EGG SIZE EVOLUTION IN TROPICAL AMERICAN ARCID BIVALVES: THE COMPARATIVE METHOD AND THE FOSSIL RECORD

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Abstract.—Marine organisms exhibit a wide range of egg sizes, even among closely related taxa, and egg size is widely considered to be one of the most important components of the life histories of marine species. The nature of the trade-off between egg size and number and the consequences of variation in egg size for offspring growth and survivorship have been extensively modeled. Yet, there is little empirical evidence that supports the relative importance of particular environmental parameters in engendering the tremendous variation in egg size seen in marine organisms. This study compares egg sizes between six geminate species pairs of bivalves in the family Arcidae to determine whether egg size differs in predictable directions between geminate species in the two oceans separated by the Central American isthmus, and whether the direction and timing of egg size evolution among geminates in this family is correlated with both modern and paleoceanographic patterns of oceanic productivity. In all modern members of six geminate pairs, egg size was larger in the species in the western Atlantic than in its sister species the eastern Pacific. This pattern supports the hypothesis that optimal egg size differs in the two oceans due to the low productivity and poor larval feeding environment in the western Atlantic relative to the eastern Pacific. The fossil record of one geminate pair shows that egg size has remained consistently large in the western Atlantic from the Miocene to the Recent, while egg size in the eastern Pacific has decreased to the current small size in less than 2 million years; this suggests that modern-day differences between egg sizes in the western Atlantic and eastern Pacific are due to either an increase in productivity in the eastern Pacific and subsequent selection for smaller eggs in that ocean, or differential patterns of extinction that occurred well after the rise of the isthmus. These results agree with ancestral character state reconstruction using linear parsimony, but differ from squared-change parsimony reconstructions.

Key words.—Ancestral character state reconstruction, Isthmus of Panama, larval development, life-history evolution.

Egg size is widely considered to be one of the most important components of the life histories of marine organisms (Thorson 1950; Vance 1973; Christiansen and Fenchel 1979; Strathmann 1985; Jaeckle 1995; Levitan 2000; McEdward and Miner 2003). In general, life-history strategies of marine invertebrates are closely correlated with egg size: species that produce small eggs have high fecundity (Thorson 1950; Crisp 1976), feeding larvae with long developmental times (Thorson 1950; Strathmann 1985; Emlet et al. 1987; Havenhand 1993), high dispersal and large geographic range (Bhaud 1993; Emlet 1990), and increased geological longevity (Hansen 1978, 1980; Jablonski and Lutz 1983; Jeffery and Emlet 2003), while the converse holds true for species with large eggs. In species with feeding larvae, egg size is thought to represent the action of natural selection balancing the advantages of high fecundity against the high mortality experienced by larvae that spend extended periods of time feeding in the plankton (Vance 1973; Christiansen and Fenchel 1979; Strathmann 1985; Emlet et al. 1987; but see Levitan 1993). The evolution of large eggs and independence from larval food may also be a prerequisite for the evolutionary transition from feeding to nonfeeding development (Havenhand 1993, 1995; Hart 1996; Hart et al. 1997).

Egg size of free-spawning marine invertebrates is likely influenced by many environmental factors and developmental constraints. High mortality of larvae in the plankton caused by starvation, predation, or advection away from suitable settlement substrate is thought to select for larger and yolkier eggs, whereas smaller egg sizes and higher fecundity should be favored when larval mortality is low (Vance 1973; and others reviewed by Havenhand 1995; Levitan 2000). In taxa

with nonfeeding larvae, increased investment per egg may also lead to increased fitness of postmetamorphic juveniles (Emlet and Hoegh-Guldberg 1997; Moran and Emlet 2001; Marshall et al. 2003). Other factors such as fertilization kinematics are likely to influence egg size evolution as well (Levitan 1993, 1998). Therefore, egg size may have predictive power for inferring other important life-history parameters that are more difficult to measure, such as fecundity, fertilization success, dispersal, and survival of larvae and juveniles from a wide range of marine taxa.

Despite the tremendous body of theory surrounding the evolution of egg size in marine invertebrates (e.g., Vance 1973; Christiansen and Fenchel 1979; Strathmann 1985; Emlet et al. 1987; Levitan 2000; and other studies reviewed by Havenhand 1995; McEdward 1997), there have been few direct tests of theoretical predictions. Experimental reductions in egg size have been shown to result in reduced larval size (Hart 1995; McEdward 1996), slower development through early stages (Sinervo and McEdward 1988; McEdward 1996), and decreased juvenile performance (Emlet and Hoegh-Guldberg 1997), as predicted by theory. It is not known whether such manipulative tests accurately mimic the effects of an evolutionary change in egg size, and these tests cannot directly identify the potential selective agents associated with long-term patterns of egg size evolution. Only the direct tracking of evolutionary changes in egg size relative to known changes in oceanic environment can provide a historical test of the ecological and evolutionary parameters that are important in shaping life histories of marine organisms.

This study applies a combined paleontological, biogeographical, and phylogenetic approach to the study of life-

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history evolution in marine systems, by examining egg size evolution in a family of marine bivalves relative to a major biogeographic event. In recent years, considerable attention has been focused on identifying evolutionary and environmental patterns associated with the rise of the Central American isthmus (e.g., Lessios 1990; Cunningham and Collins 1994; Knowlton and Weight 1998; Budd and Miller 2001; Marko and Jackson 2001; Wellington and Robertson 2001; Marko 2002; and other references in Jackson and Budd 1996). The rise of the isthmus closed the Central American Seaway (CAS) that connected the tropical western Atlantic (WA) and tropical eastern Pacific (EP) oceans until 2.8–3.1 million years ago (Keigwin 1982; Duque-Caro 1990; Coates and Obando 1996; Collins 1996), and separated the tropical American ocean into two environments that are now strikingly different. Notably, the modern equatorial EP experiences strong seasonal upwelling that drives high planktonic primary productivity, while the WA experiences little upwelling and low primary production (Glynn 1982; Keigwin 1982; Marra et al. 1987; D'Croz et al. 1991; Allmon et al. 1993, 1996b; Jackson et al. 1996). Prior to the closure of the CAS, environmental differences between the oceans are thought to have been minor (Keigwin 1982; Jones and Hasson 1985). Modern differences are thought to have arisen at approximately the same time as CAS closure and were caused largely by a substantial drop in WA productivity (references summarized in Allmon 2001) that has been implicated in the widespread faunal turnover that occurred in Late Neogene tropical America (Stanley 1986; Vermeij and Petuch 1986; Allmon et al. 1993; Jackson et al. 1993, 1996; Todd et al. 2002). In the EP, upwelling and hence productivity also intensified due to changes in circulation related to the closure of the CAS (Teranes et al. 1996; Ibaraki 1997).

The closure of the CAS also isolated populations of previously continuous species in the WA and EP basins, forming large numbers of what are known as "geminate" species pairs (Jordan 1908) that occur in many phyla. Although recent molecular and paleontological work suggests some geminate species were likely isolated long before final closure of the CAS (Bermingham and Lessios 1993; Knowlton et al. 1993; Collins 1996; Bermingham et al. 1997; Knowlton and Weigt 1998; Marko and Jackson 2001; Marko 2002), the presence of numerous closely related species pairs in which one occupies the WA and its closest relative is found in the EP nevertheless offers a unique, replicated natural experiment that can shed light on the evolutionary forces shaping life-history evolution. When comparing the life-history characteristics of geminates between the two oceans, a striking pattern of egg size variation has been found across the isthmus; in echinoderms with free-living larvae that feed in the plankton (planktotrophic), WA members of geminate pairs have larger eggs than their EP counterparts (Lessios 1990). This pattern has been attributed to the transisthmian differences in productivity set up by the closure of the CAS and primarily to the drop in productivity that occurred in the WA (summarized in Allmon 2001): large eggs in the WA may represent increased yolk reserves to offset a poor larval feeding environment in that ocean (Lessios 1990).

Whether these patterns are also found in free-spawning marine invertebrates other than echinoderms is not known.

Indirect support for the importance of productivity changes in affecting life-history evolution has also come from gastropods, corals, bryozoans, and shrimp. Among Recent bryozoans, WA species have larger eggs and larger newly settled juveniles than their EP counterparts; this may be related to the enhanced feeding ability of large bryozoan juveniles, an important trait in food-poor environments (Jackson and Herrera 1999). An unusually large proportion of Caribbean corals have nonfeeding larvae (Richmond and Hunter 1990), and strombinid gastropods show a Pliocene shift from planktotrophic to direct development in the WA (Jackson et al. 1996). Likewise, in one species pair of alpheid shrimp, the EP species has more prolonged feeding development than its WA geminate (Wehrtmann and Albornoz 2002). These patterns are consistent with evolutionary trends expected in marine organisms in response to a change in oceanic productivity that alters the amount of food available to early life-history stages.

