

ADAPTATION AND PHYLOGENY AS DETERMINANTS OF EGG SIZE
IN ECHINODERMS FROM THE TWO SIDES OF THE
ISTHMUS OF PANAMA

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Egg size is an important life-history parameter in marine invertebrates. For animals with planktonic development, the egg constitutes the only means of investment by the parent to the offspring. Size is an obvious (Strathmann and Vedder 1977; Lawrence et al. 1984) though perhaps crude (Turner and Lawrence 1979; McEdward and Carson 1987; McEdward and Coulter 1987) measure of such investment, and it can often be used to deduce the developmental mode of a species (Perron and Kohn 1985; Emler et al. 1987). Vance (1973), Christiansen and Fenchel (1979), Grant (1983), Perron and Carrier (1981), Strathmann (1985), and Emler et al. (1987) have sought to define the conditions under which a given egg size is favored by natural selection; a debate about the correlates of egg size as a life-history parameter (Vance 1973, 1974; Underwood 1974; Steele 1977; Strathmann 1977) has been waged largely on theoretical grounds. These models and theoretical arguments are useful as explanations of natural patterns if egg size is capable of evolving toward a theoretically predicted stable point under the pressure of natural selection. However, the question of how responsive egg size may be to selection is entirely open. It is possible that, as Vance (1973) has argued, the high mortality of marine-invertebrate larvae imposes severe selective pressures on early life stages. It is equally possible that the egg size of each marine-invertebrate taxon can follow only a limited number of evolutionary pathways, because it is a trait constrained by phylogeny (Gould and Lewontin 1979; Spight 1979; Stearns 1983, 1984; Cheverud et al. 1985) or by trade-offs with other attributes of each species (Stearns 1977; Law 1979). It is also conceivable that the morphological conservatism of early life stages (see, e.g., Jagersten 1972; Zimmer 1973) may extend to egg size as well.

Empirical explorations of the relationship between egg size and environmental variables or other life-history parameters (see, e.g., Thorson 1950; Spight 1976; Strathmann and Vedder 1977; Turner and Lawrence 1979; Perron 1981; Amy 1983; DeFreese and Clark 1983; Lawrence et al. 1984; Emler et al. 1987) have used data from various species and—considering each species as an independent

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datum point—examined its relationship to the variable of interest. The assumption of such independence is safe only if the egg size of a species is evolutionarily free to vary without regard to its lineage (Harvey and Mace 1982; Clutton-Brock and Harvey 1984; Felsenstein 1985). However, the influence of phylogeny (as revealed by classification) on life histories has been found in every study that looked for it (e.g., Brown 1983; Stearns 1983, 1984; Clutton-Brock and Harvey 1984; Harvey and Clutton-Brock 1985). It would be of interest for both theoretical and empirical purposes, therefore, to know the relative contributions of phylogeny and adaptation to the molding of egg size.

One way of attempting to answer the question is to compare the dimensions of eggs of related species living in different environments and of unrelated species living in the same environment. If egg size is determined by lineage, related species should have similar egg sizes regardless of their environment; if egg size can respond quickly to environmental variables, species in the same environment should have similar egg sizes regardless of lineage. This dichotomy is, of course, a gross oversimplification, because different species are not under identical selective pressures even if they inhabit the same geographical areas and because the degree of relatedness between species found in different areas (and thus the time available for adaptation) generally varies. There is, however, one set of species for which some confounding variables can be eliminated through a comparison of populations that split from the same ancestor and have been evolving in separate environments for the same period of time. These are the Neotropical shallow-water species that were separated by the rise of the Central American land bridge, forming “geminate pairs” (Jordan 1908).

