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# Diatoms on sea turtles and floating debris in the Persian Gulf (Western Asia)

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**ABSTRACT**

The current study investigated diatom communities on juvenile green turtles foraging in neritic habitats around five Iranian islands. The primary objectives were to (1) compare species composition, growth form structure, and abundance of diatom communities associated with sea turtles foraging within the restricted boundaries of local feeding pastures, and (2) assess the level of uniqueness of the epizoic diatom flora in comparison with biofilms growing on floating debris. All observations and diatom counts were performed using scanning electron microscopy. The effect of the sampling location was apparent among sea turtle samples and reflected in significantly different cell densities. Diatom abundances were significantly higher on sea turtles (758–1836 cells $mm^{-2}$) than on floating debris samples (9–189 cells $mm^{-2}$). Epizoic diatom communities were composed of 20 diatom taxa and dominated by erect forms belonging to the so-called 'marine gomphonemoids', *Chelonicola* and *Poulinea*, previously reported on sea turtles from other geographical regions. The diatom flora found on floating debris was composed of 21 taxa. Only four taxa, *Amphora* cf. *bigibba, Cocconeis* cf. *neothumensis* var. *marina, Psammodictyon constrictum*, and *Tabularia affinis,* were recorded from both sea turtles and floating debris samples, and none of these exceeded 4% of the average relative abundance on the sea turtle carapaces. The study reveals a clear substratum preference in sea turtle-associated diatoms, with no evidence for species turnover across the investigated region over different sampling seasons, thus confirming previous speculations that sea turtle diatom communities would show a high level of uniqueness and stability.

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Biofilm; *Chelonia mydas*; Epibiosis; Epizoic diatom; Substratum specificity

## INTRODUCTION

Microbes are key elements of the biosphere, affecting other organisms at multiple levels. Numerous studies show that both endo- and epizoic microflora living in close association with animals profoundly shape their host biology (Carey & Duddleston 2014; Dubilier *et al.* 2008; Miller *et al.* 2018; Venn *et al.* 2008). Although sea turtles have been extensively studied for many years, studies on the sea turtle-associated microbes are limited largely to those focused on identification and characterisation of disease-causing bacteria, fungi, and viruses (Aguirre *et al.* 2006; Brofft Bailey *et al.* 2018; Cárdenas *et al.* 2019; Glazebrook & Campbell 1990; Raidal *et al.* 1998; Santoro *et al.* 2006).

Since the publication of the first report describing sea turtle-associated diatom communities (Majewska *et al.* 2015c), interest and knowledge in this subject have grown. Several new diatom taxa have been described, and biofilms on different sea turtle species from different geographical regions investigated, using both morphology-based and molecular techniques (Frankovich *et al.* 2015, 2016; Kaleli *et al.* 2018; Majewska *et al.* 2015a, 2017a, 2017b, 2017c, 2018; Riaux-Gobin *et al.* 2017a, 2017b; Rivera *et al.* 2018). Although epizoic diatom biodiversity, ecology, and function are far from being fully understood, and baseline information collection remains a major priority, investigations testing specific hypotheses are required to improve the current balance between speculation and available data. Some reports suggest that the epizoic community of sea turtles is composed of a combination of 'core taxa' and opportunistic species that settle on the carapace once the biofilm is formed (Majewska *et al.* 2015c, 2017c). Core taxa are thought to include truly (obligately) epizoic or sea turtle-specific species, and their relative abundances may depend on local environmental conditions as well as the basibiont physiological state and behaviour. However, once established, these epibionts remain important elements of the diatom flora throughout the lifespan of the host. Although yet to be addressed, future molecular analyses will be required to identify phylogenetic relationships among morphologically similar

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forms found on sea turtles worldwide. These core taxa may, therefore, serve as an excellent model to study dispersal modes of the marine surface-associated diatoms, as well as co-evolutionary processes in the diatom–sea turtle relationship. Opportunistically settling taxa may also provide useful tools in tracking sea turtle migration routes. However, it is not known whether or how sea turtle diatom communities vary in time and space, or how similar they are to those developing on other marine substrata.

The current study explores diatom communities present on juvenile green turtles (*Chelonia mydas* Linnaeus) in the Persian Gulf. Recent investigations conducted in this area indicate that green turtles occurring along the Iranian coast are mainly (> 90%) juvenile specimens foraging in patchy seaweed and seagrass meadows (M. Rezaie-Atagholipour, personal communication). Once a juvenile individual establishes its core habitat, it usually remains there for a prolonged period, as long as sufficient food is available (Hard & Fujisaki 2010; Limpus & Walter 1980; Musick & Limpus 1997; Rees *et al.* 2013). The extent of the core habitat can be as small as 0.18 km$^2$ (Makowski *et al.* 2006). This behaviour in juvenile green turtles has been reported in other populations (Rees *et al.* 2013; Robinson *et al.* 2017). The Persian Gulf is a relatively shallow Mediterranean water body (mean depth 36 m) with some pronounced gradients in surface water salinity and temperature caused by extensive evaporation and high isolation from the open ocean (Alosairi *et al.* 2011). Feeding pastures near islands in this region provided a unique opportunity for investigating the impact of local environmental conditions on epizoic diatom communities of a single species of sea turtle inhabiting the same water body. In addition, the study evaluated the uniqueness of the epizoic diatom flora with respect to that of biofilms developing on floating debris. Microscopical observation of morphospecies attached to the substratum surface was chosen over molecular analysis as a more effective and direct approach to study marine diatom biofilm structure and functional composition (Rivera *et al.* 2018).

## MATERIAL AND METHODS

### Material collection

Samples from sea turtle carapaces were collected in April, September, and October 2016 from green turtles foraging around five islands in the northern Persian Gulf: Hormuz, Larak, Hengam, Qeshm, and Hendurabi Islands (Table 1, Fig. 1).

The approach and methodology used in this study largely followed those described in Majewska *et al.* (2017c). Juvenile and subadult specimens of green turtles were caught in the shallow coastal waters by SCUBA divers. At least three *c.* 5–10 cm$^2$ samples of carapace with visible signs of epizoic growth (brown biofilm) were shaved from lateral and posterior parts of every specimen by a qualified field researcher using a scalpel or razor blade. Turtles were released as soon as the samples had been collected. As this method affects only the external layer of carapace (i.e. tissue composed of anucleate cells), it did not cause animal suffering. In total, 20 individuals were sampled (four from each of the five islands). Sampling was conducted under the close supervision of experienced research station personnel and all procedures used in this study were approved by the Hormozgan Environmental Organization, Iran (under approval number 16.Zh.96), which acted as the ethics board. The methods applied respected ethical standards in the Declaration of Helsinki (World Medical Association 2013) and all applicable national laws. The techniques used did not involve anaesthesia, euthanasia, or any animal sacrifice.

Table 1. Dates of sea turtle (•) and floating debris material collection and geographic coordinates of sampling locations. All sampling dates in 2016.

| Sampling site | Site no | Sampling date | Geographic coordinates |
|---|---|---|---|
| Hendurabi • | 1 | 01 September | 26°41.68′N, 53°38.03′E |
| Qeshm • | 2 | 01 April | 26°41.38′N, 55°49.06′E |
| Hengam • | 3 | 07 October | 26°36.79′N, 55°54.08′E |
| Hormuz • | 4 | 21 October | 27°2.05′N, 56°29.18′E |
| Larak • | 5 | 14 October | 26°49.11′N, 56°23.33′E |
| Bandar Abbas (Posht Shahr) | 6 | 01 February | 27°10.26′N, 56°15.77′E |
| Bandar Abbas (Haghani) | 7 | 01 February | 27°10.44′N, 56°16.80′E |
| Khamir Port | 8 | 02 February | 26°56.76′N, 55°35.91′E |
| Sayeh Khosh beach | 9 | 02 February | 26°46.54′N, 55°19.90′E |
| Kong Port | 10 | 02 February | 26°35.39′N, 54°56.68′E |
| Bostaneh Port | 11 | 02 February | 26°30.46′N, 54°39.77′E |
| Javadolaemeh Port | 12 | 03 February | 27°7.66′N, 52°59.95′E |
| Khoor-e-Haleh | 13 | 03 February | 27°24.27′N, 52°38.71′E |
| Assaluyeh Port | 14 | 03 February | 27°28.32′N, 52°36.88′E |
| Dayer Port | 15 | 04 February | 27°49.84′N, 51°55.84′E |
| Bushehr Port | 16 | 04 February | 28°55.40′N, 50°49.22′E |
| Shif Island | 17 | 05 February | 29°4.42′N, 50°52.33′E |
| Genaveh Port | 18 | 05 February | 29°33.61′N, 50°30.72′E |
| Deylam Port | 19 | 05 February | 29°49.86′N, 50°15.53′E |

Samples of floating debris, including driftwood, plastic bottles, tires, and aluminium cans, were collected to enable comparison of diatom floras growing on sea turtles and physical debris present in the water. Debris items were collected in February 2016 from near 14 coastal stations located along the Iranian coastline (Fig. 2, Table 1). Only debris with visible patches of biofilm was collected. This limited the number of debris samples to 51 (35 plastic bottles, nine pieces of driftwood, three cans, and three tires), as the appropriate specimens could not always be found within the selected sampling area. Due to logistic constraints and permit delays, sampling of sea turtle and floating debris biofilm were not simultaneous.

Environmental data, including surface water temperature, salinity, pH, and concentration of phosphates and nitrates (Table 2), were obtained through the Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu; product reference: CMEMS-GLO-QUID-001-024).

