GEOGRAPHY AND EVOLUTION

Using Marine Snails to Teach Biogeography and Macroevolution: The Role of Larvae and Dispersal Ability in the Evolution and Persistence of Species

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Abstract While some marine animals are capable of traveling great distances, many have limited mobility as adults and spend the majority of their lifetimes in a small geographical area or may even be cemented to a single place. While it might be expected that species with limited mobility would have small geographic distributions, some nevertheless occur over very large areas. This is the case for some marine snails (gastropods). A key factor that impacts the geographic distribution of marine snails is the type of larvae they have during the phase of their life history that follows hatching from an egg. Because adult snails do not typically travel vast distances, the mobility of the larval stage determines the species' ability to reach new territories. Some larvae are capable of long-distance travel, while others are not. An important component of the process of speciation involves geographic isolation, so the type of larvae a snail species possesses impacts the likelihood that it will become geographically isolated and give rise to a new species. Larval form also affects how long snail species will persist on geological timescales before going extinct, as well as rates of speciation. This paper briefly reviews the evolutionary consequences of different types of larval development in marine gastropods (especially cone snails, which are one of the most diverse groups of marine animals), particularly in determining the dispersal ability and geographic ranges of individual species, the amount of genetic exchange among populations within species, and the duration of species through time. The goal of this short review is to provide context and examples for classroom discussions of the connections between biogeography and macroevolution. Furthermore, a classroom activity is presented that involves students' using information about snail life history and biogeography to develop research plans (and predicted results) that could be utilized to test (i.e., support or reject) several macroevolutionary hypotheses.

Keywords Evolution · Extinction · Gastropod · Geographic range · Larvae · Snail · Speciation

Speciation, or the origination of a new species from a preexisting species, is caused by a prolonged break in genetic exchange (interbreeding) between populations within a species. Thus, the geographic isolation of populations often plays an important role in the formation of new species (e.g., Lieberman 2000; Mayr 1942). One factor that contributes to the geographic isolation of animal populations is the dispersal ability of the animals themselves. While many groups of marine animals—ranging from great white sharks (e.g., Bonfil et al. 2005) to leatherback turtles (e.g., Shillinger et al. 2008) to humpback whales (e.g., Rasmussen et al. 2007)—have members that can travel widely as mature adults, many seafloor-dwelling (known as benthic) marine invertebrates (animals lacking a backbone) do not. For example, most corals are cemented to a single place, as are tubeworms, brachiopods, and barnacles. Other invertebrates, such as many bivalves (e.g., clams, scallops, oysters, and mussels) are cemented in place or move only small distances.

Dispersal ability may affect the likelihood that populations within a species will become geographically isolated from one another, especially if individuals with limited mobility are unable to travel the distances necessary to reproduce with members of other populations within their

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species. Ultimately, this may result in speciation. Species that are more widely distributed should also be buffered from regional environmental changes and, therefore, might be predicted to persist longer on geological time scales and have longer fossil records than species with smaller geographic ranges. This may have important macroevolutionary consequences because groups with larger geographic ranges may show different rates of speciation and extinction than groups with smaller ranges (e.g., Jablonski and Roy 2003; Rode and Lieberman 2005). Using benthic marine snails (gastropods) as an example, this paper will briefly review research on the relationships between species mobility and geographic range and how those factors affect (1) patterns of genetic connectivity, (2) species longevity on geological timescales, and (3) rates of speciation. The factors underlying these relationships operate at different scales and thus shed light on the connections between micro- and macroevolutionary processes. As such, the relationships between species mobility and geographic range serve to clarify how population-level changes may translate to the origin and long-term maintenance of species. Furthermore, they present accessible examples that could fit well into a variety of high school and college-level classroom discussions and exercises on the topic of macroevolution, which deserves far more attention in curricula at all levels (see Padian 2010). A suggestion for how this information might be discussed in the classroom in a hypothesis-testing framework is presented at the end of this paper.

