

# Variability, flexibility and plasticity in life histories of marine invertebrates

Larvae  
Life-histories  
Polytypic development  
Flexible development  
Developmental plasticity

Larves  
Stratégies de développement  
Polytypie du développement  
Développement flexible  
Plasticité du développement

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## ABSTRACT

Nearly all aspects of the life histories of individual marine-invertebrate species are characterized by ranges of sizes, seasonal variation, and functional flexibility and phenotypic plasticity in response to varying environmental conditions; that is, they are highly polytypic. Four major areas of polytypy are considered: (1) breeding seasons and cycles vary greatly in time and duration with latitude and from year to year; (2) egg and larval sizes, while showing both genetic and stochastic variability in all species, are often also flexible responses to adult and larval nutrition; (3) modes of development are variable within a number of single species, often reflecting egg-size differences between populations, or even as a result of hatching age of siblings from a single egg mass; and (4) duration of the pelagic larval phase, both before and after the onset of metamorphic competence. Planktotrophic larvae show plastic responses to phytoplankton abundance in their morphologies, and most larvae are flexible in their age at metamorphosis because this complex process requires a more-or-less specialized substratum to induce it for most invertebrate species. New data are presented that provide additional examples of broad flexibility of sibling lecithotrophic larvae to hatch and settle at greatly differing ages. Larvae of the patelloidean gastropod *Lottia pelta* settled from 8 to 28 days after fertilization, and those of the fissurelloidean *Diodora aspera* hatched over a three week period from 7 to 30 days post-fertilization; larval settlement had a similarly broad range. Even the planktotrophic-lecithotrophic dichotomy breaks down as increasing numbers of species are found to produce larvae that can metamorphose without feeding (*i.e.* lecithotrophy), or feed and greatly extend their larval durations (planktotrophy) in the absence of suitable settlement substrata. Invertebrate groups with rigidly canalized life histories are noted to be components of the fouling community, and it is conjectured that an evolutionary history on floating substrata canalized their life histories toward high inbreeding tolerance, often selfing, and brief pelagic larval durations. We note that most life-history theory has considered extremes and major modes in invertebrate development, and suffers from lack of attention to the abundance of polytypic life-history traits as evolutionary survival mechanisms at the species level. We conclude that response flexibility and plasticity increase both survivorship and fecundity of individuals, while life-history variability increases the likelihood of recruitment across populations and persistence over geological time. More data are needed on the ranges of scalar characters and flexible responses in marine-invertebrate life histories to rigorously evaluate their contributions to evolutionary success.

## RÉSUMÉ

## Variabilité, flexibilité et plasticité dans les stratégies de développement des invertébrés marins.

Les caractères démographiques des espèces d'invertébrés marins sont, pour la plupart, hautement polytypiques : gamme étendue de tailles, variabilité saisonnière, flexibilité fonctionnelle et plasticité phénotique répondent aux conditions environnementales. Les théories sur les stratégies démographiques portent généralement sur les modes principaux ou sur les cas extrêmes du développement des invertébrés et négligent de nombreux caractères démographiques polytypiques.

Les exemples discutés ici illustrent la polytypie dans les quatre principales phases du cycle de vie : 1) les cycles et saisons de ponte dont la date et la durée varient avec la latitude et d'une année à l'autre ; 2) les tailles des œufs et des larves qui présentent une variabilité génétique et stochastique chez toutes les espèces, mais aussi une flexibilité en réponse à la nutrition des adultes et des larves ; 3) les modes de développement qui varient chez de nombreuses espèces, différant souvent d'une population à l'autre et quelquefois parmi les descendants d'une même lignée ; 4) la durée de la phase larvaire pélagique, qui peut varier avant et après l'acquisition de l'aptitude à la métamorphose. Des données nouvelles illustrent la grande flexibilité des larves lécitotrophiques d'une même ponte à se développer et se fixer à différents âges : les larves du gastéropode *Lottia pelta* (patelloïde) se fixent entre 8 et 28 jours après la fertilisation ; chez *Dodora aspera* (fissurelloïde) les larves sont émises au cours de trois semaines, de 7 à 30 jours après la fertilisation et se fixent après une période équivalente. D'autres exemples sont fournis par les larves planctotrophiques dont la plasticité morphologique répond à la quantité de nourriture planctonique disponible ou dont la durée de vie varie avec la fixation et la métamorphose, complexes et plus ou moins spécialisées face au substrat disponible.

La dichotomie planctotrophie-lécitotrophie, communément admise, diminue quand augmente le nombre d'espèces produisant des larves qui peuvent se métamorphoser sans se nourrir (larves lécitotrophiques) ou qui se nourrissent et prolongent leur phase pélagique en l'absence de substrat favorable (larves qui peuvent être planctotrophiques). Les groupes d'invertébrés présentant des stratégies démographiques bien définies sont probablement courants dans la communauté polluée du fait de pressions sélectives vers une grande tolérance à la consanguinité, à l'autofécondation et à une dispersion larvaire limitée par leur fixation privilégiée sur des substrats flottants faiblement immergés, qui seraient rares sans l'intervention humaine. Chez la plupart des invertébrés marins, la flexibilité et la plasticité accroissent la survie et la fécondité des individus tandis que la variabilité des stratégies démographiques accroît la probabilité de recrutement entre les populations et leur persistance à l'échelle des temps géologiques. Il est nécessaire d'acquiescer davantage de données sur la variabilité des caractères et sur la flexibilité des stratégies démographiques chez les invertébrés marins.

