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Trophic ecology of two syntopic sciaenid species (*Micropogonias furnieri* (Desmarest, 1823) and *Ctenosciaena gracilicirrhus*) (Metzelaar, 1919) in a tropical bay in south-eastern Brazil

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Summary

Analyzed were the diets of two closely related species of Sciaenidae (*Micropogonias furnieri* and *Ctenosciena gracilicirrhus*) coexisting in high abundance in the outer zone of Sepetiba Bay. Their sizes and seasonal niche dimensions were also analysed. The tested hypothesis was that these two abundant species do not overlap in the trophic niche despite occurring in the same area and having similar sizes and body shapes and where an intraspecific overlap is likely to occur. The stomach contents of 198 *M. furnieri* specimens (85–280 mm total length) and 198 *C. gracilicirrhus* (49–131 mm total length) were examined. Quarterly diurnal fish samplings were performed using bottom trawls between winter 2012 and autumn 2013. In each season, three replicate tows were taken against the current during 20 min at the bottom with a towing speed of circa 4.5 km/hr, covering a distance of approximately 1,500 m. The trawl had an 8 m headline, 11 m ground rope, 25 mm stretched mesh and 12 mm mesh cod-end liner. Significant differences were detected in the diet between the two species (Pseudo-F = 5.16; p = .001) and among size classes (Pseudo-F = 2.23; p = .001), but not among seasons (Pseudo-F = 0.36; p = .920), according to PERMANOVA. *Micropogonias furnieri* fed mainly on Polychaeta and *Caprella*, whereas *C. gracilicirrhus* fed preferably on *Caprella*. Both species tended to specialize as they grew in size, with *M. furnieri* preferring Polychaeta, and *C. gracilicirrhus* specializing in *Caprella*. As expected, a high intraspecific niche overlap was observed among the size classes within each species, but not at an interspecific level and with the two syntopic species using different feeding resources.

1 | INTRODUCTION

Usages of the available feeding resources by fish species are crucial aspects of the trophic ecology of the fish community. Knowledge regarding their trophic levels provides important information for the development of conservation strategies and protection of the aquatic biodiversity and thus a better assessment of ecosystem services (Braga, Bornatowisk, & Vitule, 2012; Chase & Leibold, 2003; Greenstreet & Rogers, 2006; Micheli & Halpern, 2005). Knowledge of this aspect of trophic relationship can also provide valuable insight on habitat use, resource availability and behaviour (Azzurro et al., 2014; Braga et al.,

2012; Pianka, 1974). Trophic ecology is directly associated with population dynamics and is fundamental to obtain a holist understanding of how the ecosystem functions (Braga et al., 2012; Hoggarth, Mees, O'Neill, Hindson, & Krishna, 2005; Simpfendorfer, Heupel, White, & Dulvy, 2011).

According to Gerking (1994), the diets of syntopic species in different genera are not expected to overlap, plus the availability of feeding resources influences the number of individuals and species that can coexist in a given habitat (Piet, Pfisterer, & Rijnsdorp, 1998; Schuckel, Sell, Kroncke, & Reiss, 2012). Spatial, temporal and/or ontogenetic segregation among the feeding resources are common strategies

developed by species to avoid intra and interspecific competition (Baeck, Park, Choi, Hug, & Park, 2011; Lomiri, Scacco, Mostarda, & Andaloro, 2008; Young et al., 2010).

The Sciaenidae family is an important group of fishes along the south-western Atlantic coast that has a high number of important commercial fish species. Some genera of Sciaenidae that can occur in sympatry are closely related morphologically. Such is the case with *Micropogonias furnieri* (Desmarest, 1823) and *Ctenosciena gracilicirrhus* (Metzelaar, 1919), which co-occur in high abundance in the outer zone (near the marine connection) of Sepetiba Bay (Araújo et al., 2002), a coastal area in south-eastern Brazil. They have in common an elongate body, small and sub-terminal mouth, presence of barbels and pores in the head, and a long lateral line. These characteristics could lead to the use of similar feeding resources in the outer bay zone and an overlap in the trophic niche (Frehse, Valduga, Corrêa, Pinheiro, & Vitule, 2015; Pombo et al., 2013). However, *M. furnieri* reaches a maximum size of ca. 65 cm (Nakamura, Inada, Takeda, & Hatanaka, 1986), and *C. gracilicirrhus* only ca. 21 cm, therefore they are unlikely to overlap in the trophic niche as adults.

