View metadata, citation and similar papers at core.ac.uk
brought to you by CORE
provided by Crossref

Scientia Marina 81(3)
September 2017, 413-423, Barcelona (Spain)
ISSN-L: 0214-8358
doi: http://dx.doi.org/10.3989/scimar.04359.06A

Sea pen (Pennatulacea) aggregations on the northern Spanish shelf: distribution and faunal assemblages

Susana Ruiz-Pico [1], Alberto Serrano [1], Antonio Punzón [1], Álvaro Altuna [2], Olaya Fernández-Zapico [1], Francisco Velasco [1]

[1] Instituto Español de Oceanografía de Santander, Promontorio de San Martín s/n, 39004, Santander, Spain.
(SRP) (Corresponding author) E-mail: susana.ruiz@st.ieo.es. ORCID iD: http://orcid.org/0000-0003-3610-7662
(AS) E-mail: aserrano@st.ieo.es. ORCID iD: http://orcid.org/0000-0002-7806-8422
(AP) E-mail: antonio.punzon@st.ieo.es. ORCID iD: http://orcid.org/0000-0001-6703-7690
(OFZ) E-mail: olaya.fernandez@st.ieo.es. ORCID iD: http://orcid.org/0000-0002-6479-890X
(FV) E-mail: francisco.velasco@st.ieo.es. ORCID iD: http://orcid.org/0000-0002-6420-9474
[2] INSUB, Museo de Okendo, Zemoria, 12, 20013 Donostia-San Sebastián, Spain.
(AA) E-mail: alvaro.altuna@telefonica.net. ORCID iD: http://orcid.org/0000-0003-1364-7826

Summary: The sea pens *Funiculina quadrangularis*, *Pennatula aculeata*, *Pennatula phosphorea*, *Pteroeides spinosum* and *Veretillum cynomorium* are known to be characteristic species of the habitat ‘pennatulacean communities on circalittoral and upper bathyal soft bottoms’, described recently on the northern Atlantic Spanish shelf under the terms of the EU directives. Distribution, abundance and environmental data collected from 1995 to 2010 in the Northern Spanish Shelf Groundfish Surveys in the Cantabrian Sea and off Galicia (SPNGFS) were analysed. Although low densities of sea pens were commonly found over the years, some aggregations were shown. Multivariate analysis separated the aggregations of *F. quadrangularis* and of *Pennatula* spp. found on circalittoral soft bottoms. In addition, evidence of aggregations of *F. quadrangularis* on upper bathyal sites was also found. Depth and longitude, which were closely related to organic matter and sediment particle size, were key factors in determining the distribution and abundance of these aggregations. However, very little information on distribution and density of the species *P. spinosum* and *V. cynomorium* was obtained. Details of community composition of *F. quadrangularis* and *Pennatula* spp. were studied and compared with those of the OSPAR habitat “sea pen and burrowing megafauna communities” in other areas. The results improve our knowledge concerning sea pen communities in the southern Bay of Biscay and contribute to a global assessment of the status of these communities in the northeast Atlantic.

Keywords: sea pens; southern Bay of Biscay; abundance; distribution; habitat.

Agregaciones de pennatuláceos en la plataforma del norte de España: distribución y agrupaciones faunísticas

Resumen: Los pennatuláceos *Funiculina quadrangularis*, *Pennatula aculeata*, *Pennatula phosphorea*, *Pteroeides spinosum* y *Veretillum cynomorium* son especies características del hábitat “comunidades de pennatuláceos sobre fondos blandos profundos y circalitorales” descrito recientemente en la plataforma noratlántica española bajo directrices europeas. Datos de distribución, abundancia y ambientales recogidos desde 1995 hasta 2010 en las campañas demersales de la plataforma del norte de España y Galicia (SPNGFS) han sido analizados. Aunque predominan las bajas densidades de pennatuláceos a lo largo de los años, se han encontrado agregaciones. El análisis multivariante ha separado las agregaciones encontradas de *F. quadrangularis* y *Pennatula* spp. en los fondos blandos circalitorales. Además, se han encontrado agregaciones de *F. quadrangularis* en los fondos blandos profundos. La profundidad y la longitud, estrechamente relacionadas con el contenido de materia orgánica y el tamaño de partícula del sedimento, han sido los factores clave en la distribución y abundancia de estas agregaciones. Sin embargo, se ha obtenido poca información de la distribución y densidad de las especies *P. spinosum* y *V. cynomorium*. Se ha estudiado la composición de las comunidades de *F. quadrangularis* y *Pennatula* spp. y se ha comparado con el hábitat definido por OSPAR “sea pen and burrowing megafauna communities” en otras áreas. Los resultados mejoran el conocimiento de las comunidades de pennatuláceos en el sur del Golfo de Vizcaya y ayudan en la evaluación global del estatus de estas comunidades en el noreste Atlántico.

Palabras clave: pennatuláceos; sur del golfo de Vizcaya; abundancia; distribución; habitat.

Citation/Como citar este artículo: Ruiz-Pico S., Serrano A., Punzón A., Altuna A., Fernández-Zapico O., Velasco F. 2017. Sea pen (Pennatulacea) aggregations on the northern Spanish shelf: distribution and faunal assemblages. Sci. Mar. 81(3): 413-423. doi: http://dx.doi.org/10.3989/scimar.04359.06A

Editor: M. Ramón.

Received: October 21, 2015. **Accepted**: Aprill 27, 2017. **Published**: June 28, 2017.

Copyright: © 2017 CSIC. This is an open-access article distributed under the terms of the Creative Commons Attribution (CC-by) Spain 3.0 License.

INTRODUCTION

Recent studies and environmental legislation are involving sea pens in habitat conservation (OSPAR 2010, NOAA 2014, Kenchington et al. 2014). Despite their ecological value, pennatulacean coral habitats have been overlooked compared with cold-water coral ecosystems and studies of the latter mainly focus on stony corals (Order Scleractinia), sea fans and soft corals (Order Alcyonacea). Examples of sea pens forming fields (Aguilar et al. 2009, Porporato et al. 2014, Kenchington et al. 2014) and acting as nurseries for fish larvae (Pirtle 2005, Baillon et al. 2012) or as indicators of quality of mud habitats (MacDonald et al. 1996) highlight their role in benthic ecosystems. Like other corals, sea pens are slow-growing species that are particularly vulnerable because recovery after disturbances can take a long time (Kaiser et al. 2006, de Moura Neves et al. 2015). Moreover, in contrast with other corals, they are able to anchor in soft sediment (Hughes 1998), offering a shelter in a bare environment and acting as an indicator of the degradation of these sediments, which commonly sustain intensive fishing pressure or other disturbances (Thrush and Dayton 2002). The OSPAR Convention assessed the threatened habitat "sea pen and burrowing megafauna communities" in the northeast Atlantic affected by *Nephrops* trawling (Hughes 1998, Greathead et al. 2007, OSPAR 2010). Moreover, sea pens are involved in the soft-bottom coral garden habitat that is also considered threatened and/or declining (OSPAR 2008). Outside the OSPAR region, in eastern Canada, the important role of deep-sea pennatulacean corals as biogenic habitats has been reported (Kenchington et al. 2010, Baillon et al. 2014), and in the USA, under the reauthorized Magnuson-Stevens fishery Conservation and Management Act, deep-sea coral areas, including sea pens, have been protected from fishing (NOAA 2014). The Northwest Atlantic Fisheries Organization (NAFO) has also protected sea pen fields on the Flemish Cap.

After OSPAR recommendations to increase knowledge on the "sea pen and burrowing megafauna habitat" in areas where there are insufficient data and intensive fishing, such as the Cantabrian Sea (Sánchez and Olaso 2004, OSPAR 2010, ICES 2012), and under the European Marine Strategy Framework Directive (EU 2008) considerable advances in habitat definition have been made in Spain in the last few years, describing 'the pennatulacean communities on circalittoral and bathyal soft bottoms' in the North Atlantic Marine Area (MAGRAMA 2012). Despite these efforts, there is still limited information on this habitat in the area and it receives little attention and protection.

In the Bay of Biscay and nearby areas, 21 species of sea pens have been reported, 13 of them occurring off Spain south of the 44°N parallel (Altuna 2010, Supplementary Material Table S1). During several surveys undertaken every autumn by the Spanish Institute of Oceanography (IEO) in the Cantabrian Sea (southern sector of the Bay of Biscay) and off Galicia, five of these species, *Funiculina quadrangularis*, *Pennatula aculeata*, *Pennatula phosphorea, Pteroeides spinosum* and *Veretillum cynomorium*, were found on circalittoral and upper bathyal soft bottoms, sometimes in abundance. Although some of these species are of conservation significance (Hughes 1998, OSPAR 2010), knowledge of them is uneven in this area, with little information on their abundance, distribution and habitat requirements.

F. quadrangularis has a worldwide range, being common throughout the North Atlantic and the Mediterranean Sea (Manuel 1981, Gili and Pagès 1987), with a wide bathymetric range from 20 m to depths of over 3000 m (Tixier-Durivault and d'Hondt 1975, Manuel 1981, López-González et al. 2001). It is a sensitive species considered to be of conservation significance. This species is reported to be especially vulnerable to disturbances because of its inability to withdraw rapidly into the sediment (Hughes 1998). According to the European Nature Information System (EUNIS), it is a characterizing species of the circalittoral biotope 'sea pen and burrowing megafauna', as well as being common in the bathyal facies of soft muds associated with *Aporrhais serresianus* in the Mediterranean Sea. Furthermore, with the implementation of the MSFD in Spain, specifically in the North Atlantic Marine Area (MAGRAMA 2012), this species is also described as a characterizing species of 'the pennatulacean communities on circalittoral and bathyal soft bottoms' in the northern Atlantic Spanish area.

The genus *Pennatula* has a worldwide distribution (Williams 2011), and three out of the five species listed by Williams (2014) from the European Register of Marine Species area occur in the Cantabrian Sea off Spain: namely *P. aculeata*, *P. grandis* and *P. phosphorea*. Records of *P. rubra* from this area are misidentifications. The species *P. aculeata* and *P. phosphorea* are often uncertainly classified (Manuel 1981), and the latter has been confused with other species (Hughes 1998). Thus, tracing their distributions is not easy despite the fact that they are accepted species (Williams 2014). Both species may co-occur in some areas and at some depths in the southern sector of the Bay of Biscay and Galicia (Supplementary Material Table S1). *P. phosphorea* is widespread in the North Atlantic and in the Mediterranean Sea, with several records from the whole Bay of Biscay (Tixier-Durivault and d'Hondt 1975, Gili and Pagès 1987), and is also involved in conservation issues (OSPAR 2010). According to EUNIS classification, it occurs together with *Virgularia mirabilis* in the biotope 'sea pen and burrowing megafauna' in the North and Irish Sea, but also in the facies of sticky muds with *V. mirabilis* in the Mediterranean Sea. It may also be found in the biotope '*Myrtea spinifera* and polychaetes in offshore circalittoral sandy mud' in the North and Irish Sea.