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## INTRODUCTION

Life histories are too often regarded as rigidly defined and species-specific, whereas it is well known that reproductive and developmental characteristics are rarely rigidly fixed. The literature, however, tends to be limited in appreciation and reporting of this flexibility because records consist largely of mean values reported without ranges of values, anecdotal reports based on very small sample sizes, and data from populations at only a few sites within a species' range. Such limited observations and records have led to apparent acceptance of life histories with (1) specific and narrow calendar periods for reproduction, (2) invariant breeding seasons or cycles of individuals within a species, (3) species-specific egg sizes, (4) discrete and mutually

exclusive modes of development, (5) set durations for embryonic development, and (6) defined durations for larval development, usually derived from minimum times to metamorphic competence under laboratory conditions. Scientists studying life histories of benthic marine invertebrates have discussed geographic variation in pattern (e.g. Hadfield and Switzer-Dunlap, 1990), poecilogony (e.g. Thorson, 1950), and extended periods of metamorphic competence for a variety of larvae, some of them planktotrophic (e.g. Scheltema, 1971; Kempf, 1981), some of them lecithotrophic (e.g. Birkeland, Chia and Strathmann, 1971), and some both (e.g. Kempf and Hadfield, 1985; Emler, 1986). Still, focus has tended to be on extreme examples, such as ocean-crossing teleplanic larvae, leaving

us with our earlier notions that most invertebrates are relatively fixed in various life history parameters.

This paper focusses on data, some previously published and some new, on the occurrence of polytypy in invertebrate life histories and its consequences. Examination of the broad capacity for flexibility in the reproductive and larval lives of probably most marine invertebrate species leads us to suggest that differences among distributional ranges of coastal benthic invertebrate species may not be explained by differing larval durations, and to urge consideration of flexibility in invertebrate reproductive and larval characters in heuristic life-history models. We conclude that flexibility, not adherence to rigid reproductive and larval developmental patterns, is a major key to invertebrate reproductive success. We have not attempted to be exhaustive in our citations of published work, but have simply chosen useful examples.

**Terminology:** We use the term polytypy to include all of the different ways in which life-history and developmental characters may exhibit multiple states. For traits whose variance is (1) genetic or stochastic, (2) always, or nearly always present, and (3) not an individual response to an environmental condition, we use the term *variability*. In addition, we discern two classes of polytypy, both occurring at the level of the individual animal, that arise as responses to environmental differences: plasticity and flexibility. We restrict the term *plasticity* to environmentally induced phenotypic polytypy, and thus equate it to the often-used term "phenotypic plasticity". Plasticity is reflected in morphological differences among siblings brought about by environmental influences during development. *Flexibility*, as utilized here, is the capacity of individuals, sometimes encompassing an entire population, to display different functional states from others because of differing environmental conditions. Included among flexible characters are spawning time, hatching time and stage, rate of development, age at metamorphosis, and dispersal pattern, in a non-exhaustive list.

#### Four major areas of life-history polytypy

##### *Breeding seasons and cycles*

By breeding seasons and cycles, we mean the annual timing and extent of bouts of reproduction within species. Most marine invertebrate species have more-or-less fixed reproductive periods. Animals with extremely narrow reproductive seasonality have captured attention and inspired studies of mechanisms that control reproduction, perhaps leaving an impression that such patterns are typical (e.g. the crinoid *Comanthus japonicus*, summarized by Kubota, 1981, and the palolo worms, reviewed by Schroeder and Hermans, 1975). Temperature and photoperiod are major determinants of annual reproductive bouts, and thus more polar populations of shallow-water species may reproduce later in the year and for briefer periods than more equatorial ones (Giese and Kanatani, 1987). Invertebrate species with exceptionally wide north-south distributions may actually have different seasonal reproductive patterns at the extremes of their ranges, as exemplified by the sea hare *Aplysia juliana*, with continuous reproduction

and an approximately six-month lifespan in Hawaii, contrasted with a 3-4 month summer reproductive period and a one-year lifespan along the western coast of northern Japan (Hadfield and Switzer-Dunlap, 1990).

For benthic species with pelagic embryos or larvae that survive more than one or two days in the plankton, reproducing throughout the year or in more than one season will have a major influence on larval dispersal and thus range of the species. Because current patterns and velocities typically vary seasonally in most coastal areas, the annual timing of larval release will determine the dominant direction that larvae are carried; if larvae of a species are released during more than one season, the direction of dispersal may vary by as much as 180° between seasons. Recruitment conditions may also vary seasonally in different locations, and thus the potential to establish or replenish populations in a locale may well depend on larvae being available at more than one time of the year. Simply having the physiological capacity to be flexible in reproductive timing rather than inflexible and fail in years of atypical conditions should provide a strong selective advantage. The effects of rare reproductive or dispersal events brought about by extreme El Niño conditions have become apparent (Richmond, 1990) and may reflect flexibility to exploit atypical conditions.

How extensive is the capacity to breed continuously or to vary reproductive period with temperature and latitude? In their Table IV (p. 283), Giese and Kanatani (1987) provide six examples of very well known species in three major invertebrate phyla that demonstrate significant flexibility in both timing and duration of reproductive seasons: *Nereis grubei*, *Arbacia punctulata*, *Paracentrotus lividus*, *Ostrea edulis*, *Crassostrea virginica*, *Diadema setosum*, and *Triploneustes gratilla*. It seems certain that these species are not unusual, and it would be most instructive to see much new data on the temporal reproductive patterns of many shallow-water invertebrate species, traced across their latitudinal ranges and recorded for several consecutive years.

##### *Egg and larval sizes*

A range (variability) of sizes of ova within clutches is provided for nearly every species for which development has ever been described (e.g. Kohn and Perron, 1994). Differences in mean egg sizes between individuals of a species have also been noted (e.g. Turner and Lawrence, 1979), as well as between locales (e.g. barnacles, Barnes and Barnes, 1965; echinoids, George, 1990) and different seasons (Barnes and Barnes, 1965; R. Strathmann, quoted in M.F. Strathmann, 1987). McEdward and Carson (1987), studying the sea star *Solaster stimpsoni*, noted differences in the organic content of eggs among females and populations. Despite this general awareness of variance in egg sizes and organic content, there seems to have been no real exploration of the larval capacities of con-specific larvae that naturally arise from eggs of different sizes. For example, in our studies of larval development of the keyhole limpet *Diodora aspera* (see Duration of the Pelagic Phase, Planktotrophs, below), the largest ova in clutches produced by two females had, at 198 µm diameter, about 1.9 times the volume of the smallest ova,

160  $\mu\text{m}$  in diameter. If this difference is reflected in actual organic content, then we might expect that the greater yolk supply in larger eggs should lead to the development of larger larvae and perhaps larvae with a longer potential planktonic life. However, the variance in larval shell dimensions that we measured from our cultures of *D. aspera* were not particularly great, and thus provided no support for the suggestion that larger eggs give rise to larger larvae. McEdward and Carson (1987) and McEdward and Chia (1991) found egg diameter to be a poor predictor of energy content for a number of echinoderm species, all with relatively large eggs and lecithotrophic development. George (1990) recorded larger eggs and larvae, with faster developmental rates, in populations of the sea urchin *Arbacia lixula* inhabiting seemingly better habitats. The relationship between egg size and energy content seems not to have been extensively explored for most invertebrate groups, nor even for echinoderms with planktotrophic development. We have been unable to locate studies where the fates of individual eggs, naturally differing in size, have been followed in culture to look for differences among the resulting larvae, either in size or development rate.