This study aims to describe and compare the *M. furnieri* and *C. gracilicirrhus* diets to test the hypothesis whether the trophic relationship explains their coexistence in the outer zone of Sepetiba Bay. Changes in size and seasons were investigated to assess eventual intra- and interspecific overlap in the diet and to determine available resource usage by these two species during their period of high abundance and coexistence in the bay. We surmise that by building their own trophic niche to facilitate coexistence, these two species do not overlap in the use of the food resources. A high level of intra- or interspecific overlap in their diets would imply a close dietary relationship that would make coexistence difficult in the case of limited resources.

2 | MATERIAL AND METHODS

2.1 | Study area

Sepetiba Bay (22°549′–23°049′S; 43°349′–44°109′W) is a sedimentary embayment at the south-eastern coast of Brazil, with an area of 450 km^2 and encompassing a wide range of habitats, including mangroves, sandbanks and small estuarine areas (Fiszman, Pfeiffer, & Lacerda, 1984; Leal Neto, Legey, González-Araya, & Jablonski, 2006). This microtidal system has tides ranging from 0.5 to 1.5 m. Within the last decade the bay has suffered increased degradation due to industrial outflow and municipal effluents brought into the bay by rivers and drainage channels from the outskirts of the city of Rio de Janeiro. Consequently, large loads of sediment are carried into the bay, causing intensive sedimentation.

The inner zone is influenced by discharges from small perennial rivers, with increased turbidity and temperatures, and decreased salinity; the substratum is mainly muddy, with depths of usually <5 m, and an average salinity of 28‰. The outer zone located near the sea exhibits contrasting environmental conditions: a mainly sandy substratum, comparatively lower temperatures and higher salinity and transparency; a maximum depth of circa 28 m, average salinity of 33‰, and

an average temperature of 25°C. In this study, we examined fishes caught exclusively in the outer bay zone, where the two studied species coexist in high abundance (Araújo et al., 2002).

2.2 | Sampling programme and laboratory procedures

Using bottom trawls, diurnal fish samplings were performed quarterly between winter 2012 and autumn 2013. Three replicate tows were taken in the outer bay zone for each season. Tows were against the current, with 20 min at the bottom and at a towing speed of ca. 4.5 km/hr, covering a distance of approximately 1,500 m. The trawl had an 8 m headline, 11 m ground rope, 25 mm stretched mesh and 12 mm mesh cod-end liner.

Immediately after collection, fishes were anaesthetized in benzocaine hydrochloride (50 mg/L), fixed in 10% formaldehyde–seawater solution, and transferred to 70% ethanol after 48 hr. All fishes were identified to species, measured for total length (mm), and weighed (g). The stomachs were removed from the fish, and food items identified under a stereomicroscope. Each identifiable food item was separated, counted and weighed at a precision of 0.001 g. Items with less than the accuracy of the balance were considered as having a minimum value of 0.001 g.

2.3 | Data analyses

The index of relative importance (IRI) proposed by Pinkas, Oliphont, and Iverson (1971), based on the frequency of occurrence (%FO), percent of total number (%N) and percent of total weight (%W; Berg, 1979; Clark, 1985; Hyslop, 1980) was used to assess the most important food items. The IRI was calculated as: IRI = (%N + %W) × %FO and expressed on a percent basis, such that %IRI for a given food item, i (IRI_i), becomes $\%IRI_i = 100 \times IRI_i / \sum IRI_i$, $i = 1$ to n, where n is the total number of food items considered at a given taxonomic level (Cortès, 1997). Food items with %IRI < 1% and digested material were excluded from the analyses.

We compared food items of these syntopic species among seasons and size-classes. Three size-classes were considered according to the total length range (TL) for *M. furnieri*: Mf_1 < 150 mm (n = 88 individuals), Mf_2 = 150–215 mm (n = 84 individuals), and Mf_3 > 215 mm (n = 26 individuals); and three size classes for *C. gracilicirrhus*: Cg_1 < 75 mm (n = 63 individuals), Cg_2 = 75–100 mm (n = 94 individuals), and Cg_3 > 100 mm (n = 41 individuals).

