# Distribution patterns of Syllidae (Annelida: Polychaeta) from seagrass (*Zostera marina* and *Z. noltei*) meadows in the Ensenada de O Grove (Galicia, NW Spain)

## PATRICIA QUINTAS<sup>1</sup>, JUAN MOREIRA<sup>2</sup> and JESÚS S. TRONCOSO<sup>1</sup>

 <sup>1</sup> Departamento de Ecoloxía e Bioloxía Animal, Facultade de Ciencias, Campus Lagoas Marcosende s/n, Universidad de Vigo, E-36200 Vigo, Galicia, Spain. E-mail: patriquipe@gmail.com
 <sup>2</sup> Departamento de Biología (Zoología), Facultad de Ciencias, Universidad Autónoma de Madrid, Cantoblanco, E-28049 Madrid, Spain. E-mail: juan.moreira@uam.es

SUMMARY: This paper describes the distribution and composition of the syllid fauna inhabiting seagrass meadows in the Ensenada de O Grove (NW Spain). Samples were collected on muddy sediments colonized by either *Zostera marina* L., *Zostera noltei* Hornemann or by a mixed meadow with both species. Syllids were dominant (13340 individuals; 37% of total polychaete abundance), including 22 species (12 genera). The mixed meadows housed the highest number of species and the *Z. noltei* meadow had practically no syllids. The dominant species were *Exogone naidina*, *Parapionosyllis elegans*, *Parexogone hebes* and *Prosphaerosyllis campoyi* (>80% of total abundance). Carnivores (mainly species of *Parapionosyllis*, *Amblyosyllis*, and *Streptosyllis*) were dominant, especially in muddy sand with either *Z. marina* or *Z. noltei* and sandy mud with a mixed meadow. The most important abiotic variables for explaining the composition and distribution of the syllid fauna were bottom water salinity, sorting coefficient and carbonate content. The highest number of species was recorded at sites with a high sorting coefficient.

Keywords: Syllidae, seagrass meadows, Zostera marina, Zostera noltei, diversity, multivariate analysis, Atlantic Ocean, Spain.

RESUMEN: PATRONES DE DISTRIBUCIÓN DE LA FAMILIA SYLLIDAE (ANNELIDA: POLYCHAETA) EN PRADERAS DE LAS FANE-RÓGAMAS MARINAS ZOSTERA MARINA Y ZOSTERA NOLTEI EN LA ENSENADA DE O GROVE (GALICIA, NO ESPAÑA). – El presente trabajo describe la distribución y composición de los sílidos encontrados en las praderas de fanerógamas de la Ensenada de O Grove (NO España). Los fondos fangosos estudiados están colonizados por Zostera marina L., Zostera noltei Hornemann o por ambas especies de fanerógamas. Los sílidos fueron la familia de poliquetos dominante numéricamente (13340 individuos, 37% total de la abundancia total de poliquetos) representados por 22 especies (12 géneros). Los fangos arenosos con pradera mixta albergaron el mayor número de especies de sílidos mientras que en los fondos de fango con Z. noltei estuvieron prácticamente ausentes. Las especies más abundantes fueron *Exogone naidina, Parapionosyllis elegans, Parexogone hebes* y *Prosphaerosyllis campoyi* (> 80% abundancia total). Los carnívoros (principalmente especies de *Parapionosyllis, Ambl*yosyllis y Streptosyllis) fueron dominantes especialmente en arenas fangosas con Z. marina o Z. noltei y en fangos arenosos con una pradera mixta. Las variables abióticas más importantes a la hora de explicar la composición y distribución de los sílidos fueron la salinidad del agua de fondo, el coeficiente de selección y el contenido en carbonatos; así, se ha encontrado un elevado número de especies en estaciones con salinidad y contenido en carbonatos más elevados, en comparación con estaciones con un mayor coeficiente de selección.

Palabras clave: Syllidae, praderas de fanerógamas, Zostera marina, Zostera noltei, diversidad, análisis multivariante, océano Atlántico, España.

## INTRODUCTION

Seagrass meadows are of great ecological importance in shallow-water environments, as their structures (leaves, rhizomes and roots) increase the habitat complexity. They harbour numerous epiphytic and epifaunal taxa (Orth and Heck 1980, Webster et al. 1998, Attrill et al. 2000), providing shelter and protection from predators (Heck and Thoman 1981) and a variety of food resources (e.g. seagrass, detritus and epiphytes) (Kitting et al. 1984, Hily et al. 2004, Fredriksen et al. 2005) to the associated faunal assemblages. Among them, the most diverse taxa are generally polychaetes, molluscs and crustaceans (Gambi et al. 1998, Nakaoka et al. 2001, Arroyo et al. 2006), which are often represented by small-sized, interstitial species that are also usually present in bare soft sediments (San Martín et al. 1985, Sardá 1985, Brito et al. 2005). In Zostera meadows, as in other seagrass meadows, these species may be favoured by the sediment retained by the seagrasses (Parapar et al. 1994, Fredriksen et al. 2010) and by the rhizomes and roots, which create spatial complexity within sediment and enable oxygenation (Tu Do et al. 2011 and references therein).

The Syllidae Grube, 1850 are one of the most diverse and globally distributed polychaete families, in both soft and hard substrata, especially in shallow waters (Çinar 2003). Most syllids are small-sized and occur on a great variety of habitats such as algal beds, mangroves, sponges, coral reefs and rocky, sandy and muddy bottoms (Bone and San Martín 2003). Syllids are important components of seagrass assemblages all over the world, in terms of both abundance and species diversity (Bone and San Martín 2003), as has been reported for Posidonia oceanica (L.) Delile, 1813 (San Martín and Viéitez 1984, Gambi et al. 1989, San Martín et al. 1990), Cymodocea nodosa (Ucria) Ascherson, 1869 (Lanera and Gambi 1993, Brito et al. 2005), Halodule wrightii Ascherson, 1868 (Nelson and Capone 1990, Omena and Creed 2004) and Thalassia testudinum Banks ex König, 1805 (Stoner 1980, Stoner and Lewis 1985, Bone and San Martín 2003). Syllids may exploit all trophic resources and microhabitats in the meadows thanks to a wide range of body length (<1 to 90 mm), a wide range of feeding modes, including herbivores, detritivores, carnivores, scavengers and omnivores (Fauchald and Jumars 1979, Giangrande et al. 2000), and a wide range of reproductive strategies (Giangrande 1990, Franke 1999). In addition, some species are epifaunal while others (especially among the Exogoninae and Eusyllinae) are infaunal (Cinar 2003, López and Gallego 2006).

Meadows of the seagrasses *Zostera marina* L. and *Zostera noltei* Hornemann are typical of estuaries and shallow coastal areas in the northern hemisphere (Duffy and Harvilicz 2001), which are protected through the Habitat directive 92/43/EEC. On the Atlantic coast of the Iberian Peninsula, *Z. marina* and *Z. noltei* occur as extensive meadows in intertidal and shallow subtidal



FIG. 1. – Location of the Ensenada de O Grove (Galicia, Spain) showing the distribution of sampling sites with seagrass meadows.

areas, particularly in the Galician rias (Laborda *et al.* 1997). In the sheltered, inner parts of the Ensenada de O Grove, highly dense meadows extend from the intertidal to the shallow subtidal (<20 m depth), providing macrofauna with protection against desiccation during low tide.

Studies exclusively focusing on the Syllidae from the Galician coasts are scarce (but see San Martin *et al.* 1985) and are most often included in wider benthic ecology studies (Moreira *et al.* 2006, Lourido *et al.* 2008) of both hard and soft substrata (San Martín *et al.* 1985, Parapar *et al.* 1994, Parapar *et al.* 1996a,b, Cacabelos *et al.* 2010).

As part of a broader project devoted to characterizing the soft-bottom benthic fauna of the Ensenada de O Grove (NW Spain) (Project XUGA30101A98), the main objective of this paper is to describe the syllid fauna inhabiting the seagrass meadows of the inlet in terms of composition, abundance, number of species and trophic structure.

#### MATERIALS AND METHODS

#### Study area

The Ensenada de O Grove is located in the inner part of the Ría de Arousa (Galicia, NW Spain) between 42°41'N-42°28'N and 9°01'W-8°44'W (Fig. 1). The inlet has an area of 15 km<sup>2</sup> and is sheltered from wave action and dominant winds by the O Grove Peninsula. It receives freshwater inputs from rivers, both at the mouth and in the inner part. The inner and intertidal and shallow subtidal areas (<20 m) are soft bottoms largely colonized by Z. marina and Z. noltei. This inlet is of great socio-economic importance, especially with regard to mussel culture on rafts, bivalve collection (intertidal harvesting by hand and boat trawling) and fishing. Furthermore, the inlet is protected because of the seagrass meadows (Habitat Directive 92/43/CEE) and as a habitat for birds (ZEPAS, 1979 and RAM-SAR Convention, 1990). It is also a natural space of importance for the European Community, listed in the European Natura 2000 network.

