

# Environmental factors structuring polychaete communities in shallow rocky habitats: role of physical stress versus habitat complexity

Alberto Serrano · Izaskun Preciado

Received: 2 January 2006 / Revised: 4 September 2006 / Accepted: 20 September 2006 / Published online: 7 November 2006  
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**Abstract** Polychaetes inhabiting 12 different hard bottom habitats were studied. A total of 157 species belonging to 32 families were identified. Differences among habitats in polychaete density, species richness, and diversity were analysed, as well as the relationships between these ecological indices and depth range, slope and in-bay/out-bay gradient. A high faunal homogeneity was found: all biotopes were dominated by a low number of eurytopic species. Intertidal habitats and subtidal ones with scarce algal cover were typified by vagile polychaetes (syllids, nereids), while sessile polychaetes (serpulids, sabellids) appeared typically among subtidal large macrophytes, habitats with a calcareous substrate and shaded habitats. Multivariate analyses showed that habitat complexity, determined by physical disturbance, is the main structuring factor for polychaete populations. Biotopes with the highest structural complexity displayed a high number of companion species increasing ecological indices and denoting a well-structured habitat. On the other hand, communities such as those in the upper intertidal, mainly controlled by physical environmental variables, showed a poorer polychaete fauna, dominated by ubiquitous species and a few well-adapted specialists.

**Keywords** Polychaetes · Rocky environments · Physical disturbance · Habitat complexity · Cantabrian Sea

## Introduction

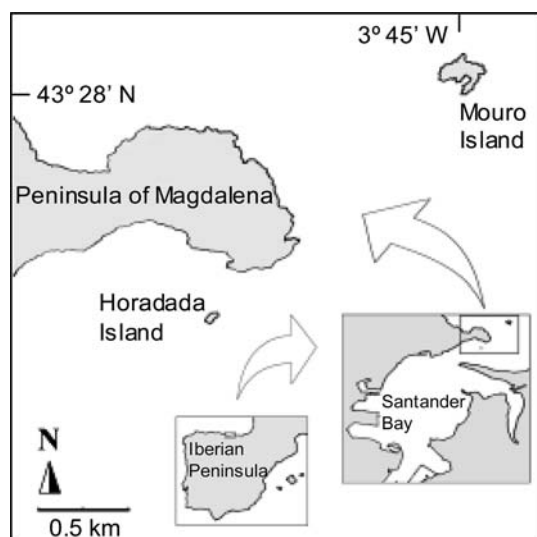
Shallow rocky ecosystems provide a great variety of habitats suitable for polychaetes, which are often one of the dominant taxa there (e.g., Bianchi and Morri 1985; Giangrande 1988). In the littoral rocky bottoms of the Santander Bay (Fig. 1), hydrodynamic and topographic variables produce a patchy distribution of benthic macrohabitats (García-Castrillo et al. 2000). Tidal rhythms generate harsh conditions, with barnacles and turf algae being the only organisms able to establish three-dimensional biotopes in the intertidal (Puente 2000). In the subtidal, sedimentation is the key factor conditioning the different habitats, as it simplifies the macrophytic coverage by decreasing the vertical stratification and replacing canopy algae by crustose and turf types (Gorostiaga and Díez 1996). Because of this, turf-forming algae monopolize subtidal localities of high luminosity and siltation. Polychaete responses to environmental changes are diverse. Polychaetes are soft-bodied organisms with low resistance to desiccation and sand abrasion (Serrano 2002). Mobile polychaetes can behaviourally avoid environmental stress. However, since most vagile polychaetes are medium- or small-sized organisms with low motility at macrohabitat scale, they rely on the existence of microhabitats or “refuges” in harsh areas or during periods of environmental stress to survive (Bailey-Brock et al. 1980). Conversely, the distribution of sessile polychaetes is much more dependent on environmental conditions,

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Communicated by H.-D. Franke.

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A. Serrano (✉) · I. Preciado  
Instituto Español de Oceanografía (IEO),  
Promontorio de San Martín s/n, P. O. Box 240,  
39080 Santander, Spain  
e-mail: aserrano@st.ieo.es



**Fig. 1** Map of Santander Bay (Cantabrian Sea, North-Atlantic coast of Spain) showing the three sampling sites: *HI* Horadada Island, *MP* Magdalena Peninsula, and *MI* Mouro Island

and morphological as well as physiological adaptations are necessary to avoid stress situations.

Well-structured macrophytic habitats are located far from environmental extremes, i.e., in the study area, on horizontal surfaces with low sedimentation rates. Calcareous encrusting algae are relatively abundant in environments of low light intensity and sedimentation rates, and are hence common underneath macroalgae (Connell 2003). Finally, invertebrate assemblages dominate shaded environments on higher slope surfaces (Preciado and Maldonado 2005), where competition with macroalgae and siltation are limited (Moore 1977).

Patchiness in macrohabitat distribution sometimes generates parallel distributions of associated populations. On the other hand, taxa may perceive environmental variability at different scales, thus exhibiting patterns of distribution, which do not match that of macrohabitats. The aim of the present work was to elucidate if polychaete spatial distribution matches the patchy distribution of benthic habitats, and to determine the main factors structuring polychaete populations in shallow rocky habitats. We examined patterns of polychaete spatial distribution along depth, slope, and in-bay/out-bay gradients in littoral rocky habitats of the Atlantic coast of northern Spain.

## Methods

The study was carried out at three different sites: Mouro Island (MI, number of quadrants ( $n$ ) = 294), Magdalena Peninsula (MP,  $n$  = 29), and Horadada

Island (HI,  $n$  = 34), located outside, at the entrance, and inside of the Bay of Santander (Atlantic coast of northern Spain; Fig. 1), respectively. Rocky bottoms reach 20 m of depth at MI, 10 m at MP, and 5 m at HI; below these depths the bottom is completely covered by sand deposits. The underwater topography at MI consists mostly of large boulders with deep vertical walls forming an intricate system of narrow channels. At MP the seascape is a large rocky platform with a moderate slope heading offshore. Finally, at HI the bottom is characterized by horizontal surfaces, with vertical walls extending from the sides of the island. MI and MP are highly exposed to wave action, while HI is sheltered from direct wave action but affected by strong tidal currents (Castillejo et al. 1984). At MI the presence of silt is confined to the bottom of the channels, whereas at MP and HI sedimentation is intense all over the bottom surface.

The benthic assemblages found in the study area were defined in previous studies (García-Castrillo et al. 2000; Puente 2000) relating to tidal level, algal coverage, and especially, to the presence of a basal encrusting layer of *Mesophyllum lichenoides*. We grouped these communities into 12 different “habitats” following previous general studies on the polychaete fauna of the area (Serrano 2002). Hence, we considered three intertidal habitats: barnacles dominated by *Chthamalus stellatus* (BAR,  $n$  = 5), the alga *Corallina elongata* (COR,  $n$  = 37) and the lower intertidal (LIA,  $n$  = 16) grouping *Bifurcaria bifurcata* and *Codium tomentosum* assemblages. Another four habitats were characterized as subtidal without *Mesophyllum lichenoides* substratum: two animal-based habitats without algal cover, *Anemonia viridis* beds (ANE,  $n$  = 3) and *Sabellaria spinulosa* “reefs” (SAB,  $n$  = 2); a seasonal small-sized algae habitat (SSA,  $n$  = 22) grouping communities dominated by several species (*Aglaothamnion* sp., *Asparagopsis armata*, *Falkenbergia rufolanosa*, *Dictyopteris polypodioides*, *Dictyota dichotoma*); and a macroalgae habitat dominated by *Cystoseira baccata* (CYS,  $n$  = 20). These four habitats showed a high siltation-resilience, and were located in rock-sand ecotones. Additionally, there were four subtidal habitats with *Mesophyllum* substrate: *Laminaria ochroleuca* (LAM,  $n$  = 48), *Gelidium sesquipedale* (GEL,  $n$  = 39), a “small red algae” habitat (SRA,  $n$  = 17) co-dominated by *Calliblepharis ciliata* and *Pterosiphonia complanata*, and a *Mesophyllum lichenoides* community without macroalgal cover (MES,  $n$  = 7). Finally, shaded walls, overhangs, and caves were grouped in a sciophilous habitat category (SCI,  $n$  = 141), dominated by macrofauna, mostly sponges and cnidarians.