On the other hand, *P. aculeata* has been mainly reported in the North Atlantic, including the Bay of Biscay, but there are some Mediterranean records as well (Tixier-Durivault and d'Hondt 1975, Langton et al. 1990, Ocaña et al. 2000). A review of the literature (Supplementary Material Table S1) indicates that it can reach deeper depths than *P. phosphorea* in the Bay of Biscay and nearby areas, and it has not been associated with a given habitat.

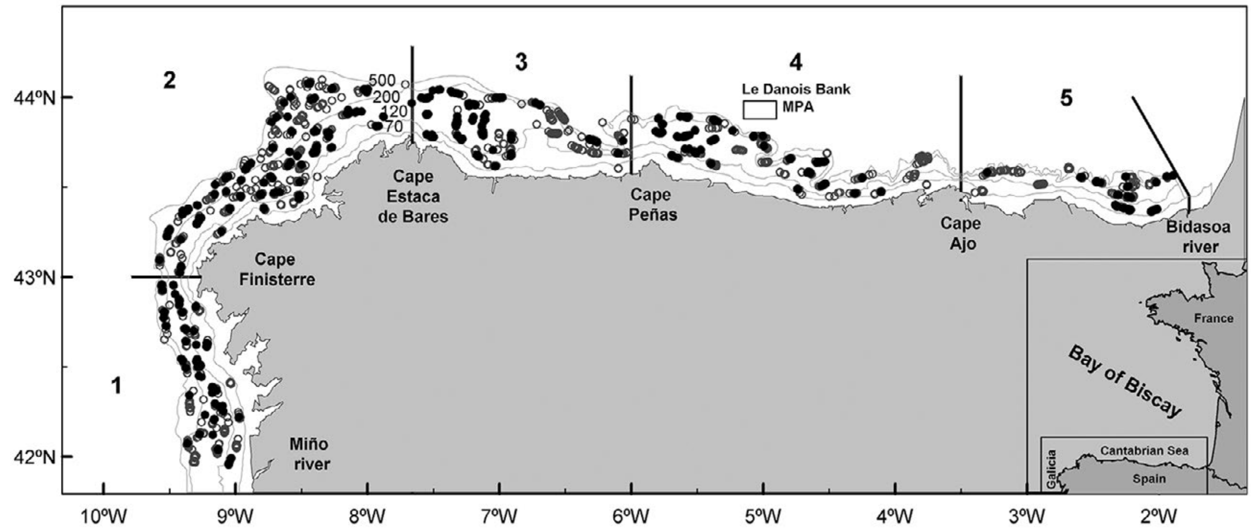

Fig. 1. – Stratification design and hauls (with sea pens, solid black circles and without sea pens, grey circles) in the Northern Spanish Shelf Groundfish Survey. Geographical sectors: 1, Miño-Finisterre; 2, Finisterre-Estaca de Bares; 3, Estaca de Bares-Peñas; 4, Peñas-Ajo; 5, Ajo-Bidasoa. Depth strata: 70-120 m; 121-200 m; 201-500 m; and >500 m.

The two genera *Pteroeides* and *Veretillum* are reported in the eastern Atlantic and West Pacific and described to be bathymetrically restricted to shallow waters (Williams 2011). Specifically, the geographical distribution of *P. spinosum* and *V. cynomorium* ranges from the Bay of Biscay to the Atlantic shores of Africa, including the Mediterranean Sea (Gili and Pagès 1987, López-González et al. 2001, Altuna, 2010). They are involved in the habitat 'the pennatulacean communities of circalittoral and bathyal soft bottoms', according to the description of the biodiversity in the North Atlantic Marine Area (MAGRAMA 2012) with the implementation of the MSFD.

The present work considers the biology and ecology of the most abundant sea pens on the shelf and in the upper bathyal of the southern Bay of Biscay and northwestern Spain (Galicia), mapping their distribution, identifying significant concentrations and describing the benthic/demersal communities associated with them.

MATERIALS AND METHODS

Study area

The study area is the northern Spanish shelf in the southern Bay of Biscay (Fig. 1). This area is included in the OSPAR Region IV in the northeast Atlantic and in the ICES Ecoregion Bay of Biscay and the Iberian Coast. It is situated at temperate latitudes and is strongly influenced by the inflow of oceanic water from the Atlantic Ocean. The bottom topography is highly variable, with noteworthy features such as seamounts, banks and submarine canyons, and a highly diverse coastline. The westernmost area (Galician shelf) in particular is fed by many rias and the large Miño River and has a wider shelf, whereas the eastern area (Cantabrian Sea) is cut by many canyons, the shelf is narrower and the slope steep. The former area falls within ICES Division IXa and the latter within Division VIIIc.

In addition, the Le Danois Bank, the Galicia Bank and the Avilés Canyon have been detected as vulnerable ecosystems off the shelf in the study area and proposed as a Marine Protected Area (MPA).

Data source

The study area has been sampled annually for 33 years by a Spanish groundfish survey to collect demersal and benthic megafauna data, oceanography and sediment characteristics, as described by Olaso (1990) and the standard International Bottom Trawl Survey (IBTS) methodology (ICES 2010). These data were used to analyse changes in the distribution and abundance of the pennatulaceans from the families Funiculinidae, Pennatulidae and Veretillidae from 1995 to 2010.

Following the IBTS methodology (ICES 2010), hauls of 30 minutes (ca. 126 hauls per survey) were performed at a speed of 3 knots with an otter trawl sampler (baca 44/60) with a 20/mm mesh cod-end liner and a mean swept area of 52504 m^2. The sampling design used was random stratified to the area, with five geographical sectors and three depth strata, two on the circalittoral (70-120 m, 121-200 m) and one on the upper bathyal (201-500 m) (Fig. 1). In addition, some extra hauls were carried out to cover shallower (<70 m) and deeper (>500 m) grounds.

The environmental variables depth, near-bottom temperature and salinity, location (longitude) and sediment characteristics were analysed to explain differences among the samples. Temperature and salinity were measured with a CTD Seabird 25. Sedimentary characteristics were determined using a sediment collector attached to the groundgear. Particle size of sediments was analysed by combining dry sieving and sedimentation techniques and the variables weight percentage of gravel and coarse sands (GCS: >500 μm), weight percentage of medium, fine and very fine sands (MFS, 63-500 μm) and weight percentage of silt (<63 μm). In addition, weight percentage of organic matter (OM) in the sediment was estimated as weight loss of dried (100°C, 24 h) samples after combustion (500°C, 24 h).

Data analysis

Density (number of colonies per haul) of *F. quadrangularis*, *Pennatula* spp., *P. spinosum* and *V. cynomorium* were obtained from the 2019 hauls (standard and extra hauls) performed between 1995 and 2010. In addition, records of *Pennatula* spp. collected on the same surveys but from 2008 and 2014 were used to shed some light on the bathymetric distribution of the two species *P. aculeata* and *P. phosphorea*, although they were not included in the density analysis.

The aggregations at or above 10.5 sea pens/haul were studied to analyse faunal assemblages, according to the threshold defined under the MSFD, of species forming habitat when abundances are at or above 200 individuals km^{-2} or biomass at or above 4 kg km^{-2} in the same area as our study area, the North Atlantic Marine Area (MAGRAMA 2012). We chose the threshold based on abundance because the biomass of sea pens is not an accurate measurement at sea for these light-weighing species.

An abundance matrix of demersal species was obtained. Highly abundant mobile invertebrates such as the decapod *Polybius henslowii*, swimming pelagic crustaceans and nektonic cephalopods, namely squids, were removed from the data set.

Density of sea pens per haul was plotted on a histogram and on a spatial context in the area to study the aggregations. Species accumulation curves were represented with the "vegan" package in R software (R Core Team 2014) to ensure that the aggregations were adequately sampled.

Environmental differences between aggregations were studied with constrained correspondence analysis (CCA) and implemented with R (Borcard et al. 2011). Unlike in unconstrained ordination, in canonical ordination the data matrix is forced or constrained by the environmental variables and performs well with species abundance data (Palmer 1993). Forward selection was used for variable reduction and partial CCA to study the effect of correlation and the power of the most significative variables when the other variables were controlled. The significance of the F-statistics associated with all variables was tested using permutation tests, and the most significant explanatory variable was selected (Blanchet et al. 2008). Significance of the adjusted model with the most significant variables was tested using an ANOVA-like permutation test for CCA. CCA results were presented graphically in a tridimensional ordination diagram generated by triplot scaling focusing on inter-species distances, in which samples were represented by symbols, species by points and environmental variables by vectors. In addition, a Mantel correlogram of the Bray-Curtis similarity matrix of the aggregations was constructed to evaluate the spatial correlation as a function of the geographic distance classes.

Table 1. – Summary of the collection data from 1995 to 2010. N, number of hauls analysed; Nseapens, number of hauls with seapens; Naggreg.C, number of hauls with densities at or above the threshold 10.5 sea pens/haul on the circalittoral; Naggreg.U, number of hauls with densities at or above the threshold 10.5 sea pens/haul on upper bathyal.

Year	N	Nseapens	Naggreg.C	Naggreg.U
1995	116	18	6	1
1996	114	32	6	2
1997	116	36	12	1
1998	114	22	1	0
1999	116	15	4	1
2000	113	12	2	1
2001	113	20	0	0
2002	109	20	3	0
2003	112	17	2	1
2004	114	29	4	1
2005	116	41	5	0
2006	116	40	1	1
2007	117	29	5	0
2008	115	22	2	0
2009	119	23	2	0
2010	114	27	1	1

Differences of the species composition between aggregations were studied with PRIMER version 6.1.13 (Clarke and Gorley 2006). Analysis of Bray-Curtis similarity (ANOSIM) was used to detect the statistical significances of these differences, and the similarity of percentages procedure (SIMPER) was used to identify higher-contributing species (at least 80%) to intragroup Bray-Curtis similarity and intergroup dissimilarities. In addition, the frequency and density of the species composition of the aggregations were obtained. Categories of the percentage of occurrence were established according to biotopes classification for Britain and Ireland and categories of density were based on a modified SACFOR scale (semiquantitative abundance scale, Connor et al. 2004), but reduced to four categories (Abundant, >1000/haul; Common, 100-999/haul; Frequent, 10-99/haul; and Occasional, 1-9/haul) due to the low abundances found in the study area.

