

Recruitment of soft-sediment infaunal invertebrates : the importance of juvenile benthic stages*

Guy BACHELET**

Abstract: Spatial and temporal variability of marine benthic communities depends, to a great extent, on the success or failure of recruitment, which is influenced itself by all the events that occur during the course of ontogenetic development. In species with a benthoplanktonic life cycle, several critical stages may be identified: (1) maturation of sexual products, (2) spawning, (3) planktonic larval phase, (4) larval settlement and metamorphosis, and (5) postlarval or juvenile stages. Invertebrates with a holobenthic life cycle do not undergo a larval phase nor metamorphosis, and the first free-living stages are benthic juveniles.

Settlement is often a transient phenomenon and settling organisms are usually found in the meiofaunal size range. Hence, the quantitative assessment of young bottom stages requires both small sieving mesh sizes and short sampling intervals, which explains, to a large extent, our lack of knowledge of settlement patterns of benthic invertebrates in the field. High mortality rates have been recorded during early benthic life of molluscs and polychaetes: 70-99% of the settled individuals disappear within about three months. This juvenile mortality is likely to be of the same order of magnitude as larval mortality in the plankton.

The growth rates of juveniles may be low, especially when settlement coincides with adverse thermal and/or nutritive conditions; in such a case, juveniles may stay within the meiofaunal-size class for several weeks or months. Estimates of production and annual P/\bar{B} ratios in populations including the juvenile stages show that the productivity of benthic macrofauna is considerably underestimated by using only 1 mm-sieves.

1. Introduction

The dynamics of natural marine benthic communities primarily results from two antagonistic processes: (1) the supply of larvae, and (2) the mortality which occurs during the whole benthic life of settled organisms. As it is generally agreed that marine invertebrates experience extremely high mortality during the early stages of their life history (THORSON, 1950), the maintenance as well as the balance of composition of benthic assemblages depend, to a great extent, upon the survival/mortality ratio of larvae and juveniles (PÈRES, 1971; MILEIKOVSKY, 1974a). Hence, most of the temporal variability of benthic communities may be ascribed to the success or the failure of recruitment.

Recruitment is not, however, a true life-

history stage, but is observer-defined (KEOUGH and DOWNES, 1982; BUTMAN, 1987); it is rarely measured at the time of larval settlement, but instead when settled organisms have survived and grown to a size collected by some sampler (HADFIELD, 1986). Therefore, the number of recruits present at a given time reflects all past events since the elaboration of gametes in the parental organisms. In his pioneering work on larval ecology of marine bottom invertebrates, THORSON (1950) stated that the heavy waste found in most marine invertebrates takes place during the free-swimming, pelagic larval life. He later (THORSON, 1966) acknowledged that survival rates after settlement might be extremely low. This implies that the causes of recruitment variability must be researched, not only during the larval period, but also during the early post-settlement period. Recent studies conducted within the framework of the French National Program on the Determinism of Recruitment

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**CNRS & Institut de Biologie Marine, Université de Bordeaux I, 2 rue du Professeur Jolyet, 33120 Arcachon, France.

have provided quantitative data on juvenile populations of infaunal molluscs and polychaetes. The present paper summarizes some of these data, which emphasize the importance of the early benthic stages as a comprehensive tool for recruitment studies.

2. Critical phases in the life histories of marine benthic invertebrates

The life history of every animal species includes several successive stages (gametes, embryos, larvae, juveniles, adults) which are more or less well protected against external factors. Since our purpose is to identify

some critical phases in the ontogenetic development of marine invertebrates, it may be useful, before going further, to specify some definitions. TURNER *et al.* (1986) draw attention to some problems of terminology dealing with embryos and larvae, because these stages may be defined morphologically or ecologically. In a morphological sense, an embryo is an early developmental stage which precedes the first distinctly recognizable, immature form—the larva. Ecological definitions were given by GIESE and PEARSE (1974), focusing on the location of the developmental stages: embryos are stages which develop