Sampling was conducted by Scuba diving. A total of 357 random quadrats were scraped, collecting all fauna and flora within them. We used 625 cm<sup>2</sup> sampling quadrats, except in the LAM community, where quadrats of 2,500 cm<sup>2</sup> were used. For further statistical analyses, abundance values were calculated as ind m<sup>-2</sup>.

Differences in polychaete density (average number of individuals m<sup>-2</sup>), species richness (average species number per quadrat) and Shannon–Wiener diversity were examined in relation to depth level, substrate inclination, site, and habitats, using a Kruskal–Wallis one way ANOVA on ranks. When significant differences were detected, pairwise “a posteriori” Dunn’s tests were run to identify the groups responsible for such differences. We considered five depth ranges: –5 to 0 m, 0 to 5 m, 5 to 10 m, 10 to 15 m, 15 to 20 m; and four substrate inclination semiquantitative ranges: horizontal to subhorizontal surfaces (HOR, substrata angling 0°–45°), vertical to subvertical walls (WVS, 46°–90°), overhangs (OVH, 91°–135°), and ceilings (CEI, 136°–180°). Sites and habitats were defined as specified above in this section. “Habitat complexity” and “physical disturbance” are concepts used along the text. McCoy and Bell (1991) stated that “habitat complexity” encompasses the absolute abundance of habitat structural components and the relative abundances of different habitat structural components. Thereby, the total abundance of structural species (algae and sponges in photophilous and sciophilous environments, respectively) was used in some analyses. In addition, *Laminaria* rhizoids, *Mesophyllum* basal stratum and three-dimensional sponges are considered as habitat structural components. Regarding physical disturbance, intertidal conditions and sand burial and abrasion have been considered as the main sources of stress (Sousa 2001). Following these criteria, habitats have been classified as follows: high habitat complexity and low physical disturbance (LAM, GEL, SCI), medium habitat complexity and physical disturbance (SRA, COR, CYS, MES, SAB), and low habitat complexity and high physical disturbance (BAR, ANE, LIA, SSA).

To cluster habitat-site groups based on polychaete fauna, Bray–Curtis pair-wise faunal similarities between groups were calculated using log-transformed abundances, and the distance matrix was then processed using the UPGMA algorithm. SIMPER analyses were also run to identify the main polychaete species responsible for dissimilarities between habitat-site groups. We used a redundancy analysis (RDA) to assess the amount of variation in polychaete densities per quadrat in relation to a set of environmental factors. The set of variables included depth, substrate

inclination, site, and habitat. Sponge and algal abundance (both calculated as wet weight per quadrat) were also included, as indicators of a darkness/light affinity gradient and also as a habitat complexity measure (see above). Density data were log-transformed to diminish the effect of uneven density distributions and rare taxa. The Monte-Carlo test was used to test the statistical significance of the first and all canonical axes together using 999 permutations under the reduced model. RDA results were represented graphically in two bi-dimensional ordinations generated by bi-plot scaling, focusing on inter-species distances, and representing species and samples by points and environmental variables by vectors.

## Results

### General faunal patterns

About 25,500 polychaetes (colonial *Filograna implexa* excluded) were collected and ascribed to 157 species belonging to 32 families (Table 1). We found polychaetes in 356 (99.7%) out of 357 samples. The most frequent family was Syllidae, which was found in 92% of the samples. Regarding species richness, Syllidae was also the best-represented family with 39 species and a mean richness of 4.3 species/sample. Other families with high species numbers were Serpulidae (15 species, 2.4 species/sample), Sabellidae (13, 0.8), Phyllodocidae (10, 1.3), Nereididae (10, 0.9), and Eunicidae (5, 1.29). Serpulidae was the numerically dominant family with 3,579.9 ind m<sup>-2</sup> and 81.9% of the total number of individual sampled, while Syllidae and Spirorbidae contributed to total polychaete density with 224.7 and 173.8 ind m<sup>-2</sup>, respectively, i.e., 18.9 and 14.6% of the individuals sampled.

Table 2 shows a high level of population overlapping across the different habitats, with a few species dominating a wide range of habitats. Nevertheless, some autoecological trends could be described. The colonial serpulid *Filograna implexa* dominated most habitats, except the upper and middle intertidal. The nereid *Platynereis dumerilii* dominated all intertidal communities, except for the upper intertidal dominated by barnacles (BAL), and shallow subtidal habitats with scarce (SSA) or without algal cover (ANE). The serpulid *Spirobranchus polytrema* dominated subtidal habitats with large algae, habitats with calcareous substrate and shaded habitats. The syllid *Syllis gracilis* was abundant in most habitats, denoting its wide environmental range, while *Serpula concharum* appeared as a companion species of *S. polytrema* in

