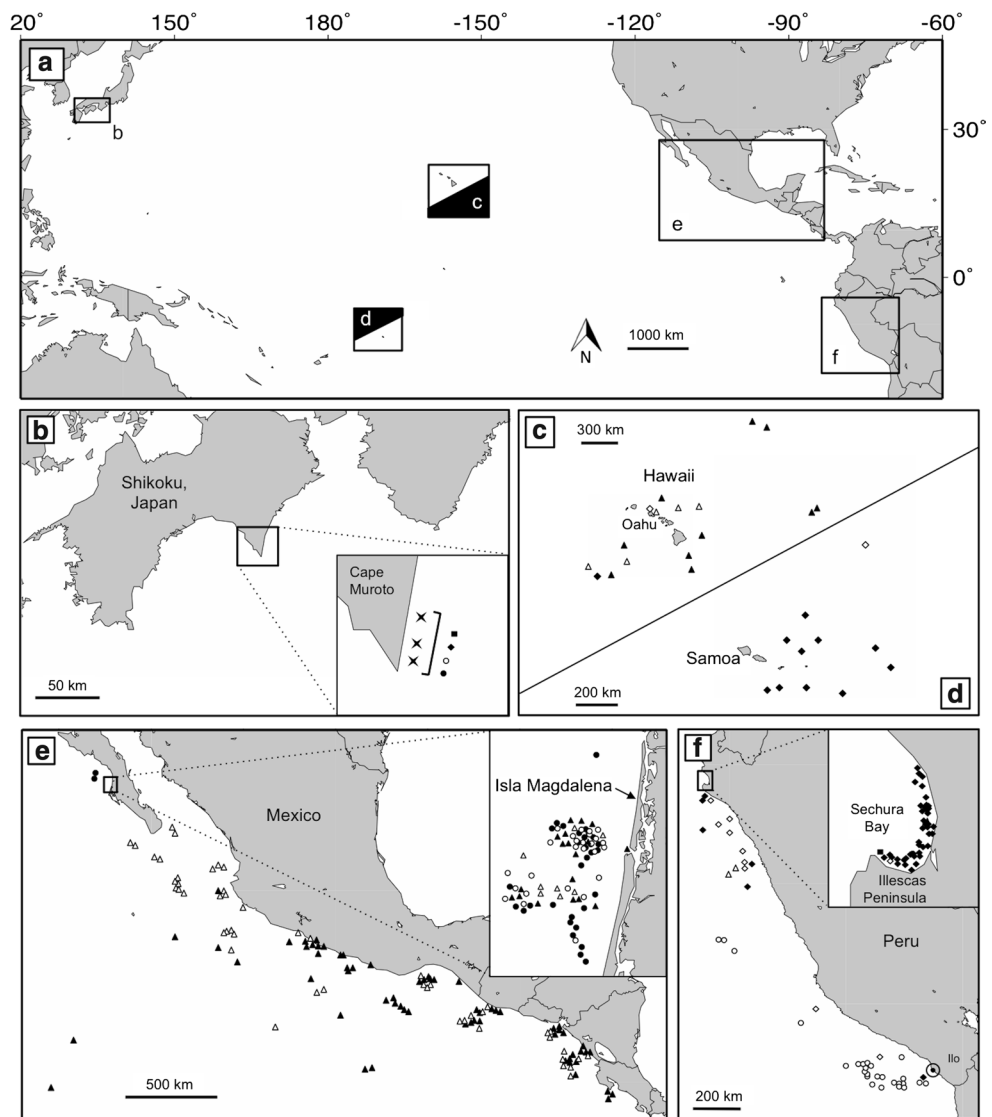
Studies of the associations between sea turtles and their epibionts have provided important information on their migratory behavior (Killingley and Lutcavage 1983; Caine 1986; Eckert and Eckert 1988) and habitat-use patterns (Pfaller et al. 2008; Reich et al. 2010; Hosono and Minami 2011). For example, the foraging grounds and migratory

corridors of nesting loggerhead turtles (*Caretta caretta*) have been inferred from the presence of particular epibiont taxa that are geographically restricted to areas away from the nesting beaches (Caine 1986; Pfaller et al. 2008). The most common dichotomy that has been used to infer inter- and intraspecific differences in habitat use among sea turtles is the presence of particular epibiont species associated with turtles occupying either epipelagic (upper 200 m in areas with >200 m depth) or neritic/benthic habitats (Limpus and Limpus 2003; Reich et al. 2010). The presence of epipelagic organisms such as pedunculate barnacles of the genera *Lepas* and *Conchoderma* and grapsid crabs of the genus *Planes* on sea turtles indicates that turtles are occupying or have recently occupied epipelagic habitats, which provides valuable insights into cryptic migratory behaviors and habitat-use patterns of sea turtle populations.

Studies of *Planes* crabs associated with sea turtles represent the most detailed information to date on sea turtle–epibiont symbiosis (Frick and Pfaller 2013). *Planes* crabs may settle on turtles as megalopal-stage larvae or colonize turtles after initially settling on floating debris. Initial colonization likely occurs while epipelagic turtles are resting or swimming slowly at the surface of the ocean. Crabs may become disassociated from turtles when turtles remain submerged for long periods of time, when turtles enter neritic waters, or when turtles come ashore to nest. Associations between *Planes minutus* and oceanic-stage loggerheads in the North Atlantic Ocean are common—82 % of turtles host crabs (Dellinger et al. 1997)—and crab dietary data suggest a cleaning association (Davenport 1994; Frick et al. 2000, 2004). More recently, similar symbiotic associations have been described for *Planes major* on sea turtles in the South Atlantic (Carranza et al. 2003; Bugoni et al. 2007; Pons et al. 2011) and Pacific oceans (Barceló et al. 2008; Frick et al. 2011). Because differences in the frequency of *Planes* crabs on sea turtles suggest inter- and intraspecific differences in the use of epipelagic habitats, quantitative surveys for crabs on turtles can provide information on cryptic behavioral traits of sea turtle populations.