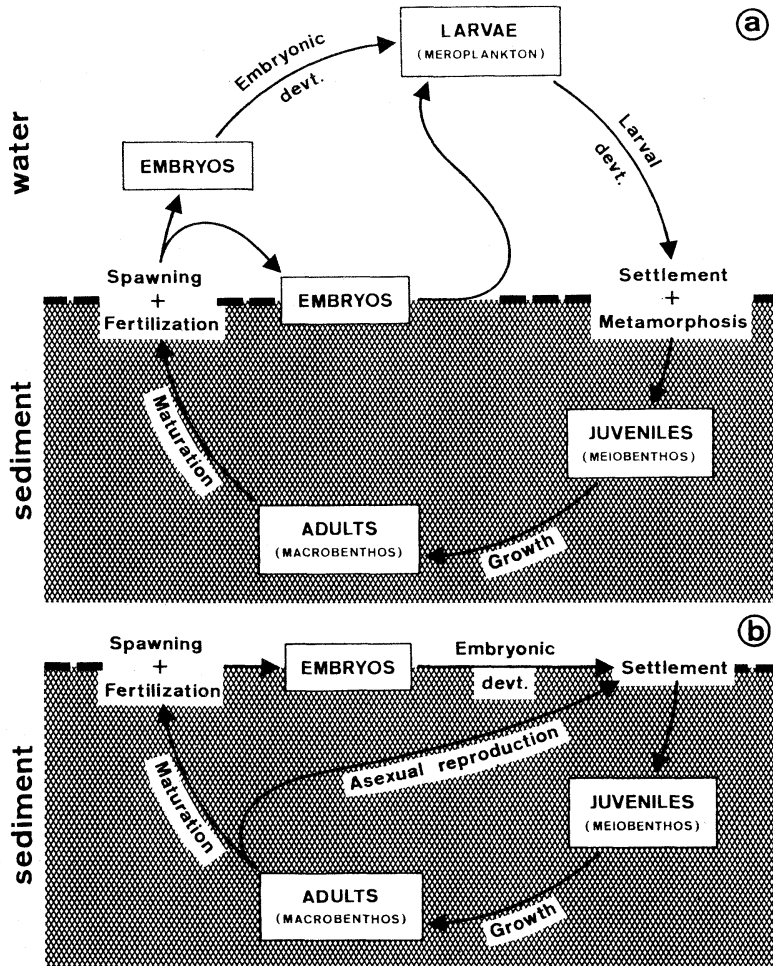


Fig. 1. Diagrammatic representation of the ontogenetic development of marine infaunal macroinvertebrates with (a) bentho planktonic or (b) holobenthic life cycle.

Fig. 1. Schéma du développement ontogénique des invertébrés de l'endofaune marine à cycle de vie ventho planktonique (a) ou holobenthique (b).

within the parent, egg mass, or egg membranes, whereas larvae are free-swimming stages, which pass through a metamorphosis to form the juveniles. HERMANS (1979) also underlined the difficulty in distinguishing between larvae and embryos in polychaetes. For example, in species whose gametes are freely liberated in seawater, HERMANS (1979) thought that there was not a true embryonic stage, but instead a lecithotrophic larval stage which may or may not, be followed by a planktotrophic larval stage before metamorphosis.

The ability to move freely is a criterion, both morphological and ecological, which facilitates clearer distinction between larvae and embryos (CAZAUX, 1981). This property will be used in our definitions. An *embryo* is an immature, prelarval form possessing two main characters: (1) lack of motility, and (2) inability to survive spontaneously after separation from the protective structure in which it normally develops. Hence, the term "embryos" may be applied to: (1) the stages which develop within the parent or some other protective structure (shell, egg capsule, etc...) until hatching, and (2) the early cleavage stages, when fertilization occurs in seawater, until the appearance of the first larval swimming devices. In the former case, embryonic development occurs at the expense of the female parent or through yolk reserves, and may last a relatively long time; in the latter, the embryonic period is relatively short. A *larva* is an immature, free-living stage, which is morphologically and biologically different from a juvenile or an adult and ends with metamorphosis; it is able to live outside any protective structure, and feeds on yolk reserves (lecithotrophy) or plankton (planktotrophy). *Juveniles*, or *postlarvae*, are recently settled organisms, possessing adult organs and behavior; their maximum size is usually limited by the smallest screen of the observer.

