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Breadth and composition of polychaete diets and the importance of diatoms to species and trophic guilds

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Abstract

Polychaetes are important components of trophic webs in sandy beaches, mainly due to their abundance and diversity of feeding modes, acting as detritivores or primary/secondary consumers. We characterized diets of several polychaete species from intertidal sandy beaches by gut content evaluation. Diet breadth (Levins Index) was calculated for each species to evaluate the influence of different feeding strategies on this metric. Diatom composition was also assessed to verify the relevance of microphtyobenthic primary production to macrobenthic feeding on sandy beaches and its relationship with feeding strategies. A total of 2583 guts from 17 species were evaluated. Diet information is compared with literature, and added to taxa with previously unknown feeding habit. Diet breadths were generally low, but surface deposit feeders had the highest values. *Scolelepis squamata* guts were dominated by foraminfera, which may either be an specialization or local conditions. Subsurface deposit feeders usually had few items and lower breadths, highlighting the importance of organic matter to this guild. Diatoms were frequently found, and benthic were more frequently consumed than planktonic ones. The high numbers of benthic diatoms found for some species highlight the importance local food sources to sandy beach food webs.

Keywords: Polychaete feeding, Gut content, Feeding guild, Diatoms, Sandy beaches

Background

Polychaetes are one of the most common and diverse components of macrofauna inhabiting soft bottoms, from the intertidal zone to the deep-sea floor. On sandy beaches, they are usually abundant, especially where conditions such as gentle currents and fine-grained sediments are present [3, 14, 37]. Due to this abundance, they are naturally important components of food webs of these ecosystems, acting as detritivores and/or primary and secondary consumers [6, 36].

Five feeding modes are usually recognized for polychaetes. Surface and subsurface deposit feeders, suspension (or filter) feeder, carnivores and omnivores (or herbivores) [22, 23]. Microphagous feeders rely mainly on particulate organic matter, but items such as diatoms, foraminifera, macroalgae and macrophyte fragments are also found in dissected guts [16, 33]. Carnivorous polychaetes may feed on prey or carrion, and mollusk, crustaceans, ophiuroids and polychaetes fragments are often consumed [27, 33, 55]. Cannibalism is also found for some species [8, 9]. Polychaetes feature different structures to trap and capture food, such as a retractable pharynx, a jawed proboscis and palps [22].

Recognition of polychaete feeding mechanisms is important to studies of benthic communities. The use of feeding guilds to evaluate trophic structures is widely applied in polychaete studies. Many of these studies were motivated by Fauchald and Jumars [22], who reviewed knowledge at the time, and proposed trophic guilds at the family level. However, many guilds were established based on generalizations, and studies were needed to validate the assumptions [21]. In the past decades, behavioral and gut content analysis [12, 16, 17], gut architecture [44], fatty acid composition [28, 56], and stable isotope analysis [18, 19] have been important methods

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to uncover feeding mechanisms, feeding structures, and trophic relationships of polychaetes. Despite those efforts, a recent review shows that there are still gaps and a lack of information for many families to be able truly uncover their feeding ecology [23].

Among the methods used to uncover the feeding mechanisms of polychaetes, analysis of gut contents can help to characterize the feeding habits of a given species to confirm or modify the original classification [16]. However, analysis of gut contents can be time consuming for species-rich communities, particularly for small specimens. This approach also usually identifies food items to higher taxonomic levels, obscuring relationships at finer taxonomic levels. Diatoms are one of the most important food items for polychaetes in estuaries and mudflats [20, 24], but their relevance on sandy beaches is less studied [35]. Identifying the origin of diatom sources (benthic or planktonic) can help to elucidate the contribution of local versus allochthonous production to sandy beach food webs [35].

The diversity of feeding strategies in polychaetes may lead to contrasting diet compositions and characteristics. In this scenario, and given the existing gaps of knowledge regarding their feeding biology, our objective was to characterize the diets of several polychaete species. Our aim was not only to identify the composition, but also the diet breadth, evaluating the diversity of items consumed by each species. Comparisons with literature descriptions were made in order to corroborate or update current knowledge. Identity of diatom items was assessed to check the importance of this food source to polychaete fauna, evaluating whether benthic or planktonic forms are more commonly consumed. Given the various feeding strategies described for polychaetes, we aimed to investigate a relationship between these strategies, diet composition and diatom consumption. Each feeding strategy has its own particularity (e.g. feeding on deposited or suspended material), and we expected that these differences would result in contrasting diet compositions. Similarly, we expected that the rate of consumption and source (benthic vs planktonic) of diatoms would change with feeding strategy.

