Mesh size effects on assessments of planktonic hydrozoan abundance and assemblage structure

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ABSTRACT

The choice of appropriate mesh-size is paramount to accurately quantify planktonic assemblages, however there is no such information available for hydrozoans. Here planktonic hydrozoan abundance and assemblage structure were compared using 200 and 500 μm meshes at Babitonga estuary (S Brazil), throughout a year cycle. Species richness and Shannon–Wiener diversity were higher in the 200 μm mesh, while evenness was typically higher in the 500 μm. Assemblage structure was significantly different between meshes (PERMANOVA, $P < 0.05$; n = 72 pairs of samples) both regarding taxa and size composition. These discrepancies are due to significant underestimation of small hydromedusae by the coarse mesh, like *Obelia* spp., young *Liriope tetraphylla*, *Podocoryna loyola* and others. Yet, larger taxa like *Eucheilota maculata* and adult *L. tetraphylla* were more abundant in the coarse mesh on some occasions and others such as *Blackfordia virginica* and *Muggiaea kochi* were similarly represented in both meshes. Overall collection efficiency of the coarse mesh (CE_{500}) was 14.4%, with monthly averages between 1.6% and 43.0%, in July (winter) and January (summer) respectively. Differences between the meshes were size-dependent; CE_{500} was ~0.3% for hydrozoans sizing <0.5 mm, ~21% for those between 1 and 2 mm, ~56% for those between 2 and 4 mm, and nearly 100% for larger ones, reaching up to 312% for hydrozoans >8 mm in October. These results suggest that both meshes have their drawbacks and the best choice would depend on the objectives of each study. Nevertheless species richness, total abundances and most taxa were better represented by the 200 μm mesh, suggesting that it is more appropriate to quantitatively sample planktonic hydrozoan assemblages.

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1. Introduction

Zooplankton communities are paramount to food web structure and energy transfer and consequently to the functioning of marine ecosystems. Therefore quantitative assessments are necessary to properly evaluate their role, and to accomplish so with reliability the choice of appropriate sampler is a key issue. Among the many variables that may influence the accuracy of zooplankton sampling – such as shape and size of the net, towing speed, filtration performance, and so on – mesh size selectivity is commonly regarded among the major sources of error when estimating zooplankton abundance and community structure (Riccardi, 2010; Sameoto et al., 2000; Skjoldal et al., 2013; Vannucci, 1968). Although many studies attempted to evaluate mesh size effects since late XIX century, the subject is still troublesome since no single mesh properly sample all taxa and/or developmental stages

in all areas and under different conditions (Hopcroft et al., 2001; Miloslavic et al., 2014; Skjoldal et al., 2013).

Mesh size selectivity is relatively well known for copepods, and many authors have shown that 200 μm meshes underestimate adults of small species, and copepodites and nauplii of all species due to extrusion. Losses are significant and may exceed 90% in abundance and 50% in biomass and production (Bernhard et al., 1973; Di Mauro et al., 2009; Favareto et al., 2009; Hopcroft et al., 1998; Hwang et al., 2007; Krsinic and Lucic, 1994; Riccardi, 2010; Wu et al., 2011). In contrast, larger copepods may not be well sampled by fine meshes due to the bow wave effect and reduced filtering efficiency (Favareto et al., 2009; UNESCO, 1968). Hopcroft et al. (2001) concluded that among 64, 200, and 500–600 μm meshes, each is more efficient for a specific copepod size range. However this seems not to be always the case, since many other authors did not find differences for larger copepods (Almeida Prado, 1962; Antacli et al., 2010; Miloslavic et al., 2014; Vidjak, 1998; Wu et al., 2011).

Among other marine invertebrate taxa, studies are considerably fewer. Bivalve larvae and the pteropod *Limacina* spp. are highly underestimated by 200 μm mesh (Miloslavic et al., 2014). Decapod larvae and ostracods are equally sampled by 125 and 250–333 μm meshes

(Krsinic and Lucic, 1994; Vidjak, 1998). The same may be true for chaetognaths (Almeida Prado, 1962; Vidjak, 1998) but the issue is disputable; small slender species such as *Parasagitta setosa* may be underestimated in more than 50% by 200–250 μm meshes (Krsinic and Lucic, 1994; Miloslavic et al., 2014), but Skjoldal et al. (2013) concluded that 330 μm is more efficient than 180 μm mesh for chaetognaths. Cladocerans are equally sampled by 125 and 250 μm meshes in Adriatic (Krsinic and Lucic, 1994; Miloslavic et al., 2014), but *Evadne nordmanni* and *Podon* sp. from Norway are better sampled by 200 μm in comparison with 400, 100 or 55 μm meshes (Skjoldal et al., 2013). Losses of 35–98% of *Oikopleura dioica* <1 mm in trunk length abundance and between 60–90% of biomass of animals <400 μm have been reported in 220 μm mesh. Conversely, 67 μm mesh may underestimate in 50–80% biomass of larger animals, and completely missed appendicularians >1 mm (Di Mauro et al., 2009). All developmental stages of three other species of *Oikopleura* were similarly sampled by 53 and 200 μm meshes (Esnal et al., 1997).

From the data depicted above particularities for each taxon are clear, which are typically related to their size, morphology, flexibility and behavior (Vannucci, 1968). Therefore, the effectiveness of a given mesh size depends on taxonomic composition and size–structure of the assemblage to be sampled (Hopcroft et al., 2001; Riccardi, 2010; Skjoldal et al., 2013; Vannucci, 1968). Moreover, retention efficiency of a given mesh size may change seasonally (Riccardi, 2010) and in different environments (Hopcroft et al., 2001; Miloslavic et al., 2014) further complicating the topic. Consequently, detailed evaluations of effects of mesh size, including different seasons and environments, are critical for proper quantitative sampling of any taxonomic group.

Planktonic hydrozoans are common, abundant, and diversified in marine systems. They are typically carnivores with high feeding rates, playing a significant role in pelagic food webs (e.g. Mills, 1995; Pagès et al., 2001). Therefore, accurately quantifying them is essential for detailed understanding of ecological processes and energy flow in water column. Most authors use meshes with pore sizing between 200 and 500 μm when attempting to quantify planktonic hydrozoans, but both finer and coarser meshes have also been employed (Mesquita et al., 2006; Pagès and Kurbjeweit, 1994; Pagès et al., 1996; Palma, 1985; Palma et al., 2007; Panasiuk-Chodnicka and Zmijewska, 2010; Persad et al., 2003; Pestoric et al., 2012; Petrova et al., 2011; Sabatés et al., 2010; Suárez-Morales et al., 2002). Notwithstanding the wide range of mesh sizes employed, there has been no effort to test the effects of different meshes on such estimates. Bouillon (1999) suggested that meshes larger than 200 μm may lose smaller hydromedusae however this hypothesis has not been tested yet. The lack of this knowledge complicates both the choice of appropriate mesh size and direct comparisons of samples – or studies – made with different meshes. Aiming to improve the knowledge of quantification of planktonic hydrozoans, in the present study we tested the hypothesis that meshes with pores sizing 200 and 500 μm provide different results regarding abundance and assemblage structure.

