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Recruitment of the Clam *Ruditapes decussatus* in the Lagoon of Thau, Mediterranean

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The spatial and temporal patterns of recruitment of juvenile clams *Ruditapes decussatus* were investigated in the Mediterranean lagoon of Thau. The periods of release of clam larvae were determined by monitoring the gonad maturity index in samples of adult females. Two massive spawnings were detected. Recruitment, deduced from spat density, was abundant in one part of the lagoon (Etang des Eaux-Blanches) in 1987 but not in the following years. Conversely, it was absent in another part of the lagoon (Grand-Etang) in 1987, although it occurred previously there. The spatial patterns of recruitment in 1987 were highly heterogeneous. They could be related to circulation, modelled for the periods following spawning. In the Grand-Etang, where no recruitment occurred in 1987, the larvae were confined to the vicinity of intensive shellfish culture zones where they presumably were depleted from the water. Episodic local anoxia also likely caused massive mortality among recruits. Recruitment of invertebrates with planktonic larvae in Mediterranean lagoons thus depends on meterological conditions which directly or indirectly determine the timing of spawning, the circulation patterns, and the occurrence of anoxias. In the lagoon of Thau, the presence of large areas of intensive shellfish culture is a potential factor of massive mortality for larvae.

Introduction

The evaluation of recruitment success is a necessary step in modelling population dynamics, of prime importance in fishery management: information about some aspects of larval life in the plankton, like patterns of dispersal and sources of mortality, are a key to understanding demographic fluctuations. It is also a major focus of an increasing number of studies on the structure of benthic communities (Underwood & Fairweather, 1989). Genetic studies have stressed the locally high genetic heterogeneity of benthic invertebrate populations (Johnson & Black, 1984; Watts *et al.*, 1990; Borsa *et al.*, 1991) which

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could possibly be attributed to heterogeneity in recruitment, caused by fluctuations in settlement of discrete swarms of larvae of different origin or history. These results, as well as ecological studies showing that recruitment is a major determinant of community patterns of sessile organisms (Connell, 1985; Menge & Farrell, 1989) stress the need of further research about patterns and determinism of their recruitment success.

The palourde *Ruditapes decussatus* (L.), is extensively fished along the European Atlantic coast (Vilela, 1950; Fernandez-Pato, 1979) and in Mediterranean lagoons (Arnaud & Rimbault, 1963; Breber, 1980; Fischer *et al.*, 1987). Data on the dynamics of its natural populations are scarce, and have resulted from a few localized studies (Vilela, 1950; Fernandez-Pato, 1979; Guelorget *et al.*, 1981) whose objectives were to estimate biomass, growth and production. In addition, gonad maturation and reproduction have been studied using histological (Gallois, 1977; Breber, 1980) and biochemical methods (Beninger & Lucas, 1984). Between the phase of gamete maturation and that of sedentary benthic life are the planktonic larval phase and the recruitment phase. Both have been neglected, up to now, in population studies on *R. decussatus*.

The objective of the present study is to investigate recruitment in *R. decussatus* in the coastal lagoon of Thau (43°20'N, 3°40'E). Large areas in this lagoon have been transformed into zones of intensive cultivation of mussels and oysters (Figure 1) whilst in other areas, the remaining natural populations of *R. decussatus* undergo intensive fishing. An important feature of the Mediterranean lagoons is that they are regularly subjected to temporary, local anoxias which cause massive mortalities among populations of benthic invertebrates (Amanieu *et al.*, 1975; Borsa *et al.*, 1992).

We attempt to relate the spatial and temporal patterns of reproduction and recruitment in *R. decussatus* with data produced by a circulation model, in order to analyse the different steps in the process leading to recruitment. Emphasis will be given to patterns of larval dispersal and potential sources of mortality in the particular case of this heavily exploited Mediterranean lagoon.

Materials and methods

Reproductive activity

The timing of gamete release and subsequent larval development was deduced from observations on gonad maturation. We checked for the presence or the absence of oocytes, and for the state of maturation in adult female gonads (Gallois, 1977) throughout summer 1987.

In hatchery conditions, at 24–25 °C, the duration of the larval development of *R. decussatus* from Thau was 8 to 10 days (P. Borsa & A. Diter, IFREMER, unpubl.). We assumed that it is similar in the wild for the same range of temperatures.

