

LITERATURE REVIEW

Free-living nematodes of Brazilian oceanic islands: revealing the richness in the most isolated marine habitats of Brazil

Virag Venekey^{a*} and Thuareag Monteiro Trindade dos Santos^a

^aGrupo de Estudos de Nematoda Aquáticos, Laboratório de Pesquisa em Monitoramento Ambiental Marinho, Universidade Federal do Pará (UFPA), Belém (PA), Brazil

*venekey@ufpa.br

HIGHLIGHTS

- A complete taxonomical list of free-living marine nematodes found in Brazilian Oceanic Islands with 9 orders, 39 families, and 143 genera.
- Higher nematode richness recorded in all Brazilian Oceanic Islands studied, compared to coastal environments.
- Lower nematode densities found in Trindade Island than in Rocas Atoll and Saint Peter and Saint Paul Rocks.
- Common dominance of epistrate feeders, predators/omnivores, or different body shapes (not vermiform) in all islands studied due to hydrodynamic processes.

ABSTRACT: The taxonomic richness of marine Nematoda in Brazilian oceanic islands and similarities among them are analyzed. Results are from surveys conducted in Saint Peter and Saint Paul Archipelago, Rocas Atoll, and Trindade Island. A complete faunal list is presented, containing 9 orders, 39 families, and 143 genera. Chromadoridae and Desmodoridae were the richest families with 21 and 13 genera, respectively. Among the genera recorded, *Pseudonchus* and *Paradraconema* had not yet been recorded in Brazilian coastal environments. So far results have pointed out high richness and low similarity in composition among the studied islands. However, further studies are required, especially more systematic samplings, to help understand and to confirm the patterns found. Furthermore, to allow for complete biogeographical studies, locations not yet sampled, e.g. Fernando de Noronha and Abrolhos, should also be studied.

Keywords: marine nematodes, beaches, taxonomy.

Cite as

Venekey V, Santos TMT. Free-living Nematodes of Brazilian Oceanic Islands: Revealing the Richness in the most isolated marine habitats of Brazil. *Nematoda*. 2017;4: e122016. <http://dx.doi.org/10.4322/nematoda.01216>.

Received: Dec. 17, 2016 **Accepted:** Mar. 29, 2017

INTRODUCTION

Phylum Nematoda has four to five thousand free-living marine species^[1] but many more remain to be discovered. They are mostly small and inconspicuous yet the most abundant metazoans in marine (littoral, estuarine, coastal, and oceanic) sediments, often numbering millions per m²^[2]. In marine environments, nematodes can be found from the high-water mark into the deepest oceanic trenches^[3].

Traditionally, nematology has its strength in agricultural applications (study of plant-parasitic species) because of its economic implications. The biodiversity/ecological side of nematode taxonomy, which often deals with free-living forms like marine species, remains in need of research input^[4]. This fact is mostly due to difficulties in identifying marine nematodes. Taxonomic literature lacked

useful pictorial keys until recently, and the first ones were launched only in the end of the 20th century, such as the “Illustrated Guide” by Tarjan^[5] and the “Free-Living Marine Nematodes”, divided into three volumes (“Enoplids” by Platt & Warwick^[6], “Chromadorids” by Platt & Warwick^[7], and “Monhysterids” by Warwick et al.^[8]). Even more recently, Internet websites have been launched with original descriptions and data on marine nematode species, e.g. the “Nemys” database^[9] and WoRMS (World Register of Marine Species)^[10], making it easier to search for literature and information.

Over the last decades, studies have increased in regions where few studies were conducted before, with many new records and species descriptions. South America is one of the continents where new studies have increasingly appeared, including Brazil, where a “taxonomic bloom” has been happening according to Venekey et al.^[11] In their review, Venekey et al.^[11] pointed out that until 2008, 11 orders, 59 families, 294 genera, and 231 species of free-living marine nematodes were recorded in Brazilian coastal ecosystems. However, according to the same authors, most of the biodiversity data regarding Brazilian marine nematodes is usually concentrated in easy access coastal environments, such as beaches and estuaries.

Oceanic islands are productive marine ecosystems that often support high concentrations of species, high endemism rate, and high dispersal abilities^[12, 13, 14]. The taxonomic richness and ecological data (i.e. densities, dominant families) of marine Nematoda in Brazilian oceanic islands and similarities among them are analyzed and discussed in this paper. Results are from surveys conducted in Saint Peter and Saint Paul Archipelago, Rocas Atoll, and Trindade Island.

Study areas

Brazil has a long coastline along which several islands can be found, and five major archipelagos stand out: Saint Peter and Saint Paul, Rocas Atoll, Fernando de Noronha, Abrolhos, and Trindade-Martim Vaz (Figure 1). Except for Fernando de Noronha and Abrolhos, the other archipelagos are military and research areas, without authorization for tourist activities. So far, free-living marine nematodes have been sampled in Rocas Atoll, Saint Peter and Saint Paul Archipelago, and Trindade Island. Their general characteristics are briefly described here. For more details and studies in Brazilian oceanic islands, see the books edited by Mohr et al.^[16] and Viana et al.^[17].

Rocas Atoll: It is the only atoll in the South Atlantic. It is situated 257 km E-NE of Natal and 148 km west of Fernando de Noronha (3°52'S, 33°49'W). The atoll is an ellipsoid reef covering approximately 5.5 km² of area, built on top of a sea mount that rises steeply from depths of 1000 m^[18]. The circular reef,



Figure 1. Map showing the location of Brazilian Oceanic Islands (Adapted from Almeida^[15]).

which is exposed at low tide, encloses a shallow lagoon (<1m at low tide). There are a number of pools distributed on the reef top, varying in form, from shallow pools with sandy bottoms to as deep as 15 m, with rocky bottoms and sand patches. Average water temperature fluctuates around 27 °C and water visibility ranges between 25 and 40 m^[19]. The region is under the influence of the South Equatorial Current. Rocas Atoll was the first site designated as a Brazilian Marine Protected Area, established in 1979. The “Brazilian Institute of Environment and Natural Renewable Resources” (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, IBAMA) maintains a permanent camp facility for scientific researchers in one of the Atoll’s islands.

