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Spongivory by nudibranchs on the coast of Rio de Janeiro state, southeastern Brazil

(Mollusca, Gastropoda)

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Nudibranch gastropods are carnivores and most dorid nudibranchs are spongivores, preying on a single or a few species of sponges. The feeding biology has important biological, ecological and evolutionary implications, and many characteristics of nudibranchs likely arose from co-evolution with diet organisms. Data on spongivory by dorid nudibranchs are available for many species from the Indo-Pacific, eastern Pacific and the Mediterranean Sea, but such information is scarce for the southwestern Atlantic. In this study we provide qualitative data on spongivory by dorid nudibranchs along the coast of Rio de Janeiro State, southeastern Brazil, including the identification of the species involved. A total of 94 spongivory events were observed between 12 nudibranch and 13 sponge species, greatly expanding our knowledge of predator-prey interactions. Among the sponges preyed upon, one species belongs to the class Homoscleromorpha (*Plakina* sp.) and 12 species to the class Demospongiae. Our observations show that spongivorous nudibranchs have a more diverse diet than previously thought. Additional observations on a higher number of species from different biogeographic regions are needed for a better understanding of the feeding preferences of the diverse and ecologically important spongivorous dorid nudibranchs.

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Introduction

Nudibranch gastropods are carnivores and many species have specialized diets, reportedly preying on a single or few species of sessile marine invertebrates (Wägele 2004, Rudman & Bergquist 2007). Nudibranchs are a key group for studying the evolution of chemical defence and feeding specialization in the marine environment (Faulkner & Ghiselin 1983, Cimino & Ghiselin 1999, Rudman & Bergquist 2007). The feeding biology has important biological, ecological and evolutionary implications, and many characteristics of nudibranchs arose from co-evolution with diet organisms (Becerro et al. 2003). There are approximately 3000 species of nudibranchs worldwide (Wägele & Klussman-Kolb 2005), of which approximately one third feed on sponges (Wägele 2004).

Dorid nudibranchs are the most diverse group of sponge predators. Many species feed on sponges of the order Chondrosida, most of which have no skeleton (except the genera *Chondrilla* Schmidt, 1862 and *Thymosia* Topsent, 1895, which have siliceous spicules and sponging fibres, respectively); Dictyoceratida and Dendroceratida, which have spongin

fibres, but no mineral skeleton; and Haplosclerida, with siliceous spicules often embedded in spongin fibres (Rudman 1984, Hooper & Van Soest 2002). Most of these sponge groups present well-developed chemical defences (Cimino & Ghiselin 1999, 2009).

Data on spongivory by nudibranchs is available for many species from the Indo-Pacific, eastern Pacific and the Mediterranean Sea (Thompson 1976, McDonald & Nybakken 1997, Rudman & Bergquist 2007, Penney 2013), but such information is scarce from the southwestern Atlantic (Granato et al. 2000, Pereira et al. 2012). For decades, nudibranchs were studied in the coast of São Paulo, southeastern Brazil (Er. Marcus 1955, 1957, 1958, Ev. Marcus & Er. Marcus 1967, Ev. Marcus 1970), but data on feeding activity included in these studies is scarce. With more than 8000 km of coastline, only two cases of spongivory by nudibranchs, with the identification of both predator and prey species involved, were recorded on the Brazilian coast: the predation of the sponge *Hymeniacion* aff. *heliophila* (Parker, 1910) by *Doris januarii* (Bergh, 1878) (Granato et al. 2000, as *Doris* aff. *verrucosa* Linnaeus, 1758), and the predation of *Dysidea* sp. by *Felimare lajensis* (Troncoso, García & Urgorri, 1998) (Pereira et al. 2012).

Table 1. Number of sponge predation events by each nudibranch species recorded in Rio de Janeiro State. Localities indicated between parentheses: **AC**, Arraial do Cabo; **BZ**, Armação dos Búzios; **TP**, Cabo Frio: tidal pool; **PI**, Cabo Frio: Papagaio island; **RJ**, Rio de Janeiro.

