ELSEVIER

Journal of Experimental Marine Biology and Ecology
257 (2001) 109–115

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.nl/locate/jembe

Combined ecological factors permit classification of developmental patterns in benthic marine invertebrates: a discussion note

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Received 12 July 2000; received in revised form 9 November 2000; accepted 10 November 2000

Abstract

Traditional classifications of developmental patterns of marine benthic invertebrates are based on combinations of embryological (direct or indirect development) and ecological (such as nutritional source or habitat) characteristics. Different schemes have been proposed for different reasons, relating to ecology, evolution and/or development. However, these classifications contain interconnected characters that do not efficiently discriminate between developmental patterns and, thus, do not fully apply to either ecological or embryological studies. An ecological multifactor classification based on three independent two-state characters (pelagic/benthic, free/protected, and feeding/non-feeding) is proposed. It discriminates between eight developmental patterns and can encompass any ecological pattern of development among marine benthic invertebrates.

Keywords: Benthos; Brood protection; Ecological characters; Larva; Lecithotrophy; Marine invertebrates; Multifactor classification; Planktotrophy

Marine benthic invertebrates are often sessile or have only very limited adult mobility. For such species, a free larval phase can be of paramount importance for dispersal, and hence, for gene flow on which the spatial and genetic structuring of a species depends. These organisms display a great diversity in developmental patterns. This observation,

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0022-0981/01/$ – see front matter
PII: S0022-0981(00)00332-4

established since the middle of the nineteenth century, generated discussions on how to classify these different types of development (Thorson, 1950; Mileikovsky, 1971, 1974; Chia, 1974; Jablonski and Lutz, 1983; Strathmann and Rumrill, 1987; Wilson, 1991; McEdward and Janies, 1993). In these attempts at classification, developmental patterns have been characterised indifferently by embryological and/or ecological characteristics. Numerous classifications have been proposed to create a universal developmental scheme that would incorporate the variety of known developmental types (see Mileikovsky, 1974 for his 'world ocean-revised scheme'). Characteristics of particular taxa have led to a variety of specific classifications (e.g., bivalves, Ockelmann, 1965; molluscs, Simpson, 1977; ophiuroids, Strathmann and Rumrill, 1987; annelids, Wilson, 1991). Generally, four developmental patterns have been proposed, namely, planktotrophy, pelagic lecithotrophy, demersal development and brooding (including vivipary). However, this basic classification does not cover all existing variants; firstly, because of the diversity of the studied groups of marine benthic invertebrates, which can present individual peculiarities, and secondly, because of the differences in the scopes of the studies for which the classification is needed. The purpose of this note is to propose a scheme reflecting the whole range of variants for the classification of developmental patterns in marine benthic invertebrates.

From an embryological point of view, development is normally described with a distinction between direct and indirect development. In the latter, the embryo or 'egg' stage is followed by intermediate larval stages with structural features (mainly related to locomotion and nutrition) that are not involved in the morphogenesis of the juvenile. The so-called larval structures disappear during metamorphosis. When some nutritional and swimming structures known in other larvae are reduced or even absent, development is called abbreviated (see Strathmann, 1978; Emlet et al., 1987; Raff, 1987; Pearse et al., 1991 for echinoderms). Such a decrease in larval morphological complexity led some authors to consider what can be called a *continuum* spanning from typical planktotrophy to the absence of any larval stage (Raff, 1987; Raff et al., 1990; Olson et al., 1993). The complete absence of larval features and of metamorphosis proper characterizes direct development, also called ametamorphic development (Bonar, 1978; Schatt and Féral, 1996). The question arises as to whether or not this designation is valid for instances of larval features and related metamorphosis occurring *prior to hatching* from an egg case ('métamorphose abritée' *sensu* Portmann, 1955); see further below.

From an ecological point of view, developmental patterns are characterized by habitat and nutritional features. The ecological perspective allows an evaluation of the importance of this period in the life-cycle of the studied species, particularly for dispersal, survival and, more generally, for the evolution of life-history traits.

The purpose of any classification is to order objects (taxa, functional groups, patterns etc.) according to criteria that permit discrimination of the classified objects. To avoid inconsistency and ambiguity, the characters used for the classification must be independent from one another. Because ecological and physiological characteristics are related to morphological and/or to embryological characteristics, mixing different classes of characteristics leads to interdependency among characteristics. For instance, a morphologic character 'cilia' is not independent of nutrition, locomotion and/or pelagic life. To consider direct development as a character implies the non-feeding state of the character 'nutrition' to reflect the time the embryo spends in more or less complex envelopes and lives on yolk. However, this is a debatable issue with regard to cephalopods (Boletzky, 1974) that develop directly (living entirely on yolk reserves) and that mimic an ecological larval phase, i.e., as planktonic feeding (predatory) off-spring while some safety is provided by the remaining yolk reserves. The term 'paralarva', based on ecological criteria, was proposed to designate this phase in planktonic cephalopods (Young and Harman, 1988).

