DISTRIBUTION PATTERNS AND DISPERSAL OF PROSOBRANCH GASTROPODS ALONG A SEAMOUNT CHAIN IN THE ATLANTIC OCEAN

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Based on qualitative data on prosobranch gastropods present at eight seamounts and islands of the Vitória-Trindade Seamount Chain off the eastern coast of Brazil, similarities at the species level are examined, and the effects of selection for different modes of development varying with increasing distance from the coast are investigated. Number of species decreases significantly from the continent towards easternmost localities. Similarity coefficients and cluster analysis suggest that similarities are greater among the western seamounts, followed by the eastern, most oceanic localities. Subtidal stations on Trindade Island show less similarity at specific level when compared with the remaining sublittoral stations. Percentages and absolute numbers of species with intracapsular metamorphosis decrease rapidly away from the coast in the sublittoral localities. However, there is little variation for the ratio planktotrophs/lecithotrophs among these localities, and their percentages remained constant over the entire Chain. In spite of the slightly wider range of distribution of planktotrophs within the Chain, the observations suggest that both planktotrophs and lecithotrophs can be effectively dispersed, probably by passive larval transport, in an 'island-hopping' pattern across the relatively small distances (100-250 km) that separate summits in the Chain. Notwithstanding shallow, subtidal conditions and intense isolation, percentages of planktotrophs and lecithotrophs also do not vary at the subtidal Trindade stations.

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The Vitória-Trindade Seamount Chain off eastern Brazil provides an opportunity to investigate several propositions on biogeography and dispersal of bottom organisms. A group of isolated, oceanic islands is present at its eastern end (Trindade Island, Martin Vaz Archipelago), at 1100 km off the Brazilian coast, and six major, linearly arranged seamounts are present between the coast and these islands. Distances of the same order of magnitude (100-250 km) separate each seamount from its closest neighbours, and lower-bathyal or abyssal (2000-5000 m) depths are present between them. Summits of seamounts come relatively close to the surface (50-150 m), but shallower, subtidal depths are present only in the oceanic islands (see description of study area below).

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High dispersal abilities in benthic marine organisms have been associated with extended length of pelagic larval life and passive dispersal of larvae by ocean currents (Scheltema, 1971, 1988; Laursen, 1981; Scheltema & Williams, 1983). Oceanic distances can be effectively crossed by pelagic larvae, and their ability to feed is usually correlated with the length of their permanence in the planktonic phase, which ranges from a few weeks to a few months in most planktotrophic species (Jablonski & Lutz, 1983; Strathmann, 1985). Also, it has been proposed that prosobranchs with teleplanic larval stages (extremely long-lived, planktotrophic larvae lasting between six weeks and one year; Scheltema, 1971) have greater temporal and geographical ranges than those with non-teleplanic development (Jablonski & Lutz, 1983); species with teleplanic larvae are less prone to reproductive isolation and allopatric speciation due to largely enhanced probabilities for maintenance of genetic integrity via dispersal (Scheltema, 1978).

Based on the taxonomic composition of the prosobranch assemblages, and under the assumption that dispersal via ocean currents is the major process bearing on colonization of these islands and seamounts, we investigated: (1) the regularity with which species occur in the different seamounts and islands of the chain, and whether patterns of occurrence could indicate dispersal via 'stepping-stones', and (2) if there are important changes in the relative frequencies of modes of development along the chain that could suggest selection for colonization by planktotrophic species in situations of enhanced isolation.

STUDY AREA

The Vitória-Trindade Seamount Chain (VTSC) (Vitória-Trindade Ridge, Columbia Fracture Zone) is a group of structures of volcanic origin which extends in an east-west direction (29°50'S 38°30'W) for 1100 km, between the latitudes 20° and 21°S in the south-western Atlantic (Figure 1). It evolves from the ocean basin off eastern Brazil towards the South American continental mass; the westernmost oceanic expression of VTSC is the Vitória Seamount, situated at the base of the slope. To the east, it is apparently limited by the islands of the Martin Vaz Archipelago (Almeida, 1965; Asmus, 1978; Guazelli & Carvalho, 1978). The whole extension of VTSC is under the influence of the southward flow of the warm, saline Brazil Current (Miranda & Castro Filho, 1982).

The basic bathymetry and contours of the main seamounts and banks of VTSC were not well established until the late 1970s; average minimum depth of the submerged structures is around 70 m below sea level, and all except Columbia Seamount exhibit depths less than 60 m (Guazelli & Carvalho, 1978). The predominantly flattened tops are the result of growth and erosion of carbonatic algal deposits over a volcanic pedestal, associated with eustatic processes during the Pleistocene glaciation (Almeida, 1965; Asmus, 1978).

