

BIOGEOGRAPHICAL RELATIONSHIPS OF THE MOLLUSCAN FAUNA OF THE ORMONDE SEAMOUNT (GORRINGE BANK, NORTHEAST ATLANTIC OCEAN)

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ABSTRACT

Thirty-six taxa (28 Gastropoda and eight Bivalvia) were collected at Ormonde Seamount (Gorringe Bank). Trochidae and Rissoidae, both with three species, were the best represented families. *Manzonina crispa* (Watson, 1873), formerly thought to be restricted to Madeira, has its range extended to the northeast. Of the 25 prosobranchs, 14 taxa have a planktotrophic type of development and 11 taxa are non-planktotrophic. Most of the species that occur at Ormonde are related to Mediterranean taxa, to those of the Portuguese continental shelf, and also to those of Madeira and the Canary Islands. The geographical position and topography of seamounts, the prevailing sets of sea-surface and depth currents, the distance to the nearest colonizing source, available area for the settlement of the larvae, mean and annual range of water temperature, larval ecology, biotic factors (interspecific competition, the history of the successive colonizers), and also anthropogenic factors are discussed, in order to provide an explanation of the biogeographical relationships of the Ormonde Seamount.

INTRODUCTION

The marine fauna of the Northeast Atlantic archipelagos and seamounts is characterized by species with very different biogeographical affinities. It is possible to find in these places species that also occur in the Boreal, Lusitanian or South Atlantic provinces, species that occur in the Mediterranean and Senegal regions, species with tropical affinities, amphi-Atlantic species, cosmopolitan species and also some endemic species (Briggs, 1970; García-Talavera, 1983; Boury-Esnault & Lopes, 1985; Lopes, Marques & Bellan-Santini, 1993; Santos, Porteiro & Barreiros, 1997; Wirtz, 1998). This complex pattern of biogeographical affinities also occurs in the molluscs (Sánchez, Ortea & Bacallado, 1987; Malaquias, 1996; Ávila, 2000).

The general pattern of sea-surface circulation, the capacity of some marine gastropod larvae to cover large distances and to stay in the water column for several months (Scheltema, 1971), and the presence of a series of submarine banks at shallow depths, play an important role in the 'stepping-stone' processes of dispersion and colonization of new areas (Gillet & Dauvin, 2000). Between Portugal and Madeira, a group of seamounts fulfil these requisites: Seine, Ampère, Gorringe (with Ormonde and Gettysburg peaks) and Josephine.

In 1987 Philippe Bouchet's, 'SEAMOUNT 1' expedition of R/V *Le Noroît* sampled the Lusitanian seamounts for molluscs, and the preliminary results on Rissoidae were published by Gofas (1992). The 'SEAMOUNT 2' expedition of R/V *Le Suroît* sampled again in 1993, and the Pyramidellidae were revised by Peñas & Rolán (1999). However, the importance of these banks in the range extension of species and in the colonization of new areas in the northeast Atlantic are still poorly understood; many of the questions posed by Hubbs in 1959 still remain unanswered (cf. Rogers, 1994, for a review). In comparison with the knowledge of the insular Macaronesian littoral malacofauna, that on the Lusitanian seamounts is poor (Gofas, 1992). In this context, the study of the molluscs of these seamounts will

help to understand the mechanisms of species range extension (Scheltema, 1995), and also provide opportunities to test theories of biogeography and speciation processes (Shuto, 1974). According to Cracraft (1994), the colonization of seamounts depends on two main factors, range extension of species and long-distance dispersal of larvae, which take place over different time scales, geological and ecological, respectively.

With this work, we intend to improve the knowledge of the malacofauna of the Ormonde Seamount (Gorringe Bank) and establish the biogeographical relationships for the shallow (<50 m depth) Ormonde molluscs. Based on the assumption that species dispersion through sea currents is one of the most important processes in the colonization of islands and seamounts, we relate range extension mechanisms to the larval development type of the Ormonde species.