Habitat-use patterns of sea turtles in the Pacific Ocean tend to be similar to those in the Atlantic Ocean (Musick and Limpus 1997). All species, excluding the flatback turtle (*Natator depressus*), use epipelagic habitats for juvenile development (Musick and Limpus 1997). In general, leatherback (*Dermochelys coriacea*) and olive ridley (*Lepidochelys olivacea*) turtles tend to remain epipelagic throughout adulthood (Plotkin 2010; Saba 2013), while loggerhead (*C. caretta*), green (*Chelonia mydas*), and hawksbill (*Eretmochelys imbricata*) turtles tend to transition to neritic habitats as juveniles and remain neritic as adults (Musick and Limpus 1997). Recently, however, several studies have shown that alternative habitat-use patterns exist among turtles in the Pacific Ocean. Satellite telemetry and stable

**Fig. 1** Maps showing sampling sites, turtle-capture locations, and *Planes major* presence (open icons) or absence (closed icons). **a** Pacific Ocean showing the five sampling areas in the present study. **b** The island of Shikoku, Japan, with inset showing Cape Muroto and the locations of three pound nets (stars) where neritic turtles were captured. **c** Hawaii, with epipelagic turtle-capture locations by the Hawaiian longline fisheries and turtle strandings on Oahu. **d** Samoa, with epipelagic turtle-capture locations by Samoan longline fisheries. **e** Mexico and Central America, with neritic and epipelagic turtle-capture locations along coast and offshore 1,800 km and inset showing turtle-capture locations off the west coast of Baja California Sur, Mexico. **f** Peru, with epipelagic turtle-capture locations along the coast and inset showing turtle-capture locations within Sechura Bay. Circles, *C. caretta*; triangles, *L. olivacea*; diamonds, *C. mydas*; squares, *E. imbricata*. Maps were created using seaturtle.org Maptool



isotope analyses of loggerhead and green turtles in the western North Pacific indicate that adult turtles use both epipelagic and neritic habitats (Hatase et al. 2002, 2006, 2010). Moreover, juvenile loggerheads in the North Pacific are known to occupy either epipelagic habitats in the central North Pacific or neritic habitats along the Baja California peninsula, where there are fundamental differences in the distribution, abundance, and quality of prey (Parker et al. 2005; Peckham et al. 2011). Because the existence of alternative strategies has emerged, more studies are needed to assess population-wide variation in habitat-use patterns and behavior among different sea turtle species and among different life stages.

In this study, we studied the interactions between *P. major* and sea turtles at five sites in the Pacific Ocean. We quantified the effects of turtle species, turtle size, and habitat (neritic or epipelagic) on the frequency of these associations. These results were then integrated with a review

of all known records of *P. major*–sea turtle interactions in the Pacific Ocean to evaluate two primary questions: (1) Do turtles display variable/flexible epipelagic–neritic transitions? and (2) do turtles display similar surface-dwelling behavior in epipelagic habitats?

## Methods

Associations between *Planes major* and sea turtles in the Pacific Ocean were surveyed at five sites (Fig. 1a): (1) Japan, in neritic habitats along the east coast of Muroto on the island of Shikoku (33.28°N, 134.15°E) (Fig. 1b); (2) Hawaii, on Oahu (21.47°N, 157.98°W) and within the surrounding epipelagic habitat (14.42–28.62°N, 140.10–166.82°W) (Fig. 1c); (3) Samoa, within the surrounding epipelagic habitat (7.13–16.47°S, 166.2–171.32°W) (Fig. 1d); (4) Mexico and Central America, in neritic and

epipelagic habitats from Baja California Sur, Mexico (25.85°N, 111.97°W) to the Nicoya Peninsula, Costa Rica (10°N, 85.42°W) to 1,800 km offshore (8.52°N, 118.25°W) (Fig. 1e); and (5) Peru, in neritic habitats in Sechura Bay (5.75°S, 80.95°W) and epipelagic habitats along the entire coast from Illescas Peninsula in the north (5.96°S, 81.05°W) to Ilo in the south (18.20°S, 73.03°W) (Fig. 1f).

In Japan, neritic turtles incidentally captured by large pound net fisheries between November 4, 2010, and November 24, 2011, were inspected for crabs within 0.5–3 h of capture. In Hawaii and Samoa, epipelagic turtles recovered dead in longline fisheries or found stranded on beaches in Oahu between October 29, 2010, and February 14, 2013, were initially frozen and inspected for crabs up to 4 weeks post-mortem. In Mexico and Central America, turtles captured by hand from a small boat between August 8, 2003, and November 16, 2003, and between July 3, 2011, and October 21, 2011, were inspected for crabs within 5–10 min of capture. In Peru, turtles incidentally captured by artisanal gillnet (neritic) and longline fisheries (epipelagic) between January 10, 2011, and May 31, 2012, were inspected for crabs within 5–10 min of capture. All turtles were removed from nets and longlines within 12 h of entanglement or hooking, while turtles captured by hand in Mexico and Central America were removed from the water within 30 s. All turtles were measured for body size (curved carapace length, CCL). When observed, *P. major* specimens were captured by hand and placed immediately in 75–95 % ethanol, or frozen and subsequently transferred to 75–95 % ethanol, for future studies. In Mexico and Central America, ocean depth (m) was measured during each capture event and turtles were separated by habitat type: neritic (<150 m depth) and epipelagic (>350 m depth). Turtles captured between 150 and 350 m depth were not included in this study.

