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Comparison between ROV video and Agassiz trawl methods for sampling deep water fauna of submarine canyons in the Northwestern Mediterranean Sea with observations on behavioural reactions of target species.

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Abstract

In this paper we present a comparison between Remotely Operated Vehicle (ROV) and Agassiz trawling methods for sampling deep-water fauna in three submarine canyons of the Northwestern Mediterranean Sea and describe the behavioural reactions of fishes and crustacean decapods to ROV approach. 10 ROV dives, where 3583 individuals were observed and identified to species level, and 8 Agassiz trawls were carried out in a depth range of 750 to 1500 meters. As noticed in previous studies, abundances of fishes and decapod crustaceans were much higher in the ROV videos than in Agassiz trawl samples, as the latter are designed for the retrieval of benthic, less motile species in permanent contact with the bottom. In our observations fish abundance was one order of magnitude higher with ROV (4110.22 ind/km^2) than with Agassiz trawl (350.88 ind/km^2), whereas decapod crustaceans were six times more abundant in ROV videos (6362.40 ind/km^2) than in Agassiz samples (1364.52 ind/km^2).

The behaviour of highly motile fishes was analysed in terms of stationary positioning over the seafloor and avoidance or attraction to ROV approach. The most frequently occurring fish species *Coelorinchus mediterraneus*, *Nezumia aequalis*, *Bathypterois dubius*, *Lepidion lepidion*, *Trachyrincuss scabrus* and *Polyacanthonotus rissoanus* did not react to the presence of the ROV in most cases (>50%). Only *B. dubius* (11%), *L. lepidion* (14.8%), *P. rissoanus* (41%) and *T. scabrus* (14.3%) reacted to ROV approach. More than 60% of less motile species, such as crustacean decapods, did not respond to ROV presence either. Only 33.3% of *Geryon longipes*, 36.2% of *Munida* spp. and 29.79% of *Pagurus* spp. were observed avoiding or defensively reacting to the ROV.

The comparison of results obtained with ROV and trawl sampling is of ecological relevance since ROV can report observations in areas where trawling is technically unfeasible. The lack of reaction by most fish and crustacean decapod specimens further confirms that ROV surveying is an efficient technique to assess abundance and species composition in deep-sea waters for these motile species and questions trawl-based estimations.

Keywords: Animal behaviour, submarine canyon, deep-sea, Northwestern Mediterranean Sea, ROV observations, Agassiz trawl

1. Introduction

Our perception of the composition, distribution and overall biodiversity of marine communities should carefully consider the spatio-temporal modulation of species behaviour (Aguzzi *et al.*, 2012). Knowledge of reaction behaviour is highly relevant to evaluate species vulnerability to commercial trawling (Lorance and Trenkel, 2006), which is of great relevance for the management of fisheries (Aguzzi *et al.*, 2014; Bahamon *et al*., 2009). However, the behaviour of deep-sea fauna is still poorly understood (Lorance and Trenkel, 2006) and is a potential source of bias in stock assessments.

The use of different sampling systems, such as Remotely Operated Vehicle (ROV) observations and trawling, may lead to variations in species composition. Small scientific bottom beam trawls, such as Agassiz trawls, are designed for the retrieval of benthic, less motile species in permanent contact with the bottom (Tecchio *et al.*, 2011), while video surveys with underwater vehicles have been used to assess densities of demersal fish populations both in trawlable and non-trawlable areas (Stoner *et al.*, 2008). Sampling variability also is tightly related to the behavior of deep-sea fauna (Lorance and Trenkel, 2006) and to the size and speed of sampling devices. Bottom trawls have higher chances to catch motile species the larger their opening and speed over the ground (Glass and Wardle, 1989; Gordon and Duncan, 1985; Merrett *et al.*, 1991; Gordon and Bergstad, 1992). Quantitative statistical comparisons between trawling and ROV-based video surveys have shown that distance off ground, body size and spatial dispersion had strong relationships with relative trawl availability, which is the ratio of population density estimates from a scientific bottom-trawl survey to those derived from ROV visual strip transects. The way different species react to an ROV is not correlated to relative trawl availability according to Trenkel *et al.* (2004a). Laboratory and field experiments using ROVs and also cabled observatories have been carried out to understand how animal behaviour influences sampling variability (Mauchline and Gordon, 1984; Uiblein *et al.*, 1998; Aguzzi *et al.*, 2012; Sarda and Aguzzi, 2012; Doya *et al.*, 2013).

1.1 Behavioural analyses from ROV observations

ROV video surveys have been increasingly used in areas where trawl hauling is technically unfeasible (Collins *et al.*, 1999; Lorance *et al.*, 2000; Priede and Bagley, 2000). ROV video records have provided valuable qualitative data on behaviour of deep-sea fauna (Lorance *et al.*, 2002; Uiblein *et al.*, 2002; Trenkel *et al.*, 2004a). They have also shown how presence and abundance of deep-sea fishes are associated to complex temporal and spatial variations in oceanographic conditions (Collins *et al.*, 1999; Lorance *et al.*, 2000; Priede and Bagley, 2000; Ryer *et al.*, 2009; d'Onghia *et al.*, 2011; Capezzuto *et al.*, 2012). Disturbance reactions rather than attraction to an approaching ROV have been reported (Uiblein *et al.*, 2002, 2003; Trenkel *et al.*, 2004b; Lorance and Trenkel, 2006). Variations in fish detection were associated to the ROV technology itself, with fishes being attracted or scared by the vehicle approaching, possibly due to artificial lighting, engine noise, electrical fields and motion-induced water pressure changes (Cailliet *et al.*, 1999; Lauth *et al.*, 2004; Trenkel *et al.*, 2004b; Stoner *et al.*, 2008).

The composition, abundance and diversity of deep-sea demersal fish and crustacean assemblages in the Northwestern Mediterranean Sea, and the biology of individual species, have been studied by several authors (e.g. Cartes and Sarda, 1992; Stefanescu *et al.*, 1993; Carrasson, 1994; Cartes *et al.*, 1994). In contrast, behavioural analyses of demersal fauna derived from ROV observations in the Mediterranean Sea are restricted to the study of the small-scale feeding behaviour of some fish species in submarine canyons of the Central Mediterranean Sea (d'Onghia *et al.*, 2015) and of conservative life strategies adapted to great depths in the Eastern Mediterranean Sea (Gates *et al.*, 2012). For crustacean decapods, ROV video behavioural data are currently scant in the deep-sea in general (Poupin *et al.*, 2012), with few examples from the Mediterranean Sea (e.g. the carrying behaviour of *Paromola cuvieri* (Risso, 1816); Capezzuto *et al.*, 2012).

1.2 The North Catalan continental margin

Three major submarine canyons dissect the North Catalan continental margin, which from north to south are the 95 km long Cap de Creus canyon, the 105 km long La Fonera canyon (also known as Palamós canyon) and the 180 km long Blanes canyon (Amblas *et al.*, 2006; Lastras *et al.*, 2011). The heads and upper courses of these canyons are deeply indented into the continental shelf (Fig. 1). The dominant bottom type is muddy, although rocky outcrops are common in the canyon heads and upper courses. The detailed characteristics of these canyons are summarized in Canals *et al.* (2013).

The three canyons are able to capture dense waters that form seasonally and descend from the continental shelf carrying sediment, food and pollutants to the deep (Canals *et al.*, 2006, 2013; Ulses *et al.*, 2008; Salvado *et al.*, 2012), as well as sediment-laden flows resulting from severe coastal storms (Palanques *et al.*, 2005; Martin *et al.*, 2006; Sanchez-Vidal *et al.*, 2012). The proximity of their heads to the shoreline, which is less than 1 km for La Fonera canyon, enhances the trapping ability of coastal and shelf flows by these canyons and strongly influences their overall dynamics (Canals *et al.*, 2013).

The oceanography of the study area is characterised by the Northern Current, a steady mesoscale current flowing south-westward over the shelf and slope incised by the submarine canyons (Millot, 1999). The Northern Current has a baroclinic component from surface to approximately 400 m depth (i.e. within the depth range of our study) and is associated to a shelf-slope density front that separates colder, fresher waters over the continental shelf from saltier, warmer waters over the outer continental margin and basin (Font *et al*., 1988).

Here, we aim at extending current knowledge on the behaviour of deep-sea demersal fishes and invertebrates by ROV video observations performed in the above-mentioned three large submarine canyons of the Northwestern Mediterranean Sea, namely Cap de Creus, Blanes and la Fonera canyons. Estimates of species abundances from video images are compared with data from Agassiz trawls, in order to evaluate the biasing effects of species behaviour in terms of motility and reaction to these sampling tools.

2. Material and methods

2.1 ROV video sampling

The investigated submarine canyons (Fig. 1) were explored in summer 2011 on board *R/V Sarmiento de Gamboa* with the "Liropus 2000", a Super-Mohawk ROV rated to 2000 m depth. The ROV was equipped with four video cameras, including a frontal full HD Kongsberg OE14-502A camera (1920 x 1080 of resolution and 10X-optical zoom), a frontal colour Kongsberg OE14-366 camera used for quantitative analyses and two movable auxiliary Kongsberg OE14-502A mini-cameras mounted on the ROV arm or, alternatively, on the tether management system (TMS). Two parallel laser beams with 15 cm separation within the field of view of the camera provided a reference scale for size measurements. Underwater positioning while in operation was performed by using a high-precision HiPAP 350P Simrad USBL acoustic system with a position accuracy of 0.3% of the range and a range of detection accuracy of less than 20 cm linked to the Differential Global Positioning System (DGPS) of the vessel.

A total of 10 dives were conducted close to the bottom (50-100 cm above seabed), with a constant speed of 1.2 knots in the upslope direction. The area inspected during each ROV transect was calculated following Tubau *et al*. (2015). The length of each transect was multiplied by the field of view width (3 m in average) of the frontal colour Kongsberg OE14-366 ROV reference camera. In total, 19 hours of video filming were recorded, resulting in a total swept area of ~35,367 m^2. Most dives were performed along the relatively flat floor of the three canyon axes at depths between 750 m and 1570 m (Table 1 and Fig. 1). The only exception was a dive conducted over the northern wall of La Fonera canyon from 985 m to 570 m depth, which traversed a steep rocky slope but no modification of the ROV operating procedure was required.

The taxonomical identification and counting of individuals was carried out for each dive by analysing the videos in a time-lapse mode (i.e. at 50% of travelling speed). All detected animals were classified to the lowest possible taxonomic level according to current faunal guides (Zariquiey, 1968; Mercader *et al*., 2001) and validated Internet resources (e.g. www.marinespecies.org, www.marbef.org/). All video frames for any given transect had a stamped time code to ensure that each detected faunal entry could be linked to a precise geographic positioning, dive timing and water depth.

2.2 Agassiz trawl sampling

In comparison to larger otter trawls, the Agassiz dredge allows better manoeuvrability in complex geomorphological environments such as submarine canyons (Holme and McIntyre, 1971). Agassiz trawling was therefore conducted in order to ground-truth ROV video observations, and to provide a comparison between the two methods. Five trawls were carried out 24 hours after ROV dives and following the previous ROV tracks along the axes of Cap de Creus, La Fonera and Blanes canyons in a depth range from 750 to 1569 m (Table 1 and Fig. 1). The trawl mouth was 2.5 m wide and had 1.2 m of vertical opening, and the net mesh was 12 mm. Hauls were carried out in a down-canyon direction, resulting in a total swept area of ~128,250 m². The area for each haul was estimated according to Tecchio *et al*. (2013) by multiplying the horizontal mouth opening of the net by the haul track length. Cable tension, presumed scope and sinking speed were used to estimate times of arrival and departure from the bottom. The vessel's navigation was used to calculate the length of each transect, using the ArcGis 10.2.1 software.