Attempts to categorize the types of larval development in marine benthic invertebrates have been proposed by various authors (THORSON, 1950; MILEIKOVSKY, 1971, 1974b; CHIA, 1974). These classifications may be redressed

in accordance with the appearance of larval stages (as defined above) and the type of developmental environment. Two main types of life history are now distinguishable: (1) species with a benthoplanktonic developmental cycle, and (2) species with a holobenthic developmental cycle (Fig. 1).

Species with a benthoplanktonic life cycle develop through pelagic larval stages of varying durations (Fig. 1a). In some species, development is entirely pelagic: fertilization of gametes, embryonic and larval development occur in the water mass. Other species undergo a partially pelagic development, with embryos protected within egg masses or brooded by the parents, before hatching of larvae. This type of life cycle is analogous to the 'pelagic development' described by MILEIKOVSKY (1971, 1974b). According to CAZAUX (1981), the 'demersal development' proposed by MILEIKOVSKY will be considered here as a particular case of pelagic development, because demersal larvae possess some swimming ability which may have an effect on their dispersal by water currents. The larval planktonic phase ends with a period of competence during which larvae are capable of settling if the appropriate environmental cues are encountered (CAMERON, 1986). SCHELTEMA (1974) defined settlement as the termination of the pelagic existence and the assumption of a sedentary life; it is a behavior, presumed to be under nervous control. The loss of swimming ability is more or less concomitant with metamorphosis, which refers to morphological and physiological changes (destruction of larval organs, differentiation of adult structures), through which a larva is transformed into a juvenile (SCHELTEMA, 1974; CHIA, 1989). As noted by BURKE (1983), settlement is a repeatable process, whereas metamorphosis is an irreversible phenomenon that happens only once in the life of an individual.

Species with a holobenthic life cycle have no free-living developmental stages (Figure 1b). The embryo gradually differentiates to the adult form without distinct stages, and hatches directly into a completely formed juvenile that begins its independent existence in the same benthic habitat as the adult.

Unlike the benthoplanktonic species, there is no metamorphosis in holobenthic species; they retain only the behavioral phase of settlement. Several developmental patterns of marine invertebrates are involved in this type of life history (MILEIKOVSKY, 1971, 1974b): (1) direct development, where embryos develop up to juvenile bottom stages inside protective egg capsules released by the parents into the bottom environment; (2) ovoviviparity (*sensu* TURNER *et al.*, 1986), where complete development up to juvenile occurs within the parental organism, without any tissue connection; (3) germiphory, or external gestation, which is known for example in syllid worms (*Exogoninae*); (4) asexual reproduction.

The distinction between these two types of life history is important as far as methodology is concerned: benthic samples will allow the collection of all the developmental stages of holobenthic species, whereas sampling of the complete cycle of benthoplanktonic species requires both plankton and benthos samples. Moreover, environmental and biological constraints are not the same for developmental stages that remain on the bottom and for larvae that undergo a change in habitat.

During the course of species development, several stages are decisive for the maintenance of benthic populations. In macrofaunal organisms with benthoplanktonic life-cycle, there are at least five such crucial stages: (1) maturation of sexual products, (2) spawning, (3) planktonic larval life, (4) larval settlement, and (5) postlarval growth, as observed from the time of settlement to a size large enough to be retained by sieves used for macrobenthos studies. The intensity of settlement is dependent upon the availability of larvae. This supply of larvae is directly influenced by mortality during the pelagic stages and by larval transport, but also by the fertilization success, and, ultimately, by the reproductive effort of adults. Unlike species with a benthoplanktonic developmental cycle, direct development and ovoviviparity are generally considered as processes ensuring good protection from predators and unfavourable environmental conditions (THORSON, 1946, 1950), and limiting dispersion of young stages. However, PECHE-

NIK (1979) found several examples where egg capsules were ineffective against predation.

3. Sampling the juvenile stages

In soft sediments, two conditions must be fulfilled in order to quantitatively sample the juveniles (WILLIAMS, 1980): (1) using sieve sizes small enough to retain the smallest settled individuals, and (2) sampling at short time intervals.