### Material processing and microscopy

Immediately after collection, samples (both carapace and debris) were placed in separate plastic containers and preserved in 4% formaldehyde solution in filtered seawater. Samples were then cut into *c.* 1-cm$^2$ pieces and dehydrated by immersion in an

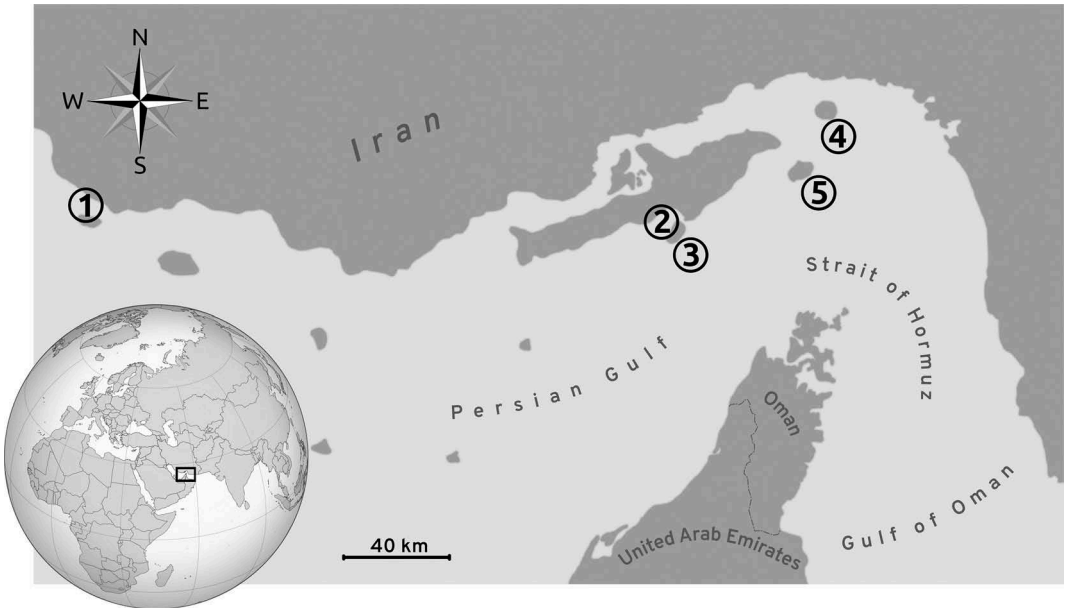


Fig. 1. Sea turtle carapace sampling locations: 1, Hendurabi; 2, Qeshm; 3, Hengam; 4, Hormuz; 5, Larak. See Table 1 for coordinates.

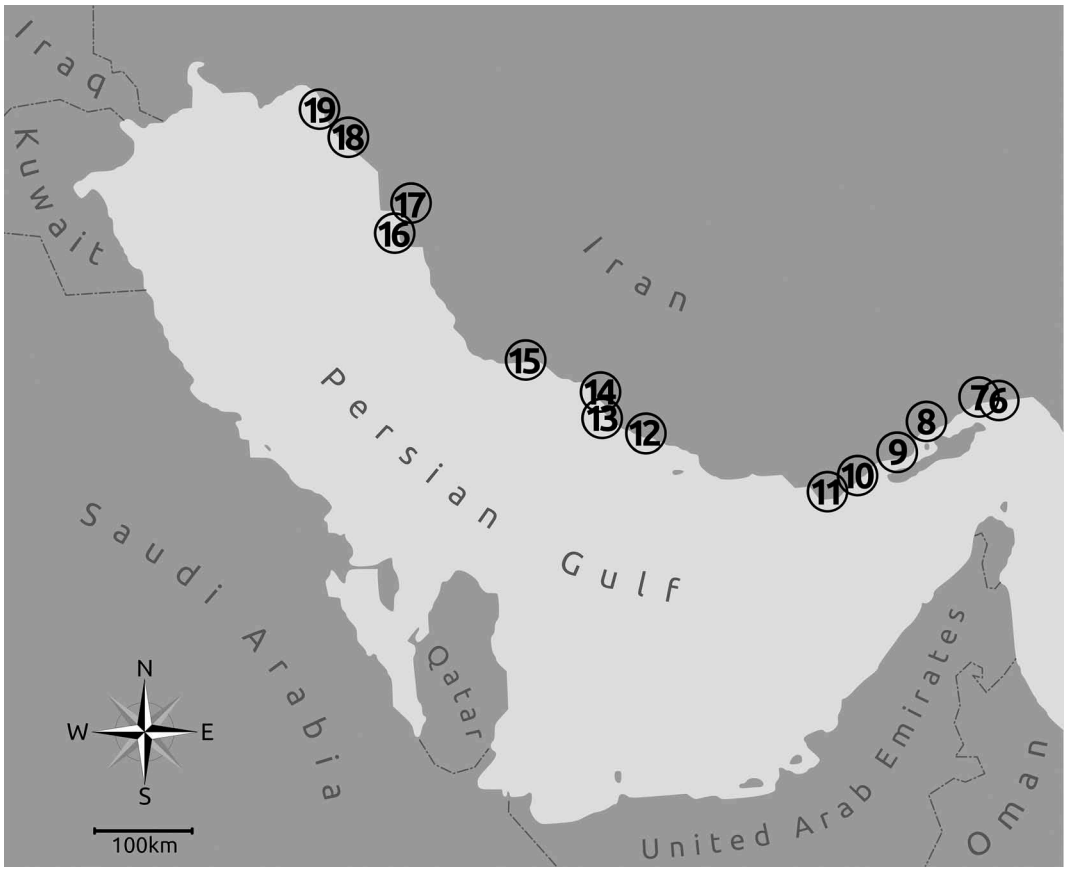


Fig. 2. Floating debris sampling locations. See Table 1 for sampling site names and coordinates.

ethanol concentration series followed by critical point drying (Majewska *et al.* 2017c). Finally, they were mounted on aluminium stubs with adhesive carbon discs. This technique preserves the entire surface-associated community, providing information on diatom growth form and spatial distribution on the surface.

For taxonomic analysis, roughly 50% of each carapace sample was digested in boiling concentrated acids using von Stosch's method (Hasle & Syvertsen 1997). The same technique was used to detach and clean frustules of diatoms growing on debris pieces. Subsequently, a few drops of

**Table 2.** Average monthly values (with standard deviation) of some of the environmental factors prevailing at the sea turtle (•) and floating debris material collection sites.

| Site no | Sampling month | Temp (°C)[a] | Salinity (PSU)[b] | $NO_3^-$ (mmol $m^{-3}$)[c] | $PO_4^{3-}$ (mmol/$m^3$)[d] | pH[e] |
|---|---|---|---|---|---|---|
| 1• | September | 31.8 | 38.2 | 0.010 | 0.001 | 8.04 |
| 2• | April | 25.1 | 37.2 | 0.009 | 0.131 | 8.07 |
| 3• | October | 30.8 | 38.1 | 0.008 | 0.019 | 8.04 |
| 4• | October | 30.7 | 38.2 | 0.008 | 0.019 | 8.04 |
| 5• | October | 30.7 | 38.2 | 0.008 | 0.018 | 8.04 |
| 6 | February | 21.6 | 37.3 | 0.008 | 0.086 | 8.12 |
| 7 | February | 21.7 | 37.3 | 0.009 | 0.078 | 8.13 |
| 8 | February | 20.8 | 37.2 | 0.007 | 0.100 | 8.12 |
| 9 | February | 21.3 | 37.5 | 0.008 | 0.104 | 8.13 |
| 10 | February | 22.0 | 37.4 | 0.008 | 0.098 | 8.13 |
| 11 | February | 22.0 | 37.4 | 0.008 | 0.082 | 8.14 |
| 12 | February | 22.2 | 37.4 | 0.007 | 0.071 | 8.14 |
| 13 | February | 22.2 | 38.0 | 0.014 | 0.026 | 8.14 |
| 14 | February | 21.9 | 38.0 | 0.008 | 0.012 | 8.18 |
| 15 | February | 20.7 | 38.1 | 0.007 | 0.008 | 8.18 |
| 16 | February | 17.2 | 37.3 | 0.020 | 0.001 | 8.19 |
| 17 | February | 17.0 | 37.2 | 0.043 | 0.001 | 8.21 |
| 18 | February | 16.7 | 37.0 | 0.170 | 0.001 | 8.22 |
| 19 | February | 16.6 | 35.6 | 0.464 | 0.001 | 8.22 |

[a]Maximum $s$ = 0.05; [b]maximum $s$ = 0.08; [c]maximum s = 0.001; [d]maximum $s$ = 0.008; [e]maximum = 0.003.

cleaned diatom material were filtered through Nucleopore polycarbonate filters (1.2-µm pore size), mounted on aluminium stubs, and air-dried at room temperature.

A Polaron SC7640 sputter coater (Quorum Technologies Ltd., Ashford, UK) was used to coat specimens with a thin layer of gold/palladium (Au-Pd). Microscopic observations were made with a Hitachi SU3500 (Hitachi High-Technologies, Tokyo, Japan) scanning electron microscope (SEM) operating at 15 kV. Diatoms attached to substratum pieces were counted in 10 randomly selected fields (0.1 $mm^2$ each) across prepared sections of each sample. To assess structural differences among surface-associated diatom communities, taxa were grouped according to growth form using the classification proposed by Round (1981) and applied in several other studies exploring epibiotic diatom flora (Majewska *et al.* 2015b, 2015c; Romagnoli *et al.* 2007). Taxonomic identifications were performed after analysis of cleaned material.

All samples and microscopy specimens produced are stored at the Department of Environmental, Biological and Pharmaceutical Sciences and Technologies, University of Campania 'Luigi Vanvitelli', Caserta, Italy.

## Statistical analysis

Statistical analyses were run using PRIMER v7 (Clarke & Gorley 2006). Non-metric multidimensional scaling (nMDS) was performed to visualise similarity among biofilm samples collected from different substrata and locations, and permutational multivariate analysis of variance (PERMANOVA) was used to test for statistical significance of those patterns. The Bray–Curtis similarity index, used to build the matrix, was calculated either on raw (one-way PERMANOVA) or square-root transformed species abundance data (two-way crossed PERMANOVA, nMDS) expressed as the number of diatoms per 1 $mm^2$ of carapace. Similarity percentage analysis (SIMPER) was run to estimate the intra- and inter-group dissimilarity. A one-way ANOVA was used to test for significant differences in total abundances and growth form structure among sea turtle biofilm samples.

# RESULTS

## Sea turtles

Diatoms (Figs 3–11) were found on all carapace pieces analysed, with densities ranging from 571 cells $mm^{-2}$ (Hendurabi) to 2153 cells $mm^{-2}$ (Hormuz). The highest average diatom abundances were recorded for the two easternmost sampling stations, Larak (1836 ± 247 cells $mm^{-2}$) and Hormuz (1730 ± 376 cells $mm^{-2}$); the lowest for the westernmost station, Hendurabi (758 ± 144 cells $mm^{-2}$; Fig. 12). ANOVA confirmed that diatom abundances were significantly higher in samples collected from Larak and Hormuz than in those from the three other islands ($P$ = 0.025 for Hengam and Hormuz; $P$ = 0.026 for Hendurabi and Hormuz and Hengam and Larak; $P$ = 0.029 for Hendurabi and Larak, Qeshm and Hormuz, and Qeshm and Larak).