Methods

Sampling procedure

Sampling of polychaete species was carried out at the municipality of São Sebastião, North coast of the state of São Paulo, Southeastern Brazil (45°26′W–23°19′S to 45°27′30″W–23°52′30″S). The area has a Cfa Koppen climate [2], with humid subtropical climate with hot summers and no dry season. The coast is composed of several beaches with distinct hydrodynamic characteristics.

Sampling took place at five different beaches along the São Sebastião Channel and Caraguatatuba Bay: Barra Velha (BV), Engenho d' Água (EA), Cigarras (Ci), São Francisco (SF), Segredo (Se) and Enseada (Ens). Environmental characterization of these beaches at the sampling period can be found in Amaral et al. [3]. In summary, Barra Velha has the highest content of silt/clay, with predominance of very fine sand and much higher organic matter content than the other beaches; Engenho d'Água and São Francisco are composed of coarser sand with rock fragments, while the remaining beaches have similar characteristics, with predominance of fine sand and low organic matter content. Monthly, from August/1997 to July/1998, five sediment samples were taken at each beach at intertidal level, with a cylindrical corer (area = 0.01 m^2, 20 cm deep). A total of 1080 samples were taken during this period. Samples were sieved on nested meshes with sieve sizes of 1.0 and 0.5 mm. Polychaetes retained were sorted, preserved in 70 % ethanol, and identified to the lowest taxonomic level possible.

Diet characterization

Gut content analysis was done only for abundant species to ensure that the number of non-empty guts would be enough to give a reliable diet estimate. Based on this criterion, seventeen taxa were selected: *Isolda pulchella* (Ampharetidae), *Eurythoe complanata* (Amphinomidae), *Capitella* spp., *Heteromastus filiformis*, *Notomastus lobatus* and *Scyphoproctus djiboutinesis* (Capitellidae), *Cirriformia filifera* (Cirratulidae), *Marphysa sebastiana* and *Nematonereis hebes* (Eunicidae), *Hemipodus rotundus* (Glyceridae), *Lumbrineris tetraura* (Lumbrineridae), *Laeonereis culveri* (Nereididae), *Diopatra aciculata* (Onuphidae), *Naineris setosa* (Orbiniidae), *Owenia fusiformis* (Owenidae), *Sigambra grubei* (Pilargidae) and *Scolelepis squamata* (Spionidae).

Every specimen was observed under a stereomicroscope in order to verify whether the gut was empty. Whenever gut contents were observed, individuals were further dissected. Contents from the dissected gut were analyzed microscopically. Food items were identified to varying taxonomic levels. Most groups of food items were identified to higher taxonomic levels, such as Foraminifera, Dinoflagellata and Radiolaria. Vegetal and animal remains were also separated under a specific category, in the latter identification to high taxonomic levels was made (e.g. Crustacea, Bryozoa). Diatoms were identified to species or genus. Identifications of food items were made with help from appropriate literature [10, 49, 53] and taxonomic expertise.

Trophic group classification was made following the standards set by Fauchald and Jumars [22]. Jumars et al.

[23] provided an update to polychate trophic guild classification reviewing published papers on the subject. Their review and additional literature was checked to classify species feeding guild (e.g. [15, 41, 50]). We compared our results from gut contents with the updated guilds proposed by Jumars et al. [23].

Data analysis

Stomach Repletion Index (RI) was estimated by the visual percentage of gut fullness under a stereomicroscope. Four repletion classes were estimated:

- RI = 0 (Completely empty)
- RI = 0.25 (≤25 % with content)
- RI = 0.5 (>25; ≤50 % with content)
- RI = 1 (>50–100 % with content).

The lack of a class RI = 0.75 (>50; ≤75 %) was due to the decision to include this class within the RI = 1. This decision was based on the very little number of individuals observed with gut fullness >50 %, and the grouping of the classes was made to increase the number of individuals in the RI = 1.0. The percentage of empty guts was calculated individually for each species. Additionally, we calculated a rate of food items per individual of each species, defined as the total number of times an item was recorded (regardless of abundance) divided by the number of individuals with non-empty guts for each species.

Diet breadth was calculated using Levins Index [30], which is based on the sum of the frequencies of each food item that was found for a given species:

$$B = \frac{1}{\sum p_j^2}$$

B: Levins' measure of niche breadth, p_j^2: proportion of individuals using resource state j.

The index was standardized for values reaching from 0 (lowest breadth) to 1 (highest breadth) following the equation [26]:

$$\mathrm{Ba} = (\mathrm{B} - 1)/(\mathrm{Bmax} - 1)$$

Ba = Levins Standardized Index, Bmax = total number of recognized food items.

Breadth measures can indicate the width of food items that compose the diet of a given species. The similarity of diet composition among species and feeding guilds was assessed by non-metric dimensional scaling (NMDS). Bray–Curtis distance was applied to the matrix of frequency of food items found for each species.

