Fauna and Flora of the Atlantic Islands

PROCEEDINGS OF THE 3rd SYMPOSIUM – PART A

PONTA DELGADA 21-25 SEPTEMBER 1998

Arquipélago – ***Life and Marine Sciences***
Supplement 2 – Part A
2000

ARQUIPÉLAGO

Life and Marine Sciences. Bulletin of the University of the Azores.

SCOPE

ARQUIPÉLAGO - Life and Marine Sciences, publishes annually original scientific articles, short communications and reviews on the natural marine environment of the archipelago of the Azores and surrounding region of the Atlantic Oceans. MSS from other Macaronesian and Atlantic islands will also be accepted.

PUBLISHER

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FINANCIAL SUPPORT

Fundação para a Ciência e Tecnologia (FCT), Lisboa
Fundação Luso-Americana para o Desenvolvimento
Governo Regional dos Açores

Indexed in:

Aquatic Sciences and Fisheries Abstracts (ASFA), BIOSIS, Current Awareness in Biological Sciences (CABS), Marine Science Content Tables (MSCT), Zoological Record.

ENDEMISM AND MODES OF DEVELOPMENT OF MARINE PROSOBRANCH GASTROPODS (MOLLUSCA) FROM OCEANIC ISLANDS OFF BRAZIL

JOSÉ H. LEAL

LEAL, J. H. 2000. Endemism and modes of development of marine prosobranch gastropods (Mollusca) from oceanic islands off Brazil. *Arquipélago*. Life and Marine Sciences. Supplement 2(Part A): 79-87. Ponta Delgada. ISSN 0873-4704.

The endemism rates and the relationships between modes of development and endemism of shallow-water (<200 m) prosobranch gastropod assemblages from oceanic islands off Brazil (302 species) are assessed. Endemism rates are 5.1% (Fernando de Noronha), 8.1% (Atol das Rocas), 9.4% (Martin Vaz), and 16% (Trindade). When studied as "island groups" Rocas and Noronha (northern group) show a combined endemism rate of 19.2%, and Trindade and Martin Vaz (southern group) of 18.3%. To test the hypothesis that endemics are mostly species with non-planktotrophic development, the basic mode of development was determined for each species. Frequencies of each mode of development were analyzed for the two island groups. Non-planktotrophic species were more frequent among the insular endemics in both island groups when compared to the entire prosobranch faunas: frequencies of non-planktotrophic species at the northern and southern groups are, respectively, 84.2 and 71.4% for endemics, 60.1 and 51.7% for all species. In contrast to planktotrophic species, which have higher dispersal abilities, inception of insular endemism in non-planktotrophic species may be favored by effective reproductive isolation, offspring retention, and allopatric speciation in the absence of repeated arrivals on the islands.

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INTRODUCTION

Since DARWIN'S (1870) observations on the fauna and flora of the Galapagos and other oceanic islands, insular assemblages of animals and plants have been considered as modified and impoverished renditions of the assemblages living in the nearest continental mass. As many authors did before him, LEAL (1991a) has shown that this applies to the shallow-water (<200 m) marine gastropods from the oceanic islands off Brazil (Atol das Rocas, Fernando de Noronha, Trindade, and Martin Vaz), in the south-western Atlantic Ocean. In spite of these expected similarities to adjacent landmasses, chance arrivals on islands when followed by reproductive isolation will eventually lead to genetic divergence from the parental populations and allopatric speciation. The number of endemic species will be directly correlated with the area, age, degree of isolation (distance from nearest source) of the islands (MACARTHUR & WILSON 1967), and other variables.

Starting with pioneer studies of THORSON (e.g., 1950, 1961), the relationship between geographic range and mode of development of marine invertebrates has been reasonably well established. Larval transport (dispersal) by ocean currents leads to increased opportunity for genetic exchange between separated populations of species with pelagic larval lives of longer duration (plankton-feeders, or planktotrophs). Planktotrophs are less prone to reproductive isolation and allopatric speciation due to enhanced probabilities for maintenance of genetic integrity via dispersal (JABLONSKI & LUTZ 1983; SCHELTEMA 1971). Species showing planktotrophic development will generally be more broadly distributed geographically. Conversely, species with planktonic larval lives of short duration (pelagic lecithotrophs) or absent

Fig. 1. Location of the study islands (names italicized) in relation to other major Atlantic volcanic islands and archipelagos.