MATERIAL AND METHODS

Study area

Ormonde peak is the top of the eastern seamount of the Gorringe Bank, situated on an old transform fault of Triassic-Liassic age (LaGabrielle & Auzende, 1982). It is located at the boundary between the European and the African plate, between the Tagus abyssal plain in the north and the Horseshoe plain in the south, some 190 km southwest of Portugal (36° 10' N to 37° 00' N, 10° 50' W to 11° 50' W; Auzende, Charveret, Le Lann, Le Pichon, Monteiro, Nicolas, Olivet & Ribeiro, 1979). Ormonde Seamount is 200 km long by 80 km wide, 110–135 million years old and rises from the bottom of the ocean at 3000–3500 m to a depth of 40 m (Pastouret, Auzende, Le Lann & Olivet, 1980; LaGabrielle & Auzende, 1982). From 40 to 60 m depth, Ormonde is characterized by the existence of rich biological communities (other than molluscs), with kelp beds and gorgonians of large dimensions (P. Neves & R. Santos, personal communication).

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Sampling

All the material examined in this study was collected during the scientific expedition 'Atlântico Selvagem—Ormonde 1999' on board the cruise vessel *Mauritius*. All samples were obtained by SCUBA-diving from 40 to 60 m depth, using a suction device or by brushing and scraping surfaces. Eight samples were collected, between the 3 and 5 August 1999, in an area about 100 m around the coordinates 36° 42' N 11° 09' W (see Table 1 for a list of stations). Qualitative scrapings were done on rocky substrates; sand and gravel bottoms were also sampled for molluscs.

All samples were preserved on board in 70% ethanol, sorted later at the ecology laboratory of the Sciences Faculty of the Sea and Environment (University of Algarve) and identified at the Marine Biology Section of the Department of Biology (University of the Azores). All samples are deposited in the collection of the Department of Biology, University of the Azores (DBUA).

Mode of development

The mode of development of the prosobranch gastropods was inferred using scanning electronic microscope pictures of the protoconch of the majority of the taxa. Data were also taken from literature when the species had a well-known life history. Two types of development were considered: planktotrophic, with a free-swimming feeding stage and non-planktotrophic (either lecithotrophic or direct development; Jablonski & Lutz, 1980).

Analysis

A table with the geographical distribution of the Ormonde species was constructed (Table 2). The biogeographical relationships of the Ormonde shallow-water marine molluscs were studied by comparing the Ormonde database with data from selected locations: Scandinavia, British Isles, Bay of Biscay to Galicia, Portugal, western Mediterranean, Morocco, Azores, Madeira, Desertas and Selvagens, Canary Islands, Cape Verde Islands, and the Caribbean (for sources of data see Ávila, 2000). A simple percentage similarity index was used to compare the molluscs of the Ormonde Seamount with those from the selected locations. This was calculated as the ratio between the shared species and the 31 benthic species confirmed for the seamount (Table 3). We have not used indices that took into account the total number of species existing in each one of the compared regions, because there are no recent checklists for some locations (e.g. Madeira, Cape Verde Islands).

RESULTS

Thirty-six taxa (28 Gastropoda, some illustrated in Fig. 1, and eight Bivalvia) were collected at Ormonde Seamount (Gorringe Bank). Trochidae and Rissoiidae, both with three species, were

Table 1. Sample number (DBUA collection), date, depth (m) and type of substrate of the samples collected at Ormonde Seamount (Gorringe Bank)

Sample	Date	Depth (m)	Substrate
DBUA 827	03 Aug 1999	46	Rocky
DBUA 828	03 Aug 1999	46	Rocky
DBUA 829	03 Aug 1999	45	Rocky
DBUA 830	03 Aug 1999	44	Rocky
DBUA 831	04 Aug 1999	40	Rocky
DBUA 832	04 Aug 1999	45	Rocky
DBUA 833	05 Aug 1999	57	Sandy
DBUA 834	05 Aug 1999	57	Gravel

the best-represented families. No endemic Ormonde species were found.

Modes of development

Of the 25 prosobranchs, 11 species have a non-planktotrophic type of development and 14 taxa are planktotrophic (see Table 2).

Composition of assemblages and similarities

Most of the species that occur at Ormonde occur also in the Mediterranean. A high number of Ormonde species occur also in the Canary Islands, as well as along the coast of Portugal and in Madeira. After removing *Cavolinia inflexa* (a pelagic species) and the four unidentified Ormonde taxa from the analysis, 29 of the 31 Ormonde species occur in the Mediterranean (93.5%), 25 are present in the Canary Islands and Portugal (both with 80.6%), followed by Madeira (24 species, 77.4%), Bay of Biscay to Galicia (18 species, 58.1%), and the Azores (17 species, 54.8%; Table 3).