When the connections between the tropical Atlantic and Pacific oceans were severed by the emergence of the Central American isthmus 3.1 to 3.5 million years ago (Saito 1976; Keigwin 1978, 1982), they separated previously continuous marine populations. Each of the isolates has been evolving for the same period of time in the same general environment as more distantly related species, and independently from its closest relative in the other ocean. Divergence between members of each pair, if not random in direction, would be due to adaptation over the past three million years to the different environments of the two oceans. Thus, differences between geminate species can be used to assess the degree to which local adaptation can overcome phylogenetic constraints in three million years. Similarities between species that live in the same ocean but are less closely related than the geminates could provide indications of whether a common environmental optimum exists and of whether co-occurring species can adapt to it. This paper presents data on the egg size of 22 species of echinoids and 2 species of asteroids found on the two sides of Central America. Of these species, 14 belong to geminate pairs, and 8 are sympatric with a congener. By examining the level of variability between members of geminate pairs, between congeners, and between less related species, I attempted to determine whether egg size is a parameter that can evolve rapidly—thus justifying the assumptions of theoretical models and empirical correlations with other variables—or whether it is a conservative character determined by the past history of each group.

MATERIALS AND METHODS

Eggs were obtained from 16 species of regular echinoids, 5 species of clypeasteroids, and 1 spatangoid by injection of 0.5-M solution of potassium chloride in the coelomic cavity (Tyler 1949). Ova from two species of asteroids were collected by incubating excised ovaries in a 10^{-4} -M solution of 1-methyladenine (Kanatani 1969). Eggs were collected from 1976 to 1987 at localities listed in table 1 and (unless otherwise noted) preserved in a 5% formaldehyde solution in seawater. In each egg, the longest axis and the axis perpendicular to it were measured with an ocular micrometer under a magnification of $400\times$ or $100\times$, depending on size. Egg volume was calculated as that of a prolate spheroid with two axes equal to these measurements. All statistical comparisons were performed on egg volume; the longest axis is also reported to facilitate comparisons with data in the literature. Data on the egg volume of *Arbacia punctulata* are those of Goldforb (1935). Corrections for possible changes in volume due to formalin preservation were calculated by comparing 50 fresh eggs with 50 preserved eggs from each of 10 females per species (as described in Lessios 1987). A rarity of ripe females or inaccessibility of a microscope at the collection sites made it impossible to measure fresh eggs of 10 species. In these cases, the uncorrected values of preserved eggs are reported. Eggs of *Mellita quinquiesperforata* were measured fresh immediately after they were shed.

A set of eggs from individuals different from the ones included in the estimation of correction factors was used to calculate the descriptive statistics of each species. In species with sample sizes of at least 10 individuals, 5 eggs per female were measured. In species for which fewer than 10 ripe females were available, 50 eggs per individual were measured. A mean value was calculated for eggs obtained from each individual and subsequently used as a raw datum for the calculation of statistics.

RESULTS

Contrasts between pairs of species with common ancestors circumvent the problem of non-independence of datum points when a set of species is used to explore the correlation of one variable with another (Felsenstein 1985). Thus, the useful and formally correct statistical comparisons between the echinoderm species discussed here are those limited to the same genus. Despite substantial amounts of intraspecific variability (Lessios 1987), significant differences exist between the egg sizes of all congeneric species, regardless of whether they are sympatric or allopatric, except for those of *Tripneustes* (table 2). The small sample size of *T. depressus*, resulting from the extreme rarity of this species in Panama, would make it difficult to show significant differences from its Atlantic counterpart unless such differences were large. In two genera, *Diadema* and *Eucidaris*, the differences are slight, and significance was obtained only after correcting for size change due to preservation. Temporal intraspecific variation in echinoid egg size exists (Lessios 1987); this makes the mean values of four species with small

