Dörjes, J., 1980. Auswirkungen des kalten Winters 1978/79 auf das marine Makrobenthos. Natur u. Museum 110: 109–115.

Essink, K., 1978. The effects of pollution by organic waste on macrofauna in the eastern Dutch Wadden Sea. Netherlands Institute for Sea Research, Publication Series No. 1, 144 pp.

Gibbs, P. E., 1968. Observations on the population of *Scoloplos armiger* at Whitstable. J. mar. biol. Ass. U.K. 48: 225–254.

Hauser, B., 1973. Bestandsänderungen der Makrofauna an einer Station im ostfriesischen Watt. Jber. Forschungsstelle f. Insel- u. Küstenschutz Norderney 24: 171–204.

Jepsen, U., 1965. Die Struktur der Wattbiozönosen im Vormündungsgebiet der Elbe. Arch. Hydrobiol., Suppl. 29: 252–370.

König, D., 1943. Vergleichende Bestandsaufnahme an bodenbewohnenden Wattieren im Bereich des Sicherungsdammes vor Friedrichskoog 1935–39. Westküste 1943: 120–172.

Kristensen, I., 1958. Differences in density and growth in a cockle population in the Dutch Wadden Sea. Arch. Neerl. Zool. 12: 351–453.

Lappalainen, A. & P. Kangas, 1975. Littoral benthos of the northern Baltic Sea. II. Interrelation of the wet, dry and ash-free dry weights of macrofauna in the Tvärminne area. Int. Revue ges. Hydrobiol. 60: 297–312.

Madsen, P. Brinch, 1984. The dynamics of the dominating macrozoobenthos in the Danish Wadden Sea 1980–1983. Rep. Mar. Pollut. Lab. 7: 1–35.

Meyer, M. & H. Michaelis, 1980. Das Makrobenthos des westlichen 'Hohen Weges'. Jber. Forschungsstelle f. Insel- u. Küstenschutz Norderney 31: 91–155.

Michaelis, H., 1981. Recent Changes in the Communities of the Wadden Sea – natural Phenomena or Effects of Pollution? In S. Tougaard & C. Helweg Ovesen (eds), Environmental Problems of the Waddensea-Region. Fiskeri-og Søfartsmuseets, Saltvandsakvariets Biologiske Meddelelser 5: 87–95.

Muus, B. J., 1967. The fauna of Danish estuaries and lagoons. Distribution and ecology of dominating species in the shallow reaches of the mesohaline zone. Medd. Danmark Fisk. Havundersøg. (n. ser.) 5: 1–316.

Obert, B., 1982. Bodenfauna der Watten und Strände um Borkum – Emsmündung. Jber. Forschungsstelle f. Insel- und Küstenschutz Norderney 33: 139–162.

Ohde, J., 1981. Entstehung von Besiedlungsmustern der Makro-Endofauna im Wattenmeer der Elbe-Mündung. Thesis, University of Hamburg, 445 pp.

Rachor, E., 1980. The inner German Bight – an ecologically sensitive area as indicated by the bottom fauna. Helgol. Meeresunters. 33: 522–530.

Rachor, E. & S. A. Gerlach, 1978. Changes of macrobenthos in a sublittoral sand area of the German Bight 1967–1975. Rapp. P.- v. Réun Cons. perm. int. Explor. Mer 172: 418–431.

Reineck, H.-E., 1976. Primärgefüge, Bioturbation und Makrofauna als Indikatoren des Sandversatzes im Seegebiet vor Norderney (Nordsee). 1. Zonierung von Primärgefügen und Bioturbation. Senckenbergiana marit. 8: 155–169.

Reise, K., 1977a. Predation pressure and community structure of an intertidal soft-bottom fauna. In B. F. Keegan, P. O'Céidigh & P. J. S. Boaden (eds), Biology of Benthic Organisms. Pergamon Press, New York: 513–519.

Reise, K., 1977b. Predation exclusion experiments in an intertidal mud flat. Helgol. wiss. Meeresunters. 30: 263–271.

Reise, K., 1985. Tidal Flat Ecology. Springer-Verlag, Berlin. 191 pp.

Schäfer, W., 1962. Aktuo-Paläontologie nach Studien in der Nordsee. Verlag Waldemar Kramer, Frankfurt a. M., 666 pp.

Smidt, E. L. B., 1944. Das Wattenmeer bei Skallingen, 3. The effects of icewinters on marine littoral fauna. Folia geogr. dan. 2: 1–36.

Smit, C. J., 1980. Production of biomass by invertebrates and consumption by birds in the Dutch Wadden Sea area. In C. J. Smit & W. J. Wolff (eds), Birds of the Wadden Sea. Balkema, Rotterdam: 290–301.

Thamdrup, H. M., 1935. Beiträge zur Ökologie der Wattenfauna auf experimenteller Grundlage. Medd. Danmarks Fisk. Havundersøg., Ser. Fisk. 10(2): 1–125.

Vlas, J. de, 1979. Annual food intake by plaice and flounder in a tidal flat area in the Dutch Wadden Sea, with special references to consumption of regenerating parts of macrobenthic prey. Neth. J. Sea Res. 13: 117–153.

Wolff, W. J., 1973. The estuary as a habitat. An analysis of data on the soft bottom macrofauna of the estuarine area of the rivers Rhine, Meuse, and Scheldt. Zoologische Verhandelingen 126: 1–242.

Ziegelmeier, E., 1964. Einwirkungen des kalten Winters 1962/63 auf das Makrobenthos im Ostteil der Deutschen Bucht. Helgol. wiss. Meeresunters. 10: 276–282.

Ziegelmeier, E., 1978. Macrobenthos investigations in the eastern part of the German Bight from 1950 to 1974. Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer 172: 432–444.

Recruitment and year-to-year variability in a population of *Macoma balthica* (L.)

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Abstract

Because of methodological problems, macrobenthic studies usually neglect the juvenile stages of invertebrate communities, due to the fact that appearance of recruits in samples is only detected some weeks or even months after their true recruitment. During this period, the temporary meiobenthos undergoes high rates of mortality. From year to year, juvenile survival rate is thus responsible for temporal patterns observed in adult population densities.

The results presented here relate to the population dynamics of the tellinid bivalve *Macoma balthica* (L.). A study of temporary meiobenthos was conducted over two consecutive years in an intertidal *Macoma*-community located at the mouth of the Gironde Estuary in southwest France. Sampling of juvenile stages required short intervals (2 weeks) between successive samplings and a fine sieving mesh size (63 μm). Other population parameters, such as temporal patterns in density, reproductive cycle, and individual growth, were recorded.

Recruitment processes showed a year-to-year variability, with regard to settlement density, settlement period, and survival rate. In 1983, recruitment was moderate and protracted over several months. Only one main recruitment period was detected in 1984, resulting in a high juvenile density. In a previous study (1977), by contrast, recruitment was almost non-existent.

This variability is discussed as a function of climatic and sedimentological conditions which prevailed in the estuary throughout the study period. However, none of these physical factors appeared to underlie the recruitment fluctuation in *Macoma balthica*. It is suggested that biological interactions are of prime importance in regulating population densities in this community.