2. Material and methods

2.1. Study site and sampling methods

Babitonga Bay is a subtropical estuary located in the state of Santa Catarina, south Brazil (26.3°S; 48.7°W). The estuary has an area of ~130 km², average depth of 6 m, and is bordered by extensive mangroves (Cremer et al., 2006). Its high biological productivity sustains a high abundance and diversity of phytoplankton and zooplankton (Brandini et al., 2006; Nogueira Júnior, 2012). Eight surveys were done on a seasonal basis between October 2007 and August 2008. On each cruise nine stations were sampled along the estuary (Fig. 1), totalizing 72 stations. On each station, two conical plankton nets were simultaneously obliquely hauled side-by-side between 2 and 5 min integrating most of the water column, one with 200 and other with

500 μm mesh–pore, 40 and 50 cm in mouth diameter respectively. The hauls were all made during daylight (between 9 a.m. and 3 p.m.) and speed was kept low, around 1.5 knots. Both nets were fitted with a calibrated mechanic flowmeter, and samples were fixed in 4% formaldehyde seawater solution.

2.2. Analysis of samples

In laboratory whole samples were analyzed under stereomicroscope and the hydrozoans sorted, identified and quantified. Voucher specimens of most species were deposited at the Zoology Museum from São Paulo University (Museu de Zoologia da Universidade de São Paulo; MZUSP 1578–1582, 1584–1632), and their taxonomy discussed in a previous study (Nogueira Júnior, 2012). The abundant hydromedusa *Liriope tetraphylla* was further classified as juvenile or adult. The former was characterized by the absence of gonads and undeveloped gastric peduncle (Nagata et al., 2014). Siphonophores calycophoran colonies were quantified as anterior nectophores and bracts. The unique physonect species sampled, *Nanomia bijuga*, was not included in the present analysis due to the well-known difficulties in accurate quantifying physonects from net samples. Medusae's bell diameter and siphonophore's largest width (both for polygastrics and eudoxids) were measured.

2.3. Data analysis

Community indexes such as Pielou's evenness (J) and Shannon–Wiener diversity (H′) were calculated for each sample (n = 72 for each mesh). Species richness, ecological indexes, and abundances of individual taxa estimated with both meshes were compared using a paired t test (Zar, 2010). A permutational multivariate analysis of variance (PERMANOVA) was used to test whether taxonomic and size structure of hydrozoan assemblage changed according to mesh size, sampling months, sampling sites and possible interactions between these factors. Both analyses were based on a Bray–Curtis similarity matrix constructed on the log (x + 1) transformed densities of each taxa or size class from all samples (n = 72 with each mesh). Significance of PERMANOVAs was evaluated by the pseudo-F statistic (Anderson et al, 2008) after 999 permutations. In case of significant differences (P < 0.05) the taxa and/or size classes most contributing to the differences were recognized using a similarity percentage analysis (SIMPER, Clarke and Warwick, 2001). The collection efficiency of the 500 μm mesh (CE_{500}, %) in relation to the 200 μm mesh was calculated as follows: $CE_{500} = (Ab_{500} * 100)/Ab_{200}$; where Ab_{500} and Ab_{200} are abundance estimated by 500 and 200 μm meshes respectively. To estimate monthly CE_{500} we used the monthly average abundance estimated with each mesh.

3. Results

3.1. Taxonomic and size class composition

A total of 31 hydromedusae and three calicophoran species were sampled, beyond actinula larvae (online supplementary Table 1). Among these 35 taxa, *Laodicea minuscula* (n = 8 individuals), *Corymorpha forbesi* (n = 9), *Amphinema dinema* (n = 1), and *Hydractinia* sp.2 (n = 1) were exclusively sampled by the 200 μm mesh, while *Eirene* sp. (n = 2) and *Stauridiosarsia reesi* (n = 6) were exclusively sampled by the 500 μm mesh. Although total number of species was similar in both meshes (33 and 31 species in 200 and 500 μm meshes respectively), the coarse mesh underestimated species richness in smaller size classes, particularly those <0.5 mm (7 against 17 species), and retrieved slightly more species than the 200 μm mesh in size classes >1 mm (Fig. 2a). Hydrozoan size composition and abundance were markedly different in the two meshes employed. Most hydrozoans retrieved by the 200 μm mesh were smaller than 1 mm,
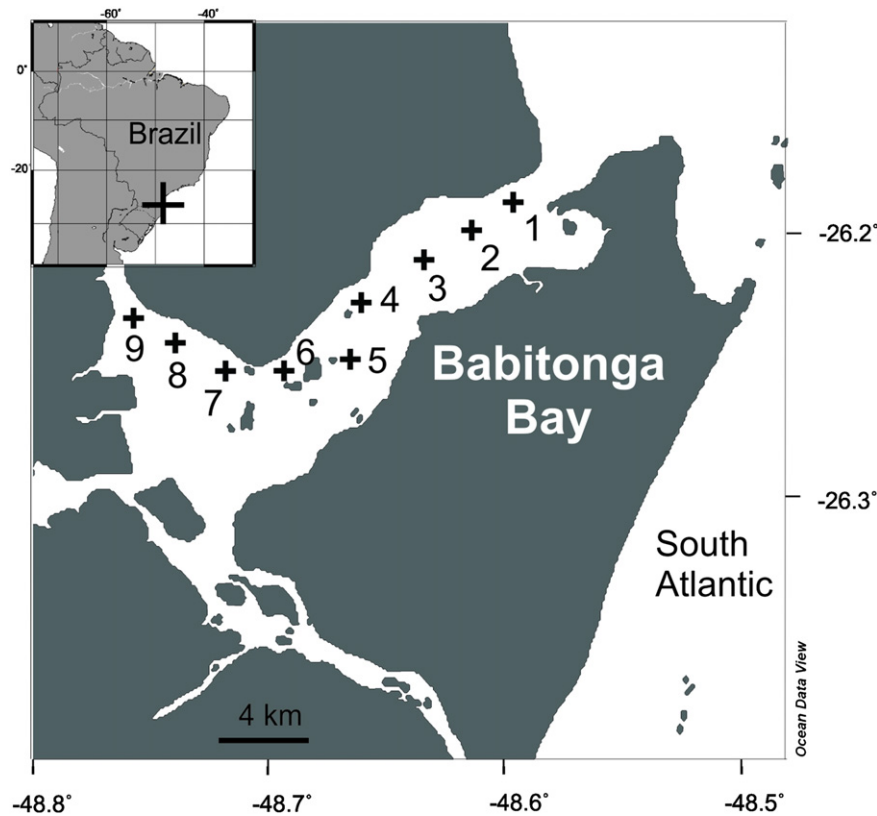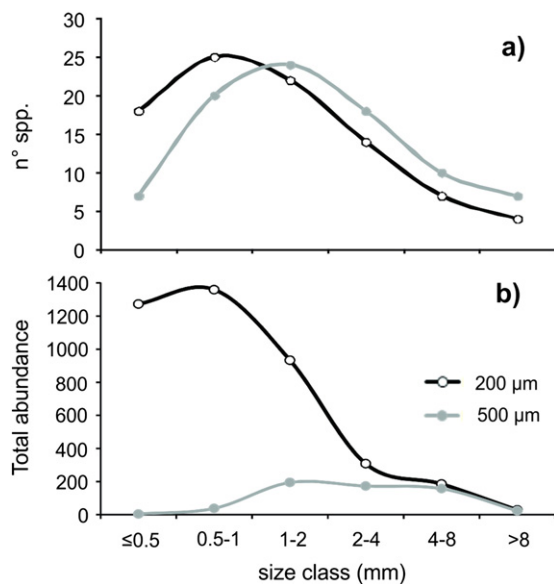
Fig. 1. Map of Babitonga Bay estuary, south Brazil, showing the nine stations sampled in October 18 and November 16, 2007, January 24, February 29, April 25, May 26, July 10 and August 8, 2008. Generated using Ocean Data View 4 software (Schlitzer, 2012).

