RECRUITMENT IN THE LIGHT OF BIOLOGICAL-PHYSICAL INTERACTIONS IN COASTAL WATERS: RESULTS OF PNDR ACTION AT THE ARAGO LABORATORY IN 1994-1995

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RECRUITMENT IN THE LIGHT OF BIOLOGICAL-PHYSICAL INTERACTIONS IN COASTAL WATERS : RESULTS OF PNDR ACTION AT THE ARAGO LABORATORY IN 1994-1995

***S. ARNOUX*[3]*, M. BHAUD*[1]*, C. CAZAUX*[2]*, J.H. CHA*[1]*, J.C. DUCHENE*[1]*, P. FRAUNIE*[3]*, G. MARCANO*[2]*, D. MARTIN*[1, 4]*, M.J. NATTERO*[1]*, C. NOZAIS*[1]*, S. PINEDO*[4]*, C. REY*[1]*, R. SARDA*[4]**

[1]Université P. et M. Curie, Observatoire Océanologique, Laboratoire Arago, 66650 Banyuls-sur-mer, France
[2]Université de Bordeaux, Institut de Biologie Marine, Rue du Professeur Jolyet, 33120 Arcachon, France
[3]Université de Toulon et du Var, Laboratoire de Sondages Electromagnétiques de l'Environnement Terrestre (L.S.E.E.T.), 83957 Lagarde Cedex, France
[4]Centre d'Estudis Avançats de Blanes (C.S.I.C.) Cami de Santa Barbara s/n, 17300-Blanes (Girona), Spain

Correspondance à adresser et tirés à part à demander à M. Bhaud
Correspondence to be sent to M. Bhaud

POLYCHAETA
RECRUITMENT
LARVAE
DISSEMINATION
LIFE CYCLE
INTERANNUAL VARIABILITY
PHYSICAL PROCESSES
CONSTRAINT
FRENCH AND SPANISH CATALAN COAST
ARCACHON BASIN
EUPOLYMNIA NEBULOSA
LANICE CONCHILEGA
OWENIA FUSIFORMIS

ABSTRACT – This paper presents the work of the Arago Laboratory larval biology team developed close to the Laboratory but also in other areas which differ either by the dominant pattern of life cycle (subantarctic area) or by the conditions of water mass transport (Arcachon area on the Atlantic coast). The ultimate objective is the identification of the factors giving rise to the variability of populations. In this context, physical processes seem of primary interest for two reasons : a) they create a structure within which biological processes may proceed, and b) they influence the rate of these biological processes. Their identification and quantification form a fundamental point in our project. In Mediterranean populations of the target species *Eupolymnia nebulosa*, the mucilaginous egg mass sheltering larvae is related to the control of larval dissemination. Broadly speaking, development with reduction or suppression of the pelagic life, is considered as a response to the negative effects of dissemination. In this conceptual frame, life cycle evolution must have gone from benthoplanktonic to holobenthic development. The former is considered plesiomorphic, the latter is expressed by a very wide range of solutions.

A rough scheme of the seasonal variability of recruitment based on larval releasing has been elaborated : spring rise of temperature is of prime importance in the success of recruitment. The study of year to year variations in recruitment shows that short term perturbations may be at the root of the variable success of the species. The biomass level of *E. nebulosa* is determined during short periods of the year such as the prolongation or shortening of the thermocline, and the temporary fall of temperature breaking the smooth profile of the spring rising temperature curve. Consequently, in order to explain variation of recruitment, it is necessary to disregard the annual or monthly means which may suppress or seriously obscure short term deviations.

Larvae-substrate relationships are complex. Larvae settle on heterogeneous substratum. A solid basis or fulcrum is a requisite for coordination of movements which make possible manipulation of particles used for tube building and for feeding. This double constraint relative to the nature of substratum reflects living conditions of adults and not feeding processes. When considered as a whole, the main function of a life cycle is to secure the return of larvae to the adult habitat. This is achieved by several strategies among which the control of dissemination and the development of an elaborate larval behaviour can be pointed out.

POLYCHÈTES
RECRUTEMENT
LARVES
DISSÉMINATION
CYCLE DE VIE
VARIABILITÉ INTERANNUELLE
PROCESSUS PHYSIQUES
CONTRAINTES
CÔTES CATALANES ESPAGNOLES
ET FRANÇAISES
BASSIN D'ARCACHON
EUPOLYMNIA NEBULOSA
LANICE CONCHILEGA
OWENIA FUSIFORMIS

RÉSUMÉ – Ce travail présente les activités de l'équipe de biologie larvaire du laboratoire Arago. Ces activités sont développées à proximité de ce laboratoire, sur la côte française catalane, mais aussi dans d'autres zones qui diffèrent par le type dominant du développement (province subantarctique) ou par les conditions de transport des masses d'eau (Bassin d'Arcachon sur la côte Atlantique). Le but essentiel est l'identification des facteurs à l'origine de la variabilité, ce qui suppose la connaissance précise des différentes étapes du développement. Dans ce contexte, les processus physiques apparaissent primordiaux pour deux raisons : a) ils créent des structures à l'intérieur desquelles les processus biologiques se développent et b) ils influencent la vitesse de ces mêmes processus. Leur identification et leur quantification constituent un point fondamental de notre programme. Chez les populations méditerranéennes de l'espèce cible *Eupolymnia nebulosa*, la structure mucilagineuse abritant les larves contrôle la dissémination de ces larves. De façon plus générale le développement avec réduction de la durée de la phase pélagique est considéré comme une réponse aux effets négatifs de la dissémination; dans ce schéma conceptuel, l' évolution des cycles de vie part du développement benthoplanctonique représentant un caractère plésiomorphe en direction du dévelopment holobenthique qui se manifeste par des solutions très diversifiées. Un schéma, encore simple de la variabilité saisonnière du succès du recrutement, a été élaboré à partir des modalités de libération des larves au cours de la saison de reproduction. Ces modalités dépendent fortement des variations de la température ambiante. L'étude des variations interannuelles du recrutement montre que des perturbations à court terme de la température, peuvent être à l'origine du succès variable d'une espèce. Ainsi le niveau de biomasse de *E. nebulosa* est déterminé durant de courtes fractions du cycle de variation de la température : lors d'une prolongation ou d'un raccourcissement de la période de thermocline ou lors de la chute provisoire de la température au cours de l'augmentation de la température printanière. En conséquence, il apparait nécessaire, pour expliquer les variations du recrutement, de négliger les moyennes annuelles ou mensuelles qui suppriment ou gomment sérieusement les déviations à court terme. L'étude des relations de la larve et du substrat met en évidence la nécessité d'un substrat hétérogène au moment de la fixation; une base stable est nécessaire pour la coordination des mouvements; cette coordination rend possible la manipulation des particules les plus fines du substrat, utilisées pour la construction du tube et la nourriture. Cette double contrainte reflète l'habitat de l'adulte et non les procédés de nutrition. Considéré globalement, le cycle de vie a comme fonction fondamentale d'assurer le retour des larves dans l'habitat des adultes, ce qui est réalisé par différentes stratégies parmi lesquelles le contrôle de la dissémination et le développement d'un comportement larvaire élaboré.

INTRODUCTION

Many of the facets of life-cycles of marine invertebrates are presently studied thoroughly, and lead to very fructifull synthesis. Study of larval settlement of soft-sediment invertebrates (Butman 1987) lead to two hypothesis : importance of active habitat selection and passive deposition of larvae. They were thought as exclusive but are probably compatible : larvae are passively deposited at a large spatial scale but are able to select actively over a much smaller scale. For organism distribution and animal-sediment relationships Snelgrove & Butman (1994) emphasize on hydrodynamic and sediment-transport processes, in addition to grain size, organic content, number of microorganisms and sediment stability. The pre- and post-settlement processes have been compared (Olafsson *et al.* 1994). Formerly Thorson (1946) stated that the longer duration of planktonic life for planktotrophic species induced a greater intrinsic variability in settlement rate and adult population than that exhibited by lecithotrophic species. Presently (Beukema 1982) abundant evidence, based on demographic features, action of epibenthic predators or hydrodynamic disturbance, food limitation and carrying capacity, exists to show that post-settlement mortality is efficace in the density regulation of soft sediment invertebrates. Different perspectives have also been addressed to study the planktonic phase : identification (Bhaud & Cazaux 1987), dispersal (Bhaud 1993; Scheltema 1986), gene flux and its importance for evolution (Jablonski & Lutz 1983; Lenaers & Bhaud 1992; Scheltema 1981), plasticity of the planktonic life length (Bhaud 1990; 1993). Oocyte growth and process of adult maturity control the number of larvae available for the formation of the next generation. Consequently, environmental and endocrine controls of maturity have been throughly investigated (Olive 1984; Franke & Pfannenstiel 1984). However, in spite of perfectly cibled studies, tentatives of integration of isolated events of life-cycle are not numerous. At best, synthesis dealt with the significance of variability in developmental patterns (Chia 1976; Giangrande *et al.* 1994; Grahame & Branch 1985; W.H. Wilson 1991) and processes related to a precise part of the life history are kept independant. For instance little is known about how initial patterns of larval settlement are related to the distribution of adults. However, we feel this point is a central problem which suppose to link the disseminative ability of the larvae, the constraints when they settle, the kind of care brought to propagules, the potential fecondity, and the habitat of adults in terms of location and area. We know (Thorson 1966; Boesch *et al.* 1976; Marcano 1994) that numerous species settle in a much broader variety of habitats than in which they can survive. What means this difference between adult area and first benthic recruites? This paper presents some results related to this research field.

This paper may also draw attention to the activity of Arago Laboratory larval biology team, working close to the Laboratory but also in other areas which differ either by the dominant pattern of life cycle (subantarctic area) or by the conditions of water mass transport (Arcachon area on the Atlantic coast). The present results are for a large part a contribution to the French National Program on Determinants of Recruitment among which objectives, the identification of factors giving rise to numerical variability of populations can be pointed out. The methods are based on the analysis of "critical" phases of the life-cycle: oogenesis, larval settlement and first benthic juveniles. The starting point of our program was the presence of perfectly delimited benthic communities in the Bay of Banyuls (Fig. 1). The problem deals with the formation and perennity of these communities. How is the selection of larvae achieved in relation to their respective communities? How do these animal communities sustain themselves? Two complementary strategies were adopted: (1) to break down the life cycle of targeted species involving the comprehensive study of this life cycle; (2) to develop experimental studies on characteristic points, considered both in the field and in the laboratory. This second point required a large program which included the development of an automatic sampling station, a hydrodynamic canal and an actographic device. The limiting conditions of Mediterranean environments without tides induced us to integrate other conditions of transport by water masses far from Mediterranean Sea. We have not limited the location of studies to the Bay of Banyuls and we also have enlarged the range of developmental patterns and used different species of polychaete (from the families Terebellidae and Owenidae), for which a large body of knowledge already existed.

