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Free-Living Marine Nematode Communities in San Jorge Gulf, Argentina

By Catalina T. Pastor de Ward, Virginia Lo Russo, and Martín Varisco

ABSTRACT. The aim of this study was to investigate the patterns of nematode diversity and community structure in San Jorge Gulf, Argentina, in order to improve knowledge of this key group of organisms. Free-living marine nematodes were sampled at 13 stations in February 2014 during an expedition aboard R/V Coriolis II. We found a total of 188 species (101 of which were new to science) belonging to 98 genera. The statistical results indicated the presence of three different assemblages of free-living marine nematodes distributed spatially in three distinct zones in the gulf: the central part, the outer thermal front at both sides of the entrance, and the south thermal front area. Diversity increased from the coast to the entrance of the gulf, and the highest diversity was found in areas with coarser sediment. Sediment and salinity were the environmental parameters that best matched nematode community distribution.
INTRODUCTION

San Jorge Gulf (45°–47°S and 65°–67°W), located in Argentinean Patagonia, is of strategic interest because it sustains important fisheries of high economic value, including the shrimp *Pleoticus mulleri* Spence Bate, 1888; the southern king crab *Lithodes santolla* (Molina, 1782); and the hake *Merluccius hubbsi* Marini, 1933. Three thermal fronts have been identified in San Jorge Gulf (Glembocki et al., 2015): (1) the south front, which has high chlorophyll-*a* concentrations throughout the year and is strongly influenced by the cold, low-salinity Beagle-Magellan waters that are distributed by tides and winds (Acha et al., 2004); (2) the outer front, which separates the stratified waters of the inner gulf from the vertically mixed waters overlaying the southeastern area (from spring to summer); and (3) the north front (also from spring to summer). In these three fronts, no pycnocline develops (Paparazzo et al., 2017), and phytoplankton blooms reach the benthos quickly (Fernández, 2006). Additionally, modeling results indicate upwelling driven by dominant strong westerly winds along the south and southwest coasts (Tonini et al., 2006; Glembocki et al., 2015).

The shrimp *P. mulleri* migrates from the nursery grounds along the south coast to the north of San Jorge Gulf (Boschi, 1989; Góngora et al., 2012; Glembocki et al., 2015). During the passage north, the shrimp feed on meiofauna and small macrofauna, mainly crustaceans, polychaetes, and bivalves, followed by nematodes (13% of the total, Albertó et al., 1993; 70% of the total, Roux et al., 2009). Although nematodes as food for an economically important species like *P. mulleri* makes them ecologically important in the area, they are also important as consumers. Wieser (1953) classified nematode feeding groups based on the morphology of their mouths. He established four feeding groups: selective deposit feeders, non-selective deposit feeders, epistrate feeders, and predators or omnivores. New information has helped improve this classification, and it remains widely used (Moen and Vincx, 1997, and references therein). Species in the same functional group may compete for the same food source unless they segregate along different microniches (Moen and Vincx, 2000). Thus, differences in the way species that share the same functional group respond to changes in food quality and quantity or to a fluctuating abiotic environment can change the nematode community structure (Schiemer, 1985, 1987).

Meiofauna (nematodes are the dominant taxa) enhance organic matter mineralization (Nascimento et al., 2012) and increase bacterial denitrification in soft sediment ecosystems (Bonaglia et al., 2014). Also, in deep-sea sediments, Pape et al. (2013) found a positive linear relation between taxon diversity and carbon mineralization in nematodes communities.

Because new offshore oil exploitation is planned for the gulf, it is urgent to define its biodiversity in order to establish appropriate environmental policies. Free-living nematodes provide a suitable environmental monitoring tool based on their abundance, species richness, broad range of sensitivity to environmental changes, low mobility, short to intermediate life cycles, interstitial life, and lack of pelagic larval dispersion (Trett et al., 2009). Consequently, a baseline survey of free-living marine nematode communities in the gulf is essential for evaluating potential future impacts.

The aim of this study was to investigate the diversity and community structure of nematodes in San Jorge Gulf and to explore their distribution, focusing on the oceanographic conditions in the area. To this end, we performed the first inventory of the group in this habitat, including the dominant taxa of free-living marine nematodes at 60–110 m depth, and mapped the nematode assemblages and diversity. We also investigated relationships between nematode communities and environmental parameters.

