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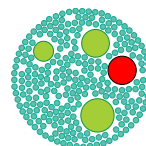
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Epizoic diatoms on sea turtles and their relationship to host species, behaviour and biogeography: a morphological approach

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ABSTRACT

Sea turtles harbour epizoic diatoms of which several taxa are considered exclusively epizoic and possible 'commensals'. The epizoic diatom communities were examined from 124 individuals representing four turtle species (*Chelonia mydas*, *Eretmochelys imbricata*, *Lepidochelys olivacea* and *Dermochelys coriacea*), from three well-defined areas: Eastern Caribbean, Equatorial West Atlantic and South Pacific. Overall, the epizoic diatoms are very small and need electron microscopy to be accurately identified. Non-Metric MultiDimensional Scaling analyses permitted us to evaluate these diatom assemblages according to turtle species and biogeography. Differentiation was mainly driven by 14 taxa in the diatom genera *Chelonocola*, *Tripterion*, *Tursiocola*, *Olifantiella*, *Navicula* and *Achnanthes*. The highest diatom species richness was found associated with *E. imbricata*. *Dermochelys coriacea* and *L. olivacea* exhibit lower diatom diversities. Some difference in colonization was detected between *C. mydas* adults and juveniles at the same site, with higher diatom diversity for the juveniles. Within *C. mydas* we show geographic differentiation of their diatom assemblages, particularly between populations of the Equatorial West Atlantic and South Pacific. Two *Tursiocola* species 'commensal' to *C. mydas* seemed to be geographically restricted to French Guiana and the Caribbean. *Dermochelys coriacea* has a diatom assemblage very different from those of the three other turtles, probably due to its particular behaviour. *Lepidochelys olivacea* is also unique in the complete lack of *Chelonocola* species. Based on our results, the diatoms *Tripterion societatis* and *Chelonocola* spp. (as currently defined) appear to be mutually exclusive on turtle hosts. This study adds significantly to our understanding of the global distribution of epizoic diatoms on sea turtles. We discuss to what extent these diatoms can be used as a geographic marker with regard to the biogeography of the diatoms themselves and their host.


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KEYWORDS biogeography; host lifestyle; epizoic diatoms; sea turtles

Introduction

The sea turtles (Order Testudines) include seven living species. Six genera of sea turtles are related to one of the most primitive groups of reptiles, the Cheloniidae (Bustard, 1972), and all are endangered or even critically endangered, as is the case of *Lepidochelys kempii* (cf. Schmid & Witzell, 2006; <https://conserveturtles.org/about-stc-archie-carr-tribute/>). These turtle species all have specific behaviours and survival strategies (Musick & Limpus, 1996; Bolten, 2003). As their habits are highly diversified, they host diverse epibionts. Some epizoic macroalgae on turtles are host-specific, e.g. *Polysiphonia caretta* was first described from *Caretta caretta* (Hollenberg, 1971; Senties *et al.*, 1999 and refs therein; Battelli & Rindi, 2016; Karaa *et al.*, 2017). Sea turtles from across the globe also appear to host unique assemblages of diatoms (Bacillariophyta) (e.g. Brady, 2010; Frankovich *et al.*, 2015a, 2016; Majewska *et al.*, 2015a,

b, 2017a; Azari *et al.*, 2016; Robinson *et al.*, 2016, 2017; Riaux-Gobin *et al.*, 2017a, b; Kaleli *et al.*, 2018; Van de Vijver *et al.*, 2020), a phenomenon which appears to be mirrored in marine mammals such as Dall's porpoise and manatees (Holmes *et al.*, 1993; Frankovich *et al.*, 2015b, 2018). The studies cited are based on diatom morphology (mainly using electron microscopy). While DNA data are used increasingly in descriptive studies (and ecological work, utilizing 'environmental DNA' data in metabarcoding and metagenomic studies), such data are still scarce relative to the number of described diatom species, particularly with regard to benthic marine taxa. This paucity of data is even more pronounced among epizoic diatoms, and the limited data that exist could potentially lead to flaws in inferring conclusions. For example, a metabarcoding study of epizoic diatoms on turtles (Rivera *et al.*, 2018) could not resolve the inconsistencies between their DNA and microscope-

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based surveys, as there are no DNA data for the most commonly observed diatom, *Labellicula lecohuiana*, and its phylogenetic position is unknown; without a known and sequenced close relative, the taxon is rendered effectively invisible to any metabarcoding assay. Instead, Rivera *et al.* (2018) chose to focus on ‘cryptic diversity’ within the *Nitzschia inconspicua* clade. There is ‘cryptic’ diversity among small *Nitzschia* spp. in many types of benthic marine habitats (Witkowski *et al.*, 2015, 2016; Lobban *et al.*, 2019) so it is hardly unique to the epizoic habitat. In possibly the best-documented molecular study of epizoic diatoms, Frankovich *et al.* (2018) sequenced more than a dozen, photodocumented and vouchered individual cells of *Tursiocola* spp. and found that *Tursiocola* was not closely related to *Rhoicosphenia abbreviata* in the same family. However, because the position of *Tursiocola* was poorly supported in the phylogeny and it did not share any synapomorphic morphological features with closely related taxa, they did not formally transfer the genus to a different family (Frankovich *et al.*, 2018). Without direct observation of these cells under a microscope, it would have been difficult to predict the identity of these diatoms as belonging to the genus *Tursiocola* solely on their position in the molecular phylogeny. Clearly, at this time, the most complete dataset to use for comparing assemblages of epizoic diatoms remains the valve and frustule morphology.

The diatom assemblages on turtles remain mostly undescribed. Majewska *et al.* (2017a), studying *Chelonia mydas* (CM) from the Persian Gulf and East Atlantic coast, listed 26 taxa (often only at the genus level), with several cosmopolitan taxa and only a few species suspected to be strictly epizoic. Based on recent literature, several species have never been found except on their host, and thus may be ‘commensals’ by the definition of commensalism proposed by Wilson (1975), as there is no evidence that the diatoms are not harmful to the host and one can theorize benefits to the diatoms in the form of expanded benthic habitat and the potential for nutrients derived from the host. However, we use ‘commensal’ conditionally, as no particular study has, to our knowledge, completely tested and described the relationship between these diatoms and their host. These possible sea turtle ‘commensals’ include *Achnanthes elongata* and *A. squaliformis* (Majewska *et al.*, 2017b), *Chelonicola costaricensis* (Majewska *et al.*, 2015a), *C. caribeana* (Riaux-Gobin *et al.*, 2017b), *Labellicula lecohuiana* (Majewska *et al.*, 2017c), *Medlinella amphoroidea* (Frankovich *et al.*, 2016), *Poulinea lepidochelicola* (Majewska *et al.*, 2015a), *Tripterion societatis* (Riaux-Gobin *et al.*, 2017b), *Tursiocola denysii* (Frankovich *et al.*, 2015a), *T. yin-yangii* and *T. guyanensis* (Riaux-Gobin *et al.*, 2017a). The presumed biogeography of these diatoms and the extent of their exclusivity to a host species and

lifestyle have not been adequately documented; this manuscript is a first attempt.