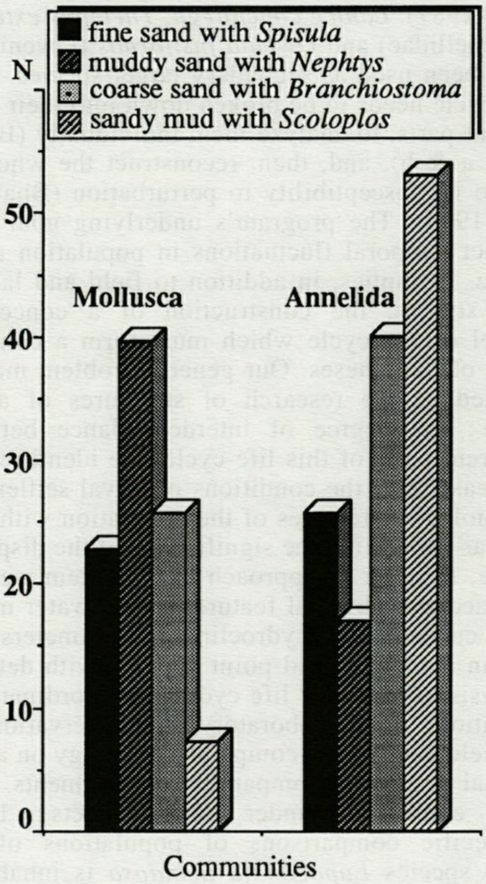


Fig. 1. – When visiting different communities in the bay of Banyuls, variation of number (N) of Annelids and Molluscs species is reversed, apart from fine sand with *S. subtruncata*. Segregation of species may take place through selective settlement of larvae from a common pool visiting all the communities or after settlement by progressive selection of benthic juvenile individuals. This situation is a typical example of one worth studying by larval biology, *in situ* and in the laboratory, with identification of settlement and dispersive constraints.

Fig. 1. – *En se déplaçant dans différentes communautés de la Baie de Banyuls, le sens de variation du nombre (N) d'espèces d'Annélides et Mollusques est inverse, exceptés les sables fins à* S. subtruncata. *La ségrégation des espèces s'effectue-t-elle au stade larvaire qui constitue un pool commun visitant les différentes communautés ou au stade postérieur à la fixation par sélection progressive des individus benthiques juvéniles? Cette situation constitue l'exemple typique méritant d'être traité par étude de la biologie larvaire, en milieu naturel et au laboratoire, avec identification des contraintes de fixation et de dissémination.*

The main target species is the polychaetous annelid *Eupolymnia nebulosa* (Montagu), which is widely distributed in the Bay of Banyuls (North Western Mediterranean Sea) but is also present throughout the world. An English Channel population has also been studied, allowing us to compare between different reproductive strategies: mucous egg-masses in the Mediterranean versus direct development in the English Channel (Bhaud *et al.* 1987). *Lanice conchilega*, *Thelepus extensus* (Terebellidae) and *Owenia fusiformis* (Oweniidae) have been used as secondary target species. Each life-cycle needs to be broken down into their component parts, to analyze them individually (Bhaud 1994 a & b), and, then, reconstruct the whole to gauge its susceptibility to perturbation (Bhaud & Cha 1993). The program's underlying goal is to predict temporal fluctuations in population abundance. It implies, in addition to field and laboratory studies, the construction of a conceptual model of life-cycle which must form a coherent body of hypotheses. Our general problem may be defined as the research of structures of a life cycle : the degree of interdependance between different parts of this life-cycle, the identification of weak links, the conditions of larval settlement, the biological features of the population with year to year variability, the significance of the dispersal phase. In order to approach this problem we take into account physical features of the water mass : both currents and hydroclimatic parameters; we use an autoecological point of view with detailed analysis of a precise life cycle; we coordinate observations in the laboratory and observations in the field and we use comparative biology on a latitudinal transect. Comparative experiments have been considered under three aspects : 1) intraspecific comparisons of populations of the same species *Eupolymnia nebulosa* is inhabiting different climatic environments : the English Channel and the Mediterranean Sea. 2) interspecific comparisons of two species with different larval strategies : *Eupolymnia nebulosa* and *Lanice conchilega.* 3) comparisons and coordination of experiments in laboratory and in the field.

MATERIAL AND METHODS

1. Lay-out of experiments in the laboratory

Larval potentialities have been studied in the laboratory with the aid of two technical devices : 1) a hydrodynamic canal for larval selection of sediments; 2) an actograph for recording passive and active displacements. The present study on mecanisms of accession to benthic life by planctonic larvae is indebted to the works of Wilson (1951, 1952, 1958) for relations between larvae and substratum; and to those of Nowell & Jumars (1984), Butman (1987), Butman *et al.* (1988), Jonsson *et al.* 1991, Andre (1994) for introduction of hydrodynamic conditions when larvae access to the bottom. Comparisons with several of these authors (see for instance Butman *et al.* 1988) command attention taking into account the similarity of goals and several differences with regard to the operative modalities. These differences affect specially the length of incubation (from 2 to 4 hours as opposed to several days in our protocol), modality of sowing larvae in the enclosure from a precise location situated up-stream of the experiment tray – formed with 25 alternating small boxes filled with two types of sediments – and last, the simultaneous use of inert particles mimetic of larvae. Accordingly, two points are investigated : the nature of the final part of the fall curve and the possible rearrangement in the distribution of larvae between the sediments. However, experimental length is both too long in order to register the nature, either passive or active, of the larval fall, and also too short to estimate ability to choose among the sediments or to allow expression of benthic behaviour. For our part, we intended to be pragmatic and we searched for the possible existence of preferential situations during larval settlement (Bhaud 1990; Bhaud *et al.* 1991; Cha & Bhaud 1991). We saved a sufficiently long incubation time to allow for the demonstration of substratum selection which supposes the development of several tests by larvae eventually leading to a new spatial distribution. This length of experimentation also allowed the development of interindividual relations, which displayed for first built tubes contagious, neutral or negative distribution. Very possibly we did not study settlement (a biological step during development, independent from the observer) but recruitment (observer– defined) because, in the context of definitions given in literature, our first observed distributional pattern reflects a new organisation, considered by several authors as an indication of recruitment. However, the observer is not prevented from condensing the sampling method to try to get superposition of settlement and recruitment. This is what we have done; we analysed changes in spatial distribution and in mortality during access to benthic life, which allowed us to telescope first contact, settlement and recruitment (Cha 1990, 1994). Actography is a device used for studies of larval displacement in still water and flumes. A set of video cameras is attached on step motors driven by a 2 or 3-axis tracking system with a 12 microns resolution. The digitized signals are read by a video capture board and analyzed by a real time software developed by J.C. Duchêne. After shape extraction and recognition, the amount of detected movement is used by the computer to displace the cameras in order to keep the object in a central position within the working frame. Displacements are recorded on a real time basis by the computer. A working field corresponding to the overall length of the tracking translators may be defined with a starting point. In studies involving the use of a flume, this allows repetitive automatic recordings of sequences of larval displacement. The system is size independent : the ratio "object pixel size" on "video camera field width" depends on the optical lens used on the camera (Nozais 1991; Duchêne & Nozais 1993, 1994).

2. Experiments in the field integrating several topographic situations

A last point of method must be added. Limitation of the Mediterranean environment, particularly due to the absence of tides, induces the integration of specific topographic situations on the Atlantic coast. The presence of the Marine Station led us to study the influence of the topography formed by the Arcachon Basin and conditions of larval circulation through the channel connecting the Basin to the Ocean. Three reasons justify studies on recruitment in this site. It allows better than elsewhere; 1) the identification of hydrodynamic processes during recruitment; these processes are not always propitious to successful recruitment; 2) the integration of concepts of theoretical ecology, for instance significance of reproductive patterns in an ecological gradient developed over a short distance, or significance of plasticity of several developmental phases like metamorphosis not linked to a precise morphological stage; 3) development of natural experiments on larval sowing on varied substrata at the mercy of ocean water intake. This Basin is a lagunar environment communicating with the open sea. The tides originate an oscillatory movement of the water that can result in a larval exchange between both ecosystems. The Basin is characterized by a marked hydroclimatic gradient from the oceanic to the inner neritic waters. Also, an increasing number of species with benthic development is observed in the inner bottoms, associated with the reduced area of the specific adult habitat. The relationships between the mode of development and the range of larval dispersal can thus be fruitfully studied in this area (Bhaud & Duchêne, 1995). A comparative study on the delay of the metamorphosis can be done in this area in terms of stimulation by the charge with suspended particles; in the Basin, planktonic stages are submitted to benthic stimuli and their transfer to the benthos is fast; on the contrary the planktonic life is prolonged in the open sea where quite old larvae can be collected for the same species. This observation indicates a plasticity at the end of the planktonic life (Bhaud *et al.* 1990) showing that the size at metamorphosis is not constant in spite of the contrary hypothesis often advanced for the establishment of reproduction models (Grant 1983).

3. Two basic features of the target species

Before describing results, two aspects of the biology of our species must be considered because they are important elements of our method and are always present in the background of our research.

Firstly, a basic element in this research is the developmental pattern of the target species. Definition of several terms (larvae, juvenile, metamorphosis, as seen for settlement and recruitment) are subject to variation. This is the consequence of independance of states of developmental traits. In other words, they are not perfectly correlated, for instance pelagic development is associated with either feeding or non feeding development; likewise autonomous developmental pattern called "non-feeding development" is associated with direct development as well as indirect development. As it has been proposed formerly (Bhaud, 1987; Mc Edward & Janies 1993) three criteria or characters are used to define developmental patterns : 1) morphological change with or without a temporary structure specific to the larva depending on whether development is direct or indirect); 2) behaviour as in feeding or non feeding; and 3) ecology connected with spatial location of development : in the water column when pelagic, or close to the substrata when benthic. These three traits by combination allow to define 8 patterns. Application of these definitions to *E. nebulosa*, shows that this species changes its developmental pattern. At the beginning of the reproductive period, development is indirect, pelago-benthic and endotrophic; larvae work on their own energy reserves when released; but when formed at the end of the reproductive period, the developmental pattern is direct, holobenthic and exotrophic; for feeding, larvae work on the environment after escaping from the egg mass. This species constitutes a model allowing us to understand the evolution from one developmental pattern to an other.

