

Poecilogony as a reproductive strategy of marine invertebrates

Poecilogony
Marine invertebrate
Reproductive strategy

Poécilgonie
Invertébré marin
Stratégie de reproduction

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ABSTRACT

Poecilogony is a polymorphism of sexual development in some marine invertebrates, in which both feeding and non-feeding or planktonic and benthic larvae are produced. Since the original report on poecilogony by Gaird in 1905, a good number of such species have been recognized. Upon close examination, however, Hoagland and Roberston (1988) have found that almost all the 64 species reported to be poecilogonous are in fact a result of miss-identification of species or due to laboratory disturbance. To be a poecilogonous species, a different mode of development has to be found from sibling offspring of a single female, or from different individuals of a single biological species, and the different modes of development cannot be altered by disturbance in laboratory handling. This being the case, there are only a few known species which are poecilogonous.

As a reproductive strategy poecilogony appears to have the advantages of both the commonly recognized patterns of development, short planktonic or benthic development (without planktonic larvae) and long planktonic development (broadcaster, with planktonic larvae). The former allows immediate recruitment to the parental habitats for fast population growth and the latter provides some degree of dispersal and gene flow.

In this paper, we briefly review the reproduction and larval development of three poecilogonous species (*Haminaea callidegenita*, *Streblospio benedicti* and *Capitella* sp.) and pose the following questions: 1) Why are the currently known examples of poecilogonous species found only in polychaetes and opisthobranchs? 2) Why are poecilogonous animals predominately located on mud flats? 3) If poecilogony is such a good reproductive strategy, why don't we see it in more species? We reasoned that polychaetes and opisthobranchs may be genetically predisposed for more flexible reproduction, and that the mud flat is among the most dynamic marine habitat, exerting greater selective pressure favoring polymorphism of reproduction than that of other habitats. We reasoned also that there may be more such species which can only be discovered through intensive and long term research on the reproductive biology of invertebrates on mud flats.

RÉSUMÉ

La poécilgonie, stratégie de reproduction des invertébrés marins - une discussion.

La poécilgonie caractérise les invertébrés marins dont le mode de reproduction présente diverses formes, avec le développement de larves, soit planctotrophiques ou lécitotrophiques, soit planctoniques ou démersales. Depuis la première description de la poécilgonie par Gaird en 1905, cette stratégie a été identi-

fiée chez de nombreuses espèces. Cependant un examen approfondi par Hoagland et Robertson (1988) a montré que, pour la plupart des 64 espèces signalées, la poécilogonie détectée résultait d'erreurs d'identification des espèces ou de biais expérimentaux en laboratoire. Pour qu'il y ait poécilogonie, il faut que l'espèce présente des modes de développement variables dans la descendance d'une même femelle, ou chez des individus issus d'une même espèce biologique, et les différents modes de développement ne peuvent être perturbés par des traitements expérimentaux. Dans ces conditions, il existe peu d'espèces douées de poécilogonie.

Comme stratégie de reproduction, la poécilogonie a les avantages des deux modes de développement communément reconnus : développement planctonique court ou benthique (sans larve planctonique) et développement planctonique long (avec émission d'œufs produisant des larves planctoniques). Le premier mode permet un recrutement immédiat à proximité de l'habitat parental et entraîne une croissance rapide de la population ; le second mode conduit à la dispersion des larves et favorise le flux génique.

Le présent article décrit brièvement la reproduction et le développement larvaire de trois espèces présentant de la poécilogonie (*Hamina callidegenita*, *Streblospio benedicti* et *Capitella* sp.) et pose les questions suivantes : 1) pourquoi les espèces les plus connues pour leur poécilogonie ne se trouvent-elles que parmi les polychaetes et les opisthobranches ? 2) pourquoi ces animaux sont-ils localisés surtout sur des laisses de vase ? 3) si la poécilogonie est une si bonne stratégie de reproduction, pourquoi ne l'observe-t-on pas chez un plus grand nombre d'espèces ?

La laisse de vase est l'un des habitats marins les plus dynamiques, exerçant la plus grande pression sélective en faveur du polymorphisme de la reproduction. Les polychaetes et les opisthobranches sont génétiquement prédisposés à ces modes de reproduction, comme probablement d'autres espèces qui ne pourront être identifiées que par des recherches intensives et de longue durée sur la biologie de la reproduction dans les zones envasées.

