DYNAMICS OF EGG PRODUCTION IN MEDITERRANEAN POPULATIONS OF THE TEREHELLID POLYCHAETE *EUPOLYMNIA* *NEBULOSA*

CHRISTIAN NOZAIS*, DANIEL MARTIN*†, JAE-HOON CHA*‡, JEAN CLAUDE
DUCHÊNE*, FRANÇOIS CHARLES* AND ANTOINE GRÉMARE*

*Observatoire Océanologique de Banyuls, Université Pierre et Marie Curie, CNRS URA 117, BP 44,
F-66650 Banyuls-sur-mer, France; †Centre d'Estudis Avançats de Blanes, 17300 Blanes-Girona, Spain.

‡Korean Ocean Research and Development Institute, Ansan PO Box 29 Seoul, 425-600 Korea

The dynamics of egg production by a Mediterranean population of the terebellid polychaete *Eupolymnia nebulosa* was assessed both in the field and in the laboratory between 1992 and 1994. Our results confirm the occurrence of several peaks of jelly mass production at the population level. They show that such peaks result from the production of several broods per individual female (the number of produced broods increasing with female size). Jelly masses produced at the end of the breeding season tend to be smaller and to contain fewer eggs than those produced at the beginning of the breeding season. Worms produced significantly larger jelly masses in 1994 than in 1993 and 1992, without noticeable change in corresponding fecundities. The computation of temporal changes in eggs produced per unit of surface area in the cove of Paulilles shows that most of the eggs are produced during the first two peaks of jelly mass production. These results are discussed relative to the different hypotheses invoked to account for the occurrence of several spawnings in Mediterranean populations of *E. nebulosa*. It is concluded that no single explanation, such as the allometry constraint hypothesis or heterogeneity in oogenesis rates, can be retained.

INTRODUCTION

As stated by Thorson (1950), ~70% of the marine benthic invertebrates produce planktonic larvae which are released in the water column where they are influenced by hydrodynamic processes such as advection and eddy diffusion. Therefore, one of the main points of interest when studying the recruitment of benthic invertebrates featuring a complex life cycle is to understand the interaction of their pelagic larvae with their physical environment (Sinclair, 1988; Butman, 1989; Mann & Lazier, 1991; Richards et al., 1995). Modelling the spatial distribution of larvae thus requires: (1) the elaboration of a physical model describing the distribution and intensity of currents within the studied area; (2) the assessment of larval production (at least in the studied area); and (3) the acquisition of data regarding the hydrodynamic characteristics (including swimming capabilities) of the larvae.

Mediterranean populations of the polychaetous annelid *Eupolymnia nebulosa* (Montagu) have been extensively studied for almost ten years now in the Banyuls area (Bhaud et al., 1987; Grémare, 1988; Bhaud & Grémare, 1991; Duchêne & Nozais, 1992; Cha, 1994;

Nozais, 1995; Bhaud et al., 1995b). This interest is mainly due to the reproductive characteristics of the Mediterranean populations of this species (extended breeding period characterized by several spawning peaks and presence of a jelly mass in which young larvae are incubated) which facilitates the collection, the ageing and the experimentation on larvae. This explains why *E. nebulosa* has been selected as a biological model in the framework of the French national programme on recruitment determinism (PNDR) which led to numerous and various studies assessing reproductive cycle (Bhaud et al., 1995a), reproductive effort (Grémare, 1986), larval development (Bhaud & Grémare, 1988; Bhaud, 1988a,b) and larval swimming performances (Duchêne & Nozais, 1994). Moreover, a physical model describing the distribution and intensity of currents in the Bay of Banyuls under different wind regimes has been developed within the same framework (Arnoux & Fraunié, 1994; Verdier-Bonnet, 1996). Coupled with the existing data on ontogenic changes in buoyancy (Nozais & Duchêne, 1996), time devoted to swimming, and swimming performances (Duchêne & Nozais, 1994), this could allow modelling of the spatial distribution of *E. nebulosa* larvae in the Bay of Banyuls-sur-Mer.

