Change from planktonic to benthic development: is life cycle evolution an adaptive answer to the constraints of dispersal?

ABSTRACT

Current research on recruitment of benthic marine invertebrates is, to a large extent, concerned with the consequences of larval planktonic development in water masses entailing dispersal, a milieu which appears unfavourable for a successful recruitment. In this paper, the origin of benthic development is tentatively considered as a response to the constraints of dispersal. Examples among annelid polychaetes are taken from personal work and from the literature. i) Life cycles in the subantarctic area provide good indications of a correlation between direct development and environmental pressure enhancing dispersal (due to turbulence and advection which would carry the planktonic larvae away from a suitable habitat). ii) Experimental analysis of the life cycle of _Eupolymnia nebulosa_ in the Mediterranean shows that gelatinous egg masses reduce the ability of larvae to spread and consequently increase retention in areas more suitable for the adults. iii) Examination of a large number of geographic sites where a very reduced habitat area is reported indicates that developmental patterns may involve weak dispersal to secure the return of larvae. From an evolutionary point of view, the direction of the transformation of life cycle patterns in the polychaete class may be inferred from the large number of solutions adopted by benthic development. The observations suggest that this pattern is derived. The case of _E. nebulosa_, which exhibits two developmental strategies, suggests also that the direct development found in populations of the Mediterranean Sea is a derived condition from the free development found elsewhere e.g. the English Channel. Evolution from benthopelagic development to benthic development is frequent, yet the reversion to planktonic development is also observed. We suggest that changes in the physical conditions of the environment disrupt and modify the life cycle; these unbalanced conditions may occur several times over the course of the evolution of a family.

RÉSUMÉ

Du développement planctonique au développement benthique : l’évolution des cycles de vie est-elle une réponse aux contraintes de dissémination ?

Les recherches actuelles sur le recrutement s’appliquent pour une large part aux conséquences du développement larvaire planctonique dans un milieu dispersif qui apparaît négatif pour un recrutement satisfaisant. A l’échelle de temps évolutive, ce couplage soulève la question de l’origine du développement benthique. On tente de montrer que ce type de développement chez les annélides polychètes est considéré comme une réponse aux contraintes de dissémination. Pour cette
démonstration on examine plusieurs situations tirées de nos propres travaux et de la littérature. a) Les cycles de vie de la province subantarctique fournissent une bonne corrélation entre le développement direct prédominant et les forces de dissémination extrêmement prononcées. b) L’analyse du cycle de vie de Eupoly­nia nebulosa permet de démontrer que les masses gélatineuses contenant les larves réduisent la capacité de dissémination de ces larves et empêchent la colonisation sur des zones défavorables au maintien des adultes. c) L’examen d’un ensemble d’espèces, caractérisées par une surface d’habitat très réduite, indique la nécessité d’une faible dissémination. Du point de vue évolutif, la direction de la transformation du type de développement peut être identifiée. À l’échelle de la classe des Polychètes, le grand nombre de solutions adoptées par le développement direct suggère une origine secondaire de ce mode de développement. Le cas particulier fourni par E. nebulosa avec deux stratégies de développement, suggère que le contrôle des larves en Méditerranée est dérivé par rapport au développement libre connu sur tout le reste de l’aire spécifique. Cependant cette direction d’évolution n’est probablement pas unique. Le retour vers le développement bentho-planktonique est aussi observé et l’on suggère que les variations des conditions physiques de l’environnement peuvent briser le cycle de vie et le modifier. Ce déséquilibre peut se produire plusieurs fois et dans des directions différentes au cours de la vie de la lignée familiale.

recognized. Three life-history patterns are available to reduce dispersal (Fig. 1): i) evolution towards benthic development through a reduction in, or the suppression of, the planktonic larval phase; ii) conservation of the benthoplanktonic life cycle but with behavioural adaptation of planktonic larvae (such as vertical migrations) or of adults during the reproductive period (such as timing and placing of spawning relatively to the tidal cycle); these reasons explain why benthoplanktonic development is still so frequent; and iii) evolution towards holoplanktonic life cycles. This latter solution of the dispersal problem seems paradoxical but it suppresses the transfer from one ecosystem to another during metamorphosis. All life history stages of a population are subject to similar transport conditions and may thus develop processes for schooling or aggregation (O’Brien, 1988; Alldredge and Hamner, 1980).

The idea of considering physical structures in the ocean to be important for success in the life cycle is not new from an evolutionary point of view. Sinclair (1988, p. 184) suggests that evolution to direct development is externally forced, in the oceans, by changes in the physical geography that disrupt the existing tight linkage between the morphological and behavioural cycles of the animal and the associated particular geography. Evolution may lead to holobenthic or holoplanktonic development. According to the same author, speciation in the oceans can be thought of as a repetitive contraction and expansion of complex life cycles in response to a nonequilibrium in the physical environment. The constraint of sexual reproduction is the requirement to find a mate in a dispersive environment and the process of life-cycle selection, in adjusting to such nonequilibrium conditions, results in speciation. Following this idea, it appears that it is possible to go back and forth from one type of life cycle to another. Two questions will be investigated: the role of spatial dispersal as a source of selection in the developmental pattern with a shift from complex development to holobenthic patterns; and the exclusive or non exclusive nature of this direction.