	<i>Felimida binza</i>	<i>Felimida paulomarcioi</i>	<i>Felimare lajensis</i>	<i>Tyrinna evelinae</i>	<i>Cadlina rumia</i>	<i>Diaulula greeleyi</i>
<i>Chelonaplysilla erecta</i>	2 (AC), 1 (TP)					
<i>Darwinella</i> sp.		4 (AC), 3 (TP)				
<i>Dysidea etheria</i>			4 (RJ), 4 (PI)	20 (TP), 3 (AC)	1 (TP)	
<i>Lissodendoryx isodictialis</i>						10 (TP)
<i>Amphimedon viridis</i>		1 (TP)				
Chalinidae unidentified				3 (TP)		
<i>Haliclona</i> sp.					5 (TP)	2 (TP)
<i>Callyspongia</i> sp.					3 (TP)	
<i>Scopalina</i> sp.					2 (TP), 1 (BZ)	
Total events recorded	3	8	8	26	12	12
	<i>Jorunna spazzola</i>	<i>Jorunna spongiosa</i>	<i>Rostanga byga</i>	<i>Discodoris hummelincki</i>	<i>Doris kyolis</i>	<i>Dendrodoris krebsii</i>
<i>Dysidea etheria</i>					2 (TP)	
<i>Lissodendoryx isodictialis</i>					3 (TP)	
<i>Mycale microsigmatosa</i>			3 (PI)			
<i>Haliclona</i> sp.		2 (TP)		1 (TP)	4 (TP)	1 (TP)
<i>Callyspongia pallida</i>	2 (TP)	2 (TP)				
<i>Callyspongia</i> sp.		2 (TP)				
<i>Chalinula</i> sp.	1 (PI)					
<i>Plakina</i> sp.					2 (TP)	
Total events recorded	3	6	3	1	11	1

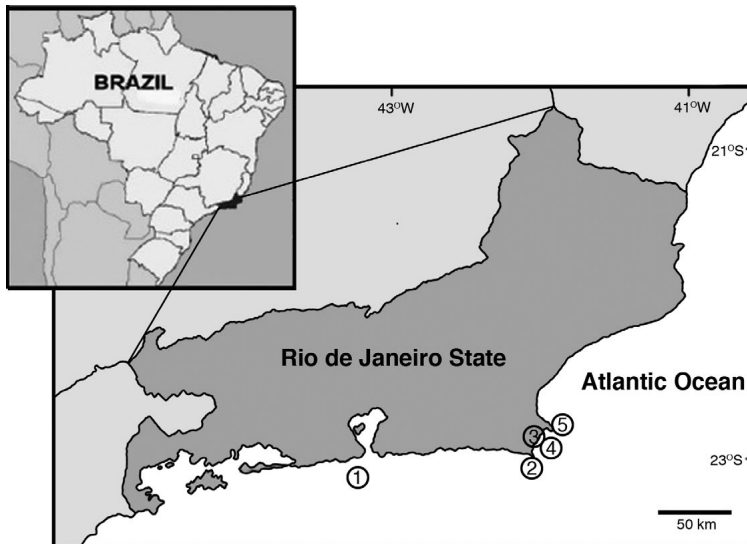


Fig. 1. Study area and collection sites on the coast of Rio de Janeiro State, southeastern Brazil. 1. Cagarras Archipelago, Rio de Janeiro; 2. Forno beach, Arraial do Cabo; 3. Tide pool near Canal do Itajuru, Cabo Frio; 4. Papagaio island, Cabo Frio; 5. Tartaruga beach, Armação dos Búzios.

In this study we provide new data on spongivory by dorid nudibranchs along the coast of Rio de Janeiro State, southeastern Brazil, including the identification of the species involved and comparing their diet patterns to those reported for species in other regions of the world.