#### Sample collection

The present study focuses on the inner soft bottoms of the Ensenada de O Grove colonized by Z. marina and Z. noltei. Ten sites were selected as representative of the different meadows (i.e. Z. marina, Z. noltei and mixed) and tidal conditions (intertidal vs subtidal). Sampling was done during October and November 1996 following the standard methodology for the XU-GA30101A98 project. We used a Van Veen grab with a sampling surface of 0.056 m<sup>2</sup> to collect five replicates per site (total area: 0.28 m<sup>2</sup>). Samples were then sieved through a 0.5 mm mesh and all retained material was fixed in a 10% buffered formalin-sea water mixture. Additional sediment samples were used to determine particle-size composition and carbonate and organic matter contents, and single measurements of water temperature (°C), pH and salinity (practical salinity units, psu) and sediment pH and temperature (°C) were obtained in situ.

### Laboratory analyses

Syllids were sorted out from the sediment under a stereomicroscope, identified to species level whenever possible, counted, and preserved in 70% ethanol. The names of species and higher taxonomic levels used follow the classification by Aguado and San Martín (2009), the MarBEF Data System (www.marbef.org) and the WoRMS database (www.marinespecies.org).

Grain-size analyses considered the following fractions (Guitián and Carballas 1976): gravel (>2 mm), very coarse sand (2-1 mm), coarse sand (1-0.5 mm), medium sand (0.5-0.25 mm), fine sand (0.25-0.125 mm), very fine sand (0.125-0.063 mm) and silt/clay (<0.063 mm). Median grain size ( $Q_{50}$ ) and sorting coefficient (S<sub>o</sub>) were also determined for each sample. Sediment types were characterized according to Junoy (1996), considering the following types for muddy sediments when silt/clay was more than 5%: muddy sand (5%-25% silt/clay), sandy mud (25%-50%) and mud (>50%). Carbonate content (%) was estimated by treating the sample with hydrochloric acid. Total organic matter (%) was estimated as weight loss after ashing (4 h at 450°C).

#### Data analyses

The structure of the syllid assemblage was analysed using the PRIMER v 6.0 software package (Clarke and Warwick 1994). For each site, total abundance (N), total number of species (S), the Shannon-Wiener diversity index (H', log<sub>2</sub>) and Pielou evenness (J') were determined using the DIVERSE routine. Affinities among sites were determined through non-parametric multivariate techniques (Field et al. 1982). Abundance data were fourth-root transformed (Currie and Small 2005, Bremec and Giberto 2006, Rueda et al. 2009) prior to constructing a matrix of similarities using the Bray-Curtis coefficient and calculating the centroids. Based on this matrix, the sampling sites were classified by cluster analysis (which was tested by the Simprof) and ordered through a non-metric multidimensional scaling (nMDS). These two analyses are complementary, so the graphic representation of the nMDS ordination includes the similarity levels derived from the cluster analysis. The SIMPER routine was used to identify the species most contributing to the dissimilarity among assemblages. Site 37 was excluded from the multivariate analyses (there was only one syllid). Also, the species in each group were classified according to the constancy and fidelity indexes (Glémarec 1964, Cabioch 1968), and those representing more than 4% of the total abundance per site or group were considered as dominant (Junoy 1996). The frequency  $\times$  dominance (F $\times$ D) index was calculated to determine the numerical importance of species. The syllid species were assigned to one of the following guilds: carnivores, herbivores, detritivores, and omnivores (Rasmussen 1973, Fauchald and Jumars 1979, Gambi and Giangrande 1985a,b, Tena et al. 1993, 2000, Giangrande et al. 2000) (Table 1), and the importance of these guilds in the whole inlet and within the groups identified in the nMDS was analysed.

Correlations between assemblage descriptors and all measured environmental variables were determined through the non-parametric Spearman rank coefficient (SPSS 15 software package). Co-linearity (r>0.7) was also detected between some environmental variables and therefore only some of them were selected for the BIO-ENV routine (see Table 2). The rationale was the following: when two variables were highly correlated, that offering the most relevant information was selected for the BIO-ENV. For example, carbonate content was highly correlated with

TAXON	Acronym	Sites	TG	Abund.
PHYLUM ANNELIDA				
CLASS POLYCHAETA				
ORDER PHYLLODOCIDA				
Family Syllidae Grube, 1850				
Subfamily Eusyllinae Malaquin, 1893				
Amblyosyllis sp.	Ambl sp.	27	С	4
Odontosyllis gibba Claparède, 1863	Odon gib	31	Ο	4
Pionosyllis sp. 1	Pion sp.1	31	С	7
Subfamily Anoplosyllinae Aguado and San Martín, 2009	-			
Streptosyllis websteri Southern, 1914	Stre web	24,27,31,39	С	79
Anoplosyllis edentula Claparède, 1868	Anop edl	38,39	D	7
Syllides edentatus Westheide, 1974	Syld edt	27,34,35,38,39,40	D	546
Syllides sp. 1	Syld sp.1	31	D	4
Subfamily Exogoninae Langerhans, 1879	· 1			,0
Brania pusilla (Dujardin,1851)	Bran pus	35,38	Н	25
Parexogone hebes (Webster and Benedict, 1884)	Parg heb	24,26,27,31,34,35,38,39,40	Ο	6361
Exogone naidina Örsted, 1845	Exog nai	24,26,27,31,34,35,37,38,39,40	Ο	12021
Exogone verugera (Claparède, 1868)	Exog ver	24,27,31,35	0	18
Salvatoria clavata (Claparède, 1863)	Salv cla	24,26,27,31,35,38,39	Ο	71
Salvatoria limbata (Claparède, 1868)	Salv lim	38,39	0	18
Parapionosyllis brevicirra Day, 1954	Para bre	34,35,38,39	С	93
Parapionosyllis elegans (Pierantoni, 1903)	Para ele	24,26,27,31,35,38,39,40	С	15418
Parapionosyllis minuta (Pierantoni, 1903)	Para min	24,26,27,31,35,38,39,40	С	2432
Sphaerosyllis hystrix Claparède, 1863	Spha hys	26,27,31,35,38,39,40	Н	1796
Prosphaerosyllis tetralix (Eliason, 1920)	Prosp tet	27,31	D	7
Prosphaerosyllis campoyi (San Martín, Acero,	1			
Contonente and Gómez, 1982)	Prosp cam	24,26,27,31,34,35,38,39,40	D	5489
Erinaceusyllis belizensis (Russell, 1989)	Erin bel	24,27,31,34,35,38,39,40	D	721
Subfamily Syllinae Rioja, 1925				
Syllis garciai (Campoy, 1982)	Syli gar	27,35,38,39,40	0	2518
Xenosyllis scabra (Ehlers, 1864)	Xeno sca	24	С	4

 

 TABLE 1. – Systematic list of syllid species identified in the study. Sampling sites, trophic guild (TG; C: carnivores, H: herbivores, D: detritivores, O: omnivores) and abundance values (Abund.) per m<sup>2</sup> (considering all sites) are indicated. The species acronym used in the nMDS ordination is also listed.

TABLE 2. – Geographical coordinates (Coord.), tidal condition (TC: S, Subtidal; I, Intertidal), temperature (°C) of sediment (TSED), temperature (°C) of surface (TSW) and bottom water (TBW), pH of sediment (pHSED), pH of surface (pHSW) and bottom water (pHBW), salinity (psu) of surface (SSW) and bottom water (SBW), and sedimentary characteristics of sampling sites at the Ensenada de O Grove. Granulometric fractions (%) (GR, gravel; VCS, very coarse sand; CS, coarse sand; MS, medium sand; FS, fine sand; VFS, very fine sand); Q<sub>50</sub>, median grain size (mm); S<sub>0</sub>, sorting coefficient; SEL, sediment selection (M, moderate; MWS, moderately well sorted; P, poor); S. type, sedimentary type (SM, sandy mud; MS, muddy sand; M, mud); OM, Organic matter content (%); CARB, carbonate content (%). Variables marked with an asterisk were selected for the BIO-ENV routine.