However, some crucial information about the dynamics of egg production is still lacking. In Mediterranean populations of *E. nebulosa*, the breeding season lasts for approximately three months (i.e. from late February to late May). During this season, several brooding peaks separated by resting periods (Grémare, 1988) occur, and it has been suggested that these peaks are synchronized by the lunar phase (Bhaud & Grémare, 1991). Although Grémare (1988) has collected indirect laboratory evidence suggesting that individual females reproduce several times during this period, little quantitative information was available about the dynamics of jelly mass and egg productions at both the individual and the population level. Duchêne & Nozais (1992) noticed that either the morphology and the age of the larvae at the emergence of the jelly mass were very different during the beginning and the end of the breeding season. These authors attributed this primarily to increasing temperature. They also showed that these differences were associated with differences in swimming behaviour thereby suggesting that eggs produced during the beginning of the breeding season were subjected to greater dissemination than those produced at the end of the breeding season. It is thus necessary to assess the dynamics of egg production by *E. nebulosa* (both at the individual and the population levels) in order to get a clear picture of temporal changes in the input of larvae for modelling their spatial distribution in the Bay of Banyuls.

This study was designed to answer this particular question. It combines: (1) a field survey of the number of jelly masses and larvae produced per unit of surface area over the whole breeding season; and (2) the monitoring of the kinetics of egg production by individual females kept in the laboratory. These results are then coupled to assess temporal changes in egg production during the breeding period.

MATERIAL AND METHODS

Field survey

Five quadrats (1 m² each) were placed at both 5 and 10 m depths in Paulilles Cove (Figure 1) during January 1994. The production (total number and newly produced), together with the volume of the jelly masses within these quadrats were then monitored weekly until the end of the breeding season (i.e. mid June 1994). The topography of each quadrat was mapped allowing for the identification of newly produced jelly masses. The volume of each jelly mass was estimated visually by SCUBA divers which led to the identification of three size classes (i.e. <5 cm³, between 5 and 10 cm³, and between 10 and 20 cm³).

Figure 1. Map showing the location of the harvesting sites (laboratory monitoring), and of the field site (field survey).

Laboratory monitoring experiments

The laboratory monitoring experiments consisted of assessing jelly mass production and corresponding fecundity in females kept individually in experimental chambers. They were carried out in 1992 on 11 females originating from the rearing units of the laboratory, in 1993 on 15 females originating from the rearing units of the laboratory, and in 1994 on 15 females originating from the rearing units of the laboratory, 11 females collected at Le Troc, 18 females collected at Port Vendres and eight females collected at Paulilles) (Figure 1).

Animals were collected in January, taken to the laboratory where they were maintained for four weeks in tanks (570x390x180 mm) filled with a thin (i.e. few millimetres) layer of sand originating from the Bay of Banyuls, and supplied with running sea-water.

One week prior the beginning of the breeding season (i.e. end of February), females (recognizable due to the presence of thoracic mucous glands) were individually transferred to experimental chambers (180x115x110 mm) filled with a thin layer of sand. Seven of these chambers were randomly assigned to a tank (570x390x180 mm) containing ten males and fuelled with running ambient sea-water. The circulation of water within the experimental chambers was ensured by 12 holes (2 mm in diameter) which proved to be efficient in precluding any escape from the experimental chambers. During both the acclimation period and the experiments, animals in each tank were fed weekly with 2 g DW of Tetramin® (Tetra).

Jelly mass production was monitored daily. All produced jelly masses were collected and assayed for volume and fecundity. Volumes were measured by recording (to the nearest 0.1 cm³) the displacement of sea-water due to the total immersion of the jelly mass. The measure of fecundities required the complete disintegration of the jelly mass. This was achieved by strong hand shaking for a few minutes. Counts were then carried out either on the whole jelly mass (when the total number of eggs was <4000) or on three 10-ml subsamples after dilution in 500 ml of filtered (1.2 µm) sea-water. At the end of the breeding season, the presence of coelomic gametes was observed by dissection of females previously anaesthetized with MS-222 (Sigma) and the dry weight (60°C, 24 h) of each female was measured. This procedure allowed for the quantification of the number of jelly masses produced by each female during the breeding season, and for the assessment of the dynamics of egg production at the individual level.

The effects of both the site of collection and the year of study were assessed by carrying out an analysis of variance (ANOVA) based: (1) on the data regarding worms collected from the rearing units of the laboratory in 1992, 1993 and 1994; and (2) on the data regarding worms collected from the rearing units of the laboratory, Port Vendres, Paulilles and Le Troc in 1994. Depending on cases, either a parametric two-way ANOVA (the rank of the brood or the position within the brooding period being the second independent variable) or a Kruskal-Wallis non-parametric ANOVA was used.

