

Comparison of the community structure of the marine molluscs of the “Banco D. João de Castro” seamount (Azores, Portugal) with that of typical inshore habitats on the Azores archipelago

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Abstract D. João de Castro Bank (DJC) is a shallow seamount with hydrothermal activity located between the islands of Terceira and São Miguel, Azores (Portugal). A survey of the molluscan fauna was conducted in this peculiar habitat. We found a smaller number of molluscan taxa and a different community structure compared to shore environments on the Azores. This coincides with impoverished environmental settings at this location. Possible reasons such as the degree of isolation (inshore vs. offshore locations), geological age, and special ecological conditions related to seamounts and hydrothermal vents are discussed.

Keywords Seamounts · Molluscs · Azores · Hydrothermal vents · Modes of larval development

Introduction

D. João de Castro Bank (38°13.3'N; 26°36.2'W) is an isolated seamount located in the archipelago of the

Azores (northern Atlantic), between the islands Terceira and São Miguel (Fig. 1a), at 36 and 40 nautical miles, respectively, from these islands. Today, the upper part of the seamount has its base at 50 m depth and reaches 13 m depth at its top. Inside the volcanic cone (300 × 600 m), the depth is around 40 m (Fig. 1b). The shallower part of the seamount was formed by several submarine eruptions during 2 weeks in December 1720. These eruptions occurred at 100 m depth and were visible from São Miguel and Terceira. The ashes accumulated, forming a small island approximately 1 km across and 150 m high, which was completely destroyed by the winter storms 2 years later (Agostinho 1934, 1960; Weston 1964; Machado 1967).

Formations such as D. João de Castro Bank with exuberant hydrothermal activity at shallow depths are rare in the Atlantic Ocean (Santos et al. 1996). The gas is released within a small area (100 × 50 m) at the bottom (16–45 m depth) in the western part of the volcanic cone. This gas, mainly CO₂ (90%) with lesser H₂S, H₂, and CH₄ (Cardigos et al. 2005), has its source in a magmatic chamber located between 1 and 5 km under the seafloor (Machado and Lemos 1998). Recently, a second area with hydrothermal activity was discovered, in the depth range of 150 to more than 400 m, south-east of the shallowest part of the seamount (Pascoal et al. 2000). For a discussion on the chemical characterization of the fluids released by the vents at D. João de Castro Bank, see Cardigos et al (2005). The molluscan fauna at D. João de Castro Bank is still poorly known and has mainly been studied from a taxonomical point of view (Ávila 1997; Ávila et al. 2004). Nevertheless, seamounts provide opportunities to study the processes and patterns of dispersion and colonization in marine animals and contribute to the theories of

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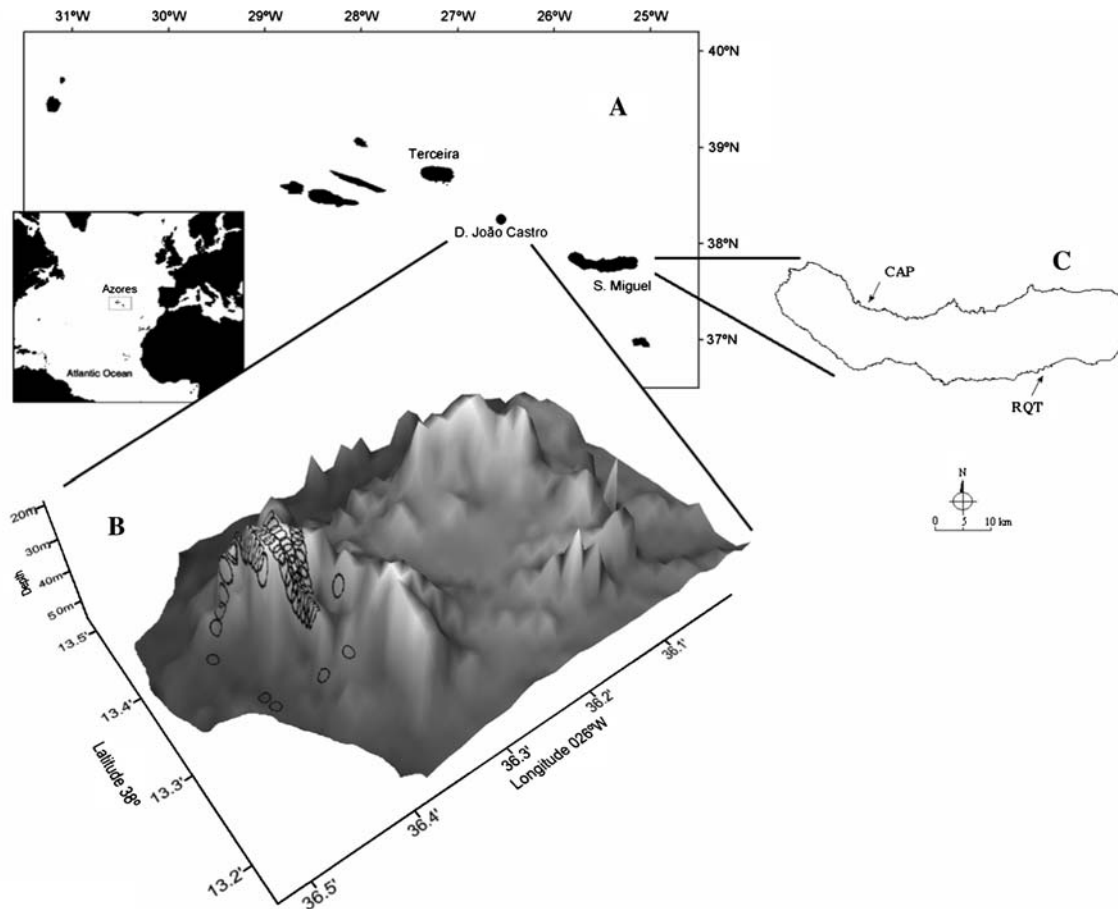


