





Article

Exploring Benthic Scavenger Assemblages, a Multi-Habitat Approach in NW Iberian Peninsula

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Abstract: Scavenging fauna plays an integral role in ecosystem functioning, nutrient cycling and circulating organic matter. Thus, baseline data of scavenger assemblages on the NW coast of the Iberian Peninsula that provides information on the abundance of species in different habitats is crucial to understanding the distribution of this understudied group. Two different types of baited traps, to capture scavenging megafaunal and scavenging benthopelagic macrofaunal assemblages, were deployed to compare them among rocky, pebbled and sandy bottoms at shallow subtidal on the northern coast of Portugal. Results showed significant differences in the structure of scavenger assemblages. Scavenging megafaunal assemblages differed between sandy and the other two studied habitats, whereas benthopelagic macrofaunal assemblages differed between pebbles and rocky habitats. This suggests that different drivers seem to shape the structure of benthopelagic macrofauna and megafauna. Regarding megafauna, the dominance of *Tritia* gastropods in sand habitats in comparison with its absence in rock and its very low abundance in pebbles was mainly responsible for the differences. However, in benthopelagic macrofauna, differences in assemblages between pebbles and rock were more related to changes in the relative abundance of crustacean species (*Cirolana cranchii* and *Socarnes erythrophthalmus*) that were less abundant in pebbles.

Keywords: scavengers; NW Iberian Peninsula; megafauna; macrofauna; baited traps; benthos



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1. Introduction

Knowledge about the functional role of species, communities and ecosystems is crucial for understanding biodiversity patterns and adopting conservation strategies [1]. Feeding traits have been studied to elucidate fundamental questions in ecology, such as the relationship between many taxonomic groups that share similar ecological functions [2–4]. Marine scavengers are those organisms that detect carrion by chemoreception and deliberately move to consume it [3].

Marine scavengers play an integral role in ecosystem functioning, nutrient cycling and circulating organic carbon [3–5]. In this way, scavenger ecology is relevant to understanding trophic relationships and anthropogenic impacts (i.e., how fisheries discards affect benthic carnivores populations) on marine environments [4]. Most studies on marine carrion consumption have reported that macrofaunal scavengers, especially amphipods, isopods and gastropods, play an important role in organic matter recycling [1,6–9]. Scavenging amphipods can rapidly reach carrion because of their high mobility and well-developed chemoreceptors [7]. Furthermore, these scavenging amphipods and isopods could play a crucial role in maintaining commercial fish and decapod stocks since they are part of their food sources. Therefore, an increase in the available carrion (e.g., commercial fishing discards) could also raise the biomass of small scavengers and, consequently, the potential

food availability for higher levels of the food chain, including species with commercial interest [10].

Marine scavengers are commonly used as a food resource for people, and fishers have taken advantage of the active scavenging behavior to reach carrion to capture some commercial species in baited traps for decades [2,4,11,12]. The importance of these fisheries continues to the present; for example, the annual landings of *Octopus vulgaris* Cuvier, 1797 in the NW Iberian Peninsula by the artisanal fleet, reaches 1500 t in 2021 [13,14]. Therefore, baseline data of scavenging megafauna on the NW coast of the Iberian Peninsula that provides information on the abundance of species in different habitats is key to understanding the distribution of this crucial but understudied group. Moreover, fish damage by scavengers (amphipods and isopods) has been reported as a concern to commercial fisheries and aquaculture production [15].

Scavenging fauna distribution depends on depth, hydrological conditions, sedimentation regime, food availability and bottom type [16–18]. Some approaches have been used: (1) baited cameras that record or take images at pre-set intervals [2,5,19,20]; (2) small baited traps (1–5 cm entrance) used to sample scavenging macrofauna (0.5 mm to 2 cm) [1,9,16–18,21,22]; and (3) big baited traps (>10 cm entrance) designed for fish, decapods and mollusc harvesting that also sample megafauna (>5 cm) [10,12]. The main advantage of baited cameras is that they are non-destructive sampling methods, but it may be difficult or impossible to identify small organisms, such as amphipods or isopods, which are relevant scavenger taxa [4]. This problem can be dealt with by using baited traps, namely by using traps with a prefixed entrance that allows scavengers to be selected by size, and after the retrieval of traps, smaller macrofauna can be fixed for later identification in the laboratory, whereas the megafauna can be returned to the environment after identification and counting in situ [9]. Baited traps are usually deployed for a few hours (i.e., 6 h) [16], 18 h [9], 24 h [10,12,17,18], or even for longer periods [10].

Scavenging fauna is already well-studied in shallow and deep areas of the Arctic Sea [5,16,18,21], shallow waters of the North Atlantic [2,12], tropical reef ecosystems of the Coral Sea [9], the North Deep Pacific [22], and Antarctica [1,19]. Most of these studies focused on commercial fishing discards [11]. However, studies in the Iberian Peninsula are still scarce and are related to scavenging fauna associated with commercial fishing discards on the southern Portuguese coast [10]. Nevertheless, these studies were not designed with robust and systematized sampling procedures to compare megafauna and benthopelagic macrofaunal assemblages separately in different habitats under the same depth conditions.

