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Improving the sampling efficiency of benthic species and communities using complementary gears: beam trawl and bottom trawl

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Abstract

Benthic species and habitats are receiving increasing attention in the framework of European regulations such as the Marine Strategy Framework Directive (MSFD) and the implementation of the Ecosystem Approach to Fisheries Management by the current European Union Common Fishery Policy. As a consequence, scientific surveys initially designed to assess demersal resources, like MEDITS, have broadened over the years from demersal species and their communities to benthic ones. At the same time, in the framework of the MSFD, new specific surveys have also started to properly identify and characterize benthic communities. This work aims to compare the efficiency of Jennings beam trawl (BT) and the experimental bottom trawl GOC-73, to sample epibenthic and nectobenthic species and communities. Thus, data from MSFD surveys were compared to data from MEDITS surveys in the Levantine-Balearic demarcation (western Mediterranean Sea). The Jennings BT provides better estimations of density and species richness for small species closely associated with the seabed and the GOC-73 of the occurrence of some macroepibenthic species presenting low abundance. The GOC-73 allows for higher spatial coverage, but the Jennings BT gives more precise information on the location of benthic species and the patchy distribution of benthic habitats. Although sampling was performed in the same habitats, an important fraction of the species was collected exclusively using one or the other sampling gear. Both sampling methods provide complementary information that improves biodiversity estimations and the description of benthic habitats, allowing a better future assessment of the anthropogenic impact, hence improving the objectives of the MSFD.

Keywords: benthic habitats; epibenthic species; nectobenthic species; Jennings beam trawl; experimental bottom trawl GOC-73; sampling efficiency.

Introduction

The studies of benthic habitats are of high relevance for the conservation of marine ecosystems and the sustainability of their living resources. The implementation of the Ecosystem Approach to Fisheries Management (EAFM) by the current European Union Common Fishery Policy (CFP) and other European regulations, such as the Marine Strategy Framework Directive (MSFD; 2008/56/EC) has increased the interest in conservation studies. For instance, two of the 11 descriptors that the MSFD uses for the assessment of Good Environmental Status (GES) are related to benthic habitats: Descriptor 1 (Biodiversity) and Descriptor 6 (Seafloor integrity). Common methodologies and indicators are currently being developed to explore the status of benthic habitats and the physical damage caused by human activities on benthic communities. Some examples are the indicators *Sentinels of the Seabed* and the *Extent of Physical Damage to Predominant Seafloor Habitat* (Elliott *et al*., 2018; Serrano *et al*., 2022). On the other hand, the EAFM aims to identify all the habitats used by humans, assessing the anthropogenic impact thereon and identifying those habitats that are critical to particular species for key ecological processes at the population level (Pikitch *et al*., 2004). Moreover, the application of EAFM requires the protection of a substantial portion of marine ecosystems from fishing impacts, so that they can serve as biodiversity reserves and reference sites (Hilborn, 2004).

In the Mediterranean Sea, within the framework of the Barcelona Convention, two common indicators have been proposed for the assessment of Ecological Objective 1 related to biodiversity: the habitat distributional range and the condition of the habitat's typical species and communities (UNEP/MAP, 2016). For the CFP and the General Fisheries Commission for the Mediterranean, Sensitive Habitats, Essential Fish Habitats, and Vulnerable Marine Ecosystems are important concepts for management (STECF, 2006; GFCM, 2019, 2022). Sensitive Habitats are fragile habitats of a high diversity that are ecologically relevant and require special protection. Essential Fish Habitats are considered essential to the development of critical phases of fishery resources whose protection enhances fishery stocks (Benaka, 1999). This is the case of the Sensitive Habitats and Essential Fish Habitats of crinoids, maërl/rhodoliths, and *Peyssonnelia* beds (Colloca *et al*., 2004; Ordines *et al*., 2009, 2015). The Council Regulation (EC) Nº 1967/2006, of 21 December 2006, concerning management measures for the sustainable exploitation of fishery resources in the Mediterranean Sea, protects the maërl/rhodoliths beds. Vulnerable Marine Ecosystems constitute areas that may be vulnerable to impacts from fishing activities; for instance, some species, like the bamboo coral *Isidella elongata,* have been acknowledged as indicator species of Vulnerable Marine Ecosystems due to their vulnerability to bottom trawling (Appendix 17 of the report of the forty-second session of the FAO-GFCM; Resolution GFCM/43/2019/6).

The identification, characterization, and mapping of benthic biocenoses contribute to fisheries management guaranteeing the preservation of biodiversity and the sustainability of fisheries, through a spatio-temporal organization of the fishing effort, based on the presence of certain habitats and their conservation status. However, the estimation of the indicators necessary for this purpose requires good quality data, based on the appropriate sampling of benthic species. The study of the structure and distribution of epibenthic communities has been historically hampered by the challenges associated with the quantitative sampling of epibenthic species, which is influenced by their small-scale, patchy distribution, depth range, ground attachment, substrate type, bottom currents, but also by the lack of information on the efficiency of sampling gears (Wennhage *et al.*,1997; Jennings *et al*., 1999; Reiss *et al*., 2006).

Since it started in 1994, the MEDITS bottom trawl survey program has represented the most important data source in the Mediterranean Sea supporting the evaluation of demersal resources, through population and community indicators, and the assessment and simulation models based on fishery-independent data (Spedicato *et al.*, 2019). MEDITS surveys are included in the Data Collection Framework (DCF), whose original regulatory framework (the Council Regulation (EC) Nº 199/2008, of 25 February 2008, concerning the establishment of a community framework for the collection, management, and use of data in the fisheries sector, and support for scientific advice regarding the CFP), establishes that research surveys at sea must provide information not only to evaluate the abundance and distribution of fisheries stocks, independently of the data provided by commercial fisheries, but also to assess the impact of the fishing activity on the environment. Within this context, the scope of MEDITS surveys has broadened over the years, from the demersal species and their communities to the benthic ones (Stamouli *et al*., 2022). MEDITS bottom trawl survey program has faced new challenges, such as the identification of Sensitive Habitats and Essential Fish Habitats, also providing new scientific insights linked to the MSFD (e.g., biodiversity, trophic webs, allochthonous species, and litter), the EAFM, and even the Marine Spatial Planning (Spedicato *et al*., 2019).

In Spain, the MEDITS surveys are an important source of data and samples for the MSFD. These data are being used to estimate indicators of the conservation status of benthic habitats. However, the experimental bottom trawl gear used in MEDITS surveys, the GOC-73, was designed to sample efficiently a great variety of macrobenthic and nectobenthic species (Bertrand *et al*., 2002; Fiorentini *et al*., 1999; Dremière *et al*., 1999). To improve the sampling of benthic species and communities, new research surveys have been conducted in the MSFD using a beam trawl. This work aims to compare the sampling efficiency of these gears to sample epibenthic and nectobenthic species and communities. Data on the abundance and biomass of the main taxonomic groups and habitat-forming species were compared for this purpose.

Materials and Methods

Study area

Within the MSFD, the Spanish marine environment is divided into five marine demarcations, based on their general biogeographic, oceanographic, and hydrological characteristics (Bellas, 2014). Our study area is the Levantine-Balearic (LEBA) demarcation, situated in the western Mediterranean Sea, and includes the Mediterranean coast of the Iberian Peninsula from Cabo de Gata to Cap de Creus and the Balearic Islands (Fig. 1). The LEBA covers around 2400 km of coastline and is subject to high anthropogenic pressure, with high fishing activity, especially in the continental shelf (López-Jurado *et al*., 2012; Serrano *et al.*, 2012).

There are some peculiarities in the different areas of the LEBA demarcation. The waters surrounding the Balearic Islands, for example, are characterized by pronounced oligotrophy, while the continental coast has higher primary productivity and a large number of terrigenous bottoms from river discharge, with a wide continental shelf in its central part (Estrada, 1996; Siokou-Frangou *et al*., 2010; Serrano *et al*., 2012). The Archipelago does not have any river discharge and, consequently, the sediments of its narrow continental shelf are mainly biogenic sands and gravels, with a high percentage of carbonates. Furthermore, whereas submarine canyons are scarce on the Balearic margin, they are abundant in the southern and northern parts of the continental margin of the LEBA demarcation.

Data source

MEDITS surveys

These surveys are performed annually during late spring and summer onboard the R/V *Miguel Oliver* (70 m long, 14.4 m wide, 2495 GT, and 2000 kW), covering

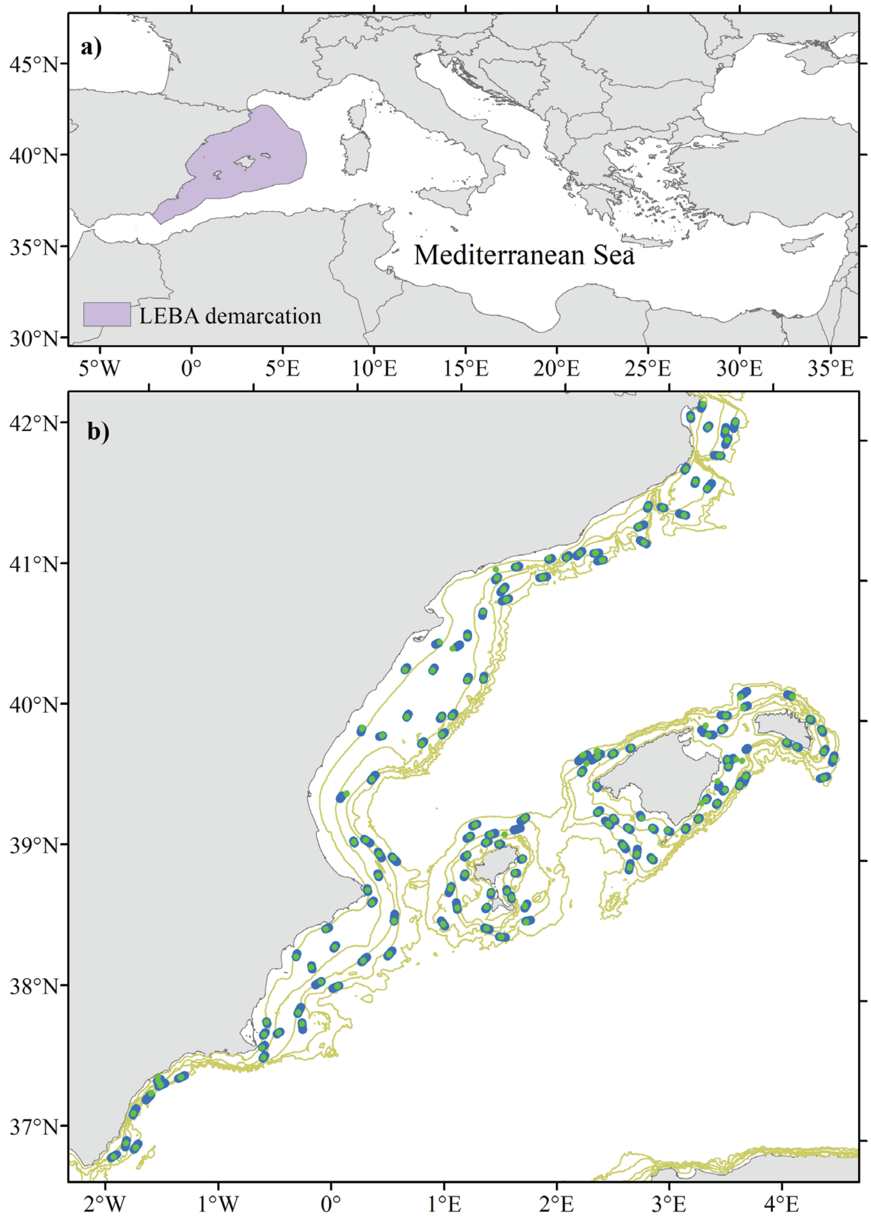

Fig. 1: Map of the study area showing: a) the LEBA demarcation, and b) the stations sampled with the Jennings beam trawl (green) and the experimental bottom trawl GOC-73 (blue), during CIRCA-LEBA and MEDITS surveys, respectively. The isobaths represent 50, 100, 200, 500 and 800 m depth.