The contribution of diatom species to polychaete feeding was evaluated by the mean number of food items and diatoms consumed per filled guts. It is important to note that not every filled gut contained food item, as sand was sometimes the only content found. Thus, the mean number can reach values lower than 1 if sand is the only gut content found for most individuals of a species. Diatom species were separated in benthic and planktonic to evaluate which form contributed most to polychaete diet and to check for differences on diatom consumption among the contrasting feeding strategies.

Results

Diet composition and breadth

Feeding guild classification revealed five carnivores, five subsurface deposit feeders, four surface deposit feeders (although two also facultative suspension feeders) and four omnivores. Six species were exclusively found at Barra Velha beach, five of those being subsurface deposit feeders, with the exception of *C. filigera*. Nine species occurred at Engenho and São Francisco beaches. Most occurred jointly at the two areas, with the exception of *E. complanata* and *O. fusiformis*, found only at São Francisco and Engenho, respectively. *S. squamata* was found at Cigarras, São Francisco and Segredo beaches, whereas *L. culveri* was only encountered at Enseada (Table 1).

A total of 2583 guts were evaluated, but only 429 had a RI higher than 0, and very few had RI = 1 (0.07 %). This pattern was commonly observed, with most species having more than 50 % of individuals with RI = 0. Three species had only empty guts (*H. rotundus*, *S. tetraura* and *S. grubei*). Aside from those, the lowest percentages of filled guts were found for *Capitella* spp. (7.5 %), *S. squamata* (8.9 %) and *N. hebes* (12.8 %). The highest percentages of filled guts were found for *L. culveri* (54.46 %), *O. fusiformis* (51.66 %) and *I. pulchella* (44.68 %) (Fig. 1).

Sand was registered in almost all non-empty guts. Some species had a low variety of food items, especially subsurface deposit feeders, such as *Capitella* spp. and *N. lobatus*, and carnivores, such as *E. complanata* and *N. hebes*. Benthic diatoms were frequently found in the guts of *O. fusiformis*, *I. pulchella* and *C. filigera*. Those species were also the ones with the highest variety of food items registered. Diatom species such as *Surirella fastuosa*, *Navicula* sp., *Biddulphia* sp. and the planktonic diatom *Cosconodiscus* sp. were registered in the guts of most species (Table 2).

Aside from diatoms, other food items were also frequently registered. Foraminifera were consumed by half of the species, and were a frequent item found in guts of *S. squamata* (~50 %). Radiolaria also occurred in many species, but was especially frequent in *O. fusiformis* and *I. pulchella*. Macrophyte detritus (i.e. fragments from marine angiosperms) were also frequently registered in polychaete guts, most notably for *L. culveri* and *O. fusiformis*. Macrophyte was remarkably found in three of the

Table 1 Proportion of empty and number of filled guts; numbers of food items registered per filled guts (rate); feeding guild classification; and sample location of polychaete species evaluated

Species	Label	Guts		Rate	Guild	Beaches
		Empty (N)	Filled (N)			
Capitella spp.	Cspp	524	42	0.33	SS	BV
Cirriformia filigera	CF	146	52	1.4	S	BV
Diopatra aciculata	DA	11	3	4	O	EA; SF
Eurythoe complanata	EC	12	4	2.5	C	SF
Heteromastus filiformis	HF	57	39	0.82	SS	BV
Hemipodus rotundus	HR	15	0	0	C	EA; SF
Isolda pulchella	IP	26	21	3.59	S	EA; SF
Laeonereis culveri	LC	51	61	1.31	O	Ens
Marphysa sebastiana	MS	21	6	1.83	O	EA; SF
Nematonereis hebes	NH	130	19	0.21	C	EA; SF
Notomastus lobatus	NL	22	12	0.67	SS	BV
Naineris setosa	NS	46	25	0.88	SS	BV
Owenia fusiformis	OF	29	31	6.48	SS/Sus	EA
Scyohoproctus djiboutinesis	SD	60	17	0.94	SS	BV
Sigambra grubei	SG	20	0	0	C	EA; SF
Scolelepis squamata	SS	887	96	0.77	SS/Sus	Ci; SF; Se
Scoletoma tetraura	ST	14	0	0	C	EA; SF

Labels are presented to be used as a code on further tables and figures

Guild lables: *C* canivore, *O* omnivore, *SS* subsurface deposit-feeder, *S* surface deposit-feeder, *Sus* suspension-feeder

Beaches labels: *BV* Barra Velha, *EA* Engenho D'Água, *SF* São Francisco, *Ens* Enseada, *Ci* Cigarras, Se: Segredo

