Are Echinoderm Egg Size Distributions Bimodal?

MARY A. SEWELL* AND CRAIG M. YOUNG

*Department of Larval Ecology, Harbor Branch Oceanographic Institution,
5600 U.S. 1 North, Fort Pierce, Florida 34946*

Marine invertebrates can be categorized into species that reproduce by producing either large numbers of small, energetically inexpensive eggs that become planktotrophic larvae, or fewer, larger eggs with more yolk and lecithotrophic development (1). The selective advantages of these alternative strategies were considered in a series of simple mathematical models by Vance (2, 3). These models predicted that intermediate egg sizes should have lower reproductive efficiency, and that only extreme egg sizes should be evolutionarily stable (2, 3). Specifically, Vance's models (2, 3), and later modifications (4–7), predict that eggs of marine invertebrates should have bimodal size distributions, reflecting the contrast between small egg/feeding and large egg/nonfeeding modes of development and the selection against intermediate egg sizes. Evidence for bimodality in egg size distributions is, however, equivocal, with unimodal distributions seen in the majority of comparative studies that are appropriate tests of the hypothesis (8–13). Bimodal distributions have been described only in a few groups of molluscs (4) and in asteroid and echinoid echinoderms (14). Here we test the prediction of bimodality in the holothuroid and ophiuroid echinoderms and show that although the natural log-transformed egg size distributions are visually unimodal, the holothurian egg size distribution is statistically composed of two discrete modes. Moreover, reexamination of the asteroid and echinoid egg size distributions (14) with the addition of data from more recent literature confirms that there are two statistical modes in the egg size distributions of these classes. Thus, in the phylum Echinodermata, there is a bimodal egg size distribution in three of the four classes in which this prediction can be tested.

In marine invertebrates there is a tradeoff between fecundity and the amount of energy that can be invested in each egg. Thus, as a rule, a species produces either many, small eggs with planktotrophic development or fewer, larger eggs with lecithotrophic development (1). As the size of eggs may differ between closely related species, egg size is assumed to be subject to considerable selective pressure (15–17). This has prompted interest in documenting patterns of egg size among species and higher taxa, and in exploring how factors such as phylogeny (15), fertilization biology (16, 18, 19), length of the prehatching (14, 20) and prefeeding periods (17), and size and organic content at metamorphosis (*e.g.,* 14, 21) might be important for selection of egg size.

In early mathematical modeling Vance (2, 3) viewed planktotrophy and lecithotrophy as extreme forms of larval development, and his models suggested that only the extreme egg sizes would confer maximum reproductive efficiency (number of newly metamorphosed adults per unit of energy devoted to reproduction). Subsequently, the prediction of bimodality in egg sizes within taxa of marine invertebrates was tested by a number of authors using previously published or new data sets. Most of these studies showed unimodal egg size distributions (see also fig. 2 in ref. 22). Examples include prosobranch gastropods (9, 10), opisthobranchs (11), muricid gastropods without nurse eggs (12), Indo-Pacific *Conus* (13), bivalves (8), chitons (23), thoracican barnacles (24), and stomatopods (25). Bimodal distributions in egg size were described in American species of the genus *Crepidula* (4), in prosobranch gastropods from Danish waters (4), and in echinoid and asteroid echinoderms (14).

Many of the early studies used data sets that were not adequate for a valid test of the distribution patterns of egg size. We defined three criteria for appropriate data sets: (a) the data should include both planktotrophic (feeding) and lecithotrophic (nonfeeding) forms of develop-

ment; (b) the egg sizes should be from species that span a broad range of habitats and a wide geographic range; and (c) the data should exclude species that provide additional maternal investment (e.g., nurse eggs, capsules). Criterion (b) is necessary because egg size may be correlated with habitat—for example, more planktotrophs in the tropics (1)—and use of species from a limited geographic area might under- or overemphasize a particular developmental type. Criterion (c) is necessary because Vance's models (2, 3) assume that reproductive energy is invested solely in the egg. Additionally, because the models (2, 3) were developed in terms of energetic content rather than egg size *per se,* for all data sets it is assumed that there is a correlation between egg size and energetic content.