Material and methods

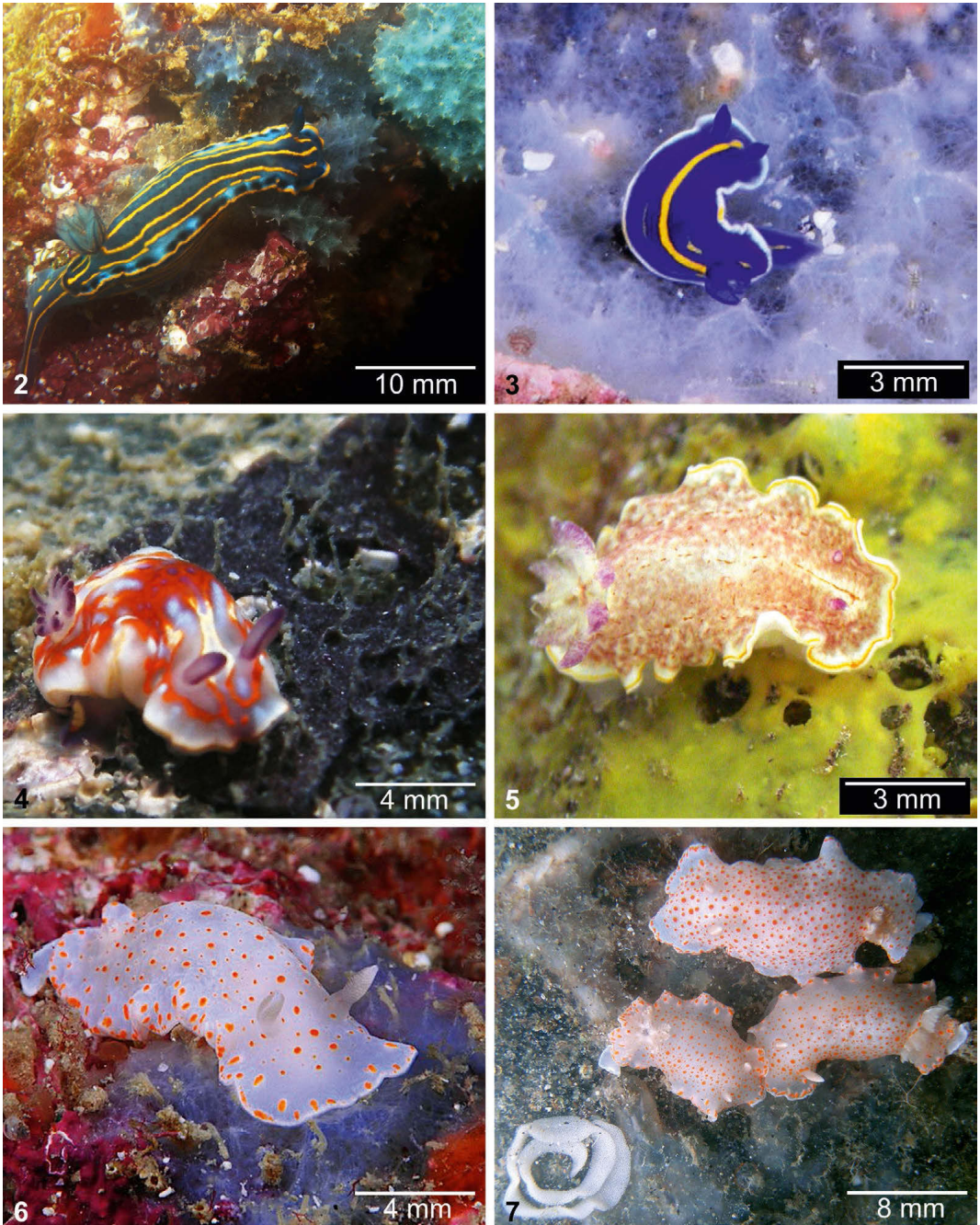
The study was performed at five sites in Rio de Janeiro State, on the southeastern Brazilian coast (Fig. 1): Site 1, Rio de Janeiro: Cagarras archipelago (0–12 m depth) (43°12' W, 23°01' S); Site 2, Arraial do Cabo: Forno beach (0–3 m depth) (42°00'52" W, 22°58'06" S); Site 3, Cabo Frio: a tidal pool in the end of Itajuru channel (intertidal) (42°00'17" W, 22°53'13" S); Site 4, Cabo Frio: Papagaio island (0–20 m depth) (41°59' W, 22°53' S); Site 5, Armação dos Búzios: Tartaruga beach (1–3 m depth) (41°54' W, 22°45' S). Sampled areas are characterized by hard substrates such as rocky shores, rocky reefs and tide pools, colonized by a rich community of benthic invertebrates and algae. Cagarras archipelago (site 1) is situated 5 km off the urban zone of Rio de Janeiro city and its waters receive more effects of the city pollution.