Computation of egg production in the field

Temporal changes in the amount of larvae produced in the Paulilles Cove during the 1994 breeding season were assessed based on: (1) the numbers of produced jelly masses per unit of surface area; (2) the volumes of produced jelly masses; and (3) the allometric relationship linking the volumes of individual jelly masses and the corresponding fecundities recorded for the 1994 breeding season.

RESULTS

Field survey

Temporal changes in the densities of observed jelly masses are presented in Figure 2. At both depths, jelly masses were observed between the beginning of March and mid June 1994. At 5 m depth, the number of observed jelly masses showed four distinct peaks: one corresponding to March, another corresponding to April and the last two corresponding to early May and from late May to early June. The picture is less clear at 10 m depth due to the impossibility of splitting the peaks of April and early May. At

Figure 2. Field survey. Temporal changes in the number of jelly masses observed within five quadrats, each of 1 m², at each of the two studied depths.

Figure 3. Field survey. Temporal changes in the number of jelly masses newly produced within five quadrats, each of 1 m², at each of the two studied depths.

this depth, there were thus three periods of high abundances of jelly masses: March, from April to mid May, and from the end of May to early June. The maximum number of observed jelly masses was found on the 11 April 1994 at both depths (21 and 12 jelly masses, respectively). Such a polymodal pattern for temporal changes in the density of observed jelly masses of *Eupolymnia nebulosa* is in good agreement with previous observations carried out in a semi-enclosed pool of the Bay of Banyuls-sur-Mer (Grémare, 1986). However, the present study is the first one in which the production of new jelly masses was also monitored. These data are presented in Figure 3 for the two studied depths. At both depths, there were four peaks of jelly mass production. The first one corresponds to March, the second one to early April, the third one to late April or early May, and the fourth one lasted from late May to early June.

Temporal changes in the volumes of the observed jelly masses are presented in Figure 4. At 5 m depth, most of the jelly masses were between 5 and 10 cm³ in volume, whereas the size distribution was much more balanced at 10 m depth. At both depths, there was no clear pattern of temporal changes in jelly mass volumes.

Figure 4. Field survey. Temporal changes in the volume of the jelly masses produced within five quadrats, each of 1 m², at each of the two studied depths.

Laboratory monitoring experiments

Dynamics of jelly mass production at the population level

Temporal changes in the number of produced jelly masses for the different treatments (i.e. years and collection sites) are shown in Figure 5. For all the treatments, the breeding season lasted between the beginning of March and the beginning of June. Most sites were characterized by the occurrence of several (i.e. 3 or 4) brooding peaks. This pattern was similar to what was observed in the field (see above), however it was less clear in some treatments (1994 rearing units for example) due to the partial fusion between consecutive peaks. This may result from the low number of produced jelly masses.

Number of jelly masses per female

All the females reproduced during the course of the study. Each of them produced between one and four jelly masses during each breeding season. The relative proportions of females producing one, two, three or four jelly masses are presented in Table 1 for the different treatments (i.e. both years and origins). There was no significant effect of the site of harvest on the number of produced jelly masses (Kruskal-Wallis ANOVA carried out on the 1994 data, $P=0.54$). This parameter was not affected by the year as well (Kruskal-Wallis ANOVA carried out on the data regarding worms collected in the laboratory, $P=0.15$). There was also no significant differences in average female dry weight among years and field sites (Kruskal-Wallis ANOVA $P=0.98$, and $P=0.22$, respectively).

Except for the females collected from the rearing units of the laboratory in 1994, the greatest proportion of females produced only one jelly mass. When looking at each treatment separately, it seems that there was a negative correlation between the number of produced jelly masses and the corresponding proportions. This trend becomes evident when pooling the data corresponding to all treatments (cf. last column of Table 1). Only one jelly mass was produced by 53.8% of the females per breeding season; 30.8% of the females produced two jelly masses; 12.8% of the females produced three jelly masses, whereas only 2.6% of the females produced four jelly masses. According to these results, the average number of jelly masses produced per female during one breeding season would be 1.64.

Figure 5. Laboratory monitoring. Temporal changes in the number of jelly masses produced for the six defined treatments (year/origin).

Table 1. Laboratory monitoring. Proportion (%) of females producing, respectively 1, 2, 3 or 4 broods. The first six columns refer to treatments (i.e. a combination of the year of study and of the harvesting site of the adult). The last column corresponds to the overall mean for all treatments.