**Table 1** Polychaetes collected in this study

	N	SD <sub>N</sub>	%	N	SD <sub>N</sub>	%	N	SD <sub>N</sub>	%	N	SD <sub>N</sub>	%	N	SD <sub>N</sub>	%
Paraonidae															
				<i>Harmothoe glabra</i>	0.04	0.85	0.28	<i>Amblyosyllis madeirensis</i>	0.04	0.85	0.28	Terebellidae			
<i>Paradoneis lyra</i>	0.43	4.57	1.12	<i>Harmothoe fragilis</i>	0.01	0.21	0.28	<i>Eusyllis assimilis</i>	0.04	0.85	0.28	<i>Nicola venustula</i>	0.84	4.75	3.92
Spionidae				Sigalionidae	*	*	*	<i>Syllis beneliahuae</i>	0.04	0.85	0.28	<i>Thelepus setosus</i>	0.40	3.47	1.68
<i>Polydora ciliata</i>	7.49	40.26	8.12	<i>Sithenelatis boa</i>	*	*	*	<i>Streptosyllis campoyi</i>	*	*	*	<i>Eupolyminia nebulosa</i>	0.24	2.24	1.40
<i>Polydora flava</i>	0.72	6.53	1.68	Pholoidae				Nereitidae				<i>Terebella lapidaria</i>	0.13	1.89	0.56
<i>Pygospio elegans</i>	0.70	12.15	0.84	<i>Pholoe inornata</i>	0.38	2.39	2.80	<i>Platynereis dumerilii</i>	50.57	139.06	35.57	<i>Polycirrus sp.</i>	0.09	1.69	0.28
<i>Aonides oxycephala</i>	0.58	3.95	2.80	Chrysopetalidae				<i>Ceratonereis costae</i>	8.47	33.50	14.29	<i>Pista cretacea</i>	0.04	0.85	0.28
<i>Pseudopolydora antennata</i>	0.31	5.93	0.28	<i>Paleanotus chrysolepis</i>	0.09	1.20	0.56	<i>Neanthes irrorata</i>	5.32	29.09	12.32	<i>Lanice conchylega</i>	*	*	*
<i>Polydora hoplura</i>	0.27	4.32	0.56	Pisionidae				<i>Websterineris glauca</i>	1.46	6.77	5.60	Trichobranchidae			
<i>Prionospio steenstrupi</i>	0.04	0.85	0.28	<i>Pisone remota</i>	*	*	*	<i>Nereis pelagica</i>	0.46	4.56	2.24	<i>Octobranchus lingulatus</i>	0.09	1.20	0.56
Chaetopteridae				Hesionidae				<i>Ceratonereis vittata</i>	0.46	3.15	2.52	Sabellidae			
<i>Phyllochaetopterus socialis</i>	37.20	253.68	5.04	<i>Syllidia armata</i>	0.09	1.20	0.56	<i>Perinereis marioni</i>	0.22	4.23	0.28	<i>Amphicorina pectinata</i>	49.84	248.68	19.61
<i>Chaetopterus varipodatus</i>	0.59	4.15	3.08	Syllidae				<i>Neanthes kerguelensis</i>	0.11	1.27	0.84	<i>Pseudopotamilla reniformis</i>	25.06	92.58	31.93
Cirratulidae				<i>Syllis armillaris</i>	56.73	94.69	64.43	<i>Nereis zonata</i>	0.04	0.85	0.28	<i>Potamilla torelli</i>	1.85	26.03	1.68
<i>Dodecaeria concharum</i>	2.69	14.63	10.08	<i>Syllis gracilis</i>	42.87	87.05	57.98	<i>Perinereis oliveirae</i>	0.04	0.85	0.28	<i>Jasmineira elegans</i>	1.18	5.95	6.72
<i>Cirriformia tentaculata</i>	0.57	10.18	0.56	<i>Syllis variegata</i>	19.98	32.62	49.58	Glyceridae				<i>Chone duneri</i>	1.13	5.60	6.44
<i>Cirratulus cirratus</i>	0.43	3.48	2.24	<i>Sphaerosyllis pirifera</i>	12.36	43.38	25.21	<i>Glycera alba</i>	*	*	*	<i>Branchioma bombyx</i>	0.72	4.74	3.08
<i>Heterocirrus sp.</i>	0.09	1.69	0.28	<i>Autolytus brachycephalus</i>	11.66	35.59	22.97	<i>Glycera cf. celtica</i>	*	*	*	<i>Perkinsiana rubra</i>	0.54	7.07	1.12
Capitellidae				<i>Syllis prolifera</i>	8.65	77.75	3.08	<i>Glycera lapidum</i>	*	*	*	<i>Fabricia stellaris</i>	0.24	1.89	1.68
<i>Capitella capitata</i>	0.99	11.65	0.84	<i>Pionosyllis lamelligera</i>	8.63	35.48	16.53	Goniadidae				<i>Sabella pavonina</i>	0.24	2.24	1.40
<i>Notomastus latericius</i>	0.04	0.85	0.28	<i>Exogone naidina</i>	6.82	48.10	6.72	<i>Goniada emerita</i>	0.09	1.20	0.56	<i>Amphiglena mediterranea</i>	0.09	1.20	0.56
Maldanidae				<i>Brania pusilla</i>	6.38	20.11	17.65	Sphaerodoridae				<i>Euchone sp.</i>	0.07	0.95	0.56
<i>Micromaldane ornitochaeta</i>	0.49	4.38	1.68	<i>Trypanosyllis zebra</i>	5.56	15.74	18.77	<i>Sphaerodorum peripattus</i>	0.65	3.32	4.48	<i>Sabella spallanzanii</i>	0.04	0.85	0.28
Opheliidae				<i>Haplosyllis spongicola</i>	5.44	15.96	20.17	<i>Sphaerodorum gracilis</i>	0.17	1.53	1.40	<i>Chone collaris</i>	0.02	0.42	0.28
<i>Polyophthalmus pictus</i>	1.58	8.87	5.04	<i>Autolytus edwardsii</i>	4.19	28.35	9.24	Euprosinidae				Serpulidae			
Scalibregmidae				<i>Procerastea nematodes</i>	4.08	34.61	3.08	<i>Euprosine foliosa</i>	0.04	0.85	0.28	<i>Filograna implexa</i>	3179.50	10229.82	33.89
<i>Sclerocheilus minutus</i>	0.04	0.85	0.28	<i>Sphaerosyllis hystrix</i>	4.06	22.18	8.68	Eunicidae				<i>Spirobranchus polytrema</i>	195.85	442.98	66.95

**Table 1** continued

	N	SD <sub>N</sub>	%	N	SD <sub>N</sub>	%	N	SD <sub>N</sub>	%	N	SD <sub>N</sub>	%	N	SD <sub>N</sub>	%
Phyllocladaceae															
<i>Eulalia expusilla</i>	6.18	16.96	21.57	<i>Proceraea aurantiaca</i>	2.99	13.37	10.64	<i>Lysidice ninetta</i>	46.38	70.82	58.54	<i>Serpula massiliensis</i>	75.43	1393.26	0.84
<i>Phyllocladace mucosa</i>	6.10	19.68	15.97	<i>Syllis amica</i>	2.98	14.24	6.16	<i>Eunice torquata</i>	11.28	24.54	34.17	<i>Serpula concharum</i>	73.02	136.28	56.02
<i>Eulalia tripunctata</i>	4.43	10.55	21.01	<i>Syllis corallicola</i>	2.02	11.48	6.16	<i>Marphysa fallax</i>	4.27	16.21	14.85	<i>Pomatoceros triquetra</i>	20.02	39.73	42.30
<i>Eulalia viridis</i>	4.41	16.80	13.17	<i>Syllis columbretensis</i>	1.92	7.78	8.96	<i>Eunice harassii</i>	3.05	8.50	16.25	<i>Josephella marenzelleri</i>	18.92	89.91	9.80
<i>Pseudomystides limbata</i>	2.33	9.95	9.24	<i>Salvatoria clavata</i>	1.73	8.73	6.16	<i>Nematoneis unicornis</i>	0.92	4.53	5.32	<i>Pomatoceros lamarki</i>	15.71	79.46	19.89
<i>Nereiphylla rubiginosa</i>	1.38	5.71	7.84	<i>Ehlersia ferrugina</i>	1.42	9.53	5.88	Lumbrineridae				<i>Serpula vermicularis</i>	0.55	3.21	3.08
<i>Eulalia aurea</i>	1.25	5.01	7.56	<i>Syllis gertlachi</i>	1.32	8.14	4.48	<i>Lumbrineris cocquina</i>	4.57	19.26	12.04	<i>Protula tubularia</i>	0.36	2.66	1.96
<i>Eumida sanguinea</i>	0.78	4.18	4.20	<i>Autolytus prolifer</i>	1.20	8.76	3.08	Lumbrineris				<i>Ficopomatus enigmaticus</i>	0.18	3.39	0.28
<i>Eulalia mustela</i>	0.40	3.86	1.68	<i>Euryssyllis tuberculata</i>	1.18	6.34	4.76	<i>Lumbrineris gracilis</i>	0.76	6.54	2.80	<i>Placostegus tridentatus</i>	0.12	1.28	1.12
<i>Notophyllum foliosum</i>	0.10	1.71	0.56	<i>Odontosyllis ctenostoma</i>	1.09	7.56	3.64	<i>Lumbrineris impatiens</i>	0.22	2.23	1.12	<i>Vermiliopsis striaticeps</i>	0.09	1.20	0.56
<i>Pterocirrus macroceros</i>	0.09	1.69	0.28	<i>Syllis krohni</i>	0.91	6.05	3.08	Arabellidae				<i>Hydroids norvegica</i>	0.04	0.85	0.28
<i>Eulalia ornata</i>	0.04	0.85	0.28	<i>Trypanosyllis coeliaca</i>	0.82	4.45	4.48	<i>Arabella iricolor</i>	3.75	12.06	19.89	<i>Metavermilia multicristata</i>	0.04	0.85	0.28
Polynoidae				<i>Syllis hyalina</i>	0.65	5.06	3.08	Dorvilleidae				<i>Semivermilia torulosa</i>	*	*	*
<i>Lepidonotus clava</i>	6.02	19.07	20.45	<i>Autolytus quindecimdentatus</i>	0.64	6.43	2.24	<i>Dorvillea rubrovittata</i>	0.36	2.37	2.24	Spirobridae			
<i>Harmothoe spinifera</i>	1.04	5.77	4.48	<i>Proceraea picta</i>	0.59	3.21	4.20	<i>Ophryotrocha hartmanni</i>	0.04	0.85	0.28	<i>Protolaeospira striata</i>	153.96	953.61	10.08
<i>Harmothoe extenuata</i>	0.64	3.87	3.64	<i>Parapionosyllis brevicirra</i>	0.58	4.19	2.80	Oweniidae				<i>Pileolaria militaris</i>	16.82	75.13	13.17
<i>Harmothoe impar</i>	0.59	5.62	2.52	<i>Syllis vivipara</i>	0.54	5.34	1.40	<i>Galatowenia oculata</i>	1.38	7.76	4.76	<i>Janua pagenstecheri</i>	2.60	38.87	0.84
<i>Harmothoe imbricata</i>	0.43	3.68	1.96	<i>Syllis garciai</i>	0.44	3.35	2.24	Sabellariidae				<i>Pileolaria berkeleyana</i>	*	*	*
<i>Harmothoe areolata</i>	0.32	2.80	1.68	<i>Syllides fulvus</i>	0.19	1.70	1.40	<i>Sabellaria spinulosa</i>	26.49	101.29	40.34	<i>Spirorbis cuneatus</i>	*	*	*
<i>Subadyte pellucida</i>	0.13	1.89	0.56	<i>Myrianida pinnigera</i>	0.16	2.18	0.56	<i>Sabellaria alveolata</i>	0.99	7.71	3.36				
				<i>Salvatoria limbata</i>	0.13	2.54	0.28								