Field observations were made by free diving and SCUBA from the intertidal zone to 20 m depth, between October 2007 and August 2013. The study sites were randomly sampled and all the nudibranchs found during 1–4 h each day were recorded, with a total of 165 h of sampling. Specimens were photographed in situ with a digital camera. The behaviour of the dorids on the sponges was observed and recorded. When a dorid was

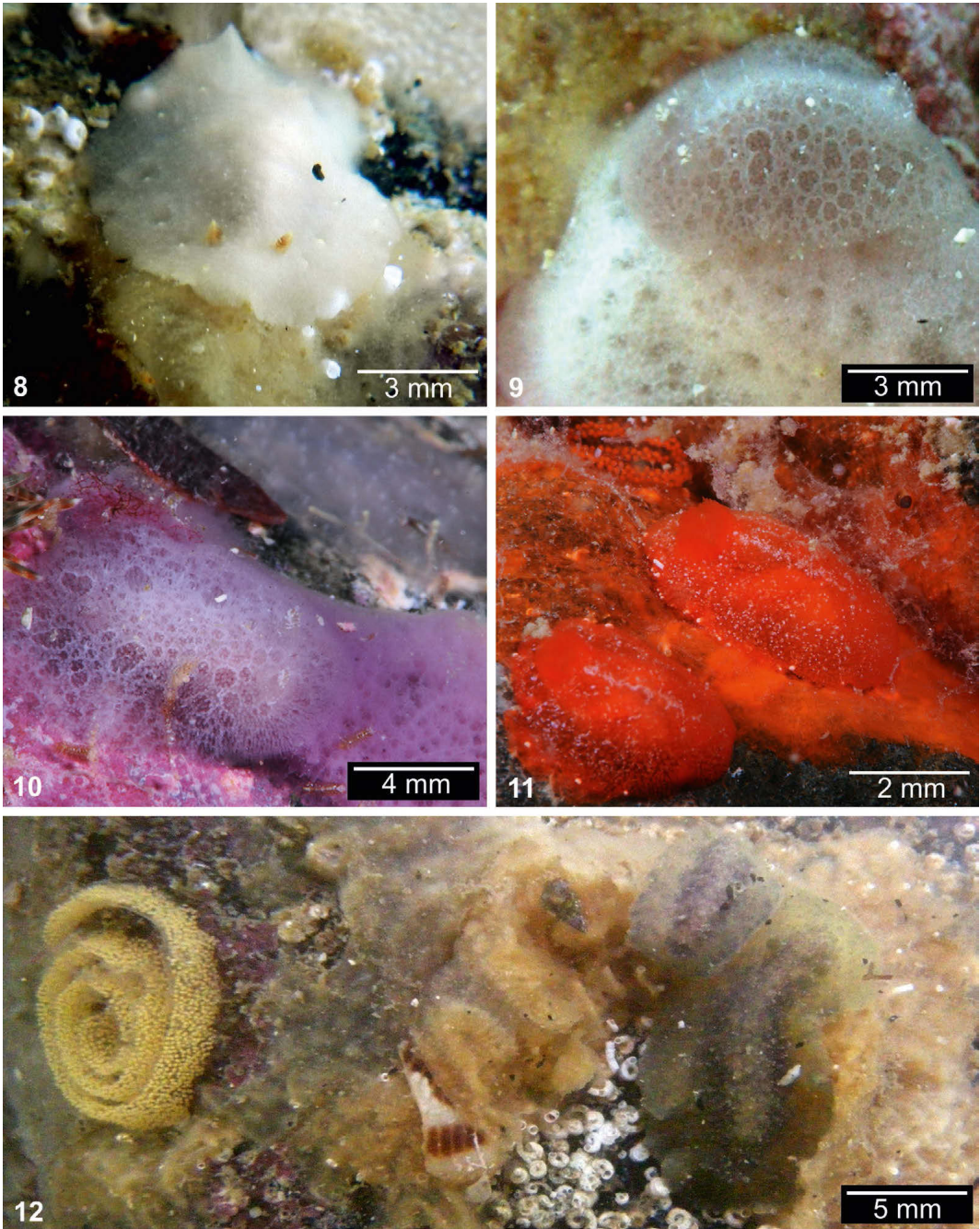
found above or near the sponge but without evidences of foraging, the predation was not confirmed. A predation event was confirmed only when the dorid nudibranch was observed effectively feeding, projecting its oral apparatus into the sponge, or when scars were visible on the sponge surface. Nudibranchs species were identified based on the external morphology and colour of in situ photographs and field records, following Er. Marcus (1955), Valdés et al. (2006) and Alvim & Pimenta (2013). When there were doubts on the identification of the nudibranchs, they were collected and preserved in ethanol 70 %. Specimens were dissected in the Laboratório de Malacologia do Museu Nacional / Universidade Federal do Rio de Janeiro (MNRJ) and the identification was confirmed through the morphology of the radula and reproductive system. Sponges were collected, preserved directly in ethanol 70 % and identified in the Laboratório de Porifera do Museu Nacional / Universidade Federal do Rio de Janeiro (MRNJ) through the analysis of external morphology, colour, organization of the skeleton and the shape and size of spicules and fibres. Sponge classification followed the *Systema Porifera* (Hooper & Van Soest 2002) and the *World Porifera Database* (Van Soest et al. 2015).

