



The distribution of marine gastropods is more influenced by larval development than by adult characteristics

Cristiane Xerez Barroso¹ · Tito Monteiro da Cruz Lotufo² · Alisson Sousa Matos¹ · Pedro Bastos de Macêdo Carneiro³ · Helena Matthews-Cascon¹

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Abstract

The larval stage is a critical aspect of the biology of most marine animals, impacting not only the species fitness but also its bathymetric and geographic distribution. To understand the role of larval dispersion and adult characteristics in the distribution of marine gastropods, the present study assesses the relationship among larval development type (planktotrophic, lecithotrophic, or intracapsular metamorphosis), adult characteristics (body size, depth range, and habitat diversity), and geographic distribution of benthic gastropods inhabiting shallow waters (up to 200 m depth) in the Western Atlantic Ocean. Results were generated using literature and linear mixed model (LMM) and variance partition analyses. Larval development type is the most important predictor of geographical distribution of marine gastropods analyzed here, unlike studies with reef fishes. Along with the type of larval development, the ability to occupy different types of habitats and depth ranges were also important to predict the geographic distribution, but to a lesser extent. The similar dispersal capabilities of planktotrophic and lecithotrophic larvae and the restricted geographic distribution of some species with planktonic larvae are also discussed.

Keywords Larval dispersion · Planktonic larvae · Atlantic Ocean · Benthic gastropods · Linear mixed model

Introduction

For any species, the distribution range is associated with dispersal mode, body size, population density, latitude, elevation, and bathymetric zonation (in marine systems), reflecting the interaction between limiting environmental conditions and dispersal/extinction dynamics (Brown et al. 1996). When we specifically address the geographical distribution of marine biota, along with these factors,

environmental conditions, such as seawater temperatures and ocean currents (e.g., Baptista et al. 2021a; Collin et al. 2021), and past vicariant events, such as the Tethys Seaway closure (e.g., Cowman and Bellwood 2013; Liu et al. 2018; Oskars and Malaquias 2019), the formation of mid-Atlantic Barrier (e.g., Floeter et al. 2008; Souza et al. 2017), and the emergence of the Isthmus of Panama (e.g., Fortunato 2004; Leigh et al. 2014), must also be considered.

The type of larval development (incubated, encapsulated, or planktonic) of marine invertebrates has far-reaching evolutionary consequences, relating to the dispersal capacity, geographical distribution, and species longevity (Carrier et al. 2018). Species with planktotrophic development are expected to have higher dispersion potential and, consequently, broad geographic distribution (e.g., Thorson 1950; Jablonski and Lutz 1983). Populations of these species tend to be less structured genetically, since larval dispersal by biophysical processes maintains gene flow among disjointed adult populations, suppressing genetic divergence required for allopatric speciation (e.g., Scheltema 1971; Berger 1973; Myers et al. 2000). Furthermore, in organisms that exhibit high dispersion potential, local disasters are unlikely to eliminate all individuals in its geographical range, because

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✉ Cristiane Xerez Barroso
barrosocx@ufc.br

¹ Laboratório de Invertebrados Marinhos do Ceará, Departamento de Biologia, Centro de Ciências, Universidade Federal do Ceará, Rua Campus do Pici, s/n Bloco 909 Pici, Fortaleza, CE 60440-900, Brazil

² Instituto Oceanográfico, Laboratório de Biologia Recifal, Universidade de São Paulo, Praça do Oceanográfico 191, São Paulo, SP 05508-120, Brazil

³ Universidade Federal do Delta do Parnaíba, Campus Ministro Reis Velloso, Av. São Sebastião 2819, Parnaíba, PI 64202-020, Brazil

the dispersion of a persistent population can replenish the populations reduced by local disappearance (Jablonski and Lutz 1983; Gunther 1992).

Contrarily, species with non-planktotrophic larvae tend to have limited and more continuous geographical distributions (e.g., Jablonski and Lutz 1980, 1983; Myers et al. 2000). Their local populations tend to remain isolated after initial colonization or separation from the parental population, and thus, the rates of speciation and extinction tend to be higher among these groups (e.g., Underwood 1979; Jablonski and Lutz 1980, 1983; Gilinsky 1981; Hansen 1983; Myers et al. 2000; Collin 2003).