Larvae that develop from "zygotes" experimentally produced by separating blastomeres of sea urchins at two-cell and four-cell stages, are smaller and develop slower than larvae from whole eggs (e.g. Sinervo and McEdward, 1988, and other references cited therein). However, the smaller larvae are able to achieve metamorphosis at sizes comparable to larvae developing from entire eggs by remaining longer in the feeding larval stage. Results of studies on experimentally produced half- or quarter-size larvae strongly suggest that variability is to be expected in the development of sibling invertebrates that arise from eggs at the ends of normal distributions of egg sizes within single clutches or between the clutches of individuals from the same or geographically separated populations.

The abundance and type of food available may lead to differences in the size of ova produced by a benthic invertebrate, as demonstrated for a polychaete (Qian and Chia, 1991) and the echinoid *Arbacia lixula* discussed above (George, 1990). Flexibility in the rate and timing of development is to be expected in such species. Sibling embryos of a nudibranch species were described by Williams (1980) as having differing amounts of yolk; both shell sizes and nutritional requirements of the resulting larvae differed significantly. These differences were not attributed to differences in egg size, nor were other explanations provided.

#### *Modes of development*

By modes of development we mean the major invertebrate developmental categories outlined by Thorson (1946) and many others: benthic (variously viviparous, ovoviviparous, brooded or encapsulated) vs. pelagic development; and, among the latter, feeding (planktotrophic) vs. non-feeding (lecithotrophic) larval development. The question is, do species adhere to only one pattern, or is there flexibility to shift from one to another or for patterns to be mixed?

Extensive work on some species once thought to include individuals with very different reproductive modes has

shown them to be clusters of sibling species with similar morphological characters (e.g. the *Capitella capitata* species complex; Grassle and Grassle, 1976). However, careful research has shown that reproductive modes do vary within single polychaete species, for example *Streblospio benedicti* (Levin, 1984; Levin *et al.*, 1987; Levin and Huggett, 1990; Levin *et al.*, 1991) and *Capitella* sp. (Qian and Chia, 1991, 1992). In both of these cases, different but sympatric or only narrowly geographically separated individuals produce eggs of different sizes that have different developmental fates; small eggs develop into planktotrophic larvae, while larger eggs develop into lecithotrophic larvae. Although Hoagland and Robertson (1988) cast doubt on most instances of such variable reproductive patterns (i.e. "poecilogony") within molluscan species, some well documented examples remain. Breeding studies have demonstrated that members of two populations of the opisthobranch mollusc *Elysia chlorotica* are indeed members of the same species, despite the fact that the developmental mode in a population that produces smaller eggs is via planktotrophic veliger larvae, while in another population whose members lay larger eggs, development is completely benthic (West *et al.*, 1984).

Variation may actually occur in the time or stage at hatching from single egg masses. For example, all individuals of the polychaete *Eupolyornia nebulosa* leave the egg mass as swimming larvae, but the time of hatching varies over a period as long as 10 days (Bhaud, 1991). Because all larvae from a single egg mass settle at the same time, the minimal pelagic period of sibling larvae varies considerably. For example, for egg masses of *E. nebulosa* laid in May, hatching begins three days after spawning and concludes eight days after spawning. Since settlement commences 10 days after spawning, minimal larval durations vary between two and seven days, seemingly guaranteeing significant spread in the recruitment of sibling larvae. In the carefully studied opisthobranch species, *Haminoea callidegenita*, both premetamorphic and post-metamorphic stages emerge from a single egg mass over a period of about a week (Gibson and Chia, 1989). From 50 to 70 percent of the embryos completed metamorphosis within the egg mass, with the remainder hatching as swimming veligers; the variable is the age of the individual at metamorphosis. Hatched veligers remained metamorphically competent for at least 20 days, and metamorphosed on contact with specific benthic green algae. These two examples thus illustrate two kinds of variability that occur within single brood masses.

#### *Duration of the pelagic phase*

The focus in this section is on species that have definitive pelagic development, either planktotrophic or lecithotrophic, and whose larvae may persist in a metamorphically competent state for periods of weeks or even months in the absence of suitable settlement stimuli.

The timing of entry into the pelagic phase is open to considerable variation, not just in breeding season and cycles as previously discussed, but also through changes in egg laying, brooding and hatching. For all benthic species with any pelagic stage at all, the beginning point of the planktic

phase will be determined by whether fertilization is internal or external and whether pre-larval development is benthic, brooded or encapsulated, or pelagic. If gametes are broadcast into the sea, as is typical for some benthic species in nearly every invertebrate phylum, even zygotes and embryos are pelagic and subject to the same hazards and dispersal as resulting larvae; if brooded or encapsulated, release to the plankton usually occurs as a swimming larva. Clearly, if all of development is pelagic or if the pelagic hatching/birth stage requires much more development before becoming competent, dispersal may be extensive before the larva is capable of settling, regardless of whether or not the larvae must feed. Development of individual larvae that encounter colder waters will always take longer than those in warmer water, as has been amply demonstrated for both feeding and non-feeding larvae (e.g. tables for many invertebrate species in M. F. Strathmann, 1987; feeding gastropod larvae, Pechenik and Lima, 1984). In the following section, flexibility in the larval lives of species with feeding and non-feeding larviparous development is discussed.