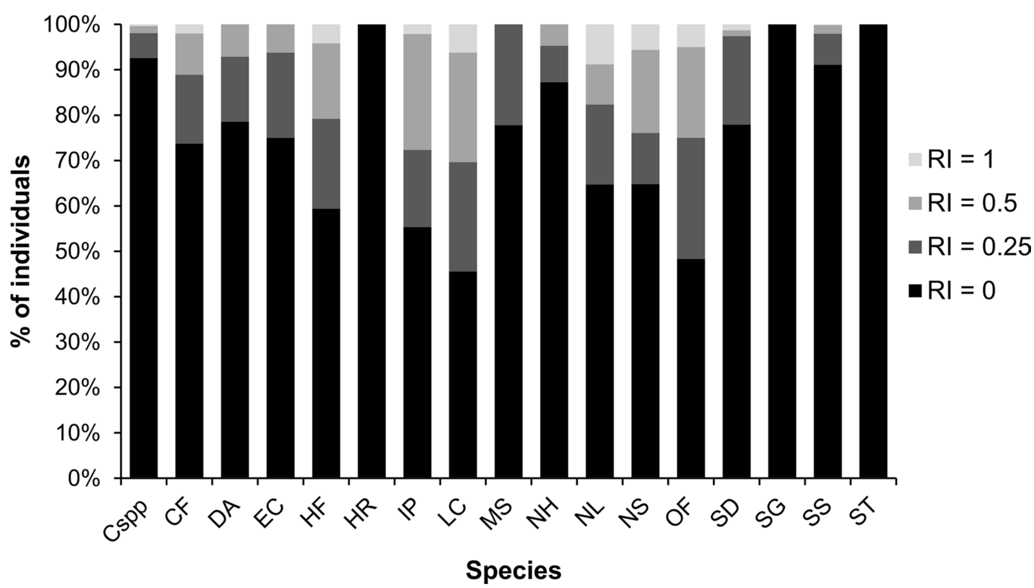

Fig. 1 Proportion of Repletion Index (RI) classes obtained for each polychaete species

four non-empty guts of *E. complanata*, a species commonly classified as a carnivore.

Food items that were rarely registered are mainly related to animal remains. Pteropoda was only found (although frequent) in guts of *D. aciculata*; Ciliophora only in *L. culveri* and *I. pulchella*; Harpacticoida in *C. filigera*; Bryozoa in *O. fusiformis*; Bivalvia in *S. squamata*; and Ostracoda and crustacean fragments in *L. culveri*.

Table 2 Diet composition and frequency (%) of food items recorded for polychaete species

Species	Cspp	Cf	Da	Ec	Hf	Ip	Lc
Item							
Macrophyte detritus		7.69		75		13.64	26.23
Macroalgae fragment				25			1.64
Foramnifera		5.77				9.09	13.11
Radiolaria		3.85			5.13	18.18	1.64
Ciliophora						4.54	9.84
Pteropoda			66.67				
Harpacticoida		1.92					
Ostracoda							1.64
Crustacean Fragment							6.56
Egg		3.85	33.33			9.09	
Centric planktonic diatom							
Bacillaria sp.						9.09	
Bacillaria paxillifera	2.38	5.77			7.69		
Coscinodiscus sp.	9.52	17.31	33.33		12.82	31.82	6.56
Coscinodiscus nodulifer			33.33				
Pinullaria sp.		5.77					
Thalassiosira eccentrica		1.92	33.33		5.13	9.09	
Triceratium sp.		1.92				4.54	
Triceratium alternans							
Triceratium favus			33.33			4.54	
Centric benthic diatom							
Biddulphia sp.	2.38	15.38		25	15.83	31.82	18.03
Biddulphia pulchella						4.54	
Melosira sp.	2.38			25		22.72	9.84
Melosira moliniformis	2.38						
Melosira sulcata						4.54	
Odontella aurita					2.56		
Pennate planktonic diatom							
Rhabdonema sp.					2.56		
Pennate benthic diatom							
Amphiophora sp.		5.77					
Climacosphenia moniligera		1.92					
Grammatophora marina		11.52		25	2.56	4.54	
Gyrosigma sp.						4.54	1.64
Licmorpha sp.		3.85				13.64	
Licmorpha abbreviata		7.69					
Navicula sp.	7.14	9.26	33.33	25	10.26	27.27	31.15
Navicula membranacea		3.85	33.33	25	12.82	45.45	
Nitzchia sp.	2.38		33.33			9.09	
Nitzchia longissima		1.92				13.64	1.64
Nitzchia paradoxa		1.92					
Nitzchia bilobata						4.54	
Plagiogramma sp.						9.09	
Pleurosigma sp.		7.69			2.56	27.52	
Surirella fastuosa	4.76	13.46	33.33	25	2.56	31.82	1.64

Species	Ms	Nh	Ns	Nl	Of	Sd	Ss
Item							
Macrophyte detritus	16.67		28	8.33	36.67		5.21