This general pattern, however, does not seem to be universal among marine organisms. In the gastropod genus *Conus*, for example, there are few narrowly distributed species with long planktonic periods, indicating that other factors may influence distribution patterns (Kohn 2012). On the other hand, for some ascidians, higher dispersal abilities and low levels of genetic structuring were observed, despite their short planktonic larval duration (Dias et al. 2006). Since the dispersal capacities of young and adults can exceed those of a larva with a low dispersive capacity, the potential for gene flow and population genetic structure should not be inferred only from the larval type (Levin and Brigdes 1995). Studies with reef fishes have shown that adult characteristics (body size, schooling behavior, and nocturnal habits), which affect the ability to survive and establish populations in new environments, are able to predict the geographic range of species better or as well as the period of larval duration (Luiz et al. 2012, 2013).

To contribute to the understanding of the role of larval dispersion and adult characteristics in the distribution of marine gastropods, species of Patellogastropoda, Vetigastropoda, Neritimorpha, and Caenogastropoda (Cunha and Giribet 2019) were used here as a model. Considered by Thorson (1950) as good models to study the influences of different ecological conditions, marine gastropods have a relatively stable taxonomy, well-known geographical distributions, and trochophore and veliger larvae as the main dispersion mechanisms, in which the former can be suppressed during development (Fiorini 1967; Hyman 1967; Fretter and Graham 1994).

The present study, therefore, aims to assess the relationship among larval development type (planktotrophic, lecithotrophic, or intracapsular metamorphosis) and geographic distribution of marine gastropod species inhabiting shallow waters. To investigate the importance of other factors, this study also analyzes three characteristics related to adults: body size, depth range, and habitat diversity. The choice of adult traits was based on previous studies that evaluated the factors that influence the geographic distribution of species (Brown et al. 1996; Luiz et al. 2012, 2013). Thus, we

consider that these characteristics may also influence the geographic distribution of marine gastropods.

Materials and methods

Data collection (species traits and geographic range)

Taking into account the studies by Luiz et al. (2012, 2013) and earlier (Scheltema and Williams 1983; Scheltema 1986, 1989), we analyzed herein the influence of larval and adult traits on the geographic distribution of marine gastropod species. The larval characteristic considered was the type of larval development, while the characteristics of adults analyzed were: (1) depth ranges (breadth between the minimum and maximum depth recorded in meters), (2) bathymetric zonation, (3) habitat diversity (how many habitats does the species inhabit), and (4) maximum adult length (maximum shell length recorded in millimeters), a proxy for body size.

To build the present database, we used initially the list of marine shallow benthic gastropods recorded in the Caribbean and South America provided by Barroso et al. (2016). To this list, we added species recorded in North America, the Gulf of Mexico, and Antarctica. Thus, our database (latitudinal range of species, bathymetric distribution, maximum adult length, habitats, and type of larval development) was built compiling information from the literature (Online Resource 1). The geographic distribution, bathymetric ranges, and maximum adult length data were obtained mainly from the Malacolog 4.1.1 (A Database of Western Atlantic Marine Mollusca) (Rosenberg 2009). However, other references were used to obtain the necessary data for the analyses and were specified in the Online Resource 1. The taxonomy adopted was that proposed by MolluscaBase (MolluscaBase eds. 2022).

Therefore, the 238 species of gastropods considered here are benthic, present in shallow (≤ 200 m) marine biogeographic regions [sensu Briggs and Bowen (2013)] of the Western Atlantic Ocean and Antarctica and belonging to groups of non-heterobranch gastropods (species of Patellogastropoda, Vetigastropoda, Neritimorpha, and Caenogastropoda) (Online Resource 1). Species with maximum depth above 200 m were not considered in this study. Considering the marine biogeographic areas proposed by Briggs and Bowen (2012), most of the species studied (200) inhabit only Warm Regions (characterized by tropical and warm-temperate waters), 12 species are found exclusively in cool regions (cold-temperate and polar waters), and 26 species are more widely distributed, being found in both Warm and Cool Regions. According to the literature consulted (see Online Resource 1), only *Littorina littorea* (Linnaeus, 1758)

is considered exotic in the areas where it occurs in the Western Atlantic Ocean.