The primary criterion, that planktotrophic and lecithotrophic forms be present, is violated by three of the taxa: thoracican barnacles (24) and stomatopods (25), neither of which groups include species with lecithotrophic development, and chitons (23), which do not include species with planktotrophic development. Criterion (b) may be violated by Ockelmann's bivalve data set (8) because planktotrophs are rare in East Greenland (26), in compilations of egg sizes in American species of *Crepidula* (4) and Danish prosobranchs (4), and in studies with low sample sizes (4, 23, 24, 25). Violation of criterion (c) has been avoided by removal of species using nurse eggs (12, fig. 2 in ref. 22). With the removal of studies that clearly violate criterion (a) there are unimodal egg size distributions in six taxa (8–13) and bimodal distributions in four taxa (4, 14).

The best known, and most widely cited, example of the bimodality in egg sizes within a taxon is the extensive data set compiled by Emlet *et al.* (14) for asteroid and echinoid echinoderms. This data set meets criteria (a)–(c) above, incorporating egg sizes from 89 asteroid species and 109 echinoid species from a variety of habitats. Moreover, in this phylum there is a strong correlation between egg size and energetic content (27). Of the four remaining classes of echinoderms, our criteria are not met in the crinoids, where there are no known planktotrophic species (28), or in the concentricycloids, where there are only two described species (29). In this paper we test the prediction of bimodality in egg sizes in the two remaining classes, the holothuroids and ophiuroids, which meet the criteria defined above, and we incorporate new data into the published egg size distributions of echinoids and asteroids (14).

The egg size data sets used in this analysis were compiled from the published literature and our own unpublished data, with the implicit assumption that all echinoderm eggs are basically alike. As noted by Turner and Lawrence (30), although egg diameter is an easy reproductive character to measure, there are shortcomings in its use for theoretical discussions of life-history patterns. Firstly, many species have oblately or prolately spheroidal eggs, so that eggs with the same diameter may have different egg volumes (30). We did not attempt to convert published egg diameters to volumes because in most cases only one of the two linear dimensions required for such a calculation was presented. Secondly, egg measurements made from histological sections will underestimate egg diameter because of tissue shrinkage during processing and the hydration of the egg during spawning (30). We used the diameters of both intraovarian and freshly spawned eggs in this paper to increase the sample sizes for statistical analysis ($n > 100$ species for all classes). Because the size classes in the raw (100 μm) and ln-transformed analyses (ln 0.25) are relatively large, we assumed that intraovarian egg diameters would have a low probability of moving into an adjacent size class should a freshly spawned egg diameter be available. Thirdly, eggs differ in their organic components—lipid, protein, etc—(27, 30) and our assumption that egg diameter is an effective measure of maternal investment may prove to be untenable.

Previous studies of egg size distributions in marine invertebrates have determined the number of modes in the distribution by visual appraisal. In this paper we instead made use of statistical techniques designed to differentiate length-frequency classes of fish populations (31). Histograms of egg diameter frequencies were generated for each class using the raw and ln-transformed diameters as shown in Figures 1–4. A modal analysis using the method of Schnute and Fournier (31) was then used to identify the Gaussian modes presented in these figures. Because the analysis is relatively insensitive to the dimensions of the size classes (31; B. Smith, pers. comm.), this method provides an objective way to examine the egg size distribution in a particular taxon and directly test the hypothesis of bimodality of egg sizes in marine invertebrates (2, 3). The complete raw data sets used for these analyses are available to interested readers from either of the authors.