Results

A total of 94 spongivory events were observed between 12 nudibranchs and 13 sponge species (Table 1). The nudibranchs observed feeding on sponges were *Felimida binza* (Er. Marcus & Ev. Marcus, 1963), *Felimida paulomarcioi* (Domínguez, García



Figs. 2-7. Spongivory events by nudibranchs from Rio de Janeiro, southeastern Brazil. 2-3. *Felimare lajensis* preying on *Dysidea etheria* (2, adult; 3, juvenile). 4. *Felimida binza* preying on *Chelonaplysilla erecta*. 5. *Felimida paulomarcioi* preying on *Darwinella* sp. 6. *Tyrinna evelinae* preying on *Dysidea etheria*. 7. *Tyrinna evelinae* and its egg mass over another prey, an unidentified chalinid species (order Haplosclerida). (Photographs 2, 4, 7 by Vinicius Padula; 5 by Thalita Belmonte; 3, 6 by Luiz Fernando Cassino).



Figs. 8-12. Spongivory events by nudibranchs from Rio de Janeiro, southeastern Brazil. 8. *Cadlina rumia* preying on *Haliclona* sp. 9. *Jorunna spongiosa* preying on *Callyspongia pallida*. 10. *Jorunna spazzola* preying on *Chalinula* sp. 11. *Rosstanga byga* preying on *Mycale microsigmatosa*. 12. *Doris kyolis* and its egg mass over *Lissodendoryx isodictyalis*. (Photograph 8 by Juliana Alvim; 9, 12 by Vinicius Padula; 10, 11 by Luiz Fernando Cassino).