Introduction

It is a well known fact that the abundance of marine and estuarine benthic invertebrate populations fluctuate seasonally. It follows that in a natural environment, without any source of pollution or man-induced changes, benthic communities may present a different specific composition from year to year, particularly when the species have a life span of about one year (Eagle, 1975). Most of the variability in the seasonal and long-term dynamics of benthic communities can be attributed to the success or failure of a larval recruitment and the subsequent survival of juvenile stages. Long-term monitoring of temporal fluctuations has often shown different levels of recruitment during consecutive years (Glémarec, 1978; Beukema, 1980, 1982; Vahl, 1982; Persson, 1983; Diaz, 1984; Holland, 1985; Nichols, 1985). It appears then that the size of the settlement as well as the survival of recruits and individual growth rate reflect good and bad conditions.

Adequate knowledge of the causes of natural variability in marine communities requires detailed

information on all the repopulation processes (including gonad development, survival of larvae, settlement density and post-settlement survival and growth) which are potentially the most sensitive to environmental constraints. Quantitative studies on recruitment are still scarce and long-term data are lacking. This lack of information on recruitment events proceeds in a great part from inaccurate sampling methods (Bachelet, 1984). In this respect, two main features in the biology of benthic invertebrates must be kept in mind. First, larval settlement is a transient phenomenon and survivorship of newly settled juveniles is usually low (Cattaneo & Massé, 1983; Diaz, 1984; Luckenbach, 1984; Powell et al., 1984). Secondly, recruits are of meiofaunal-size and thus should be extracted from soft sediments with a fine sieving mesh (Williams, 1980; Bachelet, 1985). With usual methods employed by macrobenthologists, the first appearance of recruits in samples may sometimes be detected some weeks or even months after their true recruitment. During this period, the temporary meiobenthos (i.e. the post-larvae) undergoes high rates of mortality and the level of recruitment can thus be considerably under-estimated.

The tellinid bivalve *Macoma balthica* (L.) is one of the species for which the largest amount of data on biology and ecology has been published. Occurring both intertidally and in shallow subtidal marine and estuarine waters, this species is widely distributed in North-West Europe and on the two northern coasts of North America (Bachelet, 1980; Beukema & Meehan, 1985), covering a large scale in latitude. Though long-term surveys on *M. balthica* are available, particularly in the Dutch Wadden Sea (Beukema & De Bruin, 1977; Beukema et al., 1977, 1985; Beukema, 1980, 1982), precise data relating to recruitment have only been reported by Caddy (1969) and Ankar (1980).

This paper reports on a two-year study of recruitment in an intertidal population of *Macoma balthica* located in the Gironde estuary, SW France, which represents the southern limit of the geographical distribution of the species in European waters (Bachelet, 1980). Yearly variations in reproductive cycle, recruitment and growth were examined for 1983 and 1984, and are compared with a previous survey in 1977.

Material and methods

Macoma balthica were sampled from an intertidal mud flat at Le Verdon (Station 1 in Bachelet, 1980) near the mouth and on the left shore of the Gironde Estuary (45°33′N, 1°03′W). This station was located approximately 2 m above MLW (percentage of time drained: about 50%) in a sheltered bay protected from the strongest waves by a rocky dam.

For a study of recruitment processes, a survey strategy must contain frequent samplings to monitor the large, rapid changes that occur in spatfall densities. Weekly collections are probably an ideal strategy, however, sorting of so many samples is too time-consuming. Moreover the distance between the sampling site and the laboratory (150 km) did not allow for weekly sampling. Samples were thus taken approximately every fortnight from January 1983 to January 1984. During the second year survey (1984), the sampling frequency was reduced to monthly intervals.

Faunal samples were collected on each occasion using cores of two sizes. To sample large *Macoma balthica*, three to five replicate cores were taken with an aluminium box corer (20 cm × 20 cm × 30 cm deep) from random locations within a fixed 20 × 20 m plot. *M. balthica* were never found deeper than 10 cm. The depth of excavation was thus limited to 15 cm. Juveniles were usually too numerous to be counted in large core samples, so smaller cores were used to collect them. Three to eight (mean = 5) plexiglass cores (inner diameter 3.2 cm, sampling area 8 cm², depth 2 cm) per sampling occasion were analysed for the meiofaunal-sized spat.

All cores of both sizes were fixed with 10% buffered formalin before sieving. Rose Bengal was added to small cores in order to facilitate the sorting of juveniles. Sieving was performed in the laboratory. The 400 cm² macrofaunal samples were sieved through a 400 μm screen that retained all individuals with lengths $\geq$ 0.8 mm. The 8 cm² cores were first sieved through a 400 μm mesh and then a 63 μm screen. Trials with a 100 μm screen showed that this size was sufficient enough to collect the smaller spat, so the 63 μm screen was omitted. A similar mesh size was used by Ankar (1980) with *M. balthica*, and by Williams (1980) and Luckenbach (1984) for other bivalves.

Sorting, identification of juveniles and measurements were made under a dissecting microscope with an eyepiece micrometer. The maximum shell length of all specimens was recorded with a 0.01 mm accuracy (spat < 1.5 mm length) or to the nearest 0.1 mm (other specimens). Growth rings on the shell were measured in the same way. Clams of less then 10 mm length were separated into cohorts based on plots of shell lengths vs frequency through time; in this size range, the number of rings were used to separate the generations. Unlike a previous survey (Bachelet, 1980, 1982), growth cessation rings could not be used to separate year classes when shells were marked by more than one ring, because there were no distinct rings or they were too numerous to indicate a clear biological pattern.

To determine gonad condition, 12 *Macoma* over 10 mm in length were selected from each sample and fixed in Bouin's fluid. Two approaches were used (Caddy, 1967). First, the visceral mass was examined under a dissecting microscope after removal of the shell valves and the macroscopic appearance of the gonad was used to assess grossly the state of development. When the gonad tissue was developing and imbricated in the dark brown digestive gland, the animal was considered mature and when gonad regression was observed it was ascribed to spawning. After macroscopic examination, the visceral mass was embedded in paraffin (melting point 56°C). Transverse 7 μm sections were cut along the dorso-ventral axis at the regions of the foot, crystalline style and the gut. Sections were mounted on slides and stained with hematoxylin and eosin. The state of gonad development was determined according to Caddy (1967) and Lammens (1967). The arbitrary scheme of gonad classification (spent, developing, ripe, spawning) and the mean gonad index of Brown (1982) were used to describe the seasonal gonad changes in *M. balthica*.

Analysis of grain size and organic carbon in the sediment was performed on the top 2 cm. At each sampling date, four cores (3.5 cm in diameter) were taken at the same site as the biological samples. Silt and clay content (particles < 63 μm) was estimated by wet sieving the sediment from two cores. Samples for organic carbon content were treated with N hydrochloric acid to remove carbonates and bicarbonates. As a rough estimate of organic content,

the loss on ignition (L.O.I.) was determined as the difference between the dry weight (100°C, 48 h) and ashfree dry weight (600°C, 2 h) of decalcified sediment. Silt and clay and organic matter contents are given as percentage of the dry sediment.

The only physical measurements taken on the field were sediment temperature near the surface ($\approx$ 5 mm) and at 15 cm depth. Meteorological data were gathered from the monthly weather reports issued by the Météorologie Nationale (Bulletin Climatologique du Sud-ouest); data were used from the weather station of Le Verdon. Hydrological data (water flow, temperature, salinity, nutrient contents) were obtained from stations 1 and 2 of the Réseau National d'Observation in the Gironde estuary.

Results

Environmental variables

Monthly average values (mean of the years 1976–1983) for hydrological data at the mouth of the Gironde estuary are presented in Fig. 1, together with mean monthly water flow for the period 1961–1970.