DISCUSSION

The diverse biogeographical relationships of the northeast Atlantic archipelagos and seamounts is a result of the interaction between their present geographical position and several other factors, such as the prevailing surface and depth currents, the distance to the nearest colonizing source, the size of the seamount and available area for settlement of larvae, mean and annual range of water temperature, larval ecology, biotic factors (interspecific competition, the history of the successive colonizers) and also anthropogenic factors (Scheltema, 1971, 1979; Franz, 1975; Edmunds, 1977; García-Talavera, 1983; Gofas, 1992). Geological age is also a factor that should not be neglected.

The prevailing sea-surface currents in this region of the Atlantic are one of the main factors explaining the biogeographical affinities of the species. The general sea surface circulation in the northeast Atlantic has been reviewed by Anonymous (1979), Gould (1985), Kleine & Siedler (1989), Alves (1990), Bower (1994) and Fiúza & Martins (1996). The geographic region where Ormonde Seamount is located is an area of convergence of Gulf Stream waters, waters from northern Europe (via the Madeira current) and also from the Mediterranean (via deep currents emerging to the Atlantic). The deep outflow from the Mediterranean, located along the bottom of the outlet (150–250 m and deeper westwards, down to 1000–1200 m), is usually extremely poor in nutrients and animal life. It will not contribute to the colonization of the shallow Atlantic seamounts, for at the longitude of the Gorringe Bank the Mediterranean outflow is at about 1000 m depth and should not affect the photic zone.

The lower number of species shared with Portugal than with the Mediterranean is probably an artefact, for the marine molluscan fauna of Portuguese shores is one of the least known in Europe. Improved knowledge of the Portuguese fauna will probably bring the figure to the same level as the relationship with the Mediterranean.

The high proportion of Mediterranean and Portuguese species at Ormonde Seamount could be related to local current-topographic interactions. The molluscan larvae transported in the sea-surface currents may reach Ormonde Seamount by means of eddies that usually appear southwest of Cape São Vicente (Portuguese mainland). The disintegration of these large-scale structures in the vicinity of shallow seamounts has been documented (Bower, 1994). In such cases, and in spite of its small shallow part, a Taylor column may exist, with nutrient-

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Table 2. Checklist and geographical distribution of the species collected at the Ormonde Seamount (Gorringe Bank).