This study aims to set baseline data about scavenger assemblages in three different habitats in shallow waters of the NW Iberian Peninsula. For this, two different types of baited traps, intended to capture scavenging megafaunal and benthopelagic macrofaunal scavenger assemblages, were deployed at 20 m depth on the coast of Viana do Castelo (North Portugal) and to compare them among rocky, pebbled and sandy bottoms. The hypothesis tested was that megafaunal and benthopelagic macrofaunal scavenging assemblages will differ between habitats. These baseline data could improve the knowledge of this understudied group of animals in the scope of the implementation of the European Marine Strategy Framework Directive (MSFD; 2008/56/EC), where the species composition is one basic descriptor on the evaluation of the ‘Good Environmental Status’ (GES) [23,24]. Given the economic relevance of some scavenger species, this study could also contribute to fishery management by providing information to fishermen about the habitat preferences of commercial species.

2. Materials and Methods

2.1. Study Area

The North coast of Portugal is affected by a semi-diurnal tidal regime, with the largest spring tides of 3.5–4.0 m [25]. The area is dominated by the southwards surface “Portugal Current” and bottom northwards currents [26]. This straight coast is very exposed to a particularly energetic wave action, with a dominant swell from the west and northwest.

The most frequent wave heights are 1.5–2 m with an interval period of 11–13 s. During winter wave extreme events, with maximum wave height values of about 7–11 m, the whole shelf is under the waves' influence [27,28]. In addition, the studied area is subjected to a seasonal upwelling that provides nutrients and hence increases the primary production in the water column during the spring and summer months [26,28,29].

The area of Viana do Castelo is dominated by rocky reefs derived from plutonic and metamorphic outcrops, pebbled bottoms, and soft bottoms resulting from marine erosion [27,28]. Based on existing bathymetric charts (e.g., COSMO, Navionics) complemented with our data, we categorized three main habitats in the shallow coast of Viana do Castelo (<30 m depth): sandy bottoms, rocky reefs and pebbles (Figure 1). Sandy bottoms are composed mainly of fine sand moderately well sorted, rocky reefs consist of complex rocky reefs intercalated with large boulders, and pebbled areas were composed of approximately 10 cm to 20 cm pebbles on fine sand. These data were generated from bottom charts, developed based on bathymetry and hardness data from side scan sonar (Helix 9 Chirp DI GPS G2N), processed with Quantum Gis [30] and ReefMaster software [31], and confirmed by bottom images obtained with an underwater mini ROV (Chasing M2).

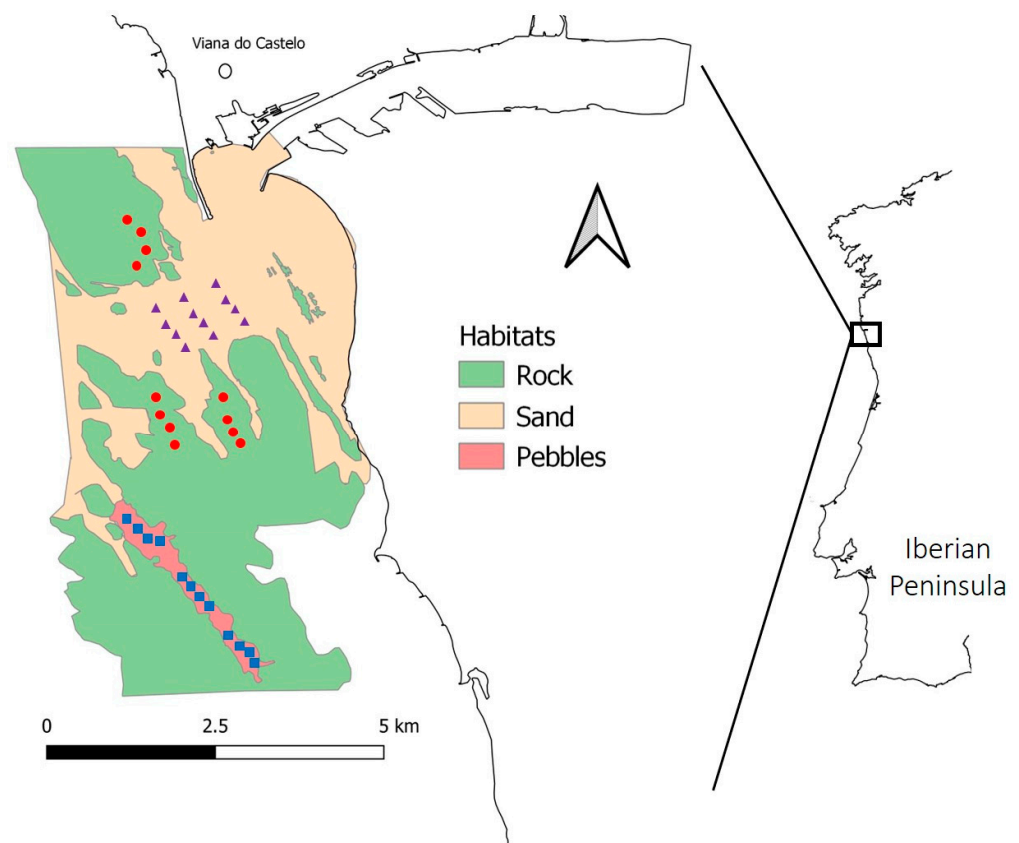


Figure 1. Main bottom habitats on the shallow coast of Viana do Castelo (<30 m depth) and baited trap deployment sites. Red dots indicate baited traps deployed in rocks; pink triangles indicate baited traps deployed in sand; blue squares indicate baited traps deployed in pebbles.