(those undergoing intracapsular metamorphosis) usually have narrower geographic distribution (Hansen 1980; Jablonski & Lutz 1983). But exceptions to this inverse relationship between length of larval life and extent of geographic range are known occur at least in the gastropod genera *Littorina* (Johannesson 1988; Reid 1996), *Dendropoma* (Safriel & Hadfield 1988), in the bivalve genus *Lasaea* (Ó Foighil 1989), and in north temperate (Vermeij et al. 1990) and subantarctic (Arnaud 1974) islands. Successful colonisation will depend not only upon chance dispersal, but also upon the establishment of viable populations; it has been suggested that rare arrivals (e.g., of gravid females transported by rafting) of non-planktotrophic species will more likely provide successful founders than frequent arrivals of larvae of planktotrophic species. Due to their decreased ability for dispersal after a rare arrival (increased retention of offspring), speciation rates should be higher for newly arrived non-planktotrophs (Abbott 1966; Hadfield et al. 1972; Hourigan & Reese 1987; Johannesson 1988; Reid 1996; Safriel & Hadfield 1988; Scheltema 1986; Strathmann 1986).

If it is true that non-planktotrophs generally have narrower geographic ranges, are more apt as coloniser species, and show higher speciation rates than planktotrophs, then in any given location the subset of narrowly distributed or endemic species should show higher frequency of non-planktotrophs when compared to all prosobranchs present—assemblages of insular endemics from any oceanic island should expectedly present a higher frequency of non-planktotrophs than that computed from the entire prosobranch fauna of that island.

Since the publication of Leal (1991a) on the prosobranchs of Brazilian islands, a number of papers dealing with or affecting the systematics and biogeography of these species have been or are being published (e.g., Absalão & Gomes in press; Absalão & Rios 1995; Harasewych et al. 1992; Houart 1991; Leal 1991b; McLean in preparation; Quinn 1991; 1992a; 1992b; Rolán 1991; 1994; Vermeij & Snyder 1998). A goal of the present study is to reassess the rates of insular endemisms based on the above mentioned new data. It also aims to evaluate and further explore the relationships between insular endemism and the two basic modes of development found in prosobranch gastropods from the Brazilian oceanic islands.

MATERIAL AND METHODS

An earlier listing of the material examined in this study was provided by LEAL (1991a). That earlier listing has, however, been modified to include data from the works mentioned above. An updated electronic version can be obtained from the author upon request. The material examined includes all records of shallow-water (<200 m) Brazilian insular prosobranch gastropods deposited in the collections at: American Museum of Natural History, New York (AMNH); Museu Nacional, Rio de Janeiro, Brazil (MNRJ); Museu Oceanográfico, Fundação Universidade do Rio Grande, Brazil (MORG); Muséum National d'Histoire Naturelle, Paris (MNHN); National Museum of Natural History, Smithsonian Institution, Washington (USNM). Also included are the stations made off Trindade and Martin Vaz Islands during the cruise MD55 of the French R/V *Marion-Dufresne*, in May 1987, and material collected by the author on the islands in 1982–87 and deposited in the above institutions. A commercially available relational database software was used in the assessment of endemism rates (frequencies of endemic species among all species occurring in a group of islands).

MODES OF DEVELOPMENT

Assessment of modes of development was made (1) from literature data for species with known life histories, (2) through comparisons of protoconch/larval shell between a species in this study and a close relative with known life history, (3) by complete inference from protoconch morphology. Mollusk shells are characterized by accretionary growth, which allows for retention of the embryonic and larval shell on the apical region of the adult shell. Inspection of the thus preserved sequence of embryonic and larval shells, or protoconch, allows for inference of basic modes of development (BOUCHET 1989; JABLONSKI & LUTZ 1983; LEAL 1991a; LEAL & BOUCHET 1991; SHUTO 1974; THORSON 1950). Species with planktotrophic development have protoconchs usually elaborately sculptured and with many whorls (Fig. 2, top), usually more than 3. Planktotrophic larval shells are usually divided into a small embryonic whorl (due to the lack of a yolk sac in the embryo), followed by the true larval shell. (After settlement, the embryonic shell remains as the protoconch 1, and the true larval