The inadequacy between settling sizes of marine infaunal invertebrates and sieving sizes used in most macrobenthic studies was stressed by THORSON (1966) who noted that about 2/3 of macrofaunal species settle on the substrate as temporary members of the meiofauna. However, THORSON used a sieve with 2 mm mesh opening to separate macro- and meiofauna, which is larger than the 0.5 or 1 mm meshes currently used in modern studies. Size at the time of settlement was reassessed from literature data for a number of infaunal bivalves and polychaetes (Fig. 2). These data show that nearly all bivalve species settle with a shell length <0.5mm; most of them are even smaller. In polychaetes, size spectrum at settlement is rather wide (up to 3 mm) when size is measured as body length. Nevertheless, worm morphology is such that body length greatly exceeds body width in most species; a size spectrum drawn with body width shows that settling polychaetes cannot be retained by meshes >0.5 mm if they fall vertically over the sieve. Therefore, sieve screen sizes >0.5 mm are too large to retain newly settled individuals of most invertebrate species. BACHELET (1990) suggested that sieves with 0.1–0.2 mm mesh openings should be used in studies involving population dynamics of macrofauna, to provide an adequate estimate of juvenile abundances.

Another important bias source in recruitment studies is the frequency of sampling (LUCKENBACH, 1984): the time between settlement and sampling must be as small as possible, due to the transience and unpredictability of settlement patterns. LIVINGSTON (1987) provided direct evidence that sampling at monthly or quarterly intervals might obscure the weekly variations of environmental and biological

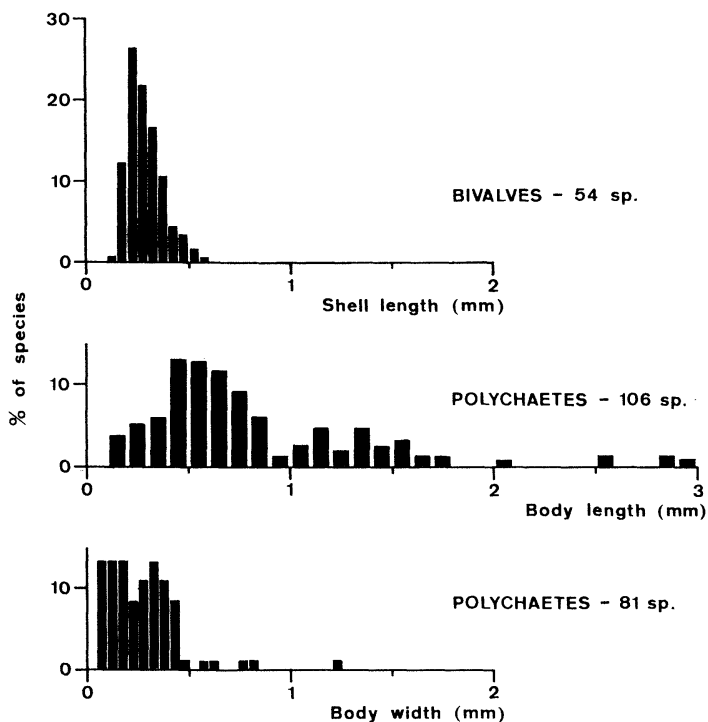


Fig. 2. Size spectrum of marine infaunal bivalves and polychaetes at settlement. In bivalves, shell length was measured along the antero-posterior axis. In polychaetes, size spectrum is shown both for body length, measured from the anterior end of prostomium to the posterior end of pygidium (palps and urites excluded), and for body width, measured at the widest segment (setae excluded); larval stages which stay on the bottom most of the time (nectochaetes, erpochaetes, etc.) are here regarded as the first benthic stages. Histograms drawn from literature data (references are available upon request to the author).

Fig. 2. Spectre de taille des bivalves et polychètes de l'endofaune lors de la sédentarisation sur la substrat. Chez les bivalves, la dimension retenue est la longueur de la coquille, mesurée selon l'axe antéro-postérieur. Chez les polychètes, le spectre de taille est représenté en considérant soit la longueur du corps, mesurée entre l'extrémité antérieure du prostomium et l'extrémité postérieure du pygidium (appendices non compris), soit la largeur du corps, mesurée au niveau du segment le plus large (à l'exclusion des soies); dans ce dernier phylum, les stades larvaires passant une grande partie de leur temps sur le fond (tels que nectochètes, erpochètes, etc.) ont été considérés comme les premiers stades benthiques. Les histogrammes ont été tracés à partir de données de la littérature (références disponibles auprès de l'auteur).