RESULTS

Distribution of sea pens in the area

Approximately 21% of the hauls were found to contain sea pens every year. The summary of these hauls with sea pens is shown in Table 1. In general, the density was low: around 65% of the hauls with sea pens showed an abundance of one colony per haul. Despite this predominance of low densities, evidence of aggregations was found during the time series (Table 1 and Fig. 2) and throughout the study area (Fig. 3). Approximately 20% of the hauls with sea pens were found to contain densities of sea pens at or above the threshold of 10.5 sea pens per tow. In addition, the Mantel correlogram showed a positive spatial correlation among near samples and negative significance in distant samples, supporting the hypothesis that sea pens form aggregations across space in the area (Supplementary Material Fig. S1). Species accumulation curves for these aggregations (Supplementary Material Fig. S2) indicated a suitable sampling.

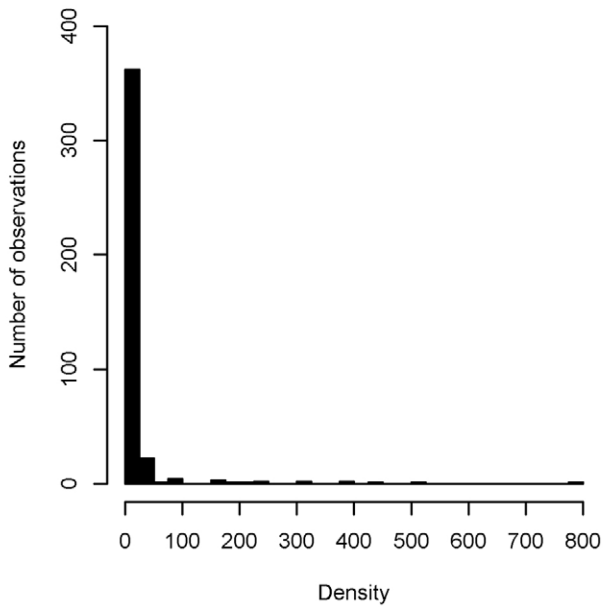

Fig. 2. – Density for all non-zero data of sea pens (colonies/haul).

The results of CCA (Fig. 4A and Table 2) showed that the first axis (Eigenvalue=0.822) splits the aggregations into two groups, depth being the most contributing variable, with higher scores associated with deeper aggregations. The second axis (Eigenvalue=0.467) also splits the sites into two groups, but in this case the most contributing variables were mainly OM and longitude, with negative scores associated with western stations. The two groups of the first axis corresponded to the circalittoral (negative scores) and upper bathyal (positive scores) aggregations, and the two groups of the second axis corresponded to the aggregations on the circalittoral of *F. quadrangularis* (positive scores) and *Pennatula* spp. (negative scores). Therefore, three groups were defined in the study area as the results of the CCA: the aggregations of *F. quadrangularis* on the circalittoral, the aggregations of *F. quadrangularis* on the upper bathyal and the aggregations of *Pennatula* spp. on the circalitttoral. Some aggregations on the upper bathyal were slightly deeper than 201 m, so they were at the border between the circalittoral and the upper bathyal. In fact, they were closer to the groups of aggregations on the circalittoral than to the group on the upper bathyal, as is shown in the CCA.

Forward selection showed a significant model (p>0.005) with depth, OM and salinity. Partial CCAs highlighted that depth, and to a lesser extent longitude, were the variables which best defined the groups of aggregations when the other variables were partialled out.

Most of the aggregations (80%) were on the circalittoral between 94 and 196 m, but some aggregations

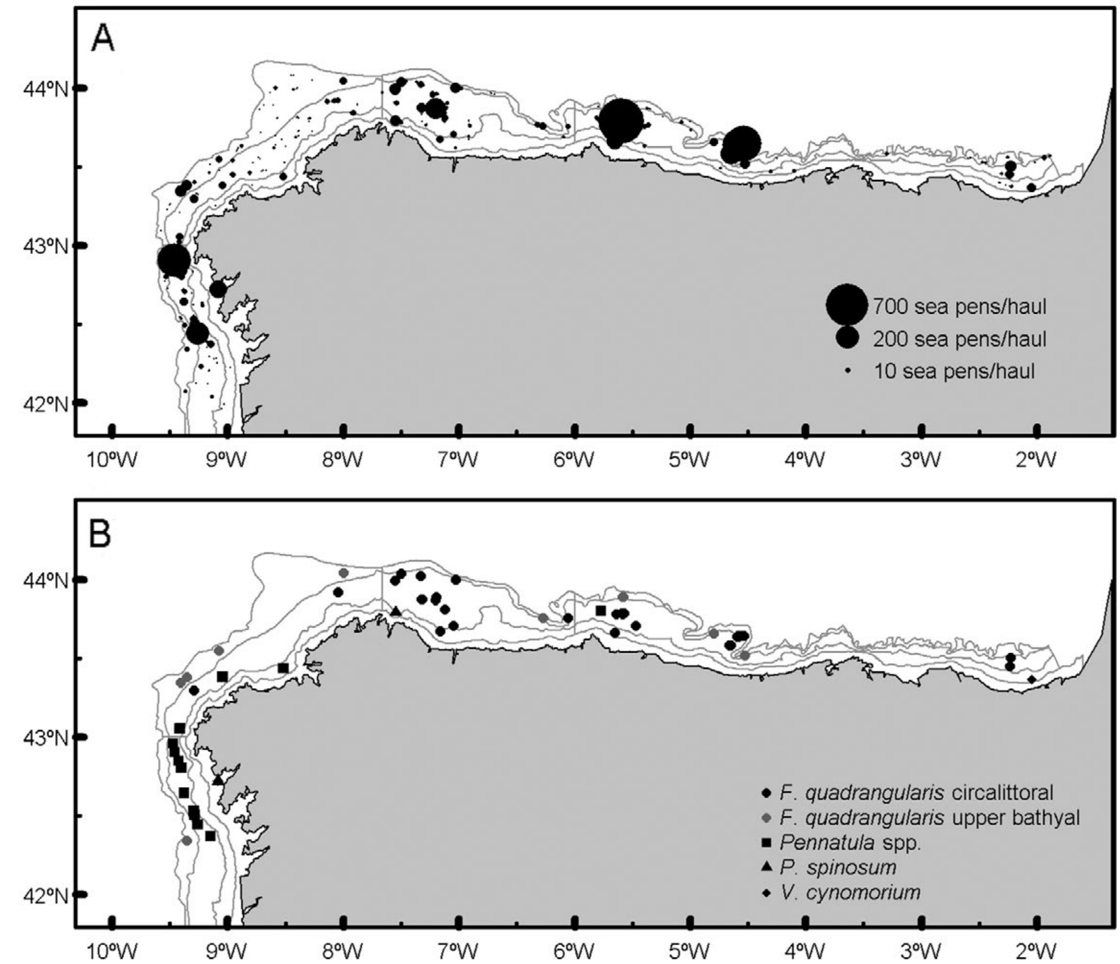

Fig. 3. – Distribution of sea pens (A) and of the aggregations (B) in the study area.

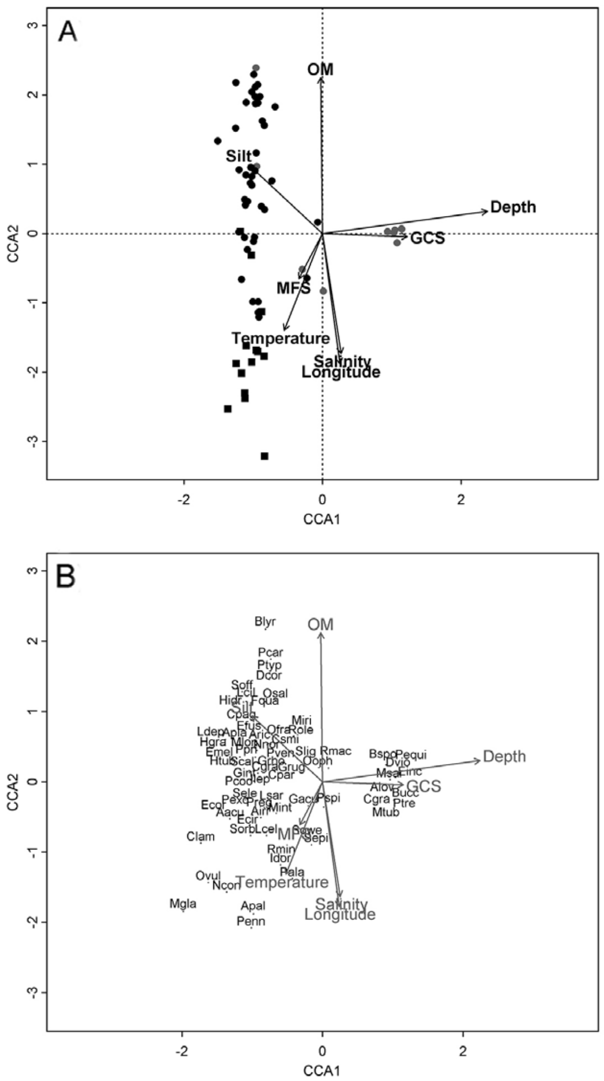

Fig. 4. – A, CCA of the aggregations (*F. quadrangularis* [dots] and *Pennatula* spp. [squares]) based on the species composition. The samples on the circalittoral in black and the samples on the upper bathyal in grey. B, CCA of the species composition of these aggregations. Species abbreviations appear in Supplementary Material Table S2. The arrows indicate the direction and magnitude of the environmental variables: depth, longitude, temperature, salinity, median particle diameter (GCS, weight percentage of gravel and coarse sands [>500 µm]; MFS, weight percentage of medium, fine and very fine sands [63-500 µm]; Silt, percentage weight of silt [<63 µm]) and weight percentage of organic matter (OM).

were also found on the upper bathyal from 194 m to 300 m. On the circalittoral, approximately 73% of the aggregations were dominated by *F. quadrangularis*, 25% by *Pennatula* spp., 1% by *P. spinosum* and 1% by *V. cynomorium*. On the upper bathyal, all aggregations were dominated by *F. quadrangularis* (Fig. 3B).

F. quadrangularis was the most abundant sea pen in the study area. This species represented about 83% of the pennatulacean mean abundance caught with an average of 23 colonies per haul. *F. quadrangularis* was widespread in the sampling area from 84 to 793 m.