Dispersal Ability and Larval Development

Almost all adult marine snails live their lives on the seafloor and have limited mobility. With a few exceptions, marine gastropods can move, but only at the proverbial snail's pace. Catch-and-release experiments have shown, perhaps unsurprisingly, that individual marine gastropods do not often travel far following their larval phase. For example, Frank (1969) showed that some cowries (*Monetaria*) and cone snails (*Conus*) may not move more than about five meters (16 feet) and 20 meters (66 feet), respectively, beyond their release areas over the course of a year. Magalhaes (1948) demonstrated that whelks (*Busycon carica*) have greater rates of movement, averaging 18 meters (59 feet) per day when they are active; but even so, the most widely ranging specimen in her study traveled only about one kilometer (0.6 miles) over the course of four months. It is known that some small species may be able to drift in ocean currents (Martel and Chia 1991), but otherwise, adult snails do not travel far enough to account for the substantial ranges of some species, which in some cases may span distances on the scale of the Indo-Pacific Ocean. How then do such species naturally achieve wide ranges? The answer comes from

understanding the early life cycles of snails (and many other types of marine animals).

After they hatch from an egg, marine snails go through an immature larval phase. During this phase of their lives, many float around in the ocean plankton before settling on the seafloor to continue the rest of their life cycle. While in the plankton, they are pushed by ocean currents to new locations–in some cases far from where they hatched. The total geographic distributions of snail species are thus mostly the result of range expansions that take place, generation after generation, during the larval phase of their life cycles (other factors, such as availability of appropriate habitats, of course, are also important). It may therefore be reasonably predicted that the amount of time that a snail spends in its larval phase (in number of days) is important in determining its overall ability to disperse to new areas. The dispersal ability of a snail's larva should, therefore, be correlated to the size of its geographic distribution (but see critical review by Lester et al. 2007). Furthermore, the larval phase must be important in expanding and maintaining the geographic range of individual marine snail species.

Marine snail species exhibit a range of larval development types (or developmental modes) (e.g., Jablonski and Lutz 1983; Krug 2011; Shuto 1974; Thorson 1950). Importantly, these different developmental modes are characterized by very different amounts of time (if any) spent in the plankton. Planktotrophic larvae emerge from eggs laid on the seafloor as swimming, feeding larvae that may spend long periods of time (weeks to months; e.g., Claremont et al. 2011) developing in the plankton (and being pushed by ocean currents) prior to metamorphosizing and settling on the seafloor, often far from where they hatched. For example, many planktotrophic *Conus* species spend 20 or more days in the plankton prior to settling (Kohn and Perron 1994; Röckel et al. 1995). In contrast, when the larvae of lecithotrophic snails emerge from their eggs, they do so as non-feeding forms and spend few, if any, days in the water column before settling to the seafloor. Finally, some species exhibit direct development. In this type of development, juveniles spend no time in the water column as plankton but rather crawl away from their eggs (see Bell 2008; Jablonski and Lutz 1983). Following Jablonski and Lutz (1983), lecithtotrophic and direct-developing species are hereafter referred to as nonplanktotrophs.

Because of the long duration of their larval phase, snails species with planktotrophic development attain larger geographic ranges than nonplanktotrophic species (e.g., Hansen 1978, 1980; Kohn and Perron 1994; Paulay and Meyer 2006; Shuto 1974). As an example, consider the geographic ranges of three closely related *Conus* species: *Conus araneosus*, *Conus bandanus*, and *Conus marmoreus* (Duda and Kohn 2005; Duda and Palumbi 1999). The planktotrophic species *C. bandanus* and *C. marmoreus*—which have larvae

that spend a minimum of seven and ten days, respectively, in the water column—span much of the Indo-Pacific. In contrast, the nonplanktotrophic species *C. araneosus* occupies three much smaller, discontinuous regions (Fig. 1; developmental and geographic range data are from Röckel et al. 1995); its populations are so different from one another that two subspecies are recognized. The correlation between larval dispersal ability and range size is not unique to snails and has been demonstrated in a variety of other organisms as well (see Lester et al. 2007).

Most marine snails possess a shell during their larval phase, just as they do as adults. This larval shell is known as the protoconch (Fig. 2). The larval shell is not shed once the larva settles on the seafloor. Instead, the shell continues to grow throughout all phases of the snail's life (some species have shells that stop growing after individuals become adults). As the oldest and often most delicate part of the shell, the protoconch is frequently broken off, highly eroded, or covered by other organisms (called bio-encrusters). Sometimes, however, this protoconch stays attached to the tip (or, apex) of the adult snail shell. When it is preserved—which is more common in juvenile shells—it is useful for interpreting the developmental histories of individual species, including fossil species.