Fig. 1 **a** Geographic location of D. João de Castro Bank; **b** topography of D. João de Castro Bank (© *ImagDOP* and *ISR/IST*); **c** geographic location of Capelas (CAP) and Ribeira Quente (RQT) at São Miguel Island

biogeography and speciation (Shuto 1974; Scheltema 1995). The aim of this paper is to compare the molluscan community on this seamount with that of more typical inshore habitats on the Azores, and to relate possible differences to differences in the degree of isolation (inshore vs. offshore locations), geological age, type of substrate, depth, and the presence/absence of hydrothermal vents.

Methods

The molluscan fauna of D. João de Castro Bank (DJC), a shallow offshore bank with hydrothermal activity, was compared with two different inshore sites: Capelas (CAP), a rocky shore, densely covered by algae, without hydrothermal activity; and Ribeira Quente (RQT), a sandy area with hydrothermal activity (located on the north and south coast, respectively, of São Miguel; Table 1). In the Azores, there are no algae-covered inshore rocky sites with hydrothermal activity that could be compared with the DJC Bank.

Samples were obtained by SCUBA-diving. At each site, 25×25 cm quadrates covered with algae were scraped off with a chisel. A total of 21 quadrates covered by algae were collected, 4 at DJC, 5 at RQT, and 12 at CAP (Table 3). The attached algae and associated organisms were collected into a labeled cotton drawstring bag with fine mesh net. In the laboratory, the samples were sieved by pouring water through a 1 mm mesh sieve. The molluscs were then removed from the algae, sorted to species level under a stereomicroscope, counted, labelled, and preserved in 70% ethanol. Only live molluscs were counted. All samples were given a number and were deposited in the collection of the Department of Biology of the University of the Azores (DBUA). The samples from CAP are a transformed subset of those published by Ávila (2003). The minimum area for subtidal quantitative ecological studies on algae, in the Azores is 50×50 cm (Neto 1997), in contrast to 25×25 cm for molluscan studies (Azevedo 1991; Ávila 1998). As scraping is a destructive technique, Ávila (2003) used the molluscan data from the algae area, so for the present study, the

Table 1 Characterization of the samples

Site	Date	Depth (m)	Hydrothermal activity	Distance to vents (m)	Type of substrate
DJC1	22 July 2000	20.5	1	0.5	Rocky
DJC2	25 July 2000	16.9	4	0.3	Rocky
DJC3	25 July 2000	17.0	3	1.0	Rocky
DJC4	25 July 2000	16.0	3	1.3	Rocky
RQT1	28 September 2000	6.1	4	0.5	Sandy
RQT2	28 September 2000	6.6	2	0.3	Sandy
RQT3	28 September 2000	6.0	1	0.4	Sandy
RQT4	28 September 2000	5.9	2	0.5	Sandy
RQT5	28 September 2000	6.5	3	0.2	Sandy
CAP1	17 July 1996	16.0	0	–	Rocky
CAP2	17 July 1996	16.0	0	–	Rocky
CAP3	17 July 1996	16.0	0	–	Rocky
CAP4	11 July 1997	15.0	0	–	Rocky
CAP5	11 July 1997	15.0	0	–	Rocky
CAP6	11 July 1997	15.0	0	–	Rocky
CAP7	18 July 1996	8.0	0	–	Rocky
CAP8	18 July 1996	8.0	0	–	Rocky
CAP9	18 July 1996	8.0	0	–	Rocky
CAP10	10 July 1997	6.0	0	–	Rocky
CAP11	10 July 1997	6.0	0	–	Rocky
CAP12	10 July 1997	6.0	0	–	Rocky

DJC D. João de Castro Bank, *RQT* Ribeira Quente, *CAP* Capelas; the hydrothermal activity level was classified as: 0 no hydrothermal activity, 1 intermittent release of gas bubbles, 2 constant release of gas bubbles, 3 two or more vents per square meter with constant release of gas bubbles, 4 water heating and two or more vents per square meter with constant release of gas bubbles

original data of the 50 × 50 cm CAP samples were transformed into a 25 × 25 cm area by a simple division by the factor 4.