Mean monthly salinity of surface waters vary between 19.4 and 29.5⁰/₀₀. Highest salinities are recorded in August–October, during a period with little rainfall and low fluvial discharge; lowest surface salinities occur in January–May, due to swellings of the Gironde estuary. At Le Verdon, the extremes of the salinity range throughout the year are $33.7 - 18.0^0/_{00}$.

Mean monthly surface water temperatures vary between 7.2 (January) and 20.1°C (August) but shallow water moving onto or off the flat with the tide may reach more extreme temperatures. Measurements of sediment temperatures at low tide showed a thermic inertia at 15 cm depth while surface sediment temperatures were always higher than air or water temperatures, due to solar irradiation during daytime. Linear relationships with highly significant correlations were found between air (T_A) and sediment temperatures (T_S):

$$T_A = 1.682 \ (T_S \ \text{deep}) - 13.309$$
$$(r = 0.962, \ P > 0.99)$$
and T_S surface $= 1.418 \ (T_S \ \text{deep}) - 3.778$
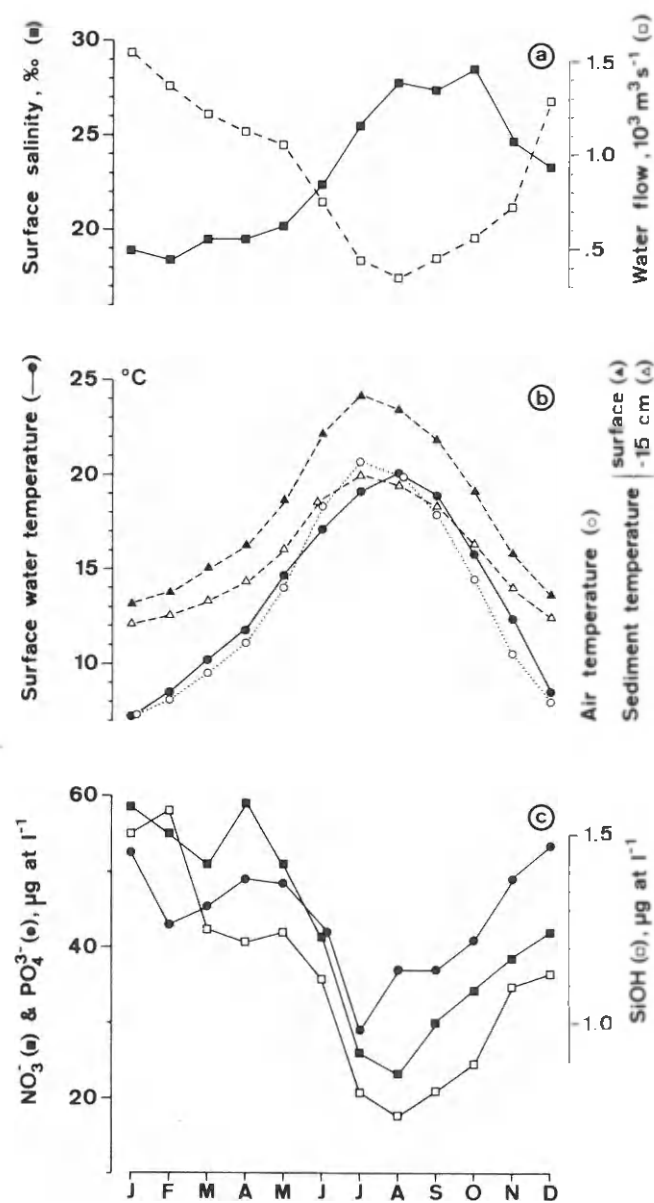$$(r = 0.901, \ P > 0.99).$$

Fig. 1. Summary of data on (a) surface water salinity and water flow, (b) surface water, air, and sediment (surface and 15 cm depth) temperatures, (c) phosphate, nitrate, and silicate contents in surface waters, at Le Verdon, Gironde estuary. Data are average monthly values calculated for the period 1976–1983, except for estuarine water flows averaged for the period 1961–1970.

The range of values used for air temperature was large (between −7.5 and 28.0 °C), but only pertinent to day-time and to emerged sediment.

Nutrient concentrations in surface estuarine waters show a seasonal evolution. Highest levels are measured in winter: 1.5 μg at P l⁻¹ in December–January, 58.4 μg at N l⁻¹ in January and 58.0 μg at Si l⁻¹ in Febuary and remain stable until April–May, when a second peak is obvious. Lowest values are recorded in July (phosphates) and August (silicates and nitrates), then increase again until winter.

During 1983 and 1984, fine particles and organic matter contents showed a great temporal variability in the sediments: 28–90% for the former, 4.2–10.9% for the latter (Fig. 2). A high silt and clay content during the summer and autumn months was the mark of a calm weather and a low fluvial discharge. In contrast, high river runoff generated strong tidal currents which accounted for the erosion of mud flats from January to May–June. Silt plus clay and organic contents were highly correlated. During the 1983–84 survey, three peaks of organic matter could be distinguished: two around 10% in December–January and August–October, and a third, less obvious, in May.

Seasonal gonad changes and spawning

In spite of the low number of individuals examined at each sampling occasion, a fairly clear pattern in reproductive condition of *Macoma balthica* occurred during the two consecutive years of detailed investigation (Table 1). However, analysis of data for individual years reveals some variation from one year to another.

Gross examination of the visceral mass showed
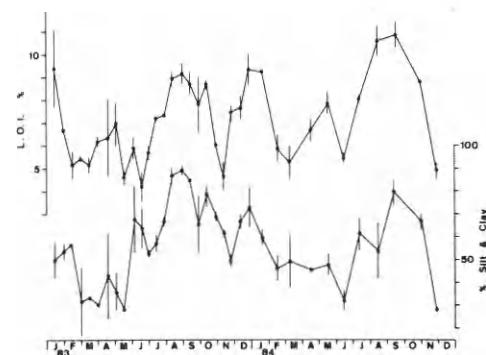
Fig. 2. Organic matter (L.O.I.) and silt plus clay contents (mean ± standard error) in the top 2 cm of sediment at station 1, Le Verdon, during the years 1983–1984.

that almost all individuals had well developed gonads, imbricated in the digestive gland, from November to March. Two drops in the percentage of mature animals were observed in early March and early June in 1983, in February and April 1984. No gonads were obvious in summer and early autumn. These observations are, however, insufficient to precisely determine the exact spawning time, because gonads are well developed when they are either ripe or in the stages 3 and 4 of both developing and spawning states (Brown, 1982). Thus the scheme of gonad classification and the calculation of a gonad index as described by Brown, *loc. cit.*, was used to describe with more details the seasonal gonad changes (Table 1).

In January 1983, nearly all the adult population of *M. balthica* was in the ripe condition, with individuals having a swollen foot filled with ripe ova and sperm. After that, the proportion of ripe individuals declined rapidly, as the spawning state became dominant. Around mid-April, there were no more clams with ripe gametes, but a small increase

Table 1. Reproductive condition of *Macoma balthica* in the Gironde estuary during 1983–1984. Gonad classification and gonad index according to Brown (1982). The mean gonad index varies from 0 (all spent) to 5 (all ripe).