METHODS

Sample Collection

Sediment samples were collected at 13 stations in a grid within San Jorge Gulf, from 42 m to 100 m depth (Figure 1; online supplementary Table S1), in February 2014. Samples were collected onboard R/V *Coriolis II* during the MArine ecosystem health of the San Jorge Gulf: Present status and RESilience capacity (MARES) project. The goal of the expedition was to study the physical, chemical, and biological characteristics of the gulf, including the benthos. Soft sediments were sampled for nematodes using a box corer (50 × 50 × 60 cm, 0.250 m² surface).

Nematode Extraction and Identification

Three meiofauna subsamples were collected at each sample site at a depth of 5 cm with a cylindrical Plexiglas corer (internal diameter 29 mm) and then preserved in 5% formaldehyde in filtered seawater with rose bengal. In the laboratory, the samples were sieved through both 500 µm (to avoid small macrofauna) and 50 µm (to retain nematodes) mesh sieves, and separated using LUDOX™ (Somerfield and Warwick, 1996). Then, 185–231 individual nematodes were randomly extracted from each sediment subsample, and permanent mounts were prepared on glass slides and sealed. The nematodes were identified to the lowest taxonomy level using standard identification keys based on morphological analysis, NeMys online identification key (Bezerra et al., 2018), and relevant literature (Platt and Warwick, 1983, 1988; Warwick et al., 1998; Lorenzen, 1994; Smol et al., 2006). Nematodes were classified by feeding type based on buccal morphology using Wieser’s classification (Weiser, 1953; Table S2).

Environmental Parameters

Total organic matter (TOM) and granulometry were measured for sediments. TOM was determined following the procedures described by Sargent et al. (1983). Sediments were analyzed by dry
sieving and classified according to the Wentworth scale (Wentworth, 1922) and divided into the following grain size categories: gravel (>2 mm), very coarse and coarse sand (2 mm–500 µm), medium sand (500 µm–250 µm), fine sand (250 µm–125 µm), very fine sand (125 µm–63 µm), and fine silt-clay fraction (<63 µm). Bottom water salinity (PSU) and temperature (°C) data were recorded with a CTD (SBE 911plus) attached to a rosette (SBE 32 Carousel), and dissolved oxygen was measured with an SBE 42 probe attached to the rosette.

**Data Analysis**

Multivariate analyses were used to determine the differences in nematode species composition between sites and between sedimentary environments. PRIMER* software was used for hierarchical cluster analysis (CLUSTER, SIMPROF), species contribution analysis (similarity percentage [SIMPER]), principal component analysis (PCA), and biota-environment routine (BEST). The resemblance matrix was calculated based on Bray-Curtis dissimilarity (fourth root transformation). PRIMER* was also used to calculate the following biological indices (Table 1): species richness (S), Shannon-Wiener diversity index (H'[^log_e^]), Margalef's diversity index (d'), Pielou's evenness index (J'), rarefaction (ES [51]), and 1-Lambda' index (Clarke et al., 2014, Chapter 8). A Kruskall Wallis test was performed to evaluate differences for diversity indices analysis. A second CLUSTER analysis based on Bray-Curtis dissimilarity (presence/absence transformation) was added to show data from a non-quantitative analysis.

The source samples and the statistical approach are presented in the online supplementary material.

**RESULTS**

**Nematode Abundances and Community Structure**

Nematode density per 10 cm\(^{-2}\) of sediment in all sampling sites ranged from 189 nematodes at site 6 to 621 nematodes at site 13 (Figure 1; Tables 1 and S2). A total of 188 species belonging to 28 families and eight orders were found. That figure includes 79 new records of known species and 101 new species (note that when we give a species a number, it is a new species), with four identified up to genus, two identified up to family, and two that remain unidentified species. The family Monhysteridae dominated (51 species), followed by Comesomatidae (29 species), Enoplidae (24 species), Cyatholaimidae (16 species), and Chromadoridae (12 species) (Table S2).

The 10 most important nematode species present in all samples were *Sabateria wieseri* (13% of total), *Hopperia americana* (5% of total), *Axonolaimus* sp. 1 (4% of total), *Daptonema concordiense* (3% of total), *Metachromadora zaixsi* (3% of total), *Mudwigglus* sp. 1 (3% of total), *Paralongicyatholaimus* sp. 1 (3% of total), *Paramonohystera megacephala* (3% of total), *Comesa* sp. 1 (2% of total), *Craspodema* sp. 1 (2% of total), *Molgolaimus* sp. 1 (2% of total), *S. flecha* (2% of total), and *Metalinhomoeus gloriae* (2% of total).

