



Epibiont Assemblages on Nesting Hawksbill Turtles Show Site-Specificity in the Persian Gulf

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Sea turtle epibionts can provide insights into the hosts' habitat use. However, at present, there is a lack of information on sea turtle epibiont communities in many locations worldwide. Here, we describe the epibiont communities of 46 hawksbill turtles (*Eretmochelys imbricata*) in the Persian Gulf. Specifically, we sampled 28 turtles from the Dayyer-Nakhiloo National Park (DNNP) in the northern Gulf and 18 turtles from Shibderaz beach in the Strait of Hormuz. A total of 54 macro, meio, and micro-epibiont taxa were identified, including 46 taxa from Shibderaz and 29 taxa from DNNP. The barnacles *Chelonibia testudinaria* and *Platylepas hexastylus*, as well as harpacticoid copepods and Rotaliid foraminifers, had the highest frequency of occurrence found on almost all turtle individuals. Harpacticoids were the most abundant epizoic taxa (19.55 ± 3.9 ind. per 9 cm^2) followed by forams (*Quinqueloculina* spp.: 6.25 ± 1.5 ind. per 9 cm^2 and Rotaliids: 6.02 ± 1.3 ind. per 9 cm^2). Our results showed significant differences between the study sites in the composition of micro and macro-epibiont communities found on hawksbill turtles. We speculate that the differences in epibiont communities were largely influenced by local environmental conditions.

Keywords: barnacles, epibionts, environmental extremes, Strait of Hormuz, sea turtles

INTRODUCTION

Epibiosis is a symbiotic relationship where one organism (epibiont) lives on the surface of the other (basibiont) (Wahl and Mark, 1999; Harder, 2008). A wide variety of epibiont communities are found on sea turtles (Wahl, 1989; Pfaller et al., 2008b; Frick and Pfaller, 2013; Majewska et al., 2015) including macro, meio, and micro-epibionts. Macro-epibiont communities encompassing cirripeds, polychaetes, hydrozoans, bryozoans, poriferans, tunicates, periphytic algae, and some motile organisms have been widely studied on different sea turtle species (Caine, 1986; Pfaller et al., 2008b; Fuller et al., 2010; Lazo-Wasem et al., 2011; Robinson N. J. et al., 2017; Robinson et al., 2019), and meiofaunal organisms such as nematodes and copepods have recently been the focus of several studies (Aznar et al., 2010; Corrêa et al., 2013; Domènech et al., 2017; Ingels et al., 2020). Likewise, micro-epibiota on sea turtles, represented mostly by colonizing diatoms, have recently been assessed (Majewska et al., 2015, 2017; Robinson et al., 2016; van de Vijver et al., 2020). Some of these epibionts, such as the barnacle *Chelonibia testudinaria*, have a wide geographical distribution (Rawson et al., 2003; Lazo-Wasem et al., 2011), whereas some others, like some short-lived diatom species, may have a relatively narrow and local distribution (Abarca et al., 2014).

Barnacles are the most prominent epibionts of sea turtles (Casale et al., 2012; Frick and Pfaller, 2013). Turtle barnacles belong to the superfamily Coronuloidea and include three families: Chelonibiidae Pilsbry, 1916, Coronulidae Leach, 1817, and Platylepadidae Newman and Ross, 1976 (Hayashi, 2012, 2013). Members of Chelonibiidae are perhaps the most studied barnacle species recorded on sea turtles. *Chelonibia testudinaria*, the most commonly reported sea turtle barnacle, has been reported on the body surface of all extant sea turtle species (Sloan et al., 2014), sirenians (Zardus et al., 2014), and some crustaceans (Cheang et al., 2013) from distant geographical regions. It is, therefore, considered a host generalist species and should not be assumed as an obligatory turtle barnacle (Cheang et al., 2013; Zardus et al., 2014). In contrast, *Chelonibia caretta*, which is considered a host specialist, is reported only in association with sea turtles, especially loggerheads (*Caretta caretta*) (Torres-Pratts et al., 2009; Farrapeira, 2010).

Several techniques have been successfully used to study habitat use and migration patterns of sea turtles, including satellite telemetry (e.g., Rees et al., 2016; Robinson D. P. et al., 2017; Hays and Hawkes, 2018; Pilcher et al., 2020), aerial surveys (Jean et al., 2010), visual surveys *via* snorkeling (Roos et al., 2005), and stable isotope analysis (e.g., Nolte et al., 2020). However, most of these techniques are costly (Pfaller et al., 2014), and/or logistically difficult to implement. As an alternative, or complementary and relatively low-cost approach, epibiont assemblages living on sea turtles can roughly indicate habitat use and migratory behavior of these highly mobile marine reptiles (e.g., Pfaller et al., 2008b; Lazo-Wasem et al., 2011; Rivera et al., 2018; Robinson et al., 2019; Nolte et al., 2020; Silver-Gorges et al., 2021). For instance, some sea turtle epibionts, e.g., *C. testudinaria* and two lepadid barnacles *Lepas hilli* and *Conchoderma virgatum*, have been proposed to be potentially used as habitat indicators of sea turtles (Casale et al., 2012; Ten et al., 2019). According to previous studies, the barnacles *L. hillii*, *C. virgatum* (Ten et al., 2019), and *Platylepas* spp. (Casale et al., 2012) preferably settle on turtles inhabiting oceanic waters. In contrast, *C. testudinaria*, *Stomatolepas elegans*, and *Stephanolepas muricata* are mainly associated with turtles occupying neritic waters (Casale et al., 2012). Epibiotic barnacles and crabs have also been used as indicators of the distribution and movement of loggerheads (Casale et al., 2004). Thus, epibiont communities could roughly reflect the environment in which the host has recently been living (Casale et al., 2012; Frick and Pfaller, 2013; Nolte et al., 2020; Silver-Gorges et al., 2021). In addition, this method could be very useful in sea turtle conservation planning efforts, as epibionts may affect their health status. Stranded turtles were frequently utilized in studies to examine factors that affect their health and mortality (Sönmez, 2018; Cheng et al., 2019; Wang et al., 2020). Turtle epibionts may cause increased drag (Logan and Morreale, 1994; Wynneken, 1997), which could be energetically expensive for the host turtles, particularly for those undertaking long-distance migrations (Frick and Pfaller, 2013). Additionally, some turtle epibionts such as leeches and barnacles may cause infections in sea turtles (George, 1997; Greenblatt et al., 2004), or enhance their vulnerability to pathogens (George, 1997). The presence of some coronuloid barnacles on eyes and wounds, as well as their

penetration into the epidermis of the host's flippers, may have a negative influence on their health (Frick et al., 2011).