MATERIAL AND METHODS

The interaction between larval behaviour and the physical structure of water masses is increasingly well understood (Rothschild, 1988; Sinclair, 1988; Lefèvre, 1990; Kingford, 1990; Pineda, 1991) for many invertebrates but studies are still scarce for polychaetes. For instance, Sinclair (1988, table 6.1, p. 104) does not mention any studies describing retention of the pelagic stages in the life of benthic species among Polychaeta. This class is useful for comparison if we consider that, among the main groups of marine invertebrates, polychaetes exhibit the largest variety of strategies (Giangrande et al., 1994). The aim of this paper is to report on numerous situations in this group. To do so, we will use our own work carried out in both subantarctic and temperate areas. The detailed analysis of Eupolyphonidae nebulosa life cycle will be of prime interest for the present objective, which is to identify relations between physical structures of the environment and specific features of the life cycle. First we will examine the reproductive pattern in a subantarctic area where turbulence and currents are extreme; then we will describe a specific case (E. nebulosa) with an analysis of the relation between habitat size and pattern of development; and finally we will attempt to widen the scope by including a series of species for which habitat components and developmental patterns are known.

RESULTS

The Kerguelen Archipelago example

The hypothesis of the emergence of direct development patterns through constraints of dispersal is perfectly illustrated by the study of polychaetes from the Kerguelen province (Duchêne, 1983, 1989, 1992; Bhaud and Duchêne, 1988). Among species with known life cycles, development is most frequently direct with large-sized eggs. It is generally accepted that there is a relation between developmental pattern and egg size. The size limit is close to 100-
150 μm, smaller-sized eggs produce larvae with planktonic development. In Kerguelen the majority of species undergo direct development (Tab. 1) and egg size is 200, 450 and 600 μm in Amphicteis gunneri, Platynereis magalhaensis and Neoleprea streptocheaeta, respectively. On the other hand, eggs of Boccardia polybranchia reach a diameter of only 80 mm and we therefore expect to find indirect development. In fact development in B. polybranchia is accomplished in capsules enclosing 40 to 90 eggs (Duchène, 1984). Some eggs develop into fast growing larvae that feed on abortive eggs, while a few planktotrophic-like larvae are kept inside the egg mass until the opening of the capsule wall (Duchène, 1992). In this species, characteristics of indirect development are perfectly reflected with marked exotrophy, but spatial dispersal cannot take place. This situation is not a demonstration of evolution going from indirect to direct development, but provides a strong correlation between direct development and the presence of enhanced dispersive conditions. In the same area but for other groups, such as crustaceans, complex development is maintained. In this case an adaption for reduced dispersal is formed by holdfasts of giant kelp like Macrocystis and Durvillaea (Bhaud and Duchène, 1988). These examples of attachment of small eggs on a fixed structure not linked to the animals are a particularly good illustration of adaptation for reduced dispersal. That the oceanographic constraints in the Kerguelen Archipelago are characterized by strong currents and dispersal is demonstrated in Duchène (1989) and Gamberoni et al. (1982).

The Eupolymnia nebulosa example

The experimental study of several parts of the life cycle of this species reveals a means of counteracting dispersal. Populations are differentiated between the Atlantic and the Mediterranean Sea in terms of the existence, in the Mediterranean Sea, and absence from the Atlantic and the Channel, of a gelatinous egg mass in which larvae undergo direct development. This divergence is probably rather recent and connected with the history of the Mediterranean Sea (Lenaers and Bhaud, 1992). In the Bay of Banyuls, E. nebulosa is one of the most abundant species for which a large body of biological information is available. Its life cycle has been described (Bhaud and Grémare, 1988 and 1991) and experimental studies investigating settlement requirements have also been undertaken (Bhaud, 1988 a, b; 1990, 1991; Cha and Bhaud, 1991; Cha, 1994). Adults are collected in a narrow area, at the periphery of the Banyuls Bay. They inhabit a tube of coarse sediment formed at the interface between stones and the underlying sediment. Spawning occurs between March and the end of May, sometimes between the end of February and early June. Spawning activity is strongly rhythmic, four or five maxima are recorded each year. The highest spawning peak occurs around the last quarter to the new moon in April. In the laboratory the larvae have the ability to use the finest fraction of heterogeneous sediments present in the centre of the Bay of Banyuls: muddy sand from the Nephys hombergii community (Bhaud and Cha, 1994). However adult E. nebulosa are never collected in this community. How then can we reconcile the absence of the species in the axis of the Bay with successful settlement on the same substratum in the laboratory? We showed, by studying tube-dwelling juveniles in a hydrodynamic canal, that displacement of tubes built on soft substrates of the Nephys hombergii community may be different according to the thickness of the sediment. When tubes are arranged on a sedimentary bed as in the centre of the Bay, they are easily washed away by water currents. On the other hand, when tubes are anchored on a thin layer of the same sediment deposited on a hard substratum like at the periphery of the bay, they offer a higher resistance to the erosion by currents. In the first case a speed of 16 cm.s⁻¹ detaches the tubes, whereas in the second case a flow rate of 24 cm.s⁻¹, which is the upper limit of the flow reached in the canal, does not detach the tubes, (Cha, 1994; Bhaud et al., 1995). These results suggest that the role of gelatinous egg masses reduces the ability of larvae to spread and prevents colonization in the centre of the Bay. Even if larvae are able to colonize this bay, it does not appear desirable that they reach this area, which forms an unsuitable habitat for adults.