Data analysis

Data analysis was carried out using the software package PRIMER v5.2 (Clarke and Gorley 2001). Species diversity was calculated using species richness (S), and the species diversity indices of Shannon–Wiener (H') (Pearson and Rosenberg 1978) and Pielou (J') (Pearson and Rosenberg 1978; Warwick and Clarke 1993). Additionally, the total number of molluscs per sample (N) was used for comparisons between sites. The associations between samples were visualized using the UPGMA clustering technique (Clarke and Warwick 1994). Prior to the analysis, data were transformed by double square root in order to standardize the data and to avoid clustering that would be determined by the most abundant species (Clarke 1993). Transformed species abundance ($n_i^{1/4}$) was used to generate triangular matrices of similarities using the Bray–Curtis similarity index (Field et al. 1982; Clarke 1993).

The ANOSIM randomization/permutation test (Warwick and Clarke 1993) was used to test for differences between sites or selected sets of sites. These sets of sites were selected “a priori”, based on their environmental conditions (e.g. sites with and without

hydrothermal activity; inshore vs. offshore sites; sites with sand vs. rocky substrate). Species with a ratio higher than 1.4 (using SIMPER subroutine—similarity percentages analysis) were considered as mainly responsible for the dissimilarity between sites/sets of sites (Warwick et al 1990). Similarity percentages analysis examines the contribution of each species to the average Bray–Curtis dissimilarity, within and between groups of samples.

Diversity (species number) of DJC and CAP was compared using previous samples from both places: DJC—Ávila (1997), ASIMOV Expeditions in 1998, 1999 and 2000; Santos et al. (1996), Ávila et al. (2004); CAP—Ávila (2000c, 2003). The number of species was summed cumulatively (using species-area analysis implemented by PRIMER v 5.2; (Clarke and Gorley 2001) over all samples taken at those particular sites (irrespective of the technique employed) and plotted against the number of samples (Williamson 1990; Morri et al. 1999). A tendency line was added to the graph.

Modes of development

The mode of development of the caenogastropods was inferred by scanning electronic microscope pictures of the protoconch in the majority of the taxa, supplemented with data from literature when the species had

a well-known life history. Two types of larval development were considered: non-planktotrophic (either lecithotrophic or direct development) and planktotrophic (i.e. with a free-swimming feeding larval stage) (Jablonski and Lutz 1983).

Results

A total of 2,360 molluscs with more than 1 mm were identified (337 at DJC, 219 at RQT, and 1,804 at CAP) (see Table 3). All taxa had already been described from the Azores (Ávila and Azevedo 1997; Ávila et al. 1998, 2000; Ávila 2000a, b). Forty-two taxa are known from the DJC Bank: 32 gastropods and 9 bivalves (some illustrated in Fig. 2), and 1 cephalopod (Ávila 1997; Ávila et al. 2004); no endemic vent species were found.

On average, species number and total number of specimens were lower at DJC and at sites with hydrothermal activity, when compared to CAP. The highest average diversity value ($H' = 1.67$) was found at RQT, the other two sites had similar and lower diversity values (see Tables 2, 3).

For each location, the maximum densities of the most common species are summarized in Table 4. A clear dominance of bivalves was found at DJC. *Gregarrella semigranata* (Reeve 1858), a small bivalve with a Macaronesian and Mediterranean distribution, was the most abundant mollusc, with an average density (\pm standard error) of $740 \pm 260 \text{ m}^{-2}$ and a maximum value of $1,296 \text{ m}^{-2}$. This species and *Crassadoma pusio* (Poli 1795) were the only species that occurred in all four samples collected at DJC. *Anachis avaroides* (Nordsieck 1975) and *Columbella adansonii* (Menke 1853) were common in only some of the DJC samples, but their densities at DJC were higher than at RQT and CAP. *Bittium latreillii* (Payraudeau 1826) occurred at DJC, but always in very low densities (maximum 192 m^{-2} , average $6 \pm 2 \text{ m}^{-2}$), while it was the most abundant species at CAP (maximum density $11,324 \text{ m}^{-2}$, average $1,377 \pm 288 \text{ m}^{-2}$) regardless of depth, followed by *Tricolia pullus azorica* (Dautzenberg 1889), an endemic subspecies that occurred in all CAP samples. *Nassarius incrassatus* (Ström 1768) was the most common species at RQT. *B. latreillii*, *Parvicardium vroomi* (van Aartsen, Moolenbeek and Gittenberger 1984), *Rissoa guernei* (Dautzenberg 1889) and also *Tricolia pullus azorica* were present with low densities in most RQT samples.