All specimens were sorted on board, cleaned, counted and weighed. Animals were split into three groups for subsequent treatment: some were fixed in 10% formalin, others were placed in absolute ethanol (for molecular analyses, not included in this study), and the last were dried. They were subsequently stored in the Biological Reference Collection of the Institute of Marine Sciences (ICM-CSIC), in Barcelona.

2.3 Behavioural analyses

Behavioural analyses were conducted for fishes, which are epibenthic swimmers, and crustacean decapods, which are both swimmers and walkers with mixed epibenthic and endobenthic behaviour (Aguzzi and Company, 2010). Notes were also made on other abundant crawling invertebrates of ecological relevance in the area, such as irregular sea urchins (Mecho *et al*., 2014).

Fish behaviour and reaction to ROV approach was divided into two categories according to Uiblein *et al*. (2002, 2003), Lorance and Trenkel (2006), Stoner *et al*. (2008), and Ryer *et al.* (2009): undisturbed and disturbed. The *undisturbed category* was divided into two sub-categories: *station-holding*, for individuals displaying slow movements in order to preserve their seabed position, and *passive drifters*, for animals that were transported by water motion since fully immobile. The *disturbed category* was also divided in two subcategories: *avoidance*, for animals quickly swimming out of the field of view, and *attraction*, for animals approaching the ROV.

Behavioural observations of crustacean decapods were annotated following the same classification used for fishes, although motionless and very low rate of movement specimens were excluded from this analysis. For crustaceans additional notes were made of species reactions in relation to aggressive territoriality, burying, shelter and the relationship with litter. Percentages of individuals observed per species and category of reaction were calculated.

A Chi-square test by means of contingency tables was performed with *Statgraphics Centurion XVII* (www.statgraphics.com/centurion-xvii) in order to test the hypothesis that different species have different reactions to the ROV approach. This analysis was carried out only for the most abundant species of fishes and crustaceans to ensure the robustness of the results.

2.4 Comparison between ROV and Agassiz trawl sampling

Data obtained with ROV video imaging and Agassiz trawls were grouped at family level and compared in order to quantify potential sampling biases at different depths and locations. The aim was to assess if species behaviour could be an important factor influencing sampling with indirect (video) and direct (haul) methods. To do so numbers of video-detected and trawl caught individuals were standardized to units of transect surface (km^2) per each family. Species densities were calculated as the ratio between the number of individuals and the inspected area during each dive or haul.

Differences in family composition and abundances due to the sampling method were screened with non-parametric statistics. In order to remove the potential effect of bathymetry and location we considered the comparison of paired-samples collected in ROV dives (D) and Agassiz hauls (A) in the same location and depth (Table 1): D8-A1, D9-A2, D31-A5, D32-A6 and D33-A7. This paired-samples comparison is justified by the assumption that animal behavioural reactions to the perturbing presence of the ROV are constant over depth and independent of location within the canyon. Therefore, these two variables were not taken into account in our analyses, with all species derived from these transects being grouped and compared considering the sampling method only. Levels of similarity among taxa composition and abundance were ordered in a two-dimensional plane through distance matrices and visualised using Nonmetric Multidimensional Scaling (NMDS) scatterplots. The "meta-MDS" function in the "vegan" library in R (R Project for Statistical Computing, http://www.r-project.org/) was used to perform the analyses of data collected using the two sampling methods. The function standardizes the scaling in the result for easier interpretation of taxa ordination. Furthermore, permutation tests were performed by the function "envfit" in "vegan", allowing investigating for potential significant effects of sampling methods (factor variables) on taxa ordination. The test uses r^2 (squared correlation coefficient) as a goodness-of-fit statistic.

3. Results

A total of 3583 individuals were observed by ROV surveying, belonging to seven different Phyla and one Subphylum (see Supplementary Material, Table S1). Agassiz trawl sampling provided 557 individuals, which were classified in seven Phyla and one Subphylum (see Supplementary Material, Table S2).

3.1 ROV behavioural analyses for fishes

Several species of deep-sea demersal fishes were commonly observed, such as *Coelorinchus mediterraneus* (Iwamoto and Ungaro, 2002), *Nezumia aequalis* (Günther, 1878), *Bathypterois dubius* (Vaillant, 1888), *Lepidion lepidion* (Risso, 1810), *Trachyrincus scabrus* (Rafinesque, 1810) and *Polyacanthonotus rissoanus* (De Filippi and Verany, 1857) (Fig. 2A-E). The behavioural reactions of these species to ROV approach are presented in Table 2. The chi-square test showed the relationship between type of reaction and species. The majority of the species were not disturbed by the ROV presence (Table 2), being the "stationary" and "drifting" behavioral reactions dominant in most of the analyzed species (i.e. accounting together for more than 50% in all cases). All undisturbed species remained horizontal with respect to the seabed, with two exceptions: *N. aequalis* maintained a nose-down body position inclined towards the bottom and *B. dubius* remained motionless resting directly on the seabed standing on the elongated rays of the caudal and pelvic fins in the classic "tripod" posture. Different avoidance reactions were observed in fishes. *Polyacanthonotus rissoanus* escaped by increasing their swimming activity with sudden zig-zag changes of direction. *Trachyrincus scabrus* and *L. lepidion* had a more complex behavioural reaction, generating mud puffs in front of the ROV, likely to confound the displacement trajectory (see Supplementary Material, Fig. S1A-B). In a single case, an individual of *L. lepidion* was found stationary, coiled on the seabed. *Bathypterois dubius* specimens also generated mud puffs while escaping, which seemed to result from irregular, awkward movements, in agreement with previous observations (Davis and Chakrabarty, 2011).

For species with less than three detected individuals no behavioural quantitative analysis was attempted: *Cyclothone braueri* (Jespersen and Tåning, 1926), *Hoplostethus mediterraneus* (Cuvier, 1829) and *Lepidorhombus boscii* (Risso, 1810) were found drifting, while *Lampanyctus crocodilus* (Risso, 1810), *Nettastoma melanurum* (Rafinesque, 1810), *Notacanthus bonaparte* (Risso, 1840) and *Chimaera monstrosa* (Linnaeus, 1758) were observed stationary. Only *Alepocephalus rostratus* (Risso, 1820) was disturbed by ROV approach, escaping without generating mud puffs.

3.2 ROV behavioural analyses for crustacean decapods and other invertebrates

Eight different species of decapods were observed and identified although only three were commonly found in all three canyons: *Geryon longipes* (A. Milne-Edwards, 1882), *Pagurus* spp. and *Munida* spp. (Fig. 2F-H). Undisturbed reactions to the presence of the ROV (Table 3) were generally observed in these species. The analysis showed that 117 individuals out of 156 remained stationary as the ROV passed by (66.67% of *G. longipes*, 82.98% of *Munida* spp. and 61.70% of *Pagurus* spp). Those individuals reacting to the presence of the ROV performed a wide range of responses (Table 3). *Pagurus* spp. were observed running away, leaving undulated tracks on the muddy seabed (see Supplementary Material, Fig. S1C). Some deep-sea *G. longipes* crabs displayed burrowing and burying behaviour, with the latter directly observed as digging activity until complete body coverage (see Supplementary Material, Fig. S1D). While doing this, these crabs triggered mud puffs that concealed their presence. In the case of *Munida* spp. some individuals (10.64%) performed a defensive behaviour, projecting their claws forwards at the entrance of their tunnels or shelters, either natural or made of marine litter (see Supplementary Material, Fig. S1E).

Specimens of the red shrimp *Aristeus antennatus* (Risso, 1816) were observed always as isolated individuals and not grouped in schools. They were always disturbed by the ROV approach showing avoidance responses, with various evasion trajectories depending on their distance to the ROV. Distant individuals (i.e. 2.5 to 3.5 m) escaped by a mixture of crawling and swimming, whereas when ROV approached closer swimming speed abruptly increased and animals escaped upwards into the water column out of the field of view.

3.3 Aggregation behavior

The holothurian *Mesothuria intestinalis* (Östergren, 1896) and the irregular echinoid *Brissopsis lyrifera* (Forbes, 1841) were observed forming aggregations, either of exposed or buried individuals. Locally, herds of hundreds of *B. lyrifera* individuals left pervasive marks on the soft seafloor. The largest *Brissopsis* herds were found in La Fonera canyon, while carcasses of dead specimens were observed both in huge aggregations forming extensive thanatocenoses and as solitary corpses in La Fonera and Blanes canyons (see Supplementary Material, Fig. S2). In some dives we also identified the regular echinoid *Gracilechinus elegans* (Düben and Koren, 1844) among *Brissopsis* herds.

3.4 Comparison of assemblages sampled by ROV and Agassiz trawls

NMDS of equivalent ROV transects and Agassiz hauls showed significant differences between the sampling methods when factors like depth and location were removed ($p = 0.01$, r2 = 0.47, p-value based on 999 permutations) (Fig. 3). The majority of taxonomic groups of fishes were most highly represented in ROV video surveys, but were rather scarce in Agassiz trawl samples. Species belonging to families Moridae, Macrouridae, Notacanthidae or Inopidae were sampled mostly by ROV and few were caught by the Agassiz trawl. Also, families belonging to crustacean decapod taxa, such as Aristeidae, Munididae and Paguridae, were best represented in ROV observations. In contrast, Agassiz mainly retrieved strictly benthic individuals belonging to different families such as Caryophylliidae and Oculinidae (Phylum Cnidaria), Aporrhaidae and Naticidae (Phylum Mollusca), and Phronimidae and Acanthephyridae (Phylum Crustacea).

3.5 Taxonomic composition and abundance from different sampling methods

Low motile individuals in Agassiz trawls accounted for more than 80% of the total number of specimens sampled (Fig. 4A), with Crustacea and Mollusca as the dominant groups. Fish species (Chordata) represented only 12.16% of the total individuals caught by Agassiz trawls compared with over 30% of the observations by ROV. The Subphylum Crustacea was slightly higher by percentage in the ROV data than in the trawls.

Abundance values of motile species were much higher in ROV observations. Fish abundance was one order of magnitude higher with ROV (4110.22 ind/km^2) than with Agassiz trawl (350.88 ind/km^2) and decapod crustaceans were six times more abundant (6362.40 ind/km^2) than in Agassiz trawls (1364.52 ind/km^2). Regarding strictly benthic groups, the trawls yielded higher abundances for Annelida (15.59 ind/km^2), Sipuncula (7.79 ind/km^2) and Mollusca (467.84 ind/km^2) than ROV observations, which detected zero Annelida and Sipuncula, and 112.61 ind/km^2 Mollusca.

Comparison between the two methods (Fig. 4B) showed that abundances for fish families such as Moridae (1970.65 ind/km^2), Macrouridae (844.57 ind/km^2) and Inopidae (506.74 ind/km^2) were one order of magnitude higher in ROV observations than within Agassiz trawl samples (163.74 ind/km^2 for Moridae, 31.19 ind/km^2 for Macrouridae and 15.60 ind/km^2 for Inopidae, respectively). Crustacean families Geryondidae, Munididae and Paguridae were also found in larger abundances in ROV video imagery than in trawl samples (Fig. 4B).

4. Discussion

The observed behaviour patterns illustrate the occurrence of different reactions to ROV presence in motile megafauna individuals, spanning from avoidance to indifference. Comparisons between ROV and Agassiz trawl sampling methods revealed that motile fauna was better sampled when using ROV than Agassiz trawl. Our results bring information on the role of behaviour as a modulator of the perceived composition of deep-sea faunal assemblages and species relative abundances, subsequently affecting biodiversity indexes calculated after one methodology or the other.

