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Co-ordination of the pelagic and benthic life history phases in marine benthic invertebrates: two examples from the Polychaeta.*

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Abstract: An introduction is presented of work carried out in the French marine station at Banyuls (Mediterranean coast) within the framework of the French national programme (PNDR) concerned with determining the factors that effect recruitment. Two terebellid polychaete species have been chosen as suitable models for recruitment studies: *Eupolymnia nebulosa* (Montagu) producing spawning egg masses and larvae with a short pelagic phase, and *Lanice conchilega* (pallas), free spawning with a long planktonic stage. The suitability of these species particularly for laboratory experimentation is discussed. Laboratory and field observation of the recruitment processes in these two species shows that: a) *E. nebulosa* larvae have weak dispersion capabilities which promote retention of the larvae in the vicinity of the adult habitat, and at least at one location, the synchronisation of the release of spawning egg masses with appearance of macroalgae which provide nursary areas for young juveniles appears to be important in controlling recruitment suceess; b) *L. conchilega* larvae with long planktonic development appear to be retained close to the adult habitat by local hydrodynamic mechanisms.

1. Introduction

The success or failure of larval settlement on the bottom is a critical feature in the maintenance of benthic invertebrate populations and to a large extent controls the temporal and spatial variability of the adult stages. Experiments in the field are, however, of limited value in the description of the actual events occurring during settlement. In-laboratory experimentation is therefore obligatory, to interpret the likely effects, on the small scale, of hydrodynamics and biological processes.

This paper provides a brief introduction to, and temporary synthesis of, work carried out by researchers in the French marine station of Banyuls (Mediterranean), in collaboration with the marine station of Archachon (Atlantic coast) and within the framework of the PNDR (a national program concerned with determining the factors that effect recruitment). More detailed results of this work are contained in the following publications; BHAUD and DUCHÊNE, 1989; BHAUD and DAUVIN, 1990; BHAUD, *et al.*, 1990.

One major programme directive requires the study of model species preferably species which are well known in term of their ecology and reproductive biology. In the two laboratories above, work is being carried out on the Polychaeta, more specifically, two species of Terebellidae: *Eupolymnia nebulosa* (Montagu) which produces spawning egg masses and larvae with a short planktonic stage (3–15 days), and *Lanice conchilega* (Pallas) which is free spawning and has a long planktonic stage (>3 weeks). Information on the basic biological features of these species can be found in BHAUD (1988 a and b; 1990 a and b).

In addition to work on model species, a project to provide quantitative and comparative field data on recruitment of the principal species in a muddy sand *Nephtys hombergii* community and in a fine sand *Spisula subtruncata* community in the bay of Banyuls, is in progress. The aim of this study is to tract settlement and early post-settlement recruitment in a number of species, especially with regards to post-settlement mortality rates. A pluridisciplinary approach has been adopted with the intention of producing an integrated model of the main physical and biological processes occurring during the spring recruitment period in the study area.

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The following results obtained from the study of *Eupolymnia nebulosa* and *Lanice conchilega,* are presented to highlight some of the more important recruitment processes in the two species.

2. Suitability of *Eupolymnia nebulosa* and *Lanice conchilega* as model species for study.

Eupolymnia nebulosa.

A laboratory study of the settlement behaviour of *Eupolymnia nebulosa* on different sediments has been carried out both in still water and using a hydrodynamic canal (BHAUD, 1990b; CHA, 1990). Laboratory experimentation on *E. nebulosa* has several advantages: a) the number of available larvae for each experiment is always high enough to allow the utilization of a container with a large volume of water, approx. 60 litres; b) this container, in the form of a self-circulating canal, facilitates the passage of water over removable plates which can be covered with various substrates; c) the duration of each experiment, 2 to 5 days, show final settlement distribution patterns and not just the initial arrival of larvae at the bottom; d) easy observation of larval tubes facilitates accurate monitoring of settlement; e) synchronisation of settlement produces individuals of the same age for experimentation; f) the short duration of planktonic larval life facilitates more rapid experimentation; g) photography of the substrate in the canal enables rapid counting of tubes without disturbing the test plates.

Lanice conchilega.

The larvae of *Lanice conchilega* are present in the plankton of the bay of Banyuls from November to February. Adult densities are never high as indicated by diver survey (<1 ind. 5m^{-2}). *L. conchilega* is an associated species in the fine sand *Spisula subtruncata* and the muddy soft sediment *Venus ovata.* community (GUILLE, 1970), and is also found in *Posidonia* sp. beds (eel grass) in the bay of Banyuls (LAUBIER et PARIS, 1962). Larvae for experimental use are obtained by plankton sampling. While the number of available larvae obtained is much less than for *E. nebulosa* (often less than 50 individuals per tow), sufficient material is obtained for canal experimentation (BHAUD *et al.*, 1991). In nature, the long duration of the planktonic stage of *L. conchilega* permits the determination of spatial distribution and thus permits study of the species larval dispersion ability.