2.2. Sampling Strategy

Two different types of baited traps were used as scavenger selective sampling devices. The first one was designed for sampling benthopelagic macrofauna, animals between 0.5 mm to 5 cm mainly composed of amphipods and isopods. The macrofauna trap consisted of a 30 cm long PVC pipe (11 cm diameter) with a 1 cm opening funnel glued and sealed at one end. The funnel allowed animals to easily enter the trap but not to exit it. The opposite end of the trap was covered with a 0.5 mm mesh bag fastened with elastic bands. The mesh allowed water to circulate inside the trap and to take a sample or replace the

bait, as it was only necessary to remove the mesh (sensu Keable, 1995) (Figure 2A). The second trap was designed for benthic and demersal megafauna sampling, consisting of animals between 5 cm and 1 m mainly composed of Gastropods, *Octopus* and fishes, and is made up of cylindrical commercial fish traps with a 1 cm mesh, 70 cm high, 40 cm diameter and 15 cm opening (Figure 2B). The opening had a conical shape that ended in a mesh that allows entry but made the exit difficult. The bait was introduced into a 0.5 mm mesh bag inside the trap.

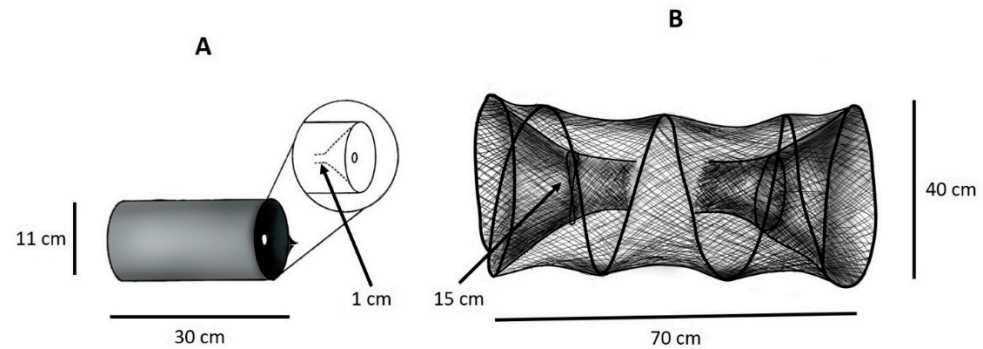


Figure 2. Benthopelagic macrofauna trap (A) and Megafauna trap (B).

In July 2022, a total of 36 megafauna traps and 27 benthopelagic macrofauna traps were deployed at three different habitats. At each habitat, three different sites were sampled, and four traps in the case of megafauna and three in the case of benthopelagic macrofauna were deployed at a minimum distance of 100 m between each other to avoid the overlapping effects of the bait (Figure 1). Both traps were marked with a buoy; megafauna traps were attached to the end of the rope close to the lead and benthopelagic macrofauna traps were attached 30 cm from the lead to ensure that the traps were not in contact with the substrate and to avoid large marine gastropods from obstructing the entrance of smaller scavengers (Figure 3). The baited traps were left for 24 h and retrieved during the morning of the following day. The determination of such period was based on a previous study in the south of Portugal [10] that reported that the main consumption of bait occurred within the first 24 h. Approximately 100 g of smashed pilchard (*Sardina pilchardus* (Walbaum, 1792)) was used as bait because this oily fish (pilchards) provided the most consistent results in baited traps [32]. Upon retrieval, the content of the megafaunal traps was sorted into large containers and the species composition of each trap was identified and counted in situ. The megafauna was then returned to the sea alive. After collection, the content of the benthopelagic macrofaunal traps was washed out into small containers, pre-filled with 70% formalin with Bengal Rose for later identification to the lowest taxonomic level (usually species), and quantification at the laboratory. The taxonomic classification followed the World Register of Marine Species (WoRMS) [33].

2.3. Data Analyses

Data were analyzed using multivariate techniques to test if scavenging benthopelagic macrofaunal and scavenging megafaunal assemblages differ between habitats (different bottom types). A non-parametric permutational multivariate analysis of variance (PERMANOVA; [34]) was based on a two-way model design with two factors: Habitat (fixed, three levels: Sand vs. Rock vs. Pebbles) and Site (Random, nested in Habitat, three levels: Site 1 vs. Site 2 vs. Site 3). Three replicates per site in benthopelagic macrofaunal bait traps and four in megafaunal traps were used. When appropriate, a posteriori multiple comparisons were made to test the differences between/within groups for pairs of levels of factors. Tests were based on 9999 permutations of residuals under a reduced model of fourth root transformed density data. When the number of unique permutations for a factor was lower than 30 (or close to 30), Monte Carlo *p*-values were considered [35]. Patterns in the assemblages were visualized by non-metric multidimensional scaling (nMDS) based

on the Bray-Curtis dissimilarity matrix. A PERMDISP procedure was undertaken to test whether differences between habitats were due to different multivariate dispersion in the location of the centroids [34]. The SIMPER procedure was used to identify the percentage contribution of each taxon to the Bray–Curtis dissimilarity between habitats. Taxa were considered important if their contribution to percentage dissimilarity was >10%. Multivariate analyses were conducted using Primer v.6 [36] with PERMANOVA + add-on [35].