Table 2 continued

Species	Ms	Nh	Ns	Nl	Of	Sd	Ss
Macroalgae fragment	16.67				6.67		1.04
Dinoflagellata					6.67		
Foramnifera		5.26	8		13.33	5.88	58.33
Radiolaria		5.26	4		26.67		3125
Bivalvia							1.04
Bryozoa					6.67		
Centric planktonic diatom							
Bacillaria paxillifera					20		
Chaetocerus sp.					6.67		
Coscinodiscus sp.	33.33		4		50	5.88	3.12
Coscinodiscus nodulifer					3.33		
Hemidiscus cuneiformis					3.33		
Thalassiosira eccentrica					10		
Triceratium alternans					10		
Triceratium favus					10		
Centric benthic diatom							
Biddulphia sp.	50	5.26	8	16.67	43.33	5.88	
Biddulphia pulchella			4		6.67		
Melosira sp.					23.33		1.04
Melosira moliniformis	16.67				3.33		
Melosira sulcata	16.67				3.33	5.88	
Odontella aurita			4			5.88	
Pennate planktonic diatom							
Striatella sp.					3.33	5.88	
Thalassiothrix sp.			4		6.67		
Pennate benthic diatom							
Achantes sp.					3.33		
Amphiophora sp.					3.33		
Climacosphenia moniligera					6.67		
Grammatophora marina			4	8.33	33.33	11.76	
Gyrosigma sp.					3.33		
Licmorpha sp.					23.33		
Licmorpha abbreviata			4		43.33	5.88	
Navicula sp.	33.33		4	16.67	56.67		2.08
Navicula membranacea				8.33	20	5.88	1.04
Nitzchia sp.					20	5.88	
Nitzchia longissima			4		40	11.76	
Nitzchia paradoxa					3.33		
Nitzhia seriata					3.33		
Plagiogramma sp.					3.33		
Pleurosigma sp.			4		46.67	5.88	
Surirella fastuosa		5.26	4	8.33	63.37	11.76	1.04

Frequency equals the number of guts a food item was found in relation to total filled guts. Number of guts and species labels are according to Table 1

Eggs were also identified in the guts of *D. culveri* and *I. pulchella*. Some diatom species were also rarely found, but this may be due to local availability rather than selectivity.

The mean number of items registered per non-empty gut shows that most species had values lower than 1. Aside from species which had no food items, the lowest ratios were found for *N. hebes* (0.22 items/ind.) and

Capitella spp. (0.33 items/ind.). In contrast, species such as *O. fusiformis* (6.48 items/ind.) and *I. pulchella* (3.48 items/ind.) had the highest number of food items registered in non-empty guts.

Diet breadth values were generally low. The higher values were registered for *O. fusiformis* (0.367), *I. pulchella* (0.294) and *C. filigera* (0.280), species presenting surface deposit feeding. Most species with lower breadth values were subsurface deposit feeders, such as *Capitella* spp. (0.097) and *N. hemipodus* (0.088), and carnivores, such as *E. complanata* (0.107) and *N. hebes* (0.061). Exception to this pattern was the interface-feeder *S. squamata*, which had the lowest diet breadth registered (0.015) (Fig. 2). This is likely due to the dominance of one food content (Foraminifera) in the dissected guts of this species. This dominance reflected on similarity analysis. Surface-deposit feeding species had similar diet compositions, with the exception of *S. squamata*. The other feeding guilds did not show a strong similar diet composition among its species, especially for macrophagous guilds (Fig. 3).

Diatom consumption

Diatoms were found in the guts of most species. Twenty-three diatom species were benthic, whereas 14 were planktonic. From the benthic species, 17 species were pennate and 6 were centric. The opposite was found for the planktonic forms, where most species were centric diatoms. Benthic forms were more frequently consumed than planktonic. Surface deposit feeder species had overall higher numbers and rates of diatom consumption, both for benthic and planktonic forms. However, the standard deviation values for the group were very high, due to the low diatom consumption by *S. squamata* (Table 3).

Subsurface deposit feeders had average values of diatoms registered, with a higher number of items, but a lower rate than omnivores. However, consumption of planktonic diatoms by subsurface species was very low. Omnivores, especially *D. aciculata* had the highest rate of planktonic forms registered, but the numbers of items were generally low. Carnivores overall had the lower values of diatom consumption and only benthic forms were registered (Table 3).

Discussion

Diet composition and breadth

Results from stomach contents showed a high number of food items consumed by polychaetes. Individual species diet breadths were generally low. Surface deposit feeders, such as *O. fusiformis* and *I. pulchella* had the highest number of food items registered per non-empty guts. Surface deposit feeding species were the main consumers of diatoms, especially benthic forms. Benthic diatoms were generally much more frequently consumed than planktonic forms by all feeding guilds.