Species	Family	DBUA	Dev	ORM	SCA	BRI	BIS	POR	MED	MOR	AZO	MAD	CAN	CAP	CAR
<i>Tectura virginea</i> (O.F. Müller, 1776)	Lottiidae	833, 834	p	1	1	1	1	1	1	0	1	1	1	0	0
<i>Diodora graeca</i> (Linné, 1758)	Fissurellidae	833, 834	np	1	1	1	1	1	1	0	0	1	1	0	0
<i>Emarginula tenera</i> Locard, 1892	Fissurellidae	833	np	1	0	0	0	1	1	0	0	1	1	0	0
<i>Haliotis tuberculata coccinea</i> (Reeve, 1846)	Haliotidae	834	np	1	0	0	0	0	1	0	1	1	1	1	0
<i>Calliostoma</i> cf. <i>conulus</i> (Linné, 1758)	Trochidae	830	np	1	0	0	0	1	1	0	0	1	1	0	0
<i>Calliostoma</i> sp.	Trochidae	827, 829, 831, 832, 834	np	1	–	–	–	–	–	–	–	–	–	–	–
<i>Jujubinus exasperatus</i> (Pennant, 1777)	Trochidae	830, 833, 834	np	1	0	1	1	1	1	0	0	1	1	0	0
<i>Bolma rugosa</i> (Linné, 1767)	Turbinidae	833, 834	np	1	0	0	1	1	1	0	1	1	1	0	0
<i>Bittium latreillii</i> (Payraudeau, 1826)	Cerithiidae	830, 833, 834	p	1	0	0	1	1	1	0	0	0	1	0	0
<i>Similiphora similior</i> (Bouchet & Guillemot, 1978)	Triphoridae	827	p	1	0	0	1	1	1	0	1	0	0	1	0
<i>Cerithiopsis</i> sp.	Cerithiopsidae	833 (Fig. 1M)	p	1	–	–	–	–	–	–	–	–	–	–	–
<i>Epitonium pulchellum</i> (Bivona, 1832)	Epitoniidae	833	p	1	0	0	1	1	1	0	0	1	1	0	0
<i>Alvania cancellata</i> (da Costa, 1778)	Rissoidae	833	p	1	0	1	1	1	1	0	1	1	1	1	0
<i>Alvania zylensis</i> (Gofas & Warén, 1982)	Rissoidae	833 (Fig. 1E-F)	np	1	0	0	0	0	1	0	0	0	0	0	0
<i>Manzonella crispa</i> (Watson, 1873)	Rissoidae	833 (Fig. 1G-J)	np	1	0	0	0	0	0	0	0	1	0	0	0
<i>Capulus ungaricus</i> (Linné, 1758)	Capulidae	833	p	1	1	1	1	1	1	?	0	1	1	0	0
<i>Lamellaria latens</i> (O. F. Müller, 1776)	Lamellariidae	833	p	1	1	1	1	0	?	0	1	0	0	0	0
<i>Trivia pulex</i> (Solander in Gray, 1828)	Triviidae	833, 834	p	1	0	0	0	1	1	0	1	1	1	0	0
<i>Coralliophila brevis</i> (Blainville, 1832)	Coralliophilidae	829	p	1	0	0	0	1	1	0	0	0	1	0	0
<i>Coralliophila meyendorffi</i> (Calcare, 1845)	Coralliophilidae	827	p	1	0	0	1	1	1	1	1	1	1	1	0
<i>Chauvetia mamillata</i> (Risso, 1826)	Buccinidae	828, 830, 833 (Fig. 1A-D)	np	1	0	0	0	0	1	0	0	0	0	0	0
<i>Gibberula</i> sp.	Cystiscidae	833	np	1	–	–	–	–	–	–	–	–	–	–	–
<i>Crassopleura maravignae</i> (Bivona Ant. in Bivona And., 1838)	Drilliidae	833	p	1	0	0	0	1	1	0	1	1	1	0	0
<i>Raphitoma</i> sp.	Conidae	833 (Fig. K-L)	p	1	–	–	–	–	–	–	–	–	–	–	–
<i>Philippia hybrida</i> (Linné, 1758)	Architectonicidae	834	p	1	0	0	1	1	1	0	1	1	1	0	0
<i>Odostomella doliolum</i> (Philippi, 1844)	Pyramidellidae	833	–	1	0	0	0	0	1	0	1	1	1	0	0
<i>Cavolinia inflexa</i> (Lesueur, 1813)	Cavolinidae	833	–	1	?	1	1	1	1	1	?	1	?	?	?
<i>Hypselodoris picta</i> (Schultz in Philippi, 1836)	Chromodorididae	*	–	1	0	0	0	1	1	1	1	1	1	1	1
<i>Arca tetragona</i> Poli, 1795	Arcidae	831, 833	–	1	1	1	1	1	1	1	1	1	1	1	0
<i>Striarca lactea</i> (Linné, 1758)	Noetiidae	833, 834	–	1	0	1	1	1	1	?	0	0	1	0	0
<i>Trichomusculus semigranatus</i> (Reeve, 1858)	Mytilidae	833	–	1	0	1	1	1	1	1	1	1	1	1	0
<i>Lima lima</i> (Linné, 1758)	Limidae	827, 833, 834	–	1	0	0	0	1	1	?	0	1	1	0	1
<i>Chama gryphoides</i> Linné, 1758	Chamidae	834	–	1	0	0	0	1	1	1	1	1	1	1	0
<i>Plagiocardium papillosum</i> (Poli, 1795)	Cardiidae	833, 834	–	1	0	1	1	1	1	1	1	1	1	1	0
<i>Gouldia minima</i> (Montagu, 1803)	Veneridae	833, 834	–	1	1	1	1	1	1	1	1	1	1	1	0
<i>Hiatella rugosa</i> (Linné, 1767)	Hiatellidae	833	–	1	1	1	1	1	1	1	0	1	0	0	0
Total number of species				36	7	13	19	26	30	9	18	25	25	10	2

*One specimen seen, but not collected.