3. Results and Discussion

To examine the interaction between larvae and sediments at settlement, several experiments were developed to assess:

- the ability of larvae to use several types of sediment in terms of the nature and size of grains,
- the ability of larvae to use a heterogeneous sediment,
- the effect of current on larval sediment choice capabilities,
- the application, if possible, of these results to explain observed variability in the field.

Eupolymnia nebulosa

A) The ability of larvae to construct primary tubes with respect to the grain size and the nature of sediments

This experiment was carried out in still water containers and concerns the ability of the larvae to manipulate a sediment (Table 1). The results show that larvae are best able to utilize decanted silt (No. 6 and 7) and microbeads (No. 5) while clay particles (No. 8) although of sufficient size are not utilized due to their morphological unsuitability for manipulation.

B) Settlement choice in the presence of two different sediments

Two of the substrates used in (A) above (N° 2 and 6, respectively FS and DS in Table 2), were deposited individually in ten separate petri-dishes arranged in two rows of five in the same aquarium. The two sediment types were presented in alternating pattern in each row and between rows. Free swimming larvae released from an egg mass were introduced to be aquarium and gave the following tube distribution after settlement five days later:

Table 1. Main biological features and recruitment characteristics examined in the two species.* The time lag between the appearance of *Lanice conchilega* larvae at Banyuls (B) (Mediterranean sea) and Arcachon (A) (Atlantic coast) increases the period of possible study.

	*L. conchilega**	*E. nebulosa*
Biological features:		
Larval availability	B: December->March A: April->July	B: March->June
Fertilization and spawning	free spawning no egg masses	benthic egg masses
Length of larval life	3 weeks in the plankton	3-15 days between release of eggmasses and settlement
Number of larvae available	30-50 per plankton tow	5,000 to 20,000 per egg mass
Recruitment processes examined:		
In-laboratory	buoyancy, floatation: role of secretion	interaction with sediment
	influence of flow: lengthening of planktonic life	influence of flow: multiplication of contacts during short period
In-field	dissemination in connection with physical structures	dissemination over a short distance; co-ordination of the life cycle.

Table 2. The preference of *E. nebulosa* larvae for several different types of sediment. The ability of these larvae to use the sediment and to construct or attempt to construct tubes is assigned a value from 0 (grains not displaced) to ++++ (well constructed tubes). FS: Fontainebleau sand; MB: glass microbeads; DS: decanted silt; PC: pure clay.

	sediment	size (mm)	strength of use
1	FS	250-200	0
2	FS	200-160	+
3	FS	160-100	++
4	MB	150-105	+++
5	MB	60-45	++++
6	DS	<60	++++
7	DS	<40	++++
8	PC	5a40	0

FS (160-200 mm): 445 375 355 370 340
DS (<60 mm): 195 230 50 245 265

There were significantly (Student's t: 4.25, $p>0.05$) less tubes on the silt, which seems to be contrary to the results in Table 2. A grain size of 160-200 μm seems to be too large to allow tube building. Closer inspection revealed that the tubes were not built from grains of fine sand but from small quantities of silt present in the running seawater supply (even after double decanta decantaion) or from contamination by neighbouring silt containing petri dishes. This experiment, in effect, shows that sediment heterogeneity may produce higher rates of settlement, i.e. the availability of small amounts of manipulable particles can render an otherwise unusable sediment suitable for settlement. After five days of this experiment, all newly constructed tubes were occupied but after a further six days approximately 2/3 of the tubes in the dishes containing sand were empty while all the tubes in the dishes containing silt were occupied. A new factor became important, i.e. food availability.

In summary, the 160–200 mm fraction of Fontainebleau Sand appears to be unsuitable for larval settlement (result in Table 2). However, by the addition of a small amount of silt, the resulting silt/sand aggregate is capable of supporting initial settlement but ultimately is inadequate for the maintenance of juvenile stages. The fine sand particles provide a firm support for settlement but are inadequate for feeding, therefore, development is quickly halted. This also indicates that the larvae possess sufficient intrinsic energy reserves to attain the benthic existence and that during the initial settlement phase, external energy supplies are not required.