Saint Peter and Saint Paul: This archipelago is a remote group of five bigger and ten smaller entirely volcanic islands lying just north of the equator on the remnants of a volcanic cone of the Mid-Atlantic ridge, approximately 500 km northeast of Fernando de Noronha and 960 km off the Brazilian coast (0°56'N, 29°22'W)^[18]. The islands do not have beaches. The major island has only 0.5 ha in area and rises 18m above sea level. Its substrate consists of rocks with algae and some patches of sand. In Belmonte Island, there are many tidal pools that are flushed with fresh seawater from the tide^[20]. Between Belmonte and Challenge islands there is a sheltered cove with unstable substrate at the bottom, comprised mainly by coarse sand. The area of shallow water marine environment (<100 m deep) surrounding Saint Peter and Saint Paul is no more than 0.5km². The islands are influenced by both South Equatorial Current and Atlantic Equatorial Undercurrent. The “Secretariat of the Interministerial Commission for the Sea Resources” (SECIRM) has maintained a scientific station in Belmonte Island since 1998.

Trindade: This island is on the eastern end of the Vitória-Trindade submarine Ridge, 1,140 km off the coast of Espírito Santo state, southeastern Brazil (20° 30' S, 29° 20' W). It has an area of 13.5 km² and is almost totally comprised of volcanic and subvolcanic rocks formed between the end of the Pliocene and the Holocene^[21]. Its coastline consists of reefs, narrow beaches, and narrow dunes. The littoral zone is comprised of approximately 2.5 km of beaches and 14 km of narrow (<1 km), steep rocky shores^[22]. Sandy substrates are characterized by volcanic sands and dominated by the presence of coarse and medium sands. The whole extension of the Vitória-Trindade Ridge is under the influence of the southward flow of the Brazil Current^[23], characterized by warm (>27°C SST), saline (37 psu), and oligotrophic waters^[24]. A tropical oceanic climate prevails in the region, ameliorated by eastern and southern trade winds, with mean water temperature of 27 °C. Air temperature is warmer in February and colder in August^[25]. The only human inhabitants at Trindade are the Brazilian Navy personnel, which have maintained a base on the island and have controlled its access since 1957.

Data collection and analysis

The data presented here were collected from papers available until November 2016, from a PhD thesis^[26], a M.Sc thesis^[27], graduation works^[28, 29], Book Chapters^[30, 31], and other manuscripts^[32, 33, 34, 35, 36]. Abstracts published at scientific meetings were not considered.

A uniform taxonomic list and table were built with nematode genus and species records, as well as other information such as substrate characteristics and densities. The genus and species names were reviewed taking into account synonyms, nomenclature changes, and new combinations available in specific literature and websites such as Nemys^[9] and WoRMS^[10]. The taxonomic classification of De Ley & Blaxter^[37] was followed.

Literature available on marine nematodes in Brazilian Oceanic Islands

The study of free-living marine nematodes in Brazilian oceanic islands started in 1999 at Rocas Atoll. Later, Saint Peter and Saint Paul Archipelago and Trindade Island were also studied. Fernando de Noronha and Abrolhos have not been studied yet, although as far as we know there was an attempt of sampling in Abrolhos but the data from those samples were lost (Fonseca-Genevois, personal communication). General information on habitat and free-living marine nematode characteristics in Brazilian oceanic islands are shown in Table 1.

The studies by Netto et al.^[32, 33, 34, 35] are results of the PhD thesis by Netto^[26] but only the latter shows a complete taxonomic list. Therefore, Table 1 shows general data extracted from the manuscripts and the taxonomic list of Brazilian oceanic islands is comprised from the PhD thesis. The book chapter by Miranda-Junior et al.^[30] shows results from the graduation paper by Miranda-Junior^[28], mostly a colonization experiment with artificial plants, but many findings of nematodes from sediments remained only in the graduation paper. We therefore show both studies in Table 1 using the latter to

Table 1. General information about habitat and free-living marine nematodes characteristics in Brazilian oceanic islands. (-): information not available. (s): number of species.

Reference	Locality	Substrate composition	Sediment granulometry	Sampling depth (m)	Density range (ind./10cm ²)	Number of Families	Number of gen./sp.	Dominant families	Dominant genera
Netto et al. ^[32]	Rocas Atoll	Carbonate	Fine to very coarse sand	5.2-24.1	-88.56-398.52	-	89(s)	Epsilonematidae	<i>Epsilonema</i> <i>Perepsilonema</i>
Netto et al. ^[33]	Rocas Atoll	Carbonate	Medium to coarse sand	intertidal	63-667	-	79(s)	Oncholaimidae Epsilonematidae Desmodoridae	<i>Metoncholaimus</i> <i>Epsilonema</i> <i>Chromaspirinia</i>
Netto et al. ^[34]	Rocas Atoll	Carbonate	Fine to very coarse sand	0-24.1	134.1-538.2	-	109(s)	Oncholaimidae Epsilonematidae Desmodroidae	<i>Metoncholaimus</i> <i>Epsilonema</i> <i>Chromaspirinia</i>
Netto et al. ^[35]	Rocas Atoll	Carbonate	Medium to coarse sand	2.15-2.70	53-2592	-	61(s)	Desmodoridae Oncholaimidae Ethmolaimidae Linhomoeidae	<i>Chromaspirinia</i> <i>Metoncholaimus</i> <i>Gomphonema</i> <i>Paralinhomoeus</i>
Miranda-Junior ^[26]	Saint Peter and Saint Paul	Volcanic	Coarse sand	0-1m	0.01-76.3*	13	24	Cyatholaimidae	<i>Marylynnia</i>
Miranda-Junior et al. ^[30]	Saint Peter and Saint Paul	Artificial plants	-	0-1m	1.1-56.4*	15	29	Chromadoridae	<i>Ptycholaimellus</i>
Venekey et al. ^[31]	Saint Peter and Saint Paul	Volcanic	Coarse sand	0-8m	5-19.01*	14	33	Cyatholaimidae Chromadoridae Oncholaimidae	<i>Paracyatholaimus</i> <i>Viscosia</i>
Nascimento ^[29]	Trindade	Volcanic	Fine to coarse sand	intertidal	1.53-6.37	10	22/23(s)	Xyalidae Cyatholaimidae	<i>Theristus</i> <i>Paracanthonchus</i>
Santos & Venekey ^[36]	Trindade	Volcanic	Fine to coarse sand	intertidal	6.2-33.7	12	27/29(s)	Xyalidae Oncholaimidae	<i>Theristus</i> <i>Viscosia</i>