To date there are no data (other than patterns noted above) from free-spawning taxa to support the hypothesis that modern egg size differences between related taxa are functionally connected to productivity differences between the two oceans. This study examines egg size distributions in the bivalve family Arcidae and shows that, as in free-spawning echinoderms, WA members of this family of largely free-spawning planktotrophic molluscs have larger eggs than their EP geminates. I also demonstrate that features of the arcid larval shell (preserved on the adult shell) can be used to infer egg size from adult fossil and Recent specimens. Using this technique, I examined the arcid fossil record of one geminate species pair from the tropical American Neogene to test the hypothesis that egg size evolution occurred contemporaneously with the inferred Pliocene drop in WA primary productivity (Keigwin 1982; Allmon 2001) and to determine the direction of egg size evolution relative to changes in productivity. I further examined the direction of egg size evolution by mapping egg size of Recent arcids onto a molecular phylogeny and reconstructing ancestral character states for all pairs. These data together provide a powerful mechanism for tracing the evolution of life-history traits in time and space, and for testing hypotheses regarding the influence of oceanic productivity changes on the evolution of larval life histories.

MATERIALS AND METHODS

Study Organisms

The organisms studied here are bivalves in the family Arcidae, a large, well-defined, and highly diverse clade of bivalves distributed worldwide consisting of at least 150 recognized species (Olsson 1961; Keen 1971; Abbott 1974). Tropical American arcids (approximately 60 nominal species) have received considerable taxonomic attention due to their abundance and diversity within the tropical Caribbean and Pacific. Arcids also have an extensive and well-dated fossil record from Neogene tropical America, and the family contains six geminate species pairs that are supported as sister taxa by a molecular phylogeny containing all geminates and 13 other nominal species from tropical America (Marko 2002).

TABLE 1. Localities of arcid collection sites. Species are grouped in geminate pairs, with the Eastern Pacific species listed first. Asterisk indicates a site from which egg size measurements were made. At sites not marked with an asterisk, specimens did not contain ripe oocytes.

Species	Ocean	Collection Locality
Arca mutabilis	Eastern Pacific	1, 3*, 4*
A. imbricata	Western Atlantic	8*, 9*
A. pacifica	Eastern Pacific	1, 3, 4
A. zebra	Western Atlantic	8*, 9*
Barbatia gradata	Eastern Pacific	3*, 4*
B. domingensis	Western Atlantic	7, 11*
B. reeveana	Eastern Pacific	1*, 3, 4
B. candida	Western Atlantic	8*, 9*
B. illota	Eastern Pacific	3*, 4
B. tenera	Western Atlantic	7, 10*
Arcopsis solida	Eastern Pacific	1*, 2, 3
A. adamsi	Western Atlantic	7*, 10, 11
Barbatia cancellaria	Western Atlantic	7*, 8*, 9*
B. bailyi	Eastern Pacific	—
B. bailyi sp.	Eastern Pacific	5*
Anadara concinna	Eastern Pacific	6*
Anadara nux	Eastern Pacific	6*

Ocean	Collection Localities
Eastern Pacific	
1	Playa Venado and Isla Venado, Panama
2	Punta Bique, Panama
3	Isla Périco, Panama
4	Isla Taboga, Panama
5	Islas Secas, Panama
6	Gulf of Chiriquí, Panama
Western Atlantic	
7	Mangrove Inn, Bocas del Toro, Panama
8	Hospital Bight, Bocas del Toro, Panama
9	Bocas del Drago, Bocas del Toro, Panama
10	Isla Magote, Colón, Panama
11	Viento Frío, Colón, Panama

Egg Size of Recent Species

Members of 16 arcid species were collected live in Panama, including specimens of each member of the six geminate pairs and four additional species that lack geminates. Species names and collection sites are shown in Table 1. Data for an additional species, *Barbatia bailyi*, were obtained from Moran (2004). Adults were brought back to the laboratory, opened, and gametes were stripped from the ovaries of females. Females contained oocytes at a variety of developmental stages, but when mature oocytes were present their size did not vary greatly within females. Mature oocytes were identified by the presence of a clearly defined germinal vesicle, detachment from the ovary wall (determined by presence or absence of an attached pedicle), and the presence of a rounded and clearly defined egg membrane. To measure oocytes, gametes were placed in sea water under a coverslip on tall (~ 1.5 mm) clay feet (to avoid compression) on a microscope slide. Fifteen ripe oocytes from each individual were randomly selected by traversing the slide from left to right and examining the first ripe oocytes that came into the field of view. The two maximum diameters of each oocyte were then measured under an Olympus (Olympus America, Inc., New York) BH-2 compound microscope at 40X, accurate to the nearest 2 μm. Volume (v) of each egg was estimated as the volume of a prolate spheroid, $v = (4/3) \pi a^2 c$, where a was the shortest (equatorial) radius and c was the longest (polar) radius. Volumes of ripe oocytes were measured from three to seven individuals each of 16 species (Table 2). For one species, *Arca pacifica* (the EP geminate of *Arca zebra*), ovaries of several females were examined but none contained ripe oocytes. Direct egg size measurements were therefore not available for this species, but *A. pacifica* egg sizes were estimated from prodissoconch I height measurements (see below) and are included in Table 2.

Within five geminate pairs of arcids, the significance of egg size differences between EP and WA species was tested (within pairs) using five mixed-model nested analyses of variance (ANOVAs). Species (EP or WA) and female were the independent variables, with female as a random factor nested under species. Egg volume was the independent variable. Five Student's t-tests in which the data were the grand mean of egg sizes of each female averaged for each species were also performed as a second way to compare egg size between EP and WA members of each geminate pair. Student's t-tests were performed in addition to nested ANOVAs because sample sizes were unequal between members of three of five geminate pairs (meaning a loss of power in the ANOVA model) and because of significant variance heterogeneity in all five geminate pairs.

Two tests were employed to compare egg sizes among oceans. First, using the means and standard deviations of egg sizes of each species, a paired Student's t-test with pairing

TABLE 2. Grand means of the longest egg diameters and egg volumes of 17 species of tropical American arcid bivalves, including six geminate pairs (the first 12 species, listed in pairs, with the EP species first) and five additional species. The raw difference and percent difference between geminates are also shown. Percent difference was calculated by dividing the volume of a species by the volume of its geminate. Volume was calculated from the two greatest diameters (shorter diameter data not shown) using the formula for an oblate spheroid ($4/3 \pi a^2c$). All sizes were directly measured except for egg diameters and volumes of *Arca pacifica*, which were estimated from prodissoconch measurements as described in the text.

Species	Ocean[1]	n	Egg diameter (longest, μm) ± SD	Difference from geminate (μm)	Egg volume[2] ± SD	Difference from geminate (μm³)*	Percent of volume of geminate
Barbatia illota	EP	6	64.8 ± 1.5	−2.7	132.9 ± 6.4	−11.2	92.2
B. tenera	WA	6	67.5 ± 0.4	+2.7	144.1 ± 10.5	+11.2	108.4
Barbatia reeveana	EP	7	55.9 ± 1.1	−5.6	85.2 ± 5.7	−25.9	76.7
B. candida	WA	5	61.5 ± 2.2	+5.6	111.1 ± 8.7	+25.9	130.4
Barbatia gradata	EP	3	69.5 ± 2.9	−5.4	157.5 ± 14.0	−43.0	78.5
B. domingensis	WA	4	74.9 ± 0.8	+5.4	200.5 ± 3.6	+43.0	127.3
Arca mutabilis	EP	5	61.4 ± 2.1	−12.6	106.1 ± 7.6	−65.3	60.8
A. imbricata	WA	5	74.1 ± 5.7	+12.6	171.4 ± 27.3	+65.3	161.6
Arcopsis solida	EP	6	65.7 ± 1.8	0.00	128.3 ± 12.2	−1.5	98.9
A. adamsi	WA	5	65.7 ± 2.0	0.00	129.8 ± 11.0	+1.5	101.1
Arca pacifica	EP	3	69.7 ± 6.1	−7.3	162.3 ± 44.0	−52.9	75.4
A. zebra	WA	5	77.0 ± 4.5	+7.3	215.2 ± 37.1	+52.9	132.6
Barbatia cancellaria	EP	6	116.5 ± 3.5	—	657.0 ± 86.3	—	—
Barbatia bailyi	EP	1	216.8 ± 5.9	—	5068.0 ± 361.7	—	—
B. bailyi sp.	EP	8	170.4 ± 10.6	—	2140.7 ± 388.9	—	—
Anadara concinna	EP	7	52.9 ± 1.0	—	63.5 ± 4.7	—	—
Anadara nux	EP	6	53.6 ± 5.5	—	55.8 ± 24.0	—	—

[1] EP, Eastern Pacific; WA, Western Atlantic.
[2] Egg volumes expressed as cubic microns × 10^4.

between geminates was performed to compare the egg size of WA species and EP species. The paired Student's *t*-test takes into account both the direction and magnitude of differences among oceans. As a second, nonparametric test of differences between oceans, a sign test was also performed to test the significance of trends in the direction (or sign) of each difference (i.e., whether there are significant differences in the direction of differences in egg size between geminates in each ocean; Zar 1984).