Secondly, we must distinguish between larval choice and opportunity. Throughout our present work we will use the expression larval choice, this is for simplicity rather task more than accuracy. A choice assumes a comparative action developed on short time and space scales which is exerted in the sensorial sphere of each individual, between alternative proposals simultaneously accessible. The analysis of the reorganisation of larval distribution indicates that this is not the case. The settling process is developed in time and it seems more correct to consider an ecological opportunity at the origin of the substratum selection. An other trait of the choice concept is the projection in the future and in this sense, choice constitutes an element of the reproductive strategy. But for *E. nebulosa* this strategy is missing : larvae must be confined in space to avoid a successful recruitment in the center of the Bay of Banyuls, followed by failure of benthic juveniles. Selection of sediment by larvae is accomplished on the short-term and does not assure the future of individuals. The result of the transition from the planktonic to the benthic phase is unrelated to the subsequent success or failure of recruitment. A contrast becomes visible between limited requirements in terms of grain size and shape defining a large potential zone for larval settlement, on the one hand, and a spatially limited adult area, on the other hand. These two features are made compatible by the existence of an egg mass in the life-cycle. Retention structures and larval plasticity are of great importance in the subantarctic environment found in Kerguelen archipelago, characterized by a narrow range of temperature variation and severe dissemination constraints (Duchêne, 1991, 1992).

RESULTS

In the frame which has just been defined, we choose to expose some results on the following points : the importance of physical parameters of environment and particularly of water mass movements considered in different space scale; function of egg-mass in the life-cycle; selection of sediment by larvae during settlement; regulation and interannual variation of biomass with qualitative and quantitative modelisation, identification of connections between different features of the life-cycle.

1. Biological-physical interactions

Physical processes create the conditions for many important biological processes. They create structures within which biological processes may proceed, and they influence the rate of these biological processes. Physical processes act on a large range of spatial scale. We have explored three of them : 1) physical conditions at the water-sediment interface, which determine the parameters of the benthic boundary layer, 2) physical conditions on the local scale of Banyuls Bay and 3) regional physical conditions in the subantarctic area.

To approach physical conditions at the benthic boundary layer we firstly identified abilities of larvae to select substrata on a bottom subject to zero rugosity, and to a shear stress lower than 0.15 cm.s^{-1} (Cha 1994). In these conditions, larvae were able to reject an unsuitable substratum and to return to the water column. Secondly, roughness created by height and distance of a set of obstacles, was introduced. Sediment and larvae were introduced successively which represent natural conditions of a temporary high perturbation. Settlement areas were controlled by obstacles; larvae were limited in their exploratory space; they were obliged to stay close to the obstacles. They were not able to settle on the area covered with a reduced quantity of sediment. Consequently, tubes were observed only on areas with a thick layer of sediment. For an intermediate current rate of 8.6 cm.s^{-1} a relation between roughness and number of settling larvae has been established (Fig. 2).

The specific situation of Banyuls Bay, sheltered from the dominant N-W winds, isolates partially internal water masses. The first thematic attempts to define the role of internal circulation in relation to the external general circulation of the western Golfe du Lion, on the dissemination of invertebrate larvae. The goal is the identification of spatial barriers in life-cycle in order to recognize spatial limitation of a population. The numeric modelling of currents in the Bay of Banyuls (Fig. 3) is based on flow simulation solving Navier-Stokes, 3 dimensional temperature and salinity equations, with a two equation closure model for the turbulence (κ-ε model). Several steps are in progress : a) the bay is considered during homogeneous sea conditions without wind and with a residual component of the liguro-provençal current; b) on the same basic scheme, dominant wind conditions frow NW are added; c) the vertical circulation with upwelling is integrated. We dispose actually of the first model step which shows a bottom recirculation area and a surface flow going off the coast (Arnoux & Fraunié 1994; Fraunié 1994).

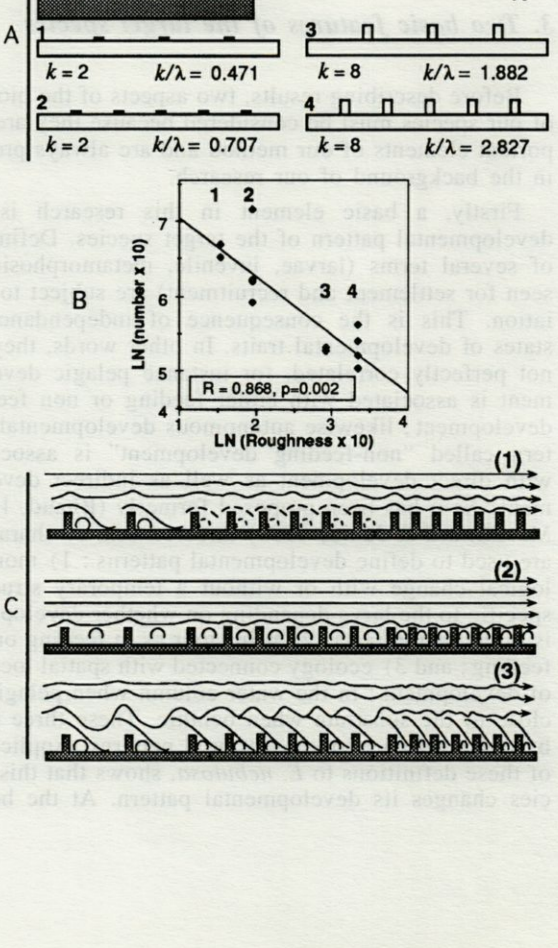


Fig. 2. – Experimentation in two phases and simulating larval settling after a period of high turbulence (flow rate at the surface : 18.5 cm.s^{-1}). Larvae are introduced after this turbulence (flow rate at surface : 8.6 cm.s^{-1}). The bottom of the enclosure is furnished with obstacles defining the roughness (A). For conditions of flow rate in this experiment, there is a negative correlation (B) between roughness and number of settled larvae. C : illustration of the benthic boundary layer in terms of the flow rate at the surface when larvae are introduced; 1 : average flow rate already illustrated in part B with number of settling larvae depending of roughness; this relation disappears when flow rates are higher (2) or lower (3); in these two situations the variation range of roughness is not large enough to differenciate larval settlement : with a high rate (2), larvae cannot pass between obstacles and with a low rate (3) larvae reach the bottom in all conditions of roughness.

Fig. 2. – *Expérimentation se déroulant en deux phases et simulant la fixation des larves après une période de forte turbulence (vitesse de surface 18.5 cm.s^{-1}). Les larves sont introduites après cette période de turbulence (vitesse de surface 8.6 cm.s^{-1}). Le fond de l'enceinte expérimentale est garni d'obstacles définissant la rugosité (A). Pour les conditions de vitesse de l'expérience, il existe (B) une relation négative entre le facteur de rugosité et le nombre de larves fixées. C : illustration de la couche limite en fonction de différentes conditions de vitesse au moment de l'introduction des larves ; 1 : vitesse moyenne déjà illustrée par la partie B avec pénétration des larves en fonction de la rugosité ; cette relation disparait pour une vitesse plus forte (2) ou plus faible (3) ; dans ces deux cas la gamme de variation de la rugosité n'est pas suffisante pour différencier la réception larvaire ; en vitesse élevée (2), les larves ne peuvent pénétrer entre les obstacles et en vitesse faible (3) les larves atteignent le fond dans toutes les conditions de rugosité.*

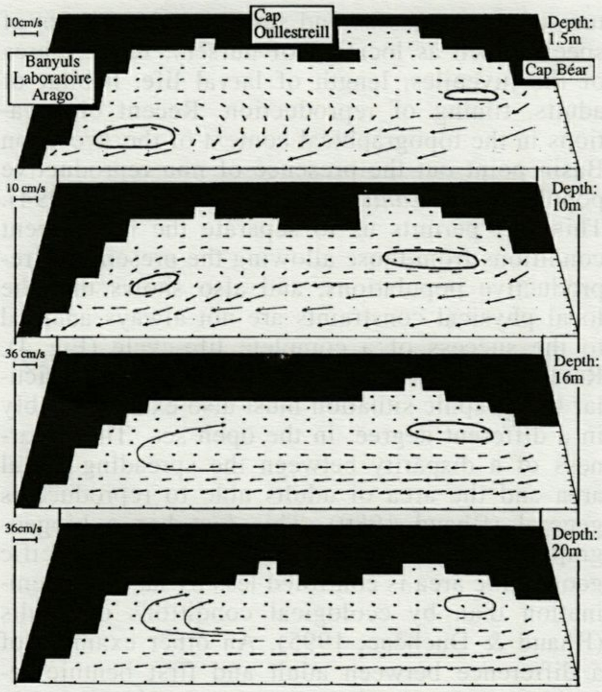


Fig. 3. – Numeric modelling of currents in the Bay of Banyuls. The graphs show the bay during homogeneous sea conditions without wind and with a residual component of the liguro-provençal current. The model shows a deep gyre and a current moving off the coast on the surface. For each depth, the length of the arrows is proportional to the scale on the left side but some arrows, too long if drawn in scale, are represented by points. The presence of rotary motion areas has been underlined.