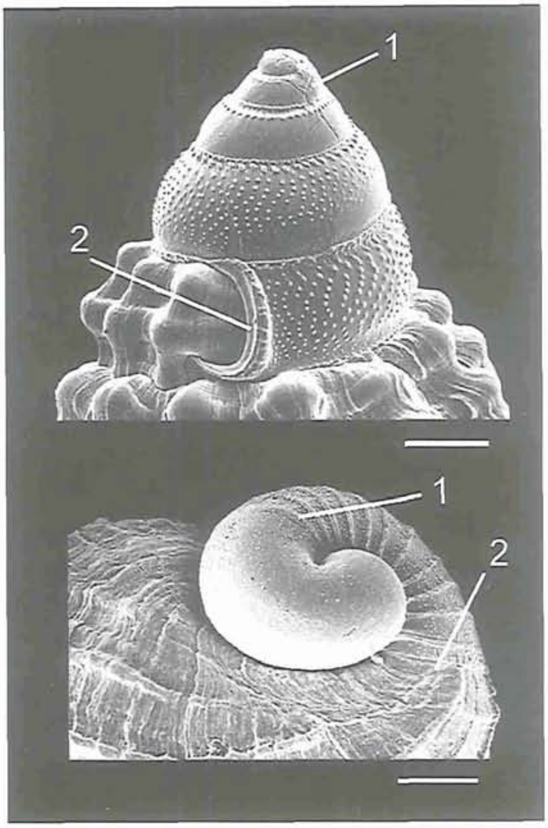

Fig. 2. Examples of the types of protoconchs representing the two basic modes of development of marine gastropods: top, *Trachypollia turricula* (von Maltzan, 1884), family Muricidae, Trindade Island, planktotrophic, with amphi-Atlantic distribution. Scale line = 200 μm; bottom, *Capulus* sp., family Capulidae, Fernando de Noronha, non-planktotrophic, restricted to SW Atlantic Ocean. Scale line = 100 μm. Lines indicate transition between (1) embryonic and larval shells and (2) larval shell and teleoconch. Note small size of embryonic shell of *T. turricula*, and its large number of whorls (4.25) when compared to number of whorls (1.5) on *Capulus* sp.

shell as the protoconch 2.) Species with lecithotrophic (intracapsular or pelagic) development, on the other hand, do not feed on external sources before metamorphosis to the bottom environment, relying instead on a reserve of yolk. The embryonic part of the shell is usually large (Figure 2, bottom) (to accommodate the yolk sac), and the shorter duration of planktonic life is reflected into a smaller number of whorls, usually not more than 2–2.5. The transition between embryonic and true larval shells in non-planktotrophs is usually blurred.

Observations of protoconchs and larval shells in this study were made under scanning electron microscope at the Rosenstiel School of Marine and Atmospheric Science, University of Miami. Number of protoconch whorls was determined following the methods of HANSEN (1980), MAES (1983), and JABLONSKI & LUTZ (1983). An annotated list of species with comments on the modes of development of each species was given by LEAL (1991a). All computations were made with using a commercially available relational database software. Computation of frequencies includes only species for which the mode of development could be determined.

STUDY SITES

The islands in this study are divided into two groups, due to geographic contiguity (Figure 1). Moreover, members of each of the two groups (see below) had similar origins as a result of the initially northwestward then westward motion of the South American tectonic plate, relative to the African plate, over two fixed hotspots (MORGAN 1983; VINK et al. 1985). For more detailed descriptions and literature of the study sites see LEAL (1991a) and LEAL & BOUCHET (1991) and the references cited below.

The Northern Group - Atol das Rocas and Fernando de Noronha.

Atol das Rocas is located at 3°52'S, 33°49'W, lying about 200 km off the coast of NE Brazil. Its bulk consists of a mixed coralline algal/vermetid reef with the ring shape characteristic of coral atolls. The atoll measures about 3.5 km in diameter, with an emerged surface at mean tide of about 7.2 km^2. It constitutes the lifted part of a much larger, relatively shallow, calcareous platform that sits on top of a submarine seamount. Sediment dredged along the bottom of the platform consists basically of calcareous sand and nodules of coralline red algae in the genus *Lithothamnium*. The age of its foundation of basaltic rock situated 80 m below sea level is unknown (OTTMANN 1963; FAIRBRIDGE & GORINI 1975).

