An Assessment of Poecilogony in Marine Invertebrates: Phenomenon or Fantasy?

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Abstract. Poecilogony, defined as more than one mode of reproduction within a single species, has been reported in various invertebrates, including mollusks and polychaetes. Many cases that have been described involve planktotrophic and non-planktotrophic development in allopatric populations, or instances of planktonic larval stages and benthic juveniles being found together, but not associated with adults. There is always the possibility of mis-assignment of larvae to adults of the wrong species. Most cases that offer these kinds of evidence are now known to involve cryptic species, not poecilogony.

There are a few species in which release of young occurs both at metamorphosis and a day or so before. There may be cases in which extracellular yolk or nurse-egg production is variable and allows the release of larvae at different stages, but no actual instance is known. A few instances are known of allopatric populations with different modes of development and other differences in reproductive characters that lack reproductive isolation when brought into the laboratory. The polychaetes *Streblospio benedicti, Cirriformia tentaculata, Boccardia proboscidea,* and the opisthobranch *Elysia chlorotica* are in this category. All examples of poecilogony require further genetic substantiation.

Despite the scarcity of proven examples of poecilogony, the presence of more than one mode of reproduction within a genus is the rule in most invertebrate phyla. The evolutionary and ecological significance of these patterns is discussed.

Introduction

There have been numerous reports of more than one pathway of development within a single species of marine invertebrate. Quotes such as these are common: "It is an established fact that some animal forms have a different mode of development under different biological conditions" (Mortensen, 1921, p. 241). "Studies . . . cast further doubt on an already-failing dogma that a particular larval mode is a set and inflexible species characteristic" (Hadfield, 1972). The term poecilogony was invented to describe the phenomenon. ". . . poecilogony was first mentioned by Giard (1904) [sic], who gives a number of examples of its occurrence . . . which, as far as the echinoderms are concerned, have proved to be wrong. . . . That the ability exists is, however, a fact." (Thorson, 1950, pp. 29–30). If poecilogony exists, it is of interest to evolutionary biologists. However, further investigation has often revealed that cryptic species were responsible for the supposed poecilogony.

The word poecilogony derives from the Greek, *poikil-*, various, and *goneia,* reproduction. Even Webster's [unabridged] *Third New International Dictionary* (1971) expressed doubt as to whether poecilogony occurs: "A *supposed* method of development occurring in invertebrate animals when in the same species there are two kinds of young although the adults are *exactly* alike" (italics ours). In this paper, we first define the phenomena we mean to include under the term poecilogony. We then review reported cases of poecilogony known to us in marine invertebrates, particularly mollusks and polychaetes. We also demonstrate that congeneric species in many invertebrate groups differ in type of larval development, hence the mode of larval development has a complex history within most invertebrate phyla. The likelihood that poecilogony is real is assessed and theoretical implications are discussed. We suggest ways of testing the hypothesis of poecilogony in some cases where the data are insufficient for a judgment to be made.

Materials and Methods

We searched the published literature for references to poecilogony. We categorized the data in each paper as to

the geographical or seasonal pattern found, the type of evidence for poecilogony, and the proposed mechanism. In some cases, we sought further information from the authors. We then evaluated the status of each claim of poecilogony.

Results

Definitions

Poecilogony is the presence of more than one distinctive kind of development in the same sexually reproducing species, *i.e.*, a polymorphism in development. In most cases, it involves differences in egg size (*e.g.*, small eggs destined to develop planktotrophically and large eggs that develop directly) or embryo size (*e.g.*, some embryos consume nurse eggs but others do not). It might occur as geographical variation between populations. In that case, it is difficult to know whether two species are involved. Some cases of poecilogony are cited as seasonal within a population. For example, a population produces brooded young in spring, but releases planktonic young in fall. A third reported kind of poecilogony is environmentally determined, as when the pattern of development is determined by salinity or amount of food available to the parent.

Giard (1891) first proposed the term "poecilogonie" in a short paper mainly discussing larval ascidians. He followed up with a paper devoted to poecilogony (1892), and then by a frequently cited lengthy article (1905). In this last paper, he said that poecilogonous differences could involve (1) certain individuals or different generations in one population (involving seasonal, nutritional factors, etc.), or (2) geographically separated populations with or without habitat differences. He believed that there are examples of poecilogony in nearly all the major groups of animals. Most if not all of these examples can be explained equally well as similar or sibling species with invariable larval development. Giard admitted that there can be differences, although slight, between different parents with different kinds of development.

In most of the proposed examples of poecilogony, observations have been made in the field, and the same individual parent or lineage could not be shown to produce two kinds of young. There have been observations of two kinds of larvae within a single egg case. If the egg cases were shown to be laid by one female without contamination and both types of larvae hatched, it would be a demonstration of poecilogony. If only the larger larvae hatch, it would be an example of cannibalism, not poecilogony.

Some marine invertebrates produce larvae that feed facultatively in the plankton (Chia, 1974; Perron and Carrier, 1981; Alatalo *et al.*, 1984; Kempf and Hadfield, 1985; Emlet, 1986). We do not consider facultative feeding to be true poecilogony because there are not two kinds of young with different developmental paths.

There is no morphological differentiation in either larvae or supportive structures (egg capsule wall, etc.) that distinguishes two kinds. We also exclude cases of diapause, such as occur in crustaceans, and heterogeneous life cycles, such as occur in cnidarians and many polychaetes with both sexual and asexual life stages. Finally, non-polymorphic, continuous variation in egg size, clutch size, or development time is not poecilogony.

This paper does not cover examples of poecilogony in freshwater invertebrates nor in plants ("amphicarpy"), where there are some well-proven examples.

A review of the literature

We searched the literature for reported cases of poecilogony. Jablonski and Lutz (1983) reviewed some molluscan examples, but most are scattered in the literature. Table I reports cases in the Mollusca; Table II gives cases in the Polychaeta. Most examples are in these two higher taxa. The kind of poecilogony is categorized as geographical (G) when reports of allopatric populations are involved, seasonal (S) when a succession of reproductive modes has been reported for a single population, sympatric (Sy) when occurring within a population simultaneously, capsular (Cp) when within a single capsule, and environmental (E) when factors such as salinity have been invoked to explain the occurrence of poecilogony. The type of evidence is also categorized: field observations of larvae without associated adults (F), field observations with adults (FA), production of young (L), or successful breeding of individuals differing in mode of reproduction in the laboratory (LB). If the different modes of reproduction were independent observations by two researchers, it is so indicated (I). If only embryonic shells or only planktonic veligers were observed, the symbols (Sh) and (P) are used, respectively. Mechanisms of poecilogony originally proposed are given: twinning (T), nurse-eggs (N), cannibalism (C), extracellular yolk (Y), and/or variable nutrition available to the parent (VN).