Clustering analysis shows a clear separation between sites with and without hydrothermal activity, all DJC samples grouping together, as well as RQT samples. There is also a split on the CAP samples, related

with depth (shallow samples versus deeper samples) (Fig. 3).

The pre-defined groups of replicates (see Table 5) were compared against random simulations. A total of 20,000 permutations were used with the subroutine ANOSIM. The test statistic R was low for the comparison between sites with rocky/sandy substrate. In the other comparisons (inshore/offshore sites; sites with/without hydrothermal activity) the differences were higher (Table 6).

SIMPER analysis indicated that *G. semigranata* (Gre) and *C. pusio* (Cra) are responsible for more than 50% of the similarity of the samples collected at DJC. At RQT, the typical species is *N. incrassatus* (Nas), which is responsible for almost 40% of the similarity between the replicates of this location. *B. latreillii* (Bit) and *Tricolia pullus azorica* (Tpa) characterize the samples from CAP, defining 45% of the similarity. Inshore sites and sites without hydrothermal activity are typified by *B. latreillii* and *Tricolia pullus azorica*, whereas offshore sites are best defined by the presence of *G. semigranata*. *B. latreillii* is associated with a rocky substrate covered by algae, and *N. incrassatus* with a sandy bottom (Table 7). The absence of *Tricolia pullus azorica* at offshore sites and the higher densities of *G. semigranata* at these sites define the main differences between inshore and offshore mollusc communities found. The presence of *Tricolia pullus azorica* also distinguishes sites with and without hydrothermal activity, being very abundant especially in the shallow waters at CAP. This species had low densities at RQT and was absent from the quantitative samples at DJC.

Despite the low number of samples collected at DJC, it is possible to infer, by extrapolation, that for a similar collecting effort, the number of species is expected to be higher at CAP than at DJC (Fig. 4).

Modes of development

Of the 29 caenogastropods reported for the DJC Bank (Ávila 1997; Ávila et al. 2004), 8 have a non-planktotrophic type of larval development, 17 species are planktotrophic and for 4 species the mode of development remained unknown (Table 8).

Discussion

A pattern that appears from this and other studies (see Costa and Ávila 2001) is that the average numbers and densities of species are lower at hydrothermal vents than at similar sites without hydrothermal activity. At



Fig. 2 **a, e** *Alvania angioyi* (van Aartsen 1982); **a** shell (DBUA 412/22-2), **e** protoconch (DBUA 335/23-3). **b, f** *Alvania sleursi* (Amati 1987); **b** shell (DBUA 446/34-1), **f** protoconch (DBUA 446/34-1). **c, g** *Manzonia unifasciata* (Dautzenberg 1889); **c** shell (DBUA 662/39-2), **g** protoconch (DBUA 181/49-2). **d, h** *Rissoa guernei* (Dautzenberg 1889); **d** shell (DBUA 662/10-2), **h** protoconch (DBUA 662/10-2). **i, j, n** *Anachis avaroides* (Nordsieck 1975); **i** shell (DBUA 785/56-1), **j** shell (DBUA 785/56-1), **n** protoconch (DBUA 785/63-2). **k, o** *Jujubinus pseudogravinae* (Nord-

sieck 1973); **k** shell (DBUA 574/125-2), **o** protoconch (DBUA 350/14-9). **l, p** *Columbella adansoni* (Menke 1853); **l** shell (DBUA 570/59-1), **p** protoconch (DBUA 570/59-1). **m, q** *Nassarius incrassatus* (Ström 1768); **m** shell (DBUA 766-F/71-3), **q** protoconch (DBUA 766-F/71-3). **r** *Bittium latreillii* (Payraudeau 1826), shell (DBUA 701/13-1). **s** *Tricolia pullus azorica* (Dautzenberg 1889), shell (DBUA 767/68-1). **t** *Gregariella semigranata* (Reeve 1858), shell (DBUA 812/176-2). **u** *Parvicardium vroomi* (van Aartsen, Menkhorst and Gittenberger 1984), shell (DBUA 355)