Fernando de Noronha, located at 3°50'S, 32°25'W and about 345 km off the NE Brazilian coast, consists of a small archipelago with Fernando de Noronha Island occupying more than 95% of its emerged area, which totals 18.4 km^2. Unlike Atol das Rocas, which probably represents an older structure, situated "downstream" in their hotspot track, Fernando de Noronha is a high volcanic island. Radiometric dating has indicated that the oldest rocks in its three major volcanic formations are 8–11 million years old (Late Miocene). The bottom around Fernando de Noronha is characterized by extensive vermetid reef formation as well as *Lithothamnium* patch reefs. The prevailing soft sediment is calcareous sand. It represents the present location of the hotspot that formed the "northern" hotspot track (ALMEIDA 1958; FAIRBRIDGE & GORINI 1975; MORGAN 1983).

The Southern Group - Trindade Island and Martin Vaz Islets.

Trindade Island is located at 20°30'S, 29°20'W, lying about 1140 km off the eastern Brazilian coast. It has an area of about 8 km^2. The island is the top of a volcanic cone rising from the ocean floor at 5.5 km depth. Most of the rocks above sea level are 2.3–2.9 million years old (Pliocene). Sediments at the narrow insular shelf consist mostly of calcareous sands, conglomerates and fragments of *Lithothamnium*, and fronds and fragments of the calcareous green alga *Halimeda tuna* Lamoroux (ALMEIDA 1961; CORDANI 1970; LEAL 1988).

Martin Vaz, consisting of three small volcanic islets, is located at 20°30'S, 28°51'W. The main islet measures about 0.6 km in maximum diameter. The three islets rise from a truncated seamount that measures about 3 km in diameter. The seamount represents the present location of the hotspot that formed the "southern" hotspot track and, like Trindade, dates from the Pliocene (ALMEIDA 1961; CORDANI 1970; MORGAN 1983). Dredgings made around the islets in 1987 (LEAL 1991a) by a French-Brazilian team that included the author indicate that the prevailing soft substrate consists of calcareous sand intermixed with volcanic gravel and pebbles.

RESULTS

A total of 302 prosobranch species were considered in this study. Of these, 86 occur at Atol das Rocas, 117 at Fernando de Noronha, 94 at Trindade, and 53 at Martin Vaz. When considered as island groups, the northern group (Atol das Rocas + Fernando de Noronha) yielded a total of 145 species occurring at one or both islands. The southern group (Trindade + Martin Vaz) was represented by 120 species occurring at one or both localities. Endemisms computed for the islands separately (Figure 3, top) are: 8.1% (7 species) at Atol das Rocas, 5.1% (6 species) at Fernando de Noronha, 16% (15 species) at Trindade, and 9.4% (5 species) at Martin Vaz. Again, when examined as island groups (Figure 3, bottom), the rate of endemism was 19.2% (23 species) at the northern group and 18.3% (22 species) at the southern group.

Modes of development were assessed and quantified as numbers of species (Figure 4, top) and frequencies (Figure 4, bottom) of planktotrophs and non-planktotrophs. The computation of frequencies includes only species for which the mode of development could be determined. Of all 145 species from the northern group, 55 species (39.9%) were planktotrophs, 83 (60.1%) non-planktotrophs, and 7 species remained undetermined. Among the endemic species at the northern group, 3 species (15.8%) were planktotrophs, 16 (84.2%) non-planktotrophs, and 4 species remained undetermined. Of all 120 species from the southern group, 57 species (48.3%) were planktotrophs, 61 (51.7%) non-planktotrophs, and 2 species remained undetermined. Among the endemic species at the northern group, 6 (28.6 %) were planktotrophs, 15 (71.4%) non-planktotrophs, and 1 species remained undetermined.

DISCUSSION

ENDEMISMS

Additions to the database since its publication (LEAL 1991a) caused the number of entries to increase from 297 to 302. These 5 additions result from the later publications by authors working on species from the Brazilian insular fauna (see listing in Introduction). Also an overall increase

