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Ecology of Syllidae (Annelida: Polychaeta) from shallow rocky environments in the Cantabrian Sea (South Bay of Biscay)

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SUMMARY: The syllids inhabiting 12 hard bottom macrobenthic habitats were studied. A total of 38 species belonging to 19 genera were identified. Differences in density, species richness, and diversity among habitats were analysed, as well as the relationships between these ecological parameters and depth range, slope and in-bay/out-bay gradient. The effect of environmental variables on syllid distribution was studied using canonical ordination. A high faunistic homogeneity has been found, since all biotopes were dominated by a low number of eurytopic species (*Syllis armillaris*, *S. gracilis* and *S. variegata*). Habitat complexity, determined by physical disturbance, is the main structuring factor in syllid 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 in upper intertidal habitats, mainly controlled by physical environmental variables, showed a poorer syllid fauna, dominated by ubiquitous species and a few stenotopic species well-adapted to those environments. However, this is not the case in some other intertidal biotopes, such as in *Corallina*, whose tangled structure prevents drying and provides shelter from predation, allowing a richer and more diverse syllid fauna.

Keywords: Polychaeta, Syllidae, physical disturbance, habitat complexity, redundancy analysis.

RESUMEN: ECOLOGÍA DE SYLLIDAE (ANNELIDA: POLYCHAETA) DE AMBIENTES ROCOSOS SOMEROS EN EL MAR CANTÁBRICO (SUR DEL GOLFO DE VIZCAYA). – Se han estudiado los sílidos que pueblan 12 hábitats macrobentónicos de fondo rocoso. Un total de 38 especies pertenecientes a 19 géneros han sido identificadas. Se han analizado las diferencias en densidad, riqueza específica y diversidad entre hábitats, rangos batimétricos, de inclinación de sustrato y en un gradiente estuárico. El efecto de las variables ambientales sobre la distribución de los sílidos se ha analizado mediante ordenación canónica. Se ha detectado una gran homogeneidad, ya que todos los biotopos están dominados por un escaso número de especies euritópicas (*Syllis armillaris*, *S. gracilis* y *S. variegata*). La complejidad del hábitat, determinada por la perturbación física, es el principal factor de estructuración de las poblaciones de sílidos. Los biotopos con mayor complejidad estructural presentan un número alto de especies acompañantes, incrementando los índices ecológicos y denotando un hábitat bien estructurado. Por otro lado, las comunidades controladas por variables físicas, como el intermareal superior, muestran una fauna de sílidos pobre, dominada por especies ubiquestas y especies estenotópicas bien adaptadas a esos ambientes. No ocurre así en otros biotopos intermareales, como *Corallina*, cuya estructura intrincada evita la desecación y proporciona cobijo frente a predadores, permitiendo una fauna de sílidos más rica y diversa.

Palabras clave: Polychaeta, Syllidae, perturbaciones físicas, complejidad de hábitat, análisis de redundancia.

INTRODUCTION

The family Syllidae is one of the dominant taxa in terms of species number and abundance in coastal

assemblages (San Martín, 1984, 2003; Serrano, 2002; Çinar and Ergen, 2002; Çinar, 2003a, b). Most of the syllids are free-living, mainly epibenthic, and they are particularly diverse and abundant in

rocky environments, inhabiting algae and kelp rhizoids, and being part of the cryptofauna. This wide environmental range is a consequence of the wide range of body dimensions (from less than 1 mm to more than 90 mm), of feeding habits (from detritivores to carnivores) (Fauchald and Jumars, 1979; Giangrande *et al.*, 2000), and of reproductive strategies (featuring epigamy or schizogamy by scissiparity or gemmiparity) (Franke, 1999). Furthermore, syllids are the only non-sessile polychaetes known to have asexual reproduction (Giangrande, 1990; López *et al.*, 2001). Not all syllid species show the same colonization success, since the family contains both eurytopic and stenotopic species.

In the study area, hydrodynamic and topographic variables acting together lead to a patchy distribution of macrobenthic communities. Barnacles and turf or encrusting algae dominate the intertidal. In the subtidal, turf-forming algae monopolize photophilous environments with high sedimentation. Sedimentation is a key factor in habitat conditioning, simplifying macrophytic coverage, decreasing vertical stratification and replacing arborescent algae with crustose and turf algae (Gorostiaga and Díez, 1996). Calcareous encrusting algae are relatively abundant in localities of low light and low sedimentation, mainly as an understory amongst macroalgae (Connell, 2003), while invertebrates dominate shaded environments with steeper slopes. Inclination of substratum is the main factor preventing siltation (Moore, 1977), and also determines the algal coverage by modifying the amount of incident light.

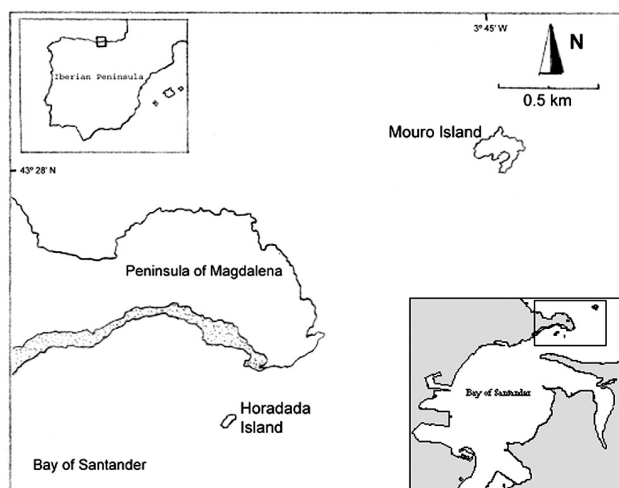


FIG. 1. – Map of Santander Bay (Cantabrian Sea, North Atlantic coast of Spain) showing the three sampling zones: Mouro Island (MI), Peninsula of Magdalena (MP) and Horadada Island (HI).