a wide bathymetric range (30-800 m) along the Mediterranean waters of the Iberian Peninsula and around the Balearic Islands. The GOC-73 gear used in the MEDITS surveys is an experimental bottom trawl gear specifically designed for this sampling program. It is equipped with two Morgére otter boards, each one weighing 350 kg and with a surface of 2.5 m^2; 100 or 200 m sweeps, depending on the depth (<200 m and >200 m, respectively); 30 m bridles; and a net with average horizontal and vertical openings of 16-18 and 2.7-3.2 m, respectively; it is also equipped with a 10 mm diamond mesh codend. The fishing time (the time in which the gear is in contact with the bottom), and the behaviour of the net, in terms of horizontal and vertical openings, is measured using a MARPORT system. For more details about the sampling gear, see the MEDITS Handbook (MEDITS Working Group, 2017).

The sampling was conducted during daylight hours, with an effective duration of 30 and 60 minutes for stations above and below 200 m depth, respectively, and a towing speed ranging from 2.7 to 3.0 knots. The MEDITS surveys follow a depth-stratified random sampling scheme, with haul allocation proportional to the surface of depth strata (Bertrand *et al*., 2002; Spedicato *et al*., 2019): A (10-50 m), B (51-100 m), C (101-200 m), D (201-500 m) and E (501-800 m). Once onboard, the catches are sorted, identified to species level or the lowest possible taxonomic level, counted, and weighed.

MSFD surveys

Two research surveys, called CIRCA-LEBA, were conducted on November 2021 and 2022 onboard the

R/V *Ramon Margalef* (46 m long, 10.5 m wide, 988 GT, and 1800 kW) to sample epibenthic species in the LEBA demarcation. For this purpose, a standard beam trawl, described by Jennings *et al.* (1999), was used (hereafter called the Jennings BT). It is a small gear, with horizontal and vertical openings of 2 and 0.5 m, respectively, and a 5 mm diamond mesh codend; its sampling efficiency has been estimated by Reiss *et al*. (2006).

Sampling was conducted during daylight hours at the same stations previously covered during the MEDITS surveys. The effective duration of hauls varied between 2 and 15 minutes, depending on the depth, with towing speed ranging from 1.8 to 2.0 knots. The arrival and departure of the gear to the bottom were measured using a SCANMAR system. Once the capture was on board, specimens were sorted, identified to species level or the lowest possible taxonomic level, counted, and weighted.

Additionally, the HORUS photogrammetric benthic sled was deployed in the CIRCA-LEBA surveys, enabling underwater filming at depths of up to approximately 1000 m; it is equipped with a 4k resolution camera and parallel linear lasers. The sled captured high-quality video footage at a distance of 0.5 m from the seabed and an acquisition angle of 45º. The effective duration of video transects, conducted at a towing speed of around 0.5 knots, varied between 15 and 45 minutes, depending on the depth. Underwater recorded videos were georeferenced with a USBL (ultra-short baseline) acoustic beacon fixed to the sled structure, providing data through the vessel's HiPAP system. In each transect, the substrate type and benthic species were identified to the lowest taxonomic group and recorded with the OFOP (Ocean Floor Observation Protocol) software. Once ashore, the video footage was meticulously reviewed using OFOP to conduct a thorough analysis of species abundance. Georeferenced observations allowed for the calculation of individual densities of the species.

Comparative analysis

To compare the efficiency of the Jennings BT and the GOC-73 for sampling epibenthic and nectobenthic communities, data from the surveys CIRCA-LEBA-1121 and CIRCA-LEBA-1122 were compared with the corresponding stations from MEDITS surveys of 2021 and 2022 in the LEBA demarcation. A total number of 144 MEDITS stations and the corresponding CIRCA-LEBA stations were selected, based on their geographical position and depth (Table 1; Fig. 1). The samples obtained in stations shallower than 50 m corresponding to A stratum (7 MEDITS and 7 CIRCA-LEBA stations) were reassigned to B stratum because of the depth similarity (ranging from 38 to 47 m) and the species composition of samples. The total swept area by gear was one order of magnitude higher with the GOC-73 than with the Jennings BT, due to the characteristics of each sampling method (i.e., vertical and horizontal opening, velocity, and duration of hauls). The total swept area was 10650700 m^2 with the GOC-73 and 213184 m^2 with the Jennings BT.

For each gear, the abundance and biomass of each species in each sample were standardized to 250 m^2, taking into account the horizontal aperture of each gear and the distance covered in each station. Pelagic species were excluded from the analysis. We calculated the total species richness by main taxonomic group and gear, the mean species richness and density (biomass in the case of algae and sponges), and elaborated a list of the 10 most abundant species by main taxonomic group, depth stratum, and gear. The paired Mann-Whitney-Wilcoxon (WMW) test was used to compare the mean values between gears.

The analysis of similarity (ANOSIM) and the similarity percentage analysis (SIMPER; Clarke *et al*., 2014) were applied to test for differences in species composition between gears in each depth stratum and to identify which species contribute most to those differences, respectively. For these analyses, we used standardized biomass data because it allowed the inclusion of species belonging to the taxonomic groups algae and sponges. Similarity between samples was calculated using the Bray–Curtis index.

To compare gear performance in terms of biodiversity estimates we calculated the species accumulation curves using the 'random' method implemented in the *Specaccum* R software function. This method calculates the mean curve of species accumulation and their standard deviation, from random permutations of sampling stations (Gotelli & Colwell, 2001), allowing us to visualize the increase of species richness with sampling size (number of stations).

The abundance and biomasses of the most important structuring species previously detected in the area (Ruiz *et al*., 2012), were compared between the GOC-73 and the Jennings BT using the WMW test. All statistical analyses and tests were performed according to standard routines using R version 4.2.2 (www.r-project.org/) except

Table 1. Number of stations and total sampled area (in km^2) by depth stratum (B, 51-100 m; C, 101-200 m; D, 201-500 m and E, 501-800 m) and sampling gear (BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73).

Stratum	Stations (n)	BT	GOC
B	53	79142	2219300
C	32	38299	1720200
D	38	57673	4431000
E	21	38070	2280200

for ANOSIM and SIMPER analyses that were performed with the PRIMER-E 7 software (Clarke *et al*., 2014).

Finally, abundance per 250 m^2 of the habitat-forming species *Funiculina quadrangularis* and *Leptometra phalangium* were obtained from both the Jennings BT and the GOC-73 and from the photogrammetric sled in all the stations where they were present.

Results

Analysis at the community level

There were significantly higher values of abundance (or biomass for Porifera and Algae) estimated with the Jennings BT than the GOC-73: for nine out of 11 taxonomic groups (Algae, Ascidiacea, Bivalvia, Cnidaria, Crustacea, Echinodermata, Pisces, Gastropoda, and Porifera) in the B stratum; for eight out of 10 taxonomic groups (Ascidiacea, Bivalvia, Brachiopoda, Cnidaria, Crustacea, Echinodermata, Pisces, and Gastropoda) in the C stratum; for six out of 10 taxonomic groups (Bivalvia, Brachiopoda, Crustacea, Echinodermata, Gastropoda, and Porifera) in the D stratum; and for four out of 10 taxonomic groups (Bivalvia, Cephalopoda, Crustacea, and Echinodermata) in the E stratum (Fig. 2; Table S1). The most abundant taxonomic groups obtained with the Jennings BT were Crustacea, Echinodermata, Mollusca (both Gastropoda and Bivalvia), and Pisces, while for the GOC-73, they were Crustacea, Echinodermata, and Pisces.

There were also differences between sampling gears in the mean values of species richness (*S*) (Fig. 3; Table S2) that varied depending on the taxonomic group. Significantly higher *S* values were obtained with the Jennings BT than with the GOC-73 for Bivalvia in all strata, Crustacea in strata B–D, Echinodermata in strata C–E, Gastropoda in strata B-D and Porifera in stratum D. The GOC-73 only provided significantly higher values than the Jennings BT for Cephalopoda and Pisces in all strata. Mean *S* values did not show significant differences between gears for Ascidiacea in any strata. Taxonomic groups showing the highest *S* mean values for the Jennings BT were Crustacea, Pisces, and Echinodermata, while for the GOC-73, they were Crustacea, Pisces, and Cephalopoda.