	1992 Lab	1993 Lab	1994 Lab	1994 Troc	1994 Paulilles	1994 Port Vendres	Mean
1 brood	72.7	60.0	33.3	54.5	87.5	38.9	53.8
2 broods	27.3	26.7	46.7	27.3	0.00	38.9	30.8
3 broods	0.00	13.3	13.3	18.2	12.5	16.6	12.8
4 broods	0.00	0.00	6.70	0.00	0.00	5.60	2.60

Interestingly, there was a significant effect of female dry weight on the number of jelly masses produced during the breeding season (Kruskal-Wallis ANOVA, $P=0.009$). The average dry weight of females producing one jelly mass was 35.3 mg DW ($N=42$, $SD=16.3$) vs 38.3 mg DW ($N=24$, $SD=18.8$), 55.4 mg DW ($N=10$, $SD=13.7$), and 62.3 mg DW ($N=2$, $SD=4.9$) for females producing one, two, three, and four broods, respectively. Thus the production of three or four jelly masses appeared to be restricted to the largest females.

Kinetics of jelly mass production by individual females

The pattern of production of jelly masses by individual females was not strictly corresponding to the brooding peaks observed for the whole population. For example, females producing only one jelly mass during the whole breeding season did not

Figure 6. Laboratory monitoring. Relationship between the average volume of jelly masses, the year of study and the position within the breeding season (A), or the rank of the brood (B). Vertical bars are standard deviations. The number of measurements is indicated above each bar.

necessarily produce their brood during the first peak. Moreover, some females producing two jelly masses indeed reproduced during the first and second peaks, but others did so during the first and third. This pattern is also apparent when comparing the average time-lag between two consecutive broods produced by a given female. A two-way ANOVA carried out on the 1994 data shows that there was no effect of the site of collection but a significant effect of the rank of the brood. This last effect was confirmed by Kruskal-Wallis ANOVAs carried out on the data regarding the animals collected in the laboratory during 1993 and 1994 ($P < 0.03$ and $P < 0.006$, respectively). When pooling the results for all treatments, the average time-lag between broods 1 and 2 was 35.6 d ($N=36$, $SD=11.7$), against 24.1 d ($N=12$, $SD=7.6$) between broods 2 and 3 and only 19.5 d ($N=2$, $SD=6.4$) between broods 3 and 4.

Volumes of jelly masses

The relation between the position within the brooding period, the year of study and the average volume of produced jelly masses are presented in Figure 6A. At the population level, the average volume of jelly masses was not significantly affected by the collection site but decreased significantly (from 12.9 to 5.6 cm³ between March and May 1994) as the breeding season progressed (two-way ANOVA carried out on the 1994 data, $P=0.397$ and $P=0.0003$, respectively). The average volume of jelly masses was also significantly affected by the year of collection (two-way ANOVA carried out on the

Figure 7. Laboratory monitoring. Relationship between the position within the breeding season (A) or the rank of the brood (B) and the number of eggs per jelly mass. Vertical bars are standard deviations. The number of measurements is indicated above each bar.

data regarding the laboratory rearing units, $P=0.0275$, and $P=0.001$, for the effect of year and position within the breeding season, respectively). The interannual variability was mostly due to differences in mean volumes of jelly masses produced in March (mean volumes of 12.9 cm^3 in 1994 vs only 8.3 cm^3 in 1993 and 6.8 cm^3 in 1992, respectively).

The relation between the rank of the brood, the year of study and the average volume of produced jelly masses are presented in Figure 6B. At the individual level, the average volume of jelly masses was not significantly affected by the place of origin but decreased significantly with the rank of the brood (two-way ANOVA carried out on the 1994 data, $P=0.337$ and $P=0.0041$, respectively). In 1994, the average volumes of the jelly masses produced during the first brood was 10.8 cm^3 vs only 5.9 cm^3 for the third brood. The decrease in volume of the jelly masses was confirmed by the analysis carried out on the data from worms collected within the rearing units (two-way ANOVA, $P=0.0283$; $P=0.045$ for the effects of the rank of the brood and the year of study, respectively). The interannual variability appeared to be caused mostly by the first brood (average volumes of 5.9 , 8.7 and 10.8 cm^3 , in 1992, 1993 and 1994, respectively).

Fecundity

At the population level, there was no significant effect of the site of harvest on the average number of eggs contained in each jelly mass but this variable was significantly affected by the position within the breeding season (two-way ANOVA carried out on the 1994 data, $P=0.934$ and $P=0.0042$, respectively). The average number of eggs per brood was not affected by the year of harvest as well (two-way ANOVA carried out on the data regarding worms collected in the laboratory, $P=0.543$; $P=0.0003$ for the position within the breeding season). When pooling the results of all treatments, the average number of eggs per jelly mass ranged between 13,826 (March) and 5576 (May) (Figure 7A).