Patchy distribution of macrohabitats may determine parallel distributions for some populations, while other taxa may perceive environmental variability at different scales and thus exhibit different patterns, not matching those of macroscale habitats. The aim of this study was to elucidate which are the main factors structuring syllid populations in shallow rocky environments. To assess it, we examined quantitatively patterns of spatial distribution with depth, slope, and in-bay/out-bay gradients, and in a variety of Atlantic littoral rocky habitats. Differences in syllid distribution across habitats could contribute to determining whether environmental forces structuring macrobenthic habitats are responsible for spatial distribution of syllids.

MATERIALS AND METHODS

The study was carried out in three zones, Mouro Island (MI, number of quadrats=294), Peninsula of Magdalena (MP, n=29) and Horadada island (HI, n=34), respectively located outside, at the entrance to, and inside the Bay of Santander (North Atlantic Coast of Spain, Fig. 1). Rocky bottoms reach 20 m depth in MI, 10 m depth in MP, and 5 m depth in HI; below these depths sand deposits completely cover the bottom. The topography at MI consists mostly of blocks of rock with large vertical walls forming an intricate system of narrow channels. At MP, the seascape is a large rocky platform with a moderate slope facing offshore. In HI horizontal surfaces predominate, with vertical walls at the sides of the small island. MI and MP are directly exposed to wave action, while HI is sheltered from direct wave action but affected by strong tidal currents (Castillejo *et al.*, 1984). In MI silt is limited to the bottom of channels, whereas in MP and HI sedimentation occurs over the whole area.

All the communities found in the study area have been defined in previous studies (García-Castrillo *et al.*, 2000; Puente, 2000) and referred to tidal level, algal coverage and especially to a basal encrusting stratum of *Mesophyllum lichenoides* (Ellis) Lemoine. These communities were grouped into 12 “habitats” following previous general studies on the whole polychaete fauna of the area (Serrano, 2002). There were three intertidal habitats, Barnacles (BAR, n=5) dominated by *Chthamalus stellatus* (Poli), *Corallina elongata* Ellis and Solander (COR,

n=37), and Lower Intertidal (LIA, n=16) grouping *Bifurcaria bifurcata* Ross and *Codium tomentosum* Stackhouse communities. Four other habitats were characterized as subtidal without a basal stratum of *Mesophyllum*: two animal-based habitats without algal cover, *Anemonia viridis* (Forsskål) (ANE, n=3) and *Sabellaria spinulosa* Leuckhart “reef” (SAB, n=2), a seasonal Small-Sized Algae habitat (SSA, n=22) grouping communities dominated by several genera (*Aglaothamnion*, *Asparagopsis*, *Dictyopteris*, *Dictyota*), and a Macroalgae habitat dominated by *Cystoseira baccata* (Gmelin) Silva (CYS, n=20). These four habitats showed a high siltation-resilience, and were located at rock-sand boundaries. There were four subtidal habitats with a *Mesophyllum* stratum: *Laminaria ochroleuca* De La Pylaie (LAM, n=48), *Gelidium sesquipedale* (Clemente) Thuret (GEL, n=39), a Small Red Algae habitat (SRA, n=17) co-dominated by *Calliblepharis ciliata* (Hudson) Kützing and *Pterosiphonia complanata* (Clemente) Falkenberg, and a *Mesophyllum lichenoides* community without algal cover (MES, n=7). Finally, shaded walls, overhangs and caves were grouped in a Sciophilous habitat category (SCI, n=141), dominated by animals, mostly sponges and cnidarians.

In the Discussion section the terms “habitat complexity” and “physical disturbance” are used. 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 the analysis. In addition, *Laminaria* rhizoids, *Mesophyllum* basal stratum and three-dimensional sponges are considered as habitat structural components. Regarding physical disturbance, intertidal conditions and burial and abrasion by sand 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).

Sampling was conducted by SCUBA diving between intertidal and 20 m depth. We examined 357 random quadrats and scraped off and collecting

all fauna and flora. Sample quadrats measured 625 cm², except for those falling within the *Laminaria ochroleuca* community, which were sized 2500 cm² because of the large algal size. Abundance values were extrapolated to abundance per square metre for further analysis.

We examined differences in syllid density (average number of individuals m⁻²), species richness (average species number per quadrat) and Shannon diversity (species densities per quadrat) referred to depth strata, substratum inclination, zone and habitats, using a Kruskal-Wallis 1-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. Depth ranges (in metres) used were: -5-0, 0-5, 5-10, 10-15, 15-20; substratum inclination semiquantitative ranges were: horizontal to subhorizontal surfaces (HOR, substratum angle 0°-45°), vertical to subvertical walls (WVS, 46°-90°), overhangs (OVH, 91°-135°), and ‘ceilings’ (CEI, 136°-180°).

To assess the amount of variation in syllid densities per quadrat related to a set of environmental factors, a redundancy analysis (RDA) was used. The set of variables comprised depth, substratum inclination, zone and habitat. Sponge and algal abundance (as wet weight per quadrat) were included, aiming to reflect a sciophilous-photophilous gradient and a habitat complexity measure (see above). Density data were log-transformed to diminish the effect of uneven densities, distribution, and rare taxa. The Monte Carlo method 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 bidimensional ordination generated by biplot scaling focused on inter-species distances, representing species and samples by points and environmental variables by vectors.