After pooling data from both gears, we detected a total of 751 taxa from all samples (Table 2). Up to 595 taxa were detected in the Jennings BT samples, and 428 were detected in the GOC-73 samples. Only 36% of the total taxa identified were collected by both samplers, 43% were just collected with the Jennings BT and 21% with

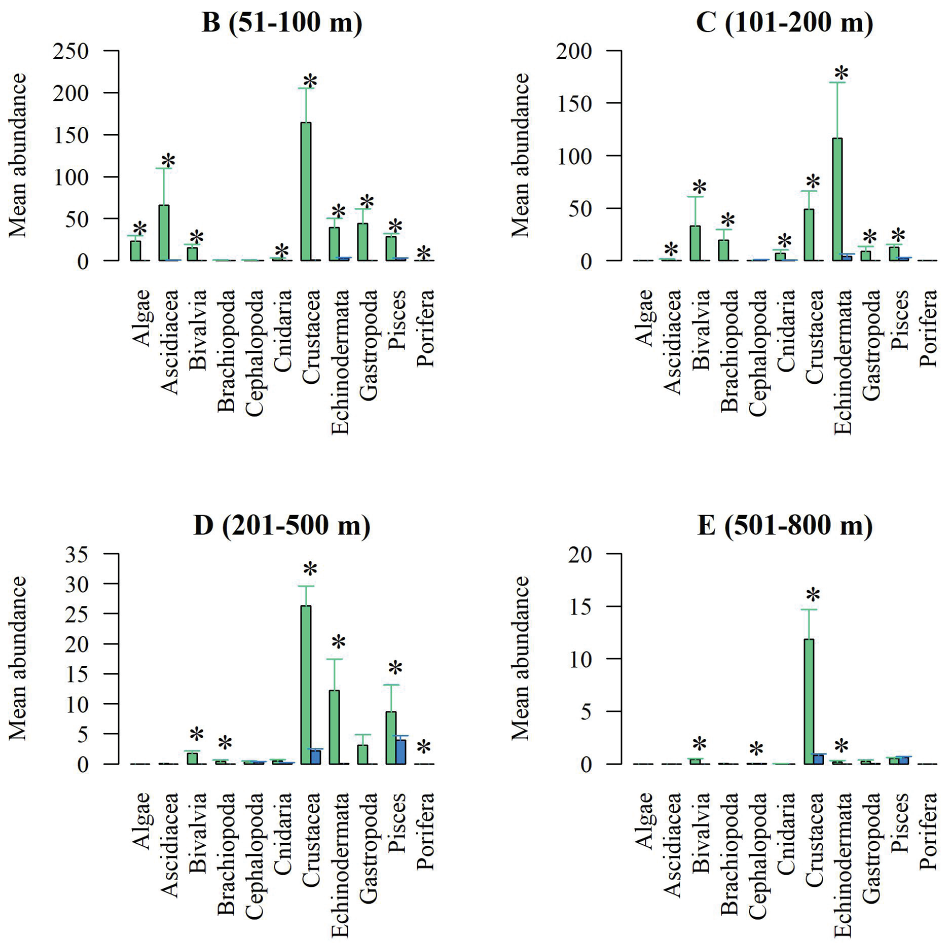

Fig. 2: Mean standardized abundance and standard error by taxonomic group and depth stratum. Values are abundance (individuals/250 m^2), for all groups, except Algae and Porifera, whose values are biomass (kg/250 m^2). Green and blue represent the Jennings beam trawl and the experimental bottom trawl GOC-73, respectively.

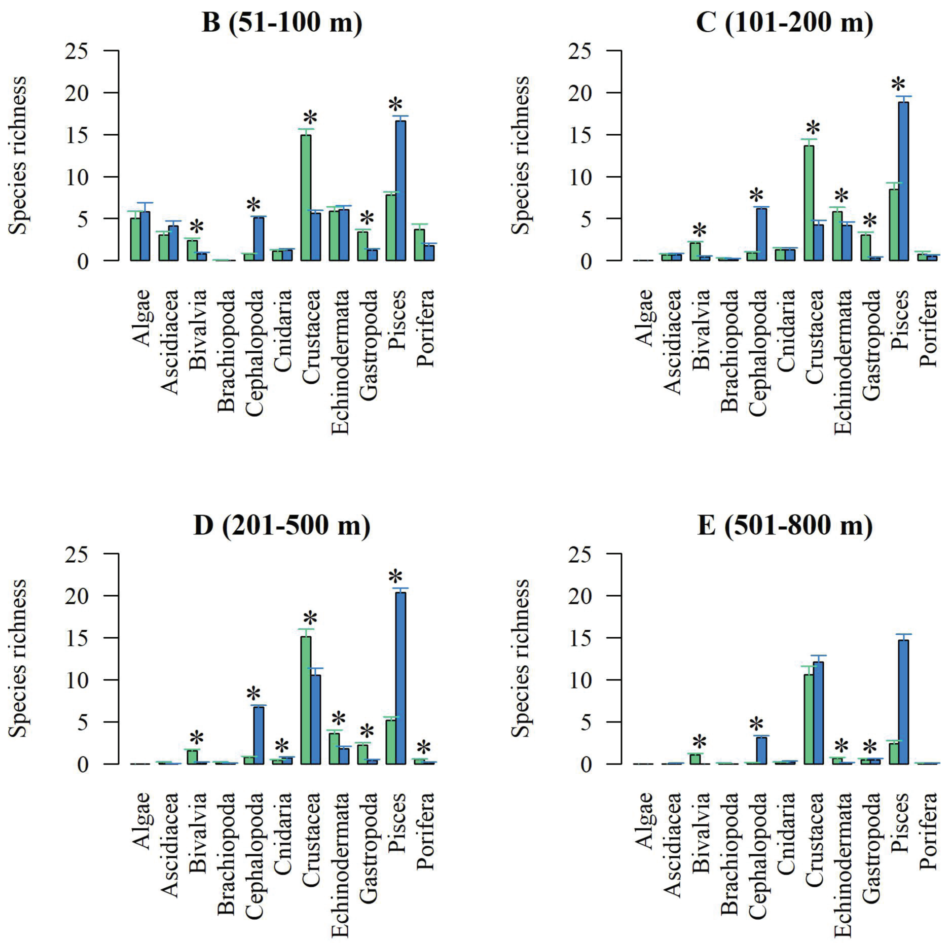

Fig. 3: Mean species richness (number of species or taxa) by taxonomic group and depth stratum. Green and blue represent the Jennings beam trawl and the experimental bottom trawl GOC-73, respectively.

the GOC-73. The percentage of total taxa detected by each gear varied with depth (Table 2). In stratum B, sampling with the Jennings BT allowed detection of 81% of the total taxa identified using both gears, while the GOC-73 detected only 53%. In stratum E, 56% of all species were detected with the Jennings BT, while the GOC-73 detected up to 71% of them. Despite these general trends, the variation of gear performance with depth was different depending on the taxonomic group (Fig. 4). For instance, the proportion of Echinodermata species detected with the GOC-73 was lower in the deeper strata (D-E) than in the shallower strata (B-C). Conversely, the proportion of Cephalopoda species detected with the GOC-73 increased with depth.

In general, the proportion of species collected with both gears decreased with depth (Fig. 4). In the B stratum, the number of taxa detected with both sampling gears was 23 for Ascidiacea, 27 for Algae, 6 for Cnidaria, 38 for Crustacea, 28 for Echinodermata, and 45 for Pisces; for the other taxonomic groups, the number of taxa detected was lower than 15. In the C stratum, the number of taxa detected with both sampling gears was higher than 15 only in Crustacea, Echinodermata, and Pisces. In the D and E strata, the number of taxa detected with both sampling gears was higher than 15 in Crustacea and Pisces, and in Crustacea, respectively. The number

Table 2. Total number of taxa by depth stratum (B, 51-100 m; C, 101-200 m; D, 201-500 m and E, 501-800 m) and sampling gear (BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73).

Stratum	BT	GOC	Total	Shared
B	471	311	585	197
C	234	183	315	101
D	213	186	304	94
E	93	117	165	44
Total	595	428	751	272

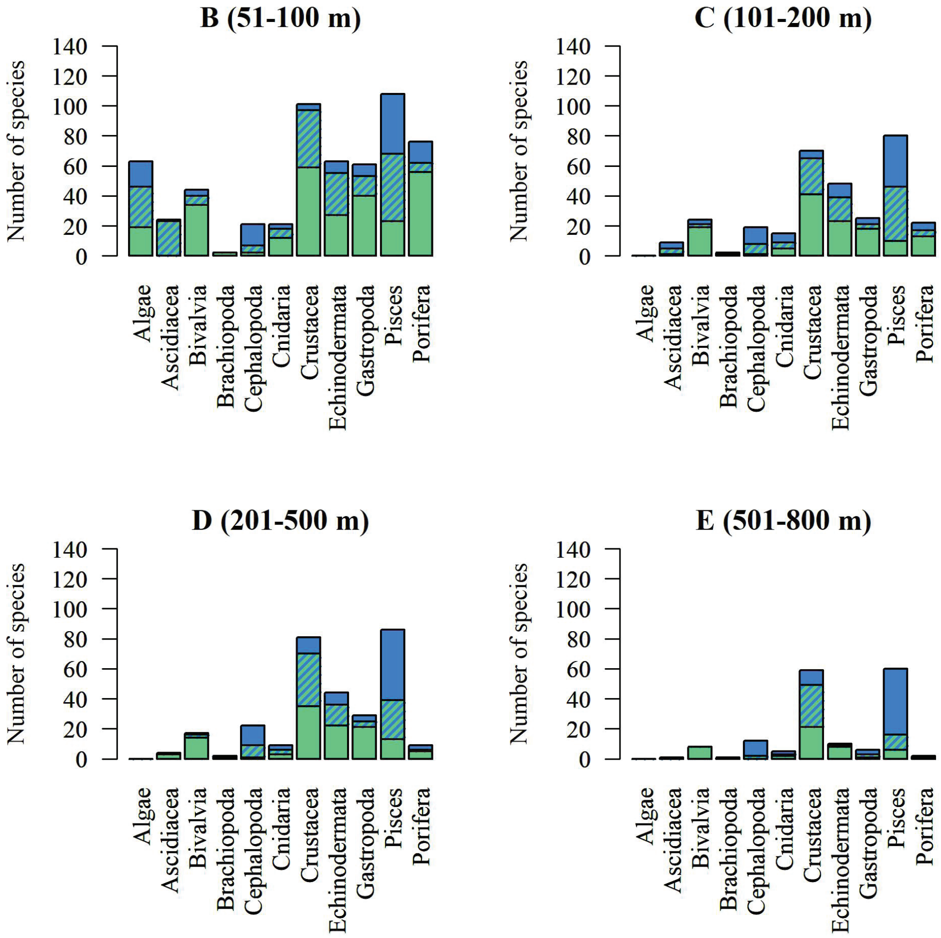

Fig. 4: Total number of species or taxa by taxonomic group and depth stratum. The number of species detected using both gears is represented as green and blue stripes. Green and blue represent the Jennings beam trawl and the experimental bottom trawl GOC-73, respectively.

of taxa detected exclusively with the Jennings BT was higher than with the GOC-73 in all strata for Crustacea, Echinodermata, Brachiopoda, and Bivalvia. In contrast, the number of taxa detected exclusively with the GOC-73 was always higher for Pisces and Cephalopoda.