Morgan (1983) and Vink *et al.* (1985), using selected magnetic anomalies isochrons on both sides of the Mid-Atlantic Ridge, indicated that VTSC is the more recent segment of a hotspot track. The segment represented by VTSC "constrains the motion of South America to be east-west for some indefinite period of time" (Morgan, 1983, p. 133). This

author has considered that the hotspot is presently in the Trindade-Martin Vaz area, as previously suggested by Asmus (1978). Trindade and Martin Vaz are Pliocene in age (2·3-2·9 My BP; Cordani, 1970). Geological evidence indicates that elements forming VTSC were never connected to any land mass; the relative chronology associated with its sequential formation is that of an earlier origin of structures at the western end, and more recent origin of the islands at the eastern extremity.
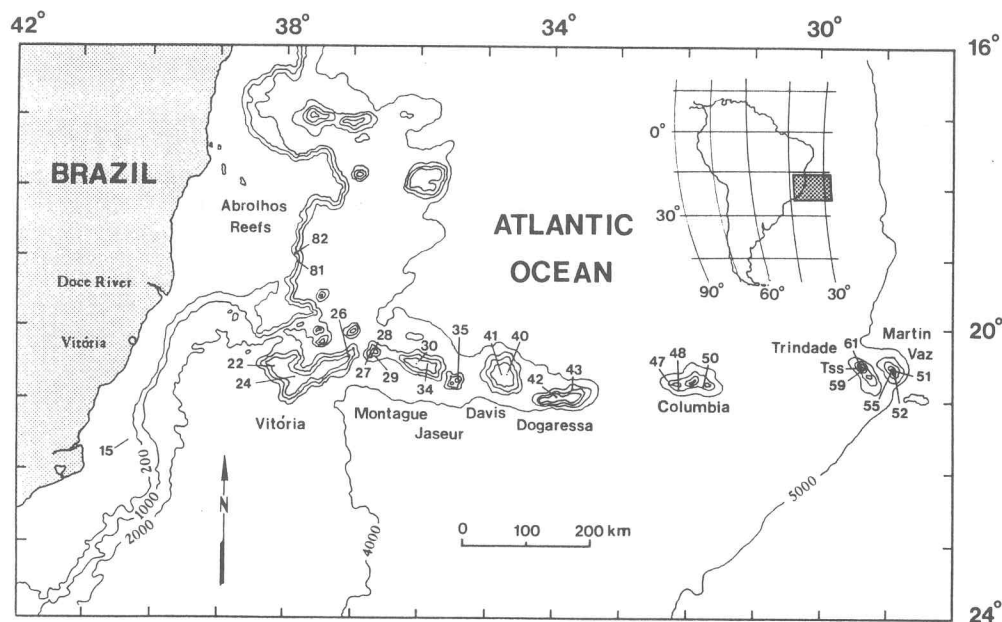

Figure 1. Location and general bathymetry of the Vitória-Trindade Seamount Chain, and stations made during the MD-55 cruise (two-digit numbers). Inset shows position of study area in the south-western Atlantic Ocean. Isobath for 3000 m is omitted.

MATERIAL AND METHODS

Sampling

All the material examined in this study, with the exception of that from Trindade Island, was collected during the Cruise MD-55 of the RV 'Marion-Dufresne', in May 1987, by P. Bouchet, J. Leal and B. Métivier (see Table 1 for a list of stations and Figure 1 for their locations). Sampling in the subtidal of Trindade Island includes not only material collected through SCUBA-monitored suction-samplings made at 10 m depth in Baía dos Portugueses (Portuguese Bay) by the authors during the cruise MD-55, but also from sediment samples dredged and collected (SCUBA) in two stations at the same locality and same depth by the senior author in December 1982. Therefore, Trindade subtidal is represented by three stations.

Bottom depths ranged from 37 to 135 m (Figure 1), for all samples except for those from four deeper stations. Stations DC-28 and DC-29 (525-600 m and 310-350 m respectively, Montague), DC-48 (250-300 m, Columbia) and DC-55 (780-795 m, Martin Vaz Archipelago)

yielded only dead shells of shallow-water material (in practically all cases species also collected in sublittoral stations) which may have fallen from the top of the seamount or been carried down by processes such as turbidity currents. A set of stations made on the adjacent continental shelf provided information on faunal assemblages present at the nearest coastal area in Brazil.

Table 1. *Position and depth of stations of the Cruise MD-55 of RV 'Marion-Dufresne' considered in the present investigation*

Locality	Stations	Latitude S	Longitude W	Depth (m)
Shelf	DC-15	21°37'	40°18'	37
	DC-81	19°00'	37°48'	120-135
	DC-82	18°56'	37°52'	85-105
	DC-83	18°50'	37°57'	60
Vitória	DC-22	20°32'	38°11'	52
	DC-24	20°42'	37°50'	48-52
	DC-26	20°21'	36°59'	97
Montague	DC-27	20°26'	36°42'	81
	DC-28	20°27'	36°42'	525-600
	DC-29	20°27'	36°41'	310-350
Jaseur	DC-30	20°27'	36°17'	60
	DC-34	20°28'	35°54'	54
	DC-35	20°42'	35°22'	82-105
Davis	DC-40	20°40'	34°41'	60
	DC-41	20°39'	34°43'	58-70
Dogaressa	DC-42	20°55'	34°01'	60
	DC-43	20°51'	33°45'	63
Columbia	DC-47	20°42'	32°13'	94-105
	DC-48	20°44'	32°08'	250-300
	DC-50	20°44'	31°50'	95-120
Trindade	TSS	20°30'	29°18'	10-12
	DC-59	20°30'	29°19'	52-60
	DC-61	20°29'	29°18'	63
Martin Vaz	DC-51	20°29'	28°54'	48-52
	DC-52	20°29'	28°52'	64-80
	DC-55	20°32'	28°52'	780-795