TABLE 1
LOCALITY WHERE EACH SPECIES WAS COLLECTED, PRIMARY HABITAT, AND
APPROXIMATE SIZE OF EACH SPECIES

Class/Order/ Family/Species	Locality	Habitat	Diameter (cm)*
Asteroidea			
Valvatida/Oreasteridae			
<i>Oreaster reticulatus</i>	Islas San Blas, Caribbean	<i>Thalassia</i> beds	20–25
<i>Oreaster occidentalis</i>	Islas Perlas, Bay of Panama	coral rubble fields	15–20
Echinoidea			
Cidaroida/Cidaridae			
<i>Eucidaris tribuloides</i>	Islas San Blas, Caribbean	coral reef, rocks	2–3
<i>Eucidaris thouarsi</i>	Isla Taboguilla, Bay of Panama	rocks, coral reef	3–5
Diadematoidea/Diadematidae			
<i>Diadema antillarum</i>	Punta Galeta and Islas San Blas, Caribbean	coral reef, sand, <i>Thalassia</i> beds	4–9
<i>Diadema mexicanum</i>	Isla Taboguilla, Bay of Panama	coral reef, rocks	2–6
<i>Astropyga magnifica</i>	Aguadilla, Puerto Rico	<i>Thalassia</i> beds, sand	10–15
<i>Astropyga pulvinata</i>	Isla Changame, Bay of Panama	sand, coral reef	5–9
Arbacioidea/Arbaciidae			
<i>Arbacia stellata</i>	Punta Paitilla, Bay of Panama	rocks	2–3
<i>Arbacia punctulata</i>	Raw data from Goldforb 1935	rocks	2–4
Temnopleuroidea/Toxopneustidae			
<i>Toxopneustes roseus</i>	Isla Taboguilla, Bay of Panama	coral rubble fields	5–7
<i>Lytechinus variegatus</i>	Islas San Blas, Caribbean	<i>Thalassia</i> beds	3–7
<i>Lytechinus williamsi</i>	Islas San Blas, Caribbean	coral reef	2–3
<i>Tripneustes ventricosus</i>	Islas San Blas, Caribbean	<i>Thalassia</i> beds	8–12
<i>Tripneustes depressus</i>	Isla Uva, Gulf of Chiriquí (Pacific)	coral rubble fields	10–15
Echinoida/Echinometridae			
<i>Echinometra lucunter</i>	Isla Margarita and Islas San Blas, Caribbean	reef flat	2–4
<i>Echinometra viridis</i>	Isla Margarita and Islas San Blas, Caribbean	coral reef	2–4
<i>Echinometra vanbrunti</i>	Isla Taboguilla and Punta Paitilla, Bay of Panama	rocky intertidal zone	3–6
Clypeasteroida			
Clypeasteridae			
<i>Clypeaster rosaceus</i>	Islas San Blas, Caribbean	coral rubble, sand	12–17
<i>Clypeaster subdepressus</i>	Islas San Blas, Caribbean	sand, subtidal zone	12–20
Mellitidae			
<i>Mellita (Leodia) sexesperforata</i>	Islas San Blas, Caribbean	sand, subtidal zone	5–8
<i>Mellita quinquesperforata</i>	María Chiquita, Caribbean coast of Panama	sand, subtidal zone	5–7
<i>Encope stokesii</i>	Playa Venado, Bay of Panama	sand, intertidal zone	3–6
Spatangoida/Brissidae			
<i>Plagiobrissus grantii</i>	Islas San Blas, Caribbean	sand, subtidal zone	20–25

* Diameter of asteroids from arm tip to arm tip; of other species, maximum diameter of adult test.