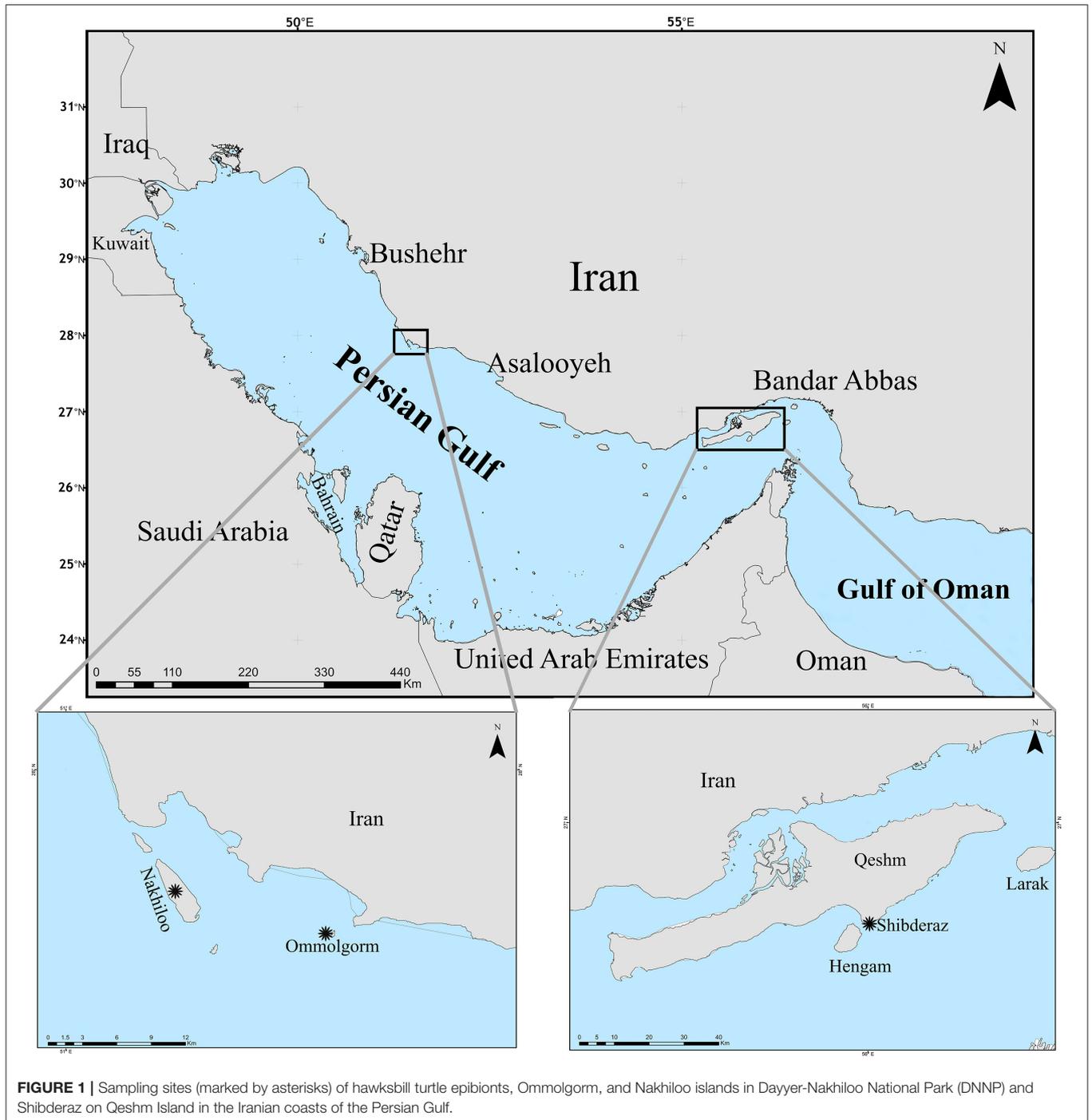
The marine environment of the Persian Gulf is characterized by high and wide-ranging temperatures [sea surface temperatures (SST) from 15° to 36°C, Riegl and Purkis, 2012] and high salinities (>39 psu in most areas, Sheppard et al., 2010). This is a challenging environment for many organisms, leading to impoverished biodiversity in this semi-enclosed body of water compared to other coastal habitats of the Indian Ocean (Sheppard et al., 2010). Satellite telemetry has partially revealed habitat use and migratory behavior of the turtles in this region. Hawksbill turtles (*Eretmochelys imbricata*) spend most of their time feeding on foraging grounds in shallow waters near the coasts of Qatar, Saudi Arabia, and UAE while spending only a small portion of their life nesting on Iranian coasts (Pilcher et al., 2014). In summer, when the SST rises to 33°C, hawksbills leave shallow foraging grounds and move northward to deeper waters (30–50 m) of the Persian Gulf (Pilcher et al., 2014; Marshall et al., 2020).

Hawksbill turtles, along with green turtles (*Chelonia mydas*), are the dominant sea turtle species in the Persian Gulf. It is assumed that hawksbill turtles nesting along the Iranian shores of the Gulf may comprise one of the most important nesting populations in the Indian Ocean region (Meylan and Donnelly, 1999). Therefore, obtaining information on epibiont communities of hawksbills in the Gulf, especially those that are likely indicators of nesting ecology, can aid in their management. Additionally, epibionts could be used as bio-indicators of ecological change in the Persian Gulf. Despite this, our knowledge about epibiont communities of the Gulf's hawksbill turtles is restricted to a few studies on turtle barnacles (Loghmani-Devin and Sadeghi, 2010; Razaghian et al., 2019). In this study, we present the first comprehensive dataset on the diversity, assemblage, and abundance of macro, meio, and micro-epibionts of hawksbill turtles nesting at two distant sites along the Iranian coastline of the Persian Gulf, one at the northwest coast, and the other at the Strait of Hormuz. Due to the differences in environmental conditions of the sites, we hypothesized that epibiont assemblages of the two turtle rookeries might show site-specific differences.

MATERIALS AND METHODS

Study Area

Ommolgorm (27° 50' N, 51° 33' E) and Nakhiloo (27° 51' N, 51° 26' E) islands in Dayyer-Nakhiloo National Park (DNNP) and located at the center of Iran's northwestern Persian Gulf coast, and Shibderaz (26° 41' N, 55° 55' E), a 2 km sandy beach on the south coast of Qeshm Island in the Strait of Hormuz (the entrance of the Persian Gulf; **Figure 1**) were used as study sites. Sea surface temperature and salinity data were obtained during 2017 and 2018 for each site (**Table 1**) from the Copernicus Marine Environment Monitoring Service (<http://marine.copernicus.eu>; product reference: CMEMS-GLO-PUM-001-024).



Field Surveys and Sample Collection

The beach areas of both sites were patrolled between March and June in 2017 and 2018. All encountered nesting turtles were examined after the completion of oviposition to avoid interrupting the nesting process. Each turtle was first measured for curved carapace length (CCL) to the nearest 1 mm, and its body was gently washed with clean seawater to remove sand and particles. Following that, a digital camera (Sony DSC-HX9V) was

used to photograph the carapace, plastron, head, and soft parts to measure barnacle abundance on each body part using a non-invasive approach. Further, three randomly chosen portions of the carapace surface (9 cm²) were gently shaved and the keratin materials collected were preserved in 4% formaldehyde solution diluted with filtered seawater. To study diatoms, ~4 cm² of the outer-most layer of the three different scutes were taken and immediately fixed in vials containing 4% formaldehyde solution

TABLE 1 | Sea surface temperature and salinity values at Shibderaz and Dayyer-Nakhiloo National Park (DNNP) during 2017 and 2018.

		Sampling areas	
		Shibderaz	DNNP
Geographical coordinates		26° 41' N, 55° 55' E	27° 51' N, 51° 26' E
Temperature (°C)	Average ± SD	28.13 ± 4.12	26.31 ± 5.46
	Min	22.22	17.73
	Max	33.60	35.09
Salinity (PSU)	Average ± SD	37.40 ± 0.48	38.25 ± 0.26
	Min	36.95	37.69
	Max	38.44	38.62

Data were obtained from Copernicus Marine Environment Monitoring Service (<http://marine.copernicus.eu>; product reference: CMEMS-GLO-PUM-001-024).

diluted by filtered seawater (Majewska et al., 2015). For precise identification of the barnacles, in addition to using photographs, a few barnacle individuals from visually distinct species were physically removed with a safe plastic knife and preserved in vials containing 96% ethanol for laboratory examinations. In total, epibiont samples were collected from 46 nesting hawksbill sea turtles (28 turtles from DNNP and 18 turtles from Shibderaz).

Species Identification and Quantification

Zoopibionts of each collected sample were isolated from algal mats under a stereomicroscope with a magnification of 80x. Specimens were then identified to the lowest possible taxonomic level and their abundance was determined. Scute samples for diatoms identification were subsampled to ca. 1 cm², dehydrated through 25, 50, 60, 70, 80, 90, and 100% ethanol series. The samples were then air-dried in a desiccator containing silica gel, placed on microscope slides, sputter-coated with gold, and identified using images taken with a Hitachi SU3500 (Hitachi High-Technologies, Tokyo, Japan) scanning electron microscope (SEM), operating at 15 kV.

We used standard morphological keys following Chan et al. (2009) and Shahdadi et al. (2014) to identify the barnacle species. Sea turtle foraminifera epibionts were identified using the Atlas of Benthic Foraminifera (Holbourn et al., 2013). To identify macroalgae epibionts on hawksbill turtles we utilized the Atlas of the sea algae of the Persian Gulf and Oman Sea coasts (Gharanjik and Rohani Ghadikolaei, 2009) and the Field Guide of Marine Macroalgae of Kuwait (Al-Yamani et al., 2014). Other epibiont taxa were identified using the relevant literature (e.g., Taylor et al., 2007; Guerra-García et al., 2010; Martin et al., 2014).