Site Coord. TC*	24 42°29'7"N 8°50'15"W S	26 42°28'45''N 8°50'45''W S	27 42°29'45''N 8°50'15''W S	31 42°28'15"N 8°50'45"W I	34 42°27'45"N 8°50'15"W I	35 42°27'45"N 8°51'45"W I	37 42°27'45''N 8°49'15''W I	38 42°27'15"N 8°52'15"W I	39 42°27'15"N 8°51'15"W I	40 42°27'15"N 8°51'45"W I
TSED TSW TBW pHSED pHSW pHBW SSW SBW* GR* VCS CS* MS* FS VFS* silt/clay	$\begin{array}{c} 12.50\\ 14.30\\ 14.60\\ 7.36\\ 7.77\\ 7.76\\ 29.50\\ 29.00\\ 1.87\\ 0.50\\ 0.97\\ 3.82\\ 40.14\\ 40.68\\ 12.01\\ 12$	$ \begin{array}{c} 11.10\\ 10.20\\ 10.00\\ 7.53\\ 7.93\\ 7.90\\ 28.00\\ 30.00\\ 4.44\\ 2.38\\ 4.56\\ 10.19\\ 46.14\\ 25.89\\ 6.41\\ 25.89\\ 6.41\\ 7.56\\ 10.17\\ 10.$	$\begin{array}{c} 11.60\\ 10.00\\ 9.90\\ 7.41\\ 7.94\\ 7.85\\ 29.00\\ 32.00\\ 0.38\\ 0.21\\ 0.45\\ 2.37\\ 37.80\\ 47.89\\ 10.90\\ 10.90\\ 10.11\\ \end{array}$	$\begin{array}{c} 13.40\\ 15.50\\ 16.70\\ 7.39\\ 7.85\\ 7.81\\ 32.00\\ 32.50\\ 1.95\\ 0.57\\ 0.91\\ 4.76\\ 58.03\\ 23.20\\ 10.59\\ 0.56\end{array}$	$\begin{array}{c} 12.70\\ 12.90\\ 13.00\\ 7.27\\ 7.94\\ 7.74\\ 20.00\\ 30.00\\ 0.23\\ 0.14\\ 1.83\\ 10.97\\ 20.85\\ 33.93\\ 32.05\\ 32.05\\ \end{array}$	$\begin{array}{c} 13.50\\ 15.40\\ 15.30\\ 7.46\\ 7.91\\ 7.89\\ 32.00\\ 30.50\\ 0.68\\ 0.53\\ 1.54\\ 14.48\\ 64.63\\ 11.40\\ 6.75\\ 11.40\\ 6.75\end{array}$	$\begin{array}{c} 12.90\\ 13.10\\ 13.20\\ 7.20\\ 7.76\\ 7.74\\ 21.00\\ 20.00\\ 1.03\\ 0.36\\ 1.86\\ 3.88\\ 11.77\\ 19.49\\ 61.61\\ 10\end{array}$	12.60 13.10 13.20 7.30 7.85 7.71 32.00 33.00 5.77 1.09 2.81 5.13 18.51 29.66 37.02	$\begin{array}{c} 12.70\\ 13.20\\ 13.00\\ 7.29\\ 7.86\\ 7.70\\ 31.00\\ 33.00\\ 1.05\\ 0.37\\ 1.00\\ 4.72\\ 43.58\\ 31.07\\ 18.22\\ 12$	12.80 13.00 13.30 7.26 7.78 7.73 28.00 32.00 22.38 3.95 5.00 9.71 18.36 13.17 27.44
Q <sub>50</sub> ° S <sub>0</sub> * SEL S. type OM CARB*	0.12 1.52 M MS 3.93 7.58	0.17 1.50 M MS 1.37 10.05	0.11 1.48 M MS 2.98 8.46	1.45 M MS 2.80 8.69	0.18 1.82 M SM 5.08 7.22	0.19 1.30 MWS MS 1.32 10.46	0.10 2.31 P M 15.55 5.41	0.11 1.70 M SM 10.75 7.40	0.13 1.61 M MS 3.32 9.59	0.18 1.99 P SM 7.10 7.17



FIG. 2. - Spatial distribution and density of the numerically dominant syllid species in the seagrass meadows at the Ensenada de O Grove.

fine sand content (CARB-FS: 0.939). In this case, the latter was non-selected because other granulometric fractions that also provide information of sediment had already been included in the analysis. Variables expressed in percentages were previously log (x+1) transformed (Lourido *et al.* 2008, Sánchez Moyano and García-Asencio 2009).

## RESULTS

#### **Environmental variables**

Sampling sites were characterized by moderate to high silt/clay contents (6%-62%). Sand content was generally greater at subtidal sites and sediment ranged

from muddy sand to mud (Table 2). Water salinity was lower than 33 psu, particularly at sites 34 and 37 (close to the river, 20 psu). Carbonate content ranged from 5% to 10% and organic matter content ranged from low at subtidal sites (1.3%) to high (10.7-15.5%) at intertidal inner sites. Site 37 also showed the highest organic matter content and the lowest carbonate content.

#### Assemblage descriptors

Syllids occurred at all sites, with 13340 individuals corresponding to 12 genera and 22 species (Table 1). The most diverse subfamilies were the Exogoninae and the Syllinae (13 and 7, respectively), the former mostly represented by *E. naidina*, *P. elegans*, *P. hebes*, and *P.* 

TABLE 3. – Total abundance (N, individuals per  $m^2$ ), number of species (S), Shannon-Wiener's diversity index (H',  $log_2$ ) and Pielou evenness (J') for each sampling site in the Ensenada de O Grove. Values: mean±standard deviation.

Site	Ν	S	H'	J,
24	6600±1971.93	6±1.14	1.70±0.24	0.64±0.11
26	3132±1171.96	5±0.55	$1.29 \pm 0.41$	$0.54 \pm 0.19$
27	2425±694.41	9±0.84	2.25±0.13	$0.72 \pm 0.03$
31	7914±6883.48	8±2.17	2.30±0.19	$0.78 \pm 0.14$
34	86±34.35	3±0.84	1.34±0.35	$0.95 \pm 0.06$
35	10818±4483.31	8±1.95	$1.86 \pm 0.18$	$0.65 \pm 0.07$
37	1	1	-	-
38	4486±534.43	11±1.30	2.61±0.15	$0.75 \pm 0.11$
39	7400±6029.99	8±1.73	$1.65 \pm 0.88$	$0.55 \pm 0.27$
40	4779±1455.91	8±1.10	$1.90 \pm 0.49$	0.64±0.13

*campoyi* (Fig. 2) and the latter by *S. garciai. Parapionosyllis elegans* (Group A1: F×D: 934.3; Group A2: F×D: 1674.3), *P. minuta* (A1: 432.7; A2: 22.8), *P. hebes* (A1: F×D: 817.5; A2: 319.7), *E. naidina* (A1: 1059.2; A2: 1024.1), *P. campoyi* (A1: 343.6; A2: 582.3) and *E. belizensis* (A2: 85.6; B: 12.3) were the most characteristic species according to their constancy (Table 6). They were present at all sites and (with the exception of *E. belizensis*) accounted for most of the total syllid abundance.

Sandy mud sediments with mixed seagrasses (sites 38-40) harboured the highest number species (10-14; Table 3). H' was generally low to moderate (1.65-2.61), being lower at sites 26 and 34 (<1.5). J' was moderate at most sites (0.55-0.75). At site 37 (close to the river mouth and having muddy sediments with Z. noltei) there was only one specimen of E. naidina.





 TABLE 4. – Results of SIMPER analysis showing the main taxa contributing to the similarity among subgroups determined from cluster analysis. Average abundance (Av.Ab.), average similarity (Av.Sim.), ratio value (similarity/standard deviation, Sim./SD) and percentage of cumulative similarity (Cum.Sim.) were also included.