Frequency of epibiosis ( $F_0$ ) was derived by dividing the number of turtles hosting *P. major* by the number of turtles surveyed. We determined  $F_0$  for each turtle species in each site separately, for each turtle species for each habitat type (neritic and epipelagic), for each site for all applicable turtle species combined, and for each turtle species regardless of site/habitat. We used contingency tables and Fisher's exact tests to test for differences in  $F_0$  (1) among turtle species within each habitat, (2) between habitats within each turtle species, and (3) among turtle species regardless of habitat (Bonferroni correction for 13 Fisher's exact tests: corrected  $\alpha = 0.004$ ). Contingency tables and Fisher's exact tests were used in place of logistic regression analyses because these methods generate more robust results for unbalanced sampling designs and when expected values are <10 (Hirji et al. 1991). To test if turtle size affected  $F_0$ , we performed binomial logistic regressions for each turtle species from each site. All statistical analyses were performed in R for Windows v. 3.0.0 (R Development Core Team 2008).

## Results

We surveyed 584 turtles for the presence of *P. major* and found 169 ( $F_0 = 28.9$  %) hosting at least one crab. All crabs were identified as *P. major* following Chace (1951), and most crabs were found as singletons or in heterosexual pairs regardless of turtle species, site, or habitat. The frequency of epibiosis for the three primary turtle species—loggerhead turtles (*C. caretta*), green turtles (*C. mydas*), and olive ridley turtles (*L. olivacea*)—varied among species, sites, and habitats (Table 1). We surveyed two hawksbill turtles (*E. imbricata*), and neither turtle hosted crabs (1 in Japan and 1 in Peru). We surveyed one leatherback turtle (*D. coriacea*) in Hawaii, and it did not host crabs. Because of small sample sizes ( $N < 5$ ), we excluded some data from statistical analyses and figures: one hawksbill in Japan, two green turtles and one leatherback in Hawaii, and two olive ridleys and one hawksbill in Peru.

We found significant differences in  $F_0$  (1) among turtle species within each habitat, (2) between habitats within each turtle species, and (3) among turtle species regardless of habitat (Table 1; see Table S1 for detailed results from contingency tables and Fisher's exact tests). In neritic habitats and when data from both habitats were combined, loggerheads and olive ridleys hosted *P. major* at the same frequency, but more frequently than green turtles. In epipelagic habitats, loggerheads hosted *P. major* more frequently than green turtles and olive ridleys, which host *P. major* with the same frequency. Turtles in epipelagic habitats hosted *P. major* more frequently than turtles in neritic habitats for each turtle species separately and for all turtle species combined.

We found a significant negative effect of turtle size on  $F_0$  for neritic loggerheads in Mexico (Table 2; Fig. 2b). We found no significant effect of turtle size on  $F_0$  for neritic loggerheads in Japan (Fig. 2a), epipelagic green turtles in Peru (Fig. 3c), epipelagic olive ridleys in Hawaii (Fig. 4a), neritic olive ridleys in Mexico and Central America (Fig. 4b), and epipelagic olive ridleys in Mexico and Central America (Fig. 4c; Table 2). The effect of turtle size on  $F_0$  was not tested for (1) epipelagic loggerheads in Peru because  $F_0$  was 100 % on turtles with CCL data (Fig. 2c), (2) neritic green turtles in Japan because  $F_0$  was 0 % (Fig. 3a), (3) epipelagic green turtles in Samoa because only one turtle hosted *P. major* (Fig. 3b), and (4) neritic green turtles in Peru because only one turtle hosted *P. major* (Fig. 3c; Table 2).

## Discussion

In this study, we quantified the interactions between *P. major* and sea turtles in epipelagic and neritic habitats

**Table 1** Comparison of frequency of epibiosis among turtle species, site, and habitat: neritic (N), epipelagic (E), *C. caretta* (CC), *C. mydas* (CM), *L. olivacea* (LO)

| Site                  | Habitat | Frequency of epibiosis (%) |                          |                           |                           |
|-----------------------|---------|----------------------------|--------------------------|---------------------------|---------------------------|
|                       |         | CC                         | CM                       | LO                        | Total                     |
| Japan                 | N       | 21.1 (147)                 | 0.0 (47)                 | –                         | 16.0 (194)                |
| Hawaii                | E       | –                          | –                        | 33.3 (15)                 | 33.3 (15)                 |
| Samoa                 | E       | –                          | 9.1 (11)                 | –                         | 9.1 (11)                  |
| Mexico and C. America | N       | 44.6 (56) <sup>†</sup>     | –                        | 26.2 (61)                 | 35.0 (117)                |
| Mexico and C. America | E       | –                          | –                        | 52.3 (105)                | 52.3 (105)                |
| Peru                  | N       | –                          | 1.0 (99)                 | –                         | 1.0 (99)                  |
| Peru                  | E       | 92.9 (28)                  | 60.0 (15)                | –                         | 81.4 (43)                 |
| All sites             | N       | 27.6 (203) <sup>a/a</sup>  | 0.7 (146) <sup>a/b</sup> | 26.2 (61) <sup>a/a</sup>  | 17.8 (410) <sup>a/–</sup> |
| All sites             | E       | 92.9 (28) <sup>b/a</sup>   | 38.5 (26) <sup>b/b</sup> | 50.0 (120) <sup>b/b</sup> | 55.2 (174) <sup>b/–</sup> |
| Total                 | N and E | 35.5 (231) <sup>–/a</sup>  | 6.4 (172) <sup>–/b</sup> | 42.0 (181) <sup>–/a</sup> | 28.9 (584)                |

Samples sizes are in parentheses

Superscripts before slash indicate significant differences between habitats, and superscripts after slash indicate significant differences between turtle species. Different superscript letters indicate values that are significantly different from each other. Bonferroni correction for 13 Fisher's exact tests of independence: corrected  $\alpha = 0.004$  (see Table S1 for statistical details)

<sup>†</sup> All turtles captured in 2011 off Baja California Sur, Mexico (see inset on Fig. 1e)

**Table 2** Results of binomial logistic regression analyses testing the effect of turtle size on frequency of occurrence: neritic (N), epipelagic (E), *C. caretta* (CC), *C. mydas* (CM), *L. olivacea* (LO), not significant (NS), significant (S)