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INTRODUCTION

Poecilogony, the intraspecific variation of development among marine invertebrates (Gaird, 1905), has been the subject of considerable studies and discussions in recent years. The reasons for this enthusiasm can perhaps be attributed to the following: 1) Ecologists believe that developmental variation with both planktonic and benthic larvae will give added advantage which allows *in situ* recruitment as well as for greater gene flow through dispersal (Levin, 1984; Qian, 1991; Gibson, 1993); 2) Taxonomists believe that the pattern of intraspecific development is quite conservative and is a dependable species-level character in taxonomy (Bouchet, 1989; Hoagland and Robertson, 1988); and 3) People who work on life-history strategies are interested in poecilogony because it may enhance our understanding of the evolutionary relationship of different developmental patterns.

Only a few species are presently considered to be poecilogonous and they include both polychaetes and opisthobranchs. Many species which were previously thought to be poecilogonous have been proved to be wrong either because of miss identification or laboratory artifacts (Hoagland and Robertson, 1988; Bouchet, 1989). The purpose of this paper is to review briefly the reproductive biology of the poecilogonous species and to discuss the subject from an evolutionary standpoint.

Developmental patterns of marine invertebrates

Although a number of people have attempted to provide schemes of developmental patterns of marine invertebrates, it appears that there is no particular one acceptable by the majority of biologists (see review of Grahame and Branch, 1985; Levin and Bridges, 1995). It is perhaps instructive for the discussion in this paper to review the developmental patterns of marine invertebrates again.

Planktotrophic vs. non-Planktotrophic development:

Planktotrophic development means there is a planktonic larval phase which feeds on plankton. Non-Planktotrophic development may or may not have a planktonic larval phase and the larvae do not feed on plankton. Based on the larval diet, non-planktotrophic development can be further divided into: a) Lecithotrophic development in which larvae do not have a functional digestive tract and hence they do not feed; nutrient for development up to juvenile stage is derived mostly from yolk stored in the egg. These larvae may or may not be pelagic. b) Adelphophagic larval development is usually viviparous or inside egg capsules (feed on nurse eggs or siblings). c) Parasitic larval development which may be pelagic or benthic depending on the habitats of the hosts; they feed on the host tissue (Chia, 1974).

Planktonic vs. benthic development:

Planktonic development means there is a pelagic larval phase which ranges in duration from a few hours to many

months or even over a year. Larvae become pelagic either immediately after gamete release or as larvae hatching from a capsule or egg mass. They may or may not feed. Benthic development includes both feeding and non-feeding larvae. These larvae remain at the sea bottom, either brooded by their parents attached to the substrates or as demersal larvae.

Direct vs. indirect development:

Indirect development means animals with a distinct larval stage in their life history. Larval structures are lost (discarded or eaten or absorbed) during metamorphosis to the juvenile stage. Direct development means animals with vestigial larval structures or completely lacking a larval stage; development is a gradual transformation from embryo to juvenile.

The above classification provides a general overview of reproductive patterns of marine invertebrates. It is noted that some of the points are overlapping. In addition, our understanding of larval types is rapidly changing. For example, it was previously thought that yolk reserves are the only nutrient source for early development in lecithotrophic larvae. There is evidence that lecithotrophic larvae can increase in biomass during development and that the direct uptake of dissolved organic molecules (DOM) from the environment plays an important role during development (Jaeckle and Manahan, 1989; Manahan *et al.*, 1989). Among marine invertebrates, there have been a number of animals found without a digestive tract. In that case the required nutrient supply has to be dependent on dissolved organic molecules or through symbiotic organisms.

Poecilogonous species

The taxonomy of polychaetes and opisthobranchs is notoriously difficult and there are many sibling and cryptic species. For example Clark *et al.* (1979) reported that the development of the sacoglossan, *Elysia subornata* changes seasonally, planktotrophic in spring, lecithotrophic in summer, and intracapsular metamorphosis in the fall and winter. However, Clark's recent work has shown that the original observation was made on a complex of sibling species (Clark, pers. comm.). It is also known that variation in development can be caused by laboratory disturbance. For example, Carroll and Kemff (1990) found that the development of an *Aeolid nudibranch*, *Berghia verrucicornis* is poecilogonous if the embryo mass is cultured in the laboratory without aeration; both larvae and juveniles hatch from the same embryo mass. When aerated, only larvae hatch. These authors believe that poecilogony may occur in natural population although this remains to be tested.

To be absolutely certain about poecilogony one should either have evidence of the polymorphism of development among siblings from a single female and show that the developmental pattern cannot be altered by laboratory disturbance, or that the species must be identified by most reliable methods including cross-fertilization (Hoagland and Robertson, 1988). Based on this definition, a few species exhibit poecilogony including *Capitella* sp., *Haminæa callidegenita*, *Streblospio benedicti*, and two other small polychaete species.