	Av.Ab.	Av.Sim.	Sim./SD	Sim. (%)
Group A1 Sites 24, 26, 27, 31 (subtidal, Z. marina)				
(Av. Sim.: 71.80%) Parexogone hebes Exogone naidina Parapionosyllis elegans Prosphaerosyllis campoyi Parapionosyllis minuta	2.52 2.55 2.37 2.06 2.16	14.76 14.07 12.78 12.43 12.41	2.82 4.04 3.74 5.52 4.74	20.55 19.60 17.80 17.31 17.29
Group A2 Sites 35 (intertidal, <i>Z. noltei</i> ), 38, 39, 40 (in (Av. Sim.: 67.36%)	tertidal, Z. marina and Z.	noltei)		
Exogone naidina Prosphaerosyllis campoyi Syllis garciai Parapionosyllis elegans Parexogone hebes Erinaceusyllis belizensis Syllides edentatus	2.95 2.55 2.04 2.37 1.89 1.31 1.09	15.31 12.90 8.77 8.40 7.97 5.04 3.30	5.16 4.76 2.32 1.25 1.75 1.26 0.86	22.73 19.15 13.03 12.47 11.83 7.48 4.89
Group B Site 34 (intertidal, Z. marina and Z. noltei) (Av. Sim.: 57.01%) Parexogone hebes Prosphaerosyllis campoyi	0.16 0.94	34.96 19.42	5.21 1.13	61.33 34.07

	Av.Ab.	Av.Ab.	Av.Disim.	Dis./SD	Disim. (%)
Group A1 vs A2					
A1: Sites 24, 26, 27, 31 (subtidal, Z. )	marina)				
A2: Sites 35 (intertidal, Z. noltei), 38	, 39, 40 (intertidal, Z. m	arina and Z. noltei)	)		
Average Dissimilarity = $41.04$	Group A1	Group A2			
Syllis garciai	0.05	2.04	6.22	2.38	15.15
Parapionosyllis elegans	2.37	2.37	4.69	1.33	11.43
Parapionosyllis minuta	2.16	0.71	4.66	1.68	11.36
Sphaerosyllis hystrix	0.98	1.08	3.59	1.25	8.75
Parexogone hebes	2.52	1.89	3.33	1.18	8.12
Syllides edentatus	0.10	1.09	3.31	1.21	8.06
Erinaceusyllis belizensis	0.74	1.31	3.00	1.33	7.31
Exogone naidina	2.55	2.95	2.96	1.53	7.22
Prosphaerosvllis campovi	2.06	2.55	2.34	1.62	5.71
Salvatoria clavata	0.26	0.35	1.40	0.83	3.40
Parapionosyllis brevicirra	0.00	0.46	1.36	0.71	3.30
Streptosyllis websteri	0.15	0.17	0.93	0.51	2.26
Group A1 vs B					
$\Delta 1$ Sites 24 26 27 31 (subtidal 7)	marina)				
B: Site 34 (intertidal 7 marina and 7	7 noltei)				
Average Dissimilarity = $69.64$	Group A1	Group B			
Average Dissimilarity = 07.04	Gloup Al	Oloup D			
Parapionosyllis elegans	2.37	0.00	13.42	3.03	19.27
Parapionosyllis minuta	2.16	0.00	12.31	4.14	17.68
Exogone naidina	2.55	0.40	12.19	2.37	17.50
Parexogone hebes	2.52	1.16	8.13	1.54	11.67
Prosphaerosyllis campoyi	2.06	0.94	6.37	1.67	9.14
Sphaerosyllis hystrix	0.98	0.00	5.18	1.00	7.44
Érinaceusyllis belizensis	0.74	0.20	3.83	1.09	5.49
Syllides edentatus	0.10	0.24	1.68	0.58	2.41
Group A2 vs B					
A2: Sites 35 (intertidal Z noltei), 38	39.40 (intertidal. Z. m	arina and Z. noltei)	)		
B: Site 34 (intertidal, Z. marina and Z	Z. noltei)				
Average Dissimilarity = $73.28$	Group A2	Group B			
c ,	1	1			
Exogone naidina	0.40	2.95	12.68	2.93	17.30
Parapionosyllis elegans	0.00	2.37	11.89	1.43	16.23
Syllis garciai	0.00	2.04	9.77	2.58	13.33
Prosphaerosyllis campoyi	0.94	2.55	7.85	2.20	10.72
Erinaceusyllis belizensis	0.20	1.31	5.72	1.70	7.81
Sphaerosyllis hystrix	0.00	1.08	4.95	1.02	6.75
Syllides edentatus	0.24	1.09	4.93	1.16	6.73
Parexogone hebes	1.16	1.89	4.80	1.53	6.54
Parapionosyllis minuta	0.00	0.71	3.31	1.05	4.52
Parapionosyllis brevicirra	0.20	0.46	2.42	0.86	3.30

TABLE 5. – Results of SIMPER analysis showing the main taxa contributing to the dissimilarity among subgroups determined from cluster analysis. Average abundance (Av.Ab.), average dissimilarity (Av.Disim.), ratio value (dissimilarity/standard deviation, Dis./SD) and percentage of cumulative dissimilarity (Cum.Disim.) were also included.

## **Trophic guilds**

Carnivores (mainly species of *Parapionosyllis*, *Amblyosyllis*, and *Streptosyllis*) dominated at sites 24, 31, 35 and 39 (density range: 2736-5275 ind. m<sup>-2</sup>) and were less abundant at sites 34, 38 and 40 (4-164 ind. m<sup>-2</sup>). Herbivores were represented by *B. pusilla*, at sites 35, 38 and 40 (4-18 ind. m<sup>-2</sup>) and by *S. hystrix*, which was highly dominant at sites 27, 31 and 38 (250-832 ind. m<sup>-2</sup>). Detritivores dominated at sites 31, 35, 38, 39 and 40 (114-1575 ind. m<sup>-2</sup>), ranging from 39 to 207-296 ind. m<sup>-2</sup> at sites 34, 26 and 27; this group was mainly represented by species of *Anoplosyllis*, *Syllides*, *Sphaerosyllis*, *Prosphaerosyllis*, and *Erinaceusyllis*. Omnivores dominated at sites 24, 26, 31, 35, 38 and 40 (1911-4318 ind. m<sup>-2</sup>) and were less abundant at sites 37 and 34 (4-43 ind. m<sup>-2</sup>). This group comprised species of *Exogone*, *Odontosyllis*, *Parexogone*, *Salvatoria* and *Syllis*.

## **Multivariate analyses**

The sampling sites were divided into two main groups at the 35.7% similarity level (Fig. 3). Group A included eight sites, which were further divided at 63.6% similarity into two subgroups: A1 (sites 24, 26, 27, 31) and A2 (sites 35, 38, 39, 40). A1 included muddy sand sites with *Z. marina* (66.9% similarity), while A2 included muddy sand and sandy mud sites with *Z. noltei* or mixed meadow (71.5% similarity). B included site 34, with sandy mud and mixed meadow.

The species that most contributed to similarity were *P. hebes, E. naidina, P. elegans, P. campoyi* and *P. minuta* at the A1 sites; and *S. garciai, E. belizensis* and



FIG. 4. – Non-metric multidimensional scaling (nMDS) ordination plot showing the syllid species ordination with a numerical dominance >4% at any given site in the study area. See Table 1 for species acronyms.

S. edentatus at the A2 sites. The species that most contributed to similarity within subgroup B were P. hebes and P. campoyi. The species that most contributed to dissimilarities between A1 and A2 were S. garciai (mostly present at A2), P. elegans (highly dominant at sites 35 and 39, A2), P. minuta (A1), S. hystrix (A2), P. hebes (A1), S. edentatus and E. belizensis (A2) (Table 5). The species that most contributed to the dissimilarity between A1 and B were E. naidina, P. hebes and P. campoyi (highly dominant in A1), and P. elegans, P. minuta and S. hystrix (absent at B). The species most contributing to the dissimilarity between A2 vs B were E. naidina, P. elegans, S. garciai, P. campoyi and E. belizensis (less abundant at A2) (SIMPER; Table 4).

The nMDS analyses based on the abundance data of the species considered as dominant at each site showed two groups at 6.6% similarity, i.e. Groups a (subdivided into a1 and a2) and b (X. scabra). Subgroups a1 and a2 clustered at 27.4% and 31.4% similarity, respectively. Within a1, there were two additional subgroups: a11 and a12 (37.9% and 52.2% similarity, respectively). Subgroup all was composed of species with few specimens from sandy mud with Zostera spp., mostly at sites 38 to 39 (i.e. A. edentula, S. limbata, P. brevicirra, and B. pusilla). Subgroup a12 included species with high densities, particularly from muddy sand with Z. noltei (site 35) and sandy mud with mixed meadows (sites 38-39) (i.e. P. campoyi, E. naidina, P. hebes and P. elegans), while S. hystrix, P. minuta, and E. belizensis were widespread and frequent but were less abundant at sites 26, 35, 39 and 40. Within a2, there were also

TABLE 6. – Best combinations of variables obtained by the BIO-ENV routine. SBW, salinity of bottom water; GR, gravel; CS, coarse sand content; MS, medium sand content; CARB, carbonate content;  $S_o$ , sorting coefficient.  $\rho W$ , Spearman's rank correlation.