Table II reports cases in the Polychaeta, including the forms of reproduction reported: planktonic development (P), benthic development (B), brooding or ovoviviparity (Br), epitoky (Ep), atoky (A), and nurse-eggs (N), which are usually in benthic capsules.

Forty-two examples from the Mollusca have been found, all marine, eighteen of which involve geographically distinct populations (Table I). Nearly all prosobranch examples are of planktotrophic veligers and either direct development or demersal eggs. The family Littorinidae contains sympatric sibling species that differ in reproductive mode as well as penial morphology and other characters (Reid, 1986; Heller, 1975). Electrophoresis has confirmed in several cases the genetic distinctness of the sibling species (*e.g.*, Ward and Janson, 1985).

Reid (1986) places *L. angulifera* in the genus *Littoraria*. Although he has no specific evidence about the reproductive anatomy of this species, he concludes, "Anatomical examination has provided no suggestion that any species of *Littoraria* is able to show both oviparous and ovoviviparous modes of development." *Tectarius muricatus* has been reported by various workers in different localities to be "viviparous" (releasing fully developed veligers) or to release pelagic capsules, but differences exist in the radula that suggest several species could be involved (Bandel, 1974).

According to Rehfeldt (1968), Rasmussen suspected poecilogony for *Rissoa membranacea*, but she doubted it, based on her own data. Indeed, *R. membranacea* has been reported incorrectly synonymized with a morphologically distinct species, *R. labiosa* [Verduin, (1986a)]. Data from *Modulus modulus, Brachystomia [Odostomia] rissoides*, and *Natica groenlandica* (Table I) are probably also based on confusion of two allopatric congeners; there is no evidence of interbreeding of the different reproductive types. Risbec's (1935) brief description of *Siphonaria atra* is insufficient to know if two reproductive types exist. The case of *Siphonaria laciniosa* was disproved, being a case of mistaken synonymy (Hulings, 1986). Gallardo (1979) disproved his own example of *Crepidula dilatata* when morphological and ecological data were collected that revealed a sibling species. Likewise, the cephalaspid (bullomorph) genus *Acteocina* is now known to be composed of sibling species with different types of reproduction (Mikkelsen and Mikkelsen, 1984).

The species in Table I with egg collars or capsules that were collected without the parent, such as *Sipho islandicus*, the Columbellidae, and the Naticidae, provide poorly documented examples of poecilogony. The two types of *Columbella rustica* had different capsule morphology and therefore are most likely distinct species. There was no basis for the claim of poecilogony for *Lunatia pallida*, because two types of hatching young were not observed. The observation of a single egg mass with two embryos per capsule led to speculation that these young might be released as veligers instead of crawling young (Thorson, 1946). Similarly, the data for *Polinices catena* show some variation in numbers of nurse-eggs but poecilogony is only an extrapolation; positively identified *P. catena* with pelagic young have not been found (Thorson, 1946). Although two types of egg collars were found for *Polinices triseriata*, the association of the egg collars with particular adults was a guess by different investigators, and the oft-quoted correlation of larval type with local weather was only a suggestion based on collections of eggs made once each in two years (Giglioli, 1955).

The finding of two different types of protoconchs in planktonic juveniles cannot be taken as proof of poecilo-gony because of the great possibility of mis-assignment of the juveniles to adults. For example, Taylor (unpub.) reported finding veligers in the plankton that belonged to several species of Vermetidae previously known to produce crawling young. Her reports, cited in Hadfield *et al.* (1972), are undocumented. Verduin (1986b) reported that *Alvania cimex* was really a species complex. Thiriot-Quiévreux's (1980a) *Seila adamsi* var. *beauforti* with a shell distinct from *S. adamsi* is probably a distinct species.

Examples of poecilogony involving nurse-eggs include *Sipho islandicus, Planaxis sulcatus, Thais canaliculata,* and *T. haemastoma.* The last three are based on geographically isolated populations. The assumption that numbers of nurse-eggs vary to produce two hatching types within a single population or from a single adult is not based on any direct observations and is not justified by the data. Spight (1977) suggested that *Thais canaliculata* was evolving nurse-eggs, from his finding of egg capsules in separate localities with and without nurse-eggs. Only two capsules were found with adults; Spight did not compare the adults that produced the capsules. He found variation in percent of developing embryos in the populations with nurse-eggs. No evidence was presented that bears on whether one or two species exist. Rivest (1981) found nurse eggs in all populations that he examined from six localities, including the one studied by Spight. It is possible that Spight examined capsules at one site after all nurse eggs had been consumed.

"*Dolium maculatum*" [=*Tonna maculosa*] is interesting in that it is reported to have brood cannibalism, in which embryos of different size and developmental stage exist in the same capsule (Thorson, 1940). There is no proof that the less-developed young ever are released from the egg mass and survive, so we cannot say that there are two kinds of larvae. This situation may just be a variant in which nurse-eggs begin to develop, albeit slowly, before being consumed.

Penchaszadeh (1981) reported poecilogony in *Tonna galea.* He found small and large larval shells (reflecting, respectively, planktotrophy and lecithotrophy) in a single egg case. However, as can be seen even from his photographs (Penchaszadeh, 1981, Figs. 1a, b), the large larval shells are not shaped like larval *Tonna*, but have a much longer anterior siphonal canal. (See Laursen, 1981, pp. 31-34, Figs. 49 and 51 for illustrations of larval *Tonna* shells.) A growth series of ten larval specimens from the Atlantic Ocean, loaned to us by Dr. Rudolf S. Scheltema, corroborates Laursen's observations: at no stage does larval *Tonna* have a long anterior siphonal canal. Even though some similar observations on *Tonna* larvae were published earlier suggesting brood cannibalism (Thorson, 1940), there is at least one other explanation. Possibly some oophagous gastropod pierced some of the compartments, ate the contained *Tonna* eggs, and

Table I

Reported cases of poecilogony in Mollusca. Abbreviations are explained in the text. The classification follows Taylor and Sohl (1962) for prosobranchs and Thompson (1976) for opisthobranchs