Development in specialized environments

In this part, we apply the situation of E. nebulosa Mediterranean populations (i.e. a reduced adult area) to other spe-

Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Egg diameter (μm)</th>
<th>Observations on larval development</th>
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<tbody>
<tr>
<td>Platynereis magalhaensis</td>
<td>450</td>
<td>eggs laid in a jelly mass inside the tube built on Macrocystis fronds</td>
</tr>
<tr>
<td>Amphicteis gunneri</td>
<td>200</td>
<td>no direct observations but likely existence of short planktonic life deduced from development of early juveniles</td>
</tr>
<tr>
<td>Thelepus extensus</td>
<td>210</td>
<td>spherical egg masses formed by the female and attached at the opening of the tube; several egg masses formed by one female</td>
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<tr>
<td>(formerly setosus)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neoleprea streptocheaeta</td>
<td>600</td>
<td>no jelly mass; incubation of embryos and larvae in the tube, hatching 20 days at 5° C after spawning; no free-swimming life</td>
</tr>
<tr>
<td>Flabelligera penningar</td>
<td>500</td>
<td>incubation of embryos and larvae in the mucus surrounding the female body</td>
</tr>
<tr>
<td>Boccardia polybranchia</td>
<td>80</td>
<td>adelphophagia and poecilogony; benthic individuals escaping from the capsules at stage of 10 to 18 setigerous segments</td>
</tr>
<tr>
<td>Cirratulus cirratus</td>
<td>500</td>
<td>larvae held between tentacular cirri; ciliated belt absent</td>
</tr>
</tbody>
</table>
cies. They inhabit a specialized topographical environment (bays, internal neritic zones, lagoons, hydrothermal vents, islands, fissured hard bottom) often coupled with a specialized ecological environment (determined by temperature, hydrodynamics, salinity). The high frequency of spawning mucilaginous structures in species inhabiting particular ecological zones supports the hypothesis of the need to control of dispersal in certain environments. For these species which inhabit an environment characterized by very peculiar ecological features, the reduction of dispersal is a prerequisite for the maintenance of populations (Tab. 2). This is the idea developed by Gibbs (1968) with regard to the study of development of Scoloplos armiger by Chapman (1965). The most important function of the cocoon in Scoloplos is thought to prevent the wide dispersal of the larvae (see also Plate and Husemann, 1991). The habitat of Scoloplos is restricted to fairly sheltered shores and thus it is probably advantageous to retain the larvae within the favorable conditions of the adult habitat. In the same way, Opheliidae (O. bicornis on the south-west coast of England or O. limacina in the Mediterranean Sea) are polychaetes living in a very restricted and specialized habitat (Harris, 1994): in clean and loose sand when the pelagic faction is totally absent, at high level in very shallow habitats in tide- or current-swept bays or estuaries. To ensure that larvae stay in this restricted habitat, planktonic larval life is short and does not last longer than 4-5 days.