Number of variables	Best combination of variables	ρW
5	SBW - GR - CS - MS - CARB	0.347
4	SBW - GR - S <sub>o</sub> - CARB	0.338
4	GR- CS - So - CARB	0.324
4	SBW - GR - CS - CARB	0.320
3	GR - S <sub>o</sub> - CARB	0.318
3	SBW - GR - So	0.286
3	GR- CS - CAŘB	0.280
2	SBW - So	0.304
1	So	0.276

two subgroups, a21 and a22 (31.4% and 91.4% similarity, respectively). Subgroup a21 included species with low abundance from muddy sand with *Z. marina* at sites 24, 27 and 31 (i.e. *Amblyosyllis* sp., *P. tetralix, S. websteri, E. verugera*, and *S. clavata*). Subgroup a22 included species with low abundance from muddy sand with *Z. marina* at site 31 (*O. gibba, Syllides* sp. 1 and *Pionosyllis* sp. 1 (Fig. 4).

The combinations of environmental variables best explaining the structure of the syllid assemblage were (1) salinity of bottom water, % of gravel, % of coarse sand, % of medium sand, and carbonate content (BIO-ENV,  $\rho$ w=0.347), and (2) salinity of bottom water, gravel content, sorting coefficient, and carbonate content (BIO-ENV,  $\rho$ w=0.338) (Table 6).

The abundance of *Parexogone hebes* and *P. elegans* increased with carbonate content (r=0.939 and 0.833, respectively; P<0.01) and decreased with organic matter content (r=-0.939 and -0.754; P<0.01), sorting coefficient (r=-0.903, P<0.01 and r=-0.748, P<0.05) and silt/clay content (r=-0.952, P<0.01 and r=-0.723, P<0.05). The abundance of *Sphaerosyllis hystrix* and *S. garciai* increased with S (r=0.887, P<0.01 and r=0.668, P<0.05), *E. naidina* with salinity of surface water (r=0.794; P<0.01), and *P. campoyi* and *S. hystrix* with salinity of surface (r=0.923, P<0.01 and r=0.728; P<0.05) and bottom water (r=0.697, P<0.05 and r=0.910, P<0.01).

#### **Description of faunal assemblages**

Subgroup A1 included subtidal sites with *Z. mari*na, mostly with muddy sand, a moderate selection, and a low organic matter content. N was high (mean  $\pm$  sd: 5018 $\pm$ 2657 ind. m<sup>-2</sup>) and total S was the highest (18), ranging from 7 to 14 per site. The group was dominated by *E. naidina*, *P. elegans*, *P. hebes*, *P. minuta*, *P. cam*poyi and *S. clavata*. H' ranged from 1.29 to 2.30 and J' from 0.54 to 0.78. Carnivores and omnivores were dominant in abundance (36% and 28%, respectively) and number of species (33% and 33%) (Table 7).

Subgroup A2 characterized by bottoms with Z. noltei and bottoms with mixed meadow with moderate values of salinity, organic matter and carbonate content

TABLE 7. – Summary of biotic and physical characteristics of the three assemblages derived from multivariate analysis (values: mean ± standard deviation). First ten constant species are listed including their fidelity (ELE, elective; PRE, preferential; ACE, accessory) and frequency x dominance values (in brackets). N, total number of individuals per m<sup>2</sup>; S, total number of species; H', Shannon-Wiener diversity; J', Pielou evenness; C, carnivores; H, herbivores; D, detritivores; O, omnivores; TC, tidal condition; SSW, salinity of surface water; SBW, salinity of bottom water; OM, organic matter content; CARB, carbonate content; Q<sub>50</sub>, median grain size. N & S of trophic categories expressed in %.

Assemblage	A1 (24, 26, 27, 31)	A2 (35, 38, 39, 40)	B (34)
Constant species	E. naidina (ACE, 1059.2) P. elegans (ACE, 934.3) P. hebes (ACE, 817.5) P. minuta (ACE, 432.7) P. campoyi (ACE, 343.6) S. clavata (PRE, 4.1)	P. elegans (ACE, 1674.3) E. naidina (ACE, 1024.1) P. campoyi (ACE, 582.3) S. garciai (ACE, 401.9) P. hebes (ACE, 319.7) S. hystrix (PRE, 155.3) E. belizensis (ACE, 85.6) A. edentula (ELE, 85.1) P. minuta (ACE, 22.8)	X. scabra (ELE, 1535.6) B. pusilla (PRE, 700.2) P. tetralix (ELE, 135.1) O. gibba (ELE, 122.9) S. limbata (ELE, 110.6) S. garciai (ACE, 24.6) S. belizensis (ACE, 12.3) Syllides sp. 1 (ELE, 0.0)
Seagrass(es)	Z. marina	Z. noltei, Z. marina + Z. noltei	Z. marina + Z. noltei
N	5018±2656.52	$6871\pm2939.69$	86
S	7±1.57	$9\pm1.64$	3
H'	1.89±0.48	$2.01\pm0.41$	1.34
J'	0.67±0.10	$0.65\pm0.08$	0.95
C (%)	N: 36, S: 33	N: 39, S: 25	N: 3, S: 17
H (%)	N: 4, S: 6	N: 4, S: 13	N: 0, S: 0
D (%)	N: 10, S: 28	N: 17, S: 25	N: 31, S: 50
O (%)	N: 50, S: 33	N: 40, S: 38	N: 67, S: 33
Tidal condition	Subtidal Intertidal	Intertidal	Intertidal
SSW	29.63±1.70	30.75±1.89	20.00
SBW	30.88±1.65	32.13±1.18	30.00
OM (%)	2.77±1.06	5.62±4.17	5.08
CARB (%)	8.70±1.02	8.66±1.62	7.22
Q <sub>50</sub> (mm)	0.14±0.03	0.15±0.04	0.18

showed similar H' and J' to A1 (1.65-2.61 and 0.55-0.75, respectively) and shared several species, with *P. elegans, E. naidina, P. campoyi, S. garciai, P. hebes, S. hystrix, E. belizensis, A. edentula*, and *P. minuta* being highly abundant. Carnivores and omnivores were also dominant in abundance (39% and 40%) and number of species (25% and 38%) (Table 7).

As stated above, group B only included site 34 (an intertidal sandy mud area with a mixed meadow), and was characterized by low salinity, carbonate content, S (6), N (86 ind.  $m^{-2}$ ) and H' (1.34). The syllid assemblage, characterized by *X. scabra*, *B. pusilla*, *P. tetralix*, *O. gibba* and *S. limbata*, was clearly different from that in A (Table 7).

## DISCUSSION

Syllids are common members of benthic assemblages associated with seagrass meadows (Çinar 2003), including those formed by Zosteraceae (Hutchings 1981), and the meadows at the Ensenada de O Grove were no exception (37% of total abundance and 24% of polychaete species richness; Quintas 2005). This contrasts with lower abundances found in other quantitative studies using the same sampling methodology on soft bottoms (coarse sand to mud; see Moreira 2003, Moreira *et al.* 2006, Cacabelos *et al.* 2008, Lourido *et al.* 2008, Lourido 2009, Cacabelos *et al.* 2010), which may be partially explained by the presence of a dense seagrass meadow in the present study rather than differences in granulometric composition or organic matter content (Table 8). In general, seagrass meadows reduce physical stress, trap sediment, reduce suspension, protect small invertebrates from predators, and enhance food availability, also adding complexity to the habitat (Orth et al. 1984). In the case of Cymodocea nodosa and Zostera noltei, syllids are among the most abundant polychaete taxa in the foliar and rhizome layers (Giangrande and Gambi 1986, Gambi et al. 1998, Brito et al. 2005). In fact, the tridimensional structure provided by those seagrasses and especially the rhizome structure make available a variety of microhabitats for small-sized taxa. Syllids are mostly interstitial animals and therefore the availability of small spaces along the rhizomes could favour their presence (Giangrande 1985, Somaschini and Gravina 1994, Brito et al. 2005). In fact, syllids require spatial structures at microhabitat rather than at macrohabitat level (Abbiati et al. 1987, Giangrande 1988), while the interactions among syllids and with other macrofaunal species have also been suggested as factors controlling the abundance and, partially, the variability of syllid assemblages (Musco 2012).

In the studied seagrass meadows, abundance, number of species, and diversity differed among sites, resulting in two distinct faunal assemblages: (1) the muddy sand with *Z. marina* and the intertidal muddy sand or sandy mud with *Z. noltei* or mixed meadows (with high values of S and H'), and (2) the intertidal sandy mud with mixed meadows and the intertidal mud flat with *Z. noltei* (low values of S and H'). These differences may be partially explained by the sediment characteristics (carbonate and silt/clay content), the proximity of a river, and the dominance of *Z. marina*, *Z. noltei* or both seagrass species; the latter determines,

 TABLE 8. – Summary of biotic and physical characteristics of three studies carried out on Galician Rias with similar sampling methodology (values: mean ± standard deviation). S. type, sedimentary type (GR, gravel; CS, coarse sand; MeS, medium sand; FS, fine sand; MS, muddy sand, SM, sandy mud, M, mud); OM, Organic matter content (%); CARB, carbonate content (%); TC, tidal condition (S, Subtidal; I, Intertidal); N polychaetes, total number of polychaetes; N syllids, total number of syllids; S syllids, total number of species; Dom Species of Syllids for each groups of sites.