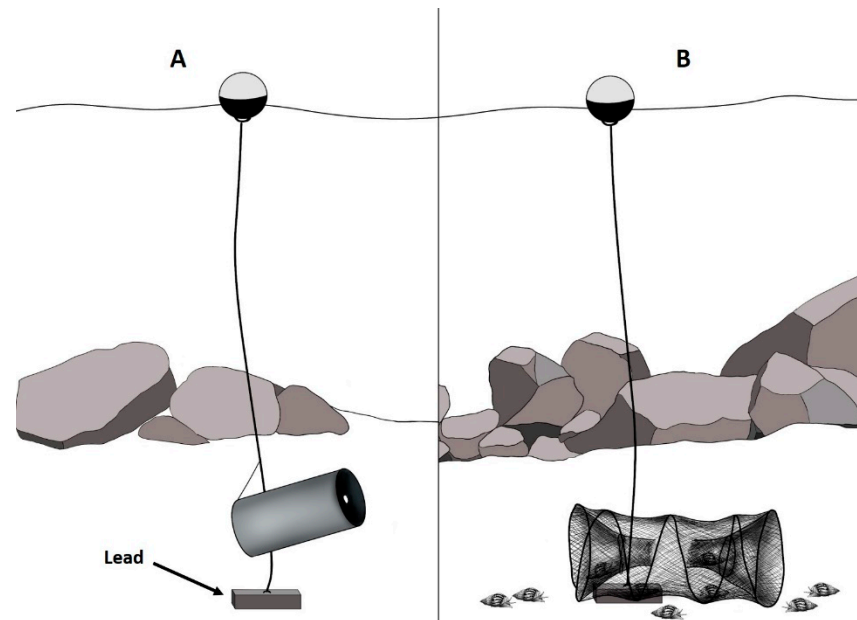


Figure 3. Deployment scheme of benthopelagic macrofauna (A) and Megafauna (B) baited traps.

3. Results

3.1. Scavenging Megafaunal Assemblages

A total of 2462 individuals and eight species were sampled in megafauna baited traps (Table 1). *Conger conger* (Linnaeus, 1758) was the most frequent fish captured by the traps, given that it is more common in rocky and pebbled areas than in sandy habitats. *Trisopterus luscus* (Linnaeus, 1758) was more abundant in sandy habitats. In sand traps, 2394 gastropods of the genus *Tritia* (*Tritia reticulata* (Linnaeus, 1758) and *Tritia varicosa* (W. Turton, 1825)) were captured, reaching a maximum number of 1296 individuals in a single trap and an average of 199.5 ± 357.53 individuals per trap. PERMANOVA results showed that scavenging megafaunal assemblages were significantly different between habitats (Table 2). Pair-wise tests showed significant differences between sand vs. rock and sand vs. pebbles. However, no significant differences were found between rock and pebbles (Table 3). Moreover, the PERMDISP analysis showed that the dispersion of replicates did not provide a significant contribution to the observed differences between habitats (Table 3). The nMDS ordination showed a clear separation of scavenging megafaunal assemblages between sand and the other two habitats (Figure 4).

The dissimilarity of scavenging megafaunal assemblages between sand and rock was 86.51%, with *Tritia* gastropods contributing to 48.95% of this dissimilarity (Table 4). The fishes *C. conger* and *T. luscus* and the echinoderm *Marthasterias glacialis* (Linnaeus, 1758), considered together, contributed 41.67% of the dissimilarity between habitats.

The dissimilarity of scavenging megafaunal assemblages between sand and pebbles was 83.01%, with *Tritia* gastropods responsible for 54.50% of this dissimilarity (Table 4). As in the previous case, *C. conger*, *T. luscus* and *M. glacialis* were also important taxa contributing to the dissimilarity between habitats.

Table 1. Summary of the number of individuals of each megafaunal species per habitat. Average and standard deviation per trap and the total number of individuals captured.

| Species | Sand | | Rock | | Pebbles | |
|--------------------------------|-----------------|-------|-------------|-------|-------------|-------|
| | Average | Total | Average | Total | Average | Total |
| <i>Tritia</i> spp. | 199.50 ± 357.53 | 2394 | 0.00 ± 0.00 | 0 | 0.08 ± 0.29 | 1 |
| <i>Octopus vulgaris</i> | 0.25 ± 0.45 | 3 | 0.08 ± 0.29 | 1 | 0.08 ± 0.29 | 1 |
| <i>Marthasterias glacialis</i> | 0.33 ± 0.89 | 4 | 0.75 ± 0.87 | 9 | 0.50 ± 1.00 | 6 |
| <i>Asterias rubens</i> | 0.08 ± 0.29 | 1 | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 |
| <i>Conger conger</i> | 0.33 ± 0.65 | 4 | 0.75 ± 0.62 | 9 | 0.67 ± 1.15 | 8 |
| <i>Trisopterus luscus</i> | 0.83 ± 0.72 | 10 | 0.25 ± 0.45 | 3 | 0.50 ± 0.67 | 6 |
| <i>Polybius henslowii</i> | 0.08 ± 0.29 | 1 | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 |
| <i>Scyllarus arctus</i> | 0.00 ± 0.00 | 0 | 0.08 ± 0.29 | 1 | 0.00 ± 0.00 | 0 |

Table 2. Permutational multivariate analysis of variance (PERMANOVA) of scavenging megafaunal assemblages.

| Source | df | MS | Pseudo-F | P (perm) | Unique Perms |
|----------------|------------|--------|----------|-----------------|--------------|
| Habitat | 2 | 8807.8 | 7.6202 | 0.01 | 280 |
| Site (Habitat) | 6 | 1155.8 | 1.2891 | 0.239 | 9933 |
| Residual | 27 | 896.65 | | | |
| Total | 35 | | | | |
| PERMDISP | F: 0.30564 | | | P (perm): 0.768 | |