& Troncoso, 2006), *Felimare lajensis* (Troncoso, García & Urgorri, 1998) and *Tyrinna evelinae* (Er. Marcus, 1958) (Chromodorididae) (Figs 2–7); *Cadlina rumia* Er. Marcus, 1955 (Cadlinidae) (Fig. 8); *Diaulula greeleyi* (MacFarland, 1909), *Jorunna spazzola* (Er. Marcus, 1955), *Jorunna spongiosa* Alvim & Pimenta, 2013, *Rostanga byga* Er. Marcus, 1958 and *Discodoris hummelincki* (Ev. Marcus & Er. Marcus, 1963) (Discodorididae) (Figs 9–11); *Doris kyolis* (Ev. Marcus & Er. Marcus, 1967) (Dorididae) (Fig. 12); and *Dendrodoris krebsii* (Mörch, 1863) (Dendrodorididae).

Among the 13 sponge species preyed upon, one belongs to the class Homoscleromorpha: *Plakina* sp. (order Homosclerophorida); and 12 species to the class Demospongiae: *Chelonaplysilla erecta* (Row, 1911), *Darwinella* sp., *Dysidea etheria* (de Laubenfels, 1936) (orders Dendroceratida and Dictyoceratida), *Lissodendoryx isodictialis* (Carter, 1882), *Mycale microsigmatosa* Arndt, 1927 (order Poecilosclerida), *Amphimedon viridis* Duchassaing & Michelloti, 1864, Chalinidae unidentified, *Haliclona* sp., *Callyspongia pallida* Hechtel, 1965, *Callyspongia* sp., *Chalinula* sp. (order Haplosclerida), *Scopalina* sp. (order Halichondrida) (Table 1).

Cadlina rumia (Fig. 8) and *Doris kyolis* (Fig. 12) were the species with the most diverse diets, each preying upon four different sponges, including spiculate and non-spiculate species (Table 1). *Felimida paulomarcioi* (Fig. 5), *Tyrinna evelinae* (Figs 6–7) and *Diaulula greeleyi* fed on two species of sponge each (Table 1). *Felimida binza* was observed feeding only on *Chelonaplysilla erecta* (Fig. 4), *Felimare lajensis* only on *Dysidea etheria* (Figs 2–3), *Rostanga byga* only on *Mycale microsigmatosa* (Fig. 11), and *Discodoris hummelincki* and *Dendrodoris krebsii* only upon *Haliclona* sp. *Jorunna spazzola* and *Jorunna spongiosa* were observed feeding on species of the order Haplosclerida: *Callyspongia pallida* (Fig. 9), *Callyspongia* sp., *Haliclona* sp. and *Chalinula* sp. (Fig. 10). *Haliclona* sp. is consumed by six different nudibranch species, of four different families (Cadlinidae, Discodorididae, Dorididae and Dendrodorididae) and *Dysidea etheria* is the prey of four different nudibranch species in three different families (Chromodorididae, Cadlinidae and Dorididae) (Table 1).

Discussion

Spongivory was commonly observed in our study, with a total of 94 observations in five different localities. Our data shows similarity to that recorded in other regions of the world, but there are divergences from previous hypotheses of feeding preferences by nudibranch families and genera, which are discussed below.

Chromodorididae

Species of the genus *Tyrinna* have been hypothesized to feed on dysideid sponges (Fontana et al. 1998, Rudman & Bergquist 2007), although direct observations of feeding have been lacking for any species of the genus. This hypothesis was derived from the presence of secondary metabolites (pallescensin A and dehydropallescensin-2), known only from *Dysidea*, which was found in the mantle of *Tyrinna delicata* (Abraham, 1877) from Patagonia (Fontana et al. 1998, Cimino & Ghiselin 2009, as *Tyrinna nobilis* Bergh, 1898). Our observations confirm that *Tyrinna evelinae* feeds extensively on a dysideid sponge, *Dysidea etheria* (total of 23 records). However, *T. evelinae* was also recorded feeding upon an unidentified chalinid species (order Haplosclerida) (three records), showing that *Tyrinna* species do not predate exclusively on dysideid sponges.