For the Jennings BT, the SIMPER analysis showed that species that most contributed to intra-group similarity were the algae species of the family Corallinaceae and the gastropod *Turrinellitela tricarinata* in the B stratum, the echinoderms *Parastichopus regalis* and *Gracilechinus acutus* in the C stratum, the crustaceans *Parapenaeus longirostris* and *Plesionika heterocarpus* in the D stratum, and *Geryon longipes* and *Calocaris macandreae* in the E stratum (Table S3). For the GOC-73, the species that most contributed to intra-group similarity were the elasmobranch *Scyliorhinus canicula* together with the cephalopod *Octopus vulgaris* in the B stratum, with the elasmobranch *Raja clavata* in the C stratum, and with the teleostei *Phycis blennoides* in the D stratum, and the elasmobranch *Galeus melastomus* and the teleost *P. blennoides* in the E stratum (Table S3). The ANOSIM showed significant differences in the species composition obtained from the Jennings BT and the GOC-73 for all depth strata (Table S4).

The species accumulation curve flattened at lower numbers of sampling stations with the GOC-73 than with the Jennings BT (Fig. 5). This difference between gears was more evident in the B and C strata, where more divergent curves were obtained.

Analysis at the species level

Catch composition for each taxonomic group varied across depth strata and there were relevant differences between gears (Tables 3-6). For instance, in the B stratum (Table 3) the crustaceans *Galathea intermedia*, *Eurynome aspera*, *Anapagurus laevis*, and *Ebalia tuberosa*; the fishes *Buenia massutii* and *Odondebuenia balearica*; and the echinoderms *Ophiura albida* and *Ophioconis forbesi*, were collected with the Jennings BT but not with the GOC-73; on the other hand, species such as *Mullus barbatus* or *Merluccius merluccius* were better collected with the GOC-73.

Abundance and biomass values of all habitat-forming species were higher for the Jennings BT, with some species (e.g., Corallinaceae, *Grypheus vitreus, Lithothamnion valens, Lithothamnion corallioides*, *Osmundaria volubilis, Peyssonnelia rosa-marina*, *Phyllophora crispa*, *Phymatolithon calcareum,* and *Spongites fruticulosus*) showing differences of two or more orders of magnitude between gears (Table 7). The percentage of stations in which habitat-forming species appeared, varied depend-

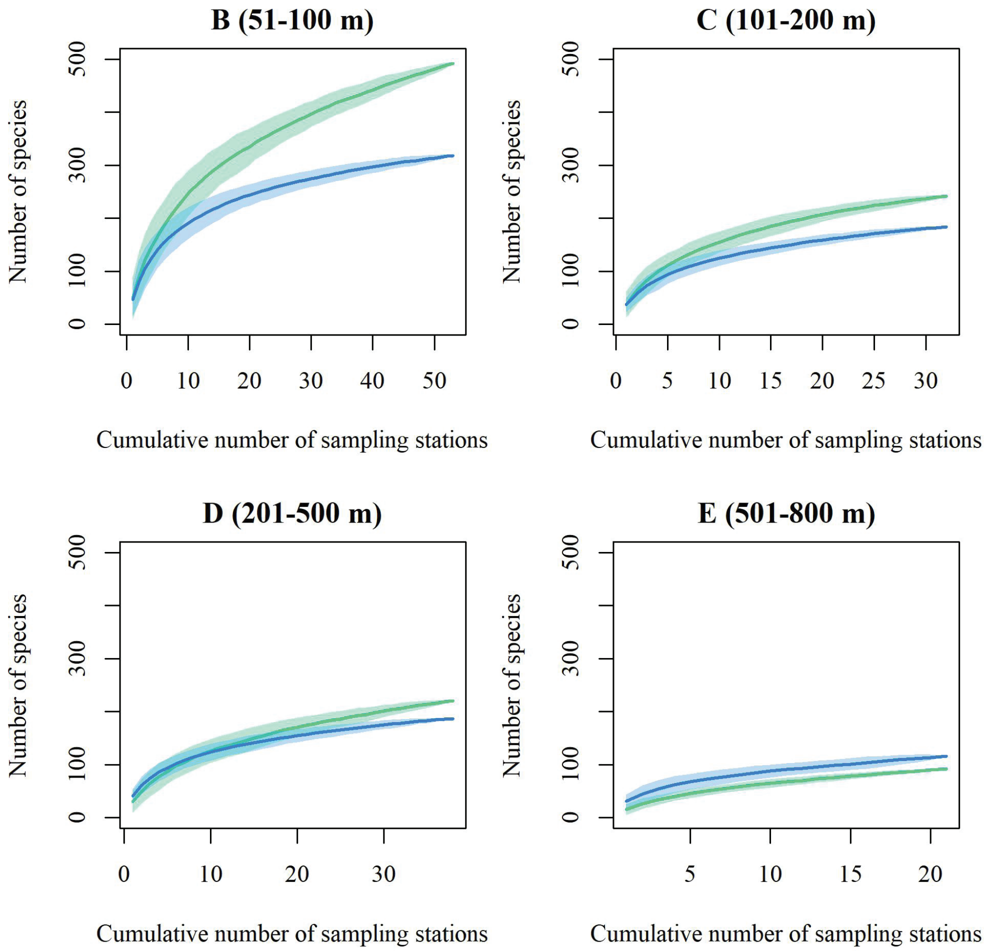

Fig. 5: Species accumulation curves for each sampler and depth stratum. Green and blue represent the Jennings beam trawl and the experimental bottom trawl GOC-73, respectively.

Table 3. Taxa showing the highest mean abundance (A, individuals/250 m^2) by taxonomic group and sampler (BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73) in stratum B (51-100 m). Algae and Porifera are presented in kg/250 m^2.

	BT		GOC	
Group	**Taxa**	**A**	**Taxa**	**A**
Algae	Corallinaceae	8.436	*Laminaria rodriguezii*	0.060
	Spongites fruticulosus	3.073	*Osmundaria volubilis*	0.052
	Lithothamnion valens	2.904	Corallinaceae	0.039
	Peyssonnelia spp.	2.329	*Peyssonnelia* spp.	0.029
	Lithothamnion corallioides	1.509	*Lithothamnion valens*	0.028
	Phymatolithon calcareum	1.265	*Spongites fruticulosus*	0.022
	Osmundaria volubilis	0.679	*Phyllophora crispa*	0.020
	Phyllophora crispa	0.582	*Halopteris filicina*	0.015
	Laminaria rodriguezii	0.553	*Halopithys incurva*	0.010
	Peyssonnelia rosa-marina	0.506	*Flabellia petiolata*	0.008
Ascidiacea	*Molgula appendiculata*	24.568	*Aplidium nordmanni*	0.200
	Polycarpa mamillaris	24.535	*Polycarpa mamillaris*	0.177
	Aplidium nordmanni	3.564	*Ciona* spp.	0.150
	Ciona spp.	3.528	*Ascidia mentula*	0.072
	Aplidium spp.	2.515	*Polyclinella azemai*	0.044
	Phallusia mammillata	1.954	*Microcosmus vulgaris*	0.041
	Ascidia mentula	1.580	*Molgula appendiculata*	0.021
	Ascidiella spp.	1.062	*Diazona violacea*	0.014
	Synoicum blochmanni	0.732	*Phallusia mammillata*	0.012
	Microcosmus vulgaris	0.683	*Botryllus schlosseri*	0.010

Continued

Table 3 continued

	BT		GOC	
Group	**Taxa**	**A**	**Taxa**	**A**
Bivalvia	*Neopycnodonte cochlear*	6.557	*Neopycnodonte cochlear*	0.101
	Aequipecten opercularis	2.807	*Aequipecten opercularis*	0.006
	Mimachlamys varia	0.816	*Pteria hirundo*	0.002
	Laevicardium crassum	0.678	*Mimachlamys varia*	0.001
	Venus verrucosa	0.603	*Venus nux*	0.001
	Nucula sulcata	0.594	*Anadara gibbosa*	0.000
	Glycymeris glycymeris	0.478	*Acanthocardia aculeata*	0.000
	Palliolum incomparabile	0.392	*Flexopecten flexuosus*	0.000
	Venus nux	0.344	*Pecten maximus*	0.000
	Talochlamys pusio	0.225	*Glossus humanus*	0.000
Brachiopoda	*Megerlia truncata*	0.351		
	Joania cordata	0.085		
Cephalopoda	*Sepietta oweniana*	0.315	*Alloteuthis media*	0.122
	Sepia elegans	0.167	*Illex coindetii*	0.066
	Rossia macrosoma	0.100	*Loligo vulgaris*	0.064
	Octopus vulgaris	0.072	*Octopus vulgaris*	0.062
	Eledone cirrhosa	0.046	*Alloteuthis subulata*	0.037
	Sepiola robusta	0.037	*Eledone moschata*	0.013
	Sepia officinalis	0.036	*Sepia elegans*	0.008
			Sepia officinalis	0.008
			Sepietta oweniana	0.003
			Abralia veranyi	0.002
Cnidaria	*Sertularella gayi*	0.867	*Alcyonium palmatum*	0.026
	Alcyonium palmatum	0.450	*Epizoanthus* spp.	0.022
	Nemertesia antennina	0.313	*Funiculina quadrangularis*	0.013
	Eunicella filiformis	0.301	*Pennatula rubra*	0.008
	Pennatula phosphorea	0.159	*Pteroeides spinosum*	0.001
	Alcyonium coralloides	0.144	*Veretillum cynomorium*	0.001
	Funiculina quadrangularis	0.055	*Pennatula phosphorea*	0.000
	Modeeria rotunda	0.026	*Pteroeides griseum*	0.000
	Alcyonium acaule	0.023	*Cerianthus membranaceus*	0.000
	Alicia mirabilis	0.023		
Crustacea	*Galathea intermedia*	33.951	*Dardanus arrosor*	0.126
	Dardanus arrosor	18.322	*Inachus thoracicus*	0.120
	Inachus dorsettensis	17.309	*Inachus dorsettensis*	0.094
	Eurynome aspera	10.468	*Pagurus prideaux*	0.072
	Anapagurus laevis	9.739	*Macropodia tenuirostris*	0.034
	Pagurus prideaux	8.300	*Macropodia linaresi*	0.028
	Inachus thoracicus	5.192	*Polybius depurator*	0.024
	Ebalia tuberosa	4.704	*Macropodia rostrata*	0.015
	Pagurus forbesii	4.169	*Parapenaeus longirostris*	0.012
	Parthenopoides massena	3.782	*Pisa armata*	0.009
Echinodermata	*Ophiura albida*	7.803	*Leptometra phalangium*	1.369
	Ophioconis forbesi	5.706	*Spatangus purpureus*	0.793
	Spatangus purpureus	4.974	*Sphaerechinus granularis*	0.590
	Sphaerechinus granularis	3.212	*Echinaster (E.) sepositus*	0.107
	Ophiura ophiura	2.161	*Trachythyone* spp.	0.038
	Echinaster (E.) sepositus	2.032	*Hacelia attenuata*	0.036
	Astropecten irregularis	1.692	*Ophiura ophiura*	0.027
	Leptometra phalangium	1.141	*Astropecten irregularis*	0.027
	Hacelia attenuata	1.089	*Ophiomyxa pentagona*	0.019
	Ophiomyxa pentagona	0.948	*Parastichopus regalis*	0.019