At the individual level, there was no significant effect of the site of harvest on the average number of eggs contained in each jelly mass but this variable was significantly affected by the rank of the brood (two-way ANOVA carried out on the 1994 data,

Figure 8. Laboratory monitoring. Relationship between female dry weight and the cumulated number of eggs produced during the whole breeding season. The regression line refers to data pooled for all treatments (year/origin).

$P=0.5162$ and $P=0.0058$, respectively). The average number of eggs per brood was not affected by the year of harvest as well (two-way ANOVA carried out on the data regarding worms collected in the laboratory, $P=0.389$; $P=0.0408$ for the rank of the brood). When pooling the results of all treatments, the average number of eggs per jelly mass ranged between 11,973 (first brood) and 6907 (fourth brood) (Figure 7B).

The total (i.e. cumulated over the whole breeding season) fecundity per female ranged between 762 and 55,166. The relationships between female dry weight and their total fecundity are presented in Figure 8 for the different treatments. When considering data originating from all the treatments, there was a significant relationship between these two parameters ($N=66$, $r=0.54$, $P=0.0001$). However, a simple linear regression model accounted for only 29% of the variance of total fecundities. This is mostly due to the fact that, for half of the treatments (i.e. rearing units 1992 and 1993 and 'Paulilles 1994'), the relationship between female dry weight and total fecundity was not significant.

The relationship between the volume of each jelly mass, and the corresponding number of eggs is presented in Figure 9A,B. For all treatments, there was always a significant relationship between these two variables. There was a significant effect of the year of study on the slope of the regression linking jelly mass volumes and corresponding fecundities (Reeve's test carried out on the rearing units data during 1992, 1993 and 1994, $P=0.034$). The variability between sites was assessed by considering the 1994 data. There was no significant effect of the site of harvest neither on the slope ($P=0.176$) nor on the interception ($P=0.460$) of the regression linking brood volumes and the number of eggs per brood. Thus all the 1994 data was pooled to infer the relationship between volume and fecundity in each brood.

Figure 9. Laboratory monitoring. Relationship between the volume of each jelly mass and the corresponding number of eggs. (A) corresponds to the worms collected from the rearing units of the laboratory in 1992, 1993 and 1994; (B) refers to the worms of different origins collected in 1994.

Figure 10. Computation of temporal changes in the number of eggs produced within the two 5 m² quadrats (z=5 and 10 m, respectively) studied during the field survey.

Estimation of the dynamics of larval production at the field site

Temporal changes in the amount of larvae produced in the field were estimated from: (1) the field estimations of temporal changes in jelly mass densities and volumes; and (2) the relationship between jelly mass volumes and fecundities. It became possible to evaluate. Regressions linking the jelly mass volumes and the corresponding number of eggs for 1994 provided us with average numbers of 2762, 7785 and 15,320 eggs for the three size classes of jelly masses defined during the field study. The estimated total number of eggs produced during each brooding peak at the field site are presented in Figure 10. At both depths, the highest peaks of egg production occurred during the beginning of April (i.e. second brood peak). When averaged for both depths, the first brooding peak accounted for about 27.6% of the total number of eggs produced during the breeding season, vs 44.0% for the second peak and only 17.0 and 11.4% for the third and fourth peaks, respectively.

DISCUSSION

Kinetics of jelly mass production by individual females

Our results confirm the existence of several brooding peaks (at the population level) during each breeding season (Bhaud & Grémare, 1991; Duchêne & Nozais, 1992). The results of the present study demonstrate that, in Mediterranean populations of *Eupolymnia nebulosa*, these peaks are caused by the fractionated emission of eggs by individual females. Preceding data were limited to those of Grémare (1988), which were based on the comparison of the total number of jelly masses produced during the 1985 breeding season, and the final number of females in a laboratory population. He reported a value of 3.17 jelly masses per female thereby suggesting the production of several jelly masses per female. His result could have been biased by mortality during the observation period of more than three months. The occurrence of several spawnings per female agrees with the report of up to five spawnings per female for another terebellid, *Nicolea zostericola*, in which no spawning peaks appear to occur at the population level (Eckelbarger, 1974).