RESULTS

A total of 38 syllid species from 19 genera were identified, being present in 92.4% of the samples (330). The subfamily Syllinae was the best represented in species number (17 species, Table 1), in terms of density (155.2 ind. m⁻²) and in frequency of occurrence (91.0%). The most common and abun-

TABLE 1. – Syllids collected in the study area listed in decreasing order of total density (ind. m⁻², standard deviation in brackets) within each subfamily (Syllinae, Eusyllinae, Autolytinae, Exogoninae), and per habitat (see acronyms in Materials and methods). Species acronym used in RDA is listed (RDA Ac)

	RDA Ac	BAR	COR	LIA	SAB	ANE
<i>Syllis armillaris</i> (Müller)	Sarm		3.9 (11.6)	12.0 (22.2)	8.0 (11.3)	37.3 (18.5)
<i>Syllis gracilis</i> Grube	Sgra	40.0 (54.8)	112.9 (134.7)	21.2 (33.6)		21.3 (18.5)
<i>Syllis variegata</i> Grube	Svar		9.1 (24.6)	30.3 (44.5)	16.0 (0.0)	32.0 (27.7)
<i>Syllis prolifera</i> Krohn	Spro		77.0 (232.5)	2.0 (8.0)		
<i>Trypanosyllis zebra</i> (Grube)	Tzeb		3.5 (14.7)	6.0 (24.0)		5.3 (9.2)
<i>Haplosyllis spongicola</i> (Grube)	Hspo					16.0 (16.0)
<i>Syllis amica</i> Quatrefages	Sami	20.0 (44.7)	21.9 (32.3)	6.0 (24.0)		
<i>Syllis corallicola</i> Verrill	Scor		2.0 (12.3)	3.1 (12.5)		
<i>Syllis columbretensis</i> (Campoy)	Scol			1.0 (4.0)		
<i>Syllis gerlachi</i> (Hartmann-Schröder)	Sger			6.0 (24.0)		
<i>Eurysyllis tuberculata</i> Ehlers	Etur			2.0 (8.0)		5.3 (9.2)
<i>Syllis krohnii</i> Ehlers	Skro		2.6 (11.6)			
<i>Trypanosyllis coeliaca</i> Claparède	Tcoe			3.0 (12.0)		
<i>Syllis hyalina</i> Grube	Shya					
<i>Syllis vivipara</i> Krohn	Sviv	3.2 (7.2)	4.8 (15.9)			
<i>Syllis garciai</i> (Campoy)	Sgar					10.7 (18.5)
<i>Syllis beneliahuae</i> (Campoy and Alquézar)	Sben					
<i>Pionosyllis lamelligera</i> Saint-Joseph	Plam			1.0 (4.0)	8.0 (11.3)	10.7 (18.5)
<i>Paraehlersia ferrugina</i> Langerhans	Pfer		0.9 (5.3)			
<i>Odontosyllis ctenostoma</i> Claparède	Octe	20.0 (44.7)	5.6 (14.7)			
<i>Syllides fulvus</i> (Marion and Bobretzky)	Sful					
<i>Amblyosyllis madeirensis</i> Langerhans	Amad					
<i>Eusyllis assimilis</i> Marenzeller	Eass					
<i>Autolytus brachycephalus</i> (Marenzeller)	Abra		1.7 (6.3)	2.0 (5.5)		
<i>Autolytus edwardsi</i> Saint-Joseph	Aedw		0.9 (5.3)			
<i>Procerastea nematodes</i> Langerhans	Pnem					
<i>Proceraea aurantiaca</i> Claparède	Paur		0.4 (2.6)	5.0 (20.0)		
<i>Autolytus prolifer</i> (Müller)	Apro					
<i>Autolytus quindecimdentatus</i> Langerh.	Aqui					
<i>Proceraea picta</i> Ehlers	Ppic					5.3 (9.2)
<i>Myrianida pinnigera</i> (Montagu)	Mpin					
<i>Sphaerosyllis pirifera</i> Claparède	Spir		41.5 (102.2)	5.0 (12.7)	8.0 (11.3)	32.0 (55.4)
<i>Exogone naidina</i> Oersted	Enai					
<i>Brania pusilla</i> (Dujardin)	Bpus		6.9 (20.5)	4.3 (9.2)		5.3 (9.2)
<i>Sphaerosyllis hystrix</i> Claparède	Shys		2.6 (15.8)	1.0 (4.0)		10.7 (18.5)
<i>Salvatoria clavata</i> (Claparède)	Scla		0.9 (5.3)			
<i>Parapionosyllis brevicirra</i> (Day)	Pbre					
<i>Salvatoria limbata</i> (Claparède)	Slim					

dant species was *Syllis armillaris* (64.4%), followed by *Syllis gracilis* (58.0%) and *Syllis variegata* (49.6%) (see abundance values in Table 1).

Depth

No significant associations were found between depth and the ecological indices. However, significant differences in densities ($H=18.2$, $p<0.01$), species richness ($H=20.6$, $p<0.01$) and diversity ($H=26.3$, $p<0.01$) between depth-strata were detected. According to the “a posteriori” test, intertidal and the 0-5 m stratum densities were significantly higher than those of the 15-20 m stratum (Fig. 2a). Richness and diversity values in the 0-5 m and 5-10 m strata were significantly higher than intertidal values (Fig. 2b, c).

Syllis gracilis was the most abundant species in the intertidal and the 0-5 m stratum, decreasing with

depth, whereas *S. armillaris* dominated in the remaining strata, increasing its density with depth. With lower values, *Syllis prolifera* and *Sphaerosyllis pirifera* were also abundant in intertidal and *S. variegata* in subtidal samples.

