



ELSEVIER

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Distribution and habitat association of benthic fish on the Condor seamount (NE Atlantic, Azores) from *in situ* observations



Filipe M. Porteiro¹, José N. Gomes-Pereira^{*1}, Christopher K. Pham, Fernando Tempera, Ricardo S. Santos

Department of Oceanography and Fisheries, Centre of IMAR of the University of the Azores and LARSyS Associated Laboratory, 9901-862 Horta, Azores, Portugal

ARTICLE INFO

Available online 23 September 2013

Keywords:

Deep-sea
Coral habitats
Seamount
Video imagery
Azores
Ichthyofauna
Biodiversity
Ecological guild

ABSTRACT

Distribution of fish assemblages and habitat associations of demersal fishes on the Condor seamount were investigated by analyzing *in situ* video imagery acquired by the Remotely-Operated Vehicles ROV SP 300 and Luso 6000. A total of 51 fish taxa from 32 families were inventoried. Zooplanktivores (10 species) were the most abundant group followed by carnivores (23 species) and benthivores (18 species). Non-metric multidimensional scaling (MDS) analyses were performed on dive segments to visualize the spatial relationships between species and habitat type, substrate type or depth, with depth being the most significant parameter influencing fish distribution. Four major fish groups were identified from their vertical distribution alone: summit species (generally to < 300 m depth); broad ranging species (ca. from 200 to 800 m); intermediate ranging slope species (ca. from 400 m to 800–850 m); and deeper species (800–850–1100 m). The fish fauna observed at the summit is more abundant (15.2 fish/100 m²) and habitat-specialized than the fish observed along the seamount slope. Down the seamount slope, the summit fish assemblage is gradually replaced as depth increases, with an overall reduction in abundance. On the summit, three species (*Callanthias ruber*, *Anthias anthias* and *Lappanella fasciata*) had higher affinity to coral habitats compared to non-coral habitats. A coherent specialized fish assemblage associated to coral habitats could not be identified, because most species were observed also in non-coral areas. On the seamount's slope (300–1100 m), no relationship between fish and coral habitats could be identified, although these might occur at larger scales. This study shows that *in situ* video imagery complements traditional fishing surveys, by providing information on unknown or rarely seen species, being fundamental for the development of more comprehensive ecosystem-based management towards a sustainable use of the marine environment.

© 2013 Elsevier Ltd. All rights reserved.

1. Introduction

Benthic habitats are physically distinct areas of seabed associated with the occurrence of particular species (see Harris and Baker, 2012). Understanding how fish associate with habitats is a central issue for an ecosystem-based approach to marine spatial planning (Agardy, 1997; Botsford et al., 1997; Schmiing et al., 2013).

The habitats formed by sessile emergent fauna are more structured and ecologically complex, harboring higher biological diversity and abundance, when compared to uniform and

monotonous sedimentary environments (e.g. Buhl-Mortensen et al., 2010; Freiwald et al., 2004). Cold-water corals (CWCs) and sponges are “habitat engineering” sessile organisms occurring on continental and insular shelves and slopes, ridges and seamounts across most oceanic regions of the world (Roberts et al., 2006). In areas where environmental conditions are favorable, they aggregate densely and form three-dimensional habitats known as deep-sea coral reefs (Freiwald et al., 2004) and gardens (Bullimore et al., 2013; OSPAR, 2010) and sponge aggregations (Cook et al., 2008). These habitats may function as nursery, recruitment, feeding and/or shelter grounds for invertebrates and fishes, but actual evidence remains weak (e.g. Baillon et al., 2012; Buhl-Mortensen et al., 2010; Costello et al., 2005; Richer de Forges et al., 2000; Fossà et al., 2002). In oceanic regions, seamounts offer favorable conditions for corals and sponges and for an assortment of fishes (Rogers et al., 2007). Fishes typically considered to be associated with seamounts are schooling benthopelagic predators, like orange roughy and alfonsinos (Koslow, 1996; Morato et al., 2006), but seamounts also

* Corresponding author. Tel.: +351 966643842.

E-mail addresses: filipe@uac.pt (F.M. Porteiro), josenunopereira@uac.pt (J.N. Gomes-Pereira), phamchristopher@uac.pt (C.K. Pham), tempera@uac.pt (F. Tempera), ricardo@uac.pt (R.S. Santos).

¹ These authors have equally contributed to the manuscript.

harbor many other bottom fish species not included in that ecological guild (e.g. Koslow et al., 2000; Fock et al., 2002a; Parin et al., 1997; Uiblein et al., 1999).

Bottom or near-bottom living-fish on seamounts are mainly known from surveys using fishing gears such as longlines and bottom trawls (e.g. Christiansen et al., 2009; Koslow et al., 2000; Kukuev, 2004; Menezes et al., 2012; Parin et al., 1997; Uiblein et al., 1999), which provide limited insights on small-scale fish behavior and habitat associations (Costello et al., 2005; Ross and Quattrini, 2007). Clearly, with each fishing method catching a particular type of fish species, the selectivity can be better tackled by using *in situ* imagery (e.g. Felley and Vecchione, 1995; Lundsten et al., 2009; Uiblein et al., 2003).

Over the last decade, image-based studies on deep-sea ecosystems have increasingly addressed fish-habitat associations, mainly in areas dominated by CWCs. The importance of gorgonians, black corals and other megafauna aggregations as fish habitats were investigated in the Northeast Pacific, from the Bering Sea to California (Krieger and Wing, 2002; Miller et al., 2012; Stone, 2006; Tissot et al., 2006), Hawaii (Parrish, 2006) and Northwest Atlantic (Auster, 2005; Baker et al., 2012). Most of the observations ranged from 27 m in Aleutian Islands to 533 m in the Bering Sea, but in the Newfoundland canyons and the New England seamounts investigations extended down to lower bathyal bottoms (i.e. 351–2245 m and 1100–2500 m, respectively). The importance of *Lophelia pertusa* reefs as habitat for fishes was investigated in the boreal Northeast Atlantic (Biber et al., 2013; Costello et al., 2005; Husebø et al., 2002; Mortensen et al., 1995; Söfker et al., 2011), Mediterranean Sea (D'Onghia et al., 2010, 2011) and subtropical Northwest Atlantic (Quattrini et al., 2012; Reed et al., 2006; Ross and Quattrini, 2007, 2009). In the Gulf of Mexico, Sulak et al. (2007) investigated both habitats.

The results obtained by these studies are somewhat inconsistent since only Ross and Quattrini (2007, 2009) and Quattrini et al. (2012) described a specialized fish community associated to CWC reefs. The remaining studies generally found that fish abundance and diversity were higher in coral habitats, but not different from other 3-D bottom structures. Moreover, these studies could not identify any specific fish species or assemblage strictly associated to coral habitats. As a result, it is still debatable whether CWCs are obligatory (or essential) fish habitats since the nature and the ecological meaning of these associations for the population is yet poorly understood (e.g., Auster et al., 2005; Auster, 2007).

The Azores region comprises more than 460 seamounts that typify the complex geomorphology of the area (Morato et al., 2013). Most are small and deep but some are large and may rise from abyssal and bathyal depths into the epipelagic layer. Due to their geomorphologic and hydrographic settings they represent optimal habitat for filter/suspension feeders such as corals and sponges (Rogers et al., 2007). Indeed, more than 20 distinct coral biotopes and 8 sponge aggregations have so far been recognized across the Azorean seamounts and island slopes (Tempera et al., 2012a) and the region harbors a considerable high diversity of CWCs (Braga-Henriques et al., 2013) and sponges (Van Soest et al., 2012). Therefore, it is expected that coral gardens and sponge aggregations habitats are widespread over seamount and islands slopes.

Since the oceanographic expeditions in the late 19th century, the Azorean fish fauna has been regularly studied (see Santos et al., 1995, 1997). Its predatory demersal component living in the seamounts is the best known, mainly because those species are targeted by the bottom longline commercial fishery operated from the islands (Menezes et al., 2006, 2012; Menezes and Giacomello, 2013; Silva and Pinho, 2007). Bottom trawling has never been introduced as a commercial fishing technique in the region and since 2005 a formal ban has been established by a European

Regulation with the aim to protect vulnerable bottom habitats, namely corals gardens and reefs (Probert et al., 2007). However, in 2000 an exploratory trawl survey directed at orange-roughy (*Hoplostethus atlanticus*) showed the limitations and bias of our knowledge on seamount-associated fishes. Apart from the unsuspected large reproductive aggregations of orange-roughy at the top of some deep seamounts (> 800 m), fifteen fish species were recorded that were previously unknown from the region (Menezes et al., 2009, 2012; Melo and Menezes, 2002).

Despite the existing knowledge on Azorean fish fauna, small-scale interactions between deep-sea fish and their benthic habitat have been virtually ignored, due to the scarcity of *in situ* visual studies. The Azores were visited by several international expeditions using underwater imagery since the advent of scientific submersibles (Tempera et al., 2012a). During the last decades, most of those have been concentrated on the Azores hydrothermal fields (e.g. Cuvelier et al., 2009; Desbruyères et al., 2001), supporting some *in situ* studies of the occurrence and behavior of fishes associated with those ecosystems (i.e. Biscoito et al., 2002; Saldanha, 1994). Only recently have the island and seamount slopes started to be more thoroughly explored using optical platforms but published literature concentrated on describing benthic invertebrate communities (e.g. Braga-Henriques et al., 2012; Wisshak et al., 2009), the presence of anthropogenic litter (Pham et al., 2013) or habitat mapping (Tempera et al., 2012a,b).

The present work provides the first detailed description of the composition, vertical distribution and habitat associations of the demersal fish communities found on a mid-Atlantic seamount between 200 and 1100 m depth, as observed by Remotely-Operated Vehicles (ROVs). It aims to contribute to an integrated understanding of the ecology and dynamics of Condor seamount, which was selected as a case study area for multidisciplinary scientific programs and projects (Giacomello et al., 2013).

2. Materials and methods

2.1. Study area

The Condor is a shallow seamount located 17 km southwest of Faial Island, in the Azores archipelago. This ridge volcano is 39 km long and 23 km wide, with sloping flanks extending to over 1800 m depth from a narrow flattened summit developing between 180 m and 250 m (Fig. 1; Tempera et al., 2012b; Tempera et al., 2013). From the 1980s until 2010, when the seamount was closed to fisheries (Giacomello et al., 2013), commercial longline fishing exploited these grounds for demersal fish (Menezes and Giacomello 2013). The benthos is characterized by dense patches of coral gardens on the summit and predominantly sediment covered slopes with discontinuous patches of coral and sponge dominated habitats (Tempera et al., 2012b).

2.2. Survey design

ROVs were used to visually assess fish occurrence, distribution and habitat association patterns on the seamount. A total of 19 dives were executed, covering 23,800 m² of seafloor and providing over 22 h of bottom imagery (Figs. 1 and 2; Table 1). The northern slope of Condor seamount was surveyed by the working class ROV *Luso* (Bathysaurus XL), operated from R/V *Almirante Gago Coutinho* in 2010. Four dives were performed, totaling 5802 m length of bottom transects surveyed corresponding to 20 h 10 min of imagery, between 210 and 1097 m depth. The seamount summit was surveyed in 2010 and 2011 by 15 short dives with the 300 m rated ROV *SP* operated from the R/V *Águas Vivas*, totaling 2 h 52 min of bottom imagery over a distance of 3613 m, between 210 and 259 m depth.

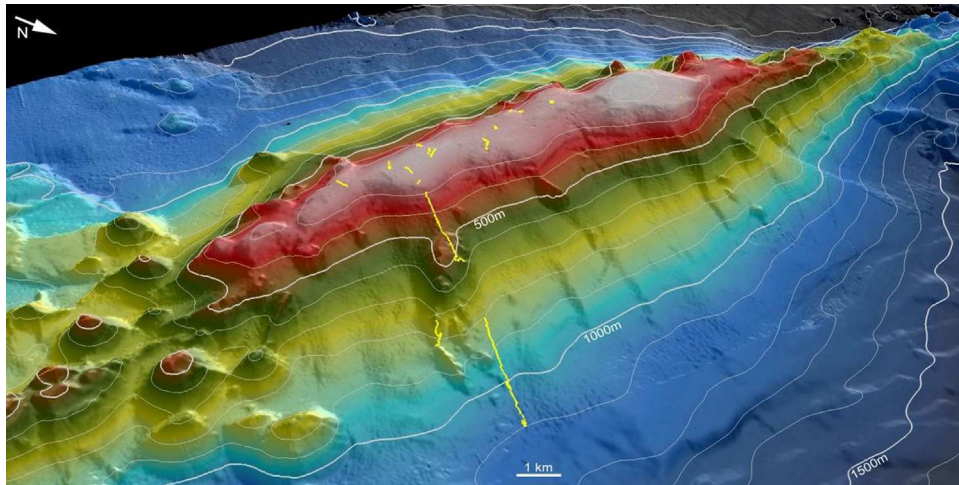


Fig. 1. View of the Condor seamount from NE (vertical exaggeration: 3x). The yellow lines indicate the dive tracks of ROV SP (summit above 300 m) and ROV Luso (long cross-slope transects below 300 m plus one short dive on the summit). See Table 1 for dive details. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

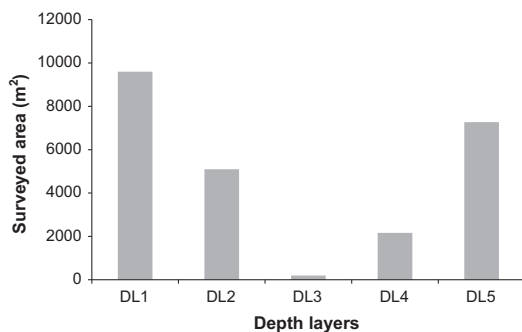


Fig. 2. Area surveyed (m²) by ROV SP and ROV Luso on Condor seamount on each depth layer (DL1 200–300 m; DL2 301–500 m; DL3 501–700 m; DL4 701–850 m; DL5 850–1100 m).