Capitella sp.

This small tube-dwelling polychaete is found at the adjacent waters of Bamfield Marine Station at the West coast of Vancouver Island, Canada. The specific identification has not yet been resolved. However, much of the work on their reproductive biology was done on sibling individuals indicating that they are poecilogonous (Qian, 1991).

In one experiment, post-hatching siblings from a single female with planktotrophic development were reared in culture trays with filtered sea water at ambient temperature (10.3 ± 1 °C). These animals reached sexual maturity within three months and the reproduction of 249 animals reared in such a way was followed. Twenty-two of the 249 individuals produced large eggs (11.24×10^{-3} mm³) and each egg contained about 74.29 µJ energy. These large eggs underwent lecithotrophic development. The remaining 227 individuals produced small eggs and underwent planktotrophic development (Qian and Chia, 1992 a).

In another experiment sibling juveniles from a single female of lecithotrophic development were marked by a vital dye and were reared in cultural trays and some of the trays were placed in a mud flat, the natural habitat where the animals were originally collected. Growth rate, fecundity, egg size and egg energy content of the marked animal reared *in situ* were identical to those reared in the laboratory, both reached sexual maturity at three months. Of the total 162 individuals reared in such a way, 42 of them were observed to release eggs. Thirty seven of the 42 produced large eggs and underwent lecithotrophic development. Five animals released small eggs ($0.63 \pm 0.40 \times 10^{-3}$ mm³) with an average energy content 8.58 ± 1.65 µJ. The fecundity of these five worms was 6890 ± 3116 eggs (per worm) at their first spawn. These small eggs underwent planktotrophic development (Qian and Chia, 1994).

Besides to having the ability to switch from one type of development (planktotrophic) to another (lecithotrophic) within generations, *Capitella* sp. is extremely flexible in many other phenotypic characteristics such as survivorship, growth, sex ratio, fecundity, egg size, egg energy contents and generation time. These characteristics can easily be influenced by age, and quantity or quality of diet (Qian and Chia, 1991, 1992 a, 1992 b). In one of their experiment, Qian and Chia (1992 b) fed the worms by four types of foods which were prepared in an identical manner. The design of this experiment is as follows (Fig. 1).

This study showed significant differences among worms fed on different diets, as well as between worms of the two types of development. Worms of lecithotrophic development grew faster and became larger when fed on *Ulva*, produced more eggs when fed on *Nereocystis*, had larger eggs when fed on *Ulva* and *Zostera* and had higher energy contents/ egg when fed on *Zostera*. These worms became sexually mature at 120 days and 95 % of them became functional hermaphrodites. In contrast, worms of planktotrophic development grew faster when fed on *Ulva* and *Nereocystis*, had higher fecundity when fed on *Zostera*, and became sexually mature at an earlier age when fed on *Zostera*. Despite these differences egg size and energy content did not differ among worms fed on the four types

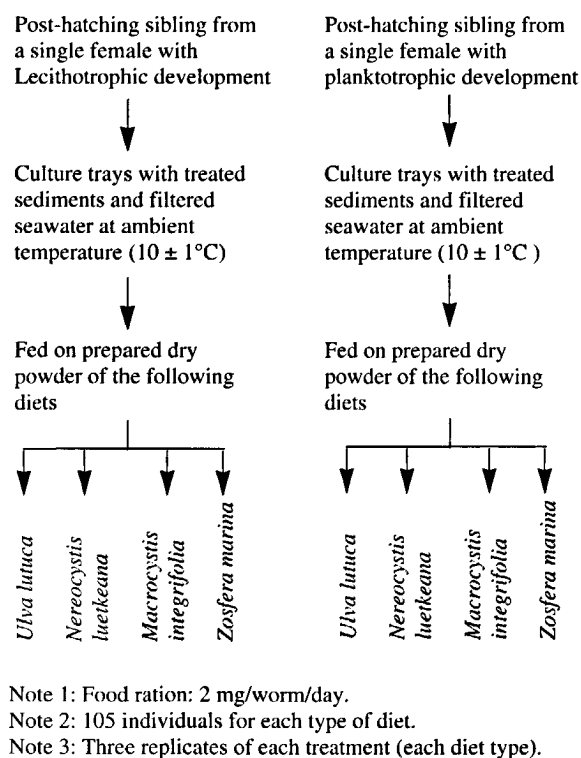


Figure 1

Flow chart of experiment design assessing effects of diet types on growth and the reproduction of *Capitella* sp., from Qian and Chia (1992 b).

of diets. As a whole, worms of planktotrophic development reached sexual maturity in 45 days.