while those sampled by the 500 μm mesh were mostly between 1 and 8 mm (Fig. 2b).

In the 200 μm mesh young *L. tetraphylla* dominated the assemblage, accounting for 55% of all hydrozoans, followed by *Obelia* spp. (14.1%), and *Clytia* sp.1 (8.2%). Other taxa, such as *Eucheilota duodecimalis*, adult *L. tetraphylla*, *Muggiaea kochi*, *Ectopleura dumortieri*, *Proboscidactyla ornata*, *Podocoryna loyola*, *Turritopsis nutricula*, *Blackfordia virginica* and

Corymorpha gracilis were also seasonally abundant, representing >10% at least in one of the campaigns (online supplementary Table 1).

Similar taxa dominated the 500 μm mesh samples, but in quite different proportions; young *L. tetraphylla* represented 35.0%, followed by adult *L. tetraphylla* (24.8%), *Clytia* sp.1 (12.8%), *M. kochi* (9.6%), and *B. virginica* (6.8%). Others like *Eucheilota maculata*, *Obelia* spp. and *Helgicirrha* sp. also were seasonally abundant, representing >10% in at least one of the months.
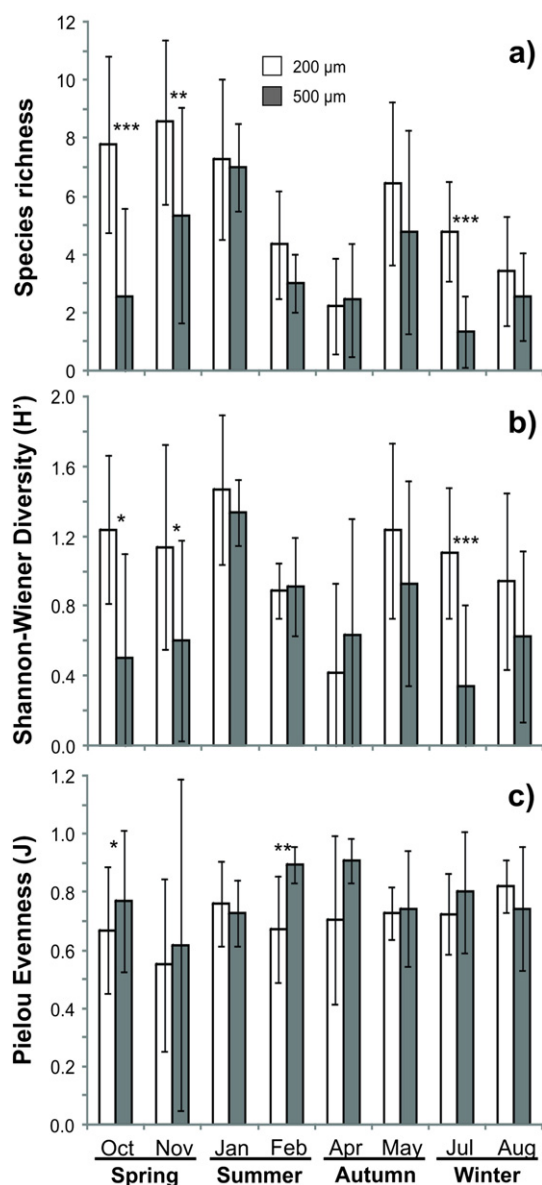
3.2. Abundance, community structure and seasonal variations

Species richness and Shannon–Wiener diversity index were typically higher in the finer mesh throughout the year, with statistical significance in October, November and July when differences were greatest (paired t test p < 0.05; Fig. 3a, b). Differently, evenness was typically higher in the 500 μm mesh throughout the year, with statistical significance in October and February (Fig. 3c). While species richness and Shannon–Wiener diversity index estimated by both meshes did not follow exactly the same seasonal trend, seasonality of evenness was roughly similar in both meshes with smaller values during spring.

Both taxonomic and size structure of the assemblage differed between meshes and months, but not between stations. The interaction between factors followed a similar pattern, with no significance whenever stations were considered (Table 1). Mesh size was the major source of variation for both taxa and size class datasets, as suggested by the markedly higher values of the PERMANOVA's pseudo F statistic (Table 1). Therefore, differences in this factor were further examined. Average dissimilarity between the two meshes datasets was 91.9% for abundance of taxa and 86.1% for size classes (Table 2). *Obelia* spp., young *L. tetraphylla*, and *Clytia* sp.1 are the taxa that mostly contributed to the differences. Considering size-classes, nearly 75% of difference between meshes was due to hydrozoans <2 mm (Table 2).

Fig. 2. Size-based (mm) total species richness (a) and abundance (b; indiv 10 m^{-3}) of planktonic hydrozoans sampled with 200 and 500 μm meshes between October 2007 and August 2008.

Fig. 3. Monthly averaged variation of planktonic hydrozoans species richness (a), Shannon–Wiener diversity (b), and Pielou evenness (c) estimated by the 200 and 500 μm meshes, between October 2007 and August 2008. The error bars indicate the standard deviation. Asterisks indicate months in which the two meshes are significantly different (paired t test, *** = p < 0.001, ** = p < 0.01, * = p < 0.05; n = 9 for each month).

In the coarse mesh average number of hydrozoan species sizing <2 mm was typically half or less than estimated with the finer mesh. Except in April when both meshes provided similar results (Fig. 4). Species richness of hydrozoans between 2 and 8 mm was approximately similar in both meshes throughout the year, again except in April when values estimated by the coarse mesh were higher. Animals larger than 8 mm were usually more species rich in the 500 μm mesh, up to 5 times greater in October. The exception was May when the finer mesh sampled slightly more species larger than 8 mm (Fig. 4).