TABLE 2

SAMPLE SIZES, LINEAR DIMENSIONS, AND VOLUME OF EGGS OF PANAMANIAN ECHINODERMS¹

SPECIES ^a	OCEAN ^b	NO. OF INDIVIDUALS	NO. OF EGGS	LONGEST AXIS ^c		VOLUME ^e		SIGNIFICANCE OF INTRASPECIFIC DIFFERENCES (P)
				Mean (SD) (μm)	Correction Factor	Mean (SD) (μm ³)	Correction Factor	
<i>Oreaster reticulatus</i>	A	11	55	197.28 (33.69)	—	4.18 × 10 ⁶ (1.82 × 10 ⁶)	—	0.000 ^{d,e}
<i>Oreaster occidentalis</i>	P	33	165	144.83 (6.23)	—	1.43 × 10 ⁶ (1.54 × 10 ⁶)	—	
<i>Euclidaris tribuloides</i>	A	71	355	94.79 (4.49)	1.074	4.27 × 10 ⁵ (6.16 × 10 ⁵)	1.249	0.014 ^d
<i>Euclidaris thouarsi</i>	P	27	135	91.06 (7.47)	1.049	3.86 × 10 ⁵ (9.77 × 10 ⁵)	1.160	
<i>Diadema antillarum</i>	A	185	925	68.11 (3.09)	0.996	1.57 × 10 ⁵ (1.98 × 10 ⁵)	0.981	0.001 ^d
<i>Diadema mexicanum</i>	P	44	220	69.54 (2.63)	1.017	1.69 × 10 ⁵ (1.92 × 10 ⁵)	1.050	
<i>Astropyga magnifica</i>	A	4	200	104.04 (1.45)	—	5.59 × 10 ⁵ (2.55 × 10 ⁵)	—	0.000 ^{d,e}
<i>Astropyga pulvinata</i>	P	9	450	89.47 (4.20)	—	3.47 × 10 ⁵ (3.61 × 10 ⁵)	—	
<i>Arbacia punctulata</i> ^f	A	25	1059	—	—	2.03 × 10 ⁵ (1.54 × 10 ⁵)	—	0.000 ^{d,g}
<i>Arbacia stellata</i>	P	17	85	66.78 (3.68)	0.999	1.47 × 10 ⁵ (2.18 × 10 ⁵)	0.997	
<i>Toxopneustes roseus</i>	P	3	150	101.72 (2.07)	—	5.23 × 10 ⁵ (3.73 × 10 ⁵)	—	—
<i>Lytechinus variegatus</i>	A	89	445	102.15 (8.52)	1.036	5.24 × 10 ⁵ (1.32 × 10 ⁵)	1.120	0.000 ^d
<i>Lytechinus williamsi</i>	A	50	250	110.34 (8.71)	1.039	6.56 × 10 ⁵ (1.49 × 10 ⁵)	1.146	
<i>Tripneustes ventricosus</i>	A	63	315	80.35 (2.66)	—	2.59 × 10 ⁵ (2.31 × 10 ⁵)	—	0.532 ^{d,e}
<i>Tripneustes depressus</i>	P	3	150	79.16 (1.41)	—	2.50 × 10 ⁵ (7.33 × 10 ⁵)	—	
<i>Echinometra viridis</i>	A	83	415	93.65 (5.24)	1.001	3.97 × 10 ⁵ (6.06 × 10 ⁵)	1.004	0.000 ^d
<i>Echinometra lucunter</i>	A	74	370	88.93 (8.59)	1.011	3.40 × 10 ⁵ (1.00 × 10 ⁵)	1.021	<0.05 ^h
<i>Echinometra vanbrunti</i>	P	21	105	72.40 (8.53)	1.023	1.94 × 10 ⁵ (6.99 × 10 ⁵)	1.065	<0.05 ^h
<i>Clypeaster rosaceus</i>	A	32	160	321.05 (18.43)	1.068	1.71 × 10 ⁷ (2.99 × 10 ⁶)	1.239	0.000 ^d
<i>Clypeaster subdepressus</i>	A	71	355	162.06 (8.82)	1.028	2.15 × 10 ⁶ (3.28 × 10 ⁵)	1.093	
<i>Mellita (Leodia) sextesperforata</i>	A	51	255	237.16 (17.81)	1.293	6.70 × 10 ⁶ (1.41 × 10 ⁷)	2.292	0.000 ^{d,g}
<i>Mellita quinquesperforata</i> ⁱ	A	15	75	137.91 (8.47)	—	1.19 × 10 ⁶ (2.72 × 10 ⁵)	—	
<i>Encope stokesii</i>	P	29	145	119.65 (7.44)	—	7.64 × 10 ⁵ (1.10 × 10 ⁵)	—	—
<i>Plagiobrissus grantis</i>	A	1	50	106.70 (9.10)	—	5.54 × 10 ⁵ (1.21 × 10 ⁵)	—	—

^a Brackets indicate presumed geminate species.^b A, Atlantic; P, Pacific.^c Reported means and standard deviations were calculated by considering the mean of all eggs from an individual as the raw datum point; they include the correction for preservation. Correction factors for preservation in formalin were calculated by dividing the mean volume of 50 fresh eggs from each of 10 females by the mean volume of 50 preserved eggs from the same female.^d F-test.^e Comparison between preserved eggs.^f Data from Goldforb 1935.^g Comparison between fresh eggs of one species and values corrected for the effect of preservation in the other.^h Student-Newman-Keuls test; significance applies to all pairwise comparisons.ⁱ Eggs measured fresh.

sample sizes suspect as descriptors of central tendency. However, there is no reason to believe that intraspecific variation has biased interspecific comparisons in any consistent direction. Thus, one can conclude that, as a rule, eggs of different species in a genus differ in volume.

