Light influence on larval emission and vertical swimming in the terebellid worm
Eupolymnia nebulosa (Montagu, 1818)

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ABSTRACT

The reproduction of a population of the terebellid worm, *Eupolymnia nebulosa*, was studied at the Arago Marine Laboratory in the western Mediterranean. As many as four spawnings occur from early March to mid June. Eggs are released within jelly masses, counted and collected from a 30 m^2 area at various times. Larval outputs from the egg masses were observed. The corresponding swimming activity of the trochophores was measured by mean of an actographic device. The apparatus developed for that purpose allowed fast localisation of sets of up to 400 larvae on a motionless area, or tracking of a single larva by means of computer driven video camera located on translators. The real time video tracking of the swimming larvae allowed precise spatial localisation within gradients. The influence of light was tested on early larvae. Cocoons were analysed in normal and controlled conditions, in order to quantify the number of emerging larvae at different temperatures and growth rates. Larval growth increased with temperature. The larval output from the jelly masses was faster at lower temperatures and high density of larvae within the cocoon. The larval output was closely related to light, increasing the larval swim : most of the larvae were emitted in the plankton during day light. Observations indicated large differences between the four spawnings with implications for recruitment. The first spawning period with lower temperatures, a high phototropy and higher swimming rate of the trochophores resulted in wide larval dissemination. The remaining spawnings, with lower egg density, a higher temperature associated with a faster growth rate, lower swimming activity and longer retention within the cocoon, ensured a good local recruitment.

RÉSUMÉ

Influence de la lumière sur l'émission et la nage verticale des larves chez le térébellide *Eupolymnia nebulosa* (Montagu 1818)

Cette étude concerne la reproduction d'une population d'*Eupolymnia nebulosa*, Annélide Terebellidae, située en face du laboratoire Arago, en Méditerranée occidentale. La période de ponte s'étend de mars à juin, avec quatre pics. Les œufs sont pondus dans des cocons muqueux, qui sont recueillis et comptés à diverses périodes sur une surface de référence de 30 m^2. L'émission larvaire à partir de ces cocons est étudiée. L'activité de nage des trochophores recueillies est mesurée à l'aide d'un système actographique, développé dans ce but. Ce système permet les enregistrements rapides des positions d'un maximum de 400 larves dans un nuage sur un champ fixe, ou le suivi en temps réel d'un seul individu au moyen de caméras vidéo fixées

sur des translateurs pilotés par un ordinateur. Les enregistrements en temps réel des larves permettent un positionnement précis des larves dans des séries de gradients avec estimation de leur vitesse de nage. L'influence de la lumière a été testée sur les jeunes larves émises à partir des cocons, maintenus en conditions contrôlées, de manière à apprécier le nombre de larves émises dans le temps. La croissance larvaire s'accroît avec la température. La sortie des larves hors des cocons est plus rapide aux basses températures et pour des hautes densités larvaires à l'intérieur des cocons. L'émission larvaire est liée à la lumière, qui augmente l'activité de nage des trochophores et provoque une sortie maximale durant la phase éclairée. Les implications des 4 pontes sur le recrutement sont très différentes : la première période de ponte, lorsque les températures sont basses, la phototropie élevée et le comportement natatoire des larves très actif, favorise une large dissémination. Les pontes suivantes, qui présentent une densité d'œufs plus faible, une température plus élevée associée à un taux de croissance supérieur, une activité de nage plus faible et une rétention accrue au sein des cocons muqueux, favorisent quant à elles un bon recrutement local.