Date	Gonads visible by macroscopic examination %	Developing %	Ripe %	Spawning %	Spent %	Gonad index
1983						
14 Jan.	100	13	87	0	0	4.8
31 Jan.	100	0	92	8	0	4.7
15 Feb.	100	0	64	36	0	4.5
01 Mar.	100	0	42	58	0	4.0
15 Mar.	67	0	18	82	0	3.2
30 Mar.	58	0	8	84	8	2.5
18 Apr.	42	0	0	92	8	2.2
02 May	33	0	8	75	17	2.0
16 May	8	0	9	55	36	1.4
03 June	25	0	25	42	33	1.8
17 June	0	20	0	30	50	0.6
29 June	0	18	0	6	66	0.5
13 July	0	17	0	8	75	0.3
27 July	0	17	0	16	67	0.3
11 Aug.	0	21	0	0	79	0.5
29 Aug.	0	21	0	4	75	0.8
13 Sep.	0	33	0	0	67	1.0
27 Sep.	0	92	0	0	8	2.3
12 Oct.	0	100	0	0	0	2.5
28 Oct.	17	83	17	0	0	2.9
12 Nov.	67	67	25	8	0	3.3
25 Nov.	92	50	50	0	0	4.0
12 Dec.	100	17	83	0	0	4.8
27 Dec.	100	8	75	17	0	4.7
1984						
19 Jan.	100	0	75	25	0	4.5
17 Feb.	92	0	84	8	8	4.3
09 Mar.	100	0	67	33	0	4.0
16 Apr.	92	0	21	71	8	2.3
17 May	75	0	10	65	25	1.5
15 June	0	13	0	29	58	1.0
11 July	0	17	0	0	83	0.3
14 Aug.	0	25	0	0	75	0.5
17 Sep.	0	33	0	0	67	1.1
29 Oct.	30	75	25	0	0	3.0
27 Nov.	100	58	42	0	0	4.3

occurred again in May and early June. No ripe specimens were found from mid-June to mid-October. Large numbers of spawning individuals were dominant from February to April, but were still found until July in a few females which exhibited gonads with residual eggs. Since the first spawning specimens were noticed on January 31 and the mean gonad index markedly declined up to May 16, the February–May period could be characterized by a first intense spawning. A rising proportion of ripe individuals, together with a new increase in the gonad index on June 3, followed by a quick drop, suggests that a second, minor spawning period took place in June–July.

Animals with developing gonads had already appeared in June. Their proportion remained stable (around 20%) until late August, then abruptly increased to 100% in October. The first specimens with ripe spermatozoa and eggs were noticed in late October. Their maximum numbers were reached from December 1983 to February 1984, so that most animals had ripe gametes from November to March. During this period, no clear decline in the mean gonad index was ascertained, but spawning individuals were present in a noticeable proportion in late December and early January, suggesting a spawning early in the year. *M. balthica* in a ripe state declined in numbers from February to June 1984. As seen by a steady decrease in the gonad index, the main spawning period during this year can be considered to be the months March–June or July.

As in the preceding year, the development started in June, as soon as spawning was completed. Recovery of condition continued throughout the summer months (increase of gonad index) so that mature gametes were again present in late October.

Age distribution and abundance

Size-frequency histograms of *Macoma balthica* were obtained by pooling 8 cm^2 and 400 cm^2 samples from January 1983 to November 1984 as shown in Fig. 3 and 4. Because of their three-dimensional shape (length > height > thickness), the same size juvenile clams were not equally retained at a given sieving mesh size, so that the smallest clam found on the 400 μm sieve was 0.54 mm in length, whereas the largest retained on the 100 μm sieve was 0.71 mm. In this overlapping

size region (0.54 to 0.71 mm), a mean density was thus determined from the data of both cores. Frequency data for each 0.5 mm length intervals were finally normalized to a standard area of 1 m^2.

From January 1983 to January 1984, the density of animals older than about one year remained relatively high (around 500 ind. m^{-2}) and formed a single size group between 10 and 15 mm shell length. It has been shown that these individuals belonged to three or four age groups (Bachelet, 1980). A few clams were larger (the maximum recorded length was 20.9 mm) but lengths greater than 16 mm were rarely found. During their growth, new recruits formed broad frequency histograms with several peaks that overlapped with the older individuals into the 10–15 mm grouping in the summer months of the next year. This size group, though well represented in January 1984, showed reducing densities thereafter, and from May onwards nearly completely disappeared. Thus, some factor led to the total extinction of the oldest generations, in such a manner that by November, the population was only composed of individuals less than 10 mm in length.

Recruitment features

In 1983, the first sign of recruitment occurred by mid April. From this date and onwards, decomposition of the size frequency histograms shown in Fig. 3 and analysis of more detailed histograms built with size classes of 0.1 mm for juvenile shell lengths led to the partition of the newly recruited generation into four successive waves named A, B, C and D (Fig. 5). A single cohort (A) was present from mid April to early June. The other three cohorts (B, C and D) were first observed at 17 June, 13 July and 27 July, respectively. Densities were almost identical at the time of settlement and relatively low (about 500 ind. m^{-2}) in these four cohorts; their maximal cumulated numbers, found in late July, were 3250 ind. m^{-2}. A steady decrease in the abundance of the 0+ year class resulted in about 1000 ind. m^{-2} in December, when the four cohorts became undistinguishable because of the junction of their modal size. Autumnal densities remained stable, then a new mortality occurred in spring months. Approximately one year after their settlement, the density of juveniles was found to be only 100/300 ind. m^{-2} at the most (see genera-

tions '82 and '83 respectively in June 1983 and 1984, Fig. 5).

During the year 1984 spat fall began sooner than in the preceding year. Densities of juveniles of up to 15000 ind. m^{-2} were found in February and a high mortality occurred after that. Only one cohort could be distinguished throughout the course of the year, with possibly a second, poorly individualized cohort in June when densities rose again (Fig. 5). However the fact that only one or two cohorts were found in 1984 could be a consequence of the monthly interval between two successive samplings, since it was fortnightly in 1983.
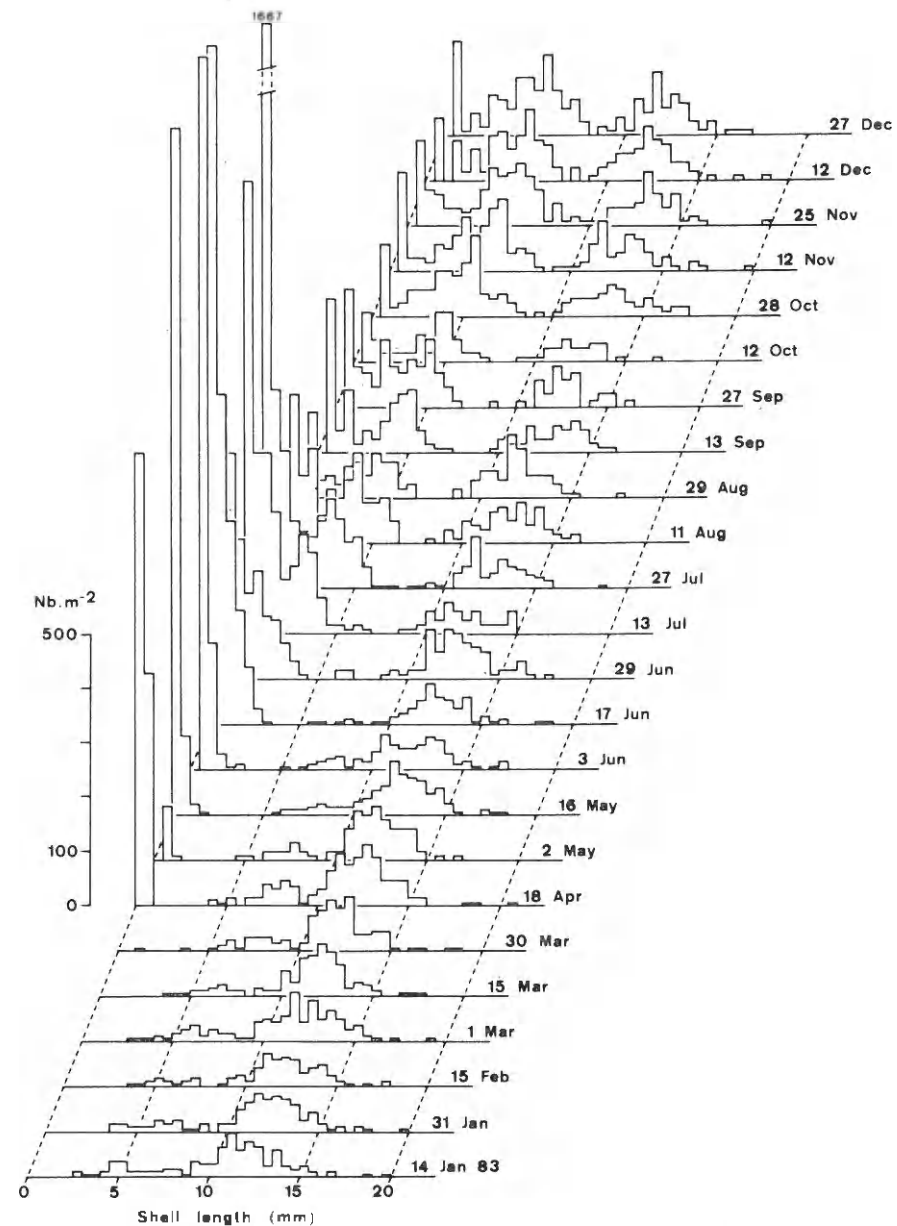