Hydrozoan abundance using the 200 μm mesh ranged from <1 indiv.10 m^{-3} in April and August to 1138 indiv.10 m^{-3} in November. On a monthly basis, higher values were found in October and November, averaging 147 and 164 indiv.10 m^{-3} respectively. Lower abundances occurred in April and August (averaging ~7 indiv.10 m^{-3}). Smaller size classes were the most abundant throughout the year in the 200 μm mesh, except for January when those >4 mm dominated and August when all sizes were in similarly low abundances (Fig. 5).

Table 1
Summary of PERMANOVA testing for differences in quantitative taxonomic composition (abundances of taxa) and size distribution (abundances of size classes) of planktonic hydrozoan assemblages considering mesh size, months and stations as factors. Differences are considered significant if P < 0.05 (in bold). df = degrees of freedom. n = 72 pairs of samples.

Variable	df	Pseudo F	P
Factors			
Taxonomic composition			
Mesh	**1**	**19.21**	**<0.001**
Month	**7**	**5.14**	**0.001**
Station	8	1.90	0.276
Month × mesh	**7**	**2.51**	**0.001**
Station × mesh	8	1.41	0.35
Month × station	55	1.31	0.298
Size composition			
Mesh	**1**	**34.99**	**<0.001**
Month	**7**	**3.54**	**0.001**
Station	8	0.89	0.705
Month × mesh	**7**	**2.32**	**0.001**
Station × mesh	8	0.70	0.831
Month × station	55	0.74	0.779

Densities estimated with the 500 μm mesh-net were considerably lower throughout the year, never surpassing 156 indiv.10 m^{-3}. Higher densities occurred in October and November, averaging 21–26 indiv.10 m^{-3}, and lower abundances were in April and July, averaging <1 indiv.10 m^{-3}. Hydrozoans sizing between 1 and 8 mm dominated the assemblage when abundances were usually higher from late winter (August) to early summer (January); hydrozoans sizing between 1 and 2 and/or 2 and 4 mm dominated between April and July (autumn–early winter; Fig. 5) when abundances were lower.

The CE$_{500}$ varied a lot throughout the year and in different size-classes (Fig. 6a, b). Overall, the CE$_{500}$ was 14.4%, varying from 1.6% in July to 43.0% in January without a well-defined seasonal tendency (Fig. 6a). The CE$_{500}$ values tended to increase with increasing body-size. For hydrozoans smaller than 0.5 mm CE$_{500}$ was always <5%, ranging from <0.1 in February, April and July to 4.8 in August, averaging ~0.3%. For those sizing between 0.5 and 1 mm CE$_{500}$ was typically smaller than 4%, but reached up to 14.4% in January. For hydrozoans between 1 and 2 mm CE$_{500}$ ranged from 2.9% to 57.2% in February and October respectively, tending to be lower in autumn and winter seasons (Fig. 6b). The coarse mesh was more efficient than the fine mesh for 4–8 mm hydrozoans between October and April, when CE$_{500}$ ranged from 120.2 to 144.8% (January except CE$_{500}$ = 63.6%). However between May and August the CE$_{500}$ of the 4–8 mm size class was considerably lower, ranging from 13.1 to 34.3% (Fig. 6b). The CE$_{500}$ for hydrozoans >8 mm remained nearly to or larger than 100% most of the time, reaching up to 312% in October. Exception of this pattern occurred in May and August when relatively and unexpectedly low values of 14.5 and 49% were respectively recorded, which may be related to patchiness.

For young *L. tetraphylla* the CE$_{500}$ ranged between 2.1 and 63.1%, with monthly averages between 2.5 and 12.5% and overall mean of 9.2%. It was very abundant during spring reaching up to 140 and 11 indiv.10 m^{-3} in November in the fine and coarse mesh respectively (Fig. 7). Significant smaller abundances also consistently occurred in the 500 μm mesh throughout the year for *Obelia* spp. In the fine mesh *Obelia* spp. average abundances ranged from 1 to 14 indiv.10 m^{-3} in August and October respectively, while in the coarse mesh this medusa was always less abundant than 0.5 indiv.10 m^{-3}. Overall CE$_{500}$ of this medusa was 1.5%, ranging from 0.5 to 3.2% in October and May respectively. *P. loyola* and *Clytia* sp.1 also were consistently less abundant in the 500 μm mesh, however for the latter species statistical significant differences occurred only in July when highest abundances were recorded. Other seasonally abundant meroplanktonic hydromedusae like *E. duodecimalis*, *B. muscus* and *E. dumortieri*, were also largely

Table 2
Summary of SIMPER showing the contribution of taxa or size classes to the differences between the 200 and 500 μm meshes (n = 72 pairs of samples), and their average abundance (indiv.10 m^{-3}) on each mesh. SD = standard deviation.

Variable	Overall average dissimilarity (200 × 500 μm)	Taxa or size-class	Average dissimilarity	Contribution (%)	Cum. (%)	Average abundance (±SD)	
						200 μm	500 μm
Taxonomic composition	91.9%	*Obelia* spp.	23.8	25.9	25.9	8.2 (±9.1)	0.1 (±0.2)
		Young *Liriope tetraphylla*	12.9	14.0	39.9	32.1 (±142)	2.5 (±11.3)
		Clytia sp.1	11.5	12.5	52.4	4.8 (±9.5)	0.9 (±2.2)
		Adult *L. tetraphylla*	8.3	9.1	61.5	1.7 (±4.4)	2.1 (±6.7)
		Eucheilota duodecimalis	5.6	6.1	67.6	2.3 (±3.6)	0.02 (±0.07)
		Podocoryna loyola	4.1	4.5	72.1	5.5 (±22.5)	0.01 (±0.6)
		Blackfordia viriginica	3.9	4.2	76.3	0.5 (±1.6)	0.5 (±1.7)
		Ectopleura dumortieri	3.2	3.5	79.8	1.4 (± <0.01)	<0.01
		Muggiaea kochi	3.0	3.3	83.1	1.7 (±6.7)	0.6 (±3.7)
		Turritopsis nutricula	2.6	2.8	85.9	1.0 (±2.5)	0.01 (±0.04)
		Proboscidactyla ornata	2.1	2.3	88.2	1.1 (±4.4)	0.01 (±0.06)
		Corymorpha gracilis	1.9	2.1	90.3	0.8 (±3.7)	0.04 (±0.01)
		Others (n = 24 spp.)		9.7	100.0	0.9 (±1.3)	0.4 (±0.7)
Size composition	86.1%	0.5–1 mm	28.6	33.3	33.3	19.4 (±38.2)	0.5 (±1.5)
		1–2 mm	18.2	21.1	54.4	13.3 (±51.4)	2.8 (±9.3)
		<0.5 mm	17.4	20.2	74.6	18.2 (±56.5)	<0.01
		4–8 mm	10.3	12.0	86.6	2.6 (±4.8)	2.2 (±6.3)
		2–4 mm	9.1	10.5	97.1	4.4 (±15.4)	2.5 (±9.1)
		>8 mm	2.5	2.9	100.0	0.4 (±1.3)	0.3 (±0.8)

underestimated by the 500 μm meshes, with statistical significant differences in periods of abundance (paired t test, p < 0.05; Figs. 7 and 8). *P. ornata* and *C. gracilis* also were consistently more abundant in the finer mesh, however without statistical significance probably due to higher variation between sampling stations.