Dysideids were reported to be the sole food of the genus *Hypselodoris* Stimpson, 1855 (Hochlowski et al. 1982, Grode & Cardellina 1984, McDonald & Nybakken 1997) with a few exceptions (Ávila et al. 1991, Rudman & Bergquist 2007, Padilla Verdín et al. 2010). Recently, the genus *Hypselodoris* was reported to be polyphyletic with eastern Pacific and Atlantic species being separated as part of another clade, not closely related, named *Felimare* Ev. Marcus & Er. Marcus, 1967 (Johnson & Gosliner 2012). *Felimare lajensis*, a common species in the southeastern Brazilian coast, was observed to feed only on *Dysidea etheria*. A total of eight feeding records were made in two different localities, suggesting a close and perhaps species-specific predator-prey relationship between these two species. In addition, Pereira et al. (2012) identified in *F. lajensis* a compound previously recorded only from *Dysidea etheria* and *Dysidea* sp., further supporting this hypothesis.

The genus *Chromodoris* Alder & Hancock, 1855 was also separated into two major groups, with eastern Pacific and Atlantic species allocated to the genus '*Felimida* Ev. Marcus, 1971' by Johnson & Gosliner (2012). Based on observations made mostly on Indo-Pacific species, *Chromodoris* was reported to feed almost exclusively on sponges from the family Darwinellidae (Rudman & Bergquist 2007). In the present study, *Felimida binza* was observed feeding only on the dark purple darwinellid sponge *Chelonaplysilla erecta* (three observations). Preserved specimens of *F. binza* generally present a digestive gland with dark purple content (V. Padula pers. obs.), corroborating our observations. The other *Felimida* species in Rio de Janeiro State, *F. paulomarcioi*, feeds on *Darwinella* sp. (seven observations). However, this species also feeds on *Amphimedon viridis* (order Haplosclerida). This is the first record of a *Felimida* species feeding on a haplosclerid sponge.

Cadlinidae

The genus *Cadlina* Bergh, 1878 was traditionally considered a basal group among the chromodoridids, but it is now allocated in a separate family, Cadlinidae (Johnson 2011). Previous records indicate that *Cadlina* feeds on sponges of the orders Halisarcida (family Halisarcidae) and Dendroceratida (families Dysideidae and Darwinellidae) (McDonald & Nybakken 1997, Rudman & Bergquist 2007). Recently, Penney (2013) reported that *Cadlina luteomarginata* MacFarland, 1966 feeds on several species of sponges in the northeastern Pacific, but shows preference for species of the orders Poecilosclerida and Halichondrida. We observed *Cadlina rumia* feeding on sponges of three different orders, including the spiculate Halichondrida (*Scopalina* sp.) and Haplosclerida (*Haliclona* sp. and *Callyspongia* sp.) and the aspiculate Dictyoceratida (*Dysidea etheria*), showing that *Cadlina* is not specialized in preying a particular group of sponges. Sponge euryphagy by *Cadlina* spp. is supported also by chemical studies that reported a remarkable variety of metabolites in these nudibranchs (Cimino & Ghiselin 1999).

Discodorididae

Few observations on feeding preferences are available for the family Discodorididae. Species of *Jorunna* are frequently associated with sponges of the orders Haplosclerida and Halichondrida, upon which many species live camouflaged (Miller 1996, Thompson & Brown 1984). Feeding data are available for six species, all of which predate upon sponges of the orders Haplosclerida and Halichondrida (Camacho-García & Gosliner 2008). In southeastern Brazil, *Jorunna spazzola* and *Jorunna spongiosa* followed this pattern and were observed feeding only on haplosclerid species: *Callyspongia pallida*, *Callyspongia* sp., *Haliclona* sp. and *Chalinula* sp. (Figs 9–10). Indo-Pacific species of *Rostanga* present a diet restricted to sponges of the family Microcionidae (order Poecilosclerida) (Rudman & Avern 1989), but some species feed on sponges from unrelated families such as Halichondriidae, Chalinidae, Acarnidae and Chondropsidae (Cook 1962). *Rostanga byga* only fed on *Mycale microsigmatosa* in our observations; this is the first record of a *Rostanga* species feeding on a species of the family Mycalidae. The only species of the genus *Diaulula* with available data about predation is *Diaulula sandiegensis* (Cooper, 1863), which feeds on sponges of the orders Halichondrida, Poecilosclerida, Haplosclerida and Hadromerida (Elvin 1976, Bloom 1981, Goddard 1984, McDonald & Nybakken 1997, Penney 2013). The prey sponges observed for the Brazilian species *Diaulula greeleyi* were *Lissodendoryx isodictialis* (Poecilosclerida) and *Haliclona* sp.