Substratum inclination

Syllid density ($H=9.94$, $p=0.02$), species richness ($H=9.16$, $p=0.03$) and diversity ($H=9.62$, $p=0.02$) were significantly higher on ceilings than on horizontal, vertical and subvertical surfaces (Fig. 2d, e, f). Overhangs did not show significant differences from the rest of the slope ranges, thus representing a transition habitat.

Syllis armillaris and *S. gracilis* were again the most abundant species in all inclination ranges, but with remarkably high values on ceilings, followed by *S. variegata* on horizontal and vertical surfaces.

SSA	SRA	CYS	MES	GEL	LAM	SCI	Total
11.4 (15.4)	67.8 (139.7)	24.0(27.2)	107.4 (117.1)	53.3 (45.3)	103.2 (74.7)	71.8 (120.9)	56.7 (94.7)
12.8 (35.2)	1.9 (7.8)	2.8 (6.4)	29.7 (26.8)	34.5 (49.9)	35.4 (39.9)	49.4 (104.5)	43.1 (87.1)
7.5 (16.8)	9.4 (15)	4.8 (9.4)	22.9 (29.0)	16.0 (24.3)	36.0 (42.6)	23.1 (34.8)	20.0 (32.6)
0.7 (3.4)	3.8 (15.5)					0.9 (7.4)	8.6 (77.8)
3.5 (11.6)	0.9 (3.9)	0.2 (0.9)		8.6 (20.1)	4.3 (7.3)	7.8 (18.5)	5.6 (15.7)
2.2 (5.6)	0.9 (3.9)	0.8 (3.6)		5.1 (10.5)	5.4 (11.4)	9.6 (22.8)	5.4 (16.0)
	0.9 (3.9)	0.8 (3.6)		0.1 (0.6)	0.1 (0.6)	0.1 (1.3)	3.0 (14.2)
1.5 (6.8)		1.4 (4.4)	2.3 (6.0)	1.6 (8.0)	2.1 (7.1)	3.0 (15.5)	2.0 (11.5)
				2.7 (8.6)	3.2 (7.6)	2.5 (10.0)	1.9 (7.8)
				1.2 (7.7)	1.5 (5.3)	1.8 (8.8)	1.3 (8.1)
				4.5 (13.2)	2.4 (9.3)	0.6 (3.5)	1.2 (6.3)
0.7 (3.4)			4.6 (12.1)		0.4 (2.4)	1.1 (6.8)	0.9 (6.1)
				1.6 (6.1)	1.4 (5.7)	0.8 (3.5)	0.8 (4.4)
0.2 (0.9)				1.2 (5.7)	0.4 (2.4)	1.1 (7.3)	0.6 (5.1)
							0.5 (5.3)
0.7 (3.4)		0.2 (0.9)		0.8 (5.1)	0.8 (4.6)	0.3 (2.2)	0.4 (3.3)
				0.4 (2.6)			0.0 (0.8)
4.4 (12.3)	0.9 (3.9)	1.6 (4.9)	4.6 (12.1)	20.1 (63.9)	5.5 (17.5)	12.7 (43)	8.6 (35.5)
	9.4 (38.8)	0.8 (3.6)		2.1 (7.5)	1.3 (4.0)	1.1 (4.5)	1.4 (9.5)
			2.3 (6.0)			0.5 (3.3)	1.1 (7.6)
1.5 (4.7)	0.9 (3.9)			0.1 (0.6)	0.3 (2.3)		0.2 (1.7)
						0.1 (1.3)	0.0 (0.8)
						0.1 (1.3)	0.0 (0.8)
6.5 (18.7)	7.5 (21.3)	2.4 (7.8)	2.3 (6)	4.6 (10.3)	4.7 (9.9)	23.6 (52.8)	11.7 (35.6)
0.7 (3.4)		0.2 (0.9)		3.3 (15.7)	1.8 (4.6)	8.7 (43.9)	4.2 (28.4)
						10.3 (54.6)	4.1 (34.6)
1.2 (5.5)	0.9 (3.9)	1.0 (4.5)		5 (23.2)	3.7 (8.4)	3.8 (14.9)	3.0 (13.4)
				1.2 (5.7)	0.6 (3.1)	2.5 (13.4)	1.2 (8.8)
		0.2 (0.9)		0.4 (2.6)		1.5 (10.1)	0.6 (6.4)
				0.8 (5.1)	1.8 (4.8)	0.6 (3.0)	0.6 (3.2)
1.2 (5.5)						0.2 (2.7)	0.2 (2.2)
14.5 (25.1)	2.8 (11.6)	2.0 (4.9)	16.0 (35.8)	10.9 (22.3)	7.9 (13.1)	9.6 (37.3)	12.4 (43.4)
2.2 (7.5)		0.2 (0.9)		4.5 (28.2)		15.7 (74.3)	6.8 (48.1)
10.2 (23.4)	3.8 (15.5)	2.0 (5.6)	11.4 (15.2)	15.3 (42.1)	5.8 (15.8)	4.7 (13.6)	6.4 (20.1)
4.4 (8.8)				4.9 (16.5)	0.5 (3.5)	7.0 (32.7)	4.1 (22.2)
2.9 (9.4)		0.2 (0.9)		3.4 (13.8)	0.3 (2.3)	2.6 (10.8)	1.7 (8.7)
0.7 (3.4)	4.7 (12.3)	0.2 (0.9)			0.9 (3.8)	0.5 (4.3)	0.6 (4.2)
						0.3 (4.0)	0.1 (2.5)

The Autolytinae preferred shaded overhangs and ceilings (Table 1), with *Autolytus brachycephalus*, *Procerastea nematodes* and *Autolytus edwardsi* quite abundant in these habitats.

