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ORIGINAL ARTICLE

Diversity, distribution and ecology of the family Syllidae (Annelida) in the Portuguese coast (Western Iberian Peninsula)

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Abstract The diversity, distribution and ecology of the family Syllidae along the Western Iberian coast was studied, based on 145 sediment samples covering the whole Portuguese coastal shelf and 30 *Saccorhiza polyschides* holdfasts sampled in the north of Portugal. A total of 55 species were identified in 2,306 specimens. A total of 33 species were recorded in the holdfasts and 36 in the shelf samples spanning a wide range of sediments, bathymetry and latitude. A total of 14 species were shared between both substrates. A total of 26 species were here firstly recorded, increasing to 80 the number of species known in Portugal, and new insights were added to the ecology and geographic distribution of several species. A multivariate analysis identified three assemblages, characterized by the species (a) *Sphaerosyllis bulbosa* and *Syllis pontxioi* in the western shelf coarse sediments, (b) *Parapionosyllis brevicirra* and *Syllis mercedesae* in the southern shelf muddy sands and (c) *Brania pusilla* and *Myrianida brachycephala* in the kelp holdfasts. The type of substrate (kelp holdfast vs. soft-bottom sediments) and the sediment grain size (coarser vs. finer) were the descriptors best related to the Syllid assemblages.

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Introduction

The family Syllidae Grube, 1850 (Annelida, Polychaeta, Phyllodocida) is one of the most complex, diverse, abundant and widespread among the annelid polychaetes. The number of valid species is estimated between 700 (Aguado et al. 2012) and 900 (Faulwetter et al. 2011), belonging to 74 genera (Aguado et al. 2012; Glasby et al. 2012; Lucas et al. 2012; Nygren et al. 2010). Syllids are very abundant and diverse among sponges, seaweed, seagrass, coral or hydrozoans and in soft bottoms, due to a generalist feeding strategy and active mode of life, moving in the interstitial space or crevices (Giangrande et al. 2000; San Martín 2003). The attention devoted to this family is shown by the several recent papers on their diversity and/or description of new species and genera (e.g., Abd-Elnaby and San Martín 2010; del Pilar-Ruso and San Martín 2012; Granados-Barba et al. 2003; Lattig et al. 2007; Lucas et al. 2012; San Martín and Hutchings 2006; San Martín and López 2003, among many others). New insights were recently given regarding the soft-bottom Portuguese continental shelf polychaete fauna (Martins et al. 2013) and macrobenthic communities (Martins et al. in press). The Syllid fauna was, however, still poorly known, with only close to 50 reported species and very few specialized papers (Ravara et al. 2004).

Along the Portuguese coast, north Atlantic colder waters mix with northern Africa and Mediterranean warmer waters. The western Portuguese continental shelf presents a complex current system and high energetic waves and tides regime, particularly in the northwestern sector, in contrast with the sheltered southern shelf, characterized by lower hydrodynamic energy and warmer waters (Fiúza 1983). According to the hydrodynamic regime, the intertidal coastal area has been classified into mesotidal exposed, from the northern border to Cape Carvoeiro on the west coast, mesotidal moderately exposed, from Cape Carvoeiro to Ponta da Piedade on the south coast, and mesotidal sheltered, from Ponta da Piedade to Vila Real de Santo António, southern coast (Bettencourt et al. 2004 and Fig. 1). The sedimentary coastal shelf seascape partially reflects this regime, mostly coarse sediments in the northwestern sector, predominance of sands at greater depths and in the southwestern sector and muds in the southern sector and off the major Portuguese rivers (Martins et al. 2012a). The Portuguese shelf is also dissected by several canyons, namely Porto, Aveiro, Nazaré, Cascais/Lisboa, Setúbal, S.Vicente and Portimão which represent important morphological, sedimentary and hydrological boundaries (Oliveira et al. 2007).

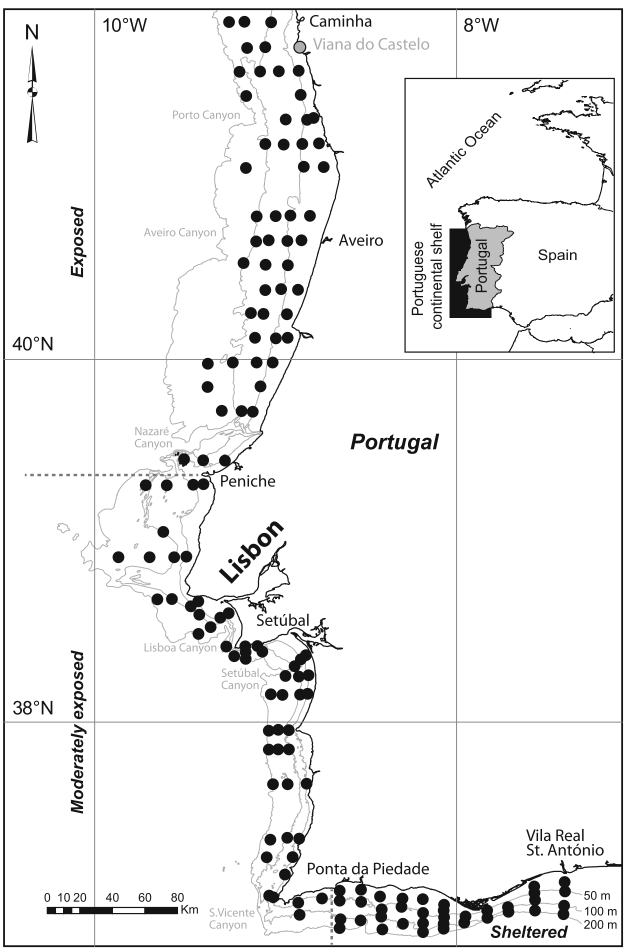

Fig. 1 Study area: the Portuguese coast (Western Iberia), indicating the positioning of the shelf sediment samples (*black circles*) and the *Saccorhiza polyschides* holdfasts samples (*gray circle*, Viana do Castelo). The hydrodynamic regime coastal subdivisions according to Bettencourt et al. (2004) are also shown

This study focus on the diversity of Syllids from the Portuguese coast (Western Iberia Peninsula) and is based on sediment samples collected on the western and southern shelf and in holdfast samples of *Saccorhiza polyschides* (Lightfoot) Batters 1902, from a northwestern rocky shore. This seaweed presents a long stipe and a large holdfast with internal channeling system, securing the algae to the rock, which can support a high biodiversity (McKenzie and Moore 1981). Few studies were developed about the faunal communities inhabiting the holdfasts of this species (McKenzie and Moore 1981; Tuya et al. 2011), when compared to other kelp species (Christie et al. 2003; Jørgensen and Christie 2003; Norderhaug et al. 2012; Tuya et al. 2011). *Sacchoriza polyschides* can be found from Norway to Portugal and is abundant on subtidal rocky shores in northern Portugal (Ardré 1970; Tuya et al. 2011).

This work is integrated in a holistic study on the diversity and distribution of the Portuguese continental shelf benthic macrofauna (Martins et al. 2012b, c, 2013, in press), and the macrofauna inhabiting *S. polyschides* holdfasts. Given the high abundance and diversity of Syllids in samples from both substrates and the lack of knowledge in this coastal European region, the aims of the present work were (a) to identify and characterize the diversity and distribution of the Syllidae fauna of the Portuguese coast; (b) to give new insights about the ecology of this fauna; and (c) to identify and discuss biological–environmental relationships.