Research has shown that it is possible to predict the larval developmental mode of extant (modern) and fossil snail species from characteristics of the protoconch (e.g., Hendricks 2009; Jablonski and Lutz 1980; Kohn and Perron 1994; Shuto 1974). This can be done by measuring the diameter of the protoconch and counting the number of 360-degree coiling turns (or volutions) of the larval shell. Because protoconchs are almost always less than 1.5 millimeters in diameter, this work requires either a high-quality dissecting microscope or access to a scanning electron microscope. As a "rule of thumb," nonplanktotrophic marine gastropods have two or fewer protoconch volutions, while planktotrophic species have three or more. Determination of
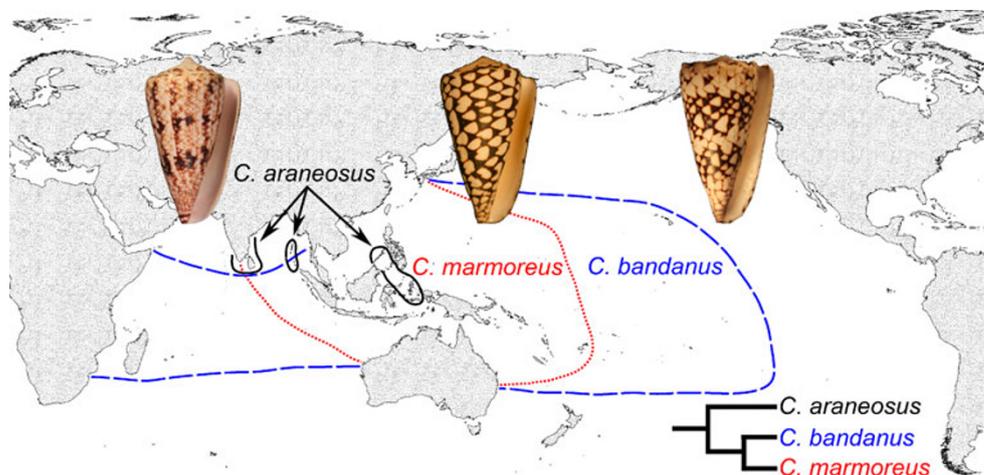
the development type of species with protoconchs that have between two and three volutions is often not possible because in this range, either developmental mode is possible (see Kohn and Perron 1994).

Developmental Mode, Genetic Connectivity, and Speciation

Because snail species with longer larval phases are more likely to be pushed further by ocean currents, it has been predicted (e.g., Hansen 1980) that distant populations will still retain strong genetic links, preventing genetic isolation. In contrast, snail species with short larval phases are less likely to disperse frequently to regions far from where they hatched and, thus, separate populations should maintain weaker genetic links (Bell 2008). Because of such potential differences in levels of genetic connectivity, populations of nonplanktotrophic species may be predicted to show, on average, greater amounts of interpopulation genetic differentiation than species with planktotrophic development, and given enough time, these genetically distinct populations may become different enough from other populations that speciation will result if members of the different populations cannot mate and produce fertile offspring (Mayr 1942). The reason for this is that the localized populations of the poorly-dispersing species are not continuously "seeded" with (i.e., connected by) new combinations of genes carried in by larvae from distant populations, which would be a more common occurrence for populations of planktotrophic species.

An interesting observation from cone snails supports the hypothesis that poorly dispersing nonplanktotrophic species show greater patterns of isolation and differentiation than planktotrophic species. Duda and Palumbi (1999) noted that *Conus* species with nonplanktotrophic development have, on average, 7.5 taxonomically equivalent (or, synonymous) names associated with them, while planktotrophic species