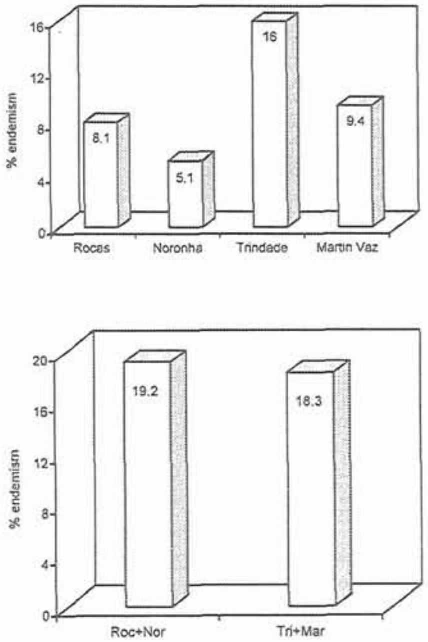

Fig. 3. Endemism rates calculated (endemic species/all species) in separate for the (top) main four study islands and (bottom) jointly for the northern (Atol das Rocas + Fernando de Noronha, **Roc+Nor**) and southern (Trindade + Martin Vaz Islets, **Tri+Mar**) island groups.

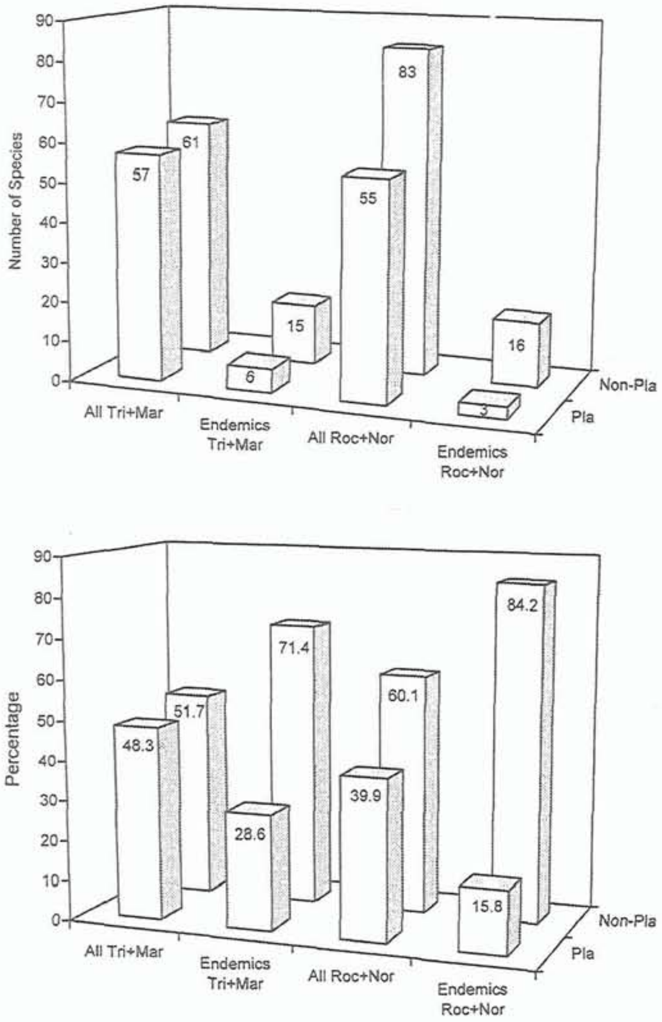

Fig. 4. Number (top) and frequencies (bottom) of basic modes of development (planktotrophic, **Pla** or non-planktotrophic, **Non-Pla**) for all species and endemics only occurring at the northern (Atol das Rocas + Fernando de Noronha, **Roc+Nor**) and southern (Trindade + Martin Vaz Islets, **Tri+Mar**) island groups.

in the taxonomic resolution of the database as it was originally established resulted from redefinition of some species, changes in knowledge about the geographic ranges of other species, and other alterations. The above mentioned alterations of the database caused the endemism rates to fall since its original publication at Martin Vaz from 15% to 9.4%, at Rocas from 14 to 8.1%, at Fernando de Noronha from 9 to 5.1%. The rate at Trindade did not change, remaining at 16%. LEAL (1991a) did not study the islands combined as island groups.

It is not an objective of this study to examine data under the assumptions of the classical theory of island biogeography (MACARTHUR & WILSON 1967). Nonetheless, it is possible that the slightly larger endemism rates of prosobranchs found at the southern group (when island rates are examined in separate) may have been determined by their greater distance from the closest landmass, represented by the Brazilian coast and continental shelf areas. Within a global framework, the prosobranch endemism rates at the two island groups (northern, 19.2%; southern 18.3%) are larger than at younger Ascension Island (12%, ROSEWATER 1975). But they are smaller than those of more isolated islands of the Hawaiian Archipelago (21%, KAY & PALUMBI 1987), Galapagos Islands (27%, FINET 1989), or than the molluscan endemisms of the Marquesas (20%, REHDER 1968), Kermadec (34%, DELL 1957), and Easter Island (42%, REHDER 1980).