2.4 | Data treatment

Logarithmic transformations of the biomass values of each food item of both species were performed to address the effects of abundant items; the results were then used to construct a Bray-Curtis similarity matrix. Analysis of Similarity (ANOSIM) was used to compare the diets between the two species. A Permutational Analysis of Variance (PERMANOVA) with 999 permutations was then applied to compare diet differences between species, seasons and size classes. The

analytical design used an approach with hierarchical factors: seasons (four levels; Fixed); species (two levels; Random) nested in seasons; and size class (three levels; Random), nested in species and seasons. The items that most contributed to within-group similarity in size and season were identified by the Similarity Percentage (SIMPER) routine. A cluster analysis based on the group average method was applied to values of %IIR of the main food items. The SIMPROF procedure was used to identify significant differences among the branches of the clustering diagram (Clarke, Somerfield, & Gorley, 2008). All procedures were performed using the PRIMER 6.0 and PERMANOVA+ software (Anderson, Gorley, & Clarke, 2008).

Levin's niche breadth that corresponds to the degree of specialization/generalization of each species was calculated using the equation: $B = 1/\sum P_j^2$, where B, is the Levin's breadth width; P_j, is the proportion of items in a given alimentary category j (estimated by the mass of a given prey/total number of items). B ranges from 1 to n, with n corresponding to the total number of items. When B is close to 1, it means a wide trophic niche and generalization; conversely, when it is close to 0, it means a narrow trophic niche associated with specialization of resource use.

Niche overlapping among size-classes for each species was calculated based on the Pianka index (Pianka, 1974), according to the equation:

$$O_{jk} = \frac{\sum P_{ij} \times P_{ik}}{\sqrt{\sum P_{ij}^2 \sum P_{ik}^2}}$$

where O_{jk} is the Pianka Niche Overlapping Index, and P_{ij} and P_{ik} is the proportion of the resource use of the item i between the species j and k.

3 | RESULTS

A total of 396 stomachs were examined (198 for each species). *Micropogonias furnieri* had 165 stomachs with identifiable food items and 33 (16.9%) empty stomachs, whereas *C. gracilicirrhus* had 186 stomachs with food items and 12 (6.2%) that were empty.

Eighteen food items were identified for *M. furnieri*, with a predominance of Polychaeta (IIR% = 66.86) and *Caprella* (IIR% = 26.04). For *C. gracilicirrhus*, a total of 17 food items were identified, with a high predominance of *Caprella* (IIR% = 92.14; Table 1). Other secondary items were Gammaridae for both species, Decapoda for *M. furnieri*, and Mysidacea for *C. gracilicirrhus* (Figure 1).

Significant differences in the diet of the two species were also detected according to Analysis of Similarity (ANOSIM; R global = .293; p = .1%). The Similarity of Percentage (SIMPER) analysis showed that the items most contributing to within-group similarity for *M. furnieri* were Polychaeta (46.6% average similarity) and *Caprella* (45.1% average similarity), whereas *Caprella* (93.4% average similarity) contributed the most to the within-group similarity for *C. gracilicirrhus*.