4.1 The behaviour of undisturbed fishes

ROV white artificial illumination represents a major source of photic interference, which is absolutely non-familiar to benthic and suprabenthic megafauna inhabiting the deep reaches of the investigated submarine canyons. Despite the majority of detected species of fishes and crustacean decapods possess large developed eyes and a distribution limit encompassing disphotic depth strata, most of them seemed to ignore the ROV. This indicates that artificial stimulation is somehow unperceived or, at least, not perceived as a threat. While monochromatic blue and green bioluminescence has been proven to be of ecological and evolutionary importance in regulating reproduction and predation in deep-sea species, high intensity white ROV lights do not seem to constitute a meaningful ecological signal (Widder, 2010), as suggested by Wilson and Smith (1984) for Macrouridae.

We observed several species showing either a passive drift by seabed currents or being engaged in active station holding while gently swimming to keep position. Other species were instead observed as performing a mixture of station holding and passive drifting. These behaviours should be analysed in relation to the energy budgets required by feeding, including prey spotting, in energetically impoverished deep-sea ecosystems (Childress, 1995).

Strict station holding was performed by *N. aequalis*, *C. mediterraneus* and *B. dubius*. *Nezumia aequalis* and *C. mediterraneus* feed on epi- and endobenthic organisms, usually hovering or actively searching into the sediment (Macpherson, 1979; Mauchline and Gordon, 1984; Carrasson, 1994). This feeding strategy may explain why *N. aequalis* has been found bending towards the bottom without touching it. When foraging, *Coelorinchus* sp. and related genera such as *Nezumia*, adopt a posture with the snout to the substrate and the tail elevated at a steep angle and the mouth protruding directly towards the substrate (Gartner *et al.*, 1997). However, we did not observe *C. mediterraneus* inclined towards the seabed, but horizontally set above it. This might be result of depth-dependent feeding strategies, as described for other *Coelorinchus* species

(Carrasson, 1994). *Coelorinchus mediterraneus* diet at great depths is based on benthopelagic and nektobenthic organisms (*sensu* Aguzzi and Company, 2010), which are not strictly associated to the sediment like epi- and endobenthic fauna. Most macrourid species use olfaction to locate baits (Gartner *et al*., 1997). This hovering behaviour has been reported in Northeastern Atlantic canyons, where most *N. aequalis* and *Coelorinchus* sp. specimens were observed actively searching into the sediment (Baker *et al.*, 2012).

Solitary specimens of *B. dubius* were found standing on their three fins on the seabed. This behaviour, also observed elsewhere (Trenkel *et al*., 2002; Baker *et al*., 2012; Gates *et al*., 2012), has been hypothesized to be a sensory mechanism. *Bathypterois* sp. are sit-and-wait predators facing into the current while feeding on small nektonic prey (Gartner *et al*., 1997). Their pectoral fins are held up in the enhanced current above the sea floor and possess well-developed sensory innervations, while the tripod formed by the caudal and pelvic fins allows them to stay in contact with the substrate (Sulak, 1977).

Lepidion lepidion, *T. scabrus*, and *P. rissoanus* displayed combined station holding and passive drifting. This alternative is the most common in demersal fishes such as macrourids, ophidiids, nothacanths and morids (Gartner *et al*., 1997). These predators are often found in loose aggregations continuously foraging while slowly moving along just above the substrate (Gartner *et al.*, 1997). Passive drift body stance seems to represent a save-energy mode for displacements over large seabed distances. Deep-sea eelpouts may use internal tidal water flows as corridors for low-energy budget displacements (Aguzzi *et al*., 2010).

4.2 Fish avoidance reactions

Avoidance reactions of deep-sea fishes to ROV approach have been attributed to illumination, motion related sound and pressure wave disturbances (Stoner *et al*., 2008) and viewed as a predator avoidance strategy (Hobson and Chess, 2001). However, resolving reasons for avoidance is not feasible with our video observations.

Studies carried out in the Bay of Biscay showed that most deep-sea species were weakly or not disturbed by ROV (Trenkel *et al*., 2002; Uiblein *et al*., 2003; Lorance and Trenkel, 2006). Less than 30% of all detected deep-sea demersal fishes showed ROV avoidance behaviours. Lorance and Trenkel (2006) found that shark species belonging to the order Squaliformes were the only ones clearly reacting to the ROV, but these species were missing from our observations.

Individuals for which avoidance reactions to our ROV were observed fast swam away with or without generation of mud puffs, the latter favoured by close proximity to the bottom along the escape trajectory. *Lepidion lepidion* and *T. scabrus* displayed zigzag escape trajectories when the ROV approached very close, likely as a means to confound predators. In the Atlantic Ocean, *Trachyrincus* spp. has been observed frantically swimming in fast short bursts as a reaction to ROV (Trenkel *et al*., 2002). Often *L. lepidion* did not completely disappear from the camera field of view, settling back again at shorter distance within the mud-cloud. To our best knowledge this short-run avoidance strategy is described for the first time here. It probably results from the balancing of opposite needs as the generation of an effective evasion response and the need to preserve energy. Such behaviour may convey information about the type of predators these species could encounter: a predator not pursuing its preys over large distances, and likely relaying on an ambushing strategy.

Conversely, *P. rissoanus* was highly disturbed by the presence of the ROV, but since it was always observed slightly more separated from the bottom, its escape did not generate mud puffs. Trenkel *et al*. (2002) also found that *Polyacanthonotus* sp. in the Atlantic Ocean had the highest sensitivity to ROV disturbance, always avoiding the vehicle with rapid movements of the caudal fin. *Bathypterois dubius* was caught by the camera escaping in one occasion, performing an awkward and irregular movement, as reported by Davis and Chakrabarty (2011). *Alepocephalus rostratus* and *L. crocodilus* were also observed reacting to ROV, but as only one individual of each was detected, no conclusions can be drawn.

4.3 Decapod crustaceans

Decapod crustaceans are the most abundant invertebrates of the deep Catalan continental margin (Abello *et al*., 1988; Company *et al.*, 2004). *Aristeus antennatus* was always observed as isolated individuals that exhibited fast swimming escape reactions to the ROV that matched with morphological adaptations recognized at rostral level (Aguzzi *et al*., 2008a). A curved rostrum redirects the individuals upwards when the swimming speed increases and animals suddenly disappear into the water column. These observations point out the occurrence of a significant behavioural bias on ROV visual observations for this species. Some fishing methods, like otter trawling, allow the commercial capture of large quantities of *A. antennatus*, suggesting aggregation in schools (Sarda *et al*., 2003). We suggest that large schools of individuals detect the ROV from distance and avoid it by leaving behind only sparse, isolated individuals to the chance of detection.

For the first time, we directly observed a mixed burying and burrowing behaviour for the deep-sea crab *G. longipes*. Once, one individual was observed sheltered in a large burrow. Previous works have only suggested such behaviour for this species, indicating it as circumstantial (Boyer *et al*., 1988; Attrill *et al*., 1991; Gates and Jones, 2010). Our observations of the capability of burying as an apparent avoidance response based on within-sediment sudden camouflage fully confirm an endobenthic life style.

The diversity of observations regarding the behaviour of *Munida* spp. suggests an opportunistic endobenthic mixed burrowing and sheltering life style. Although larger individuals were found in self-made burrows or sheltering in natural infracts, there was a significant number of animals using large litter leftovers, which are nowadays abundant in the deep-sea areas (Galil *et al*., 1995; Galgani *et al*., 2010; Ramirez-Llodra *et al*., 2011, 2013; Company *et al*., 2012) and seem to concentrate in submarine canyons according to some recent studies (Pham *et al*., 2014; Tubau *et al*., 2015). We also observed door-keeping behaviour (i.e. *Munida* spp. waiting at the entrance of their tunnels) and other sympatric burrowing species (e.g. *Nephrops norvegicus*) (Aguzzi *et al*., 2007, 2008b).

We also report for the first time avoidance responses in the Family Paguridae. Individuals were usually seen on the seafloor as running away of the ROV, leaving behind continuous rectilinear trails. Such trails are easily distinguishable from other faunal tracks (e.g. *Brissopsis* spp.; see further down), since they are markedly narrow and present lateral dot-like marks due to the animal-walking mode.

4.4 Gregarious invertebrates.

We observed in our ROV imagery large quantities of grouped live and dead irregular echinoids *B. lyrifera*, with the largest abundances of both death and alive at about 1500 m depth (dive 16) in the floor of La Fonera canyon (Fig. 1, Table 1 and Supplementary Material, Table S1). Living specimens were observed only in La Fonera canyon, while high numbers of dead specimens were reported both in La Fonera and Blanes canyons building up large thanatocenoses. This species performs displacements in large groups (Hollertz and Duchêne, 2001; Hollertz, 2002; Ramirez -Llodra *et al.*, 2008; Pawson and Pawson, 2013) and it is known to be highly abundant in submarine canyons (Mecho *et al.*, 2014). We also sampled living specimens by Agassiz trawling in all three investigated canyons.

The large amounts of *B. lyrifera* carcasses forming the observed thanatocenoses are probably the result of the transport of dead individuals from up-canyon, which is favoured by the oceanographic processes acting in these canyons and subsequent dynamics (cf. Section 1.2). Near-bottom currents in excess of 50 cm s^{-1} and occasionally 100 cm $s\text{-}^{-1}$ have been detected within the investigated canyons, being able to remobilise light sea urchin tests (Canals *et al.*, 2006; Puig *et al.*, 2008; Sanchez-Vidal *et al.*, 2012; Durrieu de Madron *et al.*, 2013). The very same processes transport down light litter that also concentrates in the axes and lower reaches of the investigated canyons as pointed out by Tubau *et al.* (2015).

We further noticed how the herds of this echinoid influenced the detection at small spatial scale of other sympatric invertebrate species. The few identified individuals of the regular echinoid *G. elegans* were always observed as associated with *B. lyrifera*. In contrast, aggregations of *M. intestinalis* were only detected in locations without *Brissopsis*, dead or alive. The absence of *M. intestinalis* nearby *B. lyrifera* might be related to the bioturbating capability of echinoids (Widdicombe and Austen, 1998), which shape the seafloor with its displacing marks. Such bioturbation could be detrimental for the settlement of *M. intestinalis* within the sediment.

4.5 Assemblage ground-truthing by ROV observations and Agassiz trawl sampling

Bottom-trawl surveys have been used to obtain abundance indices for fisheries management. Visual census methods using underwater vehicles such as ROVs and manned submersibles are increasingly applied to achieve the same goal (Trenkel *et al.*, 2004b). In submarine canyons, ROVs have been used to examine the occurrence, behavior, habitat specificity and patterns of deep-sea fauna (Baker *et al.*, 2012; Ross *et al.*, 2015). A wide range of factors can affect density estimations with both methods. In the case of trawling, these factors are related to gear configuration and fishing efficiency, and to species ecology and biology (Wardle, 1993; Engås, 1994). On the other hand, artificial illumination, motion sound and pressure wave disturbances can affect population assessments made with underwater vehicles (Stoner *et al.*, 2008). The behaviour of individuals is also an important aspect determining the species sampling efficiency (Mcintyre *et al.*, 2014). Some studies have demonstrated how the behaviour of deep-water fishes influences counts along transects (Trenkel *et al.*, 2004b). Biasing effects derived from animal's behaviour on ROV and Agassiz sampling outcomes should be higher for motile swimming species.

Agassiz trawl is not the best method for sampling fish. Otter trawl is usually considered a better method, but studies on fishes in the Atlantic Ocean have shown that video observations still provide superior density estimates in deep-sea environments (Uzmann *et al.* 1977; Adams *et al.*, 1995; Krieger and Siegler, 1996). Our results confirm this view, with higher numbers of motile species in ROV videos than in Agassiz hauls, which sampled more sessile organisms. Also, they indicate that ROV misses part of the sessile organisms either because they are poorly visible or not visible at all (e.g. when buried mostly or totally). Although species are different, recent studies on demersal fish distribution and associations in a number of habitats of the eastern Atlantic Ocean, including submarine canyons, have obtained abundance estimates that are somehow comparable to ours (Baker et al., 2012; Quattrini et al., 2015; Ross et al., 2015).

