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# Deep-sea scavenging amphipod assemblages from the submarine canyons of the Iberian Peninsula

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9, 7831–7851, 2012

## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Abstract

Submarine canyons have often been identified as hotspots of secondary production with the potential to house distinct faunal assemblages and idiosyncratic ecosystems. Within these deep-sea habitats, assemblages of scavenging fauna play a vital role in reintroducing organic matter from large food falls into the wider deep-sea food chain.

Free-fall baited traps were set at different depths within three submarine canyons on the Iberian Margin. Amphipods from the traps were identified to species level and counted. Scavenging amphipod assemblages were compared at different depths within each canyon, between individual canyon systems, and between the abyssal plain and submarine canyon sites. Samples from canyons were found to contain common abyssal plain species but in greater than expected abundances. Community composition differed significantly between the submarine canyons and abyssal plains. It is proposed that this is a result of the high organic carbon input into canyon systems owing to their interception of sediment from the continental shelf and input from associated estuarine systems.

## 1 Introduction

Large submarine canyons are complex, poorly understood, topographical features that incise deeply into the continental shelf (Shepard and Dill, 1966). They experience heightened levels of sediment input, acting as downward conduits for matter that has been transported along the continental shelf, an effect that is often amplified in the presence of contributory river systems (Vetter and Dayton, 1998; Van Weering et al., 2002; Cúrdia et al., 2004). Elevated sediment input carries with it substantial quantities of organic matter (Kiriakoulakis et al., 2011), providing food for deep-sea scavengers (Sorbe, 1999). Many submarine canyons have been identified as hotspots of secondary production (Jannasch and Taylor, 1984; Gage and Tyler, 1992; Vetter, 1995; Soliman and Rowe, 2008; De Leo et al., 2010; Van Oevelen et al., 2011). One section

**BGD**

9, 7831–7851, 2012

## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



of the Nazaré Canyon, on the Iberian Peninsula, contains an estimated biomass of megabenthic invertebrates that is 2–3 orders of magnitude greater than that found on open slopes at similar depths (Van Oevelen et al., 2011). Biomass in the Kaikoura Canyon, off the coast of New Zealand is estimated to be an order of magnitude greater again (De Leo et al., 2010).

Scavenging organisms are particularly important in the deep sea (Britton and Morton, 1994). In an environment where food-supply is often a limiting factor, they play a pivotal role in the degradation and redistribution of organic matter (Christiansen and Dielchristiansen, 1993). Scavengers breakdown, disperse, and reintegrate organic carbon from food falls into the deep-sea food web via predator-prey interactions (Payne and Moore, 2006) and by faecal enrichment of sediments (Stockton and DeLaca, 1982; Jones et al., 1998).

Of all of the scavenging organisms, members of the order Amphipoda (Crustacea, Malacostraca) have been found to be some of the most abundant and successful in the deep sea (Hessler et al., 1978; Debroyer et al., 2004). Morphological evidence suggests that scavenging has evolved independently on numerous occasions within this order, with the majority of scavenging amphipods being members of the superfamily *Lysianassoidea* (Dahl, 1979; Debroyer et al., 2004; Lowry and Stoddart, 2009, 2011). Many deep-sea scavenger species have cosmopolitan distributions and there is little evidence of endemism in individual abyssal plain communities (Thurston, 1990). Some species, such as *Eurythenes gryllus* Lichtenstein, 1822, have been found in all of the World's oceans and over a wide range of depths (Christiansen et al., 1990; Debroyer et al., 2004). There is, however, a growing body of evidence to support the theory that discrete populations inhabit the Atlantic and Pacific oceans. The extent of this separation has yet to be determined with some indication that populations are on the verge of speciation (Thurston et al., 2002, and references therein).

Assemblages of scavenging amphipods in submarine canyons have been poorly studied (e.g., Soliman and Rowe, 2008) and factors affecting the composition of these communities are yet to be identified. This study aims to determine if scavenging

**BGD**

9, 7831–7851, 2012

## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



amphipod communities in submarine canyons differ from those in other locales and identify factors that may potentially be affecting community composition and species distributions.