Family	Genus & species	Citation	Type	Mechanism	Evidence	Comments; status
POLYPLACOPHORA						
Chitonidae	*Chiton cinereus*	**Thorson, 1946	G, Sy	—	FA, I	Demersal eggs or brooding in mantle cavity; same stage at hatching.
GASTROPODA						
Littorinidae	*Littorina angulifera*	*Lenderking, 1954	G	—	FA	Probably a species complex (Reid, 1986).
		**Mileikovsky, 1971	S	—	F, I	
	Littorina scabra	**Mileikovsky, 1975	G	—	FA, I	A species complex (Reid, 1986).
	Littorina scutulata	Imai, 1964	—	—	FA	Shown morphologically that 2 distinct species exist (Murray, 1982).
		*Buckland-Nicks et al., 1973	G	—	FA, I	
	Littorina saxatilis	*James, 1968	G	—	FA	Species complex. See Heller, 1975; Ward & Janson, 1985; Hannaford Ellis, 1978, 1983. Claims of viviparity when young based on smaller species.
		Hughes, 1978	Sy	—	FA	
		*Bergerard & Sy	S	—	FA	
		Caugant, 1981	—	—	FA	
		Seshappa, 1948	Sy	—	—	
	Tectarius muricatus	*Bandel, 1974	G	—	F, I	Release of veligers vs. release of egg capsules
		Lebour, 1945	G	—	F, I	
Rissoidae	*Alvania cimex*	*Thiriot-Quiévreux, 1986b	Sy	—	Sh, P	Direct & pelagic development based on protoconch. Ornamentation differed. Verduin claimed complex of 3 species.
	Rissoa membranacea and	*Rehfeldt, 1968	—	—	—	Two species, based on morphology.
	Rissoa labiosa	Verduin, 1986a	—	—	—	Poecilogony doubted.
Vermetidae	*Dendropoma irregularis* (=*Spiroglyphus*)	*Lewis, 1960	?	—	FA	Some capsules produce briefly-planktonic young; others produce young that crawl away. Unclear if from same female or same locality.
	Dendropoma meroclista	**Hadfield et al., 1972	Sy	—	P	Usually crawling young. Taylor (unpubl.) reported veligers in the plankton, same general locality.
	Dendropoma platypus	**Hadfield et al., 1972	Sy	—	P	Same comment as just above.
	Petaloconchus keenae	**Hadfield et al., 1972	Sy	—	P	Same comment as just above.
Planaxidae	*Planaxis sulcatus*	**Thorson, 1940, 1952	G	N	F, I	Nurse eggs in only some populations.
		Risbec, 1921	—	—	F	
		Lamy, 1928	—	—	F	
Modulidae	*Modulus modulus*	*Houbrick, 1980	G, E	—	L	Shell sculpture differences. Spawn masses differ in morphology.
		Lebour, 1945	—	—	F	
		Bandel, 1976	—	—	F	
Cerithiopsidae	*Seila adamsi*	*Thiriot-Quiévreux, 1980a	Sy	—	Sh, P	Protoconch differences. S.a. var. beauforti named.
Calyptraeidae	*Crepidula dilatata*	*Gallardo, 1977; 1979	—	—	FA	Two species, morphology and microhabitat differences. C. fecunda named.

Table I (Continued)

Family	Genus & species	Citation	Type	Mechanism	Evidence	Comments; status
Naticidae	Lunatia pallida (=Natica)	*Thorson, 1946	Sy	T	F	Speculation only; variation in egg size (Thorson, 1950).
	Natica groenlandica	*Thorson, 1950	G	—	F	Latitudinal differences.
	Polinices catena (=Natica)	**Thorson, 1946	G	N	F, I	Number of nurse-eggs might vary. Thorson
		Ankel, 1930	—	—	F	questioned Lebour's
		Lebour, 1936	—	—	F	identity of N. catena with pelagic young.
	Polinices triseriata	*Giglioli, 1955	E	—	F, I	Different researchers,
		Stinson, 1946	—	—	F	different years, same
		Wheatley, 1947	—	—	F	locality. Egg collars only. Wet vs. dry yrs.
Tonnidae	Tonna maculata	*Thorson, 1940	Cp	C	F	"Brood cannibalism" cited.
	Tonna galea	*Penchaszadeh, 1981	Cp	C	F	1 egg mass fragment had 2 sizes of embryos.
Muricidae	**Murex incarnatus	*Gohar & Eisawy, 1967	C	N	L	Embryological study. Most hatch as veligers & metamorphose next day; some hatch metamorphosing.
	Thais canaliculata	*Lyons & Spight, 1973; Spight, 1977	G	N	FA, I	Yolky eggs at one locality,
			G	N	F	nurse eggs at another.
		Houston, 1971	—	—	FA	% nurse eggs varies.
	Thais haemastoma (confused with T. floridana; see Radwin & Chamberlin, 1973)	**Thorson, 1950	G	N	F, I	Nurse eggs in some
		Lamy, 1928	—	—	F	localities; error in report
		Burkenroad, 1931	—	—	F	of nurse eggs in W. Indies (D'Asaro 1966; Spight, 1975).
Columbellidae	Columbella rustica	*Knudsen, 1950	E	—	F	Nurse eggs at Naples,
		*Thorson, 1950	G	N	F, I	Banyuls; veligers
		Franc, 1943	—	—	F	elsewhere. Capsules
		Bacci, 1947	—	—	F	with nurse eggs a
		Bandel, 1975	—	N	F	different shape; not collected with adults.
Buccinidae	Sipho (Colus) islandicus	*Thorson, 1935, 1936, 1952	Sy	N	F, L	Dredged field collection; adults apart from egg capsules in many cases. Assumed that young escape when nurse eggs depleted.
Pyramidellidae	Brachystomia rissoides	*Rasmussen, 1944, 1951	G, E	—	FA, L	Salinity proposed as controlling factor. No
		Pelseneer, 1914	—	—	FA	sympatry. No
		Thorson, 1946	G	—	FA	experimental evidence.
Acteocinidaea	Acteocina candei & A. canaliculata	*Franz, 1971	G	—	L, I	Two species (Mikkelsen,
		Wells & Wells, 1962	—	—	F	1984).
Elysiidae	Elysia cauze	*Clark et al., 1979	E, S	Y	FA	Sequential seasonal change, 3 types of development. No adult produced more than one type offspring.
	**Elysia chlorotica	*West in Bonar, 1978	Cp	—	—	Lecithotrophic veligers & metamorphosing young.
		West et al., 1984	G	—	LB	Hybridization between kinds.
	Elysia evelinae	*Clark & Jensen, 1981; Jensen & Clark, 1983	Cp	—	L	Capsular metamorphosis and lecithotrophy

Table I (Continued)