5. Conclusion

Our study provides new insights on the life-style of demersal species inhabiting deep submarine canyons. Behavioural observations indicate that only some fish individuals performed ROV avoidance reactions by swimming frantically, while some decapods displayed burying or aggressive behaviour. By contrast, most fish and decapod crustaceans seem to be mainly unaffected by ROV presence, with fishes remaining stationary or drifting in front of the vehicle. Agassiz trawling and ROV video imaging reported different composition and abundance values regarding these highly motile species. ROV performance is significantly better than Agassiz trawl to obtain abundance indices for fishes and some motile crustaceans.

These findings have significant implications as behaviour diversity directly affects population assessments. The lack of reaction by most specimens evidences that ROV surveying is a useful technique to assess abundance and species composition of motile species in deep-sea environments. Our results further question trawl-based estimations on such species groups.

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References

1. Abello, P., Valladares, FJ., Castellon, A. 1988. Analysis of the structure of decapod crustacean assemblages off the Catalan coast (North-West Mediterranean). Marine Biology, 98: 39-49. doi: 10.1007/BF00392657.
2. Adams, P.B., Butler, J.L., Baxter, C.H., Laidig, T.E., Dahlin, K.A., Wakefield, W.W. 1995. Population estimates of Pacific coast groundfishes from video transects and swept-area trawls. Fishery Bulletin, 93: 446–455.
3. Aguzzi, J., Company, J.B., Sarda, F. 2007. The activity rhythm of berried and unberried females of *Nephrops norvegicus* (Crustacea, Decapoda). Crustaceana, 80: 1121-1134. doi: 10.1163/156854007782008577.
4. Aguzzi, J., Costa, C., Antonucci, F., Company, J.B., Menesatti, P., Sarda, F. 2008a. Influence of rhythmic behaviour in the morphology of decapod Natantia. Biological Journal of the Linnean Society, 96: 517-532. doi: 10.1111/j.1095-8312.2008.01162.x.
5. Aguzzi, J., Sarria, D., Garcia, J.A., Del Rio, J., Sarda, F., Manuel, A. 2008b. A new tracking system for the measurement of diel locomotor rhythms in the

Norway lobster, *Nephrops norvegicus* (L.). Journal of Neuroscience Methods, 173: 215-224. doi:10.1016/j.jneumeth.2008.06.009.

6. Aguzzi, J., Company, J.B. 2010. Chronobiology of deep-water decapod crustaceans on continental margins. Advances in Marine Biology: An Annual Review, 58: 155–225. doi: 10.1016/B978-0-12-381015-1.00003-4. –Atenció!-
7. Aguzzi, J., Costa, C., Furushima, Y., Chiesa, J. J., Menesatti, P., Iwase, R., Fujiwara, Y. 2010. Behavioural rhythms of hydrocarbon seep fauna in relation to internal tides. Marine Ecology Progress Series, 418: 47-56. doi: 10.3354/meps08835.
8. Aguzzi, J., Company, J.B., Costa, C., Matabos, M., Azzurro, E., Manuel, A., Menesatti, P., Sarda, F., Canals, M., Delory, E., Cline, D., Favali, P., Juniper, S.K., Furushima, Y., Fujiwara, Y., Chiesa, J.J., Marotta, L., Priede, I.M. 2012. Challenges to assessment of benthic populations and biodiversity as a result of rhythmic behaviour: video solutions from cabled observatories. Oceanography and Marine Biology: An Annual Review, 50: 235-286.
9. Aguzzi J., Sbragaglia V., Tecchio S., Navarro J., Company J.B. 2014. Rhythmic behaviour of marine benthopelagic species and the synchronous dynamics of benthic communities. Deep-Sea Research I: Oceanographic Research Papers, 95: 1-11. doi:10.1016/j.dsr.2014.10.003.
10. Amblas, D., Canals, M., Urgeles, R., Lastras, G., Liquete, C., Hughes-Clarke, J.E., Casamor, J.L., Calafat, A.M. 2006. Morphogenetic mesoscale analysis of the northeastern Iberian margin, NW Mediterranean Basin. Marine Geology, 234: 3-20. doi: 10.1016/j.margeo.2006.09.009.
11. Attrill, M.J., Hartnoll, R.G., Rice, A.L. 1991. Aspects of the biology of the deep-sea crab *Geryon trispinosus* from the Porcupine Seabight. Journal of the Marine Biological Association of the United Kingdom, 71: 311-328. doi: 10.1017/S0025315400051626.
12. Bahamon, N., Aguzzi, J., Sarda, F. 2009. Fuzzy diel patterns in catchability of deep-water species on the continental margin. ICES Journal of Marine Science, 66: 2211-2218.
13. Baker KD, Haedrich RL, Snelgrove PV, Wareham VE, Edinger EN, Gilkinson KD. 2012. Small-scale patterns of deep-sea fish distributions and assemblages of the Grand Banks, Newfoundland continental slope. Deep-sea Research Part I: Oceanographic Research Papers, 65: 171–188. doi: 10.1016/j.dsr.2012.03.012.

14. Boyer, L.F., Diaz, R.J., Hedrick, J.D. 1988. Computer image-analysis techniques and video-sediment-profile camera enhancements provide a unique and quantitative view of life at or beneath the sediment-water interface. Proceedings of the Oceans '88 Conference, Baltimore, Maryland, October 31 – November 2, 1988. Marine Technology Society and IEEE, Piscataway, NJ, p. 448 – 453. doi: 10.1109/OCEANS.1988.23544.
15. Cailliet, G., M., Andrews, A.H., Wakefield, W.W., Moreno, G., Rhodes, K.L. 1999. Fish faunal and habitat analyses using trawls, camera sleds and submersibles in benthic deep-sea habitats off central California. Oceanologica Acta, 22: 579-592. doi: 10.1016 / S0399-1784 (00) 88949-5.
16. Canals, M., Puig, P., Heussner, S., Durrieu de Madron, X., Palanques, A., Fabres, J. 2006. Flushing submarine canyons. Nature, 444 (7117): 354-357. doi: 10.1038/nature05271.
17. Canals, M., Company, J. B., Martin, D., Sanchez-Vidal, A., Ramirez-Llodra, E. 2013. Integrated study of Mediterranean deep canyons: Novel results and future challenges. Progress in Oceanography, 118: 1-27. doi:10.1016/j.pocean.2013.09.004.
18. Capezzuto, F., Maiorano, P., Panza, M., Indennidate, A., Sion, L., D'Onghia, G. 2012. Occurrence and behaviour of *Paromola cuvieri* (Crustacea, Decapoda) in the Santa Maria di Leuca cold-water coral community (Mediterranean Sea). Deep Sea Research Part I: Oceanographic Research Papers, 59: 1-7. doi:10.1016/j.dsr.2011.10.006.
19. Carrasson, M. 1994. Relaciones tróficas en las comunidades ícticas bentónicas (de 1000 a 2200 m) del Mar Catalán. PhD Thesis, Universitat Autonòma de Barcelona, http://hdl.handle.net/10803/3688.
20. Cartes, J. E., Sarda, F. 1992. Abundance and diversity of decapod crustaceans in the deep-Catalan Sea (Western Mediterranean). Journal of Natural History, 26: 1305-1323. doi: 10.1080/00222939200770741.
21. Cartes, J. E., Company, J. B., Maynou, F. 1994. Deep-water decapod crustacean communities in the Northwestern Mediterranean: influence of submarine canyons and seasons. Marine Biology, 120: 221-229. doi: 10.1007/BF00349682.
22. Childress, J.J. 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? Trends in Ecology and Evolution, 10: 30–36. doi: 10.1016/S0169-5347(00)88957-0.

23. Collins, M.A., Priede, I.G., Bagley, P.M. 1999. *In situ* comparison of activity of two deep-sea scavenging fishes occupying different depth zones. Proceedings of the Royal Society of London. Series B: Biological Sciences, 266(1432): 2011-2016. doi: 10.1098/rspb.1999.0879.

24. Company, J.B., Porzia, M., Tselepides, A., Politou, C.Y., Plaitu, W., Rotllant, G., Sarda, F. 2004. Deep-sea decapod crustaceans in the western and central Mediterranean Sea: preliminary aspects of species distribution, biomass and population structure. Scientia Marina, 68: 73-86. doi: 10.3989/scimar.2004.68s373.

25. Company, J.B., Ramirez-Llodra, E., Aguzzi, J., Puig, P., Canals, M., Calafat, A., Palanques, A., Sanchez-Vidal, A., Lastras, G., Tecchio, S., Koenig, S., Fernandez-Arcaya, U., Mecho, A., Fernandez, P. 2012. Submarine canyons in the Catalan Sea (NW Mediterranean): megafaunal biodiversity patterns and antrophogenic threats. In:Würts, M. (Ed.), Mediterranean Submarine Canyons: Ecology and Governance. Gland, Switzerland and Málaga, Spain, pp. 133-144. http://hdl.handle.net/10261/65402.

26. Davis, M. P., Chakrabarty, P. 2011. Tripodfish (Aulopiformes: Bathy - pterois) locomotion and landing behaviour from video observation at bathypelagic depths in the Campos Basin of Brazil. Marine Biology Research, 7: 297–303.

27. D'Onghia, G., Indennidate, A., Giove, A., Savini, A., Capezzuto, F., Sion, L., Vertino, A., Maiorano, P. 2011. Distribution and behaviour of deep-sea benthopelagic fauna observed using towed cameras in the Santa Maria di Leuca cold-water coral province. Marine Ecology Progress Series, 443: 95-110. doi: 10.3354/meps09432.

28. D'Onghia, G., Capezzuto, F., Carluccio, A., Carluccio, R., Giove, A., Mastrototaro, F., Panza, M., Sion, L., Tursi, A., Maiorano, P. 2015. Exploring composition and behaviour of fish fauna by *in situ* observations in the Bari Canyon (Southern Adriatic Sea, Central Mediterranean). Marine Ecology, 36: 541-556. doi: 10.1111/maec.12162.

29. Doya, C., Aguzzi, J., Pardo, M. Matabos, M., Company, J.B. Costa, C., Mihaly, S., Canals, M. 2014. Diel behavioral rhythms in sable fish (*Anoplopoma fimbria*) and other benthic species, as recorded by the deep-sea cabled observatories in Barkley canyon (NEPTUNE-Canada). Journal of Marine Systems, 130: 69-78. doi: http://dx.doi.org/10.1016/j.jmarsys.2013.04.003.