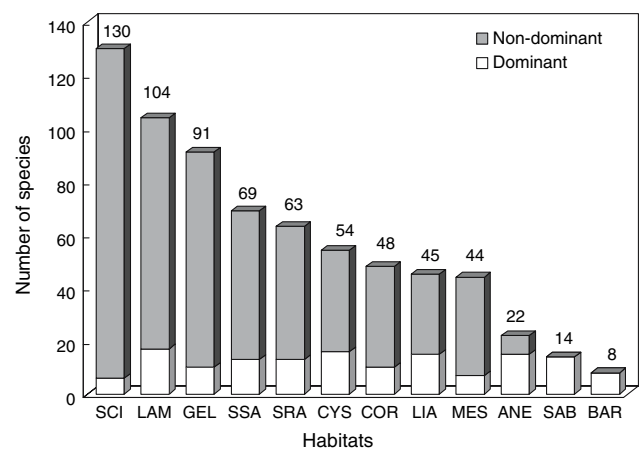
Species are arranged in decreasing order of density within each family. *SD<sub>N</sub>* standard deviation of *N*; *N* ind *m*<sup>-2</sup>; % frequency of occurrence in sampling quadrats; \* species found in qualitative samples

**Table 2** Species with high densities (ind m<sup>-2</sup>) in the 12 habitats studied

Barnacles (BAR)		<i>Corallina</i> (COR)		Lower intertidal algae (LIA)	
<i>Pomatoceros lamarckii</i>	40.0	<i>Platynereis dumerilii</i>	245.7	<i>Filograna implexa</i>	198.8
<i>Syllis gracilis</i>	23.2	<i>Syllis gracilis</i>	112.9	<i>Platynereis dumerilii</i>	87.4
<i>Amphicorina pectinata</i>	20.0	<i>Syllis prolifera</i>	77.0	<i>Janua pagenstecheri</i>	45.0
<i>Eulalia viridis</i>	20.0	<i>Sphaerosyllis pirifera</i>	41.5	<i>Pileolaria militaris</i>	37.0
<i>Odontosyllis ctenostoma</i>	20.0	<i>Syllis amica</i>	21.9	<i>Syllis variegata</i>	30.3
<i>Syllis amica</i>	20.0	<i>Eulalia viridis</i>	16.9	<i>Pseudopotamill. reniformis</i>	27.0
Small-sized algae (SSA)		<i>Sabellaria</i> reef (SAB)		<i>Anemonia</i> (ANE)	
<i>Filograna implexa</i>	243.6	<i>Sabellaria spinulosa</i>	450.0	<i>Filograna implexa</i>	506.7
<i>Platynereis dumerilii</i>	92.0	<i>Spirobranchus polytrema</i>	64.0	<i>Platynereis dumerilii</i>	42.7
<i>Spirobranchus polytrema</i>	52.0	<i>Eulalia tripunctata</i>	40.0	<i>Syllis armillaris</i>	37.3
<i>Neanthes irrorata</i>	45.6	<i>Pomatoceros triqueter</i>	40.0	<i>Lysidice ninetta</i>	32.0
<i>Serpula concharum</i>	33.2	<i>Marphysa fallax</i>	16.0	<i>Sphaerosyllis pirifera</i>	32.0
<i>Lysidice ninetta</i>	26.9	<i>Syllis variegata</i>	16.0	<i>Syllis variegata</i>	32.0
<i>Cystoseira</i> (CYS)		<i>Mesophyllum</i> (MES)		Small red algae (SRA)	
<i>Filograna implexa</i>	108.0	<i>Filograna implexa</i>	5234.3	<i>Filograna implexa</i>	734.1
<i>Spirobranchus polytrema</i>	53.4	<i>Pileolaria militaris</i>	205.7	<i>Sabellaria spinulosa</i>	158.8
<i>Pileolaria militaris</i>	45.2	<i>Sabellaria spinulosa</i>	123.4	<i>Spirobranchus polytrema</i>	155.8
<i>Syllis armillaris</i>	24.0	<i>Serpula concharum</i>	114.3	<i>Serpula concharum</i>	136.0
<i>Serpula concharum</i>	20.8	<i>Syllis armillaris</i>	107.4	<i>Pomatoceros lamarckii</i>	73.4
<i>Sabellaria spinulosa</i>	17.4	<i>Lysidice ninetta</i>	89.1	<i>Syllis armillaris</i>	67.8
<i>Gelidium</i> (GEL)		<i>Laminaria</i> (LAM)		<i>Sciophilous</i> (SCI)	
<i>Filograna implexa</i>	1186.7	<i>Spirobranchus polytrema</i>	246.2	<i>Filograna implexa</i>	7235.7
<i>Spirobranchus polytrema</i>	155.2	<i>Filograna implexa</i>	149.8	<i>Protolaeospira striata</i>	389.2
<i>Serpula concharum</i>	120.0	<i>Lysidice ninetta</i>	119.7	<i>Spirobranchus polytrema</i>	328.0
<i>Syllis armillaris</i>	53.3	<i>Serpula concharum</i>	112.5	<i>Serpula massiliensis</i>	191.0
<i>Lysidice ninetta</i>	46.7	<i>Syllis armillaris</i>	103.2	<i>Amphicorina pectinata</i>	114.4
<i>Syllis gracilis</i>	34.5	<i>Pomatoceros triqueter</i>	53.2	<i>Phyllochaetop. socialis</i>	92.8

calcareous habitats. The spirorbid *Protolaeospira striata* was predominant in SCI, and the same occurred with the microsabellid *Amphicorina pectinata* though this species was less abundant. *Syllis armillaris* was a dominant species in habitats with large macroalgae (LAM, GEL, CYS), and also in SRA, MES and ANE. *Lysidice ninetta* was found in photophilous subtidal habitats. *Sabellaria spinulosa* typified the community made by its tubes (SAB), and was also abundant in SRA, CYS, and MES. Finally, *Pomatoceros lamarckii* was the most abundant species in the upper intertidal (BAR).

All habitats presented a narrow range of dominant species (6–17), with only slight differences among them (Fig. 2). On the contrary, high differences appeared regarding rare species (0 in BAR and SAB vs 124 in SCI, and 87 in LAM), following a pattern related with habitat complexity. There was a decrease in the number of non-dominant species from more complex habitats (SCI, LAM, GEL) to simpler ones (habitats without algal cover as the upper intertidal, SAB or ANE). Therefore, differences in richness and diversity are due to rare species which occur in complex habitats and are excluded from less complex ones, although part of these results might be attributed to the different number of samples between habitats.