## 2 Methods

### 2.1 Sample collection

Three submarine canyons on the Iberian Margin, off of the west coast of Portugal, were studied; Nazaré, Setúbal, and Cascais (Fig. 1). Sampling occurred on three scientific research expeditions (RRS *Discovery* 297, RRS *Charles Darwin* 179, RRS *James Cook* 010) between August 2005 and June 2007 as part of the European HERMES (Hotspot Ecosystem Research on the Margins of European Seas) Project (Table 1). Samples were collected using a basic trap design comprising of a funnelled entrance leading into a container with bait attached inside. All deployments during D297 and CD179 utilised a free-fall lander frame with one trap at the base and one a metre above. Recovery was via an iXSea acoustic release attached to the frame alongside the trap. The JC010/094 deployment used two traps placed on the seafloor and recovered using the remotely operated vehicle (ROV) Isis. All but one of the traps were baited with a single raw mackerel (*Scomber scombrus*) of approximately equal size wrapped in muslin cloth. Trap CD179/56817 was baited with smoked fish fillets. Upon recovery, the contents of all traps were fixed in 4 % buffered formaldehyde-saline solution and subsequently preserved in 80 % industrial methylated spirits.

### 2.2 Sample analysis

All amphipods were identified to species level using morphological characteristics viewed under a stereo dissecting microscope. Following sorting, counts of each species were taken. For the purposes of this study the contents of the two traps used in each deployment were analysed as a whole.

## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abundance data were converted to percentage composition and square-root transformed. Bray-Curtis Similarity matrices were subsequently produced. A one-way analysis of similarities (ANOSIM; Clarke, 1993) was performed using PRIMER 6 (Plymouth Routines In Multivariate Ecological Research; Clarke and Gorley, 2006) statistical software to determine if community composition varied significantly between samples. A SIMPER analysis (Clarke, 1993) was used to identify which components of the community were responsible for any variability detected.

Study areas were grouped into megahabitats (e.g., canyon, abyssal plain) and macrohabitats (e.g., lower canyon, middle canyon; de Stigter et al., 2007) to facilitate comparative analyses between locales (Greene et al., 1999). Samples from the Iberian submarine canyons were classified using canyon and depth as factors to compare between macrohabitats within the submarine canyons. Canyon samples were compared to published records of scavenging amphipod community composition from traps deployed in the Iberian Abyssal Plain (Thurston, 1990). Where possible data on environmental variables were obtained from CTD casts deployed in the vicinity (<2.5 km radius) and from push-cores taken during dives of ROV Isis (Cunha et al., 2011). Temperature and total organic carbon (TOC) measurements were grouped into discrete categorical bins to facilitate subsequent factorial analysis.

The diversity of each site was measured using Simpson's Index of Diversity ( $D$ ; Simpson, 1949) calculated using the equation:

$$D = 1 - \sum_{i=1}^S \left( \frac{n_i(n_i - 1)}{N(N - 1)} \right) \quad (1)$$

where  $S$  is the total number of species,  $n_i$  the number of individuals of the  $i$ th species, and  $N$  the total number of individuals in the sample. The calculated indices were compared with those calculated for the adjacent abyssal plain using published data (Table 2; Thurston, 1990) with a Mann-Whitney  $U$  test. Evenness was measured using

Pielou's evenness index ( $J'$ ; Pielou, 1966):

$$J' = \frac{-\sum_{i=1}^S \frac{n_i}{N} \ln \frac{n_i}{N}}{\ln(S)} \quad (2)$$

and compared with a Mann-Whitney  $U$  test.

### 3 Results

5 A total of eight baited trap deployments were made, five in Nazaré Canyon, two in Setúbal, and one in Cascais. Large catches of scavenging amphipods were obtained from all but three of the deployments. During deployment D297/15734 the trap was  
10 damaged while in situ, possibly by strong currents in the canyon as recorded on the seabed lander system ROBIO (RObust BIOdiversity; OceanLab, Aberdeenshire, UK) deployed at the same time nearby (Weaver, 2005). Smoked fish was used instead of raw mackerel for deployment CD179/56817. Deployment JC010/094 was made using small traps deployed by ROV. Despite these three deployments returning smaller catches, the composition of the catches appeared to be unaffected and therefore these samples were included in analysis of community structure following standardisation for  
15 sample size.