All carapace samples were dominated by erect (including chain-forming) diatoms (Figs 3, 6–10) that contributed from 59% (Hengam) to 81.5% (Hendurabi) of total diatom number (Fig. 13). Motile and adnate forms contributed from 7% (Hendurabi) to 31% (Hengam) and from 2.5% (Hengam) to 18.3% (Hendurabi), respectively (Fig. 13). ANOVA indicated that differences in growth form structure (based on relative abundances) observed between the five sampling locations were not significant ($P$ > 0.05).

Altogether, 20 diatom taxa (17 genera) were identified from the sea turtle carapace samples, all of which occurred on sea turtles foraging in the vicinity of the five islands (Table 3). Three taxa, *Chelonicola costaricensis* Majewska, De Stefano & Van de Vijver (contributing up to 66.2% of total diatom abundance; Figs 3, 8), *Poulinea* cf. *lepidochelicola* Majewska, De Stefano & Van de Vijver (up to 31% of total diatom abundance; Figs 3, 6, 7), and *Nitzschia* sp. 1 *sensu* Majewska *et al.* (2015c; up to 17.7% of total diatom abundance), exceeded average abundance of 10% on sea turtles from at least one of the sampled islands. The former two taxa dominated every sample and together contributed from 62.2% (Hormuz) to 71.2% (Hendurabi) of total diatom number (Table 3). Six other taxa, *Amphora* cf. *bigibba* Grunow ex A. Schmidt, *Amphora* sp. 2 *sensu* Majewska *et al.* (2015c), *Cocconeis* cf. *neothumensis* var. *marina* De Stefano, Marino & Mazzella, *Microtabella interrupta* (Ehrenberg) Round, *Navicula* sp. 1 *sensu* Majewska *et al.* (2015c), and *Psammodictyon constrictum* (W. Gregory) D.G.Mann, exceeded average abundance of 3% (Table 3).

A clear pattern of sea turtle diatom communities in relation to sampling location was revealed (Fig. 14). The nMDS graph based on cluster analysis indicated four groups of samples at the 80% similarity level (Fig. 14). A pair-wise PERMANOVA test confirmed significant differences in

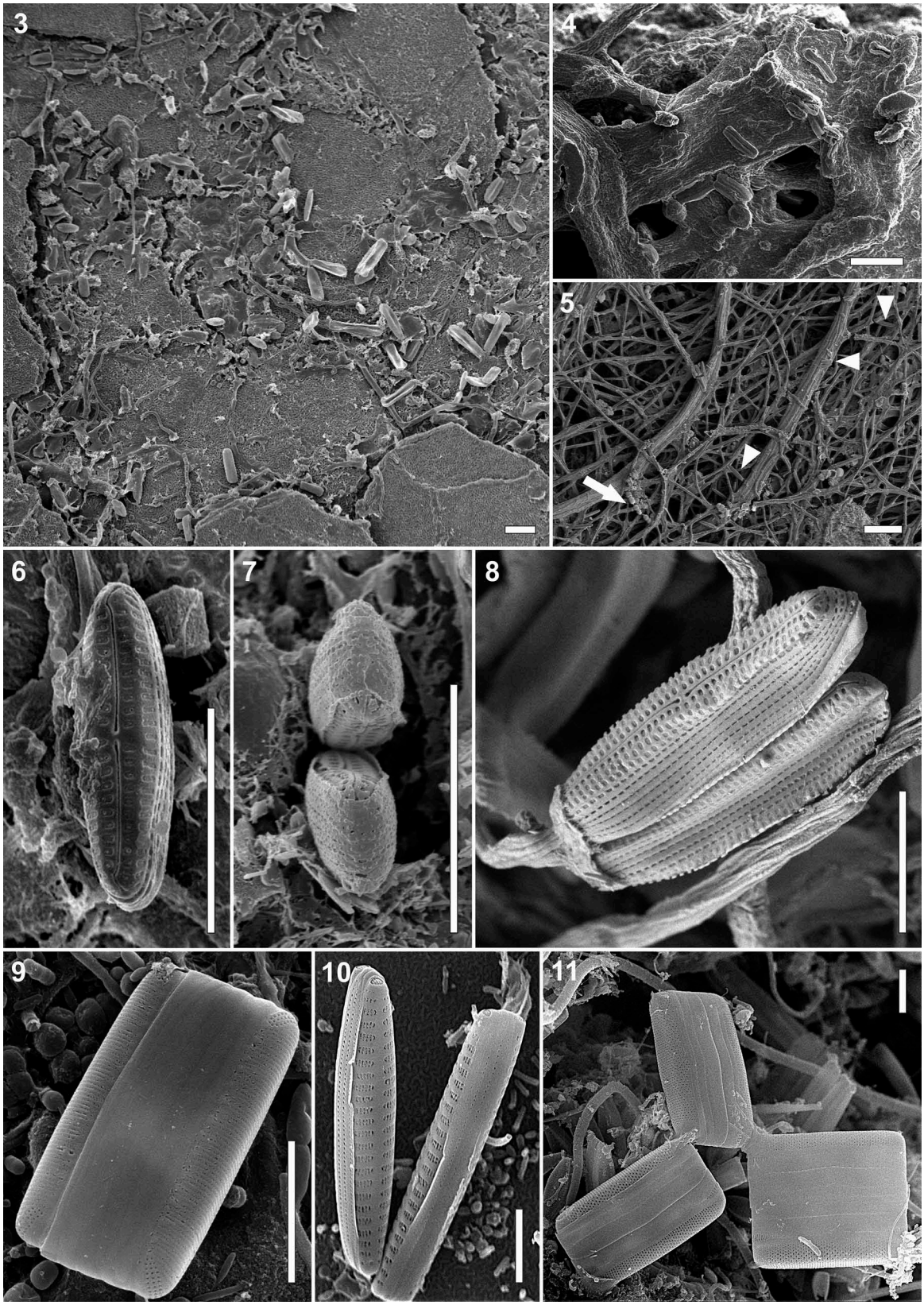


Fig. 3-11. Scanning electron micrographs showing diatoms on the surface of various substrata.
**Fig. 3**. *Chelonicola costaricensis* (larger cells) and *Poulinea* sp. (smaller cells) on sea turtle carapace. Scale bar = 10 µm;
**Fig. 4**. *Achnanthes brevipes* attached to biofilm on a plastic bottle. Scale bar = 50 µm;
**Fig. 5**. *Melosira varians* (arrow) and *Tabularia affinis* (arrowheads) on driftwood surface. Scale bar = 100 µm;
**Figs 6–7**. *Poulinea* cf. *lepidochelicola*. Scale bar = 5 µm;
**Fig. 8**. *Chelonicola costaricensis*. Scale bar = 5 µm;
**Fig. 9**. *Pteroncola inane*. Scale bar = 5 µm;
**Fig. 10**. *Tabularia investiens*. Scale bar = 5 µm;
**Fig. 11**. *Grammatophora marina*. Scale bar = 10 µm.

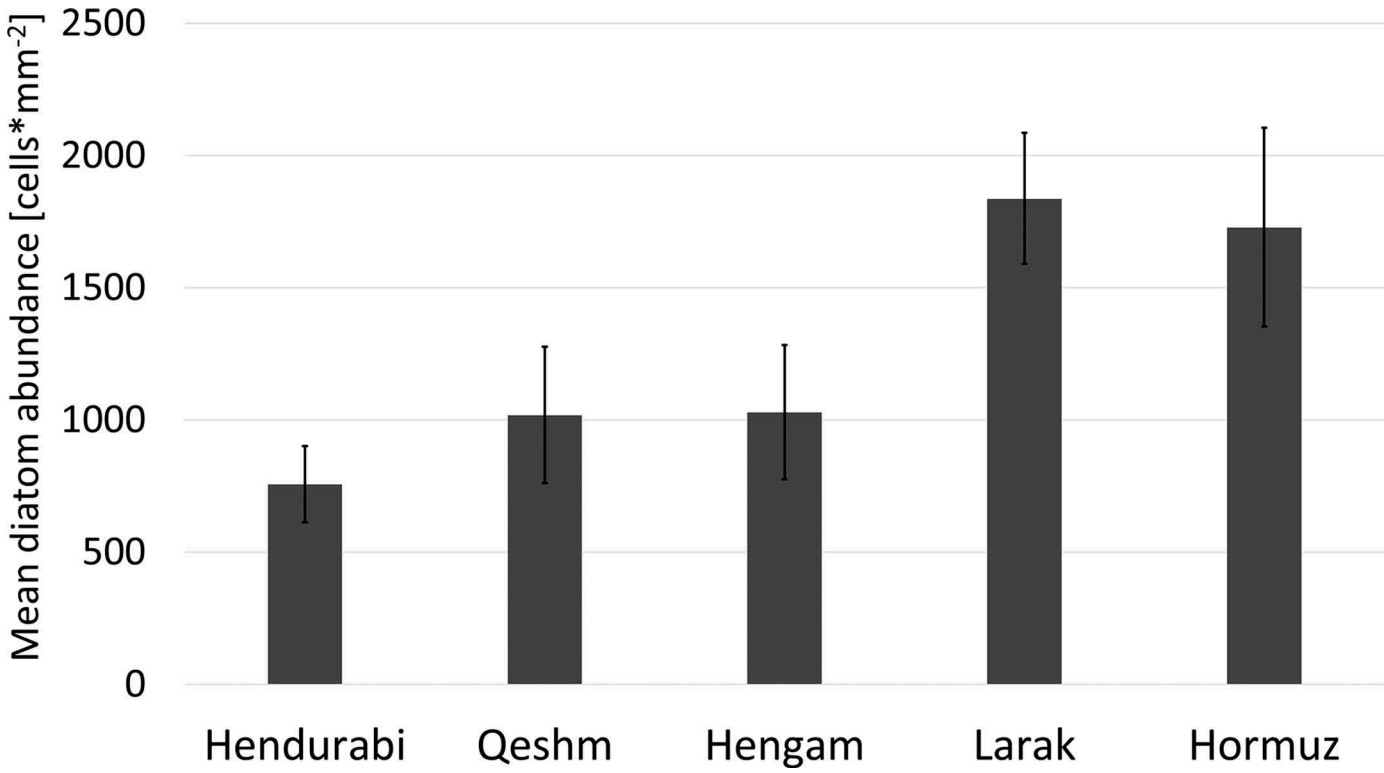


Fig. 12. Mean diatom abundance (± *s*) on sea turtle carapaces from the five islands.

diatom communities between all sample groups except for those collected from Hendurabi and Qeshm ($P$ = 0.1), Qeshm and Hengam ($P$ = 0.1), and Hormuz and Larak ($P$ = 0.1). High intra-group similarity was estimated for samples collected in the vicinity of Larak (91%), Hormuz (87.6%), and Hendurabi (86.2%; SIMPER). Inter-group dissimilarity ranged from 13.9% (Larak and Hormuz) to 26.2% (Hormuz and Hendurabi) and 26.8% (Larak and Hendurabi; Table 4).