ROVs were positioned using USBL systems (Ultra-Short Base-Line), calculated by *OLEX* for ROV Luso and by *Seanet* for ROV SP. As USBL positioning accuracy contains spurious data (e.g., created by varying distance to transducer, proximity to seafloor, ROV attitude), the data exported from these software packages were manually filtered for major outliers and smoothed with a moving average (MovAv) to mitigate fine-scale noise. The width of the MovAv window was adjusted until the ROV track did not contain stretches with average speeds above 0.5 m/s and the sequence of displacements was consistent with the ROV progress as perceived from the recorded videos. ROV Luso tracks on the seafloor were steadier and required much less smoothing and outlier removal since *OLEX* already has filters embedded that minimize positioning noise.

ROV SP possess a color camera (570 line/02 lx), with a Luxeon 6 LED array (480 lm) mounted internally and 4 additional arrays (4 × 480 lm) on the 4 front corners of the ROV. With a tilt range of 270° and panning achieved by moving the ROV itself, the camera orientation can change throughout the dive as the seafloor and its features are explored, being mainly oblique with a tilt around –30°. ROV Luso used a HDTV camera with two halogen lights with 150 watts each and four HID lights with 7500 watts each with an oblique view over the seafloor. The surveyed area was estimated from average widths of view, defined for each platform individually. Scaling lasers indicated an average field of view width of 2.33 m (± 0.8SD) in ROV SP, and 2.74 m (± 0.75SD) in ROV Luso. The areas covered were estimated by multiplying the average width of view by the distance traveled.

2.3. Video data classification

Videos were digitized, matched with the corresponding navigation and annotated systematically. Annotation interfaces were customized in the COVER package (v0.7.2, Ifremer; Carré, 2010). Videos were annotated for: (i) fish occurrence; (ii) substrate type; (iii) habitat type; and (iv) depth layers.

2.3.1. Fish occurrence and behavior

Each fish observation was considered a unique event. Fishes were identified to the lowest taxonomic level possible. Many of the fish observed were easily recognized based on our knowledge of Azores fauna. Other identifications were supported by published data (e.g. Whitehead et al., 1986–1989) and matching the images obtained with others on image archives, namely at the *ImagDOP* (IMAR-DOP/UAz).

Species behavior, including response to ROV, was annotated conservatively, highlighting unclear situations. Fish reactions to ROV annotations follow Lorange and Trenkel (2006) although they are not specifically analyzed in the current paper.

Fish exhibiting obviously altered or unclear behaviors upon being detected on the ROV video imagery were excluded from analyses to minimize biases induced by the presence of the ROV.

2.3.2. Substrate type

Substrate type was grouped in two categories: (i) sand and gravel (*S&G*), including unconsolidated sediment with scattered particles up to pebble-size; (ii) rock and mixed rock-sediment (*R&M*), including hard rock bottoms and bottoms covered with cobble-sized or larger blocks over sediments (Wentworth, 1922).

2.3.3. Habitat type

The main coral gardens occurring at Condor were described by Tempera et al. (2012b); see Table 2 and Fig. 3. The denser coral gardens of *Dentomuricea* aff. *meteor* and *Viminella flagellum* were surveyed, mostly using the ROV SP. They extend over the seamount summit with a patchy distribution pattern, colonizing boulders and rocky bottoms often covered with a thin veneer of sand and/or gravel. On the Condor upper slope, sparser gardens of *V. flagellum* and small emergent sponges were the main sessile invertebrate fauna observed. *Narella* cf. *bellissima*, along with other sparse large gorgonians, occurs deeper on hard bottoms.

Table 1

Underwater surveys performed at the Condor seamount with the ROVs *Luso* and *SP* during 2010 and 2011. See text for calculations of distance and estimated areas surveyed. ROV *SP* dives correspond to seamount summit.

ROV	Dive code	Date	Depth (min–max)	Bottom time (hh:mm:ss)	Distance (m)	Estimated area (m ²)
<i>LUSO</i>	10CF_RLU001	06-08-2010	297–520	07:23:10	1954	5355
<i>LUSO</i>	10CF_RLU002	07-08-2010	803–1097	08:44:45	2977	8156
<i>LUSO</i>	10CF_RLU003	08-08-2010	228–231	01:20:46	406	1113
<i>LUSO</i>	10CF_RLU004	08-08-2010	703–832	02:09:42	465	1274
<i>SP</i>	10CF_RSP003	12-07-2010	214–259	00:30:54	334	777
<i>SP</i>	10CF_RSP005	15-07-2010	231–247	00:11:07	48	111
<i>SP</i>	11CF_RSP031	06-07-2011	221–214	00:03:53	34	79
<i>SP</i>	11CF_RSP032	06-07-2011	212–217	00:10:23	207	481
<i>SP</i>	11CF_RSP033	06-07-2011	210–216	00:12:27	262	610
<i>SP</i>	11CF_RSP034	06-07-2011	212–219	00:08:16	157	366
<i>SP</i>	11CF_RSP035	12-07-2011	213–218	00:07:57	231	538
<i>SP</i>	11CF_RSP036	12-07-2011	227–229	00:19:39	619	1442
<i>SP</i>	11CF_RSP042	13-07-2011	245–255	00:05:11	96	224
<i>SP</i>	11CF_RSP043	14-07-2011	233–238	00:07:01	267	623
<i>SP</i>	11CF_RSP044	14-07-2011	248–258	00:04:57	104	242
<i>SP</i>	11CF_RSP060	22-07-2011	213–221	00:13:24	280	652
<i>SP</i>	11CF_RSP061	22-07-2011	237–244	00:02:57	89	208
<i>SP</i>	11CF_RSP062	22-07-2011	218–235	00:21:53	680	1585
<i>SP</i>	11CF_RSP075	14-08-2011	216–227	0:04:54	207	482
Totals			210–1097	22:23:16	9416	23,780

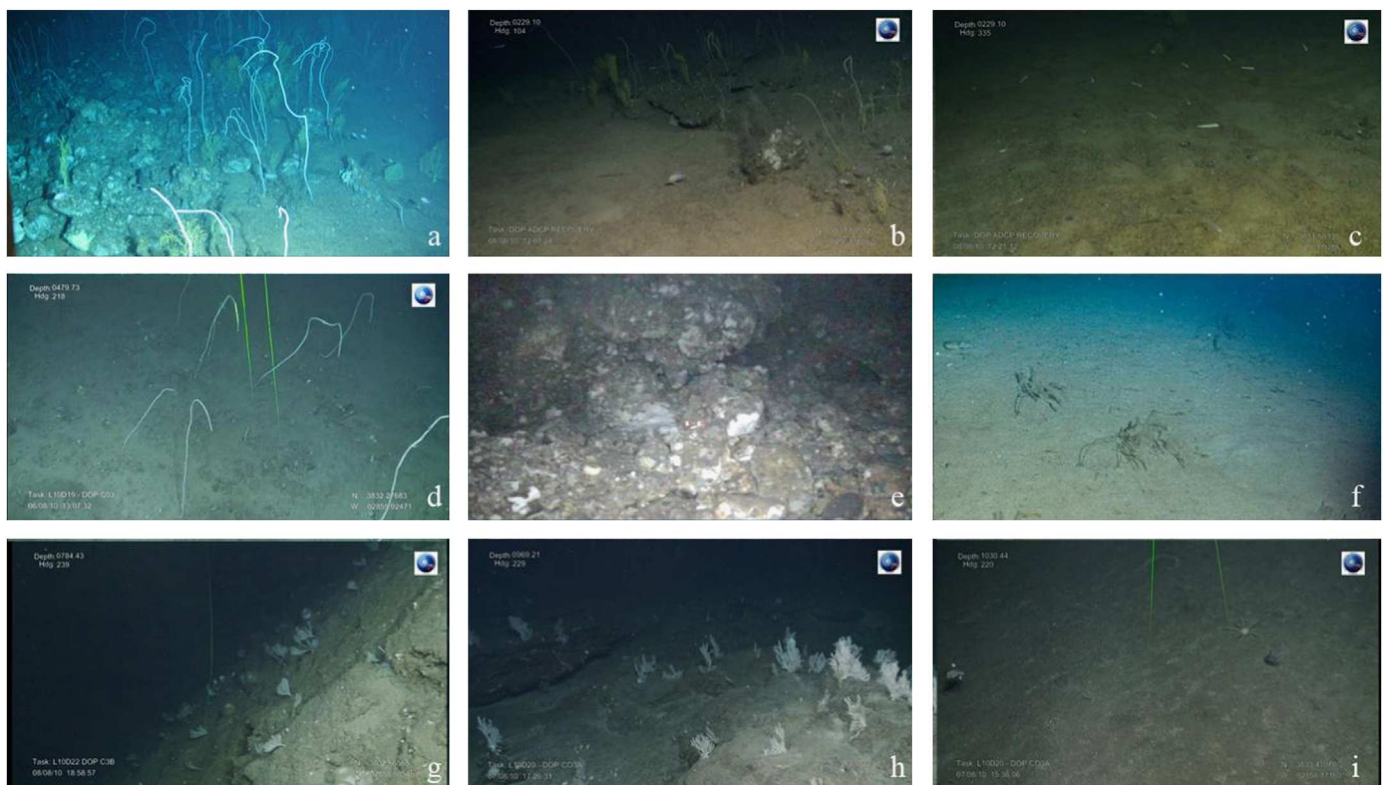


Fig. 3. Habitats surveyed on Condor seamount. Summit (210–300 m): (a) coral garden of *Dentomuricea* aff. *meteor* and *Viminella flagellum*; (b) transition of *D.* aff. *meteor* and *V. flagellum* habitat, over rocky substrate, to unconsolidated non-coral habitat; (c) unconsolidated sediment without corals. Upper slope (300–500 m): (d) sparse *V. flagellum* garden; (e) hard substrate dominated by sponges without large corals; (f) unconsolidated bottom with sparse sessile fauna (*Polyplumaria flabellata*). Mid and lower slope (750–1070 m): (g) sparse large gorgonians (e.g. *Narella* cf. *bellissima*) and bird's nest glass sponge (*Pheronema carpenteri*) over rocky bottoms; (h) gorgonian garden of *Candidella imbricata* with solitary hard corals over rocky substrate; (i) unconsolidated sediments with sparse mobile epifauna (e.g. cidarid sea-urchin). Credits: photos (a) and (f) ©Greenpeace, Gavin Newman, from Baixo de São Mateus; photos (b), (c), (d), (g), (h) and (i) ©EMEPC, ROV *Luso*; photo (e) ImagDOP/Uaz, ROV *SP*.

At the lower slope of Condor *Candidella imbricata* and small solitary scleractinians and stylasterids form a coral habitat patch over rocky areas. On unconsolidated sediments, sparse gardens of tall hydroids (i.e. *Lytocarpia myriophyllum* and *Polyplumaria flabellata*) were seen from the seamount summit to ca. 500 m depth,

while sponge aggregations of *Pheronema carpenteri* and other lithistid distributed between 717 and 780 m.

Habitats were classified in coral areas (CA) and non-coral areas (NCA). Coral areas were defined where coral densities attained at least 0.04/m² (i.e. 1 colony per 25 m²) along a transect

section. Hydroids and sponge aggregations were classified as non-coral areas.

2.3.4. Depth layers

The data were divided into 5 distinct layers based on the depth of the dominant benthic communities described by [Tempera et al. \(2012b\)](#); [Fig. 2](#). The depth layers (DL) considered were: 1: 200–300 m; 2: 301–500 m; 3: 501–700 m; 4: 701–850 m; 5: 850–1100 m. DL1 corresponds to the seamount summit, while the others correspond to the upper (DL2), mid (DL3–4) and lower slope (DL5) of the seamount. These layers should not be confused with the slope definitions early proposed by [Haedrich and Merrett \(1988\)](#). For comparative purposes DL1 to DL3 correspond to upper slope, while DL4 and DL5 are commonly referred to as middle slope elsewhere (750–1500; [Haedrich, Merrett, 1988](#)).

2.4. Data analysis

Relative fish abundance was estimated as the number of individuals observed per unit effort, calculated as the area covered by video over the seafloor, standardized per 100 m². Observation effort was computed separately for substrate type (S&G, R&M), habitat type (CA, NCA) and depth layers (DL1–5), which were used as grouping factors to create homogeneous sections of video, treated as independent samples.

Non-metric multidimensional scaling (MDS) analyses were performed to detect the spatial relationships between samples and potential species assemblages related to habitat type, substrate type or depth layers. The analyses were performed on resemblance matrices computed from two separated matrices of species abundance (43 taxa); 1-per substrate type (R&M and S&G) for the summit only, and 2-per habitat type (CA vs. NCA) including all depth layers (DL1–5). The raw data were subject to a square root transformation and the Bray–Curtis measure was applied. The ANOSIM R ([Clarke, 1993](#)) statistics tested for the significance of the null hypothesis of “there are no different fish assemblages between CA vs. NCA, R&M vs. S&G”. The *p*-values were calculated for 5000 permutations. ANOSIM R was only applied for the seamount summit (DL1) due to the limited amount of data concerning the slope. The procedures followed the techniques implemented in the ecological package PRIMER v.6 ([Clarke and Gorley, 2006](#)).