Ten species of lysianassoid amphipod were identified, representing six scavenging amphipod families (Table 3; Fig. 2). Eight of the species have been recorded previously on the abyssal plains of the North-East Atlantic (Thurston, 1990; Christiansen, 1996, unpublished data). Four species are new to science; *Cyclocaris* sp. nov., *Valettietta* sp. nov., and two species of *Paracallisoma*.  
20

*Paralicella caperesca* Shulenberger and Barnard, 1976 was the dominant species in all but one sample. *Paralicella caperesca* and *P. tenuipes* Chevreux, 1908 accounted for between 77.7% and 96.1% of all scavenging amphipod specimens in each sample (Fig. 2). The prevalence of *P. tenuipes* was reduced at shallower sites. This trend was

particularly apparent in Nazaré Canyon where this species dominated at the lower canyon site but represented less than 1 % of the total scavenging amphipod component of the middle canyon sites.

No significant difference in scavenging amphipod communities was observed between submarine canyons (one-way ANOSIM:  $R = -0.269$ ,  $P = 0.885$ ). A significant difference was evident between sample sites in the middle and lower canyon (ANOSIM:  $R = 0.494$ ,  $P = 0.040$ ). There was no significant difference between communities based upon temperature (ANOSIM:  $R = 0.124$ ,  $P = 0.248$ ) or TOC of the sediments (ANOSIM:  $R = -0.333$ ,  $P = 0.971$ ).

The scavenging amphipod assemblages from canyons differed significantly from those of the adjacent Iberian Abyssal Plain (ANOSIM:  $R = 0.219$ ,  $P = 0.018$ ). SIMPER analysis showed that the majority (~72 %) of this dissimilarity was explained by differences in catches of *E. gryllus* (34.5 %), *P. caperesca* (24.8 %), and *P. tenuipes* (12.4 %).

Simpson's Index of Diversity values ranged from 0.23 to 0.65 ( $n = 9$ , median = 0.32, Q1 = 0.25, Q3 = 0.59) and were generally lower than values calculated for the abyssal plain ( $n = 6$ , median = 0.63, Q1 = 0.59, Q3 = 0.68). This difference was significant (Mann-Whitney  $U$  test;  $P = 0.013$ ). Pielou's Evenness Index showed the composition of abyssal plain samples was more evenly spread than canyon samples (Mann-Whitney  $U$  test;  $P = 0.013$ ).

## 4 Discussion

### 4.1 Community composition

The similarity of communities between canyons demonstrates the wide distribution of deep-sea scavenging amphipods and confirms that canyons do not restrict the movement of motile scavenging fauna. A similar trend is evident in abyssal basins, with

**BGD**

9, 7831–7851, 2012

## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



little community variation between adjoining abyssal plains in the North-East Atlantic (Thurston, 1990).

While the scavenging amphipod species identified in canyons are largely identical to those on the adjacent abyssal plains, there is a significant difference in the composition of the assemblages in these two habitats. The results of the SIMPER analysis coupled with the significant difference in Pielous's Evenness Index suggest that the disparity in community composition is due to the reduced importance of *Paralicella* spp. and increased evenness of community composition in abyssal plain settings, including a greater representation of *E. gryllus*. A more even distribution of species results in a higher diversity index when measured using indices, such as Simpson's, despite few differences in species richness.

A similar trend of high abundances and low species richness in submarine canyon communities has also been observed in scavenging fish (Stefanescu et al., 1994; King et al., 2008) and various macrofauna (Cunha et al., 2011; Paterson et al., 2011). The similarity of the assemblages in the different canyons taken together with the occurrence of species with global distributions, the mobility of amphipods (Boudrias, 2002), and the interconnectivity evident between canyons and abyssal plains (Vetter and Dayton, 1998) support the theory that the observed differences within canyons are mainly due to variation in environmental conditions, notably depth-correlated variables, rather than canyons acting as physical barriers to dispersal and species distributions.

Although community composition does not vary significantly between canyons, there is a clear difference in community composition within canyons at different depths. Within the limitations of this study, it has not been possible to establish which of the many depth-correlated variables (e.g. hydrostatic pressure, temperature, salinity, oxygen concentration, POC flux) specifically leads to the community differences seen. Temperature, salinity, oxygen concentration, and sediment TOC variability were not found to contribute significantly toward variability in community composition when tested as individual factors. It may be that hydrostatic pressure alone is responsible for these differences, however, the polar emergence of *E. gryllus* (Ainley et al., 1986), a deep-sea