Hierarchical cluster analysis based on abundance fourth root transformation and presence/absence transformation of species showed similar patterns and revealed three significant groups (similarity profile [SIMPROF], p <0.05; Figures 2, S1, and S2). The three groups can be considered as nematode assemblages: group "a" (sites 1, 4, 5, 6, and 7), group "b" (sites FS [fixed station], 9, 13, and 14), and group "c" (sites 10 and 12 in the abundance cluster and sites 12 and 16 in the presence/absence cluster).

**FIGURE 1.** Map of San Jorge gulf with sampling stations indicated by numbered circles. Circle size indicates nematode density.
In the hierarchical cluster analysis of Figure 2a (fourth root), site 16 was separated from the other assemblages at the 25% similarity level. In the presence/absence cluster without influence of dominant species, group “c” was formed by sites 12 and 16, and site 10 was excluded, whereas groups “a” and “b” were the same in both clusters.

When considering only those species with an accumulated contribution of up to 62%, SIMPER analysis showed that *S. wieseri* was the most widely distributed species in San Jorge Gulf. *S. wieseri* Platt, 1985 is a non-selective deposit feeder (1B) with a body length of 1,500–1,900 µm and a body width of 10–15 µm. It was the first *Sabatieria* species re-described from the coast of Patagonia (Deseado River estuary, Santa Cruz; Pastor de Ward, 1987), and it is broadly distributed at that location (Pastor de Ward, 1998). *S. wieseri* was later found to be extremely abundant along the Patagonian Argentine coast in sedimentary environments up to 100 m depth. It has been found in intertidal areas of San Antonio Bay (Villares et al., 2016), in deeper areas of Nuevo Gulf (Pastor de Ward, 2003), and in intertidal areas of San Julián Bay (Pastor de Ward et al., 2015).

*S. wieseri* was present in San Jorge Gulf in all three groups revealed by cluster analysis, contributing 12% to group “a,” 6% to group “b,” and 7% to group “c.” Thirteen known species and five new species were found to be present in all sampled sites: *P. megacephala*, *D. concordiense*, *Campylaimus arcuatus*, *H. patagonica*, *M. retrosetosus*, *Crestanema patagonicum*, *M. parafiliformis*, *Aponema papillatum*, *Setosabatieria conicaudata*, *Terschellingia longicaudata*, *Leptolaimus vinnulus*, *Laimella longicaudata*, *L. sandrae*, *Comesa* sp. 1, *Mudwigglus* sp. 1, *Daptonema* sp. 1, and *Amphimonhystera* sp. 1, and *Paralinhomoeus* sp. 1. The average dissimilarity between groups “a” and “b” was 66.9%, with major contributions from *H. americana* (2.9% contribution), *M. zaixsi* (2.7), *Paramesacanthion inaequale* (2.1), and *Axonolaimus* sp.1 (2.0). The average dissimilarity between

### TABLE 1.
Summary of site data and nematode diversity indices for each site: species richness (S), Margalef richness (d’), Pielou’s evenness (J’), rarefaction (ES [51]), Shannon-Wiener diversity index (H’[log,]), λ-Lambda’, CLUSTER groups, and density.

<table>
<thead>
<tr>
<th>Samples</th>
<th>S</th>
<th>d’</th>
<th>J’</th>
<th>ES(51)</th>
<th>H’(log,_)</th>
<th>λ-Lambda’</th>
<th>GROUPS</th>
<th>CLUSTER</th>
<th>Density (Ind. per 10 cm–2)</th>
</tr>
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<td>1</td>
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<td>20.0000</td>
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<td>35.0000</td>
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<td>0.9895</td>
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<td>a</td>
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<tr>
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<td>24.0000</td>
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<td>3.5824</td>
<td>0.9905</td>
<td>b</td>
<td>b</td>
<td>434.24</td>
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</table>

**FIGURE 2.** Results of cluster and similarity profile (SIMPROF) analyses of species (a) fourth root and (b) presence/absence similarity matrices computed using Bray-Curtis similarity of transformed abundance data. Significant and grouped samples (p < 0.05) are identified by the black vertical lines. The red dashed bars indicate that there is no substructure within these samples. Assemblages are identified by letters a, b, and c below each cluster diagram.
groups “a” and “c” was 71.9%, with major contributions from *S. arquata* (2.3), *M. gloriae* (2.1), *S. flecha* (1.6), and *R. argentinae* (1.6). The average dissimilarity between groups “b” and “c” was 70.8%, and the species with major contributions were *M. gloriae* (2.0), *S. arquata* (1.8), *Neochromadora papillosa* (1.7), and *H. americana* (1.7). Table S3 shows the 10 species with the highest dissimilarities in each group and between groups.