Family	Genus & species	Citation	Type	Mechanism	Evidence	Comments; status
Elysiidae (cont.)	*Tridachia crispata*	*Clark & Jensen, 1981	G	—	L	Capsular metamorphosis and lecithotrophy.
Dendronotidae	*Dendronotus frondosus*	*Clark, 1975	G	—	FA, I	Europe vs. New England
		Thompson, 1967	—	—	FA	populations.
Arminidae	*Armina tigrina*	*Eyster, 1981	G	—	L	Florida and S. Carolina.
		Clark & Goetzfried, 1978	G	—	FA	Based on egg diameters.
Spurillidae	*Spurilla neapolitana*	*Clark & Goetzfried, 1978	E	VN	L	Multi-embryo planktotrophic capsules produced when adults starved; otherwise nonplanktotrophic.
Cuthonidae	*Cuthona nana*	*Harris et al., 1975, 1980	S	Y	F	Data from different years. Brown synonymized 2
		Brown, 1978	G	—	F	species; Rivest (1978) found 2 species.
	**Tenellia fuscata* (=*Embletonia*) [see text for taxomony]	*Eyster, 1979	Sy	—	LB	Sympatric individuals
		Rasmussen, 1944	G, E	—	L	bred in lab; offspring type didn't change. No proof of cross-fertilized matings. Morphological differences between larval types; adult size differed.
Siphonariidae	*Siphonaria atra*	*Risbec, 1935	Sy	—	FA	Insufficient information.
	Siphonaria laciniosa *S. kurracheensis*	Hulings, 1986	—	—	—	Two species. Incorrect synonymy demonstrated.
BIVALVIA						
Teredinidae	*Teredo navalis*	*Kudinova-Pasternak, 1957; Thorson, 1946	G	—	F, I	Misidentifications of specimens in Adriatic Sea.
	Teredo utriculus	**Kudinova-Pasternak, 1957; Roch, 1940	S	—	F, I	Misidentifications;
			—	—	F	confused with *T. navalis*.
	Teredo pedicellata	**Kudinova-Pasternak, 1957; Roch, 1940	G	—	F, I	Probably confused with *T.*
			—	—	F	*navalis*.

* Primary reference suggesting poecilogony.
** Cases with merit.
* Author reported poecilogony on the basis of the research of others.

laid one of its own eggs in each compartment that it had emptied. To prove or disprove this idea, it should be possible to ascertain whether each compartment containing large larvae had been pierced prior to hatching.

There are many reports of poecilogony in nudibranchs and ascoglossans. As with all the foregoing examples, not one adult has been directly observed to produce more than a single distinct kind of offspring (but see discussion of *Elysia evelinae* and *E. chlorotica* below). The reported seasonal progression of three types of larvae for *Elysia cauze* (Clark et al., 1979) could be the succession of three or even four species (Jensen and Clark, 1983). DeFreese and Clark (1983) report that sibling species account for two of the types of reproduction. Clark (pers. comm.) believes *E. cauze* to be a junior synonym of *E. subornata*. Allopatric populations of *Armina tigrina* and *Dendrono-*

tus frondosus are undocumented as cases of poecilogony and need further systematic study; Clark (pers. comm.) points out that there are two available names for *Armina tigrina* in the southeastern United States, and there are differences in hatching morphology between the two allopatric forms, suggesting that two species exist. Poecilogony in *Tridachia crispata* is also insufficiently documented. From original published reports, it is not clear if capsular metamorphosis and lecithotrophy occurred in the same or different populations (Clark and Jensen, 1981). Clark (pers. comm.) stated that the populations are allopatric but within about 10 kilometers of each other; one is on a reef and the other is in mangroves. The two populations differ morphologically. Rivest (1978) demonstrated that the suggested poecilogony of *Cuthona nana* was in fact a case of sibling species.

There are a few remaining cases with better data. Specimens of *Tenellia pallida* of different reproductive modes were bred in the laboratory (Eyster, 1979). Offspring of the kind of the (female) parent were produced. There was no proof that cross-fertilization took place in these hermaphrodites, and morphological differences were found in the larvae of the two types. Genetic data on such a breeding (and on an F₂ generation) are badly needed to see if the forms are truly interfertile. Rasmussen (1944) found geographically separate populations presumed to be of this species, one that produced veliger larvae and another that produced veligers that metamorphosed as they hatched. Clark (pers. comm.) believes that Rasmussen's European populations are correctly called *Tenellia pallida,* while Eyster's American specimens are properly referred to *Tenellia fuscata.* For *T. fuscata* from New England, Harris *et al.* (1980) suggest not poecilogony, but a plasticity of hatching time determined in part by breakdown of the egg mass itself. Although the species is genetically programmed to go through a veliger stage, Harris *et al.* (1980) speculated that the exact time of hatching might be determined by bacteria, water movements, or other external factors.

Spurilla neapolitana was reported to produce a different kind of capsule when adults were starved (Clark and Goetzfried, 1978). This work should be continued to verify that the same adult could produce both kinds, and both kinds of capsule produced viable young. The original work involved adults in aquaria, not isolated individuals in finger bowls, and contamination could have occurred.

The best case for poecilogony in mollusks is that of *Elysia chlorotica,* in which hybridization of individuals from allopatric populations of different reproductive characters was achieved (West *et al.,* 1984). The F₁ generation produced young of the same type as the (female) parent, but the F₂ produced young that were intermediate in egg size and developmental characteristics, as if maternal expression were a factor. The interesting findings definitely call for further study. This case could represent genetically diverging (speciating) populations that have not yet become reproductively isolated, *i.e.,* true poecilogony.

Jensen and Clark (1983) and Clark (pers. comm.) report that capsular metamorphosis and lecithotrophy both occur in a gradient of developmental patterns within the same egg capsules in *Elysia evelinae.* The time between release from the capsule and metamorphosis of lecithotrophic young varies over a period of a day or two. The same situation occurs in the nudibranch *Doto acuta* (Schmekel and Kress, 1977), in *Murex incarnatus,* and in one of the two kinds of *Elysia chlorotica:* most young hatch as very short-term veligers, but a few larvae are retained in the capsules longer and hatch metamorphosing (Gohar and Eisawy, 1967). Such a situation could be

considered incipient poecilogony, but there is no difference between the young in larval morphology or egg capsule morphology, and metamorphosis merely varies within a 24-hour period.

Williams (1980) reported two types of larvae for both *Hermissenda crassicornis* and *Aeolidia papillosa.* All eggs were the same size and all larvae were planktotrophic, but some hatched with yolk reserves and others hatched without yolk. The yolk-free larvae tended to be larger, and it was suggested that they developed faster. This situation does not quite fit the definition of poecilogony because there are not two distinct types of larvae, but it is a possible intermediate of the type needed to explain evolution of different reproductive modes.

Examples of poecilogonous bivalves (end of Table I) are limited to the genus *Teredo* of the Teredinidae. These boring bivalves are difficult to identify without dissection from the wood. Claims of poecilogony are unsubstantiated in the 30 years since Kudinova-Pasternak's 1957 paper, which was based not on laboratory anatomical comparisons or breeding studies but on various field reports. *Teredo utriculus* (*=T. norvagicus*) is oviparous and *Teredo pedicellatus* is larviparous, but both have been confused with *T. navalis* (briefly larviparous, then planktonic development ensues) (Turner, pers. comm.). Turner has found cryptic species pairs with different types of reproduction; *T. pedicellatus* is a species complex.

The case for *Chiton cinereus* is based on observations of eggs retained in the space surrounding the gills. Thorson (1946) was not sure if this retention was fortuitous or a regular occurrence; in any event, the stage at hatching does not change.