**BGD**

9, 7831–7851, 2012

## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



scavenger primarily seen at abyssal depths at mid-latitudes (Ingram and Hessler, 1983; Smith and Baldwin, 1984), suggests that temperature also plays a role in the depth distribution limitations of deep-sea scavenging amphipods (Thurston et al., 2002). A more feasible explanation is that both of these depth-correlated variables, along with others, each contribute a small amount toward the community-level differences. While their individual effects are not detectable, the cumulative and interacting influences of these factors are detectable. The synergistic effect of temperature and depth upon respiration has been found during laboratory tests on the deep-sea lysianassoid *Stephonyx biscayensis* Chevreux, 1908 (Brown and Thatje, 2011), but the physiological limits of the species in this study remain unknown.

The dominance in all samples of *Parallicella*, a genus commonly identified in traps deployed on the abyssal plains of the North-East Atlantic (Thurston, 1990, unpublished data), indicates that members of this taxon are highly efficient scavengers. Both *P. caperesca* and *P. tenuipes* have been identified as specialist scavengers with adaptations that allow them to monopolise food falls (Thurston, 1979). The reduced prevalence of *P. tenuipes* at shallower sites, as particularly apparent in Nazaré Canyon, indicates that the upper depth limit of this species is shallower than that of its congener.

## 4.2 Relative abundance

Estimating background population size based on catches from baited traps, as performed previously for scavenging fishes using baited camera data (Priede and Merrett, 1998; Sainte-Marie and Hargrave, 1987), is not possible for deep-sea scavenging amphipods, which can rarely be identified in photographs and have unknown maximum swim speeds. Despite this, the large catches found in this study can be qualitatively linked to the size of the background populations (Blankenship et al., 2006). Compared to catches from similar traps deployed on the abyssal plains of the North-Eastern Atlantic (Table 2; Thurston, 1990), submarine canyons house very large assemblages of scavenging amphipods.

**BGD**

9, 7831–7851, 2012

## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



---

## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

---

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The large background populations of deep-sea scavenging amphipods, indicated by catches from canyons sampled, can be linked to high levels of sedimentation and enhanced concentrations of associated organic matter found (Vetter and Dayton, 1998; Epping et al., 2002; Garcia et al., 2010; Masson et al., 2010). Setúbal and Cascais  
5 Canyons are fed by large river systems (Sado and Tagus Rivers, respectively; Arzola et al., 2008). The mouths of these rivers flow directly into the canyon heads. Estuarine input results in large quantities of terrigenous organic matter entering the canyon system (Cúrdia et al., 2004). The extent to which this material travels down these two  
10 canyons is thought to be limited, in comparison to Nazaré, owing to the rarity of large-scale episodic events, which are a particular feature of down-canyon sediment transport (de Stigter et al., 2011).

Nazaré Canyon has no direct link to any large river systems, yet it has been estimated to have the highest levels of organic carbon and sediment input (Masson et al., 2010; Garcia et al., 2010). Heavy metal contamination of sediments in the canyon suggests  
15 output from a number of small river systems enters the canyon (Oliveira et al., 2011), however, inputs from shelf sediments are the most likely source of organic matter input. The Nazaré Canyon experiences the highest sediment input of the three canyons sampled. This provides an explanation for why the catches from this canyon are particularly large compared to catches from Setúbal and Cascais canyons, with  
20 Nazaré Canyon supporting larger background populations of scavenging amphipods.

The largest catches of all canyon deployments were seen in the deepest sites of the Nazaré Canyon. The location of these sites correlates with flat terraces observed during a video survey of the canyon using the ROV Isis (Tyler et al., 2009). These terraces experience relatively weak currents, acting as depocentres for sediment and  
25 larger material. This could result in more frequent settling of large food-falls in this area, in turn supporting larger populations of scavengers. This may be a potential explanation for the abundant catches of the baited traps deployed in submarine canyons. The idea that these terraces are nutrient rich and high in organic matter is supported by the

existence of large communities of xenophyophores (Gooday et al., 2011), single-celled protists whose presence is associated with high nutrient environments (Levin, 1991).

Input from rivers and coastal waters will undoubtedly include carcasses of large terrestrial, freshwater, and marine organisms, a food source that will be readily exploited by deep-sea scavenging amphipods. The productive waters associated with submarine canyons also make them ideal grounds for commercial fishing. The increase in food falls, via the discard of bycatch from fisheries will have a positive effect on marine scavenger abundances (Kaiser and Hiddink, 2007) increasing secondary production (Bozzano and Sarda, 2002; Furness et al., 2007). Indeed some facultative scavengers switch from a predatory foraging strategy to a scavenging one in the presence of fisheries (Laptikhovsky and Fetisov, 1999).