**Diversity**

The nematode diversity indices—species richness (S), Shannon-Wiener (H’(log)), Margalef’s (d’), Pielou (J’), rarefaction (ES [51]), and 1-Lambda’—were normal to high at every site studied, with site 16 showing the highest values (see PCA results; Table 1; Figure S3; Table S4). PC 1 explains 96.2%, and PC 2 explains 3.8% of the variability (Table S4). In addition to the PCA results, Figure S7 visually displays how diversity varies in San Jorge Gulf (see Table 1 for the site data). The S index (Figure S7a) fluctuates from 20 (sites 4 and 7) to 75 (site 16), the species richness (Margalef’s) index (d’) value fluctuates from 5.57 (site 7) to 16.46 (site 16) (Figure S7b), the J’ index value fluctuates from 0.98 to 0.99 (Figure S7c), rarefaction (ES [51]) fluctuates from 20 (sites 4 and 7) to 44.24 (site 16) (Figure S7d), the Shannon-Wiener diversity index H’(log.) fluctuates from 2.94 (site 7) to 4.29 (site 16) (Figure S7e), and the 1-Lambda’ value fluctuates from 0.97 to 0.99 (Figure S7f). The Kruskal Wallis test for S, d’, J’, ES (51), and 1-Lambda’ shows significant differences between “a” and “c,” whereas “b” was not different from “a” or “c.” H’ showed significant differences between “a” and the other groups (“b” and “c”), but not between “b” and “c.”

When relating the groups obtained by CLUSTER (fourth root transformation) with diversity, we found that group “a” had the lowest diversity, group “b” intermediate diversity, and group “c” the highest diversity.

**Relationship to Environmental Variables**

In the PCA (Figure S4 and Table S5), the first two axes explain 73.5% of variability in nematode communities. Group “a,” located in the center of the gulf, is characterized by depths between 61 m and 100 m, a high percentage of fine sediments (3.2%–6.7%), salinity of 33.4 PSU, oxygen saturation between 47.5% and 58.1%, temperature between 8°C and 11°C, and TOM between 3.4% and 8.5% (Figure 3). Group “b,” on the inner side of the gulf entrance, is characterized by similar depths (79–110 m), a wide range of fine sediments (0.17%–7.72%), similar temperature (9°–10.8 °C), lower salinity (33.2–33.3 PSU), and higher dissolved oxygen (51.3%–73.1 %) than group “a” (Figure 3). Group “c,” at the southern part of the gulf, is characterized by depths from 42 m to 74 m, it is dominated by medium to coarse sands (0.52%–0.76%), and it has lower salinity (33.1 PSU), a larger temperature range (11.8°–14.1°C), and higher dissolved oxygen than groups “a” and “b” (77.7%–78.4%) (Figure 3). Also, sample 16, included only in the SIMPROF presence/absence cluster, is situated at the northern limits of the gulf (Figure 3) at 81 m depth and has the highest fine sand fraction (4.9%), the highest coarse sand fraction (0.7%), and high salinity (33.4 PSU).

The BEST analysis (with a correlation of 0.676) selected percent fine fraction (%FF), medium sand (Msand %), coarse sand (Csand %), and salinity (PSU) as the variables most related to the raw biological data.