As the most prominent and visible epibiont taxa, barnacles were analyzed in greater detail. Total and mean barnacle abundance were recorded on each body part (head, carapace, plastron, supra-caudals, and soft parts) using photographs (see above). Image J software (version 1.43 u) was used to measure the basal diameter (Nasrolahi et al., 2013) of each individual barnacles found on turtles.

Statistical Analysis

A Kolmogorov-Smirnov test was used to check for normality, and revealed that the data did not exhibit a normal distribution even after being transformed. The Kruskal-Wallis non-parametric test was performed to compare barnacle abundances, and a Mann-Whitney *U*-test was used to evaluate differences in *C. testudinaria* rostro-carinal diameter (RCD) among different body parts (head, carapace, plastron, supra-caudals, and soft parts). A Mann-Whitney *U*-test was also used to compare *P. hexastylus* RCD between plastron and soft parts of hawksbill turtles encountered in Shibderaz and DNNP.

A PERMANOVA statistical test was used to compare assemblage structure and species composition of sea turtle epibionts between the two study sites. Except for diatoms and other algal taxa, for which only presence-absence data were recorded, the analysis of epibiont structure was based on absolute abundance data. Species composition of the entire epibiont community (including micro, meio, and macro-epibionts) was evaluated based on presence-absence data. A SIMPER (similarity percentage) test was performed to identify the relative contribution of each epibiont taxon to any dissimilarity values between the epibiont assemblages of hawksbill turtles nesting on the two sites. Graphical representation of the similarity was carried out using non-metric multidimensional scaling (nMDS) based on the square-root-transformed abundance data and the Bray-Curtis similarity measure of all identified epibiont taxa for each turtle. Furthermore, a PERMANOVA was used to compare species composition of the macro, meio, and micro-epibionts between the two study sites. Following this, a SIMPER analysis was used to reveal the dissimilarity of epibiont groups between the two sites as well as the contribution of each taxon to the dissimilarity. All the analyses were performed and graphs generated using the statistical software SPSS 26 (George and Mallery, 2019) and Primer 6.0+PERMANOVA (Clarke and Gorley, 2006; Anderson et al., 2008). A significance level of <0.05 was used to reject null hypotheses for all tests.

RESULTS

Examined Turtles

A total of 46 hawksbill turtles were examined from both nesting sites. At Shibderaz, the mean CCL (±SE) was 73.6 ± 0.6 cm (range 69.5–78.0 cm). At DNNP, the mean CCL ± SE was 71.9 ± 0.5 cm (range 67.5–77.0 cm). The overall mean CCL (±SE) for both sites was 72.6 ± 0.4 cm, ranging from 67.5 to 78.0 cm.

Composition and Structure of Epibiont Communities

In total, 54 macro-, meio-, and micro-epibiont taxa including 28 diatoms, five filamentous algae, four barnacles, three foraminifers, and two amphipod species. In addition, single-taxon representatives of bivalves, copepods, cumaceans, gastropods, haptophytes, leeches, hydrozoans, nematodes, ostracods, polychaetes, sponges, and tanaids were identified on hawksbill sea turtles at both nesting sites (Table 2). From these, 46 taxa were found on turtles from Shibderaz, whereas only 29 taxa were identified on turtles from DNNP. The difference was

TABLE 2 | Epibiont species list, abundance (ind. per 9 cm²), and frequency of occurrence on hawksbill (*Eretmochelys imbricata*) turtles (N = 46) nesting on Shibderaz (Qeshm Island) and Dayyer-Nakhiloo National Park (DNNP; Bushehr) beaches, Iran.

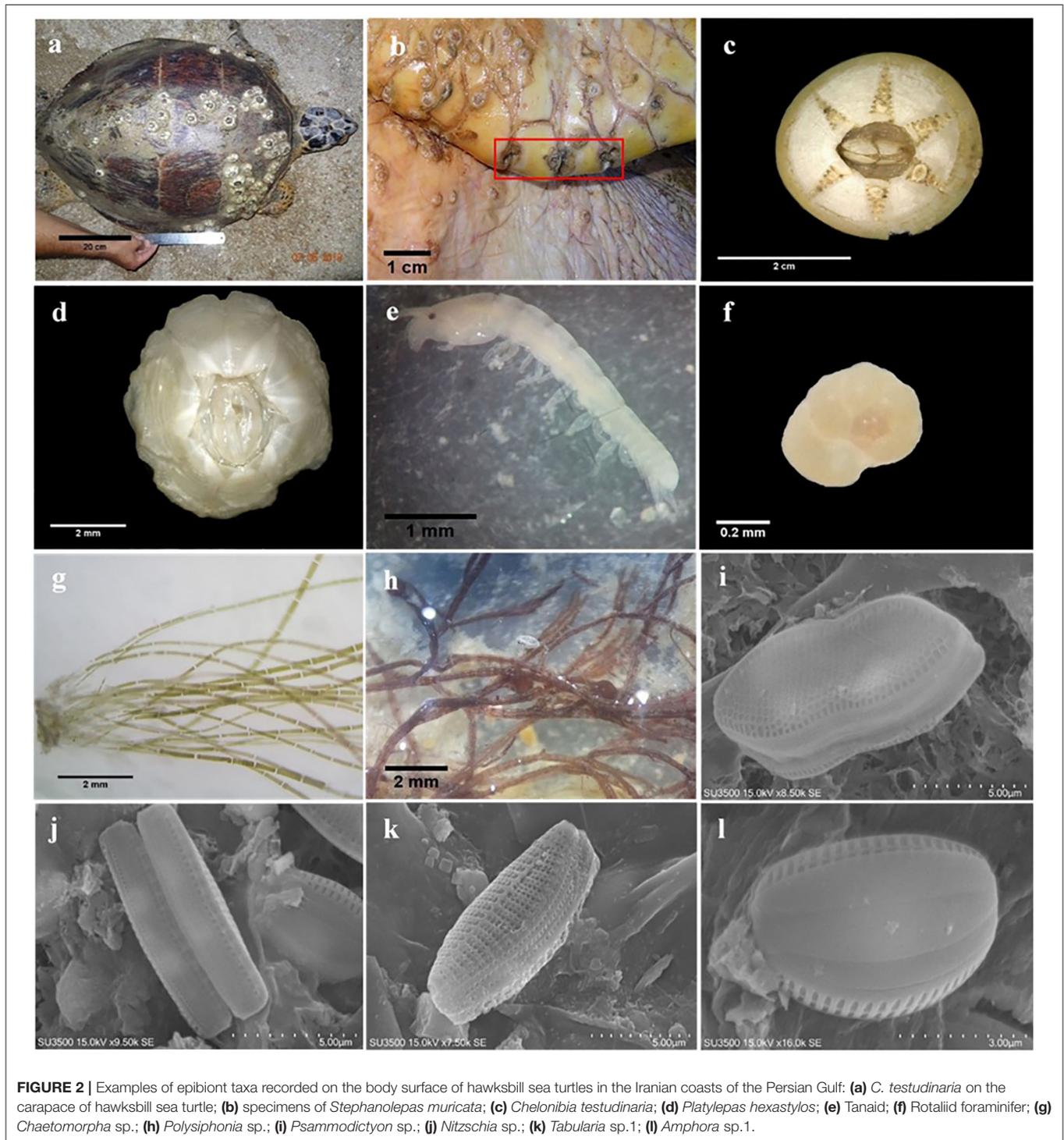
Main epibiont taxonomic groups	Identified epibionts	Epibiont type	% Frequency of epibiont occurrence on host turtle		Average abundance of epibionts on all hosts	
			Shibderaz N = 18	DNNP N = 28	Shibderaz N = 18	DNNP N = 28
Algae: Bacillariophyceae	<i>Achnanthes</i> sp.	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Achnantheidium</i> sp.	Micro	–	*	–	*
Algae: Bacillariophyceae	<i>Actinocyclus</i> sp.	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Amphicoconeis</i> sp.	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Amphora coffeiformis</i>	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Amphora</i> sp. 1	Micro	*	*	*	*
Algae: Bacillariophyceae	<i>Amphora</i> sp. 2	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Amphora</i> sp. 3	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Amphora ovalis</i>	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Berkeleya</i> sp.	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Caloneis</i> sp.	Micro	–	*	–	*
Algae: Bacillariophyceae	<i>Cocconeis convexa</i>	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Cocconeis distans</i>	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Cocconeis scutellum</i>	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Cocconeis</i> sp.	Micro	*	*	*	*
Algae: Bacillariophyceae	<i>Grammatophora</i> sp.	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Licmophora</i> spp.	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Mastogloia horvathiana</i>	Micro	–	*	–	*
Algae: Bacillariophyceae	<i>Navicula directa</i>	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Navicula</i> sp. 1	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Navicula</i> sp. 2	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Nitzschia</i> sp. 1	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Nitzschia</i> sp. 2	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Opephora</i> sp.	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Poulinea lepidochelicola</i>	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Psammodictyon</i> sp.	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Tabularia tabulata</i>	Micro	*	–	*	–
Algae: Bacillariophyceae	<i>Tabularia</i> sp. 1	Micro	*	–	*	–
Algae: Chlorophyta	<i>Chaetomorpha</i> sp.	Macro	31	–	*	–
Algae: Chlorophyta	<i>Ulva</i> sp.	Macro	88	56	*	*
Algae: Rhodophyta	<i>Ceramium</i> sp.	Macro	50	59	*	*
Algae: Rhodophyta	<i>Polysiphonia</i> sp.	Macro	–	4	–	*
Algae: Rhodophyta	Unknown	Macro	13	63	*	*
Annelida: Hirudinea	<i>Ozobranchus</i> sp.	Macro	7	–	0.07 ± 0.1	–
Annelida: Polychaeta	Unknown	Macro	–	35	–	0.36 ± 0.1
Cnidaria: Hydrozoa	Campanulariidae	Macro	47	42	*	*
Crustacea: Amphipoda	<i>Hyachelia</i> sp.	Macro	33	35	0.67 ± 0.3	0.46 ± 0.2
Crustacea: Amphipoda	<i>Caprella</i> sp.	Macro	–	4	–	0.09 ± 0.1
Crustacea: Cirripedia	<i>Chelonibia testudinaria</i>	Macro	100	100	0.21 ± 0.05	0.34 ± 0.4
Crustacea: Cirripedia	<i>Platylepas hexastylus</i>	Macro	100	100	4.55 ± 0.44	2.15 ± 0.28
Crustacea: Cirripedia	<i>Stomatolepas transversa</i>	Macro	73	85	*	*
Crustacea: Cirripedia	<i>Stephanolepas muricata</i>	Macro	73	88	*	*
Crustacea: Copepoda	Harpacticoida	Meio	100	100	22.56 ± 5.1	16.54 ± 2.7
Crustacea: Cumacea		Macro	13	4	0.07 ± 0.0	0.03 ± 0.0
Crustacea: Ostracoda		Meio	60	88	0.82 ± 0.2	4.15 ± 1.13
Crustacea: Tanaidacea	Tanaidacea	Macro	7	27	0.09 ± 0.1	0.51 ± 0.2
Foraminifera: Rotaliida		Meio	100	96	3.22 ± 0.5	8.83 ± 2.1
Foraminifera: Textulariida		Meio	–	12	–	0.08 ± 0.0
Foraminifera: Miliolida	<i>Quinqueloculina</i> spp.	Meio	87	92	2.53 ± 0.7	9.97 ± 2.3
Haptophyta: Isochrysidales	<i>Emiliana huxleyi</i>	Micro	*	*	*	*
Mollusca: Bivalvia		Macro	–	46	–	0.62 ± 0.2
Mollusca: Gastropoda		Macro	13	58	0.09 ± 0.1	0.81 ± 0.2
Nematoda	Unknown	Macro	7	42	0.02 ± 0.0	0.52 ± 0.2
Porifera		Macro	7	4	*	*