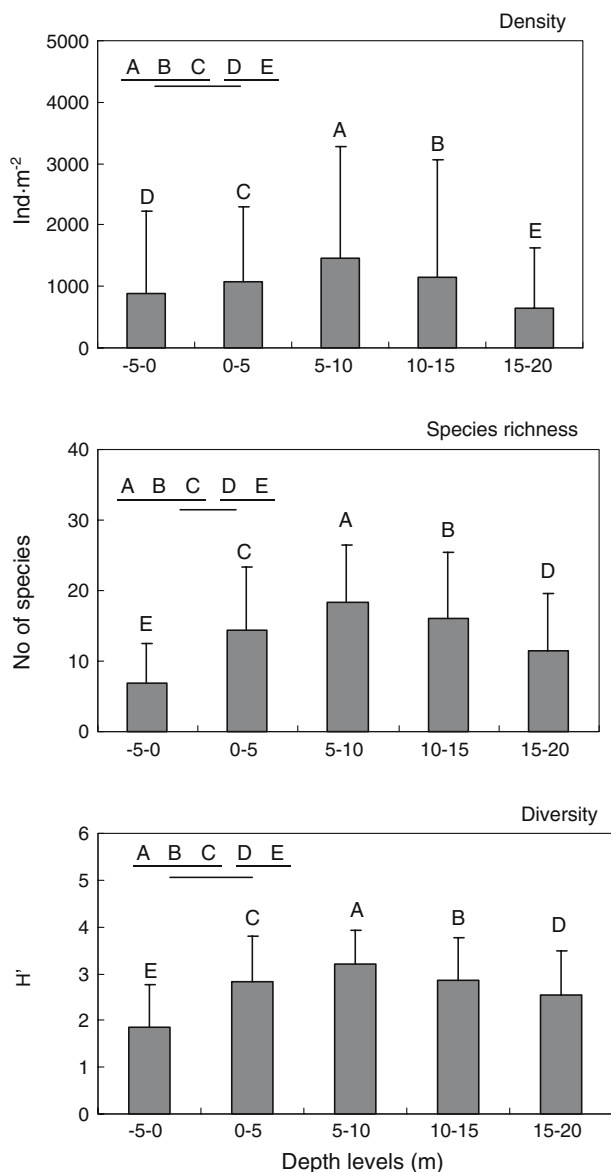


**Fig. 2** Total species richness by habitat, with the percentage of non-dominant versus dominant species. Species with abundance values of more than 1% of the total abundance per habitat were considered dominant. For abbreviations, see [Methods](#)

Polychaete distribution patterns along environmental gradients

Depth correlated positively with species richness ( $r^2 = 0.033$ ;  $P = 0.0005$ ) and diversity ( $r^2 = 0.037$ ;  $P = 0.0002$ ). However, this relationship was extremely weak. More marked effects became evident when eco-

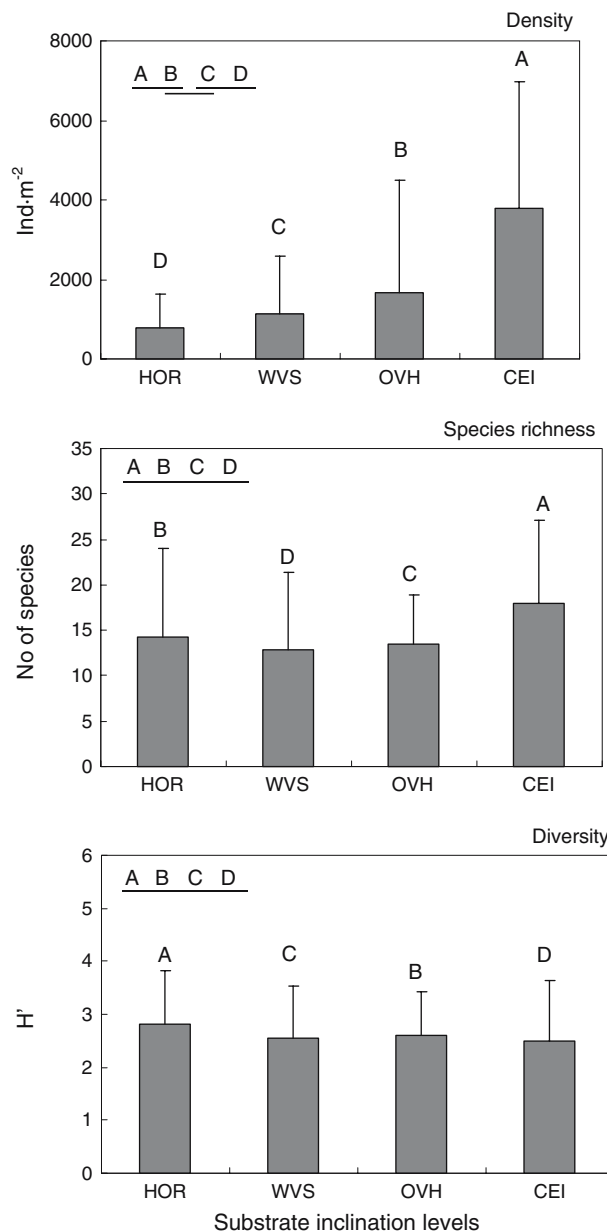
logical indices for different depth strata were compared (Fig. 3). Polychaete density, species richness and diversity in the 5–10 m stratum were significantly higher than in the intertidal (–5 to 0 m) and the deep (15–20 m) stratum. Furthermore, density and richness (but not diversity) were significantly higher in the 10–15 m than in the 15–20 m stratum. Ultimately, polychaete species richness and diversity (but not density) were significantly higher in the 10–15 m than in the –5 to 0 m stratum.



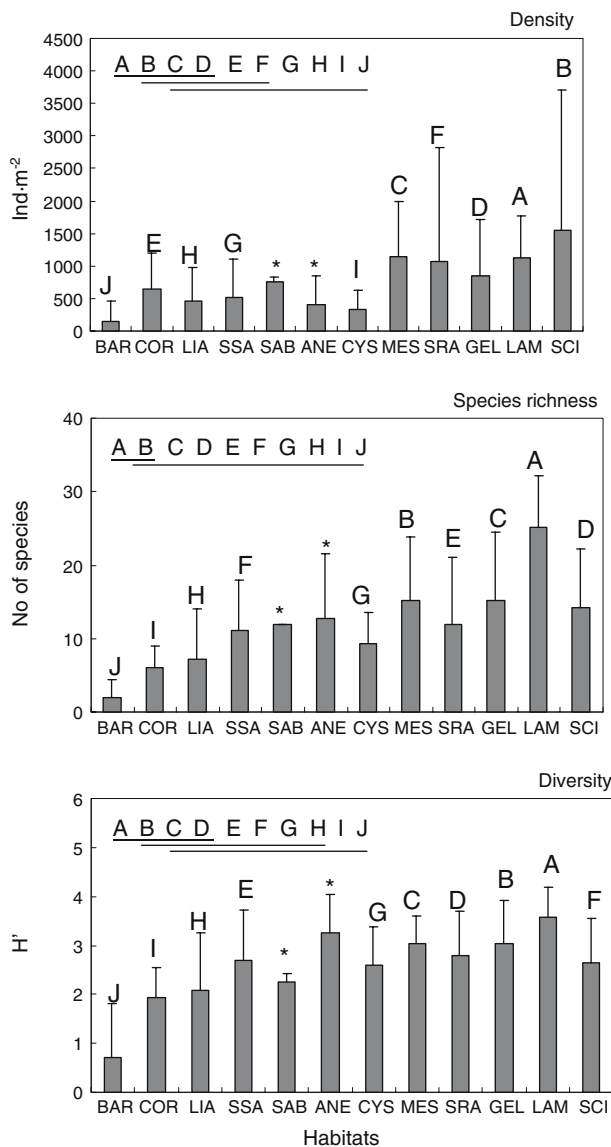
**Fig. 3** Polychaete density, species richness, and diversity ( $H'$ ) per quadrat for the different depth levels. Bars represent means + SD values. Uppercase letters (A–E) refer to mean values arranged in descending order. Groups of underlined letters indicate non-significant differences between pairs of means according to “a posteriori” Dunn’s tests following a significant Kruskal–Wallis ANOVA on ranks

With respect to substrate inclination, significant differences were found only in density (Fig. 4). Ceilings had significantly higher densities than horizontal surfaces and vertical walls, and overhangs had significantly higher densities than horizontal surfaces.