INTRODUCTION

The reproductive trends of the polychaete *Eupolymnia nebulosa* has been studied for several years in front of the Arago marine laboratory in Banyuls on the western Mediterranean. Personal field observations made by scuba diving revealed that synchronous spawning occurred. On a small submarine cliff, diver observations showed that cocoon production starts at night and lasts until the following week. There were up to four spawning peaks from early March to early June. Records are known for a breeding-ground in front of the laboratory, but concerned only the number of cocoons (GRÉMARE, 1988; BHAUD & GRÉMARE, 1988; DUCHÊNE & NOZAIS, 1992). Larval settlement was analysed in laboratory experiments involving types of sediment and settling in a hydrodynamic flume (BHAUD, 1991; CHIA & BHAUD , 1991). Observations were made in order to estimate the quantity of larvae present over the sediment (DUCHÊNE & NOZAIS, 1992). It appeared that the larval development was highly dependent on external parameters such as temperature (DUCHÊNE, 1982). This modified larval growth and the time when larvae are released from the protective cocoon. Cocoons having different eggs densities were found during the spawning period (DUCHÊNE & NOZAIS, 1992). The first peaks, in March, involve dense cocoons with up to 30,000 eggs. In late May, the mean number of eggs per cocoon had fallen to about 3,500 eggs. The larval density within the cocoon seems to have an influence on the larval release by modifying the structure of the jelly mass. A closer look indicated that larval output from the protective cocoons occured only at certain times of the day. Light appears to be an important synchronising factor for the larval release from the protective cocoon. In order to estimate the influence of the light on larval swimming and behaviour, we developed an actographic device which was able to quantify the displacement of larvae in aquaria with a precision of some microns. The small size of the young *Eupolymnia* larvae led us to adapt the recording system. This involved the use of a small video camera with a magnifying lens mounted on a set of translators allowing large displacement. The field sampled by this camera is very small and compensated by the displacement of the 10 μm precision translators. The only way to automatize this apparatus was to perform a real time analysis on a computer. The camera is then moved by the computer in order to follow the larval displacement.

MATERIAL AND METHODS

Eupolymnia nebulosa larvae are released in the plankton from protective cocoons. The age of every cocoon studied is known from quadrat recordings on the coast in front of the laboratory. The cocoons were gently collected by diver from the rocks from a depth of one meter or less. Each cocoon was isolated in a tank with controlled temperature and light. All the larvae swimming in the tanks were collected and counted every four hours. Individuals were then used for measurement of swimming speed and displacements in controlled light conditions. External recordings of light intensity were used to adapt the controlled light conditions in the tanks.

The age of all larvae used in the measurements was known with a precision of four hours for the March experiments and 12 hours for the other experiments. Larval observations were made within horizontal and vertical tanks. The horizontal tanks were small sized black coated containers with a 6 mm water layer : larvae are attracted by a lateral light source in a non-coated area and when they stop swimming they remain on the bottom of the tank. The vertical tanks were aquaria of various sizes, the most commonly used was 10 x 20 x 40 cm in height.

A set of equipment has been used in this study for locating and counting the young larvae as soon as they are liberated from the mucous cocoon (Fig. 1). Besides the delayed observations realised with the digitizing tablet and the video tape recorder, a real time computer based recording system has been developed in order to achieve a

nearly automatic record of larvae locations within an aquarium. This system is presented on the upper right side of figure 1.
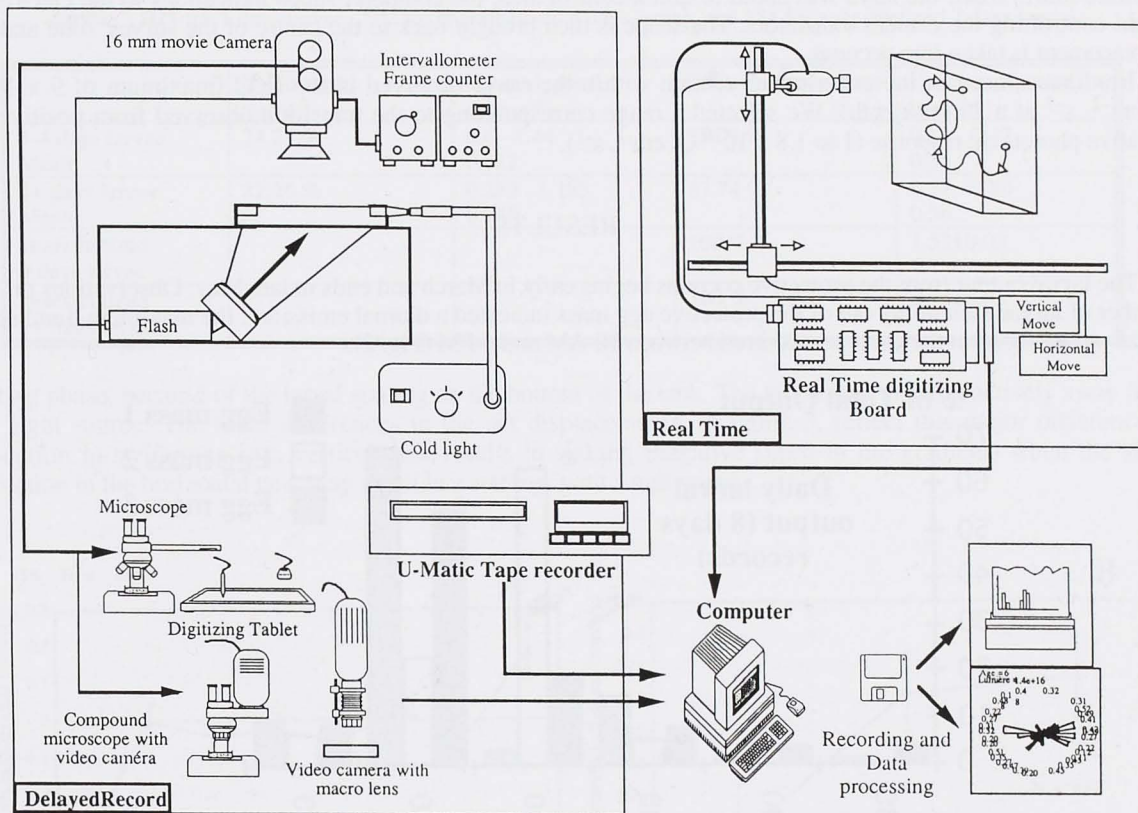