Larger taxa had different patterns; *B. virginica* abundances were similar in both meshes (p > 0.05; Fig. 8), with monthly CE$_{500}$ ranging from 61 to 145% in October and November respectively and averaging 102%. Statistically similar abundances were also observed for the siphonophore *M. kochi* (Fig. 7); yet in October when peaked, its CE$_{500}$ was
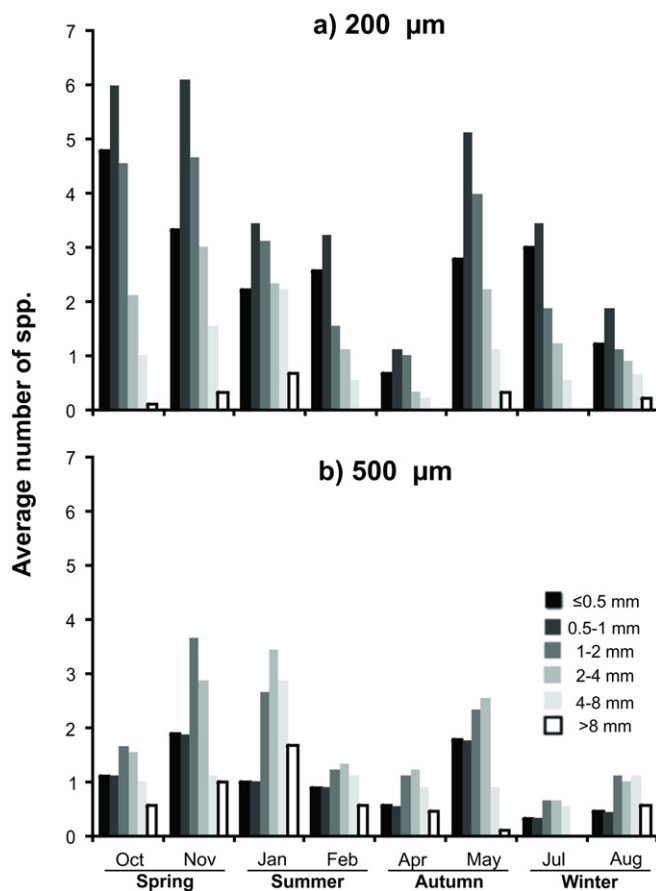

Fig. 4. Monthly averaged (n = 9) size-based planktonic hydrozoan species richness estimated with 200 (a) and 500 (b) μm meshes between October 2007 and August 2008.
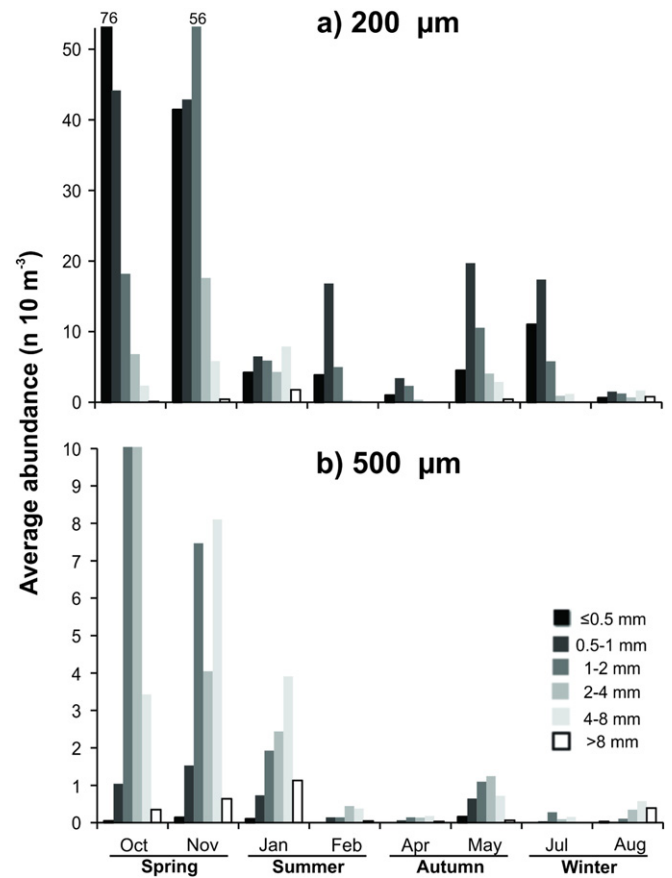

Fig. 5. Monthly averaged (n = 9) size-based abundance of planktonic hydrozoans sampled with 200 (a) and 500 (b) μm meshes between October 2007 and August 2008. Notice different scales.
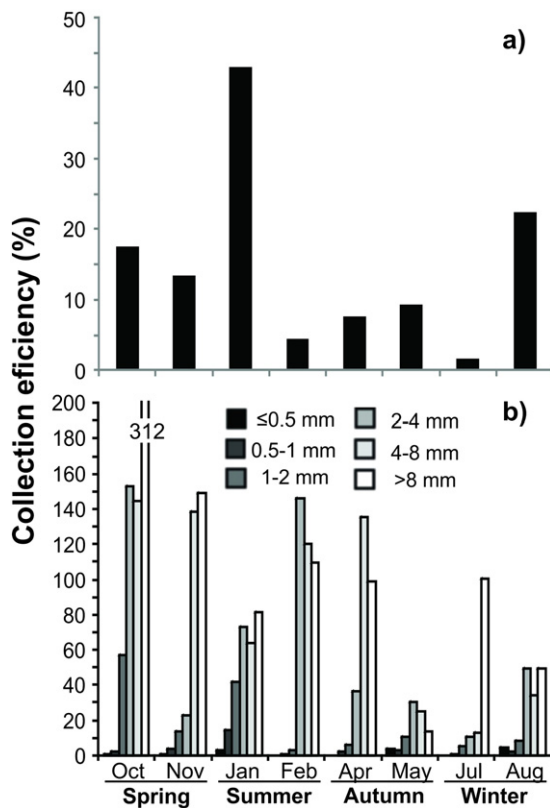
Fig. 6. Monthly variation of collection efficiency of 500 μm mesh in relation to the 200 μm of total (a) and size-based (b) planktonic hydrozoan assemblage between October 2007 and August 2008. Notice different scales.

62.6%. Although *M. kochi* is large, reaching more than 4 mm in nectophore height, its width is smaller (0.5 to 3 mm in the present material) allowing part of the population to escape through the coarse mesh. *E. maculata*, was more abundant in the 500 μm mesh throughout the year, being largely absent in the 200 μm mesh from January onward when large medusae (3–10 mm) predominated; significant differences occurred in October, November and April (Fig. 8). Adult stages of *L. tetraphylla* also were typically more abundant in the coarse mesh, with statistical significance in January when CE_{500} was 209%.