(Haplosclerida), in agreement with the reports on *D. sandiegensis*. There are no previous studies on the feeding habits of any species of the genus *Discodoris*. In Rio de Janeiro State we found one specimen of *Discodoris hummelincki* feeding on *Haliclona* sp. (order Haplosclerida, family Chalinidae).

Dorididae

Knowledge of food preferences of this family is scarce. Some *Doris* species are known to feed on Halichondriidae, Dysideidae, Suberitidae, Chalinidae and Poecilosclerida sponges (McDonald & Nybakken 1997, Bloom 1976). In Brazil, there is a single record of dorid feeding: *Doris januarii* feeds on *Hymeniacion* aff. *heliophila* (family Halichondriidae) in São Sebastião, São Paulo State (Granato et al. 2000). In our study *D. kyolis* preyed on *Dysidea etheria* (family Dysideidae), *Haliclona* sp. (family Chalinidae) and *Lissodendoryx isodictialis* (order Poecilosclerida), the same sponge clades recorded as prey of other *Doris* species (McDonald & Nybakken 1997, Bloom 1976). However, *Doris kyolis* also preyed on a sponge of the class Homoscleromorpha (*Plakina* sp.). Our observations therefore expand the taxonomic range of sponge prey recorded for the genus *Doris*.

Dendrodorididae

Species of *Dendrodoris* were previously recorded feeding on sponges of the orders Dictyoceratida, Hadromerida, Halichondrida and Poecilosclerida (McDonald & Nybakken 1997). One species, *Dendrodoris citrina* (Cheeseman, 1881), was reported to feed on ascidians (McDonald & Nybakken 1997). Ev. Marcus & Er. Marcus (1967) recorded *Dendrodoris krebsii* over *Cliona* (Hadromerida), but predation was not confirmed. Our record of *D. krebsii* feeding on *Haliclona* sp. is the first for the genus feeding on haplosclerid sponges, increasing its known diet diversity.

Conclusions

Our spongivory records for nudibranch species such as *Felimare lajensis*, *Felimida binza* (family Chromodorididae), *Rostanga byga*, *Jorunna spazzola*, *Jorunna spongiosa* and *Diaulula greeleyi* (family Discodorididae) are in agreement with previous observations for these genera and families. On the other hand, spongivory records for *Felimida paulomarcioi* (family Chromodorididae), *Doris kyolis* (family Dorididae), *Discodoris hummelincki* (family Discodorididae) and *Dendrodoris krebsii* (family Dendrodorididae) expand the known diet of these genera and families to different groups of sponges. In general, our data

indicate that some nudibranch groups have a more diverse diet than previously thought. Current theories on feeding preferences by spongivorous dorid nudibranchs groups are based mostly on species of few regions, especially the eastern Pacific and the Mediterranean Sea. Species from other regions of the world, such as the one studied here in the southwest Atlantic, may have different feeding habits and must be considered in order to have more embracing, realistic general hypotheses. Finally, differences in feeding habits of nudibranch species of a same genus but from distant regions may also be indicative of the existence of artificial groups with convergent morphology. More observations on a higher number of species are needed for a better understanding of the feeding preferences of the diverse and ecologically important spongivorous dorid nudibranchs.

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