*Taxon represents presence only and individual counts were not undertaken.
–, Taxon represents absence only.

largely driven by diatoms. Of the 28 total diatom taxa belonging to 17 genera, 25 taxa were identified in samples collected from Shibderaz whereas only five taxa were observed from DNNP (Table 2). *Chaetomorpha* sp. and *Ozobranchus* sp. were recorded only from Shibderaz and *Polysiphonia* sp., *Caprella* sp., a bivalve,

and a polychaete were only identified in DNNP. Examples of different epibiont taxa are shown in Figure 2.

Among macrofauna, *C. testudinaria* and *P. hexastylus* were present on all examined turtles. Among the meiofauna, harpacticoid copepods, and Rotaliid foraminifers were also



observed on almost all sea turtle individuals. Likewise, the filamentous alga *Ulva* sp. showed a high frequency of occurrence on turtles (88 and 56% at Shibderaz and DNNP, respectively, **Table 2**). Harpacticoids (64.5%) followed by *P. hexastylus* (13%) and Rotaliids (9.3%) were the most abundant epizoic taxa on turtles from Shibderaz, whereas harpacticoids (36.4%), *Quinqueloculina* spp. (22%) and Rotaliids (19.5%) were the most dominant taxa on turtles at DNNP (**Figure 3**).

The PERMANOVA analysis identified statistically significant site-based differences in the epibiont species composition and community structure on studied turtles [Pseudo-F = 5.89, P (perm) < 0.001; Pseudo-F = 17.51, P (perm) < 0.001, respectively, **Supplementary Table S1**]. Similarly, the nMDS plot shows that species composition and community structure were noticeably different between the two sites (**Figure 4**). The SIMPER analysis showed 35.71% dissimilarity between the two sites. Rhodophyta (7.1%), Gastropoda (6.32%), Bivalvia (5.64%), Campanulariidae (5.55%), *Ceramium* sp. (5.54%), *Ulva* sp. (5.11%), and *Hyachelia* sp. (4.93%) contributed to more than 40% of the difference (**Table 3**). When separating the epibionts into macro, meio, and micro-epibiont groups, a significant difference between the two sites in species composition of the micro and macro-epibionts was detected

[Pseudo-F = 15.32, P (perm) < 0.001, Pseudo-F = 9.02, P (perm) = 0.001, respectively]. The SIMPER analysis revealed 97.68 and 39.37% dissimilarity between the two sites, respectively. Diatom species—including *Cocconeis* spp. (23.83%), *Caloneis* sp. (9.43%), *Amphora* sp. 1 (7.14%), and *Amphora ovalis* (6.80%)—contributed around 47% to the differences of the micro-epibionts (**Table 3**). Rhodophyta (10.45%), Gastropoda (9.31%), *Ceramium* sp. (8.28%), Campanulariidae (8.23%), Bivalvia (8.19%), and *Ulva* sp. (7.66%) explained 52% of the macro-epibiont variances (**Table 3**).

Barnacle Composition and Distribution

Four barnacle species, including *P. hexastylus*, *C. testudinaria*, *Stomatolepas transversa*, and *Stephanolepas muricata* were identified on the body surface of examined turtles. About 95% of *P. hexastylus* individuals were found on the flippers and soft parts, while only 5% were recorded on the plastron scutes; no individuals were observed on the carapace. *C. testudinaria* individuals were distributed more broadly, with 51% distributed on the plastron, 37% on the carapace, 10% under the supracaudals, and 2% on the head. Individuals of *S. transversa* were only observed along the plastral sutures and *S. muricata* was only found attached to the leading edges of the front flippers.