If one compares Atlantic and Pacific geminates in each genus, a trend emerges: in six out of seven pairs (in the asteroid genus *Oreaster* and the echinoid genera *Eucidaris*, *Astropyga*, *Arbacia*, *Tripneustes*, and *Echinometra*, but not *Diadema*), the Pacific member has smaller eggs than the Atlantic one. This pattern has a small probability of being due to chance (Wilcoxon paired-sample test, $T = 1$, $0.05 > P > 0.02$). It suggests that the direction of divergence between geminates in egg size has not been random and that it results from an adaptation to an environmental variable with different values in each ocean. The three species of *Echinometra* are an example of this trend. Their egg volumes are significantly different from each other, with the Pacific representative of the genus having the smallest eggs. The Atlantic species that resembles *E. vanbrunti* more closely in egg size is *E. lucunter*, which is also the species that morphology (Mortensen 1943; Cheshier 1972; Lessios 1981a) and mitochondrial DNA (E. Bermingham and Lessios, MS) indicate to be its geminate. *Echinometra viridis*, which probably split from the *E. lucunter*-*E. vanbrunti* stock either shortly before or during the erection of the isthmus (Bermingham and Lessios, MS), has eggs that are slightly larger than those of its sympatric congener.

With the glaring exception of *Clypeaster* (and *Mellita*, in which the two species are often placed in different genera), species in the same genus, both sympatric and allopatric, tend to have eggs of roughly the same size. The volume of *Clypeaster rosaceus* eggs is eight times that of its sympatric congener *C. subdepressus*, an adaptation that reflects the different developmental modes in these species; the former is a facultative planktotroph, whereas the latter is an obligate planktotroph (Emlet 1986). The influence of common ancestry, however, does not extend to higher taxonomic categories; a cladogram based on egg size would bear little resemblance to the phylogenetic tree of the species in question (fig. 1). The Clypeasteroidea *Clypeaster* and *Mellita* have large eggs, but they resemble the eggs of the asteroid *Oreaster*, with which they have not shared an ancestor since the Ordovician, more than they resemble those of other echinoids, from which they split more recently. The eggs of *Diadema* resemble those of *Arbacia*, a genus belonging to a lineage from which the diadematoids diverged as far back as the Triassic, more than they resemble the eggs of *Astropyga*, which is in the same family. *Toxopneustes* has eggs close in size to those of *Lytechinus*; but *Tripneustes*, the third member of the family Toxopneustidae in the sample, has eggs that are only half as large.

DISCUSSION

Four trends emerge from the comparisons of egg size in 24 species of echinoderms on the two coasts of Central America. (1) Species have eggs that are significantly different from those of other, congeneric species. (2) Species evolving