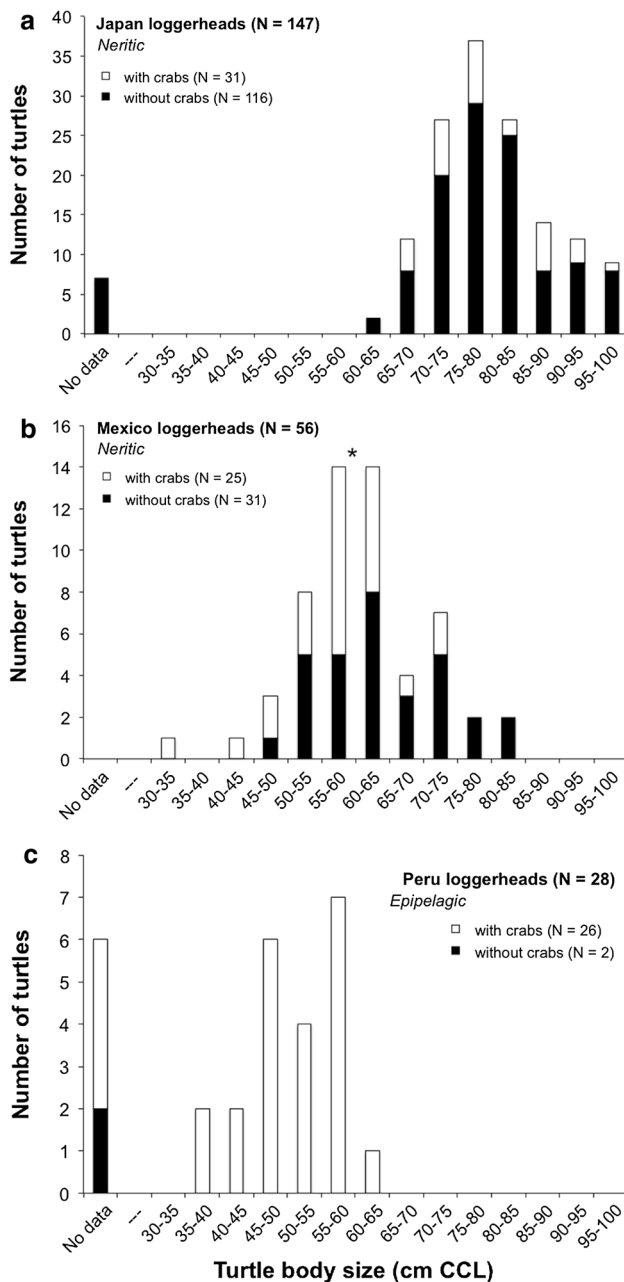
| Species | Site                  | Habitat | Binomial logistic regression |           |         |     |         |      |
|---------|-----------------------|---------|------------------------------|-----------|---------|-----|---------|------|
|         |                       |         | Slope                        | Intercept | z value | df  | P value | Sig. |
| CC      | Japan                 | N       | –0.02                        | 0.046     | –0.65   | 138 | 0.51    | NS   |
| CC      | Mexico                | N       | –0.09                        | 5.34      | –2.42   | 54  | 0.02    | S    |
| CC      | Peru                  | E       | Did not test (see text)      |           |         |     |         |      |
| CM      | Japan                 | N       | Did not test (see text)      |           |         |     |         |      |
| CM      | Samoa                 | E       | Did not test (see text)      |           |         |     |         |      |
| CM      | Peru                  | N       | Did not test (see text)      |           |         |     |         |      |
| CM      | Peru                  | E       | –0.03                        | 1.81      | –0.29   | 12  | 0.77    | NS   |
| LO      | Hawaii                | E       | –0.76                        | –49.2     | 1.78    | 13  | 0.08    | NS   |
| LO      | Mexico and C. America | N       | –0.08                        | 4.45      | –1.07   | 59  | 0.28    | NS   |
| LO      | Mexico and C. America | E       | –0.01                        | 0.92      | –0.87   | 102 | 0.38    | NS   |

in the Pacific Ocean. Several of these associations represented previously undescribed and/or un-quantified interactions. We integrated these findings with those from previous studies on *P. major*–sea turtle interactions in the Pacific Ocean (Table 3) to gain new insights into cryptic habitat-use patterns and behavior of sea turtles in this region. Because inter- and intraspecific differences in the frequency of epibiosis by *P. major* ( $F_0$ ) suggest differences in epipelagic habitat use and behavior, we used  $F_0$  data to address our two questions: (1) Do turtles display variable/flexible epipelagic-neritic transitions? and (2) do turtles display similar surface-dwelling behavior in epipelagic habitats?

Do turtles display variable/flexible epipelagic-neritic transitions?

Most sea turtles exhibit ontogenetic habitat shifts, in which juvenile turtles transition from being primarily epipelagic to being primarily neritic (Musick and Limpus 1997). When turtles transition from epipelagic to neritic habitats, *Planes* crabs—and other epipelagic epibiota—are transported away from their optimal habitat and into areas with different physiological conditions and higher predator densities. Such transitions also involve characteristic changes in turtle diving behavior, in which epipelagic turtles transition to a more benthic existence (Bolten 2003).