DC=dredge, TSS=monitored suction samples in Trindade Island

The relatively small number of stations/localities (about three) can partially be compensated for by (1) the relative constancy in the bathymetric range at the seamounts, usually around 100 m depth, and the small areas at their summits, and (2) large sample volumes and homogeneity of substrates sampled (the mixture of algal conglomerates, calcareous sand, marl, and the calcareous green alga *Halimeda discoidea* Decaisne, 1842).

The gear consisted of rectangular dredges with 1·8 m width. In addition, an air-lift type suction sampler was employed for the shallow-water samples. Each dredge sampling yielded an average of 600 kg of algal conglomerates (genus *Lithothamnium*), small colonies of the coral *Montastrea cavernosa* (Linnaeus, 1767) (usually down to depths of about 50 m), and a mixture of the alga *Halimeda discoidea* and *Halimeda*-derived sediments.

About 10% of the volume of larger conglomerates and coral colonies were opened to check for burrowing and boring organisms. All remaining sediment was sieved in 5, 2, 1 mm mesh metal sieves and each fraction sorted. Gastropods were preserved in 80° GL ethanol. Each seamount, island or the continental shelf is referred to simply as a 'locality'. Abbreviations used for the localities are: SHE, continental shelf off Brazil, adjacent to Vitória-Trindade Seamount Chain; seamounts: VIT, Vitória, MON, Montague, JAS, Jaseur, DAV, Davis, DOG, Dogaressa, COL, Columbia; TRI, Trindade Island; TSS, subtidal suction samples, Trindade Island; MAR, Martin Vaz Archipelago.

Modes of development

Modes of development of the species were determined (1) by direct data from the literature for those species with known life histories, (2) by analogy with closely related species with known life histories, or (3) by complete inference from protoconch morphology. Planktotrophic larval types have protoconchs usually elaborately sculptured and with many whorls. These larval shells are divided into a small embryonic shell (protoconch I) and a larger larval shell (protoconch II). A sinuous, double embayment in the external lip of the larval shell, the sinusigeral lip, which allows for the positioning of the velar lobes of the larva, is also sometimes present in planktotrophic species. Lecithotrophic (non-feeding), planktonic larvae lack the distinction between protoconchs I and II and have protoconchs with 1-2 whorls (Thorson, 1950; Jablonski & Lutz, 1983). Species exhibiting intracapsular metamorphosis have unusually large embryonic whorls, and are referred to as 'direct developers'. It is assumed in this work that large-scale oceanographic conditions do not vary in a west-east fashion along VTSC. Due to geographical orientation of VTSC, possible latitudinal gradients in species diversity (Pianka, 1966) and the 'latitudinal effect', or variation in frequency of modes of development along a latitudinal gradient (Thorson, 1950), are non-existent by definition.

Data processing

Species were identified, when possible, by comparison with reference material and type-collections at the Museu Oceanográfico, Fundação Universidade do Rio Grande, Brazil; Museu Nacional, Rio de Janeiro, Brazil; Muséum National d'Histoire Naturelle, Paris; National Museum of Natural History, Smithsonian Institution, Washington and The Natural History Museum, London.

To evaluate whether a particular mode, or modes of development could show significant differences in range extent within VTSC, we used a local 'range value'. The range value (RV) represents linear distance between the eastern- and western-most localities where a given species was found; RV is the number of localities situated between and including the limits of distribution along VTSC. It ranges from 1 to 9, and can be equal to or larger than the number of localities where the species was actually found. In the computation of RV it was assumed that named, well-identified species are present somewhere else on the continental shelf of the tropical western Atlantic, thus scoring positively for SHE. Species with unknown mode of development were not computed. The total number of species involved in the computation of RVs is 164.

All statistical procedures were performed according to Sokal & Rohlf (1981). Similarities between localities were calculated from an initial, binary data matrix. The number of species in each locality is represented by all the occurrences from stations made in that locality. Similarities were calculated for all possible pairs of localities (Valentine, 1966), according to the Dice coefficient (also known as Sørensen coefficient; Sneath & Sokal, 1973; Pielou, 1984). Localities were clustered according to the similarity coefficients using 'unweighted pair-group arithmetic average clustering' (UPGMA; Sneath & Sokal, 1973; Pielou, 1984). Computation of similarity coefficients and cluster analysis was performed by means of the NTSYS-PC package of programs (Rohlf, 1989).