*ind./mL

comprise the taxonomic list and data on nematodes from sediments and the former for the colonization experiment. The study published by Santos & Venekeyⁱ resulted from the M.Sc. thesis by Santos^[27]. Both studies show all relevant ecological information and also the complete taxonomic list; for this reason, only the first one is shown in Table 1. Finally, both taxonomic and ecological information have been extracted from the graduation paper by Nascimento^[29], as it has not been published yet.

Among the islands, Rocas Atoll was the most thoroughly studied, with extensive samplings covering approximately 50 stations, from intertidal to depths of 24 m, including tidal pools (for the location of stations see Netto et al.^[32, 33, 34, 35]). Saint Peter and Saint Paul was sampled three times, in September 2000, March 2004, and December 2004, covering tidal pools of Belmonte Island and depths down to 8 m in the cove between Belmonte and Challenge Islands^[30, 31]. In addition, a colonization experiment with artificial plants was also performed on Belmonte Island in one of the sampling expeditions to Saint Peter and Saint Paul^[30]. Trindade Island has been sampled twice, in August and December 2014, with intertidal stations at five sandy beaches (Cabritos, Parcel, Portugueses, Príncipe, and Tartarugas)^[29].

Abundance and richness of marine nematodes in Brazilian Oceanic Islands

Regarding nematode abundances, studies should be compared with caution. Samplings in Saint Peter and Saint Paul were performed manually, without a sampling corer, and therefore, densities were represented in volume (ind./mL), not in area (ind./10 cm²), the usual unit for marine nematodes. According to Miranda-Junior^[28], the difficulty of inserting a corer into the substrate of tidal pools in Saint Peter and Saint Paul is due to sediment characteristics (probably very coarse sand). Sampling in Rocas Atoll was performed using a corer of 2.5 cm diameter and 10 cm length and those in Trindade were performed using a corer of 3 cm diameter and 10 cm length. In an attempt to better compare data, we converted the densities found in Rocas Atoll and Trindade to individuals per volume (mL). For that purpose, we first re-calculated densities from ind./10cm² for the total area of corers ($A = \pi \cdot r^2$; 4.91 cm² in Rocas Atoll and 7.06 cm² in Trindade) and subsequently converted them into individuals per volume considering corer volumes ($V = \pi \cdot r^2 \cdot h$; 39.25 mL in Rocas Atoll and 47.1 mL in Trindade Island). As a result, we found variations of 0.66 to 32.42 ind./mL in Rocas Atoll and 0.02 to 0.50 ind./mL in Trindade. Comparing densities which were found after these new calculations, we observed that nematode densities in Trindade sediments are much lower than those in Rocas Atoll and Saint Peter and Saint Paul (0.01-76.3 ind./mL). Densities in the two latter overlap themselves, they are more similar.

Considering richness of nematode taxa until 2016, 9 orders, 39 families, and 143 genera had been recorded in Brazilian oceanic islands. A complete faunal list is presented in the Appendix A. Chromadoridae and Desmodoridae were the richest families with 21 and 13 genera, respectively. Among the genera recorded, so far *Pseudonchus* and *Paradraconema* have not been recorded in Brazilian coastal environments. Only the genus *Prorhynchonema* (in this case, from Trindade Island) has been definitely identified to the species level (*P. gourbaultae*). Other identifications in Trindade were performed for putative species. There was also an attempt to identify to the species level in Rocas Atoll determining three species to the affinity level: *Anticoma* aff. *eberthi*, *Chromadora* aff. *nudicapitata*, and *Metachromadora* aff. *remani*. Other identifications in Rocas Atoll, similar to Trindade, were also in putative species. As for Saint Peter and Saint Paul, identifications were performed only to the genus level.

There are some likely reasons for the lack of identifications to the species level in Brazilian oceanic islands. Identification to the genus level is a global pattern in marine nematode studies. In Brazil, the situation is not different. Considering the volume of studies, only very recently and only few works have attempted to identify specimens to the species level^[38, 39, 40] and none of them identified all recorded genera to the species level. The demand for considerable experience and well-equipped laboratories to allow for a correct identification to the species level^[41] has rendered marine nematode taxonomy quite stagnant. This is specially true to developing countries like Brazil. Moreover, identification to the species level is very time-consuming and all studies in Brazilian oceanic islands have had an ecological purpose, where genera offer satisfactory and reliable answers for different questions and hypothesis tested^[42]. Furthermore, Santos & Venekey^[36] stated that identification to the species level in Trindade was not possible due to the very low number of individuals or to the fact that few of them were in perfect conditions to be measured.