We investigated the diatom assemblages associated with *Chelonia mydas* (Green Turtle, CM), *Eretmochelys imbricata* (Hawksbill Turtle, EI), *Lepidochelys olivacea* (Olive Ridley Turtle, LO) and *Dermochelys coriacea* (Leatherback Turtle, DC) from three oceanic areas: the Eastern Caribbean (i.e. Lesser Antilles, Martinique), Equatorial West Atlantic (i.e. French Guiana) and South Pacific (i.e. Society Archipelago; Tables 1 and 2). These samples include the type material for several recently described epizoic diatoms: *Tursiocola yin-yangii* and *Tursiocola guyanensis* (Riaux-Gobin *et al.*, 2017b), *Tripterion societatis* and *Chelonicola caribeana* (Riaux-Gobin *et al.*, 2017a). *Navicula dermochelycola* is included here, but formally described elsewhere (Riaux-Gobin *et al.*, 2020). Among these epizoic diatom assemblages, 14 taxa are selected (Table 3), several exclusively epizoic (not found in another habitat), and the others (genus *Olifantiella*) providing good clues about the biogeography of the involved turtles. The distributions of these selected taxa are analysed. The behaviour of the host and impact on the diatom assemblages are considered here, as well as the possible influence of the hydrological conditions of the sampled coastal areas.

With the continuing discovery of epizoic diatom diversity, we should not overlook the description of this diversity and its potential applications. There is an extensive body of literature on the use of diatoms as ‘bioindicators’ of freshwater environments (e.g. Coste *et al.*, 2009; Smol & Stoermer 2010; Morin *et al.*, 2016), and with a greater understanding of the taxonomy, ecology and biogeography of epizoic diatoms it is easy to imagine their application as a non-invasive tool to track the movement of sea turtles. Just as exciting, the epizoic system has great potential in helping us to elucidate dispersal and diversification in benthic diatoms; if these taxa are in fact exclusive to the epizoic habit, how do they colonize young hosts, and how do populations of epizoic diatoms respond to subsequent colonizations by ‘cosmopolitan’ species or individuals from epizoic populations on different host animals? This study is an important foundational step to building the study system to answer these questions.

Materials and methods

Study sites and projects

Sampled turtles and their geographic location at sampling are shown in Table 1. The study is part of the FEDER Martinique (Fonds Européen de Développement Régional) and ANTIDOT (Association of New Tools to Improve the understanding of the

Table 1. Sampled turtles and geographic position. CM = *Chelonia mydas*; EI = *Eretmochelys imbricata*; LO = *Lepidochelys olivacea*; DC = *Dermochelys coriacea*.

Oceanic basin	Location	Species	Nesting	Juvenile	Latitude	Longitude
Caribbean Sea (Martinique)	Grande Anse d'Arlet	CM		8	14°30'10.95"N	61°05'13.01"W
		CM		22	14°29'13.43"N	61°04'58.89"W
	Anse du Bourg	EI		1		
		DC	1		14°29'55.06' N	60°49'25.42"W
	Les Sâlines	EI	1		14°23'45.55"N	60°52'14.74"W
		EI		1	14°31'42.47"N	61°5'20.36"W
	Anse Noire	CM		1		
		EI		1	14°49'60"N	61°12'0"W
	Prêcheur	CM		1		
		CM		4	14°42'0"N	61°10'60"W
	Carbet	CM		2	14°43'60"N	61°10'60"W
		EI		1		
	Saint Pierre	CM		1		
		CM		1	14°27'58"N	61°04'15"W
	Equatorial Atlantic Ocean (French Guiana)	Petite Anse	CM		1	14°27'58"N
DC			16		5°44'47.96"N	53°56'37.36"W
Yalimapo		CM	13			
		CM	4		5°41'12.57"N	53°43'49.07"W
Aztèque		DC	1			
		DC	3		4°55'10.54"N	52°16'5.31"W
Cayenne	LO	6				
	CM		2	17°29'39.639"S	149°52'13.527"W	
South Pacific Ocean (French Polynesia)	Te Mana O Te Moana (Moorea)	CM		7	16°59'21.5"S	149°34'48.1"W
		CM		1	16°59'37.4"S	149°32'24.0"W
	Tiararua (Tetiaroa)	CM	9		17°01'17.9"S	149°35'45.2"W
		EI		1	17°38'54"S	149°25'46"W
	Tahiti	EI		2	17°33'S	149°48'W
		CM		1	17°32'5.793"S	149°54'10.325"W
	Afareaitu (Moorea)	CM		1	17°33'56.2"S	149°52'09.9"W
	Nu'uroa (Moorea)	CM		1	17°35'09.7"S	149°50'26.8"W
	Haapiti (Moorea)	CM		1	16°59'21.5"S	149°34'48.1"W
	Atiha (Moorea)	EI		2		
	Tetiaroa	LO	1			
	Tikehau	CM		1	15°S	148°10'W
		EI		1	17°32'5.793"S	149°54'10.325"W
	Moorea Lagoon	EI		1	17°35'13.92"S	149°48'20.7036"W
	Maatea (Moorea)	CM		1	17°30'28.7352"S	149°51'23.9328"W
	Opunohu (Moorea)	CM	1		17°29'11.2591"S	149°46'1.4967"W
	Temae (Moorea)	EI	1		17°35'13.92"S	149°48'20.7036"W
	Moorea	CM		1	17°29'43"S	149°52' 27"W
Papetoai (Moorea)	CM		1	16°59'37.4"S	149°32'24.0"W	
Horoterata (Tetiaroa)	CM	1				

Table 2. Number of studied juveniles versus nesting or sub-adults, for each species and at each site. CM = *Chelonia mydas*; EI = *Eretmochelys imbricata*; LO = *Lepidochelys olivacea*; DC = *Dermochelys coriacea*.

	Caribbean		French Guiana		South Pacific		Σ n
	Juvenile	Nesting	Juvenile	Nesting	Juvenile	Nesting	
CM	39	0	0	17	8	19	83
DC	0	1	0	20	0	0	21
EI	4	1	0	0	7	1	13
LO	0	0	0	6	0	1	7
	43	2	0	43	15	21	124

Dynamic Of Threatened marine turtles), CNRS (Centre National de la Recherche Scientifique)-IPHC (Institut Pluridisciplinaire Hubert Curien) programmes for Martinique (Caribbean Basin) and French Guiana (Equatorial West Atlantic), and several projects concerning turtles in the Society Archipelago (South Pacific) under the coordination of Te Mana O Te Moana (Observatoire des Tortues marines en Polynésie française), e.g. the 'Turtle Sanctuary of the Tetiaroa Atoll' project. We took advantage of these projects to study scrapings of turtles for our diatom survey. Juvenile sea turtles were captured at sea during

Capture-Mark-Recapture (see below) and adult females were sampled in their nesting areas (Table 1).

Capture-mark-recapture and satellite tracking techniques

Capture-Mark-Recapture (CRM) and satellite tracking techniques (e.g. Servan, 1976; Polovina *et al.*, 2004; Makowski *et al.*, 2006; Baudouin *et al.*, 2015; Chambault *et al.*, 2015, 2017, 2018; Nivière *et al.*, 2018) permit us to define the lifestyle of turtles. In the Eastern Caribbean and Equatorial West Atlantic,

Table 3. List of epizoic and potentially ‘commensal’ taxa (see Introduction and Discussion), as considered in the nMDS analyses.