Table 3. Results of pair-wise tests for scavenging megafaunal assemblages between habitats.

| Groups | t | P (perm) | Unique Perms | P (MC) |
|---------------|---------|----------|--------------|--------|
| Sand, Rock | 3.5243 | 0.09 | 10 | 0.005 |
| Sand, Pebbles | 3.2689 | 0.114 | 10 | 0.008 |
| Rock, Pebbles | 0.98031 | 0.287 | 10 | 0.4764 |

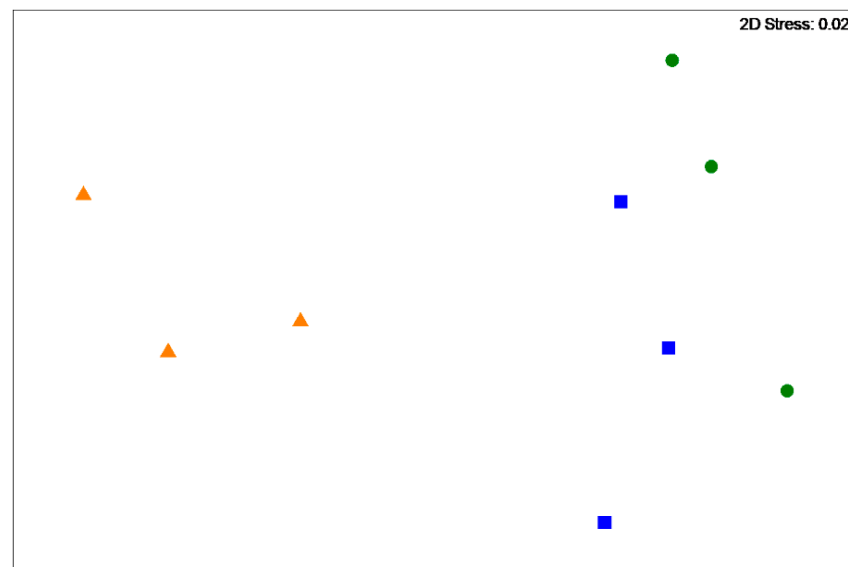


Figure 4. Non-metric multidimensional scaling (nMDS) ordination based on Bray–Curtis dissimilarity of centroids (calculated with the four replicates of scavenging megafaunal assemblages in three different habitats). (a) Orange triangles: sand; (b) Green dots: rock and (c) Blue squares: pebbles.

Table 4. SIMPER analysis results for the top contributors of the dissimilarity of scavenging megafaunal assemblages between habitats as determined by PERMANOVA based on the four root density data.

| Taxon | Average Abundance | | Average Diss | Diss/SD | Contrib% | Cum.% |
|--------------------------------|-------------------|---------|--------------|---------|----------|-------|
| | Sand | Rock | | | | |
| <i>Tritia</i> spp. | 2.78 | 0 | 42.35 | 1.88 | 48.95 | 48.95 |
| <i>Conger conger</i> | 0.27 | 0.68 | 12.58 | 0.8 | 14.54 | 63.49 |
| <i>Trisopterus luscus</i> | 0.7 | 0.25 | 12.07 | 0.98 | 13.96 | 77.45 |
| <i>Marthasterias glacialis</i> | 0.19 | 0.55 | 11.39 | 0.71 | 13.17 | 90.62 |
| | Sand | Pebbles | | | | |
| <i>Tritia</i> spp. | 2.78 | 0.08 | 45.24 | 1.9 | 54.5 | 54.5 |
| <i>Trisopterus luscus</i> | 0.7 | 0.43 | 13.66 | 0.75 | 16.45 | 70.95 |
| <i>Conger conger</i> | 0.27 | 0.45 | 9.89 | 0.72 | 11.91 | 82.87 |
| <i>Marthasterias glacialis</i> | 0.19 | 0.29 | 8.11 | 0.55 | 9.76 | 92.63 |

3.2. Scavenging Benthopelagic Macrofaunal Assemblages

A total of 3306 individuals and 22 taxa were sampled in benthopelagic macrofauna-baited traps (Table 5). Cirolanid isopods and lysianassid amphipods accounted 86.81% of the individuals. *Cirolana cranchii* Leach, 1818 was the most abundant isopod captured by the traps, where it reached a maximum number of 894 individuals in a single rocky trap and an average of 246.4 ± 340.91 individuals per trap. Isopods from the family Gnathiidae (Pranizae larvae stage) were exclusively found in rocky habitats, whereas the mysid *Siriella clausii* G.O. Sars, 1877 was more abundant in the sand. *Socarnes erythrophthalmus* Robertson, 1892 amphipods were more abundant in rocky habitats.

Table 5. Summary of the number of individuals of each benthopelagic macrofaunal species per habitat. Average and standard deviation per trap and the total number of individuals captured.