Materials and methods

Study area

A total of 145 sites were sampled, covering the entire Portuguese continental shelf, from Caminha (41°51.8′N, 9°15.6′W) to Vila Real Santo António (36°56.1′N, 7°24.7′W) (Fig. 1), and a wide bathymetric range (13–195 m depth). Two sediment samples per site were collected during 2007 and 2008, with a 0.1 m^2 Smith-McIntyre grab, one for macrofauna and the other for sediment grain size and total organic matter content. Sediment samples were sieved on board over 1-mm mesh screen, and the residue fixed in neutralized formalin (4 %) stained with rose Bengal. The study area sedimentary seascape is given in Martins et al. (2012a). The northwestern inner and mid-shelf and areas south of the Nazaré and Setúbal submarine canyons are dominated by coarse sediments with low fines content. The deep northwestern shelf and the southwestern shelf are characterized by sands with moderate fines content. The southern shelf is heterogeneous with a predominance of muds, sandy muds and muddy sands. Mud patches were also recognized off the Tagus and Douro rivers and north of the Nazaré canyon. The total organic matter was correlated with fines content (Spearman $\rho = 0.71$) and ranged from 0.3 to 9.18 % of the total sediment (Martins et al. 2012a).

A total of 30 *Saccorhiza polyschides* holdfasts were collected in the infralittoral zone of a rocky shore located in Viana do Castelo, northern coast of Portugal (41°42′N,8°51′W), in September 2011. Only submerged holdfasts were selected. They were carefully separated from the stipe and frond and kept in a plastic bag. Magnesium chloride (2 g per 5 L of seawater) was added to the bags, to anesthetize the organisms, during 5 min. The samples were sieved in the field over 0.5-mm mesh size and the residue fixed in neutralized formalin (4 %).

Laboratory analysis

In the laboratory, the samples were carefully washed to remove excess fixative. The holdfast maximum and minimum diameter was measured and used to calculate the area, according to $2(\pi \times \text{radius}^2)$. The holdfast volume was also obtained by measuring water displacement in a volumetric balloon. After hand sorting and taxonomic identification, the specimens were transferred for long-term storage in 70 % ethanol. Syllids were identified to species level, whenever possible, following San Martín (2003) and recent species descriptions references (e.g., Lucas et al. 2012).

Abundance and species richness were determined per sample. The Bray–Curtis similarity among sites was calculated after presence/absence of data transformation. Affinity groups among samples were obtained following the Unweighted Pair Group Method with Arithmetic Mean clustering (UPGMA) and visualized in Principal Coordinates Ordination analysis (PCO). These groups were characterized using total and mean species richness, mean abundance, characteristic species and quantity of exclusive species, as well as the environmental baseline data (depth, grain size and total organic matter) for the soft-bottom samples and the biometric data (diameter, area and volume) for the holdfast samples. The characteristic species per affinity group were selected from the set of species that showed the highest constancy and fidelity, according to the scaling proposed by Dajoz (1971) for constancy (constant ($C > 50.0$ %); common ($50.0 \geq C > 25.0$ %); occasional ($25.0 \geq C > 12.5$ %); rare ($C \leq 12.5$ %)) and by Retière (1979) for fidelity (elective ($F > 90.0$ %); preferential ($90 \geq F > 66.6$ %); indifferent ($66.6 \geq F > 33.3$ %); accessory ($33.3 \geq F > 10.0$ %); and accidental ($F \leq 10.0$ %).

An environmental data matrix for all samples was prepared including latitude, longitude, depth, hydrodynamic regime (1—sheltered sites; 2—moderately exposed sites; 3—exposed sites, following Bettencourt et al. 2004) and substrate type (0—kelp holdfasts; 1—shelf sediments). For the soft-bottom shelf samples, a dedicated environmental data matrix also included the sediment median grain size and the sediment content in gravel (>2 mm), sand (0.063–2 mm), fines (>0.063 mm), biogenic fraction and total organic matter. The environmental data matrices were related to the biological data using the BIOENV procedure (BEST routine) in PRIMER v.6 (Clarke and Gorley 2006). Abundance and species richness per site and the abundance of key species in the biological affinity groups were plotted using ArcGis 10.

Results

Syllidae fauna abundance and diversity

A total of 55 species in 27 genera were identified in 2,306 Syllids. These annelids were present in all 30 holdfasts and in 68 of the 145 soft-bottom samples.

In the shelf sediments and in the holdfasts, a total of 36 and 33 species were collected, respectively, 14 of which were common to both substrates (cf. Table 1). The genera *Syllis* and *Sphaerosyllis* contributed with the highest number of species (13 and 5, respectively).

In the shelf sediments 1,459 syllids were collected. The most abundant were *Sphaerosyllis bulbosa* Southern, 1914, *Syllis garciai* (Campoy, 1982), *Trypanosyllis coeliaca* Claparède, 1868, *Syllis pontxioi* San Martín and López, 2000 and *Eurysyllis tuberculata* Ehlers, 1864 (Table 1). The following species were recorded in more than 20 sites: *Syllis garciai, Sphaerosyllis bulbosa, Eurysyllis tuberculata and Syllis mercedesae* Lucas et al. 2012. The spatial distribution of Syllids abundance (Fig. 2a) and species richness (Fig. 2b) showed the highest values in coarse sediments off Peniche, Aveiro and Setúbal, mostly in shallower areas (below 60 m), in opposite to muddy or sandy mud sites from the outer shelf and the southern shelf sector. In the soft-bottom samples, the mean species richness and mean abundance reached 4.5 species and 21.5 individuals per unit sampling area (0.1 m^2).

A total of 847 Syllids were sampled in the 30 holdfasts. *Brania pusilla* (Dujardin, 1851), *Sphaerosyllis hystrix* Claparéde, 1863, *Myrianida brachycephala* (Marenzeller, 1874) and *Synmerosyllis lamelligera* (Saint Joseph, 1887) were the most abundant (total abundance >50 specimens, Table 1) and the most frequent (total frequency >50 %). The mean species richness and mean abundance were 8.2 species and 28.2 individuals. The correlation between total abundance and total species richness with the holdfast biometric data was low (area: $\rho = 0.19$ and 0.22, respectively; volume: $\rho = 0.21$ and 0.08, respectively).

Table 1 List of species occurring in the soft-bottom sediments and/or in the *S. polyschides* holdfasts collected in the Portuguese coast