The different situations shown in Table 2 may be shared in two kinds of topographic conditions: i) closed areas in which ecological situations are extreme, and where planktonic development does not exist or is present only in a small number of species, whereas benthic development is very varied, and among which egg masses are common; and ii) open sea areas with species developing with a short pelagic phase or with egg masses. With regard to the problem stated in the introduction – benthic development as a response to constraints of dispersal –, the question is to determine whether or not the benthic pattern of development is related to particular conditions of the specialized environment or to the limited dimension of the area in which these conditions occur. In other words, it seems necessary to define the role played by physical or biological structures sheltering larvae. Several advantages have been attributed to direct development: to make it easier to survive in a harsh environment (Vance, 1973a, 1973b; Christiansen and Fenchel, 1979; Wilson, 1986); to reduce energy expenditure which was thought to be high in the benthoplanktonic life cycle (Chia, 1976); to reduce the predation thought to be important during planktonic life (Pechenik, 1979); to allow gonad maturation in small-sized adults which are not able to form the minimum number of planktonic larvae required to balance loss by dispersal (Strathmann, 1982); and to prevent removing of juveniles from suitable habitats (Chapman, 1965; Gibbs, 1968). As far as we know, these various hypotheses are not supported by clear evidence even if the latter one is most likely. From situations given in Table 2, a precise and immediate answer is not possible because information on the habitat extent is not always given. However, three observations may be added. Firstly, for a part of the reported cases, particularly in the open sea or when lagoons develop large exchanges with the sea, restricted location is not associated with a modification of the environment bearing, for instance, on the concentration of organic matter or special salinity. Short planktonic life and egg masses have the same finality. This is an indication that control of dispersal is at the outset of the benthic developmental type. Secondly, when, for well known situations as for E. nebulosa or Scoloplos armiger, the length of the free developmental phase is placed in relation to the adult habitat, the physical dispersal appears negative for success of the life cycle and thus egg masses or short planktonic life are advantageous for the persistence of populations. Lastly, experiments and indirect deductions on the presence of spawning egg masses of E. nebulosa (Cha, 1994; Medernach, 1995) indicate that salinity inside the mucilaginous mass follows external conditions very quickly and that egg masses probably do not form an efficient barrier against sharp variations of salinity. These facts suggest that egg masses are more a protection against dispersal than against predation or variation of osmolarity.

Interestingly, the conclusion on the importance of spatial control of dispersal is in accordance with the findings of Swedmark (1959) who noted similar reproductive modifications to prevent horizontal dislocation in microfaunal species confined to a restricted habitat. Retention of larvae in interstitial water due to lack of reaction to light is considered by this author an absolute necessity for the survival of the populations on account of the low number of gametes.

Species living close to deep-sea hydrothermal vents are led to resolve two constraints which may appear conflicting: it is necessary to secure the survival of the population in this insular environment; but also to be able to colonize new vents as soon as they appear. For the first problem, and in the case of Paralvinella grasslei, the large size of eggs (maximum of 275 μm) is connected with lecithotrophic development which restricts dispersal. However, this adaptation seems insufficient and is completed by fertilization secured by the presence of spermatheca in females and seminal vesicles in males. These anatomical adaptations with the mating process diminish the dispersal of gametes. The presence of spermatothores in interstitial species probably has the same significance (Swedmark, 1959). McHugh and Tuniciliffe (1994) study the hydrothermal vent polychaete Amphisamymtha galapagensis (Ampharetidae); they point out that this species occurs in a wide variety of vent habitats and that reproduction is probably continuous, fertilization external, and larvae demersal and lecithotrophic. For the second problem, two possibilities have been suggested: influence of near-bottom currents and phoresy (Zal et al., 1995).

On the other hand, species developing a large habitat at great depth may have a long planktonic larval life. Thus a species of Poecilochoetaeidae reproduces by planktonic larvae (Bhaud and Cazaux, 1987). These larvae are always caught in the open sea and the surface water layer, never on the shelf, both in the Atlantic and in the Mediterranean. In the latter environment their distribution shows no sign of any concentration in a particular zone. This is probably a rare example among Polychaeta of a deep-sea species with a planktonic larval stage in the reproductive cycle.
Table 2

Developmental patterns for some Polychaeta species with a restricted adult habitat. This list is intended to be illustrative, not exhaustive. Additional examples are in Table 1 of this paper for the Kerguelen area, Table 9 in Gibbs 1968, Table XI in Bhaud and Cazaux, 1987. Note that several patterns of development are close to poecilogony but restrictions and criticisms provided by Hoagland and Robertson (1988) require a careful new examination. Two functions may be proposed for the egg masses: embryo protection, and (or) control of dispersal. The difficulty in distinguishing between the two arises from the fact that egg masses are often observed in reduced adult habitat areas with physico-chemical characteristics of water masses that are variable and different from the open sea. It is therefore interesting to focus attention on situations where these features appear separated (presence of egg masses in the open sea or absence of egg masses in lagoons).