30. Durrieu de Madron, X., Houpert, L., Puig, P., Sanchez-Vidal, A., Testor, P., Bosse, A., Estournel, C., Somot, S., Bourrin, F., Bouin, M.N., Beauverger, M., Beguery, L., Calafat, A., Canals, M., Coppola, L., Dausse, D., D'Ortenzio, F., Font, J., Heussner, S., Kunesch, S., Le Goff, H., Martin, J., Mortier, L., Palanques, A., Raimbault, P. 2013. Interaction of dense shelf water cascading and open-sea convection in the northwestern Mediterranean during winter 2012. Geophysical Research Letters, 40: 1-7. doi: 10.1002/grl.50331.
31. Engås, A. 1994. The effects of trawl performance and fish behaviour on the catching efficiency of demersal sampling trawls. In A. Fernö, and S. Olsen (Eds.): Marine Fish Behaviour in Capture and Abundance Estimation, Fishing News Books, Oxford, p. 45-68.
32. Font, J., Salat, J., Tintore, J. 1988. Permanent features of the circulation in the Catalan Sea. Oceanologica Acta, 9: 51 – 57. http://archimer.ifremer.fr/doc/00267/37808/35889.pdf.
33. Galgani, F., Fleet, D., Van Franeker, J., Katsanevakis, S., Maes, T., Mouat, J., Oosterbaan, L., Poitou, I., Hanke, G., Thompson, R., Amato, E., Birku, A., Janssen, C. 2010. Marine Strategy Framework Directive. Task Group 10 Report. Marine Litter. Luxemburg: Office for Official Publications of the European Community, 48 p.
34. Galil, B. S., Goliki, A., Turkay, M. 1995. Litter at the bottom of the sea: A sea bed survey in the Eastern Mediterranean. Marine Pollution Bulletin, 30: 22–24. doi: 10.1016/0025-326X(94)00103-G.
35. Gartner, J.V., Crabtree, R.E., Sulak, K.J. 1997. Feeding at depth. In D. J. Randall and A. P. Farrell (Eds): Deep Sea Fishes, Academic Press, San Diego, California, p. 115-182.
36. Gates, A. R., Jones, D.O.B. 2010. Recovery at Morvin: SERPENT final report. Southampton, UK, National Oceanography Centre Southampton, 74 pp. (National Oceanography Centre Southampton Research and Consultancy Report 86).
37. Gates, A.R., Jones, D.O.B., Cartes, J.E. 2012. *In situ* video observations of benthic megafauna and fishes from the deep eastern Mediterranean Sea off Egypt. African Journal of Marine Science, 34: 215-222.

38. Glass, C.W., Wardle, C.S. 1989. Comparison of the reactions of fish to a trawl gear, at high and low light intensities. Fisheries Research, 7: 249-266. doi: 10.1016/0165-7836(89)90059-3.

39. Gordon, J.D.M., Bergstad, O.A. 1992. Species composition of demersal fish in the Rockall Trough North-eastern Atlantic as determined by different trawls. Journal of the Marine Biological Association of the United Kingdom, 72: 213-230. doi: 10.1017/S002531540004889X.

40. Gordon, J.D.M., Duncan, J.A.R. 1985. The ecology of the deep-sea benthic and benthopelagic fish on the slopes of the Rockall Trough, northeastern Atlantic. Progress in Oceanography, 15: 37-69. doi: 10.1016/0079-6611(85)90037-0.

41. Hobson, E.S., Chess, J.R. 2001. Influence of trophic relations on form and behaviour among fishes and benthic invertebrates in some Californian marine communities. Environmental Biology and Fisheries, 60: 411 –457. doi: 10.1023/A:1011027312001.

42. Hollertz, K., Duchêne, J.C. 2001. Burrowing behaviour and sediment reworking in the heart urchin *Brissopsis lyrifera* Forbes (Spatangoida). Marine Biology, 139: 951-957. doi: 10.1007/s002270100629.

43. Hollertz, K. 2002. Feeding biology and carbon budget of the sediment-burrowing heart urchin *Brissopsis lyrifera* (Echinoidea: Spatangoida). Marine Biology, 140: 959-969. doi: 10.1007/s00227-001-0764-7.

44. Holme, N.A., McIntyre, A.D. 1971. Methods for the study of marine benthos. Blackwell, Oxford, 387 p.

45. Krieger, K.J., Sigler, M.F. 1995. Catchability coefficient for rockfish estimated from trawl and submersible surveys. Fishery Bulletin, 94, 282-288.

46. Lastras, G., Canals, M., Amblas, D., Lavoie, C., Church, I., De Mol, B., Durán, R., Calafat, A.M., Hughes-Clarke, J.E., Smith, C.J., Heussner, S., "Euroleón" cruise shipboard party. 2011. Understanding sediment dynamics of two large submarine valleys from seafloor data: Blanes and La Fonera canyons, northwestern Mediterranean Sea. Marine Geology, 280(1): 20-39. doi: 10.1016/j.margeo.2010.11.005.

47. Lauth, R.R., Wakefield, W.W., Smith, K. 2004. Estimating the density of thornyheads, *Sebastolobus* spp., using a towed video camera sled. Fisheries Research, 70: 39-48. doi:10.1016/j.fishres.2004.06.009.

48. Lorance, P., Latrouite, D., Seret, B. 2000. Submersible observations of elasmobranch species in the Bay of Biscay. In B. Seret and J.Y. Sire (Eds): 3rd European Elasmobranch Association Meeting, Bologne sur Mer, Societé Française d'Ichthyologie et IRD, Paris, p. 29–45.
49. Lorance, P., Uiblein, F., Latrouite, D. 2002. Habitat, behaviour and colour patterns of orange roughy *Hoplostethus atlanticus* (Pisces: Trachichthyidae) in the Bay of Biscay. Journal of the Marine Biological Association of the United Kingdom, 82: 321–331. doi: 10.1017/S0025315402005519.
50. Lorance, P., Trenkel, V.M. 2006. Variability in natural behaviour, and observed reactions to an ROV, by mid-slope fish species. Journal of Experimental Marine Biology and Ecology, 332: 106-119. doi:10.1016/j.jembe.2005.11.007.
51. Macpherson, E. 1979. Ecological overlap between macrourids in the western Mediterranean Sea. Marine Biology, 53: 149–159. doi: 10.1007/BF00389186. –ATENCIÓ!-
52. Martin, J., Palanques, A., Puig, P. 2006. Composition and variability of downward particulate matter fluxes in the Palamós submarine canyon (NW Mediterranean). Journal of Marine Systems, 60: 75-97. doi: 10.1016/j.jmarsys.2005.09.010.
53. Mauchline, J., Gordon, J.D.M. 1984. Diets and bathymetric distributions of the macrourid fish of the Rockall Trough, northeastern Atlantic Ocean. Marine Biology, 81: 107-121. doi: 10.1007/BF00393109.
54. Mcintyre, F.D., Neat, F., Collie, N., Stewart, M., Fernandes, P.G. 2014. Visual surveys can reveal rather different 'PICTUREs' of fish densities: Comparison of trawl and video camera surveys in the Rockall Bank, NE Atlanthic Ocean. Deep Sea Research Part I: Oceanographic Research Papers, 95:67-74. doi:10.1016/j.dsr.2014.09.005.
55. Mecho, A., Billett, D.S.M., Ramirez-Llodra, E., Aguzzi, J., Tyler, P.A., Company, J.B. 2014. First records, rediscovery and compilation of deep-sea echinoderms in the middle and lower continental slope in the Mediterranean Sea. Scientia Marina, 78: 281-302. doi: http://dx.doi.org/10.3989/scimar.03983.30C.
56. Mercader, L., Lloris, D., Rucabado, J. 2001. Tots els peixos del Mar Catala. Diagnosi i claus d'identificació. Institut d'Estudis Catalans, Barcelona, 350 p.

57. Merrett, N.R., Gordon, J.D.M., Stehmann, M., Haedrich, R.L. 1991. Deep demersal fish assemblage structure in the Porcupine Seabight (eastern North Atlantic): Slope sampling by three different trawls compared. Journal of the Marine Biological Association of the United Kingdom, 71: 329-358. doi: 10.1017/S0025315400051638.

58. Millot, C., 1999. Circulation in the Western Mediterranean Sea. Journal of Marine Systems, 20: 423–442. doi: 10.1016/S0924-7963(98)00078-5.

59. Palanques, A., Garcia-Ladona, E., Gomis, D., Martin, J., Marcos, M., Pascual, A., Puig, P., Gili, J. M., Emelianov, M., Montserrat, S., Guillen, J., Tintore, J., Segura, M., Jordi, A., Ruiz, S., Basterretxea, G., Font, J., Blasco, D., Pages, F. 2005. General patterns of circulation, sediment fluxes and ecology of the Palamós (La Fonera) submarine canyon, northwestern Mediterranean. Progress in Oceanography, 66: 89-119. doi: 10.1016/j.pocean.2004.07.016.

60. Pawson, D.L., Pawson, D.J. 2013. Bathyal sea urchins of the Bahamas, with notes on covering behaviour in deep sea echinoids (Echinodermata: Echinoidea). Deep Sea Research Part II: Topical Studies in Oceanography, 92: 207-213. doi: 10.1016/j.dsr2.2013.01.023.

61. Pham, C.K., Ramirez-Llodra, E., Alt, C.H.S., Amaro, T., Bergmann, M., Canals, M., Company, J.B., Davies, J., Duineveld, G., Galgani, F., Howell, K.L., Huvenne, V., Isidro, E., Jones, D., Lastras, G., Morato, T., Gomes-Pereira, J.N., Purser, A., Stewart, H., Tojeira, I., Tubau, X., Van Rooij, D., Tyler, P.A. 2014. Marine litter distribution and density in European seas, from the shelves to deep asins. PLoS ONE, 9(4): e95839. doi: 10.1371/journal.pone.0095839.

62. Poupin, J., Corbari, L., Perez, T., Chevaldonne, P. 2012. Deep-water decapod crustaceans studied with a remotely operated vehicle (ROV) in the Marquesas Islands, French Polynesia (Crustacea: Decapoda). Zootaxa, 3550: 43-60.

63. Priede, I.G., Bagley, P.M. 2000. *In situ* studies on deep-sea demersal fishes using autonomous unmanned lander platforms. Oceanography and Marine Biology: Annual Review, 38: 357–392.

64. Puig, P., Palanques, A., Orange, D.L., Lastras, G., Canals, M. 2008. Dense shelf water cascades and sedimentary furrow formation in the Cap de Creus Canion, northwestern Mediterranean Sea. Continental Shelf Research, 28: 2017-2030. doi: 10.1016/j.csr.2008.05.002.

65. Quattrini AM, Nizinski MS, Chaytor JD, Demopoulos AWJ, Roark EB, France SC, Moore, JA., Heyl, T., Auster, PJ., Ruppel, C., Elliot, KP., Kennedy, BRC., Lobecker, E., Skarke, A., Shank, TM. 2015. Exploration of the Canyon-Incised Continental Margin of the Northeastern United States Reveals Dynamic Habitats and Diverse Communities. PLoS ONE 10 (10): e0139904. doi: 10.1371/journal.pone.0139904
66. Ramirez-Llodra, E., Ballesteros, M., Dantart, L., Sarda, F. 2008. Spatio-temporal variations of biomass and abundance in bathyal non-crustacean megafauna in the Catalan Sea (North-western Mediterranean). Marine Biology, 153: 297-309. doi: 10.1007/s00227-007-0805-y.
67. Ramirez-Llodra E., Tyler, P.A., Baker, M.C., Bergstad, O.A., Clark MR Escobar, E., Levin, L.A., Menot, L. Rowden, A.A., Smith, C.R., Van Dover, C.L. 2011. Man and the last great wilderness: Human impact on the deep sea. PLoS ONE, 6(7): e22588. doi: 10.1371/journal.pone.0022588.
68. Ramirez-Llodra, E., De Mol, B., Company, J.B., Coll, M., Sarda, F. 2013. Effects of natural and anthropogenic processes in the distribution of marine litter in the deep Mediterranean Sea. Progress in Oceanography, 118: 273-287. doi: 10.1016/j.pocean.2013.07.027.
69. Ross, S.W., Rhode, M., Quattrini, A.M. 2015. Demersal fish distribution and habitat use within and near Baltimore and Norfolk Canyons, U.S. middle Atlantic slope. Deep-Sea Research Part I: Oceanographic Research Papers, 103: 137–154. doi: 10.1016/j.dsr.2015.06.004.
70. Ryer, C.H., Stoner, A.W., Iseri, P.J., Spencer, M.L. 2009. Effects of simulated underwater vehicle lighting on fish behaviour. Marine Ecology Progress Series, 391: 97-106. doi: 10.3354/meps08168.
71. Salvado, J.A., Grimalt, J.O., Lopez, J.F., Palanques, A., Heussner, S., Pasqual, C., Sanchez-Vidal, A., Canals, M. 2012. The role of dense shelf water cascading in the transfer of organochlorine compounds to open marine waters. Environmental Science & Technology, 46 (5): 2624-2632.
72. Sanchez-Vidal, A., Canals, M., Calafat, A.M., Lastras, G., Pedrosa-Pamies, R., Menendez, M., Medina, R., Company, J.B., Hereu, B., Romero, J., Alcoverro, T. 2012. Impacts on the deep-sea ecosystem by a severe coastal storm. PLoS ONE 7 (1): 1- 7, e30395. doi: 10.1371/journal.pone.0030395.