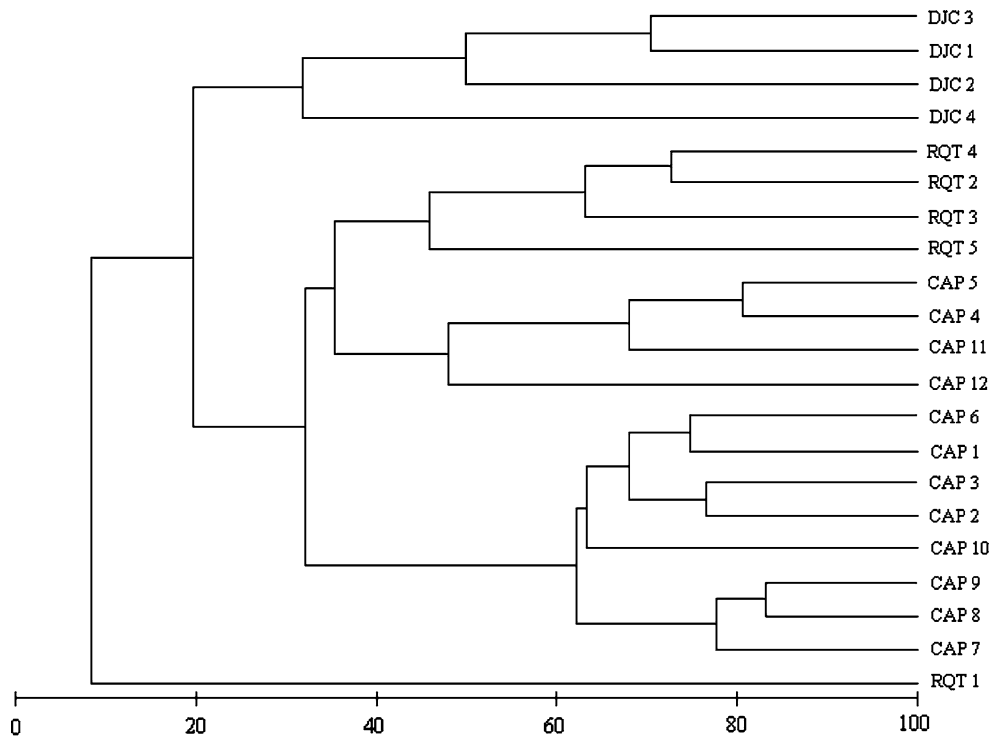


Fig. 3 Dendrogram of DJC, CAP, and RQT samples (abbreviations as in Table 3) (Bray–Curtis similarity index, UPGMA)

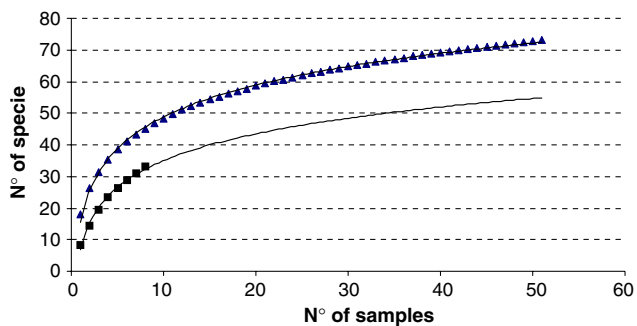


Fig. 4 Cumulative number of mollusc species plotted against the number of samples from the sites CAP (filled triangle) and DJC (filled square)

Kraternaya Bight (Kurile Islands), Tarasov et al. (1985, 1986, 1990) and Tarasov and Zhirmunskaya (1989) found that volcanic activity significantly changed the structure and specific composition of the communities. Comparable to these findings, we found striking changes in the relative densities of mollusc species in the presence of hydrothermal vents. In the Azores, in undisturbed environments (CAP), the most common littoral mollusc is *B. latreillii* (Ávila 2000c, 2003; Costa and Ávila 2001). This species, however, is not common at the shallow hydrothermal vents of RQT and DJC. The endemic *Tricolia pullus azorica* is common at RQT and in non-venting conditions (Ávila 2003), but only one operculum was found at DJC (Ávila et al.

Table 2 Diversity indices

	<i>S</i>	<i>N</i>	<i>H'</i>	<i>J'</i> = <i>H'</i> /ln <i>S</i>
DJC1	10	105	1.69	0.73
DJC2	8	69	0.81	0.39
DJC3	12	137	1.46	0.59
DJC4	7	26	1.30	0.67
<i>DJC</i>	9	84	1.32	0.60
RQT1	1	12	0.00	–
RQT2	11	62	1.94	0.81
RQT3	9	52	1.67	0.76
RQT4	8	63	1.63	0.78
RQT5	7	30	1.38	0.71
<i>RQT</i>	9	52	1.67	0.77
CAP1	25	305	1.39	0.43
CAP2	18	143	1.34	0.47
CAP3	20	115	1.82	0.61
CAP4	6	37	0.78	0.43
CAP5	5	26	0.85	0.53
CAP6	20	296	1.74	0.58
CAP7	18	126	1.65	0.57
CAP8	20	141	1.78	0.59
CAP9	19	193	1.65	0.56
CAP10	26	316	1.66	0.51
CAP11	11	95	0.55	0.23
CAP12	7	11	1.21	0.62
<i>CAP</i>	16	150	1.37	0.51

Values in italics represent the average values for DJC, RQT, and CAP samples (RQT1 was excluded from the calculation of the average values)

S Number of species, *N* total number of specimens, *H'* Shannon–Wiener diversity index, *J'* evenness; other abbreviations as in Table 1