Substrate	Species name	Sediments		Holdfasts		Depth (m)	Sediment types
		Ab	Max Ab	Ab	Max Ab		
Continental shelf soft-bottom sediments only	*Syllis pontxioi* San Martín and López, 2000	91	15	–	–	16–127	VCS, CS, G, FS
	Eurysyllis tuberculata Ehlers, 1864	88	23	–	–	13–168	VCS, CS, G, MS, FS
	Syllis mercedesae Lucas, San Martin and Parapar, 2012	69	17	–	–	29–190	All, mostly FS, CS
	Sphaerosyllis taylori Perkins, 1981	56	16	–	–	13–168	VCS, CS, MS, G, M
	Opisthodonta serratisetosa López, San Marin and Jiménez, 1997	49	28	–	–	25–93	CS, G, VCS, MS
	Plakosyllis brevipes Hartmann-Schröder, 1956	32	16	–	–	16–69	VCS, CS, G, MS
	Syllis licheri Ravara, San Martín and Moreira, 2004	32	9	–	–	33–99	VCS, CS, G, MS
	Palposyllis prosostoma Hartmann-Schröder, 1977	26	7	–	–	25–168	VCS, G, CS
	Xenosyllis scabra (Ehlers, 1864)	23	12	–	–	25–49	VCS, CS, G, MS, FS
	Streptodonta pterochaeta Southern, 1914	19	6	–	–	38–50	VCS, G, CS, MS
	Odontosyllis gibba Claparède, 1863	18	5	–	–	25–99	VCS, G, CS, MS
	Dioplosyllis cirrosa Gidholm, 1962	8	3	–	–	14–127	G, VCS, CS
	Syllides convolutus (Webster and Benedict, 1884)	7	7	–	–	25	VCS
	Parexogone gambiae Lanera, Sordino and San Martín, 1994	4	4	–	–	48	FS
	Streptosyllis bidentata Southern, 1914	4	4	–	–	74	VCS
	Exogone (Exogone) verugera (Claparède, 1868)	2	1	–	–	14–45	MS, CS
	Parexogone hebes (Webster and Benedict, 1884)	2	1	–	–	46–121	FS
	Syllis parapari San Martín and López, 2000	2	1	–	–	33–50	VCS, G
	Odontosyllis fulgurans (Audouin and Milne-Edward, 1833)	1	1	–	–	69	VCS
	Parexogone sp.	1	1	–	–	74	VCS
	Salvatoria sp.	1	1	–	–	87	VCS
	Syllis gerlachi (Hartmann-Schröder, 1960)	1	1	–	–	100	FS
Soft-bottom shelf sediments and *saccorhiza polyschides* holdfasts	*Sphaerosyllis bulbosa* Southern, 1914	311	56	1	1	0–127	All
	Syllis garciai (Campoy, 1982)	204	21	43	10	0–133	All, mostly VCS, FS
	Sphaerosyllis hystrix Claparéde, 1863	45	13	193	21	0–195	VCS, G, CS, MS
	Trypanosyllis coeliaca Claparède, 1868	103	26	1	1	0–127	All, mostly VCS
	Synmerosyllis lamelligera Saint Joseph, 1887	53	15	42	6	0–99	VCS, G, CS, MS
	Myrianida brachycephala (Marenzeller, 1874)	7	4	83	13	0–129	M, FS, VCS
	Parapionosyllis brevicirra San Martin, 1984	68	16	5	3	0–102	M, FS, MS, CS, VCS,
	Syllis armillaris (O.F. Müller, 1776)	51	32	14	3	0–179	VCS, G, MS, FS, CS, VFS
	Paraehlersia ferrugina (Langerhans, 1881)	26	13	17	3	0–127	VCS, CS, G, MS, FS, VFS
	Sphaerosyllis sp.	38	25	1	1	0–93	VCS, G, CS
	Syllides edentatus Westheide, 1974	1	1	27	18	0–99	VFS
	Haplosyllis spongicola (Grube, 1855)	11	5	1	1	0–168	MS, FS
	Syllis gracilis Grube, 1840	1	1	7	2	0–48	FS
	Exogone (Exogone) naidina Örsted, 1845	4	1	1	1	0–99	FS, M, CS

Table 1 continued

Substrate	Species name	Sediments		Holdfasts		Depth (m)	Sediment types
		Ab	Max Ab	Ab	Max Ab		
Saccorhiza polyschides holdfasts only	*Brania pusilla* (Dujardin, 1851)	–	–	234	21	0	–
	Syllis krohni Ehlers, 1864	–	–	37	4	0	–
	Syllis variegata Grube, 1860	–	–	35	5	0	–
	Syllis alternata Moore, 1908	–	–	30	6	0	–
	Syllis corallicola Verrill, 1900	–	–	23	6	0	–
	Odontosyllis ctenostoma Claparède, 1868	–	–	22	9	0	–
	Amblyosyllis formosa (Claparède, 1863)	–	–	8	2	0	–
	Nudisyllis pulligera (Krohn, 1852)	–	–	5	5	0	–
	Trypanosyllis zebra (Grube, 1840)	–	–	4	4	0	–
	Eusyllis assimilis Marenzeller, 1875	–	–	2	1	0	–
	Miscellania dentata Martin, Alós and Sardá, 1990	–	–	2	1	0	–
	Syllides fulvus (Marion and Bobretzky, 1875)	–	–	2	1	0	–
	Eusyllis blomstrandi Malmgren, 1867	–	–	1	1	0	–
	Parapionosyllis minuta (Pierantoni, 1903)	–	–	1	1	0	–
	Salvatoria clavata (Claparède, 1863)	–	–	1	1	0	–
	Salvatoria limbata (Claparède, 1868)	–	–	1	1	0	–
	Sphaerosyllis pirifera Claparède, 1868	–	–	1	1	0	–
	Syllis schulzi (Hartmann-Schröder, 1960)	–	–	1	1	0	–
	Virchowia clavata Langerhans, 1879	–	–	1	1	0	–

Ab total abundance, *Max Ab* maximum abundance per site or holdfast, – = species absent in the substrate, sediment types: *G* gravel, *VCS* very coarse sand, *CS* coarse sand, *MS* medium sand, *FS* fine sand, *VFS* very fine sand, *M* mud

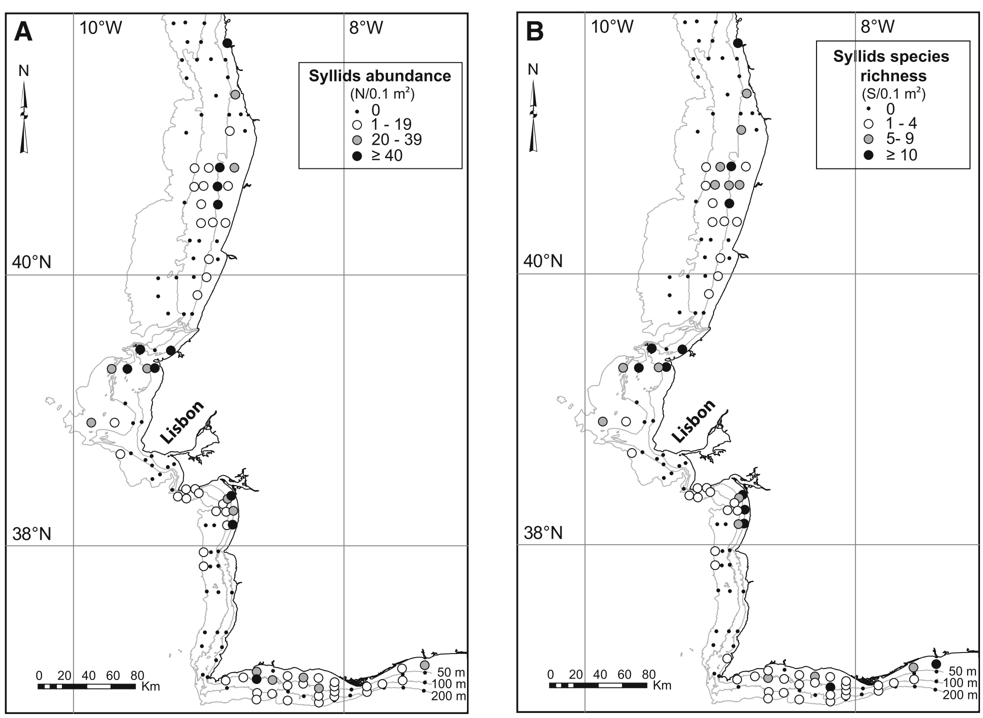

Fig. 2 Spatial distribution of the abundance (**a**) and species richness (**b**) of syllids per site (shelf sediments). Legend: *N* number of specimens, *S* number of taxa

Species spatial distribution

Total abundance, maximum abundance per site or holdfast, substrate type, bathymetric range and sedimentary data for each species are shown in Table 1. Among the 22 Syllid species recorded exclusively in the shelf sediments, 15 were found in the coarser sediments of the northwestern shelf, off Peniche and near the head of Setúbal head canyon (Table 1), such as *Odontosyllis gibba* Claparède, 1863, *Palposyllis prosostoma* Hartmann-Schröder, 1977 (Fig. 3c), *Plakosyllis brevipes* Hartmann-Schröder, 1956, *Streptodonta pterochaeta* (Southern, 1914) (Fig. 3d) and *Syllis licheri* Ravara, San Martín and Moreira, 2004. Other species were only found in the coarse sediments (Table 1) of both western and southern shelf sectors, such as *Dioplosyllis cirrosa* Gidholm, 1962, *Eurysyllis tuberculata* (Fig. 3a), *Opisthodonta serratisetosa* (López, San Marin and Jiménez, 1997) and *Syllis pontxioi*. The species *Syllis mercedesae* was recorded along the entire shelf (Fig. 3b), in a large range of sediment types, mostly in fine sands and coarse sediments (Table 1) and sometimes in symbiosis with bivalves (*Montacuta phascolionis* Dautzenberg and Fischer H., 1925) and sipunculids (*Phascolion (Phascolion) strombus strombus* (Montagu, 1804). Two species were recorded exclusively in the southern shelf, *Exogone (Exogone) verugera* (Claparède, 1868) and *Parexogone gambiae* Lanera, Sordino and San Martín, 1994. *Syllis gerlachi* (Hartmann-Schröder, 1960) was recorded in fine sand off Aveiro (Table 1).