The type of larval development, a proxy for pelagic larval duration (PLD), was classified in: 1. planktotrophic, which involves a free-swimming larva that actively feeds on the plankton; 2. lecithotrophic, when nutrient reserves allow the developing larva to reach metamorphosis after a few hours or a few days living in the plankton, but without feeding on it; and 3. intracapsular metamorphosis, when metamorphosis occurs before hatching, often called “direct development”. This classification was based on larval ecology studies of benthic marine invertebrates (Thorson 1950; Mileikovsky 1971; Jablonski and Lutz 1980, 1983; Bouchet 1989). No generalizations were made regarding the type of larval development, since studies have already shown the variation of this characteristic in marine gastropods, with different larval types occurring within the same family or genus [see, for example, Hipponicidae (Leal 1991), Calyptraeidae (Collin 2003, 2005), and Triphoridae (Fernandes and Pimenta 2019, 2020)]. Thus, we only considered species whose type of larval development has been determined through analysis of protoconch or experiments realized in the laboratory or field (Online Resource 1). This trait was, therefore, a limiting factor in the number of species used in this study, since there are still few studies on larval development compared to the great diversity of this group.

To analyze the occupied habitats by each species, we divided them in five categories: (1) marine hard bottoms (which also included species that live on Cnidaria, Porifera, and calcareous macroalgae beds); (2) estuarine hard bottoms (including species that live on mangrove trees); (3) marine soft bottoms; (4) estuarine soft bottoms; and (5) vegetated bottoms (species that live on fleshy macroalgae and seagrass beds). In the case of parasitic species (the eulimid *Hemiliostraca auricineta*, parasite of ophiuroids, and the genus *Melanella*—parasite of holothurians), we considered the habitat occupied by its host.

Regarding the bathymetric ranges, to obtain more reliable records, only the bathymetry of live specimens was used (Online Resource 1), since empty shells can be transported between different sites (post-mortem transport) [e.g., Warwick and Light 2002; Bürkli and Wilson 2017]. Along with the type of larval development, this was another factor that limited our database, since some species only present records of empty shells [e.g., *Cerithiopsis aimen* Rolán & Espinosa, 1996, *Cerithiopsis balaustium* Figueira & Pimenta, 2008, *Cerithiopsis capixaba* Figueira & Pimenta, 2008, and *Cosmioconcha helenae* (Costa, 1983)], or there is no distinction between data from live specimens and empty shells in the studies carried out [e.g., Fernandes and Pimenta (2020) about Triphoridae, Souza and Covert (2001) about Marginellidae, and Teso and Pastorino (2011) about Olividae]. We also analyzed the bathymetric zone(s) occupied by each

species, considering three zones: 0–50.99 m, 51–100.99 m, and 101–200 m. In turn, the geographical distribution range was calculated based on the latitudinal degrees of the northern and southern limits of each species (Online Resource 1). In this analysis, we considered only the latitudinal range of species in the Atlantic Ocean (including the Antarctica). The distributional ranges of species were assumed to be continuous along the northern and southern limits.