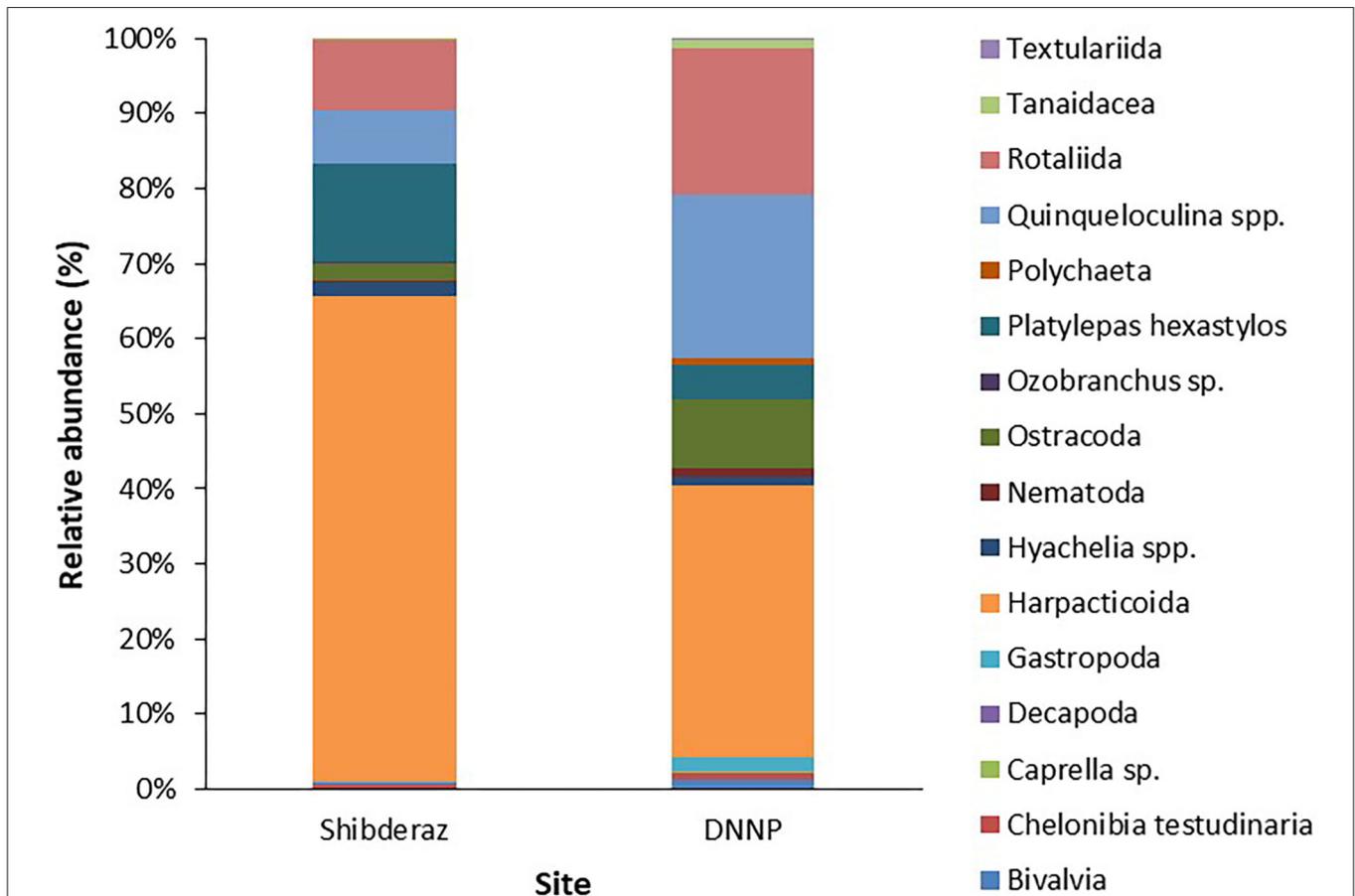
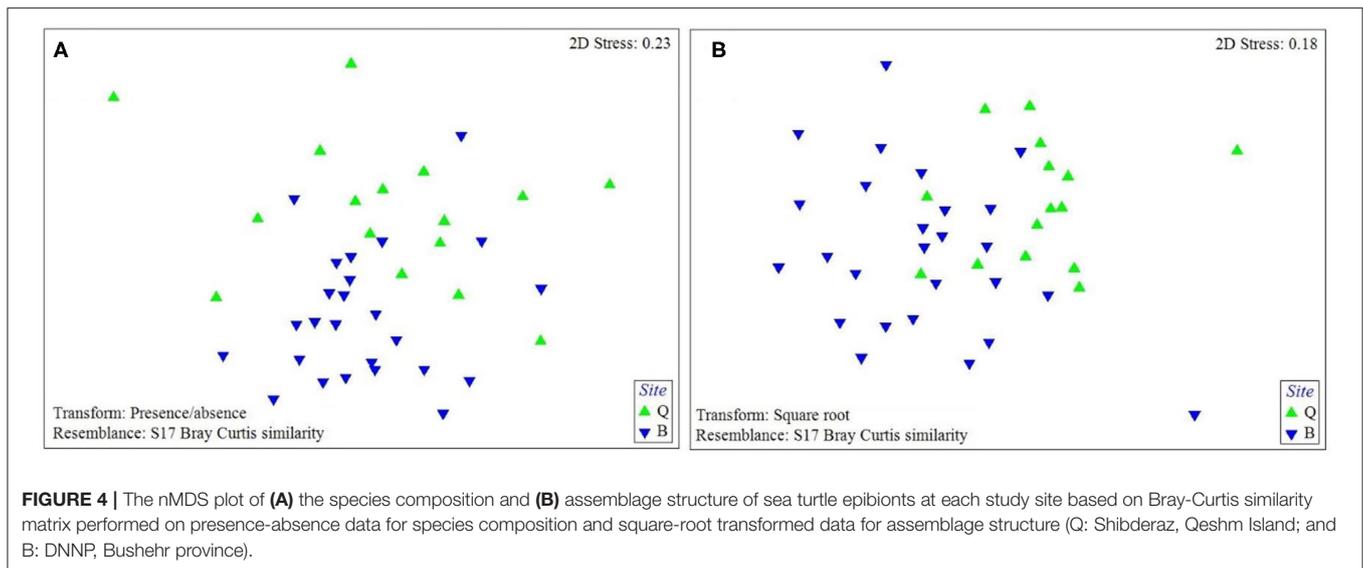


FIGURE 3 | Relative abundance (%) of epibiont taxa on the body surface of the nesting hawksbill turtles in Shibderaz and Dayyer-Nakhiloo National Park (DNNP).



In general, 85.3% of all barnacles were attached on flippers and soft parts, 9.7% on the plastron, 3.8% on the carapace, 1% under supracaudals, and 0.2% on the head (Table 4).

Barnacle Abundance

As *S. transversa* and *S. muricata* were small and difficult to distinguish from each other, which made it challenging to precisely count them using the images. We visually estimated their total abundance to be <2%. Thus, we only counted *P. hexastylus* and *C. testudinaria*. A total of 68,905 individual barnacles were counted on body parts (including carapace, plastron, head, neck, flippers, and soft parts) of turtles. Of these, there were 61,837 (90%) and 7,068 (10%) individuals of *P. hexastylus* and *C. testudinaria*, respectively. The greatest barnacle load was found on a 72 cm (CCL) turtle that had 3,774 barnacles (3,659 *P. hexastylus* and 115 *C. testudinaria*) and the lowest measured barnacle load was from a 70.5 cm (CCL) turtle that was carrying 212 barnacles (146 *P. hexastylus* and 66 *C. testudinaria*).

The overall mean (\pm SE) barnacle abundance (1497.9 ± 133.7) was significantly different on various body parts of turtles ($p < 0.05$, Supplementary Table S2). Mean barnacle abundance was 1278.0 ± 123.4 on the flippers and adjacent soft parts, 144.7 ± 16.4 on the plastron, 56.8 ± 8.2 on the carapace, 15.0 ± 2.5 under the supracaudal scutes, and 3.4 ± 1.1 on the head. The mean abundance for *C. testudinaria* and *P. hexastylus* was 153.7 ± 15.7 and 1344.3 ± 130.1 , respectively.

Barnacle Rostro-Carinal Diameter

The results of the Mann-Whitney *U*-test showed that there was no significant difference in the mean RCD of *C. testudinaria* on different body parts of turtles nesting at Shibderaz vs. DNNP ($p > 0.05$). Therefore, the data for both sites were pooled. The RCD of *C. testudinaria* was significantly different among different body parts (i.e., head, carapace, plastron, and supracaudal) (Figure 5A, $p < 0.05$, Supplementary Table S2). The highest mean barnacle RCD (22.57 ± 9.47) was observed on

the head and the lowest (12.27 ± 5.24) on the supracaudal scutes (Figure 5A). The mean RCD of *P. hexastylus* was significantly higher in Shibderaz compared to DNNP (Figure 5B, $p < 0.05$, Supplementary Table S2). The size-frequency distribution of *C. testudinaria* showed a skewness by some large barnacle individuals (Figure 6). It showed a peak at 5.01–10 mm followed by two smaller peaks at 10.01–15 and 15.01–20 mm. There were few large barnacles with a size range of 55.01–60 mm (Figure 6).