Taxon	nMDS number
<i>Achnanthes</i> cf. <i>elongata</i> Majewska & Van de Vijver	1
<i>Chelonicola caribean</i> a Riaux-Gobin, Witkowski, Ector & D.Chevallier	2
<i>Chelonicola</i> sp.	3
<i>Chelonicola</i> cf. <i>costaricensis</i> Majewska, De Stefano & Van de Vijver	4
<i>Navicula dermocheilycola</i> Witkowski, Kociolek & Riaux-Gobin	5
<i>Olifantiella</i> cf. <i>gorandiana</i> Riaux-Gobin	6
<i>Olifantiella mascarenica</i> Riaux-Gobin & Compère	7
<i>Olifantiella pilosella</i> Riaux-Gobin	8
<i>Olifantiella muscatinei</i> (Reimer & J.J.Lee) Van de Vijver, Ector & C.E.Wetzel	9
<i>Olifantiella</i> sp.	10
<i>Olifantiella societatis</i> Riaux-Gobin	11
<i>Tripterion societatis</i> Riaux-Gobin, Witkowski & Ector	12
<i>Tursiocola guyanensis</i> Riaux-Gobin & Witkowski	13
<i>Tursiocola yin-yangii</i> Riaux-Gobin & Witkowski	14

satellite tracking of the inter-nesting season, post-nesting and post-development migrations were performed for DC individuals (e.g. French Guiana, Chambault *et al.*, 2017), CM (e.g. French Guiana, Baudouin *et al.*, 2015; Chambault *et al.*, 2015 and Martinique, Chambault *et al.*, 2018; Siegwalt *et al.*, 2019), LO (e.g. French Guiana) and EI (e.g. Martinique, Nivière *et al.*, 2018). In the South Pacific (Te Mana o Te Moana, C. Gaspar *et al.* unpublished data), satellite tracking (<https://www.sprep.org/marine-turtles/marine-turtle-satellite-tracking>; <http://www.temanaotemoana.org/fr/tags/marque-satellite/>) was performed for several CM nesting at Tetiaroa (Society Archipelago) with migrations to Fiji, one migrating eastwards to Mururoa, an EI (captured and released from Moorea Island) migrating eastwards to the Tuamotu Islands, and a *Caretta caretta* (captured and released from Tahiti Island) migrating to the Marshall Islands (North Pacific). Unfortunately, no diatom collections were made on the tracked animals during these tracking experiments, nor after a turtle was re-captured. We only refer here to the bibliography cited above to define the ethology of each group of studied turtles.

Field and laboratory methods

The epibiont taxa associated with the turtle carapace or soft shell were superficially scraped with a blade off small surface areas by six different samplers from different laboratories, over a period of four years (2014–2018), with no specific instructions about the sampling. Surficial and tangential scrapings were made with no damage to the turtle. Turtle scutes have a maximum thickness of 9–12 mm (Bariand & Poirot, 1998), while the scute of CM is very thin and fragile (< 0.5 mm, pers. obs. on a specimen washed up on a beach of Madagascar, and up to 1.2 mm cf. Lebrun, 1975; López-Castro *et al.*, 2014); DC have no scutes but a reinforced leather-like skin.

The examined raw material consists of small scrapings (< 2 ml), kept in Eppendorf tubes

preserved with ethanol. As there was no defined area for scraping the turtle scutes, we only refer here to a qualitative index (presence-absence of taxa) rather than a semi-quantitative index. Every SEM stub was prepared with 2 drops of raw material filtered through a Whatman Nuclepore filter (1 µm pore size, 13 mm in diameter) rinsed twice with deionized water (Milli-Q) to remove salts. Filters were air-dried, mounted onto aluminium stubs, coated with gold-palladium alloy (EMSCOP SC 500 sputter coater) and examined with a Hitachi S-4500 SEM operated at 5 kV, calibrated with a Silicon grating TGX01 (C2M, Perpignan, France). Diatoms considered as potentially ‘exclusively epizoic’ or ‘commensal’ (see definition in Introduction), along with the epizoic *Olifantiella* taxa, were examined at high magnification, since all investigated taxa are very small (often <10 µm in length). The final presence-absence matrix comprised 124 turtle samples and 14 diatom species.

Selection of characteristic epizoic diatom taxa

Fourteen taxa epizoic on sea turtles and belonging to six genera are here considered (Table 3). Several of these taxa have been found only in epizoic habitats and may potentially be considered as ‘commensals’ (see above definition). The other epizoic taxa belong to the genus *Olifantiella* Riaux-Gobin & Compère, in which several taxa have previously been described as strictly epizoic (see below).

Statistical analyses

Diatom diversity among turtle species and locations was visually inspected by means of histogram plots using the package ggplot2 in R (Oksanen *et al.*, 2018). In order to visualize the level of similarity among samples or groups of samples as a function of their diatom assemblages, non-metric Multidimensional Scaling (nMDS) was performed using the package ‘vegan’ in R (Oksanen *et al.*, 2018). nMDS first

estimated the Bray–Curtis dissimilarity indices among samples from the presence-absence matrix described in the previous section, after removing turtle samples with no diatom counts. We then performed a nMDS by means of the metaMDS algorithm which tries to find a stable solution from several random starts. We performed the analysis forcing it into two dimensions ($k = 2$) and 1 to 500 random starts to try to find a stable solution, which was systematically achieved. This analysis was repeated after subtracting a diatom species, *Navicula dermochelycola* (Riaux-Gobin *et al.*, 2020), that was only present on most DC and one LO from French Guiana. Furthermore, a specific nMDS analysis was performed only on CMs individuals. Finally, to test if diatom composition changed as a linear function of geographic distance, Mantel tests were performed on the different data sets. These were done using the Mantel function from the vegan R package. Bray–Curtis dissimilarity matrices and geodesic geographic distance matrices were used for this analysis. Statistical significance of the correlation among distance matrices was estimated from 10 000 permutations.

Results

Epizoic and ‘commensal’ diatoms

Eighty-three CM, 13 EI, 7 LO and 21 DC sampled in 2014–2018 (Table 3) supported the presumably ‘commensal’ diatom taxa *Tursiocola*, *Tripterion*, *Chelonicola*, *Olifantiella*, *Achnanthes* and *Navicula*, and other genera commonly reported in marine benthic assemblages: *Nitzschia*, *Psammodictyon*, *Amphora*, *Seminavis*, *Mastogloia*, *Cocconeis* and *Gomphonemopsis*. Less common genera, such as *Amicula*, *Hippodonta*, *Astartiella* and *Simonsenia* were also present. The 14 taxa epizoic on sea turtles and potential ‘commensals’ belonged to six genera (Table 3); the most significant taxa and their distributions are reported below.

Tripterion societatis Riaux-Gobin, Witkowski & Ector, first described from the South Pacific (Riaux-Gobin *et al.*, 2017b), was present in Martinique and French Guiana (Figs 5–6). Characters typical of *Tripterion* include the presence of up to three rows of small areolae at one apex (Riaux-Gobin *et al.*, 2017b, Figs 5–6). There are similarities (striation, valve shape), but also slight differences (biometrics, apical pore field), between *T. societatis* and *Poulinea lepidochelycola* (Majewska *et al.*, 2015a). Because the specimens from Martinique and French Guiana (Figs 5–6) fit the diagnostic size and morphology of *T. societatis* as described from ‘Moon’ (Table 3), a CM juvenile from the Society Archipelago (see Riaux-Gobin *et al.*, 2017b), we inferred that *T. societatis* is pantropical. It is found on CM, LO and EI, but is apparently absent

from DC. Surprisingly, the LO specimens colonized by *T. societatis* do not have members of the genus *Chelonicola* attached to them.