The larvae have three basic requirements during early settlement: a need for a solid support, material for tube building and a food source for nutrition. Larvae may be fooled by certain sediment categories (e.g. 4 and 5 in Table 2). Individuals satisfy short-term needs as they arise, they do not recognise whether a sediment is compatible with the later requirements of the juvenile, and do not search for organic material on arrival at the sediment surface. This contrasts with the results obtained by Butman *et al*. (1988) for other species, as it can't be show, in this case,that larvae initially settle on a substrate commensurate with the adult needs and particularly, the need for food material.

C) The influence of current flow on settlement

The influence of sediment type and thickness on the settlement of the larvae of the polychaete *E. nebulosa*, was examined as a function of near bottom current flow. The number of larvae settling on 2 different sediment types (mud or artificial microbeads) with different thicknesses (thin layer: 60–100 mm and thick layer: 2 mm) were compared (Fig 1). Larvae showed a preference for this layered sediment which permitted access to the hard bottom. When only thick layers of the two sediment types were offered, the larvae preferred microbeads to mud. Current flow favoured settlement in terms of sediment thickness but didn't affect settlement in terms of sediment type. The effect of current flow is much more marked when the substrate is suitable. This is understandable because the current causes an increase in lateral advection and thus in the number of potential visits to the sediment surface by the larvae.

D) Observations of spatial and temporal variability in the field

Four stations with different depths have been examined in the vicinity of Banyuls. In 1990, the appearance of spawning masses in January at the shallowest station (1m) was much earlier than usual. This may have resulted from rapid growth of oocytes during the autumn coincident with higher than

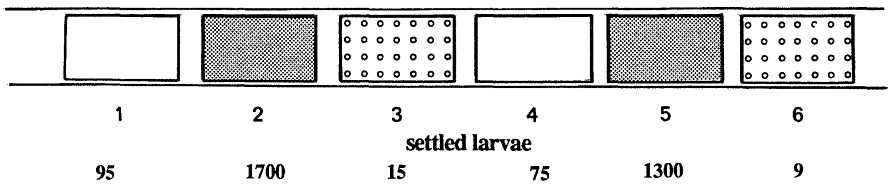

Fig. 1. Settlement by larvae of *Eupolymnia nebulosa* on a series of plates containing different sediments. The results show that there is: 1) good selection in the canal with alternating sediment choice, and 2) a larval settlement requirement for both hard and soft substrates. The current speed (2 cm over the bottom in the direction of the long axis of the canal) is 7.5 $\pm$0.7 cm s^{-1} which does not result in resuspension of the test sediments. Plate dimensions: 17$\times$9 cm (After Cha, 1990). 1 and 4 = bare plates, 2 and 5 = natural mud (<60 μm) in a thin layer (permitting access to the hard bottom), 3 and 6 = natural mud (<60 μm) in a thick layer (not permitting access to the hard bottom).

normal water temperatures due to the persistence of the summer thermocline. Early spawning at the shallow station may be disadvantageous due to an apparent dependance on macro-algae for the provision of juvenile nursary sites. These algae first appear in April, therefore, larvae which are released before this date have much higher probability of dispersion away from the adult locality. The degree of synchronisation between spawning and macro-algal appearance seems to determine to a large degree, inter-annual fluctuations in density at this location.

The variation in the maximum number of spawn masses observed at a shallow water station during a period of 7 years was as follows:

1982	1983	1984	1985	1986	1987	1990
125	190	85	85	130	92	156

The small interannual variability in adult (female) density of *E. nebulosa* at this location may be due to the following characteristics: 1) the importance of larval retention by the macro-algae; 2) pulsed spawning which ensures the success of, at least, a small number of larvae; 3) high settlement success (observed in the laboratory); and probably, 4) weak interspecific larval and adult (decreased sediment collecting activity) competition; and 5) a relatively long life span of at least 4 years.

E) Settlement on a natural sediment

If larval settlement requirements identified by experimental observations, reflect the needs of the adults in the adult location, then the larvae should be collected from soft substrates more easily than from hard substrates. A simple experiment confirmed that the silty sands of a *Nephtys hombergii* community represents a potential substrate for *E. nebulosa* larval settlement even though adults of this species are not found in any of the soft substrate populations in the bay of Banyruls (GUILLE, 1970).

The absence of adults of *E. nebulosa* in this community is potentially explained by 2 hypotheses which concern the larvae or juveniles; i) larval dispersion from adult brood stocks, located close to the shore, is sufficient to colonise the silty sand community in the middle of the bay, but after settlement other factors inhibit further development; ii) larval dispersion is insufficient to reach the *Nephtys hombergii* community. The absence of larvae in the plankton or juveniles in epibenthic sledge samples collected in the vicinity of this community tend to support the second hypothesis: i.e. current advection is too weak to transport larvae from nearshore to the *Nephtys hombergii* ground in the middle of the bay. Larvae remain close to the areas occupied by the adults which is consistent with the mode of larval developm ent, i.e., short pelagic, lecithotrophic devel opment,serving to limit dispersion.