Few species (*S. grubei*, *S. tetraura* and *H. rotundus*) had all dissected guts empty. Lack of food items within guts is a common finding in polychaetes [16, 33]. This is compatible with carnivory [16, 22], as these species

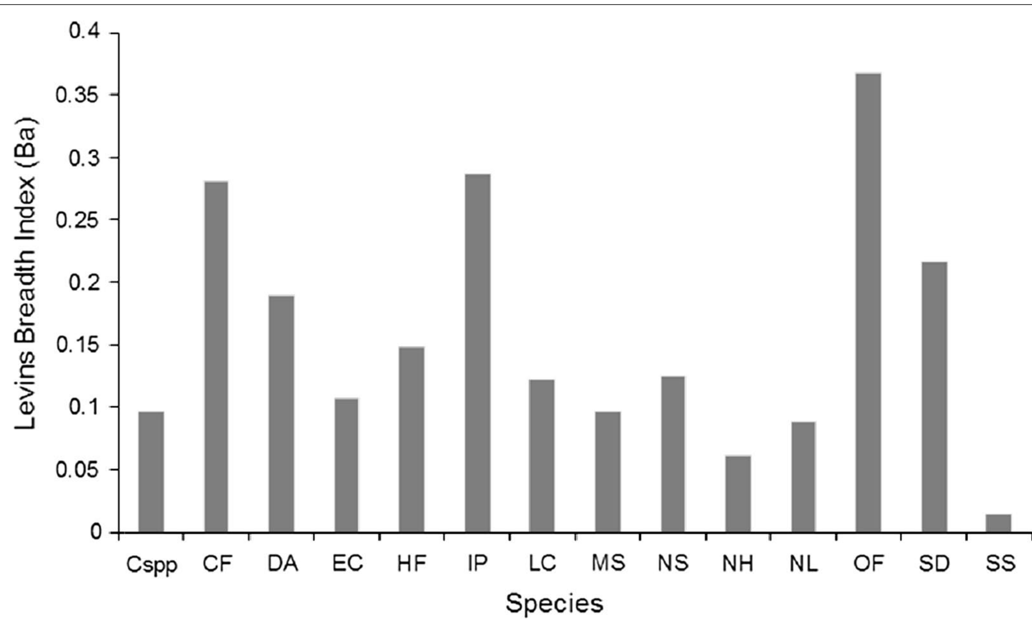

Fig. 2 Levins Standardized Index (Ba) indicating the diet breadth obtained for polychaete species. Species coded according to Table 1

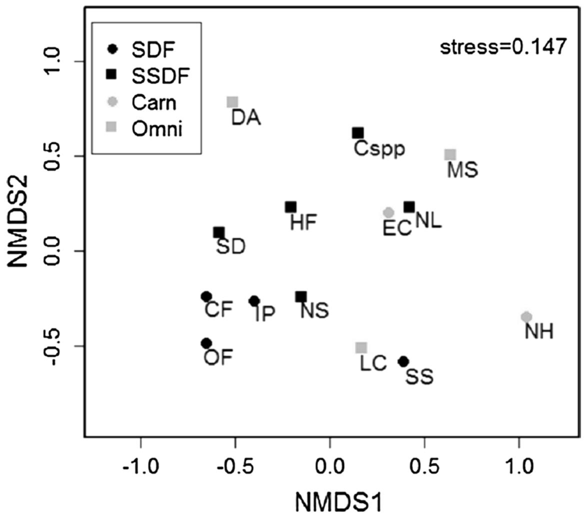

Fig. 3 Similarity of diet composition among species and feeding guilds. Species coded according to Table 1. *SDF* surface-deposit feeder, *SSDF* subsurface deposit feeder, *Carn* carnivore, *Omni* omnivore

Table 3 Diatom composition on the diet of polychaete species

	Benthic		Planktonic	
	N	Frequency	N	Frequency
Surface deposit feeders	12.15 ± 6.5	1.95 ± 1.9	5.5 ± 4.12	0.54 ± 0.5
Cirriformia filigera	12	0.86	5	0.53
Isolda pulchella	13	2.54	5	0.59
*Owenia fusiformis**	20	4.35	11	1.22
*Scolelepis squamata**	4	0.05	1	0.01
Subsurface deposit feeders	7.4 ± 2.05	0.48 ± 0.2	2 ± 1.41	0.10 ± 0.1
Capitella spp.	6	0.14	2	0.04
Heteromastus filiformis	7	0.48	4	0.3
Naineris setosa	9	0.4	2	0.88
Notomastus lobatus	5	0.66	0	0
Schyphoproctus djiboutiensis	10	0.76	2	0.11
Omnivores	4.6 ± 1.15	1 ± 0.43	2.33 ± 2.3	0.68 ± 0.8
Diopatra aciculata	4	1.33	5	1.66
Laeonereis culveri	6	0.51	1	0.33
Marphysa sebastiana	4	1.16	1	0.33
Carnivores	1.6 ± 2.6	0.43 ± 0.7	0	0
Eurythoe complanata	6	1.5	0	0
Hemipodus rotundus	0	0	0	0
Nematonereis hebes	2	0.1	0	0
Sigambra grubei	0	0	0	0
Scoletoma tetraura	0	0	0	0