Based on a series of experimental studies, Qian and Chia (1994) concluded: "The large variations in reproduction and growth of *Capitella* sp. should therefore be adaptive to accommodating whole sets of variation of environmental conditions. The uncertainty in environmental conditions may act as a selective force in the evolution of life history traits of *Capitella* sp."

Streblospio benedicti Webster

Streblospio benedicti is also a tube-dwelling worm, found on mud flats of the Atlantic and Pacific coast as well as in the Gulf of Mexico of U.S.A. They are also reported to occur in Europe and South America. The population of a given site often reproduces either lecithotrophically or planktotrophically (Levin, 1984) and development also varies among individuals of the same population (at least six populations on the Atlantic coast of the U.S.; Levin, pers. comm.). Traits of both development and larval types are summarized in the following Table 1. In at least one population from Bogue Sound North Carolina the planktotrophic and lecithotrophs are interfertile (Levin *et al.*, 1991).

Levin and Bridges (1994) also have summarized evidence indicating that environmental (food, temperature, day length) and intrinsic (age) factors can affect a number of traits in reproduction, such as survivorship, reproductive activity, body size/growth, egg size and egg number. But egg diameter, fecundity, larval packages period and some

Table 1

Developmental traits of Streblospio benedicti from Levin and Bridges (1994)

| | Planktotrophy | Lecithotrophy |
|-----------------------------------------|----------------------------------|-----------------------------------|
| <i>Ova</i> | | |
| Diameter (μm) | 60-70 | 100-200 |
| Volume ($\mu\text{l} \times 10^{-3}$) | 0.5 ± 0.06 | 3.08 ± 0.44 |
| C/embryo (μg) | 0.11 ± 0.03 | 0.85 ± 0.14 |
| N/embryo (μg) | 0.023 ± 0.003 | 0.17 ± 0.03 |
| $\mu\text{gC}/\mu\text{l}$ | 217.2 ± 48.0 | 279.7 ± 51.5 |
| $\mu\text{gN}/\mu\text{l}$ | 45.72 ± 4.67 | 57.62 ± 10.7 |
| <i>Larvae</i> | | |
| No./brood | 15-70 | 68-463 |
| No./brood pouch | 6-14 | 1-4 |
| Stage at release | 3-7 setigers | 8-10 setigers |
| Size at release | 250-300 μm | 550-650 μm |
| Swimming setae | Present | Absent |
| Planktonic period | 2-7 wk | ≤ 8 day |
| <i>Adults</i> | | |
| Lifespan | 38 wk | 30-75 wk |
| Age at first reproduction | 9-10 wk | 13-14 wk |
| No. broods/lifetime | ≥ 6 | ≥ 6 |
| Distribution (in USA) | Atlantic coast Gulf of Mexico | Pacific, Gulf, Atlantic coasts |

aspects of larval morphology also are controlled by genetic factors (Levin *et al.* 1991). Despite these development differences, demographic comparisons of planktotrophic and lecithotrophic populations revealed no differences in recruitment variation and population growth rate (Levin and Huggett, 1990).

Haminaea callidegenita

Haminaea callidegenita is a cephalospidean opisthobranch, found in seagrass beds and shallow lagoons in Washington U.S.A. Egg mass is spawned year-round (Gibson and Chia, 1991). Cylindrical egg masses, consist mainly of gelatinous muco-proteins with an average size of $15 \times 5 \times 5$ mm. Eggs are orange-yellow in color, 230×210 μm in diameter and are individually encapsulated. Eggs are arranged into a spiral string embedded in the jelly, each egg mass contains about 200-700 eggs, and the development follows a pattern similar to other opisthobranchs with lecithotrophic development. Well-developed veligers actively rotate within the capsule with propodium, heart, bilobed velum, operculum, statocyst, digestive glands, shell, and eyes. Hatching occurs 12 days after oviposition; both lecithotrophic veligers and juveniles are simultaneously released from 97 % of the egg masses examined.