For the seamount summit the association between fish and coral habitat was further assessed by comparing species total abundance inside and outside coral areas within the same depth layer using the non-parametric Mann–Whitney *U*-test. Only fish species observed six or more times were included in these analyses ([Baker et al., 2012](#); [Ross and Quattrini, 2007](#)).

To further detail and analyze the structure of the fish communities, the species were classified in the following ecological guilds:

- i) Size: small (< 10 cm); medium (10–30 cm); large (> 30 cm).
- ii) Schooling behavior: solitary; small schools (2–4 individuals); medium schools (5–10 individuals); large schools (+10 individuals).
- iii) Feeding type: zooplanktivores; carnivores/macrobenthivores; and microbenthivores.
- iv) Main habitat type: benthic; benthopelagic; mesopelagic.

The classification was made according to our observations, published information (e.g., [Whitehead et al., 1986–1989](#)) and data compiled in Fishbase (www.fishbase.org).

3. Results

3.1. Species identification

A total of 748 fish occurrences were recorded, corresponding to 2450 individual fish, classified in 51 taxa belonging to 32 families and 14 orders ([Table 3](#)). They included 28 species (plus 7 putative macrourid species), 5 taxa identified to genus, 9 taxa identified to family and 2 taxa identified to order. Synphobranchids, nettastomatids, a myctophid and a few morids were identified only to family. Fish of the genera *Deania*, *Chaunax*, *Epigonus* and *Scorpaena* could only be identified to genus level. Imagery of a gregarious Argentinidae fish, a family reported here for the first time in the Azores, were not clear enough to permit identification below family level.

Most of the individual fish events recorded could be attributed to species level (67%) with the macrourid species 1 to 7 representing an additional 18% of all the events. The remaining observations were identified to genus (1.7%), family (6%) and order (0.7%) levels. Poor image quality prevented the identification of 6.6% of the fish events which were classified as “undetermined fish”.

3.2. Ecological guild composition

The total fish sample included 10 zooplanktivorous, 23 carnivorous and 18 benthivorous taxa ([Table 3](#)). The gregarious zooplanktivores was the more abundant trophic guild representing 57% of the fish numbers followed by the carnivores and the benthivores (33% and 10%, respectively). In terms of fish events, each trophic guild represented about one third of the total.

Zooplanktivores were largely dominated by small benthopelagic fishes that swarm in large and dense schools (e.g., *Anthias anthias*, *Callanthias ruber*, *Macrorhamphosus scolopax*, an unidentified Argentinidae, among others; [Table 3](#)). The exceptions were the occasional records of a small mid-water fish (Myctophidae) and the benthic bathyal/abyssal tripod fish (i.e. *Bathypterois phenax*) that also feeds on planktonic particles.

The carnivores were numerically dominated by benthopelagic species (77%), mainly by *Pagellus bogaraveo* and *Polyprion americanus* that may form large schools and attain large body size. The guild also included seamount species known to form aggregations even if in this study just solitary individuals were observed (i.e. *Beryx* spp.). However, the benthic carnivores which were essentially solitary (e.g. *Helicolenus dactylopterus*, *Pontinus kuhlii*; *Chaunax* sp.; *Conger conger*, *Phycis phycis*, *Trachyscorpia cristulata*), represented 84% of carnivore observations.

The benthivorous fish showed a vagile near-bottom behavior, were apparently solitary and most reached a medium to large body size. The megrim (*Lepidorhombus whiffiagonis*), the Mediterranean deep-water wrasse (*Lappanella fasciata*), various forms of rattails (Macrouridae) and the duckbill eels (Nettastomatidae) were the more frequent and abundant species. Probably, *Antigonia caprus* can also profit from benthic microinvertebrates inhabiting seamount habitats.

3.3. Vertical distribution

Four major groups were identified according to their depth distribution ([Fig. 4](#)): (i) summit species that were found at depths < 300 m (some extending their vertical range to ca. 500 m depth) as *C. ruber*, *A. anthias*, *M. scolopax*, *A. caprus* and a few wrasses; (ii) broad-ranging slope species that occurred from the seamount summit down to ca. 800 m, such as *H. dactylopterus* and *Hoplostethus* spp.; (iii) intermediate-ranging slope species with vertical ranges that extended from 300–400 m to 800–850 m, including *Chaunax* sp. and Macrouridae sp. 5 and; (iv) lower seamount slope

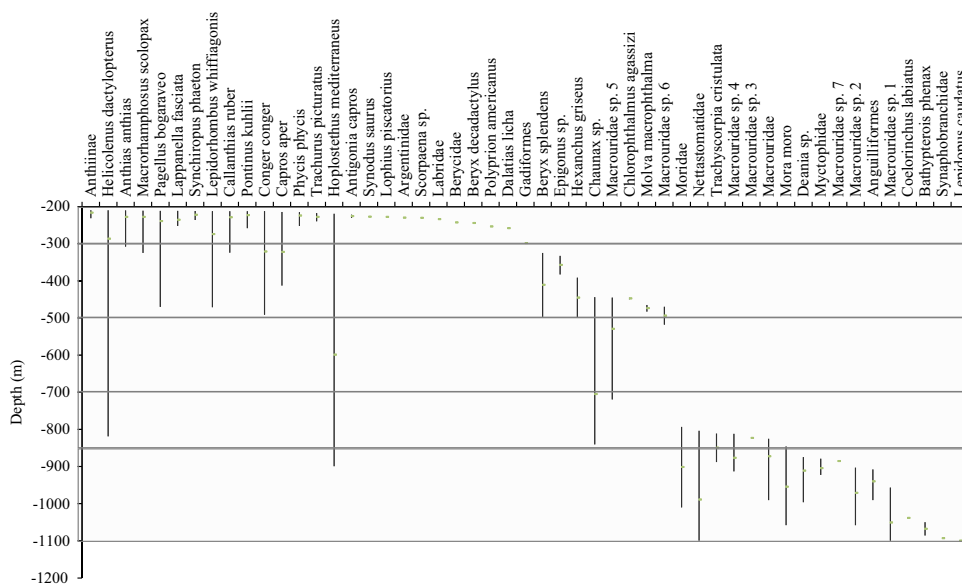


Fig. 4. Vertical distribution of fish taxa observed by ROV video surveys on the Condor seamount during 2010–2011.

fish species, such as *Mora moro*, *T. cristulata*, nettastomatids and many macrourids, which occurred below 800–850 m depth.

There was a fish fauna turnover at 800–850 m depth, where most of the species that occurred at the shallow depths disappeared and a deeper fish assemblage, dominated by rattails, emerged. However, data on vertical distribution should be interpreted with caution since the sampling effort was limited for the deeper areas. Many species showed a very narrow distribution range mainly because they were sighted very rarely.

3.4. Fish behavior

Out of the 2450 fish observations, 1522 (62.1%) did not show evident behavioral change before being detected by the ROV and these were considered for further analysis. The number represented about 70% of the events and 65% of the fish numbers recorded (Table 3). Highly mobile fishes such as the three deep water sharks recorded (*Dalatias licha*; *Deania* sp.; *Hexanchus griseus*), the blue jack mackerel (*Trachurus picturatus*) and some other fishes (i.e. *Lepidopus caudatus*, some Berycidae, Synphobranchidae, Gadiform and Myctophidae species) clearly reacted before entering the ROV's field of view and therefore were excluded from the following analyses. Other species also reacted prior to the presence of the ROVs in at least half of the encounters; these included mainly highly mobile benthopelagic schooling carnivores (i.e. *P. bogaraveo*, *Beryx splendens* and *M. moro*), zooplanktivores (Argentinidae; *Capros aper*) and some deep-sea Anguilliformes and Macrouridae species and therefore were not considered for the analysis. Only about 10% of the blackspot seabream (*P. bogaraveo*) fish observed were included in the following analyses.

3.5. Community composition, structure and habitat affinity

The spatial distribution of all samples shown on the MDS (Figs. 5A) indicates that depth is the main parameter responsible for the observed pattern. Due to the sparse and patchy distribution of coral (and sponge) areas along the slope and the low number of samples collected in this area, patterns of fish composition and abundance between habitat and bottom type were only explored for the summit (DL1) (Fig. 5B and C).

On the seamount summit species richness and abundance were higher in coral areas (CA) compared to non-coral areas (NCA). The 24 species recorded on CA showed an average density of 17.3 fish/100 m², compared to 8.47 fish/100 m² obtained for the 15 species observed in NCA (Table 3). *A. anthias*, *C. ruber*, *L. fasciata* and *Synchiropus phaeton* occurred preferentially in coral habitats (Mann–Whitney *U*-test, two-tailed $p < 0.05$; except for *C. ruber* $p < 0.1$; see Table 3), while no differences between habitats were detected for *H. dactylopterus*, *Hoplostethus* spp., *P. kuhlii*, *M. scolopax*, *L. whiffiagonis* and *P. bogaraveo*.

On the other hand, the overall multivariate analysis employed did not differentiate assemblages from both habitats. This similarity between samples from CA and NCA can be perceived by the MDS plot computed on fish abundance at DL1 per habitat type (Fig. 5B).

However, there were significant differences between fish assemblages found on R&M and on S&G substrates (ANOSIM $R = 0.233$; $p < 0.01$; Fig. 5C). The 76% dissimilarity between R&M and S&G is due mainly to differences in species abundance since the fish that primarily contributes to the discrimination between the two sample clusters are the same (i.e. *C. ruber*, *A. anthias* and *H. dactylopterus*).

3.5.1. Summit (220–300 m)

The summit of Condor seamount (DL1) hosted extensive areas of rocky and mixed consolidated/unconsolidated bottoms with gorgonian coral gardens intertwined by sediment areas, with or without sessile megafauna (Table 2; Fig. 3a–c).

Twenty-seven fish species were recorded at the summit, in all types of habitats and bottom types considered (Table 3; Figs. 4, 6 and 7a–f). The small size, zooplanktivorous gregarious fish species (mainly *C. ruber* and *A. anthias*) were the typical resident on coral gardens. They also occurred on sedimentary bottoms without emergent fauna but their density estimates in the latter were 5 times lower than on the rocky seafloor. Other species like *M. scolopax*, *C. aper* and an unidentified Argentinidae were less frequent and abundant.

Medium size benthivorous fish, mainly seen in association with coral areas, formed another guild of resident fish at DL1. The flatfish *L. whiffiagonis* was more abundant on sedimentary substrates devoid of epibenthic megafauna, but also occurred on coral areas. The relatively rare Mediterranean wrasse *L. fasciata* and the

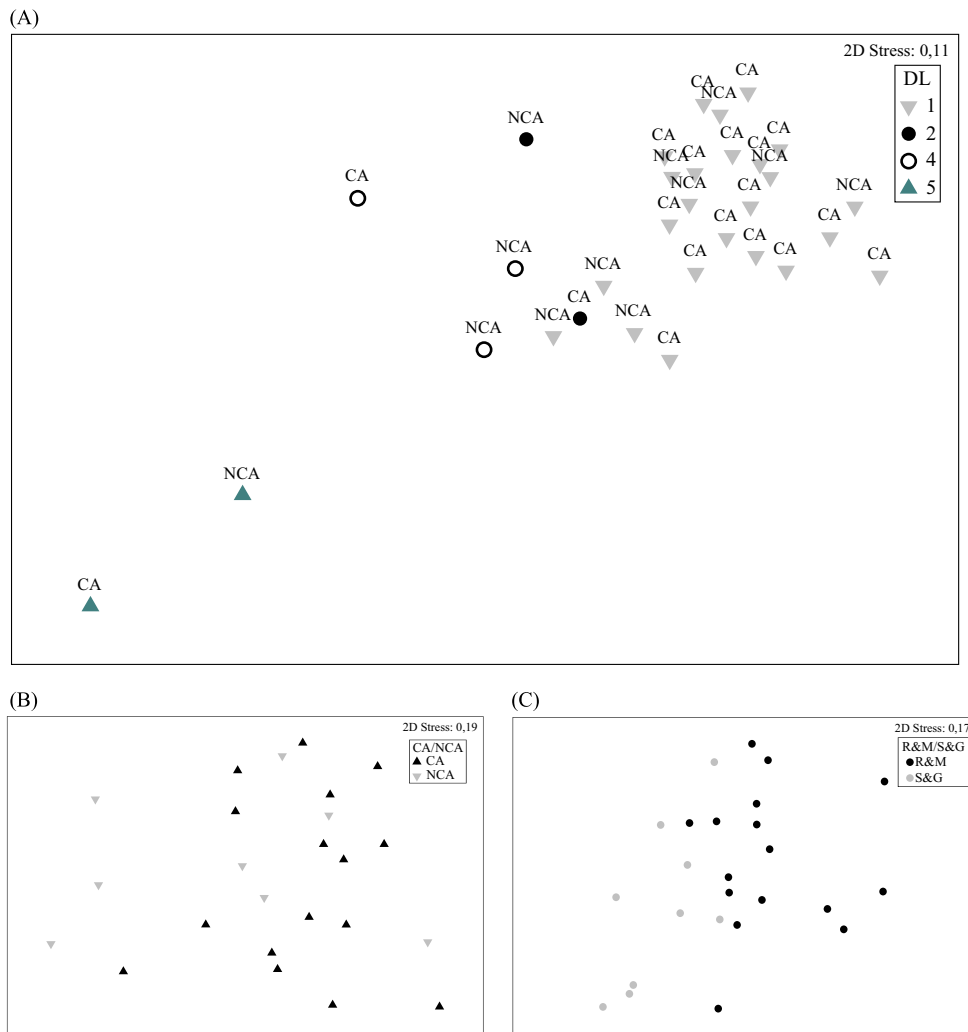


Fig. 5. Non-metric multidimensional scaling (MDS) plots based on Bray–Curtis resemblance matrices of species abundances per dive section (samples). (A) Seamount summit and slope; fish abundance per habitat type (CA: coral areas; NCA: non-coral areas) using depth layers (DL 1–5) as factor; (B) seamount summit; fish abundance per habitat type (CA: coral areas; NCA: non-coral areas); (C) seamount summit; fish abundance per substrate type (R&M: rock and/or mixed rock-sediment bottoms; S&G: sand and/or gravel).

deep body boarfish *A. capros* were only observed in CA, while the solitary *S. phaeton* occupied the fringes of that habitat.

