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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 Dam-*

age 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 man-

agement (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) N° 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) N° 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 nektobenthic 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 nektobenthic 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 (Bellás, 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

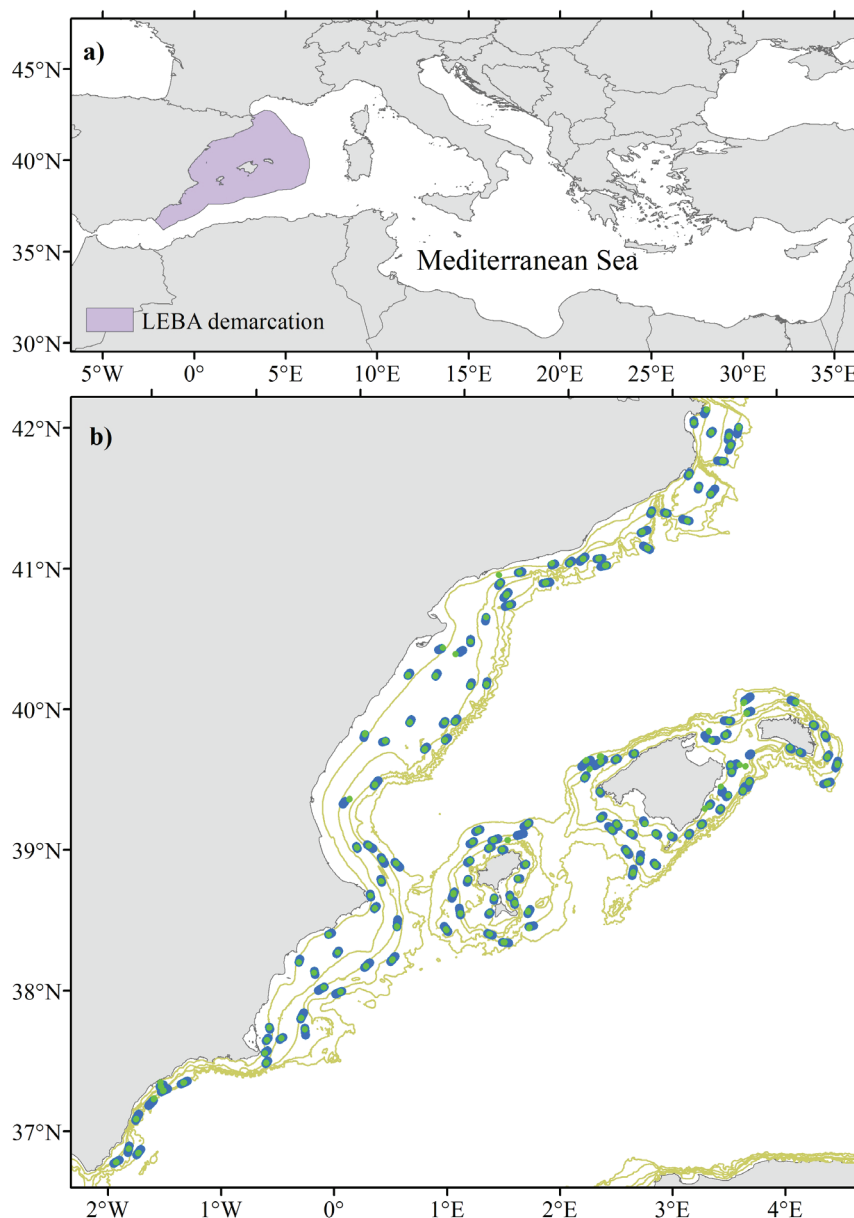


Fig. 1: Map of the study area showing: a) the LEBA demarcation, and b) the stations sampled with the Jennings beam trawl (green) and the experimental bottom trawl GOC-73 (blue), during CIRCA-LEBA and MEDITS surveys, respectively. The isobaths represent 50, 100, 200, 500 and 800 m depth.

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 Morgère otter boards, each one weighing 350 kg and with a surface of 2.5 m²; 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 45°. 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 m² with the GOC-73 and 213184 m² with the Jennings BT.