TABLE 1 Frequency of occurrence (%FO), numeric percentage (%N), mass percentage (%M), and percentage of the index of relative importance (%IRI) of feeding items for *M. furnieri* (165 stomachs with contents; Total Length = 85–280 mm) and *C. gracilicirrhus* (186 stomachs, Total Length = 49–131 mm) between winter 2012 and autumn 2013, outer Sepetiba Bay zone, Brazil
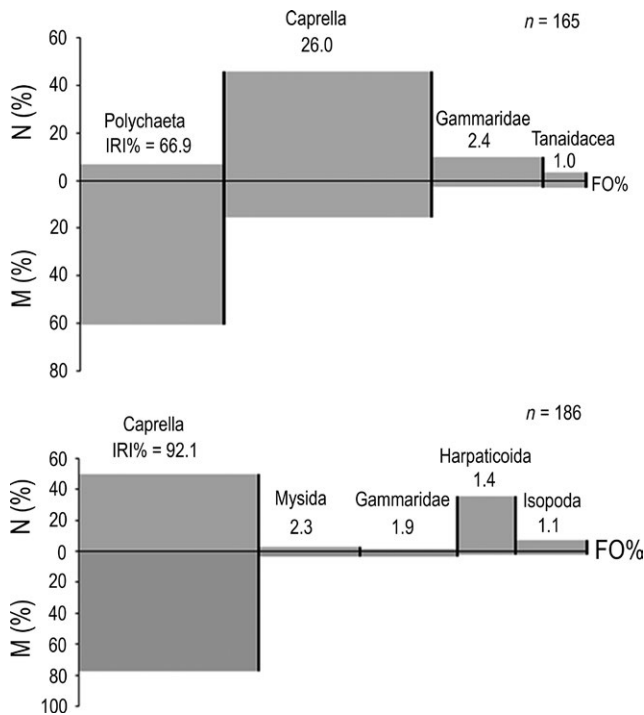
Feeding items	*Micropogonias furnieri*				*Ctenosciaena gracilicirrhus*			
	%FO	%N	%M	%IRI	%FO	%N	%M	%IRI
Crustacea								
Caprella	58.1	46.0	15.4	26.0	82.8	50.0	77.6	92.1
Tanaidacea	11.6	3.5	2.9	1.0	7.1	0.2	0.4	<0.1
Ostracoda	23.2	7.5	0.5	0.5	16.2	0.8	0.3	0.1
Gammaridea	30.8	10.0	2.5	2.4	44.9	2.0	3.0	1.9
Isopoda	11.6	1.4	0.1	0.1	33.3	7.0	2.2	1.1
Harpacticoida	17.2	3.5	0.2	0.2	26.8	36.0	2.3	1.4
Cumacea	11.6	2.4	0.8	0.3	10.6	0.3	0.2	<0.1
Decapoda	7.6	0.7	4.5	1.0	8.1	0.2	2.3	0.3
Ciclopoida	1.0	0.2	<0.1	<0.1	0.5	<0.1	<0.1	<0.1
Mysidacea	3.0	0.3	0.1	<0.1	47.0	2.7	3.4	2.3
Calanoida	5.6	14.6	1.0	0.6	7.1	0.4	0.1	<0.1
Anomura	1.0	0.1	0.9	<0.1	1.0	<0.1	0.3	<0.1
Brachyura	2.5	0.2	8.8	0.6	3.5	0.1	2.3	0.1
Brachyuralarvae	1.5	0.1	<0.1	<0.1	—	—	—	—
Polychaeta								
Polychaeta	39.9	6.7	60.5	66.9	6.6	0.1	5.1	0.5
Polichaetatubs	1.5	0.2	0.2	<0.1	—	—	—	—
Teleostei								
Teleostei	—	—	—	—	0.5	<0.1	0.2	<0.1
Teleosteiscales	9.6	2.3	0.7	0.3	7.1	0.2	0.1	<0.1
Algae	4.5	0.4	0.7	0.1	3.0	0.1	0.2	<0.1

FIGURE 1 Index of Relative Importance (IRI%) for the main food items of *M. furnieri* (above) and *C. gracilicirrhus* (below). Numerical percentage (*N*%), mass percentage (*M*%) and frequency of occurrence (FO%), winter 2012 to autumn 2013, outer Sepetiba Bay zone, Brazil. IIR% represented by rectangular area. *n*, number of examined stomachs with contents. Size range: *M. furnieri*, TL = 85–280 mm; *C. gracilicirrhus*, Total Length = 49–131 mm
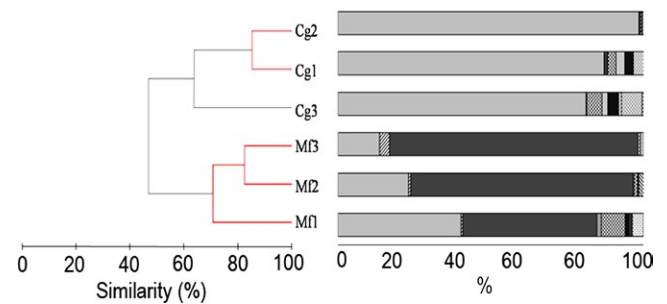