Helicolenus dactylopterus was by far the dominant benthic carnivore on coral and non-coral habitats across the seamount summit and below. *Pontinus kuhlii*, another benthic scorpionfish, follows in terms of frequency, even if ca. 30% of the individuals observed responded prior to entering the ROV field of view. The carnivore guild included also the rarely seen benthic anglerfish *Lophius piscatorius*, the Atlantic lizardfish *Synodus saurus*, the conger eel *C. conger* and the forkbeard *P. phycis*. The benthopelagic predator *P. bogaraveo* was observed in large schools, swimming over coral areas, but always at the limit of the area lit by the ROV. A large and dense school of wreckfish *P. americanus* was observed swimming over and within the coral gardens. They were detected in the same area for at least two more days (videos not analyzed in this study). In contrast with the blackspot seabream, which normally reacted to the ROV, the wreckfish were not influenced by the presence of the vehicle. The actual size of these large schools was difficult to perceive from the imagery and the numbers given here for both species (Table 3) are certainly underestimates. Few solitary individuals of *Hoplostethus mediterraneus* and *Hoplostethus* sp. were also recorded within the coral areas.

Soft sediments occurred in most areas surveyed on the Condor summit but none of the fish species observed were recorded

exclusively on this habitat, even within the sparse hydroid garden of *L. myriophyllum* and *P. flabellata*.

3.5.2. Seamount upper slope (300–500 m)

Most species recorded over the summit became less abundant on the seamount upper slope (i.e. DL2), with an overall decreasing density of ca. 85% (i.e. from an average 15.2 fish/100 m² at DL1 to 2.3 fish/100 m² at DL2).

Small schools of a cardinal fish cf. *Epigonus* sp. were observed only between 300 and 400 m deep, over sand and gravel without epibenthic fauna. Small zooplanktivores that extended below 300 m (namely, *C. aper* but also *C. ruber* and *M. scolopax*) attained densities 20 times lower than they reached in DL1.

Among the benthivores, *L. whiffiagonis* extended from the summit down to 500 m deep and typified the upper slope. A few shortnose greenfish (*Chlorophthalmus agazzisi*) appeared only between 440 and 450 m. Two unidentified rattails (mainly Macrouridae sp. 5 but also Macrouridae sp. 6) were seen abundantly sitting on the sedimentary bottoms.

Helicolenus dactylopterus was the species that attained the highest rank both in density and frequency, although in lower numbers than at DL1 (Fig. 7g). Other predators such as the Spanish ling *M. macrophtalma* and the coffinfish *Chaunax* sp. began to

occur on the Condor upper slope. The benthopelagic alfonsoino, *B. splendens* and *P. bogaraveo* were rarely detected at this depth layer. In general, the carnivores were more frequent and abundant in DL1 (ca. 10 times higher than at DL2) but they were more broadly distributed throughout the depth gradient.

3.5.3. Deeper habitats (> 500 m)

The depths between 500 and 700 m (DL3) were scarcely sampled; the single transect crossing this stratum, covered less than 200 m² and was done over a non-coral soft habitat. Only two fish were recorded, the Macrouridae sp. 6 and the six-gill shark *H. griseus*, which was attracted to the ROV.

With increasing depth, there was a noticeable change in species composition, although the total fish abundances at mid (700–850 m; DL4) and lower (> 850 m; DL5) slopes were similar to that found at DL2 (Table 3). In terms of species diversity, the slopes at those depths were dominated by deep dwelling benthic benthivorous predators, typified by rattails (Macrouridae) and by the less common duckbill eels (Nettastomatidae). Macrouridae sp. 4 was the more abundant morphotype in both depth strata, but Macrouridae sp. 1 and 2 were the typical species in the deeper layer sampled (DL5).

In DL4, *H. dactylopterus* and *Chaunax* sp. were the dominant carnivores. *Hoplostethus* sp., which is also a broad-ranging fish in terms of depth distribution, attained its maximum density at DL4. *T. cristulata*, the spiny scorpionfish, first appeared on the imagery at this depth layer.

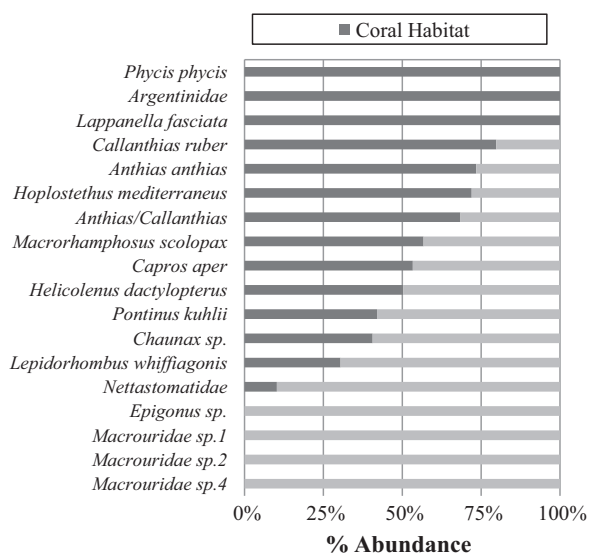


Fig. 6. Relative fish abundance (%) over coral and non-coral areas (CA vs. NCA) from *in situ* observations on the Condor seamount. Species included are small and medium-sized species (< 25 cm) or with reduced mobility, observed more than 6 times.

Table 2

Main coral vs. non-coral habitats depicted at Condor seamount, according Tempera et al. (2012b). Areas surveyed by the ROVs *Luso* and *SP* on Condor seamount. See Table 1 for survey details.

Habitat	Dives	Length (m)	Area (m ²)	Depth range (m)
Coral area (CA)				
<i>Dentomuricea</i> aff. <i>meteor</i> and <i>Viminella flagellum</i>	SP (15), Luso (2)	3083	7280	210–300
<i>Viminella flagellum</i>	Luso (1)	270	741	300–500
<i>Narella</i> cf. <i>bellissima</i> and sparse large gorgonians	Luso (1)	303	830	717–798
<i>Candidella imbricata</i> and small solitary scleractinians	Luso (1)	580	1589	960–1022
Non-Coral area (NCA)				
Non-consolidated sediment without large corals	SP (15), Luso (4)	2415	6352	210–1100
Consolidated and mixed consolidated-unconsolidated substrate without large corals	SP (15), Luso (4)	2764	6600	210–1022

In DL5, the community became more dominated by the Macrouridae and Nettastomatidae families and most of the carnivorous predators reported from the shallower layers disappeared, giving place to *M. moro* (Fig. 7h) and *T. cristulata*. At this depth layer, the planktivore tripodfish *Bathypterois phenax* was occasionally observed sitting elevated over sediments.

4. Discussion

4.1. What was observed by ROVs?

The analysis of video footage collected on Condor seamount provided a unique opportunity to increase our knowledge on the diversity of fish fauna inhabiting the area, previously documented only from experimental fishing surveys and commercial fishing activities. Despite being one of the best-reported and well studied taxonomic groups in the Azores (vd. Porteiro et al., 2010; Santos et al., 1997), and Condor seamount an historical commercial fishing ground in the region, it is remarkable that visual sampling exposed new and rarely reported species. The deep circalittoral Mediterranean wrasse *L. fasciata* had never been reported for the Azores. Additionally, the argentine fish observed on the summit belongs to a family that was documented in the region only by a doubtful record of *Argentina sphyraena* (Nobre, 1924) and by three pelagic larvae of *Glossanodon leioglossus* (Sobrinho-Gonçalves and Isidro, 2001). Although accurate identification of this fish would require specimens examination in the laboratory, it is highly likely to be *G. leioglossus*. This species occurs in Canaries, Western Mediterranean and Northwest African coasts (Cohen, 1989) but has also been documented on the seamounts south of the Azores (Fock et al., 2002a; Kukuev, 2004; Uiblein et al., 1999).

Other species commonly observed on the seamount, such as *C. ruber*, *A. capros*, *S. phaeton*, *C. agassizi* or *B. phenax* were only occasionally previously reported for the region (see Santos et al., 1997). It is probable that many more fish observed on the seamount are rare records for the Azores. For some families (e.g. epigonids, nettastomatids and macrourids), the identification at species level is difficult using video observations.

4.1.1. Comparing ROV observations with longline catches

Information about the Azores circalittoral and bathyal fish faunas results mainly from catches made with hooks and lines, targeting the carnivorous component of the community. The Condor seamount was also sampled by bottom longlines allowing for a preliminary comparison between fish caught by that gear (Menezes and Giacomello, 2013) and those observed by the ROV. In general, the information provided by the two sampling methods is complementary. Only ca. 15 species were shared between the fifty-one *taxa* list compiled from the ROV imagery and the forty-eight *taxa* caught by longlines. The common occurrences include mainly commercial species such as *P. bogaraveo*,

Table 3
Abundance (no. fish/100 m²) of fish taxa observed by ROV *Luso* and ROV *SP* on the Condor Seamount during 2010–2011 organized by feeding guilds. *R* (tot/s): total number of occurrences/occurrences selected for analysis (excluded occurrences when fish show a response time: “before detection” and “not clear”; see Section 2); *n* (% tot): number of fish individuals selected (% in relation to total); *D* (m): depth range, in meters; *DL*: depth layer (1: 200–300 m; 2: 301–500 m; 3: 501–700 m; 4: 701–850 m; 5: 850–1100 m); *H*: habitat type (CA: coral area; NCA: non-coral area); *E*: observation effort (m² surveyed); *A*: abundance (no. fish/100 m²). + Indicates that only solitary individuals of a gregarious species were observed. Species preferentially occurring on coral areas are indicated by *0.05, **0.01 (Mann–Whitney *U*-test). Taxa in gray denote those not included in the analysis due to “fish reacting to ROV” criteria.