We found no significant between-site differences in polychaete density, species richness or diversity (figure not shown). Nevertheless, some differences appeared in between-habitat comparisons (Fig. 5), although



**Fig. 4** Polychaete density, species richness, and diversity ( $H'$ ) per quadrat for the different semiquantitative levels of substrate inclination. Uppercase letters refer to median values arranged in descending order. Groups of underlined letters indicate non-significant differences between pairs of means according to “a posteriori” Dunn’s tests following a significant Kruskal–Wallis ANOVA on ranks. For abbreviations, see Methods



**Fig. 5** Polychaete density, species richness, and diversity ( $H'$ ) per quadrat for the different habitats. Uppercase letters refer to median values arranged in descending order. Groups of underlined letters indicate non-significant differences between pairs of means according to “a posteriori” Dunn’s tests following a significant Kruskal–Wallis ANOVA on ranks. Asterisks indicate under-sampled habitats that were not considered in the statistical analyses. For abbreviations, see [Methods](#)

many habitats did not differ significantly from one another. LAM presented the highest and intertidal habitats the lowest indices. SCI showed high-density indices and medium richness and diversity indices; it differed significantly from other habitats only in density. This pattern was due to the dominance of a few serpulid species. COR showed a higher polychaete density than the rest of the intertidal habitats, but did not differ significantly from those in richness and diversity. The tangled structure of the *Corallina* blades prevents desiccation and provides shelter from predation,

allowing the presence of higher numbers of some intertidal or ubiquitous species.

#### Faunal affinities between habitat-site groups

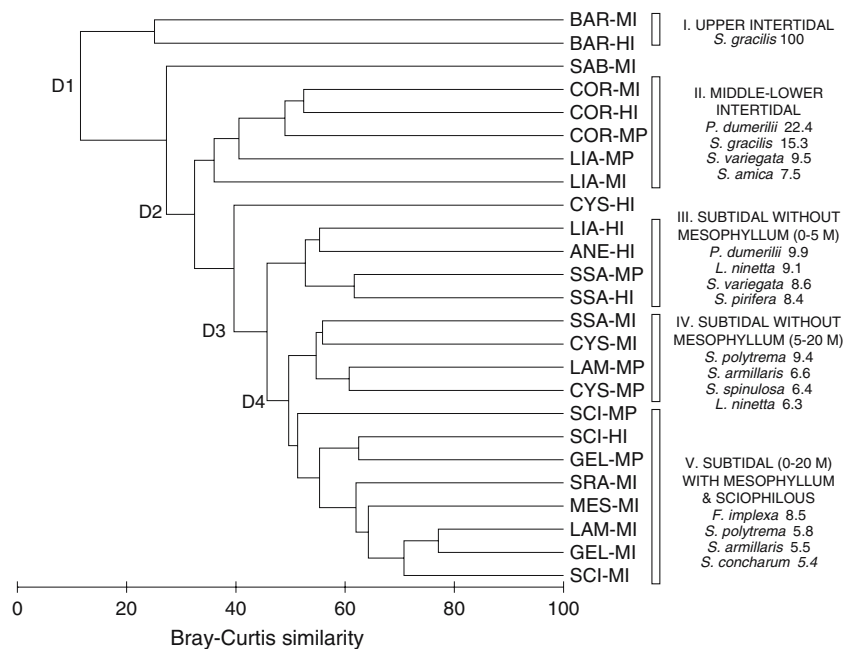
The cluster analysis between habitat-site groups (Fig. 6) showed a habitat-depth pattern of grouping, independent of site, where intertidal environment, the lack of a basal calcareous substrate of *Mesophyllum lichenoides*, and sciophilous conditions appeared as the main discriminating factors. The main groups appearing in the cluster are in order of discrimination: upper intertidal (group I), middle and lower intertidal (group II), shallow subtidal without *Mesophyllum* (group III), subtidal deeper than 5 m without *Mesophyllum* (group IV), and subtidal with *Mesophyllum*, and shaded habitats (group V). The SIMPER analysis between these major groups (Table 3) showed how this discrimination follows the appearance of vagile polychaetes (syllids, nereids) typically in groups I–III, sessile polychaetes (serpulids, sabellids) in group V, group IV being a transition group between the two others. Intertidal groups are typified by vagile polychaetes of wide ecological spectrum (*S. gracilis*, *P. dumerilii*, *Syllis variegata*), or of intertidal preference (*S. amica*, *Odontosyllis ctenostoma*). The SAB habitat is the first subtidal habitat, which is separated from the rest, due to the higher density of SAB a scarce species in the other habitats. Subtidal habitats clustering together follow a mixed pattern of depth (with a boundary around 5 m) and habitat type, the presence of a *Mesophyllum* stratum and shaded surfaces being of particular importance. Shallow habitats without a calcareous substrate are typified by the nereid *P. dumerilii*, as are the middle and lower intertidal, together with other vagile polychaetes. The density of serpuloids and other tube-building polychaetes is lower in these habitats than in the rest of the subtidal environments. The last dichotomy forms two groups, one consisting of subtidal habitats without *Mesophyllum* and deeper than 5 m, and another one consisting of a mixture of shaded habitats and habitats with calcareous substrate. This is due to the higher density of some species of Serpulidae and Sabellidae in *Mesophyllum* and shaded habitats.

#### Effect of environmental factors on polychaete distribution

The RDA explained 14.4% of faunal variation in the “species per quadrat” matrix and 64.9% in the “species-environment” matrix with its first two axes (Fig. 7). Monte–Carlo tests indicated that both the first axis ( $P = 0.002$ ) and all the canonical axes together



**Fig. 6** Dendrogram of habitat-site assemblages based on Bray-Curtis similarity of polychaete densities. For each group, the species with the highest individual contribution to total similarity are listed. For abbreviations, see [Methods](#)



**Table 3** Polychaetes contributing most to dissimilarity between groups resulting from the cluster analysis of habitat-site units

(D1) Upper intertidal (I) and rest: average dissimilarity = 88.44

	N (I)	N (rest)	DIS	DIS/SD	% SP	% CUM
<i>P. dumerilii</i>	0.0	85.4	4.22	1.40	4.77	4.77
<i>F. implexa</i>	0.0	1129.4	3.61	0.98	4.08	8.85
<i>L. ninetta</i>	0.0	36.4	3.18	2.37	3.60	12.45
<i>S. polytrema</i>	0.0	75.3	3.15	1.47	3.56	16.01
<i>S. variegata</i>	0.0	19.7	3.11	1.73	3.52	19.52

(D2) Middle-lower intertidal (II) and rest (III, IV, V): average dissimilarity = 67.55

	N (II)	N (III, IV, V)	DIS	DIS/SD	% SP	% CUM
<i>F. implexa</i>	0.8	1527.7	3.35	1.52	4.96	4.96
<i>S. polytrema</i>	5.6	96.4	1.88	1.73	2.79	7.74
<i>S. concharum</i>	5.5	57.5	1.87	1.86	2.77	10.52
<i>S. spinulosa</i>	0.0	35.2	1.71	1.40	2.53	13.05
<i>S. amica</i>	0.2	17.5	1.64	1.74	2.42	15.47

(D3) Subtidal III and rest (IV, V): average dissimilarity = 54.3

	N (III)	N (IV, V)	DIS	DIS/SD	% SP	% CUM
<i>S. polytrema</i>	9.0	133.0	2.12	1.98	3.90	3.90
<i>F. implexa</i>	660.4	1854.2	1.99	1.10	3.67	7.57
<i>S. spinulosa</i>	0.0	47.2	1.86	2.76	3.42	10.99
<i>P. militaris</i>	24.0	29.5	1.15	1.21	2.12	13.11
<i>P. mucosa</i>	0.0	10.3	1.08	1.95	1.99	15.11