Concerning the species recorded both in the shelf sediments and in the alga holdfasts, some presented a wide spatial distribution (e.g., *Myrianida brachycephala*), while others were mostly recorded in the western coarse sediments, such as *Haplosyllis spongicola* (Grube, 1855), *Paraehlersia ferrugina* (Langerhans, 1881), *Sphaerosyllis bulbosa* (Fig. 3e), *Synmerosyllis lamelligera* (Fig. 3f) and *Trypanosyllis coeliaca* (Table 1). *Sphaerosyllis hystrix* higher abundance was recorded in the holdfasts but was

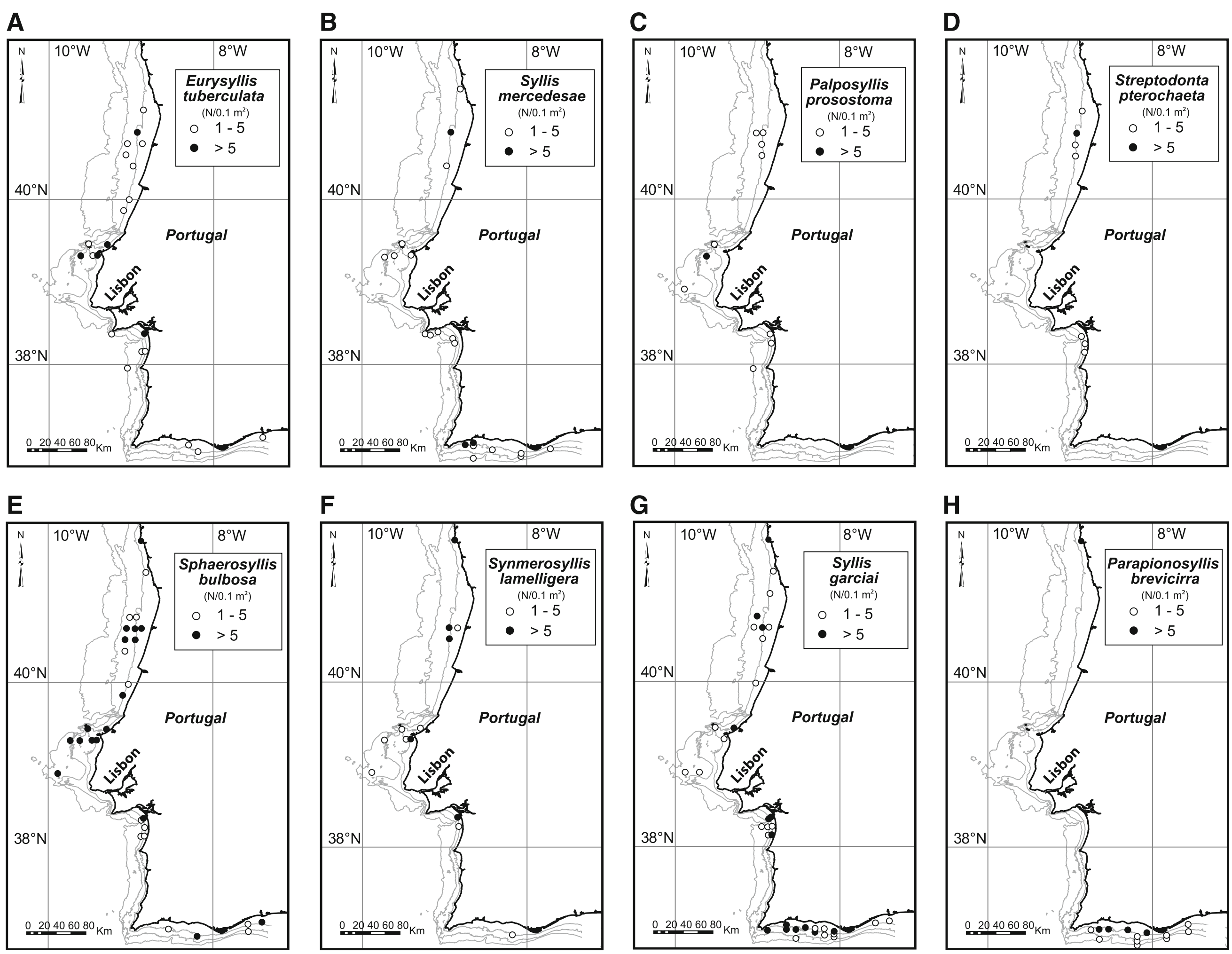

Fig. 3 Abundance distribution on the shelf sediments of *Eurysyllis tuberculata* (**a**), *Syllis mercedesae* (**b**), *Palposyllis prosostoma* (**c**), *Streptodonta pterochaeta* (**d**), *Sphaerosyllis bulbosa* (**e**), *Synmerosyllis lamelligera* (**f**), *Syllis garciai* (**g**) and *Parapionosyllis brevicirra* (**h**)