Taxa	<i>R</i> (tot/s)	<i>n</i> (% tot)	<i>D</i> (m)	<i>DL</i>	1		2		3		4		5	
					<i>H</i>	CA	NCA	CA	NCA	CA	NCA	CA	NCA	CA
Zooplanktivores														
<i>Benthopelagic; schooling</i>														
<i>Callanthis ruber</i> ⁺	57/36	657 (90.7)	212–324		8.90	1.09		0.05						
<i>Anthias anthias</i> **	127/87	325 (79.8)	210–307		4.15	1.40								
<i>Anthiinae</i>	14/14	120 (100)	210–231		0.80	2.85								
<i>Macrorhamphosus scolopax</i>	20/18	24 (92.3)	211–325		0.24	0.27		0.02						
<i>Argentinidae</i>	2/1	25 (59.5)	229–230		0.35									
<i>Epigonus</i> sp.	2/2	18 (100)	332–383							0.42				
<i>Capros aper</i> ⁺	14/7	7 (50)	214–412		0.06			0.07						
<i>Trachurus picturatus</i>	4/0		217–239											
<i>Mesopelagic; schooling</i>														
<i>Myctophidae</i> ⁺	4/0		878–922											
<i>Benthic; solitary</i>														
<i>Bathypterois phenax</i>	2/2	2 (100)	1049–1086											0.04
Carnivores/macro-benthivores														
<i>Benthic; solitary</i>														
<i>Helicolenus dactylopterus</i>	114/102	105 (89.7)	210–818		0.86	0.86	1.23	0.26			0.38			
<i>Pontinus kuhlii</i>	40/28	29 (70.%)	212–258		0.34	0.23								
<i>Scorpaena</i> sp.	1/1	1 (100)	230–230		0.01									
<i>Chaunax</i> sp.	7/6	6 (85.7)	443–840				0.14	0.02		0.12	0.23			
<i>Synodus saurus</i>	2/2	3 (100)	227–227		0.04									
<i>Lophius piscatorius</i>	1/1	1 (100)	228–228			0.05								
<i>Conger conger</i>	5/3	3 (60)	212–491		0.01	0.05	0.14							
<i>Phycis phycis</i>	9/7	7 (77.7)	215–252		0.10									
<i>Moridae</i>	2/2	2 (100)	793–1010							0.12				0.02
<i>Trachyscorpia cristulata</i>	2/2	2 (100)	811–887							0.12				0.02
<i>Benthopelagic; schooling</i>														
<i>Pagellus bogaraveo</i>	31/13	55 (9.8)	211–470		0.35	1.31		0.02						
<i>Polyprion americanus</i>	1/1	40 (100)	254–254		0.56									
<i>Lepidopus caudatus</i> ⁺	1/0		1100–1100											
<i>Mora moro</i> ⁺	8/3	3 (37.5)	845–1057										0.06	0.04
<i>Berycidae</i> ⁺	1/0		243–243											
<i>Beryx decadactylus</i> ⁺	1/1	1 (100)	245–245		0.01									
<i>Beryx splendens</i> ⁺	2/1	2 (66.6)	325–497					0.05						
<i>Benthopelagic; solitary</i>														
<i>Hoplostethus</i> spp.	8/7	7 (87.5)	219–899		0.03			0.02		0.37	0.08			
<i>Molva macrophthalma</i>	2/2	2 (100)	465–482				0.14	0.02						
<i>Gadiformes</i>	1/0		298–298											
<i>Dalatias licha</i>	1/0		258–258											
<i>Deania</i> sp.	4/0		874–996											
<i>Hexanchus griseus</i>	2/0		391–499											
Benthivores														
<i>Benthic; solitary</i>														
<i>Lepidorhombus whiffiagonis</i>	26/26	27 (100)	212–471		0.18	0.32		0.16						
<i>Lappanella fasciata</i> **	12/12	13 (100)	211–252		0.18									
<i>Synchiropus phaeton</i> **	4/4	4 (100)	212–236		0.06									
<i>Antigonia capros</i>	2/1	1 (50)	221–230		0.01									
<i>Labridae</i>	1/1	1 (100)	234–234			0.05								
<i>Chlorophthalmus agassizi</i>	2/2	3 (100)	444–450					0.07						
<i>Macrouridae</i>	9/2	2 (22.2)	825–990							0.08				0.02
<i>Coelorrhinus labiatus</i>	1/1	1 (100)	1038–1038											0.02
<i>Macrouridae</i> sp. 1	30/13	13 (33.3)	956–1100											0.23
<i>Macrouridae</i> sp. 2	10/5	5 (50)	903–1058											0.09
<i>Macrouridae</i> sp. 3	1/1	1 (100)	823–823							0.08				
<i>Macrouridae</i> sp. 4	84/43	72 (60.5)	811–913							0.46				1.18
<i>Macrouridae</i> sp. 5	4/4	4 (100)	444–719					0.07		0.12				
<i>Macrouridae</i> sp. 6	2/2	2 (100)	469–518					0.02	0.52					
<i>Macrouridae</i> sp. 7	1/1	1 (100)	885–885											0.02
<i>Anguilliformes</i>	5/2	2 (40)	907–990											0.04
<i>Nettastomatidae</i>	11/7	7 (63.6)	803–1100							0.08	0.13			0.07
<i>Synphobranchidae</i>	1/0		1093–1093											
Fish No. ID	50/16	16 (24.2)	212–1100		0.07			0.05					0.32	0.07

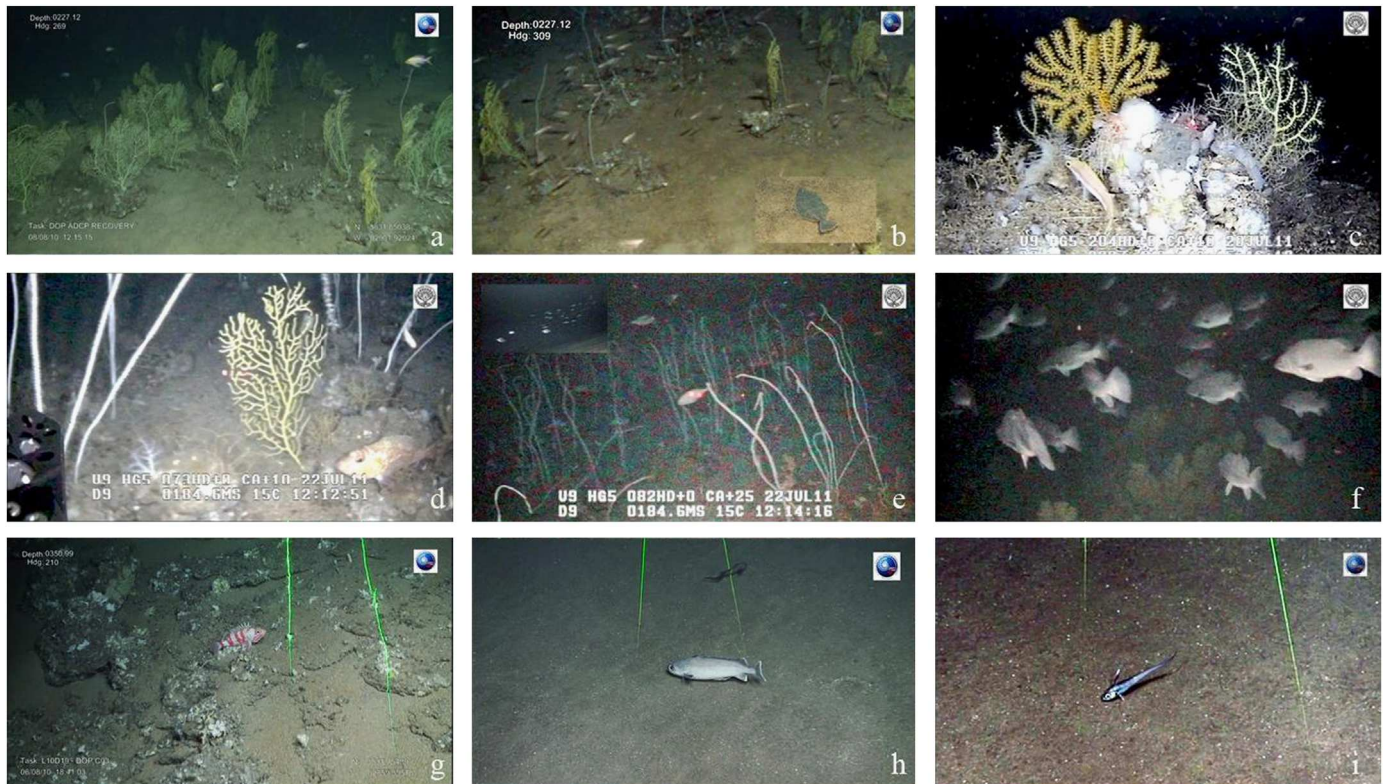


Fig. 7. Representative demersal fish species from Condor seamount. (a) *Anthias anthias* swimming over fan-shaped *Dentomuricea* aff. *meteor* gorgonians; (b) school of *Callanthias ruber* near the bottom; inset of the flat-fish *Lepidorhombus whiffiagonis*; (c) *Lappanella fasciata* swimming close to gorgonian corals, (d) *Pontinus kuhlii* sitting on rocky bottom near corals, (e) several *Pagellus bogaraveo* swimming among *V. flagellum* whip-corals; inset: large school of the same species over sandy bottom; (f) large school of *Polyprion americanus* swimming over coral garden; (g) *Helicolenus dactylopterus* on mixed bottom; (h) *Mora moro* swimming close to the bottom, with *Macrouridae* sp. 1 avoiding the ROV on top of image and; (i) *Macrouridae* sp. 2 swimming diagonally in contact with the bottom; green lasers are 60 cm apart. Credits: photos (a), (b), (g), (h) and (i), ©EMEPC, ROV *Luso*; photos (c), (d), (e) and (f), ©ImagDOP/Uaz, ROV *SP*.

B. splendens, *H. dactylopterus*, *P. kuhlii*, *P. phycis*, *C. conger*, *M. macrophthalmia* and *M. moro*.

The selectivity of both methods arises from fish size, species specific behavior related to feeding ecology (i.e. attractiveness to bait), mobility and response to ROV (see Stoner et al., 2008). Species only observed by ROVs were mainly small zooplanktivores, which are unable to bite the standard hooks used in fishing lines but also the benthivores that behaviorally are not attracted by the bait (e.g. *L. fasciata*, *S. phaeton* and most macrourids and nettastomatids). Conversely, the fishes caught by longlines and not observed (or sporadically so) by the ROV includes mainly deep-water squalid sharks (e.g. *Deania* spp., *Etmopterus* spp., *Centrophorus squamosus*, among others), scabbard fishes (Trichiuridae) and some gadiforms (see Menezes et al., 2006).

This comparison shows that ROVs overlook many large mobile top-predators that are also commercially important fish while longlines are inefficient in assessing other benthic and bathypelagic fish components. Bottom trawls are less selective than fishing lines and catch species not usually attracted by hooks (e.g. Menezes et al., 2012). However, bottom trawls were never used by local commercial fisheries and since 2005 they are prohibited in the region, to protect vulnerable benthic habitats and species (Probert et al., 2007; Santos et al., 2009). Therefore, the combination of hook and line fishing gear with ROVs provides a more complete characterization of fish communities living in circalittoral and bathyal systems (e.g. Ralston et al., 1986; Willis et al., 2000) especially in regions like the Azores where bottom trawling is not allowed.

4.2. Fish fauna diversity of Condor seamount

The combination of our results with that of longline surveys, suggests that more than 80 fish species inhabit the bottom and near-bottom layers of Condor, representing approximately 14% of the fish species reported for the Azores (Porteiro et al., 2010). However, the fish diversity found on this seamount is probably not exhaustively documented (see also Menezes and Giacomello, 2013), since other species expected to occur on this seamount have not been reported yet (e.g. *Epigonus telescopus*). Moreover, crustacean bottom traps used on Condor caught also other species recorded neither by longlines nor by ROVs (e.g. *Acantholabrus palloni*; *Benthocometes robustus*; *Simenchelys parasitica*) (Giacomello and Menezes, 2011).

Considering the current number of species reported so far, the Condor seems to harbor more fish species than Seine (Christiansen et al., 2009; Menezes et al., 2009), Great Meteor Seamount (Fock et al., 2002a; Uiblein et al., 1999) and other south Azores seamounts (Kukuev, 2004; Pakhorukov, 2008; Shcherbachev et al., 1985), which have summits within the same depth range and were intensively sampled. The observed discrepancy is not easily explained, and falls out of the scope of this work. We hypothesize that those seamounts are naturally less diverse than Condor (and other seamounts in the Azores region) due to the proximity of Condor to insular circalittoral habitats, and possibly from other factors such as lower regional topographical complexity or biogeographic constraints (e.g. Rex et al., 2005), deserving further research. Nevertheless, the fauna from Condor includes many species also known from seamounts south of the Azores and

Seine (Menezes et al., 2009; Pakhorukov, 2008; Uiblein et al., 1999), showing the close biogeographic affinities shared by these seamounts within the Macaronesia (Menezes et al., 2006), a sub-region of the Lusitania-Mediterranean province in the Northeast Atlantic (e.g. Briggs and Bowen, 2012).

4.3. Fish community structure and ecological links to habitats

4.3.1. Condor summit

The summit of Condor seamount is numerically dominated by abundant zooplanktivores, particularly *A. anthias* and *C. ruber*, which thrive mainly in the gorgonian gardens but occur also on the adjacent bottoms devoid of sessile megafauna.

Zooplanktivorous fish are common on the summits of shallow and intermediate subtropical Northeast Atlantic seamounts (i.e. Christiansen et al., 2009; Fock et al., 2002a,b; Kukuev, 2004; Pakhorukov, 2008; Shcherbachev et al., 1985; Uiblein et al., 1999). These fish are expected to occur where the supply of potential prey is abundant and predictable. Similar to other seamounts, the primary production generated at Condor probably cannot sustain the secondary production detected (e.g., Colaço et al., 2013) and therefore zooplanktivores should rely on an external food source. Fock et al. (2002b) suggested that zooplanktivores from the Meteor seamount rely on the daily vertically-migrating fauna associated with the Sound Scattering Layers (SSL). However, at Seine, Hirsch and Christiansen (2010) found that they feed mainly on allochthonous epipelagic non- or weakly migrating zooplankton unrelated to the SSL. This may also be the case for the zooplanktivores living at the narrow and flat Condor summit and feeding during daytime.

Although the high standing stocks of large fish predators associated with seamounts are thought to be supported mainly by allochthonous biomass (e.g. Morato et al., 2009), the high biomass of zooplanktivorous fish should constitute an important food source for the benthic and benthopelagic piscivores inhabiting the seamount summit. In fact, ROV observations revealed possible predatory behavior towards *A. anthias* and *C. ruber* from the two dominant scorpaenid fish living there, *H. dactylopterus* and *P. kuhlii* (Gomes-Pereira et al., in press). Moreover, acoustic telemetry studies showed that sub-adults and adults blackspot seabream (*P. bogaraveo*) remain at the seamount summit longer than expected, which may be justified by the availability of food in that habitat (Afonso et al., 2012). Likewise, it is conceivable that the wreckfish (*P. americanus*) observed within the gorgonian gardens may also profit from the high abundance of the small seamount-associated fish preys. The importance of zooplanktivores in transferring energy from the water column to benthic and benthopelagic predators was also reported for the Pinnacles Reefs at the Gulf of Mexico (Weaver et al., 2001). Nevertheless, this does not exclude the direct use of SSL prey by the blackspot seabream, which show frequent diel vertical migrations (Afonso et al., 2012) and are known to include myctophids in their diet (Morato et al., 2001). The same may apply to the wreckfish that elsewhere also feed on pelagic migrating organisms (Goldman and Sedberry, 2011).