MODES OF DEVELOPMENT AND ENDEMISMS

Frequency data in Figure 4 (bottom) show that there is a substantial increase in the ratio non-planktotrophs/planktotrophs among endemic species when compared to all prosobranch species both at northern and southern island groups. Although the type of data and sample size hamper statistical evaluation of the statistical significance of these differences, non-planktotrophs appear to be better represented within the assemblages of insular endemics. Although the overall ratio planktotrophs/non-planktotrophs in tropical oceanic islands may in some cases be higher when compared to adjacent continental areas (KAY & PALUMBI 1987; PERRON & KOHN 1985; REID 1985; SCHELTEMA & WILLIAMS 1983; TAYLOR 1971), retention of offspring, reproductive isolation, speciation and endemism rates in many groups of organisms should be higher for non-planktotrophs (ABBOTT 1966; HADFIELD ET AL. 1972; HOURIGAN & REESE 1987; JOHANNESSON 1988; REID 1996; SAFRIEL & HADFIELD 1988; SCHELTEMA 1986; STRATHMANN 1986). Increase in frequency of non-planktotrophs among endemics may be a result of rare chance arrivals followed by enhanced reproductive isolation in the absence of repeated, steady input via dispersal from external sources (which is consistent for planktotrophic, but reduced or absent in non-planktotrophic species) and repeated arrivals. Because some of the insular non-planktotrophic endemics are closely similar to non-insular planktotrophic species (sometimes differing conchologically from them only by protoconch morphology), it is also possible that these non-planktotrophic endemics derived from a planktotrophic ancestor that lost its free-feeding mode of development in conditions of enhanced isolation.

ACKNOWLEDGEMENTS

This stage of the project could not have been completed without the assistance of a group of people too numerous to mention here. Most of all, I am indebted to Arnaldo C. S. Coelho (Museu Nacional, Rio de Janeiro, Brasil), Eliézer de C. Rios (Museu Oceanográfico, Fundação Universidade do Rio Grande, Brasil), Philippe Bouchet (Muséum National d'Histoire Naturelle, Paris), for allowing me unlimited access to the collections under their charge. Gilbert L. Voss and Donald R. Moore (Rosenstiel School of Marine and Atmospheric Science, Miami, both now deceased) were enthusiastic supporters in the first stages of this project. I thank also J. H. McLean (Los Angeles County Museum of Natural History), Ricardo A. Absalão and Renata S. Gomes (Universidade Federal do Rio de Janeiro), and Geerat J. Vermeij (University of California, Davis) for access to unpublished information. I am also grateful to Geerat J. Vermeij and one anonymous reviewer for comments that helped improve the manuscript. The Bailey-Matthews Shell Museum provided much-needed support in the final stages of this work. I dedicate this study to my Azorean ancestors and to islanders everywhere.

REFERENCES

ABBOTT, D. P. 1966. Factors influencing the zoogeographic affinities of the Galapagos inshore marine fauna. Pp. 108-122 in: Bowman, R.I. (Ed.) *The Galapagos - Proceedings of the Symposia of the Galapagos International Scientific Project*. University of California Press, Berkeley.

ABSALÃO, R. S. & E. C. RIOS 1995. Descriptions of two new species of *Caelatura* (Gastropoda, Rissoidea, Barleeidae). *Apex* 10(2/3): 87-93.

ABSALÃO, R. S. & R. S. GOMES In press. The subgenus *Brochina* of the genus *Caecum* (Gastropoda: Caenogastropoda) in Brazil, with notes on type-specimens from the western Atlantic. *The Nautilus*.

ALMEIDA, F. F. M. 1958. *Geologia e Petrologia do Arquipélago de Fernando de Noronha*. xi + 181 pp. Monografia no. 13. Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro.

ALMEIDA, F. F. M. 1961. *Geologia e Petrologia da Ilha da Trindade*. xi + 197 pp. Monografia no. 18. Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro.

ARNAUD, P. M. 1974. Contribution à la bionomie marine benthonique des régions antarctiques et subantarctiques. *Téthys* 6: 567-653.

BOUCHET, P. 1989. A review of poecilogony in gastropods. *Journal of Molluscan Studies* 55: 67-78.