* Can also suspension feed

usually have smaller guts than deposit-feeders [44] and the high-quality protein food reduces the need for constant feeding, in comparison to detritus feeding. The finding for these species is compatible with literature [15], and is especially important for *S. grubei*, as feeding data for pilargids are severely lacking [23]. Our findings for *S. grubei* are compatible to the findings of Magalhães and Barros [33], reinforcing the likelihood of carnivory for the family. However, some species usually classified as carnivores presented guts with macrophyte and macroalgae fragments (*E. complanata*) or diatoms (*N. hebes*). In laboratory conditions, *E. complanata* was found to ingest and respond to fish stimuli instead of ingesting algae [42]. This result reinforces the assumption that every carnivore polychaete, lacking prey or carrion, may act as a herbivore and this omnivory potential should be considered when guild classification is concerned [46]. Nonetheless, the lack of gut content in some species explains the overall low breadth values and frequency of diatoms found for the carnivore guild.

In contrast, surface deposit feeders overall had the highest diet breadth values and rate of food items, enabling a more in depth evaluation of their diets. Ampharetid species are usually considered as surface deposit feeders. Small species (<1 cm) are suggested to feed on diatoms, but incidental ingestion of animal remains is expected [23]. No other feeding evaluation was found for the genus *Isolda* in literature, but our results suggest that the species feed extensively on benthic diatoms. Macrophyte detritus and macrophagous items such as foraminifera, radiolaria and ciliophora were less frequent but also found. These results indicate that diatoms are an important food item to *I. pulchella*. Further studies with other *Isolda* species may help elucidate whether this feature is common for the genus.

Owenia fusiformis had the highest breadth, and highest mean number of items recorded among the species evaluated. This species feeds using a tentacular crown, and is considered an interface feeder, due to the capacity of shifting its habit between surface and suspension feeding depending on the flow intensity [39]. This dual habit favors the ingestion of both suspended and deposited material, likely resulting in the higher number of records and breadth. *O. fusiformis* was also found to feed frequently and extensively on benthic diatoms, but also on Radiolaria. This reinforces findings from stable isotopes results indicating the species to fall under omnivore category in $^{15}\delta N$ content [57]. Caution is needed, however, as evidence suggests that *O. fusiformis* is a species complex [25], and generalizations may not be suitable.

In contrast, *S. squamata* is also considered to have an interface-feeding habit [12, 41], but had one of the lowest diet breadths. In fact, this species had a very distinct diet composition in comparison to other surface deposit feeders. We believe that this result might be due to the origin of the main food source. *S. squamata* fed mainly on foraminiferans, which was not identified to lower taxonomic levels. Thus, identification of foraminiferans may reveal a higher breadth than the results for *S. squamata* first indicates. The large consumption of foraminifera is intriguing. Specialization on foraminifera is not mentioned for Spionidae in a recent review, despite being a well-studied family [23], and is more commonly found for carnivorous polychaetes [5, 31, 45]. Location may play a role in our results, as *S. squamata* was the only species found at Segredo Beach. Further studies could also investigate whether the high ingestion of Foraminifera is caused by selection or local conditions.

Omnivore species also had remarkably high values of mean food items, reflecting the diversity of food items that this feeding strategy allows. *D. aciculata* had especially high numbers of food items, even though the number of filled guts was low. Dagli et al. [11] found that *D. neapolitana* preferred living prey items or carrion in laboratory, but found mostly leaves and algae within their guts. This species also deposit fed when there was a lack of food items [11]. This variety of strategies may result in the observed breadth. Another omnivore species, *L. culveri*, was found to feed abundantly on diatoms, but also on macrophyte fragments, foraminifera, tintinnida and crustacean fragments. Nereididae species are usually classified as omnivores, but deposit-feeding has been suggested for some species [23, 40], including *L. culveri* [33]. However, our results indicate this species as an omnivore, in accordance to isotope results [1], reinforcing the omnivore aspect of nereidids.