<table>
<thead>
<tr>
<th>Species</th>
<th>Pattern of development</th>
<th>Nature of the adult habitat</th>
<th>Source</th>
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<tbody>
<tr>
<td>Nereis virens</td>
<td>eggs adhering to the sediment; max diam of eggs: 233; larval dispersal during 12 to 15 h; migration of young benthic stages to reach adult habitat.</td>
<td>muddy sand of protected environments with low hydrodynamism; nets of roots in salt marshes; mouth of rivers and estuaries.</td>
<td>Desrosiers et al., 1991 Caron et al., 1993</td>
</tr>
<tr>
<td>Neanthes japonica</td>
<td>two types, probably reproductively isolated; 1: small-egg type: 140-170 μm, embryos hatched as free-swimming trochophores; 2: large-egg type: 200-240 μm, embryos hatched as 3-setiger nectochaetes which did not swim.</td>
<td>type 1: larvae in river mouth; early development in the lower reaches of rivers when the epipods worm spawned after having been carried downstream; then larvae move upstream into the adult habitat with the rising tide. (optimal S: 19-34) type 2: juveniles and post-spawners within the intertidal sediment of the adult habitat (optimal S: 9-21).</td>
<td>Sato and Tsuchiya, 1991</td>
</tr>
<tr>
<td>Streblospio benedicti</td>
<td>eggs 115 μm diameter incubated in dorsal pouches.</td>
<td>estuaries.</td>
<td>Fonsèca-Genevois and Cazaux, 1987</td>
</tr>
<tr>
<td>Scolecolepis fuliginosa</td>
<td>Mediterranean sea: eggs spawned in a mucus bag.</td>
<td>exclusive salient feature of polluted areas; close to urban outlet</td>
<td>Guérin, 1974</td>
</tr>
<tr>
<td>Scolecolepis fuliginosa</td>
<td>Atlantic ocean: free eggs on the bottom.</td>
<td></td>
<td>Guérin, 1975</td>
</tr>
<tr>
<td>Ramex californiensis</td>
<td>eggs 270-330 μm deposited by females in capsules within the tubes.</td>
<td>rocky habitats in the Marin and San Mateo County; beneath aggregating tunicate colonies attached to large rocks in the low intertidal zone.</td>
<td>Blake, 1991</td>
</tr>
<tr>
<td>Alkmaria romijni</td>
<td>eggs 180 × 130 μm, retained in mucus between external wall of the female body and internal wall of the tube.</td>
<td>muddy bottom of the intertidal belt of Arcachon Basin; mesopolyhaline (5-35 %) lagoons in the same Bassin.</td>
<td>Cazaux, 1982</td>
</tr>
<tr>
<td>Boccardia proboscidea</td>
<td>eggs 100 μm (emerging stage 3 setigers) and eggs 150 μm (emerging stage + 5 setigers)</td>
<td>muddy sand (California) two reproductive patterns seem present in the same stations.</td>
<td>Woodwick, 1977</td>
</tr>
<tr>
<td>Boccardia polybranchia</td>
<td>eggs 70-80 μm; 90 eggs per capsule; emergence at 10-18 setigers.</td>
<td>sand and blocks; poecilogony: two reproductive patterns present in the same egg mass.</td>
<td>Duchène, 1984 and 1992</td>
</tr>
<tr>
<td>Malacoceros fuliginosus</td>
<td>benthic larvae and brood protection, poecilogonic when specific area considered.</td>
<td>small brackish basin, island of Elba, Mediterranean Sea.</td>
<td>Lardicci, 1992</td>
</tr>
<tr>
<td>Spio decoratus</td>
<td></td>
<td></td>
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<tr>
<td>Polydora ciliata</td>
<td></td>
<td></td>
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<tr>
<td>Nereis diversicolor</td>
<td>abolition of the planktonic step.</td>
<td></td>
<td></td>
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<tr>
<td>Perinereis cultrifera</td>
<td></td>
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<tr>
<td>Eupolympnia nebulosa (Mediterranean Sea)</td>
<td>mucilaginous egg-masses deposited by females at the opening of the tube.</td>
<td>a narrow belt at the boundary between rocky shore and first soft bottoms.</td>
<td>Bhaud and Cha, 1994</td>
</tr>
<tr>
<td>Eupolympnia nebulosa (English Channel)</td>
<td>Free development without egg-masses.</td>
<td>larger distribution in areas with mixed soft and hard (blocks) bottoms.</td>
<td>Bhaud et al., 1987</td>
</tr>
<tr>
<td>Nicolea zostericola</td>
<td>5 cocoons per female; 55 to 90 eggs per spawning, 188-238 μm for spawned eggs; 1-2 days benthic life from escaping to tube building.</td>
<td>holdfasts of Chondrus crispus, intertidal and sublittoral, mussel beds, migration or transport of larvae from the intertidal zone to the adjacent deeper waters.</td>
<td>Eckelbarger, 1974</td>
</tr>
<tr>
<td>Pygospio elegans</td>
<td>duration of brood protection dependent upon season; 12 segments for free planktonic larvae or development in egg-capsules.</td>
<td>sand bottom to about 2 m deep.</td>
<td>Hannerz, 1956</td>
</tr>
</tbody>
</table>
Axiothella mucosa

500-1000 eggs embedded in a gelatinous mass; 250-260 μm in diameter; juveniles assume a benthic existence when they crawl from the egg mass.

Naineris laevigata

eggs 240 μm in diameter spawned within thin ribbon gelatinous masses containing 500 to 1200 eggs.

Scoloplos armiger

one egg cocoon by breeding season and by female; from 800 to 4000 eggs produced by female.

Melinia cristata

eggs sink to the bottom, tend to stick together, adhere to the tubes of the parents, negative plankton tests for the larvae.

Natomastus latericeus

diam. 150 μm, lecithotrophic larvae with demersal behaviour.