Pennatula spp. represented about 14% of the mean abundance of pennatulaceans caught. Despite their low percentages, *Pennatula* spp. was found every year, with an average of nine colonies per haul. It was mainly found in the Galician area from 91 to 793 m, with two species identified, namely *P. aculeata* and *P. phosphorea*. All specimens verified as *P. aculeata* in the study area occurred deeper than 700 m, while those of *P. phosphorea* were caught on the shelf (Supplementary Material Table S1). Among the few colonies of *P. aculeata* identified, four were found at 793 m on the surrounding slope of the Le Danois Bank MPA and, out of the study time series, three colonies were found at 811 m in the southwest of the Le Danois Bank MPA in 2013 and 2014 (unpublished data).

Table 2. – Canonical coefficients for each environmental variable on each canonical axis (CCA) on the aggregations of *F. quadrangularis* and *Pennatula* spp. GCS, weight percentage of gravel and coarse sands (>500 µm); MFS, weight percentage of medium, fine and very fine sands (63-500 µm); Silt, percentage weight of silt (<63 µm); OM, weight percentage of organic matter.

	CCA1	CCA2
Longitude	0.10	–0.72
Depth	0.91	0.12
Temperature	–0.21	–0.54
Salinity	0.10	–0.67
OM	–0.01	0.86
GCS	0.47	–0.02
MFS	–0.13	–0.25
Silt	–0.41	0.38

P. spinosum represented a small percentage of the mean abundance of pennatulaceans caught (3%), but it was found every year from a minimum of 1 colony to a maximum of 42 colonies per haul and with an average of 3 colonies per haul. *P. spinosum* occurred from 50 m to 296 m, although it was mostly found shallower than 150 m. Two aggregations were found, one in Galician waters at a depth of about 48 m and one in the western Cantabrian Sea at about 120 m (Fig. 3B).

V. cynomorium was scarce in the sampling area and it was not found every year. A maximum of 118 colonies per haul was found in 2009 at about 50 m depth in the Galician area, although this species mainly ranged between 90 and 170 m in the easternmost area of Cantabrian Sea and exceptionally occurred around 370 m. Two aggregations were found, one together with the aggregation of *P. spinosum* in the southern Galician waters and one in the easternmost area of Cantabrian Sea at about 98 m (Fig. 3B).

The density of these two last species may be underestimated in the present study as depths shallower than 70 m were under-sampled. This scarcity prevented us from assessing their ecological importance.

Faunal assemblages

Aggregations of Funiculina quadrangularis *on circalittoral and upper bathyal soft bottoms*

The aggregations of *F. quadrangularis* were mainly found on the circalittoral of the central area of the Cantabrian Sea between 95 and 301 m (80%), although, as stated above, some aggregations were also observed on the upper bathyal in the study area (Fig. 3B).

Differences in species composition between aggregations on the circalittoral and the upper bathyal and ecological information of species were obtained by

Table 3. – Results of the SIMPER analysis of the aggregations of *F. quadrangularis* on the circalittoral (1) and upper bathyal (3) and of *Pennatula* spp. on the circalittoral (2). Av abund, average abundance; Contrib.% and Cum.%, contribution and cumulative percentage respectively of the higher-contributing species.

Intragroup similarity	Av abund	Contrib%	Cum%	Intergroup dissimilarity	Av.Abund (1)	Av.Abund (2)	Contrib%	Cum%
(1) *F. quadrangularis* on the circalittoral s: 24.08%				(1) and (2) d: 89.4%				
Funiculina quadrangularis	116.16	62.15	62.15	*Funiculina quadrangularis*	116.16	0.36	21.11	21.11
Astropecten irregularis	13.07	7.14	69.29	*Leptometra celtica*	70.26	79.50	11.58	32.70
Eledone cirrhosa	9.88	4.95	74.25	*Pennatula* spp.	0.00	69.50	10.99	43.69
Pagurus prideaux	20.95	4.91	79.16	*Pagurus prideaux*	20.95	22.57	7.69	51.38
Leptometra celtica	70.26	4.11	83.27	*Eledone cirrhosa*	9.88	32.14	7.05	58.43
				Astropecten irregularis	13.07	36.14	6.60	65.03
(2) *Pennatula* spp. on the circalittoral s: 29.93%				*Sepiola* sp.	1.00	20.00	3.76	68.79
Pennatula spp.	69.50	30.35	30.35	*Munida intermedia*	18.42	5.93	3.10	71.89
Eledone cirrhosa	32.14	25.96	56.30	*Liocarcinus depurator*	11.23	6.50	2.86	74.75
Astropecten irregularis	36.14	21.11	77.42	*Munida sarsi*	8.86	5.71	2.39	77.15
Sepiola sp.	20.00	7.51	84.93	*Sepia orbignyana*	2.21	8.86	2.34	79.48
				Rondeletiola minor	0.88	8,43	1.85	81.34
(3) *F. quadrangularis* on upper bathyal s: 37.20%				(1) and (3) d: 93.08%				
Munida sarsi	1852.75	86.39	86.39	*Munida sarsi*	8.86	1852.75	63.12	63.12
				Funiculina quadrangularis	116.16	25.25	7.05	70.17
				Macropipus tuberculatus	0,95	147.88	5.75	75.92
				Sepiola sp.	1	32.5	5.64	81.56

combining the results of CCA (Fig. 4B), the density data (Supplementary Material Table S2) and SIMPER (Table 3). ANOSIM identified significant dissimilarities between the samples of *F. quadrangularis* on the circalittoral and the samples on the upper bathyal (R=0.678; p=0.001), and the SIMPER showed an intergroup dissimilarity between these groups of 93.1%. The SIMPER results showed that the species *Munida sarsi*, *F. quadrangularis*, *Macropipus tuberculatus* and *Sepiola* sp. mainly drove the intergroup dissimilarities. In the shallower (circalittoral) aggregations, the species *F. quadrangularis* and the crinoid *Leptometra celtica* showed the highest densities, although the highest-contributing species to the similarity were *F. quadrangularis*, the seastar *Astropecten irregularis*, the cephalopod *Eledone cirrhosa*, the hermit crab *Pagurus prideaux* and *L. celtica*. In the deeper aggregations, *M. sarsi* overshadowed the rest of the species due to its high density and contribution to the communities. If we do not cut off the low contributions, we can see that the cephalopod *Sepiola* sp., *F. quadrangularis* and the portunid crab *M. tuberculatus* contributed 4.82%, 3.15% and 1.66%, respectively. Regarding density, *M. tuberculatus* was the second most abundant species despite its lowest contribution.

In addition, the CCA (Fig. 4B) confirmed the segregation of samples into two groups together with a segregation of species. The eurybathic species were found in both aggregations and located near the CCA centroid, but the positive axis 1 of CCA also showed species with deeper habits and associated with larger sediment (GCS) on upper bathyal soft bottoms, and the negative axis 1 of CCA showed species with shallower habits and associated with fine sediment (silt and MFS) on circalittoral soft bottoms.

The results of the Mantel correlogram (Supplementary Material Fig. S1) also confirmed a variability of species composition along a spatial gradient. The species composition of the aggregations was significantly spatially similar at short distances, whereas when they were spatially separated they did not show significant similarity.

Aggregations of Pennatula *spp. on circalittoral soft bottoms*

The aggregations of *Pennatula* spp. were mainly found on the circalittoral in the southern Galician area between 95 and 179 m. No evidence of aggregations was found on upper bathyal (Fig. 3B).

Differences of species composition between the aggregations on the circalittoral of *F. quadrangularis* and *Pennaluta* spp. were found (CCA [Fig. 4B], density data [Supplementary Material Table S2] and SIMPER [Table 3]). ANOSIM identified significant dissimilarity between these samples on the circalittoral (R=0.629; p=0.001), and the SIMPER showed an intergroup dissimilarity between groups of 89.4%. The SIMPER showed that the species *F. quadrangularis*, the crinoid *L. celtica, Pennatula* spp., the hermit crab *P. prideaux*, the cephalopod *E. cirrhosa,* the seastar *A. irregularis,* the cephalopod *Sepiola* sp.*,* the anomuran crab *Munida intermedia,* the portunid crab *Liocarcinus depurator,* the anomuran crab *M. sarsi,* and the cephalopods *Sepia orbygnyana* and *Rondeletiola minor* mainly drove the intergroup dissimilarities between the aggregations of *F. quadrangularis* and of *Pennatula* spp. on the circalittoral in descending order of contribution. In the aggregations of *Pennatula* spp., the species*, E. cirrhosa, A. irregularis and Sepiola* sp. were the highest-contributing species to the similarity.

DISCUSSION

Our results provided further evidence of sea pens in the southern Bay of Biscay. Pennatulaceans have been previously reported in the area, not only in the proposed MPAs on the Galicia Bank (IEO 2014a) and in the Avilés Canyon (IEO 2014b), but also in the inner basin of the Le Danois Bank MPA (BOE 2011) and in Galician waters (Aguilar et al. 2009). Moreover, under the MSFD, Spain has recently identified pennatulacean communities as the most diverse and richest habitats on circalittoral and bathyal soft bottoms of the northern Atlantic Spanish area (MAGRAMA 2012). Our results also provided further evidence of sea pens forming aggregations on the northern Atlantic Spanish shelf. Although sea pens were broadly found at low density in the study area, the aggregations with a noteworthy high density in the central part of the Cantabrian Sea and in the southern Galician area and the high spatial autocorrelation among near samples supports the hypothesis of sea pens forming aggregations in the area. The hotspots in the Cantabrian Sea were of the species *F. quadrangularis*, while in the Galician area they were of *Pennatula* spp. Though the sea pens *V. cynomorium* and *P. spinosum* were scarce, they showed two hotspots in the southern Galician area and in the easternmost area of the Cantabrian Sea, respectively.

In addition, differences in the distribution of sea pen aggregations were supported by the fact that longitude was among the variables contributing most to the differentiation of the aggregations. This factor is a result of environmental differences between the western (Galicia area) and eastern (Cantabrian Sea) zones of the study area, the Galician and Cantabrian Sea, respectively. In general, there is higher primary production in Galician waters (López-Jamar et al. 1992, OSPAR 2000) and, in particular, a heterogeneous grain size and a higher OM content have been reported to the south of Cape Finisterre (López-Jamar et al. 1992), where *Pennatula* spp. was highly abundant. *Pennatula* spp. are known to be much stouter and fleshier than *F. quadrangularis* (Manuel 1981), which probably helps them to settle in less homogeneous sediments. In fact, both species are known to occur in muddy substrata, but Manuel (1981) also reported *P. phosphorea* in sandy substrata and Greathead et al. (2015) reported the absence of *F. quadrangularis* in sediment with gravel content above 30%.