Data analysis

To analyze the effect of larval and adult characteristics on the geographical distribution of marine gastropods, we used a linear mixed model (LMM), treating geographical distribution (range in degrees of latitude) as response variable and type of larval development (planktotrophic, lecithotrophic, and intracapsular metamorphosis), depth ranges (in meters), bathymetric zonation, habitat diversity (number of used habitats), and maximum shell length (in millimeters) as fixed variables. The non-independence of characteristics shared by related species was controlled treating taxonomic rank (genus and/or family) as a random effect (see Luiz et al. 2012, 2013). The LMM was fitted using the function “lme” from the package “nlme” (Luiz et al. 2013; Pinheiro et al. 2021) in R software (R Core Team 2022). For the construction of the predictive model, we followed the recommended procedure (e.g., Zuur et al. 2009) of fitting a model with all possible factors and interactions (i.e., the full model) and gradually removing terms that did not contribute to the explanation (considering the significance level, the Akaike information criteria, and a likelihood ratio test). This procedure was executed first for the random effects and then for the fixed terms, and the adequacy of the selected models were assessed by checking residual normality and homoscedasticity. The parameters of the final model were estimated by Restricted Maximum Likelihood (REML), but the competing models used for variable selection were fitted by Maximum Likelihood (ML) to allow meaningful comparisons (Zuur et al. 2009). We also conducted a partitioning of variance analysis to determine the relative importance (percent of explained variance) of each fixed variable in the model (independent effects), using the “hier.part” package (Nally and Walsh 2004) in R. An ANOVA was performed to find out which variables were significant in the model. The script used in the R software is available in the GitHub repository (<https://github.com/alissonfeijjaum/Barroso-et-al.git>). The data are available in the Online Resource 1.

Since the ability to cross biogeographic barriers can influence the geographic distribution of species, we analyzed the presence of marine gastropod species on both sides of the two major biogeographic barriers in the Atlantic Ocean—the mid-Atlantic Barrier and Orinoco-Amazon freshwater outflow (Floeter et al. 2008) (Fig. 1). The observed proportion

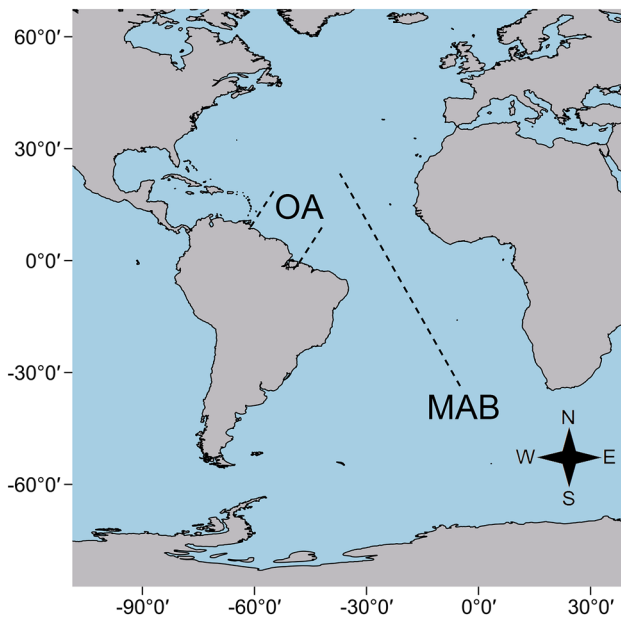


Fig. 1 Location of the studied area—Western Atlantic Ocean and Antarctica, indicating the two major biogeographic barriers in the Atlantic Ocean—the mid-Atlantic Barrier (MAB) and Orinoco–Amazon freshwater outflow (OA)

of each larval type, considering the biogeographic barriers, was compared to the proportions expected by chance, as estimated by bootstrapping with 1000 replications of the whole dataset.

Results

The most representative type of larval development was planktotrophic, with 118 species (49.6%), followed by lecithotrophic, with 61 species (25.6%), and intracapsular metamorphosis with 59 species (24.8%), totaling 238 species of marine gastropods analyzed. The maximum shell length varied from 1.25 to 492 mm. In relation to the ability to occupy different habitats, 29% of species are able to inhabit more than one type of habitat.

Our partitioning of variance analysis showed that larval development type is the most significant predictor of geographical distribution of marine gastropods (62.66%), followed by depth range (13.65%) and use of multiple habitat diversity (13.32%) (Table 1). This result was corroborated by the selected predictive model (Table 2), which excluded bathymetric zonation and maximum shell length, retaining only the three types of larval development, the depth range, and the diversity of habitats as significant predictors of the amplitude of the geographic distribution of the analyzed species (Table 3). As expected, model coefficients indicated that planktotrophic species tend to have the largest distribution

Table 1 Fixed variables ranked according to their independent effects, considering geographical distribution (range in degrees of latitude) as response variable