The overall low diet breadth is an expected outcome for organisms such as polychaetes. Carnivores usually have empty guts, so low or null breadth can be expected, as found for the guild on this study. Also, deposit-feeding species rely on deposited organic matter within sand, as detritus, for energy intake [24, 32, 52]. Some subsurface species, such as *Capitella* spp. and *Heteromastus filfiormis* are common in organically enriched communities [7, 43, 54]. As this organic matter comes with ingested sand, especially for non-selective deposit feeders, it is not classified as a food item and thus is not included in breadth analysis. Although the ingested diatoms may represent an important food component, and subsurface deposit feeders are found to rapidly bring surface diatoms to bottom layers [24, 29], the low breadth indicates these species rely more on deposited organic matter than macrophagous items in the area. Granted, subsurface deposit feeders were mainly found at Barra Velha beach, which has a significantly higher organic matter content (~8 %) than other sampled beaches [3].

Diatom consumption

A great number of diatom species were found in polychaete guts. Diatoms are an important content of benthic food webs due to the high assimilation and low gut residence [32, 38]. Microalgae assimilation by polychaetes may be enough to supply the carbon demands, although harsh climatic conditions may require detritus feeding [4]. Our results are in accordance to these findings, but the importance of diatoms was variable among species and trophic groups.

In accordance to our expectation, species with different feeding strategies showed a varied rate of diatom consumption. Surface deposit feeders overall had a higher frequency and number of food items and diatoms registered. The values presented by those species, coupled with the highest breadth recorded, suggest that they may actively select food items such as diatoms over particles. In fact, evidence from behavioral studies supports this assumption. Particle selectivity has been demonstrated for other species of oweniids and ampharetids [48, 51]. Furthermore, tentacle-bearing polychaetes, as is the case for every surface-feeder in the study area, can select particles by roughness and organic coating, which may include microphytobenthic organisms [34, 38, 47].

Contrary to our expectation, source of diatom consumption did not differ with feeding strategy, as benthic diatoms were more commonly consumed than planktonic ones by all feeding groups. Suspension feeders were previously shown to depend more on pelagic food sources, whereas benthic grazers and deposit feeders relied more on microphytobenthic production, through stable isotopes analysis [20, 24]. However, no obligatory suspension-feeder was found to corroborate this hypothesis by gut content analysis. Surface deposit-feeders moderately fed on planktonic diatoms, indicating that the sinking planktonic diatoms may be an important food source for these species and guild, and more readily available for surface than subsurface deposit feeders. Nonetheless, our evaluation of stomach contents showed the importance of benthic diatoms to deposit feeders and omnivore species, as those items were more frequently found in polychaete guts.

This higher consumption of benthic diatoms also shows the importance of local benthic primary production for food webs on sandy beaches. Our results contradict those found by Bergamino et al. [6], which reported a higher phytoplanktonic input in sandy beach food-webs. It is worth noting, however, that beach hydrodynamics may influence these results. Strong wave action (such as that in exposed beaches) is known to negatively affect microphytobenthos establishment and production [6, 13]. The study area, however, is characterized by an overall low hydrodynamic [3]. Thus, the results observed here are more likely to be generalized easily to beaches with similar conditions. Although benthic diatom importance to sandy beach food webs was also reported by Maria et al. [35], the authors found no significant diatom uptake by polychaete species, evidence presented by our results, which add information regarding intertidal benthic trophic structure on sandy beaches.

The results presented here show the diet composition of several polychaete species inhabiting beaches with varied sediment types. Diet for species was compared with literature, and information was added to gaps such as *I. pulchella* and pilargids diet. With the exception of three species (*M. sebastiana*, *H. rotundus and S. grubei*), which are endemic, other species have wider distributions, highlighting the importance of individual species diet results, and enabling comparison between areas. Surface deposit feeders usually had higher breadth values and a higher mean number of food items registered than subsurface feeders, suggesting a higher dependence of the latter on organic matter detritus. The identity of diatoms found in polychaete guts was assessed and the results revealed a high diversity, especially of benthic diatoms, highlighting the importance of microphytobentic sources to macrobenthic species. This dominance of benthic diatoms consumption provides an evidence of the importance of autochthonous food sources to sandy beach food webs.

Abbreviations

B: Levins Index of niche breadth; Ba: Levins Standardized Index of niche breadth; Ci: Cigarras beach; BV: Barra Velha beach; EA: Engenho d'Água beach; Ens: Enseada beach; RI: Repletion Index; Se: Segredo beach; SF: São Francisco beach.

Authors' contributions

We acknowledge that every author have participated from the study and contributed to the manuscript. HHC developed the manuscript scope and carried out data analysis and discussion. EVP developed and carried out the sampling and gut content evaluation, as well a part of data analysis. ACZA helped develop and supervise the study, also helping with sampling and commenting on the manuscript. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

The dataset supporting the conclusions of this article is available in the FigShare repository, in https://figshare.com/s/058c88f9d7e798cc360a.

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