## 5 Conclusions

This study shows that scavenging amphipod assemblages in submarine canyons are dominated by a few common abyssal species occurring in large numbers with no evidence for endemic canyon species. There is strong evidence that submarine canyons provide a nutrient-rich environment in which scavenging amphipods can maintain larger populations than they do on the open slope or abyssal plains at similar depths. These large scavenging amphipod populations play an important role in the recycling of concentrated inputs of organic matter, driving secondary production to orders of magnitude greater than at similar depths on the open continental slope. Depth-correlated variables appear to control scavenging amphipod distributions with a discernible difference observed between communities at different depths within submarine canyons.

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**BGD**

9, 7831–7851, 2012

## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)


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**Scavenging  
amphipods in  
submarine canyons**

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



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## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

**Table 1.** Trap deployments made within the Iberian Margin submarine canyons during research expeditions RRS *Discovery* 297, RRS *Charles Darwin* 179, and RRS *James Cook* 010.

| Canyon  | Deployment  | Duration (hh:mm) | Depth (m) | Latitude | Longitude |
|---------|-------------|------------------|-----------|----------|-----------|
| Nazaré  | JC010/094   | 43:16            | 3400      | 39.4983  | −09.9367  |
|         | CD179/56855 | 23:02            | 3499      | 39.5027  | −09.9050  |
|         | D297/15734  | 21:28            | 3600      | 39.4963  | −09.9648  |
|         | D297/15741  | 24:22            | 4286      | 39.5825  | −10.2750  |
|         | CD179/56847 | 24:34            | 4403      | 39.5917  | −10.3167  |
| Setúbal | CD179/56817 | 31:14            | 3194      | 38.1528  | −09.6000  |
|         | CD179/56839 | 24:12            | 4445      | 38.1095  | −09.9697  |
| Cascais | CD179/56837 | 30:17            | 4230      | 38.3662  | −09.8834  |

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



## Scavenging amphipods in submarine canyons

G. A. Duffy et al.

**Table 2.** Species composition for scavenging amphipod samples collected from baited trap deployments made on the abyssal planes adjacent to the Iberian Margin submarine canyons as part of the 1981 ABYPLANE research expedition. Taken from Thurston, 1990. Species richness ( $S$ ), Pielou's Evenness ( $J'$ ), and Simpson's Index of Diversity ( $D$ ) shown.

| Station                          | na09 | na10 | na11 | na12 | na13 | na14 | na15 |
|----------------------------------|------|------|------|------|------|------|------|
| Depth (m)                        | 3400 | 3499 | 3600 | 4286 | 4403 | 3194 | 4445 |
| Species richness ( $S$ )         | 3    | 6    | 3    | 5    | 5    | 6    | 1    |
| Simpon's Index ( $D$ )           | 0.61 | 0.73 | 0.59 | 0.67 | 0.58 | 0.65 | –    |
| Pielou's Evenness ( $J'$ )       | 0.82 | 0.82 | 0.84 | 0.75 | 0.68 | 0.71 | –    |
| <i>Paralicella caperesca</i>     | –    | 26   | 5    | 11   | 36   | 58   | –    |
| <i>Paralicella tenuipes</i>      | 1    | 7    | 2    | 1    | 16   | 20   | –    |
| <i>Eurythenes gryllus</i>        | 5    | 20   | 10   | 13   | 4    | 15   | 1    |
| <i>Orchomenella gerulicorbis</i> | 2    | 6    | –    | 2    | 4    | 11   | –    |
| <i>Cyclocaris</i> sp. nov.       | –    | 2    | –    | –    | –    | –    | –    |
| <i>Valetietta gracilis</i>       | –    | 4    | –    | –    | –    | 1    | –    |
| <i>Abyssorchomene chevreuxi</i>  | –    | –    | –    | 2    | 1    | 2    | –    |
| Total                            | 8    | 65   | 17   | 29   | 61   | 107  | 1    |

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Scavenging amphipods in submarine canyons