Holothuroids show an extreme range in egg diameter, from a minimum of 50 μm in the apodid *Synaptula reciprocans* to a maximum of 4400 μm in the elasipod *Psychropotes longicauda* (Fig. 1A). About 80% of the species have eggs smaller than 1000 μm in diameter (Fig. 1A), with four modes in the size-frequency distribution (Table I). The first mode is at an egg diameter of 194 μm (Fig. 1A, Table I), and comprises species with eggs from 50 to about 300 μm with planktotrophic or unknown development (Fig. 1A). A second, but overlapping, mode is seen at 421 μm, with species with lecithotrophic, brooded, or unknown development (lecithotrophs: 150–950 μm; Fig. 1A). A large number of species in the unknown category in this mode are dendrochirote holothurians with
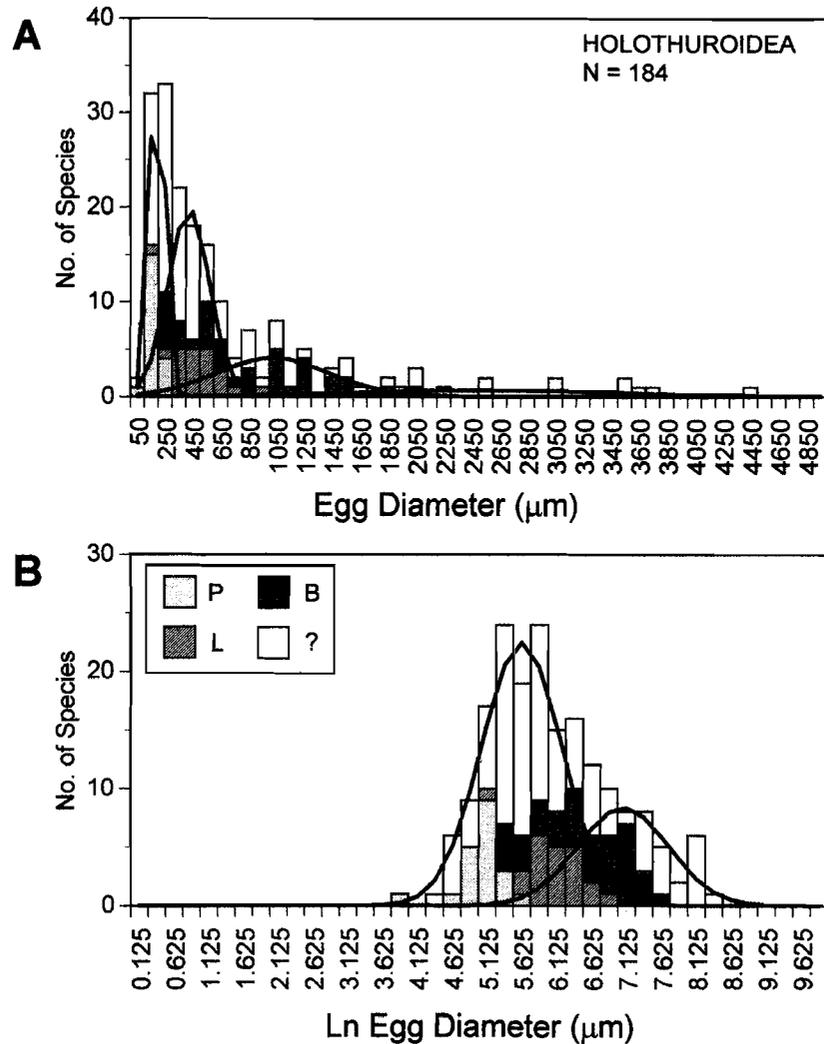
Figure 1. Egg size distribution pattern in the class Holothuroidea (n = 184). Information on the egg size of species of holothurians was compiled from the published literature and our own unpublished data. If more than one egg size was reported for a particular species, the maximum value was used in the figure. The type of larval development (planktotrophic, lecithotrophic, brooding) was based on the known development of that species from laboratory or field collections. This resulted in a large number of species with unknown developmental type; egg size was not used to infer developmental mode. Species were categorized as having an auricularia larva (planktotrophic), a doliolaria larva only (lecithotrophic), or internal/external brooding. Two species, *Holothuria floridana* and *Thyone fusus*, that are reported to have pelagic direct development were included with the lecithotrophs. The complete raw data set for this figure can be obtained from either of the authors. (A) Histogram of the untransformed egg diameters in the class Holothuroidea; x-axis shows the midpoint of the 100-μm size class. (B) Histogram of the natural log-transformed egg diameters in the class Holothuroidea; x-axis shows the midpoint of the ln 0.25 size class. Part B follows Emlet *et al.* (14) in using the natural log transformation of egg diameter to combine species with large lecithotrophic eggs into a smaller number of categories. Legend to developmental type is as shown in part B: P = planktotrophic (n = 20); L = lecithotrophic (n = 22); B = brooded (n = 38); ? = unknown development (n = 104). Solid line differentiates modes identified in the statistical analysis (see Table I for details).