Lanice conchilega: *dispersion capabilities of the planktonic larvae*

A) Buoyancy observed in the laboratory

Observation of the aulophore larva of *L. conchilega* has been made in a sufficiently large volume of water for the conditions of displacement to be similar to those occurring in nature (Fig. 2.). The position and the stability of these larvae in the water column depends on the secretion of a mucus thread and not on the circulation of the water between the body of the larvae and the wall of the larval tube (BHAUD and CAZAUX, 1990). After initial settlement the larvae still retains its ability to return to the water column. This suggests that the conditions which permit larvae to re-enter the pelagic sphere may be as important as those which control the sinking rate in determining the eventual settlement location.

B) Field observation of the larvae

In spite of the long duration of the planktonic life, the local hydrodynamic conditions in the bay of Banyuls do not necessarily have a dispersive action: regular planktonic sampling at the same location recovers successive different stages of development, i.e. the primary detritic benthic tubes and mucus planktonic tubes occupied by larvae having between 1 and 5 tentacles (MARCANO, 1991).

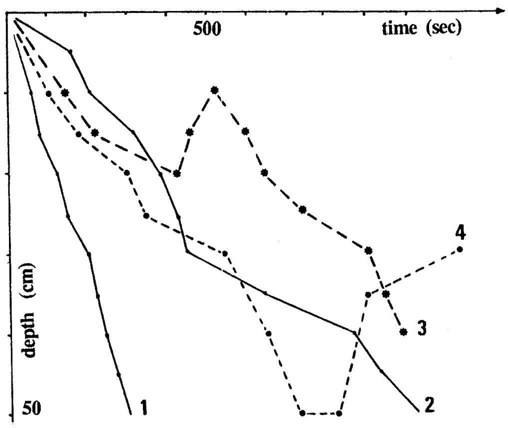

Fig. 2. A study of the buoyancy characteristics of *Lanice conchilega* larvae in an experimental chamber with still water.
1: An example of the vertical all profile of an empty tube; mean time (s^{-1}) for a 50 cm descent (n=6, m=516, s=62).
2: An example of the vertical fall profile of a larva without a tube; mean time (s^{-1}) for a 50 cm descent (n=7, m=804, s=119).
3 and 4: Vertical displacement profiles of aulophore larvae. After observations of 2500s, larvae were still in the water column after a more or less short passage at the bottom.

However, this observation doesn't definitely prove larval retention in the bay of Banyuls. It is likely that some exchange occurs between larvae inside and outside of the bay; but the extent of this possible exchange hasn't been quantified. Preliminary biological data (quantitative differences between material recovered from stations of 25m and 60m depth in the bay, and differences in the age of the larval stages) indicate that there is at least partial isolation between the bay and the exterior. Wind and wind driven currents have been studied. Two directions predominate; i) a westerly wind which causes a circular current movement which when combined with the residual north-south moving current results in the retention of the larvae in the bay; and ii) an easterly wind (coming from off-shore) which causes large disruption of the water mass. The hydrodynamic features in the bay of Banyuls are source of variability which have a direct influence on the amount of competent larvae available for settlement and can in part explain the success of failure of recruitment in *L. conchilega* (SINCLAIR, 1988). The degree of retention controls directly the quantity of larvae arriving at the end of their development and capable of settling in the bay.

4. Conclusions and prospectives.

Important factors controlling the availability of competent larvae and the success or failure of recruitment in the two polychaete species studied in the bay of Banyuls are as follows: A) *E.nebulosa*. The weak dispersion capabilities of the larvae promote retention in the vicinity of the adult habitat and perhaps serve to prevent larvae from reaching the middle of the bay where the substrate is suitable for initial settlement (laboratory results) but would result in subsequent high mortality of juveniles. The synchronisation of the release of spawning egg masses with the local appearance of macro-algae (at least at one shallow location) concurs with weak larval dispersion potential. Further work will be carried out to determine the cause of early spawning in the shallow water population. The potential link between the rate of oocyte development and the degree of summer thermocline persistence (with the consequent prolongation of high water temperature) will be investigated experimentally. B) *L.conchilega*; Large scale retention structures, rather than variation in fecundity, seem to play the most important role in determining the variation in the abundance of *L. conchilega* larvae in the bay of Banyuls. Future expeimental work with this species will focus on the effects of microscale hydrodynamic processes. Observations on the effects of near bottom turbulent flow on the settlement ability of component larvae will be assessed through flume studies.

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