Fig. 3. – *Modélisation numérique de la circulation des courants en Baie de Banyuls. Les figures représentent la baie pour des conditions de mer homogènes, sans vent avec comme seul forçage, la présence du courant Liguro-Provençal. Le modèle met en évidence une zone de recirculation en profondeur et un flux qui s'éloigne de la côte en surface. Pour chaque profondeur, la longueur des flèches est proportionnelle à l'échelle présentée sur la gauche du plan mais les flèches qui auraient été trop longues sont remplacées par des points. La présence des gyres a été surlignée.*

Physical environment considered on a regional scale controls several biological traits. For instance, the hypothesis of emergence of a direct development pattern governed by constraints of dissemination is perfectly illustrated by study of the Polychaeta from the Kerguelen province (Duchêne 1982, 1983, 1984, 1989; Bhaud & Duchêne 1988; Bhaud & Duchêne 1995). For species with known life-cycles, the most frequent development is direct, with large size eggs. This situation of the subantarctic area furnishes a strong correlation between direct development and the presence of exacerbated disseminative conditions. In the same area but for other groups (*i.e.* Crustacea), indirect development is conserved. In this case, however, a retensive structure is formed by holdfasts of giant kelps like *Macrocystis* and *Durvillea* (Bhaud & Duchêne 1988). These examples of preservation of planktonic egg size in a structure of retention are particularly conclusive in an adaptation for reduced dissemination.

2. *Function of egg masses in the life cycle of E. nebulosa*

Laboratory experiments showed that larvae were able to use the finest fraction of the heterogeneous sediments present in the axis of the Bay of Banyuls (Bhaud & Cha 1994) : muddy sand with *Nephtys hombergii* and fine sand with *Spisula subtruncata* community. However, adults are never been collected in these communities. They can be collected in a narrow belt (from 0 to 20 m depth) at the periphery of the Bay where blocks and boulders are progressively embedded in the soft substratum. Accordingly, it does not appear desirable that larvae by their dissemination reach the axis of the Bay which is not suitable for the adults. How then reconcile the absence of the species in the axis of the Bay with successful settlement on the same substratum ? The negatif aspect of this dissemination in the axis of the bay, followed by a successful larval settlement and a failure of juvenile grown, has been explained by studying the dragging of juvenile tubes built on soft substrata of *Nephtys hombergii* community in a hydrodynamic canal. According to the thickness of the sediment, tube anchorage is different. When tubes are arranged on a sedimentary bed, (*e.g.*, the center of the Bay), they can be easily washed away by hydrodynamic strength. On the other hand, when tubes are anchored on a thin layer of the same sediment, deposited on a hard substratum (*e.g.*, the periphery of the Bay), they offer a higher resistance to the erosion by currents (Cha 1994, Bhaud *et al.* 1995). These results transposed to the field suggest that the function of gelatinous egg-masses is to reduce the ability of larvae to spread and to prevent then settlement in the axis of the Bay. Even if larvae are able to settle on this area of Bay, it does not appear desirable that they reach this area which is an unsuitable habitat for adults. Mucilaginous structures shortened the length of the planktonic larval life thus securing settlement inside adult habitat areas. In the Kerguelen environment the egg masses reduce the pelagic life of *Thelepus* larvae to a maximum of 24 hours thus preventing larval drift off the coasts of this isolated island located in the westward currents of the southern Indian Ocean (Duchêne 1993).

3. *Larvae-substratum relationship when settling*

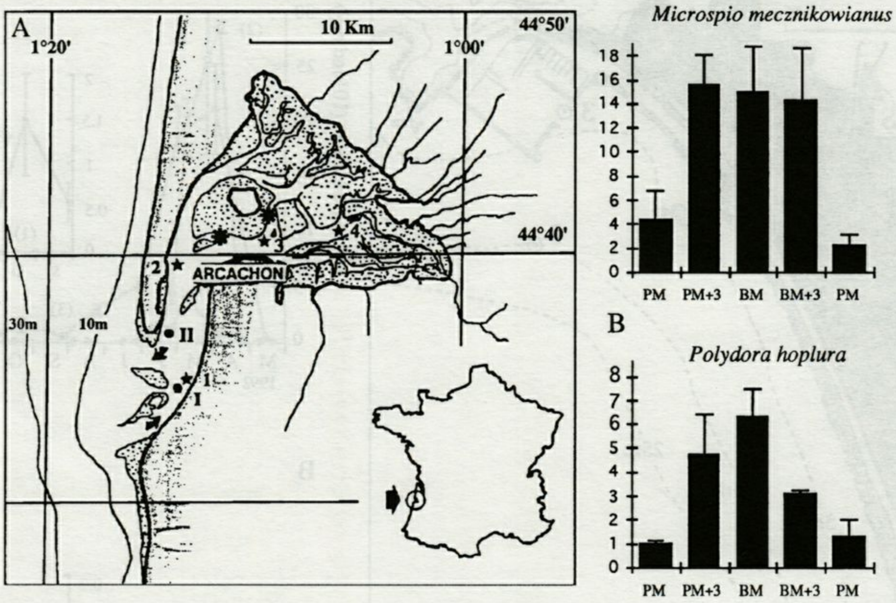
The transition from the plankton to the benthos has been investigated experimentally using *E. nebulosa* (Bhaud & Cha 1994). Tests on artificial and natural sediments lead to the following results. 1) Larvae are able to displace particles with a greater weight than their own, but this is possible only if larvae have access to a perfectly immobile platform. 2) Larvae require two kinds of substrata for settlement, one forming support and allowing coordination of movements, the other being tube-building material. This dual constraint, solid base plus manipulable building particles, is related to the nature of substrata. Such statement differs from previous conclusions, suggesting that only grain size was important for settlement. This has been demonstrated for the subantarctic terebellid *Thelepus extensus* (Duchêne 1982). Our observations also show the importance to settlement of the thickness of the sediment layer (Bhaud *et al.* 1995).

Larvae of a given stage of development are able to manipulate only a well defined size-range of particles. This range increased as development proceeded, and the result was the progressive utilisation of increasing grain sizes. This reduced selectivity of aged-larvae corresponded to an increasing ability to use particles. The older the larvae are when they touch the substratum for the first time, the weaker their ability to return to the water column is, when the substratum is unsuitable. In the same way, the suitable size range of particles increases with age, and the probability of a succesful settlement increases. As a consequence, a delay in the contact of planktonic larvae with substrata is not necessarily a negative point, because the probability to settle successfully increases with this delay. *E. nebulosa* does not form the sole model for larva-substrate relationships. Recently, we observed that larvae of *O. fusiformis* are able to metamorphose on a very large range of sediments and even without soft substrata but in contact with hard substrata (notwithstanding numerous partially metamorphosed larvae collected in the water column). The acquisition of the first benthic morphology seems non related to the nature of substrata. The ability of larvae to select at a fine spatial scale seems non-existent. The first tube is secreted by the benthic worm and is made of mucus. From this step on, the nature of the sediment (size of grains, content in organic matter) may play a role in forming the definitive distribution of the adult population. In the case of *Thelepus* larvae released from the cocoons over a muddy substrate the presence of hard structures, mainly the adult tubes and *Macrocystis* canopy appears to be essential (Duchêne 1983).

Until now, we have worked with considering a perfect adjustment between the hydrologic structure of water masses and several caracteristics of species such as location of nursery, feeding area of the juveniles, length of larval life, habitat of adults, timing of reproduction. Recent observations in the topographical context of the Arcachon Basin point out the presence of non reproductive populations of *Lanice conchilega* (Marcano 1994). This fact permits us to separate the recruitment conditions from those allowing the presence of reproductive populations, and also shows that the local physical constraints are not always adapted to the success of a complete life-cycle (Fig. 4). Retention process like that observed in a particular topographic situation must also exist, probably in a different degree, in the open sea. This clearness of a disparity between the spreading larval area and the area of adults able to reproduce is general (Bhaud 1989). This fact has a biogeographic consequence : variation of the specific geographic area is controled less by larval dissemination than by ecological conditions of adults (Bhaud & Duchêne, 1995). An other example of a difference between adult and first benthic recruitment areas is given by a survey developed in the Bay of Blanes, Spanish Catalan coast (Pinedo *et al.* 1995 ; Sarda *et al.* 1995). The population structure of *Owenia fusiformis* from this Bay was studied from March 1992 to March 1993 (Fig. 5). Seasonal pattern in abundance was characterized by a peak during spring (recruitment period), a sharp decrease through summer and lower densities during autumn and winter. This population was stable from August to March with 500 ind m^{-2} approximately. High density of small-sized individuals were observed at three stations during the recruitment period followed by high mortality. Adults were clearly detected at St 3 and more rarely at St 1 ; they disappeared completely at St 2. Area covered by young benthic recruites is larger than adult area. Settlement of larvae seems to be associated with a range of sediments larger than sediments associated with adults. As Thorson (1966) pointed out, many species set in a much broader variety of habitats than those in which they can survive (*cf* also Boesch *et al.* 1976). If there is not correspondence between distributional areas of both first benthic recruits and reproductive adult populations, the direct consequence is the obligation during benthic studies to specify the age of collected benthic specimens. Characteristics of a sediment containing young recruits or juvenile stages of a given species are not necessarily a specific trait ; only the location of the reproductive phase is relevant.