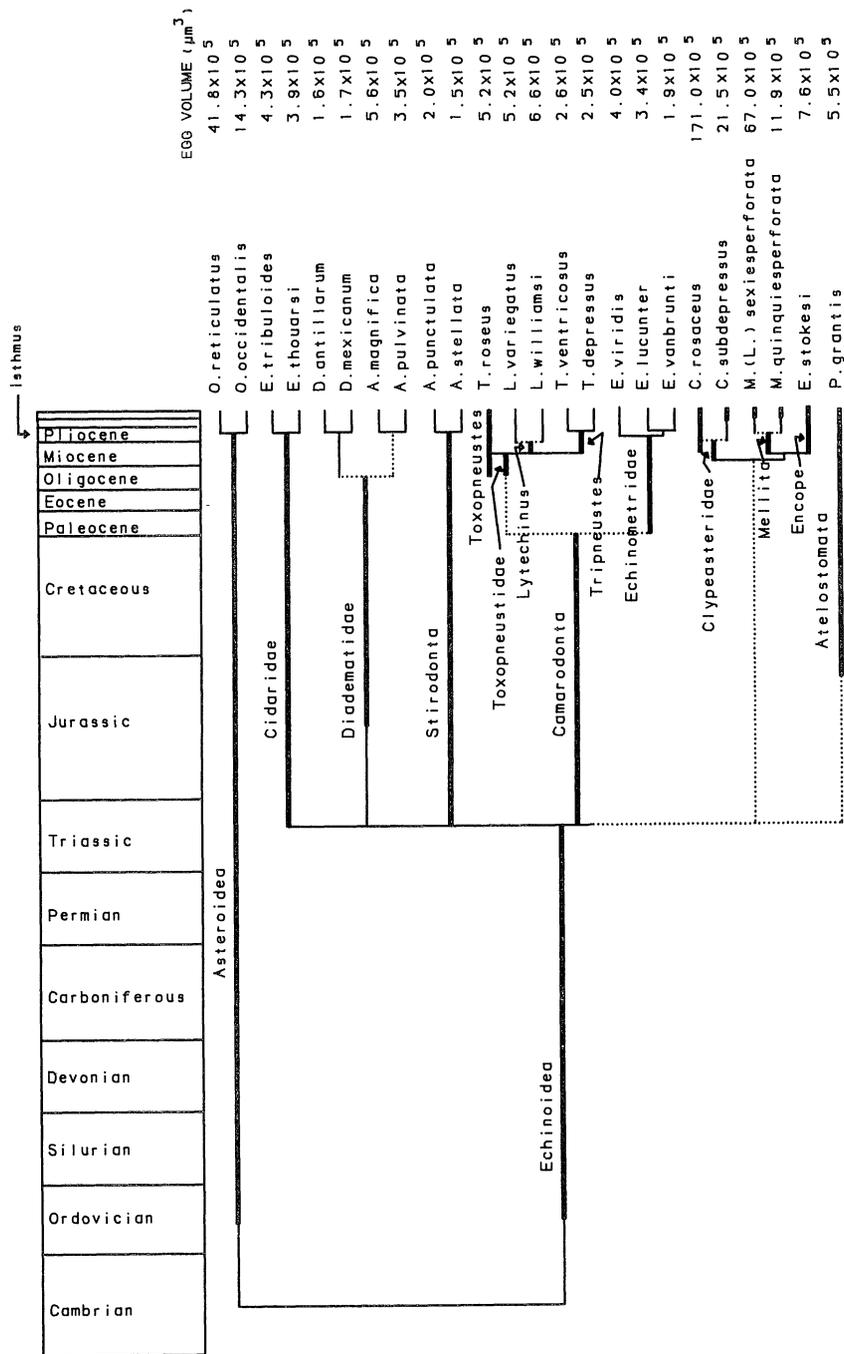


FIG. 1.—Phylogenetic relationships between species included in this study, and their respective egg sizes. The stratigraphic range of the highest category that helps establish the most recent common ancestor with the rest of the groups is shown by a heavy continuous line (the taxon is indicated next to the line). Thin solid lines indicate relationships for which there is evidence regarding times of divergence. Dotted lines indicate times of splitting about which no estimate is available. Stratigraphic ranges of species are from Mortensen 1948 and Kier 1963, of genera from Moore 1966, and of families and higher categories from Smith 1984. The time of splitting between the species of *Echinometra* is estimated from mitochondrial-DNA divergence (Bermingham and Lessios, MS).

for three million years in separate environments have accumulated differences in their egg sizes; the direction of these differences is not random. (3) Egg size of congeneric species is similar where developmental modes are similar. (4) There is no similarity between the egg sizes of species belonging to the same family or higher taxonomic category, even if these species inhabit the same ocean.