Fig. 1 Distribution patterns, modified after Röckel et al. (1995), of three closely related *Conus* species, *C. araneosus* (*black solid lines*; eastern two occurrences are the subspecies *C. araneosus nicobaricus*), *C. marmoreus* (*red dotted line*), and *C. bandanus* (*blue dashed line*). Phylogenetic relationships are based on molecular sequence data from Duda and Kohn (2005). See text for discussion
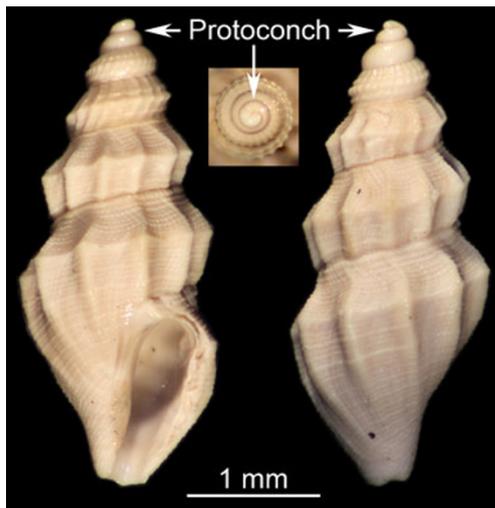
Fig. 2 Fossil snail shell from the Pinecrest Beds of the Tamiami Formation, Sarasota County, Florida. *Arrows* indicate the position of the protoconch (larval shell), which can be utilized to determine developmental mode. Images are focal stacks constructed from multiple images using Helicon Focus 5.2 (Kozub et al. 2011)

have an average of 2.2. This likely means that many of these synonymous nonplanktotrophic species are regional varieties (subspecies) in the process of differentiating into new species. Careful comparison by a team of experts (Röckel et al. 1995), however, showed these regional varieties to be synonymous based on anatomical and ecological similarities.

A second example of the relationship between dispersal ability and genetic connectivity concerns repeated observations of an aberrant population of sinistral, or left-handed, *Conus ventricosus*. Almost all marine snail species are dextral: The shell opens on the right side when held with the spire pointing upwards (shell coiling direction is controlled by a single, but unknown, gene; e.g., Ueshima and Asami 2003). This is also typically the case in *C. ventricosus*. Donati et al. (1984), however, reported several sightings over an eight-year period of sinistral *C. ventricosus* living alongside normal dextral individuals in shallow waters near Sardinia. Sinistral and dextral conspecific snails may not be able to orient their mirror-image shells correctly for mating (e.g., Ueshima and Asami 2003), and it is assumed that this is the case for oppositely coiling *C. ventricosus*. This suggests that a persistent population of reproductively compatible sinistral individuals has been maintained near Sardinia over time. Furthermore, this assertion is supported by the fact that *C. ventricosus* has nonplanktotrophic development (Kohn and Perron 1994). Were *C. ventricosus* larvae planktotrophic, it is not likely that such a viable population could be maintained because similarly coiled, reproductively compatible sinistral individuals would be scattered by the currents during their larval stage and the chance that they would meet as adults and

successfully reproduce would be very low. For further discussion, see Hendricks (2009).

Phylogeographic studies consider degrees of relatedness among individuals of the same species across geographical space, allowing measurement of the amount of genetic connectivity between different populations. The hypothesis that planktotrophic species should show greater genetic connectivity across vast ocean distances relative to nonplanktotrophic species (e.g., see Palumbi 1994) has been supported by some phylogeographic studies (e.g., Johnson and Black 2006a). A growing number of studies have recently suggested, however, that the story may sometimes be more complicated than this. For example, Van den Broeck et al. (2008) demonstrated the existence of genetically differentiated populations of the periwinkle *Tectarius striatus* across a stretch of ocean separating the Cape Verde Islands from other archipelagos in Macronesia, despite the fact that this species has planktotrophic development. They demonstrated that none of the haplotypes considered in their study—which "showed 0.10–1.61 % sequence divergence" (p. 424)—were shared by populations separated by this stretch of ocean. Johnson and Black (2006b) demonstrated that populations of a planktotrophic snail species, *Austrocochlea constricta*, showed considerable genetic differences over short distances. This work suggests an important role for currents near islands in limiting dispersal of planktotrophic larvae and favoring their retention near the location from which they hatched. As suggested by these studies, there is a growing view that a significant proportion of marine invertebrate larvae may settle close to their birthplace, thereby limiting long-distance genetic connections in some species regardless of their potential for long-distance larval dispersal (see recent reviews in Hellberg 2009; Weersing and Toonen 2009). More phylogenetic studies will need to be conducted to determine the extent to which larval dispersal ability affects genetic connectivity—and, therefore, the likelihood of speciation—in marine snails. For additional information on the varied factors that may contribute to divergence and speciation in marine snails, see Allmon and Smith (2011).