egg sizes in the 200–800 μm range. As there are no known planktotrophs in this order (32), this mode may additionally include 20 lecithotrophic species. The last two modes, at 1024 and 2603 μm, are primarily composed of species that are lecithotrophic, brood, or have unknown

development type (Fig. 1A)—the majority of the latter species are elasipod holothurians and may have direct development (33). Thus, in the holothurians the first mode contains mainly species with planktotrophic development; the following three modes are species with nonfeeding

Table I

Results of modal analysis for egg size distributions in asteroid (n = 149), echinoid (n = 131), holothuroid (n = 184), and ophiuroid echinoderms (n = 132)

Class	No. of modes	Mean egg diameter (μm)	SD	No. of species in mode	K-S test statistic
(a) Raw numbers					
Asteroidea	4	162	29	55.32	0.026
		475	89	25.99	
		1008	206	55.42	
		2472	806	12.25	
Echinoidea	4	102	15	91.99	0.014
		317	140	20.76	
		1157	160	14.00	
		2000	18	4.00	
Holothuroidea	4	194	45	51.09	0.021
		421	147	74.40	
		1024	409	41.42	
		2603	970	16.50	
Ophiuroidea	3	165	50	58.46	0.055
		450	210	71.34	
		1528	3	1.00	
(b) Natural log transformation					
Asteroidea	2	5.03	0.24	55.32	0.040
		6.75	0.58	93.68	
Echinoidea	2	4.60	0.25	89.07	0.043
		6.22	0.92	41.93	
Holothuroidea	2	5.62	0.57	129.43	0.018
		7.08	0.65	54.57	
Ophiuroidea	1	5.46	0.69	132	0.051

The number and position of modes within each distribution were determined using a computer program developed by Dr. B. Smith (Environment Canada, Vancouver) using the method of Schnute and Fournier (31). For these analyses the mean and standard deviation of the modes were assumed to be independent of each other, and were not constrained to conform to any particular function (31). Competing models were ranked using the χ^2 procedure suggested by Schnute and Fournier (31), in combination with likelihood ratio tests (39) and the Akaike Information Criterion (AIC, 40). The table presents the parameters of the modal structures that best explained the observed data: the number of statistical modes in each distribution, the mean egg diameter and standard deviation of each mode, and the number of species in mode (the proportion of observations in each mode multiplied by the total number of species in the distribution). The Kolmogorov-Smirnov (K-S) test statistic (41) was used as a measure of the fit of the predicted model to the observed distribution, and is not rejected at the 0.05 level in any case.

(planktonic or brooded lecithotrophs) or unknown development.

The natural log-transformed distribution appears visually to be unimodal with a slight right skew (Fig. 1B). Statistical analysis, however, reveals two modes with means of ln 5.62 and 7.08 respectively (Table I). There is no clear demarcation between planktotrophic, lecithotrophic, and brooding species, with representatives of all

three developmental types in the first mode (Fig. 1B). The second mode, however, is almost exclusively composed of species with lecithotrophic or brooded development.

Examination of the egg size distribution in the ophiuroids reveals a similar distribution in the untransformed egg sizes (Fig. 2A). Ophiuroid eggs are smaller than holothuroid eggs, ranging in diameter from 50 μm in *Ophiactis kroeyeri* to 1500 μm in *Astrospartus mediterraneus* (Fig. 2A). Ninety-five percent of the species produce eggs smaller than 800 μm, and only two species have egg sizes greater than 1000 μm (Fig. 2A). There are three statistical modes in the egg size distribution: the first, at 165 μm, of species with primarily planktotrophic (80–185 μm) development; the second, at 450 μm, of species with abbreviated (150–350 μm), brooded (100–1000 μm), or unknown development; and the third, at 1528 μm, which results from a single species (*Astrospartus mediterraneus*) with unknown development (Fig 2A, Table I).

The ln-transformed egg size distribution in the ophiuroids appears visually to be unimodal (Fig. 2B) and similar in shape to that observed in the holothuroids (Fig. 1B). Although there are lower numbers of species with eggs in the ln 4.75–5.0 size class (115–148 μm), there is only one statistical mode (ln 5.46, Table I). In this class, therefore, all developmental types are included within the single mode of the distribution.