FIG. 1. — Actographic device used for larval displacement measures. Delayed records are made with a video camera connected to U-Matic tape-recorder and with a 16 mm movie camera with intervallometre in order to obtain various recording speeds. The treatment involves a set of digitizers. The real time recordings are made by a computer driven system with video cameras attached on translators allowing size independant measurements (with various optical devices). In the present analysis the size of *Eupolymnia* larvae was between 100 and 220 µm. Motionless measurement of up to 400 larvae or tracking of a single larva over a 1 m distance (length of the longer 12.5 microns precision translator) is possible with the home made software. The real time measurements allow shape extraction and treatment of 4 to 12 frames per second.

A video camera was attached on a X-Y translator driven by step motors. A second camera was mounted at a right angle on the same support to provide depth indications. The step motor translator (CharlyRobot™) allows displacement of video cameras with 12.5 µm steps. Twenty four frames per second are sent to a video digitizer board (MCB™ from Lumiere Technology) connected to a micro-computer (Apple MacIntosh IIcx). A program was developed to insure the video signal analysis. It used MPW-Pascal and MPW-C for the program shell and specific machine language routines (using MPW-Asm) for fast computing related to video acquisition. This resulted in the storage and computation of a pixel matrix followed by the saving of larval location information on text files usable by standard spread sheet programs. The program drives the translators and computes relative displacements. The recording/computing process allowed a mean speed of about 4-12 frames. s[-1], depending on the type of recording.

Two different modes were tested during larval analysis :

- a "cloud" analysis of a set of up to 400 larvae (generally we used 50 larvae) with recordings of the analysed video field every tenth of a second. In this case the computer system is used like the standard tape recording video

analysis systems with a real time analysis instead of a delayed study of the shapes. We used a motionless camera mode for the study (the barycenter of the larval group may be calculated with associated camera translation). This allowed us to make precise estimations of the light conditions for every place in the video field.

- a single individual tracking, with long displacements (the larger translator allows a maximum displacement of 1,020 mm). When the larva was about to quit a control area, the computer sends indications to the electronic board controlling the camera translators. The shape is then brought back to the centre of the survey zone and its displacement is taken into account.

Irradiances used in the experiments remain within the range observed in the field (maximum of 9×10^{16} Q. cm^{-2}. s^{-1} at a 20 cm depth). We selected a range corresponding to the transition observed from positive to negative phototaxic response (1 to 1.8×10^{16} Q. cm^{-2}. s^{-1}).