Out-bay / in-bay

Significant ‘between-zone’ differences were found in density (H: 10.6, $p < 0.01$) (Fig. 2g), richness (H: 13.9, $p < 0.01$) (Fig. 2h) and diversity (H: 12.2, $p < 0.01$) (Fig. 2i). The in-bay zone (HI) showed higher indices than the out-bay zone (MI), a transitional zone being at the entrance to the bay (MP).

In MI *S. armillaris* dominated (62.6 ind. m^{-2}), followed by *S. gracilis* (33.1) and *S. variegata* (19.3), whereas in HI *S. gracilis* showed the highest average density (135.3 ind. m^{-2}), followed by the Exogoninae *S. pirifera* (46.1) and *Exogone naidina* (45.2), and *A. brachycephalus* (38.1). The higher

syllid density in MP was due to *Syllis prolifera*, followed by *S. pirifera*, *S. gracilis* or *S. armillaris* that also dominated in one of the other two zones.

Macrobenthic habitats

Significant differences in the three ecological indices were found (H: 58.8, H=60.9, H=48.6 in density, richness, and diversity respectively, $p < 0.01$ in all indices), but a high between-habitat homogeneity is apparent, according to an ‘a posteriori’ test. COR showed average densities higher than those of SRA, SSA and CYS, without other differences between habitats (Fig. 2j). Regarding species richness and diversity (Fig. 2k, l), values were significantly higher in LAM than in the rest of the environments except for SCI, GEL and MES.

In analysing faunal dominances two patterns were found. In the intertidal (Table 1, Fig. 3), the

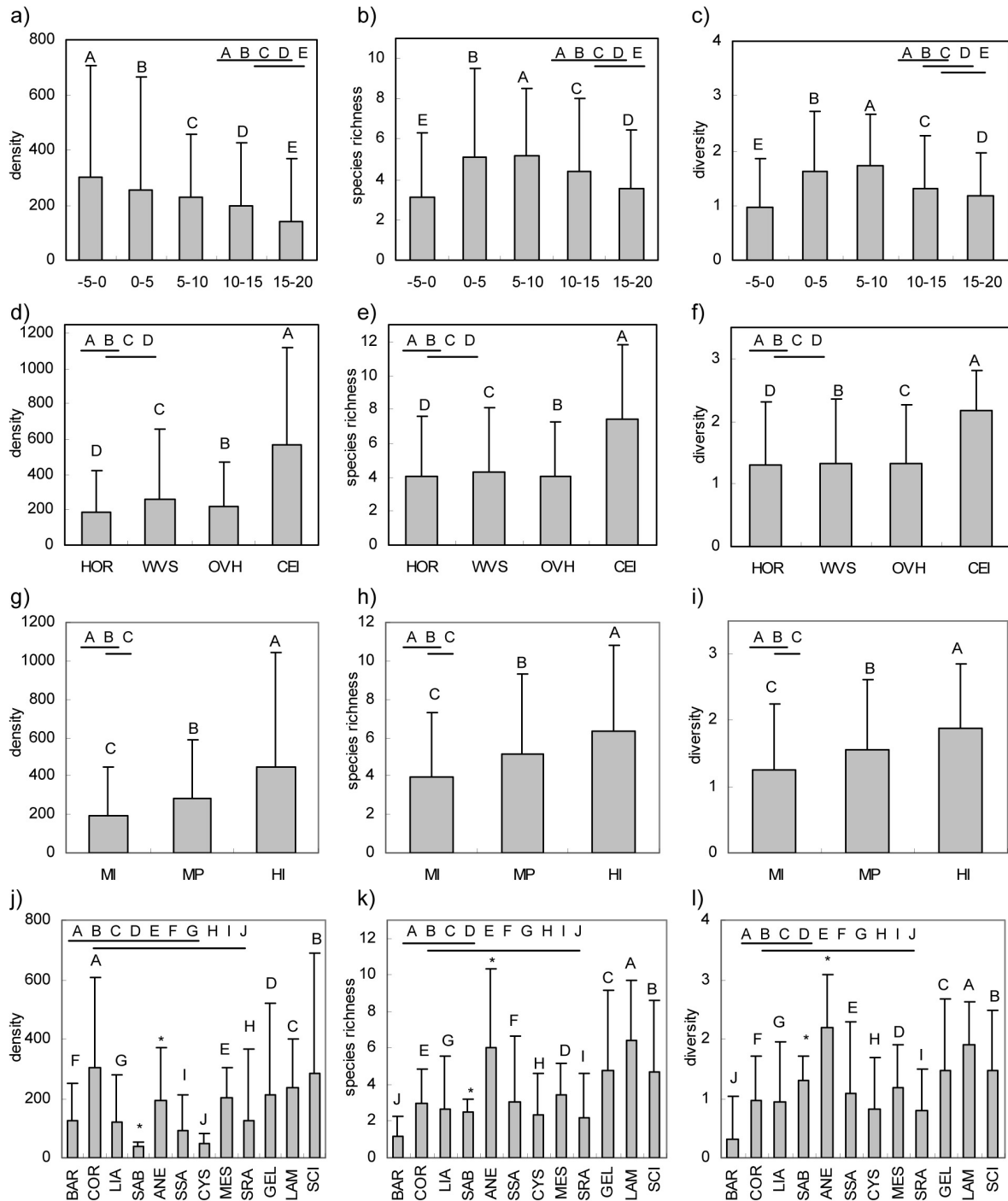


FIG. 2. – Syllid density (ind m⁻²), species richness, and diversity at depth ranges (a, b, c), at semiquantitative levels of substratum inclination (d, e, f), at zone (g, h, i), and habitat (j, k, l). See acronyms in Material and methods section. Uppercase letters indicate mean values arranged in descending order. Groups of underlined letters indicate non-significant differences between pair treatments.