In literature published since the review of Emlet *et al.* (14) and in our own unpublished data, we added egg sizes for 61 asteroid species. Asteroids have four modes in the untransformed egg size distributions (Fig. 3A, Table I). The first mode is of species with primarily planktotrophic development; the following three modes comprise species with lecithotrophic, brooded, or unknown development (Fig. 3A).

The addition of the new asteroid data to the natural log-transformed egg size distribution does not alter the bimodality described by Emlet *et al.* (14). Statistically there are two separate modes, at ln 5.03 and 6.75 (Fig. 3B, Table I)—the first (Fig. 3B) contains almost exclusively planktotrophic species (79%), with one lecithotrophic species (*Astropecten latespinosus*) and three brooders, two of which are intraovarian brooders, *Patiriella vivipara* and *P. parvivipara* (34). The second mode (Fig. 3B) is predominantly lecithotrophic (62%) and brooding (12%) species, with the exception of the planktotrophic *Porania antarctica* (35). The asteroid species with the exceptional developmental type for that mode are often species with rare developmental types. For example, *Astropecten latespinosus* (300 μm) has an abbreviated lecithotrophic development, lacks both a bipinnaria and a brachiolaria stage, and is in the plankton for only about 4 days (36). *Porania antarctica* similarly has a large egg (550 μm) and
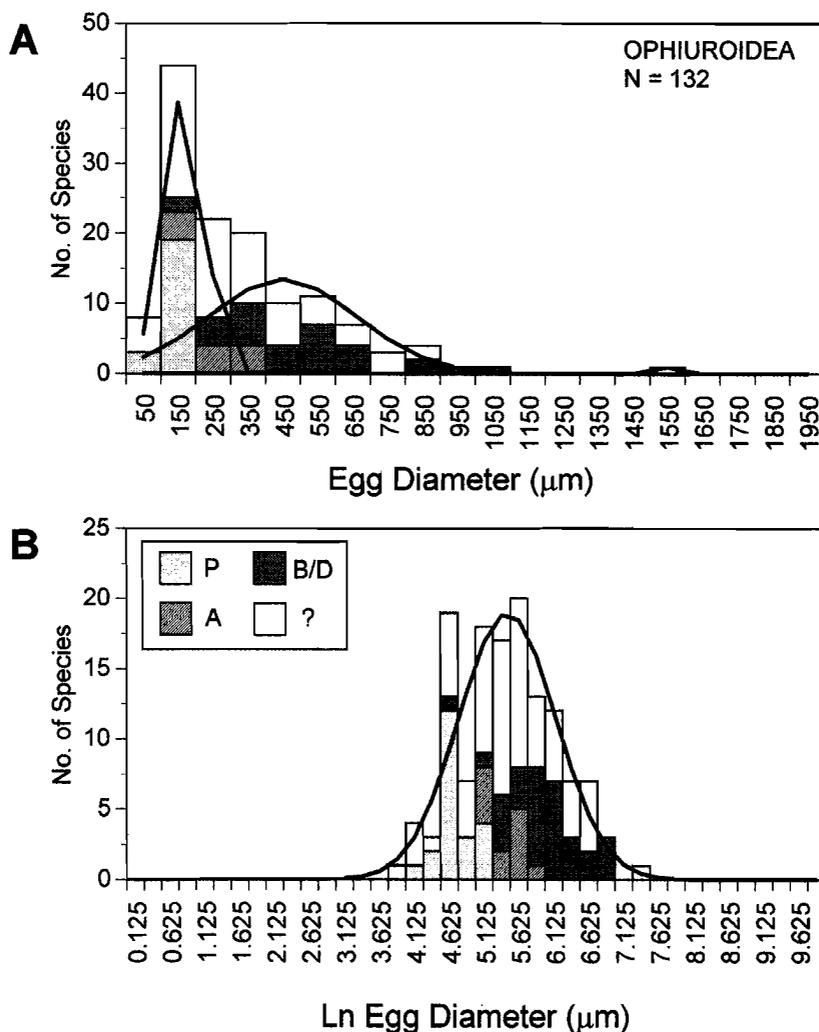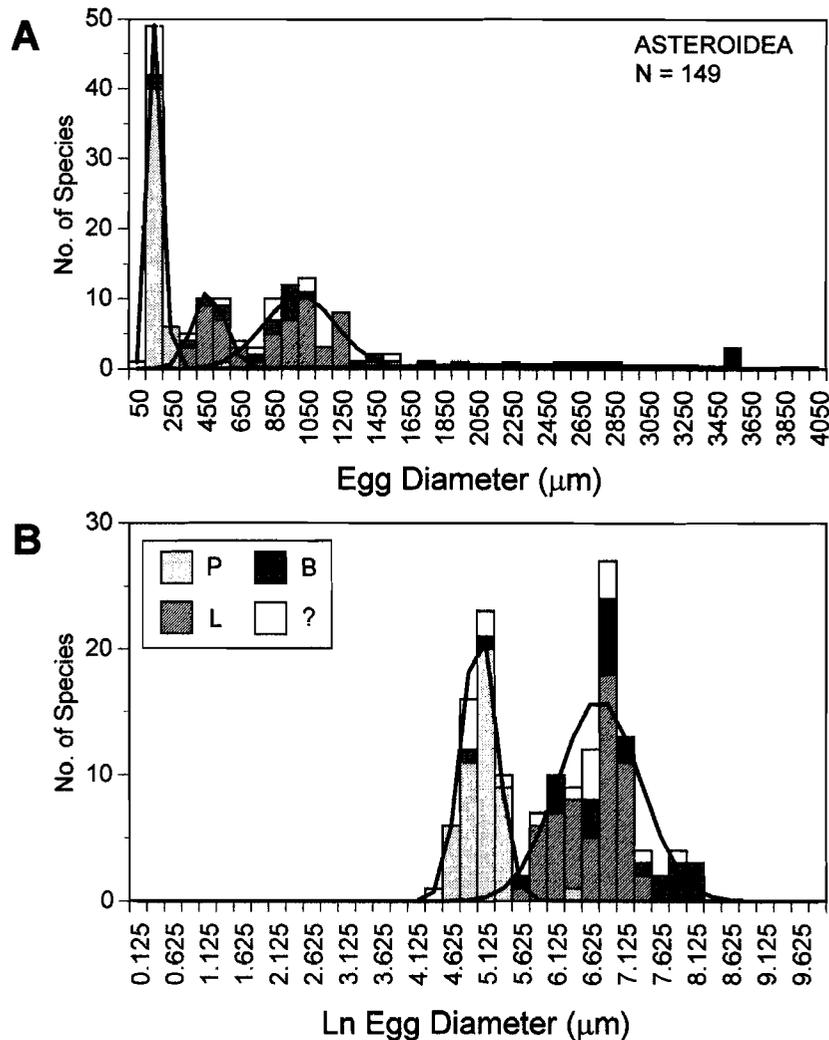