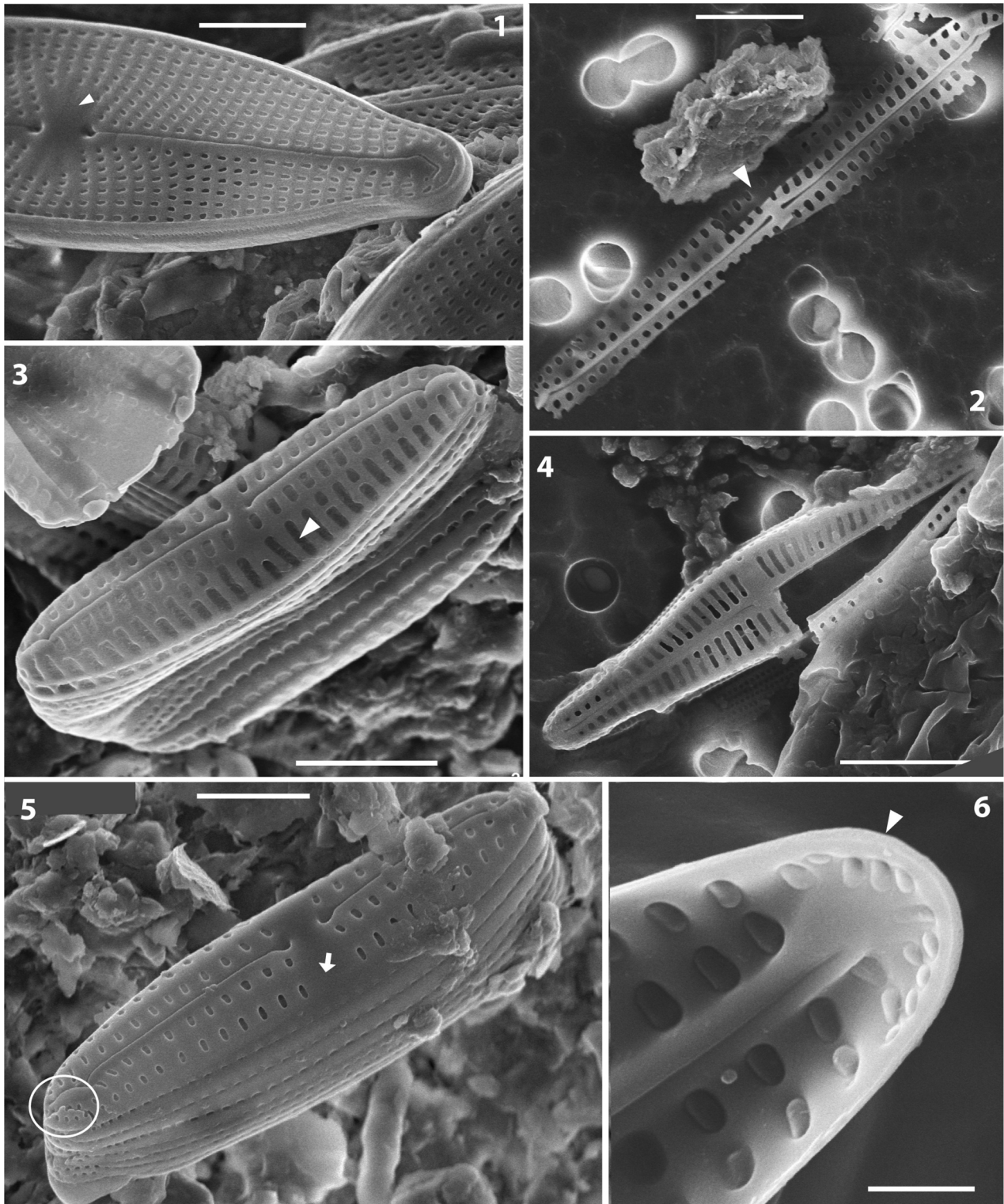
Chelonicola caribearia Riaux-Gobin, Witkowski, Ector & D.Chevallier (Fig. 3, Table 3), first described from Martinique (Riaux-Gobin *et al.*, 2017b) was also found in the South Pacific. *Chelonicola caribearia* is present on all the studied turtles, except for DC. This taxon is particularly abundant in Martinique and French Guiana, but present in the Society Archipelago. The morphometrics of specimens observed in the South Pacific (Table 3) fit the diagnostic description from the Lesser Antilles.

Chelonicola sp. (Fig. 2, Table 3). Present on juvenile CM from Society Archipelago and Eastern Caribbean (Martinique) and EI from Martinique (Fig. 2). This taxon was not found on French Guiana. *Chelonicola* sp. has characters diagnostic of *Chelonicola* (terminal raphe fissures strongly hooked on the same side, proximal raphe endings slightly bent on the side opposite of that of terminal endings, one row of slightly elongate areolae on each side of the raphe and one row of short areolae on the mantle). *Chelonicola* sp. has a fascia reaching the margins of the valve (Fig. 2, arrowhead). While grossly similar in morphology to *C. caribearia* (Fig. 3), *C.* sp. is longer, has lower stria density, higher length/width (L/W), and a fascia reaching the margins of the valve (Table 4). Furthermore, the row of areolae on the mantle is much shorter than that observed on *C. caribearia*. The cingulum of the putative new species is composed of numerous copulae, with puncta smaller and less quadrangular than those of *C. caribearia*. Overall, this taxon has a very fragile, brittle frustule and was considered a distinct entity in the statistical analyses.

Chelonicola cf. *costaricensis* Majewska, De Stefano & Van de Vijver, first described from Costa Rica (Pacific coast, locality Ostional, Majewska *et al.*, 2015a), was rare in collections from Martinique, French Guiana and South Pacific (not illustrated). This taxon has striae composed of several short areolae and no real delineation between the valve face and the mantle. It is very similar to *C. costaricensis*, but *C.* cf. *costaricensis* is often narrower, with slender apices and oblong areolae rather than the more rounded areolae in the original description.

Navicula dermochelycola Witkowski, Kocielek & Riaux-Gobin (Riaux-Gobin *et al.*, 2020; Fig. 1). This taxon was found on most nesting DC and one nesting LO in French Guiana but is apparently absent from the other turtle species and was only observed in French Guiana.

Olifantiella Riaux-Gobin & Compère. Several rare *Olifantiella* species were observed in our samples (Table 3), with *Olifantiella* cf. *gorandiana* present on several turtles; except for LO, all turtle species from the three studied areas were colonized by *Olifantiella*.



Figs 1–6. (SEM) **Fig. 1.** *Navicula dermochelycola* with large and irregular central area (arrowhead) and alternatively long and short striae around the central area, note the decussate pattern of areolae. **Fig. 2.** *Chelonicola* sp. with a narrow fascia up to the margins (arrowhead), showing the valve face and mantle with oblong areolae (one or two, arrowhead). **Fig. 3.** *Chelonicola caribeana*, frustule in external view, showing the valve face and mantle with oblong areolae (one or two, arrowhead). **Fig. 4.** *Olifantiella* sp., frustules in valve view, with slender apices, and position of the buciniportula aperture. **Figs 5, 6.** *Tripterion societatis*; note the fascia (arrowhead) and the small areolae on two rows on apex (6, arrowhead). Scale bars 2 μ m (1–5); 500 nm (6).

Specimens with narrow valves and protracted to slender-sharp (tapered as an arrow) apices (*Olifantiella* sp., Fig. 4, Table 3), similar to other members of the *O. gorandiana* complex, were noted separately. However, we recently concluded that these fit within the range of variation in *O. gorandiana* (Riaux-Gobin

et al., 2019). *Olifantiella* sp. (Fig. 4, Table 3) was present on a CM juvenile ('G5-Manahere') from Opunohu Bay (Moorea, South Pacific), and on several EI and CM juveniles from Martinique. The latter *Olifantiella* sp. (Fig. 4, Table 3) has similarities in valve shape, striation with *Labellicula lecohuiana*

Table 4. Features of *Tripterion societatis* (specimens from Caribbean and French Guiana), *Chelonicola caribeana* (specimens from South Pacific), *C. sp.* (Caribbean and South Pacific), *C. cf. costaricensis* (Caribbean, French Guiana and South Pacific), *Navicula dermochelycola* (French Guiana) and *Olifantiella sp.* (Caribbean and South Pacific). Morphometrics expressed as min-max and mean \pm SD (μ m, stria density in 10 μ m). SD = standard deviation. n = specimens observed in SEM.