In the 22 examples of polychaetes (Table II), most cases clearly involve cryptic species in which the nonreproductive adults look alike, but the juvenile stages and/ or reproductive adult stages differ. Often (*e.g.,* Thorson, 1946), researchers found larvae in the plankton and made an educated guess as to which species they belonged. Brooded larvae, of course, and most epitokes were associated with adult females.

Many supposed cases of poecilogony are found in the Spionidae, a group of small worms that can undergo copulation or produce spermatophores (Rice, 1978) and often brood young or have nurse eggs (Woodwick, 1960). *Spio setosa, S. martinensis,* and *Polydora quadrilobata* involve cryptic species and failure of researchers to associate larvae with the proper adults. Larvae of the benthic and planktonic types differ in numbers of setigers, setal pattern, color pattern, and ciliation, characters that are of taxonomic importance. *Spio filicornis* was misidentified and wrongly synonymized with *S. martinensis* (see Hannerz, 1956). Hannerz (1956) also disproved seasonal poecilogony for *Pygospio elegans,* finding only one morphology, but the possibility remains that the relative

lengths of brooded and pelagic stages vary seasonally. However, Anger (1984) found in laboratory studies that temperature and salinity changes do not cause changes in developmental pattern of *P. elegans*. Thorson's (1946) three types of pelagic larvae of *P. elegans* differed in color, bristle lengths, etc. and obviously were different species.

Boccardia proboscidea has been confused with another species, *B. columbiana* (Woodwick, 1963). However, Woodwick (1977) found sympatric populations of *B. proboscidea* with lecithotrophic and pelagic larvae at Moss Landing, California. The two types of larvae differed in length of setae at the three-setiger stage. Not only were the eggs of lecithotrophically developing worms larger, but the capsules and three-setiger larvae were also larger. Therefore, the reproductive differences involve more than simple availability of nutrients. Hartman's (1941) descriptions of reproduction in this species dealt mainly but not exclusively with pelagic larval forms; all her adult specimens came from hard substrata. Woodwick, on the other hand, collected his specimens in sand and soft mud; his populations were mostly lecithotrophic. Whether interbreeding occurs in nature between the adults of the two different larval types could be assessed easily by comparing allozyme frequencies of sympatric individuals.

Blake and Kudenov (1981) reported *Boccardia proboscidea* from Australia with single egg capsules containing at the same time unfertilized nurse eggs, small larvae, and precocious larvae feeding on both the eggs and small larvae. They believed that the small larvae could have a long pelagic period if they survived brood cannibalism. However, none were observed to be released into the environment. If they were artificially removed from capsules in the laboratory, the small larvae could feed on suspended food particles (Blake and Kudenov, 1981). However, evidence that both types of larvae survive and contribute to future generations is needed. Production of developing embryos of two distinct size classes in one adult demonstrates that two modes of oogenesis can evolve in spionids. This is a most interesting population for further study of evolution of life history, and could be an example of true poecilogony. The Australian population with two sizes of larvae in the same capsule is believed to be a recent introduction (Blake and Kudenov, 1981).

In addition to *Boccardia proboscidea,* four other species in the genus have been reported by Read (1975) to reproduce with or without nurse eggs. He did not say whether two types of reproduction occurred in the same locality. He listed all localities together in a "material examined" section, apart from the reproductive data. Although he stated, "Some polydorids vary the form of larval development. . . by alteration of the amount of food supplied", no data were given. For *B. acus,* specimens

from Wellington were larger, with more segments, branchiae, and setae, than specimens from Otago (New Zealand). It would be interesting to know if these localities represented the two reproductive types. If so, we predict that the Wellington specimens are a different species, with pelagic development.

Streblospio benedicti and *Cirriformia tentaculata* are the most interesting examples in the Polychaeta because breeding data are available. Levin (1984) crossed allopatric adults of two larval types of *S. benedicti,* planktotrophic and lecithotrophic. Inter-fertility was indicated. Further studies using sympatric specimens of the two reproductive types from Bogue Sound, North Carolina, indicated that F_1 and F_2 offspring were intermediate between the two parental types in egg size, brood size, and planktonic period (Levin and Creed, 1987, unpub. abstract, Second International Polychaete Conference). Hybrid individuals are sometimes observed in the field. Genetic data in the form of allozyme studies of field populations would be of high interest, to see if the two developmental types are fixed for alternative alleles at any locus in the sympatric population. If so, they are not breeding in nature and are functionally separate species. If not, they may well be a single polymorphic species, but the mechanism for maintaining such a polymorphism is difficult to imagine. Genetic studies of the laboratory-reared specimens would confirm whether cross-fertilization did occur in the breeding experiments. It is interesting that morphological differences between the two kinds of *S. benedicti* do occur: planktotrophic larvae have long swimming setae lacking in the non-feeding larvae, yolk in the two forms differs in composition, and ovaries first occur in setigers 9–11 of the planktotrophic females but in setigers 11–14 of the lecithotrophic females. "Females with planktotrophic development were longer, had more segments, bore the first gametogenic segment more anteriorly, had half the ovum diameter, . . . [and] more paired brood pouches . . . [than] those with lecithotrophic development." (Levin and Creed, 1986).

The initial hypothesis that *S. benedicti* is an example of incipient speciation between Atlantic and Pacific North American populations, with interbreeding still possible, was weakened by Levin's find of sympatric specimens in North Carolina. However, in some months planktotrophic reproduction only was found, suggesting that the two reproductive types were possibly partially segregated by maturing at different times. Animals reared under a variety of food levels and temperature regimes mimicking fall, summer-fall, and winter-spring did not change reproductive mode (Levin and Creed, 1986), so it is unlikely that the same individuals vary their reproduction seasonally. The genetic structure of *S. benedicti* cannot allow free interbreeding of the forms, or there would be a full range of forms rather than only occasional intermediates.

Coincidentally, Levin (1984) found a third type of *Streblospio benedicti* in the Gulf of Mexico that differed in adult reproductive structures; in particular, it had vascularized branchiae instead of brood pouches. It may represent a distinct species (Levin, pers. comm.).

George (1967) bred *Cirriformia tentaculata* from Plymouth, England, by mixing eggs of one female with male gametes in the laboratory. The gametes were naturally released. He reared both free-swimming and demersal larvae from single broods. No morphological differences were reported in the larvae. There was no detailed description of the methods of rearing so contamination cannot be ruled out, but the data certainly warrant further examination of *C. tentaculata*. Some populations are reported to be demersal only, with smaller adults (George, 1963), suggesting that two species could be involved. Grassle and Grassle (1976) showed the power of careful morphological study and electrophoresis when they found that differences in reproduction in *Capitella capitata* actually involved at least six sympatric species. Healy and Wells (1959) found new taxonomic characters that divide *Arenicola claparedei* into three species.