Recruitment

The abundance of young recruits was inferred from the density of spat. The sampling sites for spat are shown in Figure 2. Sampling was carried out in winter, between November 1987 and March 1988, and was repeated at three sites, Barrou (station 5), Balaruc-Z.I. (station 12) and Balaruc-Port (station 4), in the following winters (1988–89 and 1989–90). The total area sampled at each site varied from 0·25 to 2·0 m^2. The first 0·01 m of sediment was removed using an Eckman grab (area 0·05 m^2), or a spade in a delimited area, and was sieved through a 2 mm sieve. The professional fisherman's hand dredge, locally called 'arseillère', was used at two stations: Plan de Roquerols (station 6) and Plan de Mèze

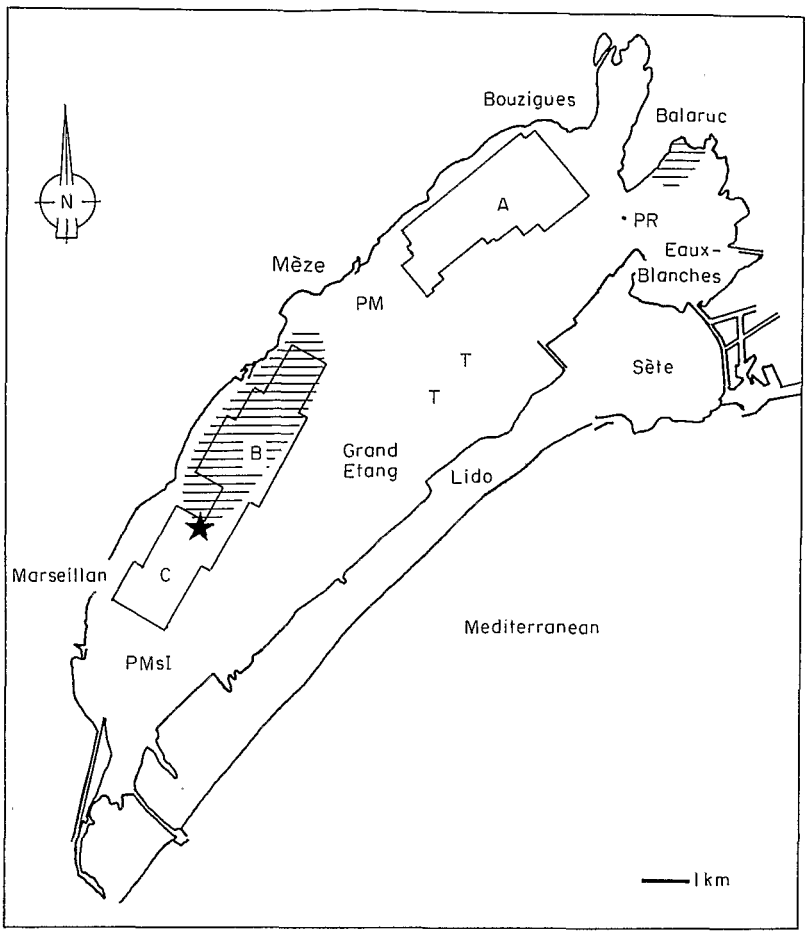

Figure 1. Map of the lagoon of Thau, with location of the intensive shellfish culture zones (A, B and C), and fishing areas for *R. decussatus* (PM Plan de Mèze; PMsl Plan de Marseillan; PR Plan de Roquerols; T toques). *Location of the meteorological station. Shaded: zones affected by the malaigue of July 1987 (see text).

(station 18) (Figure 2). Despite its 20 mm mesh size, this tool was useful in determining whether spat were abundant at a given site, because young individuals have a long byssus by which they attach to a fragment of shell or to a stone, so they are retained by the net.

Within-site sampling variance was estimated for a few stations (station 4, station 5, station 12 and station 15) and was found to be negligible, compared to between-site differences.