Fig. 3. Length-frequency distributions of *Macoma balthica* from Le Verdon, Gironde estuary, in 1983 (size classes 0.5 mm). 8 cm^2 cores and 400 cm^2 quadrats are pooled and the densities of *M. balthica* converted for 1 m^2.
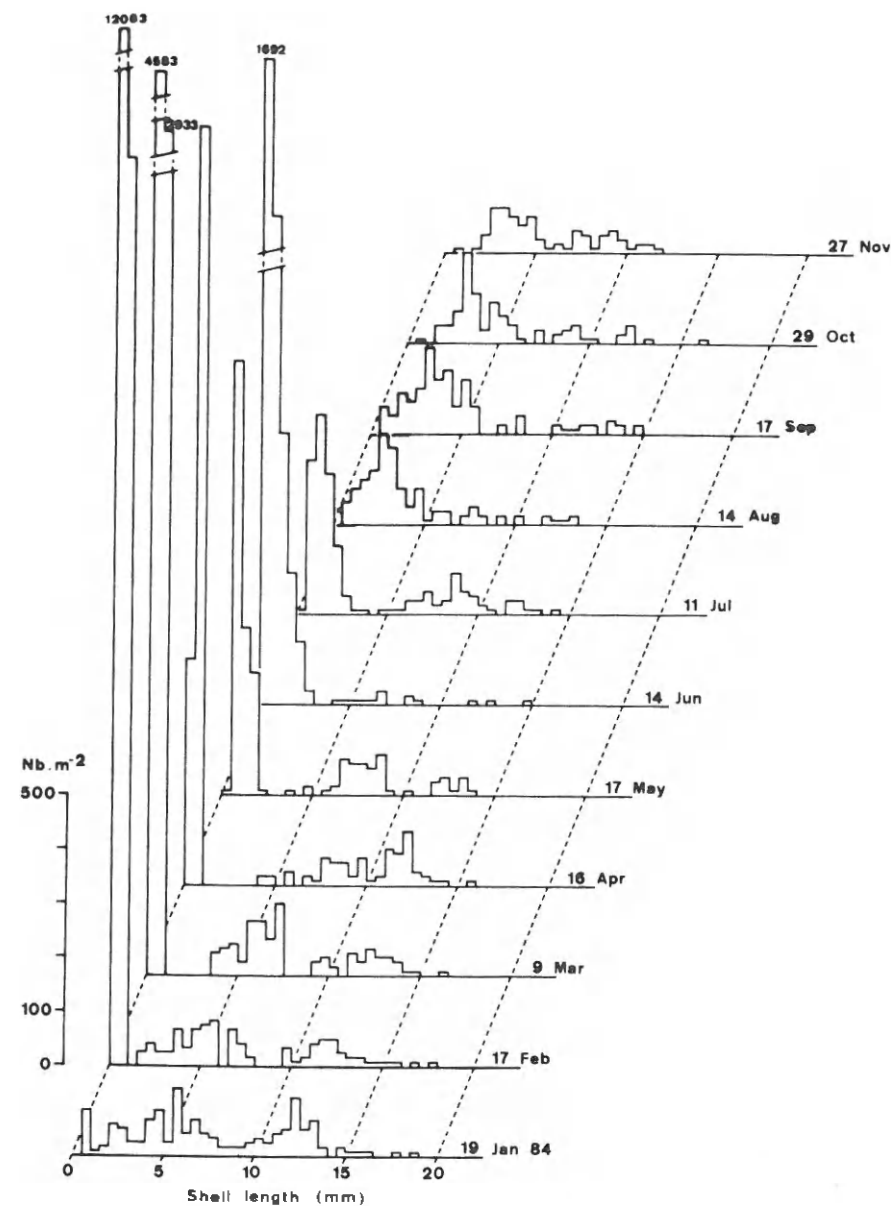
Fig. 4. Length-frequency distributions of *Macoma balthica* from Le Verdon in 1984.

Postlarval and juvenile growth

At the time of settlement, the smallest benthic stages of *M. balthica* were usually 270 to 310 μm long, but the minimal size recorded was 200 μm. Measurements of prodissoconch II shells (Pd) in postlarval clams of about 1 mm shell length

showed a range of 240–300 μm for Pd length (mean = 272 μm). Metamorphosis therefore occurred at around 250–300 μm shell length.