Continued

Table 3 continued

Group	BT Taxa	A	GOC Taxa	A
Pisces	*Buenia massutii*	8.213	*Trisopterus minutus*	0.594
	Arnoglossus laterna	2.028	*Mullus barbatus*	0.305
	Odondebuenia balearica	1.668	*Pagellus acarne*	0.230
	Gobius xoriguer	1.522	*Mullus surmuletus*	0.198
	Serranus hepatus	1.333	*Serranus hepatus*	0.176
	Lesueurigobius friesii	1.288	*Serranus cabrilla*	0.170
	Lesueurigobius suerii	1.228	*Scyliorhinus canicula*	0.170
	Diplecogaster bimaculata	1.220	*Merluccius merluccius*	0.164
	Vanneaugobius dollfusi	1.190	*Chelidonichthys lastoviza*	0.152
	Gobius gasteveni	0.870	*Lepidotrigla cavillone*	0.131
Gastropoda	*Turritellinella tricarinata*	33.379	*Berthella aurantiaca*	0.017
	Turritella spp.	3.393	*Pleurobranchus testudinarius*	0.007
	Calyptraea chinensis	2.029	*Umbraculum umbraculum*	0.007
	Gibbula magus	1.476	*Bolma rugosa*	0.004
	Calliostoma granulatum	0.696	*Turritella* spp.	0.003
	Calliostoma conulus	0.486	*Diodora graeca*	0.002
	Bolma rugosa	0.361	*Aporrhais pespelecani*	0.002
	Ocinebrina aciculata	0.315	*Aplysia fasciata*	0.001
	Fusinus sp.	0.309	*Bolinus brandaris*	0.001
	Jujubinus exasperatus	0.245	*Xenophora crispa*	0.001
Porifera	*Haliclona* sp.1	0.073	*Suberites domuncula*	0.011
	Phorbas tenacior	0.046	*Chondrosia reniformis*	0.002
	Dictyonella incisa	0.040	*Axinella damicornis*	0.000
	Lissodendoryx sp.	0.036	*Scalarispongia scalaris*	0.000
	Axinella damicornis	0.025	*Haliclona (R.) mediterranea*	0.000
	Siphonochalina sp.	0.011	*Mycale (A.) contarenii*	0.000
	Tethya sp.	0.009	*Desmacella annexa*	0.000
	Haliclona sp.2	0.007	*Petrosia (P.) ficiformis*	0.000
	Dysidea sp.	0.007	*Aplysina aerophoba*	0.000
	Suberites domuncula	0.006	*Axinella verrucosa*	0.000

Table 4. Taxa showing the highest mean abundance (A, individuals/250 m^2) by taxonomic group and sampler (BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73) in stratum C (101-200 m). Porifera are presented in kg/250 m^2.

Group	BT Taxa	A	GOC Taxa	A
Ascidiacea	*Ascidiella* spp.	0.999	*Diazona violacea*	0.010
	Diazona violacea	0.068	*Ascidiella* spp.	0.008
	Polycarpa mamillaris	0.059	*Ascidia mentula*	0.001
	Ascidia virginea	0.012	*Dendrodoa grossularia*	0.000
	Ascidia mentula	0.006	*Microcosmus vulgaris*	0.000
			Ciona spp.	0.000
			Polycarpa mamillaris	0.000
			Phallusia mammillata	0.000
Bivalvia	*Neopycnodonte cochlear*	29.032	*Neopycnodonte cochlear*	0.058
	Pseudamussium clavatum	2.584	*Venus nux*	0.007
	Nucula sulcata	0.345	*Pteria hirundo*	0.001
	Cuspidaria cuspidata	0.172	*Donax trunculus*	0.000
	Fabulina fabula	0.154	*Anadara gibbosa*	0.000
	Peronidia albicans	0.119		
	Arcopella balaustina	0.083		
	Cuspidaria rostrata	0.082		
	Abra longicallus	0.079		
	Anomia ephippium	0.070		

Continued

Table 4 continued

Group	BT Taxa	BT A	GOC Taxa	GOC A
Brachiopoda	*Gryphus vitreus*	19.260	*Gryphus vitreus*	0.026
	Joania cordata	0.064		
Cephalopoda	*Sepietta oweniana*	0.189	*Alloteuthis media*	0.438
	Rossia macrosoma	0.056	*Illex coindetii*	0.204
	Sepia orbignyana	0.031	*Loligo forbesii*	0.090
	Eledone cirrhosa	0.025	*Sepia orbignyana*	0.013
	Sepiola robusta	0.018	*Scaeurgus unicirrhus*	0.011
	Rondeletiola minor	0.016	*Sepietta oweniana*	0.007
	Sepia elegans	0.013	*Alloteuthis subulata*	0.006
	Scaeurgus unicirrhus	0.006	*Abralia veranyi*	0.006
			Eledone cirrhosa	0.005
			Octopus vulgaris	0.005
Cnidaria	*Funiculina quadrangularis*	5.377	*Funiculina quadrangularis*	0.404
	Alcyonium palmatum	0.708	*Alcyonium palmatum*	0.033
	Kophobelemnon stelliferum	0.238	*Pennatula rubra*	0.015
	Pennatula phosphorea	0.196	*Pennatula phosphorea*	0.013
	Veretillum cynomorium	0.148	*Veretillum cynomorium*	0.000
	Sertularella gayi	0.070	*Pteroeides spinosum*	0.000
	Nemertesia antennina	0.055	*Cerianthus membranaceus*	0.000
	Acryptolaria conferta	0.046	*Eunicella* spp.	0.000
	Sertularella polyzonias	0.012	*Pteroeides griseum*	0.000
			Epizoanthus spp.	0.000
Crustacea	*Anapagurus laevis*	22.212	*Parapenaeus longirostris*	0.130
	Lophogaster typicus	3.472	*Iridonida speciosa*	0.039
	Inachus dorsettensis	2.854	*Macropodia tenuirostris*	0.025
	Alpheus glaber	2.520	*Dardanus arrosor*	0.021
	Parapenaeus longirostris	2.407	*Macropipus tuberculatus*	0.017
	Solenocera membranacea	1.331	*Pagurus prideaux*	0.010
	Ebalia cranchii	1.227	*Polybius depurator*	0.005
	Pagurus prideaux	1.174	*Scalpellum scalpellum*	0.005
	Chlorotocus crassicornis	1.074	*Inachus dorsettensis*	0.003
	Ebalia deshayesi	1.045	*Chlorotocus crassicornis*	0.002
Echinodermata	*Leptometra phalangium*	102.412	*Leptometra phalangium*	3.773
	Antedon mediterranea	3.107	*Gracilechinus acutus*	0.112
	Astropecten irregularis	2.634	*Astropecten irregularis*	0.063
	Ophiura (D.) carnea	1.754	*Parastichopus regalis*	0.041
	Sclerasterias richardi	1.218	*Cidaris cidaris*	0.027
	Ophiopsila annulosa	1.107	*Echinus melo*	0.008
	Gracilechinus acutus	1.020	*Ophiura ophiura*	0.008
	Psammechinus microtuberculatus	0.656	*Tethyaster subinermis*	0.006
	Paraleptopentacta tergestina	0.537	*Antedon mediterranea*	0.005
	Ophiura ophiura	0.263	*Peltaster placenta*	0.005
Pisces	*Lesueurigobius friesii*	4.571	*Merluccius merluccius*	0.596
	Buenia massutii	2.496	*Trisopterus minutus*	0.373
	Symphurus nigrescens	1.169	*Scyliorhinus canicula*	0.229
	Arnoglossus laterna	0.907	*Chelidonichthys cuculus*	0.223
	Pomatoschistus norvegicus	0.732	*Gadiculus argenteus*	0.165
	Callionymus maculatus	0.587	*Serranus hepatus*	0.161
	Serranus hepatus	0.499	*Lepidotrigla dieuzeidei*	0.155
	Arnoglossus rueppelii	0.218	*Mullus barbatus*	0.127
	Deltentosteus quadrimaculatus	0.141	*Lepidotrigla cavillone*	0.127
	Diplecogaster bimaculata	0.121	*Micromesistius poutassou*	0.091

Continued

Table 4 continued

	BT		GOC	
Group	**Taxa**	**A**	**Taxa**	**A**
Gastropoda	*Turritellinella tricarinata*	5.400	*Xenophora crispa*	0.011
	Calliostoma granulatum	0.976	*Scaphander lignarius*	0.001
	Turritella spp.	0.608	*Galeodea rugosa*	0.001
	Xenophora crispa	0.441	*Tethys fimbria*	0.000
	Gastropteron rubrum	0.366	*Umbraculum umbraculum*	0.000
	Pseudofusus pulchellus	0.326	*Bivetiella cancellata*	0.000
	Pleurobranchaea meckeli	0.191	*Turritella* spp.	0.000
	Scaphander lignarius	0.187		
	Calliostoma gubbiolii	0.093		
	Euspira fusca	0.068		
Porifera	*Thenea muricata*	0.006	*Haliclona poecillastroides*	0.000
	Penares helleri	0.000	*Desmacella annexa*	0.000
	Poecillastra compressa	0.000	*Poecillastra compressa*	0.000
	Suberites domuncula	0.000	*Chondrosia reniformis*	0.000
	Myxilla (M.) rosacea	0.000	*Suberites domuncula*	0.000
	Bubaris sp.	0.000	*Ircinia oros*	0.000
	Calcarea sp.	0.000	*Thenea muricata*	0.000
	Hemiasterella elongata	0.000	*Hamacantha falcula*	0.000
	Suberites sp.	0.000	*Myxilla (M.) rosacea*	0.000
	Eurypon sp.	0.000		

Table 5. Taxa showing the highest mean abundance (A, individuals/250 m^2) by taxonomic group and sampler (BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73) in stratum D (201-500 m). Porifera are presented in kg/250 m^2.