RESULTS

Composition of assemblages and similarities

A total of 244 species was examined in this study, including samples obtained from four stations at the continental shelf. The number of species at each locality (computed from all samples taken at that locality) ranges from 33 (TRI) to 99 (VIT); arithmetic mean ±standard deviation is $60 \cdot 0^{\pm} 22 \cdot 1$ (Table 2). Frequencies of occurrence for species in the study localities are indicated in Figure 2. Not a single species has been found in all 10 localities, and about 44% of the total number of species was obtained in only one locality. The binary data matrix has 598 presences in a total of 2440 data points ($P=0 \cdot 25$).

Table 2. *Statistics for number of species and percentages of the three basic developmental types in the study localities at the Vitória-Trindade Seamount Chain*

	Mean	SD	Range
Total species/locality	60.0	22.1	33-99
Planktotrophs	27.9	9.1	15-43
Lecithotrophs	26.8	9.5	14-43
Direct developers	4.9	4.0	0-11
Archaeogastropods	12.0	3.6	7-17
Percentage/locality			
Planktotrophs	47.2	4.1	43.1-54.5
Lecithotrophs	44.9	3.9	40.3-53.1
Direct developers	7.3	5.2	0.0-14.7
Archaeogastropods	21.9	8.0	10.1-32.6

Archaeogastropods are computed separately for comparative purposes (N=10)

The total number of species per locality decreased significantly along VTSC with increasing distance from the shelf to the oceanic islands (Figure 3A). As shown below, similarly inverse relationships were found for the three basic modes of development. Reduction in number of species is apparently steeper between DAV and DOG, TRI, but there was an unexpected increase in MAR. That reduction could be correlated with the successively increasing distances that separate DAV→DOG→COL→TRI+MAR. About
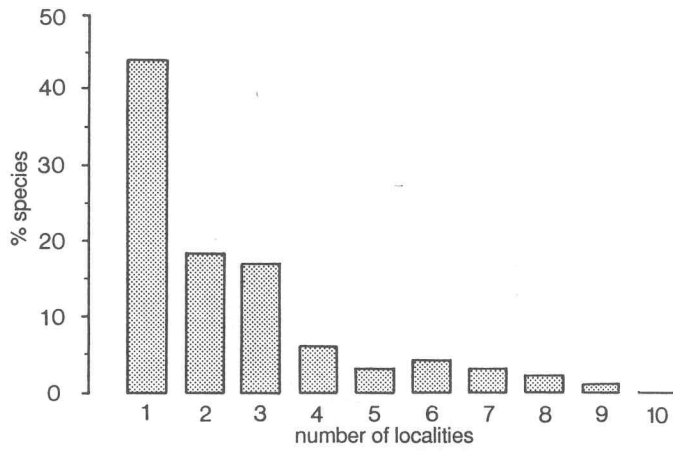
Figure 2. Distribution of frequencies of occurrence for species in the 10 study localities (N=244).
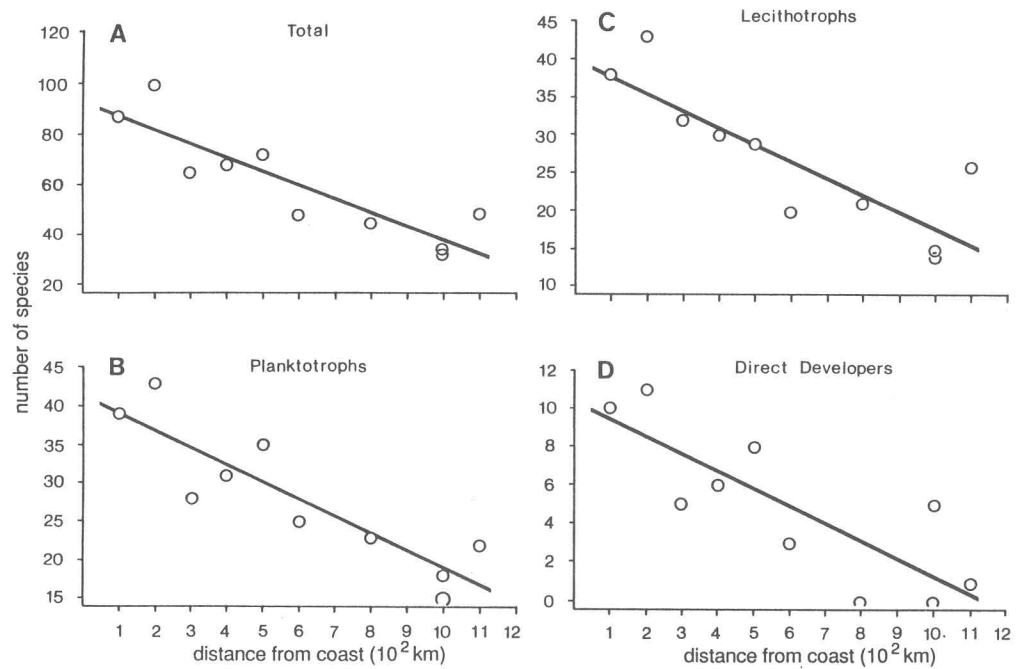

Figure 3. Model I linear regression of number of species in each locality with approximate distance between study localities and the adjacent coast. (A) Total for species; regression line is y=92·6-5·4x, r=-0·89, P=0·0006. (B) Planktotrophs; regression line is y=41·3-2·2x, r=-0·89, P=0·0006. (C) Lecithotrophs; regression line is y=40·2-2·2x, r=-0·84, P=0·002. (D) Direct developers; regression line is y=10·3-0.9x, r=-0·81, P=0·004.