Fixed variables	numDF	F value	P value	IE (%)
Larval development type	2	46.856	<0.0001	62.66
Depth range	1	12.6900	0.00	13.65
Habitat diversity	1	13.3404	0.00	13.32
Bathymetric zonation	5	3.1685	0.0118	9.88
Size (maximum shell length)	1	0.1446	0.7048	0.49

The values of the independent effects (IE) are in decreasing order of contribution (percentage of explained variance), which was calculated using hierarchical partitioning. *P* values in bold are significant ($P < 0.05$) for variables

Table 2 Linear mixed models (LMMs), treating geographical distribution (in degrees of latitude) as response variable and type of larval development (Larval), depth ranges (Depth), use of multiple habitats (Habitats), Bathymetric zonation (Zonation), and maximum shell length (Length) as fixed variables

Model	AIC	P value
Random effects		
Full model without random effects	2043.5	
Full model with genus	2023.4	
Full model with genus nested in Family	2025.4	
Full model with family	2015.8	
Fixed effects		
Full model with family as random effect	2015.8	
Larval + Habitats + Depth + Zonation + Length	2002.6	0.84
Larval + Habitats + Depth	1993.2	0.94

Genera and family taxonomic ranks were treated as possible random variables. The selected predictive model (indicated in bold) was chosen based on simplicity (fewer explanatory terms), likelihood ratio test, and the Akaike Information Criteria Akaike (AIC) value. The significance (*P* value) of the likelihood ratio tests (between the model and the one listed immediately above) is also shown. All models were computed by traditional maximum likelihood (ML) to allow comparisons. Not all possible models are shown

Table 3 Parameters of the selected predictive linear mixed model (LMM), treating geographical distribution (in degrees of latitude) as response variable and type of larval development (planktotrophic—PLA, lecithotrophic—LEC, and intracapsular metamorphosis—Intercept), depth range, and the ability to use of multiple habitats as fixed variables

Variables	Estimate	SE	T value	P value
(Intercept)	13.8	3.6	3.9	0.00
LEC	18.0	3.0	5.9	0.00
PLA	25.9	2.8	9.2	0.00
Depth range	0.13	0.03	38	0.00
Habitat diversity	6.3	1.9	3.3	0.001

Family (taxonomic rank) was treated as a random variable
P values in bold are significant ($P < 0.05$) for coefficients

ranges, whereas species with intracapsular metamorphosis have the smallest. At the same time, the ability to use multiple habitats and wide depth ranges also resulted in broader distributions (Table 3, Fig. 2). Additionally, the final model, besides the fixed effects, included family as a random factor, indicating that taxonomy also plays an important role in determining species distribution range.

Regarding the presence on both sides of biogeographic barriers, among the 122 species (51.3% of 238) observed to have distributions in the two sides of the Orinoco–Amazon freshwater outflow Barrier, 70 (57.4%) have planktotrophic larvae, 39 (32%) have lecithotrophic larvae, and 13 (10.6%) show intracapsular metamorphosis. The expected proportions for each of these larval types, as estimated by bootstrapping of the whole dataset, were, respectively, 49.6% (95% C.I. 40.6%–58.6%), 25.5% (95% C.I. 17.8%–33.3%), and 24.8% (95% C.I. 17.0%–32.8%). Therefore, particularly, the number of species with intracapsular metamorphosis is significantly lower than expected by chance. *Bostrycapulus odites* Collin, 2005 is the only species (0.4% of 238) recorded on both sides of the mid-Atlantic Barrier (it is distributed in the Southwestern Atlantic and Eastern Atlantic) and shows intracapsular metamorphosis. Twenty-nine species (12.2% of 238) are widely distributed, both being recorded to the north and south of the Amazon barrier as in the Eastern Atlantic. Among them, 24 (82.8%) have planktotrophic larvae, four (13.8%) have lecithotrophic larvae, and one (3.4%) shows intracapsular metamorphosis (all three proportions are different than expected by chance). Among the 86 species (36.1% of 238) with geographic distribution restrict to one side of the Orinoco–Amazon Barrier, there are 24 (27.9%), 18 (20.9%), and 44 (51.2%) with planktotrophic larvae, lecithotrophic larvae, and intracapsular metamorphosis, respectively (again, a lower-than-expected proportion of species with planktotrophic larvae and a