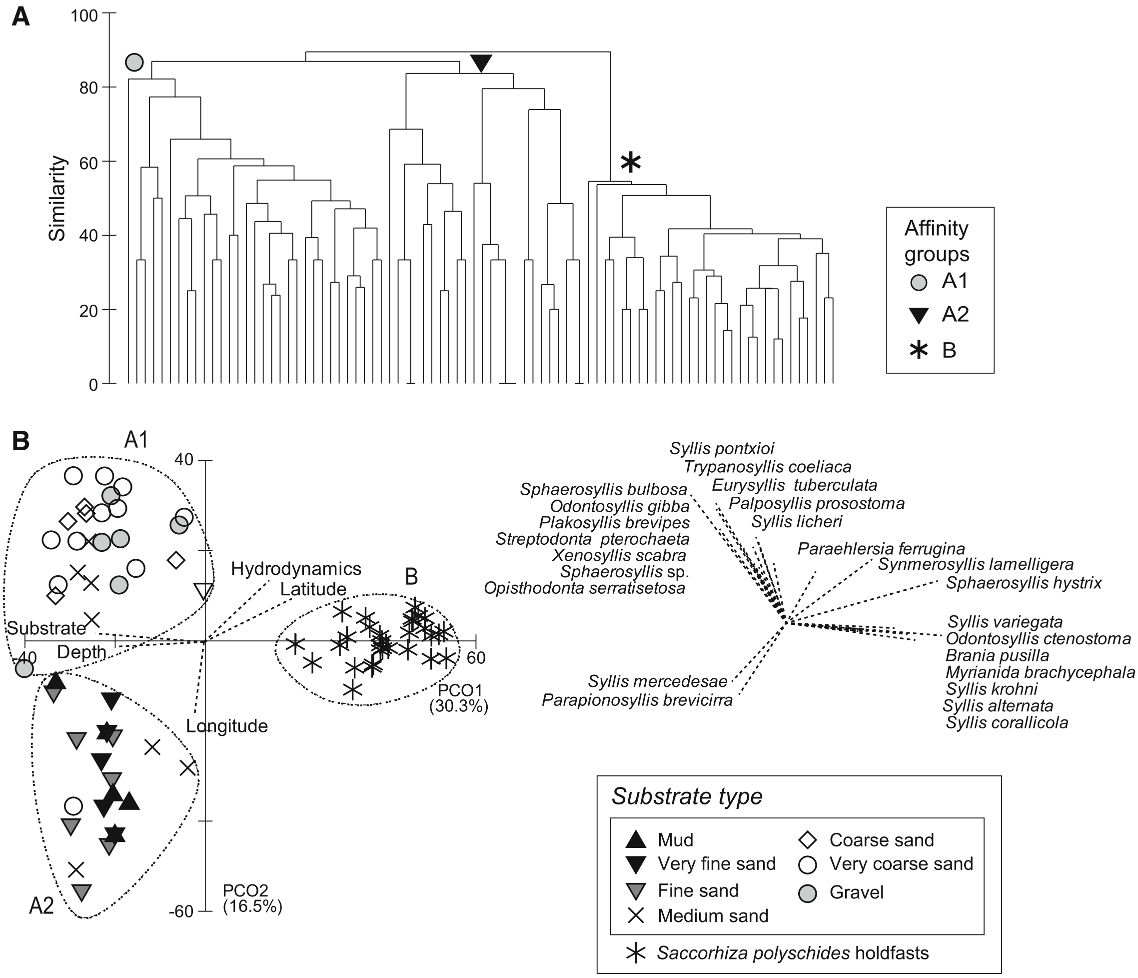

Fig. 4 Classification (**a**) and ordination diagrams (**b**) based on the presence/absence of Syllids. The clusters (*A1*, *A2*, *B*) are overlaid on the ordination diagram, which also represent the substrate type for each sample. Spearman's correlation vectors of environmental data are provided as supplementary variables. The species with the highest Spearman's correlation ($\rho > 0.4$) are represented as vectors in a separate ordination

also found in coarser sediments (Table 1). *Syllis armillaris* (O.F. Müller, 1776) and *S. garciai* (Fig. 3g) were found in a wide range of sediments and in the holdfasts (Table 1). Other species were found in the southern shelf and in the holdfasts, such as *Exogone (Exogone) naidina* Örsted, 1845, *Parapionosyllis brevicirra* Day, 1954 (Fig. 3h), *Sphaerosyllis* sp., *Syllides edentatus* Westheide, 1974 and *Syllis gracilis* Grube, 1840 (Table 1).

Finally, 19 species were recorded exclusively in the kelp holdfasts of which *Brania pusilla* in all the samples. *Syllis krohni* Ehlers, 1864, *S. variegata* Grube, 1860, *Odontosyllis ctenostoma* Claparède, 1868, *S. alternata* Moore, 1908 and *S. corallicola* Verrill, 1900 were recorded in 63, 57, 37, 33 and 30 % of the samples, respectively.

Multivariate analysis

The multivariate analysis results are shown in Fig. 4 and the spatial representation of the affinity groups in Fig. 5. Three major affinity groups were identified, A1, A2 and B (Figs. 4 and 5). Their overall characterization is shown in Table 2 and the species succession in Table 3. Thirteen samples with a single specimen were excluded from the analysis.

The PCO axis 1 (cf. Fig. 4b) gathered 30.3 % of the total variation and opposed A1 and A2 to B. Group B included all the holdfast samples, and so PCO axis 1 made the partition between Syllids from the shelf sediments and from the coastal kelp holdfasts. This was also shown by the superimposed vectors representing the environmental variables. Axis 2 accounted for 16.5 % of the total variation and separated A1 from A2. Fig. 4b also illustrates the sediment type of each sample showing that PCO axis 2 separated the sites located on coarser sediments in the northern exposed shelf (A1) from the sites on finer sediments in the southern sheltered shelf (A2). The vectors of the most correlated species (Fig. 4) showed two large sets of species, one in the top left side, associated with A1 (e.g.,

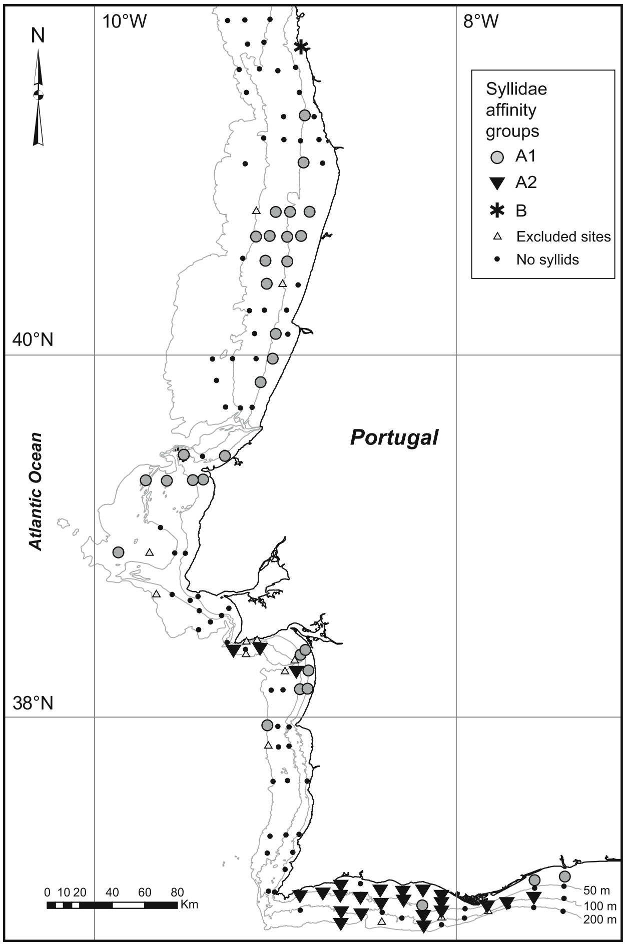

Fig. 5 Spatial distribution of the Syllids assemblages along the Portuguese coast

Plakosyllis brevipes), and the other in the right side, exclusively found in group B (e.g., *Brania pusilla*). Other species, represented in the top right, were shared by two or three groups (e.g., *Sphaerosyllis hystrix*), and in the bottom left, the species *Syllis mercedesae* were more related with group A2.

Group A1 comprised 31 sites mostly located on the mid-western shelf (Fig. 5), characterized by coarse sediments with the highest gravel content and by low fines and total organic matter content (Table 2). This group presented the highest mean abundance and high mean species richness (Table 2). A1 was characterized and dominated by *Sphaerosyllis bulbosa, Syllis pontxioi* and *Trypanosyllis coeliaca* (all constant and elective) (Tables 2, 3). Sixteen species were exclusively found in this group (Table 2).

Group A2 comprised 24 sites located in finer sediments, mostly on the southern shelf (Fig. 5). Sand, fines and total organic matter content were high (Table 2). Abundance and species richness were the lowest among all groups (Table 2). Group A2 was characterized by *Parapionosyllis brevicirra, Syllis mercedesae* and *S. garciai* (cf. Tables 2, 3). *Parexogone gambiae* and *P. hebes* (Webster and Benedict, 1884) were exclusively found here (cf. Tables 2, 3).

Group B corresponded to the Syllids collected in the kelp holdfasts. The *S. polyschides* holdfasts were collected at the end of the growing season and reached mean values of 21.7 cm for maximum diameter, 188.9 cm^2 for area and 198.7 cm^3 for the volume (cf. Table 2). Total and mean species richness values were the highest (Table 2). The group was characterized by *Brania pusilla*, *Myrianida brachycephala, Syllis krohni* and *S. variegata* (cf. Tables 2, 3). A total of 19 species occurred exclusively in this group.

The BIOENV procedure identified latitude, depth and substrate type as the best related variables with the Syllids spatial distribution along the Portuguese coast ($\rho = 0.592$). Considering the soft-bottom samples alone, the best related variables were latitude, depth, median grain size, fines and organic matter content ($\rho = 0.475$). If only the sedimentary variables were used, the correlation slightly decreased ($\rho = 0.438$), and fines content was the best related variable.