4. *Oocyte growth*

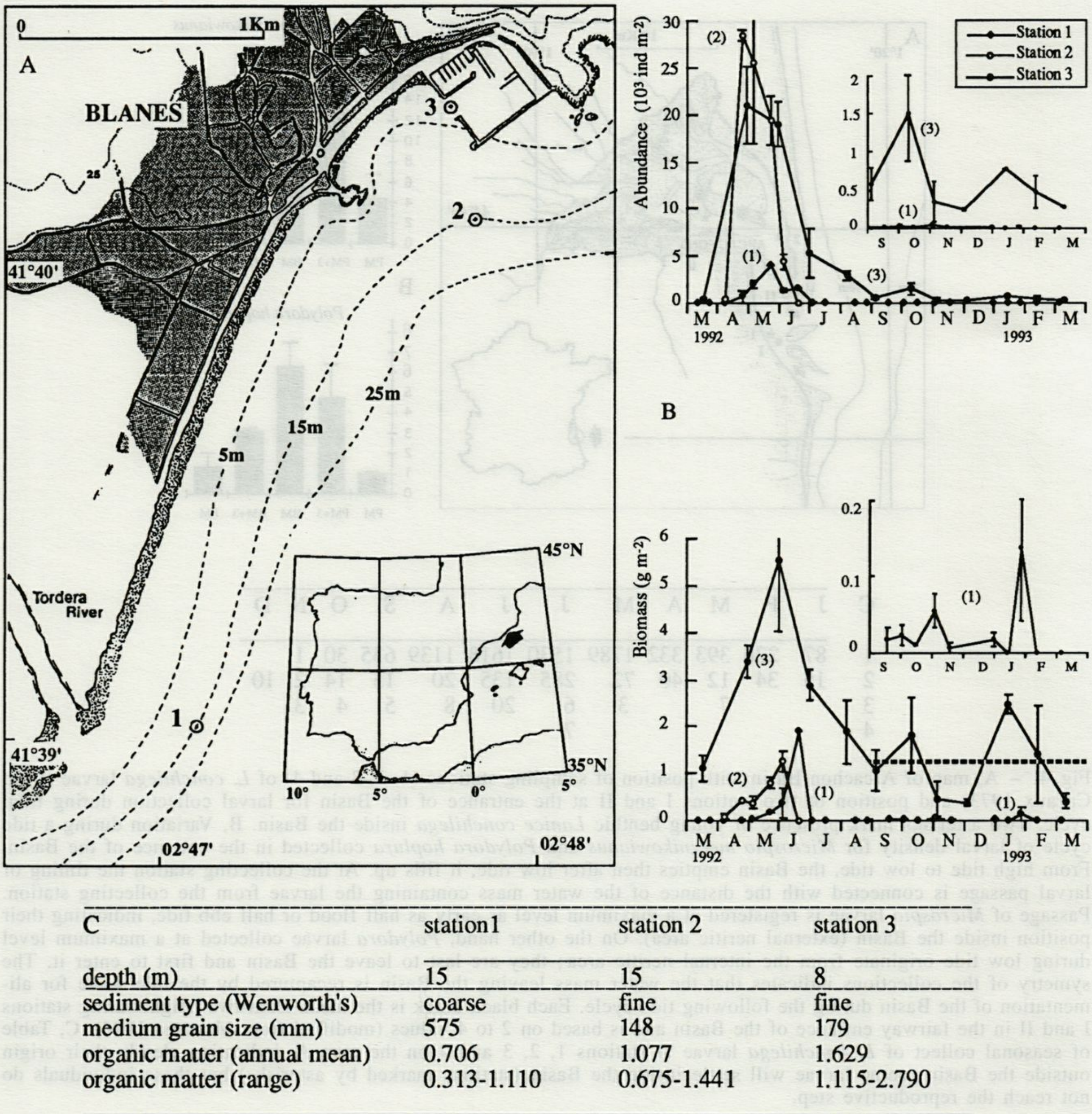
From a long-term survey carried out in the Bay of Banyuls (North Western Mediterranean Sea),



C	J	F	M	A	M	J	J	A	S	O	N	D
1	87	226	393	332	1789	1530	1618	1139	635	30	1	
2	15	34	12	40	72	285	135	20	15	14	2	10
3			7		3	6	20	8	5	4	3	
4						7						

Fig. 4. – A, map of Arcachon Basin with position of sampling stations (1, 2, 3 and 4) of *L. conchilega* larvae (from Cazaux 1973) and position of two stations I and II at the entrance of the Basin for larval collection during tidal cycle. Two asterisks mark presence of young benthic *Lanice conchilega* inside the Basin. B, Variation during a tide cycle of larval density for *Microspio mecznikowianus* and *Polydora hoplura* collected in the entrance of the Basin. From high tide to low tide, the Basin empties then after low tide, it fills up. At the collecting station the timing of larval passage is connected with the distance of the water mass containing the larvae from the collecting station. Passage of *Microspio* larvae is registered at a maximum level as early as half flood or half ebb tide, indicating their position inside the Basin (external neritic area). On the other hand, *Polydora* larvae collected at a maximum level during low tide originate from the internal neritic area; they are last to leave the Basin and first to enter it. The symetry of the collections indicates that the water mass leaving the Basin is recaptured by the tide wave for alimentation of the Basin during the following tide cycle. Each black block is the mean from two neighbouring stations I and II in the fairway entrance of the Basin and is based on 2 to 4 values (modified from Marcano 1994). C, Table of seasonal collect of *L. conchilega* larvae at stations 1, 2, 3 and 4 on the map A, indicating clearly their origin outside the Basin; some larvae will settle inside the Basin (stations marked by asterisks) but these individuals do not reach the reproductive step.

Fig. 4. – *A, carte du Bassin d'Arcachon avec situation des stations de récolte des larves de* L. conchilega *1, 2, 3 et 4 (d'après Cazaux 1973) et des stations I et II des passes d'entrée utilisées pour la récolte des larves au cours des cycles de marée; les deux astérisques figurent la présence de jeunes* Lanice conchilega *à l'intérieur du Bassin. B, Densités larvaires des deux espèces* Microspio mecznikowianus *et* Polydora hoplura *récoltées dans les passes d'entrée du Bassin. A partir de la pleine mer et jusqu'en basse mer, on assiste à une vidange du bassin puis entre la basse mer et la pleine mer à son remplissage. En une station donnée, l'ordre de passage des larves est lié à la distance de la masse d'eau qui contient les larves par rapport à la station d'observation. Le moment du plus fort passage des* Microspio *est situé dès la mi-marée montante ou descendante indiquant leur position à l'intérieur du bassin dans la zone néritique externe. En revanche le maximum des* Polydora *est enregistré en basse mer indiquant la présence des adultes dans la zone interne du bassin; ils sont les derniers à sortir et les premiers à entrer. Dans les deux cas, la symétrie des récoltes indique que la masse d'eau qui sort est reprise par la marée pour alimenter le bassin au cours d'un nouveau cycle. Chaque barre verticale noire représente la moyenne de deux à quatre valeurs obtenues aux stations I et II situées dans la passe d'entrée du Bassin (Marcano 1994, modifié). C, Tableau de récolte saisonnière des larves de* L. conchilega *aux stations 1, 2, 3 et 4 de la carte A indiquant clairement la source des larves à l'extérieur du Basin; certaines larves se fixeront à l'intérieur du Bassin (station indiquée par les deux astérisques); cependant ces individus n'atteindront pas l'étape de la reproduction.*



C	station1	station 2	station 3
depth (m)	15	15	8
sediment type (Wenworth's)	coarse	fine	fine
medium grain size (mm)	575	148	179
organic matter (annual mean)	0.706	1.077	1.629
organic matter (range)	0.313-1.110	0.675-1.441	1.115-2.790

Fig. 5. – A, map of the area of Blanes with three sampling benthic stations. B, seasonal variation of abundance (above) and biomass (below) of *Owenia fusiformis.* The dotted curve superimposed from September to March on curve 3, bottom graph, shows as an hypothesis the mean of monthly biomass which is relatively stable. C, abiotic parameters of the three stations : mean and range of organic matter is given as % of dry weight.

*Fig. 5. – A, carte de la zone de Blanes avec emplacement des trois stations de prélèvement benthique. B, variation saisonnière de l'abondance (graphique du haut) et de la biomasse (graphique du bas) d'*Owenia fusiformis. *Le trait en pointillé superposée sur la courbe 3, graphique du bas, indique à titre d'hypothèse la moyenne mensuelle de biomasse relativement stable. C, paramètres sédimentaires des trois stations : moyennes et extrêmes de matière organique sont exprimées en % du poids sec.*

the coincidence of an advancement of the spawning period with a delay of the thermocline breakdown was described. These persistent high temperatures could act on the gamete development by stimulating oocyte growth, subsequently causing the advancement of cocoon release. To achieve a better understanding of this interactions between temperature and oocyte growth in *E. nebulosa*, an experimental approach to the individual level was applied (Cha, Martin & Bhaud 1995).

Three methodological steps were progressively used : 1) The identification of net growth component of intracoelomic oocyte population. 2) The identification of differential growth rates related to mean oocyte sizes. 3) The determination of statistically comparable pairs of oocyte size distributions at the onset of the experiment. Three main results were found : 1) A positive response of oocyte growth to the maintaining of high temperatures can be detected. 2) This positive response could not be demonstrated for all females but only for certain individuals. 3) The lack of non significant level population responses to changes of a given parameter should not be immediately attributed to the absence of any kind of response. It could eventually be related to the degree of variability among individuals. The existence of changes from discoid oocytes to spherical newly spawned eggs has also been noted for *E. nebulosa* (Martin, Cha & Bhaud 1995). Although there are not direct demonstrations, the existence of a size-dependent selection mechanism during the spawning process was strongly supported. This mechanism results in an effective selection of a short size-range of large mature oocytes and can be directly linked with the life-cycle strategy of the Mediterranean *E. nebulosa* populations. The implications of its existence in the English Channel populations remains unclear. The results underline the importance of considering the real form of gametes when dealing with the study of life history strategies viz. oocyte growth linked to different environmental or endogenous controllers or spawning mechanisms (Martin, Cha & Bhaud 1995).

5. *Age at first maturity*

The comparative study of the English Channel and the Mediterranean Sea populations of *E. nebulosa* (Bhaud *et al.* 1987) displayed a difference in the age at first maturity which was 1 and 2 years, respectively. The origin of this difference remained unknown ; it could be the consequence of a reversible adaptation or the expression of a genetic trait. Breeding experiments in the laboratory showed that age at first reproduction (2 years) estimated in the Mediterranean from the number of maxima in the frequency diagram of adult weight, was not a definitive feature. Effectively, his age has been put forward to 1 year by modification of breeding conditions. These modifications deals mainly with the quantity and quality of food (Cha 1994). These results incited us to propose 2 models, both able to take into account gonads development in terms of available food. 1) The energetic transfer to the gonads is only possible after soma reaches a given size limit ; in this case morphological development and size are always the same when first maturity is reached. 2) The second model is based on the accumulative rate of external energy ; this input rate is variable ; if reduced, the whole energy is attributed to somatic growth ; above a given rate, a fraction of energy input is attributed to gonads, and consequently reproduction may occur early. In this model, the body size can be different from one individual to another when maturation begins. The choice between these two models will be dictated by examination of morphological structures at the time of first maturity.