(including recruitment) data in estuarine habitat.

4. The extent of juvenile mortality vs. larval mortality

To a large extent, our lack of knowledge of settlement patterns of benthic invertebrates in the field is likely to result from sampling biased towards small sizes. It is clear that

densities of juveniles can be assessed only through specific benthic sampling schemes, focusing on the "temporary meiobenthos". Such a study was conducted in an intertidal mudflat located in the polyhaline zone of the Gironde Estuary, SW France. In order to obtain quantitative, reliable data on early post-settlement survival of infaunal macro-invertebrates, sampling was performed at

fortnight intervals using a 100 μ m sieving mesh size (see BACHELET, 1987, for further details on sampling methodology). In this low-diversity estuarine community, nine species showed clear recruitment patterns from which juvenile mortality rates could be determined; they included five polychaetes (*Nephtys hombergii* Aud & M. Edw., *Nereis*

diversicolor O.F.Müller, *Polydora ligni* Webster, *Pygospio elegans* Claparède, *Streblospio shrubsolii* (Buchanan)), three bivalves (*Abra tenuis* (Montagu), *Cerastoderma edule* (L.), *Macoma balthica* (L.)), and a gastropod (*Hydrobia ulvae* (Pennant)). As reproduction (and settlement) period extended over several weeks in most of these species, juvenile

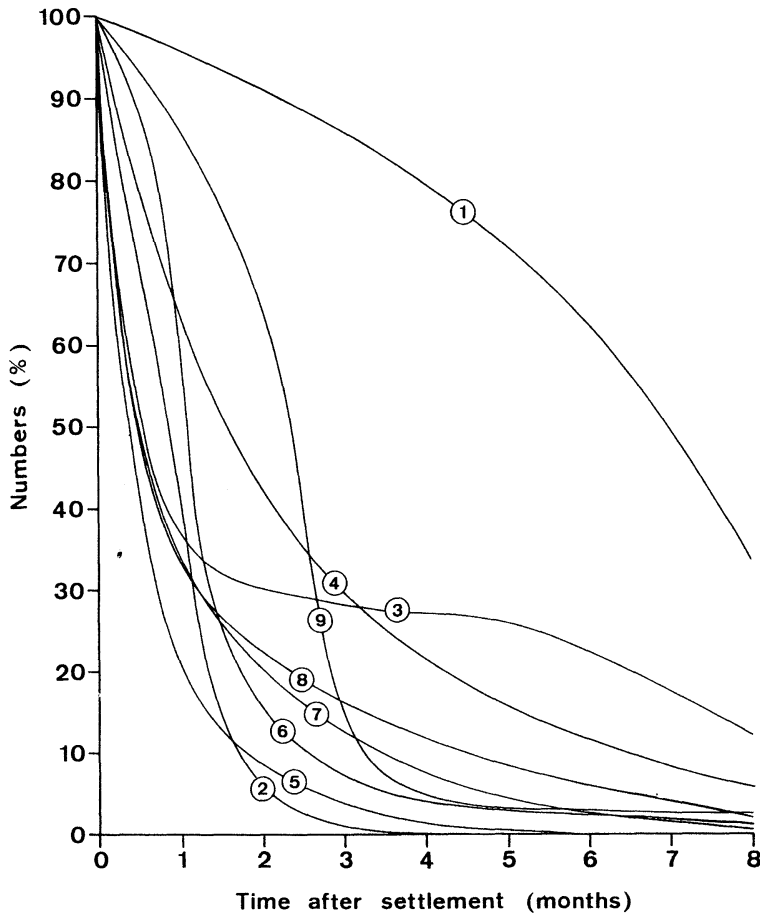


Fig. 3. Survival curves of some infaunal species from an intertidal mudflat of the Gironde Estuary. Seven species have a benthoplanktonic life cycle: development is entirely pelagic in *Nephtys hombergii* (1), *Cerastoderma edule* (2), and *Macoma balthica* (3), and partially pelagic in *Nereis diversicolor* (4), *Polydora ligni* (5), *Pygospio elegans* (6), and *Hydrobia ulvae* (7). Direct development (i.e., holobenthic life cycle) occurs in *Streblospio shrubsolii* (8) and *Abra tenuis* (9).