4.3.2. Coral vs. non-coral areas

Zooplanktivorous fish and filter-feeding CWCs both depend on planktonic food particles which makes them co-occur in areas where food supply is enhanced. Coral gardens may function as shelter and reproductive grounds for those gregarious fish (see Gomes-Pereira et al., 2012). Therefore, a tight spatial relationship between zooplanktivores and CWCs is expected, as seen for some of the most abundant fish species. Moreover, one can assume that carnivores and benthivores would converge where their potential preys are more abundant (i.e. fish and macro-invertebrates).

However, this assumption was not statistically confirmed for the benthic carnivores. The explanation for the observed pattern is not straightforward but spatial auto-correlation problems, induced by the fact that small video segments classified as non-coral areas were likely to be influenced by adjacent coral gardens, and hence did not represent strictly independent samples is a possible explanation (Gonzalez-Mirelis et al., 2009). The Condor summit seascape is a patchy mosaic of rocky outcrops and boulders covered with the dominant gorgonians interspersed by areas of hard or soft bottoms devoid of emergent megafauna. The survey method itself might induce undetected species specific behavioral responses which difficult the identification of fine-scale distribution patterns (i.e. attraction to the ROV moving fish outside of coral areas; forward swimming behavioral response pushing gregarious fishes into narrow non-coral patches; or predatory strategies of the carnivores, inhabiting the surrounding of coral areas). The differences found between assemblages over rocky (even when devoid of megafauna) and mixed bottoms vs. sand and gravel bottoms are mainly due to differences in abundance of zooplanktivores. This may indicate that over soft bottoms the prey delivery rate is lower.

In contrast to the summit, we did not find any species or assemblages linked to coral habitats over the seamount slopes. This may reflect the distribution pattern of sessile megafauna found on the slopes, which occurred in isolation or forming small coral patches among vaster sedimentary areas intersected by rocky outcrops and crests. The spatial coupling between fishes and discrete colonies, or conspicuous geological structures, was not evaluated in this study (Miller et al., 2012; Quattrini et al., 2012). Future research should examine the relationship between fish distribution and CWCs over larger spatial scales in order to elucidate the importance of CWCs as essential fish habitats.

4.4. Comparison to other deep-sea coral habitats

Soft coral habitats in the Northeastern Pacific (Miller et al., 2012; Stone, 2006; Tissot et al., 2006) and boreal Northwest Atlantic (Auster et al., 2005; Baker et al., 2012) and shallow reefs (< 400 m) in the Northeast Atlantic (Costello et al., 2005; Husebø et al., 2002; Mortensen et al., 1995) are dominated by an assortment of *Sebastes* spp., a fish genus absent from the Azores. North Atlantic cold-temperate reefs are dominated by several gadiform families (i.e. Gadidae, Lotidae, Phycidae, Moridae and Macrouridae), while in the subtropical North American and Mediterranean reefs Anguilliformes (Congridae and Synphobranchidae), Beryciformes (Trachichthyidae) and Scorpaeniformes (Scorpaenidae) are also important components of the fish fauna. In general, those taxa are characteristic of the North Atlantic bathyal environments and correspond to the assemblages observed on the Condor slopes. Aside from some deep-sea predators (e.g. *P. bogaraveo*, *P. americanus* and some serranids) reported from the Mediterranean and the warm Northwest Atlantic reefs, and cold-temperate North Atlantic fish families (e.g. Zoarcidae and Anarhichadidae), the perciforms associated to the studied coral habitats are scarce, contrasting with the fish found at the Condor summit.

Similarly to the observations made on the Condor summit, some studies have found higher fish species richness and abundance associated with CWCs habitats than in non-coral habitats (Costello et al., 2005; D'Onghia et al., 2012; Husebø et al., 2002; Söfker et al., 2011).

Nevertheless, some researchers suggests that coral habitats are not more important for fish than other 3D structured habitats, like rocky outcrops, boulders and other megafauna aggregations (Auster, 2005; Auster et al., 2005; Baker et al., 2012; Biber et al., 2013; Miller et al., 2012; Parrish, 2006; Tissot et al., 2006). These ecologically (or functionally) equivalent habitats have similar

attributes (Auster, 2005, Auster et al., 2005; Miller et al., 2012; Tissot et al., 2006) used opportunistically by fishes. Even if different fish assemblages were found between hard and soft substrates in the Condor summit (see Fig. 5C) it is not clear if boulders and rocky bottoms devoid of sessile megafauna have the same ecological role as coral gardens.

Contrastingly, Ross and Quattrini (2007) and Quattrini et al. (2012) identified a unique, probably obligatory, fish assemblage associated with deep-sea corals reefs at the Western North Atlantic. They found that 19% of the species observed (mainly pertaining to Bythitidae, Scorpaenidae, Chaunacidae, Acropomatidae and Serranidae) were unknown or rarely reported from the area, due to trawling constraints over rough coral bottoms (Ross and Quattrini, 2007). Nevertheless, those specialized fishes were mainly bathyal since none or few occur on the adjacent shelf habitats (e.g. on the *Oculina* reefs at eastern Florida; Reed et al., 2006; Ross and Quattrini, 2007) contrasting with the fish fauna from the Condor summit where the dominant fauna clearly have circalittoral affinities.

The functional linkage between fishes and coral habitats remains less well-known in the deep-sea than in shallow water (Auster, 2005). In trophic terms, the filter-feeding habitat-forming species and the zooplanktivorous fish should aggregate in areas where the rate of planktonic prey delivery is high. However, Sulak et al. (2007) noted that planktivores were rarer than expected in Gulf of Mexico and in several other CWC systems, where plankton occur in high concentrations. The absence of schooling planktivores is explained by the low levels of light at bathyal depths, which constrain the predatory performance of those fishes. Indeed, the vertical distribution of the gregarious zooplanktivores found on the Condor summit ranges from ca. 50 m (25 m for *A. anthias*) to about 300 m depth, similarly to other warm water planktivorous fish found elsewhere (e.g. Hobson, 1991; Thresher and Colin, 1986). Possibly, the *Sebastes* spp. often seen hovering on the top of Northeast Atlantic shallow reefs, benefiting from the enhanced zooplankton abundance (Costello et al., 2005; Söfker et al., 2011), occupy a niche equivalent to that of the zooplanktivores found at Condor.

In most deep-sea CWC areas investigated, macro- and megacarnivorous fishes (such as many gadiforms) are among the dominant group, but the micro and mesobenthivores are almost absent, as noted again by Sulak et al. (2007). The false boarfish *Neocyttus helgae* and *Grammicolepis brachiusculus* were found to be the only deep-sea members of this trophic guild, which associate to structurally complex habitats (Auster et al., 2005; Baker et al., 2012; Moore et al., 2008; Söfker et al., 2011; Sulak et al., 2007). While in the cold-temperate Pacific the fishes of the families Cottidae and Agonidae may occupy this niche (Miller et al., 2012; Stone, 2006), in the Condor coral gardens the wrasses *L. fasciata* and *A. palloni* and probably *A. caprus* are the representatives of that trophic guild.

Despite the numerous observations of fish-coral associations, generally in small discrete areas, the actual importance of CWCs and other complex habitats for fish should be evaluated at the population level, throughout their spatial distribution range and ontogenetic phases (Auster et al., 2007). Most of the fish preferentially reported to be associated with CWCs (e.g. *Sebastes* spp., *Brosme brosme*, *Anarhichas lupus* or *Guttigadus latifrons*; Biber et al., 2013; Costello et al., 2005; Husebø et al., 2002; Mortensen et al., 1995; Söfker et al., 2011) are not restricted to those habitats, neither at fine-scales nor at larger geographical scales. For the Condor seamount, it is difficult to evaluate the importance of coral gardens in mediation of population processes due to the scarcity of data on spatial extent of coral habitats vs. distribution of fish populations, hampering any definitive conclusion regarding a specialized linkage between those two groups. Nevertheless, in

the Azores *A. anthias* and *C. ruber* were also reported to be the dominant fish in a dense black coral garden (De Matos et al., 2013) and *L. fasciata* has only been recorded in the circalittoral depths on rocky habitats covered with sessile emergent epifauna (J. Gomes-Pereira, unpublished data). Those habitats are thought to be common across the Azores seascape, based on the numerous scattered records of the main sessile engineering species, such as soft and hard corals (Braga-Henriques et al., 2013). Elsewhere, *A. anthias*, *C. ruber* and *L. fasciata* were also commonly observed associated with complex habitats often formed by corals and/or other epifauna (Bo et al., 2011, 2012; Dulčić et al., 2006; Fabria et al., 2013; Sartoretto et al., 1997). Therefore, it seems that at least for those fish species, aggregations of sessile megafauna function as essential habitats, across the geographical distribution range of their populations.

Pakhorukov (2008) observed *A. anthias* and *C. ruber* over complex bottoms such as basalt outcrops, caves and crevices but nothing is mentioned about corals or other sessile megaorganisms. Studies of Christiansen et al. (2009), Fock et al. (2002a) and Uiblein et al. (1999), used fishing gears to sample the Seine and the Great Meteor seamounts and naturally failed to detect the fine-scale habitats of the species considered. Of these, the Great Meteor harbors a relatively diverse coral community, including gardens of *Dentomuricea aff. meteor* and *Viminella flagellum* (Grasshoff, 1977, 1985) most similar to those found at Condor seamount.

5. Conclusions

The Condor summit harbors a modified deep-circalittoral fish community shaped by (i) specialized perciform circalittoral species tightly associated with coral gardens (and probably to other structurally complex habitats) depending on pelagic planktivores (i.e. *A. anthias*, *C. ruber*) or benthic small invertebrates (i.e. *L. fasciata* and *A. palloni*); (ii) habitat generalist deep-circalittoral species occurring in both coral and non-coral habitats and having diverse feeding ecologies (e.g. *S. phaeton*; *P. kuhlii*); (iii) eurybathymetric benthic species that spread out from the adjacent bathyal environment (e.g. *H. dactylopterus*; *Hoplostethus* sp.), and; (iv) opportunistic bathyal benthopelagic predators that visit the seamount summit to likely feed on the resident fish (i.e., *P. bogaraveo* and *P. americanus*).

In contrast, the fish assemblages detected on the slopes are formed by species with broad distributions apparently not related to emergent megafauna habitats, although some may favor association with individual biogenic or geomorphological 3-D structures.

Future research should investigate the association between fishes and their habitats at different spatial scales, increase sample effort by sub-sampling dive transects and incorporate additional data on biotic and abiotic habitat attributes that may better explain the actual fish spatial distribution. In a region like the Azores, where trawling is not allowed, data on fish groups observed by ROVs and not sampled by fishing gears are essential to improve our knowledge on fish diversity and behavior that will help develop more robust ecosystem-based management models to support a sustainable use of the marine environment.

Acknowledgments

IMAR-DOP/UAZ is a Research and Development Unit no. 531 and LARSyS-Associated Laboratory no. 9 funded by the Portuguese Foundation for Science and Technology (FCT) through pluriannual and programmatic funding schemes (OE, FEDER, POCI2001, FSE), through PEST project (Pest/OE/EEI/LA0009/2011–2014) and by the Azores Directorate for Science and Technology (DRCTC). Surveys

and data analysis have been supported by projects CORALFISH (FP7 ENV/2007/1/21314 4), CORAZON (PTDC/MAR/72169/2006), CONDOR (EEA Grants PT0040/2008) and HERMIONE (FP7 ENV/2008/1/226354). Further acknowledgments are due to the Portuguese Task Group for the Extension of Continental Shelf (EMEPC) for sharing the ROV team and equipment during the Condor CORALFISH 2010 cruise. Thanks are also due to Paulo Martins and Victor Rosa crew members of the R/V *Águas Vivas* and to Renato Martins the pilot of the ROV *SP*. JNGP was supported by a CORAZON fellowship grant and by the doctoral grant (Ref. M3.1.2/F/062/2011) from the Regional Directorate for Education, Science and Culture, of the Regional Government of the Azores. FT was supported by a post-doctoral grant (Ref. SFRH/BPD/79801/2011) from the Fundação para a Ciência e a Tecnologia (FCT). CKP was supported by the doctoral grant (SFRH/BD/66404/2009) also from FCT. The authors acknowledge Gui Menezes and Telmo Morato for helpful contributions and three anonymous referees for valuable commentaries.