	BT		GOC	
Group	**Taxa**	**A**	**Taxa**	**A**
Ascidiacea	*Polycarpa mamillaris*	0.019	*Phallusia mammillata*	0.000
	Pyura spp.	0.005		
	Microcosmus vulgaris	0.004		
Bivalvia	*Nucula sulcata*	0.478	*Neopycnodonte cochlear*	0.001
	Fabulina fabula	0.413	*Spisula solida*	0.000
	Abra longicallus	0.350	*Pteria hirundo*	0.000
	Bathyarca philippiana	0.159		
	Cuspidaria rostrata	0.082		
	Neopycnodonte cochlear	0.057		
	Cuspidaria cuspidata	0.056		
	Tropidomya abbreviata	0.048		
	Venus nux	0.019		
	Cuspidaria sp.	0.016		
Brachiopoda	*Gryphus vitreus*	0.357	*Gryphus vitreus*	0.000
	Joania cordata	0.004		
Cephalopoda	*Sepietta oweniana*	0.229	*Illex coindetii*	0.116
	Rossia macrosoma	0.067	*Sepietta oweniana*	0.081
	Rondeletiola minor	0.029	*Abralia veranyi*	0.039
	Sepia orbignyana	0.010	*Rondeletiola minor*	0.025
	Eledone cirrhosa	0.009	*Loligo forbesii*	0.007
	Loligo vulgaris	0.005	*Alloteuthis media*	0.006
	Octopus salutii	0.005	*Eledone cirrhosa*	0.005
	Sepia elegans	0.005	*Todaropsis eblanae*	0.005
	Bathypolypus sponsalis	0.004	*Alloteuthis subulata*	0.004
			Sepia orbignyana	0.002

Continued

Table 5 continued

	BT		GOC	
Group	**Taxa**	**A**	**Taxa**	**A**
Cnidaria	*Funiculina quadrangularis*	0.392	*Funiculina quadrangularis*	0.143
	Veretillum cynomorium	0.015	*Alcyonium palmatum*	0.002
	Pennatula phosphorea	0.011	*Epizoanthus* spp.	0.000
	Sertularella gayi	0.010	*Pennatula rubra*	0.000
	Alcyonium palmatum	0.005	*Cerianthus membranaceus*	0.000
	Eunicella spp.	0.005	*Veretillum cynomorium*	0.000
Crustacea	*Alpheus glaber*	3.250	*Plesionika heterocarpus*	1.056
	Plesionika heterocarpus	2.608	*Parapenaeus longirostris*	0.386
	Plesionika antigai	2.254	*Pasiphaea sivado*	0.218
	Chlorotocus crassicornis	2.101	*Plesionika gigliolii*	0.167
	Lophogaster typicus	1.884	*Plesionika martia*	0.063
	Iridonida speciosa	1.701	*Plesionika antigai*	0.057
	Calocaris macandreae	1.421	*Nephrops norvegicus*	0.044
	Parapenaeus longirostris	1.382	*Iridonida speciosa*	0.032
	Goneplax rhomboides	1.250	*Solenocera membranacea*	0.025
	Anapagurus laevis	1.172	*Plesionika edwardsii*	0.024
Echinodermata	*Leptometra phalangium*	7.450	*Parastichopus regalis*	0.008
	Ophiura (D.) carnea	2.423	*Cidaris cidaris*	0.004
	Astropecten irregularis	0.841	*Astropecten irregularis*	0.003
	Ophiocten affinis	0.249	*Brissopsis atlantica mediterranea*	0.001
	Brissopsis lyrifera	0.220	*Leptometra phalangium*	0.001
	Amphiura filiformis	0.141	*Holothuria (P.) forskali*	0.001
	Oestergrenia digitata	0.122	*Tethyaster subinermis*	0.001
	Brissopsis atlantica mediterranea	0.094	*Gracilechinus acutus*	0.001
	Ophiocten abyssicolum	0.093	*Anseropoda placenta*	0.000
	Ophiura albida	0.071	*Echinus melo*	0.000
Pisces	*Gadiculus argenteus*	4.822	*Gadiculus argenteus*	1.248
	Symphurus nigrescens	1.051	*Micromesistius poutassou*	0.793
	Buenia lombartei	0.676	*Chlorophthalmus agassizi*	0.347
	Lesueurigobius friesii	0.499	*Coelorinchus caelorhincus*	0.255
	Gaidropsarus biscayensis	0.395	*Scyliorhinus canicula*	0.201
	Arnoglossus rueppelii	0.206	*Helicolenus dactylopterus*	0.191
	Lepidorhombus boscii	0.117	*Phycis blennoides*	0.163
	Scyliorhinus canicula	0.098	*Galeus melastomus*	0.145
	Phycis blennoides	0.096	*Lepidotrigla dieuzeidei*	0.110
	Callionymus maculatus	0.087	*Merluccius merluccius*	0.073
Gastropoda	*Callumbonella suturalis*	1.787	*Aporrhais serresiana*	0.000
	Euspira fusca	0.289	*Bivetiella cancellata*	0.000
	Turritellinella tricarinata	0.280	*Scaphander lignarius*	0.000
	Aporrhais serresiana	0.248	*Xenophora crispa*	0.000
	Calliostoma granulatum	0.093	*Pseudosimnia carnea*	0.000
	Scaphander lignarius	0.072	*Aporrhais pespelecani*	0.000
	Pagodula echinata	0.065	*Galeodea rugosa*	0.000
	Turritella spp.	0.052	*Galeodea echinopora*	0.000
	Fusiturris similis	0.025		
	Pseudosimnia adriatica	0.025		
Porifera	*Thenea muricata*	0.003	*Desmacella annexa*	0.000
	Dictyonella cf. *marsilii*	0.000	*Thenea muricata*	0.000
	Cladorhiza abyssicola	0.000	*Rhizaxinella pyrifera*	0.000
	Crella sp.	0.000	*Haliclona poecillastroides*	0.000
	Heteroxya sp.	0.000		
	Sympagella sp.	0.000		

Table 6. Taxa showing the highest mean abundance (A, individuals/250 m^2) by taxonomic group and sampler (BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73) in stratum E (501-800 m). Porifera are presented in kg/250 m^2.

	BT		GOC	
Group	**Taxa**	**A**	**Taxa**	**A**
Ascidiacea			*Ciona spp.*	0.000
Bivalvia	*Abra longicallus*	0.282		
	Nucula sulcata	0.097		
	Palliolum incomparabile	0.007		
	Cuspidaria rostrata	0.006		
	Nucula nitidosa	0.006		
	Bathyarca philippiana	0.006		
	Cuspidaria cuspidata	0.006		
	Delectopecten vitreus	0.006		
Brachiopoda	*Gryphus vitreus*	0.012		
Cephalopoda	*Sepietta oweniana*	0.009	*Abralia veranyi*	0.015
	Bathypolypus sponsalis	0.006	*Histioteuthis reversa*	0.007
			Todarodes sagittatus	0.004
			Illex coindetii	0.004
			Sepietta oweniana	0.002
			Loligo forbesii	0.001
			Bathypolypus sponsalis	0.001
			Histioteuthis bonnellii	0.001
			Heteroteuthis dispar	0.000
			Octopus salutii	0.000
Cnidaria	*Alcyonium palmatum*	0.019	*Isidella elongata*	0.001
	Sertularella gayi	0.006	*Funiculina quadrangularis*	0.000
	Isidella elongata	0.006	*Veretillum cynomorium*	0.000
Crustacea	*Calocaris macandreae*	7.411	*Plesionika martia*	0.243
	Amalopenaeus elegans	0.507	*Aristeus antennatus*	0.157
	Geryon longipes	0.354	*Geryon longipes*	0.096
	Monodaeus couchii	0.344	*Plesionika acanthonotus*	0.074
	Robustosergia robusta	0.304	*Plesionika gigliolii*	0.070
	Processa nouveli	0.281	*Pasiphaea multidentata*	0.046
	Plesionika acanthonotus	0.260	*Parapenaeus longirostris*	0.036
	Polycheles typhlops	0.251	*Polycheles typhlops*	0.024
	Aristeus antennatus	0.230	*Nephrops norvegicus*	0.023
	Alpheus glaber	0.196	*Robustosergia robusta*	0.019
Echinodermata	*Brissopsis lyrifera*	0.096	*Astropecten irregularis*	0.000
	Oestergrenia digitata	0.022	*Tethyaster subinermis*	0.000
	Astropecten irregularis	0.019		
	Ophiura (D.) carnea	0.013		
	Ophiocten abyssicolum	0.013		
	Brissopsis atlantica mediterranea	0.012		
	Molpadia musculus	0.006		
	Amphiura filiformis	0.006		
	Amphiura chiajei	0.006		
Pisces	*Gaidropsarus biscayensis*	0.198	*Galeus melastomus*	0.166
	Nezumia aequalis	0.075	*Phycis blennoides*	0.146
	Phycis blennoides	0.056	*Hymenocephalus italicus*	0.085
	Symphurus ligulatus	0.045	*Nezumia aequalis*	0.058
	Callionymus maculatus	0.019	*Coelorinchus caelorhincus*	0.055
	Hymenocephalus italicus	0.019	*Hoplostethus mediterraneus*	0.022
	Symphurus nigrescens	0.019	*Etmopterus spinax*	0.010
	Gadella maraldi	0.013	*Gadiculus argenteus*	0.008
	Mora moro	0.013	*Stomias boa*	0.007
	Galeus melastomus	0.013	*Notacanthus bonaparte*	0.006

Continued

Table 6 continued

Group	BT Taxa	A	GOC Taxa	A
Gastropoda	*Aporrhais serresiana*	0.204	*Aporrhais serresiana*	0.004
	Euspira fusca	0.032	*Ranella olearium*	0.000
	Cavolinia inflexa	0.009	*Semicassis saburon*	0.000
			Galeodea rugosa	0.000
			Euspira fusca	0.000
Porifera	*Thenea muricata*	0.000	*Penares helleri*	0.000

Table 7. Mean values (Mean) and standard errors (SE) of forming habitat species abundance (A, individuals/250 m^2) and biomass (B, g/250 m^2). BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73.