In addition, longitude also means differences in topography, which leads to an apparent absence of aggregations of sea pens on the narrow shelf and steep slope of the eastern part of the Cantabrian Sea, with the exception of the easternmost shelf area. Therein, mud deposits (Jouanneau et al. 2008) could be supporting the settlement of the few aggregations of *F. quadrangularis*.

On the other hand, depth was also an influential factor in the distribution of the sea pens in the study area. The few aggregations of *P. spinosum* and *V. cynomorium* were found at about 50 m depth, although some specimens were recorded at unusual depths in the area if compared with data in the literature (Supplementary Material Table S1). We found that 70% of the occurrences of *V. cynomorium* in our study area were detected above 100 m and three colonies were even found at an unusual depth of 372 m, despite the fact that these two species are known to be continental-shelf species with a distribution related to terrigenous sediments (Gili and Pagès 1987, Williams 2011, Sardá et al. 2012). López-González et al. (2001) reported, in the eastern Atlantic, a wider depth range (25-188 m) than Williams (1990, 13-91 m), and Gili and Pagès (1987) showed an even deeper limit in the Mediterranean Sea (around 260 m). However, neither of them mentioned such a deep distribution for the species. In addition to this interesting result, the highest aggregation of colonies of *V. cynomorium* (118 colonies), together with some colonies of *P. spinosum* (19 colonies), were found near the Arousa Ría (Galicia, Spain), where fields of *V. cynomorium* have been previously reported (Fernández et al. 2005, Aguilar et al. 2009). This result provides further evidence of sea pens forming aggregations, widely recognized as key benthic habitats (OSPAR 2008, DFO 2010, Kenchington et al. 2011).

Another result of the influence of depth on the distribution of sea pen species was found in the Galician area, where *Pennatula* spp. was abundant from 100 to 200 m, while the few occurrences of *F. quadrangularis* were mainly between 200 and 300 m. Hughes (1998) and Greathead et al. (2007) also suggest the preference of *F. quadrangularis* for deeper habitats where the conditions may be more stable. In addition, also relating depth to sediment particle size and organic content, finer and organic-rich sediments have been reported on the inner shelf off the Rías Bajas (Galicia, Spain), where *Pennatula* spp. was more abundant, while on the outer shelf the sediments are sandier and have low organic content (López-Jamar et al. 1992). Nevertheless, Greathead et al. (2007) suggest that depth is a more important factor than sediment type in the distribution of *F. quadrangularis*.

Tracing the distributions and bathymetric ranges of *P. phosphorea* and *P. aculeata* in the Bay of Biscay and nearby areas from the literature is not easy, as we highlighted in the Introduction. However, our results provide evidence of different bathymetric distributions between the two species. Hence, the fact that *P. aculeata* extends deeper than *P. phosphorea* suggests that the aggregations of *Pennatula* spp. found in the study area do not include specimens of *P. aculeata* but only of *P. phosphorea*, although more data are still sorely needed. *P. aculeata* has also been found at similar depths in the southern Bay of Biscay, as a result of the bathyal surveys carried out by the ECOMARG project (www.ecomarg.com). During these surveys, *P. aculeata* was found only at 745 and 761 m in the Le Danois Bank MPA, at 786 m on the Galicia Bank (northwestern Spain) and at 828 m in the Avilés Canyon (northern Spain) (A. Altuna, personal communication). All these records of upper bathyal presence of *P. aculeata*, and to a large extent, the lack of reliable data of *P. phosphorea* from these areas, highlight the need for more research on the bathymetric distribution and ecological needs of these two species.

With respect to the sampling of sea pen communities in the southern Bay of Biscay, the present study adds long-term information on the distribution of sea pens in an extensive area, despite the use of trawling sampling. Techniques such as beam trawl and demersal otter trawl are often used in benthic community studies, although monitoring is extensively recommended for the management of sea pens and burrowing megafauna (Hughes 1998, Greathead et al. 2007). Monitoring and assessment of vulnerable habitats have been carried out in the area with non-destructive monitoring techniques such as remotely-operated vehicles and photogrammetric sledges (Aguilar et al. 2009, www.ecomarg.com, Sánchez et al. 2009), but they were short-term or spatially isolated studies. In addition, sampling of some sea pen communities is not easy and very inaccurate, as some pennatulaceans can withdraw below the sediment surface and bias the results of monitoring. The density of some such sea pens in a given area can change by over 200% in a few hours (Birkeland 1974). *Virgularia mirabilis* is known to withdraw into the sediment and *P. phosphorea* and *P. aculeata* are also able to do so, although not as quickly, but *F. quadrangularis*, *P. spinosum* and *V. cynomorium* do not show this feature (Langton et al. 1990, Hughes 1998).

The species composition of the aggregations of sea pens in the study area agrees with previous studies in the area, which showed depth as a key factor structuring communities (Olaso 1990, Serrano et al. 2006). Many species that occur in the aggregations of *F. quadrangularis* and *Pennatula* spp. coincided with the eurybathic species described in the area by Olaso (1990), such as the portunid crab *Liocarcinus depurator*, the spider crab *Macropodia longipes* and the sea snail *Neptunea contraria*, or with the characteristic species of the shelf (between 140 and 300 m), such as the sea anemone *Actinauge richardi*, the sea snail *Ranella olearium* and the sea cucumber *Parastichopus regalis*. Specifically in the shallower samples of *F. quadrangularis*, the higher-contributing species *Astropecten irregularis*, *Eledone cirrhosa*, *Pagurus prideaux* and *Leptometra celtica* were reported by Olaso (1990) on the upper edge of the shelf (between 90 and 140 m), whereas the anomuran *Munida sarsi*, as the most abundant and the highest-contributing species in the deeper samples of *F. quadrangularis*, was reported as a dominant species on the shelf. This author compared the different distribution of *M. sarsi* with the other common anomuran in the area, *Munida intermedia* and described both species as dominant species on the shelf, but *M. sarsi* showed greater density at 275 m in the Cantabrian Sea, and *M. intermedia* showed greater density at 175 m in the Galician area. This explains the higher abundance of *M. sarsi* in the deeper aggregations of sea pens in the area and the greater occurrence of *M. intermedia* in the aggregations of *Pennatula* spp., which are mainly distributed in Galician waters. In addition, Olaso (1990) and Serrano et al. (2006) showed depth and sediment characteristics to be priority factors determining species composition.

Large differences were found between the aggregations described in the present study and the habitat "sea pen and burrowing megafauna communities" defined by OSPAR. This habitat was reported in the North Sea, the Irish Sea and the Bay of Biscay and may include populations of *V. mirabilis*, *P. phosphorea* or *F. quadrangularis* with burrowing crustaceans such as *Nephrops norvegicus*, in fine mud at depths of between 15 and 200 m. In the southern Bay of Biscay, we found aggregations of *F. quadrangularis* on circalittoral soft bottoms but also on the upper bathyal deeper than 200 m. In addition, we also found aggregations of *Pennatula* spp. in the Galician area, all of them on circalittoral bottoms. Finally, *V. mirabilis* was absent and *N. norvegicus* was found at low densities in the study area, despite its general distribution between 90 and 600 m in the study area (ICES 2012). Other species not mentioned by OSPAR, *M. sarsi*, *A. irregularis*, *L. depurator*, *Ophiura ophiura* and *M. intermedia*, were frequent in the aggregations found in the study area. Although the southerner area and the deeper and trawling sampling in the present study marked differences from the methodology used to define this habitat in Northern Europe, and the community composition and density of the aggregations of sea pens on the northern Spanish shelf might be biased by some other factors.

Some of these frequent species, *L. depurator*, *O. ophiura* and *A. irregularis*, are known to be opportunistic species in trawled areas (Kaiser et al. 1998, Vergnon and Blanchard 2006, de Juan et al. 2007) like our study area which support an intensive fishing pressure (Sánchez and Olaso 2004, ICES 2012). In contrast to the North Sea, the Irish Sea and northern Bay of Biscay, where *Nephrops* is one of the most important fisheries, in the southern Bay of Biscay *N. norvegicus* has stopped being a target species over time due to its low abundance. Nevertheless, it is a valued component of the mixed bottom trawl fishery together with hake, anglerfish, megrim, horse mackerel, mackerel and blue whiting (Fariña and Herraiz 2003, Punzón et al. 2010, ICES 2012). The *Nephrops* stock is declining in the study area (Fariña and Herraiz 2003) and recovery plans were adopted in 2005 (Council Regulation (EC) 2166/2005). This decline in *Nephrops* stock could have coincided with a decline in sea pens in the past, which could partially explain the low densities of sea pens found in the study. Now, this mixed bottom trawling could be a similar threat for sea pens in the Cantabrian and Galician waters to that of *Nephrops* trawling in the North Sea, the Irish Sea and the northern Bay of Biscay, but this possibility has not been assessed. Evidences like the intensive fishing pressure, the declining *Nephrops* stock, the presence of opportunistic species in the aggregations and the low densities of sea pens found in the present study suggest that trawling might be affecting sea pen abundance in the southern Bay of Biscay and highlight the need for further information to assess the status of these important communities in this region.

ACKNOWLEDGEMENTS

We are grateful to all the participants of the Northern Spanish Shelf Groundfish Surveys carried out in the Cantabrian Sea and off Galicia and to the crew of the R/V *Cornide de Saavedra*. We also thank the ECOMARG and INDEMARES projects for the information on benthic communities in the Le Danois Bank MPA, the Galicia Bank and the Avilés Canyon.

The manuscript was improved thanks to the careful revision and constructive comments of Ellen Kenchington.