References

- Afonso, P., Graça, G., Berke, G., Fontes, J., 2012. First observations on seamount habitat use of blackspot seabream (*Pagellus bogaraveo*) using acoustic telemetry. *J. Exp. Mar. Biol. Ecol.* 436–437, 1–10.
- Agardy, T., 1997. Advances in marine conservation: the role of marine protected areas. *Trends Ecol. Evol.* 9, 267–270.
- Auster, P.J., 2005. Are deep-water corals important habitats for fishes?. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin Heidelberg, pp. 747–760.
- Auster, P.J., 2007. Linking deep-water corals and fish populations. In: George, R.Y., Cairns, S.D. (Eds.), *Conservation and Adaptive Management of Seamount and Deep-sea Coral Ecosystems*. Rosenstiel School of Marine and Atmospheric Science, University of Miami, USA, pp. 93–99.
- Auster, P.J., Moore, J., Heinonen, K.B., Watling, L., 2005. A habitat classification scheme for seamount landscapes: assessing the functional role of deep-water corals as fish habitat. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin Heidelberg, pp. 747–755.
- Baillon, S., Hamel, J.-F., Wareham, V.E., Mercier, A., 2012. Deep cold-water corals as nurseries for fish larvae. *Front. Ecol. Environ.* 10, 351–356.
- Baker, K.D., Haedrich, R.L., Snelgrove, P.V.R., Wareham, V.E., Edinger, E.N., Wilkinson, K.D., 2012. Small-scale patterns of deep-sea fish distributions and assemblages of the Grand Banks, Newfoundland continental slope. *Deep-Sea Res.* 1 65, 171–188.
- Biber, M.F., Duineveld, G.C.A., Lavaleye, M.S.S., Davies, A.J., Bergman, M.J.N., van den Beld, I.M.J., 2013. Investigating the association of fish abundance and biomass with cold-water corals in the deep Northeast Atlantic Ocean using a generalized linear modelling approach. *Deep-Sea Res.* II.
- Biscoito, M., Segonzac, M., Almeida, A.J., Desbruyères, D., Geistdoerfer, P., Turnipseed, M., Van Dover, C., 2002. Fishes from the hydrothermal vents and cold seeps – an update. *Cah. Biol. Mar.* 43, 359–362.
- Bo, M., Bavestrello, G., Canese, S., Giusti, M., Angiolillo, M., Cerrano, C., Salvati, E., Greco, S., 2011. Coral assemblage off the Calabrian Coast (South Italy) with new observations on living colonies of *Antipathes dichotoma*. *Ital. J. Zool.* 78, 231–242.
- Bo, M., Canese, S., Spaggiari, C., Pusceddu, A., Bertolino, M., Angiolillo, M., Giusti, M., Loreto, M.F., Salvati, E., Greco, S., Bavestrello, G., 2012. Deep coral oases in the South Tyrrhenian Sea. *PLoS ONE* 7 (11), e49870.
- Botsford, L.W., Castilla, J.C., Peterson, C.H., 1997. The management of fisheries and marine ecosystems. *Science* 277 (5325), 509–515.
- Braga-Henriques, A., Porteiro, F.M., Ribeiro, P.A., De Matos, V., Sampaio, Í., Ocaña, O., Santos, R.S., 2013. Diversity, distribution and spatial structure of the cold-water coral fauna of the Azores (NE Atlantic). *Biogeosciences* 10, 4009–4036.
- Braga-Henriques, A., Carreiro-Silva, M., Tempera, F., Porteiro, F.M., Jakobsen, K., Jakobsen, J., Albuquerque, M., Santos, R.S., 2012. Carrying behavior in the deep-sea crab *Paromola cuvieri* (Northeast Atlantic). *Mar. Biodiv.* 42, 37–46.
- Briggs, J.C., Bowen, B.W., 2012. A realignment of marine biogeographic provinces with particular reference to fish distributions. *J. Biogeogr.* 39, 12–30.
- Buhl-Mortensen, L., Vanreusel, A., Gooday, A.J., Levin, L.A., Priede, I.G., Buhl-Mortensen, P., Gheerardyn, H., King, N.J., Raes, M., 2010. Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins. *Mar. Ecol. Evol. Persp.* 31, 21–50.
- Bullimore, R.D., Foster, N.L., Howell, K.L., 2013. Coral-characterized benthic assemblages of the deep Northeast Atlantic: defining “coral gardens” to support future habitat mapping efforts. *ICES J. Mar. Sci.* 70, 511–522.
- Carré, C., 2010. COVER – customizable observation video image record, User Manual v0.8.4. Ifremer.
- Christiansen, B., Martin, B., Hirsch, S., 2009. The benthopelagic fish fauna on the summit of Seine Seamount, NE Atlantic: composition, population structure and diets. *Deep-Sea Res.* II 56, 2705–2712.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Austr. J. Ecol.* 18, 117–143.
- Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.
- Cohen, D.M., 1989. Argentinidae. In: Whitehead, P.J., Bauchot, M.L., Hureau, J.C., Nielsen, J., Tortonese, E. (Eds.), *Fishes of the Northeast Atlantic and the Mediterranean*, vol. 2. UNESCO, Paris, pp. 386–391.
- Colaço, A., Giacometti, E., Porteiro, F., Menezes, G.M., 2013. Trophodynamic studies on the Condor seamount (Azores, Portugal, North Atlantic). *Deep-Sea Res.* 98 (PA), 178–189.
- Cook, S.E., Conway, K.W., Burd, B., 2008. Status of the glass sponge reefs in the Georgia Basin. *Mar. Environ. Res.* 66 (Suppl. 2008), S80–S86.
- Costello, M.J., McCrear, M., Freiwald, A., Lundalv, T., Jonsson, L., Bett, B.J., van Weering, T.C.E., de Haas, H., Roberts, J.M., Allen, D., 2005. Role of cold-water *Lophelia pertusa* coral reefs as fish habitat in the NE Atlantic. In: Freiwald, A., Roberts, M. (Eds.), *Cold Water Corals and Ecosystems*. Springer, Verlag, pp. 771–805.
- Cuvellier, D., Sarrazin, J., Colaço, A., Copley, J., Desbruyères, D., Glover, A.G., Tyler, P., Santos, R.S., 2009. Distribution and spatial variation of hydrothermal faunal assemblages at Lucky Strike (Mid-Atlantic Ridge) revealed by high-resolution video image analysis. *Deep-Sea Res.* II 56, 2026–2040.
- D’Onghia, G., Maiorano, P., Sion, L., Giove, A., Capezzuto, F., Carlucci, R., Tursi, A., 2010. Effects of deep-water coral banks on the abundance and size structure of the megafauna in the Mediterranean Sea. *Deep-Sea Res.* II 57, 397–411.
- D’Onghia, G., Indennitate, 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. *Mar. Ecol. Prog. Ser.* 443, 95–110.
- D’Onghia, G., Maiorano, P., Carlucci, R., Capezzuto, F., Carlucci, A., Tursi, A., Sion, L., 2012. Comparing deep-sea fish fauna between coral and non-coral “Megahabitats” in the Santa Maria di Leuca Cold-Water Coral Province (Mediterranean Sea). *PLoS ONE* 7 (9), e44509.
- De Matos, V., Pereira, J.N.G., Tempera, F., Ribeiro, P.A., Braga-Henriques, A., Porteiro, F., in press. Newly recorded garden of *Antipathella subpinnata* (Anthozoa, Antipatharia) extends species distribution to the Azores. *Deep-Sea Res.* II.
- Desbruyères, D., Biscoito, M., Caprais, J.C., Colaço, A., Comtet, T., Crassous, P., Fouquet, Y., Khrifounoff, A., Le Bris, N., Olu, K., Riso, R., Sarradin, P.-M., Segonzac, M., Vangriesheim, A., 2001. Variations in deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge near the Azores plateau. *Deep-Sea Res.* I 48, 1325–1346.
- Dulčić, J., Furlan, B., Lipej, L., 2006. First confirmed record of *Lappanella fasciata* (Cocco, 1833) in the Adriatic Sea. *J. Appl. Ichthyol.* 22, 536–537.
- Fabria, M.C., Pedel, L., Beuck, L., Galgani, F., Hebbeln, D., Freiwald, A., 2013. Megafauna of vulnerable marine ecosystems in French Mediterranean submarine canyons: Spatial distribution and anthropogenic impacts. *Deep Sea Research Part II: Topical Studies in Oceanography*. In Press, Available online 2 July 2013.
- Felley, J.D., Vecchione, M., 1995. Assessing habitat use by nekton on the continental slope using archived videotapes from submersibles. *Fish. Bull.* 93, 262–273.
- Fock, H., Uiblein, F., Köster, F., von Westernhagen, H., 2002a. Biodiversity and species-environment relationships of the demersal fish assemblage at the Great Meteor Seamount (subtropical NE Atlantic), sampled by different trawls. *Mar. Biol.* 141, 185–199.
- Fock, H.O., Matthiessen, B., Zidowitz, H., von Westernhagen, H., 2002b. Diel and habitat-dependent resource utilization by deep-sea fishes at the Great Meteor seamount: niche overlap and support for the sound scattering layer interception hypothesis. *Mar. Ecol. Prog. Ser.* 244, 219–233.
- Fosså, J.H., Mortensen, P.B., Furevik, D.M., 2002. The deepwater coral *Lophelia pertusa* in Norwegian waters: distribution and fisheries impacts. *Hydrobiologia* 471, 1–12.
- Freiwald, A., Fosså, J.H., Grehan, A., Koslow, T., Roberts, J.M., 2004. Cold-water Coral Reefs. UNEP-WCMC, Cambridge, UK.
- Giacometti, E., Menezes, G. (Eds.), 2011. CONDOR Observatory for Long-term Study and Monitoring of Azorean Seamount Ecosystems. Final Project Report. Arquivos do DOP, Série Estudos 1/2012, 261 pp+9 annexes.
- Giacometti, E., Bergstad, O.A., Menezes, G.M., 2013. An integrated approach for studying seamounts: CONDOR observatory. *Deep-Sea Res.* II 98 (PA), 1–6.
- Goldman, S.F., Sedberry, G.R., 2011. Feeding habits of some demersal fish on the Charleston Bump off the southeastern United States. *ICES J. Mar. Sci.* 68, 390–398.
- Gomes-Pereira, J.N., Porteiro, F.M., Santos, R.S., 2013. Deep-sea scorpionfish predatory behavior on seamount coral habitat. *Acta Ethologica*. In press.
- Gomes-Pereira, J.N., Tempera, F., Ribeiro, P.A., Porteiro, F.M., 2012. Notes on fauna associated with an opportunistic artificial reef near cold-water corals. *Arquipelago. Life Mar. Sci.* 29, 69–75.
- Gonzalez-Mirelis, G., Bergström, P., Lundäl, T., Jonsson, J., Lindgarth, M., 2009. Mapping the benthos: spatial patterns of seabed dwelling megafauna in a Swedish fjord, as derived from opportunistic video data. *Mar. Biodiv.* 39, 291–302.
- Grasshoff, M., 1977. Die Gorgonarien des östlichen Nordatlantik und des Mittelmeeres III. Die Familie Paramuriceidae (Cnidaria, Anthozoa). *“Meteor” Forsch-Ergeb Sect. D* 27, 5–76.
- Grasshoff, M., 1985. Die Gorgonaria und Antipatharia der Großen Meteor-Bank und der Josephine-Bank (Cnidaria: Anthozoa). *Senckenbergiana Marit.* 17, 65–87.
- Harris, P.T., Baker, E.K., 2012. Seafloor Geomorphology as Benthic Habitat. *Geohab Atlas of Seafloor Geomorphic Features and Benthic Habitats*.