Claims made for poecilogony in geographically separated populations of polychaetes such as those of *Eupolymnia nebulosa* from the Mediterranean and the Atlantic coasts of France are without proof unless breeding studies have been done. Daly (1972) described brooding in *Harmothoe imbricata* outside Greenland, whereas Thorson (1936) found brooding in Greenland and pelagic development elsewhere, but no sympatric populations with two types of reproduction have been reported. Cases of poecilogony where adults differ consistently in size (incorrectly assumed to be age-related) are suspect; they include *Syllis vivipara* and *Ehlersia nepiotoca* (Table II).

Although Rasmussen (1956) found sympatric reproductive differences in *Nereis pelagica,* one of his adult types was a tube-builder and the other was not, indicating that he had two species distinct in microhabitat. *Nereis* (*=Platynereis*) *dumerilii* needs further examination because sympatric populations were found (Thorson, 1936). Simple allozyme studies might easily resolve the issue. Hempelmann's (1911) observation of two allopatric reproductive types was based on his synonymy of *Platynereis massiliensis* (Moquin-Tandon, 1869) with *P. dumerilii*. The former is atokous and produces benthic young in tubes protected by the male; the latter produces pelagic young via epitoky. Hauenschild (1951) showed that these are different species, on the basis of sperm morphology as well as on larval and adult behavioral characters that prevent cross-fertilization. Likewise, *P. megalops* (Verrill) of the North American Atlantic has been synonymized with *P. dumerilii* of Europe, but Smith (1958) showed that reproductive behavior (sexual dimorphism of heteronereids and copulation of *P. mega-*

lops prior to release of eggs) prohibits interbreeding between the two species under natural conditions. Martin (1933) rejected poecilogony in favor of an interpretation of a complex of species for *Dodecaceria concharum;* there could be at least three species (Clark, 1977).

The phenomenon of embryos feeding on non-developing eggs or on other embryos is widespread in prosobranch gastropods and in spionid polychaetes, in which the term adelphophagy is often used (Mileikovsky, 1971). In the gastropods *Thais emarginata, Crepidula cerithicola,* and *Searlesia dira,* embryos from a single brood hatch at different sizes depending on the number of nurse eggs consumed (Spight, 1976; Rivest, 1983; Hoagland, 1986). However, there was only one stage at hatching for each species, despite size differences.

Very few examples of poecilogony have been given for higher taxa other than mollusks and polychaetes. Giard's (1891, 1892, "1904" [1905]) original examples included ascidians, coelenterates, crustaceans, flatworms, and many other groups; none of his cases were documented. Mortensen (1921) disproved the echinoderm examples. In the crustaceans, variation in egg size is fairly common, e.g., in *Palaemonetes varians* (Boas, "1889" [1890]) and *Crangon crangon* (Thorson, 1946). However, we found no documented examples of poecilogony. The closest possibility is *Balanus balanoides,* reported to release naupliae ordinarily, but cypris-stage larvae in special circumstances (Runnström, 1925). Cryptic species cannot be ruled out. Most of the smaller phyla are too poorly known to provide data on poecilogony.

Several species of parasitic nematodes in at least three genera produce two types of eggs: thick-coated ones that pass to the exterior and thin-coated ones that go through an endogenous cycle (Adamson, 1984). These species also have haplodiploidy as a means of sex determination. These phenomena have been called poecilogony. No similar phenomena are known for marine invertebrates. Rotifers, freshwater sponges, copepods and other freshwater invertebrates do have resting eggs as a part of complex life cycles.

While documented cases of poecilogony are few to none, depending on the rigor of proof one is willing to accept, there are many genera in numerous phyla that have more than one mode of larval development (Giese and Pearse, 1974; 1975a, b). A complete list would be very long indeed. Radwin and Chamberlin (1973) summarized data for the Recent stenoglossan neogastropods. The few families whose living representatives apparently lack planktonic larval stages are the Buccinidae, Melongenidae, Fasciolariidae, Volutidae, Marginellidae, and Cancellariidae. Most other families of meso- and neogastropods contain genera with more than one type of development; these include the Littorinidae, Rissoidae, Cerithiidae, Hipponicidae, Calyptraeidae, Cypraeidae, Naticidae, Muricidae, Thaididae, Columbellidae,

Table II

Reported poecilogony in polychaetes. Asterisks as in Table I

Family	Genus & species	Citation	Type	Larval forms	Evidence	Comments; status
Polynoidae	*Harmothoe imbricata*	*Thorson, 1936, 1946	G	Br, P	FA	Eggs beneath elytra in Greenland, pelagic elsewhere.
		Izuka, 1912	—	P	FA	
Syllidae	*Syllis vivipara & S. prolifera*	**Thorson, 1950	Sy	Br, P	—	Synonymized by Thorson.
		Mesnil & Caullery, 1917	—	Br, P	F	Smaller are viviparous.
	Ehlersia nepiotoca & E. sexoculata	**Thorson, 1950	Sy	Br, P	—	Synonymized by Thorson.
		Mesnil & Caullery, 1917	—	Br, P	F	Smaller are viviparous.
Nereidae	*Nereis (=Ceratonereis) costae*	*Durchon, 1957	G	Ep, B	F	Epitokous form not studied. Atokes live in tubes.
	Nereis pelagica	*Rasmussen, 1956	Sy	B, P	F, L	Rasmussen's adults differed in microhabitat.
		Herpin, 1925	G	B	L, I	
		Wilson, 1932	G	P	L, I	
	Nereis zonata	*Thorson, 1950	G	Ep, B	FA, L	Epitokes or non-pelagic eggs, inner *vs.* outer fjords.
	Platynereis dumerilii	*Thorson, 1936	Sy	Ep, P	FA	Epitokes and non-pelagic eggs at Naples.
		Hempelmann, 1911	G	—	F	
		Wistinghausen, 1891	G	—	F	
	Perinereis cultrifera	*Durchon, 1957	G, Sy	A, Ep	F	Major life history differences between atokous and epitokous forms. Sympatry is relatively rare.
Onuphidae	*Diopatra cuprea*	*Monro, 1924	G	Br, P	F	Brooding in Panama.
Spionidae	*Polydora quadrilobata*	*Blake, 1969	G	N, P	F	Middle population differs from the two geographic extremes. Larvae differ morphologically.
	Spio filicornis	*Thorson, 1936	S	N, P	F	Nurse eggs in autumn. Söderström's (1920) incorrect synonomy with *S. martinensis* confused larval types (Hannerz, 1956).
		*Mesnil & Caullery, 1917	—	—	F	
	Spio martinensis	Hannerz, 1956	Sy	P	F	Adults differ in size; larvae in pigment and morphology. Probably 2 species.
		*Mesnil & Caullery, 1917	S	N, P	F	
	Spio setosa	*Simon, 1968	S	B, P	L	Young cultured from plankton. Adults not associated. Larvae differ in setae, pigment, etc.
		Hannerz, 1956	—	—	F	
		Blake & Kudenov, 1981	S	N, P	—	
	Boccardia acus	*Read, 1975	—	N, P	F	Morphological differences between 2 populations.
	Boccardia androgyna	*Read, 1975	—	N, P	F	Percent nurse eggs varies; may be none. Constant within an egg string.
	Boccardia chilensis	*Read, 1975	—	N, P	F	Two types cited but no data.
		*Blake & Kudenov, 1981	G	N, P	—	
	Boccardia otakouica	*Read, 1975	—	N, P	F	No larvae found in plankton. Percent nurse eggs varies.
	Boccardia proboscidea	*Hartman, 1941	Sy	N, P	L	Some morphological differences.
		*Blake & Kudenov, 1981	Cp	N, P	L	

