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Do the morphological and functional traits of free-living marine nematodes mirror taxonomical diversity?

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A B S T R A C T

The taxonomical structure and diversity of nematode assemblages are the main attributes analyzed in ecology, but nematode adaptations to their habitats are still understudied. Accordingly, a survey on some known and other newly proposed morpho-functional traits was carried out in order to: determine if the morpho-functional diversity of nematodes mirrors their taxonomical diversity; and assess potential nematode adaptations to sediment type and hydrodynamic stress. Morpho-functional traits were investigated both singularly and together and showed significant differences related to these environmental factors. The greatest taxonomical and morpho-functional diversity was found in medium-coarse sand (M-CS) and at an intermedium energy level (IEL). The M-CS and IEL were probably richer in micro-habitats and subject to a low selective pressure, hosting nematodes with a wide range of adaptations. The mirroring of morpho-functional diversity with taxonomical diversity is crucial for the future growth of the use of nematodes in biomonitoring. This is because the study of their morpho-functional traits could reduce the level of work involved and the costs of any analyses.

1. Introduction

Nematodes are arguably the most successful free-living metazoans on Earth (Da Rocha et al., 2006). They have colonized all climatic regions and environments, even the most extreme. *Halicephalobus mephisto*, for instance, which is a free-living terrestrial nematode, has been found at a depth of 3.6 km below the Earth's crust (Borgonie et al., 2011). This phylum is considered to be "plastic" (Tahseen, 2012), because it is able to change or adapt under selective pressures or in stressful conditions (Semprucci and Balsamo, 2014a). Nematodes are key organisms in marine ecosystems, with a documented role in trophic chains and the recirculation of nutrients (Zeppilli et al., 2015; Semprucci et al., 2016).

In recent decades, the interest in the use of marine nematodes as bioindicators in ecological assessments has increased greatly (see Semprucci et al., 2017 for review). In this regard, the taxonomical structure of their assemblages and their diversity indices are often used as tools of comparison in ecological studies. The nematodes' adaptations, which allow them to live in specific ecological conditions or to survive perturbations, have not yet been the subject of targeted studies, although they are very important in understanding the ecology of the group. There is evidence, for instance, that the loss of nematode trophic diversity is closely related to the loss of marine ecosystem functioning (Danovaro et al., 2008). Accordingly, to properly use nematodes in monitoring programs, it is crucial to collect as much information as possible about how their morphological and functional traits vary when ecological conditions change, especially natural variables. It is documented that nematode assemblages may be influenced by various environmental parameters (Raes et al., 2007; Giere, 2009), but the relationship between sediment features and the composition of nematode assemblages in particular has been a central theme in meiobenthic ecology (Fonseca et al., 2014). Sediment type is recognized to affect both the horizontal and vertical distribution of meiobenthic assemblages (e.g. Steyaert et al., 1999, 2003; Vanaverbeke et al., 2002; Boufahja et al., 2016). In turn, the sedimentological characteristics of a study area are closely linked to its hydrodynamic conditions, which allow the deposition or removal of sediment and food, thus indirectly modifying the micro-habitats in which meiofauna live (Raes et al., 2007).

Several morpho-functional traits of free-living nematodes are thought to be related to important ecological functions. First, Wieser (1959) associated the morphological characteristics of nematodes with their habitat features and suggested that the morphology of the buccal cavity might be related to a particular trophic role in the ecosystem (Wieser, 1953). Several authors have underlined the possible limitations of this classification (Jensen, 1987; Moens et al., 2004), and Moens and Vincx (1997) in particular suggested the need for laboratory experiments at the species level to document the real trophic role of

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each species. Despite these criticisms, Wieser's scheme has been the one most widely applied thus far in studies of marine ecosystems.

Tail shape is another nematode trait that seems to play an important role in locomotion, feeding and reproduction. Thistle and Sherman (1985) divided nematode species into 11 functional categories based on their tail shape, with Thistle et al. (1995) subsequently reducing this number to four.

Life-style is an important biological and ecological characteristic of nematodes, with Bongers (1990) using it to create a classification that was then enlarged and modified (Bongers et al., 1991, 1995). Bongers (1990) classified nematodes into five classes along a scale from extreme *r*–strategists (c) (short life-cycle, high reproduction rates, high colonization ability, and tolerance to stress) to *k*–strategists (p) (long life-cycle, very few offspring, low colonization ability and sensitivity to stress). The c–p ranking is mainly recognized as a functional trait, but it is also related to the body size of nematodes: *r*–strategists are generally small, while *k*–strategists have larger body dimensions.

Other morpho-functional traits may have an adaptive role and can be easily identified, because they are diagnostic characteristics for taxonomical identification. Among them, amphids are the largest and most complex sensorial organs of the nematode cephalic region (Decraemer et al., 2014), and are used in the search for food and partners. It has been observed that terrestrial nematodes have small, sometimes punctiform, amphids, probably because they inhabit environments with a rich food supply, while large amphids are generally more common in species from open fresh water, where chemical information travels for greater distances (see Cesaroni et al., 2017). Despite their importance, there is no data available concerning whether amphids are related to particular habitat features in marine environments. In our study, we recognized eight main categories of amphids on the basis of the shape of the amphideal fovea and the extent of the area exposed to chemical information.