### Planktotrophs

In the case of planktotrophic larvae, food availability obviously governs length of the precompetent pelagic period. Studies on gastropod veligers by Pechenik (1984) and Bell (1993) clearly demonstrate that these larvae may survive extremely low food concentrations, and that their retarded growth during food-limited conditions reflects retarded progress toward metamorphic competence. However, these veligers typically do become competent eventually, and, if they survive the longer exposure to planktonic predators, they may find settlement sites far from their parents. Similar data are available for echinoids (Highsmith and Emler, 1986; Fenaux *et al.*, 1994), polychaetes (Wilson, 1970a; Pechenik and Cerulli, 1991; Qian and Chia, 1993; Toonen and Pawlik, 1994), crustaceans (Anger *et al.*, 1981; Harms, 1992; Harvey, 1993), bivalves (Pechenik *et al.*, 1990) and a number of other groups (Paulay *et al.*, 1985).

Even without the situation of semi-starvation, many – perhaps most – planktotrophic invertebrate larvae have great flexibility in their moment of metamorphosis. This has been demonstrated for gastropods (Kempf, 1981), bivalves (Bayne, 1965), polychaetes (Wilson, 1968, 1970b), barnacles (Lucas *et al.*, 1979), echinoids (Cameron and Hinegardner, 1974), and many other invertebrate groups. Larvae of the nudibranch *Phestilla sibogae* showed the same post-settlement life-history dynamics, whether they were induced to metamorphose after three days or three weeks as feeding pelagic larvae (Miller and Hadfield, 1990). Even granting that late metamorphosis may, in some forms, produce juveniles that grow slower (Highsmith and Emler, 1986) or mature later than earlier settled siblings, reduced survivorship and reproduction are decidedly advantageous compared with the alternative of loss of metamorphic competence and eventual larval death or spontaneous settlement into hostile benthic habitats. Extensive survivorship in the competent stage provides for extensive dispersal, as well as increased likelihood that lar-

vae carried offshore during precompetent development may persist long enough to be transported back toward hospitable shallow-water habitats (Jackson and Strathmann, 1981).

The sea hare *Aplysia juliana* serves as a useful example here. Extensive laboratory studies wherein food quality and quantity were experimentally optimized, indicate that this species, like many of its congeners, requires about a month after hatching to achieve metamorphic competence (Switzer-Dunlap and Hadfield, 1977). Larvae of this species settle specifically on the green algae *Ulva spp.*, both in the laboratory (*op. cit.*) and in the field (Sarver, 1979). Kempf (1981) demonstrated that larvae of *Aplysia juliana* reach maximal size at about the time of metamorphic competence and thereafter can persist for more than 300 days, without growing, but maintaining the ability to metamorphose on encounter with *Ulva spp.* While few workers have been willing to undertake the labor of maintaining a single larval culture for a year, lengthy pelagic existences have been inferred for a series of “teleplanic” invertebrate larvae by Scheltema (1971, 1974) and others. One of us (MFS) has maintained planktotrophic veligers of the gastropod *Fusitriton oregonensis* in laboratory culture for 42 months as of this writing. Some teleplanic larvae may survive to cross ocean basins, but nearly all of them should have the capacity to survive through extensive along-shore transport.

An additional type of developmental polytypy, phenotypic plasticity (*sensu* Hadfield, 1995), with significant survivorship value, has been experimentally demonstrated in planktotrophic larvae of echinoids and bivalve molluscs. When sibling sea urchin larvae were exposed to different concentrations of phytoplankton, the plutei developed longer arms when food was less abundant (Boidron-Metairon, 1988; Strathmann *et al.*, 1992; Fenaux *et al.*, 1994). Because the feeding mechanism of the sea urchin larva is a continuous ciliated band that runs along the larval arms, increasing arm length directly increases the magnitude of the food catching mechanism (Hart and Strathmann, 1994). Variable arm length in a pluteus species was also seen in nature when larvae were collected in seasons of high and low productivity; when productivity was low, the plutei had longer arms than during periods of high productivity (Fenaux *et al.*, 1994). When veliger larvae of the oyster *Crassostrea gigas* were exposed to different food concentrations, the results were similar; larvae in lower food concentrations developed larger velar lobes, structures that serve both propulsion and food gathering (Strathmann *et al.*, 1993). In addition, the larvae in lower food levels had longer velar cilia, an apparently plastic response for enhanced food-gathering.

### Lecithotrophs

Many lecithotrophic larvae, seemingly destined for a limited pelagic life by the nonrenewable food reserves provided in egg yolk, are capable of extended pelagic life. Echinoderm larvae that develop from very large eggs, especially many holothurians and asteroids, provide numerous examples. Larvae of the seastar *Mediaster aequalis* complete precompetent pelagic development in about

30 days, but Birkeland *et al.* (1971) maintained healthy larvae, still capable of metamorphosis, for 17 months by withholding appropriate settlement substrata. While this example may be extreme, pelagic lecithotrophic periods of several weeks are not uncommon. Barnacles molt to a lecithotrophic, competent cyprid larva after six feeding naupliar stages, and the cyprid of *Balanus balanoides* was shown capable of retaining metamorphic competence for at least four weeks when appropriate settlement substrata were absent (Lucas *et al.*, 1979). Pechenik (1990) extensively reviewed extended metamorphic competence in pelagic invertebrate larvae; his Table 1 (p. 72-73) includes many species with lecithotrophic larvae and their experimentally determined competent periods.

There are invertebrate taxa for which there is a lingering assumption that lecithotrophic larval development must be brief, and among these are most "lower" prosobranch gastropods: the limpets, keyhole limpets, abalones, top shells and turban shells. Actually representing several distinctive lineages (*see* Hickman, 1988), these gastropods share reproductive habits that include free-spawning of gametes, external fertilization, and development without feeding larval stages. Thorson (1946), Jablonski (1986) and others concluded that larvae of lower prosobranch gastropods have only a limited, if any, dispersal capacity as larvae. However, studies of several trochoidean species demonstrated both lecithotrophy and the ability to persist in the plankton for one to two weeks or more (Underwood, 1972; Heslinga, 1981; Hadfield and Strathmann, 1990).