In *E. nebulosa*, the dynamics of jelly mass production are not fully synchronized at the individual and the population levels. Simply put, all the females are not reproducing for the first time during the first brooding peak, for the second time in the second brooding peak, and so on. This pattern implies the existence of a synchronization factor for each brooding peak (i.e. something explaining that a female which has not reproduced during the first peak will wait for another one to do so).

It was initially thought that, in the Mediterranean populations of *E. nebulosa*, brooding peaks were synchronized by the lunar cycle (Bhaud & Grémare, 1991; but see also Duchêne & Nozais, 1992). Our results are not in good agreement with this hypothesis since the average time-lag between two consecutive broods tends to decrease (i.e. from 35.5 to 19.5 d) with the rank of the brood. This pattern is consistent with the decreases in the volume of individual jelly masses and the corresponding fecundities. One possible cause for the reduction of jelly mass volumes could be the occurrence of increasing temperatures which reduce dissolved oxygen concentrations in sea-water and may thereby limit the maximal size of jelly mass suitable for a good development of embryos (Chaffee & Strathmann, 1984; Strathmann & Chaffee, 1984; Hunter & Vogel, 1986; Strathmann & Strathmann, 1995). It is different from what was observed in *N. zostericola* (a constant time-lag of ~3 d between two consecutive broods throughout the breeding period) by Eckelbarger (1974). He provided no information on the corresponding fecundities. However, these masses were probably much smaller than those of *E. nebulosa* since the maximal number of eggs contained in one jelly mass was only 200. Thus the decrease in the time-lag between two consecutive broods observed during the breeding season in Mediterranean populations of *E. nebulosa* may be partly linked to the concomitant decrease in the average jelly mass volumes via the restoration of the mucous gland function, a process which could contribute to synchronization of females after the emission of the first brood.

Dynamics of egg production during each breeding season: consequences for larval dissemination

The main weakness of our estimation of temporal changes of *in situ* egg production lies in our evaluation of jelly mass volumes (i.e. only three size classes). This procedure was retained because we also wanted to assess the intensity of recruitment within the studied quadrats (Nozais, 1995), which precluded collection of the jelly masses in order to carry out direct counts. In the laboratory, average volumes of jelly masses decreased significantly during the breeding season. We did not find the same trend during the field survey. This is probably due to the resolution limits of our approach. Nevertheless, our estimation of the dynamics of larval production is in agreement with what was obtained for another site of the bay (i.e. a semi-enclosed pool located near the Banyuls observatory) (Nozais, 1995). We believe that this study provides a reliable estimation of the relative importance of the different brooding peaks in the Mediterranean population of *E. nebulosa*.

The results show that most of the larvae (72.6%) are produced during the first two brooding peaks. The possible bias associated with the evaluation of jelly mass volumes (see above) could even have resulted in a slight underestimation of the importance of these two peaks. In the Banyuls area, larvae produced during the first two peaks quit the jelly masses after 6–7 d (vs 12 and 15 d for the third and the fourth peaks, respectively) (Duchêne & Nozais, 1992). More interestingly such larvae can swim upward (average speed of 0.7 mm s^{-1}) which is no longer the case for those produced during the third and the fourth peaks (Duchêne & Nozais, 1994; Nozais, 1995). The emission of the majority of larvae at the beginning of the breeding season, thus increases the dissemination potential of the species (which probably remains relatively limited in any case due to the characteristics of the larvae). This result is surprising given that one hypothesis for the adaptive significance of brooding in marine invertebrates is that limitation of larval dispersion reduces mortality (Pechenik, 1979) and ensures the colonization of a suitable habitat (Chapman, 1965; Gibbs, 1968).

The data on temporal changes in egg production recorded during the present study will be coupled with an hydrodynamic model of the currents in the Bay of Banyuls, and with measurements of larval swimming performances to describe the dissemination of *E. nebulosa* under different wind regimes (Duchêne & Bhaud, in preparation).

The origin of the fractionation of gamete emission in Mediterranean populations of Eupolymnia nebulosa

In many invertebrates, brooding is associated with fractionation of the emission of larvae (Daly, 1972; Eckelbarger, 1974; Grémare, 1986; Grémare & Olive, 1986; Duchêne, 1991; McHugh, 1993). It is thus tempting to relate these two traits (Grémare, 1988). The hypothesis most common for this association assumes the existence of an allometry between the number of gametes produced and the size of the protective structure. Indeed, if the fecundity increases faster than the size of the protective structure, then an optimal strategy of larval production would require the occurrence of several broods. In polychaetes, this hypothesis seems to be sustained by the data recorded by

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