Spirorbis spirorbis

maximum oocyte diameter: 225 μm embryos develop in strings; release of larvae at 6-10 days; pelagic stage more or less photonegative; larvae liberated around the moon's quarters.

Spirorbis spirillum

simultaneous hermaphrodite; brooding 2-20 larvae within opercular chambers; short period of planktonic behaviour (minutes).

Arenicola brasiliensis

Mucus cocoons are attached by a stalk for 4-5 days; egg number estimated 230 to 250.10³.

Parapronospio sp

small eggs (140 μm in diameter) large fecundity (3000-43000 eggs); no brood protection; planktotrophic larvae of 2 months.

Pseudopolydora paucibranchiata, Polydora ligni, Rhyhachopora arenicola, Streblopsis benedicti, Exagone laurei, Fabricia limnicola, Capitella sp

Italian coastal lagoon (Lago Fusaro) no special adaptation of life history strategies relatively to the open sea species.

Polydora ciliata, Priomospio multibranchiata, Pseudopolydora antennata, Genolytis rubiginosa, Leocrates chinensis, Ophiodromus pallidus, Cirriformia tentaculata...

fauna dominated by species with either a short-lived or no planktonic larval phase; rafting of adults may be an effective dispersal mode.

15 species among which 5 abundant or common: Crucigera zygophora, Phyllochaetopterus prolifica, Lumbrineris inflata, cirratulid sp1, spirorbid sp

typical representatives of reduced and variable salinity environments are absent; a good exchange with the sea gives rise mainly to the presence of marine taxa.

Polydora variegata

three-setiger larvae hatch from the egg capsules; the long diameter of the oval fertilized egg is 150-160 μm; egg string contains 300-1000 eggs; 800 to 5,700 eggs per batch; larvae are planktotrophic until 17-setiger stage (after 2 months at 15 °C).

Polydora variagata

散装 phase present in most species but always reduced.

Several species of nereids

dispersal phase present in most species but always reduced.

Phyllochaetopterus prolifica, Polydora variegata, Lumbrineris inflata, cirratulid sp1, spirorbid sp

typical representatives of reduced and variable salinity environments are absent; a good exchange with the sea gives rise mainly to the presence of marine taxa.

Severa! means of controlling larval dispersal.

Axiothella mucosa

interstitial and very shallow subtidal habitats.

Scoloplos armiger

brackish-water environments, lagoon of Acquatina.

Melinia cristata

lower beaches of estuaries; able to tolerate conditions of low salinity.

Natomastus latericeus

Acquatina lagoon, brackish water, coastal environment, 2 m depth, t °C: 10-32, S 10-40 °/o.

Spirorbis spirorbis

at low tide, in a series of interconnected shallow pools and drainage channels; attached on Fucus serratus and also on F. vesiculosus arranged in a narrow belt.

Daly, 1978

Knight-Jones and Knight-Jones, 1977; Doyle, 1974

Arenicola brasiliensis

colonizer on blades of the seagrass Thalassia testudinum; in shallow bays behind a barrier-island; seagrass bed: 300-600 m across.

Dinnberger, 1993

Parapronospio sp

exclusive occupant of organically polluted areas suffering depleted oxygen concentrations; subtidal areas.

Yokoyama, 1995

Pseudopolydora paucibranchiata, Polydora ligni, Rhyhachopora arenicola, Streblopsis benedicti, Exagone laurei, Fabricia limnicola, Capitella sp

mudflats and salt marshes inside southern California lagoons, isolated from one another by long stretches of sandy, high-energy coastline, support a preponderance of infanual species with brooding behaviour and reduced larval dispersal potential.


15 species among which 5 abundant or common: Crucigera zygophora, Phyllochaetopterus prolifica, Lumbrineris inflata, cirratulid sp1, spirorbid sp

oceanic seamount in the northeast Pacific; 510 km west of the Oregon coast; (colonization of seamounts must be re-examined; inclusion of tropical seamounts will probably lead to different results).

Parker and Tunnicliffe, 1994

present authors

Sato-Okoshi, 1994

Several species of nereids

estuaries.

Mettam, 1980

Severa! species of nereids

Phyllochaetopterus prolifica, Polydora variegata, Lumbrineris inflata, cirratulid sp1, spirorbid sp

boring into molluscan shells (scallops); in Okhotsk Sea: Abashiri Bay; small habitats in a large area; settlement during the drift-ice period; several means of controlling larval dispersal.
The sampling area suggests that this species is present at a depth of more than 1500-2000 m and lives on more or less homogeneous bottoms. At settling, the morphological organization of the larvae with more than fifty setigerous segments is very elaborate; this permits the use of a wide variety of sediment particles; consequently, the larvae can dispose of a large area for settling.