- Haedrich, R.L., Merrett, N.R., 1988. Summary atlas of deep-living demersal fishes in the North Atlantic Basin. *J. Nat. Hist.* 22 (5), 1325–1362.
- Hirsch, S., Christiansen, B., 2010. The trophic blockage hypothesis is not supported by the diets of fishes on Seine Seamount. *Mar. Ecol. Prog. Ser.* 31 (Suppl. 1), 107–120.
- Hobson, E.S., 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: Sale, P.F. (Ed.), *The Ecology of Fishes on Coral Reefs*. Academic Press, San Diego, CA, pp. 69–95.
- Husebø, A., Nøttestad, L., Fosså, J.H., Furevik, D.M., Jørgensen, S.B., 2002. Distribution and abundance of fish in deep-sea coral habitats. *Hydrobiologia* 471, 91–99.
- Koslow, J.A., 1996. Energetic and life-history patterns of deep-sea benthic, benthopelagic and seamount-associated fish. *J. Fish Biol.* 49 (Suppl. A), 54–74.
- Koslow, J.A., Boehlert, G.W., Gordon, J.D.M., Haedrich, R.L., Lorange, P., Parin, N., 2000. Continental slope and deep-sea fisheries: implications for a fragile ecosystem. *ICES J. Mar. Sci.* 57, 548–557.
- Krieger, K.J., Wing, B.L., 2002. Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. *Hydrobiologia* 471, 83–90.
- Kukuev, E.I., 2004. Ichthyofauna research on underwater mountain within the North-Atlantic ridge and adjacent areas. *Arch. Fish. Mar. Res.* 51, 215–232.
- Lorange, P., Trenkel, V.M., 2006. Variability in natural behavior, and observed reactions to an ROV, by mid-slope fish species. *J. Exp. Mar. Biol. Ecol.* 332, 106–119.
- Lundsten, L., McClain, C.R., Barry, J.P., Cailliet, G.M., Clague, D.A., De Vogelaere, A.P., 2009. Ichthyofauna on three seamounts off southern and central California, USA. *Mar. Ecol. Prog. Ser.* 389, 223–232.
- Melo, O., Menezes, G.M., 2002. Exploratory Fishing of the Orange Roughy (*Hoplostethus atlanticus*) in Some Seamounts of the Azores Archipelago. *ICES CM 2002/M:26*, 11 pp.
- Menezes, G.M., Rosa, A., Melo, O., Pinho, M.R., 2009. Demersal fish assemblages off the Seine and Sedlo seamounts (northeast Atlantic). *Deep-Sea Res. II* 56, 2683–2704.
- Menezes, G.M., Rosa, A., Melo, O., Porteiro, F.M., 2012. Annotated list of demersal fishes occurring at Sedlo Seamount, Azores north-east central Atlantic Ocean. *J. Fish Biol.* 81, 1003–1018.
- Menezes, G.M., Sigler, M.F., Silva, H.M., Pinho, M.R., 2006. Structure and zonation of demersal fish assemblages off the Azores Archipelago (mid-Atlantic). *Mar. Ecol. Prog. Ser.* 324, 241–260.
- Menezes, G.M., Giacomello, E., 2013. Spatial and temporal variability of demersal fishes at Condor seamount (Northeast Atlantic). *Deep-Sea Res. II* 98 (PA), 101–113.
- Miller, R.J., Hovecar, J., Stone, R.P., Fedorov, D.V., 2012. Structure-forming corals and sponges and their use as fish habitat in Bering Sea submarine canyons. *PLoS ONE* 7 (3), e33885, <http://dx.doi.org/10.1371/journal.pone.0033885>.
- Moore, J., Auster, P., Calini, D., Heironen, K., Barber, K., Hecker, B., 2008. The false boarfish *Neocyttus helgae* in the western North Atlantic. *Bull. Peabody Mus. Nat. Hist.* 49, 31–41.
- Morato, T., Bulman, C., Pitcher, T.J., 2009. Modelled effects of primary and secondary production enhancement by seamounts on local fish stocks. *Deep-Sea Res. II* 56, 2713–2719.
- Morato, T., Cheung, W.W.L., Pitcher, T.J., 2006. Vulnerability of seamount fish to fishing: fuzzy analysis of life-history attributes. *J. Fish Biol.* 68, 209–221.
- Morato, T., Solà, E., Grós, M.P., Menezes, G., 2001. Feeding habits of two congener species of seabreams, *Pagellus bogaraveo* and *Pagellus acarne*, off the Azores (northeastern Atlantic) during spring of 1996 and 1997. *Bull. Mar. Sci.* 69, 1073–1087.
- Morato, T., Kvile, K.Ø., Taranto, G.H., Tempera, F., Narayanaswamy, B., Hebbeln, D., Menezes, G., Wienberg, C., Santos, R.S., Pitcher, T.J., 2013. Seamount physiography and biology in the north-east Atlantic and Mediterranean Sea. *Biogeosciences* 10, 3039–3054.
- Mortensen, P.B., Hovland, M., Brattegard, T., Farestveit, R., 1995. Deepwater bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64°N on the Norwegian Shelf: structure and associated megafauna. *Sarsia* 80, 145–158.
- Nobre, A., 1924. Contribuições para a fauna dos Açores. *An. Inst. Zool. Univ. Porto* 1, 41–90.
- OSPAR, 2010. Background Document for Coral Gardens. OSPAR Commission Biodiversity Series.
- Pakhorukov, N.P., 2008. Visual observations of fish from seamounts of the Southern Azores region (the Atlantic Ocean). *J. Ichth.* 48, 114–123.
- Parin, N.V., Mironov, A.N., Nesis, K.N., 1997. Biology of the Nazca and Sala y Gómez Submarine Ridges, an outpost of the Indo-West Pacific fauna in the Eastern Pacific Ocean: composition and distribution of the fauna, its communities and history. *Adv. Mar. Biol.* 32, 145–242.
- Parrish, F.A., 2006. Precious corals and subphotic fish assemblages. *Atoll Res. Bull.* 543, 425–438.
- Pham, C.K., Gomes-Pereira, J.N., Isidro, E.J., Santos, R.S., Morato, T., 2013. Abundance of litter on Condor seamount (Azores, Portugal, Northeast Atlantic). *Deep Sea Research Part II: Topical Studies in Oceanography* 98 (PA), 204–208.
- Porteiro, F.M., Menezes, G.M., Afonso, P., Monteiro, J.G., Santos, R.S., 2010. Peixe Marinhos/marine fishes (Chondrichthyes, Actinopterygii). In: Borges, P.A.V., Costa, A., Cunha, R., Gabriel, R., Gonçalves, V., Martins, A.F., Melo, I., Parente, M., Raposo, P., Rodrigues, P., Santos, R.S., Silva, L., Vieira, P., Vieira, V. (Eds.), *A List of the Terrestrial and Marine Biota From the Azores. Princípiã, Cascais*, pp. 331–344.
- Probert, P.K., Christiansen, S., Gjerde, K.M., Gubbay, S., Santos, R.S., 2007. Management and conservation of seamounts. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, R.S., Haggan, N., Santos, R.S. (Eds.), *Seamounts: Ecology, Fisheries and Conservation*. Blackwell Publishing, Oxford, UK, pp. 442–475.
- Quattrini, A.M., Ross, S.W., Carlson, M.C.T., Nizinski, M., 2012. Megafaunal-habitat associations at a deep-sea coral mound off North Carolina, USA. *Mar. Biol.* 159, 1079–1094.
- Ralston, S., Gooding, R.M., Ludwig, G.M., 1986. An ecological survey and comparison of bottom fish resource assessments (submersibles versus handline fishing) at Johnston. *Atoll Fish. Bull.* 84, 141–155.
- Reed, J.K., Weaver, D.C., Pomponi, S.A., 2006. Habitat and fauna of deep-water *Lophelia pertusa* coral reefs off the Southeastern U.S.: Blake Plateau, Straits of Florida, and Gulf of Mexico. *Bull. Mar. Sci.* 78, 343–375.
- Rex, M.A., McClain, C.R., Johnson, N.A., Etter, R.J., Allen, J.A., Bouchet, P., Waren, A., 2005. A source-sink hypothesis for abyssal biodiversity. *Am. Nat.* 165 (2), 163–178.
- Richer de Forges, B.R., Koslow, J.A., Poore, G.C.B., 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* 405, 944–947.
- Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. *Science* 312 (5773), 543–547.
- Rogers, A.D., Baco, A., Griffiths, H., Hart, T., Hall-Spencer, J.M., 2007. Corals on seamounts. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), *Seamounts: Ecology, Conservation and Management. Fish and Aquatic Resources Series*. Blackwell, Oxford, UK, pp. 141–169.
- Ross, S.W., Quattrini, A.M., 2007. The fish fauna associated with deep coral banks off the southeastern United States. *Deep-Sea Res. I* 54, 975–1007.
- Ross, S.W., Quattrini, A.M., 2009. Deep reef fish assemblage patterns on the Blake Plateau (Western North Atlantic). *Mar. Ecol. Prog. Ser.* 30, 74–92.
- Saldanha, L., 1994. Fishes observed and collected during the Alvin dives at the Lucky Strike thermal vent site (Mid-Atlantic Ridge – 1993). *Cybiurn* 18, 460–462.
- Santos, R.S., Hawkins, S., Monteiro, L.R., Alves, M., Isidro, E.J., 1995. Marine research, resources and conservation in the Azores. *Aq. Conserv.: Mar. Freshwater Ecosyst.* 5 (4), 311–354.
- Santos, R.S., Porteiro, F.M., Barreiros, J.P., 1997. Marine fishes of the Azores: an annotated checklist and bibliography. *Arquipélago. Life Mar. Sci. Suppl.* 1, 1–231.
- Santos, R.S., Christiansen, S., Christiansen, B., Gubbay, S., 2009. Towards the conservation and management of Sedlo seamount: a case study. *Deep Sea Res. II: Top. Stud. Oceanogr.* 56 (25), 2720–2730.
- Sartoretto, S., Francour, P., Harmelin, J.-G., Charbonnel, E., 1997. In situ observations of two deep-water labrids, *Lappanella fasciata* and *Acantholabrus palloni*, in the northwestern mediterranean. *Cybiurn* 21, 37–44.
- Shcherbachev Yu, N., Kukuev, E.I., Shlibanov, V.I., 1985. Composition of the benthic and demersal ichthyocenoses of the submarine mountains in the southern part of the North Atlantic Range. *J. Ichthyol.* 25, 110–125.
- Silva, H.M., Pinho, M.R., 2007. Small-scale fishing on seamounts. In: Pitcher, T.J., Morato, T., Hart, P.J.B., Clark, M.R., Haggan, N., Santos, R.S. (Eds.), *Seamounts: Ecology, Fisheries and Conservation*. Blackwell Publishing, Oxford, UK, pp. 335–360.
- Schmiing, M., Afonso, P., Tempera, F., Santos, R.S., 2013. Predictive habitat modelling of reef fishes with contrasting trophic ecologies. *Mar. Ecol. Prog. Ser.* 474, 201–216.
- Sobrinho-Gonçalves, L., Isidro, E., 2001. Fish larvae and zooplankton biomass around Faial Island (Azores archipelago). A preliminary study of species occurrence and relative abundance. *Arquipélago. Life Mar. Sci.* 18, 35–52.
- Söffker, M., Sloman, K.A., Hall-Spencer, J.M., 2011. In situ observations of fish associated with coral reefs off Ireland. *Deep-Sea Res. I* 58, 818–825.
- Stone, R.P., 2006. Coral habitat in the Aleutian Islands of Alaska: depth distribution, fine-scale species associations, and fisheries interactions. *Coral Reefs* 25, 229–238.
- Stoner, A.W., Ryer, C.H., Parker, S.J., Auster, P.J., Wakefield, W.W., 2008. Evaluating the role of fish behavior in surveys conducted with underwater vehicles. *Can. J. Fish. Aquat. Sci.* 65, 1230–1243.
- Sulak, K.J., Brooks, R.A., Luke, K.E., Norem, A.D., Randall, M., Quaid, A.J., Yeargin, G.E., Miller, J.M., Harden, W.M., Caruso, J.H., Ross, S.W., 2007. Demersal fishes associated with *Lophelia pertusa* coral and hard-substrate biotopes on the continental slope, northern Gulf of Mexico. *Bull. Mar. Sci.* 81 (1), 65–92.
- Tempera, F., Pereira, J.N., Braga Henriques, A., Porteiro, F., Morato, T., Matos, V., Souto, M., Guillaumont, B., Santos, R.S., 2012a. Cataloguing deep-sea biological facies of the Azores. *Rev. Inv. Mar.* 19, 36–38.
- Tempera, F., Giacomello, E., Mitchell, N.C., Campos, A.S., Braga-Henriques, A., Bashmachnikov, I., Martins, A., Mendonça, A., Morato, T., Colaço, A., Porteiro, F.M., Catarino, D., Gonçalves, J., Pinho, M.R., Isidro, E.J., Santos, R.S., Menezes, G., 2012b. Mapping Condor seamount seafloor environment and associated biological assemblages (Azores, NE Atlantic). In: Harris, P.T., Baker, E.K. (Eds.), *Seafloor Geomorphology as Benthic Habitat. Geohab Atlas of Seafloor Geomorphic Features and Benthic Habitats*, pp. 807–818.
- Tempera, F., Hipólito, A., Madeira, J., Vieira, S., Campos, A.S., Mitchell, N.C., 2013. Condor seamount (Azores, NE Atlantic): A morpho-tectonic interpretation. *Deep Sea Research Part II: Topical Studies in Oceanography* 98 (PA), 7–23.
- Thresher, R.E., Colin, P.L., 1986. Trophic structure, diversity and abundance of fishes of the deep reef (30–300 m) at Enewetak, Marshall Islands. *Bull. Mar. Sci.* 38, 253–272.

- Tissot, B.N., Yoklavich, M.M., Love, M.S., York, K., Amend, M., 2006. Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep sea coral. *Fish. Bull.* 104, 167–181.
- Uiblein, F., Geldmacher, A., Köster, F., Nellen, W., Kraus, G., 1999. Species composition and depth distribution of fish species collected in the area of the Great Meteor Seamount, Central Eastern Atlantic, during cruise M42/3, with seventeen new records. *Inf. Téc. Inst. Canario Cienc. Mar.* 5, 47–85.
- Uiblein, F., Lorange, P., Latrouite, D., 2003. Behaviour and habitat utilisation of seven demersal fish species on the Bay of Biscay continental slope, NE Atlantic. *Mar. Ecol. Prog. Ser.* 257, 223–232.
- Van Soest, R.W.M., Boury-Esnault, N., Vacelet, J., Dohrmann, M., Erpenbeck, D., De Voogd, N.J., Santodomingo, N., Vanhoorne, B., Kelly, M., Hooper, J.N.A., 2012. Global diversity of sponges (Porifera). *PLoS ONE* 7 (4), e35105, <http://dx.doi.org/10.1371/journal.pone.0035105>.
- Weaver, D.C., Dennis, G.D., Sulak, K.J., 2001. Northeastern Gulf of Mexico Coastal and Marine Ecosystem Program: Community Structure and Trophic Ecology of the Fishes on the Pinnacles Reef Track. Final Synthesis Report. U.S. Department of the Interior, Geological Survey, USGS BSR-2001-0008 and Minerals Management Service Gulf of Mexico OCS Region, New Orleans, LA, OCS Study MMS 2002-034.
- Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. *J. Geol.* 30 (5), 377–392.
- Whitehead, P.J., Bauchot, M.L., Hureau, J.C., Nielsen, J., Tortonese, E. (Eds.), 1986–1989. *Fishes of the Northeast Atlantic and the Mediterranean*, vol. 1–3. UNESCO, Paris.
- Willis, T.J., Millar, R.B., Babcock, R.C., 2000. Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Mar. Ecol. Prog. Ser.* 198, 249–260.
- Wisshak, M., Neumann, C., Jakobsen, J., Freiwald, A., 2009. The 'living-fossil community' of the cyrtocrinid *Cyathidium foresti* and the deep-sea oyster *Neopycnodonte zibrowii* (Azores Archipelago). *Palaeo3* 271, 77–83.