Table 3 Molluscs collected at D. João de Castro Bank (DJC), Ribeira Quente (ROT), and Capelas (CAP); CAP samples from Ávila (2003), transformed by 1:4

	DJC1	DJC2	DJC3	DJC4	DJC4	ROT1	ROT2	ROT3	ROT4	ROT5	CAP1	CAP2	CAP3	CAP4	CAP5	CAP6	CAP7	CAP8	CAP9	CAP10	CAP11	CAP12
<i>Alvania angioyi</i>	1	0	2	0	0	0	0	0	0	1	0	2	0	0	8	2	4	4	16	0	0	0
<i>Alvania cancellata</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2	0	2	0	0	0	0
<i>Alvania mediotoralis</i>	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0
<i>Alvania poucheti</i>	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	0	1	1	2	0	0	0
<i>Alvania sleursi</i>	2	0	0	0	0	0	0	0	1	5	2	3	0	0	6	3	6	5	12	0	0	0
<i>Anachis avaroides</i>	12	0	19	16	0	2	8	2	8	6	1	1	1	1	4	0	0	0	1	1	0	0
<i>Arca tetragona</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bittium latreilli</i>	12	5	7	0	0	14	17	2	2	187	89	56	30	20	162	51	65	97	187	83	6	6
<i>Calliostoma</i> sp.	0	0	2	1	0	0	0	0	1	2	1	1	1	0	19	0	0	1	2	0	1	1
<i>Cardita calyculata</i>	0	0	0	0	0	0	0	0	0	1	2	3	0	0	1	1	2	2	3	0	0	0
<i>Cerithiopsis</i> sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0
<i>Cheirodonta pallescens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Columnella adansonii</i>	14	0	4	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Crassidoma pusio</i>	15	1	10	1	0	0	0	0	0	8	7	7	0	0	3	1	1	1	0	0	0	0
<i>Crisilla postrema</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	2	0	0	0
<i>Gibbula delgadensis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	3	12	0	0	0
<i>Gregariella semigranata</i>	45	56	81	3	0	1	0	1	0	1	1	2	0	0	3	0	0	0	2	0	0	0
<i>Jujubinus pseudogravinae</i>	0	0	0	1	0	0	0	0	0	11	2	6	0	1	13	4	15	11	2	0	0	0
<i>Limaria hians</i>	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Limea loscombi</i>	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Manzonita unifasciata</i>	0	0	0	0	0	0	0	0	0	4	1	1	0	0	2	14	26	36	8	0	0	0
<i>Marshallora adversa</i>	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Miomorpha azorensis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	0
<i>Nassarius incrassatus</i>	0	0	0	0	0	12	4	16	14	15	1	0	1	0	1	0	0	2	4	1	0	0
<i>Ocenebrina aciculata</i>	0	0	1	0	0	0	0	0	0	5	1	1	2	2	13	0	0	0	1	1	0	0
<i>Omalogyra atomus</i>	2	0	8	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
<i>Pallium incomparabile</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Papillicardium papillosum</i>	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Parvicardium vroomi</i>	0	0	0	0	0	0	15	1	6	3	3	5	0	0	22	2	5	4	31	1	0	0
<i>Patella</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Pseudochama gryphina</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Raphitoma linearis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Rissoa guernei</i>	0	0	0	0	0	0	19	1	19	0	0	0	0	0	0	2	2	2	2	0	0	0
<i>Runcina</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Setia</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Setia subvaricosa</i>	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	2	0	1	1
<i>Similiphora similior</i>	0	0	0	0	0	0	0	0	0	1	0	1	0	0	2	0	0	0	0	0	0	0
<i>Sinezona cingulata</i>	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Skeneopsis planorbis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stramonita haemastoma</i>	0	0	1	0	0	1	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Tectura virginea</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
<i>Tricolia pullus azorica</i>	0	0	0	0	0	6	5	18	1	65	30	22	2	2	32	42	11	24	25	7	3	3
Triphoridae n. id.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Vermetus</i> cf. <i>triquetrus</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	105	69	137	26	12	62	52	63	30	305	143	115	37	26	296	126	141	193	316	95	11	11

Table 4 Maximum densities of the most common molluscs collected at DJC, RQT and CAP (ind m⁻²)

	DJC	RQT	CAP
<i>G. semigranata</i>	1,296	16	92
<i>C. pusio</i>	240	0	200
<i>A. avaroides</i>	304	128	144
<i>C. adansoni</i>	224	48	4
<i>N. incrassatus</i>	0	256	76
<i>B. latreillii</i>	192	272	11,324
<i>Tricolia pullus azorica</i>	0	288	1,032
<i>P. vroomi</i>	0	240	984
<i>R. guernei</i>	0	304	184
<i>A. angioyi</i>	32	0	256

For abbreviations, see Table 1

Table 5 Pre-defined groups (with respective sampling sites) used for ANOSIM and SIMPER analysis