200 km separates DOG from COL, and this latter is in turn separated from TRI by 250 km (compare Figure 1 with Figure 3A-D). Fluctuations in the pattern of reduction in number of species towards the open ocean have occurred, probably because of the small number of stations per locality. The symmetrical matrix of similarities computed from Dice
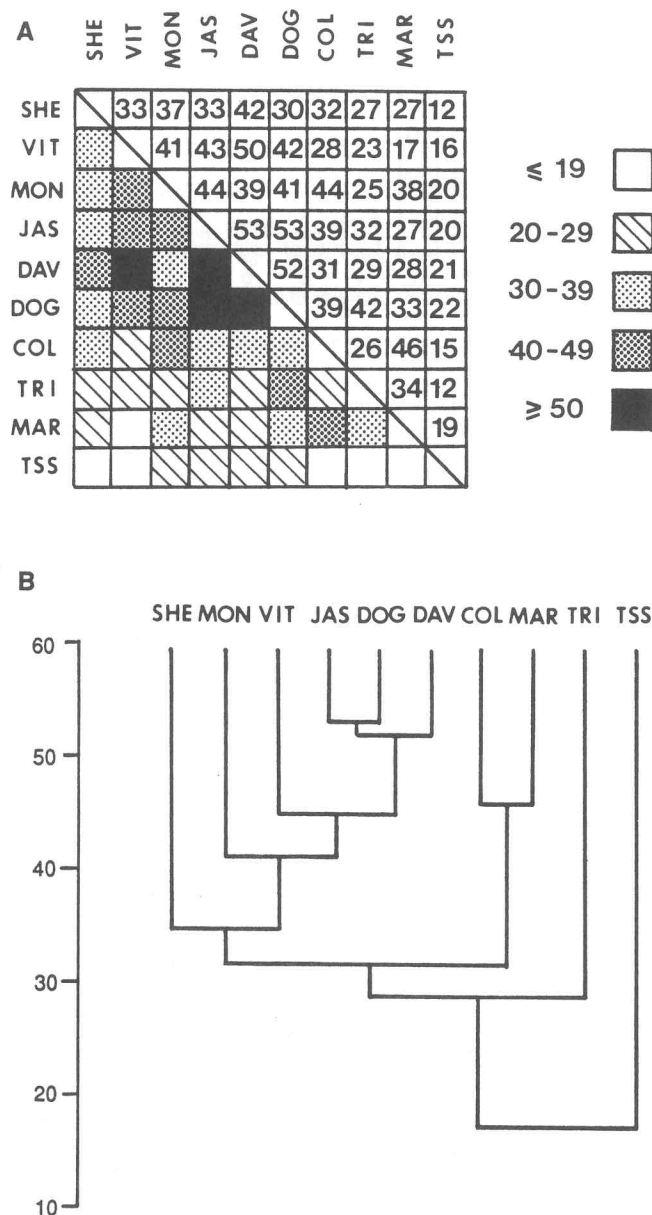
Figure 4. (A) Similarity matrix for species showing all possible Dice coefficients between localities. Matrix is symmetrical; numerical values above diagonal are depicted in coded shades below it. West-east progression from SHE→MAR. (B) UPGMA phenogram resulting from clustering of Dice coefficients for species. Localities: SHE, Continental shelf off Brazil; VIT, Vitória; MON, Montague; JAS, Jaseur; DAV, Davis; DOG, Dogaressa; COL, Columbia; TRI, Trindade; MAR, Martin Vaz; TSS, Subtidal Trindade.

coefficients for species (Figure 4A) indicates higher similarities for the geographically intermediate group of seamounts, JAS+DAV+DOG. The phenogram resulting from UPGMA clustering of the similarity coefficients in the matrix is shown in Figure 4B. Clustering with higher values occurred respectively for JAS+DOG, then +DAV+VIT+MON. This whole cluster joined the eastern TRI, COL+MAR, then SHE. Shallow TSS showed the lowest values of similarity compared with other groups.

