Primary Research Article

Phytal marine nematode assemblages and their relation with the macrophytes structural complexity in a Brazilian tropical rocky beach

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Received 23 August 2004; in revised form 26 May 2005; accepted 4 June 2005

Key words: nematoda, phytal assemblage, Brazilian coast

Abstract

The nematofauna from the seaweeds Sargassum polyceratium Montagne, Hypnea musciformis Küetzing, Padina gymnospora Küetzing and the seagrass Halodule wrightii Ascherson was studied in March 2001, at Pedra do Xaréu, Pernambuco, Brazil, in order to investigate the associations of organisms, as well as the relation between the plant architecture and the associated fauna. Soft sediments adjacent to phytal environments were also investigated. Thirty-eight genera were found, including two new records (Odontanticoma sp. and Wieseria sp.) for the Brazilian coast. Multivariate analyses were carried out in order to verify the relation between nematode assemblages on plants and in sediments. The results showed that these assemblages were different in structure and composition between macrophytes and sediments. They were different in structure but not in composition among macrophytes, so the nematode biodiversity was related to the structural features of macrophytes' habitats.

Introduction

Nematodes are probably the most successful infaunal metazoans, living in great abundance and diversity inside sediments as well in close association with other organisms, or even parasitic. Although some species are only found in very specific biotopes, others are more widely distributed (Bouwman et al., 1984).

The free-living meiofaunistic nematodes have a vertical and horizontal distribution on a global scale and are, frequently, dominant in sediments from coastal areas to great ocean depths, at all latitudes. They colonize all types of substrates such as sediments, macrophytes and even artificial substrates (Sharma & Webster, 1983; Bell et al., 1984; Heip et al., 1985; Hall & Bell, 1993; Gourbault et al., 1998; Atilla et al., 2003). Esteves (2002) observed that, taking into consideration the extension

of the Brazilian coastland and the limited number of studies carried out so far, there is a shortage of knowledge about the biodiversity of this group.

The presence of seaweed increases both the availability of food and the complexity of habitat. It also provides a refuge for the fauna, in the marine environments. The abundance of epifauna and epiphyte on seaweed has been noted since beginning of the 20th century (Mukai, 1971). Plant species and their architecture and density have a strong effect on the development of epiphytic organisms (Heck & Wetstone, 1977; Hicks, 1977a; Heck & Orth, 1980; Hicks, 1980; Bell & Westoby, 1986; Edgar & Moore, 1986; Gibbons & Griffiths, 1986; Johnson & Scheibling, 1987; Preston & Moore, 1988; Albay & Aykulu, 2002).

The meiofauna can attain high densities on algae with a complex surface morphology, which facilitates the deposition of sediments and detritus (Hicks, 1980). According to Warwick (1977) the faunal composition appears to be directly related to the coarseness, silt content, growth form and texture of the seaweed. Studies about phytal have been carried on seaweeds or seagrasses, either in relation to the meiofauna community structure (Gunnil, 1982a; Coull & Wells, 1983; Gibbons & Griffiths, 1986; Preston & Moore, 1988; De Troch et al., 2001, 2003), or on specific groups as Nematoda (Moore, 1971; Warwick, 1977; Kito, 1982), Copepoda (Hicks, 1977a, b), Amphipoda (Tararam & Wakabara, 1981; Gunnil, 1982b) and Acari (Somerfield & Jeal, 1996).

Analyzing the structure of nematode communities in phytal aquatic environments, Heip et al. (1985) detected common patterns, such as the fact that the most abundant species are frequent on different species of seaweed, although the dominant genera on each seaweed seems to be different.

The present work analyzes the relationship between the free-living community of nematodes and the physical structures of three seaweeds and one seagrass species. Hypotheses are raised to explain the question whether phytal marine nematodes associations are distinct from those observed in surrounding sediments, and whether the habitat complexity influences the structure of these communities.

