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Eretmochelys imbricata shells present a dynamic substrate for a facilitative epibiont relationship between macrofauna richness and nematode diversity, structure and function

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ABSTRACT

Although nematodes are the most abundant metazoans in marine environments and present an important biological and ecological model organism to assess marine ecosystem processes and functions, there are in fact very few studies that use nematodes to investigate ecological communities and relationships on "mobile" ecosystems. Arguably one of the most mobile or dynamic marine ecosystems is a sea turtle carapace, hosting tens to hundreds or even thousands of epibiotic organisms; and as the turtle breeds, feeds and migrates, provides an ecosystem that is continuously exposed to changes and potential colonizers. In this study we investigated the nematode communities associated with 19 Hawksbill sea turtle carapaces (*Eretmochelys imbricata)*, and compared nematode structural (composition, richness and diversity) and functional (trophic types and gender/life stages) community parameters with those of other comparable epibiotic substrates (macrophytes, natural and artificial hard substrates) to see whether turtle carapaces are hotspots of nematode diversity and function among substrates suitable for epifauna. We also addressed potential epibiotic macrofauna-nematode interactions by looking at the relationships between macrofauna richness and nematode richness, diversity and community composition. Results suggest that the macrofauna play a bioconstructing role, creating several microenvironments, and thereby enhancing the richness and diversity of the associated nematode assemblages. This was supported by a direct and positive relationship between macrofauna and nematode richness, and implies a genera enrichment process across size classes and phyla. All heterotrophic nematode feeding guilds were recovered from the carapaces, with dominance of predators/omnivores and epistrate feeders. Nematode juveniles dominated in terms of abundance, and a female/male ratio of 1.11 was observed. Nematode richness and diversity were higher than found on other substrates, but feeding guild, gender and life stage structure did not differ compared to nematode communities from all other epibiotic substrates. As a result, we argue that turtle carapaces can be seen as hotspots for nematode biodiversity compared to other epibiotic substrates, but this is not reflected in the function of the nematode community. This study is the first to investigate in detail sea turtle carapace nematode communities, their richness, diversity, trophic and life cycle structure, and potential interactions with their co-epibionts, the macrofauna.

1. Introduction

Marine turtles play many important functional roles in marine ecosystems; they act as consumers, prey, competitors, hosts for parasites and pathogens, and they contribute to nutrient transport (Bjorndal and Jackson, 2002); they are also modifiers of the marine landscape and serve as substrate for hundreds of species of epibionts (Frick and Pfaller, 2013). During the reproductive season, marine turtles travel long distances to their nesting site (Broderick et al., 2007). The behavior, habitat and movements of each turtle individual are to a large extent responsible for the associated fauna on their carapace (Caine, 1986) which is dependent on the environmental and geographical overlap between the turtle and the potential epibiotic colonizers (Corrêa et al., 2014; Frick et al., 2003; Frick et al., 2004). Marine turtles

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provide habitats that are favorable to a diverse range of organisms, which, in turn, can play bio-constructing or bio-engineering roles on the carapaces themselves by modifying the carapace habitat and interacting with other species, thereby affecting community structure and diversity of the whole epibiont community, and this on different spatial and temporal scales (Breitburg et al., 2010; Corrêa et al., 2014; Jones et al., 1997).

The ecological associations that may be present in turtle epibiont communities (and marine communities in general) can be divided in three different categories: I - positive (harmonic); II - negative (disharmonic) and; III - neutral (indifferent). The latter is trivial from an ecological point of view, because it does not necessarily affect dynamic community processes. These ecological relationships can be considered direct or indirect depending on the level of species involvement and the resulting effects. Commensal relationships (harmonic) can indirectly affect the local biodiversity of a community through the provision of food, shelter and oxygen by some organisms to others, without the former receiving benefit nor harm, and may involve biological activities (Goto and Kato, 2011). Mutually beneficial interactions (harmonic) between two species, on the other hand, imply a direct or indirect benefit to both parties. Disharmonic relations may include predation by some organisms, affecting prey abundance directly (Spieth et al., 2011) and competitive interactions, which may lead to reduced abundance or removal. Both commensal and mutually beneficial interactions may support species enrichment processes leading to increased diversity, but also predation and competitive interactions may lead to enhanced diversity through colonization or invasion by new colonizers or success of low-abundance species that are able to exploit the available niche. That being said, organisms often exhibit both positive and negative interactions, which can affect the communities in stochastic and complex ways (Meziane et al., 2002). All these interactions may apply to epibiont communities associated with sea turtle carapaces and govern the dynamics of the epimacro- and meiofauna; with for instance increased meiofauna abundance when the number of microhabitats on the sea turtle carapace increases (Corrêa et al., 2014) or when recruitment of fouling organisms such as bivalves and bryozoans occurs (Bell and Coull, 1978; Janiak and Osman, 2012). To date however, we have very little understanding of the mechanistic processes that act on the carapace region of sea turtles and how colonization and biodiversity enhancement may occur on these mobile habitats. The present study aims to advance our knowledge in this respect by assessing the meiofaunal and macrofaunal epibionts, focusing on the abundant free-living marine nematodes.