Environmental variables

Daily temperature and wind data were obtained from an automatic meteorological station located at the northern edge of shellfish-culture zone C (see Figure 1). Water temperature was measured 50 cm below the surface. Daily wind speed was computed from the cumulative value of wind passing over the anemometer (approximately 4 m above surface) over the day. The anemometer in zone C failed to record wind direction during the period considered, hence wind direction (mode over 10 min. every 3 h) was obtained from the

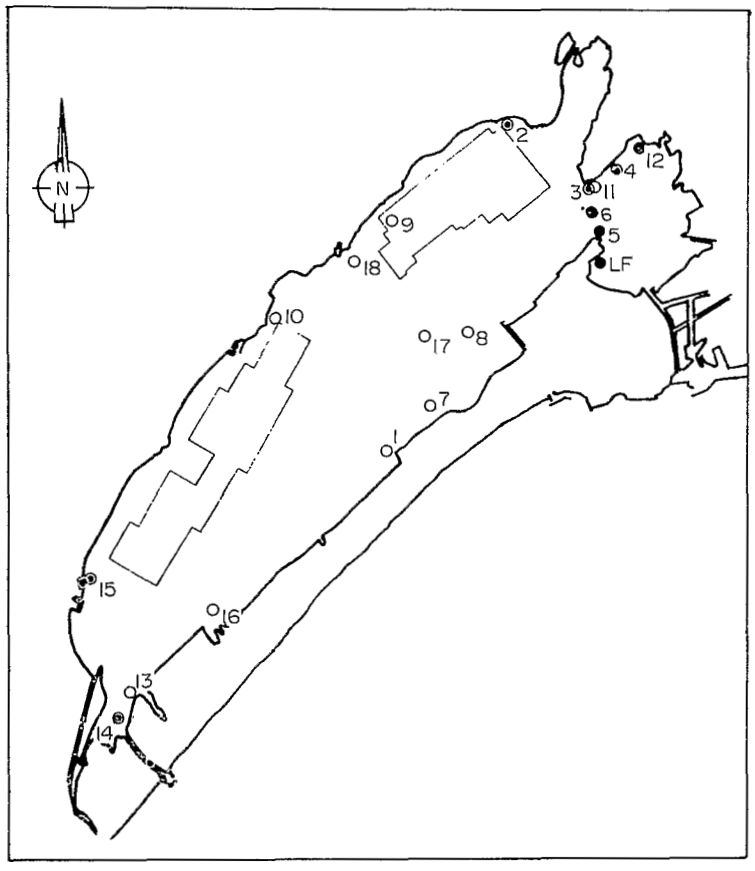

Figure 2. Map of the lagoon of Thau with locations of the stations surveyed for juvenile *R. decussatus* recruited in summer 1987. 1 Lido; 2 Bouzigues; 3 Pointe Balaruc (*Zostera* bed); 4 Balaruc-Port; 5 Barrou; 6 Plan de Roquerols; 7 Ecothau 11.5; 8 Ecothau 10.7; 9 Ecothau 14.7; 10 Mourre-Blanc; 11 Pointe Balaruc (beach); 12 Balaruc-Z.I.; 13 Maldormir; 14 Pisse-Saume; 15 Marseillan; 16 Marchepied; 17 Toque; 18 Plan de Mèze. Densities of spat: ○no spat; ⊙ < 10 ind.m^{-2}; ● > 100 ind.m^{-2}. Minimal area surveyed at each station: 0·25 m^{-2}.

national meteorological station of Sète (Figure 1). Daily data of wind speed and direction are presented in Figure 3: the record with highest speed is presented for each day.

For a few stations (1, 4, 5, 12, 14), the biotope was characterized by its redox potential. This was measured in a core of sediment using a Ponselle Eh-meter (Dutrieux, 1989) with the Pt electrode introduced 2 cm below the surface.

Circulation model

The circulation in the lagoon of Thau was simulated using an A.D.I.-type, two-dimensional (horizontal) numerical model (Leendertse, 1970; Leendertse & Gritton, 1971). This model was used to compute the wind-induced fields of flow and elevation values, according to the lagoon bathymetry, wind stress and bottom friction. The Coriolis force (weak) was considered, and the non-linear advection terms were taken into account because of the steep bathymetric gradients, and the small size of the numerical grid