That in six of seven transoceanic comparisons the Pacific species of each geminate pair has smaller eggs than the Atlantic one suggests that egg size responds to selective regimes imposed by the different environments of these oceans. Though various aspects of echinoderm phylogeny are contested (see, e.g., Durham and Melville 1957; Moore 1966; Smith 1984), fossil evidence leaves no doubt that the Asterozoa split from the Echinozoa no later than the Ordovician and that many of the clades to which the echinoid geminate species belong diverged no later than the Triassic (see the figure). That the phenomenon of smaller eggs in the Pacific holds for lineages that have not shared a common ancestor for such a long time also supports the notion of independent adaptation by the members of each pair to the environments of the two oceans during the last three million years.

As adults, these species are found in diverse habitats and reach different body sizes, which are not correlated with the size of their eggs (tables 1, 2; Spearman's $r_s = 0.29$, $P > 0.05$). It is hard to see how ocean-specific allometric constraints in the adult stages of life history could explain the differences between the egg sizes of geminate species. Data on the annual fluctuations in gonadal content in *Echinometra* and *Diadema* (Lessios 1981b) indicate that reproductive effort varies between conspecific populations in wave-swept areas and in protected areas, presumably as the result of varying resource availability or varying needs for the apportionment of resources into growth (Lessios 1979a); yet, the eggs of the same populations do not differ in size (Lessios 1987). This lack of correspondence between annual gonadal production and egg size suggests that resource limitations may affect the total reproductive output of sea urchins but not the size of their eggs. Thus, ocean-specific resource limitations acting on the adults are also an unlikely cause of the differences between egg sizes of geminate species.

However, all echinoid species included in transoceanic comparisons have planktotrophic larvae (Mortensen 1921); the development of *Oreaster* is unknown, but given the size of its eggs, it is safe to assume that its species also possess planktotrophic larvae. Thus, all species in each ocean may encounter different sets of environmental variables as adults, but they probably share conditions in the water column as larvae. An environmental variable important to the larvae is, therefore, a more likely cause of the observed differences between the members of each pair. Primary productivity is a general characteristic of each ocean expected to affect the planktotrophic larvae of all species, regardless of adult habitat. The coastal waters of the tropical eastern Pacific have greater primary productivity than the Caribbean (Bayer et al. 1970; Glynn 1982; Bishop and Marra 1984; Goodwin 1987; Marra et al. 1987). If the size and feeding ability of planktotrophic larvae are positively correlated with the size of the eggs from which they came (Strathmann 1975; Sinervo and McEdward 1988) and if greater availability of food results in faster developmental rates of larvae (for a discussion

of the validity of these relationships in echinoderms, see Emlet et al. 1987), then the Pacific species could produce more eggs by making them smaller than those of their Caribbean congeners without suffering adverse consequences in terms of increased time in the hazardous planktonic stage or of smaller size at metamorphosis.

The differences between geminate species indicate that adaptation to environmental regimes can bring significant shifts in mean egg size in three million years; what is more, the generally consistent direction of differences between the inhabitants of each ocean suggests that some environmental variables affect all species in a similar manner, regardless of phylogeny. Does this mean that the egg size of marine invertebrates can vary independently of the lineage from which they came, as has been assumed in theoretical models (Vance 1973; Christiansen and Fenchel 1979; Perron and Carrier 1981; Grant 1983; Strathmann 1985; Emlet et al. 1987) and in empirical comparisons (Thorson 1950; Spight 1976; Strathmann and Vedder 1977; Turner and Lawrence 1979; Perron 1981; Amy 1983; DeFreese and Clark 1983; Lawrence et al. 1984; Emlet et al. 1987)? An extreme hypothesis of unhindered response to the environment would predict that if environmental variables affect all species in each ocean in the same manner, they would define a common optimum on each side of the isthmus toward which egg sizes of all echinoderms would tend to converge. Clearly, the data do not fit such a simple hypothesis. There is no such thing as a characteristic egg size for the Pacific and another for the Caribbean. The eggs of Pacific species may be smaller than those of their Atlantic counterparts, but they are still larger than those of Atlantic species belonging to different genera.