Fig. 3. Courbes de survie des principales espèces endogées d'une vase intertidale de l'estuaire de la Gironde, établies à partir de l'installation des juvéniles sur le sédiment. Sept espèces présentent un cycle benthoplanktonique, avec un développement soit entièrement pélagique (1: *Nephtys hombergii*; 2: *Cerastoderma edule*; 3: *Macoma balthica*), soit partiellement pélagique (4: *Nereis diversicolor*; 5: *Polydora ligni*; 6: *Pygospio elegans*; 7: *Hydrobia ulvae*). Un développement direct (c'est-à-dire un cycle holobenthique) se rencontre chez *Streblospio shrubsolii* (8) et *Abra tenuis* (9).

mortality was only assessed for the most easily distinguishable cohorts. Figure 3 shows the decrease in population densities from the time of maximum settlement as a function of (benthic) age. For eight species, 70–99% of the settled individuals disappeared within three months, and only 1–13% of them survived the first eight months of benthic life (*C. edule* totally collapsed after 4 months in this site). In some species, the largest loss occurred during the first month after settling when the density decreased by 42% in *P. elegans*, 57% in *C. edule*, 65% in *M. balthica*, *H. ulvae*, and *S. shrubsolii*, and 80% in *P. ligni*.

The survival curve of *Nephtys hombergii* notably diverged from the pattern found in other species (Fig. 3). Actually, biometrical data suggested that *Nephtys* larvae settled subtidally, then migrated to the intertidal (BACHELET, 1987); therefore, the survival curve in Figure 3 might represent the survival of juveniles some weeks old, after a secondary

recruitment.

Although different cohorts may have a different survival rate depending on whether they stem from early or late spawnings, our data show two important features:

1/With the exception of *Nephtys hombergii*, the mortality rates recorded during the early benthic period are high and the bulk of the population of settled juveniles is decimated within 2–4 months. These data are consistent with previously published estimates (Table 1). In a *Venus*-community in the Øresund, Denmark, THORSON (1966) also estimated that approximately 98.6% or even more of the young, settling on the bottom, died during the post-larval period; in a study of eleven species of bivalves in the same area, MUUS (1973) found post-larval mortality rates of 67–100% for all species.

2/Juvenile mortality is of the same order of magnitude, whatever the type of development (see Fig. 3). Assuming a low mortality rate during embryonic development in species

Table 1. Summary of literature data on post-settlement mortality rates of marine infaunal invertebrates. Only studies involving sampling with sieving mesh sizes small enough to retain early juveniles are included.

| Species | Mortality rate % | Period after settlement (months) | References |
|-------------------------------|---------------------|--|-------------------------------|
| Polychaetes | | | |
| <i>Nephtys hombergii</i> | 90 | 4 | SMIDT(1951) |
| <i>Nereis diversicolor</i> | 99 | 3 | " |
| <i>Lagis koreni</i> | 96 | 2 | KIRKEGAARD(1978) |
| <i>Myriochele oculata</i> | 96 | 8 | " |
| <i>Nephtys hombergii</i> | 97 | 12 | " |
| <i>Scoloplos armiger</i> | 99 | 9 | " |
| <i>Nereis diversicolor</i> | 99 | 3 | MÖLLER(1985) |
| <i>Polydora ligni</i> | 90 | 2 | LAMBECK and VALENTIJN(1987) |
| Bivalves | | | |
| <i>Macoma balthica</i> | 95.4 | 5 | ANKAR(1980) |
| <i>Tapes japonica</i> | 57 | 2 | WILLIAMS(1980) |
| " | 90 | 6 | " |
| " | 98.8 | 9 | " |
| <i>Cerastoderma edule</i> | 91 | 6 | MÖLLER and ROSENBERG(1983) |
| <i>Mya arenaria</i> | 98 | 6 | " |
| Echinoderms | | | |
| <i>Dendraster excentricus</i> | 88 | 12 | CAMERON and RUMRILL(1982) |
| <i>Amphiura filiformis</i> | 90 | 8 | DUINEVELD and VAN NOORT(1986) |
| " | 97 | 9 | " |

with a holobenthic life cycle implies that fecundity and/or fertilization success must be higher in species with benthoplanktonic life history to compensate for embryonic and larval mortalities during the pelagic phase.