	Abundance (n/250 m^2)				Biomass (g/250 m^2)			
	BT		GOC		BT		GOC	
Species	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
Ascidia mentula	3.497	1.475	0.110	0.034	98.339	41.517	3.356	1.073
Botryllus schlosseri	1.019	0.459	0.078	0.023	71.809	43.146	4.651	1.626
Corallinaceae	NA	NA	NA	NA	22355.962	8307.803	123.108	35.481
Diazona violacea	3.412	2.341	0.090	0.034	42.324	19.693	20.675	15.968
Funiculina quadrangularis	7.912	4.002	0.657	0.208	11.300	6.030	2.142	0.803
Gracilechinus acutus	2.015	0.615	0.172	0.064	47.389	12.717	7.670	3.012
Gryphus vitreus	48.472	23.956	0.104	0.047	264.471	125.499	1.033	0.502
Halopteris filicina	NA	NA	NA	NA	830.222	249.231	64.692	25.411
Isidella elongata	0.129	NA	0.004	0.002	7.218	NA	0.009	0.004
Laminaria rodriguezii	NA	NA	NA	NA	7325.098	4983.914	289.283	172.252
Leptometra phalangium	134.101	62.366	17.578	6.976	169.189	82.390	34.018	12.658
Lithothamnion corallioides	NA	NA	NA	NA	4998.114	2446.295	18.839	5.963
Lithothamnion valens	NA	NA	NA	NA	8099.376	2786.840	91.473	26.390
Microcosmus vulgaris	2.795	1.084	0.095	0.048	41.730	15.194	2.070	0.959
Molgula appendiculata	118.371	100.475	0.160	0.068	158.041	86.444	1.496	0.675
Osmundaria volubilis	NA	NA	0.010	0.005	2569.741	1118.395	182.549	72.555
Parastichopus regalis	0.742	0.135	0.044	0.009	64.932	12.321	7.326	1.690
Peyssonnelia rosa-marina	NA	NA	NA	NA	3831.689	1341.152	37.408	21.754
Peyssonnelia spp.	NA	NA	NA	NA	7261.458	4140.499	101.600	88.104
Phallusia mammillata	2.230	1.030	0.041	0.013	72.362	21.157	5.760	1.944
Phyllophora crispa	NA	NA	NA	NA	1401.370	594.251	59.800	21.250
Phymatolithon calcareum	NA	NA	NA	NA	5157.914	1971.322	40.675	20.613
Polycarpa mamillaris	81.435	76.131	0.520	0.364	90.813	38.018	17.180	12.995
Polyclinella azemai	6.625	2.070	0.332	0.169	15.281	10.025	2.685	1.252
Spatangus purpureus	17.650	16.936	1.828	0.588	3154.145	3052.721	419.005	140.794
Spongites fruticulosus	NA	NA	NA	NA	16284.914	8016.240	72.195	21.443

ing on the species by sampling gear (Fig. 6). In general, both common and abundant species, especially Algae, were well detected with both gears, while less abundant species such as the ascidian *Botryllus schlosseri* or the bamboo coral *Isidella elongata* were better detected with the GOC-73. Taking into account the total set of stations, the Jennings BT showed a higher ratio of stations with occurrence of some relevant habitat-forming species, both from shallower (e.g., *P. calcareum, L. corallioides,* and *Halopteris filicina*) and deeper waters (e.g., *G. vitreus* and *Leptometra phalangium*).

In all the stations, the abundance observed with the photogrammetric sled from video images of both *Funiculina quadrangularis* and *L. phalangium* obtained was higher than the abundance obtained with the GOC-73 or the Jennings BT (Table 8).

Discussion

Our results show big differences between samples obtained with beam trawl and bottom trawl gears, in terms of abundance, biomass, and species composition of the main taxonomic groups, but also abundance and biomass of benthic habitat-forming species. These differences varied along the bathymetric gradient and depended on the taxonomic group, species size, and behaviour.

In general, sampling with the Jennings BT resulted in higher estimates of abundance and biomass than the GOC-73 for all taxonomic groups and depth strata. This was also true for species richness, especially in molluscs, crustaceans, and echinoderms, but not for fish and cephalopods, which showed greater values in samples obtained with the GOC-73. Although sampling was performed in the same habitats, an important fraction of the species was collected exclusively using one or the other sampling gear. The percentage of species collected with both gears

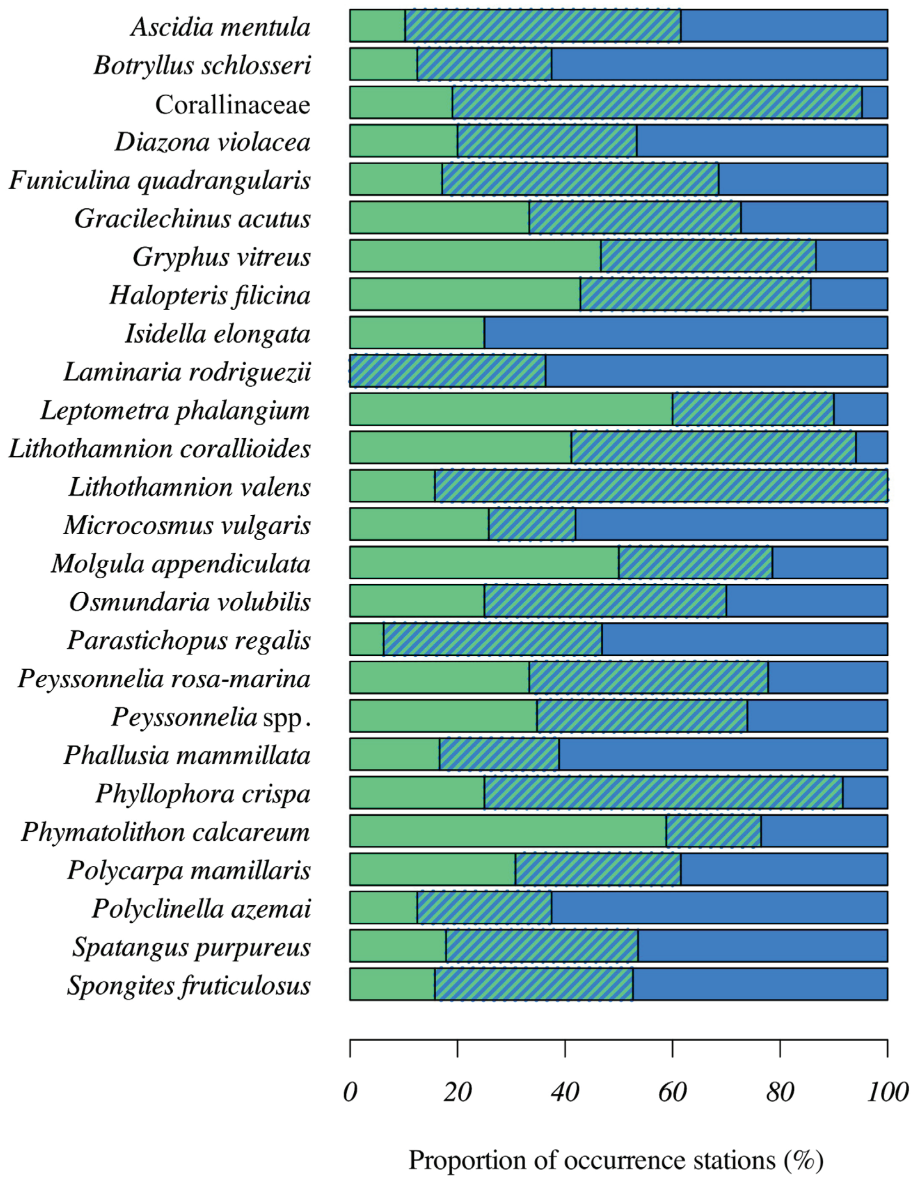

Fig. 6: Percentage of stations in which each of the habitat-forming species apperared. Percentage of stations detected using both gears is represented as green and blue stripes. Green and blue represent the Jennings beam trawl and the experimental bottom trawl GOC-73, respectively.

Table 8. Abundance (individuals/250 m^2) of *Leptometra phalangium* and *Funiculina quadrangularis* obtained from Jennings beam trawl (BT), the experimental bottom trawl GOC-73 (GOC), and a photogrammetric sledge (PS). Only stations where the species where caught with all samplers are shown.

Species	Station	BT	GOC	PS
	1	2.37	0.04	5.38
	2	113.04	0.03	477.86
Leptometra phalangium	3	58.29	46.02	1221.64
	4	970.72	7.74	1872.03
	5	96.72	74.80	1040.21
	6	2.22	0.05	4.31
	7	2.41	2.82	95.59
	8	1.03	0.01	10.73
	9	10.12	2.85	105.69
	10	1.64	0.67	4.76
Funiculina quadrangularis	11	1.24	1.60	13.35
	12	35.92	4.31	2454.16
	13	0.60	0.47	32.49
	14	43.81	2.86	195.36
	15	2.15	0.10	44.45
	16	0.20	0.03	0.96

was lower than 50% for all taxonomic groups and depth strata, with the only exception of ascidians on the shallow shelf. Sampling with the Jennings BT yielded data on a large number of species (approximately 75% of the total number of species identified), while the GOC-73 yielded data on only 25% of species that were not detected in the Jennings BT samples.

The location of species relative to the seabed, as well as their behavior (in terms of swimming capacity and escape reactions), are key factors determining their catchability by particular sampling gears. In general, smaller species closely associated with the seabed predominated in the list of the most abundant species collected by the Jennings BT, while larger demersal species were most abundant in samples from the GOC-73. These observations are explained by the fact that these sampling gears were specially designed to catch epibenthic (Jennings BT gear) or nectobenthic species (GOC-73 gear) (Fiorentini *et al*., 1999; Reiss *et al*., 2006). The higher horizontal and vertical opening of the GOC-73 together with its higher towing speed make this gear more suitable to capture species with a higher swimming capacity and the ability to move upwards from the bottom. The differences in catch composition between the Jennings BT and the GOC-73 were more evident in the taxonomic groups composed of nectobenthic and epibenthic species, like fishes and cephalopods.

On the deep shelf, where the proportion of fish species caught by both samplers was 45%, higher abundance values were estimated from the Jennings BT but higher species richness was estimated from the GOC-73 samples. The gobies *Lesueurigobius friesii* and *Buenia massutii*, and the flatfish *Symphurus nigrescens* were among the most abundant species from the Jennings BT samples. Three species from the order Gadiformes (i.e., *M. merluccius*, *Trisopterus minutus*, and *Micromesistius poutassou*) were among the most abundant species from the GOC-73 samples. In the middle slope, where the number of species caught by both trawls was only 17%, the use of the GOC-73 resulted in higher abundance and species richness values of cephalopods, with *Abralia veranyi*, *Histiotheuthis reversa*, and *Todarodes sagittatus* being the most abundant species; it is worth mentioning that these species were not present in the Jennings BT samples. The higher abundance values for ascidians and echinoderms (both taxonomic groups including exclusively epibenthic species) estimated from the Jennings BT samples also showed the higher efficiency of this sampling method to capture species attached to the sea bottom.

Species size is another important factor influencing catchability that can explain the differences in species composition obtained with different gears. On the deep shelf, with 34% of species of crustaceans being present in samples from both gears, small crustaceans like *Anapaguris laevis*, *Lophogaster typicus*, and *Alpheus glaber* were more abundant in the Jennings BT samples, while the bigger ones *Iridonida speciosa*, *Macropodia tenuirostris*, and *Macropipus tuberculatus* were more abundant in the GOC-73 samples. Also on the deep shelf, small echinoderms like *Psamechinus microtuberculatus*, *Ophiura (D.) carnea*, or *Sclerasterias richardi* were more abundant in the Jennings BT samples, whereas larger species like *Tethyaster subinermis* or *Parastichopus regalis* were more abundant in the GOC-73 samples. Differences in the catches from both sampling gears are possibly related to the smaller codend mesh size of the Jennings BT, which allows retaining smaller specimens.