## Floating debris

Diatom density on floating debris ranged from 9 cells mm$^{-2}$ (plastic bottle; Station 16; Figs 4, 15) to 189 cells mm$^{-2}$ (driftwood, Station 13; Figs 5, 15). The diatom flora was composed of 21 taxa (13 genera; Table 5). All of these occurred on floating plastic bottles and pieces of wood (Table 5). Three taxa, *Achnanthes brevipes* C.Agardh (contributing up to 20.5% of total diatom abundance), *Cocconeis convexa* M.H.Giffen (up to 19.1% of total diatom abundance), and *Tabularia affinis* (Kützing) Snoeijs (up to 17.7% of total diatom abundance), exceeded average abundance of 10% on floating wood; four taxa, *Amphora* cf. *bigibba* (up to 15%), *Navicula* cf. *cancellata* Donkin (up to 17.5%), *N. directa* (W. Smith) Ralfs (up to 17.5%), and *Pleurosigma strigosum* W. Smith (up to 13%), exceeded average abundance of 10% on floating cans; two taxa, *A. brevipes* (up to 40.5%) and *T. affinis* (up to 25.4%), exceeded average abundance of 10% on floating tires; and one taxon, *N. directa* (up to 25.8%) exceeded average abundance of 10% on plastic bottles.

## Comparative analysis

PERMANOVA test results on standardised abundance data (relative abundances) and a univariate PERMANOVA (ANOVA) test on raw abundance data confirmed a significant difference in both growth form structure ($P$ = 0.0001) and total abundances ($P$ = 0.0001) between sea turtle and debris samples (Figs 3–5, 12, 15). Of all 21 taxa growing on floating debris, only four, *A.* cf. *bigibba, C.* cf. *neothumensis* var. *marina, P. constrictum* (W. Gregory) D.G. Mann, and *T. affinis*, were also found in sea turtle carapace samples, and these contributed on average 3%, 3.9%, 2.7%, and 1.8%, respectively, of the total number of diatoms growing on sea turtle carapaces (Tables 3, 5).

Sea turtle diatom communities differed from those found on floating debris to such a high degree that the two sample sets could not be reliably plotted on the same nMDS graph (see Figs S1, S2). Thus, two separate graphs were produced to better visualise relationships of diatom communities associated with different substrata (Figs 14, 16).

Debris samples were grouped according to substratum type (plastic, wood, can, tire) and the part of the gulf they were collected (mouth, central, head). Despite the uneven number of samples representing different substrata, PERMANOVA partitioning showed significant ($P$ = 0.0001) effects of both substratum and location, with the former being relatively stronger ($s$ = 27 vs $s$ = 19, Table 6), whereas the effect of the interaction term ('Sub x Loc') was not significant ($P$ = 0.06; Table 6). The patterns were apparent in the nMDS graph showing samples grouped by both Substratum and Location (Fig. 16). A pair-wise PERMANOVA test confirmed significant compositional differences in diatom communities

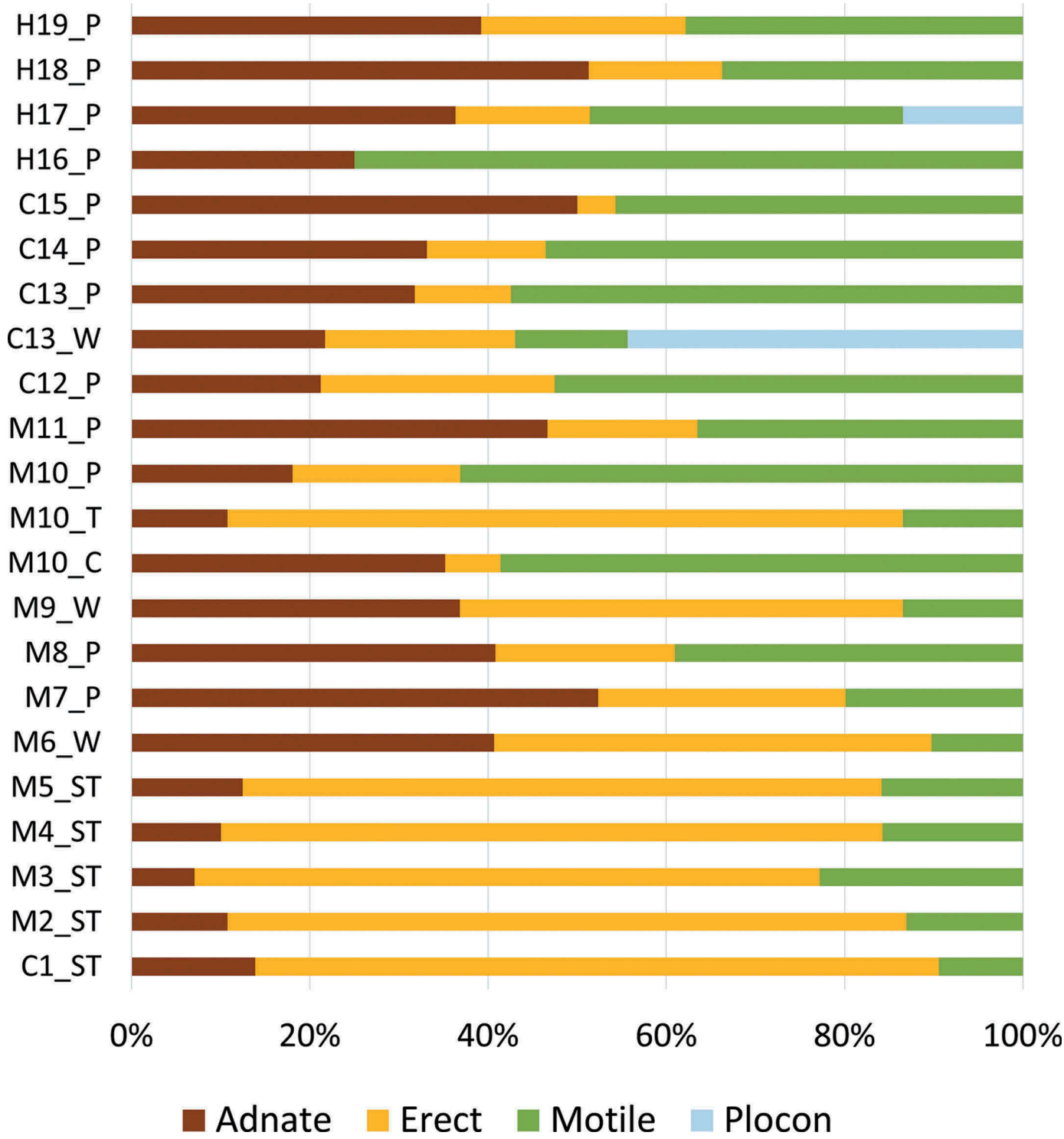


Fig. 13. Relative diatom growth form abundance on sea turtle carapaces and floating debris. Numbers in sample labels correspond to station numbers (Table 1, Fig. 2). C, central part of gulf; M, gulf mouth; H, gulf head; ST, sea turtle; W, wood, P, plastic; C, can; T, tire.

between all substratum types ($P$ = 0.0001 for wood and plastic, and plastic and tires, and $P$ = 0.0002 for wood and tires, and wood and cans) except for those associated with plastic bottles and cans ($P$ = 0.06) and cans and tires ($P$ = 0.1). Similarly, significant differences were found between samples collected from different parts of the gulf ($P$ = 0.0001 for the gulf mouth and head, $P$ = 0.0005 for the mouth and the central part of the gulf, and $P$ = 0.002 for the head and the central part).

No correlations were found between diatom density and environmental factors considered (T, S, pH, $NO_3^-$, $PO_4^{3-}$). As samples were collected from stations located along the entire Iranian coast and over different months, the range of values measured varied considerably, with average surface water

**Table 3.** Diatom taxa found on green turtles from five Iranian islands with relative abundance ranges (%) and mean relative abundance (in parentheses).