**Trophic Structure**

Non-selective deposit feeders (1B) or selective deposit feeders (1A) dominated the San Jorge Gulf samples, comprising more than 55% for most sites, followed by carnivorous and predatory feeders (2B).
DISCUSSION

Nematodes and San Jorge Gulf Oceanography

The benthic environment of San Jorge Gulf exhibits spatial heterogeneity in sediment grain size and organic matter content that may be associated with seasonal variations in productivity and circulation dynamics (Akselman 1996; Fernández, 2006; Fernández et al., 2006). As mentioned earlier, three thermal fronts were identified in San Jorge Gulf: a south front, an outer front, and a north front (Glenbocki et al., 2015). These fronts make waters at the gulf’s entrance and along its coasts highly biologically productive. Areas close to the north and south caps are characterized by coarse sediment with low organic matter content, while the central area is blanketed by fine sediment with high organic matter content (Fernández, 2006). Our results are consistent with this framework and show clear spatial distribution of nematode fauna related to benthic environmental heterogeneity in San Jorge Gulf. Waters at the south front area enter San Jorge Gulf at Cape Tres Puntas. The tidal flow there is considered to be among the highest in the world (Tonini et al., 2006), and waters have the lowest salinities and contain coarse sediments (Fernández, 2006).

Nematode assemblage “c” is influenced by the south front. This group is characterized by high diversity, intermediate density, a high number of selective and non-selective deposit feeders (1A and 1B, 60%), and a large number (22) of exclusive species, 10 of which were new. We identified Richtersia argentiniae (Pastor de Ward and Lo Russo, 2007) and S. flecha (Pastor de Ward, 2003) as an exclusive species to group “c.” S. flecha (Pastor de Ward, 2003) was found mostly in group “c” but was also present in group “b.” Richtersia argentiniae was previously found at 48–141 m depth in San José Gulf and off the south coast of San Matías Gulf, and S. flecha in Nuevo Gulf (all located north of San Jorge Gulf along the Argentinian coast) in areas also characterized by high phytoplankton production. Similar results were found close to Cape Tres Puntas, where filter species dominated the macrobenthic assemblages, suggesting more direct dependence on primary productivity with respect to assemblages found in the central area (Kaminsky et al., 2018, in this issue).

Group “b” was located within the outer front, spanning both sides of the gulf’s entrance, an area rich in phytoplankton blooms. Waters here are in constant motion. Frontal currents (Paparazzo et al., 2017) in the upper waters have low salinities and low organic matter content. Deeper waters are likely very turbulent because of tidal currents (Tonini et al., 2006) that move in opposite directions. This group has the highest percentage of non-selective deposit feeders (1B), intermediate to highest densities (sample station 13), and 17 exclusive species (seven of which were new). This group is characterized by Metachromadora zaixsi (Pastor de Ward, 2004) and Croconema otti (unpublished data of author Pastor de Ward); the former species was previously found in San José Gulf and the latter in Nuevo Gulf.

Site 16, which was excluded in the fourth root cluster (and included in the presence/absence cluster), is influenced by the north front (Boschi, 1989). It presented the highest diversity of the entire gulf, a high density of individuals, and the highest number of exclusive species and new species (26 and 20 respectively); the four buccal types were equally represented here.

Some remnants of these phytoplankton blooms, in the form of fresh organic matter and detritus, are deposited at the entrance (all along the gulf mouth) or on the north coast of the gulf, whereas others are deposited in the deeper water layers of the central gulf (Piola and Rivas, 1997). The organic matter enriches fine sediments, which are mixed with the help of residual tidal currents that circulate counterclockwise in this area (Tonini et al., 2006). The combination of phytoplankton blooms and tidal currents also allows high nutrient conditions to build up if water residence time in the deep basin is longer than that of the overlying shelf water (Krock et al., 2015). This area, which is isolated by a strong pycnocline during austral summer (Paparazzo et al., 2017), has the highest salinity, the most organic matter, and the highest percentage of fine sediment fraction (Fernández, 2006). These characteristics agree with our findings in the sense that the central area of the gulf (up to 75 m of depth, near the coast), where assemblage...
“a” is located, has very fine sediments (<63 µm), high salinity, a low density of nematodes, and high organic matter content. Group “a” displayed the highest number of known species of nematodes recorded for Patagonian coasts, only two exclusive species (Laimella annae and Molgolaimus sp. 1), and 14 new species that were shared with the other groups.