Prodissoconch Measurements

It has been well established that certain morphological characters on the shell of larval bivalves can be used to infer certain life-history characteristics, including both larval developmental mode (feeding, nonfeeding, or brooded) and egg size (Ockelmann 1965). Because the initial larval shell, or prodissoconch I (PD I), is formed directly around the yolk mass of the egg early in development, egg size is tightly correlated with PD I height both among species (Ockelmann 1965) and within species (Goodsell and Eversole 1992, for *Mercenaria mercenaria*). To determine whether this relationship also held for arcid bivalves, PD I height was measured and regressed on measurements of maximum egg diameter (as measured above) for 12 arcid species. Shell specimens for PD I measurements were either collected in Panama by the author or P. Marko (at sites listed in Table 1) or borrowed from museum collections at the Los Angeles County Museum of Natural History (LACM), the Smithsonian Natural History Museum, Washington, D.C. (UNHM), or the Naturalhistorisches Museum, Basel (NMB). Shells were first visually examined for the presence of an intact prodissoconch under a dissecting microscope (Wild Model 5A or Olympus SZX9, Wild Leitz, Ltd., Heerbrugg, Switzerland). It was generally

evident under the dissecting microscope whether the prodissoconch was present and in good condition. If the prodissoconch was obscured with dirt or detritus, shells were briefly (~ 1/min) immersed in boiling bleach to clean. If the prodissoconch was hidden by the coiling of the adult shell, as was regularly the case in large adults of several species, the obscuring adult shell was gently abraded away with a slow-speed hand-held drill (Dremel, Racine, WA) equipped with a fine sandstone point until the prodissoconch was visible (this technique was not performed on museum specimens).

To make closer observations of the prodissoconch, prepared adult or juvenile shells were mounted on double-sided adhesive carbon tabs (Ted Pella, Inc. Redding, CA), coated with gold/palladium, and examined on a Jeol (Jeol USA, Peabody, MA) JSM 6300 scanning electron microscope (SEM) operated at 15 kV. Images were digitally recorded and the height of the PD I was measured on digital images with Olympus BioSuite software (Olympus Corp.). PD I height was measured as the longest distance across the D-hinge larval shell.

Prediction of Egg Size from Prodissoconch Size

To obtain the relationship between egg size and PD I size for arcids, egg diameter measurements were regressed against PD I width for each of the 12 species for which both datapoints (egg size and PD I width) were collected. The slope of the best fit line was estimated using ordinary least squares regression (Sigmaplot 5.0, Jandel Scientific, SPSS Inc., Chicago, IL), and this equation was used to predict the egg diameter of adult animals from their PD I.

To estimate changes in egg diameter over time relative to the closure of the CAS, fossil arcid shells from the Neogene (i.e., Miocene, Pliocene, Pleistocene) of tropical America

were examined and the PD I values of well-preserved specimens were photographed and measured as above for Recent specimens. Estimated egg diameter was then calculated using the regression equation obtained from egg size and PD I measurements of Recent specimens. Fossils all came from the Panama Paleontology Project collections held at NMB, and to preserve specimen integrity, museum specimens were not cleaned with bleach or drilled prior to examination. Prodissoconchs are microscopic (generally <300 μm in width) and are found on the oldest part of the adult shell. Therefore, well-preserved prodissoconchs were rare in the fossil collections (fewer than one in 200 shells) and were mostly found on shells of juveniles under 1 cm in length. Of all the geminate species pairs, *Arca mutabilis/ Arca imbricata* was by far the best represented in the fossil collection and had the largest number of specimens with intact prodissoconchs, and only data from this fossil lineage is considered here. In addition to this lineage's excellent fossil record, it was particularly amenable to the paelontological study because unlike some other pairs, specimens from the *Arca mutabilis/A. imbricata* lineage could be readily identified based on shell shape and ornamentation (characteristics in Olsson 1961). Likewise, the Recent *A. mutabilis/A. imbricata* pair shows the greatest difference in egg size between oceans of all geminate pairs, which makes it the most likely lineage in which to detect evolutionary changes in egg size in the fossil record.

To determine the significance of patterns of egg size between oceans and over time, I calculated the egg volume of fossils by taking the estimate of egg diameter from the prodissoconch as the longest diameter of a prolate spheroid and assuming the shorter diameter was equivalent to 90% of the longest diameter (estimated from the actual difference between longest and shortest diameters of Recent specimens of both *A. mutabilis* and *A. imbricata*). Egg volume was then calculated using the formula for a prolate spheroid (as above). This method was also used to predict the egg size of the Recent species *Arca pacifica* from PD I measurements of three shells of that species.

Ancestral Character State Reconstruction of Egg Size Using Phylogenetic Data

An increasingly common method for inferring the direction of character evolution is phylogenetic ancestral character state reconstruction (Swofford and Maddison 1987; Harvey and Pagel 1991; Martins and Hansen 1997; Schluter et al. 1997; Martins 1999; Omland 1999; Forbis et al. 2002), which is often used to estimate ancestral character states when fossil evidence is lacking (e.g., Omland and Lanyon 2000; Butler and Losos 2002; Chang et al. 2002; Forbis et al. 2002; Ackerly 2004). I used two of the oldest and most commonly used ancestral character state reconstruction algorithms (Martins and Hansen 1997; Losos 1999) to reconstruct ancestral states from a known molecular phylogeny of the arcids (Marko 2002; Marko and Moran 2002): linear parsimony (LP) and sum-of-squared changes parsimony (SCP). Both methods use parsimony algorithms, but LP (Farris 1970; Swofford and Maddison 1987) uses the absolute value of the evolutionary change occurring on each branch of the tree and minimizes the sum of these values over the entire tree (Martins and

Hansen 1997; Butler and Losos 1997), whereas SCP (Maddison 1991) uses the square of evolutionary change along each branch of the tree and minimizes the sum of the squares over the entire tree (Butler and Losos 1997; Cunningham et al. 1998; Maddison and Maddison 2004).

With SCP, I estimated ancestral states in two ways; first, with all branch lengths set to one, which matches a punctuated model of evolution with all change occurring at speciation events (SCPP; Martins and Garland 1991; Ryan and Rand 1995; Losos 1999); and second, with branch lengths scaled to molecular distance (distances from Marko 2002; Marko and Moran 2002; P. B. Marko unpubl. data). The latter assumes that the amount of change occurring on a particular branch is a function of time and matches a gradual mode of evolution (SCPG; Losos 1999). Of the methods I used, each assumes that the phylogeny is accurate and that all relevant taxa are included (Schluter et al. 1997; Omland 1999). I also assumed that rates of character change are relatively slow and constant along each branch, and that a character is as likely to change in one direction as another (Schluter et al. 1997; Omland 1999). When evolutionary motion is Brownian, SCPG has a close relationship to maximum likelihood and generalized least-squares character state reconstructions (Schluter et al. 1997; Martins 1999).

Different reconstruction methods can lead to considerably different reconstructions of ancestral states (Swofford and Maddison 1992; Losos and Miles 1994; Martins and Hansen 1997; Omland 1997; Cunningham et al. 1998; Cunningham 1999; Losos 1999; Webster and Purvis 2002). SCP and LP frequently give different ancestral state reconstructions; because SCP minimizes the amount of squared change along each branch across the entire tree simultaneously, this method forces some change to occur along all branches and large changes in a character are spread through the tree (Schluter et al. 1997). In contrast to SCP, LP algorithms minimize the total amount of evolution occurring on the tree and isolate large changes onto fewer branches (Losos 1999). Thus, SCP will lead to incorrect ancestral state reconstructions when large changes occur on only a few branches (Radtkey et al. 1997; Giannasi et al. 2000).