Recently, we have investigated various aspects of development in the patelloidean *Lottia pelta*, and the fissurelloidean *Diodora aspera*, both common littoral species along the temperate west coast of North America. What we found suggests that flexibility in development may be the key to wide geographical ranges and numerical abundance in both species.

#### *Lottia pelta*

Within a few hours of collection between April and June, 1994, in the San Juan Islands, Washington, these limpets spawned epidemically. Rose-colored ova, 128-144  $\mu\text{m}$  in diameter (three clutches: (1)  $n = 10$ ,  $r = 128-140$ ,  $\bar{x} = 133.6 \pm 3.9$ ; (2)  $n = 10$ ,  $r = 136-144$ ,  $\bar{x} = 139.6 \pm 2.5$ ; (3)  $n = 10$ ,  $r = 128-144$ ,  $\bar{x} = 134.2 \pm 4.7$ ), developed to hatching early trochophores in less than 24 hours (11-12 °C). In 3-4 days, post-torsional, shelled veligers, capable of contracting completely into their shells had developed (Fig. 1 A). By four days after fertilization, the larvae possessed highly mobile podia and may have been capable of crawling and metamorphosis, although this wasn't tested by provision of suitable bacterial/algal-filmed substrata. At six days, the veligers were observed to "crawl" on the glass of the culture containers, as well as to swim near the surface. At eight days, some larvae were placed in small bowls containing small (*ca.* 1 cm) rocks collected from the intertidal zone at the Friday Harbor Laboratories. The rocks had coatings of bacteria, diatoms and fine green algae. By the following day, most of the larvae had settled (Fig. 1 D), and some had metamorphosed and begun to add juvenile shell (teleoconch) to the dorsal apertural lip of the larval shell.

On day 12, additional larvae were taken from the stock culture and placed with small intertidal pebbles in a bowl; by day 13 they had metamorphosed. On day 23 post-fertilization, some larvae had metamorphosed in the stock culture without contacting filmed rock (Fig. 1 C), probably in response to diatom-containing biofilm on the glass culture bowl. Additional swimming, 23-day old larvae were exposed to biofilmed beach pebbles, and by day 28, many of them had also completed metamorphosis. That juvenile-shell growth does not occur until after settlement and metamorphosis in *L. pelta* can be seen by comparing the two, 24-day old individuals shown in Figs. 1B and 1E; the former was still a swimming veliger, while the latter had settled on day 8 and produced a relatively large juvenile shell. At day 32, we were able to glean yet another 50 swimming larvae from the original culture to introduce to a bowl containing beach rocks; only one of these was found to have metamorphosed two days later, and the remainder were dead. We can thus estimate a minimal pre-competent pelagic period of probably 6-7 days, followed by a potential settlement phase lasting three weeks or longer. Such an extensive dispersal period is consistent with the wide range of this species, from Baja California to the Aleutian Islands of Alaska (Morris *et al.*, 1980).

#### *Diodora aspera*

Although this keyhole-limpet is abundant in intertidal locales in the San Juan Islands of Washington, the only specimens that we observed spawning in the laboratory in April and May 1994 had been dredged from about 80 m depth in San Juan Channel. It is probable that intertidal populations had already completed their spawning by late spring; B. Pernet (personal communication) observed *D. aspera* spawning in the intertidal on San Juan Island and in the laboratory in late January 1995. Both males and females shed gametes in the excurrent flow through the dorsal aperture and over the head as well; males released clouds of sperm which dispersed in the water, while females released large numbers of eggs, singly but in a continuous string, that sank to the bottom of the unstirred bowl and then stuck tightly to one another and other surfaces. We observed spawning individuals on two occasions. Each pale-green ovum, 160-198  $\mu\text{m}$  in diameter (two clutches: (1)  $n = 20$ ,  $r = 173-198$ ,  $\bar{x} = 179 \pm 7.5$ ; (2)  $n = 10$ ,  $r = 160-168$ ,  $\bar{x} = 167 \pm 2.5$ ) was surrounded by a thick coat whose inner diameter was 256-306  $\mu\text{m}$  and outer diameter 368-421  $\mu\text{m}$ ; the coat was about 57  $\mu\text{m}$  thick (Fig. 2 A). The clear coat had a single conspicuous "micropyle" which, as development progressed, had no defined location relative to the polarity of the embryo. Numerous fine channels penetrated the egg coat, and these probably provided paths for sperm entry; after insemination, sperm could be seen in most of the channels and swimming in the space between the egg coat and the surface of the ovum.

The eggs are probably normally spawned into the narrow crevices and intertidal and subtidal grottoes where adults reside. In such settings, the eggs would be likely to stick to each other and to rocks and a variety of algae, and some may be swept up into the water column. Depending on where these eggs stick, they will be exposed to varying