	Lourido <i>et al.</i> 2008 Lourido, 2009	Moreira, 2003 Moreira <i>et al</i> . 2006	Cacabelos <i>et al.</i> 2008, 2010	Quintas <i>et al</i> . (present study)
Total Number of sites Number of sites with <i>Zostera</i> S. type	27 A1: MeS; A2: CS B1: M; B2: FS	21 1 A1: G B1: CS; B2: MeS C1: FS to MS; C2: FS to MS; C3: SM to M	29 5 A1: MS to M; A2: MS to M B: CS, MS, SM to M	10 10 A1: MS; A2: MS to SM B: SM
OM (%)	A1: 1.20±0.14; A2: 1.26±0.81 B1: 5.43±3.89; B2: 2.08±0.51	A1:1.48 B1: 1.40±0.12; B2: 2.18±0.11 C1: 2.40±0.54; C2: 2.15±0.30; C3: 6.76±3.81	A1:16.89±5.13; A2: 18.62±7.66 B:14.66±16.07	A1: 2.77±1.06; A2: 5.62±4.17 B: 5.08
CARB (%)	A1: 48.22±11.46; A2: 48.89±21.53 B1: 36.74±3.05; B2: 59.98±4.68	A1: 24.26 B1: 65.01±5.40; B2: 80.89±1.57 C1: 54.37±20.46; C2: 39.30±7.16; C3: 5.93±1.25	A1: 8.64±11.29; A2: 3.97±1.26 B: 6.22±1.70	A1: 8.70±1.02; A2: 8.66±1.62 B: 7.22
TC N polychaetes (ind.) N syllids (ind.) N syllids (% polychaetes) S syllids Dom Species of syllids S. websteri P. hebes E. naidina P. brevicirra P. elegans P. minuta Parapionosyllis cabezali Para- par, San Martín and Moreira, 2000	A1, A2, B1, B2: S 28,878 3728 12,91 28 A1 A2	A1, B1, B2, C1, C2, C3: S 15,453 4154 26.88 26 B2, C1 C1, C2, C3 B2 B1	A1, A2: S; B: I 24,581 1057 4.30 14 A1 <i>B</i> B B	A1: S; A2: I; B: I 36,131 13,340 37 22 A1, A2 A1, A2 A1, A2
S. hystrix P. campoyi S. garciai	В		A1, A2	A1, A2 A2, B

in turn, the availability of microhabitats (size and shape of the leaves and rhizomes), food and amount of sediment retained by the rhizomes.

The overall composition of the syllid assemblage in the meadows from the Ensenada de O Grove is similar to those reported from other seagrass meadows. *Streptosyllis websteri* occurred in mud, muddy sand and shallow muddy gravel bottoms with *Zostera* in the Ría de Ferrol (Parapar *et al.* 1994). At the island of Ischia (Tyrrhenian Sea, Italy) 33 syllid species (mostly Exogoninae: *Exogone* spp., *Sphaerosyllis* spp., *Parapionosyllis* spp.) were associated with *C. nodosa* and *Z. noltei* meadows, with *E. naidina* and *P. elegans* being positively correlated with the foliar substrate (Gambi *et al.* 1998). On the other hand, *E. verugera*, *E. naidina*, *S. hystrix*, *B. pusilla*, and *S. clavata* are cosmopolitan and ubiquitous species that are common in other habitats including bare bottoms (soft and hard substrata) (Sardá 1985). Exogone naidina, P. hebes, P. tetralix, P. campoyi, P. elegans, S. websteri were previously recorded in intertidal bare and soft sediments near to the seagrass meadows studied here (San Martín et al. 1985). Fredriksen et al. (2010) reported higher abundance of P. hebes and S. hystrix in Z. marina meadows than in bare soft sediments in Norway. Prosphaerosyllis campoyi is also abundant in C. nodosa and P. oceanica meadows (San Martín 2003) and bare intertidal (San Martín et al. 1985) and subtidal sedimentary substrata (Parapar et al. 1994). Similarly, Syllis garciai is common in C. nodosa and Z. noltei meadows (Gambi et al. 1998) and bare muddy sand (Parapar et al. 1996b, Lourido et al. 2008).

In the Ensenada de O Grove, E. belizensis showed a noteworthy presence in subtidal muddy sand with Z. marina and intertidal sandy mud with a mixed seagrass meadow. This species has been reported from warm and tropical seas, including those of the Iberian Peninsula (López and San Martín 1997, Olano et al. 1998, San Martín 2003) and also in low densities in muddy sediments of the Ensenada de San Simón, Galicia (Cacabelos et al. 2010). In the Ensenada de O Grove, specimens were similar to those from the western Atlantic according to morphological characters. However, it has not yet been elucidated whether they have been accidentally introduced by human activities or have a true amphiatlantic distribution. Some warm-water species (mainly Mediterranean molluscs) have been previously collected in O Grove (Rolán et al. 1985, Rolán 1992, Quintas 2005, Quintas et al. 2005). The introduction of these species in this area has been attributed to commercial activities such as oyster importation (Rolán et al. 1985). In some cases, these accidental introductions may result in significant alterations in the composition of assemblages and biotic interactions (Grall and Hall-Spencer 2003). There is, however, no evidence of oyster importation being the cause of the presence of S. belizensis in the study area and direct dispersion should not be discarded as an alternative hypothesis.

Syllids were less abundant in the intertidal sandy mud with a mixed meadow at site 34, and, particularly, they were nearly absent in the nearby muddy sediment with Z. noltei at site 37, in the inner part of the inlet. This absence can be explained by the vicinity of the river mouth, which is associated with regular freshwater inputs, high silt/clay content and low salinity. In particular, the salinity and/or resulting horizontal stratification of waters is a key factor structuring the macrozoobenthic communities (mainly infauna and small, slowly motile epifauna) of Z. noltei meadows in the inner part of Arcachon Bay, France (Blanchet et al. 2004). Our results also agree with those of Cacabelos et al. (2010), who found that syllids were also scarce in Z. noltei meadows subjected to environmental conditions similar to those in the Ensenada de O Grove.

The wide spectrum of feeding habitats among syllids allows them to find a variety of suitable feeding resources on seagrass meadows. In the Ensenada de O Grove, carnivorous syllids were mostly represented by species of Parapionosyllis, Amblyosyllis and Streptosyllis. Omnivores such as P. hebes have been reported in other studies of leaf development of the plant (Gambi et al. 1995). S. hystrix and S. garciai have been considered as herbivorous and omnivorous, respectively (Giangrande et al. 2000, Sánchez Moyano and García-Asencio 2009). In the studied meadows, surface and sub-surface deposit feeding polychaetes were numerically dominant (Quintas 2005), as has been found in other seagrass meadows (Jacobs et al. 1983, Kiting et al. 1984, Thayer et al. 1984, Junoy 1996). However, in this study, the collection of a high number of syllids, including carnivores, herbivores, detritivores and

omnivores, shows the importance of syllids for understanding the trophic structure of these habitats.

In conclusion, the present study shows that Syllidae were well represented and had a high diversity in the Z. marina and Z. noltei meadows in the Ensenada de O Grove compared with bare soft bottoms of the inlet (Quintas 2005). This information suggests that seagrass meadows are biodiversity preservation hot spots. This is the first quantitative and systematic study based on the Syllidae family associated with the seagrass meadows of the inlet. Therefore, this paper can be considered as a baseline study for future monitoring and environmental management studies aimed at increasing the protection of seagrass meadows of the inlet. However, detailed long-term studies considering separately different spatial scales or microhabitats in the plant (blades, rhizomes) and the sediment are needed to better understand the temporal dynamics of syllid assemblages and the environmental factors governing them in the studied meadows.

#### ACKNOWLEDGEMENTS

The authors are very grateful to the colleagues of the laboratory of Adaptaciones de Animales Marinos (Univ. Vigo) for their invaluable assistance in the fieldwork. This work was financially supported by the XUGA30101A98 project. Comments from two anonymous referees and the editor are greatly appreciated.