Pre-defined groups	Sampling sites
Inshore	RQT, CAP
Offshore	DJC
Hydrothermal vents	DJC, RQT
Rocky substrate	DJC, CAP
Sandy substrate	RQT

For abbreviations, see Table 1

Table 6 ANOSIM results

Group comparisons	R	Significance level (%)
Inshore/offshore	0.672	0.1
Hydrothermal activity/no activity	0.526	0.1
Rocky substrate/sandy substrate	0.349	1.7

Sampling sites are grouped according to Table 5

2004). At CAP, a non-venting site, *B. latreillii*, *T. pullus azorica*, *Ocenebrina aciculata* (Lamarck 1822) define almost 50% of the similarity of the samples. Nassariid gastropods were reported as dominant forms at Milos Island (Aegean Sea) reaching densities higher than 200 m⁻² (Southward et al. 1997) and at Matupi Harbour (Rabaul Caldera, New Britain Island, Papua New Guinea) with densities of 13 m⁻² (Tarasov et al. 1999); both sites exhibit submarine hydrothermal activity. In the Azores, *N. incrassatus* is a common species in sandy and muddy habitats, being especially abundant inside harbours (personal observation). This species was found at RQT in high numbers (maximum density 256 m⁻²), but although present at DJC (Ávila et al. 2004) and at CAP, its density in these locations was very low. Its abundance at RQT is thus probably related to the sandy type of bottom rather than to the hydrothermal conditions.

Many species associated with hydrothermal areas have adaptations (Ballard 1977; Grassle 1985) that

allow them to survive in these extreme environments under the form of chemical contamination (Grassle et al. 1979) and/or extremely high temperatures (Jollivet et al. 1995). The trophic structure of shallow-water hydrothermal ecosystems differs from that of deep-sea hydrothermal ecosystems, which are dominated by chemosynthetic communities (Kharlamenko et al. 1995). At shallow-water hydrothermal vents, bacteria constitute a more important food source than at typical coastal ecosystems (Tarasov and Zhirmunskaya 1989; Kharlamenko et al. 1995). Rock samples collected from around the vent outlets at DJC were partially covered with bacterial mats, mainly an attached form of *Beggiatoa* (Cardigos et al. 2005).

The dominance of bivalves in DJC might thus be related to their filter-feeding habit which allows these animals to take advantage of the additional primary production by chemosynthetic bacteria living nearby the vents. This relationship was also used to explain the high diversity and density of Serpuloidea (Annelida: Polychaeta), also filter-feeders, in venting conditions on Milos Island (Bianchi and Morri 2000). No specialized hydrothermal molluscs were found at DJC or RQT, similarly to what was reported from other locations with shallow-water vents (Tarasov et al. 1986, 1990, 1999; Kamenev et al. 1993; Dando et al. 1995). Nevertheless, physiological and ecotoxicological tests are needed to study the tolerance to the toxic compounds that are released by these vents, such as Cu, Pb, Ba, Fe, Mn, Co, and Cd (Cardigos et al. 2005).

Similar to other seamounts around the Azores, DJC has a predominance of molluscs with a planktotrophic mode of development (17 taxa or 58.6%). Although there is still a high number of Azorean caenogastropod species with unknown mode of development, preliminary results indicate that there is a slightly higher number of planktotrophic (33.9%) relative to non-planktotrophic caenogastropods (29.8%) (Table 8).

At Ormonde peak (the top of the eastern seamount of the Gorringe, located southwest of Portugal) Ávila and Malaquias (2003) investigated the mode of development of the caenogastropods located in the photic zone (down to 50 m depth) and found that from a total of 25 taxa, 11 species (44%) were non-planktotrophic, whereas 14 taxa (56%) were planktotrophic (Table 8). Leal (1991) did a similar study at Atol das Rocas (ROC) and Fernando de Noronha islands (NOR), located off the northeastern Brazilian coast, and at Trindade (TRI) and Martin Vaz Islands (MAR), located off the eastern Brazilian coast. We have modified his data by pooling his littoral and sublittoral species (down to 30–40 m depth) into a single category

Table 7 SIMPER results

Groups of sites	Average similarity	Species	Species % (ratio of each species)	Cumulative (%)
DJC	44.55	Gre–Cra	33.22–19.23 (3.59–5.53)	52.45
RQT	47.67	Nas	39.58 (2.37)	39.58
CAP (all stations)	51.19	Bit–Tpa	27.14–17.84 (2.81–2.93)	44.98
CAP (15–16)	55.92	Bit–Tpa–Oci–Ana	23.91–14.64–10.93–10.10 (2.77–3.21–1.91–2.18)	59.58
CAP (6–8)	48.54	Bit–Tpa	28.20–19.93 (3.17–3.06)	48.14
Inshore	42.00	Bit–Tpa	23.77–19.79 (1.44–1.99)	43.56
Offshore	44.55	Gre–Cra	33.22–19.23 (3.59–5.53)	52.45
With hydrothermal activity	31.11	–	No species with ratio >1.4	–
No hydrothermal activity	51.19	Bit–Tpa	27.14–17.84 (2.81–2.93)	44.98
Rocky substrate	40.36	Bit	27.49 (1.82)	27.49
Sandy substrate	47.67	Nas	39.58 (2.37)	39.58