DISCUSSION

The direction of evolution and its persistence

According to prevailing opinion, the benthoplanktonic developmental pattern is probably the ancestral condition from which a developmental pattern emerged that is characterized by reduced dispersal ability and limited fecundity. Indeed, Agassiz (1874, p. 11) observed that "the higher we rise in the scale of animal life the more restricted is the number of offspring". Jägersten (1972) presented several arguments in favour of this opinion, among which is that the benthoplanktonic life cycle is spread over the whole phylogenetic tree of the metazoans. It is not the high number of species with planktonic development which forms the centre of the argument; there is no link between the frequency of a situation expressed by the number of species and its primary or secondary position on a genealogic axis. Rather, the representation of the benthoplanktonic pattern in nearly all phyletic lines forms the basis of the argument. Moreover, in several groups with a holobenthic life cycle, larval development reveals traces of features from the primary larva which are adaptations to pelagic life. We wish to add two arguments with regard to this evolutionary trend (cf. Mc Edward and Janies, 1993, for echinoderms).

a) In Polychaetes, benthic development uses a large number of solutions (Wilson, 1991; Duchêne, 1992; Bhaud, 1994; Premoli and Sella, 1995) such as: gelatinous egg masses outside the tube of the female, associated or not with this tube; brooding in the maternal tube, inside egg masses or capsules, or free; conservation of the initial number of eggs in each capsule, or decrease of this number by adelphophagy; incubation in dorsal brood pouches; larval not incubated in an individualized structure, but kept in the tube by adult tentacles; viviparity with fracture of the tegument. Accordingly, the large spectrum of solutions adopted by direct development can only be derived and leads us to propose an evolutionary direction from benthoplanktonic to benthic development.

b) From the precise situation furnished by the two strategies found in E. nebulosa it is possible to argue that the protection of larvae by mucilaginous masses in the Mediterranean Sea is secondary relative to free development. It has been proposed (Lenaers and Bhaud, 1992) that during the last Ice Age, relict populations survived during a period of generally low sea temperatures in the Mediterranean Sea. During subsequent global warming, E. nebulosa began a gradual colonization of Atlantic waters with development of the free larval pattern. However, three reasons prevent us from accepting this interpretation: i) populations from low latitudes are not affected by ice-age fluctuations (Scavotto, 1986; Ruddiman, 1990); ii) tropical populations of E. nebulosa do not produce brooding egg-masses (personal observations of J. D. Delgado, La Laguna, Canarias); and iii) the large geographical distribution area in the Atlantic, Pacific and Indian Oceans (Lang, 1986) in which mucilaginous masses have never been observed. It is more than likely that the Mediterranean pattern with control of larval dispersal is secondary. This pattern evolved during colonization following the salinity crisis of the Messinian (6.5-5.3 MY BP) (Hsü, 1972; Busson, 1990)

To illustrate the persistence or interruption of this direction, the Terebellidae are used once again. This family is an example which displays a secondary planktonic life and shows a remarkable heterogeneity in terms of developmental strategies and larval ecology. From this basis it is possible to separate species belonging to the genera Lanice and Loimia from all other species (Marcano and Bhaud, 1995). Representatives of these two genera exhibit a long planktonic larval life related to the presence of a thick-walled slime-tube (Fig. 2). This aulophore stage, probably a recent acquisition in terms of life style (the aulophore morphology being "neutral" in this respect), corresponds to a relatively late morphological stage which is benthic in other species of the family. This new feeding planktonic stage is not a return to the first pattern of the trochophore-metarotrophorganophore series, but represents a new developmental type with the addition of a planktonic phase during the postlarval or juvenile stage. However, with regard to the
dispersal process, there is a return to an ancestral phase. Accordingly, there is no definitive establishment of benthic
development. If the probability of an evolution from benthopelagic development to direct development is high,
taking into account the diversity of solutions in direct
development, return to benthopelagic development is also
observed, as in the case of Terebellidae. In either case,
changes in physical conditions may break the life cycle and
this disequilibrium may occur in several phases of the life
history of a family. Movement back and forth from one
type of life cycle to another may be possible, as is observed
in Terebellidae. To explain the secondary acquisition of
a dispersal stage by several species of this family, we do
not have a definitive theory. However, we suggest that
the extension of the planktonic phase acts to postpone and to
decrease settlement constraints which are exerted during
benthic settlement. If there is a decrease of settlement
constraints with age, as has been demonstrated for E. nebu-
losa (Cha, 1994), settlement at a late developmental stage
allows an increase of the area compatible with the presence
of the species. In such a context, it is not surprising that in
the Bay of Banyuls Lanice conchilega which postpone
planktonic life during juvenile development are collected
in four communities out of a total of seven. This is not the
first example of a secondary evolution. Westheide (1982)
described a new species of Hesionidae which he argued
convincingly to be an example of evolution leading from
the interstitial fauna, generally assumed to have originated
from larger forms living in other marine biotopes (West-
theide, 1987), to the macrofaunal mode of life.