6. *Life cycle regulation and year to year variation : qualitative model*

The sequence of biological events in the life-cycle of *E. nebulosa* is superimposed on the hydroclimatic features of the seasons (Bhaud 1994b ; Bhaud *et al.* 1995). The adjustment between these two series is governed by the placement of the growing period of juveniles during the spring rise of temperature. The demographic structure of juveniles is, then, distributed in a narrow range of sizes which involves weak competition between individuals. This regulation is open to external influences. A delay in the fall thermocline break down and an early rising of spring temperatures have two consequences : the displacement in time of the formation of egg masses and the lessening of the spring temperature gradient. The final result is a conservation of size structure of juveniles in a large range which produces interindividual competition. The sequence of events forming the life-cycle is the result of a long term developed balance. This balance is interpreted by two coordination processes identified in the life-cycle : 1) limitation of dispersal by egg masses, related to the narrow area of adult distribution ; 2) size structure of juveniles. The need for reduced competition between juveniles, observed in the English channel as well as in the Mediterranean, controls the position of biological events on the hydrological calendar. Once this adjustement obtained, the remaining biological events are placed in relation to particular values of physical parameters but this situation may not be ideal. This allows to introduce the notion of imperfection or price to pay for instance existence of a spread period of larval formation apparently not coordinated with development of a mucous protection or poor success of early released larvae in spite of a protection. The coordination or adjustment of biological events on the hydroclimatic calendar is not insensitive to external influences. The oocyte growing phase and the period of releasing larvae from a cocoon are sensitive to temperature deviations in fall and spring, respectively. The earlier the cocoons develop, the more important the spreading of larvae and the more limited their success. The source of year to year variability in settlement and adult biomass (the success of a life-cycle) appears to be located in the interference of two types of determinisms : 1) evolutionary biology, which addresses ultimate causes such as the specific adjustment of biological events superimposed on the climatic calendar ; 2) functional biology which addresses proximate causes and deals with a physiological function on a short term scale such as oocyte growth linked with temperature. Absence (in the Atlantic and English channel) or presence (in the Mediterranean) of a mucous egg-mass in the life-cycle appears to be independent of the coordination setting in action the two circles representing biological and hydrological events. It seems to be linked to the control of dissemination. In the Mediterranean, where the adults are distributed in a very limited narrow belt perpendicular to the coast, a reduction of larval dissemination appears to be relevant. On the other hand, in the English channel, at the term of a maximal dissemination, larvae are still in an area where adults are collected and control of dissemination seems to be less significant.

7. *Year to year variation : quantitative model*

Study of year to year variations in recruitment shows that short term perturbations may be the root-cause of the variable success of species. The biomass level of *E. nebulosa* is determined during short periods of the year (Bhaud *et al.* 1995a). A methodological consequence obliges to disregard the analysis of annual means which may suppress or seriously obscure the short-term deviations. It is an obligation to use fine scale observations and to look at act precise periods of life-history when modeling. Our first models were proposed for a spawning period which extended during the spring increase of temperature (Fig. 6). In an earlier publication (Bhaud *et al.* 1995b) five reproductive traits were integrated in a first step model : 1) distribution of egg-masses during the spawning period with 4 peaks occurring during this period, at intervals of 28 days ; 2) range from 30000 to 5000 larvae per egg-mass, at the beginning and end of the reproductive period, respectively ; 3) temperature curve from January to June established from a 10 year series of observations ; 4) the pattern of larval release from the mucilaginous masses (Duchêne & Nozais, 1992) ; and 5) the lo-

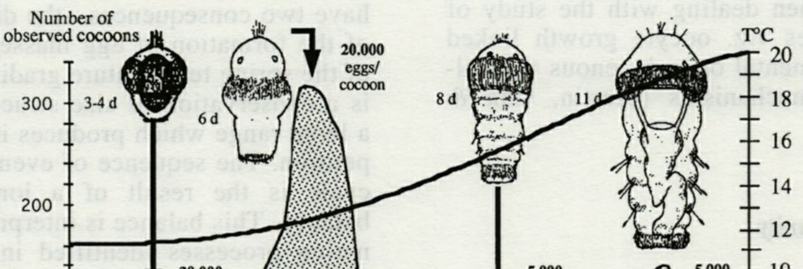


Fig. 6. – Variation during the reproductive period of the number of egg-masses (distributed in 4 distinct peaks), and variation of the morphology of larvae when escaping from mucilaginous masses. Morphological steps are function of the temperature. The mean number of larvae per egg-mass is given from five year observations. Variation of morphology and ability to disseminate when larvae are released is a factor of outstanding importance for success of recruitment. Timing of peaks of egg masses depends on moon phases which are not superposable from year to year ; consequently border between months is not given. Variation of sea water temperature is given from four year observations (Bhaud 1991 ; Duchêne & Nozais 1993).

Fig. 6. – *Variation au cours de la période de reproduction du nombre de masses mucilagineuses distribuées en 4 pics, et de la morphologie des larves au moment de leur libération ; cette morphologie est fonction de la valeur de la température. Le nombre moyen d'œufs par masse muqueuse est donné à partir de cinq années d'observation. La variation de la morphologie et de la capacité de nage lors de la libération des larves est une composante essentielle du succès du recrutement. L'emplacement des maximums des masses d'œufs dépend des phases de la lune qui ne sont pas superposables d'une année à l'autre ; en conséquence les limites entre les mois ne sont pas indiquées. La courbe de variation de la température de l'eau de mer repose sur quatre années d'observations (Bhaud 1991 ; Duchêne & Nozais 1993).*

cation of the spawning period : the first peak more frequently located in early March, the latter at the end of May. Posteriorly, a modulation in the releasing period of larvae was introduced. The new model was based on 1 000 cocoons distributed during the reproductive season following data already given (Bhaud *et al.* 1995) and derives from models developed on *Thelepus* (Duchêne 1990, 1992). Two steps were described (Fig.7). First, the seasonal variation of the number of larvae leading a planktonic life of 2 days at least can be estimated. Accordingly, these larvae were free to move away from the area inhabited by adults of the preceeding generation. The seasonal variation of the number of larvae directly reaching the substratum after being released from cocoons is also represented (in Fig. 7 with the graph between January and April on the top diagram and from March to June on the lower diagram). The earlier the formation period of the cocoon, the higher the number of released larvae at a planktonic stage, and the lesser the probability of a successful settlement. Thus, when the reproductive season begins in January, the number of swimming and benthic larvae reaches 29×10^6 and 0.45×10^6, respectively. When reproduction is delayed until March, the same figures are 23×10^6 (swimming larvae) and 6.8×10^6 (benthic larvae). Secondly, we represent in rectangles A, B and C, the relative variation of protected larvae (inside the cocoon), planctonic larvae (free swimming larvae), and last, benthic larvae (or tubicolous larvae). The place of the maximum is given by a vertical straight line and the detail of the releasing by a bell shaped curve. During the reproductive season, the proportion of free larvae, at first important in A, decreases in B and disappears in C. In this last situation, this means that larvae when released reach the tubicolous benthic life directly.

Until now, a fixed number of oocytes was considered as well defined; and their distribution along reproductive period was modeled accordingly. In the future we will apply a refined model to the variation in oocyte formation by integration of the growing phase during fall; in this particular case, between year variations will depend on the duration of the thermocline.