Groups	Average dissimilarity	Species	Species % (ratio of each species)	Cumulative (%)
Inshore/offshore	76.86	Gre–Tpa	9.94–7.67 (1.64–2.91)	17.60
Hydrothermal activity/ no activity	71.72	Tpa	6.90 (1.47)	6.90
Rocky substrate/ sandy substrate	72.09	–	No species with ratio >1.4	–

Ana *A. avaroides*, Bit *B. latreillii*, Cra *C. pusio*, Nas *N. incrassatus*, Oci *O. aciculata*, Tpa *Tricolia pullus azorica*, Gre *G. semigranata*; other abbreviations as in Table 1

Table 8 Number of caenogastropod species and mode of development

Dev	DJC ^a	RQT	CAP ^b	SMG ^c	AZO ^d	ORM ^e	ROC ^f	NOR ^f	TRI ^f	MAR ^f
np	8	5	21	35	37	11	50	57	39	15
p	17	5	21	41	42	14	25	48	38	11
Unknown	4	0	7	39	45	0	3	5	0	0
# Caen	29	10	49	115	124	25	78	110	77	26
# Total	42	10	71	223	347	36	–	–	–	–

np non-planktotrophic, p planktotrophic, # *Caen* number of caenogastropods, # *Total* total number of molluscan taxa, *ORM* Ormonde seamount (Gorringe bank), *ROC* Atol das Rocas, *NOR* Fernando de Noronha, *TRI* Trindade Island, *MAR* Martin Vaz; other abbreviations as in Table 1

^a Ávila (1997); Ávila et al. (2004)

^b Ávila (2003)

^c Ávila et al. (2000)

^d Ávila (2000a, b, c, 2005)

^e Ávila and Malaquias (2003)

^f Leal (1991)

and by using only two modes of development: non-planktotrophic (with pooled lecithotrophic and direct development) and planktotrophic. At TRI there is an equilibrium between both modes of development, whereas at ROC, NOR and MAR there is a higher

number of species with non-planktotrophic development (Table 8). This is especially evident at ROC, the island nearest to Brazil, located just 200 km off the coast, with 64% of non-planktotrophic and 32% of planktotrophic species.

The bias in favour of planktotrophic developers is probably related to the relatively early age of the DJC Bank (less than 300 years), its higher degree of isolation from source populations, and the small area (only 300 × 600 m above 50 m depth). For non-planktotrophic species such as *Calliostoma* sp., *Jujubinus pseudogravinae*, *Alvania angioyi*, *Alvania sleursi*, *A. avaroides* and *Omalogyra atomus*, and especially for those with direct development, the major problem is to reach this seamount. Once there, and provided the species' ecological demands are met, gravid females may give rise to new successful populations (Leal 2000). Planktotrophic species may reach DJC Bank with higher frequencies than non-planktotrophic ones, but they will meet with greater difficulties in establishing self-sustained populations, because most larvae will get lost by drifting away from the small area of the seamount. As a consequence, these "pseudopopulations" (Bouchet and Taviani 1992) can persist only by a regular input of larvae from other source-locations, in the case of DJC from nearby islands of the Azores archipelago (e.g. Terceira and São Miguel).

The absence at DJC of species common on the intertidal zone of the Azorean shores (e.g. the littorinids: *Littorina striata* and *Melarhaphé neritoides*, the little skeneopsid: *Skeneopsis planorbis*, the anabathrid: *Pisinnia glabatra*, and the rissoids: *Cingula trifasciata* and *Alvania mediolittoralis*) must be related to a lack of the physical and/or biotic conditions typical of littoral zones. The highest elevation of DJC is at around 13 m depth. Consequently, species that usually live in the upper 10 m can be expected to be absent from the DJC Bank. Ávila (2003) established the zonation pattern for the most common shallow marine molluscs of the Azores. From these data and the mollusc checklists of DJC (Ávila 1997; Ávila et al. 2004) it is evident that why many common littoral Azorean shore species are missing at DJC (e.g. the rissoids: *R. guernei* and *Manzonia unifasciata*, the trochid: *Gibbula delgadensis*).

Features inherent to offshore shallow seamounts, such as turbulent hydrodynamic conditions, both currents and waves, are likely to result in reduced diversity and abundance of species, as seen at DJC. On the other hand, this may explain the higher numbers of the two mentioned bivalves, one (*Crassadoma*) cemented to the substrate, and the other (*Gregariella*) attached byssally.

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