Although mortality of the larval stages is supposed to be enormous (THORSON, 1950), very little is known whether mortality is greater during planktonic larval development or during the post-settlement period. Actual estimates of larval mortality are rather rare in the literature because of the obvious technical problems of following a cohort of larvae in the plankton (HINES, 1986). Moreover, some of these estimates are conflicting. For example, high mortality rates during larval life have been found in bivalves with high fecundity: 98–99% in *Ostrea edulis* (KORRINGA, 1941), about 98% in *Crassostrea gigas* (QUAYLE, 1964), 97.4% from the straight-hinged to the setting stage of *Mercenaria mercenaria* (CARRIKER, 1961), 98.5% in *Mytilus edulis* (JØENSEN, 1981). On the other hand, BHAUD (1979) calculated high survival rates during the planktonic phase of three Mediterranean polychaetes: 50–60% in *Lanice conchilega*, about 50% in *Poecilochaetus serpens*, and 44–53% in *Mesochaetopterus minutus*; he also noted that these figures were probably underestimated because of larval emigration and displacement of water masses, and hypothesized that larval mortality rates might actually be only 30% for these species.

In addition to methodological problems, several reasons make reasonable estimates of larval mortality rates difficult to obtain; (1) the rate of mortality is unlikely to remain constant throughout larval life (SCHELTEMA, 1986), (2) the longer the larval life the higher the mortality by predation and/or starvation (THORSON, 1950; CHIA, 1974), and (3) disappearance of larvae may be due to mortality as well as passive transport out of the area of investigation. Nevertheless, the existing data do not support THORSON's (1950) view on the prevalence of pelagic events over post-settlement processes in the mortality of early life history stages. Mortality rates of benthic juveniles are likely to be within the

same range of values as mortality rates of pelagic larvae.

5. Growth rate and production of juvenile benthic stages.

Although these points are not directly related to the determinism of recruitment, it is interesting to point out some recent results about the individual growth rate during the juvenile phase and the contribution to production estimates of young bottom stages.

In her study of growth of young bivalves in the Øresund, MUSS (1973) found very low growth rates during the first year after settlement which disagreed with previous data on the same species. Such a depressed growth was also found in some intertidal and shallow subtidal molluscs by BACHELET (1986, 1987, 1989), BACHELET and YACINE-KASSAB (1987), and MADANI (1989). These observations could be made only because the small size of the sieving mesh which was used allowed the collection of the juveniles as soon as they settled. The size frequency distributions gained with a coarse sieving mesh are biased by a methodological truncation against the smaller sizes, and the juveniles may remain hidden from the macrobenthologist during several weeks or months. For example, BACHELET (1989) showed that the very slow growth rate of *Abratenuis* during its initial benthic life caused the bulk of newly settled animals to remain within the meiofaunal size range for almost 1 year; in this special case, the numbers recruited into the macrobenthos (i.e., the numbers established by census with standard sieve sizes of 0.5–1.0 mm) were thus a consequence of events extending over a considerable period.

Other reasons may be set forth to explain low growth rates during the juvenile phase. In bivalve populations from northern areas, low seawater temperatures may depress growth (MUUS, 1973). In more southerly situations, it has been shown (BACHELET, 1986, 1987) that some cohorts of juveniles might experience a slow growth rate during settlement in adverse thermal and nutritive conditions: in the Bay of Arcachon, autumnal

cohorts of *Abra alba* showed low growth rates, similar to those found by MUUS (1973) in Danish waters, whereas the growth was faster for cohorts which settled in spring and summer, when phytoplankton concentration was high (MADANI, 1989).