Considering richness in each island, Rocas Atoll was the richest with 103 genera, followed by Saint Peter and Saint Paul with 58 genera, and Trindade with only 36. The genera *Eurystomina*, *Metachromadora*, *Metacyatholaimus*, *Metalinhomoeus*, *Paracanthochus*, *Paralongicyatholaimus*, *Rhynchonema*, *Sabatieria*, *Spilophorella*, and *Theristus* were the only ones common to the three islands. All islands showed exclusive genera. Trindade has 14 exclusive genera, Saint Peter and Saint Paul has 21 exclusive genera, and Rocas Atoll showed the highest number of exclusive genera, 63.

The higher genera richness and number of exclusive genera found in Rocas Atoll was expected as this location was the most extensively sampled, including at different depths (0 – 24 m), and different habitats (subtidal, intertidal, and tidal pools). The few genera found in common among the three locations are probably also due to the lower number of samples and habitats studied in Saint Peter and Saint Paul and Trindade. Nevertheless, considering the few sampling expeditions to each of these islands, richness can be considered high.

The relationship between diversity estimates and sampling effort is well known and documented in literature on marine nematodes^[43]. Venekey et al.^[11], in their review of biodiversity of marine nematodes in Brazil, considered the high richness found in oceanic islands surprising. The authors mentioned that a high sampling effort is generally employed in locations with difficult access. At the time of their review, Trindade had not yet been studied and, even then, the richness in Brazilian islands was considered high by the authors (29 families and 110 genera at that time, with no studies in Trindade).

Genera composition of marine free-living nematodes in Brazilian oceanic islands, based on the genera common to the three islands/archipelagos, has shown few similarities so far. However, if we observe the information presented in Table 1, one fact stands out: the dominant families and genera. In all islands the dominant genera/families are mostly epistrate feeders (type 2A according to Wieser^[44]), such as Cyatholaimidae and Chromadoridae, or predators/omnivores (type 2B according to Wieser^[44]), such as Oncholaimidae and Ethmolaimidae. In addition, when neither 2A nor 2B types are dominant, families with different body shapes (Draconematidae and Epsilonematidae), not vermiform, are very abundant.

All studies have reported the intense hydrodynamic movement in the islands. Netto et al.^[32, 34] observed the difference in hydrodynamics between inner and outer areas of Rocas Atoll and considered it as one of the main causes for sediment and faunal characteristics. Concerning Saint Peter and Saint Paul and Trindade, Miranda-Junior et al.^[30] and Santos & Venekey^[36], respectively, also suggested the influence of hydrodynamic processes on nematodes. Sediments found in all islands, both carbonate and volcanic, and their size (medium to coarse sand in most cases) are possible indications of strong currents and wave stress. In this kind of environment, nematodes are frequently characterized by low density and a relatively high diversity^[2]. Also in these habitats, Epsilonematidae and Draconematidae can be dominant as genera from these families are well adapted to substrate instability^[44] due to differential body morphologies (not the classical vermiform shape, presence of ambulatory setae, and sediment-trapping capacity). Furthermore, other studies^[46, 47, 48, 49] have reported dominance of epistrate feeders or predators/omnivores as numerically dominant in coarse and medium sands of reef, carbonate, and volcanic habitats.

Studies on nematofauna in oceanic islands are scarce due to logistic difficulties. For this reason, most studies concentrate high sampling efforts in few occasions. This is probably the reason why only Santos & Venekey^[36] have attempted to study seasonal patterns of marine nematodes in Brazilian Oceanic Islands so far. This is possibly also the cause for the lack of studies in Fernando de Noronha and Abrolhos Islands. Although these islands seem to be easier to access, even open to tourist visits, programs of Brazilian funding agencies do not contemplate/prioritize these islands. As a direct consequence, a complete biogeographic study about connectivity between Brazilian islands is not yet possible for marine nematodes.

CONCLUSIONS

The results found so far for free-living marine nematodes in Brazilian oceanic islands indicate high richness and few similarities in composition among the sites. However, further studies are required with more systematic samplings to fully understand and confirm these patterns. In addition, locations which have not yet been studied, e.g. Fernando de Noronha and Abrolhos, should be sampled to allow biogeographical studies. On the other hand, an effort must be employed towards identification at species level to make it possible to detect new and endemic species.

ACKNOWLEDGEMENTS

The authors are very grateful to the Brazilian Navy (Marinha do Brasil), IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis) and SECIRM (Comissão Interministerial para os Recursos do Mar) for all logistical support to study different aspects of Brazilian oceanic islands. The authors are also very grateful to CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico),

funding agency of research projects within the program “Arquipelagos e Ilhas Oceânicas” (Arquipelagos and Oceanic Islands). The projects 48.0033/2004-8 and 405418/2012-4 funded by CNPq allowed the authors to visit and study Saint Peter and Saint Paul Archipelago and Trindade Island, respectively. A special thanks to Dr. Claudia Dolinski is in place for suggesting and encouraging the writing of this manuscript and to Dr. Sergio Netto for providing the taxonomic list of nematodes from Rocas Atoll.