The seasonal increase in shell length of the postlarval and juvenile *M. balthica* (age classes 0+ and 1+) can be seen in Fig. 6. For all the newly recruited cohorts, mean length at first sampling was near
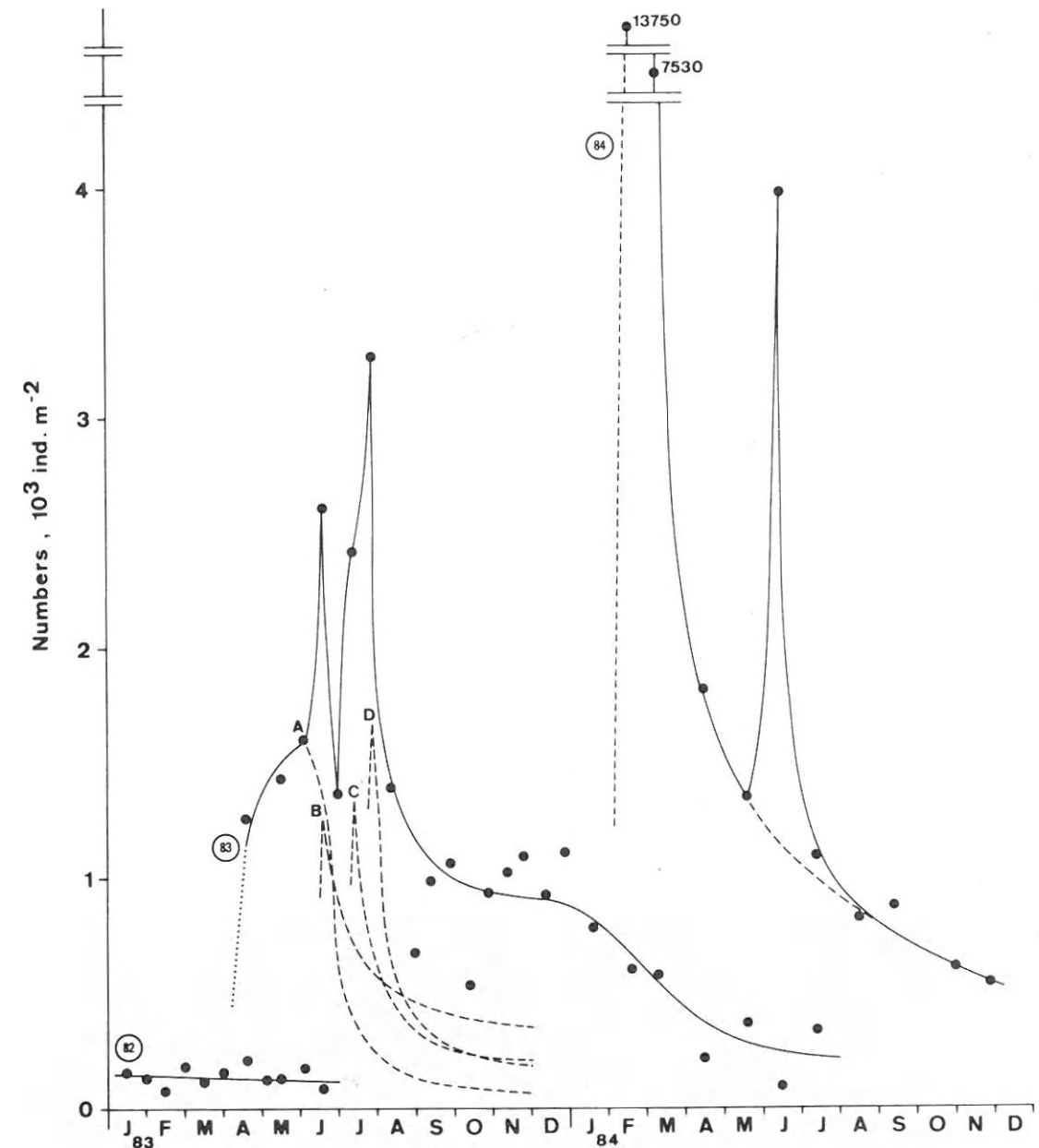
Fig. 5. Survivorship curves (ind. m^{-2}) for the generations of *Macoma balthica* born in 1982, 1983 and 1984, followed throughout 1983 and 1984. Curves are fitted by eye and are shown only for the first year of life. Points are mean densities at each sampling date. The four cohorts identified for the '83 year class are marked by a letter (A to D) and their survivorship curves are delineated with dashed lines (observed densities not shown).
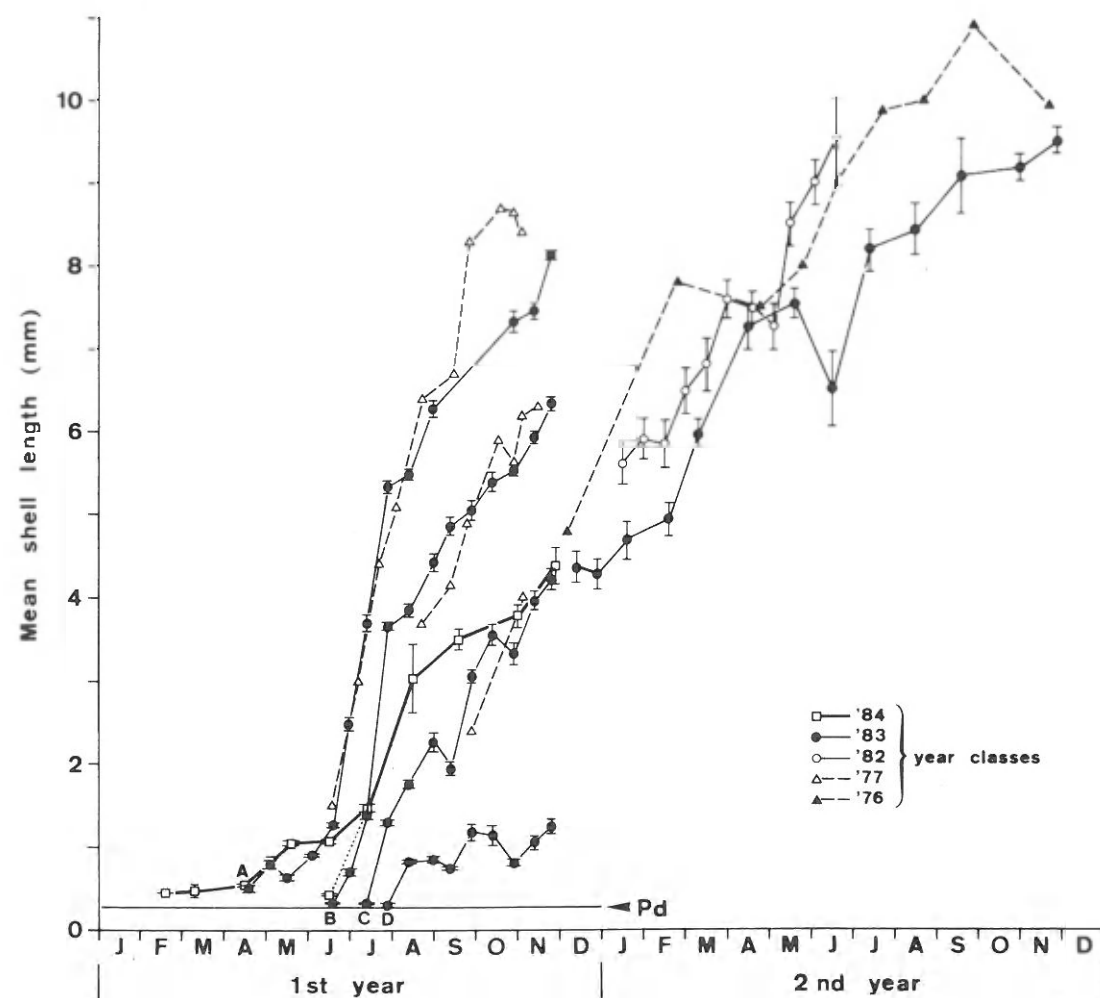
Fig. 6. Seasonal growth in shell length (mm) of juvenile *Macoma balthica* during their first and second growing seasons. Symbols are means ± standard errors. Cohorts of the 0+ year class are marked by letter. Pd = mean size of prodissoconch shell.

the Pd size; 0.51 mm (S.D. = 0.05), 0.33 mm (0.01), 0.32 mm (0.01), and 0.30 mm (0.02) respectively for the four '83 cohorts, 0.44 mm (0.01) and 0.42 mm (0.02) for the two '84 cohorts, which confirms the validity of sampling strategy.