Materials and methods

This study was performed on the north-eastern Brazilian coast-Pedra do Xaréu Beach, Pernambuco (8° 18' 14" S; 34° 56' 45" W), a rocky beach where Sargassum beds are present in the sublittoral areas throughout the year (Fig. 1). Sampling was carried out at low tide in March, 2001, in the lower intertidal zone. Four species, three seaweeds and one seagrass, were chosen due to their morphology and abundance: Sargassum polyceratium, Halodule wrightii, Padina gymnospora and Hypnea musciformis. H. wrightii (seagrass) was collected in sandy sediments, and the algae were collected from hard substrates. Ten samples of each species were collected. Each one of them was carefully enveloped in a plastic bag; the holdfast was removed and kept in 4% formalin solution. Ten samples of sediment were sampled using a PVC corer with 10 cm² internal area, as described by Hope (see Higgins & Thiel, 1988), and then also



fixed with formalin 4% solution. At the laboratory, the faunistic samples were treated using routine methods for meiofauna (humid sieving and manual centrifugation) suggest by Elmgren (1973) and sorted out using Dollfus plates and stereoscopic microscope. The animals were removed manually using a needle, and permanent slides were made for taxonomic and biological studies of Nematoda, as described by Cobb (1917) and De Grisse (1969). They were sorted into functional groups according to Wieser (1953):

- 1A: selective deposit feeders: nematodes with a very small unarmed buccal cavity;
- 1B: non-selective deposit feeders: nematodes with unarmed buccal cavities of moderate size;
- 2A: epistratum feeders: nematodes with medium size buccal cavities, provided with small teeth;
- 2B: predators or omnivores: nematodes with wide buccal cavities, large teeth or other powerful buccal structures.

The volume, height and width of the weeds were measured after the animal extraction from the substrate, as described by Montouchet (1979) and Hacker & Steneck (1990). The density is expressed by ml of seaweed. The K coefficient was calculated to show the substrate structural complexity: K=Volume/(heigth×width).

The similarity of nematode associations among seaweeds and sediments was determined by nonmetric multidimensional scaling ordination (MDS) on $\text{Log}_{10} (X+1)$ transformed data, using the Bray Curtis similarity index (Clarke, 1993). Formal significance tests for differences in nematoda community structure between habitats were performed using the one-way ANOSIM test (Clarke, 1993).

The SIMPER (Clarke & Warwick, 1994) procedure was performed in order to determine which nematodes genera were responsible for differences between algal types (cut off 40%). The differences between functional groups were tested with *G*-test (Zar, 1996).

Data analysis was performed using the PRI-MER (Plymouth Routines In Multivariate Ecological Research) version 5.1.2 software package (Clarke & Gorley, 2001). very similar among them, showing means from 6.95 to 8.44 mm (Fig. 2), with no significant differences (Table 1). All macrophytes were significantly different in height. In relation to volume data, only *S. polyceratium* was significantly different from other macrophytes, with a means of 16.7 ml. *P. gymnospora* was significantly higher in relation to *K*, an indication of a larger area, at least potentially, for nematodes colonization (Table 2). *H. wrightii* was the tallest weed, but with the lowest *K. H. musciformis* presented similarity in width, height and volume values.

The nematodes were found on 26 macrophytes out of 40 sampled phytal substrates. The gathering of taxonomic data from a tropical phytal environment resulted in a list with 38 genera, including two new records in Brazil (Odontanticoma sp. and Wieseria sp.). The richness per macrophyte ranged from 17 (Halodule wrightii) to 26 genera (Hypnea musciformis). Only five genera occurred on all macrophytes analyzed (Acanthonchus, Euchromadora, Halalaimus, Paracyatholaimus and Viscosia), corresponding to 37% of the total number of organisms. Halalaimus and Viscosia occurred only on phytal substrates. 22 nematode genera occurred only on one species: two on H. wrigthi (Metalinhomoeus and Monoposthia), eight on H. musciformis (Anticoma, Cyatholaimus, Graphonema, Longicyatholaimus, Odontanticoma, Prochromadora, Pseudochromadora, and

Results

The physical structure of the macrophytes presented some distinct characteristics. The width was



Figure 2. Comparison between measures of the macrophytes (means + Standard deviation, SD, n=10); Height and Width in cm; Volume in ml. K=[Volume/(height × width)] × 100.

Independent factor	Dependent factor	df	MS	df	MS	F	p-level
		Effect	Effect	Error	Error		
Weeds	Height	3	631.5289	36	7.5400	83.7568	0.0001*
	Width	3	4.8151	36	10.7540	0.4477	0.7204
	Volume	3	209.2010	36	28.6354	7.3057	0.0006*
	Κ	3	1052.0700	36	69.6968	15.0949	0.0001*

Table 1. ANOVA one-way of macrophytes' measures

df = degree of freedom; MS = mean square.