CORDANI, U. G. 1970. Idade do vulcanismo no Oceano Atlântico Sul. *Boletim do Instituto de Geociências da Universidade de São Paulo* 1: 9-76.

DARWIN, C. 1870. *Naturalist's Voyage Round the World. Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world, under the command of Capt. Fitz Roy, R.N.* (New Edition), London, Murray.

DELL, R. K. 1957. The marine Mollusca of the Kermadec Islands in relation to molluscan faunas in the southwest Pacific. *Proceedings of the 8th*

Pacific Science Congress 3: 499-503.

FAIRBRIDGE, R. W. & M. GORINI 1975. Fernando de Noronha, Rocas, Trindade, Martin Vaz, and Saint Paul Rocks. Pp. 274-277 in: Fairbridge, R.W. (Ed.) *The Encyclopedia of World Regional Geology, Part 1: Western Hemisphere (including Antarctica and Australia)*. Encyclopedia of Earth Sciences, volume 8. Dowden, Hutchinson & Ross, Stroudsbourg.

FINET, Y. 1989. Recent molluscan fauna in the Galapagos: taxonomic composition of the fauna. *Annual Reports of the Western Society of Malacologists* 21: 7.

HADFIELD, M. G., E. A. KAY, M. U. GILLETTE & M. LLOYD. 1972. The Vermetidae (Mollusca: Gastropoda) of the Hawaiian Islands. *Marine Biology* 12: 81-98.

HANSEN, T.A. 1980. Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology* 6(2): 193-207.

HARASEWYCH, M. G., R. E. PETIT & A. VERHECKEN 1992. Two new species of Cancellariidae (Gastropoda: Neogastropoda) from Brazil. *The Nautilus* 106(2): 26-37.

HOUART, R. 1991. The southeastern Brazilian Muricidae collected by RV *Marion-Dufresne* in 1987, with the description of three new species. *The Nautilus* 105(1): 26-37.

HOURIGAN, T. F. & E. S. REESE 1987. Mid-ocean isolation and the evolution of Hawaiian reef fishes. *Trends in Ecology and Evolution* 2(7): 187-191.

JABLONSKI, D. & R. A. LUTZ 1983. Larval ecology of marine benthic invertebrates. *Biological Reviews* 58: 21-89.

JOHANNESSON, K. 1988. The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*). *Marine Biology* 99: 507-513.

KAY, E. A. & S. R. PALUMBI 1987. Endemism and evolution in Hawaiian marine invertebrates. *Trends in Ecology and Evolution* 2(7): 183-186.

LEAL, J. H. & P. BOUCHET 1991. Distribution patterns and dispersal of prosobranch gastropods along a seamount chain in the Atlantic Ocean. *Journal of the Marine Biological Association of the United Kingdom* 71(1): 11-25.

LEAL, J. H. 1988. Trindade: grandeur and instability in the South Atlantic. *Sea Frontiers* 34(2): 94-99.

LEAL, J. H. 1991a. *Marine Prosobranch Gastropods from Oceanic Islands off Brazil*. Dr. W. Backhuys/U.B.S. Oegstgeest, 418 pp.

LEAL, J. H. 1991b. *Arene boucheti*, a new intertidal liotiine turbinid (Mollusca: Gastropoda: Trochoidea) from Trindade Island, South Atlantic Ocean. *Proceedings of the Biological Society of Washington* 104(2): 241-246.

MACARTHUR, R. H. & E. O. WILSON 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, 203 pp.

MAES, V. O. 1983. Observations on the systematics and biology of a turrid assemblage in the British Virgin Islands. *Bulletin of Marine Science* 33(2): 305-335.

MCLEAN, J. H. In preparation. The subfamily Liotiinae (Gastropoda: Turbinidae) in the western Atlantic.

MORGAN, W. J. 1983. Hotspot tracks and the early rifting of the Atlantic. *Tectonophysics* 94: 123-139.

Ó FOIGHIL, D. 1989. Planktotrophic larval development is associated with a restricted gene flow in *Lasaea*, a genus of brooding, hermaphroditic bivalves. *Marine Biology* 103: 349-358.

OTTMANN, F. 1963. 'L'Atol das Rocas' dans l'Atlantique Sud tropical. *Revue de Géographie Physique et Géologie Dynamique* 5(2): 101-107.