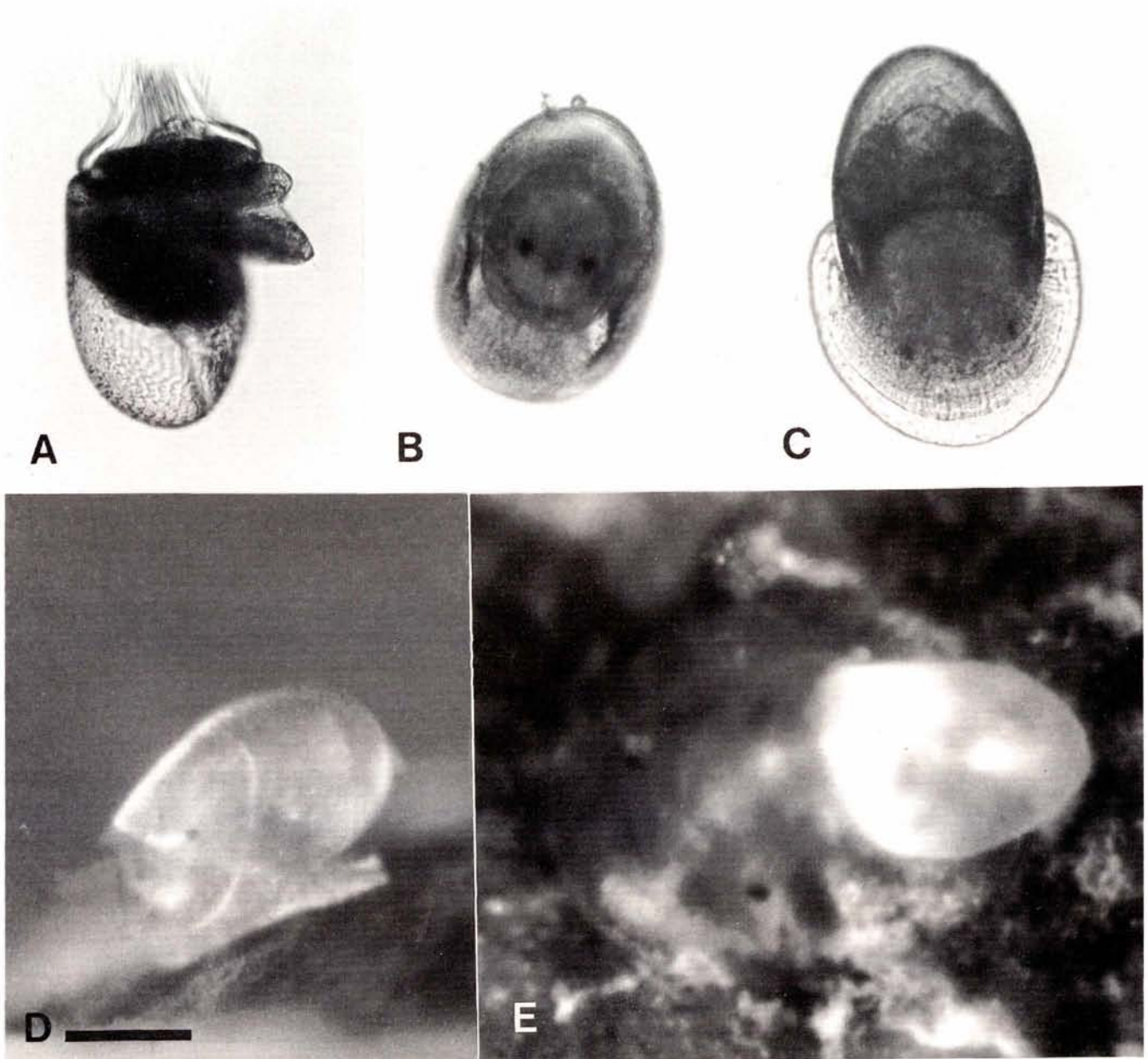


Figure 1

*Lottia pelta*. **A.** Hatched veliger, age 4 days post-fertilization, right-side view. **B.** Pediveliger, age 24 days, eyespots and retracted velum with large ciliated peripheral cells visible through transparent protoconch. **C.** Recently metamorphosed juvenile, age 24 days, dorsal view, eyespots visible but velar cells no longer present, teleoconch extends from apertural edge of protoconch. **D.** Pediveliger, age 8 days, left-side view, crawling on rock, large velar cells faintly visible. **E.** Metamorphosed juvenile, age 24 days, dorsal view, crawling on rock, eyespots and tentacles visible through transparent teleoconch anterior to opaque white protoconch. Specimens A, B, and C were from a culture maintained in a glass beaker. Specimens D and E were from a culture provided with biofilmed rocks at age 8 days. All shown to same scale; scale bar = 100  $\mu\text{m}$ .

degrees of water current, wave action and abrasion. If the eggs are spawned in still water, they probably stick to each other, creating sheet-like gelatinous egg masses, and rates of development of individual embryos may vary depending on depth in the egg mass (*see above*). The eggs released by two different females in our study were also considerably different in their stickiness. Eggs from the first spawning were very sticky, those from the second spawning much less so. If this variation exists in nature, the dispersal of eggs may be quite different either between females or between spawns. Bruno Pernet (personal communication) found an intertidal *D. aspera* "standing on a mass of really sticky, unfertilized eggs..."

In our first laboratory culture, fertilized on April 12, 1994, post-torsional shelled veligers had developed by day 6. Some cultures were agitated by bubble aeration beginning on day 6, and, in these, hatching began by day 7 or 8 (Figs. 2 B, C). Hatching appeared to be a two-part process, with the inner capsule membrane first disappearing, apparently due to enzymatic action. The capsule gel broke down as the larva swam in the enlarging space, but the outer capsule boundary appeared to break in response to mechanical action. It remained after being rent, either by the larva's swimming or by external abrasion. In the bubbled culture, some larvae continued to hatch over at least the next 26-30 days. On day 13, unhatched larvae from the