| Taxa | Hormuz | Larak | Hengam | Qeshm | Hendurabi | Average |
|---|---|---|---|---|---|---|
| *Achnanthes* sp. | < 1 | 0.3–3.3 (1.4) | < 1 | 1.2–2.7 (2) | < 1 | < 1 |
| *Amphora* cf. *bigibba* Grunow ex A.Schmidt* | < 1 | 1.7–4.7 (3) | 0.4–2.5 (1.8) | 3.6–7 (4.7) | 3.5–6 (4.9) | **3** |
| *Amphora* sp. 1 | < 1 | < 1 | < 1 | < 1 | < 1 | < 1 |
| *Amphora* sp. 2 *sensu* Majewska *et al.* 2015c | 2.6–7 (5) | 4–5 (4.5) | 1.5–4.6 (2.9) | 3.2–6.2 (4.5) | 1.5–3.9 (2.5) | 3.9 |
| *Chelonicola costaricensis* Majewska, De Stefano & Van de Vijver | 36–52 (43.9) | 48.7–60.3 (53) | 27.9– 47 (40) | 44.8–62 (54.4) | 55–66.2 (60.2) | 50.3 |
| *Cocconeis* cf. *neothumensis* var. *marina* De Stefano, Marino & Mazzella* | 3.2–10.3 (6.8) | 1.4–3.6 (2.5) | 0.6–5.2 (2.4) | 0.5–2.2 (1.5) | 2.5–9.9 (6.5) | 3.9 |
| *Dimeregramma* sp. | < 1 | < 1 | 0.7–4.1 (2.5) | < 1 | < 1 | 1 |
| *Haslea amicorum* Herwig, Tiffany, Hargraves & Sterrenburg | < 1 | < 1 | < 1 | 0.9–2.8 (1.8) | < 1 | 1 |
| *Microtabella interrupta* (Ehrenberg) Round | 2–5.3 (3.3) | 2.7–5 (3.5) | 0.3–3 (1.4) | 0.8–3.7 (2) | 1.8–2.1 (2) | 2.4 |
| *Navicula* sp. 1 *sensu* Majewska *et al.* 2015c | < 1 | < 1 | 1.9–7 (4.2) | 0.3–2.8 (1.3) | 0.6–1–9 (1.2) | 1.5 |
| *Nitzschia fasciculata* Grunow | < 1 | < 1 | < 1 | < 1 | < 1 | < 1 |
| *Nitzschia* sp. 1 *sensu* Majewska *et al.* 2015c | 4.5–9.6 (7.4) | 7.2–10.2 (8.7) | 7–17.7 (10.6) | 2.6–11.1 (6.8) | 0.6–3 (2.4) | 7.2 |
| *Parlibellus* sp. | < 1 | < 1 | < 1 | < 1 | 0.6–1.6 (1) | < 1 |
| *Pinnularia* sp. | 1.7–5.1 (2.8) | 0.7–1.7 (1.2) | < 1 | < 1 | < 1 | 1.3 |
| *Poulinea* cf. *lepidochelicola* Majewska, De Stefano & Van de Vijver | 13.9–23 (18.3) | 10–17 (12.3) | 13.5–31 (23.6) | 11.6–17 (15.4) | 5.6–15.6 (11) | 16.3 |
| *Psammodictyon constrictum* (W.Gregory) D.G.Mann* | 1.3–3.1 (2.5) | 2.8–4.9 (4) | 1.6–9.4 (4.5) | < 1 | 0.9–3.7 (2.1) | 2.7 |
| *Pteroncola inane* (Giffen) Round | 1–3.6 (2.1) | 0.7–1.4 (1.1) | < 1 | < 1 | < 1 | 1 |
| *Seminavis strigosa* (Hustedt) Danieledis & Economou–Amilli | 1.4–3 (1.9) | < 1 | 0.2–2.6 (1.2) | 1.5–4.2 (2.3) | < 1 | 1.3 |
| *Tabularia affinis* (Kützing) Snoeijs* | 1.3–3.9 (2.7) | 0.8–1.4 (1.1) | 0.6–5.6 (2.2) | 0.2–2.5 (1.3) | 0.7–3 (1.9) | 1.8 |
| *Tabularia investiens* (W.Smith) D.M. Williams & Round | <1 | <1 | <1 | <1 | <1 | <1 |

*Species found on both floating debris and sea turtles.

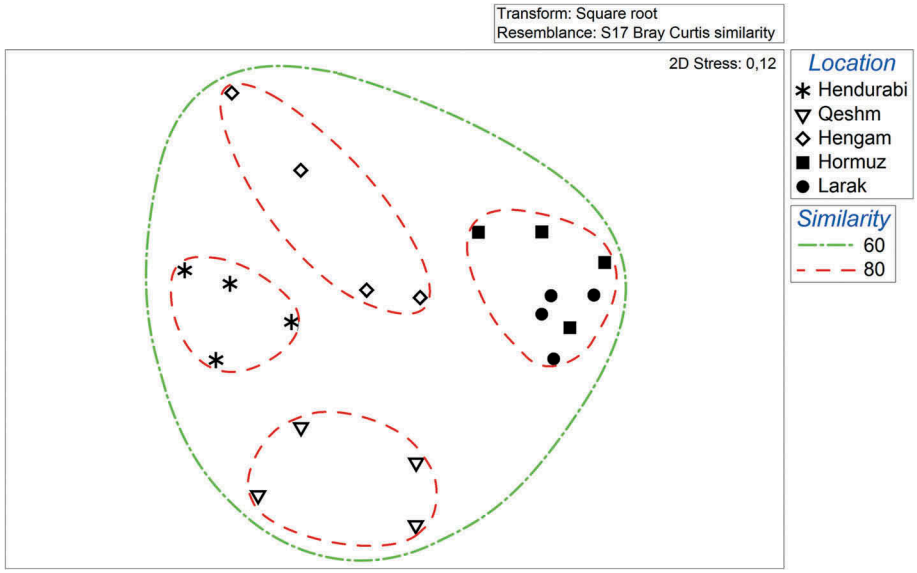


**Fig. 14.** Graph of non-metric multidimensional scaling showing distances between diatom samples as their compositional dissimilarity, with four groups of samples identified by cluster analysis at 80% similarity level.

**Table 4.** Between-group dissimilarity (%) in diatom communities associated with green turtles from five Iranian islands (SIMPER).

| | Hormuz | Larak | Hengam | Qeshm |
|---|---|---|---|---|
| Hormuz | – | – | – | – |
| Larak | 13.9 | – | – | – |
| Hengam | 23.9 | 22.8 | – | – |
| Qeshm | 25.1 | 24.8 | 23.7 | – |
| Hendurabi | 26.2 | 26.8 | 20.9 | 22.2 |

temperature being significantly higher and pH significantly lower for the sea turtle (25.1–31.8 °C and 8.04–8.07) than for debris samples (16.6–22.2 °C and 8.12–8.22; Table 2).

## DISCUSSION

We confirmed that diatoms are a regular, abundant, and likely important component of the microflora inhabiting sea turtle carapaces. The number of epizoic diatom taxa found was relatively low (20) and differed only slightly among sampled sea turtles, similar to previous observations (Majewska *et al.* 2015c, 2017c). Diatom communities were dominated by so-called 'marine gomphonemoids', i.e. species belonging to *Chelonicola* and *Poulinea*. The two genera were recently described from olive ridleys (Majewska *et al.* 2015c), and later found on several sea turtle species from different geographical regions (Majewska *et al.* 2017c, 2018; Riaux-Gobin

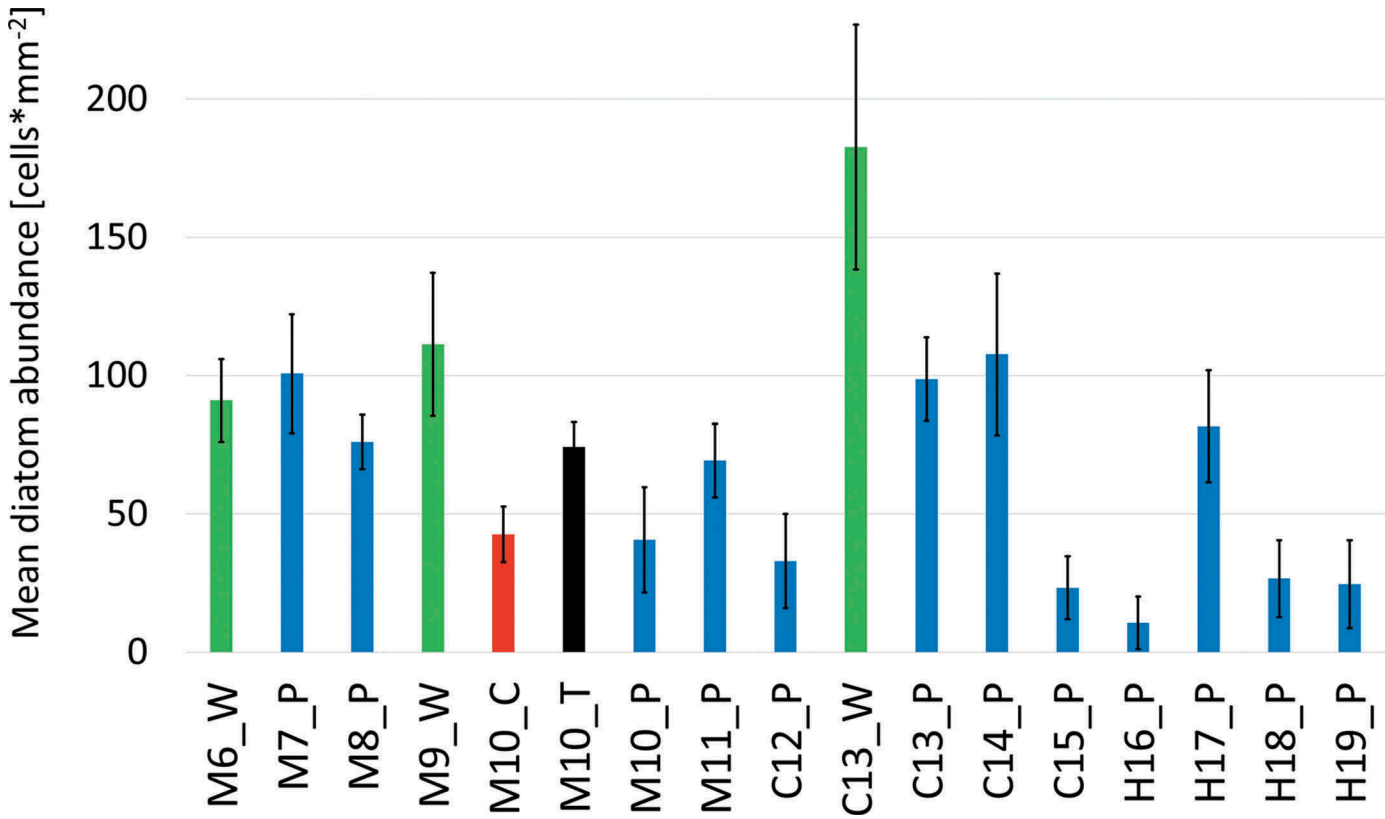


Fig. 15. Mean diatom abundance (± *s*) on floating debris. Numbers in the sample labels correspond to station numbers (Table 1, Fig. 2). C, central part of gulf; M, gulf mouth; H, gulf head; ST, sea turtle; W, wood, P, plastic; C, can; T, tire.