REFERENCES

- Lorenzen S. 1994. The phylogenetic systematics of free-living nematodes. The Ray Society, London, 383 pp.
- Heip C, Vincx M, Vranken G. 1985. The ecology of marine nematodes. *Oceanography and Marine Biology: An Annual Review*, 23: 399-489.
- Giere O. 2009. *Meiobenthology: the microscopic fauna in aquatic sediments*. Springer-Verlag, Berlin, 527 pp.
- Abebe E, Mekete T, Thomas WK. 2011. A critique of current methods in nematode taxonomy. *African Journal of Biotechnology*, 10: 312-323.
- Tarjan AC. 1980. *An illustrated guide to the marine nematodes*. Institute of Food and Agricultural Sciences, University of Florida, Florida, 135 pp.
- Platt HM, Warwick RM. 1983. Free-living Marine Nematodes. Part I. British Enoplids. In: Kermack DM, Barnes RSK (eds.). *Cambridge University Press, Cambridge*, 307 pp. *Synopses of the British Fauna (New Series)*, 28.
- Platt HM, Warwick RM. 1988. Free-living Marine Nematodes. Part II. British Chromadorids. In: Kermack DM, Barnes RSK (eds.). *Brill, Leiden*, 502 pp. *Synopses of the British Fauna (New Series)*, 38.
- Warwick RM, Platt HM, Sommerfield PJ. 1998. Free-living Marine Nematodes. Part III. British Monhysterids. In: Barnes RSK, Crothers JH (eds.). *Field Studies Council, Shrewsbury*, 296 pp. *Synopses of the British Fauna (New Series)*, 53.
- Guilini K, Bezerra TN, Eisendle-Flöckner U, Deprez T, Fonseca G, Holovachov O, Leduc D, Miljutin D, Moens T, Sharma J, Smol N, Tchesunov A, Mokievsky V, Vanaverbeke J, Vanreusel A, Venekey V, Vincx M. 2016. NeMys: World Database of Free-Living Marine Nematodes [on line]. Accessed on December 12, 2016. Available from: www.nemys.ugent.be
- WoRMS Editorial Board. 2016. World register of marine species [on line]. Accessed on December 12, 2016. Available from: <http://www.marinespecies.org>
- Venekey V, Fonseca-Genevois VG, Santos PJP. 2010. Biodiversity of free-living marine Nematodes on the coast of Brazil: a review. *Zootaxa*, 2568: 39-66.
- Allen GR. 2008. Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18: 541-556. <http://dx.doi.org/10.1002/aqc.880>.
- Clark MR, Rowden AA, Schlacher T, Williams A, Consalvey M, Stocks KI, Rogers AD, O'Hara TD, White M, Shank TM, Hall-Spencer JM. 2010. The ecology of seamounts: structure, function, and human impacts. *Annual Review of Marine Science*, 2: 253-278. PMID:21141665. <http://dx.doi.org/10.1146/annurev-marine-120308-081109>.
- Rowden AA, Dower JF, Schlacher TA, Consalvey M, Clark MR. 2010. Paradigms in seamount ecology: fact, fiction and future. *Marine Ecology*, 31: 226-241. <http://dx.doi.org/10.1111/j.1439-0485.2010.00400.x>.
- Almeida FFM. 2006. Ilhas oceânicas brasileiras e suas relações com a tectônica Atlântica. *Terrae Didática*, 2: 3-18.
- Mohr LV, Castro JWA, Costa PMS, Alves RJV. 2009. *Ilhas oceânicas brasileiras: da pesquisa ao manejo*. Ministério do Meio Ambiente, Brasília, 501 pp. vol. II.
- Viana DL, Hazin FHV, Souza MAC. 2009. *O Arquipélago de São Pedro e São Paulo: 10 anos de Estação Científica*. Secretaria da Comissão Interministerial para os Recursos do Mar. Brasília, 348 pp.
- Mabesoone JM, Coutinho PN. 1970. Littoral and shallow marine geology of northern and northeastern Brazil. *Trabalhos Oceanográficos da UFPE*, 12: 1-214.
- Machado LA, Leite LG, Goulart RM, Guedes C, Tavares FM. 2002. Pathogenicity of *Heterorhabditis* spp. and *Steinernema* spp. against the citrus root weevil, *Naupactus* sp. In: *Society for Invertebrate Pathology – SIP. Program and Abstracts of the 35th Annual Meeting of the Society for Invertebrate Pathology*, Foz do Iguaçu, Brazil, 55 pp.
- Edwards A, Lubbock R. 1983. The ecology of Saint Paul's Rocks (Equatorial Atlantic). *Journal of Zoology*, 200: 51-69. <http://dx.doi.org/10.1111/j.1469-7998.1983.tb06108.x>.
- Almeida FFM. 2002. Ilha da Trindade: registro de vulcanismo Cenozóico no Atlântico Sul. In: Schobbenhaus C. *Sítios geológicos e paleontológicos do Brasil*. DNPM, Brasília, pp. 369-377.
- Pereira-Filho GH, Amado-Filho GM, Guimarães SMPB, Moura RL, Sumida PYG, Abrantes DP, Bahia RG, Güth AZ, Jorge RR, Francini RBF Fo. 2011. Reef fish and benthic assemblages of the Trindade and Martin Vaz island group, Southwestern Atlantic. *Brazilian Journal of Oceanography*, 59: 201-212. <http://dx.doi.org/10.1590/S1679-87592011000300001>.
- Miranda LB, Castro BM Fo. 1982. Geostrophic flow conditions of the Brazil Current at 19° S. *Ciência Interamericana*, 22: 44-48.
- Silveira IC, Schmidt ACK, Campos EJD, Godoi SS, Ikeda IA. 2000. Corrente do Brasil ao largo da costa leste brasileira. *Revista Brasileira de Oceanografia*, 48: 171-183. <http://dx.doi.org/10.1590/S1413-7739200000200008>.
- Alves RJV. 1998. *Ilha da Trindade & Arquipélago Martin Vaz: um ensaio geobotânico*. Rio de Janeiro, Serviço de Documentação da Marinha, 144 pp.
- Netto SA. 1999. *Meiofauna and macrofauna communities of Rocas Atoll* [thesis]. University of Plymouth, Plymouth, England, 117 pp.
- Santos TMT. 2016. *Distribuição espaço-temporal da meiofauna em praias arenosas da Ilha de Trindade com especial referência aos Nematoda livres* [dissertation]. Universidade Federal do Pará, Belém, Brazil, 69 pp.