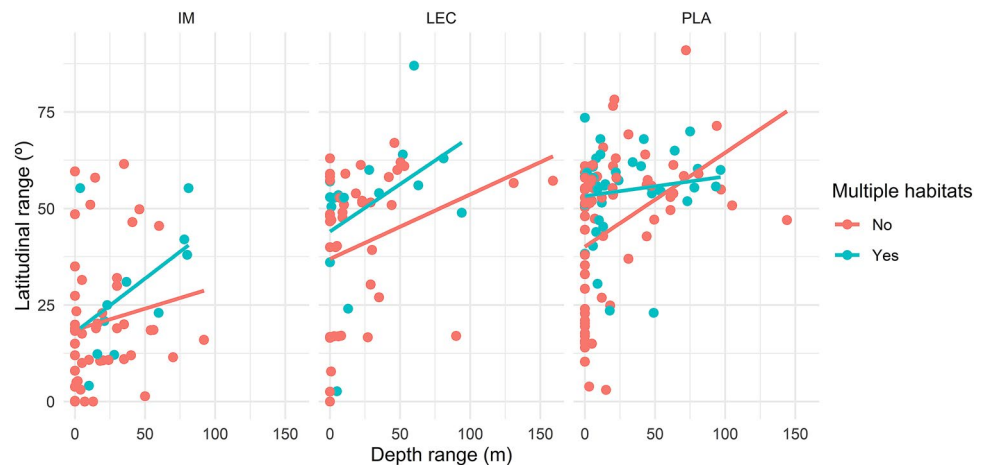
higher-than-expected proportion of species with intracapsular metamorphosis).

Discussion

Since the larval development types of marine organisms have consequences on the macro (dispersion, speciation, and extinction) and microevolutionary (gene flow) processes, understanding their variation and their role in the geographic distribution of a species becomes an important instrument for future conservation actions. Unlike studies with reef fishes (Luiz et al. 2012, 2013), the present study shows that larval development type is the most important predictor of geographical distribution of marine shallow-water gastropods when compared with the adult characteristics analyzed here. The limited mobility capacity of gastropod adults may be the main factor that differentiated our results from those of Luiz et al. (2012, 2013).

In general, our results agreed with the theoretical premises: species with planktonic (planktotrophic and lecithotrophic) larvae have a greater dispersive capacity and, therefore, broader geographic distributions than species with non-planktonic larvae (intracapsular metamorphosis) (Thorson 1950; Scheltema 1971; Berger 1973; Jablonski and Lutz 1980, 1983; Gilinsky 1981; Myers et al. 2000; Collin 2001; Guzmán et al. 2011). These broader geographic distributions of species with planktotrophic larvae (recorded on both sides of the Orinoco–Amazon freshwater outflow Barrier and, sometimes, also in the Eastern Atlantic Ocean) may result from a long period of pelagic larval duration (PLD), which could provide both a greater ability to cross large barriers of inadequate substrate and colonization of oceanic islands, promoting a wider distribution of the species (Claremont et al. 2011). The dispersal capacity can also be increased

Fig. 2 Relationship between the geographical distribution range of marine gastropods (in degrees of latitude) and their larval and adult characteristics (larval development type, depth ranges, and number of used habitats). PLA—planktotrophic, LEC—lecithotrophic, IM—intracapsular metamorphosis



in species that present, in addition to planktotrophic larvae, pelagic egg capsules, as is the case of *Echinolittorina* species (Williams and Reid 2004). In the present study, six of the ten analyzed species of *Echinolittorina* corroborate this statement, with geographic ranges greater than 20° degrees of latitude.