*et al.* 2017b; Robinson *et al.* 2016). In line with previous speculations, these presumably obligately epizoic small-celled taxa were not observed among diatoms developing on the floating debris, which supports the hypothesis that in the natural environment this group of microalgae may require the sea turtle substratum to thrive. Eleven of the 12 diatom taxa found on green turtles collected in near Hengam Island in June 2015 (Majewska *et al.* 2017c) were also recorded in the

Table 5. Diatom taxa found on various types of floating debris with relative abundance ranges (%) and mean relative abundance (in parentheses).

| Taxa | Wood | Can | Tire | Plastic | Average |
|---|---|---|---|---|---|
| *Achnanthes brevipes* C. Agardh | 7.7–20.5 (14.2) | 2.3–4.3 (3.1) | 34.5–40.5 (37.7) | 0–16.7 (4.4) | 14.8 |
| *Amphora* cf. *angusta* W. Gregory | 0.9–3.9 (2.1) | 5–10.9 (8.5) | 1.3–2.7 (2.2) | 0–14.3 (7.4) | 5.1 |
| *Amphora* cf. *bigibba** | 1.1–3.7 (2.5) | 6.5–15 (11.1) | 1.3–2.7 (1.8) | 0–17.8 (8.2) | 5.9 |
| *Amphora costata* W. Smith | 0–4.7 (2) | 4.3–10 (7.2) | – | 0–21.7 (7) | 4 |
| *Amphora marina* W. Smith | 0–2.6 (1.5) | 7.5–9.5 (8.6) | – | 0–16.7 (5.5) | 3.9 |
| *Cocconeis* cf. *neothumensis* var. *marina** | 2.8–14 (8.9) | – | 1.3–2.7 (1.8) | 0–11.5 (3.4) | 3.5 |
| *Cocconeis convexa* M.H. Giffen | 3.7–19.1 (10.1) | – | 2.7–4 (3.1) | 0–11.6 (3.8) | 4.3 |
| *Cocconeis scutellum var. scutellum* Ehrenberg | 3.7–10.2 (5.9) | – | 1.3–2.7 (1.8) | 0–8 (1.7) | 2.3 |
| *Grammatophora marina* (Lyngbye) Kützing | 0–6.1 (3.3) | – | 6.7–9.4 (8.1) | 0–5.2 (0.8) | 3.1 |
| *Haslea* sp. | 0–2.3 (0.4) | 5–7.1 (6.2) | – | 0–18.6 (4.5) | 2.8 |
| *Licmophora* cf. *communis* (Heiberg) Grunow | 2.6–7 (5.4) | – | 5.4–6.7 (6.3) | 0–3.5 (0.8) | 3.1 |
| *Melosira varians* C. Agardh | 0–46 (14.8) | – | – | 0–14.1 (1.1) | 4 |
| *Navicula* cf. *cancellata* Donkin | 0–3.7 (1.7) | 16.7–17.5 (17.2) | 1.3–2.7 (2.2) | 0–17.1 (5.6) | 6.7 |
| *Navicula directa* (W. Smith) Ralfs | 0.6–4.2 (2) | 13–17.5 (14.9) | 2.7–4 (3.1) | 2.5–25.8 (12.6) | 8.2 |
| *Nitzschia constricta* (Kützing) Ralfs | 0–7.9 (3) | – | 2.7–4 (3.1) | 0–33.3 (8.5) | 3.6 |
| *Nitzschia martiana* (C. Agardh) Schütt | 0.9–3.9 (2.2) | – | 1.3 | 0–14.4 (6.1) | 2.4 |
| *Pleurosigma strigosum* W. Smith | 0–1.9 (0.6) | 9.5–13 (10.8) | – | 0–11.1 (3.8) | 3.8 |
| *Pleurosigma diversestriatum* F. Meister | 0–2.8 (0.8) | 7.5–10.9 (9.3) | – | 0–11 (4) | 3.5 |
| *Psammodictyon constrictum** | 0.9–2.1 (1.4) | – | 2.7–4.1 (3.6) | 0–5.2 (0.8) | 1.5 |
| *Pseudogomphonema* sp. | 0–2.2 (0.4) | – | – | 0–5 (1.1) | 0.3 |
| *Tabularia affinis** | 9–22.4 (16.6) | 2.4–4.3 (3.1) | 21.6–25.4 (23.8) | 0–29 (8.9) | 13 |

*Species found on both floating debris and sea turtles.

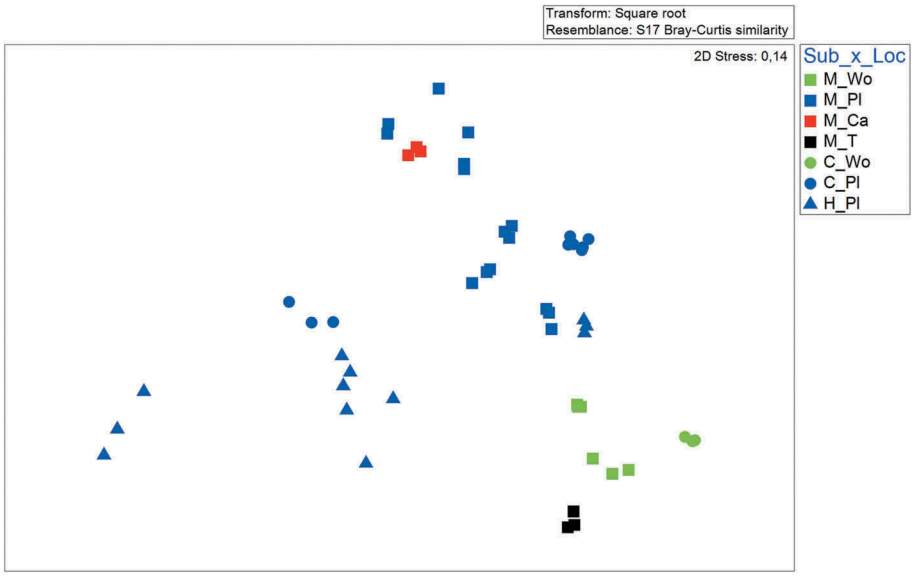


**Fig. 16.** Non-metric multidimensional scaling graph showing distances between the diatom samples collected from the floating debris as their compositional dissimilarity. C, central part of gulf; M, gulf mouth; H, gulf head; ST, sea turtle; W, wood, P, plastic; C, can; T, tire.

**Table 6.** PERMANOVA analysis of diatom communities associated with various types of floating debris, based on square-root-transformed abundances and Bray–Curtis dissimilarities.

| Source | df | SS | MS | Pseudo *F* | *P* | Var | SD |
|---|---|---|---|---|---|---|---|
| Substratum | 3 | 16 361 | 5 453 | 9.79 | 0.0001 | 751.32 | 27.41 |
| Location | 2 | 9 416 | 4 708 | 8.45 | 0.0001 | 345.9 | 18.60 |
| Sub × Loc | 1 | 1 261 | 1 261 | 2.26 | 0.0579 | 117.37 | 10.83 |
| Residual | 44 | 24 507 | 557 | – | – | 516.98 | 23.6 |
| Total | 50 | 51 643 | – | – | – | – | – |

current study, which suggests high stability of the local sea turtle-associated community composition over time, with no clear seasonal shifts or species turnover. Although both nMDS and PERMANOVA indicated that the sea turtle diatom communities clearly differed among the five sampling locations, observed differences were due to neither differences in alpha diversity nor community growth form structure. The main overall difference was associated with a significant difference in diatom abundances.

## Impact of environmental conditions

Diatom abundances on sea turtles were significantly higher in samples collected from the easternmost stations (Hormuz and Larak), which were closest to the Strait of Hormuz. The strait acts as a hydraulic control, regulating water circulation and exchange between the Persian Gulf and the Indian Ocean (Alosairi *et al.* 2011; Reynolds 1993). As evaporation in the Persian Gulf significantly exceeds both the inflow from rivers and the contribution of precipitation, the gulf is in effect a reverse estuary, where the bottom higher-density masses of water flow towards the ocean, and surface lower-salinity water masses disperse towards the estuary head (Reynolds 1993). Although river inflow may affect the water column structure locally, water parameters in our sampling area depend largely on the magnitude of oceanic water inflow, that varies throughout the year (Reynolds 1993). During early autumn (i.e. when most sea turtle samples were collected) surface water salinity and temperature ranged from 36.5 PSU to 38.5 PSU and from 27 °C to 32 °C, respectively, with both parameters increasing towards the northwest (Al Azhar *et al.* 2016; Hassanzadeh *et al.* 2011; Hume *et al.* 2018; Reynolds 1993). The nutrient-rich waters trapped near the Strait of Hormuz due to its shape, bathymetry, and wind regime (German & Elderfield 1990; Longhurst *et al.* 1995) may enhance diatom productivity, as was suggested in a study of the particularly abundant diatom communities found on olive ridleys from the Pacific coast of Costa Rica (Majewska *et al.* 2015c), a high productivity zone (Fiedler 2002). Although no correlation between nitrate and phosphate concentrations and diatom abundances was observed, it cannot be excluded that other nutrients or micro-elements associated with oceanic water influx influence sea turtle diatom productivity. In spring, salinity in the study region remains within the range of 36.5–38.5 PSU, while temperatures drop to 24–28 °C (Al Azhar *et al.* 2016; Hassanzadeh *et al.* 2011; Hume *et al.* 2018; Reynolds 1993). This is consistent with temperature and salinity fluctuations observed during the current study (Table 2). However, while samples from Qeshm were collected in April, the diatom community composition did not seem to be affected by these seasonal changes. This agrees with the observations of Majewska *et al.* (2018), who examined samples from nine juvenile sea turtles stranded on Long Island Beach (New York, USA), finding no correlation between species composition of carapace-associated diatom flora and sampling season.

## Substratum specificity

Interestingly, diatom abundances were significantly greater on the sea turtles than on the floating debris. It is conceivable that both types of substratum, the actively moving sea turtles and the free-floating physical debris, would inherently

constitute a demanding habitat for many diatom taxa. However, while the presumably sea turtle-specific taxa growing on animal surfaces might have evolved eco-physiological adaptations that allowed them to colonise and dominate the unusual substratum, species developing on the floating objects were most likely opportunistic species, for which neither the floating plastic bottle nor piece of tire necessarily provided an optimal environment.