Differences in abundance of some species of cephalopods could also be attributed to seasonality. While surveys using the Jennings BT were conducted in autumn, surveys with the GOC-73 were conducted in late spring and summer. The short-life cycle and single seasonal breeding of cephalopods make them particularly sensitive to environmental conditions (Pierce *et al*., 2008; Quetglas *et al*., 2016). For example, *Illex coindetti* showed higher abundance in the GOC-73 samples, but *Octopus vulgaris* and *Eldone cirrhosa* had similar abundance in samples from both gears. These three species have seasonal landing fluctuations in bottom trawl fisheries in the Levantine-Balearic demarcation with different trends in the Balearic Islands and the Mediterranean coast of the Iberian Peninsula (Puerta *et al*., 2016). However, taking into account the higher biomass values of the three species obtained with the GOC-73, the higher attachment to the bottom of the octopus species *E. cirrhosa* and *O. vulgaris* compared to the squid *I. coindetii* and the larger size of the individuals captured with the GOC-73 would be a more reasonable explanation for those differences than seasonality.

The spatial distribution scale of benthic species also affected their catchability by both gears (Fig. 7). The GOC-73 provided better estimates of the occurrence of some macroepibenthic species with low abundance (e.g., the ascidian *Botryllus schlosseri)*, because the higher area sampled in each haul increases the probability of finding them. The swept area is one order of magnitude higher with the GOC-73 than with the Jennings BT. The spatial distribution scale can also be relevant in the case of structuring species. Although structuring species always showed higher abundance and biomass values in the Jennings BT, the number of samples where they are present varied depending on their distribution. For example, the crinoid *Leptometra phalangium*, that showed high abundance values with both gears, presented a higher occurrence in the Jennings BT samples, whereas the bamboo coral *Isidella elongata*, which showed low abundance with both gears, presented a higher occurrence in the GOC-73 samples. Both species have aggregated distributions in the western Mediterranean, are sensitive to bottom trawling (Colloca *et al*., 2004; Maynou & Cartes, 2011), and have been spatially assessed from MEDITS data (Colloca *et al*., 2004; Carbonara *et al*., 2022; Georges *et al*., 2024). However, while populations of *L. phalangium* are still widely present in the area, *I. elongata* populations have suffered a clear reduction (González-Irusta *et al*., 2022). On the other hand, while biomass of algae species was higher in the Jennings BT samples, the big and structuring species *Laminaria rodriguezii* presented higher occurrences with the GOC-73 than with the Jennings BT. This is especially relevant, because algal communities are of high importance in the shallow shelf of the western Mediterranean, increasing biodiversity and secondary production, structuring habitats, and providing food and shelter to fishing resources (e.g., Ballesteros, 1994; Ordines & Massutí, 2009; Ordines *et al*., 2009; Barberá *et al*., 2012). These bottoms, together with cri-

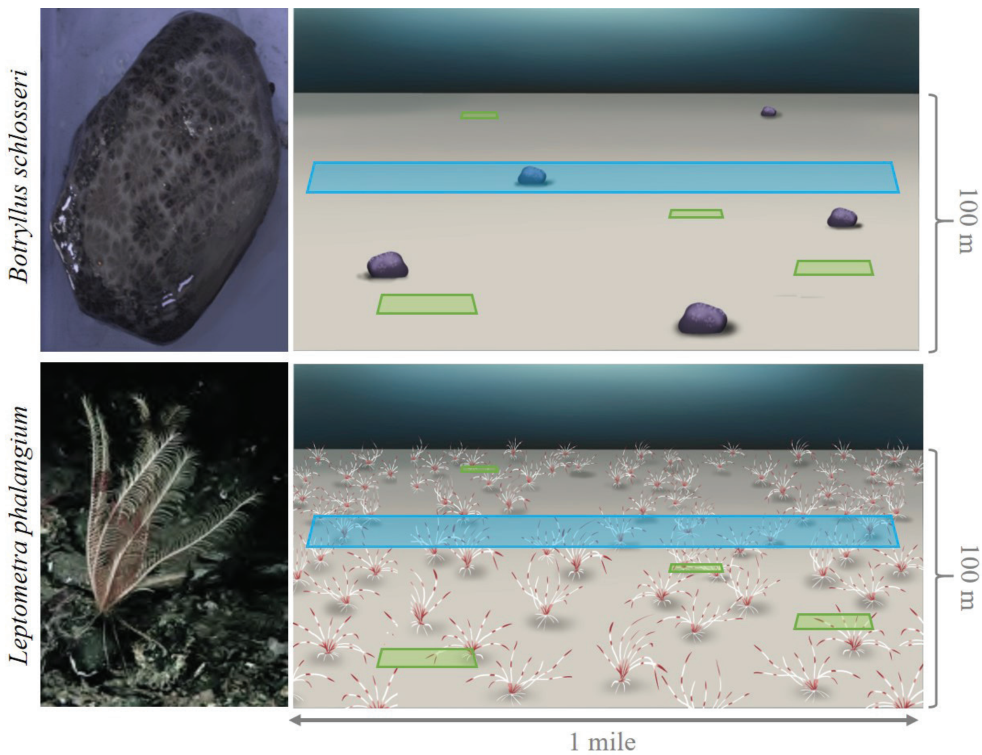

Fig. 7: Diagram showing the complementarity of the Jennings beam trawl (in green) and the experimental bottom trawl GOC-73 (in blue) for sampling the ascidian species with low frequency of appearance *Botryllus schlosseri* and the crinoid species distributed in patches *Leptometra phalangium*.

noids and bamboo coral beds are considered Sensitive Habitats and Essential Fish Habitats of the Mediterranean (STECF, 2006), so their location and characterization is a priority of the scientific advice for the management in the area to identify and delimit priority areas for the protection of these species and habitats.

The larger area sampled with the GOC-73 relative to that sampled by the Jennings BT can be a disadvantage for an accurate sampling of benthic communities, because several benthic biocenosis may be present in the sampled area during a single GOC-73 haul. Despite the smaller area covered by the Jennings BT, its use gives more precise information about the location of benthic species and the patchy distribution of benthic habitats, which is a highly relevant factor to properly characterize and map epibenthic communities. According to Callaway *et al*. (2002), bottom trawl sampling allows increased spatial coverage while providing information for broad a description of the community structure. It should be noted that the registration of non-commercial invertebrate species is not mandatory in the MEDITS protocol (Stamouli *et al*., 2022). Also, there is a faster flattening of species accumulation curves for the GOC-73 than with the Jennings BT. These two facts reveal that GOC-73 is not precise enough for a detailed and comprehensive description of the components of the benthic communities, as the maximum number of detectable species is much lower than that obtained using the Jennings BT. However, evident differences from the point of view of biomass per species obtained from both samplers make more difficult the recognition of facies than habitats from GOC-73.

The low accuracy of the GOC-73 to estimate the abundance and biomass of epibenthic species is especially relevant for the MSFD framework, as benthic habitat indicators are used to assess the GES of the ecosystem, which relies on the appropriate estimations of abundance and/or biomass of epibenthic species for the cartography and characterization of benthic communities and the assessment of the sensitivity of habitats to anthropogenic impact.

Although estimations of abundance and biomass from the Jennings BT are better, its catching efficiency is below 50% for most epibenthic species (Reiss *et al*., 2006). The density of *L. phalangium* and *Funiculina quadrangularis* estimated from video sampling was higher than that obtained with the Jennings BT. The low profile of *L. phalangium* over the seafloor could explain why some individuals can escape, specially from the GOC-73; in the case of the stem-like sea pen *F. quadrangularis*, its flexibility and body partially buried in the sediment make it difficult to sample using both the GOC-73 and the Jennings BT. These characteristics of *F. quadrangularis* make it less sensitive to trawling (Pierdomenico *et al*., 2018). Other species traits like the withdrawal behavior of the sea pen *Pennatula rubra* (Chimienti *et al*., 2018) could make sampling through images easier.

Because of these species characteristics, the inclusion of other sampling methodologies such as images of the seabed and its biota taken with photogrammetric sleds, is necessary to complement sampling with both the Jennings BT and the GOC-73; this approach would give more precise and valuable information on the abundance of some species and their distribution. Imagery acquisition systems have better geographical precision, which aids in determining the exact location of species and provides higher spatial resolution data than both the Jennings BT and the GOC-73. This is especially relevant for mapping patchily distributed species and identifying the protected ones, and can allow monitoring of their protection. *In situ* images can also give relevant information about the life-history traits of species that could help to implement indices or indicators (based on species sensitivity to specific stressors) to assess habitats' conditions (González-Irusta *et al*., 2018; Serrano *et al*., 2022).

The Jennings BT and the GOC-73 samplers are undoubtedly useful tools that provide biomass estimations and allow better species identification than photogrammetric sleds, particularly those that are hidden among structuring species. For instance, image video sampling has not been able to detect the ophiuran species *Ophiomyces grandis* (Ordines *et al*., 2019), which is highly abundant on the Mallorca Channel Seamounts (Massutí *et al*., 2022).

In conclusion, beam trawls and bottom trawls are complementary sampling methods that, together with imagery acquisition systems, are needed to get an accurate estimation of the epibenthic and nectobenthic communities. The use of these methodologies will improve the biodiversity estimations and the description of benthic habitats, allowing a better assessment of the anthropogenic impacts that affect them, hence improving the objectives posed by the MSFD.

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Supplementary Data

The following supplementary information is available online for the article:
Table S1. Mean values (Mean) and standard errors (SE) of the abundance (individuals/250 m2) by taxonomic group, depth stratum (B, 51-100 m; C, 101-200 m; D, 201-500 m and E, 501-800 m), and sampling gear (BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73). Algae and Porifera are presented in kg/250 m2. Results of the paired-samples Wilcoxon test are shown (WX statistic and WX p-value). Significant differences are denoted by asterisks: * (<0.05), **(<0.01), *** (<0.001).
Table S2. Mean values (Mean S) and standard errors (SE) of Species richness (number of species or taxa) by taxonomic group, depth stratum (B, 51-100 m; C, 101-200 m; D, 201-500 m and E, 501-800 m) and sampling gear ('BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73). Results of the paired-samples Wilcoxon test are shown (WX statistic and WX p-value). Significant differences are denoted by asterisks: * (<0.05), **(<0.01), *** (<0.001).
Table S3. Results of SIMPER analysis, estimated from standardized biomass data showing mean biomass (B, g/250 m^2) and percentage contribution (%C) of each taxon contributing up to 90% of within-group similarity by depth stratum, and sampler (BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73).
Table S4. ANOSIM results comparing the composition of the Jennings beam trawl samples and the experimental bottom trawl GOC-73 samples by depth stratum (B, 51-100 m; C, 101-200 m; D, 201-500 m and E, 501-800 m). Significant differences are denoted by asterisks: * (<0.05), **(<0.01), *** (<0.001).