The traditional classifications were very heterogeneous in this sense, mixing embryological and ecological considerations. Characteristics such as pelagic development alluding to the habitat were opposed to embryological characteristics such as direct development or vivipary (Thorson, 1950; Mileikovsky, 1971, 1974; Chia, 1974). Given the need for character independence, classifications ought to be purely embryological, purely morphological or purely ecological. To avoid any bias, Simpson (1977) has proposed to restrict the dichotomy direct/indirect to embryological statements and, therefore, used only environmental considerations. Noting that, in traditional classifications, the developmental patterns cannot be mutually exclusive, McEdward and Janies (1993) proposed a multifactor classification for asteroid developmental patterns. However, the two-state characters used in their classification, namely direct/indirect, pelagic/benthic and feeding/non-feeding, are still based on both embryological and ecological considerations. Consequently, this classification remains heterogeneous and covers neither ecological nor embryological features entirely. Two major inconsistencies appear: (1) contrary to the statement of McEdward and Janies (1993), the characters they used are not independent. The category 'pelagic, feeding, direct development' is not possible for a direct developer that does not feed during the major part of its development. The same applies for the category 'benthic, feeding, direct development'. (2) A given pattern corresponds to very different types of development. For instance, the category 'benthic, feeding, indirect development' includes feeding demersal development and adelphophagy, the category 'non-feeding, benthic, indirect development' includes demersal lecithotrophic development and some protected developments, and the category 'non-feeding, pelagic, indirect development' includes pelagic lecithotrophy and floating capsules. Even if this classification was useful for asteroids, it cannot be generalised to other marine benthic invertebrates.

In the context of ecological studies, a way to improve the classification of developmental patterns in benthic marine invertebrates is to use characteristics that define the niche occupied by offspring during their development. Three two-state characteristics appear necessary. Developmental patterns are distinguished by habitat, using both the distinction (1) between pelagic and benthic development and (2) between free and protected development (from an ecological point of view, there is no difference between protected larvae and direct development), and by nutrition, using the distinction (3) between feeding and non-feeding development, or between endo- and exotrophy. We consider that extraembryonic nutrition by absorption is not to be taken into account at the same level as grazing. It is important to distinguish cases where the larva has to feed, through differentiated organs, from cases where the main source of nutrients is provided by the parents, either as yolk or in the form of nurse eggs (see further below). Even dissolved organic matter (DOM) is taken up through the mouth, i.e., by way of swallowing, in planktotrophic larvae as well as in adults (Féral, 1985).

In the three-dimensional representation of this multifactor classification (Fig. 1), eight

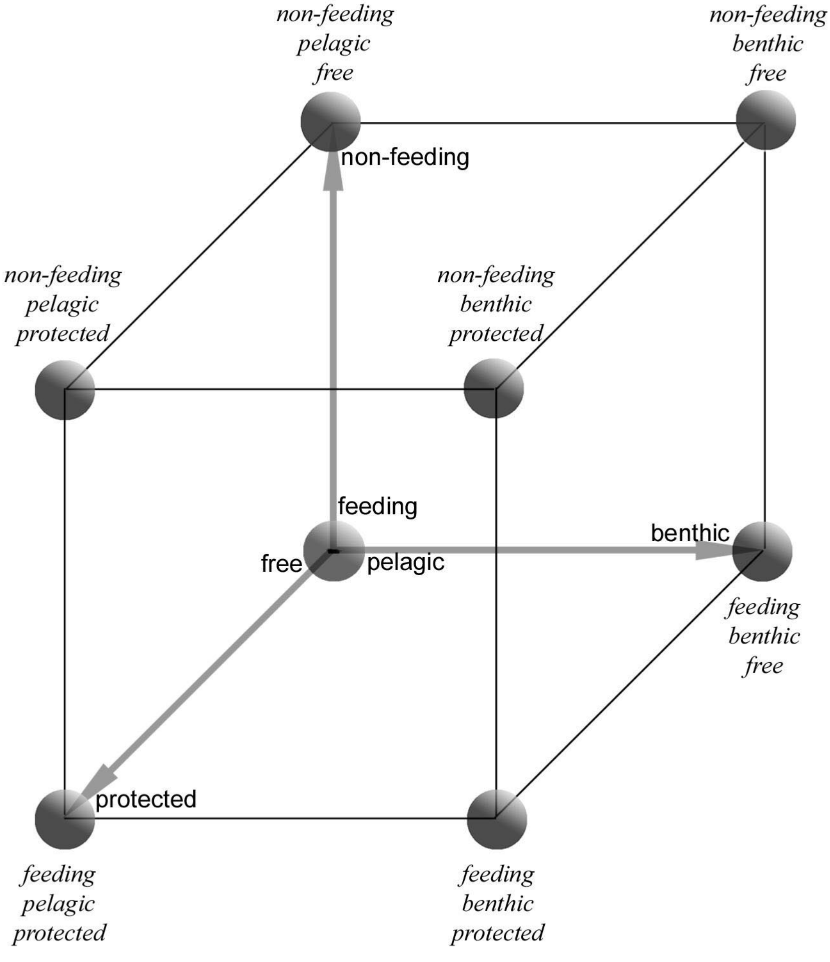

Fig. 1. Multifactor classification of developmental patterns in benthic marine invertebrates. The basic structure of the diagram is centered on the most frequently encountered (except in Antarctica) combination of free pelagic feeding conditions. The other seven corners of the diagram cube display all of the conceivable alternatives explained in the text.