| Species | Sand | | Rock | | Pebbles | |
|----------------------------------|---------------|-------|-----------------|-------|--------------|-------|
| | Average | Total | Average | Total | Average | Total |
| Crustacea, Zoea larvae | 12.00 ± 23.91 | 109 | 0.22 ± 0.44 | 2 | 0.00 ± 0.00 | 0 |
| <i>Cirolana cranchii</i> | 5.56 ± 8.06 | 47 | 246.44 ± 340.91 | 2218 | 3.56 ± 7.40 | 32 |
| <i>Eurydice affinis</i> | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 | 0.44 ± 0.73 | 4 |
| <i>Cymodoce truncata</i> | 0.11 ± 0.33 | 1 | 0.11 ± 0.33 | 1 | 0.11 ± 0.33 | 1 |
| Gnathiidae juvenile | 0.00 ± 0.00 | 0 | 7.00 ± 11.18 | 63 | 0.00 ± 0.00 | 0 |
| <i>Gammarus crinicornis</i> | 9.67 ± 21.99 | 87 | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 |
| <i>Nototropsis guttatus</i> | 5.67 ± 12.94 | 50 | 0.33 ± 0.71 | 3 | 0.33 ± 0.50 | 3 |
| <i>Stenotoe monoculoides</i> | 0.56 ± 1.01 | 5 | 0.44 ± 1.01 | 4 | 0.00 ± 0.00 | 0 |
| <i>Metopa</i> sp. | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 | 0.22 ± 0.44 | 2 |
| <i>Socarnes erythrophthalmus</i> | 4.33 ± 8.85 | 15 | 54.67 ± 138.80 | 492 | 7.33 ± 13.57 | 66 |
| <i>Tryphosella sarsi</i> | 0.11 ± 0.33 | 1 | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 |
| <i>Ampelisca</i> sp. | 0.11 ± 0.33 | 1 | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 |
| <i>Podocerus</i> sp. | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 | 0.11 ± 0.33 | 1 |
| <i>Caprella</i> sp. | 0.00 ± 0.00 | 0 | 0.22 ± 0.44 | 2 | 0.00 ± 0.00 | 0 |
| Aoridae spp. | 0.67 ± 1.12 | 6 | 1.56 ± 1.67 | 14 | 0.22 ± 0.67 | 2 |
| Calanidae | 0.11 ± 0.33 | 1 | 0.33 ± 0.71 | 3 | 0.67 ± 1.41 | 6 |
| Harpacticoida sp1 | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 | 0.11 ± 0.33 | 1 |
| Harpacticoida sp2 | 0.00 ± 0.00 | 0 | 0.11 ± 0.33 | 1 | 0.11 ± 0.33 | 1 |
| <i>Siriella clausii</i> | 2.78 ± 6.16 | 25 | 0.44 ± 0.88 | 4 | 0.22 ± 0.67 | 2 |
| <i>Ophiura</i> sp. | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 | 0.11 ± 0.33 | 1 |
| <i>Asterina gibbosa</i> | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 | 0.11 ± 0.33 | 1 |
| Gastropoda, juvenile | 0.00 ± 0.00 | 0 | 0.00 ± 0.00 | 0 | 0.11 ± 0.33 | 1 |

PERMANOVA results showed significant differences in scavenging benthopelagic macrofaunal assemblages between habitats, but only between rock vs. pebbles (Tables 6 and 7). Moreover, despite the PERMDISP analysis indicating that the dispersion of replicates was significant among habitats (Table 6), the PERMDISP pairwise comparisons showed that the dispersion of replicates did not provide a significant contribution to the observed differences between rock and pebbles ($t = 3.4025$; $P(\text{perm}) = 0.016$), which were clearly separated in the nMDS plot (Figure 5).

Table 6. Permutational multivariate analysis of variance (PERMANOVA) on scavenging benthopelagic macrofauna assemblages.

| Source | df | MS | Pseudo-F | P (perm) | Unique Perms |
|----------------|-----------|--------|--------------------|----------|--------------|
| Habitat | 2 | 6561.2 | 1.7498 | 0.042 | 280 |
| Site (Habitat) | 6 | 3749.7 | 1.8697 | 0.0045 | 1997 |
| Residual | 18 | 2005.5 | | | |
| Total | 26 | | | | |
| PERMDISP | F: 7.8212 | | P (perm): 0.006 | | |

Table 7. Results of pair-wise tests for scavenging benthopelagic macrofaunal assemblages between habitats.

| Groups | t | P (perm) | Unique Perms | P (MC) |
|---------------|--------|----------|--------------|--------|
| Sand, Rock | 1.3454 | 0.101 | 10 | 0.139 |
| Sand, Pebbles | 1.0434 | 0.598 | 10 | 0.398 |
| Rock, Pebbles | 1.6577 | 0.111 | 10 | 0.046 |

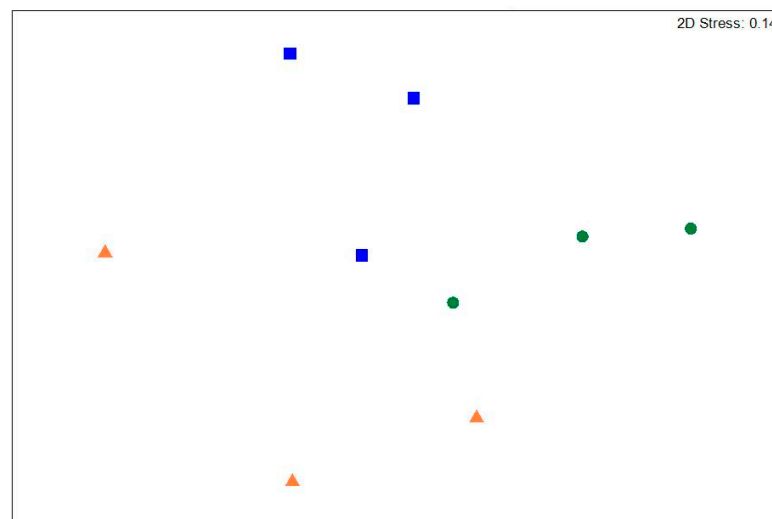


Figure 5. Non-metric multidimensional scaling (nMDS) ordination based on Bray–Curtis dissimilarity of centroids (calculated with the four replicates of scavenging benthopelagic macrofaunal assemblages in three different habitats). (a) Orange triangles: sand; (b) Green dots: rock; and (c) Blue squares: pebbles.