(D4) Subtidal IV and subtidal V: average dissimilarity = 50.33

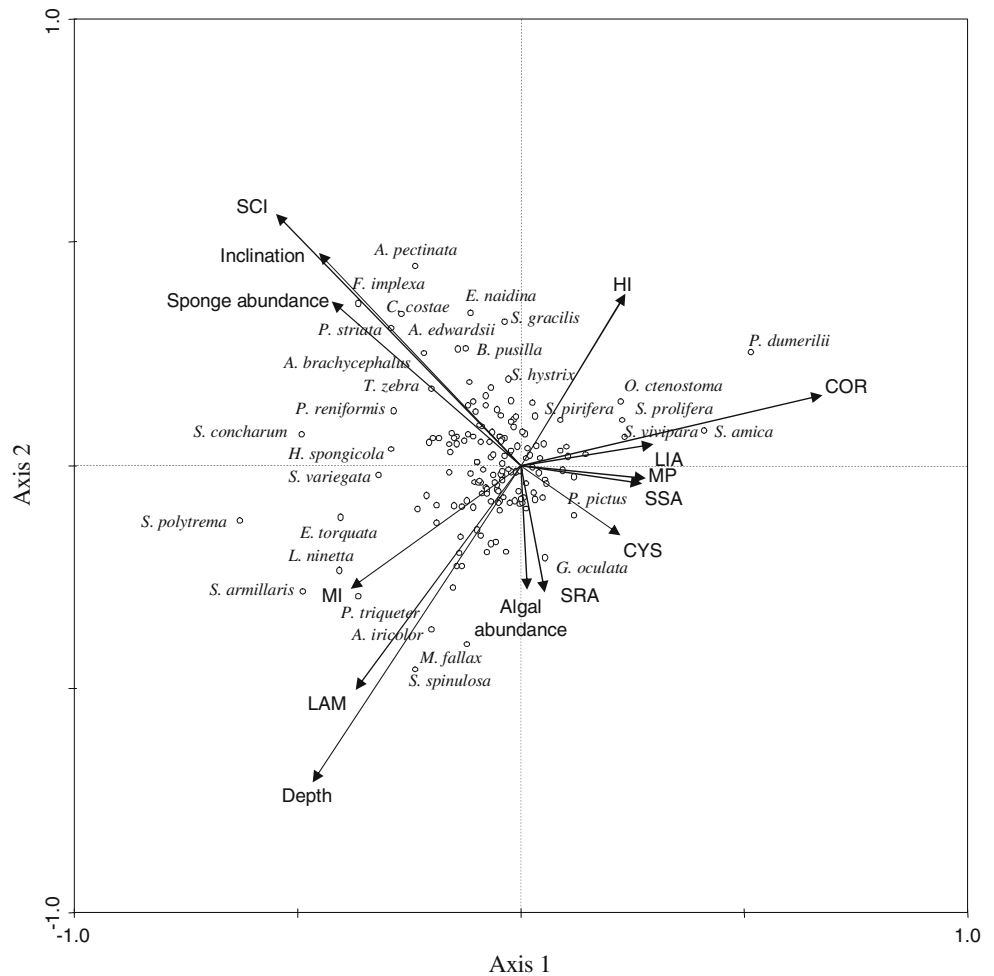
	N (IV)	N (V)	DIS	DIS/SD	% SP	% CUM
<i>F. implexa</i>	8.0	2777.3	3.14	2.53	6.24	6.24
<i>J. marenzelleri</i>	0.0	30.6	1.33	1.46	2.65	8.89
<i>A. pectinata</i>	1.5	87.0	1.12	1.25	2.22	11.11
<i>P. reniformis</i>	2.2	27.9	1.10	2.15	2.20	13.30
<i>E. expusilla</i>	0.0	8.0	1.04	4.63	2.06	15.36

*DIS* mean dissimilarity; *DIS/SD* mean dissimilarity standard deviation ratio; *N* average density (ind m<sup>-2</sup>) in the cluster group; *%SP* individual species contribution to total dissimilarity; *%CUM* cumulative percentage of species contributions

( $P = 0.002$ ) were significant. Several variables showed a moderate correlation with both axes, e.g., COR ( $r = 0.51$ ), SCI ( $r = -0.42$ ), depth ( $r = -0.36$ ) and inclination ( $r = -0.35$ ) with axis 1 and depth ( $r = -0.54$ ), SCI ( $r = 0.43$ ), LAM ( $r = -0.39$ ) and inclination ( $r = 0.36$ ) with axis 2. The lack of importance of a single variable over the others indicates the mixed effect of all

of them in the discrimination of polychaete species (Fig. 7). The ordination of samples (Fig. 8) showed a higher weight of habitat over site, with samples from the same habitat being grouped together. However, a higher than habitat pattern of ordination of these groups of samples was evident, as occurred with the cluster analysis. Axis 1 discriminated samples with a

**Fig. 7** Redundancy analysis (RDA) ordination diagram of species, with superimposed vectors representing environmental variables. Species are represented as circles, except in the most discriminating ones, for which the scientific name is added. The less discriminatory variables have been removed from the plot. For abbreviations, see [Methods](#)



*Mesophyllum* substrate (LAM, GEL, MES, SRA) and shaded habitats (SCI) from intertidal and subtidal ones without a calcareous substrate (Fig. 8). Axis 2 discriminated between shaded and steep sloped samples (animal dominated habitats with high sponge and low algal abundance) and horizontal surface samples (algal dominated habitats with high algal and low sponge abundance).

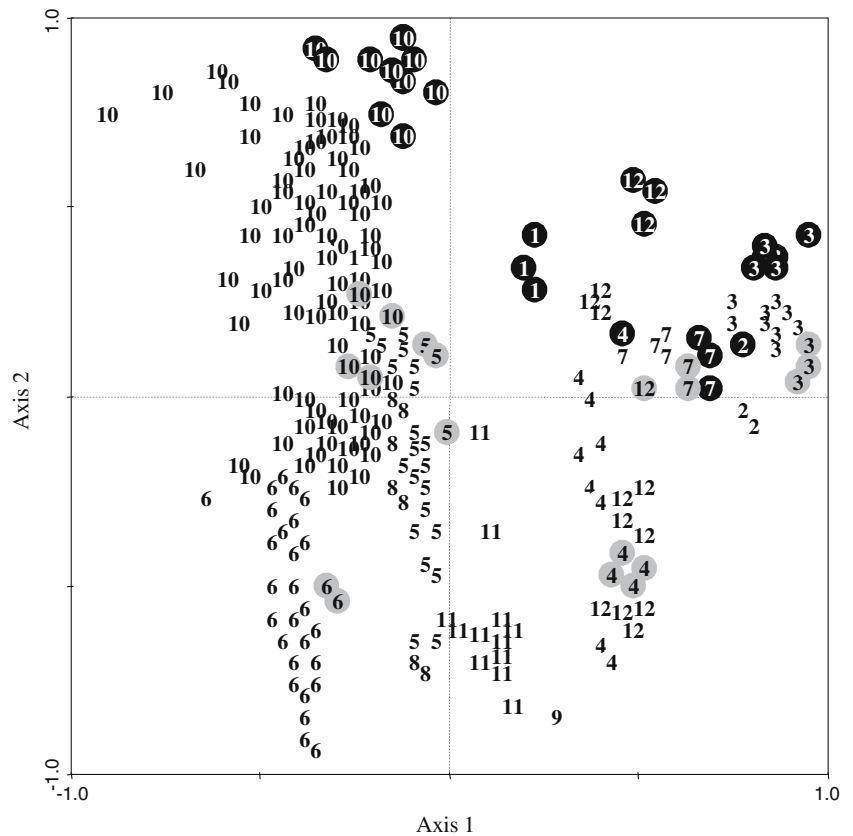
Most species showed a low discrimination regarding the set of environmental variables studied (Fig. 7). However, several species appeared well separated from the centroid, showing a response to one or more of the environmental variables considered. Species with higher densities in intertidal and in non-calcareous subtidal habitats, such as the nereid *P. dumerilii*, and exclusively intertidal species such as *S. amica*, *S. proliferata*, *S. vivipara*, and *O. ctenostoma* were located on the right side of axis 1 (Fig. 7). Other species appeared on the opposite side of axis 1, such as the serpulids *S. polytrema* and *S. concharum*. Inside this group, the gradient described by axis 2 becomes clear, with species having a higher affinity for shaded animal-dominated habitats, such as the microsabellid

*A. pectinata*, the colonial serpulid *F. implexa*, the nereid *C. costae*, and syllids of the subfamily Autolytinae, or to calcareous habitats e.g., *S. armillaris*, *Arabella iricolor*, *Pomatoceros triquetra*, *S. spinulosa*, and *Marphysa fallax*.