Mesquite 1.01 (Maddison and Maddison 2004) was used to estimate egg sizes of the common ancestor of each geminate pair using a phylogenetic tree with topology taken from a published phylogeny of the Arcidae (Marko 2002) that contains the majority (13 of 17) of species represented in the egg-size database. Four additional species that are also in the database (*Arca zebra, Barbatia bailyi, Barbatia bailyi* sp., and *Anadara concinna*) are not represented in Marko's (2002) phylogeny, but were added to the tree using recent unpublished molecular sequences (P. B. Marko, unpubl. data). For SCPG, branch lengths were calculated from COI sequence data (Marko 2002; Marko and Moran 2002; P. B. Marko, unpubl. data) and two species (*A. zebra* and *A. concinna*) were pruned from the tree prior to analysis because COI sequence data were lacking. The molecular placement of all taxa concurred with standard morphological classification of arcid bivalves (Olsson 1961).

The reconstructed egg size of the ancestor of each pair was then compared to the egg size of both geminate descendants to determine whether modern-day differences between mem-
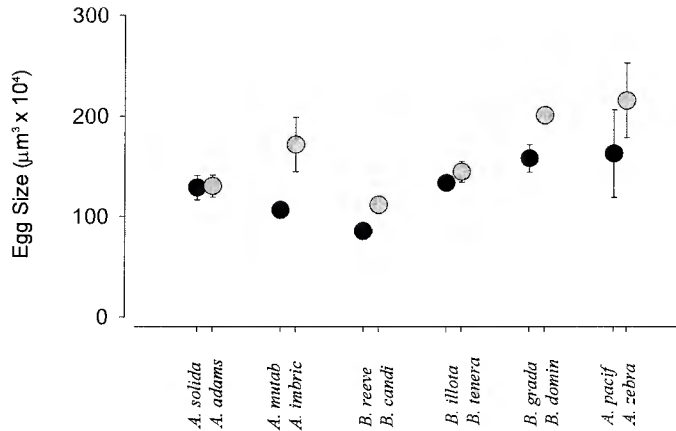
FIG. 1. Egg size of arcids from the six geminate pairs. Egg size is expressed in cubic microns × 10⁴. Abbreviated species names are given on the x-axis, and geminates are grouped by pair. Black circles represent animals from the Eastern Pacific, and gray circles represent Western Atlantic species. Error bars are standard deviations. Each point represents the mean of measurements of 15 oocytes from three to seven specimens, except for *Arca pacifica*, whose egg size was estimated from three prodissoconch measurements (see Materials and Methods). Data are shown in Table 2.

largely to planktotrophic species whose larvae must feed in the plankton to reach metamorphosis, but detailed information on the life histories of marine taxa is difficult to obtain directly. Prodissoconch morphology provides a powerful tool for inferring the developmental mode of a bivalve species without labor-intensive direct observations of larval development. Of the arcid species examined in this study, the majority (14 of 17) had prodissoconchs typical of planktotrophic bivalve larvae with small PD Is and a large, concentrically ribbed PD II (indicating substantial growth in the plankton) with a clear demarcation between PD I and PD II (Ockelmann 1965). All species that were members of geminate pairs had prodissoconchs indicating obligatory planktotrophic development, suggesting that under models of egg size evolution (e.g., Vance 1973; Levitan 2000), egg sizes of geminates would likely evolve in response to changes in the larval feeding environment. Among the three species with prodissoconch morphologies that indicate nonplanktotrophic development, one species (*B. cancellaria*) had a large smooth PD I and no PD II, indicating nonplanktotrophic but likely planktonic development (Ockelmann 1965). Two additional species (*B. bailyi* and *B. bailyi* sp.) had large, unusual, hat-shaped prodissoconchs indicative of brooded and nonplanktonic development (Moran 2004).

bers of each pair was the result of: (1) an increase in egg size in the WA (i.e., the ancestor of a pair had smaller eggs than the Recent WA member of the pair); (2) a decrease in egg size in the EP (i.e., the ancestor had larger eggs than the Recent EP species); (3) change in both oceans (i.e., the ancestral egg size of a geminate pair was intermediate between the two descendants); or (4) another scenario not directly predicted by life-history theory, such as a decrease or increase in egg size in both oceans.

RESULTS

Developmental Mode of Recent Species

Models of egg size evolution in marine taxa in response to planktonic feeding environment (e.g., Levitan 2000) apply

Egg Size of Recent Species

When comparing sister species within each geminate pair, mean egg size of the WA species was larger than its EP geminate in six of six pairs. In three pairs, *A. mutabilis/A. imbricata*, *B. reeveana/B. candida*, and *B. gradata/B. domingensis*, these differences were significant at the *P* < 0.05 level in both the Student's *t*-test and nested ANOVA models (data are shown in Table 2, Fig. 1; analyses shown in Table 3). The difference between eggs of the WA member of a fourth pair, *B. illota/B. tenera*, was marginally nonsignificant (*P* < 0.05004, Table 3). The size difference between eggs of the *A. solida/A. adamsi* pair was small (~1% difference in volume) and was not significant in either test, though like

TABLE 3. Analyses of variance and Student's two-sample *t*-tests comparing egg volumes of geminates. In each species pair, the Eastern Pacific member is listed first. All statistics were performed on egg volumes divided by 10³ for convenience of number handling.

Nested mixed-model ANOVA	Effect	df effect	MS effect	df error	MS error	F	P
Barbatia illota/tenera	female	10	1138.85	168	98.58	11.55	<0.001
	species	1	5651.46	10	1138.85	4.96	>0.050
Barbatia reeveana/candida	female	8	632.56	128	86.96	7.27	<0.001
	species	1	27292.42	8	60	43.14	<0.001
Barbatia gradata/domingensis	female	4	1502.16	100	99.19	15.14	<0.001
	species	1	46409.71	4	1502.16	30.90	<0.005
Arca mutabilis/imbricata	female	8	5884.88	138	217.82	27.02	<0.001
	species	1	157887.9	8	5884.88	26.83	<0.001
Arcopsis solida/adamsi	female	8	1928.95	165	204.79	9.42	<0.001
	species	1	165.41	8	1928.95	0.086	0.777

t-test	*t*	df	*P*
B. illota/tenera	−2.228	10	0.05004
B. reeveana/candida	−6.224	10	<0.0001
B. gradata/domingensis	−6.077	5	<0.005
A. mutabilis/imbricata	−5.185	8	<0.001
A. solida/adamsi	−0.209	9	0.839

TABLE 4. Width of prodissoconch (PD) I of 12 arcid species. Species are listed in geminate pairs with the Eastern Pacific (EP) member first, followed by the Western Atlantic (WA) member. No specimens of *Barbatia reeveana* were found that had intact prodissoconchs. These data were used with egg size data from Table 2 to generate Figure 2.

Species	Ocean	n	PD I width (μm) ± SD
Barbatia illota	EP	3	103.0 ± 1.4
B. tenera	WA	5	106.9 ± 2.8
Barbatia reeveana	EP	0	—
B. candida	WA	3	102.2 ± 3.6
Barbatia gradata	EP	1	114.8
B. domingensis	WA	4	119.6 ± 4.9
Arca mutabilis	EP	3	108.6 ± 6.1
A. imbricata	WA	3	125.6 ± 6.7
Arcopsis solida	EP	3	106.1 ± 1.7
A. adamsi	WA	5	115.1 ± 1.7
Arca pacifica	EP	3	114.6 ± 9.1
Arca zebra	WA	4	131.8 ± 2.3
Barbatia cancellaria	EP	3	181.7 ± 7.9

FIG. 2. Relationship between egg diameter and the width of the first larval shell (prodissoconch I, PD I) for 12 species of arcid bivalves. Solid line is the least-squares regression of egg diameter on PD I width; species and measurements are listed in Table 2 (egg diameter) and Table 4 (PD I width). Regression equation: $y = 0.67x - 7.0$, $r^2 = 0.96$.

all other geminate pairs the WA species (*A. adamsi*) had larger eggs than the EP species (*A. solida*). Egg size of *A. pacifica*, the Pacific member of the *A. pacifica*/*A. zebra* pair, was not measured directly (none of the adult animals collected were ripe) but was instead estimated from the prodissoconch height of three Recent specimens using the regression equation of egg diameter on prodissoconch width (below) to generate the longest egg diameter, then assuming the shorter diameter was 90% of the longest diameter (as above for fossils). In agreement with size differences in the other five geminate pairs, estimated egg size of *A. pacifica* was smaller than the egg sizes measured from its WA geminate, *A. zebra* (Table 2, Fig. 1). Because egg size of *A. pacifica* was estimated from prodissoconchs and from only three specimens, the significance of this difference was not tested.