4. Discussion

Sampling using paired nets such as in the present study is of great interest bringing two-fold benefits. By one side it allows direct inter-comparisons between different gears providing valuable background to support researchers when deciding between them, and on the other it expands knowledge of community structure (Antacli et al., 2010). Although we provide a glimpse on hydrozoan abundance, assemblage structure and seasonal dynamics, information which is largely missing from Southwestern Atlantic estuaries (Nogueira Júnior, 2012), emphasis was given on the differences between meshes because this factor accounted for most variability of the assemblage both considering taxa and size composition (Table 1). The overall efficiency of the 500 μm mesh was 14.4%, which corroborates initial assumptions that this mesh underestimates planktonic hydrozoan abundance (Bouillon, 1999) and species richness, particularly in the smaller size-fraction. For larger hydrozoans the results of both meshes were variable and not too discrepant, yet the coarse mesh represented up to 312% of the fine mesh in October for organisms >8 mm. Six species were exclusively sampled by one or another mesh. These were all rare (1–9 individuals each; present in <5 samples), and therefore their absence in one of the meshes may be the result of randomness and cannot be clearly attributed to

mesh selectivity. Yet, the four species exclusively sampled with the 200 μm mesh are small-sized (<1 mm) and delicate and may have been lost through the coarse mesh.

Although mesh size effect on quantitative estimations of marine zooplankton communities has been addressed by many authors (e.g. Favareto et al., 2009; Skjoldal et al., 2013 and references therein), to our knowledge this is the first study carefully comparing mesh efficiency for planktonic hydrozoans, and may serve as a basis for future research. Given the great variability of mesh size efficiency in different ecosystems (Hopcroft et al., 2001; Miloslavic et al., 2014), more studies are desirable in order to expand the results obtained herein to different taxonomic- and size-composition assemblages. Moreover, the results of this study apply particularly for hydromedusae since siphonophores were represented by quite few species and a single abundant one, as typical of estuaries. Other well-known variables affecting the accuracy of zooplankton sampling include tow speed, shape and size of the net, volume of water sampled, active avoidance, and patchiness (Sameoto et al., 2000; Skjoldal et al., 2013; UNESCO, 1968). Their effects on estimates of planktonic hydrozoans abundance and assemblage structure are yet to be tested.

In general, the minimum total retention width of a particular mesh is a linear function of pore size, which should be about 3/4 of the size of the smallest organism to be sampled (Bernhard et al., 1973). Therefore the 500 and 200 μm mesh would efficiently sample organisms >667 μm and >267 μm respectively. However, the 500 μm mesh in the present study largely under sampled not only hydrozoans smaller than 667 μm but also those between 1 and 2 mm (and between 2 and 4 mm in a lesser extent). Escapement may be influenced by tow speed; water pressure flowing through the net may force extrusion, enhancing escapement of larger organisms (Bernhard et al., 1973; Sameoto et al., 2000). This probably was not the case here since we kept the speed low in all our tows. Escapement is also related to morphology, behavior (Vannucci, 1968) and body consistency of the organisms; therefore the absence of spines, long hard appendices or more stiff body consistency, may result in higher escapement rates. The hydromedusae fragile nature facilitates body deformation and perhaps also facilitates extrusion through the meshes during the hauls, and may partially account for the observed underestimation of organisms larger than the minimum total retention width of the 500 μm mesh–pore observed here.

The results regarding hydrozoans larger than 4 mm were variable. Overall abundance in both meshes was similar in those >4 mm, although CE_{500} in these size-classes varied considerably between different months. Similarly, differences for larger sized copepods are variable and may (Favareto et al., 2009; Hopcroft et al., 2001) or may not occur (Almeida Prado, 1962; Antacli et al., 2010; Vidjak, 1998; Wu et al., 2011). These differences in larger organisms are commonly attributed to the bow–wave effect that is stronger in finer meshes, larger filtration efficiency of larger meshes, larger net opening and water volume sampled (Miloslavic et al., 2014; Sameoto et al., 2000; UNESCO, 1968), what may have been the case herein since the coarse mesh–net had a larger mouth opening, and a higher open mesh area to mouth opening ratio. In parallel to the one observed here, the larger size fractions typically have higher variance, probably due to their greater mobility (Sjkoldal et al., 2013). Moreover, these larger taxa are typically less abundant and larger volumes of filtered water are required to obtain a lower variance (Wiebe, 1971) and therefore a more accurate estimate of their abundance.

Although total number of taxa was similar in both meshes, average species richness on each sample was higher in the finer one, particularly in spring and early winter, as well as the diversity index. This is because the under-representation of small-sized organisms in the coarse mesh is larger than the under-representation of large-sized organisms in the finer mesh, resulting in higher evenness in the coarse mesh. When very abundant small species are largely underestimated relative abundance of remaining species is more even. The issue is variable for
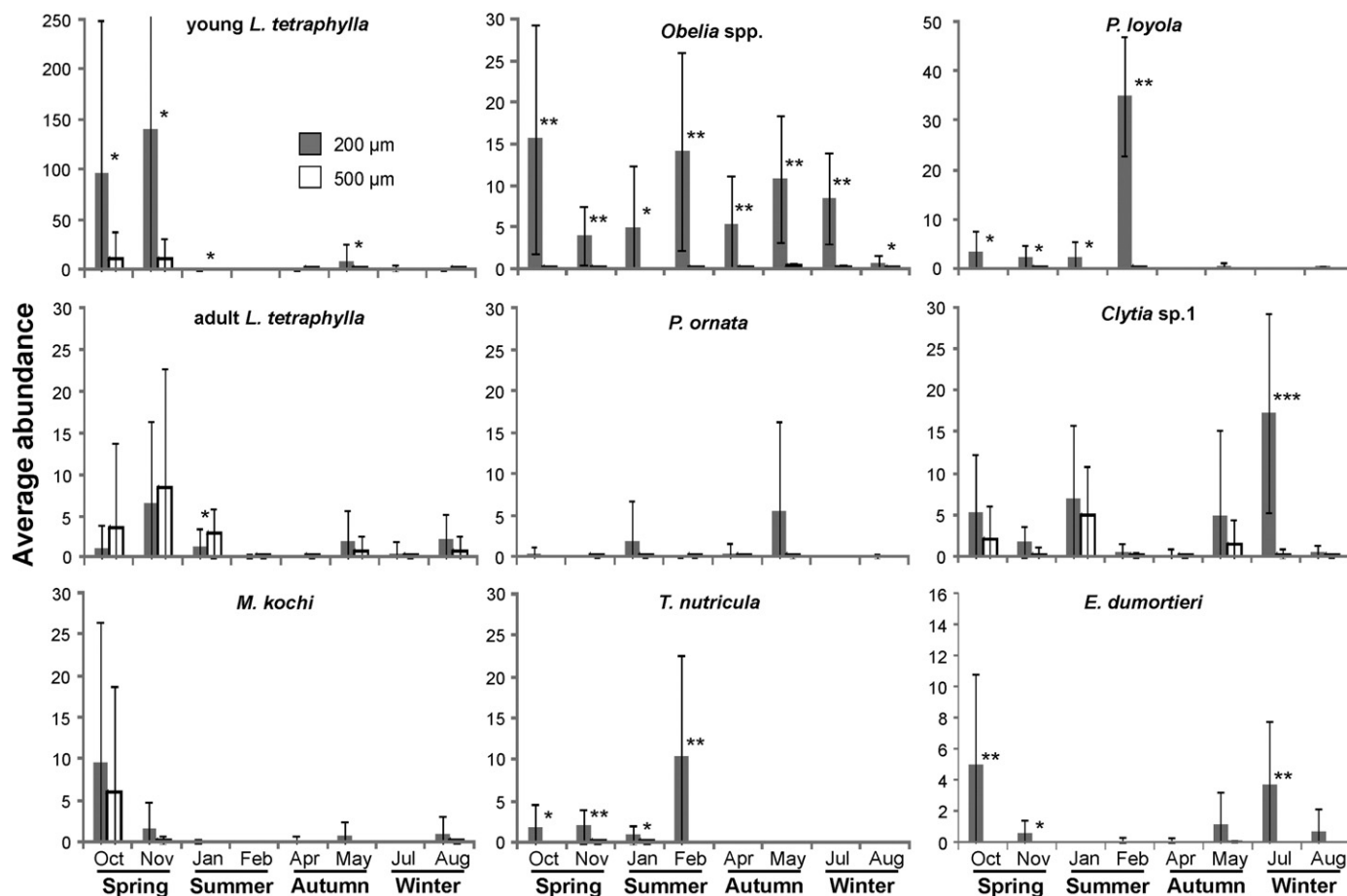
Fig. 7. Monthly averaged abundance (n 10 m^{-3}) of *Liriope tetraphylla*, *Obelia* spp., *Podocoryna loyola*, *Proboscidactyla ornata*, *Clytia* sp.1, *Muggiaea kochi*, *Turritopsis nutricula* and *Ectopleura dumortieri* sampled with 200 and 500 μm mesh between October 2007 and August 2008. Notice different scales. Error bars show the standard deviation. Asterisks indicate months in which the two meshes significantly differ (paired t test; *** = p < 0.001, ** = p < 0.01, * = p < 0.05; n = 9 for each month).