For each gear, the abundance and biomass of each species in each sample were standardized to 250 m², 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 km²) 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 m² 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

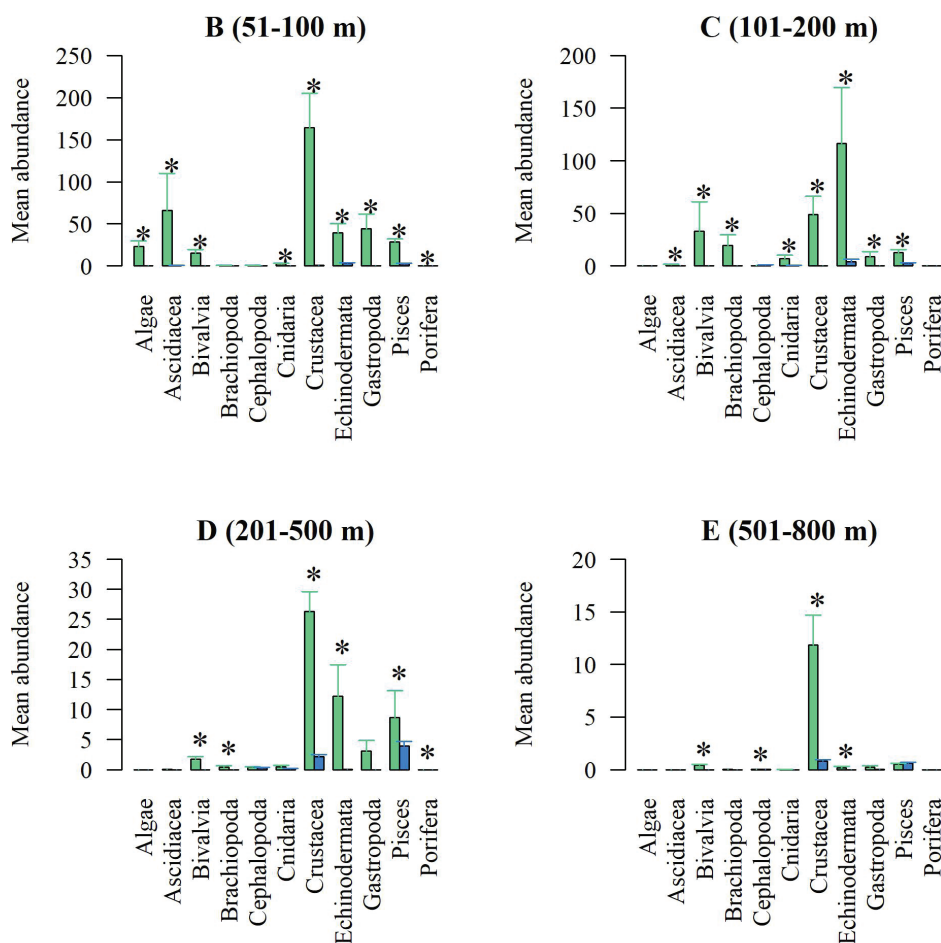


Fig. 2: Mean standardized abundance and standard error by taxonomic group and depth stratum. Values are abundance (individuals/250 m²), for all groups, except Algae and Porifera, whose values are biomass (kg/250 m²). Green and blue represent the Jennings beam trawl and the experimental bottom trawl GOC-73, respectively.