PERRON, F. E. & A. J. KOHN 1985. Larval dispersal and geographical distribution in coral reef gastropods of the genus *Conus*. *Proceeedings of the 5th International Coral Reef Congress*, Tahiti, 4: 95-100.

QUINN, J. F. JR. 1991. *Lamellitrochus*, a new genus of Solariellinae (Gastropoda: Trochidae), with descriptions of six new species from the western Atlantic Ocean. *The Nautilus* 105(3): 81-91.

QUINN, J. F. Jr. 1992a. New species of *Solariella* (Gastropoda: Trochidae) from the western Atlantic Ocean. *The Nautilus* 106(2): 50-54.

QUINN, J. F. Jr. 1992b. New species of *Calliostoma* Swainson, 1840 (Gastropoda: Trochidae) and notes on some poorly known species from the western Atlantic. *The Nautilus* 106(3): 77-114.

REHDER, H. A. 1968. The marine molluscan fauna of the Marquesas Islands. *Annual Report of the American Malacological Union for 1968*: 29-32.

REHDER, H. A. 1980. The marine mollusks of Easter Island (Isla de Páscua) and Sala y Gomez. *Smithsonian Contributions to Zoology* 289:1-167.

REID, D.G. 1985. Habitat and zonation patterns of *Littoraria* species (Gastropoda: Littorinidae) in the Indo-Pacific mangrove forests. *Biological Journal of the Linnean Society* 26: 39-68.

REID, D.G. 1996. *Systematics and Evolution of Littorina*. The Ray Society, London. 463 pp.

ROLÁN, E. 1991. El género *Amphitalamus* Carpenter, 1864 en Cuba (Mollusca, Gastropoda, Rissoidae), con descripción de tres nuevas espécies. *Iberus* 10(1): 131-141.

ROLÁN, E. 1994. Una nueva espécie de *Sinezona* (Gastropoda, Scissurellidae) del Caribe. *Iberus* 12(1): 1-5

ROSEWATER, J. 1975. An annotated list of the marine mollusks of Ascension Island, South Atlantic Ocean. *Smithsonian Contributions to Zoology* 189: 1-41.

SAFRIEL U.N. & M.G. HADFIELD 1988. Sibling speciation by life-history divergence in *Dendropoma* (Gastropoda: Vermetidae). *Biological Journal of the Linnean Society* 35: 1-13.

SCHELTEMA, R.S. & I.P. WILLIAMS 1983. Long-distance dispersal of planktonic larvae and the biogeography and evolution of some Polynesian and western Pacific mollusks. *Bulletin of Marine Science* 33(3): 545-565.

SCHELTEMA, R.S. 1971. Larval dispersal as a means of genetic interchange between geographically separated populations of shallow-water benthic marine gastropods. *Biological Bulletin* 140: 284-322.

SCHELTEMA, R.S. 1986. On dispersal and planktonic larvae of marine invertebrates: an eclectic overview and summary of problems. *Bulletin of Marine Science* (39)2: 290-322.

SHUTO, T. 1974. Larval ecology of prosobranch gastropods and its bearing on biogeography and paleontology. *Lethaia* 7: 239-256.

STRATHMANN, R.R. 1986. What controls the type of larval development? Summary statement for the evolution session. *Bulletin of Marine Science* 39(2): 616-622.

TAYLOR, J.D. 1971. Reef-associated molluscan assemblages in the western Indian Ocean. Pp. 508-536 in: STODDARD, D.R. & C.M. YONGE (Eds.) *Regional variations in Indian Ocean coral reefs*. Academic Press, New York.

THORSON, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* 25: 1-45.

THORSON, G. 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. Pp. 455-474 in: Sears, M. (Ed.) *Oceanography*, Publication 87, American Association for the Advancement of Science, Washington, D.C.

VERMEIJ, G.J. & M.A. SNYDER 1998. *Leucozonia ponderosa*, a new fasciolariid gastropod from Brazil. *The Nautilus* 112(4):117-119.

VERMEIJ, G.J., A.J. PALMER & D.R. LINDBERG. 1990. Range limits and dispersal of mollusks in the Aleutian Islands, Alaska. *The Veliger* 33(4): 346-354.

VINK, G.E., W.J. MORGAN & P.R. VOGT. 1985. The earth's hotspots. *Scientific American* 252: 50-57.

Accepted 11 November 1998