28. Miranda-Junior GV. 2006. Meiofauna do Arquipélago de São Pedro e São Paulo (Nordeste, Brasil), com ênfase aos Nematoda [graduation work]. Universidade Federal de Pernambuco, Recife, Brazil, 60 pp.
29. Nascimento WC. 2016. Composição e distribuição espacial e vertical da meiofauna, com ênfase na nematofauna, em praias arenosas da Ilha de Trindade (Brasil) [graduation work]. Universidade Federal do Pará, Belém, 49 pp.
30. Miranda-Junior GV, Venekey V, Esteves AM, Fonseca Genevois V. 2009. Colonização da meiofauna em substratos artificiais: um exemplo de experimento, enfatizando os Nematoda, no arquipélago de São Pedro e São Paulo (Nordeste, Brasil). In: Mohr LV, Castro JWA, Costa PMS, Alves RJV (eds.). Ilhas Oceânicas Brasileiras: da Pesquisa Ao Manejo. Ministério do Meio Ambiente, Brasília, pp. 369-386. vol. II.
31. Venekey V, Esteves A, Fonseca-Genevois V. 2009. Distribuição espacial da meiofauna no arquipélago de São Pedro e São Paulo, com especial referência aos Nematoda livres. In: Mohr LV, Castro JWA, Costa PMS, Alves RJV (eds.), Ilhas Oceânicas Brasileiras: da pesquisa ao manejo. Ministério do Meio Ambiente, Brasília, pp. 369-386. vol. II.
32. Netto SA, Attrill MJ, Warwick RM. 1999. Sublitoral meiofauna and macrofauna of Rocas Atoll (NE Brazil): indirect evidence of a topographically controlled front. *Marine Ecology Progress Series*, 179: 175-186. <http://dx.doi.org/10.3354/meps179175>.
33. Netto SA, Attrill MJ, Warwick RM. 1999. The effect of a natural water-movement related disturbance on the structure of meiofauna and macrofauna communities in the intertidal sand flat of Rocas Atoll (NE Brazil). *Journal of Sea Research*, 42: 291-302. [http://dx.doi.org/10.1016/S1385-1101\(99\)00033-7](http://dx.doi.org/10.1016/S1385-1101(99)00033-7).
34. Netto SA, Warwick RM, Attrill MJ. 1999. Meiobenthic and macrobenthic community structure in carbonate sediments of Rocas Atoll (Northeast, Brazil). *Estuarine, Coastal and Shelf Science*, 48: 39-50. <http://dx.doi.org/10.1006/ecss.1998.0398>.
35. Netto SA, Attrill MJ, Warwick RM. 2003. The relationship between benthic fauna, carbonate sediments and reef morphology in reef-flat tidal pools of Rocas Atoll (North-East Brazil). *Journal of the Marine Biological Association of the United Kingdom*, 83: 425-432. <http://dx.doi.org/10.1017/S0025315403007288h>.
36. Santos TMT, Venekey V. Meiofauna and free-living nematodes in volcanic sands of a remote South Atlantic, Oceanic Island (Trindade, Brazil). *Journal of the Biological Association of the United Kingdom*, in press.
37. De Ley P, Blaxter ML. 2004. A new system for Nematoda: combining morphological characters with molecular trees, and translating clades into ranks and taxa. *Nematology Monographs and Perspectives*, 2: 633-653.
38. Brustolin MC, Thomas MC, Lana PC. 2013. A functional and morphological approach to evaluate the vertical migration of estuarine intertidal nematodes during a tidal cycle. *Helgoland Marine Research*, 67: 83-96. <http://dx.doi.org/10.1007/s10152-012-0306-3>.
39. Venekey V, Santos PJP, Fonseca-Genevois VG. 2014. Effect of environmental factors on intertidal Nematoda in a tropical sandy beach (Tamandaré Bay, Pernambuco, Brasil). *Journal of Coastal Research*, 30: 785-794. <http://dx.doi.org/10.2112/JCOASTRES-D-12-00041.1>.
40. Venekey V, Santos PJP, Fonseca-Genevois VG. 2014. The influence of tidal and rainfall cycles on intertidal nematodes: a case study in a tropical sandy beach. *Brazilian Journal of Oceanography*, 62: 247-256. <http://dx.doi.org/10.1590/s1679-87592014061706204>.
41. Coomans A. 2001. Present status and future of nematode systematics. *Nematology*, 4: 573-582. <http://dx.doi.org/10.1163/15685410260438836>.
42. Warwick RM. 1988. The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. *Marine Pollution Bulletin*, 19: 259-268. [http://dx.doi.org/10.1016/0025-326X\(88\)90596-6](http://dx.doi.org/10.1016/0025-326X(88)90596-6).
43. Boucher G, Lambshead PJD. 1995. Ecological biodiversity of marine nematodes in samples from temperate, tropical and deep-sea regions. *Conservation Biology*, 9: 1594-1604. <http://dx.doi.org/10.1046/j.1523-1739.1995.09061594.x>.
44. Wieser W. 1953. Die Beziehung zwischen Mundhoehlstalt, Ernahrungsweise und Vorkommen bei frelebenden marinen Nematoden. Eine oekologisch: morphologische studie. *Arkiv för Zoologi*, II: 439-484.
45. Raes M, Decraemer W, Vanreusel A. 2008. Walking with worms: coral-associated epifaunal nematodes. *Journal of Biogeography*, 35: 2207-2222. <http://dx.doi.org/10.1111/j.1365-2699.2008.01945.x>.
46. Alongi DM. 1986. Population structure and trophic composition of the free-living nematodes inhabiting carbonate sands of Davis Reefs, Great Barrier Reef, Australia. *Australian Journal of Marine and Freshwater Research*, 37: 609-619. <http://dx.doi.org/10.1071/MF9860609>.
47. Jesús-Navarrete A. 2007. Littoral free living Nematode fauna of Socorro Island, Colima, Mexico. *Hidrobiológica*, 17: 61-66.
48. Riera R, Núñez J, Brito MC, Tuya F. 2011. Temporal variability of a subtropical intertidal meiofaunal assemblage: contrasting effects at the species and assemblage-level, Vie et milieu. *Life and Environment*, 61: 129-137.
49. Semprucci F, Colantoni P, Baldelli G, Sbrocca C, Rocchi M, Balsamo M. 2013. Meiofauna associated with coral sediments in the Maldivian subtidal habitats (Indian Ocean). *Marine Biodiversity*, 43: 189-198. <http://dx.doi.org/10.1007/s12526-013-0146-7>.