crustaceans, while species richness and evenness are usually dependent on mesh size, diversity indexes are typically less influenced by mesh selection (Favareto et al., 2009; Miloslavic et al., 2014; Riccardi, 2010; Wu et al., 2011).

Not only hydrozoan abundances differ between 200 and 500 μm meshes, but also their assemblage structure, as evidenced by the differences in average species richness, diversity and evenness indexes, dominant taxa, and size composition. For instance, adult *L. tetraphylla* were the second most abundant taxa in the 500 μm mesh, but represented only 3% in the 200 μm. Contrary, the relative abundance of *Obelia* spp. in the 500 μm mesh was almost 10 times smaller than in the 200 μm. This medusa shifted from the second most abundant cnidarian taxa in the finer mesh to the seventieth, being replaced in the coarse net mainly by *Clytia* sp.1, *M. kochi* and adult *L. tetraphylla*. These differences may lead to misinterpretations about functioning of the assemblage and their role in the ecosystem. These taxa have distinct feeding habits — *Obelia* feeds on small protists and bacterians whereas *Clytia* and *Muggiaea* feed on planktonic crustaceans (Boero et al., 2007; Purcell, 1982) — and therefore have different roles in pelagic communities.

Due to their high abundance, young *L. tetraphylla* and *Obelia* spp. (and also *P. loyola* in a lesser extent) were the most biased taxa in terms of total numbers lost. These taxa are common and abundant worldwide in many coastal, shelf and oceanic ecosystems (e.g. Nogueira Júnior et al., 2014; Pagès and Gili, 1992; Palma and Apablaza, 2004), and sampling with 500 μm mesh may provide an unreliable account on their abundance. For instance, Sabatés et al. (2010) found

that hydromedusae were not abundant in NW Mediterranean using 500 μm mesh–net. Considering our results, their view is probably largely biased by the mesh employed. Species like *Obelia* spp., *Podocoryna* spp. and *L. tetraphylla* had low abundances in their samples, but were likely to have been highly underestimated as they were here. Under sampling abundant small taxa is significant not only in terms of abundance and biomass, but the effects may be still higher on estimates of rates and processes such as feeding impact on prey populations and production (Turner, 2004).

Patchiness has long been recognized as a common distributional feature of most planktonic assemblages (e.g. Steele, 1978), and may have been a source of error contributing to the observed differences in both nets. We repeated the haul with the 500 μm mesh net right after the first one in all stations and surveys (not shown), and both 500 μm data sets do not differ significantly in taxonomic or size class composition (PERMANOVA; P > 0.05; n = 72 pairs) suggesting that patch formation was not particularly important here. The absence of statistical significance in all months for species like *P. ornata* and *C. gracilis*, as well as other species in particular months (e.g. *E. maculata* and adults *L. tetraphylla* in October, *Clytia* sp.1 in October and May, or *E. dumortieri* and "other species" in May) may be related to the relatively low sample size within each month (n = 9 pairs). Although this may not pose a big problem for the paired t test, lower number of samples may reduce the sensibility of the test and not allow us to detect small differences (Zar, 2010). Moreover the great variability of these species abundances across the estuary, as noticed by their large standard deviation in Figs. 7 and 8, also provides noise to this analysis. Such
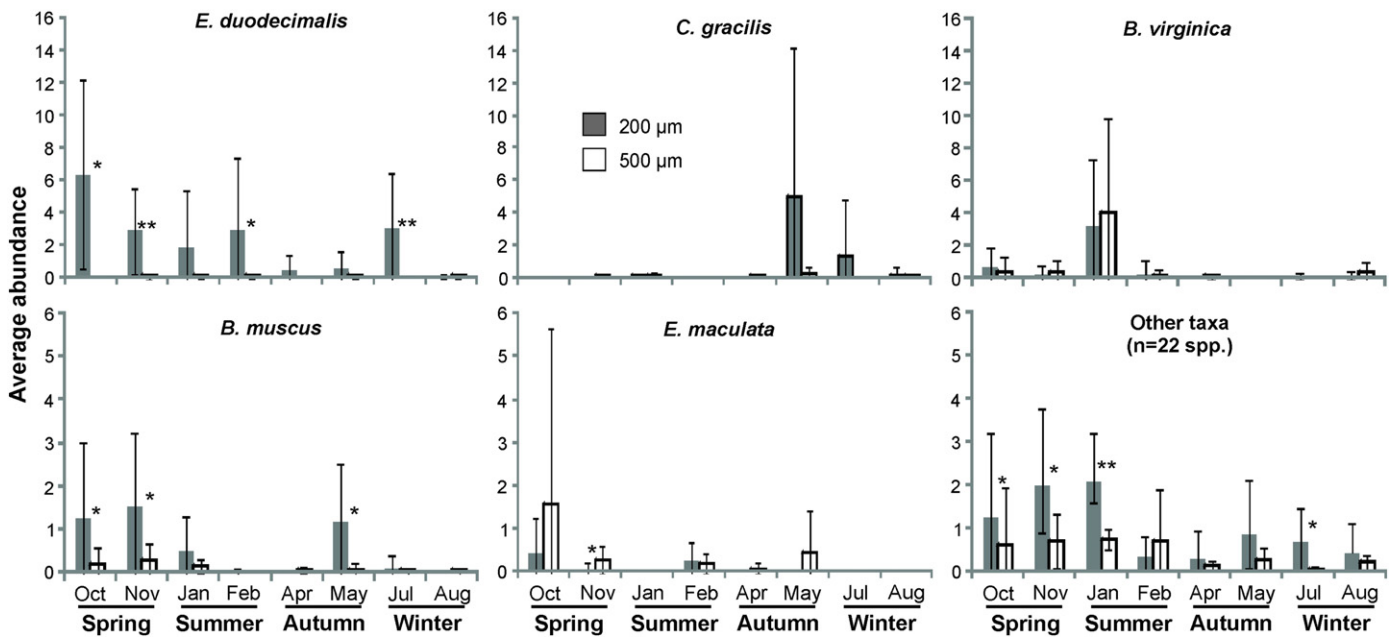
Fig. 8. Monthly averaged abundance (n 10 m^{-3}) of *Eucheilota duodecimalis*, *Corymorpha gracilis*, *Blackfordia virginica*, *Bougainvillia muscus*, *E. maculata*, and other taxa not included in Figs. 7 or 8, sampled with 200 and 500 μm mesh between October 2007 and August 2008. Notice different scales. Error bars show the standard deviation. Asterisks indicate months with signif-icant differences between the two meshes (paired t test; ** = p < 0.01, * = p < 0.05; n = 9 for each month).