RESULTS

The larval output from the protective cocoons begins early in March and ends in late May. Observations on the number of larvae swimming out of the protective egg mass indicated a diurnal emission : the maximum number of larvae emerging from the cocoons occurred between 10 AM and 6 PM (Fig. 2).
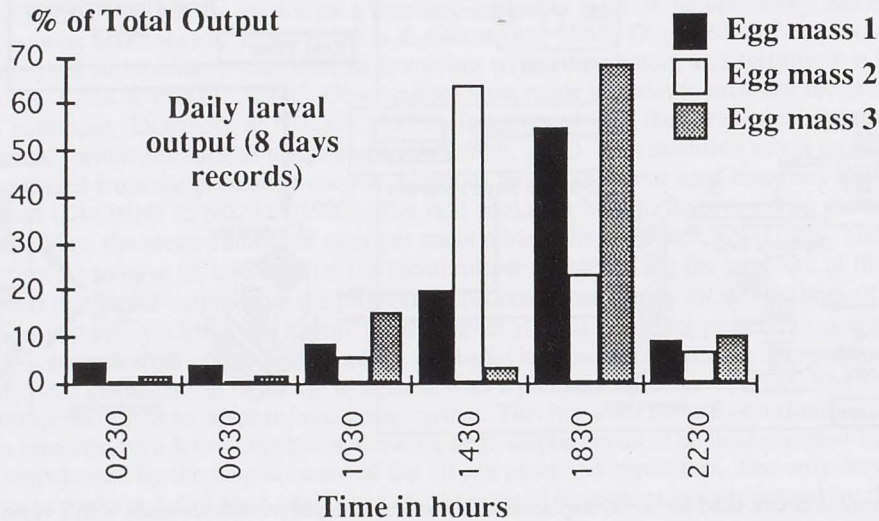

FIG. 2. — Number of larvae swimming out of the protective cocoon at different hours of the day. The cocoons are empty after 8 days. The presented percentages are summed up for every class of time and for 3 different egg masses in March 91. The main larval output occurs between 10h30 and 18h30.

Clear photopositive reaction was measured in the first free swimming stages: all the individuals between three and 10 days were found close to the light source within a few minutes. The swimming speed of the three day old larvae increased with light intensity. The four day old larvae swim actively toward the light source and remain 1.0 mm from the surface. The photopositivity decreased with age: the 10 day old larvae were found in a 5 mm layer below the surface.

The swimming behaviour of *E. nebulosa* larvae consists of short periods of fast swimming towards the light source and long, scattered periods of rest or slow motion. As shown in Table 1, 24 % of the swimming of a three day old larva is directed toward the light with an average speed of 0.982 mm. s^{-1}, and 76 % of the displacement are active sinking periods with a slow upward motion compensating passive sinking, resulting in a downward movement with a mean speed of 0.35 mm. s^{-1}. This is demonstrated by records of anaesthetized larvae presenting a downward displacement with values ranging from 1.3 to 1.7 mm. s^{-1}.

Observations were made to find the illumination corresponding to a general switch from photopositive to negative displacement in a light gradient (Fig. 3). For the observations made in the vertical tanks, the negative displacements consisted in a reduction of the active upward swimming phases, resulting in semi-passive sinking.

In horizontal tanks movements were active in both directions. The illumination level did not change during the

TABLE 1. — Swimming speed of *Eupolymnia nebulosa* larvae of different ages. The range and the mean of the upward and downward speeds of non anaesthetized animals are given, for the variations are important depending on the intensity of the light. The 95 % confidence interval is shown for anaesthetized individuals. Numbers of measures is 4,275 for 3-4 days larvae, 1,023 for 7 days larvae, 502 for anaesthetized 4 days larvae, and 184 for anaesthetized 7 days larvae.

	% Upward moves	Upward speed (mm. s^{-1})	% Downward moves	Downward speed (mm s^{-1})
3-4 days larvae Mean	24.21 %	0.6 - 1.44 0.982	75.79 %	0.18 - 0.47 0.35
7+ days larvae Mean	32.26 %	0.289 - 1.183 0.740	67.74 %	0.27 - 0.80 0.56
anaesthetized 4 days larvae			100 %	1.52±0.02
anaesthetized 7+ days larvae			100 %	0.94±0.05