However, a long PLD does not always seem to be the determining factor for the wide geographic range of the species, as demonstrated by the exceptions to the theoretical premises observed in the present study (e.g., *Bostrycapulus odites* Collin, 2005, a species with intracapsular metamorphosis recorded on both sides of the mid-Atlantic Barrier) and the similar geographical ranges presented by species with lecithotrophic and planktotrophic larvae observed here and in the previous works (e.g., Scheltema 1989; Leal and Bouchet 1991; Collin 2001). Since PLD is taxon-specific and influenced by environmental conditions (such as temperature and ocean currents), dispersal distances can be specific to species, seasons, and locations (Cowen and Sponaugle 2009). Thus, the effects of factors, such as passive transport (e.g., Thorson 1950; Cumming et al. 2014), dispersion by stepping stones (e.g., Scheltema 1989; Crandall et al. 2012), dispersion by rafting (e.g., Leal and Bouchet 1991; Castilla and Guinez 2000; Aliani and Molcard 2003; Donald et al. 2005; Thiel and Gutow 2005; Bird et al. 2011; Cabezas et al. 2013; Cumming et al. 2014; Baptista et al. 2021b), dispersion by other animals (e.g., Frazier et al. 1985; Cadeé 2011; Miura et al. 2012), and changes in ocean currents (Baptista et al. 2021a), may explain the wide geographic distributions of species with lecithotrophic larvae or intracapsular metamorphosis. Johannesson (1988) argued that, in certain cases, species with non-planktonic larvae could be better dispersers on long distances than ones with planktonic larvae, highlighting the effects of passive transport of adults and mortality and diffusion during pelagic life on two species of the genus *Littorina*. Baptista et al. (2021b) discussed the role of rafting and changes in ocean currents in expanding the distribution of the gastropod *Phorcus sauciatus*, which has a pelagic short-lived lecithotrophic larvae.

Along with these factors, studies have shown that the ecological conditions required by larvae and adults of each species interfere in their dispersal capabilities and, consequently, in their geographic distributions (e.g., Scheltema 1989; Bhaud 1993; Andrade et al. 2003; Fortunato 2004; Bird et al. 2011; Claremont et al. 2011; Albaina et al. 2012). These ecological requirements could explain, for example, the restricted geographical distribution of species with planktotrophic larvae (e.g., *Crepidula argentina* Simone, Pastorino & Penchaszadeh, 2000, and *Crepidula depressa* Say, 1822). In turn, the observed wide geographic distribution of *Columbella mercatoria* (Linnaeus, 1758) and *Morum oniscus* (Linnaeus, 1767), species with intracapsular metamorphosis, could also be a result of the ability of adults to

occupy three different types of habitats (an adult characteristic considered here that plays a role in the geographic range of the analyzed marine gastropods, but to a lesser extent), together with other factors cited above.

The larval settlement is the combined result of biophysical processes, which transport the larva to potential habitats, and the exploratory behavior of the larva, after the first contact with the substrate (Abelson and Denny 1997). The ability to delay metamorphosis in the absence of suitable conditions, like adequate substrate, shown by some species (e.g., Scheltema 1971; Pechenik 1979, 1999) can also interfere with their geographical ranges. In addition to availability of natural substrate, other factors, such as habitat preferences, food availability, or inter- and intraspecific interactions, may be acting and shaping the observed distributional patterns (Cacabelos et al. 2021). Stortini et al. (2020) also observed that physical habitat characteristics were more important for the structuring of those groups with less mobile larvae in terms of dispersion than those considered more dispersive mobile, such as crustaceans.

Davis et al. (1993) argued that the ecological conditions (e.g., food availability, temperature, and salinity) during the planktonic period and the ontogenetic behavior of veligers, especially in relation to vertical migration, are factors that also interfere with the potential transport of larvae of two species of Strombidae analyzed here [*Macrostrombus costatus* (Gmelin, 1791) and *Lobatus raninus* (Gmelin, 1791)], in addition to the type of larval development. Although their planktotrophic larvae can be transported for approximately 1,400 and 1,800 km, respectively, taking into account the surface currents of the Caribbean (Davis et al. 1993), *M. costatus* and *L. raninus* have different geographical distribution ranges (59.39 and 40.33 degrees of latitude, respectively). Johannesson (1988) also discussed the effects of oceanic circulation, predation, and temperature on the larvae planktonic stage. Recent studies showed that the thermal tolerance of the early stages of development is an important factor influencing the geographical ranges of marine species (Dahlke et al. 2020; Collin et al. 2021). Dahlke et al. (2020), studying marine and freshwater fish species, which showed that the most temperature-sensitive life stages are spawning adults and embryos. Similar results were obtained for shallow-water echinoids, whose thermal tolerance of embryos is smaller than that of adults (Collin et al. 2021).