Figure 2. Egg size distribution pattern in the class Ophiuroidea ($n = 132$). Information on the egg size of species of ophiuroids was compiled from Hendler (109 ophiuroid species, ref. 38) and later published literature. The type of larval development was based on Hendler's classification (ref. 38, p. 456): planktotrophic = with a relatively long-lived ophiopluteus larvae; abbreviated = reduced ophioplutei, embryos in an attached fertilization envelope, lecithotrophic vitellaria larvae, or demersal larvae; brooded/direct = viviparous, internal or external brooding, or with an egg capsule. The complete raw data set for this figure can be obtained from either of the authors. (A) Histogram of the untransformed egg diameters in the class Ophiuroidea; x-axis shows the midpoint of the 100-μm size class. (B) Histogram of the natural log-transformed egg diameters in the class Ophiuroidea; x-axis shows the midpoint of the ln 0.25 size class. Legend to developmental type is as shown in part B: P = planktotrophic ($n = 22$); A = abbreviated ($n = 12$); B/D = brooded/direct ($n = 31$); ? = unknown development ($n = 67$). Solid line differentiates modes identified in the statistical analysis (see Table I for details).

planktotrophic development, but has the shortest period of development (65 days) of any of the Antarctic asteroids studied by Bosch and Pearse (35). For these species, particularly, it would be of interest to examine whether the energetic content or biochemical composition of their eggs differs from those of other asteroids of the same developmental type.