Abbreviations: Dev, type of development (p, planktotrophic; np, non-planktotrophic); DBUA, reference collection of the Department of Biology, University of the Azores; 1, presence; 0, absence; ?, dubious record; ORM, Ormonde Seamount; SCA, Scandinavia; BRI, British Isles; BIS, Bay of Biscay to Galicia; POR, Portugal; MED, Western Mediterranean; MOR, Morocco and Mauritania; AZO, Azores; MAD, Madeira, Porto Santo and Desertas; CAN, Canary Islands; CAP, Cape Verde Islands; CAR, Caribbean.

rich water located in the euphotic zone of the Ormonde Seamount. This column may retain larvae over the summit of the seamount, thus providing suitable conditions for larvae to settle (Nellen, 1974; Scheltema, Williams & Lobel, 1996; Mullineaux & Mills, 1997). These Taylor columns may also be

responsible for the isolation of populations, especially of those of species with short-lived planktotrophic larvae, by trapping autochthonous larvae in the vicinities of the seamount and promoting self-recruitment (Shomura & Barkley, 1980).

The conjunction of prevailing sea currents and the type of

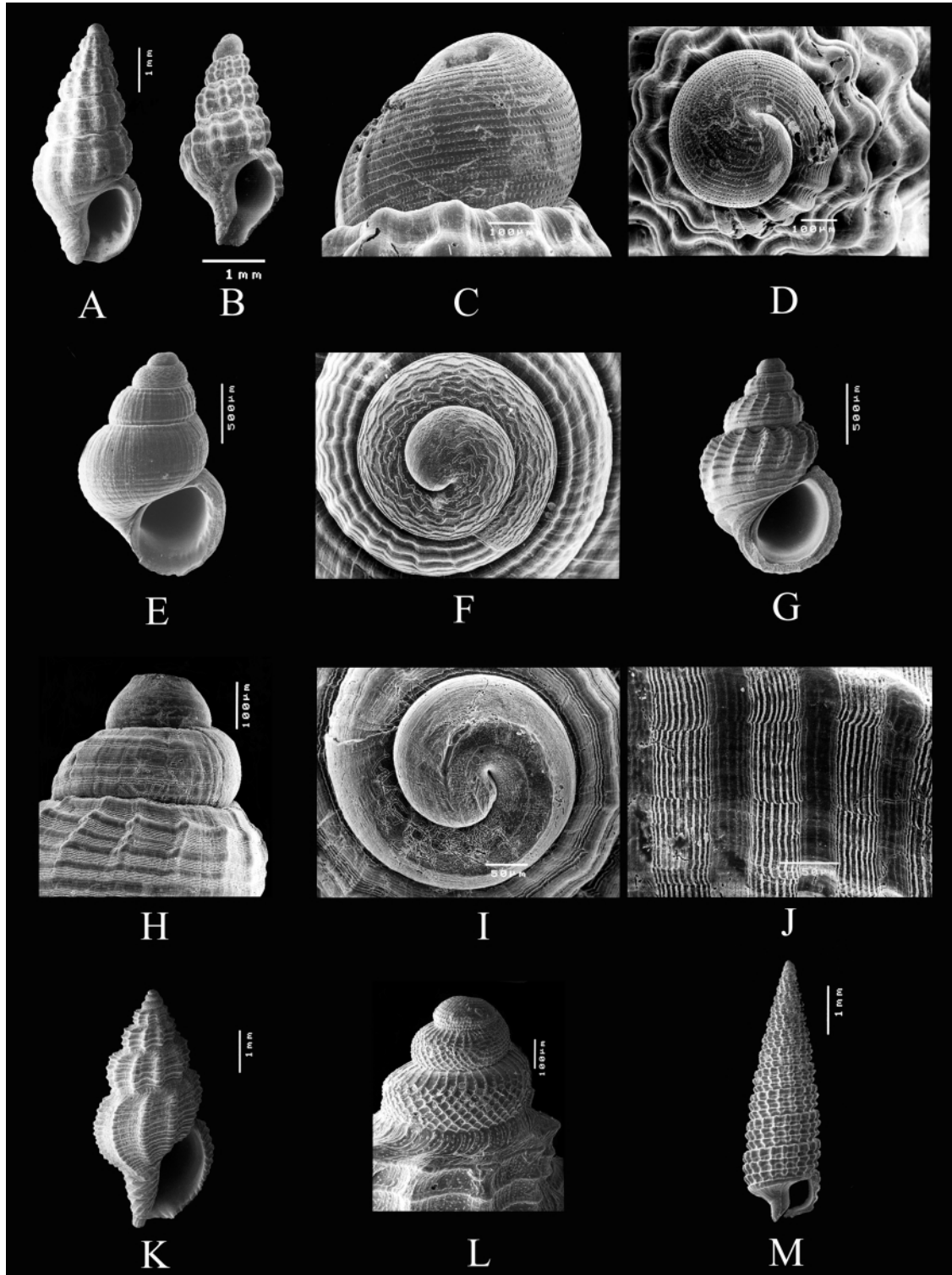


Figure 1. A–D. *Chauvetia mamillata* (Risso, 1826). A. Shell (DBUA 833/76–2) 5.4 × 2.0 mm. B. Shell (DBUA 833/78–4) 3.8 × 2.3 mm. C, D. Protoconch (DBUA 833/78–4), lateral and frontal views. E, F. *Alvania zylensis* Gofas & Warén, 1982. E. Shell (DBUA 833/78–4) 3.8 × 2.3 mm. F. Protoconch (frontal view). G–J. *Manzonina crista* (Watson, 1873). G. Shell (DBUA 833/75–3) 3.5 × 2.3 mm; H, I. Protoconch (lateral and frontal view); J. Microsculpture of body whorl. K, L. *Raphitoma* sp. K. Shell (DBUA 833/78–1), 5.6 × 2.7 mm; L. Protoconch (lateral view). M. *Cerithiopsis* sp., shell (DBUA 833/77–3) 5.4 × 1.6 mm.

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Table 3. Biogeographical relationships of the Ormonde Seamount (Gorringe Bank) (*Cavolinia inflexa* and unidentified Ormonde taxa excluded)

	ORM	%
ORM	31	100.0
SCA	7	22.6
BRI	12	38.7
BIS	18	58.1
POR	25	80.6
MED	29	93.5
MOR	8	25.8
AZO	17	54.8
MAD	24	77.4
CAN	25	80.6
CAP	10	32.3
CAR	2	6.4

Abbreviations as in Table 2.

development may be key factors explaining the occurrence of mollusc species on the Lusitanian seamounts. Gofas' (1992) data include 25 rissoid species, of which only four, *Alvania cancellata* (da Costa, 1778), *Alvania cimicoides* (Forbes, 1844), *Alvania punctura* (Montagu, 1803) and *Rissoa violacea* Desmarest, 1814, have planktotrophic larval development. This bias in favour of non-planktotrophic taxa is explained by the apparent facility of rissoids to loose their planktotrophic phase. There is an evident advantage in this pattern, for the majority of planktotrophic larvae would be lost by drifting away from the small area of the seamount (Gofas, 1992).