Appendix A. List of nematode genera and species recorded in Brazilian oceanic islands. In the list are identified the oceanic islands where the taxa were found (R – Rocas Atoll; S – Saint Peter and Saint Paul; T – Trindade Island).

PHYLUM NEMATODA
CLASS ENOPLEA
SUBCLASS ENOPLIA
ORDER ENOPLIDA
Suborder Enoplina
Superfamily Enoploidea

Family Enoplidae

Enoplus Dujardin, 1845 (R)

Fenestrolaimus Filipjev, 1927 (R)

Family Thoracostomopsidae

Enoplolaimus De Man, 1893 (R)

Epacanthion Wieser, 1953 (R) (S)

Mesacanthion Filipjev, 1927 (R)

Family Phanodermatidae

Crenopharynx Filipjev, 1934 (R)

Phanoderma Bastian, 1865 (R)

Phanodermopsis Ditlevsen, 1926 (R)

Family Anticomidae

Anticoma Bastian, 1865 (R)

Anticoma aff. *eberthi* (R)

Suborder Trefusiina
Superfamily Trefusioidea

Family Trefusiidae

Rhabdocoma Cobb, 1920 (R)

Trefusia De Man, 1893 (R)

Trefusialaimus Riemann, 1974 (S)

Family Xenellidae

Xenella Cobb, 1920 (R)

Suborder Oncholaimina
Superfamily Oncholaimoidea

Family Oncholaimidae

Adoncholaimus Filipjev, 1918 (R)

Metoncholaimus Filipjev, 1918 (R)

Oncholaimus Dujardin, 1845 (S) (T)

Pontonema Leidy, 1855 (T)

Viscosia De Man, 1890 (S) (T)

Family Enchelidiidae

Bathyeurystomina Lamshead & Platt, 1979 (R)

Belbolla Andr ssy, 1973 (T)

Eurystomina Filipjev, 1921 (R) (S) (T)
Pareurystomina Micoletzky, 1930 (R)
Polygastrophora De Man, 1922 (S) (T)
Symplocostoma Bastian, 1865 (R)

Suborder Ironina
 Superfamily Ironoidea

Family Ironidae

Syringolaimus De Man, 1888 (R) (S)
Thalassironus De Man, 1889 (R)
Trissonchulus Cobb, 1920 (T)

Family Leptosomatidae

Cylicolaimus De Man, 1889 (R)
Leptosomatium Bastian, 1865 (R)
Platycoma Cobb, 1894 (R)

Family Oxystominidae

Halalaimus De Man, 1888 (R)
Oxystomina Filipjev, 1921 (R) (T)

Suborder Tripyloidina
 Superfamily Tripyloidoidea

Family Tripyloididae

Bathylaimus Cobb, 1894 (R) (T)
Tripyloides De Man, 1886 (R)

ORDER TRIPLONCHIDA

Suborder Tobrilina
 Superfamily Tobrioloidea

Família Rhabdodemaniidae

Rhabdodemia Baylis & Daubney, 1926 (R)

CLASS CHROMADOREA
 SUBCLASS CHROMADORIA
 ORDER CHROMADORIDA
 Suborder Chromadorina
 Superfamily Chromadoroidea

Family Chromadoridae

Actinonema Cobb, 1920 (R)
Chromadora Bastian, 1865 (R) (S)
 Chromadora aff. *nudicapitata* (R)
Chromadorella Filipjev, 1918 (R) (S)
Chromadorina Filipjev, 1918 (R) (S)
Chromadorita Filipjev, 1922 (R) (S)
Dichromadora Kreis, 1929 (R) (S)
Endeolophus Boucher, 1976 (S)
Euchromadora De Man, 1886 (R)
Graphonema Cobb, 1898 (R)
Hypodontolaimus De Man, 1886 (R)

Innocuonema Inglis, 1969 (T)
Neochromadora Micoletzky, 1924 (R) (S)
Nygmatochus Cobb, 1933 (R)
Prochromadora Filipjev, 1922 (S)
Prochromadorella Micoletzky, 1924 (R) (S)
Ptycholaimellus Cobb, 1920 (S) (T)
Rhips Cobb, 1920 (R) (S)
Spiliphora Bastian, 1865 (R) (S)
Spilophorella Filipjev, 1917 (R) (S) (T)
Steineridora Inglis, 1969 (S)
Trochamus Boucher & Bovée, 1972 (R) (S)

Family Neotonchidae

Gomphonema Wieser & Hopper, 1966 (R)

Family Cyatholaimidae

Acanthonchus Cobb, 1920 (S)
Longicyatholaimus Micoletzky, 1924 (R) (T)
Marylynnia Hopper, 1977 (R) (S)
Metacyatholaimus Stekhoven, 1942 (R) (S) (T)
Paracanthonchus Micoletzky, 1924 (R) (S) (T)
Paracyatholaimoides Gerlach, 1953 (S)
Paracyatholaimus Micoletzky, 1922 (S) (T)
Paralongicyatholaimus Stekhoven, 1942 (R) (S) (T)
Pomponema Cobb, 1917 (R) (T)