	<i>Tripterion societatis</i>	<i>Chelonicola caribeana</i>	<i>Chelonicola sp.</i>	<i>Chelonicola cf. costaricensis</i>	<i>Navicula dermochelycola</i>	<i>Olifantiella sp.</i>
n	41	11	65	21	21	16
Number in the nMDS	12	2	3	4	5	10
Frustule in girdle view	wedge-shaped	slightly wedge-shaped	wedge-shaped	very slightly wedge-shaped	symmetrical	symmetrical (?)
Frustule shape	elliptic to elongate-elliptic	elliptic to elongate-elliptic	linear	elliptic to oblong with slender apices	linear elliptic with capitate apices	oblong-lanceolate, with sagittate apices
Length	7-12 (9.3 \pm 1.2)	5-8 (6.1 \pm 0.9)	6-13 (9.7 \pm 2.1)	6-15 (9.8 \pm 3.0)	14.5-25 (19.4 \pm 3.0)	5-9 (8.0 \pm 1.2)
Width	0.9-2.3 (1.5 \pm 0.6)	0.5-0.9 (0.7 \pm 0.1)	0.6-1.9 (1.1 \pm 0.3)	0.8-1.9 (1.3 \pm 0.4)	3.7-5.0 (4.4 \pm 0.3)	1.1-1.9 (1.5 \pm 0.3)
Stria density	6.7 \pm 2.4	7.9 \pm 1.5	9.40 \pm 3.4	7.7 \pm 3.5	4.4 \pm 0.8	5.4 \pm 1.0
Denser on apices	25-39 (28.5 \pm 2.9)	41-50 (44.9 \pm 3.1)	34.2-45 (39.6 \pm 3.2)	36-47 (41.4 \pm 3.8)	24.5-30 (27.8 \pm 1.6)	46-59 (54.9 \pm 3.6)
Areolae on the valve face	one row, elongate, divergent	one row, elongate, no real delineation between valve face and mantle	one row, round-elongate, parallel, separated from the mantle by a hyaline area	striae parallel, composed of up to 5 round-elongate areolae	radiate to arched striae, apically elongate areolae	macroareolae, radiate
Areolae on the mantle	one row of oblong areolae (rarely two shorter ones)	one row of often elongate areolae (rarely two shorter)	one row of round to elongate areolae	no discontinuity between valve face and mantle	mantle without areolae	oblong areolae
Central area	fascia large, delineated or not by one short areola on the mantle up to three rows of scattered small areolae at foot pole	fascia delineated by one oblong areola on both sides	fascia narrow, up to the margins	absent to reduced	distinct, bow-tie/butterfly like, expanded	asymmetrical
Pore field	present study	absent	absent	absent	absent	absent
Reference	present study	present study	present study	present study	present study and Riaux-Gobin <i>et al.</i> in press	present study

(Majewska *et al.*, 2017c), and with *Olifantiella seblae* (Kaleli *et al.*, 2018).

Achnanthes Bory. A large *Achnanthes* was mainly found on CM juveniles from Martinique, but also occasionally on CM nesting from French Guiana and South Pacific nesting LO. Based on the elongate shape of the valve, striation, and curvature in cingular view, this species may be close to *Achnanthes elongata* Majewska & Van de Vijver (described as epizoic on LO from Costa Rica in Majewska *et al.*, 2017b).

'Commensal' diatom richness versus biogeography and nMDS analyses

Samples with few to no diatoms and no 'commensals' were excluded from the factorial analyses. The turtles without evident 'commensals' mostly come from French Guiana, locality Yalimapo and to a lesser extent, Cayenne and Aztèque. Nineteen turtles (CM, EI) from the Pacific and 2 CM from the Caribbean were also void of 'commensal' diatoms.

'Commensal' diatom species richness varied greatly amongst the host species, maturity and location (Fig. 7). The highest species richness was found on all EI, with up to six taxa present per individual, particularly in the Caribbean (Fig. 7). LO and DC appeared to be characterized by relatively low species richness (Fig. 7).

The first axis of the nMDS, when applied to the full data set (turtles without any 'commensal' diatoms were excluded from the nMDS) separates turtles into two groups (Fig. 8a, b, c), driven mostly by the presence or absence of *N. dermochelycola*. This diatom was found on almost all DC (except one specimen from Martinique) and on one LO (from Cayenne, Guiana) (Fig. 8b, right ellipse). The second axis roughly discriminates EI from CM (Fig. 8b, left ellipses). There was no evidence to suggest that the area or maturity stage (adult, juvenile) had an effect on the diatom community (Fig. 8a, c).

A second group of analyses (Fig. 9) undertaken on the same data set (see above) excluding *N. dermochelycola* roughly grouped EI and CM together (Fig. 9b, ellipses), with LO excentrically positioned. Here again, neither maturity stage nor area affected the composition of the diatom assemblage (Fig. 9a, c).

Among CM the diatom species richness varied within areas (Fig. 7). An nMDS (Fig. 10) indicated some degree of spatial segregation with a trend in dissociation of the Pacific and Atlantic samples. A Mantel test analysis applied only on CM indicated a weak but significant correlation between species composition and geographic distance (Mantel statistic $r = 0.2030$, $p = 0.013$) (Fig. 11).

Figure 12 shows all diatom species except *N. dermochelycola* (sp. 5) (cf. Table 3) plotted on the nMDS analysis. *Olifantiella cf. gorandiana* (sp. 6) appears as a characteristic taxon for the grouped EI samples. In addition, *Tripterion societatis* (sp. 12), and *Achnanthes cf. elongata* (sp. 1) seem to be strongly associated with

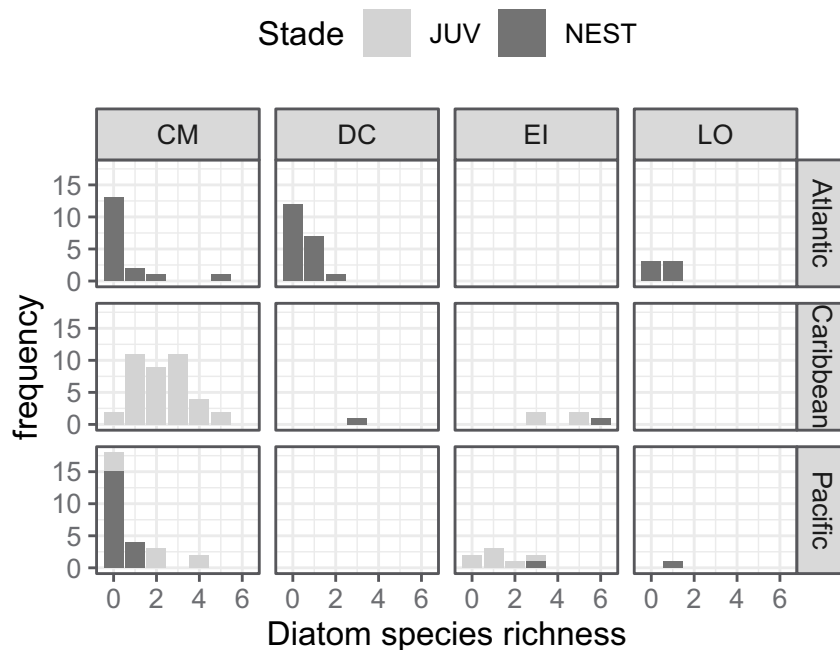


Fig. 7. ‘Commensal’ diatom species richness (cf. Table 3) per host species (*Chelonia mydas*, CM; *Dermochelys coriacea*, DC; *Eretmochelys imbricata*, EI; *Lepidochelys olivacea*, LO) and area (Equatorial West Atlantic = Atlantic, Eastern Caribbean = Caribbean; South Pacific = Pacific). Stade: juvenile (grey), nesting (black).