In paired tests comparing egg sizes between all WA and EP geminates using the mean egg size of each species, egg size of WA species was significantly larger overall than egg size of EP species (paired Student's t-test; df = 5, $t = -3.240$, $P < 0.023$; sign test, no. of nonties = 6; v < V 100%; $Z = 2.041$; $P < 0.04$).

Relationship between Egg Size and Size of Prodissoconch I

There was a positive and significant relationship between egg size and width of prodissoconch I when data from all species were combined and analyzed with linear regression (Table 4, Fig. 2). This relationship was used to estimate the egg size of *A. pacifica* from three intact shell specimens, and this species was estimated to have considerably smaller eggs than its WA counterpart (Table 2; see above).

Estimating Egg Size of Fossils from Prodissoconch Data

The size of PD I was measured from a total of 14 fossil shells in the *A. mutabilis*/*A. imbricata* geminate pair. The specimens ranged in age from the late early Miocene (16–23.3 million years ago), well before the closure of the CAS,
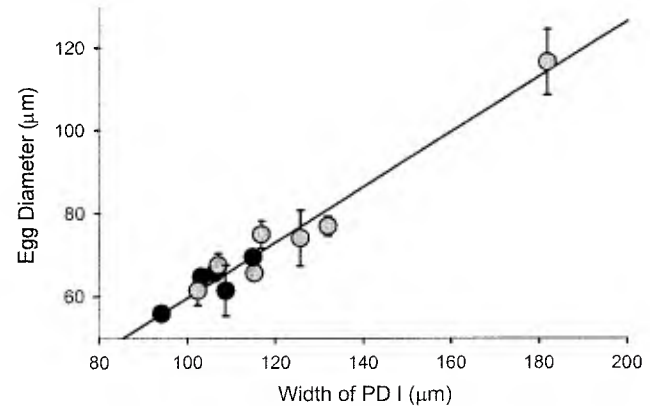
to the Plio-Pleistocene (< 1.7 million years ago), well after final closure.

Using the linear regression equation defined in Figure 2, estimated egg sizes from PD I length of *A. mutabilis*/*A. imbricata* fossils were all as large as measured egg sizes from Recent members of the WA member of this geminate pair (*A. imbricata*; see Table 5, Fig. 3). Fossil specimens included 10 from the preisthmian WA and four from the postisthmian EP; localities and collection numbers for all fossils are given in Table 5. Within fossils from the WA, all of which were preisthmian, there were five fossil specimens from Venezuelan deposits from the early Miocene, four specimens from the Dominican Republic (one from the mid to late Miocene, one from the late Miocene/early Pliocene, and two from the lower Pliocene), and one from the Bocas del Toro region of Panama (early to mid Pliocene). This study also included four Plio-Pleistocene fossils from the same geminate lineage (*A. mutabilis*/*A. imbricata*) from the postisthmian EP.

Based on PD I size, every fossil from either the WA or EP, and every fossil from all time periods (both before and after closure of the CAS), had estimated egg diameters that were as large as, or in a few cases larger than, eggs of the modern WA species (*A. imbricata*). When contrasted with the Recent EP member of this lineage (*A. mutabilis*), all fossils had estimated egg sizes that were larger than the largest measured mean egg diameter of any Recent EP specimen. The average egg diameter (±SD) estimated from the four Pleistocene fossils in the EP was 74.0 ± 3.3 μm, considerably larger than the actual measured egg diameter of the Recent EP species, *A. mutabilis* (61.4 ± 2.1 μm). This represents a significant decrease in egg volume (Student's t-test, $t = -7.0$, $P < 0.0005$, df = 7), and suggests that egg diameter in the EP decreased by about 11% in less than 2 million years (equivalent to a ~57% decrease in volume). In contrast to the EP, there was no evidence for a change in egg size in the WA in the *A. mutabilis*/*A. imbricata* lineage from the Miocene to the present. The average egg diameter volume of all preisthmian fossils from the WA was 77.2 ± 4.8 μm, while the average diameter of the Recent WA species (*A.

TABLE 5. Locality, formation, width of prodissoconch (PD) I, museum and lot number, and approximate age of all fossil arcids.

Locality (N)[1]	Formation	Width of PD 1 (μm)	Museum and lot number[2]	Approximate age[3]
1. Cayo Agua, Bocas del Toro, Panama (1)	Cayo Agua	118.2	NMB 18596, PPP 352	Early-mid Pliocene[a]
2. Rio Gurabo, Domincan Republic (1)	Cercado	133.3	NMB 15912	Middle-late Miocene[b]
3. Rio Cana, Domincan Republic (2)	Gurabo	136.5, 135.7	NMB 16828	Lower Pliocene[b]
4. Rio Cana, Dominican Republic (1)	Gurabo	121.53	NMB 16856	Late Miocene/Early Pliocene[b]
5. Paraguana Peninsula, Venezuela (5)	Cantaure	117.6, 119.5, 119.3, 124.4, 130.0	NMB 17516	Late Early Miocene[c]
6. Playa Cocalito, Nico-ya, Costa Rica (3)	Cocalito	124.0, 123.3, 113.6	NMB 17767, PPP 291	Plio-Pleistocene[d]
7. Burica, Panama (1)	Charco Azul	122.7	NMB 18413, PPP 86	Pleistocene[d]

[1] N, number of fossils with well-preserved PD I from which egg size was estimated.
[2] NMB, Naturalhistoriches Museum, Basel; PPP, Panama Paleontology Project.
[3] a, Dowsett and Cotton (1996); b, Saunders et al. (1986); c, Diaz de Gomero (1974); d, L. Collins, pers. comm.

imbricata) was 74.1 ± 5.7 μm. These two numbers are statistically indistinguishable (Student's *t*-test, $t = 1.1$, $P = 0.3$, $n = 13$) and suggest that egg volume in this geminate lineage has remained constant in the WA from the Miocene (~20 million years ago) to the present.

Because of the possibility that the relationship between PD I and egg size might vary among genera of arcids, I also regressed egg size against PD I for the three closely related

FIG. 3. Estimated egg sizes of fossils from the *Arca mutabilis/A. imbricata* lineage over time, and measured egg sizes of Recent *Arca mutabilis* (Eastern Pacific, EP) and *A. imbricata* (Western Atlantic, WA) for comparison. Recent egg sizes are plotted above the solid line marking time 0; black circle, EP species; gray circle, WA species; error bars, standard deviation. The y-axis is in units of millions of years before present, and the x-axis shows egg diameter. The y-axis age coordinate of each fossil point represents the mid-point between the oldest and youngest possible age. Dotted line indicates approximate time of the rise of the Central American isthmus. Data are shown in Table 5.

Arca species only (*A. mutabilis, A. imbricata,* and *A. zebra*; no Recent egg sizes were measured on *A. pacifica*) and used this regression equation to recalculate estimated egg sizes for all *Arca* fossils. Because the two regression equations were virtually the same ($y = 0.69x - 13.1$ for *Arca* vs. $y = 0.67x - 7.0$ for all arcids combined), results were very similar and egg size estimates from family-level regression were used because of this equation's broader applicability to future studies on other arcid geminate pairs.
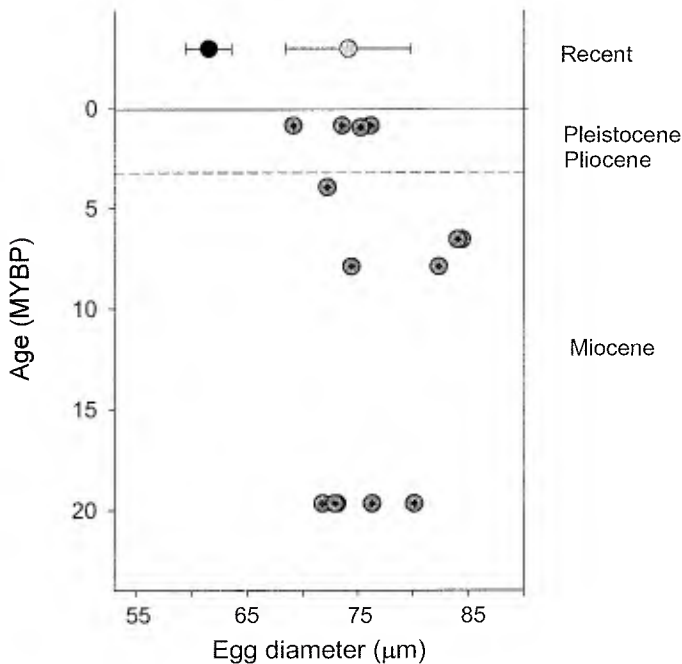
Ancestral Character State Reconstruction of Egg Size Using Phylogenetic Data

LP gave specific estimates of the ancestral state at five of 15 ancestral nodes in the tree. As is typical of the method (Losos 1999), at the other 10 nodes LP gave a range of estimates that all give equally parsimonious trees (Fig. 4). Despite this ambiguity, LP predicted a specific direction of evolutionary change in egg size for all six geminate pairs (Fig. 4). In four of six pairs (*A. solida/A. adamsi, A. mutabilis/A. imbricata, B. gradata/B. domingensis, B. reeveana/B. candida*) the reconstructed ancestor had eggs the same size or within the range of the Recent WA species, suggesting that in these pairs there was no increase in egg size in the WA, but rather that egg sizes shrank in the EP. The opposite pattern was seen in the other two geminate pairs, *A. pacifica/A. zebra* and *B. illota/B. tenera*. In these pairs, the reconstructed ancestral state was equivalent to the Recent EP species but smaller than the Recent WA species, suggesting that egg size increased in the WA but remained the same in the EP.