Energy available and pattern of development

It has been proposed (Chia, 1976) that the main selective
force for shifting from feeding to non-feeding larvae (or
from bentho-planktonic to holobenthic) is the limitation of
energy for gamete production. The major part of energy
expenditure of an individual is threefold: maintenance (respi-
ration); growth; and gamete production. This third activi-
ity is the last to be provided with energy and it may there-
fore be limited. The animal has a choice, evolutionarily
speaking, in gamete production: it may produce numerous
small eggs or a small number of large eggs. This hypo-
thesis states that the shifting from planktotrophic to leci-
thotrophic development is due to the limitation of available
energy for gamete production. The condition for this shift
is that the energy for gamete production is at a minimum
and, in order to maintain a steady population state, the
reproductive strategy shifts to a more efficient way of
reproduction in terms of per unit energy cost, but incurs the
penalty of limited dispersal and mutation. For Chia (1976),
this means that in the long run, lecithotrophic development
is an inferior method of reproduction when compared with
planktotrophy. The question calls for three comments.

a) The choice, in terms of evolution, is not as straightfor-
ward as is supposed. The choice of direction must originate
from something; that means evolutionary trends towards
benthoplanktonic or holobenthic development are not
equally probable. Basically, the pattern of development
probably does not depend on the energy expenditure for
gamete production at the level of the organism as a whole,
but on the constraints of packaging energy in a variable
number of eggs.

b) Among Polychaeta, Bridges (1993) showed from meas-
suring reproductive investment in four developmental
morphs of Streblospio, that lecithotrophic development
involved twice the C and N investment in reproduction as
in the planktotrophic development.

c) Efforts to determine which reproductive pattern, plank-
trophy or lecithotrophy, uses more energy have yielded
equivocal results (Grahame and Branch, 1985; Strathmann,
1985). Grahame and Branch (1985) reported an equal num-
ber of works in both directions and concluded that there is
as yet no consensus as to whether lecithotrophy or plankto-
rophy require more energy from the parent. Grahame
(1982) from his work on Lacuna suggests that there may
be very little difference, and Grant (1990) raises the ques-
tion of whether there is a link between mode of develop-
ment and reproductive effort. In short, these works suggest
that there may be little overall difference in energy alloca-
tion between the two different modes of reproduction (see
also Reznick, 1992).

CONCLUSION

The constraint of dispersal is linked to the necessity of
returning to a suitable substratum for adult life. Accordin-
gly, a connection must exist between habitat area and the
duration of the planktonic larval stage. From the example
of E. nebulosa, the length of the planktonic larval life and,
therefore, the ability for dispersal, seem correlated with the
locally available area for the adults. To attempt a generali-
ization from this situation requires us to query, not the
absolute value of the length of the planktonic life, but the
meaning of this length integrated with all the elements for-
ming the life cycle. Against such a background a paradoxi-
cal result emerges. A species with a reduced distributional
area in terms of adult habitat and with a limited ability to
disseminate does not act differently from another species
with larvae which wander for several weeks in the plank-
ton without really leaving the adult habitat. It is a mistake
to argue from absolute values: number of days of larval
life, the supposed travelled distance, the mean current
speed, the use of a residual vector without taking the vari-
ability into account.

However the relation between habitat area and the length
of life of planktonic larvae is confused by the adaptation of
larvae to the hydrodynamic structures of water masses
(Boicourt, 1982; Christy and Stancyk, 1982; Rothschild,
1988). Through these adaptations, control of dispersal is
carried out without any relation to the size of the adult
habitat. The observation of a short larval life leads us to
suppose the probability of a control of dispersal and a
reduced area of adult habitat. We cannot however, infer the
reverse: a long larval life may be coupled with a large
adult area as well as a reduced adult area. The first situa-
tion allows the reception of a sufficient number of larvae
probably at the price of large loss by passing over the adult
area. The second situation occurs only when the physical
structure taken by larvae is developed on a large spatial
scale (Rothlisberg et al., 1983) and when retention process

has been selected for, by means of larval behaviour. The fundamental necessity in a life cycle is to secure mating; for that, in gonochoric species, the important point is not to reduce the ability to disseminate but to find the adult habitat or not to leave it. This goal is achieved by different strategies such as reduction of dispersal period and development of elaborate larval behaviour. Exploration of the polychaete life cycle leads to the identification of two sources for selection: one related to larval behaviour with control of spatial dispersal, the other related to reduction or suppression of dispersal. In both cases, larvae resist being swept along; even in the case of a long course, they are able by their behaviour, to control advective strength.

These conclusions are partly speculative and are based upon a relatively reduced amount of data, at least with regard to polychaetes. In this class, development and autonomy of larvae, implication of advection in the dispersal, are neglected fields of investigation. The interpretation of the selective advantages of the wide range of life cycles of polychaetes is, however, consistent with the literature on other marine forms. Excessive dispersal in an oceanic environment is a constraint to the persistence of benthic populations with specific adult substratum requirements.

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REFERENCES


344