Nematodes, or roundworms, play important roles in functional processes and biodiversity dynamics in the marine benthic environment (Danovaro et al., 2008; McIntyre, 1969; Nascimento et al., 2012; Schratzberger and Ingels, 2017). Nematodes are ubiquitous (Bongers and Ferris, 1999; Kiontke and Fitch, 2013), from marine, to freshwater and terrestrial environments, and as parasites in a vast range of plants and animals. On a global scale, nematodes are the most abundant metazoans and their high diversity has been used as a tool to assess the functioning of ecosystems (Heip et al., 1985; Ingels et al., 2012; Santorufo et al., 2012; Schratzberger and Ingels, 2017). Next to biodiversity, there are other useful ways to characterize nematode communities, such as the trophic structure, life cycle, and gender information (Bongers and Bongers, 1998; Moens et al., 2006; Wieser, 1953). These community characteristics can provide crucial functional information beyond pure numerical diversity measurements. Functional diversity measurements have gained much attention in more recent literature (Bremner et al., 2003) and provide a way in assessing ecological processes of ecosystems in general. Functional diversity can reflect ecosystem stability and resilience potential in situations where various stressors act on the community level (Stuart-Smith et al., 2013). Moreover, it has been shown that functional measures are important in assessing nematode community structure and composition, and their stability on the community level (Moens et al., 2013), with for instance gender and life-stage data providing information on the reproductive state and population turnover. Applying these to mobile habitats such as sea turtle carapaces yield a new way of increasing our understanding of the ecological roles and life histories of various epibiotic organisms, whilst at the same time providing information on the potential of turtle carapaces in providing suitable habitat for mobile and sessile fauna as well giving insights into the migration of these fauna through colonization processes and community dynamics on turtle carapace habitats.

Eretmochelys imbricata carapaces are considered vagile, hard substrates that can harbor a large number of species (Corrêa et al., 2014; Frick and Pfaller, 2013). Nematodes are known to live on two-dimensional consolidated substrates (e.g. turtle carapaces, macrophytes, reef surfaces, pier columns, ship hulls, etc.) (Raes et al., 2008) and three-dimensional unconsolidated or soft bottom substrate (e.g., sand, gravel, mud) (Leduc and Probert, 2011). These substrates can be made of organic or inorganic material and characterize the ecology of the present nematode fauna. However, to our knowledge, very few studies have engaged in comparing different consolidated substrates and how the substrate and its microhabitat structure may shape nematode community structure and function. However, such comparison can indicate whether different consolidates substrates comprise preferential habitats for nematode colonization and whether they are able to sustain viable ecological communities. Despite the increasing number of studies focusing on the free-living nematodes from a wide range of habitats, the biodiversity and functioning of the nematode communities associated with marine turtle carapaces remains completely unknown.

The aim of this research was to characterize nematode abundance, community composition, structure, diversity and function on Hawksbill sea turtle carapaces and assess the influence of the epibiotic macrofauna richness on these biological parameters. We tested the hypotheses that increasing richness of epifaunal macrobenthos on sea turtle carapaces 1) affects epibiotic nematode community structure and 2) enhances nematode community function. We tested these hypotheses to address the overall question whether turtle carapaces can be seen as hotspots for nematode diversity and function compared to other epibiotic substrates. In addition to this, our objective was to improve our understanding of genera enrichment processes on hard substrates, turtle carapaces in particular, that may enable enhanced epifaunal nematode diversity and function.

2. Material and methods

2.1. Study area

This study was performed in the municipality of Ipojuca (08°24′ S e 35°03′ W) along the south coast of Pernambuco state, Brazil, where the beaches of Cupe, Muro Alto, Merepe, Porto de Galinhas and Maracaipe are located. A beach line > 14 km were monitored daily with vehicle support, during the low tide periods between 10 September 2009 and 11 May 2010. Every year during the reproductive period (September to May), 4 out of the 5 marine turtle species that nest occur along the Brazilian coast (*Eretmochelys imbricata*, *Caretta caretta*, *Chelonia mydas* and *Lepidochelys olivacea*) arrive at these beaches to nest.

2.2. Sampling

The epifauna of 19 hawksbill turtles, *Eretmochelys imbricate*, were scraped off the carapace region. Since marine turtles only leave the sea for nesting, samples were taken while female turtles were digging their nest. The carapace surface, independent of the total adult size, was subdivided into 9 subareas as established by Pfaller et al. (2006) and 5 subareas of equal size were randomly selected (Urbaniak and Plous, 2011). These 5 subareas were scraped to remove all epibiothic fauna and pooled to make one sample (adapted methodology of Pfaller et al., 2006). The 3D micro-habitat structure and epibiotic coverage of every single sub area would vary depending on the associated epibiothic