Discussion

Diversity, distribution and ecology of syllids in the Portuguese coast

Before this study, a total of 54 Syllid species were known in the Portuguese coast (e.g., Amoureux 1974; Amoureux and Calvário 1981; Campoy 1982; Carvalho et al. 2001; Fauvel 1914; Freitas et al. 2011; Hartmann-Schröder 1977; Gil and Sardá 1999; Marques 1987; Rodrigues et al. 2006, 2011; Saldanha 1995; San Martín 2003, and unpublished data). From the 55 species reported here, 26 are new records for the Portuguese fauna, namely *Odontosyllis fulgurans* (Audouin and Milne-Edward, 1833), *Opisthodonta serratisetosa*, *Parexogone gambiae, Plakosyllis brevipes*, *Streptodonta pterochaeta, Streptosyllis bidentata* Southern, 1914, *Syllides convolutus* (Webster and Benedict, 1884), *Syllis mercedesae, Syllis parapari* San Martín and López, 2000 and *Syllis pontxioi* (species exclusively found in the soft-bottom samples); *Amblyosyllis formosa* (Claparède, 1863), *Miscellania dentata* Martin, Alós and Sardá, 1990, *Nudisyllis pulligera* (Krohn, 1852), *Salvatoria clavata* (Claparède, 1863), *Salvatoria limbata* (Claparède, 1868), *Syllides fulvus* (Marion and Bobretzky, 1875), *Syllis alternata*, *Syllis corallicola, Syllis schulzi* (Hartmann-Schröder, 1960) and *Virchowia clavata* Langerhans, 1879 (species only found in the holdfasts); *Myrianida brachycephala*, *Parapionosyllis brevicirra*, *Sphaerosyllis bulbosa*, *Sphaerosyllis* sp. (accordingly to San Martín 2003), *Syllides edentatus* and *Synmerosyllis lamelligera* (species found in both substrates). This study increased the number of valid Syllid species known in Portugal from 56 to 80.

Table 2 Characterization of the syllids assemblages identified on the Portuguese coast (Western Iberia)

Affinity groups	A1	A2	B
No. of sampling sites	31	24	30
Substrate type	Coarser shelf sediments	Finer shelf sediments	Kelp holdfasts
Sediment type	VCS (11/31); CS (7/31); G (7/31); MS (3/31); FS (2/31); n.a. (1/31)	FS (13/24); M (9/24); MS (5/24); VFS (4/24); VCS(3/24); CS (1/24)	–
Gravel content (mean; %)	26.5	2.6	–
Sand content (mean; %)	69.7	61.8	–
Fines content (mean; %)	3.7	35.5	–
TOM content (mean; %)	1.2	4.3	–
Depth (mean; m)	57.8	70.8	0
Max holdfast diameter (mean; cm)	–	–	21.7
Holdfast area (mean; cm^2)	–	–	188.9
Holdfast volume (mean; cm^3)	–	–	198.7
Abundance (mean)	38.7	10.2	28.2
Total species richness	31	16	33
Mean species richness	7.5	2.5	8.2
No. of exclusive species	16	2	19
Characteristic species	*Sphaerosyllis bulbosa* (Cn/P)	*Parapionosyllis brevicirra* (C/P)	*Brania pusilla* (Cn/E)*
(with Constancy and Fidelity indications)	*Syllis pontxioi* (Cn/E)*	*Syllis mercedesae* (C/P)	*Myrianida brachycephala* (Cn/E) *Sphaerosyllis hystrix* (Cn/P)
	Trypanosyllis coeliaca (Cn/E)	*Syllis garciai* (Cn/A)	*Syllis krohni* (Cn/E)*
	Eurysyllis tuberculata (Cn/P)	*Sphaerosyllis taylori* (O/I)	*Syllis variegata* (Cn/E)*
	Odontosyllis gibba (C/E)*	*Syllis armillaris* (O/I)	*Synmerosyllis lamelligera* (Cn/I)
	Palposyllis prosostoma (C/E)*	*Exogone (Exogone) naidina* (R/I)	*Odontosyllis ctenostoma* (C/E)*
	Plakosyllis brevipes (C/E)*	*Parexogone gambiae* (R/E)*	*Syllis alternata* (C/E)*
	Syllis garciai (Cn/I)	*Parexogone hebes* (R/E)*	*Syllis corallicola* (C/E)*
	Streptodonta pterochaeta (O/E)*	*Eurysyllis tuberculata* (R/A)	*Amblyosyllis formosa* (O/E)*
	Syllis licheri (O/E)*	*Haplosyllis spongicola* (R/A)	
Most abundant species (top ten)	*Sphaerosyllis bulbosa*	*Syllis garciai*	*Brania pusilla**
	Syllis garciai	*Parapionosyllis brevicirra*	*Sphaerosyllis hystrix*
	Trypanosyllis coeliaca	*Syllis mercedesae*	*Myrianida brachycephala*
	*Syllis pontxioi**	*Sphaerosyllis taylori*	*Syllis garciai*
	Eurysyllis tuberculata	*Syllis armillaris*	*Synmerosyllis lamelligera*
	*Synmerosyllis lamelligera**	*Haplosyllis spongicola*	*Syllis krohni* *
	*Opisthodonta serratisetosa**	*Parexogone gambiae**	*Syllis variegata**
	Syllis armillaris	*Exogone (Exogone) naidina*	*Syllis alternata**
	Sphaerosyllis hystrix	*Sphaerosyllis bulbosa Eurysyllis tuberculata*	*Syllides edentatus*
	Sphaerosyllis taylori		*Syllis corallicola**

Mean values are reported to the unit sampling area for the soft-bottom samples (0.1 m^2) and per holdfast. The top 10 characteristic species in each group were defined according to the highest product between constancy and fidelity

Sediment types: *G* gravel, *VCS* very coarse sand, *CS* coarse sand, *MS* medium sand, *FS* fine sand, *VFS* very fine sand, *M* mud, *TOM* total organic matter, Constancy: *Cn* constant, *C* common, *O* occasional, *R* rare, Fidelity: *E* elective, *P* preferential, *I* indifferent, *A* accessory, * = exclusive species in each group, – = not applicable, *n.a.* not available data

Table 3 Mean species abundance per affinity group A1, A2 (ind. 0.1 m^{-2}) and B (holdfast)