resting phase, because of the larval settling on the bottom of the tank. The larvae had to swim actively away from the light source. The scale differences in the net displacements, in figure 3, reflect this major difference: a reduction in swimming in a vertical tank results in sinking (negative speed in the gradient) when the same reduction in the horizontal tank may result in a settling, with a null speed.
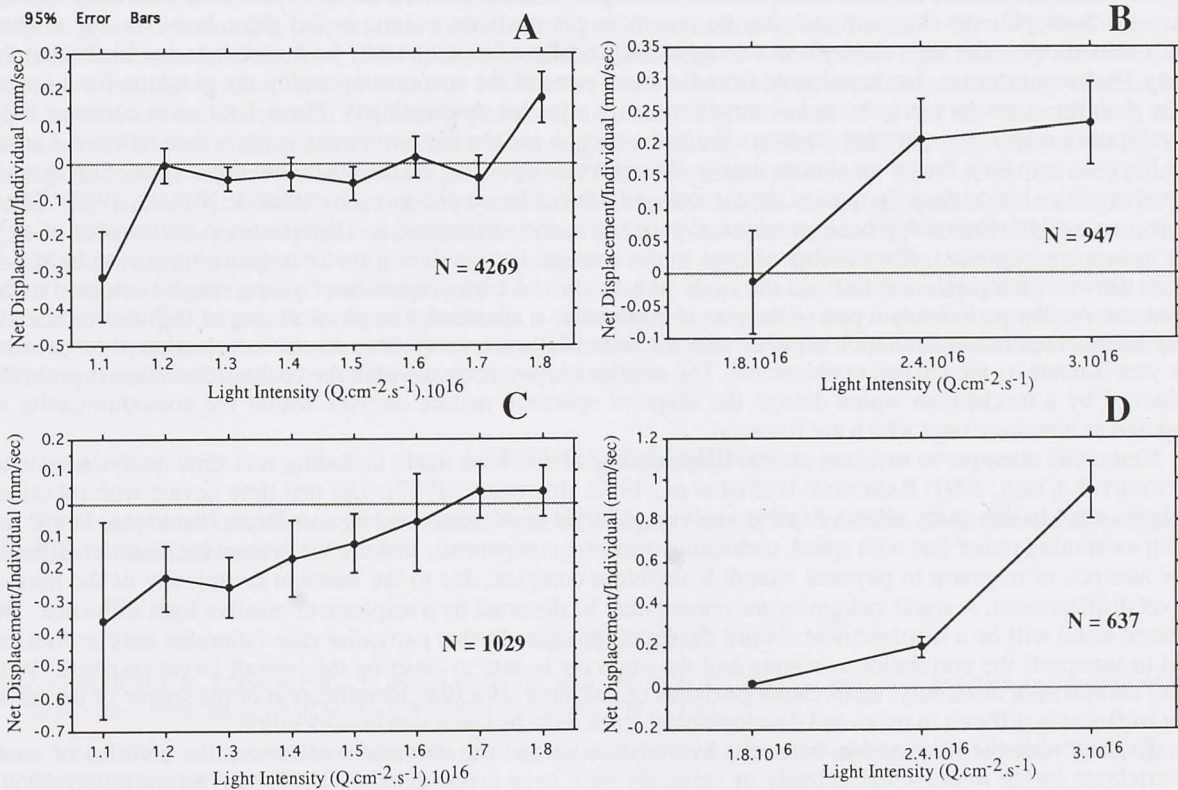

FIG. 3. — Measurements on larval swimming as a function of light intensity in vertical (A and C) and horizontal (B and D) tanks. Net displacements correspond to the mean displacement of a set of several larvae for 2 different ages (A-B: 4 day old larvae; C-D: 7 day old larvae). The grey line corresponds to neutral buoyancy. N represents the number of larvae used for the 95 % confidence interval.

From figure 3 it appears that the switch from positive to negative swimming occurs for light intensities ranging from 1 to 2 x 10^{16} Q.cm^{-2}. s^{-1}. Lower illuminations always correspond to sinking, higher illuminations to upward swimming. The differences between four day and seven day old larvae depended on the position and the pattern of the inversion: older larvae needed a stronger stimulus to increase their swimming rate. The maximum mean speed toward the stimulus, computed by considering only the positive displacements is :

- 1.34± 0,09 mm. s^{-1} for an illumination of 1.6 x 10^{16} Q. cm^{-2}. s^{-1} for 4 day old larvae;
- 1.17± 0,04 mm. s^{-1} for an illumination of 1.4 x 10^{16} Q. cm^{-2}. s^{-1} for 7 day old larvae.