Table 2. Post hoc Scheffé test of macrophytes' measures

Factor	Scheffé
Height	1 2 3 4
Volume	1 2 4 3
K	1 2 3 4

Halodule wrightii (1), Hypnea musciformis (2), Sargassum polyceratium (3) and Padina gymnospora (4).

Thalassomonystera), seven on S. polyceratium (Comesa, Crenopharynx, Gammonema, Parachromadora, Paramesacanthion, Terschellingia, Wieseria), and five on P. gymnospora (Belbola, Paracomesoma, Paralongicyatholaimus, Pomponema and Spirinia). The mean richness was 5.7 genera per sample (SD=5) (Fig. 3). The mean diversity (Shannon–Wiener index) did not present a significant difference (ANOVA, df=4; F=0.526; p=0.717) within macrophytes neither between macrophytes vs. sediment (Fig. 4).

Mean density ranged from 0.6 to 4 individuals/ ml per macrophyte (Fig. 5). The five most abundant genera comprised 50% of the total density and 17 genera made up 95% of it. The densities ranged from 0.0014 ind./ml (*Hypodontolaimus*) on *Halodule wrightii* to 0.6 ind./ml (*Chromadora*) on *Sargassum polyceratium* (Fig. 5).

A total of 32 genera were found in adjacent sediments (mean = 10.1, SD = 5.75, n = 9). From these, 17 genera occurred only in this habitat. Two genera comprised 55% of the total number of

28 28 Mean 24 24 20 20 Density (ind /ml) 0 16 16 Richness cumulative 2 12 8 8 4 4 a Halodule Hypnea Sargassum Padina (n=9) (n=7) (n=6) (n=4)

Figure 3. Nematodes genera richness and density (means + SD) on macrophytes at Pedra do Xaréu-PE; Brazil.



Figure 4. Nematofauna diversity (Shannon-Wiener index) on macrophytes at Pedra do Xaréu-PE; Brazil.

organisms. Among these, *Dichromadora* comprised 32.7%. The abundances ranged from 7 to $103 \text{ ind.}/10 \text{ cm}^2$, with a mean of 54 ind./10 cm² (n=9; SD=34.8). The presence of *Euchromadora* and *Chromadorina* explained most of differences between *P. gymnospora* and other macrophytes (Table 3). *Eurystominia* had the greatest dissimilarity between *H. musciformis* and *H. wrightii*, and between *H. musciformis* and *S. polyceratium* (Table 3). The most common feeding type was epistratum feeders (2A). Thirty-two genera presented this kind of buccal cavity. These individuals were dominant on all substrates, followed by the carnivores/omnivores (2B), and deposit feeders (1A and 1B). Almost half of epigrowth feeders genera were specific to one substrate. *S. polyceratium* and *H. musciformis*, with seven exclusive genera, showed the highest specificity, while *H. wrightii* had the lowest one, with two exclusive genera.



Figure 5. Mean density of major nematodes genera on macrophytes (means + SD) at Pedra do Xaréu-PE; Brazil.

Table 3. Average dissimilarity	between macrophytes and	l individual taxa with maj	or contributions (cut off 40%)
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	H. wrightii	H. musciformis	S. polyceratium	P. gymnospora
Halodule wrightii		Eurystomina (24.0); Acanthonchus (5.4); Halalaimus (5.2); Chromadorina (5.2)	Euchromadora (19.7); Oncholaimus (12.8); Chromadora (7.5)	Euchromadora (29.5); Chromadorina (14.0)
Hypnea musciformis	85.72		Eurystomina (21.5); Euchromadora (15.3) Oncholaimus (8.7)	Euchromadora (24.8); Chromadorina (14.5)
Sargassum polyceratium	76.70	82.65		Euchromadora (29); Chromadorina (14.9)
Padina gymnospora	81.56	85.88	72.53	

Table 4. Nematode feeding types found on macrophytes and in sediments at Pedra do Xaréu, PE, Brazil

Feeding types	H. wrightii	H. musciformis	S. polyceratium	P. gymnospora	Sediments	Total
1 A	1	1	4	1	2	4
1 B	1	4	1	3	6	10
2 A	9	15	9	12	18	32
2 B	5	6	5	6	6	14
G-value	1.789	0.484	5.962	0.441	0.448	
					$G_{3;0.05} =$	7.815

(1A = selective detritivores; 1B = non-selective detritivores; 2A = epigrowth feeders/herbivores; 2B = carnivores/omnivores).