Family Selachinematidae

Choanolaimus De Man, 1880 (T)
Halichoanolaimus De Man, 1886 (R) (S)
Latronema Wieser, 1954 (R)

ORDER DESMODORIDA
Superfamily Desmodoroidea

Family Desmodoridae

Catanema Cobb, 1920 (R)
Chromaspirinia Filipjev, 1918 (R)
Croconema Cobb, 1920 (R)
Desmodora De Man, 1889 (R) (S)
Desmodorella Cobb, 1933 (R)
Eubostrichus Greef, 1869 (R)
Leptonemella Cobb, 1920 (R)
Metachromadora Filipjev, 1918 (R) (S) (T)
Metachromadora aff. *remanei* (R)
Molgolaimus Ditlevsen, 1921 (S)
Polysigma Cobb, 1920 (R)
Pseudochromadora Daday, 1889 (R)
Pseudonchus Cobb, 1920 (T)
Spirinia Gerlach, 1963 (R) (S)

Family Epsilonematidae

Epsilonema Steiner, 1927 (R)*Metepsilonema* Steiner, 1927 (S)*Perepsilonema* Lorenzen, 1973 (R)

Family Draconematidae

Dracognomus Allen & Noffsinger, 1978 (R)*Draconema* Cobb, 1913 (R)*Notochaetosoma* Irwin-Smith, 1918 (R)*Paradraconema* Allen & Noffsinger, 1978 (S)*Prochaetosoma* Micoletzky, 1922 (R)

Superfamily Microlaimoidea

Family Microlaimidae

Calomicrolaimus Lorenzen, 1971 (R)*Microlaimus* De Man, 1880 (R) (S)

Family Aponchidae

Synonema Cobb, 1920 (S)

Family Monoposthidae

Monoposthia De Man, 1889 (R)ORDER DESMOSCOLECIDA
Suborder Desmoscolecina
Superfamily Desmoscolecoida

Family Desmoscolecidae

Desmogelachia Freudenhammer, 1975 (R)*Desmoscolex* Claparède, 1863 (R) (S)*Quadricoma* Filipjev, 1922 (R)*Tricoma* Cobb, 1893 (R) (T)

Family Cyartonematidae

Cyartonema Cobb, 1920 (R)ORDER MONHYSTERIDA
Suborder Monhysterina
Superfamily Monhysteroidea

Family Monhysteridae

Thalassomonhystera Jacobs, 1987 (R) (S)

Superfamily Sphaerolaimoidea

Family Xyalidae

Amphimonhystera Allgén, 1929 (R)*Amphimonhystrella* Timm, 1961 (T)*Cobbia* De Man, 1907 (R) (S)*Daptonema* Cobb, 1920 (R) (S)*Metadesmolaimus* Stekhoven, 1935 (R) (T)*Paramonhystera* Steiner, 1916 (R)

Prorhynchonema Gourbault, 1982 (T)

P. goubaultae Nicholas & Stewart, 1995 (T)

Rhynchonema Cobb, 1920 (R) (S) (T)

Theristus Bastian, 1865 (R) (S) (T)

Xenolaimus Cobb, 1920 (T)

Suborder Linhomoeina
Superfamily Siphonolaimoidea

Family Siphonolaimidae

Siphonolaimus De Man, 1893 (R)

Family Linhomoeidae

Desmolaimus De Man, 1880 (S)

Didelta Cobb, 1920 (R)

Eleutherolaimus Filipjev, 1922 (S)

Linhomoeus Bastian, 1865 (R) (S)

Metalinhomoeus De Man, 1907 (R) (S) (T)

Paralinhomoeus De Man, 1907 (R)

Terschellingia De Man, 1888 (R) (S)

ORDER ARAEOLAIMIDA
Superfamily Axonolaimoidea

Family Axonolaimidae

Ascolaimus Ditlevsen, 1919 (T)

Odontophora Bütschli, 1874 (R) (T)

Synodontium Cobb, 1920 (S)

Family Comesomatidae

Laimella Cobb, 1920 (R)

Paracomesoma Hope & Murphy, 1972 (S)

Pierrickia Vitiello, 1970 (S)

Paramesonchium Hopper, 1967 (T)

Sabatieria Rouville, 1903 (R) (S) (T)

Family Diplopeltidae

Araeolaimus De Man, 1888 (T)

Diplopeltis Cobb in Stiles & Hassal, 1905 (R)

ORDER PLECTIDA
Superfamily Leptolaimoidea

Family Leptolaimidae

Dagda Southern, 1914 (R)

Leptolaimus De Man, 1876 (S)

Onchium Cobb, 1920 (R)

Procamacolaimus Gerlach, 1954 (S)

Family Aegialoalaimidae

Aegialoalaimus De Man, 1907 (S)

Family Diplopeltooididae

Diplopeltooides Gerlach, 1962 (R)

Superfamily Ceramonematoidea

Family Tarvaiidae

Tarvaia Allgén, 1934 (R)

Family Ceramonematidae

Ceramonema Cobb, 1920 (R)*Dasynemoides* Chitwood, 1936 (R)*Metadasynemella* De Coninck, 1942 (R)*Metadasynemoides* Haspeslagh, 1973 (S)*Pselionema* Cobb, 1933 (T)*Pterygonema* Gerlach, 1914 (T)

Superfamily Haliplectoidea

Family Haliplectidae

Haliplectus Cobb, 1913 (S)

ORDER RHABDITIDA

Suborder Rhabditina

Infraorder Rhabditomorpha

Superfamily Rhabditoidea

Family Rhabditidae

Rhabditis Dujardin, 1845 (S)