The dissimilarity of scavenging benthopelagic macrofaunal assemblages between pebbles and rock was 76.03%, with the isopod *C. cranchii* and the amphipod *S. erythrophthalmus* contributing to 51.97% of this dissimilarity (Table 8).

Table 8. SIMPER analysis results for the top contributors of the dissimilarity of scavenging benthopelagic macrofaunal assemblages between habitats as determined by PERMANOVA based on the four root density data.

| Taxon | Average Abundance | | Average Diss | Diss/SD | Contrib% | Cum.% |
|---------------------------------|-------------------|------|--------------|---------|----------|-------|
| | Sand | Rock | | | | |
| <i>Cirolana cranchii</i> | 2.94 | 0.87 | 18.87 | 1.52 | 24.83 | 24.83 |
| <i>Socarnes erythropthalmus</i> | 1.87 | 0.8 | 12.91 | 1.5 | 16.98 | 41.81 |
| Gnathiidae juvenile | 1.06 | 0 | 7.73 | 1.22 | 10.16 | 51.97 |

4. Discussion

Results showed that the initial hypothesis was partially supported. On one hand, scavenging megafaunal assemblages differed between sand vs. rock and sand vs. pebbles. On the other, scavenging benthopelagic macrofaunal assemblages differed between pebbles vs. rock. Therefore, differences in the assemblage structure of scavengers among habitats showed different patterns for macrofauna and megafauna, with sand habitats different than the others in megafaunal assemblages and with non-differences between sand vs. pebbles and sand vs. rock in macrofaunal assemblages. This suggests that different drivers seem to shape the structure of species assemblages that we categorized as scavenging benthopelagic macrofaunal and megafaunal assemblages. Regarding megafauna, the dominance of *Tritia* gastropods in sandy habitats in comparison with its absence in rock and its very low abundance in pebbles was the main factor responsible for differences between habitats. However, in benthopelagic macrofauna, differences in assemblages between pebbles and rocky habitats were more related to changes in the relative abundance of crustacean species (*C. cranchii* and *S. erythropthalmus*) that were less abundant in pebbles.

As it has been verified with the bathymetric maps obtained in this study, the nearby of Viana do Castelo is a very heterogeneous landscape, where sandy, rocky and pebbled habitats are mixed in a relatively small area. Despite this, with this multi-habitat approach, it was possible to observe differences between the habitats based on scavenging megafaunal and benthopelagic macrofaunal assemblages.

Nassariidae gastropods accounted for 97.23% of megafaunal scavengers, almost exclusively in sand habitats. According to Keable, 1995, common obligate scavenger gastropods of the family Nassaridae occurred in large numbers in the marine benthos [9]. Our results showed that gastropods of the genus *Tritia* (*T. reticulata* and *T. varicosa*) reached the maximum abundance in sandy habitats. This high dominance of *T. reticulata* and *T. varicosa* on sandy bottoms can be explained because both species' distribution is limited to sandy habitats [37]. Other Nassarids such as *Tritia incrassata* (Strøm, 1768) are typical scavengers of rocky intertidal habitats, but in this study, *T. incrassata* was not found on rocky shores, as this species is limited to low intertidal levels and very shallow subtidal ones [37]. Therefore, based on our results, the scavenging activity of *Tritia* in the shallow sublittoral waters of the NW Iberian Peninsula could be mostly restricted to sandy habitats. This result is also in accordance with previous studies where Nassarids typically present a lie-in-buried-response behavior in soft bottoms [38,39].

Sea stars have been reported as successful scavengers in previous studies [40,41]. *M. glacialis* is a chemoreception-based opportunistic feeder and a dominant benthic predator that plays a key role in structuring benthic assemblages [42]. In our study, *M. glacialis* was the third most abundant megafaunal taxon, appearing in the three studied habitats. Our results agree with Onghia et al., 2014, that reported the preference of *M. glacialis* for rocky and boulder bottoms because the abundance of *M. glacialis* in rock was more than double compared to the reported abundance in sandy habitats [42].

For British shallow waters, Nickell and Moore, 1991 reported that a 24 h period of deployment was not enough to collect megafaunal scavengers such as *Octopus* or predator fishes in baited traps [12]. In contrast, our results showed that within 24 h, scavenging

macrofaunal species, some with commercial interest in the Iberian Peninsula, were captured, such as *C. conger*, *O. vulgaris* and *T. luscus* [13,43–45].

Conger conger is considered a large opportunistic scavenger and predator typical of shallow and deep rocky areas where it finds refuge and foraging areas [43,45]. Our results agree with Castro et al., 2005, who reported *C. conger* as the most common fish sampled with bait traps in southern Portugal between 1997 and 2001 [10]. Our results pointed out a preference of *C. conger* for rock and pebbles, in accordance with Xavier et al., 2010, who reported that *C. conger* was mostly associated with rocky bottoms on the south coast of the Iberian Peninsula [45]. *C. conger* is also a common scavenger of deep and shallow waters and one of the main target species of commercial fishing [43], with more than 1500 t of annual landings and close to EUR 3 million in profits northwest of the Iberian Peninsula (Galicia) in 2021 [14].