Three exclusive genera found on *S. polyceratium* were deposit feeders. On *H. musciformis*, from the seven exclusive genera, six were epistratum feeders (Tables 4 and 5). According to the *G*-test, the proportions of feeding types among macrophytes were not significatively different (Table 4).

Taking into account sediment and macrophytes, *Dichromadora* sp., an epistratum feeder genus, was the most abundant genus. Yet, this genus represented only 4.8% of the number of individuals on the macrophytes, from which 86% were found on *P. gymnospora*, and 32.7% of the number of individuals in sediment.

Deposit feeders were represented by only four species. However, the dominant genus on macrophytes was one of them: *Halalaimus* sp. Those organisms were almost restricted (94%) to *H. musciformis* and *P. gymnospora*.

The MDS analysis did not present a clear difference for the nematode communities among macrophytes or between macrophytes and sediment (Fig. 6). Results of ANOSIM tests confirmed that the structure of nematode assemblages were



Figure 6. MDS ordination (stress = 0,12) from transformed abundances of nematodes on *Sargassum polyceratium* (Δ), *Hypnea musciformis* (∇) *Halodule wrigthii* (**•**), *Padina gymnospora* (\diamond) and sediment (\Box).

not different among macrophytes, but showed significative differences in nematode communities present on macrophytes and those present in sediments (R=0.388, p=0.001). These differences were more evident when each macrophyte and sediment were analyzed separately: *H. wrightii* (R=0.736; p=0.001), *H. musciformis* (R=0.657; p=0.002), *S. polyceratium* (R=0.778; p=0.001) and *P. gymnospora* (R=0.461; p=0.001).

Feeding types	H. wrightii	H. musciformis	S. polyceratium	P. gymnospora	Sediments	Total
1 A	0	0	3	0	0	3
1 B	1	1	0	1	2	5
2 A	1	6	2	3	3	15
2 B	0	0	2	1	1	4

Table 5. Exclusive nematode genera on macrophytes and in sediments at Pedra do Xaréu, PE, Brazil

Discussion

Studying meiofauna and seagrasses, Hall & Bell (1993) found that resources provided by epiphytic algae are probably related to algal morphology. In experiments Lee et al. (1977) saw that the attractiveness of a particular algal species varied presumably depending on the specific animals available in the community for recruitment at the time of the experiments. The animals seem to be selectively recruited to patches of some species of algae but not to others, supporting the hypothesis that selective recruitment of meiofauna can be one of the mechanisms that establishes the spatial heterogeneity so often observed in natural colletions of meiofauna.

Jarvis & Seed (1996) suggested that the linkage between phytal meiofauna and microorganisms might be as strong as that between the sediment meiofaunal distribution and microorganisms patches. Literature suggests attraction of meiobenthic taxa and particularly nematodes to microalgal patches, explaining patchiness and distribution of these animals both in the sediment and in the water column (Warwick, 1977; Admiraal et al., 1983; Trotter & Webster, 1983; Preston & Moore, 1988; Blanchard, 1991; Martin-Smith, 1993; Jarvis & Seed, 1996; Moens et al., 1999; Ullberg & Ólafsson 2003; Ólafsson et al., 2004).

Differences among the fauna of dissimilar algal species has been shown by several authors (e.g., Edgar, 1983; Chemello & Milazzo, 2002), although faunal variation among macrophytes within a single locality is certainly more subtle (Edgar, 1983). These affirmations match with our results, from which we can deduce that, although the dominant genera among the macrophytes are not the same, the composition of nematode assemblages at Xaréu Beach is similar on all phytal substrates.

In this study, Sargassum polyceratium and Padina gymnospora showed larger structural

complexity (as revealed by their highest values of K), when compared to other macrophytes. However, the higher diversities of genera were found on H. musciformis and S. polyceratium. Our results match those of Wieser (1951, 1959) where despite the significant differences found among the structural complexity of the macrophytes, the structure of nematode communities were not different among the four substrates investigated. Studying seagrasses (Halophila ovalis, H. stipulacea, Halodule wrightii, Thalassia hemprichii and Syringodium isoetifolium), De Troch et al. (2001) found no significant effect of morphology on total meiofauna and nematode densities; the overall effect of leaf morphology and related biomass of the seagrass species on meiofauna was indirect. They pointed out that the habitat selected by the seagrass species in view of its role in the succession, in terms of grain size, organic matter and pigments determine the associated meiofauna.