Although to a lesser extent, in our LMM, the depth range was also a significant predictor of the amplitude of the geographic distribution of marine gastropods, since a greater bathymetric amplitude can increase the probability of larvae finding areas with favorable conditions (such as adequate substrate) for their settlement. However, the bathymetric zone in which the species are found was not a significant predictor. The influence of bathymetric zonation on the geographic distribution was discussed by Ávila (2006), for

insular species of the Azores Archipelago, in which intertidal species have a wider geographic distribution than subtidal and deeper species, since they would be more prone to be rafted. In the present study, we did not directly assess the role of rafting in the geographic distribution of species. In addition to, the way how geographical distribution ranges are performed here (without distinguishing between continental and insular records) may also have obscured the role of bathymetric zones at least for insular species.

The regional scale of the present study (Western Atlantic Ocean) may have obscured the role of body size in the geographic distribution of marine gastropods. The body size can influence, for example, the passive transport (e.g., rafting and dispersion by other animals) of adults (Ávila 2006) and predation rates [gastropods with larger body sizes are less subject to predation than smaller ones, since the primary function of the molluscan shell is protection (Vermeij 1993)]. Analyzing abundance data of non-planktotrophic species, Cacabelos et al. (2021) argued that processes operating at local scales (scale of site) (not addressed in this study), such as biotic interactions, could be the main drivers of the geographic distribution of these species. Therefore, local-scale studies may clarify whether this factor has an influence or not on the geographic distribution of marine gastropods.

Another factor that cannot be ignored for the geographic distribution of many species is human interference, which can act to expand or reduce geographic distributions (Elton 1958; Capinha et al. 2015; Chan and Briski 2017). Human interventions created challenges for the understanding and interpretation of the ecology, evolution, biogeography, and conservation of marine communities. Habitat fragmentation, for example, is an increasing threat to species with limited dispersal (Cacabelos et al. 2021). Species introduction is another more obvious problem. The only exotic species included in the present study—*Littorina littorea*—is native to the northeast Atlantic Ocean and was introduced to North America by humans (Chapman et al. 2007). As Carlton (2003) suggests, presumably natural distributions of some species must be called into question.

Thus, the present study contributes to a better understanding of the role of larval and adult characteristics in the evolutionary history of marine invertebrate species. The dispersal ranges and, consequently, geographical distribution of marine gastropods studied here were shaped mainly by larval development type, followed by depth range and use of multiple habitats. Nevertheless, alternative dispersal strategies, such as rafting (González-Wevar et al. 2018) and human-mediated transport (Darling and Carlton 2018), must also be considered, as well as the factors that affect larval dispersal [e.g., food availability (Marshall et al. 2012), temperature (O'Connor et al. 2007; Ewers-Saucedo and Pappalardo 2019), ocean and coastal currents (Pringle et al. 2017),

biogeographic barriers (Tosetto et al. 2022), and climate change (Ávila et al. 2019)]. A better comprehension of how different factors act by shaping the distributions of marine species can help us understand the effects of the anthropogenic climate changes in their geographic ranges, enabling more effective conservation actions.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-022-04069-0>.

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Author contributions CXB, TMCL, and HMC conceived the ideas and designed the study; CXB, ASM, and PBMC performed statistical analyses; CXB led the writing; all the authors contributed to the writing and discussions. All authors gave the final approval for publication.

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Data and code availability All data generated or analyzed during this study are provided in Online Resource 1.

Declarations

Conflict of interest The authors have not disclosed any conflict of interest.

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Consent to participate Not applicable.

Consent to publish Not applicable.

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