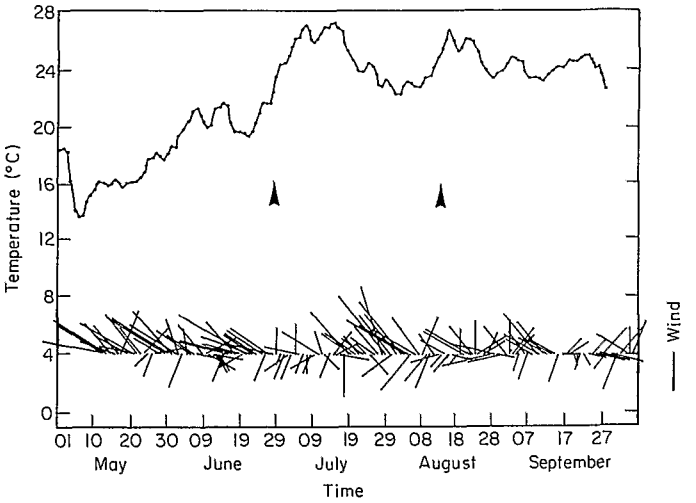

Figure 3. Daily temperature in the lagoon of Thau, from 1 May to 25 September 1987 (redrawn from Lemoalle & Millet, 1988). Below: daily values of wind speed and direction during the same period. Two dramatic increases in temperature were observed (arrows), one between 23 June and 7 July (20·0 °C to 27·1 °C) the other one between 11 and 16 August (23·7 °C to 26·8 °C). Temperature and wind data were those from the meteorological stations of zone C (Figure 1), and Sète (wind directions). Scale bar: 10 $m.s^{-1}$.

(250 m). Models taking into account the connection with the sea *via* the canals of Sète (see Figure 1) showed that the circulation induced by tides was negligible compared to the effect of wind (Millet, unpubl.). The wind was therefore considered as to be the only forcing variable in the model. Because of the inertia of water circulation, the average values of wind direction were estimated to represent the direction of the actual dominant atmospheric forcing.

A complete description of the properties of the model, its calibration, and results on spatial heterogeneity of current fields in the lagoon of Thau, obtained by stochastic analysis on an annual scale, are presented in Millet (1989). In one instance, modelled flow direction has been verified *in situ* using current-meters deployed within the shellfish culture zones by Grenz (1989).

Lagrangian trajectories of larvae, assumed to behave as passive particles, were deduced from the two-dimensional current fields considering that the wind conditions (i.e. force and direction) observed during the period of release of larvae were stationary. The two starting points chosen were Plan de Mèze and Plan de Roquerols (see Figure 1). These two localities were the most productive fishing grounds for palourdes in 1987 (J.-L. Audibert, pers. comm.). It was thus assumed that these localities had the highest densities of spawners in the lagoon.

Results

Reproduction

The qualitative gonad maturity indexes (GMI) for samples of palourdes collected during summer 1987 are given in Table 1. The surface temperatures during the same period are presented in Figure 3. GMI values showed sudden changes when surface temperature increased dramatically. These changes in GMI, which we interpret as massive spawnings,

TABLE 1. Qualitative gonad maturity index (GMI) in samples of adult female *R. decussatus* (shell length >25 mm) collected in the lagoon of Thau throughout summer 1987.

Date	Locality	*n*	GMI O	+	++	+++
10 April	Mèze	4	—	4	—	—
09 May	Bouzigues	3	—	—	3	—
07 June	Balaruc	5	—	—	3	2
11 June	Plan de Roquerols	11	—	—	—	11
16 June	Plan de Roquerols	8	—	—	—	8
24 June	Plan de Roquerols	5	—	—	—	5
27 June	Bouzigues	4	2	—	—	2
27 June	Balaruc	10	9	—	—	1
29 June	Bouzigues	5	5	—	—	—
30 June	Mèze	3	3	—	—	—
20 July	Mèze	1	—	—	1	—
27 July	Balaruc	4	—	3	1	—
01 August	Balaruc	4	—	—	4	—
12 August	Lido	31	—	—	8	23
24 August	Bouzigues	4	4	—	—	—
24 August	Balaruc	3	3	—	—	—
14 September	Lido	3	3	—	—	—
04 November	Bouzigues	12	4	1	6	1

n sample size; O gonad empty; + immature (pedunculated) oocytes only; ++ immature and mature oocytes; +++ mature (spherical or polyedrical) oocytes only.

were observed twice in summer 1987, the first one between 24 and 29 June, the second one between 12 and 24 August.

Larval trajectories

The hypothetical trajectories of larvae were deduced from the computed circulation patterns. One simulation (Figure 4) was run using the wind conditions averaged over the period 25 June–10 July: direction SW 230°, speed 3·5 $m.s^{-1}$. These were assumed to be constant for the whole period. The wind conditions were similar for the period 13–20 August direction SW 205°, speed 3·5 $m.s^{-1}$, so the same simulation was also valid for this period. The circulation patterns shown in Figure 4 were robust to this minor change in wind direction.