FIGURE 2 Cluster analysis on % IRI (Index of Relative Importance) for feeding items of *M. furnieri* (Mf) and *C. gracilicirrhus* (Cg) and size classes (1, smallest; 2, intermediate; 3, largest), winter 2012 to autumn 2013, outer Sepetiba Bay zone, Brazil. Feeding items (%): *Caprella* (light gray), Tanaidacea (right diagonal line), Polychaeta (dark gray), Ostracoda (horizontal line), Gammaridea (square), Isopoda (zigzag), Hapacticoida (black), Cumacea (black with white circles), Decapoda (dashes), Mysidacea (Diamond), Brachyura (left diagonal line). Cutoff point of the groups at 65% of similarity

Resources differed between the two species (Pseudo-*F* = 5.16; *p* = .001) and were influenced by size (Pseudo-*F* = 2.22; *p* = .001), but not by seasons (Pseudo-*F* = 0.36; *p* = .920) according to PERMANOVA (Table 2).

Four groups of species/size-classes were detected by cluster analysis and the SIMPROF test (Figure 2). Group 1 was formed by the smallest size-classes of *C. gracilicirrhus* (Cg$_1$ and Cg$_2$), which fed mainly on *Caprella* and with Mysidacea and Gammaridea as secondary items. Group II was formed by only the largest size *C. gracilicirrhus* (Cg$_3$) that fed almost exclusively on *Caprella*; group III was formed by the largest *M. furnieri* (Mf$_3$ and Mf$_2$) individuals that fed mainly on Polychaeta and to a lesser extent on *Caprella*. Group IV was formed by the smallest size-classes of *M. furnieri* (Mf$_1$), and which fed mainly on Polychaeta and *Caprella* (Figure 2).

According to the niche breadth, both species had a trend toward specialization as they reached larger sizes. *Micropogonias furnieri* decreased its niche breadth from 3.87 in the smaller size class (Mf$_1$) to 2.43 in the intermediary size class (Mf$_2$), and to 1.72 in the largest size class (Mf$_3$). Similarly, *C. gracilicirrhus* decreased its niche breadth from 2.53 in the smallest size class (Cg$_1$) to 2.0 in the intermediary size class (Cg$_2$), and then to 1.23 in the largest size class (Cg$_3$). Overall, *M. furnieri* had a comparatively higher niche breadth than did *C. gracilicirrhus*, with the first species specializing on Polychaeta and the second on *Caprella* as the species grew.

Intraspecific niche overlapping was found in each species among the different size classes, but no significant interspecific overlapping was found among size-classes between both species (Table 3).

4 | DISCUSSION

Micropogonias furnieri and *C. gracilicirrhus*, as expected, use different trophic resources in the outer Sepetiba Bay zone, where they co-exist with overlapping size ranges. In this period, both species tend

TABLE 2 PERMANOVA results for comparisons of feeding items between species (2 levels), seasons (4 levels) and size classes (3 levels), for *M. furnieri* and *C. gracilicirrhus*, winter 2012 to autumn 2013, outer Sepetiba Bay zone, Brazil

Source	df	Pseudo-F	p (perm)	Unique-perms
Seasons	3	0.36	.920	999
Species (Seasons)	4	5.16	.001*	999
Size (Species (Seasons))	14	2.23	.001*	997
Residual	354			
Total	375			

df, degrees of freedom; *p* (perm), probability; Pseudo-*F*, statistics; Uniqueperms, number of permutations.
*Significant results.

TABLE 3 Pianka overlaping niche for trophic resources between species and size classes of *M. furnieri* (Mf) and *C. gracilicirrhus* (Cg), outer Sepetiba Bay zone, winter 2012 to autumn 2013, Brazil

	Mf_1	Mf_2	Mf_3	Cg_1	Cg_2
Mf_1					
Mf_2	**0.96**				
Mf_3	**0.94**	**0.97**			
Cg_1	0.44	0.26	0.18		
Cg_2	0.52	0.35	0.30	**0.98**	
Cg_3	0.44	0.27	0.21	**0.98**	**0.99**

Significant overlapping according to Labropoulou and Eleftheriou (1997) > 0.6 in bold. Codes for sizes in data analysis section: 1, smallest size class; 2, intermediate size class; 3, largest size class.