Gadiformes, and especially those belonging to the family Gadidae, have been reported as typical scavengers captured by baited traps [40]. In the shallow waters of the NW Iberian Peninsula, one of the most common was *T. luscus*. This species is distributed along rock and sand sea bottoms on the continental shelf at depths of 20–100 m [46]. Despite the fact that the knowledge of its ecology is scarce [47], *T. luscus* has also been reported as one of the most common fish fauna in NW Iberia [48]. Our results showed that the abundance of *T. luscus* was similar to that of *C. conger*, also widely distributed along the three studied habitats, but showing a preference for sand as hunting grounds. As *T. luscus* is also a commercial species, knowledge about its ecology is also of special relevance; its annual landings reached around 700 t in 2021, with an economic value of direct auction sale of more than EUR 1.7 million [14].

The very mobile opportunistic carnivore *O. vulgaris* is well adapted to live in different habitats (sandy and muddy bottoms, rocks, and seagrass meadows) [49]. Our results also showed that *O. vulgaris* was present in the three studied habitats. Even so, Guerra et al., 2014 reported the sandy inlet of Rodas in the National Park of the Atlantic Galician Islands as a preferential habitat for *O. vulgaris* [49]. In our study, *O. vulgaris* was more abundant in sandy bottoms than in rocky and pebbled habitats. Nevertheless, it was observed that the apparent fishing effort in the study area dedicated to *Octopus* pots was substantially greater in the rocky habitats than in the sandy ones. This fact, together with the enormous fishing effort in the area, could be influencing our results. Moreover, taking into account that the annual landings of *O. vulgaris* in the NW Iberian Peninsula in 2021 were more than 1700 t with an economic value of the direct sale of more than EUR 15 million [14], additional data with regard to *O. vulgaris* ecology and distribution could be very helpful for fishers and the scientific community to achieve a more sustainable exploitation of this resource.

Since scavenging megafaunal assemblages included many species with commercial interest, overfishing could also contribute to the decline of these species. In this way, the effect of commercial fishing on scavengers could cause an imbalance in ecosystem functioning and nutrient cycling.

Nickell and Moore, 1991, [12] pointed out the importance of assuring the non-interference in the baited traps of large scavengers with small ones to not bias the results. Furthermore, according to Legezyńska et al., 2000, some studies based on baited traps were not able to capture both scavenging megafaunal and benthopelagic macrofaunal assemblages [21]. Thus, the implementation of two different bait traps in this study also guarantees no interference from the megafaunal scavengers with the capture of the macrofaunal ones. Moreover, our results showed different patterns among habitats for scavenging megafaunal and benthopelagic macrofaunal assemblages, reinforcing the implementation of the simultaneous deployment of the two types of baited traps.

The diversity of scavenging benthopelagic macrofaunal assemblages of the NW Iberian Peninsula is difficult to compare to other studies due to differences in trap design, deployment scheme, and target habitats [9]. Even so, there are common patterns that can be discussed. Within scavenging benthopelagic macrofauna, lysianassoid amphipods and cirrolanid isopods are reported as the most important scavengers in playing a key role

to transfer the energy of dead organic matter to higher trophic levels [7,10]. Lysianasids and Cirolanids had been identified as the most important component for the recycling of organic matter in the deep waters of south Portugal [10]. Our results showed that *C. cranchii* and *S. erythrophthalmus* are the most widespread and abundant benthopelagic macrofaunal scavengers in the three habitats. Our results are also in accordance with Keable, 1995 and Ellis et al., 2013, which reported that cirolanids constituted the major portion of the macrofaunal assemblages and that *C. cranchii* was highly abundant and also a voracious scavenger [9,20].

Keable, 1995, [9] reported that the composition of scavenger assemblages differs between temperate and cold waters. The NW Iberian Peninsula is an especially important area because it constitutes the transition between two biogeographic regions, the Mediterranean-Atlantic (warm-temperate) and the Boreal-Atlantic (warm-cold). Our results are more similar to those reported in temperate zones where Cirolanids dominate the abundance (i.e., Keable, 1995 [9]), as compared to those for cold waters, where Lysianassids are usually numerically dominant in baited traps (i.e., [17,18,21]).

In contrast with scavenging megafaunal assemblages, differences between benthopelagic macrofaunal assemblages from pebbles and rocky bottoms were not the result of the presence of exclusive species at any of the two habitats. The two species that explain differences between pebbles and rocky bottoms (i.e., *C. cranchii* and *S. erythrophthalmus*) were present in the three studied habitats. Therefore, differences between habitats for benthopelagic macrofauna seem to be explained by changes in the relative abundance of *C. cranchii* and *S. erythrophthalmus* between habitats. This result suggests a differential preference of these two species for the studied habitats, rocky shores being the more preferred habitat and pebbles the less preferred one.

5. Conclusions

Our results showed different patterns among habitats for scavenging benthopelagic macrofaunal and megafaunal assemblages. Scavenging megafaunal assemblages differed between sand and the other two studied habitats, whereas scavenging benthopelagic macrofaunal assemblages only differed between pebbles and rocky habitats. Our results suggest that different drivers seem to shape the structure of scavenging benthopelagic macrofaunal and megafaunal assemblages. Regarding megafauna, the dominance of *Tritia* gastropods in sandy habitats was mainly responsible for the differences. However, in benthopelagic macrofauna, differences in assemblages were more related to changes in the relative abundance of the main species among habitats. This first baseline data by habitat type on the distribution and ecology of scavengers and especially of those species with commercial interest is a starting point for future studies.

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