73. Sarda, F., Company, J.B., Maynou, F. 2003. Deep-sea shrimp (*Aristeus antennatus*, Risso 1816) in the Catalan sea, a review and perspectives. Journal of Northwest Atlantic Fishery Science, 31: 127-136.

74. Sarda, F., Aguzzi, J. 2012. A review of burrow counting as an alternative to other typical method of assessment of Norway lobster populations. Reviews in Fish Biology and Fisheries, 22: 409-422. doi: 10.1007/s11160-011-9242-6.

75. Stefanescu, C., Lloris, D., Rucabado, J. 1993. Deep-sea fish assemblages in the Catalan Sea (western Mediterranean) below a depth of 1000 m. Deep Sea Research Part I: Oceanographic Research Papers, 40: 695-707. doi: 10.1016/0967-0637(93)90066-C.

76. Sulak, K.J. 1977. The systematics and biology of *Bathypterois* (Pisces: Chlorophthalmidae) with a revised classification of benthic myctophiform fishes. Galathea, 14: 49-108.

77. Stoner, A.W., Ryer, C.H., Parker, S.J., Auster, P.J., Wakefield, W.W. 2008. Evaluating the role of fish behaviour in surveys conducted with underwater vehicles. Canadian Journal of Fisheries and Aquatic Sciences, 65: 1230-1243. doi: 10.1139/F08-032.

78. Tecchio, S., Ramirez-Llodra, E., Sarda, F., Company, J. B., Palomera, I., Mecho, A., Pedrosa, R., Sanchez-Vidal, A. 2011. Drivers of the deep Mediterranean megabenthos communities along longitudinal and bathymetric gradients. Marine Ecology Progress Series, 439: 181-192.

79. Tecchio, S., Ramirez-Llodra, E., Aguzzi, J., Flexas, M.M., Company, J.B., Sarda, F. 2013. Seasonal fluctuations of deep megabenthos: Finding evidence of standing stock accumulation in a flux-rich continental slope. Progress in Oceanography, 118: 188-198. doi: 10.1016/j.pocean.2013.07.015.

80. Trenkel, V.M., Bailly, N., Berthele, O., Brosseau, O., Causse, R., De Corbiere, F., Dugornay, O., Ferrant, A., Gordon, J.D.M., Latrouite, D., Le Piver, D., Kergoat, B., Lorance, P., Mahevas, S., Mesnil, B., Poulard, J.C., Rochet, M.J., Tracey, D., Vacherot, J.P., Veron, G., Zibrowius, H. 2002. First results of a quantitative study of deep-sea fish on the continental slope of the Bay of Biscay: visual observations and trawling. ICES Annual Science Conference, 1–5, Copenhagen, Denmark, ICES CM 2002/L18, 18 p.

81. Trenkel, V.M., Francis, R., Lorance, P., Mahevas, S., Rochet, M.J., Tracey, D.M. 2004a. Availability of deep-water fish to trawling and visual observation

from a remotely operated vehicle (ROV). Marine Ecology Progress Series, 284: 293-303. doi: 10.3354/meps284293.

82. Trenkel, V.M., Lorance, P., Mahevas, S. 2004b. Do visual transects provide true population density estimates for deepwater fish? ICES Journal of Marine Science, 61: 1050-1056. doi: 10.1016/j.icesjms.2004.06.002.
83. Tubau, X., Canals, M., Lastras, G., Rayo, X., Rivera, J., Amblas, D. 2015. Marine litter on the floor of deep submarine canyons of the Northwestern Mediterranean Sea: The role of hydrodynamic processes. Progress in Oceanography, 134: 379-403. doi: 10.1016/j.pocean.2015.03.013.
84. Uiblein, F., Bordes, F., Castillo, R., Ramos, A. 1998. Spatial distribution of shelf- and slope-dwelling fishes collected by bottom longline off Lanzarote and Fuerteventura, Canary Islands. Marine Ecology, 19:53–66. doi: 10.1111/j.1439-0485.1998.tb00453.x.
85. Uiblein, F., Lorance, P., Latrouite, D. 2002. Variation in locomotion behaviour in northern cutthroat eel (*Synaphobranchu kaupi*) on the Bay of Biscay continental slope. Deep-Sea Research I: Oceanographic Research Papers, 49: 1689–1703. doi:10.1016/S0967-0637(02)00065-1.
86. Uiblein, F., Lorance, P., Latrouite, D. 2003. Behaviour and habitat utilization of seven demersal fish species on the Bay of Biscay continental slope, NE Atlantic. Marine Ecology Progress Series, 257: 223–232. doi: 10.3354/meps257223.
87. Ulses, C., Estournel, C., Puig, P., Durrieu de Madron, X., Marsaleix, P. 2008. Dense shelf water cascading in the northwestern Mediterranean during the cold winter 2005. Quantification of the export through the Gulf of Lion and the Catalan margin. Geophysical Research Letters, 35, L07610, doi: 10.1029/2008GL033257.
88. Uzmann, J.R., Cooper, R.A., Threoux, R.B., Wigley, R.L. 1977. Synoptic comparison of three sampling techniques for estimating abundance and distribution of selected megafauna: submersible vs. camera sled otter trawl. Marine Fisheries Review, 39: 11-19.
89. Wardle, C. 1993. Fish behaviour and fishing gear. In T.J. Pitcher (Ed.): Behaviour of Teleost Fishes, Chapman and Hall, London, p. 609-643.
90. Webb, P.W. 1989. Station-holding by three species of benthic fishes. Journal of Experimental Biology, 145: 303-320.

91. Widder, E.A. 2010. Bioluminescence in the ocean: Origins of biological, chemical, and ecological diversity. Science, 328: 704-708. doi: 10.1126/science.1174269.

92. Widdicombe, S., Austen, M.C. 1998. Experimental evidence for the role of *Brissopsis lyrifera* (Forbes, 1841) as a critical species in the maintenance of benthic diversity and the modification of sediment chemistry. Journal of Experimental Marine Biology and Ecology, 228: 241-255. doi: 10.1016/S0022-0981(98)00032-X.

93. Wilson, R.R., Smith, K.L. 1984. Effect of near-bottom currents on detection of bait by the abyssal grenadier fishes *Coryphaenoides* spp., recorded *in situ* with a video camera on a free vehicle. Marine Biology, 84: 83-91. doi: 10.1007/BF00394530.

94. Zariquiey, R. 1968. Decápodos ibéricos. Investigaciones Pesqueras, 24: 113–127.

Table 1. Metadata of ROV dives (D) and Agassiz trawls (A) including identification codes, locations, depth range (m), length of dive or trawl (m) and swept area of dive or trawl (m^2). ROV depth ranges go from deeper to shallower as dives were performed up canyon axis and wall. Trawl depth ranges go from shallower to deeper as hauls were performed down canyon axis. CCC: Cap de Creus canyon; LFC: La Fonera canyon; BC: Blanes canyon.

Sampling transect code	Location	Geographic coordinates		Depth range (m)	Length (L) (m)	Swept area (A) (m^2)
		Latitude (ºN)	Longitude (ºE)			
D8	CCC axis	42.2227	3.8298	1570-1490	2152.1	6456.3
D9	CCC axis	42.2847	3.6399	1215-1200	1929.7	5789.1
D16	LFC axis	41.8545	3.4062	1570-1510	1378.5	4135.5
D18	LFC axis	41.8660	3.3348	1215-1155	1161.8	3485.4
D19	LFC axis	41.8761	3.2788	985-860	822.2	2466.6
D20	LFC northern wall	41.8620	3.3988	1500-980	1860.8	5582.4
D21	LFC northern wall	41.8747	3.3990	985-750	687.6	2062.8
D31	BC axis	41.4589	2.8797	1520-1500	623.4	1870.2
D32	BC axis	41.5227	2.8456	1225-1200	630.8	1892.4
D33	BC axis	41.5730	2.8474	910-900	584.2	1752.6
ROV Total				**750-1570**	**11831.1**	**35493.3**
A1	CCC axis	42.3255	3.5057	1408-1554	5660	10090
A2	CCC axis	42.2942	3.6224	1018-1236	4780	13680
A5	BC axis	41.4417	2.8836	1477-1570	2480	5840
A6	BC axis	41.5004	2.8544	1204-1424	4620	6270
A7	BC axis	41.5927	2.8508	752-864	2150	92370
Agassiz Total			-	**752-1570**	**43495.3**	**128250**

	Attraction	Avoidance	Drifting	Stationary	N
Bathypterois dubius	0	1	0	8	9
%	0	11.11	0	88.89	3.85
Coelorinchus mediterraneus	0	0	0	9	9
%	0	0	0	100	3.85
Lepidion lepidion	2	16	14	89	121
%	1.65	13.22	11.57	73.55	51.71
Nezumia aequalis	0	0	3	17	20
%	0	0.00	15.00	85.00	8.58
Polyacanthonotus rissoanus	1	15	10	13	39
%	2.56	38.46	25.64	33.33	16.67
Trachyrincus scabrus	0	5	16	14	35
%	0	14.29	45.7	40.00	14.96
Total fish response	3	37	43	150	233
%	1.28	15.89	18.45	64.38	100

Table 2. Observed reaction behavior to the approaching ROV of selected fish species. The first number in each cell of the table is the count or frequency and the second number shows the percentage. N: number of individuals.

Table 3. Observed behavior to the approaching ROV of selected crustacean decapod species. The first number in each cell of the table is the count or frequency and the second number shows the percentage. N: number of individuals.

	Avoidance	Defensive	Drifting	Stationary	N
Geryon longipes	5	0	0	10	15
%	33.33	0	0	66.67	9.62
Munida spp.	6	10	0	78	94
%	6.38	10.64	0	82.98	60.26
Pagurus spp.	14	0	4	29	47
%	29.79	0	8.51	61.70	30.13
Total crustacean response	25	10	4	117	156
%	16.03	6.41	2.56	75.00	100.00

Supplementary information

	CCC				LFC				BC	
Dive code	8	9	16	18	19	20	21	31	32	33
Species										
Cnidaria										
Unidentified anemona	154.9	1036.4		1434.6	2432.5	2507.9	13089		2113.7	1711,7
Ctenophora										
Unidentified Ctenophora	309,8	1036,4	1209,0			716,5	484,8			
Annelida										
Bonellia viridis						895.7				
Mollusca										
Aporrhais serresianus				286.9						
Euspira fusca							484.8			
Bathypolypus sponsalis		345.5								
Crustacea										
Meganitctyphanes spp.							484.8			
Sergestes arcticus							484.8			
Aristeus antennatus		172.7				358.3	1454.3	1604.1	528.4	
Plesionika spp.						179.1	1454.3		528.4	
Bathynectes longispina						358.3				
Geryon longipes	619.5	691.0				895.7	969.6			
Munida spp.	2942.9	6391.3	2659.9	286.9		2866.2	0.0	4277.6	1056.9	
Pagurus spp.		691.0	1450.9	2295.3	3243.3		1939.1	1604.1	5812.7	2852.9
Unidentified decapoda	154.9		241.8	286.9		537.4	484.8	3208.2		1711.7
Echinodermata										
Brissopsis lyrifera (alive)		172.7	666424.9	20370.7	48244.5	9494.1				
Brissopsis lyrifera (dead)		1727.4	1332849.7	67711.0	66488.3	3224.4	5332.6	267885.8		276731.7
Ceramaster grenadensis	154.9									
Gracilechinus elegans			1209.0							
Mesothuria intestinalis	929.3									
Unidentified holothurian	154.9									
Chordata										
Ascideacea										
Dicopia antirrhinum						895.7				
Actinopterygii										
Notacanthus bonaparte				573.8	405.4	179.1				
Polyacanthonotus rissoanus	154.9	1209.2	1692.7	2295.3	405.4	2507.9				570.6
Nettastoma melanurum						179.1				