mentioned cases would perhaps result in statistical significance if more stations were sampled. However, it would be impracticable to sample more stations in due time. Moreover, for the PERMANOVA the nine pairs of observations within a single month are enough to give a robust power to the analysis (Anderson et al., 2008), not to say all 72 pairs when analyzing the whole data set. Therefore, if some small differences of specific less abundant taxa or size class within particular months were not completely conclusive herein, the general tendencies of the assemblage differences, as well as differences of dominant taxa and size fractions could be clearly emphasized.

The statistical significance of the interaction between mesh size and month factors for both abundance of taxa and size structure (Table 1) suggests that differences between both meshes were not maintained throughout the year. Indeed, monthly CE$_{500}$ changed, reflecting varia-tions of taxa and size composition of the hydrozoan assemblage. The lowest CE$_{500}$, in July, occurred when *Obelia* spp. was the most abundant species. This medusa was always smaller than 2 mm, and among the most underestimated species by the coarse mesh (more than 95% of this medusa was always lost). In January, when the highest CE$_{500}$ occurred, larger size-classes dominated both meshes (Fig. 5), being represented mostly by larger *Clytia* sp.1, *Blackfordia virginica* and adult *L. tetraphylla* (Figs. 7 and 8; online supplementary Table 1), and there-fore a better accuracy of the coarse mesh would be expected in this cam-paign. These monthly variations in relative efficiency of a given mesh emphasize previous observations for crustaceans (Miloslavic et al., 2014; Riccardi, 2010; Vannucci, 1968), and provide serious implications when inferring patterns with coarse meshes since the error embedded is not always the same but it rather depends on taxonomic composition and dominant life history stages of main taxa, further complicating accurate conversions between different meshes. While differences in abundance of taxa and size composition on each mesh are clear and the CE$_{500}$ varied on a monthly basis, the seasonal trend of total hydrozoan abundance was roughly similar in both meshes indicating higher abundances during spring. In parallel, aside from the marked differences in abundance and biomass, the relationship of copepod assemblages and water masses is maintained in different mesh sizes (100 × 330 μm; Wu et al., 2011), however Riccardi (2010) observed

that 80 and 200 μm meshes depict different annual mesozooplankton cycles. Although mesh catchability may vary between environments with different characteristics (Hopcroft et al., 2001; Miloslavic et al., 2014), the absence of spatial variations in the relative efficiency of the meshes was expected in the present study, due to the general proximity and similarity of the stations sampled, corroborating Antacli et al. (2010).

While both meshes provided similar results for a few taxa such as *B. virginca* and *M. kochi*, this is not true for most taxa and our results clearly show the limitations of each mesh size. i) The 500 μm mesh may lead to significant underestimation of planktonic hydrozoan as-semblage mainly due to the escape of high proportions of small abundant hydromedusae like *Obelia* spp., young *L. tetraphylla* and many other hydromedusae species. This mesh also underestimates species richness and the diversity index. ii) The 200 μm mesh may underestimate a few larger taxa such as *E. maculata* and adult *L. tetraphylla* on some occasions. Another disadvantage of finer meshes is that they may clog more easily, especially in estuarine high productive waters (UNESCO, 1968), such as the one studied herein (Brandini et al., 2006). We kept the hauls short and no obvious clogging was noticed, moreover our net has an open mesh area higher than five times the area of its mouth which is enough to keep good filtration efficiency (Miloslavic et al., 2014; Skjoldal et al., 2013; Tranter and Smith, 1968).

Further information on the effect of mesh size selectivity of plank-tonic hydrozoans is necessary, and efficiency of the 200 μm mesh size compared to finer meshes is yet to be tested. Considering that 200 μm mesh efficiently retains organisms larger than 270 μm (see above), it can be assumed this mesh will quantitatively sample hydrozoans with relative good accuracy since they are mostly larger than this size (e.g. Bouillon, 1999). For instance, the dominant taxa of the present study are typically larger than 270 μm even in youngest stages; 7-day old *L. tetraphylla* is larger than 300 μm (Russell, 1953); newly released Brazilian *Obelia* spp. measure between 200 and 350 μm in diameter (Migotto, 1996; Vannucci and Ribeiro, 1955), *Clytia* spp. between 420 and 660 μm (Lindner and Migotto, 2002) and *P. loyola* more than 500 μm (Haddad et al., 2014).

5. Conclusions

In conclusion, this study draws attention to the importance of correctly choosing zooplankton sampling methods, particularly mesh size, to produce accurate data necessary to describe their role in marine ecosystems. Notwithstanding the drawbacks of both meshes outlined above, overall abundances as well as most hydrozoan taxa were better sampled by the 200 μm mesh. These results suggest that the 500 μm mesh does not produce an accurate description of hydrozoan abundance and assemblage structure. Yet, the best choice will always depend on the main goals of each study. If one is trying to describe the biodiversity, for instance, a combination of nets and meshes increases total number of species sampled (Nogueira Júnior, 2012) and would probably be desirable; if focus is solely on larger species (>4 mm), the 500 μm mesh would be more suitable, since it produces general similar results and is less-time-consuming to analyze than finer meshes due to the virtual absence of copepods and other abundant smaller organisms.

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