eurytopic *S. gracilis* was the most abundant species, accompanied by such intertidal-adapted species as *Syllis amica*, *Odontosyllis ctenostoma* and *Syllis prolifera* (in COR), or subtidal species in lower intertidal levels such as *S. variegata* (in LIA). In the subtidal *S. armillaris* dominated all environments, with higher densities in shaded and algae-with cal-

careous-stratum habitats (Table 1). However, this homogeneity in indices and faunal dominances did not exist with respect to total species richness (Fig. 3): of 38 species sampled in the area, 35 were found in shaded habitats, 28 in GEL and 27 in LAM (Table 1). CYS (19 species), COR (18), LIA (17), SRA (15), ANE (12) and MES (10) presented medium

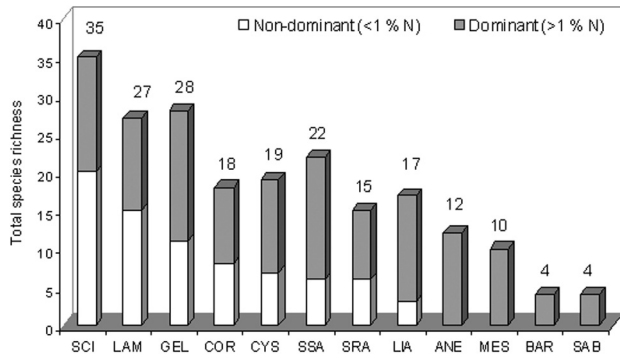


FIG. 3. – Total species richness by habitat, representing the percentage of non-dominant species vs dominant species, in decreasing order of non-dominant percentage. Only those species with abundances higher than 1% of the total habitat abundance were considered dominant.

values, while BAR and SAB were the poorest habitats (4 species each). The low total species richness found in some habitats (e.g. BAR and SAB) has to be considered cautiously due to the different sampling effort. Richness was higher in SCI, GEL and LAM as a consequence of the number of non-dominant species (Figure 3), with slight differences concerning dominant species. It is remarkable that the four dominant species (*S. armillaris*, *S. gracilis*, *S. variegata* and *S. pirifera*) were found in 11 out of 12 habitats (Table 1).

Spatial patterns of syllids in relation to environment

The first three axes of RDA accounted for 15.1% of syllid variation in the species per sample matrix, and 77.5% of variation in the “species-environment” matrix. The option of deleting rare species in the analysis was rejected (due to their main role in the species-environment relationship), this explaining the low percentage of variance obtained. The Monte Carlo tests indicated that both the first axis (P=0.002) and all canonical axes together (P=0.002) were significant. Axis 1 showed moderate correlation with depth (r=-0.65) and COR habitat (r=0.59), denoting the intertidal-subtidal gradient as the major pattern in syllid distribution (Fig. 4). Axis 2 was correlated with the in-bay zone (r=0.31) and out-bay zone (r=-0.24) showing the estuarine gradient as the second factor in structuring syllid populations. However, both axes together depicted a habitat complexity gradient diagonally opposing intertidal and subtidal without *Mesophyllum* habitats to the more complex SCI, LAM and GEL habitats. These axes determined the aggregation of samples into several

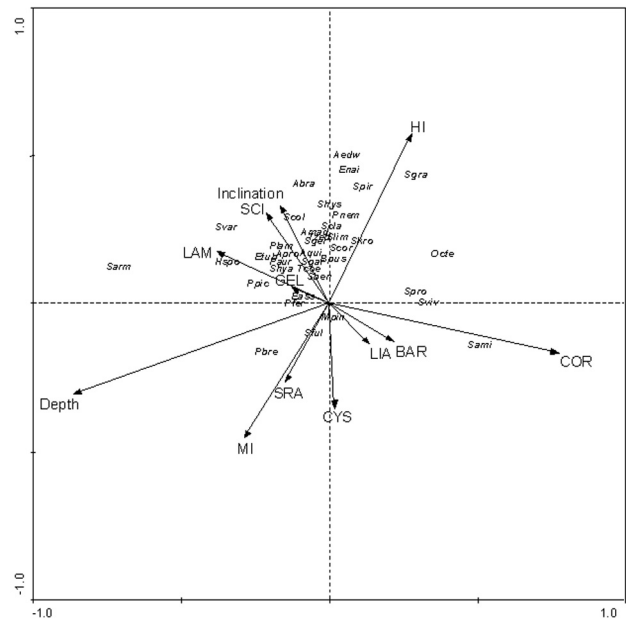


FIG. 4. – Redundancy analysis (RDA) showing the bidimensional ordination of species with superimposed vectors representing the environmental variables (represented only those variables making a major contribution to the axes). Acronyms of species in Table 1, and habitat acronyms in Materials and methods section.

groups (Fig. 5). Groups I, II and III gathered all intertidal samples of MI, MP and HI respectively, showing a higher aggregation of the in-bay samples (HI). Subtidal sample points formed a less clustered