REFERENCES

Aguilar R., Torriente A., García S. 2009. Propuesta de Áreas Marinas de Importancia Ecológica. Zona galaico-cantábrica. Oceana-Fundación Biodiversidad, 252 pp.
Altuna Á. 2010. Listado de los cnidarios (Cnidaria) bentónicos del Golfo de Vizcaya y zonas próximas (Atlántico NE). Proyecto Fauna Ibérica. Museo Nacional de Ciencias Naturales, Madrid, 27 pp.
Baillon S., Hamel J.F., Wareham V.E., et al. 2012. Deep cold-water corals as nurseries for fish larvae. Front. Ecol. Environ. 10: 351-356.
https://doi.org/10.1890/120022
Baillon S., Hamel J.F., Mercier A. 2014. Diversity, distribution and nature of faunal associations with deep-sea pennatulacean corals in the Northwest Atlantic. PloS ONE 9: e111519.
https://doi.org/10.1371/journal.pone.0111519
Birkeland C. 1974. Interactions between a sea pen and seven of its predators. Ecol. Monogr. 44: 211-232.
https://doi.org/10.2307/1942312
Blanchet F.G., Legendre P., Borcard D. 2008. Forward selection of explanatory variables. Ecology 89: 2623-2632.
https://doi.org/10.1890/07-0986.1
BOE. 2011. Real Decreto 1629/2011, de 14 de noviembre, por el que se declara como Área Marina Protegida y como Zona Especial de Conservación el espacio marino de El Cachucho, y se aprueban las correspondientes medidas de conservación. BOE 295: 130084-130138.
Borcard D., Gillet F., Legendre P. 2011. Numerical Ecology with R. Springer, New York.
https://doi.org/10.1007/978-1-4419-7976-6
Clarke K.R., Gorley R.N. 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.
Connor D.W., Allen J.H., Golding N., et al. 2004. The marine habitat classification for Britain and Ireland, version 04.05. JNCC, Peterborough.
de Juan S.D., Cartes J.E., Demestre M. 2007. Effects of commercial trawling activities in the diet of the flat fish *Citharus linguatula* (Osteichthyes: Pleuronectiformes) and the starfish *Astropecten irregularis* (Echinodermata: Asteroidea). J. Exp. Mar. Biol. Ecol. 349: 152-169.
https://doi.org/10.1016/j.jembe.2007.05.003
de Moura Neves B., Edinger E., Layne G.D., et al. 2015. Decadal longevity and slow growth rates in the deep-water sea pen *Halipteris finmarchica* (Sars, 1851) (Octocorallia: Pennatulacea): implications for vulnerability and recovery from anthropogenic disturbance. Hydrobiologia 759: 147-170.
https://doi.org/10.1007/s10750-015-2229-x
DFO (Fisheries and Oceans Canada). 2010. Occurrence, susceptibility to fishing and ecological function of corals, sponges and hydrothermal vents in Canadian waters. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2010/041.
EU (European Union). 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008, Establishing a Framework for Community Action in the Field of Marine Environmental Policy (Marine Strategy Framework Directive). Official Journal of the European Union L164: 19-40.
Fariña A.C., Herraiz I.G. 2003. Trends in catch-per-unit-effort, stock biomass and recruitment in the North and Northwest Iberian Atlantic *Nephrops* stocks. Fish. Res. 65: 351-360.
https://doi.org/10.1016/j.fishres.2003.09.025
Fernández J.A., Bonache J., Gordillo E. 2005. Parque Nacional das Illas Atlánticas de Galicia. Recursos rurais. Serie cursos 2: 91-102.
Gili J.M., Pagès F. 1987. Pennatuláceos (Cnidaria, Anthozoa) recolectados en la plataforma continental catalana (Mediterráneo occidental). Misc. Zool. 11: 25-39.
Greathead C.F., Donnan D.W., Mair J.M., et al. 2007. The sea pens *Virgularia mirabilis*, *Pennatula phosphorea* and *Funiculina quadrangularis*: distribution and conservation issues in Scottish waters. J. Mar. Biol. Assoc. U.K. 87: 1095-1103.
https://doi.org/10.1017/S0025315407056238
Greathead C., González-Irusta J.M., Clarke J., et al. 2015. Environmental requirements for three sea pen species: relevance to distribution and conservation. ICES J. Mar. Sci. 72: 576-586.
https://doi.org/10.1093/icesjms/fsu129
Hughes D.J. 1998. Sea pens and burrowing megafauna (volume III). An overview of dynamics and sensitivity characteristics for conservation management of marine SACs. Scott. Assoc. Mar. Sci. (UK Marine SACs Project). 105 pp.
ICES. 2010. Manual for the International Bottom Trawl Surveys in the Western and Southern Areas Revision III. Agreed during the meeting of the International Bottom Trawl Survey Working Group 22-26 March 2010, Lisbon. Addendum 2: ICES CM 2010/SSGESST: 06. 58 pp.
ICES. 2012. Report of the ICES Advisory Committee 2012. Book 7, Bay of Biscay and Atlantic Iberian waters. ICES Advice, 2012. Book 7. 205 pp.
IEO. 2014a. Caracterización ecológica del banco de Galicia. Informe final del proyecto LIFE+ INDEMARES (LIFE07/NAT/E/000732), subproyecto LIC. IEO. Coordinación: Fundación Biodiversidad, Madrid, 237 pp.
IEO. 2014b. Caracterización ecológica del área marina del sistema de ca-ones submarinos de Avilés. Informe final área LIFE+INDEMARES (LIFE07/NAT/E/000732). IEO. Coordinación: Fundación Biodiversidad, Madrid, 243 pp.
Jouanneau J.M., Weber O., Champilou N., et al. 2008. Recent sedimentary study of the shelf of the Basque country. J. Mar. Sys. 72: 397-406.
https://doi.org/10.1016/j.jmarsys.2007.03.013
Kaiser M.J., Edwards D.B., Armstrong P.J., et al. 1998. Changes in megafaunal benthic communities in different habitats after trawling disturbance. ICES J. Mar. Sci. 55: 353-361.
https://doi.org/10.1006/jmsc.1997.0322
Kaiser M.J., Clarke K.R., Hinz H., et al. 2006. Global analysis and recovery of benthic biota to fishing. Mar. Ecol. Prog. Ser. 311: 1-14.
https://doi.org/10.3354/meps311001
Kenchington E., Lirette C., Cogswell A., et al. 2010. Delineating Coral and Sponge Concentrations in the Biogeographic Regions of the East Coast of Canada Using Spatial Analyses. DFO Canadian Scientific Advisory Secretariat Research Document 2010/041. iv + 207 pp.
Kenchington E., Murillo F.J., Cogswell A., et al. 2011. WG on the ecosystem approach to fisheries management Serial No. N6005 NAFO SCR Doc. 11/75.
Kenchington E., Murillo F.J., Lirette C., et al. 2014. Kernel Density Surface Modelling as a Means to Identify Significant Concentrations of Vulnerable Marine Ecosystem Indicators. PLoS ONE 9: e109365.
https://doi.org/10.1371/journal.pone.0109365
Langton R.W., Langton E.W., Theroux R.B., et al. 1990. Distribution, behavior and abundance of sea pens, *Pennatula aculeata*, in the Gulf of Maine. Mar. Biol. 107: 463-469.
https://doi.org/10.1007/BF01313430
López-González P.J., Gili J.M., Williams G.C. 2001. New records of Pennatulacea (Anthozoa: Octocorallia) from the African Atlantic coast, with description of a new species and a zoogeographic analysis. Sci. Mar. 65: 59-74.
https://doi.org/10.3989/scimar.2001.65n159
López-Jamar E., Cal R.M., González G., et al. 1992. Upwelling and outwelling effects on the benthic regime of the continental shelf off Galicia, NW Spain. J. Mar. Res. 50: 465-488.
https://doi.org/10.1357/002224092784797584
MacDonald D.S., Little M., Eno N.C., et al. 1996. Disturbance of benthic species by fishing activities: a sensitivity index. Aquat. Conserv. 6: 257-268.
https://doi.org/10.1002/(SICI)1099-0755(199612)6:4<257::AID-AQC194>3.0.CO;2-7
MAGRAMA (Ministerio de Agricultura, Alimentación y Medio Ambiente). 2012. Estrategia Marina para la demarcación marina noratlántica, parte IV: descriptores del buen estado ambiental, descriptor 1: biodiversidad. Evaluación inicial y buen estado ambiental.
http://www.magrama.gob.es/es/costas/temas/estrategias-marinas/em_noratlantica.aspx.
Manuel R.L. 1981. British Anthozoa. Synopses of the British Fauna (New Series). No 18. Linnean Society Academic Press, Lon-

don, 241 pp.
NOAA. 2014. Deep Sea Coral Research and Technology Program 2014 Report to Congress. NOAA, Silver Spring, MD. 54 pp.
Ocaña A., Sánchez-Tocino L., López-González P.J. 2000. Consideraciones faunística y biogeográficas de los antozoos (Cnidaria: Anthozoa) de la costa de Granada (Mar de Alborán). Zool. Baetica 11: 51-65.
Olaso I. 1990. Distribución y abundancia del megabentos invertebrado en fondos de la plataforma cantábrica. Ph.D. thesis, Inst. Esp. Oceanogr.
OSPAR. 2000. Quality Status Report 2000. Region IV- Bay of Biscay and Iberian coast. OSPAR Commission, London, 123 pp.
OSPAR. 2008. Case Reports for the OSPAR List of Threatened and/or Declining Species and Habitats. OSPAR Commission, London, 261 pp.
OSPAR. 2010. Background document for seapen and borrowing megafauna communities. OSPAR Commission, London, 27 pp.
Palmer M.W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. Ecology 74: 2215-2230.
https://doi.org/10.2307/1939575
Pirtle J.L. 2005. Habitat-based assessment of structure-forming megafaunal invertebrates and fishes on Cordell Bank, California. Ph.D. thesis, Univ. Washington, 74 pp.
Porporato E.M., Mangano M.C., De Domenico F., et al. 2014. First observation of *Pteroeides spinosum* (Anthozoa: Octocorallia) fields in a Sicilian coastal zone (Central Mediterranean Sea). Mar. Biodiv. 44: 589-592.
https://doi.org/10.1007/s12526-014-0212-9
Punzón A., Hernández C., Abad E., et al. 2010. Spanish otter trawl fisheries in the Cantabrian Sea. ICES J. Mar. Sci. 67: 1-13.
https://doi.org/10.1093/icesjms/fsq085
R Development Team. 2014. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
http://www.R-project.org/
Sánchez F., Olaso I. 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem. Ecol. Model. 172: 151-174.
https://doi.org/10.1016/j.ecolmodel.2003.09.005
Sánchez F., Serrano A., Gómez Ballesteros A.M. 2009. Photogrammetric quantitative study of habitat and benthic communities of deep Cantabrian Sea hard grounds. Cont. Shelf Res. 29: 1174-1188.
https://doi.org/10.1016/j.csr.2009.01.004
Sardá R., Rossi S., Martí X., et al. 2012. Marine benthic cartography of the Cap de Creus (NE Catalan Coast, Mediterranean Sea). Sci. Mar. 76: 159-171.
https://doi.org/10.3989/scimar.03101.18D
Serrano A., Sánchez F., García-Castrillo G. 2006. Epibenthic communities of trawlable grounds of the Cantabrian Sea. Sci. Mar. 70: 149-159.
https://doi.org/10.3989/scimar.2006.70s1149
Thrush S.F., Dayton K. 2002. Disturbance to Marine Benthic Habitats by trawling and Dredging: Implications for Marine Biodiversity. Ann. Rev. Ecol. Syst. 33: 449-473.
https://doi.org/10.1146/annurev.ecolsys.33.010802.150515
Tixier-Durivault A., d'Hondt M.J. 1975. Les Octocoralliaires de la campagne Biaçores. Bull. Mus. Natn. Hist. Nat. Paris, Zool. 174: 1361-1433.
Vergnon R., Blanchard F. 2006. Evaluation of trawling disturbance on macrobenthic invertebrate communities in the Bay of Biscay, France: Abundance Biomass Comparison (ABC method). Aquat. Living Resour. 19: 219-228.
https://doi.org/10.1051/alr:2006022
Williams G.C. 1990. The Pennatulacea of Southern Africa (Coelenterata, Anthozoa). Ann. S. Afr. Mus. Cape Town 99: 31-119.
Williams G.C. 2011. The Global Diversity of Sea Pens (Cnidaria: Octocorallia: Pennatulacea). PloS ONE 6: e22747.
https://doi.org/10.1371/journal.pone.0022747
Williams G.C. 2014. Pennatulacea. In: Costello M.J., Bouchet P., et al. 2014. European Register of Marine Species. Accessed on 2014-11-21 at
http://www.marbef.org/data/aphia.php?p=taxdetails&id=1367

SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article and at the following link: http://scimar.icm.csic.es/scimar/supplm/sm04359esm.pdf

Table S1. – Pennatulacea occurring in the southern sector of the Bay of Biscay (off Spain) south of the 44°N parallel and Galicia after a review of the literature contrasting with our results in the study area from 1995-2010 (* data collected from 2008-2014). Only references with the shallow-most and deep-most data included.