DISCUSSION

The majority of research on turtle epibionts has focused on the epibiont loads on the carapace (see Caine, 1986; Pfaller et al., 2008a,b; Fuller et al., 2010), presuming that the abundance of epibionts is highest on this body part. However, this notion has been contradicted by more recent studies (e.g., Robinson et al., 2019) that have found epibiont abundance on soft skin to be higher than on the carapace and plastron. To provide a holistic qualitative or quantitative data set of the epibiont communities of sea turtles, it is therefore essential to conduct a full-body examination (Robinson et al., 2019). Although most prior research concentrated on macro-epibiota (e.g., Frazier et al., 1985; Fuller et al., 2010; Lazo-Wasem et al., 2011; Casale et al., 2012), meio and micro-epibiota have recently received increasing attention due to their high diversity and abundance in sea turtles, as well as advancements in microscopic techniques that have facilitated greater study of these smaller organisms (e.g., Corrêa et al., 2013; Majewska et al., 2015, 2017; Robinson et al., 2016; Azari et al., 2020; Ingels et al., 2020; Silver-Gorges et al., 2021). Some of these taxa, such as diatoms, are found on all sea turtle species (Majewska et al., 2015; Robinson et al., 2016) and are considered ecological indicators (El-Semary, 2016; Majewska et al., 2017). A comprehensive baseline study on the epibionts of sea turtles should, therefore, encompass both macroscopic and microscopic epibiota to depict a better picture of the turtle epibiont assemblages (Majewska et al., 2015). To the best of our

TABLE 3 | Results of the SIMPER procedure to identify the relative contribution of each epibiont taxa to the dissimilarity between the epibiont assemblages of hawksbills (*Eretmochelys imbricata*) nesting on Shibderaz (Qeshm Island) and Dayyer-Nakhiloo National Park (DNNP; Bushehr) beaches, Iran: (a) all epibionts, (b) micro-epibionts and (c) macro-epibionts.

Systematic group	Epibiont taxon	Shibderaz vs. DNNP		
		Average dissimilarity	Contribution (%)	Cumulative (%)
a				
Algae: Rhodophyta	Unknown	2.53	7.10	7.10
Mollusca: Gastropoda		2.26	6.32	13.42
Mollusca: Bivalvia		2.02	5.64	19.07
Cnidaria: Hydrozoa	Campanulariidae	1.98	5.55	24.62
Algae: Rhodophyta	<i>Ceramium</i> sp.	1.98	5.54	30.16
Algae: Chlorophyta	<i>Ulva</i> sp.	1.82	5.11	35.27
Crustacea: Amphipoda	<i>Hyachella</i> sp.	1.76	4.93	40.20
Nematoda		1.74	4.88	45.07
Crustacea: Ostracoda		1.51	4.23	49.31
Algae: Chlorophyta	<i>Chaetomorpha</i> sp.	1.49	4.18	53.48
Crustacea: Cirripedia	<i>Stomatolepas transversa</i>	1.39	3.90	57.38
Annelida: Polychaeta	Polychaeta	1.37	3.84	61.22
Crustacea: Cirripedia	<i>Stephanolepas muricata</i>	1.29	3.61	64.83
Algae	Algae sp. 1	1.28	3.58	68.41
Crustacea: Tanaidacea	Tanaidacea	1.16	3.25	71.66
Foraminifera: Miliolida	<i>Quinqueloculina</i> spp.	0.75	2.11	73.77
Algae: Bacillariophyceae	<i>Amphora ovalis</i>	0.67	1.86	75.63
Crustacea: Cumacea		0.59	1.64	77.27
Algae: Bacillariophyceae	<i>Amphora</i> sp. 1	0.52	1.45	78.72
Foraminifera: Textulariida		0.50	1.41	80.13
Algae: Bacillariophyceae	<i>Cocconeis scutellum</i>	0.48	1.34	81.47
Porifera		0.42	1.17	82.64
Haptophyta: Isochrysidales	<i>Emiliana huxleyi</i>	0.36	1.00	83.64
Algae: Bacillariophyceae	<i>Cocconeis</i> spp.	0.30	0.84	84.48
Algae: Bacillariophyceae	<i>Achnanthes</i> spp.	0.27	0.77	85.25
Algae: Bacillariophyceae	<i>Licmophora</i> spp.	0.27	0.77	86.02
Algae: Bacillariophyceae	<i>Navicula</i> sp. 1	0.27	0.77	86.79
Algae: Bacillariophyceae	<i>Opephora</i> sp.	0.22	0.63	87.41
Algae: Bacillariophyceae	<i>Actinocyclus</i> sp.	0.22	0.61	88.02
Algae: Bacillariophyceae	<i>Amphicocconeis</i> sp.	0.22	0.61	88.63
Algae: Bacillariophyceae	<i>Amphora coffeiformis</i>	0.22	0.61	89.23
Algae: Bacillariophyceae	<i>Berkeleya</i> sp.	0.22	0.61	89.84
Algae: Bacillariophyceae	<i>Cocconeis distans</i>	0.22	0.61	90.45
b				
Algae: Bacillariophyceae	<i>Cocconeis</i> spp.	23.28	23.83	23.83
Algae: Bacillariophyceae	<i>Caloneis</i> sp.	9.21	9.43	33.26
Algae: Bacillariophyceae	<i>Amphora</i> sp. 1	6.97	7.14	40.40
Haptophyta: Isochrysidales	<i>Emiliana huxleyi</i>	6.68	6.84	47.24
Algae: Bacillariophyceae	<i>Amphora ovalis</i>	6.65	6.80	54.04
Algae: Bacillariophyceae	<i>Achnantheidium</i> sp.	5.66	5.80	59.84
Algae: Bacillariophyceae	<i>Mastogloia horvatiana</i>	5.66	5.80	65.63
Algae: Bacillariophyceae	<i>Cocconeis scutellum</i>	4.67	4.78	70.42
Algae: Bacillariophyceae	<i>Achnanthes</i> spp.	3.44	3.53	73.94
Algae: Bacillariophyceae	<i>Licmophora</i> spp.	3.44	3.53	77.47
Algae: Bacillariophyceae	<i>Navicula</i> sp. 1	3.44	3.53	80.99
Algae: Bacillariophyceae	<i>Amphicocconeis</i> sp.	1.98	2.02	83.02
Algae: Bacillariophyceae	<i>Grammatophora</i> sp.	1.98	2.02	85.04

(Continued)

TABLE 3 | Continued

Systematic group	Epibiont taxon	Shibderaz vs. DNNP		
		Average dissimilarity	Contribution (%)	Cumulative (%)
Algae: Bacillariophyceae	<i>Opephora</i> sp.	1.98	2.02	87.06
Algae: Bacillariophyceae	<i>Actinocyclus</i> sp.	1.23	1.26	88.32
Algae: Bacillariophyceae	<i>Amphora coffeiformis</i>	1.23	1.26	89.57
Algae: Bacillariophyceae	<i>Berkeleya</i> sp.	1.23	1.26	90.83
c				
Algae: Rhodophyta	Unknown	4.11	10.45	10.45
Mollusca: Gastropoda		3.67	9.31	19.76
Algae: Rhodophyta	<i>Ceramium</i> sp.	3.26	8.28	28.05
Cnidaria: Hydrozoa	Campanulariidae	3.24	8.23	36.27
Mollusca: Bivalvia		3.23	8.19	44.47
Algae: Chlorophyta	<i>Ulva</i> sp.	3.02	7.66	52.13
Crustacea: Amphipoda	<i>Hyachelia</i> sp.	2.82	7.17	59.30
Nematoda		2.79	7.09	66.39
Algae: Chlorophyta	<i>Chaetomorpha</i> sp.	2.31	5.87	72.26
Crustacea: Cirripedia	<i>Stomatolepas transversa</i>	2.27	5.76	78.02
Annelida: Polychaeta		2.16	5.48	83.50
Crustacea: Cirripedia	<i>Stephanolepas muricata</i>	2.09	5.30	88.80
Crustacea: Tanaidacea	Tanaidacea	1.83	4.65	93.45

TABLE 4 | Occurrence of barnacles on different body parts of the hawksbill sea turtles nesting on Shibderaz (Qeshm Island) and Dayyer-Nakhiloo National Park (DNNP) in the Persian Gulf.