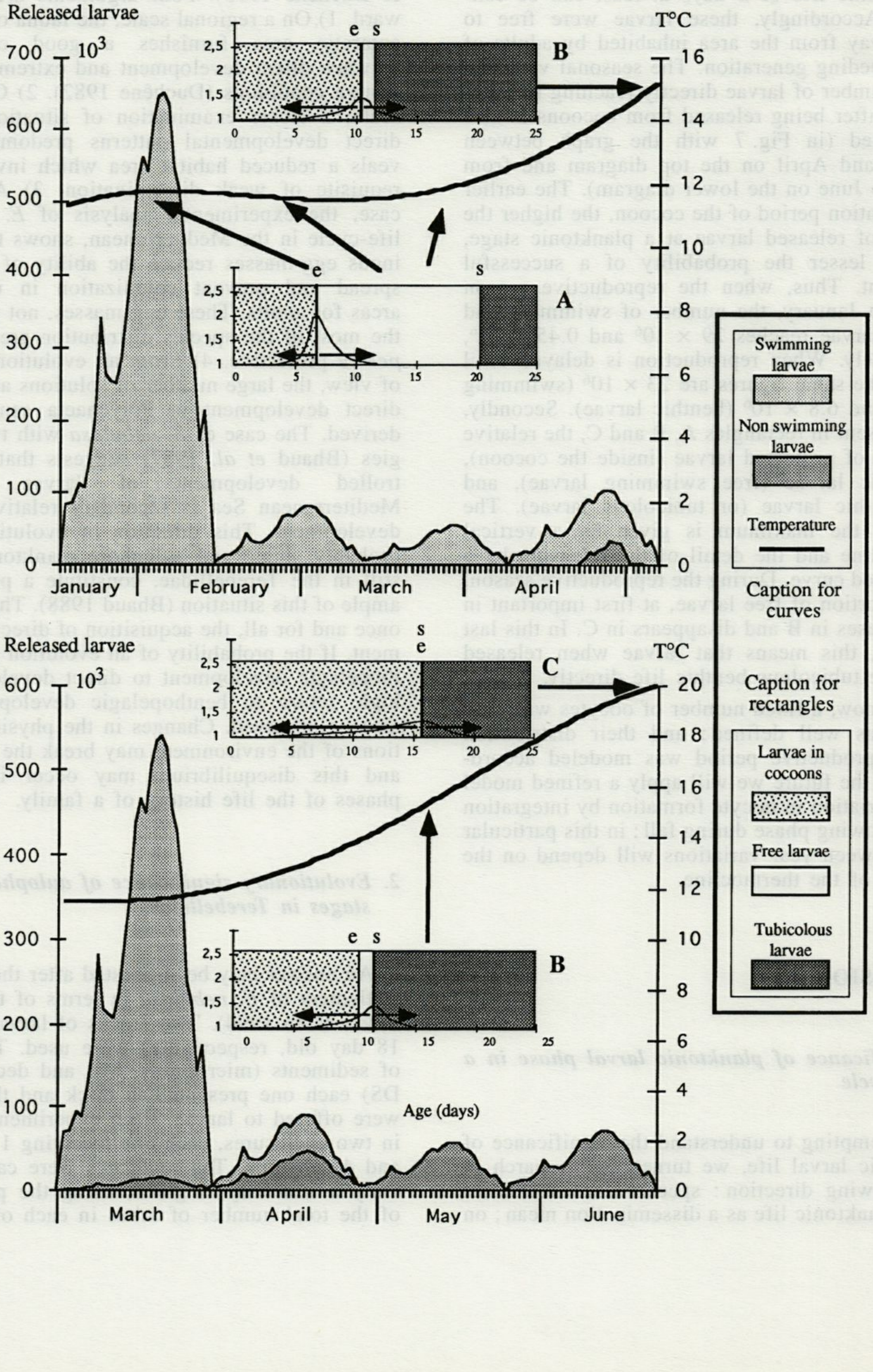
DISCUSSION

1. Significance of planktonic larval phase in a life-cycle

In attempting to understand the significance of planktonic larval life, we turned our research in the following direction : species does not select larval planktonic life as a dissemination mean; on the contrary, species attempt to break free from this constraint. At the present time, research on recruitment is concerned, to a large extent, with the consequences of larval planktonic development within the physical structures of water masses which appear negative for a successful recruitment. On an evolutive time-scale, this coupling raises the question of the origin of direct development. This pattern has been considered as an answer to constraints of dissemination (Bhaud & Duchêne 1995). Four arguments are put forward. 1) On a regional scale, the fauna of the subantarctic area furnishes a good correlation between direct development and extreme disseminative conditions (Duchêne 1982). 2) On a local scale, a closer examination of situations where direct developmental patterns predominate, reveals a reduced habitat area which involves the requisite of weak dissemination. 3) A specific case, the experimental analysis of *E. nebulosa* life-cycle in the Mediterranean, shows that gelatinous egg-masses reduce the ability of larvae to spread and prevent colonization in unsuitable areas for adults. These egg-masses, not present in the most of the species distribution area, are not *per se* protective. 4) From an evolutionary point of view, the large number of solutions adopted by direct development in Polychaeta can only be derived. The case of *E. nebulosa* with two strategies (Bhaud *et al.* 1987) suggests that the controlled development of larvae in the Mediterranean Sea is secondary relative to free development. This direction of evolution is not probably single and aulophore planktonic stages still in the Terebellidae, constitute a perfect example of this situation (Bhaud 1988). There is not, once and for all, the acquisition of direct development. If the probability of an evolution from benthopelagic development to direct development is high, return to benthopelagic development can also be observed. Changes in the physical conditions of the environment may break the life-cycle and this disequilibrium may occur in several phases of the life history of a family.

2. Evolutionary significance of aulophore larval stages in Terebellidae

An answer may be suggested after the study of settlement of *E. nebulosa* in terms of the age of larvae (Cha 1994). Two stocks of larvae (14 and 18 day old, respectively) were used. Two types of sediments (microbeads, MB and decanted silt DS) each one presented in thick and thin layers were offered to larvae. Each experiment was run in two enclosures, each one receiving 1 age class and 4 substrata. Ten replicates were carried out. Only a summary is given, using the percentage of the total number of tubes in each of the four sediments. Younger larvae preferred the thin layer of sediment. Presence (in DS) or absence (in MB) of organic matter was not a source of variance. The nature and the thickness of the sediment were of lesser importance for old than for young larvae. An age difference of four days resulted in highly modified settlement. Older larvae were less susceptible to differences between substrata; they had a greater settlement capability than younger larvae, and they were distributed more evenly between different sediments. Likewise, observation of settlement during a prolonged time of incubation, in presence of several grain sizes of the same sediment, displays the progressive development of the ability to use this sediment. In this experiment, the sediment not used after 24 h is perfectly used at the end of 3 or 4 days (Cha 1994). This suggests the acquisition of new abilities by larvae.



Due to development larval size increase, parapodia are more numerous, first tentacles larger, mucous secretions more intensive and uncinal plates more numerous. These modifications explain why a sediment first unusable becomes usuable (Fig. 8). These experiments show that a planktonic individual having an advanced developmental stage when contacting substrata for the first time, has a larger probability of settling than a younger one. Constraints linked to an uncompleted morphological organization are suppressed. Lengthening the planktonic life during stages with juvenile morphology results in the decrease of settlement constraints. The presence of mature *L. conchilega* in the Bay of Banyuls in a large range of sediments (sand with *Branchiostoma lanceolata*, muddy sand with *Nephtys hombergii*, detritic communities with *Venus ovata* and *Auchenoplax crinita*) is a consequence of this lengthening. The situation of aulophore larvae Terebellidae is interesting because : 1) It means a return towards a benthopelagic life-cycle. 2) The planktonic larva is not a trochophore but a postlarva; this is what Jägersten (1972) names a secondary planktonic larva. 3) The evolution does not come back throughout the same way used during the first transformation (Bhaud 1988); the second acquisition of a planktonic stage is made by a new process (Dollo Law). 4) Conditions for recruitment are probably original. This last point is supported by three reasons : 1) the first contact with substrata is early and takes place when larvae build detritic tubes; 2) the second contact concerns a post larval or juvenile stage, from a morphological point of view; 3) the ability to use a large spectrum of sediment for building tubes is increased as showed formerly.

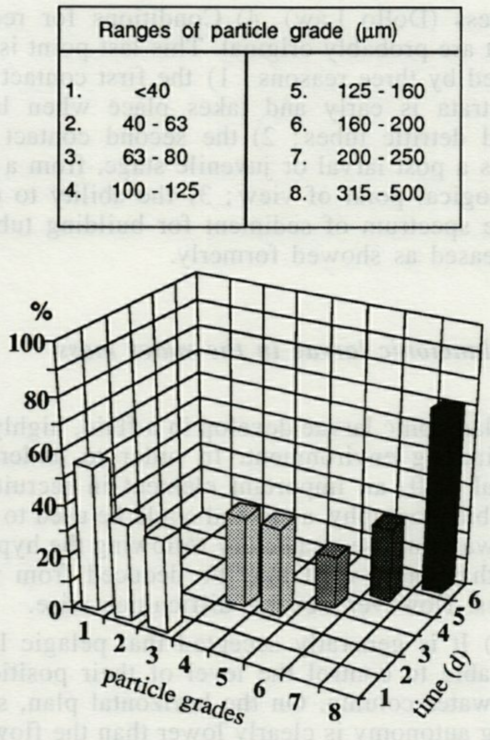
3. *Planctonic larvae in the water mass*

Planktonic larvae develop in a fluid, highly disseminating environment. In order to understand larval drift, an important element in recruitment and biogeography, a method could be used to track the water masses trajectory following the hypothesis that larval drift may be deduced from water flows. However, several difficulties arise.

1) It is generally accepted that pelagic larvae are able to control the level of their position in the water column. On the horizontal plan, swimming autonomy is clearly lower than the flow rate observed in the field. Consequently, it was proposed that horizontal dissemination is passive. This opinion is a simplification : by vertical migration, larvae are able to use different flow direc-

Fig. 7. – Model of seasonal variability in the planktonic larval emission from egg masses. The model is based on data collected over several years. The curves show the numeric variation of the number of larvae released from 1 000 egg masses for different spawning seasons and, accordingly, for variable temperatures. The upper graph presents the most common case : a spawning season starting in early March. The lower graph is for a spawning period starting in mid-January. The number of larvae with a longer planktonic larval life is more important when spawning occurs early in the year. Rectangular graphs present the length, (days), after egg-mass production of three steps : protected development in the egg mass, free planktonic stages and tubicolous life. The relative importance of these steps is given in terms of different temperatures : A, B and C are for 12 °C, 15 °C and 20 °C, respectively. The date of release (e) is variable and this variability is indicated by horizontal arrows. The associated curve indicates the intensity of larval releasing from the egg-masses. The onset of tubicolous life (s) is assumed from observations on behaviour of tube building and from the disappearance of larval vitelline reserves. Sensitivity of larval growth to varying temperatures is responsible to a large extent for the planktonic larval phase. It contributes defining the position of the metamorphosis, either within (when temperature is high) or outside (when temperature is low) the protected cocoon. In the first case, the local recruitment is particularly successful.

Fig. 7. – *Modélisation de la variabilité saisonnière dans l'émission larvaire planctonique. A partir d'une situation moyenne obtenue sur plusieurs années d'observations, la modélisation permet de simuler la libération des larves à partir des cocons. Les courbes présentent la variation numérique du nombre de larves libérées à partir de 1 000 cocons en fonction des périodes de ponte et par conséquent de la température ambiante ; de plus on a dissocié les larves planctoniques libres et les larves n'ayant pas ou plus de possibilité de nage. Le graphique du haut représente le cas le plus fréquent : celui d'une période de ponte qui débute au mois de mars. Le graphique du bas s'applique à une période de ponte qui débute en janvier. Le nombre de larves ayant une vie planctonique longue est plus important si la ponte débute tôt dans l'année. Les médaillons rectangulaires représentent la durée en jours, après la production du cocon, des trois phases dites protégée, libre et tubicole en fonction de la température : A, B et C correspondent respectivement à 12 °C, 15 °C et 20 °C. La date d'émission (e) est variable. Cette variabilité est figurée par deux flèches horizontales, qui matérialisent l'étendue de la libération, et par une courbe qui donne une idée de l'intensité de cette libération à partir des cocons. Le début de la phase tubicole (s) est déduit des observations comportementales liées à la construction du tube et aussi déduit de la disparition des réserves vitellines. La sensibilité de la croissance larvaire à la température est largement responsable de la durée de vie planctonique et contribue à positionner la période de métamorphose soit à l'intérieur de la masse mucilagineuse lorsque la température est élevée, soit à l'extérieur du cocon lorsque la température est basse. Dans le premier cas, la phase planctonique est supprimée ce qui favorise le recrutement local.*



Ranges of particle grade (µm)			
1.	<40	5.	125 - 160
2.	40 - 63	6.	160 - 200
3.	63 - 80	7.	200 - 250
4.	100 - 125	8.	315 - 500

Fig. 8. – Progressive use by *E. nebulosa* of increasingly large sediment particles. Average of three experiments. For each size of sediment particle we have shown (%) the maximum number of tubes built and the time required to obtain this maximum after the introduction of larvae. The bigger the size of the particles, the later the tubes appear.

Fig. 8. – *Utilisation progressive de grains de sédiment de taille croissante par* E. nebulosa. *Moyenne de 3 expériences. Pour chaque taille de grain, on a indiqué (%) le nombre maximum de tubes construits et le délai de ce maximum après l'introduction des larves. Plus la taille des grains augmente et plus l'apparition des tubes est tardive.*

tions and on a regional scale there is a decoupling of the length of planktonic life and the distance covered from location of larval emission to settling point.