Table II (Continued)

Family	Genus & species	Citation	Type	Larval forms	Evidence	Comments; status
Spionidae (cont.)	*Pygospio elegans*	*Hannerz, 1956	S	N, P	FA	Spring, summer difference in length of pelagic stage reported.
		*Rasmussen, 1956	Sy	N, P	F	
		Thorson, 1946	Sy, G	N, P	F	
		Söderström, 1920	S	N, P	F	
	***Streblospio benedicti*	*Levin, 1984	G, S	B, P	LB	Breeding of 1 generation.
Cirratulidae	*Cirratulus cirratus*	*Fauvel, 1916	G	Br	FA, I	Falklands vs. North Seas.
		Cunningham & Ramage, 1888	G	B	L, I	
	Dodecaceria concharum	**Thorson, 1950	Sy, G	Br, B	FA, I	Total of 5 types of reproduction, 3 of them sexual. Martin (1933) concluded species complex.
		Dehorne, 1927	G	Br, B	FA	
		*Mesnil & Caullery, 1898a, b	Sy	Br, E-P	FA	
	***Cirriformia tentaculata*	*George, 1963, 1967	G	B, P	L	Adults differ in size (George, 1963). Single female produced both types (George, 1967).
			Sy	B, P	LB	
Terebellidae	*Eupolymnia nebulosa*	Gremare, 1986	G	B, P	FA	No discussion of taxonomy or morphology.
Capitellidae	*Capitella capitata*	*Rasmussen, 1956	Sy	N, P	F, L	Grassle & Grassle (1976) demonstrated a species complex.
Arenicolidae	*Arenicola claparedei*	*Okuda, 1938	G	B, P	F, I	Japan vs. Puget Sound.
		Guberlet, 1934	—	—	F	Found to be 2 species (Healy & Wells, 1959).
Serpulidae	*Pomatoceros triqueter*	*Gravier, 1923 v.	G	P	F, I	Short pelagic stage.
		Drasche, 1884	—	Br	F	

Nassariidae, Turridae, and Conidae. All major groups of opisthobranchs also have such genera (Thompson, 1976), as do many bivalves (the Teredinidae are just one example).

Several forms of reproduction occur in many genera of polychaetes, but especially those of the Capitellidae, Spionidae, Nereidae, and Syllidae (Mileikovsky, 1971; Wilson, 1928). Two kinds of development occur in the archiannelid genus *Protodrilus* (Schroeder and Hermans, 1975). Sipunculids of the genus *Golfingia* can undergo direct development or can release pelagic trochophores (Rice, 1967). In enteropneusts, direct and indirect development correlate with taxonomic grouping at the family level (Hadfield, 1975). Both sponges and tunicates can be oviparous or viviparous at various taxonomic levels (Fell, 1974; Berrill, 1975). Some species of ctenophores have brood chambers (Pianka, 1974). Nemertinea have species with pelagic and species with non-pelagic larvae (Riser, 1974); there are also several kinds of larvae in the polyclad flatworms (Henley, 1974).

Many crustacean genera have species with differing modes of development. For example, one abyssal family of decapod crustaceans contains a few species with pelagic young while most are benthic; the same is true in abyssal echinoderms (ophiuroids). As an example from decapods, both brooding and pelagic development are known in the genus *Sclerocrangon* (Makarov, 1918 in Mileikovsky, 1971). Many echinoderm genera including *Asterias, Asterina, Heliocidaris,* and *Echinocyamus,* as well as several ophiuroids, have more than one mode of development, usually viviparity and ovoviviparity (Mortensen, 1921).

Discussion

Most reports of poecilogony have been made by well-known and respected marine biologists, yet few reports have come from workers who are or were primarily systematists. The available data on poecilogony are scant. Nonetheless, examples have been quoted repeatedly in the literature, obscuring the speculative nature of the original reports. For example, Houbrick (1973) has been quoted to say that poecilogony occurs in *Cerithium,* but actually he did not find any evidence for it. He only suggested that researchers look for examples. The impression has been given that there are cases in which environmentally induced variation of the amount of yolk or nurse-egg material leads to different developmental stages at hatching (Clark *et al.,* 1979), yet we found no example in the literature that was backed by data. Clark

and Jensen (1981) stated "*If* hatching is controlled by exhaustion of nutrient reserves, then change of albumen content *could* provide a simple mechanism for extending or abbreviating intracapsular development in response to environmental change . . . even single egg masses *may* yield different larval types" [italics ours]. In support of the hypothetical statement are three references; one of these in turn cites a "personal communication," and the other two we judge irrelevant to the subjects of poecilogony and control of hatching. Jensen and Clark (1983) elsewhere use the pattern of development of the ascoglossan *Oxynoe antillarum* to distinguish it from *O. azuropunctata.*

Whether a particular species has two different types of larvae produced by the same female (at different times or from the same egg capsule) is the critical question. Thorson (1946) concludes that such cases exist, yet supports his statement with text describing *allopatric* populations. Hadfield (1972) states that in the vermetids ". . . some larvae from a single capsule will hatch with, others without, a velum. . . ," yet the only published account we have read is of veligers found in plankton samples (Hadfield *et al.,* 1972). In none of the cases in Tables I and II has a single female been proven to produce two kinds of hatching offspring, except when metamorphosis occurs within a day of hatching.

Production of viable offspring by parents with different types of reproduction (that is, individuals sharing a common gene pool) is sufficient to demonstrate poecilogony. Only two breeding experiments in polychaetes and two in gastropods have been attempted, and all are incomplete in that they lack published genetic data in the form of allozyme or other studies. It is particularly important that genetic data be included to test claims of geographic or seasonal poecilogony. Care must be taken in interpreting breeding data for opisthobranchs and other invertebrates that can possibly self-fertilize, and with all invertebrates that store sperm.