Two major, independent cells of circulation were observed, one for the whole Grand-Etang, the other one for the Etang des Eaux-Blanches (see Figure 1). The rate of exchange of larvae between these two confined systems was likely to be low.

The hypothetical trajectories of larvae are shown in Figure 5. After 54 h, larvae originating from Plan de Mèze had crossed the shellfish-cultivated zone A and were trapped in the rotary circulation of the western part of the Grand-Etang, whose period was about 75 h. Larvae originating from Plan de Roquerols were subject to the rotary circulation of the Etang des Eaux-Blanches, whose period was about 30 h. Thus, larvae originating from the Grand-Etang remained there during their whole planktonic life, possibly crossing two-three times the zones of concentration of cultivated bivalves, whereas those originating from the Etang des Eaux-Blanches remained circulating in the latter. Because of this confined circulation pattern, it was not necessary to draw the trajectories of larvae

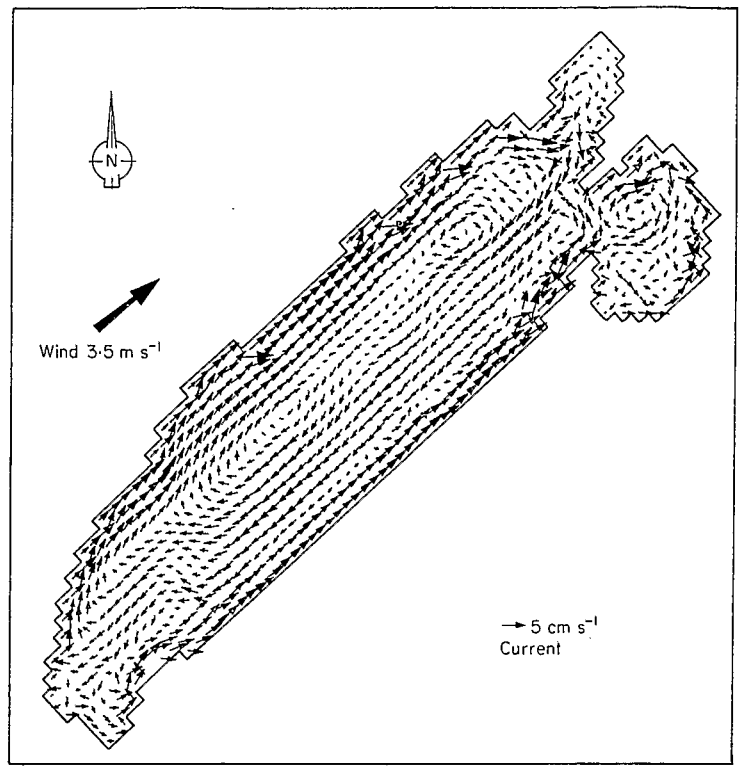

Figure 4. Simulated current fields in the lagoon of Thau, under constant wind of direction SW 230° and speed 3.5 m^{-1} (corresponding to the periods 25 June–10 July and 13–20 August 1987). Each current vector was defined as the vertical average vector. The grid used was a square of side 250 m.

further. Also, the probability that the modelled trajectory departs from the actual trajectory increases with the duration considered (A. Norro, Université de Liège, pers. comm.).

Recruitment: spatial variations

The results of the spatial survey of spat concentrations are presented in Figure 2. At three sites, all in the Etang des Eaux-Blanches, spat densities were greater than 100 individuals.m^{-2} (see Table 2: data for year 1987). T. Maître-Allain (pers. comm.) reported similar densities of spat on the shore of La Fangade (site LF). Hand dredging at Plan de Roquerols (site 6) revealed large concentrations of spat, even within the patchy areas where adult individuals were also found in large numbers. At all the other sites sampled, no spat was collected (most of the sites, see Figure 2) or its densities were extremely low (site 15, Marseillan: 4·5 individuals.m^{-2}, site 14, Pisse-Saume: 4 individuals.m^{-2}; site 2, Bouzigues: 1·5 individuals.m^{-2}).

The habitat characteristics of the sites where recruitment was abundant were the following: station 4: sandy mud, $E_h = -230$ mV; station 5: sand, $E_h = 50$ mV; station 12: black mud, $E_h = -630$ mV. Stations 1 and 14 (Grand-Etang; no recruitment) presented characteristics intermediate to stations 4 and 5.