Table S2. – Species composition of the aggregations of *F. quadrangularis* on circalittoral and upper bathyal soft bottoms and of *Pennatula* spp. on circalittoral soft bottoms. Taxon: A, ascidian; C, cnidarian; CR, crustacean; E, echinoderm; M, mollusc, P, polychaete worm; S, sponge. Species: * species that occur in the aggregations of *F. quadrangularis* on circalittoral soft bottoms but not in the upper bathyal soft bottoms; ** species that occur in the aggregations of *F. quadrangularis* on bathyal soft bottoms but not on circalittoral soft bottoms; *** species that occur in the aggregations of *Pennatula* spp. on circalittoral soft bottoms but not in the aggregations of *F. quadrangularis* on circalittoral soft bottoms. %: percentage of frequency of occurrence (occurs in 81-100% of the samples (•••••), 61-80% (••••), 41-60% (•••), 21-40% (••) and 1-20% (•)). D: density (col/haul): A (>1000/haul), C (100-999/haul), F (10-99/haul) and O (1-9/haul). Abbreviations used in Figure 4 appear in brackets after the species name.

Fig. S1. – Mantel correlogram for the abundance data of aggregations as a function of the geographic distance classes among the study locations. The black squares indicate significant spatial correlation.

Fig. S2. – Species accumulation curve for the locations with density at or above the threshold 10.5 sea pens/haul of *F. quadrangularis* and *Pennatula* spp.

Scientia Marina 81(3)
September 2017, S1-S4, Barcelona (Spain)
ISSN-L: 0214-8358

Sea pen (Pennatulacea) aggregations on the northern Spanish shelf: distribution and faunal assemblages

Susana Ruiz-Pico, Alberto Serrano, Antonio Punzón, Álvaro Altuna,
Olaya Fernández-Zapico, Francisco Velasco

Supplementary material

Table S1. – Pennatulacea occurring in the southern sector of the Bay of Biscay (off Spain) south of the 44°N parallel and Galicia after a review of the literature contrasting with our results in the study area from 1995-2010 (* data collected from 2008-2014). Only references with the shallow-most and deep-most data included.

Species	Depth range (m)	References	Depth range (m) Present study
Suborder Sessiliflorae Kükenthal, 1915			
Anthoptilum grandiflorum (Verrill, 1879)	1400	Louzao et al. (2010)	
Cavernularia pusilla (Philippi, 1835)	25-100	Rallo et al. (1988), Altuna et al. (2008)	
Funiculina quadrangularis (Pallas, 1766)	100-468	Altuna (1994), Louzao et al. (2010)	84-793
Kophobelemnon stelliferum (Müller, 1776)	151-1005	Rallo et al. (1993), Altuna (1994)	
Protoptilum thomsoni Kölliker, 1872	790-1200	Louzao et al. (2010)	
Umbellula lindahli Kölliker, 1874	896-2320	Gourret (1906), Thomson (1927)	
Veretillum cynomorium (Pallas, 1766)	15-75	Thomson (1929), Altuna (1994)	50-373
Suborder Subselliflorae Kükenthal, 1915			
Pennatula aculeata Danielssen, 1860	161-1225	Gourret (1906), Louzao et al. (2010)	793-811*
Pennatula grandis Ehrenberg, 1834	1228-1980	Grasshoff (1982), unpublished data	
Pennatula phosphorea Linnaeus, 1758	112-135	Grasshoff (1982), Paulmier (1997)	133-366*
Pteroeides spinosum (Ellis, 1764)	60-208	Thomson (1927), Urgorri et al. (2011)	50-296
Virgularia mirabilis (Müller, 1776)	3.7-468	Cacabelos et al. (2009), Louzao et al. (2010)	
Virgularia tuberculata Marshall, 1883	No data		

Table S2. – Species composition of the aggregations of *F. quadrangularis* on circalittoral and upper bathyal soft bottoms and of *Pennatula* spp. on circalittoral soft bottoms. Taxon: A, ascidian; C, cnidarian; CR, crustacean; E, echinoderm; M, mollusc, P, polychaete worm; S, sponge. Species: * species that occur in the aggregations of *F. quadrangularis* on circalittoral soft bottoms but not in the upper bathyal soft bottoms; ** species that occur in the aggregations of *F. quadrangularis* on bathyal soft bottoms but not on circalittoral soft bottoms; *** species that occur in the aggregations of *Pennatula* spp. on circalittoral soft bottoms but not in the aggregations of *F. quadrangularis* on circalittoral soft bottoms. %: percentage of frequency of occurrence (occurs in 81-100% of the samples (•••••), 61-80% (••••), 41-60% (•••), 21-40% (••) and 1-20% (•)). D: density (col/haul): A (>1000/haul), C (100-999/haul), F (10-99/haul) and O (1-9/haul). Abbreviations used in Figure 4 appear in brackets after the species name.