The net displacement is not only related to the mean speed of movement toward the light source but also to the swimming/rest ratio. The data in figure 3 suggest that this ratio increased with the intensity of the stimulus and reached higher values for older larvae at higher light intensities. In the vertical tanks the records concerning larvae remaining close to the surface have been eliminated.

DISCUSSION AND CONCLUSIONS

Studies involving terebellid polychaetes revealed the importance of early protection during the first developmental stages within egg masses. The positive phototropic response of trochophores of *Eupolymnia* in first stages increased the dispersion of larvae by causing them to swim toward the surface. This had been observed with the subantarctic polychaete, *Thelepus extensus* (DUCHÊNE, 1982). In both cases the first free swimming stages emerging from the cocoon were usually strongly sensitive to light. Larvae may change their response toward specific physical parameters during their planktonic life. A late negative phototropy was found in many cases which lead to increased settling on the benthos.

When the larvae were released to the plankton they can remain in a free swimming period for varying lengths depending upon the environmental conditions and the specific abilities of the larvae. These terebellid trochophores have lecithotrophic development and may be present in the plankton as long as 2-3 days, however, the settling trials start shortly after the release from the egg mass. Local modifications may be found: it seems likely that the early *Thelepus extensus* larvae released from the outer parts of the cocoon stay within the plankton for a longer time than the inner larvae (personal observations, in Kerguelen Archipelago). These later ones continue their development within the spherical chambers inside the cocoon and the free swimming stage is then reduced. Larvae are likely to stay for a longer or shorter time in the plankton depending on the positionin the cocoon. *Eupolymnia* larval densities inside the jelly masses appear to modify the emission patterns (DUCHÊNE & NOZAIS, 1992). There is also a possible relationship between physical parameters and vitellogenesis. Differences in the number of eggs per spawn are important. The number of eggs in the cocoons is high during the first spawning period in March when the water temperature is low and the larval growth slow. A high proportion of young stages is emitted to the plankton. At that period only a part of the oocyte production is spawned. The physical size of the mucous cocoon may be involved in this limitation together with the state of oocyte maturation. An active selection of large-sized oocytes is made by the ciliated nephrostome. The smaller oocytes remain within the coelom. Selection is probably achieved by a mechanism which detects the shape of spherical mature oocytes within the coelomic cavity as opposed to immature ones which are flattened.

Numerous attempts to measure animal displacements have been made including real time analysis systems (ROONEY & COBB, 1991; BAKCHINE-HUBER *et al.*, 1992; BOISCLAIR, 1992). The real time device with robotized cameras used in this study allows flexible analysis of larval movements on large surfaces. Planktonic larvae are often swimming rather fast with spiral, undulating direction components, making the precise localisation difficult. The analysis of response to physical stimuli is therefore complex, due to the inherent complexity of the normal larval displacement. A spiral swimming movement may be distorted by a response to positive light influence. The general trend will be a displacement toward the light emission. In that particular case (stimulus easy to localize and to interpret) the correlation is simple and the observer is able to describe the overall larval response. With other stimuli such as salinity, temperature gradients or sediment attraction, identification of the source of the larval displacement is difficult to make and developmental stage must be taken into consideration.

To determine the relationship between hydrodynamics and the movement of larvae, the abilities of some invertebrate larvae to move horizontally or vertically have been investigated by KONSTANTINOVA (1966, 1969), MILEIKOVSKY (1973) and CHIA *et al.* (1984); but swimming direction was not always specified. More recently BUTMAN *et al.* (1988) measured swimming speeds and sinking velocities of two sibling species of *Capitella*. Their swimming speed varied between 2 and 4 mm. s^{-1}. Horizontal movements of large amplitude or the transportations of long duration seem to be the characteristic of ciliated larvae endowed with efficient trochae. This is found in the

larvae of Nephtyidae, Spionidae or Chaetopteridae (CAZAUX, 1981). The use of parapodia is found in the nectochaetes of Aphroditidae. Nectosomes of Poecilochaetidae move by snake-like undulating movements (BHAUD & CAZAUX, 1988). Larvae without swimming apparatus or reduced cilia, for example Orbiniidae, Lumbrineridae, do not possess the ability to rise in the water column and are observed rarely in planktonic samples. However, some species such as *Lanice conchilega* with aulophore larvae lack a swimming device and are collected in large numbers in the water column.