The body cuticle is a morphological trait that numerous studies relate to sediment type and hydrodynamic conditions, even if no functional category has been recognized thus far on this basis (i.e. Raes et al., 2007; Semprucci et al., 2014a). According to this relationship, we have characterized the body cuticle morphology into six categories, based on the observations carried out under light and electron scanning microscopy.

Accordingly, the present study aims to test how some selected nematode traits may change over the spectra of both sediment grain-size and hydrodynamic energy level. Some traits cited above have already found a wide application in marine ecology as functional categories (e.g. trophic groups, tail shapes, c-p classes) (see Schratzberger et al., 2007 for review), whereas the relationships of amphids to habitat have never been investigated and those of cuticle traits were only considered in a study in the 1950s (Wieser, 1959).

We selected the Maldivian archipelago for our analysis, in which some localities characterized by a low level of anthropogenic disturbance have previously been studied (Semprucci et al., 2014a) and a huge dataset (a total of 29 stations) on nematode assemblages obtained (see Semprucci and Balsamo, 2014b for review). To avoid the potential interference of depth, only datasets from samples collected using the same sampling process and in shallow subtidal stations were utilized (Fonseca et al., 2014). All these criteria appear to be fundamental when it comes to distinguishing the effects of natural or anthropogenic factors as best as possible.

We thus addressed three main questions: does the sediment type influence the morpho-functional traits of nematodes? Does the hydrodynamic energy level affect the morpho-functional traits of nematodes? Does the morpho-functional diversity mirror the taxonomical diversity trends?

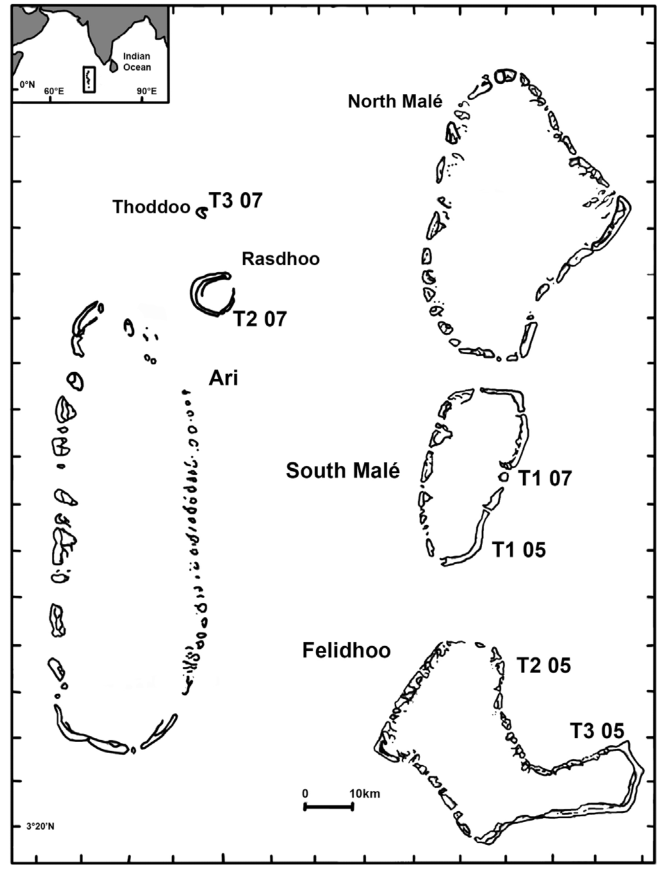

Fig. 1. Map with the location of the sampling transects investigated during the scientific cruises in 2005 (T105, T205, T305) and 2007 (T107, T207, T307).

2. Materials and methods

2.1. Study area

The Maldives comprises a double chain of 22 atolls and more than 1200 islands in the central part of the Indian Ocean (6°57′N to 0°34′S) (Fig. 1). The Maldivian archipelago is situated on a carbonate bank that rises from the deep ocean to an approximate depth of 2000 m (Kench et al., 2008). The sediments found here are completely of a carbonate origin and were formed due to the erosion of the coral reefs (Duncan and Hargraves, 1990).

In detail, the first study was carried out at the South Malé and North and East Felidhoo atolls in May 2005 (Semprucci et al., 2010). Sediment samples were collected from three transects along three back-reef platforms located on the eastern rim. A total of 18 stations were sampled at water depths that ranged from 0.40 to 5 m (Fig. 1). The texture of the sediments ranged from very coarse to fine sands, and so the samples were marked as VCS (very coarse sand), CS (coarse sand), MS (medium sand), and FS (fine sand) (Table 1).

The second investigation was carried out at a total of 10 stations in the South Malé, Rasdhoo and Thoddoo atolls (central eastern and western Maldivian Archipelago) in May 2007 (Semprucci et al., 2011). Samples were collected from three back-reef platforms differently exposed to wave energy, with water depths ranging from 0.20 to 1.1 m (Fig. 1). Accordingly, the transects can be regarded as being characterized by increasing hydrodynamic conditions moving from stations T107 (low energy level - LEL) to T307 (high energy level - HEL) (Table 1).

In this study, the different current and wave exposure of the areas selected enabled us to identify the gradient of the hydrodynamic stress on the nematode assemblages and, consequently, detect potential