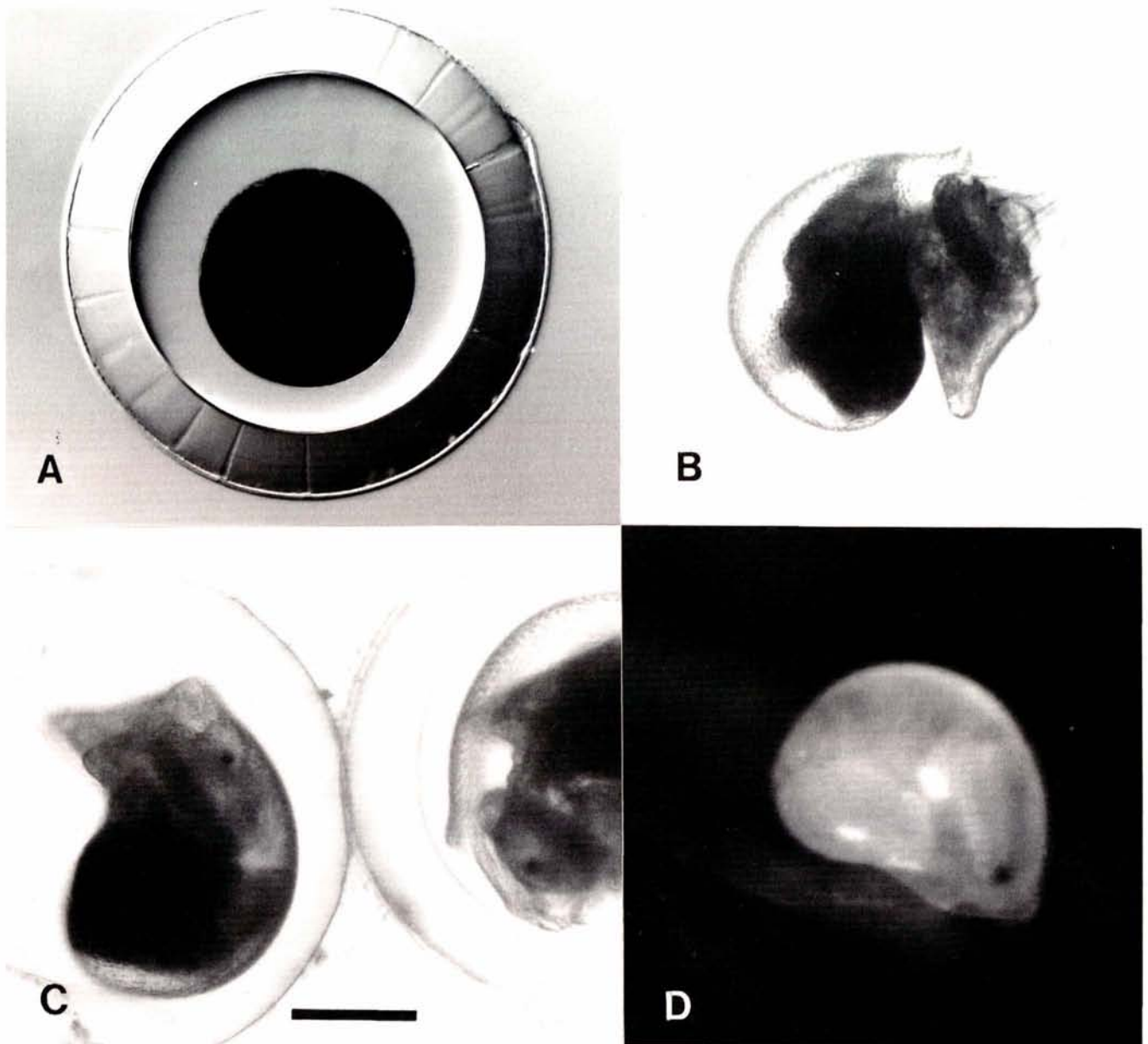


Figure 2

*Diodora aspera*. **A.** Fertilized egg, 2.25 hours after insemination, sperm visible in two of many channels that penetrate the clear colorless surrounding coat. **B.** Hatched veliger, age 8 days, right-side view showing visceral mass and retractor muscle through transparent shell, and extended foot and velum; cilia are held in arrested-swimming position folded over the frontal surface of velum. **C.** Unhatched veligers, age 9 days, both in right-side view inside adhering capsules. The capsule on the left is torn open and no longer shows the distinct inner boundary still evident in the capsule on the right. **D.** Pediveliger crawling on rock, age 26 days, right-side view with eyespot and large velar cells visible through translucent shell. All shown to same scale; scale bar = 100  $\mu$ m.

bubbled culture were put into a small vial half-filled with water and shaken vigorously; all of them hatched, their torn capsules remained otherwise intact, and the liberated larvae appeared healthy. On day 10 larvae were observed crawling on the bottoms of culture dishes, and thus settlement experiments were set up as described above for *L. pelta*. By day 13, larvae in the settlement experiment were all attached to rocks and observed to move around on them with foot ciliation. Sixteen days after these larvae had been exposed to small biofilmed rocks and had been crawling on the rocks, most were found still capable of swimming by velar action if disturbed. However, velar cells and cilia could still be observed through the shell of some crawling pediveligers at 26 days (Fig. 2 D). Other settled

individuals showed juvenile shell growth in the form of a flared lip from the dorsal margin of the aperture so had probably metamorphosed. Even 24 days after fertilization, many larvae remained unhatched in both static and bubbled cultures. If shaken in bottles of water, they hatched into apparently healthy swimming larvae. Although no additional settlement experiments were attempted, these larvae appeared capable of completing metamorphosis.

What is most interesting about larval development in *Diodora aspera* is the apparent plasticity of the hatching moment. Probably secretion of hatching enzymes by the larva, about day 7 and later, causes breakdown of the inner capsule wall and makes the outer wall weaker and suscep-



tible to rupture by external factors. This is a more or less likely event, depending on where the egg resides. Based on our observations, we predict that hatching of different larvae from the same spawn in the field occurs over a period of days or even weeks.

From our limited observations, it is unclear exactly how soon and how long larvae of *Diodora aspera* are competent to metamorphose. If the larvae that attached to rocks and remained there were competent, then metamorphic competence develops as early as day 10 (but it was not tested earlier), about two to three days after hatching. If the last date when we found crawling larvae still capable of swimming is the end point of competence, then the competent period would last about 26 days. However, if larvae that had not hatched by 34 days were still capable of metamorphosis, then the maximum competent larval age may be longer. The extensive geographic range of *D. aspera*, from Afognak Island, Alaska to Baja, California (Morris *et al.*, 1980) is easily explained by larval dispersal over a period of 10-26 days or more. While all aspects of the developmental biology of *Diodora aspera* need additional observation and confirmation, the species is clearly yet another benthic invertebrate with considerable built-in flexibility in its developmental history.