At Pedra do Xaréu, Brazil, the nematode biodiversity was related to the structural features of macrophytes' habitats and the dominant genus varied accordingly. Chromadora was dominant on Sargassum polyceratium; Chromadorina, on Halodule wrighti; and Halalaimus on Hypnea musciformis and Padina gymnospora. The shape of Padina gymnospora with a large surface helps detritus settlement that provides more food sources since generally phytal meiofauna do not feed on the host plant tissues (Gee & Warwick, 1994; Chemello & Milazzo, 2002; De Troch et al., 2003). Particularly increased levels of detritus cause large increases in nematode population (Wieser, 1954; Mukai, 1971; Findlay, 1982; Findlay & Tenore, 1982; Trotter & Webster, 1983; Preston & Moore, 1988; Gourbault & Decraemer, 1993).

The highest densities were observed on *Padina* gymnospora although the highest genera richness was found on *Hypnea musciformis*. Albay & Aykulu (2002) found that the plant architecture

and their position in the littoral region affected the epiphytic algal colonization and their consumption by invertebrates. In our case we observed that nematodes found only on Padina gymnospora and Halodule wrightii did not exhibit well developed sensilla. Perhaps because of the higher amount of detritus present on the algae, these animals do not need well developed sensilla to look for food. Among the nematodes found only on Sargassum polyceratium and Hypnea musciformis, it was possible to find nematodes with well developed sensilla, specially on Sargassum polyceratium that shows a more elaborate morphology with vesicles and curled loaves. This shape allows less deposit of detritus and the animals must be capable of looking for their food. The same was reported by Bouwman et al. (1984) where nematodes from Aufwuchs (nematode associations on macro-

phytes, cyanophytes and decaying materials drifted ashore) do not need to select food, so sensory organs are not essential in this biotope. This agrees with Edgar (1999) when he says that invertebrate communities are primarily structured by food availability.

In this study, the most abundant phytal nematodes genera belong to the Chromadoridae. Chromadorids are frequently associated with marine macrophytes (Trotter & Webster, 1983). This predominance is the same for Plymouth area and Chile (Heip et al., 1985). Chromadoridae is always dominant or well represented on phytal habitats (Moore, 1977; Kito, 1982; Trotter & Webster, 1983; Bouwman et al., 1984; Heip et al., 1985; Wetzel et al., 2002; Atilla et al., 2003). Among the genera of the family, *Chomadora* is the most commonly found on different algae and in different locations. Palmer (1988) reports the presence of Chromadoridae in the water column or at the sediment surface, which may facilitate settlement on the algae. Wieser (1954) used dominance of Chromadoridae as an indicator of the degree of sedimentation in littoral areas.

Oncholaimidae is greatly abundant in nematode associations among algae in Great Britain (Warwick, 1977), but at Xaréu Beach this family was poorly represented. The dominance of Monhysteridae as observed by Wieser (1954), where *Theristus* was the main genus, and by Hopper & Meyers (1967) did not match our results either, since this family was also poorly represented. The dominance of Chromadoridae also reflects the dominance of epigrowth-feeders (2A). Some researchers have suggested that population of epigrowth feeders increases during the summer months. This might be associated with the increase of light and consequently the epiflora, especially diatoms, which are a major food source for these species (Hagerman, 1966; Tietjen & Lee, 1973; Warwick, 1977; Trotter & Webster, 1983, Wetzel et al., 2002). The NE region of Brazil has 'summer' conditions during almost the entire year. Light is always present and temperature is never under 20 °C. This may explain the dominance of this feeding type.

Trotter & Webster (1983) emphasized that some recent studies have considered the abundance and distribution of particular feeding types and the parameters affecting this ecological pattern. On the other hand, Warwick (1981) said that the occurrence of a species in a specific biotope is not only determined by its feeding behavior, but also factors such as reprodutive capacity, tolerance to environmental conditions, competition and predation, which all play roles in the survival strategy of nematode species (Bowman et al., 1984). Based on experimental studies in a soil food web, Mikola and Setälä (1998) found out that species-specific effects were observed more than functional group effects, so the functional group probably does not perform the same or a very similar function but in marine environments similar studies are scarce (Moens & Vincx, 1997; De Mesel et al., 2003). Riera & Hubas (2003) mentioned that previous experimental and field studies have revealed the complexity of feeding strategies of meiobenthos. In spite of plant and shore site choice potentially competing species are frequently encountered on the same plant (Seed & Boaden, 1977).