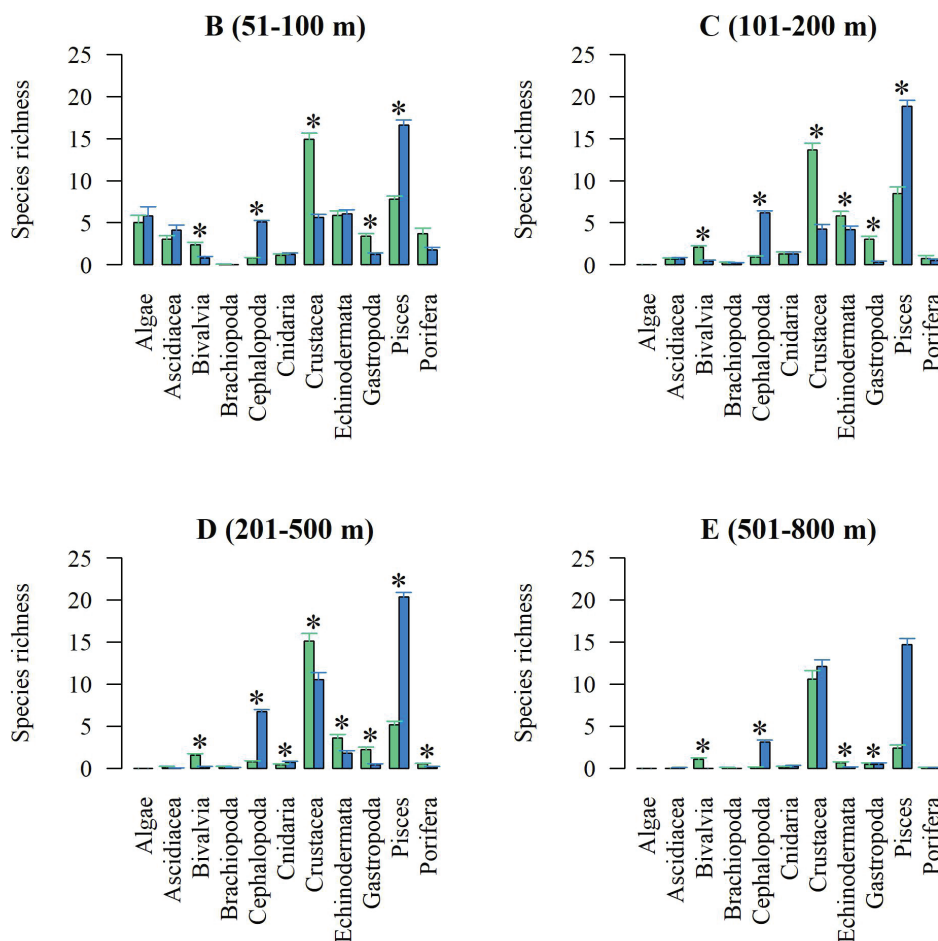


Fig. 3: Mean species richness (number of species or taxa) by taxonomic group and depth stratum. Green and blue represent the Jennings beam trawl and the experimental bottom trawl GOC-73, respectively.