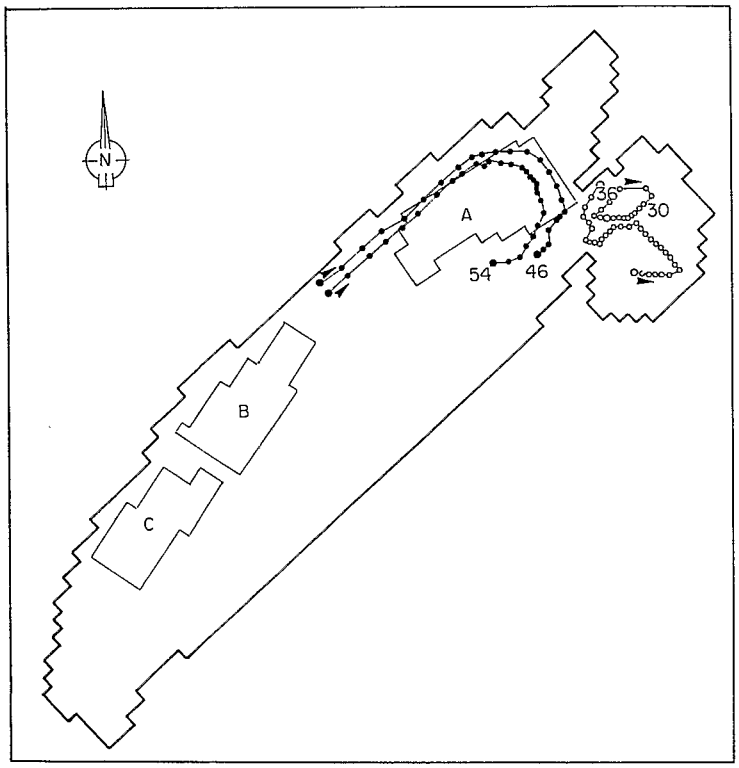

Figure 5. Trajectories of larvae of *R. decussatus* released at Plan de Mèze and Plan de Roquerols, for the durations indicated (in hours), as deduced from the results of the simulation presented in Figure 4. A, B, C intensive shellfish culture zones.

TABLE 2. Density (individuals.m^{-2}) of spat *R. decussatus* in three stations of the Etang des Eaux-Blanches for four consecutive years: 1986–89. For year 1987, the number of sub-cohorts is indicated in brackets (see Borsa, 1990). 0 no recruitment; — no data

Year	Barrou	Balaruc-Z.I.	Balaruc-Port
1986	0	—	—
1987	177·4 (2)	390·0 (1)	106·7 (1)
1988	2·9	33·5[a]	3·0
1989	0·8	—	—

[a]Value computed after resolution of the sample's length frequency distribution into its 1987 and 1988 Gaussian components (Hasselblad, 1966).

Recruitment: temporal fluctuations

Densities of spat at three sites in the Etang des Eaux-Blanches (site 4, Balaruc-Port; site 5, Barrou; site 12, Balaruc-Z.I.), for years 1986-1989 are presented in Table 2. These results showed that recruitment at a given site was highly variable from one year to the next.

Maximum likelihood analysis of the shell-length distributions in the populations of spat referred to in Table 2 (Borsa, 1990) indicated that two separated sub-cohorts settled at site 5 during summer 1987 while only one sub-cohort settled at site 4 and site 12.

Discussion

Spawning

Spawning occurred twice during the summer of 1987, first between 24 and 29 June, then between 12 and 24 August (most likely between 12 and 16 August, when the water temperature increased by several degrees within a few days). This confirms and extends the observations of Gallois (1977), who has suggested the possibility, and existence in 1971, of two annual spawnings in *R. decussatus* in the lagoon of Thau, at the beginning and the end of summer, within a period during which the temperature was above 20 °C. A single summer spawning has been observed by Breber in Venice Lagoon, during the period of maximum temperature (> 25 °C). This author noted that a similar gonadal cycle had been observed by Vilela (1949) in the Faro lagoon.

P. Borsa and A. Diter (unpubl. data) have been able to induce spawning in laboratory-matured palourdes from the lagoon of Thau by creating a double heat shock, consisting of cooling from the rearing temperature (24 °C) to 18 °C, followed by rapid reheating (30 min.) to 27 °C. They could not induce a second spawning one month later, however, either with individuals involved in the preceding spawning (which were unable to achieve a second gonadal maturation) or with individuals not used in the first experiment, whose gonads were still full and probably over-matured.