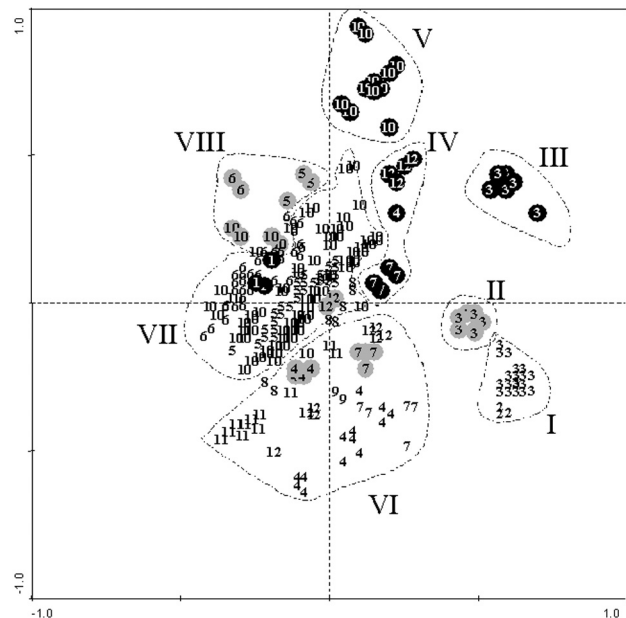


FIG. 5. – Redundancy analysis (RDA) showing the bidimensional ordination of samples. Dotted lines and roman numbers indicate groups of samples discussed in the text. Infill colours represent zone (no colour-MI, grey-MP, black-HI) and numbers represent habitats (1-ANE, 2-BAR, 3-COR, 4-CYS, 5-GEL, 6-LAM, 7-LIA, 8-MES, 9-SAB, 10-SCI, 11-SRA, 12-SSA). Habitat acronyms in Materials and methods section.

group, showing slight differences in syllid composition. However, a spatial pattern was recognizable allowing several groups to be defined. The subtidal samples of the in-bay zone showed a higher clustering compared with other subtidal samples, especially the shallow shaded habitats (group V). Algae without *Mesophyllum* of HI (group IV) were located close to the rest of the subtidal samples. In the negative segment of axis 2, group VI encompassed samples of algae without a basal calcareous stratum of MI and MP together with some samples with a *Mesophyllum* stratum, but with low vertical development, the SRA habitat. Finally, quadrats sampled in the shaded habitats of MP and MI and all the samples of macroalgae with a calcareous basal stratum (there were no macroalgae with calcareous stratum habitats in HI) were grouped near the centroid of the plot with a low affinity to each other. These samples showed a slight splitting between zones, with group VII corresponding to MI and group VIII to MP.

When projecting syllid species on the plot (Fig. 4), it was noteworthy that most of the species were located on the patches of shaded and calcareous basal stratum habitats, especially in the Mouro Island group (group VII, Fig. 5). Except for a few species located in the intertidal, there weren't species occurring on the rest of the patches. This fact means that more complex habitats have higher densities for most species, whereas habitats without a calcareous stratum do not have an unique syllid fauna. Intertidal communities had an exclusive fauna of a few well-adapted species such as *Syllis amica*, *Odontosyllis ctenostoma*, *Syllis prolifera* and *Syllis vivipara*, to which *S. gracilis*, an eurytopic species, was added. *Syllis gracilis* typified shallow water samples in clear bathymetric opposition to *S. armillaris* (Fig. 4). Other species occupied positions out of the main group with higher abundance in certain habitats. In this way, *Autolytus edwardsi*, *Exogone naidina* and *Autolytus brachycephalus* showed affinity with shallow shaded habitats, *S. pirifera* with shallow habitats, especially inside the bay, and *Parapionosyllis brevicirra* with Small Red Algae (Fig. 4, Table 1).

DISCUSSION

The results of this study strongly support the view that the spatial distribution patterns of syllids on shallow rocky environments are determined by

the interrelationship between physical disturbance and habitat complexity. In the past few decades it has become increasingly clear that environmental disturbance plays a critical role in determining biological provision of habitat heterogeneity and, as a result, in determining the abundance of diversity of species in hard-bottomed littoral communities (e.g. Sanders, 1968; Dayton, 1971; Thompson *et al.*, 1996; Sousa, 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 diminishes because disturbance affects primarily the large sessile species that determine the three-dimensional structure of the assemblages and provide food, shelter and habitat for the rest of the species (Dean and Connell, 1987). Mobile animals can behaviourally avoid environmental stresses, depending on the intensity and rapidity of the development of the harsh conditions, as well as on the motility of the species. Syllids are medium or small-sized free-living organisms, mostly a few millimetres long, with a low motility at the macrohabitat scale, and therefore need the existence of microhabitats or "refuges" in harsh areas or during periods of environmental harshness (Bailey-Brock *et al.*, 1980).

Rocky intertidal habitats experience a wide range of physical conditions, determining a high disturbance level. Wave exposure, degree of immersion, thermal conditions, nutrient concentrations, and climate present a harsh environment to polychaetes, that show a low endurance to desiccation. Intolerance of these severe conditions leads to the absence of most of syllid species, and therefore low values for ecological indices, especially in upper intertidal habitats. Species richness and diversity are also related to the predator efficiency in controlling the monopolization of environmental resources by a few dominant species (Paine, 1966; Russ, 1980). Menge (1978) concluded that this efficiency decreases in exposed intertidal habitats with low algae coverage. These processes are evident in the intertidal of the study area, where physical conditions promote an increase of the density of resilient species, not biologically controlled by predation or competition as a consequence of the absence of most of the fauna. Thus intertidal habitats are dominated by a few stenotopic (e.g. *Syllis amica*, *Odontosyllis ctenostoma*, *Syllis prolifera*, *Syllis vivipara*) and eurytopic (*S. gracilis*) species. In the upper intertidal

areas these large-sized syllid species are the only ones found. The lack of small-sized species in the harshest environments could be due to the ability of individuals to reach a refuge in order to avoid stresses. In the midtidal areas physical forces are still predominant, but the tangled morphology of *Corallina* turf alleviates the environmental stress during low tide, retaining water and providing shelter (Bailey Brock *et al.*, 1980). *Corallina* turfs also trap considerable quantities of sediment (Stewart, 1983), favouring the presence of interstitial Exogoninae (*S. pirifera*, *Brania pusilla*, see Table 1).