LO. *Olifantiella* spp. seem to be driving the position of DC (i.e. *O. societatis* (sp. 11), *O. mascarenica* (sp. 7), *O. pilosella* (sp. 8), *O. muscatinei* (sp. 9), *O. sp.* (sp. 10)). Centrally positioned on the graph, *Chelonicola caribbeana*, (sp. 2), *C. cf. costaricensis* (sp. 4) and *C.sp.* (sp. 3) are associated with CM.

Discussion

Host specificity

The nMDS analyses suggest that the commensal diatom communities differ between turtle species. DC, EI and CM are grouped differently (Figs 8, 9), with LO being marginally positioned. The most surprising and salient result concerns DC, which is distinct from the other turtle species (Fig. 10), probably driven primarily by *N. dermochelycola* (sp. 5), which is only present on DC (except for one LO). So, while it cannot be inferred that *N. dermochelycola* is restricted in its distribution exclusively to DC, the fact remains that this taxon, absent from EI and CM, contributes significantly to the nMDS analysis. The particular ethology of DC can probably explain this difference in commensal colonization.

Excluding *N. dermochelycola* from the analyses (Figs 9–12), the nMDS grouping was less clearly defined, but some degree of segregation could be observed for CM and EI, with LO being excentrically positioned (Fig. 9). Furthermore, from our data, EI host the most species-rich commensal flora (Fig. 7), possibly due to their lifestyle of foraging in coastal shallow areas and the sedentary individuals in Martinique (Nivière *et al.*, 2018).

Thus, the commensal assemblages seem to depend *pro parte* upon the host species with some particular taxa associated with, if not exclusive to, each turtle species.

Biogeography

From our data, some ‘commensal’ diatoms appear to have restricted distributions and a particular biogeography. For example, both *Tursiocola guyanensis* (sp. 13) and *T. yin-yangii* (sp. 14) are absent from the South Pacific, but are found on CM juveniles from Martinique and nesting individuals from French Guiana, and on one DC from Martinique, with an apparent mutual exclusivity between the two taxa; both taxa co-occur only on one nesting CM from French Guiana.

When considering the CM assemblages within the three areas, the species richness varies among areas but also among turtle stages (Fig. 7). A Mantel test on these data (Fig. 11) permits us to recognize geographic differentiation between samples. A nMDS analysis further illustrates the differences between these areas (Fig. 10), with CM being well separated in the Pacific from the Equatorial West Atlantic.

DC were mainly observed as nesting individuals in French Guiana with a reduced pool of ‘commensals’, but the only nesting DC from Martinique hosted *Chelonicola caribbeana* (sp. 2). *Navicula dermochelycola* (sp. 5), was mainly limited to most of the DC sampled (and one LO) from French Guiana, but the only DC observed from Martinique did not host this *Navicula*. More investigations on nesting DC from Martinique

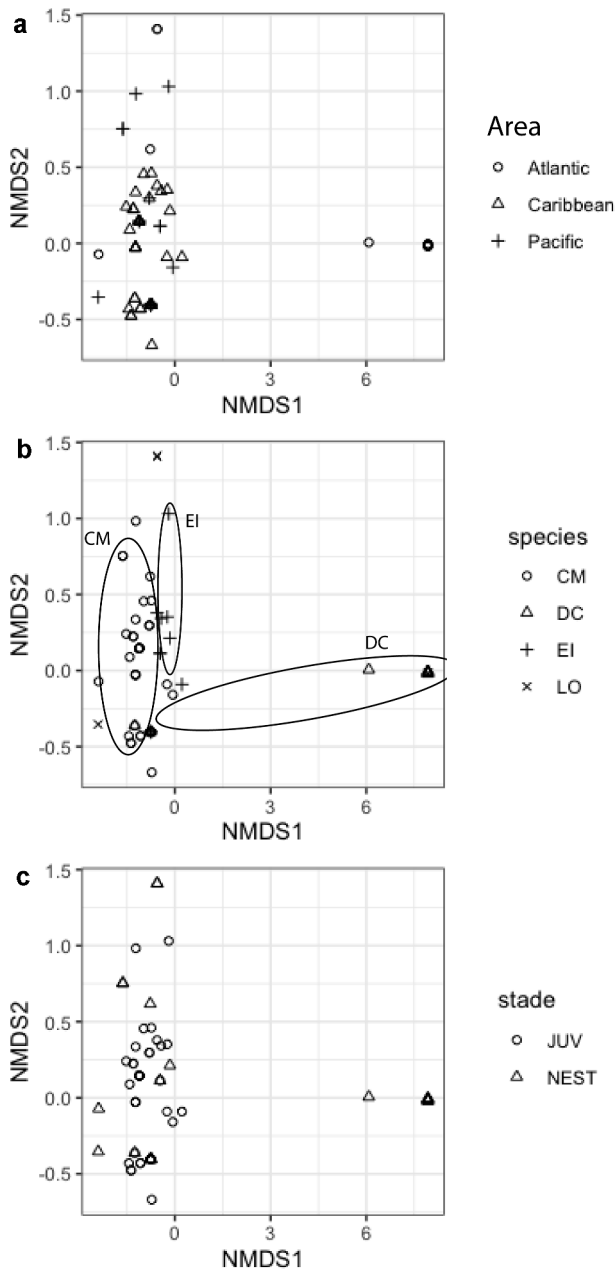


Fig. 8 a-c. Non-metric Multidimensional Scaling (nMDS) performed on the presence-absence of all ‘commensal’ diatom species observed (a) in three marine areas (Equatorial West Atlantic = Atlantic, Eastern Caribbean = Caribbean; South Pacific = Pacific), (b) on four host species (*Chelonia mydas*, CM; *Dermochelys coriacea*, DC; *Eretmochelys imbricata*, EI; *Lepidochelys olivacea*, LO), and (c) on juveniles and nesting individuals (JUV, NEST), Ellipses in Fig. 8b roughly materialize groupings amongst host species (DC, CM and EI).

are needed to discern the role of the biogeography on the occurrence of *N. dermochelycola*.

Based on our results, we would propose that only *N. dermochelycola* (sp. 5), *Tursiocola guyanensis* (sp. 13) and *T. yin-yangii* (sp. 14) are considered as ‘endemic commensals’ from French Guiana and Caribbean on DC, LO (sp. 5) and CM (sp. 13, sp. 14).