Taxa	A1	A2	B
Opisthodonta serratisetosa (López, San Marin and Jiménez, 1997)	**1.6**		
Syllis pontxioi San Martín and López, 2000	**2.9**		
Plakosyllis brevipes Hartmann-Schröder, 1956	**1.0**		
Syllis licheri Ravara, San Martín and Moreira, 2004	**1.0**		
Palposyllis prosostoma Hartmann-Schröder, 1977	**0.8**		
Xenosyllis scabra (Ehlers, 1864)	**0.7**		
Streptodonta pterochaeta (Southern, 1914)	**0.6**		
Odontosyllis gibba Claparède, 1863	**0.6**		
Dioplosyllis cirrosa Gidholm, 1962	**0.3**		
Syllides convolutus (Webster and Benedict, 1884)	**0.2**		
Streptosyllis bidentata Southern, 1914	**0.1**		
Exogone (Exogone) verugera (Claparède, 1868)	**0.1**		
Syllis parapari San Martín and López, 2000	**0.1**		
Odontosyllis fulgurans (Audouin and Milne-Edward, 1833)	*		
Parexogone sp.	*		
Salvatoria sp.	*		
Sphaerosyllis bulbosa Southern, 1914	*10.0*	0.1	*
Syllis garciai (Campoy, 1982)	*3.7*	3.6	1.4
Trypanosyllis coeliaca Claparède, 1868	*3.3*		*
Eurysyllis tuberculata Ehlers, 1864	*2.8*	0.1	
Synmerosyllis lamelligera (Saint Joseph, 1887	*1.7*		1.4
Syllis armillaris (O.F. Müller, 1776)	*1.3*	0.4	0.5
Sphaerosyllis taylori Perkins, 1981	*1.3*	0.7	
Sphaerosyllis sp.	*1.2*		*
Paraehlersia ferrugina (Langerhans, 1881)	*0.8*	0.1	0.6
Parexogone gambiae Lanera, Sordino and San Martín, 1994		**0.2**	
Parexogone hebes (Webster and Benedict, 1884)		*	
Parapionosyllis brevicirra Day, 1954	0.1	*2.7*	0.2
Syllis mercedesae Lucas, San Martin and Parapar, 2012	0.6	*1.9*	
Haplosyllis spongicola (Grube, 1855)	0.2	*0.2*	*
Exogone (Exogone) naidina Örsted, 1845	*	*0.1*	*
Sphaerosyllis hystrix Claparéde, 1863	1.3	*	*6.4*
Myrianida brachycephala (Marenzeller, 1874)	0.1	*	*2.8*
Syllides edentatus Westheide, 1974		*	*0.9*
Syllis gracilis Grube, 1840		*	*0.2*
Brania pusilla (Dujardin, 1851)			**7.8**
Syllis krohni Ehlers, 1864			**1.2**
Syllis variegata Grube, 1860			**1.2**
Syllis alternata Moore, 1908			**1.0**
Syllis corallicola Verrill, 1900			**0.8**
Odontosyllis ctenostoma Claparède, 1868			**0.7**
Amblyosyllis formosa (Claparède, 1863)			**0.3**
Nudisyllis pulligera (Krohn, 1852)			**0.2**
Trypanosyllis zebra (Grube, 1840)			**0.1**
Eusyllis assimilis Marenzeller, 1875			**0.1**
Miscellania dentata Martin, Alós and Sardá, 1990			**0.1**
Syllides fulvus (Marion and Bobretzky, 1875)			**0.1**
Eusyllis blomstrandi Malmgren, 1867			*
Parapionosyllis minuta (Pierantoni, 1903)			*
Salvatoria clavata (Claparède, 1863)			*
Salvatoria limbata (Claparède, 1868)			*
Sphaerosyllis pirifera Claparède, 1868			*
Syllis schulzi (Hartmann-Schröder, 1960)			*
Virchowia clavata Langerhans, 1879			*

Values in bold—exclusive species. Values in italics—group where non-exclusive species present their highest mean abundance

* mean abundance below 0.05 ind. 0.1 m^{-2}

Recent appropriate taxonomic developments and the heterogeneity and taxonomic complexity of these polychaetes (e.g., San Martín 2003) could explain such increase. This is key knowledge for future studies. Syllids are good faunal and ecological indicators of the physical environment, and therefore, they could be used in studies of long-term changes in marine areas and to validate the taxonomic sufficiency effectiveness (e.g., Musco et al. 2009). These 80 species represent half of the reported species for the Iberian Peninsula mainland and Spanish Islands (Lattig et al. 2007; Lucas et al. 2012; San Martín 2003), one of the best studied areas for Syllids worldwide. Other well-studied areas include Australia (160 species, San Martín and Hutchings 2006; San Martín 2005; San Martín et al. 2008a, b, 2010), the Mediterranean Sea (approximately 190 species; Musco and Giangrande 2005), the Great Caribbean Region (167 species; Salazar-Vallejo 1996), México (more than 60 species in the Pacific Mexican coast and more than 70 in the Atlantic Mexican coast; Granados-Barba et al. 2003) and Brazil where 139 species are known (Fukuda 2010; Nogueira and San Martín 2002; Nogueira and Yuanda-Guarin 2008; Nogueira et al. 2001, 2004). Other areas with a longer coastline than Portugal have fewer reported species, such as the US Gulf of México (44 species, Uebelacker and Johnson 1984), Egypt (nearly 60 species, Abd-Elnaby and San Martín 2010) or Venezuela (40 species in *Thalassia testudinum* (Bank and Köning, 1805) meadows, San Martín and Bone 2001; 26 species in different substrates, Liñero-Arana and Díaz 2011).

This study gives new insights about the ecology and geographic distribution of several species. The meridional distribution limit of the Lusitanean species *Syllis mercedesae*, recently described for the continental slope off Ártabro Gulf (Galicia, NW Spain; Lucas et al. 2012), is now set in the southern Portuguese shelf. The distribution limit of *Syllis licheri,* firstly described off Aveiro (northwestern Portuguese coast; Ravara et al. 2004), is now established between the Chausey Islands (English Channel; Olivier et al. 2012) and the Setúbal canyon (southwestern Portuguese continental shelf; this study). Other species considered so far endemic to the Mediterranean Sea, *Parexogone gambiae* and *Sphaerosyllis* sp. (Musco and Giangrande 2005; San Martín 2003), are recorded here for the first time in the Atlantic Ocean, in the southern Portuguese continental shelf and off Peniche, respectively. The temperate species *Miscellania dentata* and *Virchowia clavata*, known for the Mediterranean Sea and the Macaronesia biogeographic provinces (San Martín 2003), are here firstly reported for the Lusitanean biogeographic province. This study also sets the first record of the 33 species found in *S. polyschides* holdfasts, previously only known from other substrate types, namely hard bottoms, *Posidonia oceanica* rhizomes (or other seagrass meadows), photophilic algae, coralline bottoms, sponges, maërl or below infralittoral stones (San Martín 2003). *Sphaerosyllis bulbosa,* previously known from coarse sediments, sand and maërl, between 30 and 70 m (San Martín 2003), was reported in this study for kelp holdfasts and wider sedimentary (mud to gravel) and bathymetric (up to 127 m) range. The habitat preferences of *Haplosyllis spongicola*, *Opisthodonta serratisetosa*, *Parexogone gambiae*, *Syllis gerlachi*, *S. armillaris*, *S. gracilis* and *S. mercedesae* now also include soft bottom, as they were previously associated with different hard-bottom types only, such as sponges, *Posidonia oceanica* rhizomes, photophilic or sciaphilic algae (Lucas et al. 2012; San Martín 2003).

The present study also sets wider bathymetric range for several species. Some species were recorded for deeper waters compared to San Martín (2003) namely *Dioplosyllis cirrosa* (127 m), *Parexogone gambiae* (43 m), *Plakosyllis brevipes* (69 m), *Streptodonta pterochaeta* (50 m), *Syllis gerlachi* (100 m), *S. pontxioi* (127 m), *Exogone (Exogone) naidina* (99 m), *Haplosyllis spongicola* (179 m), *Myrianida brachycephala* (129 m), *Paraehlersia ferrugina* (127 m), *Parapionosyllis brevicirra* (102 m), *Sphaerosyllis hystrix* (195 m), *Syllides edentates* (29 m), *Syllis armillaris*, *S. garciai* (133 m) and *Synmerosyllis lamelligera* (99 m).Other species were recorded at lower depth, as *Syllis mercedesae*, 29–1,132 m (Lucas et al. 2012), and *Palposyllis prosostoma*, between 25 and 200 m (San Martín 2003) and for *Syllis licheri* new minimum and maximum depth were set (25 and 99 m).