Geographic Range and the Persistence of Species

The geographic range and persistence of species on geological time scales may be closely related (e.g., Gould 2002; Jablonski 1986, 1987; Jackson 1974; Stanley 1979). For instance, a regionalized environmental perturbation (such as a major pollution event) could cause the extinction of a narrowly ranging species. A more broadly dispersed species, however, may go extinct locally (that is, become extirpated), but survive on elsewhere (e.g., Jablonski 1986). Following the environmental perturbation, the broadly ranging species might be able to reoccupy the full extent of its former range. On

geological timescales, this would result in widely ranging species showing longer stratigraphic ranges (i.e., the period of time between speciation and extinction for a given species) relative to narrowly distributed species. Paleontologists have used the fossil record to investigate whether such an association exists in a variety of different marine animals (e.g., Hansen 1978, 1980; Harnik 2011; Hendricks et al. 2008; Jeffery and Emlet 2003; Rode and Lieberman 2004) and have also studied how the scale of the environmental perturbation (e.g., Jablonski 1986) has affected any such associations. I will review several examples from the fossil record of snails.

Hansen (1978) investigated the fossil records of volutid snails from the southeastern United States and showed that planktotrophic species had paleogeographic ranges that were over two times greater than nonplanktotrophic species. This difference in geographic ranges also extended to species survivorship on geological time scales: Planktotrophic volute species survived an average of 4.4 million years, while nonplanktotrophic species lasted only half as long (Hansen 1978). Similarly, Gili and Martinell (1994) found that planktotrophic species of *Nassarius* from European and Mediterranean fossil deposits have a median duration of 9.8 million years, while the median duration of nonplanktotrophic species was 2.8 million years. Crampton et al. (2010) also demonstrated strong correspondence between species longevity and geographic range in a variety of snails (and bivalves) from New Zealand. These and other studies lend support to the hypothesis that species with greater geographic ranges may be buffered against regional environmental perturbations and therefore have higher rates of survivorship over long periods of geological time.

Jablonski (1986) investigated the hypothesis that greater geographic range confers a survival advantage against extinction. He tested this hypothesis by studying fossil snails and bivalves from sediments laid down before and after the end-Cretaceous mass extinction event (which was caused by an asteroid impact that resulted in the extinction of the dinosaurs and many other organisms; Alvarez et al. 1980). He found that while more broadly distributed species are buffered against extinction relative to more restricted species during "normal times" (characterized by steady rates of background extinction that have existed throughout the history of animal life; see Raup and Sepkoski 1982), this advantage was not conferred to species across the end-Cretaceous mass extinction boundary. Jablonski showed, however, that widespread lineages (genera, or collections of closely related species) did have a survival advantage during the mass extinction interval, suggesting that different types of selection processes operate during mass extinction events relative to those that are important during normal times (for additional details, see Jablonski 1986, 1987).

An additional interesting line of macroevolutionary study has considered the question of whether larval developmental mode can affect rates of speciation (for recent reviews, see Allmon and Smith 2011; Krug 2011; Lester et al. 2007). The argument is that nonplanktotrophic species should become isolated, on average, more frequently than planktotrophic species (see related discussion above) and therefore should show higher rates of speciation. Hansen (1983) demonstrated that this was the case in some fossil snail groups, although his study was not conducted within an explicit phylogenetic framework (a phylogeny is an hypothesis of how a group of organisms are related to one another; it can be thought of as an evolutionary tree). Phylogenetic context is important for exploring this issue because it makes a significant difference whether species with nonplanktotrophic development are found to be grouped closely together on phylogenetic trees or whether they are found to show multiple independent origins within predominantly planktotrophic groups. The former type of evidence would support a hypothesis of increased speciation rates in poorly dispersing taxa, while the latter would not. For examples of studies that conducted such research, see Lieberman et al. (1993) and Duda and Palumbi (1999); evidence seems to suggest that different groups may show different patterns. Differential speciation rates between lineages with differing capabilities of becoming widely dispersed have also factored importantly into discussions of species selection (analogous to natural selection, but operating on entire species rather than individual organisms). This interesting idea will not be discussed further here, but the reader is referred to Lieberman and Vrba (2005) and Jablonski (2008) for recent overviews.