Circular reasoning is easy when analyzing cases of poecilogony. If one is inclined to believe that poecilogony occurs, an example of two types of reproduction in morphologically similar adults is taken on face value as poecilogony without rigorous systematic analysis. On the other hand, if one is inclined to doubt poecilogony, the same example is taken to demonstrate the existence of two species. We suggest that each putative case of poecilogony should be a flag to alert researchers to the need for careful systematic study, including anatomical and molecular genetical analyses. Studies on interbreeding are particularly important.

Taxa that retain the early larval stages, *e.g.,* the velum in mollusks, within an egg capsule are more likely to reverse the evolution of capsular development (Strathmann, 1978, 1979, 1985). A change between planktotrophy and lecithotrophy in polychaetes requires changes

in swimming setae and other features. Thorson (1950) correlated the proposed ecological plasticity of mode of reproduction in polychaetes with their cosmopolitan distributions; however, this result might well have been due to errors in polychaete systematics. Some early polychaete workers such as Fauvel had a rather broader species concept than we do today. In polychaetes, taxonomists have traditionally ignored reproductive and juvenile characteristics as taxonomic characters. Smith (1958) pointed out that to do so is to ignore potential reproductive isolation. He also emphasized that *mature* adult morphology should be used to compare species; this includes reproductive specializations such as the characters of heteronereids. *Nereis japonica* and *N. limnicola* differ morphologically at sexual maturity, but not in the non-reproductive state (Smith, 1958). Careful systematic work in gastropod taxa such as the Littorinidae, Rissoidae, and the Aeolidiidae have greatly reduced the number of potential cases of poecilogony (Heller, 1975; Rivest, 1978).

It is interesting that size of adults is bimodal in many mollusks and polychaetes thought to have poecilogony (*Littorina saxatilis, Tenellia pallida, Spio martinensis, Cirriformia tentaculata*). In every case, the smaller adults produce non-pelagic young; the larger adults produce pelagic young. Rather than invoking a shift in egg type with age or size, one can as easily hypothesize that different species are involved. Similarly, seasonal shifts in mode of reproduction might be explained by poecilogony (Mileikovsky, 1971 for *Littorina angulifera*), but the staggering of egg production by sympatric congeners is a common phenomenon in marine invertebrates and must be considered to be a viable alternative hypothesis.

Several theoretical papers have dealt with poecilogony, or with the problem of evolution of modes of larval development. Some (Vance, 1973a, b; Christiansen and Fenchel, 1979; Grant, 1983) conclude that there are dichotomous adaptive egg sizes, but these authors do not provide a model for the evolution of poecilogony within a species. Kishi's (1979) model of disruptive selection on offspring size (of fish) could be used to explain poecilogony as an intermediate stage in speciation for those taxa in which neither larval form possessed specialized structures. Many papers (*e.g.,* Underwood, 1974) do not clearly distinguish between intra- and interspecific variability in reproductive characters. Knowledge of the true extent of intraspecific variation in existing populations could illuminate proper theoretical approaches. Caswell (1981) was misled by erroneous examples of poecilogony given by Spight (1975) and Gallardo (1977) into overemphasizing the switching of a species from one form of development to another.

The theoretical advantages of poecilogony are often cited, *e.g.,* "Pelagic larvae are dispersed by tides and currents, exposing individuals to new habitats. Once estab-

lished, non-pelagic larvae produced by these newly-settled forms may rapidly establish large populations themselves . . ." (Blake and Kudenov, 1981, p. 181). The assumption is that a single genetic lineage can switch developmental mode to its best ecological advantage. In no case has such switching been demonstrated in the field or laboratory.

The rarity of examples of possible poecilogony in marine invertebrates is perhaps surprising, when we consider the theoretical framework for the concept. First of all, there *is* great intraspecific variability in other reproductive characters, such as brood size, fecundity, age at maturity, and sometimes, egg size (Brown, 1983). But these are all quantitative differences, while poecilogony is, by definition, a qualitative difference involving ecological as well as morphological differences. Secondly, the number of cases of congeneric reproductive differences shows the relative ease of evolutionary shift of reproductive modes. But reproductive change of the type required by poecilogony could lead quickly to reproductive isolation, if offspring of an intermediate type were dysfunctional.

Valentine and Jablonski (1982) theorized that a shifting proportion of individuals within a population with genetically determined longer or shorter larval lives was responsible for the evolution of mode of reproduction based on local selection. The mechanisms of nurse eggs and extracellular yolk would seem to provide a way to slide gradually from one reproductive strategy to another without dysfunction, yet we cannot demonstrate from available data that this is happening in any single population. Tests of the theory could be made using members of the prosobranch gastropod families Calyptraeidae with nurse eggs, the opisthobranch ascoglossans, the Vermetidae, and the spionid polychaetes.

Conclusion

Our literature review leads us to conclude that poecilogony is at best poorly documented as a phenomenon in marine invertebrate reproduction. The pattern of development is indeed a generally reliable species character in invertebrate systematics, and differences often signify unrecognized species. While shifts in egg nutrition by varying extracellular yolk or nurse-eggs is an attractive way to explain evolution of reproductive modes, we have no examples of facultative shifts occurring in modern populations, nor do we find clear examples of polymorphism in type of reproduction within a single population of marine invertebrates. Therefore it appears that shifts in mode of reproduction usually occur rapidly and completely within populations, leading to reproductive isolation and hence speciation.

One example of poecilogony in the literature appears to represent incomplete reproductive isolation in allopatric populations (*Elysia chlorotica*). Poecilogony in *Streblospio benedicti* could represent a recent contact between formerly allopatric, speciating populations. More breeding experiments are needed for *Tenellia pallida* and *Cirriformia tentaculata* to verify cross-fertilization in sympatric populations, but poecilogony is not ruled out. The fate of egg types in the natural environment must be known for *Boccardia proboscidea* to know if it is an example of adelphophagy, poecilogony, or both. One other possible type of poecilogony has been found: some species produce very short-term lecithotrophic veligers that metamorphose a few hours after hatching; sometimes some individuals hatch while metamorphosing (*e.g., Murex incarnatus*). All other cases of poecilogony in the literature have been disproven, or are not supported by sufficient data to judge them.

To support the hypothesis of poecilogony, at least one of three kinds of data is needed:

1) Genetic (allozyme) data for sympatric individuals, to see if interbreeding occurs between individuals with different larval types or if the individuals are fixed for alternate alleles and hence are *not* interbreeding.
2) A single individual observed in the laboratory to produce two types of larvae, *i.e.*, under varying environmental or nutritional conditions.
3) Cross-breeding data for normally allopatric populations, combined with allozyme or other molecular genetic studies, to show that (a) cross-fertilization occurred, (b) viable offspring were produced, (c) the offspring in turn are capable of breeding and reproducing with each other and the parental types, and (d) the cross-breeding event could plausibly occur in nature as well as in the laboratory. The heritability and genetics of mode of larval development need to be established.

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