Environmental disturbance in the area is also caused by burial and scour by sand (Hartnoll, 1983), particularly in the habitats located close to sand-rock boundaries. Algae living under these conditions have small thalli and most of them are seasonal (Gorostiaga and Díez, 1996). The seasonal disappearance of this algal cover is another agent of disturbance. As in the intertidal, there is a simplification of the habitat structure, and a paucity of polychaete assemblages occurs (Tena *et al.*, 2000; Çinar, 2003a, b), resulting in low indices values (Warwick and Davies, 1977). Unlike the intertidal habitats these less complex subtidal habitats do not have a unique syllid fauna, but are dominated by the same species as the more complex ones but with lower densities and without the presence of rare and scarce species.

In contrast, environments with stable and uniform physical conditions not critical in controlling the presence of species are inhabited by stable, complex and buffered communities. This results in biologically accommodated ecosystems (controlled by predation, competition, food availability) characterized by a large number of occasional and rare stenotopic species (Sanders, 1968; Menge and Sutherland, 1976; Russ, 1980; Somaschini *et al.*, 1997). In the study area, shaded habitats and macroalgae with a calcareous stratum (*Laminaria*, *Gelidium*) have the lowest physical disturbance and the highest habitat complexity. In this environments a great variety of cryptic habitats are available (e.g. crevices, sponges, *Laminaria* rhizoids or *Mesophyllum* calcareous layers). Several associations involve syllids with structural species like sessile invertebrates, especially sponges (López *et al.*, 2001; San Martín, 2003), in animal-dominated shaded habitats, or with calcareous concretions (Martín, 1987; San Martín and Aguirre, 1991). These environmental conditions increase species richness and

diversity, denoting well-structured communities where eurytopic syllids are in equilibrium with other species of polychaetes and/or with other taxa. For this reason, densities in these “climax” habitats were lower than in the *Corallina* turf.

The in-bay/out-bay gradient was the second factor in canonical ordination below intertidal conditions, but the absence of a unique syllid fauna in the in-bay zone rejects the hypothesis of the preponderance of the estuarine factor over other variables. The weight of that gradient depicts the presence of intertidal and shallow subtidal shaded ceilings at the sides of the in-bay island, which represent one of the most favourable habitats for syllids, both generalists (*S. gracilis*) and specialists (e.g. Autolytinae). However, *S. gracilis* may be a complex of two genetically divergent species (Maltagliati *et al.*, 2000), with affinity to brackish environments (Cognetti and Maltagliati, 2000), this likely explaining its high abundance in the in-bay zone.

Syllids require spatial structures at microhabitat level not at macrohabitat level (Abbiati *et al.*, 1987; Giangrande, 1988), this producing a high faunal homogeneity between habitats according to several workers (e.g. Cognetti, 1957; Giangrande, 1988; López and Viéitez, 1999; Tena *et al.*, 2000). All biotopes were dominated by a low number of species such as *S. armillaris*, *S. gracilis* and *S. variegata*. Differences occur between disturbance levels in terms of the number of occasional and rare species and in the relative dominance of ubiquitous species, *S. gracilis* being dominant in intertidal and shallow subtidal areas and *S. armillaris* and *S. variegata* in subtidal areas. *Syllis gracilis* has been quoted as a species with high densities in physically controlled and less structured environments (Bellan, 1980; Çinar, 2003a). On the other hand, other stenotopic species limit their presence to more complex habitats. The subfamily Autolytinae showed higher densities in animal-dominated habitats as a consequence of their trophic (Hamond, 1969) and reproductive links with hydrozoa (Britayev and San Martín, 2001).

Reproductive types probably play a key role in syllid zonation along disturbance gradients. Giangrande (1990) found that syllid species with continuous reproduction were linked to shallower depths (higher physical fluctuation), and the species which reproduced seasonally were linked to greater depths (major interspecific competition). *Syllis proliferifera*, mainly intertidal in the study area, is a con-

tinuously reproducing species (Cognetti, 1957), likewise *S. pirifera*, a eurytopic species but with a higher density intertidally. Colonization success and intertidal endurance of *S. gracilis* could be related to its high regenerative power (San Martín, 2003). This type of fission, or architomy, occurs when the worm divides into two or more fragments without any prior cellular differentiation, allowing it to reach high densities after colonization of a new habitat by a single larva (López *et al.*, 2001; San Martín, 2003). True asexual reproduction by architomy is rare in syllids, *Syllis gracilis* being the only species known to have this ability (Franke, 1999). However, López *et al.* (2001) found asexually reproductive specimens of *S. armillaris*. All these facts indicate that future investigations must be focused on the relation between species reproductive strategies and ecological features.

In conclusion, the spatial distribution of syllids in shallow rocky environments is not controlled by a single environmental factor. Habitat complexity determined by physical disturbance seems to be the main structuring factor. 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 mainly controlled by physical environmental variables showed a poorer syllid fauna dominated by ubiquitous species and a few well-adapted ones.

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