In the four echinoderm classes analyzed, it is only the

asteroids that show two separate, distinct, and statistically differentiated modes (Fig. 3B). There are few species with egg sizes in the size class ln 5.5 to 5.75, equivalent to egg diameters of 245 to 314 μm (Fig. 3B).

Twenty-two egg sizes were added to the echinoid data set of Emlet *et al.* (14). The untransformed distribution comprises four modes (Fig. 4A, Table I). The first two modes, at 102 and 317 μm, overlap considerably and are
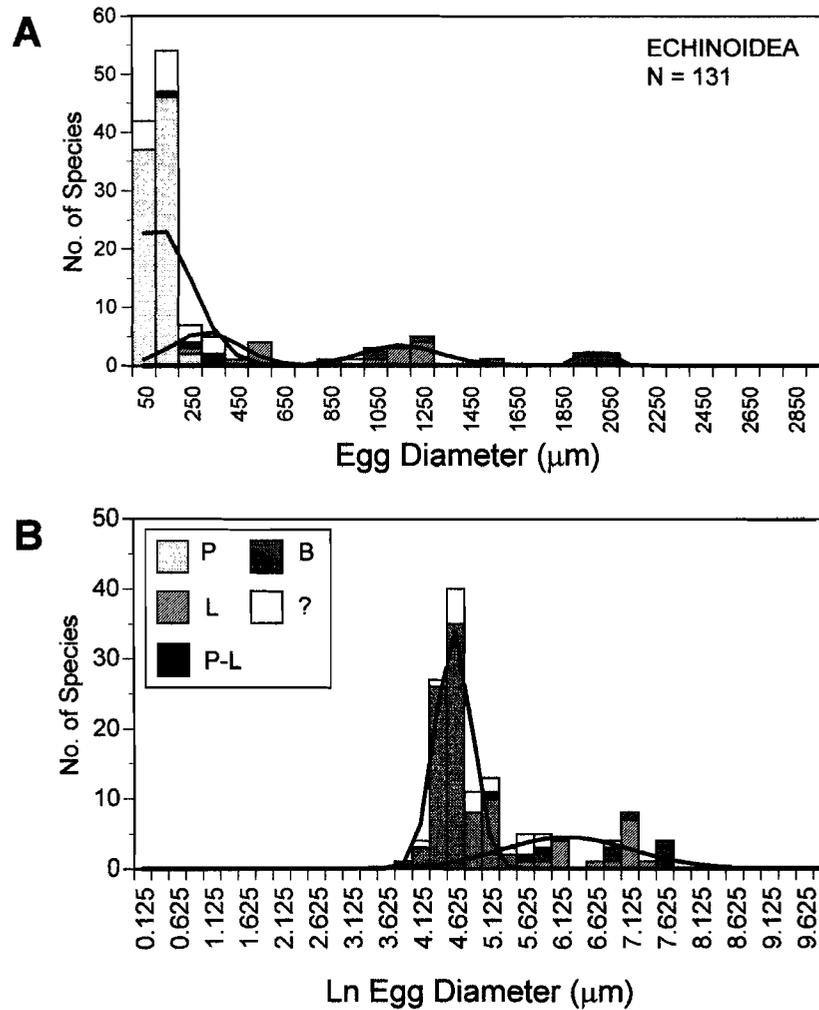
Figure 3. Egg size distribution pattern in the class Asteroidea (n = 149). Information on the egg size of species of asteroids derived from Emlet *et al.* (14) and more recent literature. The complete raw data set for this figure can be obtained from either of the authors. (A) Histogram of the untransformed egg diameters in the class Asteroidea; x-axis shows the midpoint of the 100-μm size class. (B) Histogram of the natural log-transformed egg diameters in the class Asteroidea; x-axis shows the midpoint of the ln 0.25 size class. Legend to developmental type is as shown in part B: P = planktotrophic (n = 47); L = lecithotrophic (n = 57); B = brooded (n = 26); ? = unknown development (n = 19). Solid line differentiates modes identified in the statistical analysis (see Table I for details).

composed of planktotrophic, facultative planktotrophic, and some lecithotrophic species (Fig. 4A). The last two modes are of lecithotrophic and brooding species (Fig. 4A).