In marine macrofaunal studies, the computation of secondary production is usually restricted to the macrobenthic phase of organisms. Estimates of the "true" production of a macrofaunal population over its whole lifespan should, however, include production of both larvae and juveniles (WARWICK, 1980). Because larvae usually settle in very high numbers and survival rates and biomass are often low in juveniles, high production and production/biomass ratio may be expected in early benthic life. Comparison of figures calculated according to size-selective sampling methods (sieving mesh ≥ 0.5 mm) or with techniques allowing the capture of juveniles

(sieving mesh < 0.5 mm), showed that the former results in an underestimate of the annual P/B ratio (Table 2). Using a mesh size too large to retain small benthic stages was previously suspected to overwhelmingly bias production estimates in macrobenthos (ROBERTSON, 1979; WATERS, 1979). Table 2 shows, in any case, that estimates of production based on literature values must be treated with caution and that annual population P/B are probably higher than it is usually accepted in macrobenthic species.

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Table 2. Estimates of annual P/B ratios in some populations of benthic marine molluscs. Values are compared between populations sampled with 0.5-1 mm mesh and populations with juveniles included.

| Species | Sieving mesh size (mm) | P/B ratios (yr ⁻¹) | References |
|---------------------------------|------------------------|--------------------------------|--|
| <i>Abra alba</i> (Wood) | 0.5-1.0 | 1.3-3.4 | Review of literature data by DAUVIN (1986) |
| | 0.2 | 7.5-17.0 | MADANI(1989) |
| <i>Abra ovata</i> (Philippi) | 1.0 | 1.2-2.5 | GUÉLORGET and MAZOYER -MAYÈRE(1982) |
| | 0.2 | 0.9-4.2 | MADANI(1989) |
| <i>Cerastoderma edule</i> (L.) | 10.0 | 1.1-2.6 | HIBBERT(1976) |
| | 0.2 | 2.2-21.0 | MÖLLER and ROSENBERG(1983) |
| <i>Mya arenaria</i> L. | 0.7 | 2.5 | BURKE and MANN(1974) |
| | 0.2 | 2.0-13.5 | MÖLLER and ROSENBERG(1983) |
| <i>Hydrobia ulvae</i> (Pennant) | 0.5-1.0 | 1.1-1.8 | Review of literature data by BACHELET and YACINE-KASSAB (1987) |
| | 1.0 | 0.9-4.8 | BACHELET and YACINE-KASSAB (1987) |
| | 0.1 | 5.1-6.1 | (1987) |

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Résumé: La variabilité spatio-temporelle des peuplements benthiques marins est, en grande partie, conditionnée par la réussite ou l'échec du recrutement, qui est, lui-même, la résultante de l'ensemble des événements intervenant à tous les stades du développement ontogénique des organismes, depuis la phase de reproduction. Chez les espèces à cycle de vie benthoplanctonique, plusieurs étapes critiques peuvent être identifiées: (1) la maturation des produits sexuels, (2) la ponte, (3) la phase larvaire planctonique, (4) l'installation des larves sur le substrat et leur métamorphose, (5) la phase postlarvaire ou juvénile. Dans le cas des espèces à cycle de vie holobenthique, il n'existe pas de phase larvaire au sens strict, donc pas de métamorphose, et les premiers stades libres sont des juvéniles benthiques.

La sédentarisation des larves s'effectue dans la phase dimensionnelle du méiobenthos, et il s'agit d'un phénomène souvent fugace: l'évaluation quantitative des jeunes stades benthiques nécessite donc une méthodologie contraignante (finesse des mailles de tamisage pour l'extraction du sédiment, fréquence rapprochée des échantillonnages) qui explique, dans une large mesure, notre méconnaissance de la phase postlarvaire. L'application de cette méthodologie a permis de mettre en évidence l'importance du taux de mortalité des juvéniles, qui atteint rapidement des valeurs élevées: 70-99% des individus disparaissent ainsi dans un délai voisin de 3 mois après leur installation sur le sédiment. Cette mortalité juvénile est probablement du même ordre de grandeur que la mortalité larvaire dans le plancton, alors que cette dernière a longtemps été considérée comme déterminante pour les fluctuations du recrutement.

Les taux de croissance des juvéniles sont, par ailleurs, parfois très faibles, en particulier lorsque l'installation des cohortes coïncide avec de mauvaises conditions thermiques et/ou trophiques; dans ce cas, la population de juvéniles peut rester durant plusieurs semaines ou même plusieurs mois au sein de la phase méiobenthique. Inversement, les taux de renouvellement de la biomasse (rapports P/\bar{B}) des populations sont très élevés si l'on incorpore les stades juvéniles dans les estimations de production.