A lineage-dependent, historical reason must exist for the variation in egg size within each ocean. The members of geminate species have been separated from each other recently, are still quite similar morphologically and genetically (Leslios 1979*b*, 1981*a*), and would be expected to perceive selective pressures and respond to them in a similar manner. Sympatric members of different genera, by contrast, have split at various times during the entire Phanerozoic (see the figure). It is to be expected, therefore, that each of these groups has developed into a unique epistatic and epigenetic system, with different larval morphologies and feeding efficiencies and with dissimilar adult reproductive and developmental designs. Given these differences in the basic biology of the genera, it may be that there is no common optimal egg size in each ocean. Each taxon may have its own optimum, resulting from different trade-offs with other parameters of life history, different degrees of investment in reproduction, different additional selective pressures or resource limitations imposed by its basic biology, or different strategies employed to maximize the number of larvae that survive to metamorphosis. For example, each genus may respond to the larval needs for organic material by changing the concentration, rather than the size, of each egg, or different concentrations (imposed by other aspects of the reproductive system) may make the optimal egg size vary between taxa (Turner and Lawrence 1979). *Clypeaster rosaceus* provides an example of a shift in strategy for provisioning the larvae that necessitates a drastic change in egg size; though this shift may be a response to the same selective pressures that have been proposed as responsible for the differ-

ences between the geminates—namely, the relative paucity of larval food in the Caribbean—its sympatric congener, *C. subdepressus*, has not devised the same solution. Another possibility is that, in contrast to the geminate species, sympatric members of different genera started out, for historical reasons, with different egg sizes, and relatively weak selection has not been able to make them conform to common optima that have existed only for the past three million years. None of these possibilities denies the importance of selection, but each can be classified under the general category of “phylogenetic constraints,” in that they invoke previously acquired adaptations to explain differences in the present ecological context.

That phylogeny on a taxonomic level higher than the genus does not seem important—that is, that there may be a characteristic egg-size range for a genus but not for a family—is not surprising. Given that egg size comprises a single character and given that the observed upper and lower limits of its range are fairly close together, it is to be expected that as two genera diverge, they eventually come to resemble members of a different family more than they resemble each other.

Thus, the mean egg sizes of echinoderm species are capable of changing in as little as three million years, presumably under the influence of natural selection. Such shifts, however, occur within the constraints imposed by phylogeny (or by selective regimes as they are defined by interactions of the basic biology of each species with its environment, which would still be a function of lineage), and these constraints seem fairly stringent. This would mean that theoretical formulations can predict the direction of divergence between congeneric species but not an absolute value to be attained by a heterogeneous sample of species, even if they are all subject to the same environmental variables.

SUMMARY

Theoretical models and empirical observations have attempted to determine selective pressures that influence the egg size of marine invertebrates. Both approaches generally assume that egg size is free to evolve toward an evolutionarily stable point without any constraints imposed by phylogeny. The size of eggs in 22 species of echinoids and 2 species of asteroids from the two sides of the Isthmus of Panama was determined in an effort to assess the rate at which differences between species can accumulate. Of these 24 species, 14 belong to pairs of geminate species, presumed to have been divided by the rise of the isthmus 3.1–3.5 million years ago. Comparisons between egg size in related species evolving in separate environments for the same period of time, and in related and unrelated species living in the same environment, were used to evaluate the relative importance of adaptation and phylogeny in determining the egg size of a species. In 12 of 13 comparisons, the mean egg size of each species was significantly different from that of all other species of the same genus, whether allopatric or sympatric. In 6 of 7 pairs, the Pacific member had eggs that were smaller than those of the Atlantic one, a pattern attributed to adaptation to the higher levels of primary productivity in the eastern Pacific. Therefore, shifts in mean egg size are possible in three

million years of independent evolution. However, there was no egg size characteristic for each ocean, and (except for the sand dollar *Clypeaster*, in which one species has evolved a facultatively planktotrophic larva) the differences between congeneric species were small compared with the differences between members of different genera. Thus, though adaptation to different environments can push egg size in a particular direction, differences in the basic biology of genera, accumulated over the course of their phylogenetic history, either constrain the possible sizes to be attained by each genus or cause selective regimes within the same environment to be dissimilar.

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