Modes of development

Values for number of species and percentage of planktotrophs, lecithotrophs and direct developers in the study localities are given in Table 2 and Figures 3 and 5. The decrease from west to east in number of planktotrophs, lecithotrophs and direct developers is indicated in Figure 3A-D. The ratio planktotrophs/lecithotrophs among localities is nearly constant (Figure 5A). Mean percentages of planktotrophs and lecithotrophs in each of the 10 localities are not significantly different (Figure 5A-B). From the 12
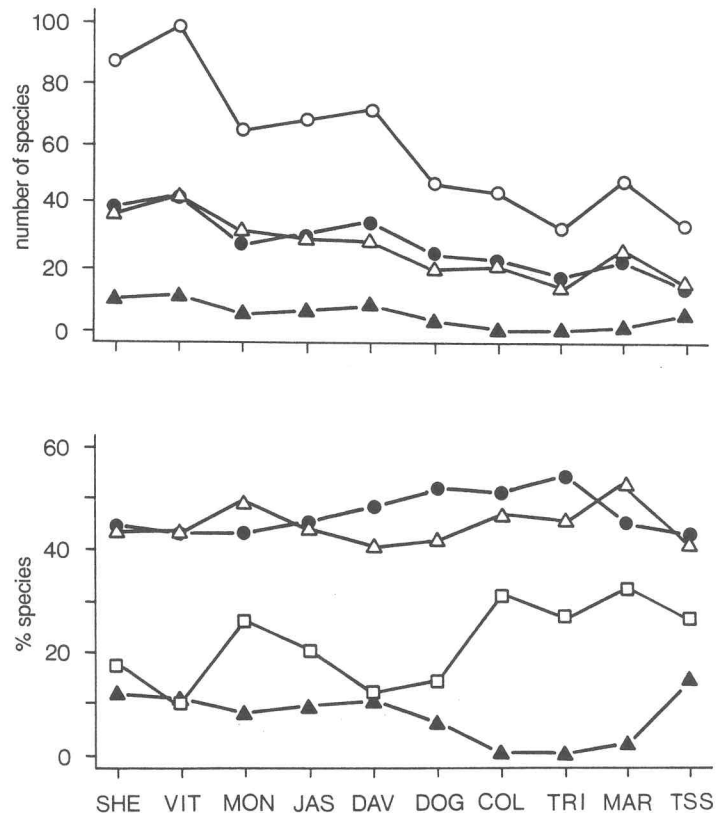

Figure 5. Variation of total number of species (open circles) and basic types of reproductive strategies (planktotrophs, occluded circles; lecithotrophs, open triangles; direct developers, occluded triangles) in study localities. Percentage of archaeogastropods (open squares) are computed separately for comparative purposes. (A) Number of species. (B) Percentages. West-east progression from SHE→MAR. Localities: SHE, continental shelf off Brazil; VIT, Vitória; MON, Montague; JAS, Jaseur; DAV, Davis; DOG, Dogaressa; COL, Columbia; TRI, Trindade; MAR, Martin Vaz; TSS, Subtidal Trindade.

planktotrophic species that occurred in more than 50% of the 10 localities (6 or more localities), 6 are characterized by teleplanic larvae.

Our data show that maintenance of geographically separated populations of several species with lecithotrophic development occurs among localities at VTSC, including several archaeogastropods. The ratios of planktotrophs/lecithotrophs in the 10 localities did not show significant variation (compare plots for planktotrophs and lecithotrophs in Figure 5) following the geographical gradient of VTSC (isolation increasing from west to east): no significant alterations in the percentages of modes of development were detected. However, with exception of the shallow TSS, there was a general decrease both
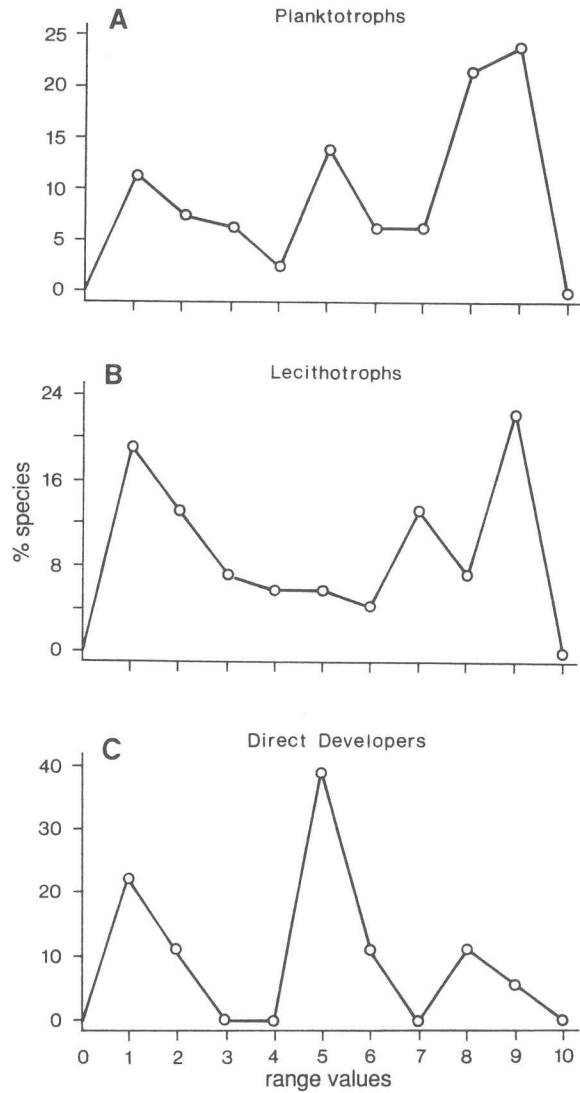