Observations on larval motion appear to be of interest when dissemination and settling considerations are analyzed. If large-scale dispersal of planktonic larvae is determined mainly by oceanic circulation (SCHELTEMA, 1971; PALMER, 1988), larval behaviour may influence settling probability at very small spatial scales (CRISP, 1974; ECKMAN, 1983). The larval swimming speed is generally too low in comparison with currents to have an effect on horizontal movements. As pointed out by CHIA *et al.* (1984) larval swimming may however influence the vertical migrations. Vertical distribution is likely to be controlled by vertical motions except when stratification exists (MILEIKOVSKY, 1973). THORSON (1964) proposed vertical movements could be the result of ontogenic changes in photoresponse which appear sometimes during larval life. Those predictions have been confirmed by laboratory observations (MARSDEN, 1984, 1986, 1990), field observations (YOUNG & CHIA, 1982a, b) and correlated data (FORWARD *et al.*, 1984). Many studies show that light strongly influences larval behaviour (FORWARD & COSTLOW, 1974; VIA & FORWARD, 1975).

The larval emission recorded in these experiments shows that the release in the plankton of more than 90% of the larvae occurs during the day and generally during the highest local illumination period. Light intensities at this period recorded close to the water surface level (20 cm depth) were between 2.4 and 9 x 10^{16} Q. cm^{-2}. s^{-1}.

Light intensity necessary to switch from positive to negative motion appears to be located in a rather narrow range for the young *E. nebulosa* studied in this set of experiments (4-7 days old). The response to a light stimulus corresponds to an increase of the swimming speed with a positive/negative heading and to a modification of the larval behaviour (rest/swim ratio or settling tendency/light stimulation constraint). In March, response to light induces upward swimming proportional to the intensity of the stimulus. In this case, the light stimulus seems to increase the dissemination phase (first spawning). Later in the season, when natural light intensity increases, the larvae are emitted in the plankton in lower densities and at a later developmental stage, resulting in a reduced photosensitivity and a reduced swimming phase. The positive displacement of seven day old stages at high illumination levels is still possible, but most these stages are usually found within the jelly masses. In the bay facing the marine laboratory in Banyuls, rotary motion currents allow planktonic larval retention over precise areas. The continuous current speed observations indicate clearly that the larvae are unable to swim against the current flow. On the contrary, the vertical motions observed indicate clearly a possible vertical displacement from the shallow water sediment, where the larvae are emitted to the surface and back. The vertical structure of the water masses shows a clear and rather constant reversal of the current direction depending on the depth (DUCHÊNE, 1994, in prep.). In these conditions a short vertical migration may induce a complete reversal in passive transportation by the currents. The vertical swimming observed in the *Eupolymnia* larvae is sufficient to allow this transition from an out of the bay to an inward motion.

ACKNOWLEDGEMENTS

REFERENCES

BAKCHINE-HUBER, E., MARION-POLL, F., PHAM-DELEGUE, M.H., MASSON, C., 1992. — Real-time detection and analysis of the exploratory behavior of small animals. *Naturwissenschaften*, **79** : 39-42.

BHAUD M., 1991. — Larval release from the egg mass and settlement of *Eupolymnia nebulosa* (Polychaeta, Terebellidae). *Bull. mar. Sci.*, **48** : 420-431.

BHAUD, M. & C. CAZAUX, 1988. — Description and identification of Polychaete larvae; their implications in current biological problems. *Oceanis*, **13** : 596-753.

BHAUD, M., GRÉMARE A., 1988. — Larval development of the terebellid Polychaete *Eupolymnia nebulosa* (Montagu, 1818) in the Mediterranean Sea. *Zool. Scripta*, **17** : 347-356.

BOISCLAIR, D., 1992. — An evaluation of the stereocinematographic method to estimate fish swimming speed. *Can. J. Fish. Aquat. Sci.*, **49** : 523-531.

BUTMAN, C.A., GRASSLE, J.P., BUSKEY, E.J., 1988. — Horizontal swimming and gravitational sinking of *Capitella capitata* sp.I (Annelida: Polychaeta) larvae: implications for settlement. *Ophelia* , **29** : 43-57.

CAZAUX, C., 1981. — Evolution et adaptation larvaires chez les Polychètes. *Oceanis*, **7** : 43-77.