**Fig. 2** Size–frequency histograms showing loggerhead turtles (*C. caretta*) that did not host *P. major* (black bars) and turtles that hosted at least one *P. major* (white bars) from **a** neritic habitats in Japan, **b** neritic habitats in Mexico, and **c** epipelagic habits in Peru. Turtles on the border of two size increments were placed in the larger increment. Asterisks indicate when a significant effect of turtle size on crab presence was detected ( $\alpha = 0.05$ )

These changes in behavior likely have a strong detrimental effect on the association between crabs and their host turtles. Our data support this premise:  $F_0$  in epipelagic habitats (55.2 %) was significantly greater than  $F_0$  in neritic habitats (17.8 %). Based on this assumption, the presence of crabs on neritic turtles strongly suggests that turtles

recently occupied epipelagic habitats. Differences in  $F_0$  should therefore reflect differences in epipelagic-neritic transitions. Three hypotheses emerge to explain differences in  $F_0$  among neritic turtles: (1) If turtles transition unidirectionally (epipelagic  $\rightarrow$  neritic) at small body sizes, then neritic turtles should show relatively high  $F_0$  at small body sizes and relatively low (or 0)  $F_0$  at larger body sizes; (2) if turtles transition unidirectionally (epipelagic  $\rightarrow$  neritic) at variable body sizes, then neritic turtles should show relatively high  $F_0$  across all sizes; (3) if turtles transition bidirectionally (epipelagic  $\leftrightarrow$  neritic), then neritic turtles should show relatively high  $F_0$  across all sizes. Because hypotheses (2) and (3) are indistinguishable using data on  $F_0$ , we can combine these two hypotheses into one; if turtles display variable/flexible epipelagic-neritic transitions, then neritic turtles should show relatively high  $F_0$  across all sizes. Support for this hypothesis would suggest that turtle species and/or populations exhibit a high degree of epipelagic habitat use. We can explore these two hypotheses (1 vs. 2/3) using the  $F_0$  data to distinguish differences in epipelagic-neritic transitions among different turtle species in different locations.

Loggerhead turtles surveyed in neritic habitats off Japan were found hosting crabs relatively frequently ( $F_0 = 21.1$  %) across a wide range of body sizes (60–100 cm CCL). These subadult and adult turtles are thought to exhibit unidirectional transitions to neritic habitats at a relatively narrow range of body sizes (60–80 cm CCL—modified from Ishihara et al. 2011). However, our data suggest that the transition to neritic habitats is more variable and/or flexible. Moreover,  $F_0$  for neritic loggerheads in Japan was considerably higher than for neritic aggregations in the Atlantic Ocean (<5 %—Frick et al. 1998, 2006), suggesting a greater use of epipelagic habitats by neritic-stage loggerheads in Japan. Previous studies applying satellite telemetry and stable isotope analysis suggest that adult loggerheads in Japan display persistent alternative foraging strategies (oceanic vs. neritic) (Hatase et al. 2002, 2010). However, our results based on  $F_0$  suggest that this habitat-use dichotomy is less clear-cut, and some individual turtles may actually use both foraging areas. Thus, our data support the hypothesis that (at least some) subadult and adult loggerheads in Japan display variable/flexible epipelagic-neritic transitions.

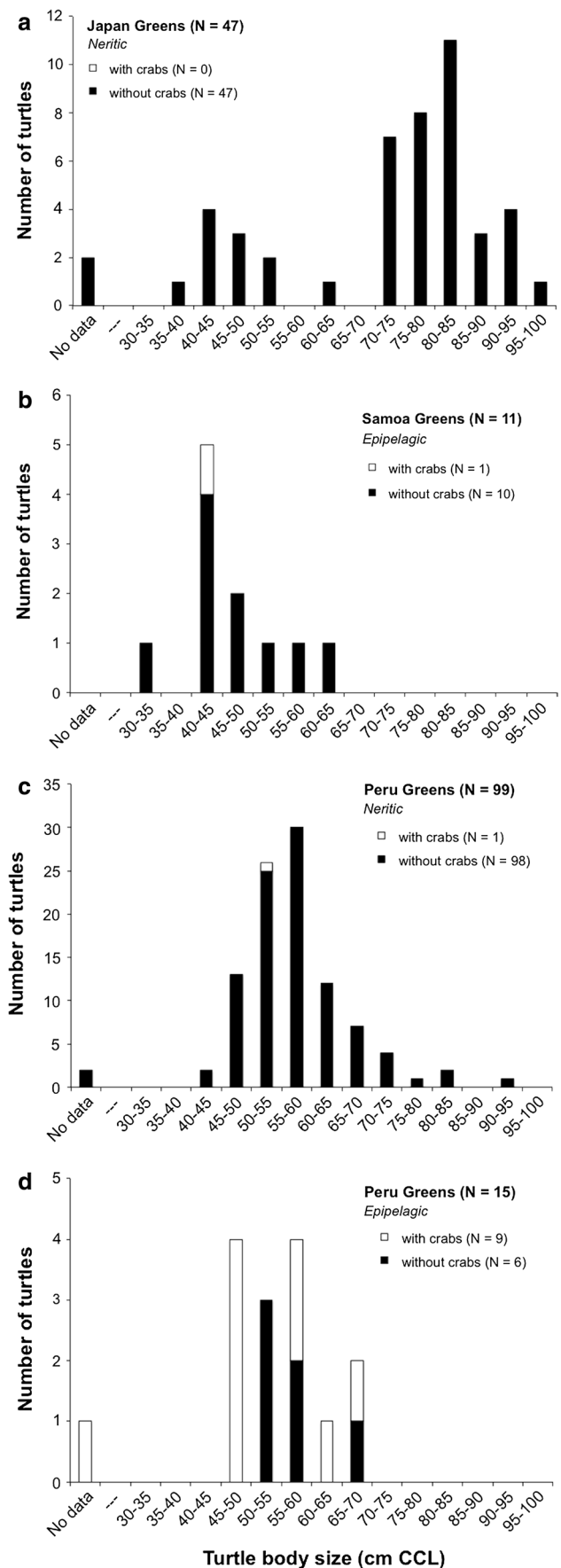
Loggerheads surveyed in neritic habitats in Mexico were mostly juvenile turtles (39–86 cm CCL—modified from Nichols et al. 2000; this study) and were found hosting crabs frequently (44.6 %), especially within the lower portion of the observed size range (30–65 cm CCL). Dietary and demographic data for juvenile loggerheads (40–80 cm CCL) in the eastern North Pacific suggest that turtles occupy either epipelagic habitats in the central North Pacific or neritic habitats along Mexico's Baja California