SCPG and SCPP made predictions about egg size evolution in geminates that were similar to each other, but substantially different from those made using LP (Table 6). In both types of SCP, the predicted egg size of the most recent common ancestor of each of the six geminate pairs was considerably larger than that predicted by LP and larger than the egg size of either Recent geminate descendent, suggesting that evolutionary reductions in egg size were a universal occurrence in both the EP and the WA. Both types of SCP also reconstructed egg sizes at many deeper nodes that were larger than any of that ancestor's descendant taxa (data not shown); thus,
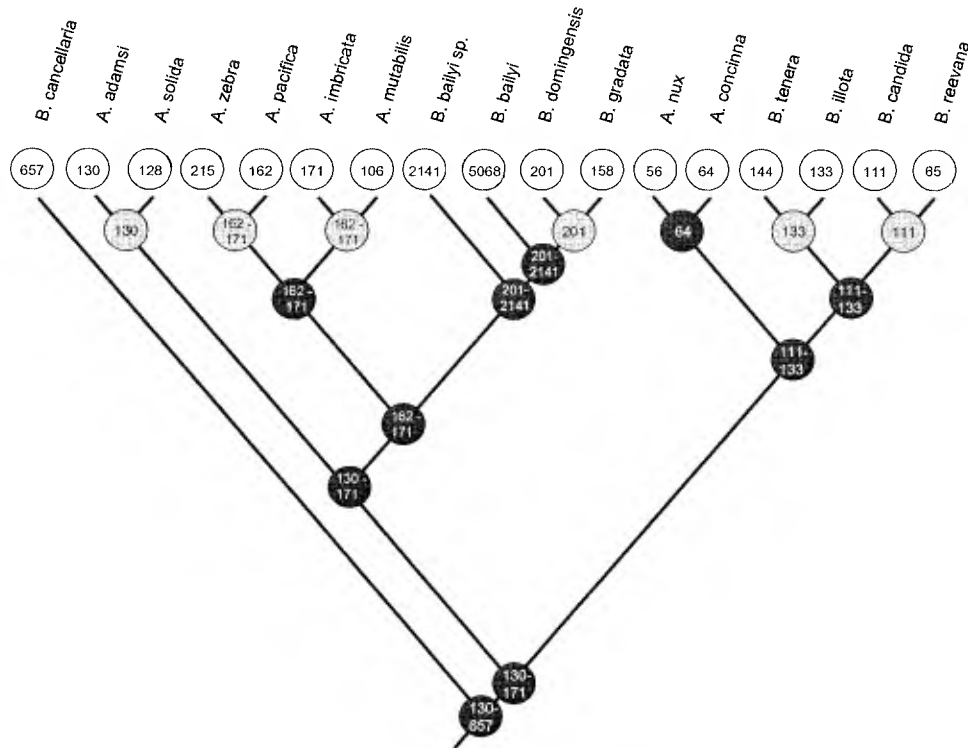
FIG. 4.   Phylogeny of 17 arcid bivalve species, showing measured egg sizes of Recent species and egg sizes at ancestral nodes calculated with the linear parsimony algorithm using Mesquite 1.01 (Maddison and Maddison 2004). Tree topology taken from Marko and Moran (2002) with three additional species added using more recent molecular data (described in text). Numbers in white circles at branch tips indicate the measured egg volumes (expressed in cubic microns $\times$ 10^4) of 17 Recent arcid species including all six geminate pairs (data also shown in Table 2). Black circles indicate the estimated egg size at ancestral nodes; gray circles are the estimated egg sizes of the immediate ancestors of each geminate pair.

this method indicated a general evolutionary trend toward reductions in egg sizes in all lineages except those leading to the three Recent species with very large eggs (*B. bailyi*, *B. bailyi* sp., and *B. cancellaria*).

DISCUSSION

Egg Size of Recent Geminate Species Pairs

One of the major findings of this study is that WA arcid bivalves have larger eggs than their EP geminates. This pattern is also seen between geminate echinoderms (Lessios 1990), which strongly suggests the presence of an underlying environmental factor that affects members of these two phyla

TABLE 6.   Estimated ancestral egg sizes (in μm^3 $\times$ 10^4) for all geminate arcid pairs using linear parsimony (LP), squared-change parsimony with a punctuated model of evolution (SCPP), and squared-change parsimony with a gradual model of evolution (SCPG). No value is given for *Arca pacifica/zebra* under SCPG because branch lengths were lacking for *A. zebra*.

Geminate pair	LP estimate	SCPP estimate	SCPG estimate
Barbatia illota/tenera	133.0	147.6	168.4
Barbatia reeveana/candida	111.0	120.7	130.0
Barbatia gradata/domingensis	201.0	1011.0	709.1
Arca mutabilis/imbricata	162.0–171.0	270.6	299.4
Arcopsis solida/adamsi	130	281.9	199.9
Arca pacifica/zebra	162.0–171.0	309.9	—

in similar ways despite their distant phylogenetic relationship. A likely ecological factor that might act in this fashion is oceanic productivity (Lessios 1990). Current models of life-history evolution in marine systems predict that egg size should be negatively correlated with productivity, because large eggs represent an increase in maternal investment per offspring that offsets the effects of low productivity and a poor feeding environment (Vance 1973; Thresher 1982; Lessios 1990; Havenhand 1995; Levitan 2000). The underlying force that drives the relationship between productivity and optimal egg size in these models is mortality. All other factors being equal, a poor larval feeding environment will result in longer larval development and increased exposure to sources of mortality such as predation and advection away from suitable settlement substrate; larger eggs are thought to compensate for a poor larval feeding environment by shortening the larval period (the fecundity time hypothesis; Hart 1995; Levitan 2000). In contrast, where high oceanic productivity provides a better larval feeding environment, selection should favor mothers who produce smaller and more numerous eggs.

Because productivity regimes differ strongly between the EP and WA (D'Croz et al. 1991; Wellington and Robertson 2001) and productivity has long been thought to be a major factor driving egg size evolution in marine taxa (Thorson 1950; Vance 1973; Thresher 1982; Cushing 1990; Havenhand 1995; Levitan 2000), the hypothesis that species in the WA have larger eggs than their geminates in the EP because of

differences in larval feeding environment is an attractive one. There are, however, several other environmental factors that also must be considered. First, temperature has known effects on size of ectothermic organisms at many levels, including the whole animal (reviewed by Atkinson 1994), single cells (van Voorhies 1996), and eggs (Azevedo et al. 1996; Armbruster et al. 2001; Blanckenhorn 2001). In general, these studies find an increase in size with decreasing temperature. The WA and EP represent different thermal environments; on average the WA is 2°C warmer than the EP (Keigwin 1982; Broecker 1989), largely due to the seasonal cooling effects of winter upwelling in the EP which peaks in February–March (STRI Marine Environmental Sciences Program long-term dataset; www.stri.org/mesp/MESP.htm). However, because animals for egg size measurements were collected in October–November when temperatures on the two sides of the isthmus are essentially the same and have been for about five months, oogenesis and larval development in the EP and WA likely occurred in similar thermal environments. In addition, if temperature were the dominant factor influencing egg size in arcids, egg size trends should be opposite to those observed in that eggs should be larger in the EP than the WA, because the EP is seasonally colder.