All these observations indicate that the factor which triggers spawning is, or is correlated to, increase in temperature, but that release of gametes occurs only when the maturational state of the gonads allows it (see Gallois, 1977 and Breber, 1980 in *R. decussatus*; see also Holland & Chew, 1974 in *R. philippinarum*, and Loosanoff, 1937*a,b* and Manzi *et al.*, 1985 in the closely related *Mercenaria mercenaria*).

The first spawning of summer 1987 (24–29 June) was massive, since all individuals observed just after this date had empty gonads. It was also simultaneous (in less than four days) throughout the lagoon. Because of this, it can be assumed that the whole offspring constituted one single cohort. The same phenomenon probably occurred once again between 11 and 16 August, during the second sudden increase in temperature of summer 1987, with individuals that had achieved a second gonadal maturation. However, data available for that period are not sufficient to demonstrate it clearly.

From comparing the present data with those of Gallois (1977), it can be concluded that the spawning dates vary considerably from year to year in the lagoon of Thau. These seem to depend, at least partly, on temperature patterns, which also vary from year to year.

Recruitment

Dramatic spatial variations in recruitment were observed, within the lagoon, in year 1987. The abundance of recruits was high in the Etang des Eaux-Blanches, whereas it was very low in the whole Grand-Etang. These discrepancies in recruitment repetitively concerned two sub-cohorts of recruits. These corresponded, respectively, to the two massive spawning events of summer 1987, although only one sub-cohort apparently was recruited at two of the three sites surveyed in the Etang des Eaux-Blanches.

In the Etang des Eaux-Blanches, abundant spat was found either within or out of dense concentrations of adults, and either at sites with sand and high redox potential (site 5), extremely reduced black mud (site 12), or an intermediate type of sediment (site 4). In the Grand-Etang, areas displaying the same range of habitat characteristics as those of the Etang des Eaux-Blanches were surveyed, but the densities of spat were, everywhere, very low. Moreover, recruitment had been successful there some years ago, so putative benthic

habitat differences cannot be invoked for explaining the lack of recruitment in the Grand-Etang in summer 1987.

Southwesterly winds rarely occur in the region of Thau (Millet, 1989). Such conditions were encountered in the beginning of July 1987 and once again in the second half of August. These winds induced a two-cell circulation (whole Grand-Etang/Eaux-Blanches). Swarms of larvae originating from the Grand-Etang followed its rotary circulation, so they were driven through the intensive shellfish culture zones. The filtering capacity of the latter is enormous: Hamon and Tournier (1984) have estimated that the cultivated populations of oysters and mussels of Thau filter a quantity of water equivalent to that of the Grand-Etang in two and a half days. The ingestion of bivalve larvae by filtering organisms is known to be a significant factor of mortality (Bayne, 1964; Thorson, 1966). Jouffre (1989, p. 213) has estimated the summer abundance of zooplankton in 63 stations screening the whole lagoon of Thau. His data have shown that the abundance of venerid larvae at the stations situated within the intensive shellfish culture zones or at their nearest neighbours were significantly lower than the values reported for all the other stations (Wilcoxon-Gros-Chessel rank test for comparison of two distributions; Gros & Chessel, 1982; $P<0{\cdot}001$). This indicates that the larvae present in these areas were depleted from the water.

If the presence of intensive shellfish culture zones is the main factor affecting recruitment in the lagoon of Thau, one may expect the shoals of the Grand-Etang to recruit abundantly when circulation patterns are such that larvae do not drift through these aquaculture zones. This would be possible, for example, when the circulation is induced by North Easterly winds, the annual frequency of which in the lagoon of Thau is about 15% (Millet, 1989).

Anoxic conditions may also have been a significant cause of massive mortality for clam larvae. This statement is supported by demographic structure patterns within the populations of spat recruited at three stations in the Etang des Eaux-Blanches: at two of them, subjected to the episodic anoxia of July 1987, the population of spat consisted of one single cohort, whereas that of the third station, unaffected by anoxia, consisted of two cohorts. The separation of the spat population into two distinct cohorts reflects the observed temporal pattern of spawning. Where only one cohort was recruited, anoxia is left as the most likely factor causing the elimination of the other cohort.

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