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

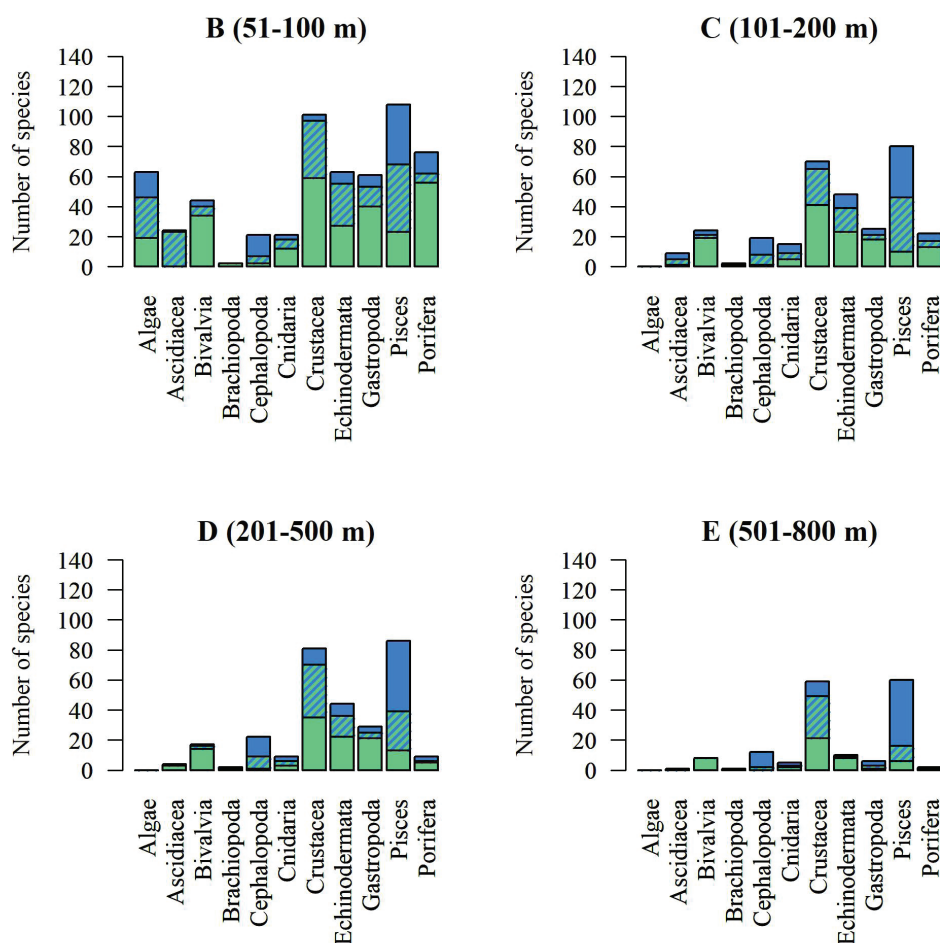


Fig. 4: Total number of species or taxa by taxonomic group and depth stratum. The number of species detected using both gears is represented as green and blue stripes. Green and blue represent the Jennings beam trawl and the experimental bottom trawl GOC-73, respectively.

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 *Odondebuena 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-

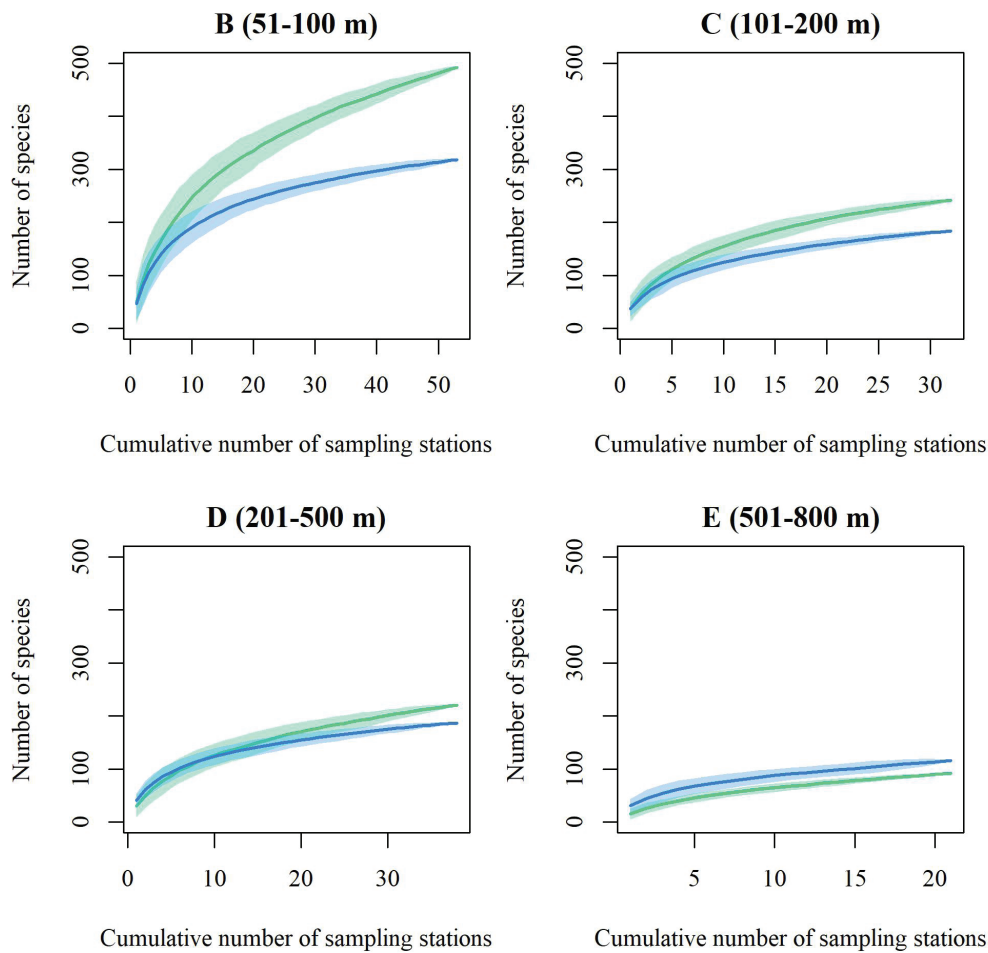


Fig. 5: Species accumulation curves for each sampler and depth stratum. Green and blue represent the Jennings beam trawl and the experimental bottom trawl GOC-73, respectively.