#### Facultative planktotrophs

There are marine invertebrates whose larvae are able to metamorphose without feeding (*i.e.* are lecithotrophic) but which can also feed on phytoplankton (*i.e.* are facultative planktotrophs). Veligers of two nudibranchs, *Adalaria proxima* (Thompson, 1958) and *Phestilla sibogae* (Kempf and Hadfield, 1985; Miller and Hadfield, 1990), are able to complete larval development without feeding, but will ingest phytoplankton if it is present. In *P. sibogae*, the larval stage may be considerably extended when larvae feed and an obligate metamorphic cue is absent. Facultative planktotrophy has also been recorded in an echinoid, *Clypeaster rosaceus* (Emler, 1986), and it seems likely that other examples might be found if biologists attempting to rear invertebrate larvae exposed otherwise "lecithotrophic larvae" to various cultured phytoplankton. Facultative planktotrophy bestows significant flexibility on species where it occurs, allowing larvae to metamorphose soon after hatching, thus potentially recruiting to nearby adult populations, or to persist in the plankton longer, leading to broad species dispersal.

#### Why is flexibility in development not universal ?

Despite the foregoing, there are, of course, species with pelagic larvae of very limited durations. Colonial ascidians, most bryozoans, and the small tubicolous polychaetes of the family Spirorbidae share a common pattern of brooded development and release of competent larvae that must settle within a few hours or perish. Even most solitary ascidians, whose development is entirely pelagic, have a total pelagic period of less than two days. Why is development in these groups so markedly different from the larval patterns discussed above that are common for many polychaetes, molluscs, crustaceans and echino-

derms? Most of these species with very short-term larvae are brooders, and they are all also small-bodied, sessile filter-feeders. At least some members of each group are capable of self-fertilization (ascidians, Berrill, 1975; bryozoans, Reed, 1991; *Spirorbis spp.*, Potswald, 1968). All of these species are typical of the so-called "fouling community" on piers, floating docks and ship bottoms, but they must once have been limited mostly to floating logs, algae and perhaps protected tide pools. During the evolution of these species, suitable habitats may have been so rare that selection operated strongly against dispersal. Such selection may also have led to high inbreeding tolerance. In fact, an advantage to larval settlement near siblings is suggested for some colonial ascidians (Grosberg and Quinn, 1986). Because these species with larvae of severely limited duration are sessile organisms, they are subject to rafting from locale to locale on floating logs or seaweed, a factor that readily accounts for their broad, in many cases world-wide, distributions.

#### Significance of polytypy to life-history theory

If polytypy characterizes the reproduction and development of most benthic marine invertebrates, as accumulating data suggest, then some suppositions about limited dispersal may be in need of re-examination. The well-studied tables of some Thorson papers (1946, 1950) were not necessarily inaccurate, but they led us to classify benthic invertebrate species according to developmental patterns that are often simple dichotomies: benthic or pelagic, and, if pelagic, lecithotrophic or planktotrophic, and short-term or long-term in their planktonic existence. Using such dichotomies, we then looked for evidence in nature of their effects on species' distribution ranges and survivorship in geological time. Thorson (1961), when considering, "Length of pelagic larval life in marine bottom invertebrates" had something rather specific in mind when he divided larvae into short and longer term planktors: could they or could they not survive long enough to disperse across oceans? However, this question addresses a rare and perhaps trivial example of distance dispersal in a geological time frame. Most larvae are undoubtedly transported not across oceans but along shores in coastal currents, so the dispersal and recruitment of individual larvae will determine how far a benthic species may spread in one generation and how widely that species will ultimately be distributed. The distance over which dispersal by advection will occur is a function of time and rate: how long a pelagic larva can remain metamorphically competent, and how fast the current moves it. Two assumptions, (1) that lecithotrophic larvae do not remain in the plankton long enough to effect genetic dispersal between populations over significant geological time and (2) that species with lecithotrophic development have narrow geographic ranges and are more vulnerable to extinction caused by localized environmental disasters, appear to have no support for coastal species with pelagic larvae. Pelagic development in *Lottia pelta*, a "lower prosobranch" species and thus assumed to have lecithotrophic development, may be as brief as 6-7 days, but under some conditions lasts as long as a month, providing ample explanation for a north-south dis-

tribution in excess of 3300 km and 30 degrees of longitude. Larval-dispersal variation and broad geographic ranges similarly characterize *Diodora aspera* and some trochoid gastropods (Hadfield and Strathmann, 1990). If the correlation between the occurrence of protoconchs associated with lecithotrophy and shorter geological species longevity, as noted by Powell (1942), Hansen (1980), Jablonski and Lutz (1983) and others, is not due to limited larval dispersal, as now seems clear, then other causal hypotheses should be examined. Bhaud (1989, 1993) suggested that the tolerance of species to different ranges of physical parameters is probably a greater determinant of species' ranges among benthic marine invertebrates than the dispersal capacities of their larvae.

Models and arguments put forth by Vance (1973), Strathmann (1974, 1978), Christiansen and Fenchel (1979), Pechenik (1980), Jackson and Strathmann (1981) and others considered aspects of selection for different durations of the precompetent larval phase, the competent phase, or both, to explain the distribution of developmental modes in marine invertebrates. Advantages for dispersal and growth, substrate selection, and return to favorable habitats after precompetent dispersal are inherent in one or more of these models or arguments. The present summary of recent data suggests that dispersal in most marine invertebrate species is not limited by the duration of the pelagic developmental period, whether it includes both precompetent and competent phases or only the latter. Except for the few higher taxa and species discussed above, there seems no valid reason to expect that the competent phase will be of shorter duration than the precompetent phase, and, mostly in species with planktotrophic larvae but also in many lecithotrophs, it will be longer. Thus the modal distribution of egg sizes explored by Vance's model – while it may be descriptive of what occurs in nature – may tell far

more about the number of ova produced by a species than about the potential duration of its pelagic development.

## CONCLUSION

Polytypy in terms of individual responses to environmental variables occurs at nearly every stage of the reproductive and developmental lives of benthic marine invertebrates. In almost each instance it is clear that flexibility and plasticity imbue the individual with an increased probability of survival, while variability gives the population and species greater likelihood of reproductive success, dispersal, recruitment and persistence in geological time. Having recognized this, it becomes important to document additional instances of polytypy in the reproductive and larval life histories of benthic marine invertebrates. Interesting explanatory patterns may emerge, ones with the capacity to generate greater understanding of invertebrate biology and evolution.

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