The nematode densities ranged from 0 to 0.6 ind./ml. Low densities of Nematoda are well recognized in phytal habitats, (Mukai, 1971; Kito, 1975; Hicks, 1977b; Coull & Wells, 1983; Johnson & Scheibling, 1987; Preston & Moore, 1988; Curvêlo & Corbisier, 2000; Oliveira et al., 2000), and perhaps due to this fact, few authors have worked with density data (Kito, 1982; Mukai 1971). Kito (1975) measured densities in square centimeters of seaweed. He found values ranging from 2.05 to 1287.77 ind./10 cm, and 1.40 to 368.90 ind./g, while Mukai (1971), reported

densities ranging from 44.90 to 116.35 ind/seaweed on *Sargassum serratifolium* in the Japan sea. We can deduce nematode phytal densities from our results multiplying those values obtained by known plant volume. Thus, we have 0 to 175 ind./ plant in this work, a similar range to those values reported by Mukai (1971).

The presence of a different nematode community associated to the macrophytes compared to the interstitial community confirmed one of the initial hypotheses of this work.

While 22 genera out of 38 were exclusive for phytal, in the sediment more than 50% were exclusive for interstitial habitat. Hopper & Meyers (1967) found that nematodes living on seagrass beds were not really epiphytic due to the large amount of detritus derived from the plants. These authors said that these habitats contain a typical fauna, including Metoncholaimus, Daptonema, Spirinia and Gomphionema the dominant genera. However, the epigrowth feeders Dichromadora, Nudora, Paracyatholaimus, Spirobolbolaimus, Desmodora and Epacanthion were the most abundant interstitial genera in our results. Nevertheless, the dominant feeding type was similar in sediments and on plants. Several authors affirmed that the presence of macrophytes increase food availability, habitat complexity and shelter for the fauna. It could explain the similar trophic pattern found between the two communities, phytal and interstitial.

Moore (1971) pointed out a characteristic phytal genera association: *Anticoma, Thoracostoma, Phanoderma, Enoplus, Oncholaimus, Paracanthonchus, Chromadora* and *Euchromadora* and most of these were found at Pedra do Xaréu, Brazil.

Epigrowth feeders/herbivores dominated on all substrates at Xaréu Beach. These results are similar to those obtained by Warwick (1977), Moore (1971) and Kito (1982), who described epistratum feeders' dominance on phytal environments. The presence of predators/omnivores on *H. musciformis*, an algae generally found in tide pools and sheltered habitats, might be the consequence of the seaweed structure, which is fine, occurs in tufts, and does not offer physical protection to the associated communities. Moore (1971) pointed out that some trophic groups may be related to the habitat structure and/or environmental condition: bigger individuals, predators, are better able to exploit the macrophytes habitats, which are exposed to wave

action, while the smaller individuals, epistrate feeders, usually dominate sheltered areas. Wieser (1959), studying the nematode fauna associated to macroalgae holdfasts in Chile, has found in an exposed beach, a co-dominance between epistratum feeders and predators/omnivores genera. The dominance of epigrowth feeders in this study suggests that the food webs in these shallow systems (phytal and sediment) are based on detritus and benthic primary producers (Moore, 1971; Warwick, 1977; Findlay, 1982; Findlay & Tenore, 1982; Coull & Wells, 1983; Edgar, 1983; Trotter & Webster, 1983, Gee & Warwick, 1994; Wetzel et al., 2002).

Bouwman et al., (1984) concluded that the nematode species are adequately adapted to interstitial biotopes not only in their morphology but also in their behavior, which was the reason they found quite different species on phytal habitat.

Conclusions

The phytal nematofauna from Xaréu Beach (Pernambuco, Brazil) was not different among the macrophytes, but the dominant genera associated to each species were different, suggesting that the substrate structural complexity may influence each genus' biology, but not the assemblage structure. The major trophic groups are epigrowth feeders, suggesting the existence of a benthic food web based on detritus and benthic primary producers.

Acknowledgements

The authors acknowledge Dr Verônica da Fonsêca-Genevois for her guidance on the theses which originated this article; Alessandra Botelho who helped with genera identification; Dr Tom Moens for interesting discussions and helpful comments on an earlier version of this manuscript and the anonymous referees for their useful suggestions.

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