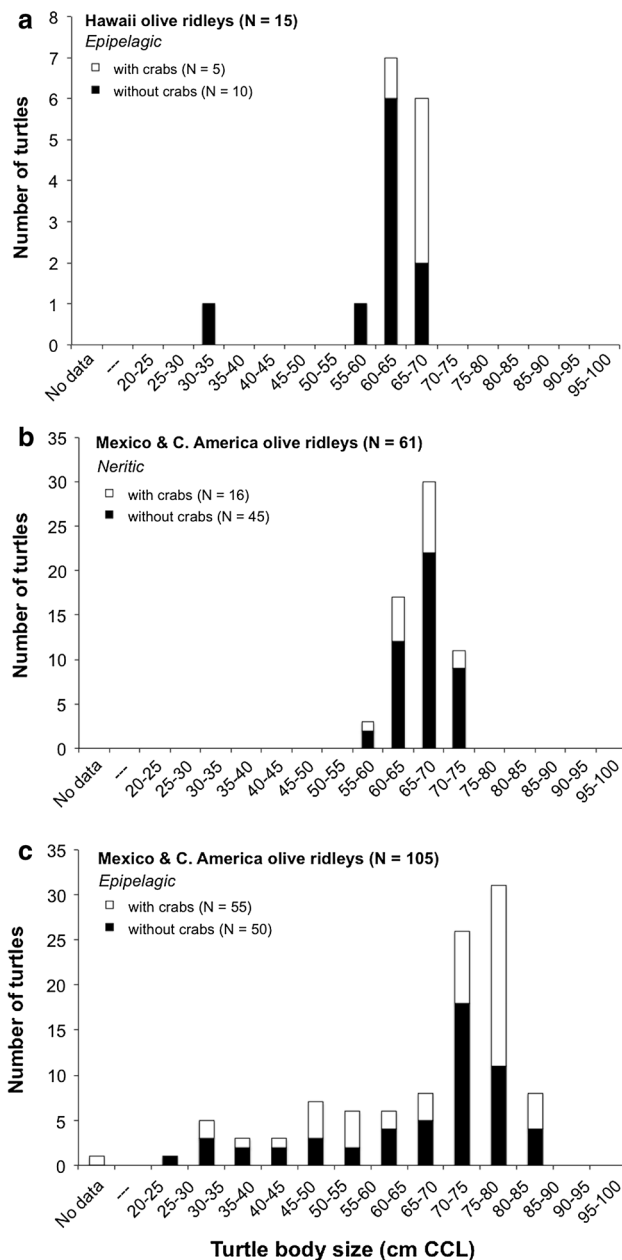
**Fig. 3** Size–frequency histograms showing green turtles (*C. mydas*) that did not host *P. major* (black bars) and turtles that hosted at least one *P. major* (white bars) from **a** neritic habitats in Japan, **b** epipelagic habitats near Samoa, **c** neritic habitats in Peru, and **d** epipelagic habitats off Peru. Turtles on border of two size increments were placed in the larger increment

peninsula (Parker et al. 2005; Peckham et al. 2011). Our results suggest that turtles that transition to neritic habitats may transition unidirectionally or bidirectionally, but tend to do so less frequently with increasing body size. Those that remain epipelagic may host crabs frequently (e.g., epipelagic juvenile loggerheads off Peru,  $F_0 = 93\%$ —this study), but were not surveyed in this study. Nevertheless, our data support the hypothesis that (at least some) juvenile loggerheads in Mexico display variable/flexible epipelagic-neritic transitions.

Green turtles surveyed in neritic habitats in Japan and Peru almost invariably did not host crabs ( $F_0 = 0$  and  $1\%$  in Japan and Peru, respectively). This result is in stark contrast to neritic loggerhead ( $F_0 = 27.6\%$ ; see above) and olive ridley ( $F_0 = 26.2\%$ ; see below) turtles. That green turtles in epipelagic habitats hosted crabs frequently ( $38.5\%$ ), albeit less frequently than epipelagic loggerheads ( $F_0 = 92.9\%$ ), suggest that green turtles that transition to neritic habitats tend to do so unidirectionally at small body sizes and remain there throughout development. Because very few small neritic green turtles (<45 cm CCL) were surveyed, we cannot evaluate whether  $F_0$  is indeed high on these small post-epipelagic turtles. It is plausible that small green turtles transition to shallow protected foraging areas where crabs are lost, then move to more high-energy coastal waters where they were captured and surveyed in this study. Such habitat-use behavior has been described for green turtles in the eastern Pacific Ocean (Seminoff et al. 2003). Demographic studies of green turtles in Peru indicate that turtles are primarily neritic (Alfaro-Shigueto et al. 2011), but data from fisheries bycatch and satellite telemetry also indicate some epipelagic habitat use (Seminoff et al. 2007). Interestingly, green turtles in Peru were found hosting crabs frequently in epipelagic habitats ( $F_0 = 60.0\%$ ) and rarely in neritic habitats ( $F_0 = 1\%$ ). Because turtles were similar in size, this suggests that these turtles may exhibit persistent alternative foraging strategies: epipelagic versus neritic. More work is needed to understand the consistency of this habitat-use dichotomy. Nevertheless, our results support the hypothesis that green turtles in neritic habitats do not display variable/flexible epipelagic-neritic transitions.