Floristic analysis of diatom biofilms on various types of floating physical debris showed that diatom taxa growing on sea turtles overlapped with those on the debris to a small degree. Of the 21 diatom taxa (13 genera) associated with floating debris, only four were included in the 20 taxa found on sea turtles. In epizoic samples, none of the shared species exceeded a relative abundance of 4%, and it was clear that the sea turtle diatom communities differed significantly from those developing on other substrata present in the water column. This is not unexpected since conditions experienced by diatoms growing on actively moving sea turtles will likely differ from those present on the surface of floating debris. Similarly, biotic (sea turtle carapace) and abiotic (floating debris of various kinds) substrata will differ in terms of, for example, their surface chemistry, adhesiveness, wettability, and roughness. All the factors mentioned above affect surface-associated diatoms, and different combinations of the values of these parameters will create unique microhabitats. As the debris samples were collected in February, when the average water surface temperature was significantly lower (16.6–22.2 °C) than during the sea turtle material collection (25.1–31.8 °C), the possible effect of thermal changes on diatom communities cannot be excluded. However, it is unlikely that this sole factor inhibited the growth of typically sea turtle-associated diatoms on other substrata so effectively, as numerous diatom strains isolated from the sea turtle biofilm, including the presumably exclusively epizoic marine gomphonemoids, develop normally at 18–22 °C (Majewska *et al.* 2019; R. Majewska, unpublished; M. P. Ashworth, personal communication). Moreover, green turtles during their migrations do not avoid waters < 25 °C and can survive periods in temperatures as low as 10 °C (Spotila *et al.* 1997). Therefore, it is expected that the diatom taxa contributing to the original sea turtle microbiome would cope rather well with changes in environmental factors within the ranges normally encountered by the host. To our knowledge, this study is the first to provide direct evidence of the uniqueness and stability of sea turtle diatom communities. As the benthic diatom flora of the Gulf is poorly characterised, further studies are required to reveal the diversity of local surface-associated diatoms across various biotic and abiotic substrata and habitats.

## Impact of sampling and material processing techniques

Both the number of diatom taxa and the diatom densities reported here are higher than those recorded by Majewska *et al.* (2017c), who found only 12 diatom taxa on 30 green turtles sampled in October 2015 in the vicinity of Hengam Island, with average diatom densities of 348 ± 140 cells $mm^{-2}$. This difference may be an artefact caused by modifications applied to the sampling methodology: while random carapace samples were collected by Majewska *et al.* (2017c), only samples with visible biofilm patches were taken in the current study. It has been reported that macro-epibionts show an uneven distribution on sea turtle carapaces (Caine 1986; Fuller *et al.* 2010; Pfaller *et al.* 2008), and the same may be true for sea turtle-associated diatoms, as some may prefer different patterns of water flow or disturbance, or the presence of other epibionts (Majewska *et al.* 2016). Two studies that examined preserved and dehydrated pieces of sea turtle carapaces reported low numbers of diatom species (Majewska *et al.* 2015c, 2017c). Twenty-two diatom taxa were found in samples taken from 38 green turtles from Tortuguero (Pacific coast of Costa Rica; Majewska *et al.* 2017c), and 21 were reported from 38 olive ridleys from Ostional (Atlantic coast of Costa Rica; Majewska *et al.* 2015c). In contrast, much higher numbers of diatom species were reported from seven green turtles from Mayotte Island (south-western Indian Ocean; Rivera *et al.* 2018). Furthermore, molecular analyses reported in the same study suggested that the number of species might, in fact, be significantly higher than the 57 based on microscopic observation due to cryptic (or pseudo-cryptic) diversity, a common feature of microalgae (Mann *et al.* 1999; Šlapeta *et al.* 2006; Vanelslander *et al.* 2009). This striking difference between the number of diatom taxa, even ignoring the possible (pseudo-)cryptic diversity, detected in the different studies might again be caused by differences in sampling techniques. Samples used in morphological observations by Rivera *et al.* (2018) consisted of digested material scraped from the entire carapace with a toothbrush. Such samples would contain not only the truly epizoic diatom taxa, but also those associated with other organisms occurring on the sea turtle carapace (e.g. macroalgae; Serio *et al.* 2020) as well as planktonic or sand-associated forms that were present on (though not attached to) the wet carapace surface at the time of sampling. The authors highlight that the ecology and architecture of turtle biofilms can be characterised only through microscopic (not molecular) analyses, and speculate that the contribution of low profile (adnate) diatoms indicates whether a sea turtle was a slow or fast swimmer.

Although we believe that relative contributions of different diatom growth forms (or ecological guilds) may provide valuable information about the host animal, adequate methods must be used to gather the necessary information, and correctly assign the diatoms to their ecological groups. It has been shown that, for example, diatom-associated bacteria may have a profound impact on diatom ecophysiology, including growth form and ability of diatom to attach to the substratum surface (Gawne *et al.* 1998). Further investigations are required to shed more light on the complex relationships between epizoic diatoms and their bacterial partners. Moreover, an appropriately designed experimental study is necessary to assess the type and range of changes in diatom flora that would indicate different behavioural (e.g. swimming) patterns in sea turtles.

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## REFERENCES

Aguirre A.A., Gardner S.C., Marsh J.C., Delgado S.G., Limpus C.J. & Nichols W.J. 2006. Hazards associated with the consumption of sea turtle meat and eggs: a review for health care workers and the general public. *EcoHealth* 3(3): 141–153. DOI: 10.1007/s10393-006-0032-x.

Al Azhar M., Temimi M., Zhao J. & Ghedira H. 2016. Modeling of circulation in the Arabian Gulf and the Sea of Oman: skill assessment and seasonal thermohaline structure. *Journal of Geophysical Research, Oceans*. 121. DOI:10.1002/2015JC011038.

Alosairi Y., Imberger J. & Falconer R.A. 2011. Mixing and flushing in the Persian Gulf (Arabian Gulf). *Journal of Geophysical Research* 116(C3): C03029. DOI: 10.1029/2010JC006769.

Brofft Bailey J., Lamb M., Walker M., Weed C. & Stephenson Craven K. 2018. Detection of potential fungal pathogens *Fusarium falciforme* and *F. keratoplasticum* in unhatched loggerhead turtle eggs using a molecular approach. *Endangered Species Research* 36: 11–119. DOI:10.3354/esr00895.

Caine E.A. 1986. Carapace epibionts of nesting loggerhead sea turtles: Atlantic coast of USA. *Journal of Experimental Marine Biology and Ecology* 95(1): 15–26. DOI: 10.1016/0022-0981(86)90084-5.

Cárdenas D.M., Cucalón R.V., Medina-Magües L.G., Jones K., Alemán R. A., Alfaro-Núñez A. & Cárdenas W.B. 2019. Fibropapillomatosis in a green sea turtle (*Chelonia mydas*) from the southeastern Pacific. *Journal of Wildlife Diseases* 55(1): 169–173. DOI: 10.7589/2017-12-295.

Carey H.V. & Duddleston K.N. 2014. Animal-microbial symbioses in changing environments. *Journal of Thermal Biology* 44: 78–84. DOI:10.1016/j.jtherbio.2014.02.015.

Clarke K. & Gorley R. 2006. *PRIMER v6: user manual/tutorial*. PRIMER-E Ltd, Plymouth, UK.

Dubilier N., Bergin C. & Lott C. 2008. Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nature Reviews Microbiology* 6(10): 725–740. DOI: 10.1038/nrmicro1992.

Fiedler P.C. 2002. The annual cycle and biological effects of the Costa Rica Dome. *Deep Sea Research Part I: Oceanographic Research Papers* 49(2): 321–338. DOI: 10.1016/S0967-0637(01)00057-7.

Frankovich T.A., Ashworth M.P., Sullivan M.J., Vesela J. & Stacy N.I. 2016. *Medlinella amphoroidea gen. et sp. nov*. (Bacillariophyta) from the neck skin of loggerhead sea turtles (*Caretta caretta*). *Phytotaxa* 272(2): 101–114. DOI: 10.11646/phytotaxa.272.2.1.

Frankovich T.A., Sullivan M.J. & Stacy N.I. 2015. *Tursiocola denysii* sp. nov. (Bacillariophyta) from the neck skin of loggerhead sea turtles (*Caretta caretta*). *Phytotaxa* 234(3): 227–236. DOI: 10.11646/phytotaxa.234.3.3.

Fuller W.J., Broderick A.C., Enever R., Thorne P. & Godley B.J. 2010. Motile homes: a comparison of the spatial distribution of epibiont communities on Mediterranean sea turtles. *Journal of Natural History* 44(27–28): 1743–1753. DOI: 10.1080/00222931003624820.

Gawne B., Wang Y., Hoagland K.D. & Gretz M.R. 1998. Role of bacteria and bacterial exopolymer in the attachment of *Achnanthes longipes* (Bacillariophyceae). *Biofouling* 13(2): 137–156. DOI: 10.1080/08927019809378377.

German C.R. & Elderfield H. 1990. Rare earth elements in the NW Indian Ocean. *Geochimica et Cosmochimica Acta* 54(7): 1929–1940. DOI: 10.1016/0016-7037(90)90262-J.

Glazebrook J.S. & Campbell R.S.F. 1990. A survey of the diseases of marine turtles in northern Australia. I. Farmed turtles. *Diseases of Aquatic Organisms* 9: 83–95. DOI:10.3354/dao009083.

Hard K.M. & Fujisaki I. 2010. Satellite tracking reveals habitat use by juvenile green sea turtles *Chelonia mydas* in the Everglades, Florida, USA. *Endangered Species Research* 11(3): 221–232. DOI: 10.3354/esr00284.

Hasle G.R. & Syvertsen E.E. 1997. Marine diatoms. In: *Identifying marine phytoplankton* (Ed. by C.R. Tomas), pp. 5–386. Academic Press, San Diego, California, USA.

Hassanzadeh S., Hosseinibalam F. & Rezaei-Latifi A. 2011. Numerical modelling of salinity variations due to wind and thermohaline forcing in the Persian Gulf. *Applied Mathematical Modelling* 35(3): 1512–1537. DOI: 10.1016/j.apm.2010.09.029.

Hume B.C.C., D'Angelo C., Burt J.A. & Wiedenmann J. 2018. Fine-scale biogeographical boundary delineation and sub-population resolution in the *Symbiodinium thermophilum* coral symbiont group from the Persian/Arabian Gulf and Gulf of Oman. *Frontiers in Marine Science* 5: 138. DOI: 10.3389/fmars.2018.00138.