The ln-transformed histogram shows statistically two modes (Fig. 4B, Table I). The first (ln 4.60) comprises 68% of the species and is composed almost entirely of planktotrophic species, with the facultative planktotroph *Encope michelini* (37) at the point of overlap between modes 1 and 2 (Fig. 4B). The second mode, at ln 6.22, has a high standard deviation (Table I) and includes two species of facultative planktotrophs (*Clypeaster rosaceus,*

Brisaster latifrons, 14) as well as all the lecithotrophic and brooding species (Fig. 4B).

Two conclusions can be drawn from the statistical analyses presented here. Firstly, in all classes the untransformed egg size distributions show three to four modes, the first being primarily of planktotrophic species, and the remaining two to three containing mainly species with nonfeeding development (*i.e.,* lecithotrophic, abbreviated, brooded, or direct development). Secondly, the ln-transformed distributions are bimodal in the holothurians, asteroids, and echinoids, but unimodal in the ophiuroids. In

Figure 4. Egg size distribution pattern in the class Echinoidea ($n = 131$). Information on the egg size of species of echinoids derived from Emlet *et al.* (14) and more recent literature. The complete raw data set for this figure can be obtained from either of the authors. (A) Histogram of the untransformed egg diameters in the class Echinoidea; x-axis shows the midpoint of the 100-μm size class. (B) Histogram of the natural log-transformed egg diameters in the class Echinoidea; x-axis shows the midpoint of the ln 0.25 size class. Legend to developmental type is as shown in part B: P = planktotrophic ($n = 85$); L = lecithotrophic ($n = 16$); P–L = facultative planktotroph ($n = 3$); B = brooded ($n = 8$); ? = unknown development ($n = 19$). Solid line differentiates modes identified in the statistical analysis (see Table I for details).

those classes with a bimodal distribution, it is only the asteroids and echinoids that show a demarcation between modes with feeding and nonfeeding development. In the holothuroids, the modes are less visually distinct, and lecithotrophic and brooding developmental types are found in both modes.

The egg size data examined here (Figs. 1–4) illustrate the need to view marine invertebrate development as a reproductive continuum (5, 17, 22). Histograms of the egg size distribution show species with planktotrophic development forming a distinctive group at smaller egg sizes (max. egg size <300 μm; Figs. 1–4). However, in

all classes, there is some overlap in egg size between these planktotrophic species and species with lecithotrophic or brooded development (Figs. 1–4). Egg sizes of species with "intermediate" forms of development, such as facultative planktotrophy (*e.g.*, 17) or modified benthic development (*e.g.*, *Patiriella exigua*, egg 400 μm; 34), generally fit within the mode for other lecithotrophic and brooding species (Figs. 3 and 4).

An important direction for future research on echinoderm eggs is examination of the assumption made here, and in other comparative studies (*e.g.*, 14), that all eggs are basically equal (27). This question should be ad-

dressed at two levels. Firstly, within an echinoderm class we need information on the energetic content and biochemical composition of species with a particular developmental type. For example, in the Holothuroidea it would be of interest to determine whether the eggs of known lecithotrophs (egg diameter 150–950 μm) differ in any way from those of the planktotrophic species or from the large (150–4400 μm) eggs of the deep-sea elasipods that are suspected of having direct development (33). Secondly, when sufficient data have been compiled, it would be of interest to compare egg characters (size, energetic content, and composition) between echinoderm classes. In a recent review of the relationship between egg size and energetic content in echinoderms, Jaeckle (27) showed that there were average differences in egg size, energetic content, and biochemical composition between developmental types, but the low number of available studies made it necessary to combine egg parameters from different echinoderm classes. With increasing study on the energy content and biochemical composition of eggs of the less well known echinoderm classes (holothuroids, ophiuroids, crinoids) we may be better able to interpret patterns of egg size distribution (Figs. 1, 2) and formulate or test new hypotheses on factors important for the selection of egg size.

Acknowledgments

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