CHA, J.H., BHAUD, M., 1991. — Etude expérimentale du recrutement benthique en canal hydrodynamique et en milieu calme. *C.R. Acad. Sci.*, **312** Sér.3 : 113-118.

CHIA, F.S., BUCKAND-NICKS, J., YOUNG, C.M., 1984. — Locomotion of marine invertebrate larvae: a review. *Can. J. Zool.*, **62** : 1205-1222.

CRISP, D.J., 1974. — Factors influencing the settlement of marine invertebrate larvae. *In*: P.T. GRANT & A.M. MACKIE (eds), *Chemoreception in marine organisms*, Academic Press, 1974.

DUCHÊNE, J.C., 1982. — *Étude comparée de la biologie d'Annélides Polychètes considérées en différentes zones climatiques.* Thèse de Doctorat d'Etat, ès Sci. Nat., Univ. P. & M. Curie, 1-315 pp.

DUCHÊNE J.C., NOZAIS, CH., 1992. — Etude de l'émission des stades larvaires précoces d'*Eupolymnia nebulosa* (Polychaeta : Terebellidae). *Annales Inst. Océanogr.*, **68** : 15-24.

ECKMAN, J.E., 1983. — Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.*, **28** : 241-257.

FORWARD, R.B., Jr., COSTLOW, J.D., Jr., 1974. — The ontogeny of phototaxis by larvae of the crab *Rhithropanopeus harrisii*. *Mar. Biol.*, **26** : 27-33.

FORWARD, R.B., Jr., CRONIN, T.W., STEARNS, D.E., 1984. — Control of diel vertical migration: Photoresponses of a larval crustacean. *Limnol. Oceanogr.*, **29** : 146-154.

GRÉMARE, A., 1988. — *Aspects quantitatifs de la reproduction chez quelques Annélides Polychètes : Intérêts et perspectives.* Thèse Doctorat d'Etat, Univ. P. & M. Curie, 218 pp.

KONSTANTINOVA, M.I., 1966. — Characteristic movement of pelagic larvae of marine invertebrates. *Dokl. Akad. Nauk. SSSR*, **170** : 726-729.

KONSTANTINOVA, M.I., 1969. — Movement of polychaete larvae. *Dokl. Akad. Nauk. SSSR*, **188** : 942-945.

MARSDEN, J.R., 1984. — Swimming in response to light by larvae of the tropical serpulid *Spirobranchus giganteus*. *Mar. Biol.*, **83** : 13-16.

MARSDEN, J.R., 1986. — Response to light by trochophore larvae of *Spirobranchus giganteus*. *Mar. Biol.*, **93** : 13-16.

MARSDEN, J.R., 1990. — Light responses of the planktotrophic larva of the serpulid polychaete *Spirobranchus polycerus.*. *Mar. Ecol. Prog. Ser.*, **58** : 225-233.

MILEIKOVSKI, S.A., 1973. — Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Mar. Biol.*, **23** : 11-17.

PALMER, M.A., 1988. — Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. *Mar. Ecol. Prog.Ser.*, **48** : 81-91.

ROONEY, P., COBB, J.S., 1991. — Effects of time of day, water temperature, and water velocity on swimming by postlarvae of the American Lobster, Homarus americanus. *Can. J. Fish. Aquat. Sci.*, **48** : 1944-1950.

SCHELTEMA, R.S., 1971. — Larval dispersal as a means of genetic exchange between geographically separated populations of shoal-water benthic marine gasteropods. *Biol. Bull.*, **140** : 284-322.

THORSON, G., 1964. — Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. *Ophelia*, **1** : 167-208.

VIA, S.E., FORWARD, JR., R.B., 1975. — The ontogeny and spectral sensitivity of polarotaxis in larvae of the crab *Rhinthropanopeus harrisi* (Gould). *Biol. Bull.*, **149** : 251-266.

YOUNG, C.M., CHIA, F-S., 1982a. — Ontogeny of phototaxis during larval development of the sedentary polychaete, *Serpula vermicularis* (L.). *Biol. Bull.*, **162** : 457-468.

YOUNG, C.M., CHIA, F.S., 1982b. — Factors controlling spatial distribution of the sea cucumber *Psolus chitonoides*: settling and post-settling behavior. *Mar. Biol.*, **69** : 195-205.