Second, in free-spawners such as arcid bivalves, water temperature might also affect the optimal egg size for a given species through its effects on fertilization kinetics. Because sperm become rapidly diluted in the ocean and sperm dilution reduces fertilization success, it has been argued that under the correct circumstances, natural selection should act to increase egg size to increase the "effective target area" for sperm and enhance fertilization success (Levitan 1993, 1998, 2000). Seasonally higher temperatures in the WA might increase sperm limitation by decreasing sperm longevity, therefore selecting for larger eggs. However, higher ocean temperatures in the WA could also increase sperm swimming speeds and thus increase sperm-egg encounter rates, alleviating the need for an increase in egg size. Because it is difficult to predict the direction of selection that temperature and fertilization kinetics would place on egg size in either ocean, currently this hypothesis for observed trends in egg size among geminates is difficult to evaluate. Regardless, the effect of small differences in seawater temperature on fertilization kinetics would likely be small (Rupp 1973).

Third, larval mortality might differ between the EP and the WA in ways not directly related to the larval feeding environment, for example, advection away from suitable settlement substrate or differential mortality due to disease or predation. Because these factors have not been suggested to vary between the WA and EP, it is difficult to evaluate their potential importance. Likewise, WA waters differ from those in the EP by being both more saline and more carbonate-rich (Weyl 1968; Maier-Reimer et al. 1990). The effects of these factors on selection for egg size (if any) are not known, and neither has been implicated in models of marine invertebrate egg size evolution. Therefore, the hypothesis that productivity differences between the WA and EP have selected for different egg sizes in the two oceans (the productivity hypothesis; Lessios 1990) currently remains the best explanation for the modern-day pattern of egg size differences across the Central American isthmus.

Paleontological Reconstructions of Egg Size from Fossil Arcids

If productivity is indeed a major factor driving observed patterns of egg size evolution in marine invertebrates, then the timing and direction of egg size evolution in the WA and EP should coincide both temporally and spatially with changes in oceanic productivity levels. This hypothesis can be tested directly by estimating egg size from fossil arcids dating from before, during, and after the closure of the CAS and comparing these to paleoceanographic reconstructions of oceanic productivity changes over the same period. Paleoceanographic data places the closure of the CAS in the middle Pliocene, at 3.8–3.1 million years ago (Coates and Obando 1996). Prior to this event, productivity differences between the oceans are thought to have been minor (Keigwin 1982; Jones and Hasson 1985). Shoaling of the isthmus caused a progressive decrease in productivity in the WA (Allmon et al. 1996b; Collins et al. 1996), while in the EP productivity increased after seaway closure (Keigwin 1982; Jones and Hasson 1985; Teranes et al. 1996; Ibaraki 1997; Anderson 2001). Therefore, if the productivity hypothesis is correct, the fossil record should show that, within geminate pairs and after the rise of the isthmus, egg size either increased in the WA, decreased in the EP, or both.

The apparent postisthmian decrease in egg size in fossils of the EP member (*A. mutabilis*) of the *A. mutabilis/A. imbricata* geminate pair does indeed support the productivity hypothesis. Fossils indicate that eggs of this geminate lineage were large throughout the Miocene and Pliocene, followed by stasis in the WA after closure and a rapid decrease in egg size in the EP that occurred between the Pleistocene and the present. Indeed, the presence of large-egged individuals in the EP as recently as the Pleistocene (Fig. 3) suggests that the decrease in egg size was recent and relatively rapid, occurring over the course of less than 2 million years (the oldest possible age of the youngest fossil with a large egg). These data are consistent with the hypothesis that increases in oceanic productivity selected for smaller egg size in the EP, because upwelling and productivity have likely intensified in the EP since the closure of the CAS (Teranes et al. 1996; Ibaraki 1997), increasing the amount of food available to planktotrophic larvae. Thus, when the larval environment improves in nature, egg size may evolve rapidly toward a smaller size to enhance parental fecundity. This idea is supported by a recent study of salmonid reproduction; salmon egg size showed a very high rate of evolutionary shrinkage when larvae were reared in a benign (i.e., hatchery) environment, presumably due to a reduction in the survival advantage of large eggs coupled with intense selection for high maternal fecundity (Heath et al. 2003).

In contrast to the EP, egg size trends in the *A. mutabilis/ A. imbricata* lineage in the WA do not meet the expectations of the productivity hypothesis. In the WA, despite a well-documented drop in productivity that occurred at approximately the same time as the closure of the CAS (Allmon et al. 1996a; Collins 1996; Collins et al. 1996), egg size has remained the same for more than 20 million years. Why, despite this decrease in productivity, was there no corresponding increase in egg size in the WA? Though necessarily

speculative, there are a number of possible explanations. First, a major advantage of large eggs in a low-productivity environment is thought to be that the greater energy contained in a large egg permits the shortening of developmental time, thus minimizing exposure of larvae to the hazards of plank-tonic life (Hart 1995; Levitan 2000). Egg size, however, is not always correlated with egg energetic content (McEdward and Carson 1987; McEdward and Coulter 1987). Potentially, adult females could increase the energetic density of eggs without a change in size, and hence decrease developmental time without producing eggs that are physically larger. How-ever, a comparative examination of egg size and energetic density over a wide range of planktotrophic taxa (Jaeckle 1995) found that, between planktotrophic species, energetic density does not change substantially over a wide range of egg sizes.

Second, biological indicators of a change in productivity in the WA include size trends and extinction patterns of adult molluscs (Jackson et al. 1996; Roopnarine 1996; Anderson 2001). Even today, the diets and food requirements of larvae in the ocean are poorly understood (Olson and Olson 1989; Moran and Manahan 2004) and they may differ from those of adults. Thus, if larvae and adults consume different re-sources, environmental changes that affect the adult stage of the life history might not affect larvae (and hence optimal egg size) in the same way.

Third, there were other changes to the environment of the WA after closure of the CAS that may have altered selection on egg size and masked the effects of changing productivity. For example, sea-surface temperature in the WA may be slightly warmer today than in the Pliocene (Cronin 1991; Dowsett et al. 1992; Cronin and Dowsett 1996). Warmer temperatures reduce the developmental time of most marine invertebrate larvae (reviewed in Strathmann 1987; Levitan 2000), thus shortening exposure of larvae to planktonic mor-tality. Therefore, an increase in temperature in the WA could have reduced selective pressure to shorten the larval period via the evolution of larger eggs. In addition, zooplankton concentrations today are considerably higher in the EP than in the WA (D'Croz et al. 1991), and predation by large zoo-plankters is thought be an important source of bivalve larval mortality (Strathmann 1974; Morgan and Christy 1995). If predation pressure decreased in the WA along with primary productivity, such a reduction in predation-related mortality might reduce the penalty for a long larval duration and, like an increase in temperature, alleviate selective pressure for an increase in egg size.

Fourth, it is possible that an increase in egg size did not occur in the WA because of developmental constraints that might limit the evolution of large eggs in planktotrophic taxa. In marine invertebrates, substantial evolutionary increases in egg size are associated with a change in developmental mode from feeding to nonfeeding development (Thorson 1950; Strathmann 1985). A change in developmental mode is gen-erally accompanied by major alterations to larval morphology (Ockelmann 1965; Emlet 1990), larval physiology, egg com-position (Villinski et al. 2002), developmental timing and regulation, and possibly changes to adult structures such as ovaries and gonoducts. There is a considerable gap between the egg sizes of planktotrophic arcids (eggs between 53- and

77-μm diameter) and nonplanktotrophs (eggs > 117 μm); the lack of any transitional egg sizes in this dataset suggests that developmental constraints may indeed limit the upper egg sizes of planktotrophic species. Regardless of underlying mechanisms, however, it is clear that the low productivity levels in the modern-day WA have not driven an egg size increase in that ocean, contrary to the predictions of the pro-ductivity hypothesis.

Models such as the regional productivity hypothesis and the fecundity-time hypothesis invoke microevolutionary change within lineages to explain modern geographic and phylogenetic distributions of life-history patterns. In the case of geminate species pairs separated by the Isthmus of Pan-ama, macroevolutionary mechanisms may also play a role. There is increasing evidence that many geminate species pairs diverged long before the rise of the isthmus (references in Collins 1996); in the arcid bivalves, Marko and Jackson (2001) found that *A. mutabilis* and *A. imbricata* were mor-phologically distinct species several million years prior to closure of the CAS. In this case, Recent transithsmian egg-size patterns may be explained by differential extinction of species with large eggs in the EP and species with small eggs in the WA after closure of the CAS, or by a combination of both differential extinction and microevolutionary change within lineages. Suites of morphological characters have been developed that can distinguish between Recent *A. imbricata* and *A. mutabilis* (Marko and Jackson 2001). This technique could be useful in determining whether fossil specimens bear-ing large prodissoconchs indeed belonged to the WA species (*A. imbricata*). To date, however, well-preserved fossil prod-issoconchs have only been obtained from small specimens (generally <1-cm shell length). While these juvenile fossils can be easily identified as belonging to the *A. mutabilis/A. imbricata* lineage, this species pair shows considerable on-togenetic shape change during growth (A. L. Moran, pers. obs.) and it is not clear whether suites of adult shell characters are adequate to discriminate between juveniles of the two species.