to specialize, with a high trophic overlap among their different size groups. While *M. furnieri* had Crustacea and Polychaeta as main food categories with a trend for specialization in the latter category, the *C. gracilicirrhus* fed mainly on Crustacea, with a trend to specialization in *Caprella*. The preferential use of Polychaeta by *M. furnieri* was already reported by Mendoza-Carranza and Vieira (2008) for the Patos Lagoon estuary in southern Brazil (lat. 33°S), for the Sepetiba Bay in south-eastern Brazil (lat. 23°S) by Pessanha and Araújo (2014) and Guedes, Araújo, Pessanha, and Milagre (2015), and for Caraguatatuba Bay (lat. 23.4°S) by Denadai et al. (2015). Those studies also emphasized the high trophic plasticity of this species, as in the Caraguatatuba Bay, where *M. furnieri* feeds mainly on crustaceans, bivalve siphons and polychaets, with the ingestion of bivalve siphons being an opportunistic behaviour due to the presence of a large bank of the bivalve *Tivela mactroides* in the study area (Denadai et al., 2015). For the *C. gracilicirrhus*, information is more scarce, but the preference for crustaceans was previously reported for Ubatuba Bay (Cunningham, 1989) and Caraguatatuba Bay (Pombo et al., 2013), both areas on the northern São Paulo coast (24°S), and for Sepetiba Bay (Guedes et al., 2015) that reported this species as an opportunist feeder.

Both species had slight changes in their diets as they grew. In the smaller size classes *Micropogonias furnieri* preferably ate crustaceans, then shifted to Polychaeta and narrowed their breadth niche when they reached larger sizes. Other studies also indicate ontogenetic changes in the diet of *M. furnieri*, with shifts in forage to the bottom of water column in their earliest life cycle (Pessanha & Araújo, 2014) as a result of constraints in their feeding apparatus (e.g., mouth position, increase in the gape, position of the pores and barbels, etc.).

Ctenosciena gracilicirrhus fed preferably on *Caprella* especially after reaching larger sizes, with a trend for specialization on this feeding resource. Guedes et al. (2015) found that this species consumes several other items, such as Caprellidae, Amphipoda and Decapoda and is thus classified as an opportunist feeder. These findings were also corroborated by Amezcua, Nash, and Veale (2003), who reported several secondary feeding items as a means to reduce competition with other species.

Low trophic overlap is expected for these two morphologically close and syntopic species that seem to use this strategy to allow their

coexistence in high abundance in the outer zone of the Sepetiba Bay. Whereas Polychaeta, and to a lesser extent *Caprella*, were the preferable feeding items for *M. furnieri*, *C. gracilicirrhus* had *Caprella* as the main food item. Other crustaceans, mainly Gammaridae, Decapoda and Mysidacea were secondary items for these two species. Moreover, interspecific differences in the diet along with the size dimension were found between the two species, but there was a high intraspecific overlap within size groups of each species. Therefore, some levels of intraspecific niche-overlapping are allowed, and which tend to lead to structural adaptations that allow small variations in the acquisition of resources that ultimately result in the sharing of resources.

Differences in the diet of these two studied species tended to increase as they reached larger sizes, with a tendency of both species to specialize. The *M. furnieri* had a strong trend to specialize on Polychaeta whereas *C. gracilicirrhus* tended to specialize on *Caprella*. The combined influence of factors to search and acquire feeding resources, such as swimming capacity, and morphological features that determine prey selection (e.g., mouth size, stomach capacity) and visual capacity for prey detection, have great importance for the coexistence of species (Frehse et al., 2015).

Both studied species had a strong tendency for specialization as they grew, with decreasing in niche breadth. In the smaller size classes, both species tend to use a higher number of available resources, than specializing in a given food item as they reach large sizes, thus avoiding inter and intraspecific competition (Pessanha & Araújo, 2014; Wootton, 1990). As reported by Amundsen, Gabler, and Staldvik (1996), a fish population with narrow niche breadth necessarily has individuals with specialized and narrow niches, whereas populations with a wide trophic niche can be formed either by individuals with a wide or narrow niche breadth or by a combination of both.

Low trophic niche overlapping between the two studied species suggests a stable coexistence developed by both species, which allowed them to reach great abundance in the outer bay zone. Our findings suggest this well-established coexistence and the probable availability of resources that allow intraspecific diet overlapping within each species, but not between the two different species. This confirms that partitioning of the feeding resources and ontogenetic changes are among the most important niche dimensions used by fish species to coexist.

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