Both planktotrophic larvae and juveniles hatch throughout the hatching period (3-11 days). About half of them hatch as planktonic veligers which will metamorphose after a swimming period of 1-30 days. This long period indicates clearly that they are not larvae which are released prematurely. The remainder of the siblings undergo intracapsular metamorphosis and hatch as juveniles. It is noted that juvenile hatching is highly variable among egg masses (4-100 %) and this situation is consistent among clutches, populations and years. Moreover, the percentage of hatching varies among populations (Fig. 2). The percentage of

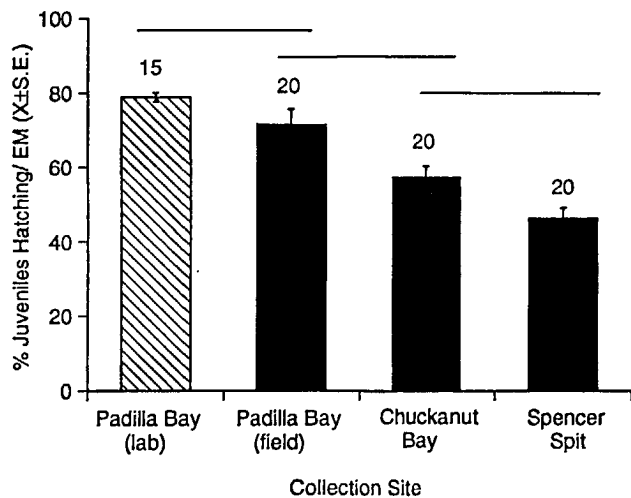


Figure 2

Haminaea callidegenita:

Percentage of juveniles hatching from egg masses collected at three natural populations 10-25 km apart (solid bars, including Padilla Bay, Chuckanut Bay and Spencer Spit) and from a laboratory population originally collected from Padilla Bay (hatched bar). Values are means and standard errors for each site, and sample size is indicated above each column. Horizontal bars indicate no significant differences were found between indicated groups from Gibson and Chia (1994).

hatching has been subjected to a number of experimental tests such as physical manipulation of egg masses and culture conditions and the result remains unaltered. In addition, the hatching percentage is not related to fecundity, female size, and seasonal changes (Gibson and Chia, 1994). Poecilogony in *H. callidegenita* is also influenced by parental environment. For example, food-deprived females produced more dispersive larvae than did control females (on continuous food ration) (Gibson and Chia, in press). One of the interesting findings is that the larvae can be induced to metamorphose by a diffusible compound in the egg jelly. A juvenile and adult food source (the green algae, *Chaetomorpha linum*) also can induce extracapsular larvae to metamorphose. The egg jelly inducer has been purified by using High Performance Liquid Chromatography (HPLC). It proves to be a small (less than 1000 Da), polar, non-proteinaceous, stable compound (Gibson and Chia, 1994). The percentage of offspring released as juveniles is highly variable, with variability estimated of 0.76 (Gibson, 1993).

Poecilogony also has been reported in a few other species of polychaetes, such as *Boccardia proboscidea*, and the *Cirriformia tentaculata*. Blake and Kudenov (1981) found

that *Boccardia proboscidea* produce two larval types within a single egg capsule; one is planktotrophic and the other feeds on nurse eggs and sibling larvae in the egg capsule, and hatching as juveniles. George (1967) found that a single brood of the polychaete *Cirriformia tentaculata* contained both free-swimming and demersal larvae (all lecithotrophic); the adults are morphologically identical.

Some Theoretical Consideration

Considering the general situation of poecilogony presented above, three questions can be asked: 1) Why are the currently known examples of poecilogonous species found only in polychaetes and opisthobranchs? 2) Why are poecilogonous animals predominately located on mud flats? 3) If poecilogony is such a good reproductive strategy as suggested by Levin (1984) and Qian and Chia (1992 b), why don't we see it in more species?

Both Levin (1984) and Qian and Chia (1994) have suggested that the success of the polychaete worms, mentioned in previous sections, are partially due to their reproductive flexibility. These worms share the following characters: small body size, infaunal, relatively short lived, tube dwelling, mud flat habitat, suspension or deposit feeders and with metropolitan distributions. On the other hand, the opisthobranch, *Haminaea callidegenita*, a new species described in 1989 by Gibson and Chia, is found so far only in three sites which all are mud flats; they are also a seasonal species. It is possible that these animals are all predisposed genetically for more flexible reproduction.

For the second question, we would like to suggest that mud flats are a very dynamic marine habitat with greater and more frequent fluctuation in temperature, salinity, oxygen, sediment and organic nutrient (including pollutant) that can exert intensive selective pressure which favors polymorphism of reproduction. With regard to the third question, there can be several answers. First of all, the so called "good strategy" is a term invented by biologists and may not be relevant to the animal. Secondly, there may be more poecilogonous species that remain to be discovered. Levin (1984), Gibson (1993) and Qian (1991) all spent long years at marine stations and studied intensively the reproduction of their animals. The poecilogonous nature of these animals could have not been discovered without such effort.

The direction of future studies of poecilogony should be focused more on genetic control of various reproductive characteristics such as studies by Gibson (1993), Levin *et al.* (1991) and Levin and Bridges (1994).

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