Alepocephalus rostratus	154.9									
Cyclothone braueri		172.7								
Bathypterois dubius	1084.2	345.5								
Lampanyctus crocodilus		172.7					484.8			
Coelorinchus mediterraneus	154.9		1450.9			179.1		534.7		
Nezumia aequalis		1381.9		573.8	1621.7	716.5	969.6			
Trachyrincus scabrus		691.0	241.8	2582.2	2432.5	1612.2	2423.9		528.4	
Lepidion lepidion	929.3	2245.6	5319.8	2869.1	2837.9	7344.5	2908.7	3742.9	2113.7	2852.9
Hoplostethus mediterraneus					405.4					
Lepidorhombus boscii				286.9						
Epigonus telescopus					405.4					
Unidentified fishes										
Chimaeriformes										
Chimaera monstrosa	172.7		573.8	810.8	1612.2	484.8		528.4		

Table S1

	CCC		BC		
Trawl code Species	1	2	5	6	7
Cnidaria					
Unidentified anemona	396.4	146.2			43.3
Desmophyllum dianthus				*	*
Madrepora oculata				*	
Lophelia pertusa					*
Annelida					
Bonellidae spp.		146.2			
Sipuncula					
Aspidosiphon muelleri					
Golfingia vulgaris					
Mollusca					
Antalis entalis					
Aporrhais serresianus	1090.2				
Euspira fusca				319.0	443.9
Bathypolypus sponsalis		73.1			
Galiteuthis armata					
Abra longicallus		73.1			43.3
Crustacea					
Phronima spp.					
Acanthephyra eximia	198.2	292.4	684.9	478.5	
Acanthephyra pelagica	198.2				
Pontocaris lacazei				159.5	10.8
Aristeus antennatus		950.3		1275.9	86.6
Bathynectes maravigna	198.2				
Calocaris macandreae					21.7
Gennadas elegans					
Geryon longipes		511.7			
Macropodia spp.				159.5	
Monodaeus couchii		73.1			86.6
Munida intermedia					43.3
Munida tenuimana	991.1	1388.9			21.7
Munidopsis serricornis					97.4
Pagurus alatus		731.0		478.5	303.1
Pagurus spp.					10.8
Pasiphaea multidentata					
Pasiphaea sivado					
Plesionika martia					21.7
Polycheles typhlops		219.3			
Pontophilus norvegicus	99.1	73.1			
Sergia robusta			171.2		
Stereomastis sculpta	99.1	146.2			
Meganyctiphanes norvegica					

Natatolana borealis					
Unidentified Decapoda	99.1				
Echinodermata					
Mesothuria intestinalis	99.1				
Ypsilothuria bitentaculata					
Hedingia mediterranea				638.0	
Molpadia musculus					
Brissopsis lyrifera			2739.7		32.5
Ceramaster grenadensis	99.1				
Chordata					
Bathypterois dubius	198.2				
Galeus melastomus				159.5	
Lepidion lepidion	99.1	657.9		1594.9	
Mora moro		73.1			
Nezumia aequalis		73.1			10.8
Trachyrincus scabrus				319.0	
Lampanyctus crocodilus		365.5			10.8
Symbolophorus barnardi			513.7		
Notacanthus bonaparte		73.1		159.5	
Cataetyx alleni					
Alepocephalus rostratus		219.3			
Melanostigma atlanticum		146.2			
Argyropelecus hemigymnus					
Chauliodus sloani		73.1			
Other					
Bivalvia spp.					10.8
Gryphus vitreus					10.8
Myctophidae spp.					10.8
Radiella sarsi	4261.6			638.0	

Table S2

Figure 1. (A) Location map of the studied submarine canyons. (B, C, D) Bathymetric maps of Cap de Creus, Blanes and La Fonera canyons. ROV dives are indicated with white lines and letter "D" and Agassiz trawls by yellow lines and letter "A". ROV dives were performed at 50-100 cm above the seafloor.

Figure 2. Fish and crustacean decapod species observed in ROV dives. (A) *Coelorinchus mediterraneus*. (B) *Nezumia aequalis*. (C) *Batyptherois dubius*. (D) *Lepidion lepidion*. (E) *Trachyrincus scabrus* (F) *Munida* spp. (G) *Geryon longipes*. (H) *Pagurus* spp. Laser beams are spaced 15 cm.

Figure 3. NMDS analysis representing the spatial ordination of different taxonomic families related to sampling methodology (ROV and Agassiz trawl). Centroids and average dispersion of taxa clustered around each sampling method were used to drawn the convex hulls.

Figure 4. (A) Percentage of total Phyla observed with ROV (left) and retrieved by Agassiz trawls (right). (B) Comparison of abundance (ind/km^2) values of different families sampled by Agassiz trawl (grey bars) and video-imaged by ROV (black bars).

Supplementary information: Table and Figure captions

Table S1. Species list and abundance of individuals per dive (individuals/km^2) in the studied submarine canyons. Location of dives is shown in Figure 1. CCC: Cap de Creus canyon; LFC: La Fonera canyon; BC: Blanes canyon.

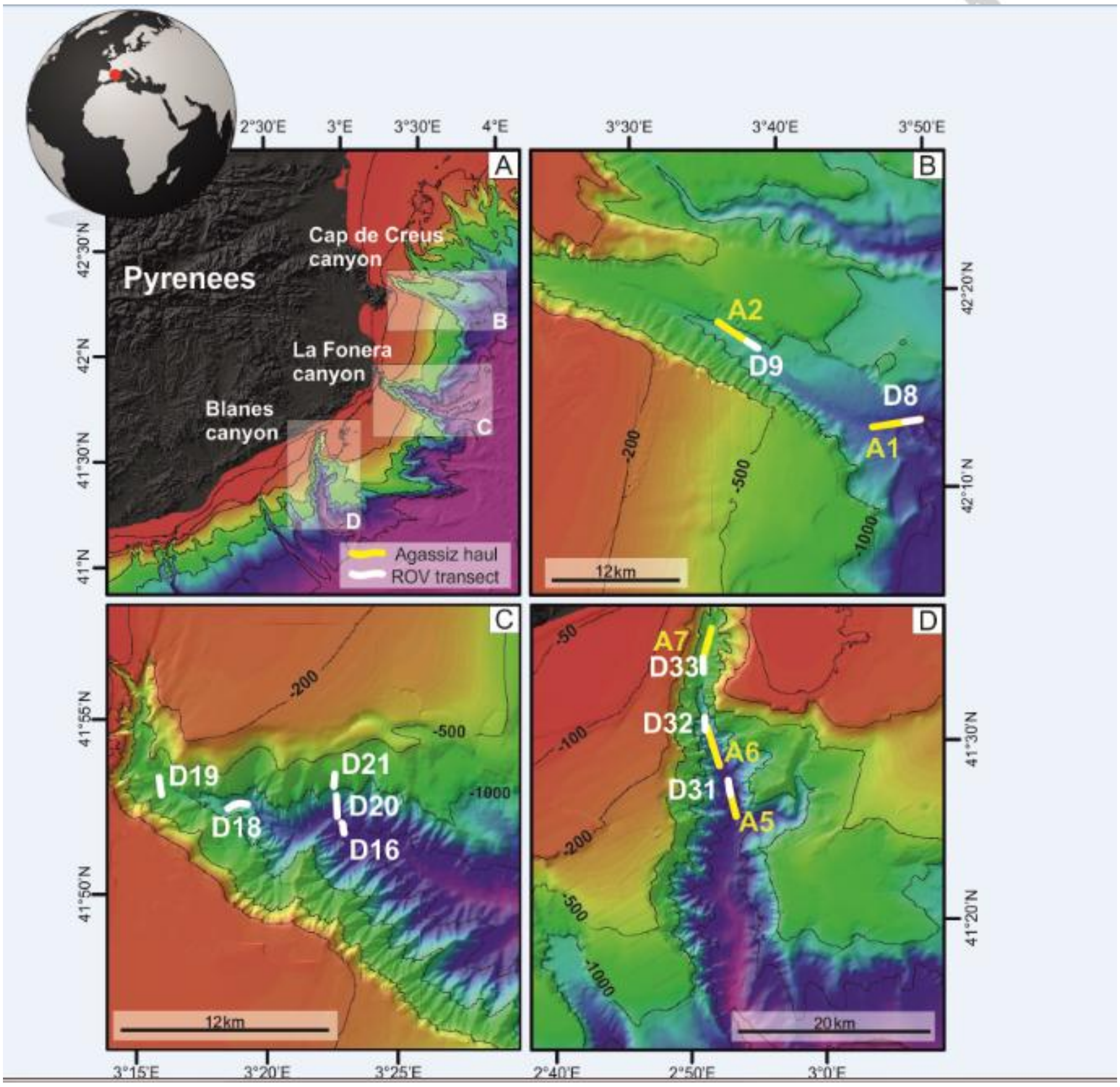
Table S2. Species list and abundance of individuals per Agassiz trawl (individuals/km^2) in the studied submarine canyons. Location of trawls is shown in Figure 1. CCC: Cap de Creus canyon; BC: Blanes canyon. *Number of individuals not available.