different developmental patterns are distinguished, as marked at the corners of a cube, and each of them is characterized by one state of each of the three characters. These eight developmental patterns permit to describe each extant type of development in marine benthic invertebrates. If the overall scheme proposed here is operational for all taxa, the eight recognized patterns are not necessarily demonstrated for each taxon. Some of these developmental patterns fit fairly well the identified patterns of the traditional classifications. Indeed, planktotrophy corresponds to a free, pelagic and feeding development, and pelagic lecithotrophy to a free, pelagic and non-feeding development. Numerous examples, such as pluteus, brachiolaria, veliger or trochophora larvae, illustrate these widespread alternative developmental patterns in most of the marine benthic invertebrate groups. In the proposed classification, demersal development is characterised by a free benthic development, but corresponds to two different patterns following the distinction between feeding and non-feeding larvae. Indeed, some demersal larvae feed on the bottom (e.g. *Eupolymnia crescentis*, McHugh, 1993; *Yoldiella oblonga*, Hain and Arnaud, 1992) while others are lecithotrophic and develop by living exclusively on yolk reserves (e.g. *Asterina gibbosa*, McEdward and Janies, 1993; *Abarenicola vagabunda*, Strathmann, 1987; *Poromya adealides*, Hain and Arnaud, 1992).

Generally, protected development has been associated with brooding (internal and external) and with development in egg masses and in capsules. However, when using the ecological characteristics described above, protected development can fall under four different patterns. These patterns are discriminated on the basis of the respective dispersal capacities and feeding types rather than on heterologous criteria such as morphological features of supposedly protective structures (e.g. egg masses, egg capsules, brooding pouches etc.), embryological characters (direct and indirect development) or behaviour (parental care). Most of the examples correspond to a benthic, non-feeding development. Indeed, yolky eggs develop in egg capsules (e.g. *Arenicola marina*, Wilson, 1991, in egg masses (e.g. *Margarella antarctica*, Picken, 1979), inside the parental organism (e.g. *Leptosynapta minuta*, Becher, 1906; *Paraonuphis bermudensis*, Wilson, 1991), or simply externally, in brood pouches (e.g. *Abatus cordatus*, Verrill, 1876) or on the body of the parent animal (e.g. *Flabelligera mundata*, Wilson, 1991). On the other hand, capsules in some polychaetes and molluscs contain both nurse eggs and embryos. The latter develop into larvae that feed on nurse eggs (e.g. *Bocardia polybranchia*, Duchêne, 1989; *Searlesia dira*, Strathmann, 1987). This developmental pattern, termed adelphophagy, is thus characterised by a protected, benthic and feeding development. In some species, egg capsules float, and are thus found drifting in the surface water (e.g. *Laternula elliptica*, Pearse et al., 1986; *Axiothella mucosa*, Wilson, 1986). This corresponds to a supposedly protected pelagic development. The distinction between these different types of encapsulated development, often included by previous authors in categories like brooding or vivipary, is necessary in the context of any study about larval nutrition, dispersal capacity, population structure or gene flow measurements.

Most marine benthic invertebrates are viewed in relation to only one developmental pattern, but some species can develop through several patterns. This complexity corresponds to different situations. (1) In a single population, two developmental patterns can coexist. Here, the difference occurs at the individual level. (2) In some other species, this difference in developmental pattern is located at the population level. Indeed, such species exhibit differences between geographically isolated populations. These two cases correspond to poecilogony (see Bouchet, 1989 for gastropods). (3) More numerous are the species that develop through different successive developmental patterns. In such mixed strategies, offspring develop for some time in egg capsules or in other protective structures, and then emerge to spend some time as a pelagic larva before metamorphosing (Pechenik, 1979; Grahame and Branch, 1985). However, boundaries separating characteristics are not always well defined, as, for example, in facultative planktotrophy (Emlet et al., 1987). All of these additional developmental schemes do not require a more complex classification, as proposed by Wilson (1991), who counted 18 different patterns for Polychaetes. Indeed, these schemes are only a combination in space or in time of some of the eight developmental patterns of the multifactor classification proposed in the present article.

Our ecological classification of development is not a scheme that can cover all evolutionary/developmental aspects. It may, however, provide a basis from which to start to understand aspects of the evolution of larval development.

Acknowledgements

We thank Michel Bhaud and Philippe Bouchet for stimulating discussions and Jan Pechenik for his useful suggestions. We are also indebted to Raoul Taddei for the art work. This work was funded in part by IFRTP (Program 195). [RW]

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