G. A. Duffy et al.

**Table 3.** Species composition (percentage contribution in parentheses) for scavenging amphipod component of samples collected from baited trap deployments in Iberian Margin submarine canyons (NC: Nazaré Canyon, SC: Setúbal Canyon; CC: Cascais Canyon). Species richness (*S*), Pielou’s Evenness (*J'*), and Simpson’s Index of Diversity (*D*) shown.

| Expedition Station                | JC010 #094 | CD179 #56855 | D297 #15734 | D297 #15741 | CD179 #56847 | CD179 #56817 | CD179 #56839 | CD179 #56837 |
|-----------------------------------|------------|--------------|-------------|-------------|--------------|--------------|--------------|--------------|
| Canyon                            | NC         | NC           | NC          | NC          | NC           | SC           | SC           | CC           |
| Depth (m)                         | 3400       | 3499         | 3600        | 4286        | 4403         | 3194         | 4445         | 4230         |
| Species richness ( <i>S</i> )     | 3          | 6            | 5           | 10          | 9            | 4            | 8            | 6            |
| Simpson’s Index ( <i>D</i> )      | 0.30       | 0.23         | 0.25        | 0.59        | 0.59         | 0.41         | 0.25         | 0.65         |
| Pielou’s Evenness ( <i>J'</i> )   | 0.48       | 0.27         | 0.30        | 0.47        | 0.49         | 0.52         | 0.29         | 0.66         |
| <i>Paralicella caperesca</i>      | 38 (82.6)  | 889 (87.1)   | 259 (86.0)  | 1424 (40.7) | 4217 (55.6)  | 66 (74.2)    | 825 (86.0)   | 558 (47.9)   |
| <i>Paralicella tenuipes</i>       | 7 (15.2)   | 8 (0.8)      | 35 (11.6)   | 1716 (49.0) | 2287 (30.1)  | 19 (21.3)    | 71 (7.4)     | 360 (30.9)   |
| <i>Eurythenes gryllus</i>         | –          | 18 (1.8)     | –           | 77 (2.2)    | 23 (0.3)     | 2 (2.2)      | 14 (1.5)     | 10 (0.9)     |
| <i>Orchomenella gerullicorbis</i> | –          | 99 (9.7)     | 2 (0.7)     | 191 (5.5)   | 845 (11.1)   | 2 (2.2)      | 22 (2.3)     | 197 (16.9)   |
| <i>Cyclocaris</i> sp. nov.        | –          | –            | 1 (0.3)     | 40 (1.1)    | 3 (<0.1)     | –            | 1 (0.1)      | –            |
| <i>Valetietta gracilis</i>        | –          | 6 (0.6)      | –           | 3 (0.1)     | 134 (1.8)    | –            | 12 (1.3)     | 29 (0.9)     |
| <i>Valetietta lobata</i>          | –          | 1 (0.1)      | –           | 1 (<0.1)    | 1 (1.8)      | –            | –            | –            |
| <i>Valetietta</i> sp. nov.        | –          | –            | –           | 6 (0.7)     | –            | –            | –            | –            |
| <i>Paracallisoma</i> sp. nov. 1   | 1 (2.2)    | –            | 4 (1.3)     | 42 (1.2)    | 75 (1.0)     | –            | 12 (1.3)     | 10 (0.9)     |
| <i>Paracallisoma</i> sp. nov. 2   | –          | –            | –           | 1 (<0.1)    | 5 (<0.1)     | –            | 2 (0.2)      | –            |
| <b>Total</b>                      | <b>46</b>  | <b>1021</b>  | <b>301</b>  | <b>3501</b> | <b>7590</b>  | <b>89</b>    | <b>959</b>   | <b>1164</b>  |

