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

JOSE H. LEAL


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.

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
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
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-planktrophs 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 km². 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 km². 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 km². 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 "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. 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.

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 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).

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
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.

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REFERENCES


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


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


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.


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