Figure 6. Range values (RV) for (A) planktotrophs (N=79), (B) lecithotrophs (N=67), (C) direct developers (N=18). RV represent distance between extremes of distribution within the Vitória-Trindade Seamount Chain (assumptions made in the calculation of RV are detailed in the text).

in number and percentage of direct developers away from the coast (Figure 5). Percentages of archaeogastropods have increased from 17·2% at SHE to 32·7% at MAR, with large fluctuations for this value in intermediate seamounts (Figure 5B). Examination of 'range values' (RVs) for each mode of development indicates that planktotrophs show a slight tendency towards larger RVs than lecithotrophs or direct developers; 46% (36 species) of all planktotrophs (Figure 6A) have RV equal to 8 or 9, while only 29% (20 species) of the lecithotrophs (Figure 6B) and 16% (3 species) of the direct developers (Figure 6C) fall within that range. Frequency graphs for lecithotrophs (Figure 6B) show an unexpected distribution with maxima at RV=1 (despite the removal of most unnamed, restricted species) and RV=9.

DISCUSSION

Composition of assemblages and similarities

Wilson & Kauffman (1987) observed that "over 596 species of invertebrates have been reported from at least 59 seamounts ranging from 27 to 3800 m depth". Molluscs comprised "specifically 72 species from seamounts in 5 regions". The total number of species (244) represents about one-third of the total number of prosobranchs (735) given by Rios (1985) for the Brazilian coast (roughly 8000 km in linear extension). Consequently, we consider relevant the mean number of prosobranch species per locality defined in the present study (mean ± standard deviation=60·0±22·1). Despite the markedly inverse relationship between total number of species and distance from west to east, it is not possible to define the exact causal mechanism for this geographical gradient. Reduction in number of species could be induced by (1) the decrease in age along VTSC in the same direction (an 'age effect' expected from the known direction of movement of the South American Plate over a fixed hotspot), (2) by the smaller surface areas above 200 m (Guazelli & Carvalho, 1978) in the eastern localities at VTSC ('area effect' of MacArthur & Wilson, 1967), by (3) a supposed decrease in general biological diversity and abundance (as theoretized by Case & Cody, 1987) in more isolated localities ('overall diversity effect'), or by any combination of these factors. Drilling through the biogenic 'cap' of the seamounts could provide an estimate of any change in diversity along their geological history, especially in regard to sea level changes, but at present such information is not available. Higher similarities among seamounts at the western half of VTSC suggest that dispersal among these localities is more effective than to the eastern, more isolated seamounts and islands. The smaller distances between intermediate and western seamounts could favour dispersal by a 'stepping stones' effect in that area.

The subtidal at Trindade (TSS) showed the smaller values of similarity when compared to all other localities. Even the sublittoral stations (52-63 m depth) in the same island (TRI) were more similar to any other locality than to TSS. Again, the factors that might account for this divergence in faunal composition can be either ecological or biogeographical, or both. Due to probably unique ecological conditions, a higher degree of differentiation can be expected from a subtidal environment (10-12 m depth) when compared to all sublittoral localities (although *Halimeda discoidea* and calcareous rubble constituted the

basic substrate in all localities, including TSS). Geographically, the nearest subtidal environment (not considering the neighbouring Martin Vaz Archipelago) is 1100 km distant, while for all other localities in this study, similar bathymetric conditions are never more than 250 km apart. This represents almost an order of magnitude difference between TSS and all other localities when comparing geographical isolation from possible 'source' areas. Then, by interaction of bathymetric and geographical factors, TSS is the locality where higher degrees of environmental isolation are present, whereas MAR is in fact the 'more distant' locality.

Modes of development

Kay (1967), Scheltema & Williams (1983) and Vermeij *et al.* (1984) observed that isolated, oceanic islands tend to have high percentages of 'good dispersers' or species derived from them. Similar views were espoused by Rex & Warén (1982) concerning abyssal caenogastropods from the western North Atlantic. Higher incidence of planktotrophs with increasing depth supposedly represents the need for dispersal to patchy (habitat islands) recruitment sites and food sources in the deep-sea environments.

Our results concerning the widespread distribution of lecithotrophic types indicate that either (1) the average distance separating study localities is not broad enough to hamper regular transport of short-lived, lecithotrophic larvae, or (2), if any 'filter' effect is defining the species compositions along VTSC, factors other than larval dispersal are acting (*e.g.* dispersal of adults or egg masses by rafting; Scheltema & Carlton, 1984; Highsmith, 1985).