Separate analysis of each cohort growth curve of the age class 0+ gives interesting information on growth rates as a function of settlement dates. 1) Cohort '83$_A$ showed three distinct growth periods: slow growth (0.0125 mm d^{-1}) from 18 April to 17 June, rapid growth (0.1014 mm d^{-1}) from 17 June to 27 July, and moderate growth (0.0269 mm d^{-1}) until 25 November. 2) Length increments for the co-

hort '83$_B$ were similar (0.0808 mm d^{-1} from 17 June to 27 July, with 0.1629 mm d^{-1} during the period 13 July−27 July), but as mean length by late July was lower than that of cohort '83$_A$ (3.7 against 5.3 mm) the final length by late November was also lower (6.3 against 8.1 mm); shell length increase for cohort '83$_B$ (0.0220 mm d^{-1}) was the same as for '83$_A$ from 27 July to 25 November. 3) During a fortnight following its settlement, cohort '83$_C$ exhibited good growth in shell length (0.0693 mm d^{-1}), but from 27 July forward its daily increase was of the same magnitude as cohorts '83$_A$ and '83$_B$ (0.0246 mm d^{-1}). 4) The main

growth of cohort '83$_D$ took place from 27 July to 11 August (0.0343 mm d^{-1}). After this date, it was almost null (0.0047 mm d^{-1}). 5) Generation '84, that had appeared already in February, showed small growth until July (0.0071 mm d^{-1}); it increased in July−August (0.0456 mm d^{-1}), then decelerated (0.0136 mm d^{-1}).

As cohorts were undistinguishable after the end of the first calendar year, they could be pooled at that time into one age group whose individuals were about 4.5 mm (generations 1983 and 1984) or 5.5 mm length (generation 1982). Growth more or less ceased in the colder months. The second growing season had already begun by the end of February and the first ring on the shells became obvious in the samples from 1983, 1st March and 1984, 9 March, when mean shell length was about 6 mm (mean length of 1st growth ring: 6.6 mm, Bachelet, 1980). For generation '83, a rapid increase in shell length (0.0429 mm d^{-1}) took place from 17 February to 16 April; growth did not end at this date but continued at a slower rate (0.0102 mm d^{-1}), at least until late November 1984. Growth of the generation '82 began by 15 February and did not show any slowing until 17 June (average increased: 0.0343 mm d^{-1}); from this date and onwards, the shells could not be aged with accuracy.

Discussion

During the course of species development, several stages are decisive for the maintenance of benthic communities. In macrofaunal organisms with benthoplanktonic life-cycle, there are at least five such crucial stages: 1) maturation of sexual products, 2) spawning, 3) planktonic larval life, 4) larval settlement, and 5) post-larval growth, as observed from time of settlement to a size large enough to be retained by sieves used for macrobenthos studies (i.e. a 0.5- or 1 mm mesh-size). Strictly defined, the term 'recruitment' only refers to the last two stages, but its size closely depends on the first ones. In order to ascertain the reasons for a success or a failure in recruitment therefore requires the study of potential contributory factors, not simply restricted to the time of settlement, but also encompassing preceding events and early benthic life.

The timing of reproductive cycle and recruitment

During the first two years of a long-term study on recruitment in a population of *Macoma balthica*, a certain year-to-year variability in the reproductive cycle as well as in the production and survival of newly settled spat was observed. Results concerning seasonal gonad changes and settlement may be recapitulated for each year as follows:

Year 1983: ripe individuals: January/March, May/early June;
spawning: February/mid May, June/mid July;
recruitment: April, June, July (4 cohorts).

Year 1984: ripe individuals: November (1983)/May;
spawning: January, March/mid July;
recruitment: February, June (2 cohorts).

With regard to gonadal regeneration, no significant difference was found between the two years; gonads started to develop by mid June, and proliferation of the sex cells was accelerated from September to November and ceased by the end of December.

In a previous survey (1977), spawning was detected in May/July, then in October (Bachelet, 1980). At that time, only macroscopic examination of the visceral mass was performed and an arbitrary state of gonad development was assigned according to the extent to which the gonad tissue had migrated downwards or upwards from the line of attachment of palps and gills (Caddy, 1967). As has already been mentioned, this method does not allow us to distinguish between ripe specimens, developing specimens approaching sexual maturity, and specimens that have already started to spawning. Thus, the actual onset of spawning periods in 1977 probably occurred sooner than recorded.

A correction must also be made for the dates of recruitment in 1977, because a sieve with 0.5 mm mesh size was employed. Three cohorts of newly recruited spat were found from June to September. When the subsequent growth in shell length of these cohorts (Bachelet, 1980: 109, Fig. 4) is superimposed on to the growth of the recruits in 1983 (Fig. 6), a clear parallel is found between growth of the cohorts A, B, and C of both years. Hence, the recruitment periods in 1977 may be assumed to be

the same as in 1983. A further settlement was observed in autumn at site 1 (Bachelet, *loc. cit*).

In summary, the most likely sequence of events in 1977 was as follows:

spawning: March or April/July, October;

recruitment: April, June, July, November (4 cohorts).

Comparison of reproductive cycle in 1977, 1983 and 1984 shows that *M. balthica* spawns twice a year in the Gironde estuary. The animals always undergo a prolonged spawning period that lasts from March through July, but a time-lag may occur in its onset. For instance, spawning started in February during 1983 and in January 1984, which involved the spliting of the spawning period in two. In other European waters, intertidal populations of *M. balthica* shows a spring spawning that more or less coincides with our observations: late February/April in the Ythan estuary (Chambers & Milne, 1975); March/April (Lammens, 1967) or April/May (De Wilde & Berghuis, 1978) in the Dutch Wadden Sea; April/June in the Thames estuary (Caddy, 1967). The Gironde population has a more protracted spawning time (4–5 months) than the others (2–3 months).

As a result of the generally extended periods over which spawning took place, settlement occurred several times a year, at different periods and with a variable intensity from year to year. Recently settled spat can usually be found from February to July, but occasionally in autumn as well, such as in 1977. The present data on spawning and recruitment corroborate the estimate made by Caddy (1969) who determined a planktonic life of 2–5 weeks in *M. balthica*.

It has been established that spawning normally occurs in the period March/July in the Gironde estuary, however two major deviations must be emphasized: the early spawning in January 1984 and the late one in October 1977. Such a variation in the timing of the spawning season from one year to another has been found for subtidal bivalves (Brown, 1982). Intertidal invertebrates are directly submitted to climatic factors and though these organisms are ecologically adapted to fluctuating parameters, they are subjected to environmental stimuli which are likely to start up physiological processes when such stimuli exceed a certain threshold. Temperature is probably the most fluctuating parameter, both annually and daily, in inter-

tidal areas. Thus it is not surprising that a relationship was found between spawning activity and temperature in *M. balthica* (De Wilde, 1975; De Wilde & Berghuis, 1978). Expulsion of the gametes in field populations is restricted to seawater temperatures in the range 7–14 °C (Caddy, 1967). Such a range normally occurs between November to May in the Gironde estuary (Fig. 1) where the lowest monthly average temperature is recorded in January (7.2 °C), and may explain why *M. balthica* is able to spawn there in January/February. However spawning occurs until mid July when water temperatures are about 19 °C and air temperatures may be up to 30 °C on tidal flats, which is clearly above optimal temperature for spawning. De Wilde & Berghuis (*loc. cit.*) showed that in the laboratory, spawning in *M. balthica* was induced by administration of a temperature shock, consisting of a rise in temperature from 5 to 12.5 °C in 5 min. Thermic stress could be the factor inducing spawning, rather than a slow increase in temperature. Thus, when specimens still posess ripe gametes, as is the case in June/July, sudden changes of temperature (daily or nycthemeral) possibly could induce some egg release. The complete exhaustion of the sexual products in July coincides with the maximal sediment temperature (Fig. 1).