Classroom Discussion: Macroevolutionary Hypothesis Testing

The information presented above provides background that may allow high school and undergraduate students to discuss biogeography and macroevolution in a hypothesis-testing framework. The following format for such a discussion is suggested:

1. Introduce students to the idea of speciation resulting from barriers to gene flow, particularly geographic isolation.
2. Discuss with students the varied mobilities of marine animals. Ask them to provide examples of animals that may travel great distances over the life span of the animal, as well as examples of those that may not travel far. Consider purchasing an inexpensive "Sea Monkey" (registered trademark, Transcience Corp.) exhibit for your classroom to demonstrate basic features of plankton, in this case, brine shrimp called *Artemia*; these are available at many toy stores.
3. Discuss with students what factors might contribute to the total geographic range of an individual species. Ask

them to present reasons why they think that some species might have wide geographic ranges, while others are narrowly distributed.

4. Introduce your students to marine snails. Ask them if they have ever observed or collected snail shells at the beach. Show your students photographs of living marine snails so that they have a better understanding of the animal that makes and lives in the shell. If you have any shells available, show them to your students.

5. Present a brief overview of snail larvae to students, stressing the fundamental life history differences between planktotrophic and nonplanktotrophic species: Planktotrophic species often have larvae that feed in the water column for periods of weeks to months, while nonplanktotrophic species do not feed in the water column and settle on the seafloor soon (if not immediately) following hatching. Explain to students how the developmental modes of many marine snail groups can be determined from inspection of protoconchs (Fig. 2) and stress that it is possible to make such observations on both modern and fossil shells.

6. Given this background, ask students to break into groups to develop research plans for testing each of the following hypotheses. Ask your students to be as specific as possible about how they would actually carry out their research plans and ask them to brainstorm about why each of the hypotheses was proposed in the first place. Furthermore, ask your students to make predictions about the expected results; what results would provide support for the hypothesis, and what results could instead cause the hypothesis to be rejected?

   a. Planktotrophic species are more widely distributed than nonplanktotrophic species.
   b. Planktotrophic species show greater amounts of gene flow across their ranges than nonplanktotropic species.
   c. Planktotrophic species are more resistant to extinction and therefore persist longer on geological time scales relative to nonplanktotrophic species.
   d. Planktotrophic groups of species show lower rates of speciation than nonplanktotrophic groups.

7. Conclude with a discussion of current research results (reviewed above) that relate to these hypotheses. Describe to your students how scientists have tested these hypotheses, and highlight studies that have provided support for or evidence against each hypothesis.

Conclusion

Padian (2010, p. 206) convincingly argued that "macroevolution must take a much more prominent place in K-12

science teaching" as well as at the college level. The shells of marine snails—if not their animal inhabitants—are familiar natural objects to many people and, with a small amount of introduction to their life histories, provide opportunities to discuss a number of core macroevolutionary principles in the classroom. Marine snail species have varied larval developmental modes, and these correspond with their ability to become dispersed by ocean currents: Species with planktotrophic larvae tend to have greater geographic ranges than species with nonplanktotrophic development. Because a key factor in speciation is geographic isolation, these differences in dispersal ability may factor importantly in the breakdown of genetic connectivity between isolated populations over time. It is possible to infer the developmental modes of well-preserved, extinct snail species from features of their larval protoconch and therefore the role that life history characters play in marcoevolutionary processes that operate over geological time scales. Paleontological studies (see above) have demonstrated that greater geographic range (as often exhibited by planktotrophic species) frequently confers a survival advantage (as measured by stratigraphic longevity) to species over long time spans, but not necessarily during mass extinction intervals. While more narrowly ranging species have higher rates of extinction than widely ranging species, they also often exhibit higher rates of speciation. In summary, with a little introduction, marine snails provide many accessible opportunities to bring discussions of natural history, biogeography, and macroevolution into the classroom.

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