Body part	Number of barnacles	Percentage (%)
Flippers and adjacent soft parts	58,790	85.3
Plastron	6,654	9.7
Carapace	2,613	3.8
Under supracaudals	692	1
Head	156	0.2
Total	68,905	100

knowledge, our study is the first study that has simultaneously assessed macro-, meio-, and micro-epibionts on sea turtles. Some of these epibionts may distinguish groups of sea turtles (see Ingels et al., 2020) and reveal their movement pathways. Sea turtle conservation and management might benefit from research into the identification and origin of epibiont species or communities that are likely to be indicators of feeding or nesting sites.

Our results showed a statistically significant difference in the structure and species composition of epibiont assemblages in the two study sites (**Supplementary Table S1**), with higher species diversity in the Shibderaz at the entrance of the Persian Gulf compared to that of DNNP at the mid part of the sea. We suggest that these differences in turtle epibiont assemblages among different habitats in the Persian Gulf might result from differences in environmental conditions at each study site. Extreme and wide-ranging temperature fluctuations and high salinity in the Persian Gulf have led to the selection of tolerant taxa, which may result in impoverished biodiversity in the region

(Sheppard et al., 2010). However, the environmental extremes are not similar in all marine habitats of the sea. The Gulf receives incoming currents from the Gulf of Oman *via* the Strait of Hormuz, which flow counterclockwise through the Gulf and exit *via* the bottom of the Strait (Sheppard et al., 2010). Along the Iranian coastline of the Gulf, temperature and salinity increase with incrementing distance from the Strait (Reynolds, 1993). This is also evident from the temperature and salinity data presented in this study for the sites investigated (**Table 1**). Further, as a result of shape, bathymetry, and wind regime, waters close to the Strait of Hormuz are nutrient-rich (German and Elderfield, 1990; Longhurst et al., 1995).

Azari et al. (2020) studied diatoms on foraging green turtles in the Persian Gulf and found that diatom abundance on turtles collected from the Strait of Hormuz was higher than that of on turtles collected from the Gulf habitats found farther from the Strait. However, their findings were based on green turtles that dwell in foraging habitats, while our study examined hawksbill turtles in their nesting habitats, where they reside temporarily. The results of a previous post-nesting satellite tracking study showed that most of the Gulf hawksbills nesting along the Iranian coastline migrate to foraging grounds in the southeastern Persian Gulf and establish home ranges of 40 to 60 km² (Pilcher et al., 2014). The same study revealed that the Gulf hawksbill turtles spend only 6% of their time at the nesting grounds, whereas they spend about 68% in foraging grounds, about 20% conducting summer seasonal movements, and 5% migrating between foraging and nesting areas (Pilcher et al., 2014). Therefore, variable epibiont taxonomic composition at each nesting site is thought to be the outcome of various environmental conditions at the nesting grounds during a short period of time (i.e., about 6% of their time as reported by Pilcher

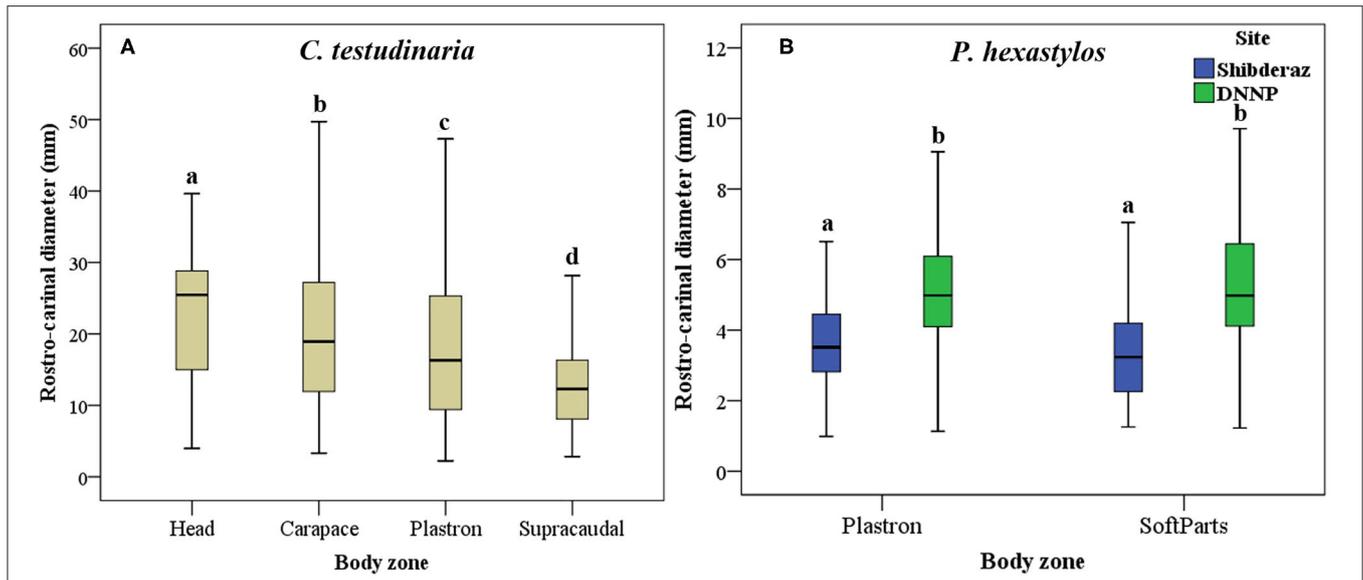


FIGURE 5 | Box plot showing Rostro-Carinal Diameter (RCD) of the turtle barnacles on different body parts of hawksbill turtles (*E. imbricata*) in Shibderaz and Dayyer-Nakhiloo National Park (DNNP): **(A)** *Chelonibia testudinaria* on head, carapace, plastron, and supracaudal and, **(B)** *Platylepas hexastylus* on plastron and soft parts.