Another example supporting this view relates to the rissoid genus *Manzonina*. In Europe, 16 species of *Manzonina* have been reported (two on the mainland, the others insular on the Canary Islands or Madeira, and one in the Azores). Only one species, *M. crassa* (Kanmacher, 1798) has planktotrophic development, all other species having a non-planktotrophic type of development, as a result of one or (more probably) several radiations in the Macaronesian Archipelagos or on the Lusitanian seamounts (M. Oliverio, personal communication). The range extension of *Manzonina crispa*, formerly thought to be restricted to Madeira (Moolenbeek & Faber, 1987) is one of the results of the present work.

In such isolated and small seamounts, to maintain viable resident populations must be a problem for all species. At Ormonde Seamount, there are molluscan species with planktotrophic and with non-planktotrophic development, as also found in polychaetes from four Atlantic seamounts (Gillet & Dauvin, 2000). Apparently, neither type of development is clearly favoured in the colonization of such isolated places. Colonization of this seamount may have happened long ago, perhaps under different geographical conditions, when it was not so isolated. Concerning the species with planktotrophic development, regular input of larvae may occur from distant sources. These 'pseudopopulations' (Bouchet & Taviani, 1992) or 'dependent populations' (Boehlert, Wilson & Mizuno, 1994) rely on long-lived dispersive larvae for their maintenance (Rogers, 1994). Species with a low capacity for dispersal (that is, with non-planktotrophic type of development) are restricted to one or two of the seamounts (Gofas, 1992). As in planktotrophic larvae, they reach other islands or seamounts by chance events, but with the difference that in planktotrophic developers the larvae are the colonizing agents, whereas in non-planktotrophic developers the adults (by means of rafting) are the most probable colonizing agents. The quantification of this genetic flux

between seamounts, islands and the mainland should be an objective of future work.

The number of taxa collected at the Ormonde Seamount is surely not representative of its total malacofauna. Further information would be gained if similar collecting were done at Ampère (18–40 m depth). Josephine (178 m depth), Seine (152 m depth) and Dacia (86 m depth) are all below the photic zone, so could not provide direct comparisons.

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