Olive ridleys surveyed in neritic habitats along Mexico and Central America were mostly adults (>60 cm CCL) and were found hosting crabs frequently ( $F_0 = 26.2\%$ ), though not as frequently as in Barceló et al. (2008) ( $F_0 = 50\%$ ;





**Fig. 4** Size–frequency histograms showing olive ridley turtles (*L. olivacea*) that did not host *P. major* (black bars) and turtles that hosted at least one *P. major* (white bars) from **a** epipelagic habitats near Hawaii, **b** neritic habitats along Mexico and Central America, and **c** epipelagic habitats along Mexico and Central America. Turtles on the border of two size increments were placed in the larger increment

Table 3). While there is a paucity of data on the life-history patterns of olive ridleys (Jones and Seminoff 2013), recent studies that apply satellite telemetry and demographic data have shown that both juveniles and adults in the eastern Pacific Ocean are highly epipelagic and nomadic (Work and Balazs 2010; Plotkin 2010). Our data suggest that some adult olive ridleys (>60 cm CCL) make forays into

neritic habitats, likely during foraging bouts. This result is consistent with results from dietary analyses of eastern Pacific olive ridleys (Kopitsky et al. 2005). Because epipelagic olive ridleys hosted crabs frequently ( $F_0 = 50\%$ ), turtles may remain in neritic habitats for somewhat extended periods of time—long enough for  $F_0$  to decline from 50 to 26 %—before returning to epipelagic habitats. Alternatively, neritic forays that involve nesting events may be relatively short in duration, but highly detrimental to associations with *P. major* (see  $F_0$  for nesting olive ridleys in Table 3). That a large proportion of the olive ridleys surveyed in Mexico and Central America in this study were surveyed during the nesting season (July–December) lends support to this idea. Our results support the hypothesis that olive ridleys in eastern North Pacific Ocean display variable/flexible epipelagic-neritic transitions.

Do turtles display similar surface-dwelling behavior in epipelagic habitats?

As “free-living” individuals, *Planes* crabs colonize floating debris as megalopal-stage larvae and spend the remainder of their lives rafting at the surface in the open ocean (Chace 1951). For this reason, crabs likely colonize turtles at the surface and remain associated with turtles that spend a significant proportion of time at or near the surface. Conversely, crabs may abandon, avoid, and/or infrequently colonize turtles that remain submerged for long periods of time. Based on these assumptions, interspecific differences in  $F_0$  among epipelagic turtles would suggest differences in epipelagic surface-dwelling behavior. Two alternative hypotheses emerge that might explain differences in  $F_0$  among epipelagic turtles: (1) If turtles display similar surface-dwelling behavior in epipelagic habitats, then  $F_0$  should be similar among species, and (2) if turtles display different surface-dwelling behavior in epipelagic habitats, then  $F_0$  should be different among species. Additionally,  $F_0$  should be proportional to the amount of time spent at or near the surface, such that turtles with high  $F_0$  spend more time at or near the surface than turtles with low  $F_0$ .

We surveyed epipelagic turtles for *P. major* at four different sites (Hawaii, Samoa, Mexico/Central America, and Peru). We found that epipelagic loggerheads hosted crabs ( $F_0 = 92.9\%$ ) more frequently than epipelagic olive ridleys ( $F_0 = 50\%$ ) and green turtles ( $F_0 = 38.5\%$ ). Although we surveyed epipelagic loggerheads in only one location in this study (Peru),  $F_0$  for epipelagic loggerheads in the North and South Atlantic Ocean are also high ( $F_0 = 82\%$ —Dellinger et al. 1997;  $F_0 = 83\%$ —Carranza et al. 2003), which supports the consistency of this pattern. High  $F_0$  in epipelagic loggerheads suggests that these turtles spend a large proportion of their time at or near the surface. This is consistent with the dive patterns of epipelagic loggerheads, in



**Table 3** Summary of all known references to *Planes major* on sea turtles in the Pacific Ocean: frequency of epibiosis ( $F_0$ ), epipelagic (E), neritic (N), nesting beach (B), stranding (D), *C. caretta* (CC), *C.**mydas* (CM), *D. coriacea* (DC), *E. imbricata* (EI), *L. olivacea* (LO), unknown turtle species (UNK), juvenile (J), subadult (S), adult (A)

| Site                | Habitat | Species | Stage   | N    | $F_0$ (%) | References                                    |
|---------------------|---------|---------|---------|------|-----------|-----------------------------------------------|
| Japan               | N       | UNK     | –       | 1    | –         | Sakai (1939) via Chace (1951)                 |
|                     | N       | CC      | S, A    | 147  | 21        | This study                                    |
|                     | N       | CM      | J, S, A | 47   | 0         | This study                                    |
|                     | N       | EI      | J       | 1    | 0         | This study                                    |
| Australia           | N       | CC      | S, A    | >100 | –         | Limpus and Limpus (2003)                      |
| Samoa               | E       | CM      | J       | 11   | 9         | This study                                    |
| (Rose Atoll)        | E       | EI      | J       | 1    | –         | Van Houtan, unpubl data                       |
| Hawaii              | E, D    | CM      | J       | 2    | 50        | This study                                    |
|                     | E       | DC      | J       | 1    | 0         | This study                                    |
|                     | E, D    | LO      | J, S, A | 15   | 33        | This study                                    |
| California          | N       | CC      | J       | 1    | –         | Guess (1981)                                  |
|                     | N       | CM      | –       | 1    | –         | Wicksten and Behrens (2000)                   |
|                     | N       | LO      | A       | 1    | –         | Hubbs (1977)                                  |
| Mexico              | N       | CC      | J, S    | 87   | 43        | Barceló et al. (2008)                         |
|                     | N       | CC      | J, S    | 56   | 45        | This study                                    |
|                     | N       | CM      | –       | >1   | –         | Faxon (1895) via Chace (1951)                 |
|                     | N       | CM      | –       | 1    | –         | Crane (1937)                                  |
|                     | B       | CM      | A       | 6    | 0         | Lazo-Wasem et al. (2011)                      |
|                     | N       | EI      | –       | 1    | –         | Steinbeck and Ricketts (1941)                 |
|                     | B       | LO      | A       | 44   | 9         | Hernández-Vásquez and Valadez-González (1998) |
|                     | B       | LO      | A       | 12   | –         | Angulo-Lozano et al. (2007)                   |
|                     | N       | LO      | S, A    | 14   | 50        | Barceló et al. (2008)                         |
|                     | B       | LO      | A       | 124  | 3         | Lazo-Wasem et al. (2011)                      |
| Mexico & C. America | N       | LO      | J, S, A | 61   | 26        | This study                                    |
|                     | E       | LO      | J, S, A | 108  | 52        | This study                                    |
| Galápagos           | E       | CM      | –       | 1    | –         | Rathbun (1902) via Chace (1951)               |
| Peru                | E       | CC      | J       | 28   | 93        | This study                                    |
|                     | N, E    | CM      | J, S, A | 416  | –         | Brown and Brown (1995)                        |
|                     | E       | CM      | J, S    | 15   | 60        | This study                                    |
|                     | N       | CM      | J, S, A | 99   | 1         | This study                                    |
|                     | N       | EI      | J       | 1    | 0         | This study                                    |
|                     | –       | LO      | –       | 1    | –         | Schweigger (1964)                             |
|                     | E       | LO      | A       | 2    | 100       | This study                                    |
| Chile               | D       | LO      | –       | 5    | 20        | Miranda and Moreno (2002)                     |