#### REFERENCES

- Abbiati M., Bianchi C.N., Castelli A. 1987. Polychaete vertical zonation along a littoral cliff in the western Mediterranean. *P.S.Z.N.I. Mar. Ecol.* 8: 33-48.
- Aguado M.T., San Martín G. 2009. Phylogeny of Syllidae (Polychaeta) based on morphological data. *Zool. Scr.* 38(4): 379-402.
- Arroyo M.C., Salas C., Rueda J.L., Gofas S. 2006. Temporal changes of mollusc populations from a *Zostera marina* bed in southern Spain (Alboran Sea), with biogeographic considerations. *Mar. Ecol.* 27: 417-430.
- Attrill M.J., Strong J.A., Rowden A.A. 2000. Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* 23: 114-121.
- Blanchet H., De Montaudouin X., Lucas A., Chardy P. 2004. Heterogeneity of macrozoobenthic assemblages within a Zostera noltii seagrass bed: diversity, abundance, biomass and structuring factors. Est. Coast. Shelf Sci. 61(1): 111-123.
- Bone D., San Martín G. 2003. Ecological aspects of syllids (Annelida: Polychaeta: Syllidae) on *Thalassia testudinum* beds in Venezuela. *Hydrobiologia* 496: 289-298.
- Bremec C., Giberto D. 2006. Polychaete assemblages in the Argentinean Biogeographical Province, between 34° and 38°S. *Sci. Mar.* 20: 249-257.
- Brito M.C., Martín D., Núñez J. 2005. Polychaetes associated to a *Cymodocea nodosa* meadow in the Canary Islands: assemblage structure, temporal variability and vertical distribution compared to other Mediterranean seagrass meadows. *Mar. Biol.* 146: 467-481.
- Cabioch L. 1968. Contribution a la connaissance des peuplements benthiques de la Manche occidentale. *Cah. Biol. Mar.* 9: 493-720.
- Cacabelos E., Moreira J., Troncoso J.S. 2008. Distribution of Polychaeta in soft-bottoms of a Galician Ria (NW Spain). *Sci. Mar.* 72(4): 655-667.
- Cacabelos E., Moreira J., Troncoso J.S. 2010. Distribution and ecological analysis of the Syllidae (Annelida, Polychaeta) from the

Ensenada de San Simón (Galicia, NW Spain). Thalassas 26(2): 93-102.

- Çinar M.E. 2003. Ecological features of Syllidae (Polychaeta) from shallow-water benthic environments of the Aegean Sea, eastern
- Mediterranean. J. Mar. Biol. Ass. UK 83: 737-745. Clarke K.R., Warwick R.M. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Natural Environmental Research Council, UK, 144 pp.
- Currie D.R., Small K.J. 2005. Macrobenthic community responses to long-term environmental change in an east Australian subtropical estuary. *Est. Coast. Shelf Sci.* 63: 315-331. Duffy J.E., Harvilicz A.M. 2001. Species-specific impacts of
- grazing amphipods in an eelgrass-bed community. Mar. Ecol. Progr. Ser. 223: 201-211
- Fauchald K., Jumars P.A. 1979. The diet of worms: a study of polychaete feeding guilds. Oceanogr. Mar. Biol. Annu. Rev. 17: 193-284.
- Field J.G., Clarke K.R., Warwick R.M. 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol. Progr. Ser. 8: 37-52.
- Franke H.D. 1999. Reproduction of the Sylllidae. In: Reproductive Strategies and Developmental patterns in Annelids. Dorrestiejn A., Westheide W. (eds). Hydrobiologia 402: 39-55.
- Fredriksen S., Christie H., Sæthre B.A. 2005. Species richness in macroalgae and macrofauna assemblages on Fucus serratus L. (Phaeophyceae) and Zostera marina L. (Angiospermae) in Skagerrak, Norway. Mar. Biol. Res. 1(1): 2-19.
- Fredriksen S., De Backer A., Boström C., Christie H. 2010. Infauna from Zostera marina L. meadows in Norway. Differences in vegetated and unvegetated areas. Mar. Biol. Res. 6(2): 189-200.
- Gambi M.C., Conti G., Bremec C.S. 1998. Polychaete distribution, diversity and seasonality related to seagrass cover in shallow soft bottoms of the Tyrrhenian Sea (Italy). Sci. Mar. 62(1-2): 1-17.
- Gambi, M.C., Giangrande, A. 1985a. Analisis della struttura trofica del popolamento dei policheti nei fondi mobili di due aree del Mar Tirreno. Oebalia 11: 215-222
- Gambi M.C., Giangrande A. 1985b. Caratterizzazione e distribuzione delle categorie trofiche dei policheti nei fondi mobili del Golfo di Salerno. *Oebalia* 11: 223-240.
- Gambi M.C., Giangrande A., Chessa L.A., Manconi R., Scardi M. 1989. Distribution and ecology of polychaetes in the foliar stratum of a Posidonia oceanica bed in the bay of Porto Conte N.W. Sardinia. In: Boudouresque C.F., Meinesz A., Fresi E., Gravez V. (eds), International Workshop on Posidonia oceanica beds. GIS Posidonie publ., Fr. 2: 175-187
- Gambi M.C., Giangrande A., Martinelli M., Chessa L.A. 1995. Polychaetes of a Posidonia oceanica bed off Sardinia (Italy): Spatio-temporal distribution and feeding guild analysis. Sci. Mar. 59: 129-141.
- Giangrande A. 1985. Policheti dei rizomi di Posidonia oceanica (L.) Delile (Helobiae, Potamogetonaceae) di una prateria dell'isola di Ischia (Napoli). Atti Soc. Tosc. Sci. Nat. Meme. 92: 195-206.
- Giangrande A. 1988. Polychaete zonation and its relation to algal distribution down a vertical cliff in the western Mediterranean (Italy): a structural analysis. J. Exp. Mar. Biol. Ecol. 120: 263-276.
- Giangrande A. 1990. Distribution and reproduction of Syllids (Annelida, Polychaeta) along a vertical cliff (west Mediterranean). Oebalia 16: 69-85.
- Giangrande A., Gambi M.C. 1986. Polychètes d'une pelouse de Cymodocea nodosa (Ucria) Aschers. du Golfe de Salerno (Mer Tyrrhénienne). Vie Milieu 36: 185-190.
- Giangrande A., Licciano M., Pagliara P. 2000. The diversity of diets in Syllidae (Annelida: Polychaeta). Cah. Biol. Mar. 41: 55-65.
- Glémarez M. 1964. Bionomie benthique de la partie orientale du Golfe de Morbihan. *Cah. Biol. Mar.* 5: 33-96.
  Grall J., Hall-Spencer J.M. 2003. Problems facing maerl conserva-
- tion in Brittany. Aquat. Conserv. 13(1): 55-64.
- Guitián F., Carballas J. 1976. Técnicas de análisis de suelos. Ed. P. Sacro. Santiago de Compostela, Spain.
- Heck K.L. Jr., Thoman TA. 1981. Experiments on predator-prey interactions in vegetated aquatic habitats. J. Exp. Mar. Biol. Ecol. 3: 125-134.
- Hily C., Connan S., Raffin C., Wyllie-Echeverria S. 2004. In vitro experimental assessment of the grazing pressure of two gastropods on Zostera marina L. epiphytic algae. Aq. Bot. 78: 183-195.