Kaleli A., Krzywda M., Witkowski A., Riaux-Gobin C., Solak C.N., Zgłobicka I., Płociński T., Grzonka J., Kurzydłowski K.J., Car A. *et al.* 2018. A new sediment dwelling and epizoic species of *Olifantiella* (Bacillariophyceae), with an account on the genus ultra-structure based on focused ion beam nanocuts. *Fottea* 18(2): 212–226. DOI: 10.5507/fot.2018.007.

Limpus C.J. & Walter D.G. 1980. The growth of immature green turtles (*Chelonia mydas*) under natural conditions. *Herpetologica* 36: 162–165.

Longhurst A., Sathyendranath S., Platt T. & Caverhill C. 1995. An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research* 17(6): 1245–1271. DOI: 10.1093/plankt/17.6.1245.

Majewska R., Ashworth M.P., Lazo-Wasem E., Robinson N.J., Rojas L., Van de Vijver B. & Pinou T. 2018. *Craspedostauros alatus* sp. nov., a new diatom (Bacillariophyta) species found on museum sea turtle specimens. *Diatom Research* 33(2): 229–240. DOI: 10.1080/0269249X.2018.1491426.

Majewska R., Bosak S., Frankovich T.A., Ashworth M.P., Sullivan M.J., Robinson N.J., Lazo-Wasem E.A., Pinou T., Nel R., Manning S.R. *et al.* 2019. Six new epibiotic *Proschkinia* (Bacillariophyta) species and new insights into the genus phylogeny. *European Journal of Phycology* 54(4): 609–631. DOI: 10.1080/09670262.2019.1628307.

Majewska R., Convey P. & De Stefano M. 2016. Summer epiphytic diatoms from Terra Nova Bay and Cape Evans (Ross Sea, Antarctica) - a synthesis and final conclusions. *PLOS One* 11(4): e0153254. DOI: 10.1371/journal.pone.0153254.

Majewska R., De Stefano M., Ector L., Bolaños F., Frankovich T.A., Sullivan M.J., Ashworth M.P. & Van de Vijver B. 2017a. Two new epizoic *Achnanthes* species (Bacillariophyta) living on marine turtles from Costa Rica. *Botanica Marina* 60(3): 303–318. DOI: 10.1515/bot-2016-0114.

Majewska R., De Stefano M. & Van De Vijver B. 2017b. *Labellicula lecohuiana*, a new epizoic diatom species living on green turtles in Costa Rica. *Nova Hedwig, Beihefte* 146: 23–31. DOI:10.1127/1438-9134/2017/023.

Majewska R., Kociolek J.P., Thomas E.W., De Stefano M., Santoro M., Bolaños F. & Van De Vijver B. 2015a. *Chelonicola* and *Poulinea*, two new gomphonemoid diatom genera (Bacillariophyta) living on marine turtles from Costa Rica. *Phytotaxa* 233(3): 236–250. DOI: 10.11646/phytotaxa.233.3.2.

Majewska R., Kuklinski P., Balazy P., Yokoya N.S., Paternostro Martins A. & De Stefano M. 2015b. A comparison of epiphytic diatom communities on *Plocamium cartilagineum* (Plocamiales, Florideophyceae) from two Antarctic areas. *Polar Biology* 38(2): 189–205. DOI: 10.1007/s00300-014-1578-7.

Majewska R., Santoro M., Bolaños F., Chaves G. & De Stefano M. 2015c. Diatoms and other epibionts associated with olive ridley (*Lepidochelys olivacea*) sea turtles from the Pacific coast of Costa Rica. *PLOS One* 10 (6): e0130351. DOI: 10.1371/journal.pone.0130351.

Majewska R., Van De Vijver B., Nasrolahi A., Ehsanpour M., Afkhami M., Bolaños F., Iamunno F., Santoro M. & De Stefano M. 2017c. Shared epizoic taxa and differences in diatom community structure between green turtles (*Chelonia mydas*) from distant habitats. *Microbial Ecology* 74(4): 969–978. DOI: 10.1007/s00248-017-0987-x.

Makowski C., Seminoff J.A. & Salmon M. 2006. Home range and habitat use of juvenile Atlantic green turtles (*Chelonia mydas* L.) on shallow reef habitats in Palm Beach, Florida, USA. *Marine Biology* 148(5): 1167–1179. DOI: 10.1007/s00227-005-0150-y.

Mann D.G., Chepurnov V.A. & Droop S.J.M. 1999. Sexuality, incompatibility, size variation, and preferential polyandry in natural populations and clones of *Sellaphora pupula* (Bacillariophyceae). *Journal of Phycology* 35(1): 152–170. DOI: 10.1046/j.1529-8817.1999.3510152.x.

Miller E.T., Svanbäck R. & Bohannan B.J.M. 2018. Microbiomes as metacommunities: understanding host-associated microbes through metacommunity ecology. *Trends in Ecology and Evolution* 33(12): 926–935. DOI: 10.1016/j.tree.2018.09.002.

Musick J.A. & Limpus C.J. 1997. Habitat utilization and migration in juvenile sea turtles. In: *Biology of sea turtles* (Ed. by P.L. Lutz & J. A. Musick), pp. 137–164. CRC Press, Boca Raton, Florida, USA.

Pfaller J., Bjorndal K., Reich K., Williams K. & Frick M. 2008. Distribution patterns of epibionts on the carapace of loggerhead turtles, *Caretta caretta*. *Marine Biodiversity Records* 1: E36. DOI: 10.1017/S1755267206003812.

Raidal S.R., Ohara M., Hobbs R.P. & Prince R. 1998. Gram-negative bacterial infections and cardiovascular parasitism in green sea turtles (*Chelonia mydas*). *Australian Veterinary Journal* 76(6): 415–417. DOI: 10.1111/j.1751-0813.1998.tb12392.x.

Rees A.F., Al-Hafez A., Lloyd J.R., Papathansopoulou N. & Godley B.J. 2013. Green Turtles, *Chelonia mydas*, in Kuwait: nesting and movements. *Chelonian Conservation and Biology* 12(1): 157–163. DOI: 10.2744/CCB-1030.1.

Reynolds R.M. 1993. Physical Oceanography of the Persian Gulf, Strait of Hormuz, and the Gulf of Oman – results from the Mt. Mitchell Expedition. *Marine Pollution Bulletin* 27: 35–59. DOI:10.1016/0025-326X(93)90007-7.

Riaux-Gobin C., Witkowski A., Chevallier D. & Daniszewska-Kowalczyk G. 2017a. Two new *Tursiocola* species (Bacillariophyta) epizoic on green turtles (*Chelonia mydas*) in French Guiana and Eastern Caribbean. *Fottea* 17(2): 150–163. DOI: 10.5507/fot.2017.007.

Riaux-Gobin C., Witkowski A., Kociolek J.P., Ector L., Chevallier D. & Compere P. 2017b. New epizoic diatom (Bacillariophyta) species from sea turtles in the Eastern Caribbean and South Pacific. *Diatom Research* 32(1): 109–125. DOI: 10.1080/0269249X.2017.1299042.

Rivera S.F., Vasselon V., Ballorain K., Carpentier A., Wetzel C.E., Ector L., Bouchez A. & Rimet F. 2018. DNA metabarcoding and microscopic analyses of sea turtles biofilms: complementary to understand turtle behaviour. *PLOS One* 13(4): e0195770. DOI: 10.1371/journal.pone.0195770.

Robinson D.P., Jabado R.W., Rohner C.A., Pierce S.J., Hyland K.P. & Baverstock W.R. 2017. Satellite tagging of rehabilitated green sea turtles *Chelonia mydas* from the United Arab Emirates, including the longest tracked journey for the species. *PLOS One* 12(9): e0184286. DOI: 10.1371/journal.pone.0184286.

Robinson N.J., Majewska R., Lazo-Wasem E., Nel R., Paladino F.V., Rojas L., Zardus J.D. & Pinou T. 2016. Epibiotic diatoms are universally present on all sea turtle species. *PLOS One* 11(6): e0157011. DOI: 10.1371/journal.pone.0157011.

Romagnoli T., Bavestrello G., Cucchiari E.M., De Stefano M., Di Camillo C.G., Pennesi C., Puce S. & Totti C. 2007. Microalgal communities epibiontic on the marine hydroid *Eudendrium racemosum* in the Ligurian Sea during an annual cycle. *Marine Biology* 151(2): 537–552. DOI: 10.1007/s00227-006-0487-x.

Round F.E. 1981. *The ecology of algae*. Cambridge University Press, Cambridge, UK.

Santoro M., Hernandez G., Caballero M. & Garcia F. 2006. Aerobic bacterial flora of nesting green turtles (*Chelonia mydas*) from Tortuguero National Park, Costa Rica. *Journal of Zoo and Wildlife Medicine* 37(4): 549–552. DOI: 10.1638/05-118.1.

Serio D., Furnari G., Moro I. & Sciuto K. 2020. Molecular and morphological characterisation of *Melanothamnus testudinis sp. nov*. (Rhodophyta, Rhodomelaceae) and its distinction from *Polysiphonia carettia*. *Phycologia* 59: 281–291. DOI: 10.1080/00318884.2020.1752531.

Šlapeta J., López-García P. & Moreira D. 2006. Global dispersal and ancient cryptic species in the smallest marine eukaryotes. *Molecular Biology and Evolution* 23(1): 23–29. DOI: 10.1093/molbev/msj001.

Spotila J.R., O'Connor M.P. & Paladino F.V. 1997. Thermal biology. In: *Biology of sea turtles* (Ed. by P.L. Lutz & J.A. Musick), pp. 297–314. CRC Press, Boca Raton, Florida, USA.

Vanelslander B., Créach V., Vanormelingen P., Ernst A., Chepurnov V. A., Sahan E., Muyzer G., Stal L.J., Vyverman W. & Sabbe K. 2009. Ecological differentiation between sympatric pseudocryptic species in the estuarine benthic diatom *Navicula phyllepta* (Bacillariophyceae). *Journal of Phycology* 45(6): 1278–1289. DOI: 10.1111/j.1529-8817.2009.00762.x.

Venn A.A., Loram J.E. & Douglas A.E. 2008. Photosynthetic symbioses in animals. *Journal of Experimental Botany* 59(5): 1069–1080. DOI: 10.1093/jxb/erm328.

World Medical Association. 2013. World Medical Association Declaration of Helsinki, ethical principles for medical research involving human subjects. *JAMA* 30: 2191–2194.