2) In order to include larvae in a model, we must define some characteristics of their displacement like size and density. However, displacement rates are difficult to determine when a visual or actographic recording clearly indicates something other than a direct run towards the bottom or the surface. Larval movements reveal slowing, acceleration, reversal, immobility, in quick alternation with upward and downward runs linked with mucous secretion or modification of behaviour (Nozais 1995). Larvae may vary its fall rate only by opening setigerous bundles after contact of a foreign particle. Finally, when at the proximity of substratum they can reach the water column after testing the sediment-water boundary if it is not clear enough supposing a fluid middle layer of fine particles. Briefly, if each elementary segment of the run may be characterized by a given rate, it is only possible to chart the whole displacement at the price of a simplification based only on extreme points of the course.

3) We suppose now that the obstacle of the variability on a short-time scale and also the variability linked with morphological development, can be resolved by determining the relatively constant fall rates from narcotized specimens. This method allows the introduction of artificial particles with the same fall rate than larvae in a hydrodynamic enclosure. Active or passive fall of larvae when reaching two kinds of sediment arranged in different squares of a checker may then be tested. However, the use of these mimetic particles supposes a short length for incubation of living larvae in the experimental enclosure. It cannot pass beyond some minutes if we wish the distribution achieved at the end of the fall to be correlated only with active or passive falls and not altered by new benthic larval distribution following the fall. Accordingly, larvae do not appear as passive as it may be thought from rapid observations. Consequently, larval travel cannot be deduced from mean flow or residual vectors.

CONCLUSION

We wish to emphasize only the two following points.

How to consider life-cycle parameters? It seems more interesting and profitable to examine the significance of the length of life of planktonic larvae integrated with other traits, rather than its absolute value. The level of this dissemination in the loss or the maintenance of individuals is probably connected with the size of the area suitable for larval reception, that is to say the size of the area suitable for adults. In such a situation, a species with a reduced distributional area and a weak capability to disseminate, would not work differently from another species which would lead a planktonic larval life for several weeks without going outside its adult distributional area, either because this adult area is very important or because larvae are put through antispreading hydrological structures. Life-cycles or life-histories have not got an unitary character but are composed by several groups of traits evolving for their own part. These traits are neither completely in concert nor completely independent. Our target species develops two groups of traits; from one group to another, these elements are independent. The coupling of these traits may be difficult. For instance, the existence of gelatinous egg-masses may be in connection with control of larval

E. nebulosa: Mediterranean population or invertebrate species with a short larval life

E. nebulosa: English Channel and Atlantic population, or invertebrate species with a longer larval life

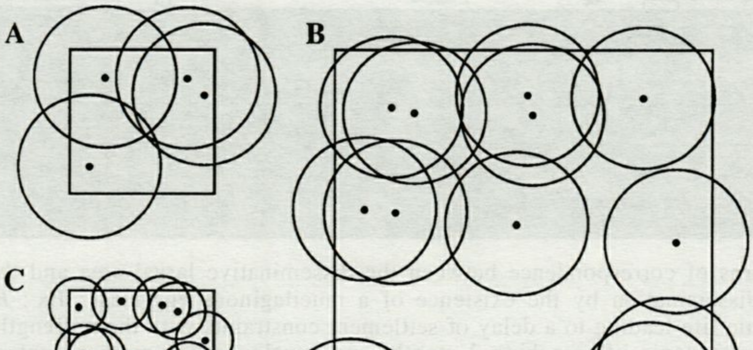


Fig. 9. – Co-ordination in *E. nebulosa* between surface area inhabited by adults (squares) and presence or absence of egg masses; these structures delay larval escaping therefore limit the ability to disseminate (circles). Supposing that the ability to disseminate in the Mediterranean populations (A), is similar to that of the Atlantic populations (B), the expected result would be : in A nearly all larvae would reach the borders of the habitat, thus the maintenance of the species would be unlikely. Species response is as follows : Mediterranean populations are able to overcome the constraint of small habitat by reducing the ability to disseminate (C); egg-masses become essential. This basic model does not take into account possible behavioural adaptations to hydrodynamic structures by larvae.

Fig. 9. – *Coordination chez* E. nebulosa *entre la grandeur de l'aire des adultes (carrés) et la présence ou l'absence des masses d'œufs; ces structures retardent la libération des larves et par conséquent limitent la capacité de dissémination (cercles). En supposant que la capacité de dissémination des populations méditerranéennes (A) et d'Atlantique (B) soient similaires, le résultat prévisible est qu'en A l'ensemble des larves atteint la limite de l'habitat, ce qui rend improbable le maintien de l'espèce. La réponse de cette dernière en Méditerranée est la réduction de la dissémination (C) par l'existence de sac muqueux emprisonnant les larves.*

spreading or with energy management. Only fine observations, experimental and comparative approaches allow one correct decisions.

How to define the ultimate constraints of a life-cycle? Organisms, through the game of selection, attempt to free themselves from advection, either by elaboration of larval behaviour or by suppression of the free larval stage with evolution towards a direct life-cycle. From the double set of solutions we can see there is not a direct relationship between area habitat and planktonic life length. However, the observation of a short larval life leads to the probably reduced area of adult habitat (Bhaud & Duchêne 1995). Our strategy is based on the hope of finding biological laws or features of general application. It could be put forward that the diversification and the variety of responses often observed could be a limitation in this attempt of generalization. However, correctly used, this disadvantage is not real and leads to a better identification of the function. For instance, the ability of larvae to disseminate constitutes a numeric value to introduce in a conceptual model of the life-cycle of the species. Dissemination requirements are present in all species, and the large range of their values is not an obstacle to use a common model. If parameters are highly variable between species, the functional structures are not so varied and their identification must be exact. Comparison of Mediterranean and Atlantic populations of *E. nebulosa* (Fig. 9) perfectly indicates that the ultimate goal is the quest of an agreement between the adult habitat and the first recruitment area. Such a constraint secures a connection between the old benthic adult phase and the terminal planktonic larval phase by the link of the respective inhabited field area. The difference between

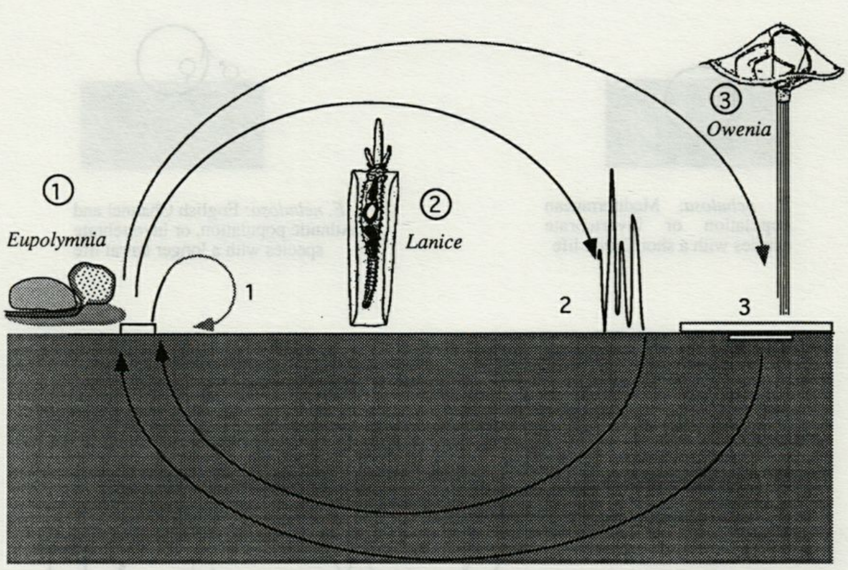


Fig. 10. – Several patterns of correspondence between the disseminative larval area and the habitat area of adults. 1) Checking of larval dissemination by the existence of a mucilaginous egg-mass; Ex : *Eupolymnia nebulosa.* 2) Prolongation of planktonic life leading to a delay of settlement constraints with their strength decreasing. Ex : *Lanice conchilega* with a long planktonic life reaching 2 months and developping numerous contacts with the sediment. 3) Larvae are passive; they suffer limited constraints during settlement and make the best of a large range of substrata; they settle on an area larger than adult habitat and during jevenile development there is a progressive reduction of the recruitment area by mortality of individuals at the periphery. Ex : *Owenia fusiformis.*

Fig. 10. – *Les différentes modalités d'un accord entre l'aire de dissémination larvaire et l'habitat des adultes. 1) Le contrôle de la dissémination larvaire s'effectue par développement d'une structure mucilagineuse. Ex :* Eupolymnia nebulosa. *2) La prolongation de la vie planctonique entraine un retard des contraintes sédimentaires avec diminution de leur intensité. Ex :* Lanice conchilega *avec une vie planctonique très longue (2 mois) qui se termine par des touchers sédimentaires nombreux. 3) La dissémination des larves est passive; elles subissent peu de contraintes au moment de leur établissement; elles s'accomodent d'une large variété de substrats et se fixent sur une aire qui dépasse largement l'habitat des adultes reproducteurs; l'accord se fait progressivement au cours du développement de la phase juvénile par mortalité des individus de la périphérie de l'aire de recrutement. Ex :* Owenia fusiformis.

both areas is an estimation of the mortality rate during the juvenile phase. However, the fundamental constraint in a life-cycle is not to reduce the ability of dissemination but to return to the adult habitat or to preserve this habitat, the ultimate goal being to ensure mating. This is achieved by different strategies, the control of dissemination and the development of elaborate larval behaviour, among them. Strategies reported in Fig. 10 may be schematized as follows. 1) The future of larvae is secured by controlling their dissemination as soon as they are formed. 2) The species does not control dissemination, and what's more, they use their dissemination by transforming it in advantage through prolongation of life in open water or through the development of a return process supported by physical structures of water masses. These two solutions aim to delay settlement constraints and, as a consequence, to diminish the strength of these constraints when larvae settle on the substratum. Moreover, the test of substrata are made possible by balooning processes. 3) A generalized dissemination allows to an overlapping of the adult area, and, accordingly, to a renewal of individuals in adult area but the price is a large loss after the overflowing of the adult area by larvae. Consequently, a general and fruitful idea emerges : the place of the largest loss of individuals is probably located during the benthic phase and is represented by the difference between the area receiving first recruits and the area where mature individuals are limited.

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