Nematodes as Food
As mentioned earlier, P. mulleri shrimp migrate from south to north along the entrance to San Jorge Gulf. During their passage, the shrimp feed on meiofauna (Albertó et al., 1993; Roux et al., 2009). If nematodes are important in P. mulleri food intake, this meiofauna/nematode predation pressure could affect the entrance to the area (it is coincident with nematode assemblage group “b”), which overlaps with the P. mulleri migration route, modifying the diversity of meiofauna in general and nematodes in particular. Also, the squat lobster Munida gregaria Fabricius, 1793, due to its abundance and trophic niche, plays a key role in the benthic-demersal community of San Jorge Gulf (Vinuesa and Varisco, 2007; Lovrich and Thiel, 2011; Diez et al., 2016). Nematodes were found in the stomach contents of the squat lobster M. gregaria, with occurrence frequency ranging from 17% to 43% and relative abundance from 1.51% to 5.3% (Varisco and Vinuesa, 2007).

Relationships with Nematodes from Other Locations
The density of nematodes in San Jorge Gulf at all sample sites is within the values observed in other continental shelf areas (Danovaro et al., 2000; Sajan et al., 2010).

We found four species of the genus Mudwigglus in San Jorge Gulf: two similar to those described by Leduc (2013) for Chatham Rise (New Zealand)— M. plebeius and M. nellyae—and two new species, probably vicariate. These species will be described in a future article.

The origin of nematode fauna is difficult to establish because not all of them have been studied with the same intensity. To our knowledge, the nematode assemblages of San Jorge Gulf include fauna from both Argentine and Magellan zoogeographic provinces (Balech and Ehrlich, 2008), plus species introduced when Drake Passage opened, connecting the Atlantic and Pacific Oceans. In this context, San Jorge Gulf can be considered an ecotone, a designation that agrees with previous macrobiota findings (Fernández, 2006).

Nematodes and Organic Carbon Cycling in San Jorge Gulf
Nematodes graze on microalgae and bacteria (Montagna, 1995; Muresan, 2012). In an early experiment, Findlay and Tenore (1982) found that at natural densities of the nematode Diplolaimella chitwoodi, the rate of detrital algal carbon mineralization doubled in the presence of this species and demonstrated the nematode’s ability to rapidly utilize settled particulate organic matter (POM). We hypothesize that advection from open waters transports great quantities of food (microalgae, bacteria, and detritus), driven by tidal mixing and currents, to the bottom of the gulf as POM. In addition, we hypothesize that this increase in organic carbon recycling at the entrance to the gulf, plus in its north and south frontal zones, could increase nematode diversity, as demonstrated by Vanaverbeke et al. (2004) for North Sea environments. In addition, organic matter recycling could sustain P. mulleri migration, for which nematodes are principal prey.

A weakness in using a box corer is that, upon insertion, it creates a bow wave that likely disturbs the sediment surface (Montagna et al., 2017). This action can significantly impact surface-dwelling meiofauna by resuspending organisms, with consequent underestimation of the real abundance. Some studies have found that use of a box corer can result in losing half the meiobenthic fauna present as compared to a multicorer, which produces less of a bow wave (Bett et al., 1994). However, other studies that compared meiofauna abundance sampled with box corers versus multicorers showed that there is no difference (Galéron et al., 2000; Mokievskii et al, 2007; Montagna et al, 2017). The bow wave effect can be eliminated if the meiofauna are sampled using corers mounted within a box core, which reduces edge effects and ensures an undisturbed surface (Galéron et al, 2000; Montagna et al, 2017).

CONCLUSIONS
1. In San Jorge Gulf, we identified 188 species of free-living marine nematodes belonging to 98 genera: 101 new species, 79 new records of known species, four identified up to the genus level, two identified up to the family level, and two unidentified species. The 101 new species were compared taxonomically with all the species of each genera and were not found to be similar to any described up to 2018. We think they are new to science and should be described in the future.
2. Our results indicate the presence of three different assemblages of free-living marine nematodes (“a,” “b,” and “c”) distributed in distinct zones in San Jorge Gulf.
3. Nematode diversity increases from the coast toward the entrance to the gulf. The highest diversity of nematodes coincides with areas containing coarser seafloor sediment.
4. Sediment composition (% fine fraction, % medium sand, % coarse sand) and salinity were the environmental parameters that best matched the biota data.
5. This work provides new insights about nematode assemblages in a region that has a paucity of information about this important topic, and it provides data essential for understanding the cycling of organic matter. In addition, our findings provide quantitative and qualitative baseline data, useful as indicators of anthropogenic and climatic disturbances.
Supplementary materials are available online at https://doi.org/10.5670/oceanoq.2019.4.1.5.

References


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