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

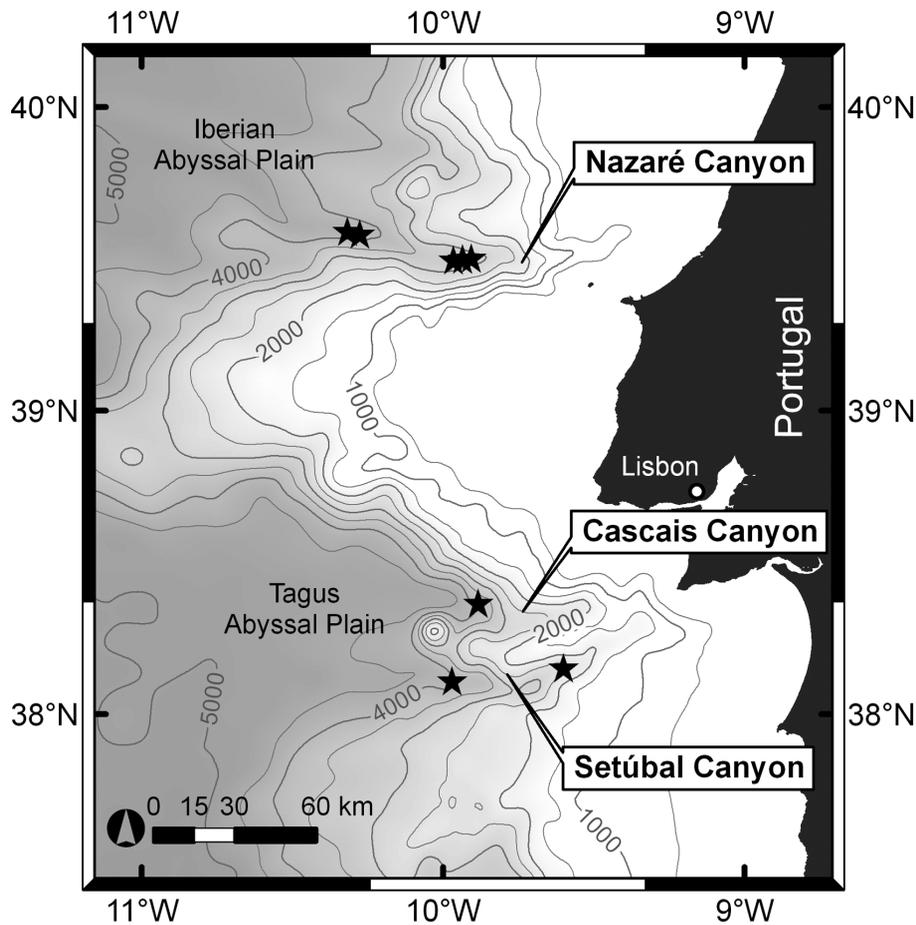
Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion





**Fig. 1.** Map of Iberian Peninsula submarine canyon trap deployments as part of research expeditions RRS *Discovery* 297, RRS *Charles Darwin* 179, and RRS *James Cook* 010.

**Scavenging  
amphipods in  
submarine canyons**

G. A. Duffy et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

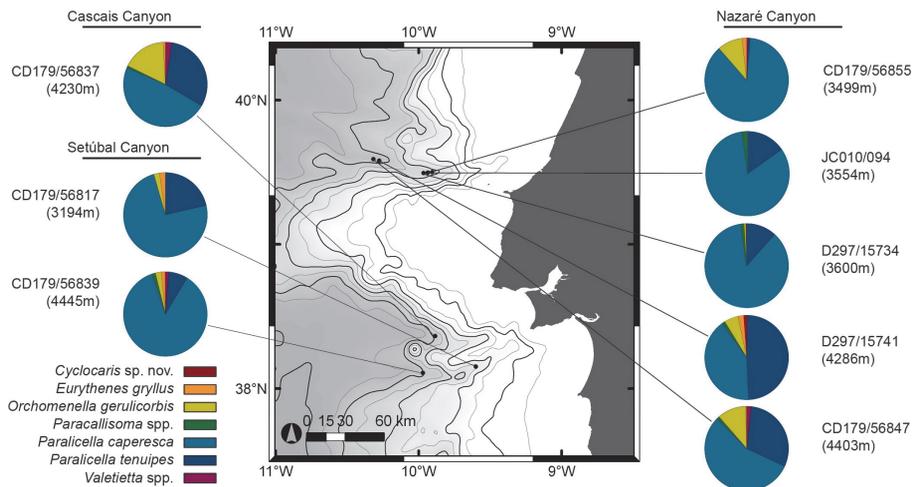
Printer-friendly Version

Interactive Discussion



Scavenging amphipods in submarine canyons

G. A. Duffy et al.



**Fig. 2.** Species composition of samples collected from trap deployments in submarine canyons off the Iberian Peninsula.

Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper | Discussion Paper

Title Page

Abstract Introduction

Conclusions References

Tables Figures

◀ ▶

◀ ▶

Back Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