F. quadrangularis on circalittoral				*F. quadrangularis* on upper bathyal				*Pennatula* spp. on circalittoral			
Taxon	Species	%	D	Taxon	Species	%	D	Taxon	Species	%	D
C	*Funiculina quadrangularis* (Fqua)	•••••	C	C	*Funiculina quadrangularis* (Fqua)	•••••	F	C	*Pennatula* spp. (Penn)	•••••	F
CR	*Macropodia longipes*(Mlon)	•••••	O	M	*Rossia macrosoma* (Rmac)	•••••	O	E	*Astropecten irregularis*(Airr)	•••••	F
E	*Astropecten irregularis*(Airr)	•••••	F	E	*Astropecten irregularis*(Airr)	•••••	F	M	*Eledone cirrhosa* (Ecirr)	•••••	F
M	*Eledone cirrhosa* (Ecirr)	•••••	O	CR	*Munida sarsi* (Msar)	•••••	A	M	*Sepia elegans* (Sele)	•••••	O
C	*Actinauge richardi* (Aric)	••••	O	M	*Eledone cirrhosa* (Ecirr)	••••	O	CR	*Liocarcinus depurator* (Ldep)	••••	O
CR	*Pagurus prideaux* (Ppri)	•••	F	CR	*Macropipus tuberculatus* (Mtub)	••••	C	M	*Sepiola* sp. (Sepi)	••••	F
CR	*Liocarcinus depurator* (Ldep)	•••	F	CR	*Macropodia longipes*(Mlon)	••••	O	M	*Sepia orbignyana* (Sorb)	•••	O
M	*Sepia elegans* (Sele)*	•••	O	E	*Ophiura ophiura* (Ooph)	•••	F	M	*Calliostoma granulatum* (Cgran)	•••	O
E	*Ophiura ophiura* (Ooph)	•••	O	M	*Sepietta oweniana* (Sowe)	•••	O	CR	*Munida intermedia* (Mint)	•••	O
E	*Parastichopus regalis* (Preg)	•••	O	C	*Actinauge richardi* (Aric)	•••	O	CR	*Pagurus prideaux* (Ppri)	•••	F
M	*Rossia macrosoma* (Rmac)	•••	O	CR	*Liocarcinus depurator* (Ldep)	•••	O	M	*Octopus vulgaris* (Ovul)	•••	O
E	*Leptometra celtica* (Lcel)	•••	F	CR	*Pontophilus spinosus* (Pspi)	•••	O	E	*Parastichopus regalis* (Preg)	•••	O
C	*Hydrozoa* (Hydr)	••	O	M	*Scaphander lignarius* (Slig)	•••	O	M	*Scaphander lignarius* (Slig)	•••	O
M	*Octopus salutti* (Osal)	••	O	CR	*Munida intermedia* (Mint)	••	O	M	*Sepietta oweniana* (Sowe)	•••	O
M	*Sepia orbignyana* (Sorb)	••	O	CR	*Nephrops norvegicus*(Nnor)	••	O	CR	*Macropodia longipes*(Mlon)	••	O
CR	*Munida intermedia* (Mint)	••	F	M	*Octopus salutti* (Osal)	••	O	M	*Neptunea contraria* (Ncon)	••	O
CR	*Munida sarsi* (Msar)	••	O	E	*Parastichopus regalis* (Preg)	••	O	CR	*Pagurus excavatus* (Pexc)	••	O
CR	*Scalpellum scalpellum* (Scal)	••	O	M	*Sepiola* sp. (Sepi)	••	F	CR	*Pagurus alatus* (Pala)***	••	O
M	*Calliostoma granulatum* (Cgran)	••	O	E	*Anseropoda placenta* (Apla)	••	O	CR	*Pontophilus spinosus* (Pspi)	••	O
E	*Ophiotrix fragilis*(Ofra)	••	O	M	*Bathypolipus sponsalis* (Bspo)**	••	O	P	*Aphrodita aculeata* (Aacu)***	•	O
M	*Sepiola* sp. (Sepi)	••	O	M	*Neptunea contraria* (Ncon)	••	O	M	*Charonia lampas* (Clam)	•	O
E	*Gracilechinus acutus* (Gacu)	••	O	CR	*Pagurus alatus*(Pala)**	••	O	CR	*Galathea intermedia* (Gint)	•	O
CR	*Macropipus tuberculatus* (Mtub)	•	O	E	*Parastichopus tremulus* (Ptre)**	••	O	E	*Leptometra celtica* (Lcel)	•	F
C	*Pennatula* spp. (Penn)*	•	O	CR	*Philocheres equinulatus* (Pech)**	••	O	M	*Euspira fusca* (Efus)	•	O
E	*Anseropoda placenta* (Apla)	•	O	M	*Ranella olearium* (Role)	•	O	CR	*Nephrops norvegicus*(Nnor)	•	O
CR	*Pagurus excavatus* (Pexc)*	•	O	E	*Asteronyx loveni* (Alov)**	•	O	E	*Ophiura ophiura* (Ooph)	•	O
M	*Scaphander lignarius* (Slig)	•	O	M	*Buccinum* sp. (Bucc)**	•	O	M	*Rondeletiola minor* (Rmin)	•	F
M	*Galeodea rugosa* (Grug)	•	O	M	*Calliostoma granulatum* (Cgran)	•	O	M	*Rossia macrosoma* (Rmac)	•	O
M	*Euspira fusca* (Efus)*	•	O	M	*Colus gracilis* (Cgra)**	•	O	C	*Actinauge richardi* (Aric)	•	O
CR	*Nephrops norvegicus*(Nnor)	•	O	A	*Diazona violacea* (Dvio)**	•	O	A	*Corella parallelogramma* (Cpar)	•	O
M	*Octopus vulgaris* (Ovul)*	•	O	C	*Epizoanthus incrustatus* (Einc)**	•	F	E	*Echinus melo* (Emel)***	•	O
CR	*Pontophilus spinosus* (Pspi)	•	O	CR	*Galathea intermedia* (Gint)	•	O	C	*Funiculina quadrangularis* (Fqua)	•	O
M	*Sepietta oweniana* (Sowe)	•	O	M	*Galeodea rugosa* (Grug)	•	O	CR	*Goneplax rhomboides* (Grho)	•	O
A	*Corella parallelogramma* (Cpar)*	•	O	E	*Gracilechinus acutus* (Gacu)	•	O	E	*Gracilechinus acutus* (Gacu)	•	O
CR	*Galathea intermedia* (Gint)	•	O	C	*Hydrozoa* (Hydr)	•	O	P	*Hyalinoecia tubicola* (Htub)	•	O
S	*Phakelia ventilabrum* (Pven)*	•	O	CR	*Inachus dorsettensis* (Idor)**	•	O	CR	*Macropipus tuberculatus* (Mtub)	•	O
M	*Ranella olearium* (Role)	•	O	E	*Leptometra celtica* (Lcel)	•	O	CR	*Munida sarsi* (Msar)	•	O
M	*Rondeletiola minor* (Rmin)	•	O	CR	*Munida iris* (Miri)	•	O	M	*Octopus salutti* (Osal)	•	O
M	*Sepia officinalis*(Soff)*	•	O	E	*Ophiotrix fragilis*(Ofra)	•	O	S	*Phakelia ventilabrum* (Pven)	•	F
P	*Hyalinoecia tubicola* (Htub)*	•	O	CR	*Pagurus prideaux* (Ppri)	•	O	S	*Alcyonium palmatum* (Apal)***	•	O
CR	*Inachus leptochirus* (Idor)*	•	O	M	*Rondeletiola minor* (Rmin)	•	O	CR	*Cancer pagurus* (Cpag)	•	O
E	*Luidia ciliaris* (Lcil)*	•	O	CR	*Scalpellum scalpellum* (Scal)	•	O	C	*Caryophyllia smithii* (Csmi)	•	O
E	*Luidia sarsi* (Lsar)*	•	O	M	*Sepia orbignyana* (Sorb)	•	O	E	*Echinocardium cordatum* (Ecor)	•	O
CR	*Munida iris* (Miri)	•	O					M	*Galeodea rugosa* (Grug)	•	O
M	*Neptunea contraria* (Ncon)	•	O					CR	*Homarus gammarus* (Hgra)***	•	O
M	*Neopygnodonte cochlear* (Ncoc)*	•	O					CR	*Inachus dorsettensis* (Idor)***	•	O
E	*Brissopsis lyrifera* (Blyr)*	•	O					CR	*Inachus leptochirus*(Ilep)	•	O
CR	*Cancer pagurus*(Cpag)*	•	O					E	*Luidia sarsi* (Lsar)	•	O
C	*Caryophyllia smithii* (Csmi)*	•	O					E	*Marthasterias gracialis* (Mgla)	•	O
M	*Charonia lampas* (Clam)*	•	O					M	*Ranella olearium* (Role)	•	O
C	*Dendrophyllia cornigera* (Dcor)*	•	O					CR	*Scalpellum scalpellum* (Scal)	•	O
E	*Echinocardium cordatum* (Ecor)*	•	O								
CR	*Goneplax rhomboides* (Grho)*	•	O								
E	*Marthasterias glacialis* (Mgla)*	•	O								
CR	*Polycheles typhlops* (Ptyp)*	•	O								
M	*Pseudosimnia carnea* (Pcar)*	•	O								

REFERENCES

Altuna, Á. 1994. Estudio faunístico, ecológico y biogeográfico de los cnidarios bentónicos de la costa vasca. Ph.D. thesis, Univ Navarra, 769 pp.

Altuna Á., Aguirrezabalaga F., Martínez J. 2008. An exceptional occurrence of *Cavernularia pusilla* (Anthozoa: Pennatulacea) off the Basque coast (south-east Bay of Biscay, north-eastern Atlantic). Mar. Biodivers. Rec. 1(e 29): 1-3

Cacabelos E., Gestoso L., Troncoso J. S. 2009. Inventario de la macrofauna bentónica de sustratos blandos de la Ensenada de San Simón (NO España). Bol. R. Soc. Esp. His. Nat. (Secc. Biol.). 103: 103-119.

Gourret P. 1906. *Alcyonium palmatum*, *Funiculina quadrangularis*, *Pennatula aculeata*, *Kophobelemnon stelliferum*, *Isis* (*Mopsea*) *elongata*, *Muricea paucituberculata*, *Plexaura desiderata*, *Umbellula ambigua*. In: Marion A.F., Étude des Coelentérés atlantiques recueillies par la Commission de dragages de l'aviso le Travailleur durant les campagnes 1880 et 1881. Exp. Scient. Travailleur et Talisman, Paris, pp. 143-147.

Grasshoff M. 1982. Die Gorgonaria, Pennatularia und Antipatharia des Tiefwassers der Biscaya (Cnidaria, Anthozoa). II.-Taxonomischer Teil. Bull. Mus. Natn. Hist. Nat. Paris. (4)3(A) 4: 941-978.
Louzao M., Anadón N., Arrontes J., Álvarez-Claudio C., Fuente M., Ocharán F., Anadón A., Acuña J.L. 2010. Historical macrobenthic community assemblages in the Avilés Canyon, N Iberian Shelf: baseline biodiversity information for a marine protected area. J. Mar. Syst. 80 : 47-56.
Paulmier G. 1997. Atlas des invertébrés du Golfe de Gascogne inventoriés dans les captures des chaluts-campagnes Ressgasc 1992–1995 et Evhoe 1995. Ifremer. L'Houmeau, 100 pp, pl. 117.
Rallo A., García-Arberas L., Isasi I. 1993. Fauna macrobéntica de los fondos del cañón de Capbretón: análisis faunístico de poliquetos, crustáceos y cnidarios y caracterización de puntos de muestreo según estos descriptores. Cah. Biol. Mar. 35: 69-90.
Rallo A., Gorostiaga J.M., Saiz J.I., Isasi I. 1988. Comunidades bentónicas del Abra de Bilbao y su entorno. Cah. Biol. Mar. 29: 3-19.
Thomson J.A. 1927. Alcyonaires provenant des campagnes scientifiques du Prince Albert Ier de Monaco. Résult. Camp. Scient. Prince Albert Ier. 73: 1-77, pl. 1-6.
Thomson J.A. 1929. Alcyonaires des environs de Monaco et de localités diverses. Bull. Inst. Océanogr. Monaco. 534: 1-10.
Urgorri V., Díaz-Agras G., Besteiro C., Montoto G. 2011. Additions to the inventory of *Mollusca Opisthobranchia* of Galicia (NW Iberian Peninsula). Thalassas. 27: 77-100.

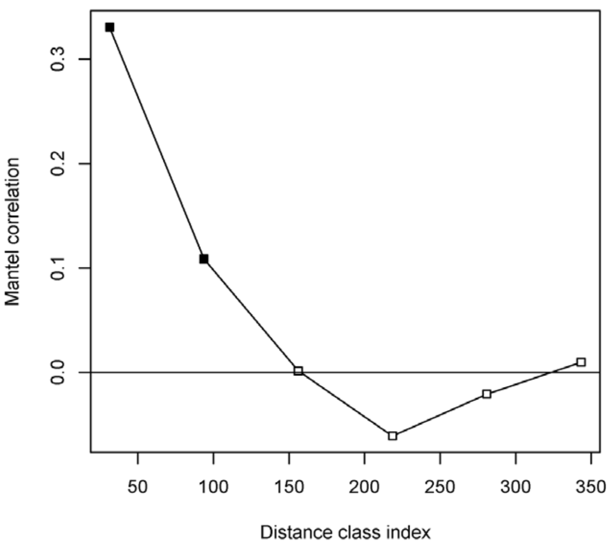

Fig. S1. – Mantel correlogram for the abundance data of aggregations as a function of the geographic distance classes among the study locations. The black squares indicate significant spatial correlation.

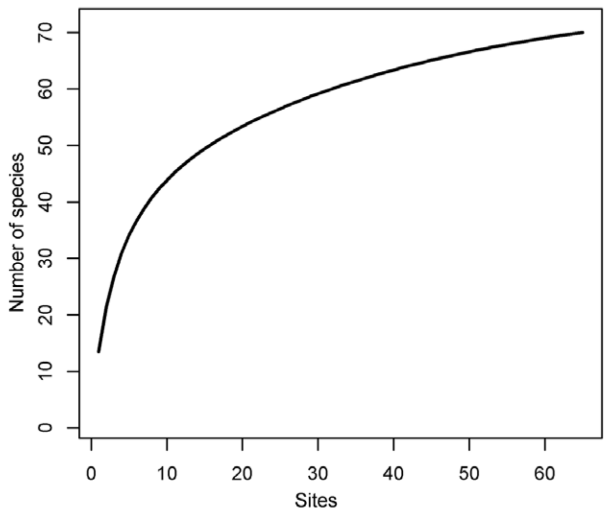

Fig. S2. – Species accumulation curve for the locations with density at or above the threshold 10.5 sea pens/haul of *F. quadrangularis* and *Pennatula* spp.