Does the pattern of egg size evolution seen in the *A. mu-tabilis/A. imbricata* geminate pair also occur in other gemi-nate arcid pairs? This cannot currently be determined from the fossil record, because no other geminate lineages had sufficient numbers of fossil specimens with intact prodis-soconchs to infer the direction or timing of egg size evolution relative to the closure of the CAS. However, because the phylogeny of arcid bivalves has been characterized using molecular sequences (Marko 2002), an indirect method of ancestral character state reconstruction (e.g., Swofford and Maddison 1987; Schluter et al. 1997; Pagel 1998; Cunning-ham 1999) can be used to infer the direction of evolutionary change in egg size in geminate lineages that lack a fossil record, thus testing the hypothesis that changes in produc-tivity have driven predictable, directional evolutionary changes that occur in many geminate pairs.

Phylogenetic Ancestral Character State Reconstructions

LP reconstructions were consistent with the fossil record; LP predicted that the ancestor of *A. mutabilis/A. imbricata* geminate pair had a large egg that was similar in size to the

Recent WA species, *A. imbricata*, and that the difference between egg sizes of these two modern-day geminates is due to a reduction in egg size in the EP. In contrast, both SCPP and SCPG reconstructed ancestors for each of the six geminate pairs that had larger eggs sizes than either Recent species in a given pair, including *A. mutabilis/A. imbricata*.

The differences between LP and SCP result from the fact that LP algorithms minimize the total amount of evolution on the tree, therefore tending to isolate large changes onto relatively few branches (Losos 1999). Both SCPP and SCPG, in contrast, minimize the amount of squared change along each branch across the entire tree simultaneously, forcing some degree of change to occur along all branches and spreading large changes in a character across the tree (Schluter et al. 1997). The arcid phylogeny contains three species (*B. bailyi*, *B. bailyi* sp. and *B. cancellaria*) with nonfeeding larval development and, hence, eggs with a volume of three-fold to more than 23-fold greater than the eggs of the planktotroph with the largest eggs (*A. zebra*). SCP spreads the evolutionary change from small to large eggs throughout the tree, inflating estimated egg sizes of all ancestral nodes. In LP, in contrast, the evolution of large eggs is isolated onto the three branches leading directly to the three nonplanktotrophic species.

The ancestral states predicted by both types of SCP seem unlikely to be correct for two reasons. First, SCP predicts that the most recent common ancestor of the *A. mutabilis/A. imbricata* pair had a substantially larger egg than either Recent descendant (Table 6). There is no support for this hypothesis in the fossil record, which instead shows that egg size has remained the same in the Caribbean for at least 20 million years (Fig. 3; it is possible, however, that *A. mutabilis* and *A. imbricata* split more than 20 million years ago; Marko and Jackson 2001). Second, both SCP methods predict very large egg sizes at many ancestral nodes in the tree; for example, under these models the direct ancestor of the *B. gradata/B. domingensis* geminate pair had eggs between three- and more than fivefold larger than either descendant (Table 6). SCP also reconstructs very large eggs at many deeper nodes in the tree as well (data not shown). Because very large eggs in the arcids and other bivalves are associated with nonplanktotrophic development (Strathmann 1987; Moran 2004), this scenario implies that planktotrophy has evolved from nonplanktotrophy numerous times in the arcid tree. This evolutionary scenario is unlikely; planktotrophy is considered to be the ancestral state in the majority of higher invertebrate taxa, and the switch from nonplanktotrophy to planktotrophy is thought to be rare in most marine invertebrate groups (Strathmann 1985; Strathmann and Eernisse 1994; Havenhand 1995; Hart et al. 1997; Cunningham 1999; Duda and Palumbi 1999; Jeffery and Emlet 2003; but see Reid 1989; Rouse 2000; Kupriyanova 2003).

Under LP, in contrast, the ancestral state is ambiguous in many cases but in no instance does this method predict the evolution of planktotrophic development from lecithotrophic ancestors in the arcid phylogeny. Also, unlike SCP, LP does not reconstruct a large decrease in egg size from the most recent common ancestor of *A. mutabilis/A. imbricata* or any other geminate pair. LP reconstructions for three geminate pairs (Fig. 4) showed a pattern similar to *A. mutabilis/A.*

imbricata (a decrease in egg size in the EP but no change in the WA), while the remaining two pairs showed the opposite pattern (no change to egg size in the EP and an increase in egg size in the WA). Though all species in this study were in the same family, the generic groupings are deeply divergent (i.e., $\gg$ 30 million years ago; Marko 2002). It is conceivable, therefore, that taxon-specific differences among the different geminate pairs might cause differences in the degree or direction of evolutionary response to environmental change (e.g., Lessios 1990).

Although ancestral states reconstructed by LP are consistent with the fossil record and with prevailing models of life-history evolution in marine invertebrates, these results must be interpreted with caution. There are many evolutionary scenarios that violate the assumptions of SCP and LP and will lead to substantial error, such as the presence of strong evolutionary constraints, trends, rapid evolutionary change, or strong directional selection (Cunningham et al. 1998; Garland et al. 1999; Martins 1999; Omland 1999; Polly 2001; Webster and Purvis 2002). Another important assumption of LP, and most other methods, is that all relevant extant and extinct taxa are included in the phylogeny (Omland 1999). This assumption is not often met, and this study is no exception; there are more than 150 species of living arcids and egg size data are currently only available for 17. As egg size data become available for additional species and are added to the phylogenetic analysis, it is possible that reconstructions of ancestral egg sizes may change.

Few empirical studies have compared estimates of ancestral states derived from phylogenies directly to the fossil record to test whether the predictions of ancestral character state reconstruction are robust to potential violations of these assumptions, and results of these studies vary. In one study that compared reconstructed states to actual ancestral states from the fossil record, SCP provided estimates of states that were reasonably close to the actual states (Polly 2001). In two other studies, however, no method of ancestral character state reconstruction performed well when reconstructed states were compared to actual ancestral values (Oakley and Cunningham 2000; Webster and Purvis 2002). In arcid bivalves, ancestral states reconstructed with SCP were inconsistent with the fossil record and with prevailing patterns in marine invertebrate life-history evolution. LP, in contrast, provided estimates of ancestral egg size that were closer to fossil data and more consistent with life-history theory. If LP is indeed a suitable method for reconstructing ancestral egg sizes in arcids, these results suggest that different geminate pairs had opposite responses to environmental changes: in four pairs egg size decreased in the EP after closure, while in two pairs egg size increased in the WA. Whether this result represents an accurate depiction of different organisms responding in contrasting ways to changing environmental conditions can only be determined by further examination of the fossil record and through improved taxon sampling of living arcids.

Conclusions

A major tenet of life-history evolution in marine organisms is that, all else being equal, egg size of planktotrophic species will evolve in response to the quality of the larval feeding

environment (Vance 1973; Thresher 1982; Lessios 1990; Havenhand 1995; Levitan 2000). Yet, there is very little experimental or observational data testing the assumptions that underlie this or any other hypotheses surrounding the principles of life-history evolution in marine invertebrates. Both the fossil record and ancestral character state reconstruction suggest that egg size has decreased in some lineages in the EP along with an increase in oceanic productivity; this supports the hypothesis that a life-history strategy of producing numerous small eggs and larvae that are highly dependent on exogenous phytoplankton foods is advantageous in high-productivity environments. These data suggest that when the larval environment improves in nature, egg size may evolve rapidly toward a smaller size to enhance parental fecundity. In contrast, the fact that egg size has not changed in the last 20 million years in the WA in one arcid geminate pair, despite the well-documented drop in productivity in the WA that occurred after closure of the CAS, suggests that the opposite is not always true: a reduction in productivity will not inevitably drive an evolutionary increase in egg size among free-spawning marine taxa. This lack of change may be attributable to opposing selection on egg size from other factors described above or to constraints on egg size evolution caused by linkages between increases in egg size and other life-history characters that cannot readily evolve.

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