Families that almost exclusively have long-lasting, teleplanic larvae (Cypraeidae, Ovulidae, Ranellidae, Tonnidae, Cassidae, Architectonicidae, Bursidae, Thaididae, Coralliophilidae, see Scheltema, 1971; Laursen, 1981; Scheltema & Williams, 1983), are not well represented in this study. In fact, Cypraeidae, Ranellidae and Bursidae were represented by three species each, Ovulidae by two, Cassidae by one and Architectonicidae were not collected. Furthermore, these families did not contribute with potentially endemic (*i.e.* unidentified and geographically restricted) species. Absence of endemic, restricted teleplanic species in situations of geographical isolation conforms to Scheltema's (1971, 1978) observations on the maintenance of 'genetic integrity' via dispersal in groups with teleplanic larvae. Intracapsular metamorphosis occurs in the families Marginellidae (Ponder, 1970; Bouchet & Warén, 1985; Gofas & Fernandes, 1988) and Volutidae (Penchaszadeh, 1988; Bouchet & Poppe, 1988). Representatives of both families lay egg capsules on the bottom, with usually one or a few juveniles hatching from each egg capsule. The two volutids examined (*Plicoliva zelindae* (Petuch, 1979) and *Odontocymbiola americana* (Reeve, 1856)) have the restricted range exhibited by most members of the family, being known only from the shelf in eastern and southern Brazil (this study; Rios, 1985). The sharp decrease in marginellid species (Figure 7) coincides with the large gaps between localities at the eastern half of VTSC. This suggests that the relatively small distances that separate the western seamounts are not acting as complete barriers to dispersal, even to some direct developers, perhaps due to dispersal of eggs or juveniles by rafting on floating algal holdfasts or debris in these small species (Gofas & Fernandes,

1988). Significantly, the largest marginellid examined, *Bullata* sp. 1 (aff. *bullata* (Born, 1778)) was found only at SHE. Its apparent absence from the seamounts and islands (also the case for the volutids, see Figure 7) could be related to the increasing difficulty for passive dispersal by rafting of species with proportionally larger, non-planktonic eggs, juveniles or adults, as opposed to what might happen with smaller species.
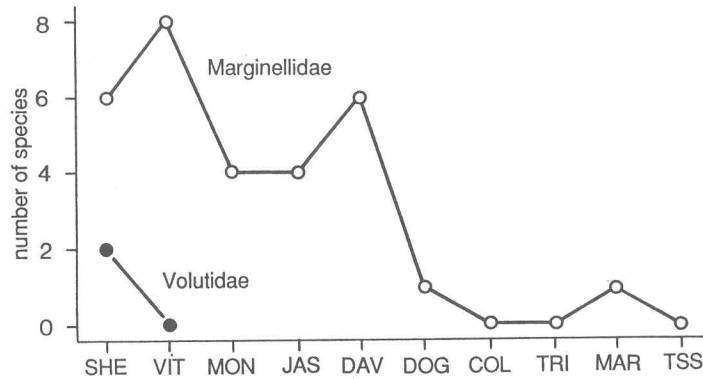

Figure 7. Variation in number of species from the families Volutidae (2 species) and Marginellidae (12 species) between the study localities. Localities: SHE, Continental shelf off Brazil; VIT, Vitória; MON, Montague; JAS, Jaseur; DAV, Davis; DOG, Dogaressa; TRI, Trindade; MAR, Martin Vaz; TSS, Subtidal Trindade.

Are the enhanced isolation and faunal dissimilarity observed for TSS and MAR characterized by significant shifts in percentages of modes of development? Percentages of lecithotrophs at both the 'less similar' TSS (53·0%) and the 'more distant' MAR (55·0%) were the highest among the 10 localities. These higher values do not deviate significantly from the remaining percentages of lecithotrophs (Dixon's and Grubb's tests for detecting outliers (Sokal & Rohlf, 1981, $\alpha \gg 0\cdot10$). Both number and percentage of direct developers decreased along VTSC, but at the subtidal TSS there is an increase in these values. However, from the 5 species, only one is probably endemic, *Granulina* sp. 1 (Marginellidae). The other four are known from elsewhere in the western Atlantic (three Hipponicidae and *Leucozonia nassa* (Gmelin, 1791) (see Bandel, 1975).

Our data indicate that, in spite of the slightly broader range of occurrence of planktotrophs (larger percentage of range values in the 8-9 classes) within the Chain, there is no significant prevalence either of planktotrophs or lecithotrophs at any particular locality, and consequently no correlation with the differing degree of geographical isolation that characterizes each of the 10 study localities. Such is true also for the subtidal at Trindade Island, which, in spite of a rather distinctive prosobranch assemblage, does not show deviation from the frequencies found in the deeper sublittoral localities. The distribution of a large number of lecithotrophs with short-lived pelagic larvae (*e.g.* archaeogastropods) indicates that oceanic barriers of the order of magnitude found between localities at VTSC probably do not prevent passive crossing by these organisms, but apparently do hamper dispersal of particular species with direct development.

Finally, it is suggested that the constant ratio of planktotrophs/lecithotrophs verified along the entire chain results from a trade-off between dispersal and colonization abilities inherent in the species assemblages at each island or seamount.

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