## Discussion

The spatial distribution of polychaete communities on shallow rocky environments is not controlled by a single environmental factor such as depth or slope, not by the algal or faunal species providing habitats. The results of this study strongly suggest that the relationship between physical disturbance and habitat complexity determines polychaete abundance and distribution. In the past decades it has become increasingly clear that environmental disturbance plays a crucial role in the biological contribution to local habitat heterogeneity and, as a result, in determining the abundance and diversity of species in hard bottom littoral communities (e.g., Sanders 1968; Dayton 1971; Thompson et al. 1996; Therriault and Kolasa 2000; Sousa

**Fig. 8** Redundancy analysis (RDA) ordination diagram of samples. No circle MI, grey circle MP, black circle HI. Habitats as numbers: 1 ANE, 2 BAR, 3 COR, 4 CYS, 5 GEL, 6 LAM, 7 LIA, 8 MES, 9 SAB, 10 SCI, 11 SRA, 12 SSA. For abbreviations, see [Methods](#)



2001). Environmental stresses affect populations in two ways, through direct effects on individuals, and indirectly, through changes in the physical and biogenic structure of the habitat (Sousa 2001). Habitat complexity decreases because disturbance affects primarily large sessile species that determine the three-dimensional structure of the assemblages and provide food, shelter and habitat to others (Dean and Connell 1987).

In our study, intertidal habitats presented the most differing polychaete fauna in the area. Rocky intertidal habitats experience a wide range of physical disturbances. Intolerance of these severe conditions causes the absence of most polychaete species, and therefore low values of ecological indices, especially in the upper intertidal habitats. Species richness and diversity are also related to predator efficiency; where this is high, environmental resources may be monopolized by a few dominant species (Paine 1966; Russ 1980). Menge (1978) concluded that this efficiency decreases in exposed intertidal habitats with low algal coverage. All these processes are evident in the intertidal of the study area, where physical conditions promote the increase in density of some resilient species, released from high predation and/or competition pressure in the absence of most of the fauna. In the study area, these habitats are dominated by eurytopic species (*S. gracilis*, *P. dumerilii*) accompanied by a few stenotopic inter-

tidal species (e.g., *P. lamarckii*, *Syllis amica*, *Eulalia viridis*, *Odontosyllis ctenostoma*, *Syllis prolifera*). The upper intertidal dominated by barnacles is the habitat with the harshest conditions, therefore presenting rather unstructured communities due to the lack of an efficient biological control. In the middle intertidal, physical forces are still predominant, but the tangled morphology of *Corallina* alleviates the environmental stress during low tides, by retaining water and providing shelter (Bailey-Brock et al. 1980). *Corallina* turfs also trap considerable amounts of sediment (Stewart 1983), favouring the presence of interstitial species such as *S. pirifera* and *Brania pusilla*.

In the subtidal, in habitats located close to sand-rock boundaries, the main sources of environmental disturbance are burial and scour by mobile sand (Hartnoll 1983). Algae living under these conditions present small thalli and most of them are seasonal (Gorostiaga and Díez 1996). The seasonal disappearance of algal coverage is another agent of disturbance (Prathec et al. 2003). In these habitats, as in intertidal communities, there is a simplification of habitat structure, which results in a paucity of polychaete assemblages (Tena et al. 2000; Çinar 2003), and hence, in low values of ecological/diversity indices (Warwick and Davies 1977). However, unlike those in the intertidal, these less complex subtidal habitats do not have a character-

istic stenotopic polychaete fauna, but are dominated by the same species as more complex habitats (e.g., *Filograna implexa*, *Spirobranchus polytrema*, *Syllis armillaris*) albeit in lower densities and not accompanied by a set of rare species. The comparison of ecological indices showed that the intermediate depth level had higher values than the shallower and deeper ones, not because of depth itself, but due to the occurrence of well-structured communities in the absence of stress typical of the other levels.

Environments with temporally stable physical conditions are inhabited by established, complex and buffered communities, resulting in biologically accommodated ecosystems (controlled by predation, competition, or food availability) and characterized by a large number of occasional and rare stenotopic species (Sanders 1968; Menge and Sutherland 1976; Somaschini et al. 1997; Therriault and Kolasa 2000). In the study area, shaded habitats and macroalgae occurring on calcareous substrates (*Laminaria*, *Gelidium*) are subjected to the lowest physical disturbance and present the highest habitat complexity. In these environments a great variety of cryptic microhabitats are available such as crevices, sponges, *Laminaria* rhizoids and *Mesophyllum* calcareous layers. The importance of cryptic habitat availability becomes obvious when comparing SSA and SRA in the study area. Both habitats are characterized by the presence of algae with small and non-rigid morphologies, bearing few epiphytes, and exposed to siltation, hence forming an environment in principle not favourable for polychaete occurrence. Despite this, SRA is one of the habitats with higher polychaete densities, while SSA is one of the least populated. This difference is due to the presence in SRA of a structurally complex *Mesophyllum* calcareous layer, which is lacking in SSA. The most paradigmatic case is that of the *Laminaria* community (LAM), which presents the calcareous algal layer and very complex attaching structures, the rhizoids, and showed the highest diversity indices. We conclude that structural complexity increases polychaete species richness and diversity, denoting well-structured communities where eurytopic species are in equilibrium with other species of polychaetes or other taxa.

Polychaetes require spatial structures at the microhabitat rather than the macrohabitat level (Abbiati et al. 1987; Giangrande 1988); this results in a high faunal homogeneity among macrohabitats (e.g., Giangrande 1988; López and Viéitez 1999; Tena et al. 2000). Most biotopes in our study were dominated by a low number of species such as *S. polytrema*, *P. dumerilii*, *S. armillaris*, *S. gracilis*, *S. concharum*, and *S. variegata*. Differences between disturbance levels were due to the

amount of occasional and rare species and the relative dominance of ubiquitous species (Therriault and Kolasa 2000). *Syllis gracilis*, one of the ubiquitous species in the area, has been quoted as a species with high densities in physically controlled and less-structured environments (Bellan 1980; Çinar 2003). On the other hand, stenotopic species are limited to more complex habitats. The subfamily Autolytinae showed higher densities in animal-dominated habitats, probably as a consequence of its trophic (Hamond 1969) and reproductive links with hydrozoa (Britayev and San Martín 2001). Several sessile species (serpulids, sabellids, spirorbids) are limited to shaded and steep sloped habitats to avoid siltation or competition with algae.

Reproductive types probably play a key role in polychaete zonation along disturbance gradients. Giangrande (1990) found that syllid species with continuous reproduction were linked to habitats subjected to strong physical fluctuations, and species reproducing seasonally were more linked to habitats with high interspecific competition. All these facts indicate that future investigations must focus on the relationship between ecological features, reproductive strategies and trophic habits of polychaetes.

**Acknowledgments** We are grateful to Dr. Gerardo García-Castrillo and all dive buddies of the Asociación Científica de Estudios Marinos (ACEM) from Santander (Spain) for their help during fieldwork and their fruitful collaboration. Drs. Lara Arroyo and Emil Olafsson are also thanked for the language revision and scientific comments. This study was co-financed by the Marcelino Botín Foundation and ACEM.

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