Syllis mercedesae was in this study sometimes found in gastropod shells, in symbiosis with a bivalve (*Montacuta phascolionis*) and a sipunculid (*Phascolion (Phascolion) strombus strombus*). A symbiotic mode of life is known for nearly 20 Syllid species, mostly with decapods, cnidarians and sponges (López et al. 2001; Martin and Britayev 1998; Martin et al. 2002). Symbiotic species have developed morphological adaptations, such as the simplification of chaetae, camouflage coloring or particular behavior (e.g., short-distance host recognition; Martin et al. 2002). Among the genus *Syllis,* only *S. armillaris*, *S. cornuta* Rathke, 1843, *S. gracilis, S. onkylochaeta* Hartmann-Schröder, 1991 and *S. sclerolaema* Ehlers, 1901 show commensal habits. The symbiotic associations and the morphological features of those species are very different from *Syllis mercedesae,* suggesting that this can correspond to a distinct symbiotic association. In fact, Cutler (1994) refers that only *Syllis cornuta* is usually found with one of the following sipunculans: *Phascolion (Phascolion) strombus strombus*, *Aspidosiphon (Aspidosiphon) muelleri muelleri* Diesing, 1851 (in shells) or *Phascolosoma (Phascolosoma) meteori* (Hérubel, 1904) (in mud tubes). On the other hand, *Phascolion (Phascolion) strombus strombus* was already found with the bivalve *Montacuta phascolionis* [or *Epilepton clarkiae* (Clark W., 1852)] and the gastropod *Ondina diaphana* (Jeffreys, 1848), but never before with Syllids.

The present study also revealed that the total number of species in the soft-bottom shelf sediments was only slightly higher than in the kelp holdfasts (36 and 33, respectively), despite the range of sediment types, depth and latitude covered by the soft-bottom samples. The complexity of the internal channeling system of the *S. polyschides* holdfast may offer larger and more protective areas for this fauna (McKenzie and Moore 1981) than the sediment interstitial spaces. Several studies also suggest that hard substrates are more important for Syllids than soft substrates (e.g., Antoniadou et al. 2004; Liñero-Arana and Díaz 2011; San Martín 2003; Serrano et al. 2006). Faulwetter et al. (2011) recorded only 23 species in soft-bottom samples (in Israel) when compared to the 62 species found in several hard substrates (e.g., filamentous Phaeophyceae and Chlorophyceae, *Jania* sp., *Cystoseira* sp.), in Crete, in the Mediterranean Sea. Granados-Barba et al. (2003) also described a lower Syllid diversity and abundance in the soft bottom of the eastern coast of Mexico when compared to coralline hard bottoms. Authors attributed this to the complexity of the coral habitat, with crevices and fissures furnishing shelter. From the 45 species they reported, 38 were found in hard bottom (corals), 31 in soft bottoms (mostly in coarse carbonate sands) and 21 were shared by the two substrates.

Syllids assemblages and relationships with environmental factors

The present study found three major assemblages, one associated with coarser sediments, another with finer sediments and another with *S. polyschides* holdfasts. Syllids have been reported from several habitats showing differential affinity for hard or soft bottom (San Martín 2003). The coarse sand Syllid assemblage here described with *Sphaerosyllis bulbosa, Syllis pontxioi* and *Trypanosyllis coeliaca* is part of the coarse sediment macrobenthic community reported by Martins et al. (in press), for the Portuguese continental shelf. This is a similar community to the gravels dominated by *Astarte sulcata—Venus casina* (Glémarec 1973) or the *Venus* community (Thorson 1957), identified in several European coasts, in Portugal with a high number of warm water species (e.g., *Opisthodonta serratisetosa, Palposyllis prosostoma* or *Syllis licheri*) co-occurring with boreal, Atlantic–Mediterranean, amphi-Atlantic or cosmopolitan species (e.g., *Odontosyllis gibba, Plakosyllis brevipes* or *Sphaerosyllis bulbosa*; Musco and Giangrande 2005; San Martín 2003). The fine sand Syllids assemblage dominated by the warm water species *Parapionosyllis brevicirra, Syllis mercedesae* and *S. garciai* is part of the Lusitanean macrofauna assemblage found in muddy sands of the southern Portuguese shelf (Martins et al. in press). Granados-Barba et al. (2003) found a decreasing abundance and diversity of Syllids from carbonate (coarse sands with coral and shell fragments) to terrigenous sediments (mud and sandy mud). This agrees with our results, in which the assemblage installed in coarser sediments was more diverse and abundant than that from finer sediments. It is recognized that polychaete communities exhibit a close relationship with sediments, depth, hydrodynamics and other abiotic parameters (e.g., Labrune et al. 2007; Simboura et al. 2000). The coarse sediments from the northwestern Portuguese continental shelf provide interstitial space to the small-sized and highly motile syllids and pisionids (Martins et al. 2012c), but also lumbrinerids (Martins et al. 2012b). The space between the gravel and sand particles, the internal channeling system of *S. polyschides* holdfasts or the cracks and crevices in the coralline hard bottoms create adequate shelter and therefore support a high abundance and diversity of small-sized polychaetes, such as the Syllids. They use those spaces to move through, to feed, to hide from predators and to reproduce, which explain why Syllids are considered one of the most successful polychaete groups in both soft and hard bottoms (e.g., Faulwetter et al. 2011; Granados-Barba et al. 2003; San Martín 2003).

The group associated with kelp holdfasts was characterized by *Brania pusilla*, *Myrianida brachycephala, Syllis krohni* and *S. variegata,* species showing primary affinity for hard bottom, including seagrass and/or kelp rhizomes, photophilic algae, corals and sponges. Among the holdfasts inhabitants, the majority have been regarded cosmopolitan or to have an Atlantic–Mediterranean distribution and only few species showed Mediterranean and/or Macaronesian distribution (*Miscellania dentata, Sphaerosyllis* sp., *Virchowia clavata*) (San Martín 2003). Several works have studied the faunal communities associated with kelp species, mostly *Laminaria* (e.g., Christie et al. 2003; Jørgensen and Christie 2003; Norderhaug et al. 2012; Tuya et al. 2011) and with seagrass meadows (rhizomes and leaves), namely *Posidonia oceanica* (e.g., San Martín 2003; San Martín et al. 1990; Somaschini et al. 1994) or *Thalassia testudinum* (San Martín and Bone 2001; Stoner and Lewis 1985). In such habitats, a high number of Syllid species and specimens have been found (e.g., San Martín 2003). Christie et al. (2003) and Jørgensen and Christie (2003) revealed important differences on the fauna abundance and diversity associated with the holdfast, the stipe and the frond of the kelp *Laminaria*. Polychaetes of the genera *Anaitides, Eulalia, Harmothoe, Hediste, Kefersteinia, Lagisca* and *Lepidonotus* were recorded in the holdfasts, while the syllids *Amblyosyllis, Brania, Pionosyllis* and *Trypanosyllis* were found mostly in the stipe (Christie et al. 2003; Jørgensen and Christie 2003). In our case, the later genera were all found in the holdfasts of *S. polyschides*. No specific studies were found in the literature focusing on Syllids associated with holdfasts of *S. polyschides* and only very few dedicated to the overall fauna. A study undertaken by McKenzie and Moore (1981) highlighted that in the space between the base of the holdfast and the hard substrate (to which it is attached), several amphipods, ophiuroids and polychaetes were found, while many polychaetes, amphipods, decapods and fish were recorded inside the holdfasts. McKenzie and Moore (1981) recorded a total of 77 species, while in our study, considering Syllids alone, we reported a total of 33 species. Gestoso et al. (2012) comparing the epifaunal assemblages in native and invasive seaweed species found mostly gastropods (45 % of the total taxa), polychaetes and ophiuroids in *S. polyschides*.

Conclusions

A total of 2,306 syllids belonging to 55 species were identified with only 14 species shared by the shelf sediments and *Saccorhiza polyschides* holdfasts. A total of 26 species were firstly recorded in this study, increasing to 80 the number of Syllid species known to Portugal. This study sets 20 new bathymetric ranges and gives new insights about the geographic distribution of six species and the ecology of several others (7 species first record in soft bottom; first record of several Syllids in the holdfasts). The type of substrate (holdfast vs. soft bottom) and the sediment grain size (coarser vs. finer) were the descriptors best related to the Syllids assemblages.

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