Dashes indicate insufficient data for determining stage, habitat, or  $F_0$ 

which >80 % of dives occur to depths less than 5 m and 40 % of time is spent within 1 m of the surface (Polovina et al. 2003, 2004; Howell et al. 2010). Dietary data indicate that these turtles forage primarily on surface-dwelling prey, including organisms associated with floating debris (e.g., *Planes* crabs and *Lepas* barnacles—Parker et al. 2005; Peckham et al. 2011). This foraging behavior would provide frequent opportunities of *P. major* to colonize epipelagic loggerheads, and, once colonized, the tendency of these turtles to spend time at the surface would likely facilitate the persistence of these associations. Both behavioral

characteristics might contribute to higher  $F_0$  in epipelagic loggerheads.

In contrast, comparably lower  $F_0$  values for epipelagic olive ridleys and green turtles suggest that these turtles display different surface-dwelling behavior than epipelagic loggerheads and tend to spend less time at or near the surface. Differences in  $F_0$  between loggerheads and olive ridleys are consistent with data from depth–time recorders, which show that epipelagic olive ridleys spend less time at the surface and make deeper dives than epipelagic loggerheads (Polovina et al. 2003, 2004). Dietary data also

support this pattern: epipelagic olive ridleys consume more subsurface prey (e.g., pyrosomes and salps) than epipelagic loggerheads (Kopitsky et al. 2005; Polovina et al. 2004). Although comparable depth–time and dietary data are not available for epipelagic green turtles, epipelagic green turtles in the North Pacific Ocean are known to conduct “resting” dives, in which turtles appear to obtain neutral buoyancy at ~35–40 m depth and remain there for some period of time (Hays et al. 2001; Rice and Balazs 2008). Subsurface-diving behavior displayed by epipelagic olive ridleys and green turtles might deter *P. major* from colonizing and/or persisting on these turtles in epipelagic habitats, which would contribute to lower  $F_0$ . Moreover, if these turtles do not frequently associate with floating debris in epipelagic habitats, as loggerheads do, then there may be fewer opportunities for colonization by *P. major*. Our data support the hypothesis that epipelagic loggerheads display different surface-dwelling behavior than epipelagic olive ridleys and green turtles, in which loggerheads spend more time at or near the surface. However, more work is needed to better understand the mechanisms driving the observed differences in  $F_0$  among epipelagic turtles.

### Caveats

Methodological differences at different sampling sites (see [Methods](#)) may have affected  $F_0$ . Turtles that spent more time within capture gear or out of the water before being inspected for crabs (Japan, Hawaii and Samoa) may have had  $F_0$  values that were biased low. However, the affect of these potential biases would not change our interpretations of the results, and therefore, our primary insights and conclusions would remain the same. (1) If  $F_0$  was slightly higher for both neritic turtles in Japan and epipelagic turtles in Hawaii and Samoa, then  $F_0$  for epipelagic and neritic turtles overall would each be slightly higher, maintaining the general pattern. (2) If  $F_0$  was slightly higher for neritic turtles in Japan, then support for variable/flexible epipelagic-neritic transitions among neritic loggerheads would be strengthened and support for unidirectional epipelagic-neritic transitions among neritic green turtles would be somewhat weakened, but not sufficiently to change our interpretation. (3) If  $F_0$  were higher for epipelagic olive ridleys and green turtles in Hawaii and Samoa, respectively, then support for the frequency of surface-dwelling behavior would increase for both species, but  $F_0$  for epipelagic loggerheads would still be considerably higher, maintaining our initial interpretation.

### Perspectives

In this study, we used the occurrence of epipelagic epibionts to infer cryptic habitat-use patterns and behavior of sea turtles in the Pacific Ocean. Because epibiosis necessitates

spatial overlap between the habitats occupied by hosts and free-living populations of potential epibionts, researchers can use the presence of particular epibiont species with more limited habitat distributions to identify the habitats that the host has recently occupied (Frick and Pfaller 2013). This approach may prove to be informative for other sea turtle populations, as well as other marine vertebrates. In addition to epibionts associated with epipelagic versus neritic/benthic habitat use, other epibiotic assemblages that reflect habitat-use dichotomies in the aquatic environment (e.g., freshwater versus marine, polar versus equatorial) may reveal important information on cryptic host movements and behavior. Studies on the epibionts of marine vertebrates represent a time- and cost-effective method to infer population-wide patterns, especially when more expensive technologies are unavailable. Future studies that utilize more advanced technologies could integrate epibiont data to elucidate a more detailed and complete picture of the ecological interactions, as well as habitat-use patterns, of large, highly mobile marine vertebrates.

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