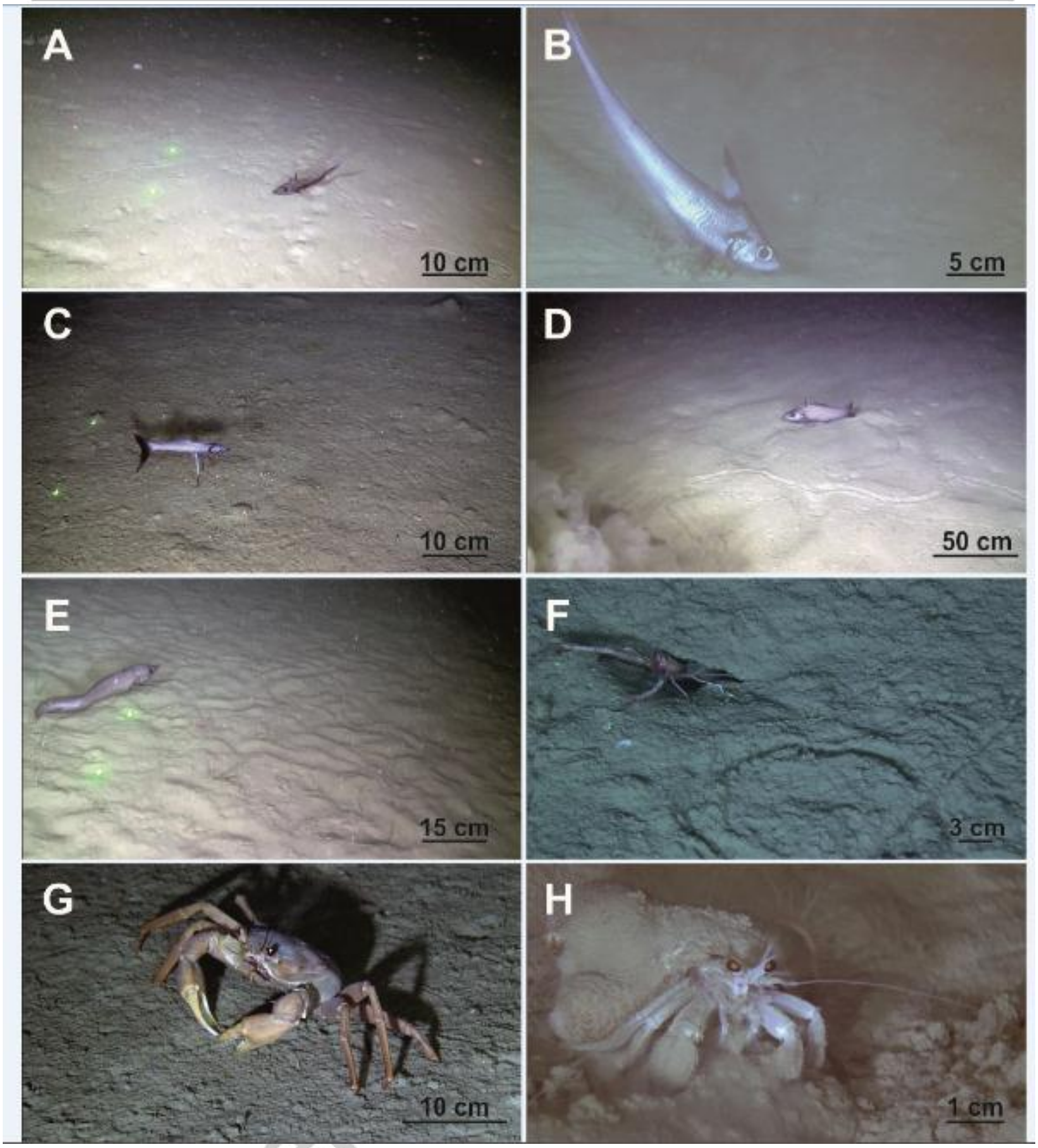
Figure S1. Sequences of different behaviours to ROV approach by demersal fishes and decapod crustaceans. Sequences are to be viewed from top down. (A) Disturbed avoidance behaviour showing a *T. scabrus* generating a mud puff at 1200 m depth (from top down). Laser beams are spaced 15 cm. (B) Disturbed behaviour showing a *L. lepidion* generating a mud puff at 1000 m depth. Another individual on the upper left corner displays a stationary behaviour. (C) Detail of an undisturbed individual and example of seabed marks left by *Pagurus* spp. at 1200 m depth in Blanes canyon. (D) *G. longipes* specimen performing an avoidance response to ROV approach by burying itself, at 1000 m depth. (E) Examples of individuals of *Munida* spp. performing aggressive responses by projecting their claws at the entrance of their shelter, either natural or artificial. Laser beams are spaced 15 cm.

Figure S2. ROV images of *B. lyrifera* individuals and aggregations either alive or dead. (A) Detail of a *B. lyrifera* individual during displacement, leaving a trail mark on the soft seabed. (B) Live *B. lyrifera* herd. (C) Field of displacement trails left by a herd of *B. lyrifera* with one visible live individual. (D) Tanathocenosis made of multiple carcasses of *Brissopsis* spp. A to C are from La Fonera canyon at 1200 m, while D is from Blanes canyon at 1100 m depth. Laser beams are spaced 15 cm.

HIGHLIGHTS

- A comparison between Remotely Operated Vehicle (ROV) and Agassiz trawling methods is presented.
- The behavior of deep-sea fishes and invertebrates of the Northwestern Mediterranean submarine canyons was studied by ROV imaging.
- The comparison between ROV sampling efficiency and Agassiz trawling highlighted that fish captures were 20 times higher with the ROV, with a lower efficiency for epibenthic invertebrates.
- Ethological observations for fishes showed minor response to the ROV presence and new insights on decapods behavior were obtained.
- ROV surveying is an efficient technique to assess abundance and species composition in deep-sea waters for these motile species and questions trawl-based estimations.

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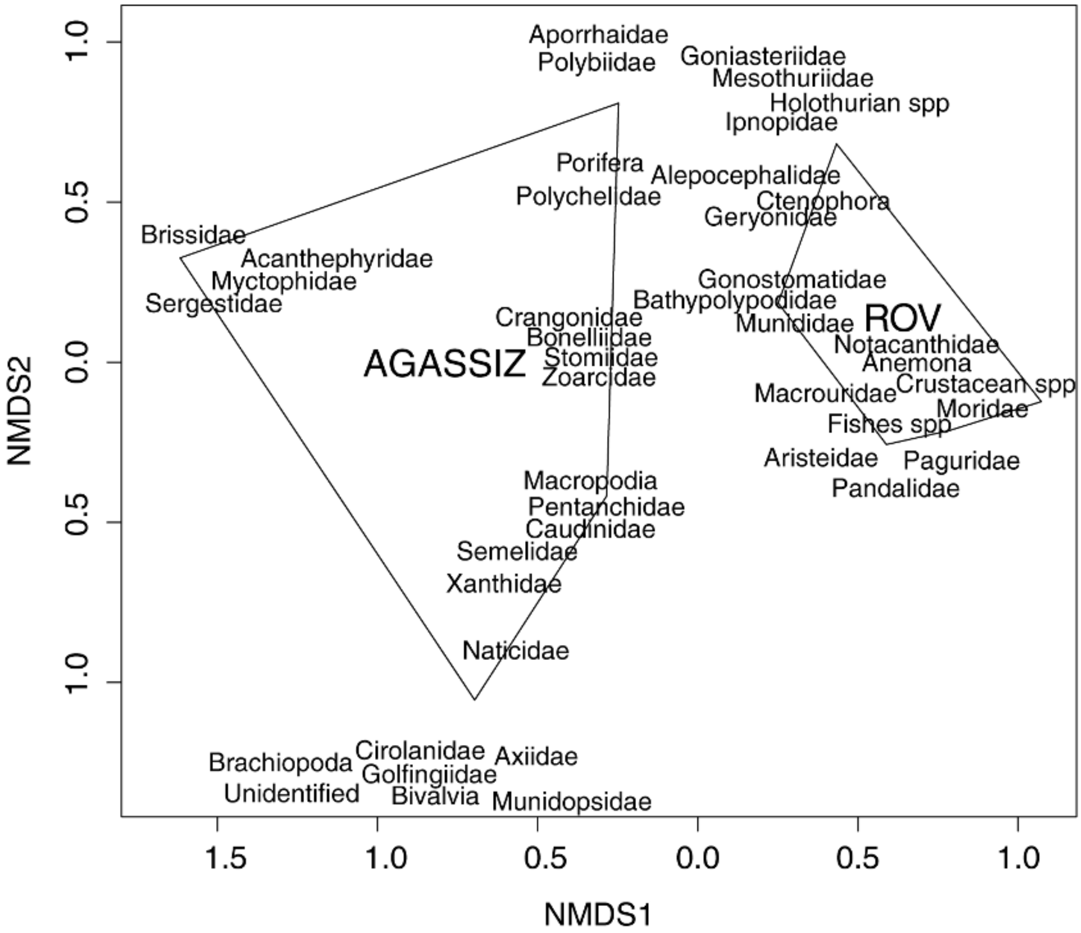
Aporrhaidae
Polybiidae
Goniasteriidae
Mesothuriidae
Holothurian spp
Ipnopidae
Porifera
Alepocephalidae
Polychelidae
Ctenophora
Geryonidae
Brissidae
Acanthephyridae
Myctophidae
Sergestidae
Gonostomatidae
Bathypolypodidae
Crangonidae
Munididae
ROV
Bonelliidae
Notacanthidae
AGASSIZ
Stomiidae
Anemona
Zoarcidae
Crustacean spp
Macrouridae
Moridae
Fishes spp
Aristeidae
Paguridae
Pandalidae
Macropodia
Pentanchidae
Caudinidae
Semelidae
Xanthidae
Naticidae
Brachiopoda
Cirolanidae
Axiidae
Golfingiidae
Unidentified
Bivalvia
Munidopsidae
NMDS2
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1.0
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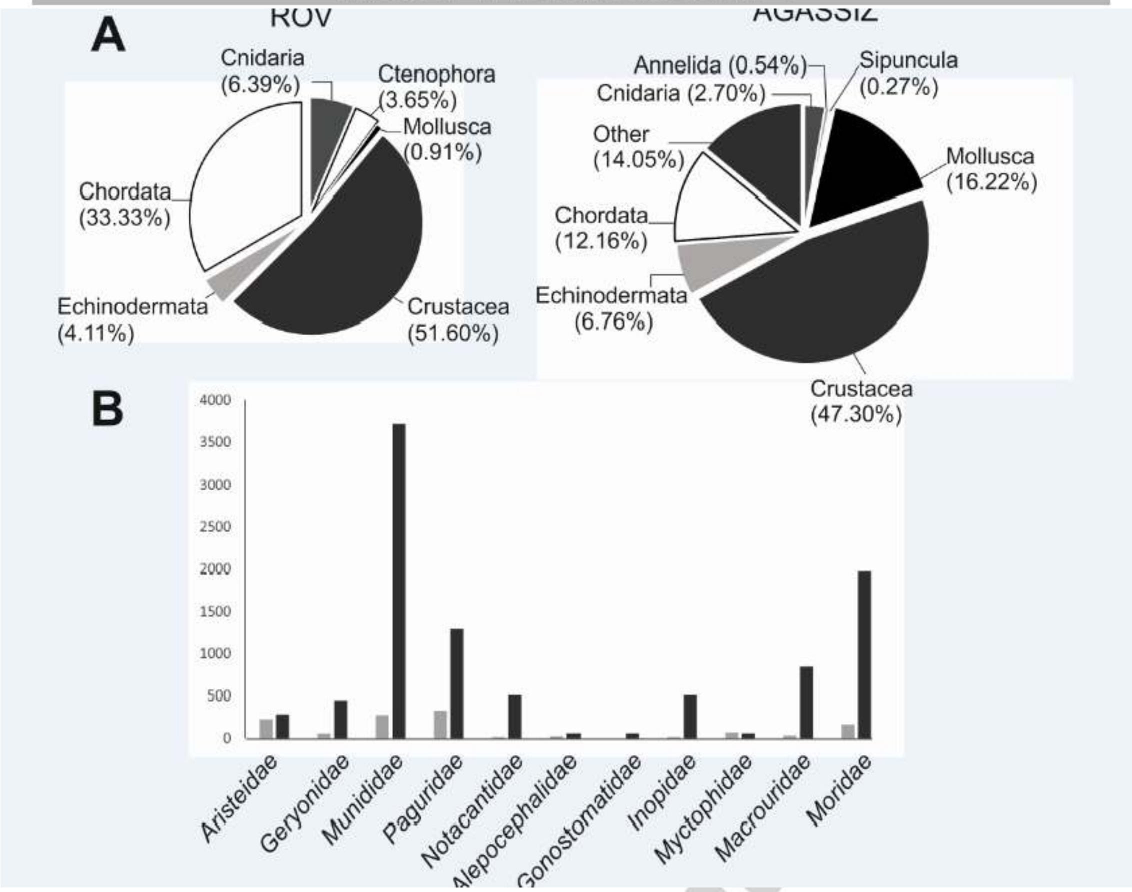
0.5
1.0


A
ROV
Cnidaria (6.39%)
Ctenophora (3.65%)
Mollusca (0.91%)
Chordata (33.33%)
Echinodermata (4.11%)
Crustacea (51.60%)
AGASSIZ
Annelida (0.54%)
Sipuncula (0.27%)
Cnidaria (2.70%)
Other (14.05%)
Mollusca (16.22%)
Chordata (12.16%)
Echinodermata (6.76%)
Crustacea (47.30%)
B
4000
3500
3000
2500
2000
1500
1000
500
0
Aristeidae
Geryonidae
Munididae
Paguridae
Notacantidae
Alepocephalidae
Gonostomatidae
Inopidae
Myctophidae
Macrouridae
Moridae