- Hutchings P. 1981. The Fauna of Australian Seagrass Beds. P. Linn. Soc. N. S. W. 106: 181-200.
- Jacobs R.P.W.M., Hegger H.H., Ras-Willems A. 1983. Seasonal variations in the structure of a Zostera community on tidal flats in the SW Netherlands, with special reference to the benthic fauna. *P. K. Ned. Akad. Wetensc.* 86(3): 347-375.
- Junoy J. 1996. La Ría de Foz, comunidades bentónicas. Servicio de Publicaciones de la Diputación Provincial de Lugo, 210 pp.
- Kitting C.L., Fry B., Morgan M.D. 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. Oecologia 62: 145-149
- Laborda A.J., Cimadevilla I., Capdevila L., García J.R. 1997. Distribución de las praderas de Zostera noltii Hornem., 1832 en el litoral del norte de España. Publ. Espec. Inst. Esp. Oceanogr. 23: 273-282
- Lanera P., Gambi M.C. 1993. Polychaete distribution in some Cymodocea nodosa meadows around the Island of Ischia (Gulf of Napoles, Italy). Oebalia 19: 89-103.
- López E., Gallego R. 2006. Temporal variation of a syllid (Syllidae: Polychaeta) taxocoenosis associated with Stypocaulon scoparium (Stypocaulaceae: Phaeophyceae) in the western Mediterranean. J. Mar. Biol. Ass. UK 86: 51-59.
- López E., San Martín G. 1997. Eusyllinae, Exogoninae and Autolytinae (Syllidae, Annelida, Polychaeta) from the Chafarinas Islands (Alboran Sea, W Mediterranean). Misc. Zool. 20(2): 101-111
- Lourido A. 2009. Distribución especial de la macrofauna bentónica de sustratos sedimentarios de la Ría de Aldán (Galicia, NO de *España*). PhD thesis, Vigo University, Galicia, Spain, 483 pp. Lourido A., Cacabelos E., Troncoso J.S. 2008. Patterns of distribu-
- tion of the polychaete fauna in subtidal soft sediments of the Ría de Aldán (north-western Spain). J. Mar. Biol. Ass. UK 88: 263-275
- Moreira J. 2003. La fauna bentónica de la Ensenada de Baiona (Galicia, NO península Ibérica): diversidad, análisis de las comunidades, dinámica de poblaciones y distribución vertical. Ph.D. thesis, Vigo University, Galicia, Spain, 676 pp.
- Moreira J., Quintas P., Troncoso J.S. 2006. Spatial distribution of soft-bottom polychaete annelids in the Ensenada de Baiona (Ría de Vigo, Galicia, north-west Spain). Sci. Mar. 70(3): 217-224.
- Musco L. 2012. Ecology and diversity of Mediterranean hardbottom Syllidae (Annelida): a community level approach. Mar. Ecol. Prog. Ser. 461: 107-119.
- Nakaoka M., Toyohara T., Matsumasa M. 2001. Seasonal and between-substrate variation in mobile epifaunal community in a multispecific seagrass bed of Otsuchi Bay, Japan. P.S.Z.N.I: Mar. Ecol. 22: 379-395
- Nelson W.G., Capone M.A. 1990. Experimental studies of predation on polychaetes associated with seagrass beds. Estuaries 13(1): 51-58.
- Olano M.L., López E., San Martín G. 1998. Dos nuevas especies de Sílidos (Polychaeta, Syllidae, Exogoninae) para el litoral ibé-rico: Sphaerosyllis belizensis Russell, 1989 y Exogone (Parexogone) cognettii Castelli, Badalamenti & Lardicci, 1987. Bol. R. Soc. Esp. Hist. Nat. 94(1-2): 83-88.
- Omena E., Creed J.C. 2004. Polychaete fauna of seagrass beds (Halodule wrightii Ascherson) along the coast of Rio de Janeiro (Southeast Brazil). Mar. Ecol. 25(4): 273-288.
- Orth R.J., Heck K.L. Jr. 1980. Structural components of eelgrass (Zostera marina) meadows in the lower Chesapeake Bay Fishes. Estuaries 3: 278-288.
- Orth R.J., Heck K.L., Van Montfrans Fr. 1984. Faunal communities in seagrass beds: A review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7(4Å): 339-350.
- Parapar J., San Martín G., Besteiro C., Urgorri V. 1994. Aspectos sistemáticos y ecológicos de las Subfamilias Eusyllinae y Exogoninae (Polychaeta, Syllidae) en la Ría de Ferrol (Galicia, NO España). Bol. R. Soc. Esp. Hist. Nat. (Sec. Biol.) 91: 91-101. Parapar J., San Martín G., Besteiro C., Urgorri V. 1996a. Aspectos
- sistemáticos y ecológicos de la Subfamilia Autolytinae (Polychaeta, Syllidae) en la Ría de Ferrol (Galicia, NO España). Bol. *R. Soc. Esp. Hist. Nat.* 92(1/4): 139-149. Parapar J., San Martín G., Urgorri V., Besteiro C. 1996b. Aspectos
- sistemáticos y ecológicos de la Subfamilia Syllinae (Polychaeta: Syllidae) en la Ría de Ferrol (Galicia, NO España). Bol. R. Soc. Esp. Hist. Nat. 92(1/4): 55-63.

- Quintas P. 2005. Distribución espacial y temporal de los moluscos y anélidos poliquetos asociados a las praderas de Zostera marina L. y Zostera noltii Hornem. en la Ensenada de O Grove (Galicia, España). PhD thesis, Vigo University, Galicia, Spain, 488 pp.
- 488 pp. Quintas P., Rolán E., Troncoso J.S. 2005. Sobre la presencia de un ejemplar de *Hexaplex trunculus* en la Ensenada de O Grove (Ría de Arousa, Galicia). *Noticiario SEM* 43: 77-78.
- Rasmussen E. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* 11: 1-482.
- Rolán E. 1992. Dos especies más de moluscos mediterráneas introducidas en la bahía de O Grove (Galicia, Spain). *Thalassas* 10: 135.
- Rolán E., Trigo J., Otero-Schmitt J., Rolán-Álvarez E. 1985. Especies implantadas lejos de su área de su distribución natural. *Thalassas* 3: 29-36.
- Rueda J.L., Marina P., Urra J., Salas C. 2009. Changes in the composition and structure of a molluscan assemblage due to eelgrass loss in southern Spain (Alboran Sea). J. Mar. Biol. Ass. UK 89: 1319-1330.
- San Martín G. 2003. Fauna ibérica. Annelida, Polychaeta II Syllidae. In: Ramos M.A. *et al.* (eds), *Fauna Ibérica* 21. Museo Natural de Ciencias Naturales. CSIC. Madrid, 554 pp.
- San Martín G., Estapé S., García Ocejo A., Gómez C., Jiménez P. 1990. Estudio de la taxocenosis de Anélidos Poliquetos de rizomas de *Posidonia oceanica* en las costas de Almería. *Bol. Inst. Esp. Oceanogr.* 6(1): 41-58.
- San Martín G., González G., López-Jamar E. 1985. Aspectos sistemáticos y ecológicos sobre algunas especies de Sílidos (Polychaeta: Syllidae) de las costas gallegas. *Bol. Inst. Esp. Oceanogr.* 2(2): 27-36.
- San Martín G., Viéitez J.M. 1984. Anélidos Poliquetos de los rizomas de Posidonia oceanica en las costas de Cabo Palos (Murcia, España). International Workshop on Posidonia oceanica Beds 1: 149-157.
- Sánchez-Moyano J.E., García-Asencio I. 2009. Distribution and trophic structure of annelid assemblages in a *Caulerpa prolifera*

bed from southern Spain. Mar. Biol. Res. 5(2): 122-132.

- Sardá R. 1985. Anélidos Poliquetos del Estrecho de Gibraltar. I. Amphinomida, Spintherida y Phillodocida. *Misc. Zool.* 9: 65-78.
- Somaschini A., Gravina M.F. 1994. Ecological analysis of some Syllidae (Annelida, Polychaeta) from the central Tyrrhenian Sea (Ponza Island). In: Dauvin J.C., Laubier L., Reish D.J. (eds), Actes de la 4ême Conférence internationale des Polychètes. Mém. Mus. Natn. Hist. Nat. 162: 567-573.
- Stoner A.W. 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bull. Mar. Sci.* 30(3): 537-551.
- Stoner A.W., Lewis F.G. 1985. The influence of quantitative and qualitative aspects of habitat complexity in tropical sea-grass meadows. *J. Exp. Mar. Biol. Ecol.* 94: 19-40.
- Tena J., Capaccioni-Azzati R., Torres-Gavila F.J., García-Carrascosa A.M. 2000. Polychaetes associated with different facies of the photophilic algal community in the Chafarinas archipelago (SW Mediterranean). *Bull. Mar. Sci.* 67(1): 55-72.
- Tena J., Capaccioni-Azzati R., Torres-Gavila F.J., Porras R. 1993. Anélidos poliquetos del antepuerto de Valencia: distribución y categorías tróficas. Publ. Espec. Inst. Esp. Oceanogr. 11: 15-20.
- Thayer G.W., Bjorndal K.A., Ógden J.C., Williams S.L., Zieman J.C. 1984. Role of larger herbivores in seagrass communities. *Estuaries* 7(4): 351-376.
- Tu Do V., De Montaudouin X., Lavesque N., Blanchet H., Guyard H. 2011. Seagrass colonization: Knock-on effects on zoobenthic community, populations and individual. *Est. Coast. Shelf Sci.* 20: 458-469.
- Webster P.J., Rowden A.A., Attrill M.J. 1998. Effect of shoot density on the infaunal macro-invertebrate community within a *Zostera marina* seagrass bed. *Est. Coast. Shelf Sci.* 47: 351-257.

Scient. ed.: D. Martin.

- Received November 5, 2012. Accepted May 27, 2013.
- Published online July 26, 2013.