Table 3. Taxa showing the highest mean abundance (A, individuals/250 m²) 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 m².

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

Continued

Table 3 continued

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

Continued

Table 3 continued

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

Table 4. Taxa showing the highest mean abundance (A, individuals/250 m²) 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 m².

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

Continued

Table 4 continued

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

Continued

Table 4 continued

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

Table 5. Taxa showing the highest mean abundance (A, individuals/250 m²) 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 m².

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

Continued

Table 5 continued

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

Table 6. Taxa showing the highest mean abundance (A, individuals/250 m²) 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 m².

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

Continued

Table 6 continued

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

Table 7. Mean values (Mean) and standard errors (SE) of forming habitat species abundance (A, individuals/250 m²) and biomass (B, g/250 m²). BT, Jennings beam trawl; GOC, experimental bottom trawl GOC-73.

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

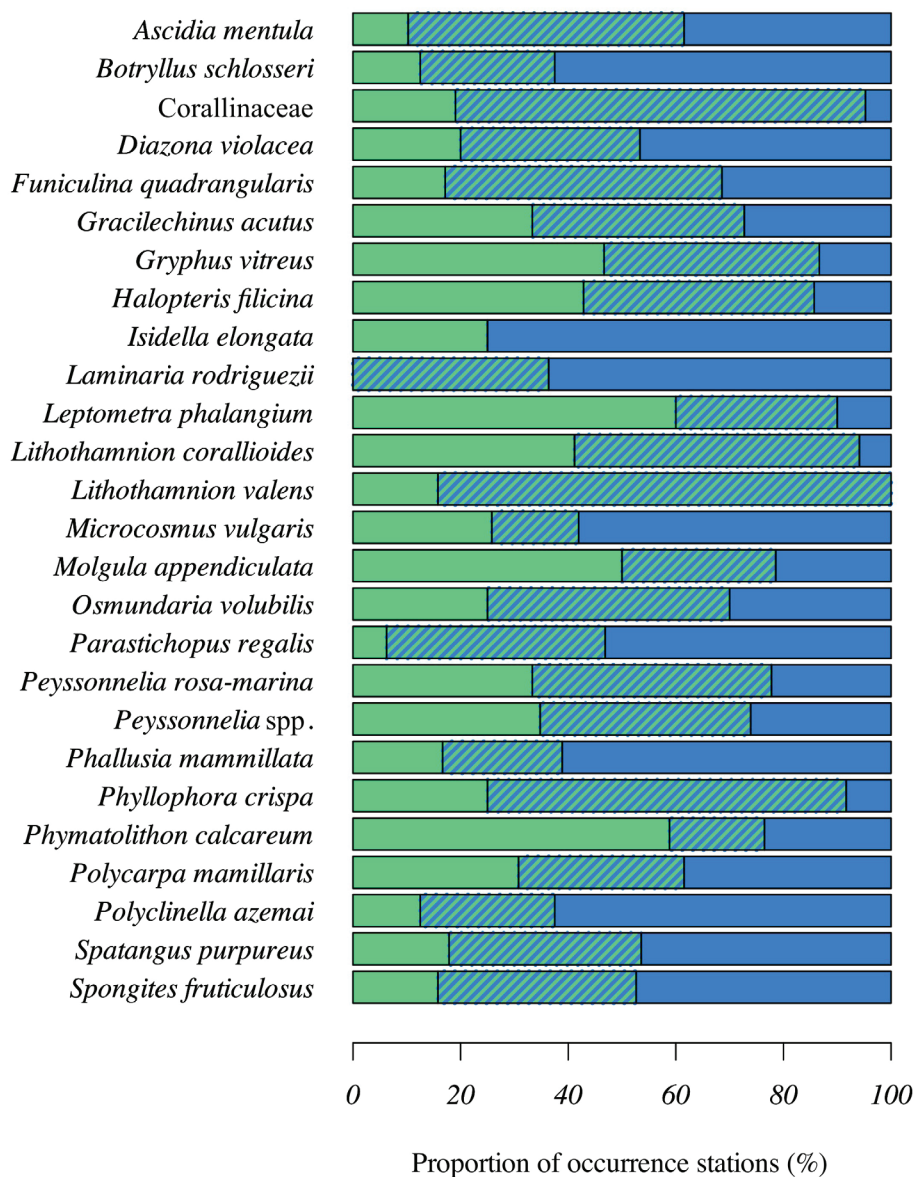


Fig. 6: Percentage of stations in which each of the habitat-forming species appeared. Percentage of stations detected using both gears is represented as green and blue stripes. Green and blue represent the Jennings beam trawl and the experimental bottom trawl GOC-73, respectively.

Table 8. Abundance (individuals/250 m²) 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 were caught with all samplers are shown.

Species	Station	BT	GOC	PS
<i>Leptometra phalangium</i>	1	2.37	0.04	5.38
	2	113.04	0.03	477.86
	3	58.29	46.02	1221.64
	4	970.72	7.74	1872.03
	5	96.72	74.80	1040.21
<i>Funiculina quadrangularis</i>	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
	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 mas-*

sutii, 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*, *Histioteuthis 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 coindetii* 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-

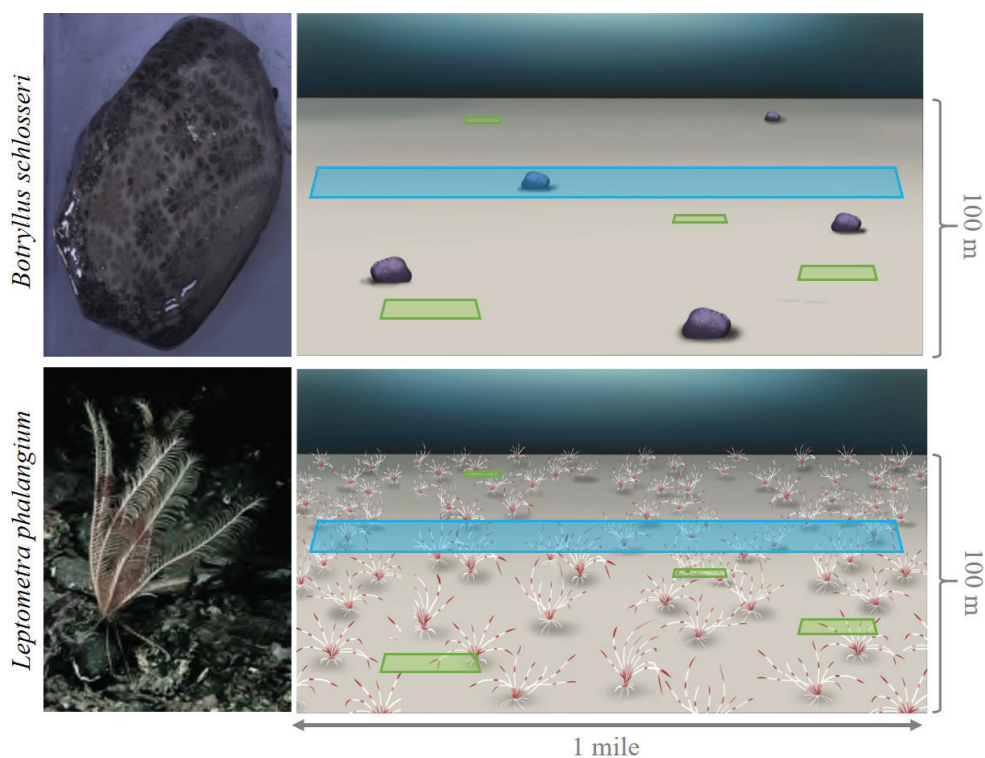


Fig. 7: Diagram showing the complementarity of the Jennings beam trawl (in green) and the experimental bottom trawl GOC-73 (in blue) for sampling the ascidian species with low frequency of appearance *Botryllus schlosseri* and the crinoid species distributed in patches *Leptometra phalangium*.

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 m²) 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).