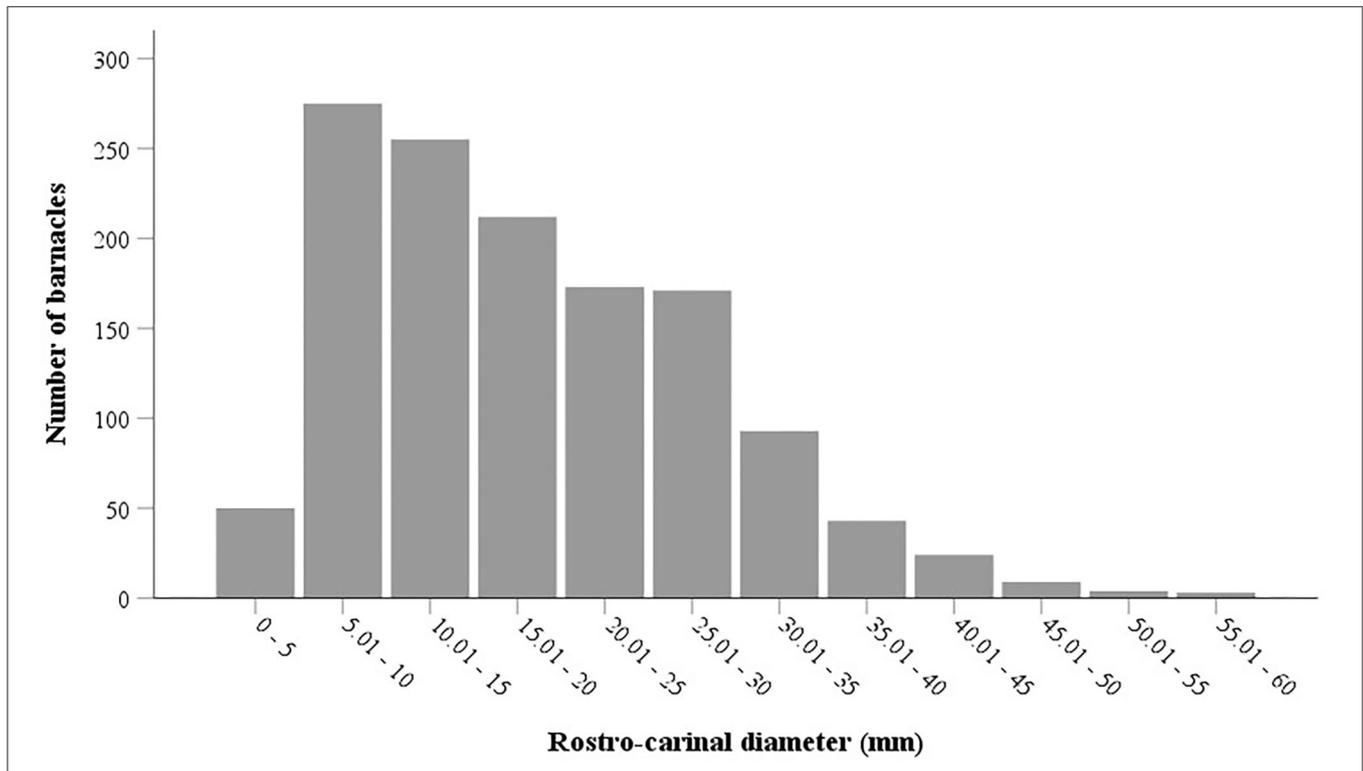


FIGURE 6 | Size frequency distribution of the barnacle *Chelonibia testudinaria* on different body surfaces of the hawksbill sea turtles nesting on Shibderaz and Dayyer-Nakhiloo National Park (DNNP).

et al., 2014). This mostly includes the short-living taxa such as diatoms.

In this research, we found more diverse diatoms on hawksbills and recorded only 11 taxa that were also found by Azari et al.

(2020). Although these studies were carried out almost in the same area, the host species was different; hawksbills were studied here whereas green turtles were the focus of Azari et al. (2020). We, therefore, speculate that the difference in diatom species

composition between our study and that of Azari et al. (2020) is partially due to differences in the behavior and local habitat use between these two Gulf turtle species. However, we acknowledge that it could also be a result of annual variations in the abundance and composition of diatom communities.

Some turtle epizoic taxa have a wide geographic distribution. Barnacle species including *C. testudinaria*, *P. hexastylus*, *Stomatolepas* sp., and *S. muricata*, for example, have been found on sea turtles from various locations (see Hayashi and Tsuji, 2008; Fuller et al., 2010; Lazo-Wasem et al., 2011; Casale et al., 2012; Domènech et al., 2015; Robinson et al., 2016, 2019). In addition to barnacles, harpacticoids (especially, *Balaenophilus manatorum*) and the amphipod, *Caprella* sp. have also shown a wide range of distribution on sea turtles (Caine, 1986; Pfaller et al., 2008b; Sezgin et al., 2009; Aznar et al., 2010; Casale et al., 2012; Domènech et al., 2015). The presence of these epibionts is seemingly not affected strongly by local environmental conditions. This wide distribution has also been locally observed in our study shown by the frequency of occurrence of some macro- and meio-epizoic taxa including barnacles (*C. testudinaria* and *P. hexastylus*), harpacticoid copepods, and rotaliid foraminifers. Our results revealed that while macro- and meio-epibiont taxa assemblages are relatively similar at both sites (16 macro- and 4 meio-epibiont taxa at Shibderaz; 18 macro- and 4 meio-epibiont taxa at DNNP, **Table 1**), micro-epibionts (26 taxa at Shibderaz and 6 taxa at DNNP, **Table 1**), represented mostly by diatoms, differ significantly. This was also evident by the high dissimilarity in species composition of micro-epibionts between the two sites (>97%, **Table 3**). We suggest that micro-epibionts may be considered as more sensitive bioindicators.

The most prominent turtle epibionts, barnacles, have shown contrasting spatial patterns on different body parts of studied turtles (Hayashi and Tsuji, 2008; Pfaller et al., 2008b; Fuller et al., 2010; Nájera-Hillman et al., 2012; Razaghian et al., 2019; Robinson et al., 2019). We also found a relative niche partitioning among different barnacle species. *P. hexastylus* individuals were observed mostly on the flippers and soft parts, while *S. transversa* was seen along the plastral sutures and *S. muricata* was mostly embedded in the gaps between scales in the leading edges of the front flippers. *C. testudinaria* showed a wider distribution attaching to both plastron and carapace. These distribution patterns are mainly driven by factors associated with feeding and attachment, including water flow (Pfaller et al., 2008a) and substratum characteristics (Fuller et al., 2010). These factors may also influence the barnacle size as was reflected by the RCD of our measured barnacles. Our results show that the most frequent RCD size range of *C. testudinaria* was 5–10 mm with a unimodal size-frequency distribution probably indicating only a single-age class of barnacles. These results are in line with those of Lim et al. (2020) on the size-frequency distribution of *C. testudinaria* on sea turtles, but are contradictory to Ewers-Saucedo et al. (2015) and Ten et al. (2019) who detected a bimodal size-frequency distribution of *C. testudinaria* in their studies. We speculate that the year-round reproduction of *C. testudinaria* in the Persian Gulf as a warm subtropical sea is the reason for

the lack of age classes compared to those from more seasonally affected areas.

In this research, the most abundant barnacle species on sea turtle bodies was *P. hexastylus*. A similar result was also found by Habibi Motlagh et al. (2020) who studied foraging green turtles in the Gulf. Similar to Robinson et al. (2019), we found that barnacle abundance on soft parts, including flippers, neck, and tail was considerably higher than on the carapace and plastron (**Table 4**). In contrast, Razaghian et al. (2019) studied the distribution pattern of epibiont barnacles on nesting hawksbills in DNNP and found that barnacle abundance was much higher on the plastron and carapace than on soft parts. The latter authors did not report *P. hexastylus* in their research but rather introduced only *C. testudinaria* as the epibiont barnacle of the examined turtles. We believe that this might be due to the lack of accurate identification of barnacle species which resulted in the taxonomic assignment of all individuals to *C. testudinaria*. We suggest that, in addition to the hard parts (carapace and plastron), soft parts of sea turtles should also be considered when assessing distribution and abundance of epibionts. Recently, Lim et al. (2020) examined different body parts of hawksbill turtles in Mabul Island (southeastern Sabah, Malaysia). They only examined barnacles larger than 5 mm on the carapace, plastron, and head of the turtles and concluded that *C. testudinaria* mainly settled on the plastron (94.6%) and just a few individuals tended to dwell on the carapace (1.4%) and head (4%). We also found a relatively similar pattern (but with different data values) in the settlement of *C. testudinaria*, with more individuals on the plastron (51%) compared to carapace and head (37 and 2%, respectively). The difference in data values may be a result of differences in the local barnacle larval supply, migratory behavior of turtles, and possibly barnacle removal by local people in some areas.

As a complementary study, these baseline data on turtle epibionts might be highly beneficial for future directions in adopting proper management strategies and making effective conservation decisions for these threatened species. In the face of climate change, the data are highly relevant considering the naturally harsh environment of the Persian Gulf. Furthermore, conducting such qualitative and quantitative assessments as regular monitoring studies can be used to track potential ecological changes in the Gulf. The epibiont assemblages of the two examined nesting turtle rookeries were significantly different, as revealed in this study, and may necessitate separate conservation approaches for the two populations. We encourage assessing epibionts of the other common turtle species in the region, the green turtle, to provide a clearer picture of sea turtle epibionts in the Persian Gulf and to better understand sea turtle habitat use and behavior in the region.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/Supplementary

Materials, further inquiries can be directed to the corresponding authors.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because we did the sampling under the Environmental Protection Organization role and received help from their local expert while sampling. As we have done this kind of sampling several times (and have published them), we used totally non-invasive protocols.

AUTHOR CONTRIBUTIONS

JL: conceptualization, methodology, sampling, analyses, and writing the first draft. AN: conceptualization, methodology, analyses, supervision, writing, review, and editing. BK: conceptualization, methodology, and supervision. MR-A: conceptualization, methodology, sampling, supervision, writing, review, and editing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.690022/full#supplementary-material>

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