Chelonicola caribbeana (sp. 2), *Chelonicola cf. costaricensis* (sp. 4), *Chelonicola sp.* (sp. 3) and *Tripterion societatis* (sp. 12) are ‘commensal’ diatoms present

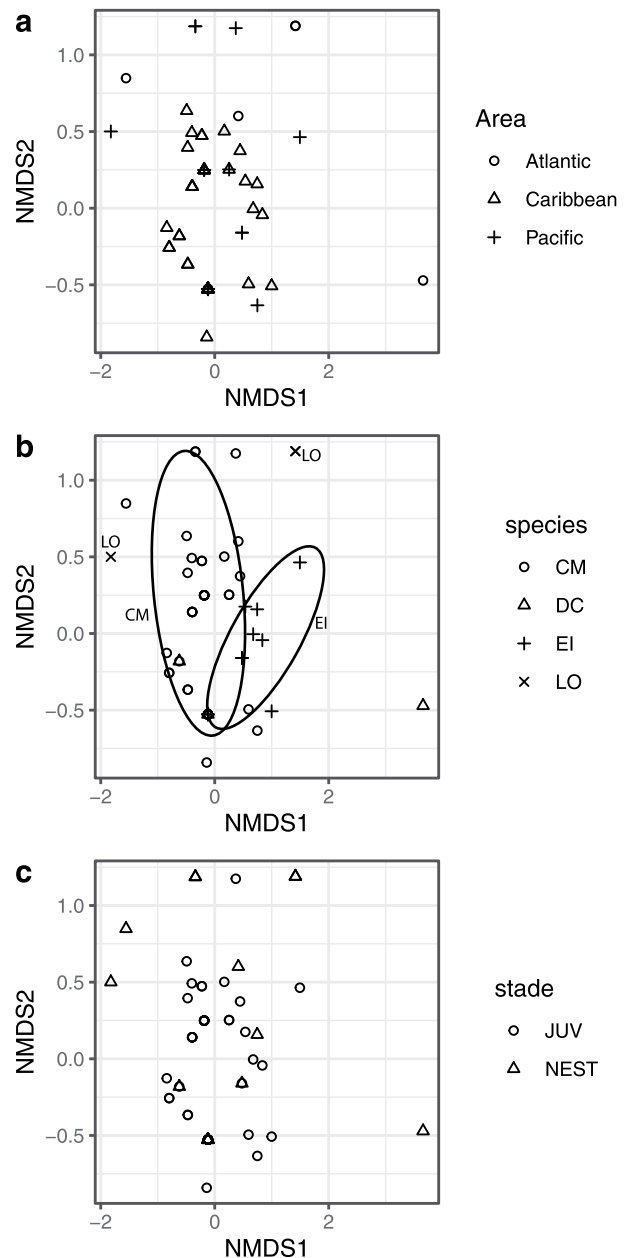


Fig. 9 a-c. Non-metric Multidimensional Scaling (nMDS) performed on the presence-absence of all ‘commensal’ diatom species, except for *Navicula dermochelycola*, observed (a) in three marine areas (Equatorial West Atlantic = Atlantic, Eastern Caribbean = Caribbean; South Pacific = Pacific), (b) on four host species (*Chelonia mydas*, CM; *Dermochelys coriacea*, DC; *Eretmochelys imbricata*, EI; *Lepidochelys olivacea*, LO), and (c) with juveniles and nesting individuals (JUV, NEST). Ellipses in Fig. 9b roughly materialize groupings amongst host species (CM and EI).

both in the Atlantic and South Pacific (*Chelonicolasp.* is apparently absent from French Guiana), so these commensals may be considered ‘pan-tropical epizoic’ taxa.

Several species of *Olifantiella* were observed in the present study. *Olifantiella cf. gorandiana*, present on coral sediments and macroalgae, shows a high morphological plasticity (with respect to valve shape, dimensions and orientation of striae) when found epizoic on sea

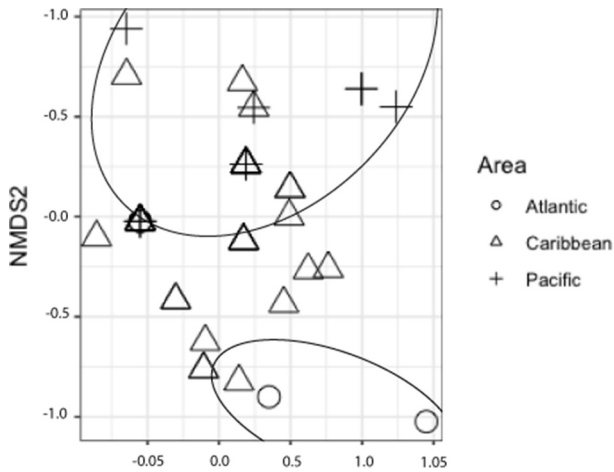


Fig. 10. Non-metric Multidimensional Scaling (nMDS) performed on presence-absence of all ‘commensal’ diatom species observed on *Chelonia mydas* (CM): in three marine areas (Equatorial West Atlantic = Atlantic, Eastern Caribbean = Caribbean; South Pacific = Pacific). Ellipse (top) roughly materializes grouping amongst South Pacific samples, ellipse (bottom) roughly materializes grouping amongst Atlantic samples.

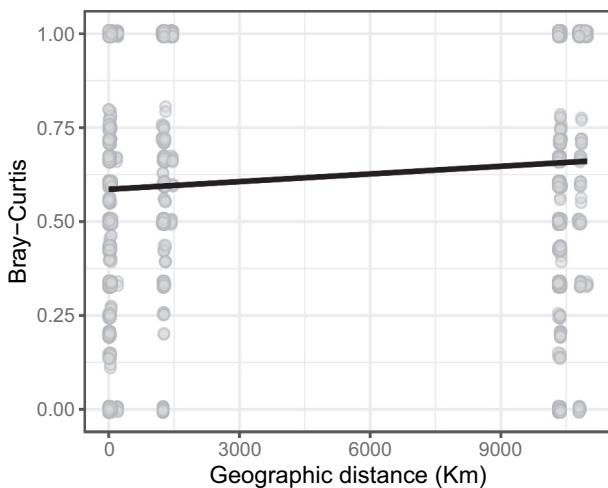


Fig. 11. Mantel test analysis, conducted on CM ‘commensal’ assemblages (see text). Mantel’s r statistic = 0.2038, p = 0.0136.

turtles (Riaux-Gobin *et al.*, 2019). This taxon is apparently widely distributed across tropical seas, and not exclusively epizoic, adapting to each niche, but particularly flourishing on turtles. Except for *Olifantiella* sp. (sp. 10) a ‘morph’ (see Riaux-Gobin *et al.*, 2019) that was only found as epizoic, several other taxa, present in the Caribbean and West Atlantic, were not epizoic in the South Pacific: *O. mascarenica* (sp. 7), *O. muscatinei* (synonym *O. pseudobiremis*) (sp. 9) (present in sediments from Moorea and Marquesas, locality Nuku Hiva, pers. obs.), *O. societatis* (sp. 11) (present on sediments from Moorea; Riaux-Gobin, 2015). On the other hand, *Olifantiella pilosella* (sp. 8) was not observed as epizoic (nor as epipsammic) in the Atlantic (French Guiana, Martinique). It is difficult to identify a particular

biogeography for such taxa, where several are only occasionally epizoic and most of them are rare.

Turtle behaviour and lifestyle

The different ethologies of the marine turtle species studied here probably influence the diatom assemblages. Foraging habits differ amongst sea turtle species and also depend on their maturity stages. LO is known to be a pelagic carnivore (Polovina *et al.*, 2004: 49; Chambault *et al.*, 2016): ‘their most common prey are pyrosomes (*Pyrosoma atlantica*) and salps (Salpidea) which are found subsurface’. CM feeds principally on seagrasses and macroalgae, but also sponge fragments (Bjorndal, 1985; Makowski *et al.*, 2006; Bresette *et al.*, 2010; Holloway-Adkins & Hanisak, 2017; Siegwalt *et al.*, 2019) and juvenile CM show long-term fidelity in restricted sites used as feeding areas over several years (Makowski *et al.*, 2006; Siegwalt *et al.*, in press). Following hypotheses by Bresette *et al.* (2010: 105), ‘adult and large subadult’ CM ‘use deeper water habitats than juveniles’. EI feed on sponges (mainly demosponges) and commonly qualifies as one of the most sedentary (and neritic) sea turtles (Bjorndal, 1996; Nivière *et al.*, 2018). DC is believed to be the most pelagic and deep-diving sea turtle, foraging on jellyfish and salps, but also foraging in coastal waters during the nesting period; leatherbacks are reported to be the most migratory and wide ranging of sea turtle species (Bjorndal, 1996; Dodge *et al.*, 2011, 2014; Chambault *et al.*, 2017).

Differences in colonization of sea turtles have been reported for macroalgae: *Caretta caretta* carries a large number of macroalgae, while CM ‘maintains a relatively clean carapace, even when exposed to high number of potential colonizing algae’ (Senties *et al.*, 1999). On the other hand, EI ‘are thought to be more sedentary’ than *C. caretta* ‘and forage near shallow reef habitats’ (Magnuson *et al.*, 1990), ‘conditions which expose them for longer periods of time to potential colonizing algae’ (Senties *et al.*, 1999).

Accounting for these different ethologies, can we point to a relationship between the ‘commensal’ diatom assemblages and the lifestyle of the host? Microalgae, as well as macroalgae, need light, though some diatoms can adapt to a shaded environment (cf., Admiraal *et al.*, 1987) or a non-photosynthetic lifestyle, such as the epizoic *Tursiocola* described in Frankovich *et al.* (2018). Thus, environmental factors which influence available light, such as the excessive particle discharge of rivers near the coast, may negatively influence the acclimation and survival of photoautotrophic ‘commensals’. For example, in French Guiana the Amazon has the highest level of freshwater and sediment discharge and the largest

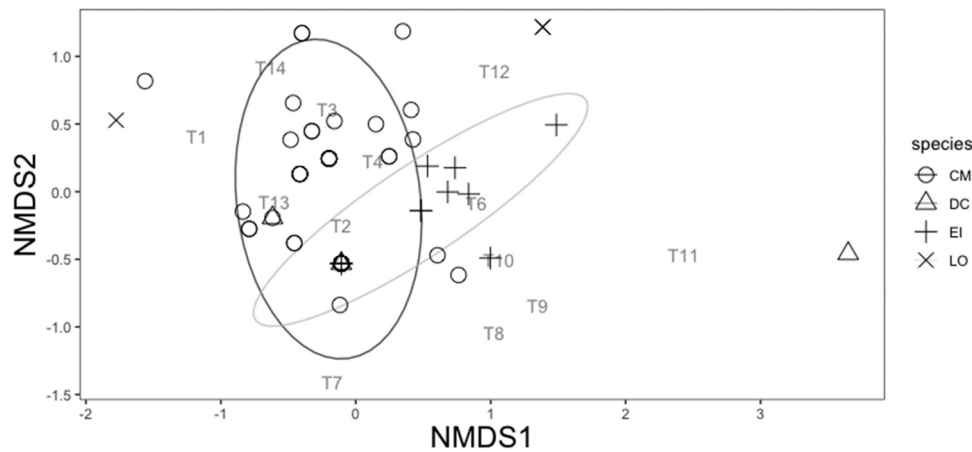


Fig. 12. nMDS analysis, as presented in Fig. 9b, with all diatom species plotted (grey numbers, see Table 3) (except for *Navicula dermochelycola*). Note the rough grouping concerning the EI and CM (ellipses), the excentric positions of DC and LO and the associated diatom species (see comments in the text).

drainage basin in the world, with 115 107 tons of sediments discharged into the Equatorial Atlantic per year (Péron *et al.*, 2013; Chambault *et al.*, 2015), providing a possible explanation for the low diatom richness on CM, DC and LO in that area (Fig. 7, west Atlantic area).

Turtles are also a moving substratum subject to reduced light during long dives. The pressure may also negatively affect microalgal survival, and some of the sampled turtle species dive very deep e.g. DC (Bjørndal, 1996). Among the four studied species in our survey, DC (all from French Guiana) have unusual diatom assemblages, with the rare presence of diatoms and a very low species richness, which could possibly be due to this deep diving inhibiting efficient diatom growth. In fact, this behaviour might drive diatom diversification, as these DC host a particular diatom (*N. dermochelycola*) never found elsewhere, except on one LO from the same environment. Alternatively, the specialization of this taxon may also be due to the particular structure of the DC leather-like carapace. This pattern of unique epibiont assemblages in DC was also pointed out by Robinson *et al.* (2017), who observed ‘the leatherback turtles’ ... have epibiont communities ... statistically distinct from those of the sympatrically nesting olive ridley and green turtles’.

From the present study, few to no planktonic diatoms (only rare Coccolithophoridae) were present, even on the mostly pelagic DC (Bjørndal, 1996). Only benthic diatoms seem to successfully colonize the turtle shell. The discussed ‘commensal’ diatoms do not passively sediment on the host carapace but are, most probably, actively growing taxa (e.g. Majewska *et al.*, 2015a: fig. 5) produced photographs of ‘clusters of cells attached to the turtle carapace’).

The high ‘commensal’ diversity shown in EI might be due to the fact that they are the most sedentary turtle species, and used to shallow environments,

whereas LO and DC have pelagic life stages which might limit diatom colonization. The nMDS analyses clearly illustrate the particular status of the DC (Fig. 8), and to a lesser extent the differentiation between CM and EI diatom assemblages (Figs 8, 9). Nevertheless, it would be interesting to refine our sampling strategy to obtain fully comparable data sets (comparable pools of juveniles and adults for each turtle species and area), and to obtain quantitative data (per scraped surface of carapace). From our present data it is difficult to ascertain the role of maturity versus biogeography in the colonization of turtles.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Ethics statement

The study in Martinique meets the legal requirements of the countries in which the work was carried out and follows all institutional guidelines. The protocol was approved by the 'Conseil National de la Protection de la Nature' (CNP, <http://www.conservation-nature.fr/acteurs2.php?id=11>), and the French Ministry for Ecology, Sustainable Development and Energy (Permit number: 2013154-0037 afforded to CNRS-IPHC), which acts as an ethics committee in Martinique. After the evaluation of the project by the CNPN, fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of Martinique in order to minimize the disturbance of animals. The protocol applied in French Guiana has been approved by the 'Conseil National de la Protection de la Nature' (CNP, <http://www.conservation-nature.fr/acteurs2.php?id=11>), which is under the authority of the French Ministry for Ecology, Sustainable Development and Energy (Permit number: 09/618 afforded to CNRS-IPHC), and acts as the ethics committee for French Guiana. The protocol applied in the South Pacific was approved by French Polynesia (Permit number 2157 of the 'Ministère de la promotion des Langues, de la culture, de la Communication et de l'Environnement' afforded/granted to 'Te mana o te moana'), particularly concerning this project.

Author contributions

C. Riaux-Gobin: conceived the project, produced all SEM imagery, determinations and countings, and drafted and edited the manuscript; M.P. Ashworth: drafted and edited the manuscript; J.P. Kociolek: drafted and edited the manuscript; D. Chevallier: collected the field samples, and drafted and edited the manuscript; P. Saenz-Agudelo: conducted nMDS and Mantel tests, drafted and edited the manuscript; A. Witkowski: helped with the taxonomy, drafted and edited the manuscript; G. Daniszewska-Kowalczyk: worked several samples and produced type slides, edited the manuscript; C. Gaspar: collected the field samples, edited the manuscript; M. Lagant: collected the field samples, edited the manuscript; M. Tournon: collected the field samples, edited the manuscript; A. Carpentier: collected the field samples, edited the manuscript; V. Stabile: collected the field samples, edited the manuscript; S. Planes: provided material support and funding for this project, edited the manuscript.

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