An autumn spawning took place in October 1977. Similar observations have been previously described in some populations where a spring spawning also occurred (Shaw, 1965; Caddy, 1967; Rasmussen, 1973; Nichols & Thompson, 1982). Developing gonads were present in this period in 1983 and 1984 as well, but no ripe specimens were found. In fact, climatic conditions in 1977 were quite different from the other years in that maximum air temperatures were unusually low from April to September (Fig. 7). Furthermore, water nutrient concentrations were relatively high during the entire year 1977, whereas they generally show a marked drop in the summer months. Reduced thermic variations and a high level of metabolites could have favoured a second gonad development in the second half of this year.

Juvenile growth

At the time of settlement, the larvae have a size of about 300 μm in shell length. The mean size of Pd II (270 μm) is close to that reported by various
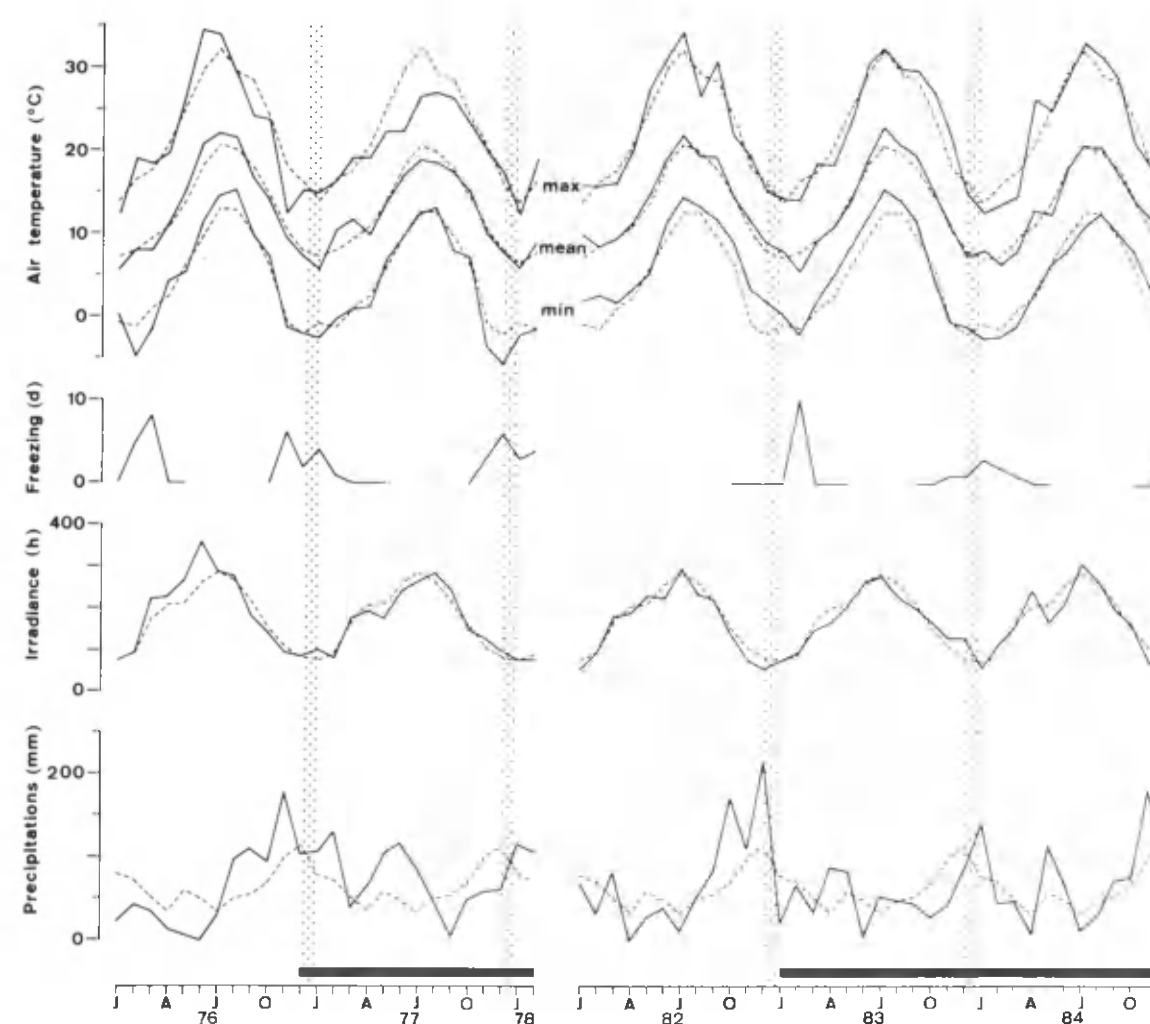
Fig. 7. Air temperature, irradiance, and rainfall fluctuations recorded near the sampling station during the years 1976–1978 and 1982–1984. Monthly numbers of freezing days are also shown. Mean values for ten years (1974–1984) are represented by a dotted line and thick horizontal bars indicate periods of sampling.

authors: 294 μm in the Øresund (Jørgensen, 1946), 255 μm at Prince Edward Island (Sullivan, 1948), 285–301 μm in the Thames estuary (Caddy, 1969). Depending on the period of recruitment, juvenile growth and size attained by the first winter were largely variable (Fig. 6). For the cohorts '83, the earlier they settled, the better they grew; individuals of each cohort were about 8, 6, 4 and 1 mm long respectively in December 1983. In this year-class, the highest growth rate was found from mid-June to the end of July, but the growing season continued at least until the end of November. After this

date, cohorts were not separable one from the other. The last cohort ('83$_D$) showed a very low growth rate. The three cohorts '77 showed the same increase in shell length as the first three cohorts '83.

The 1984 recruitment seems rather peculiar in that it occurred very early in the year (February) and had a slow growth rate until June which increased from July forward. There is an uncertainty however about growth rate during this year for the following reasons: 1) the spat had reached a length of around 4 mm in November which was the mean length of the whole generation '83 in the preceding

Chambers, M. R. & H. Milne, 1975. The production of *Macoma balthica* (L.) in the Ythan Estuary. Estuar. coast. mar. Sci. 3: 443–455.

De Wilde, P. A. W. J., 1975. Influence of temperature on behaviour, energy metabolism, and growth of *Macoma balthica* (L.). In H. Barnes (ed.), Proc. 9th Europ. mar. biol. Symp. Aberdeen University Press: 239–256.

De Wilde, P. A. W. J. & E. M. Berghuis, 1978. Laboratory experiments on the spawning of *Macoma balthica*; its implication for production research. In D. S. McLusky & A. J. Berry (eds), proc. 12th Europ. mar. biol. Symp. Pergamon Press, Oxford: 375–384.

Diaz, R. J., 1984. Short term dynamics of the dominant annelids in a polyhaline temperate estuary. Hydrobiologia 115: 153–158.

Eagle, R. A., 1975. Natural fluctuations in a soft bottom benthic community. J. mar. biol. Ass. U.K. 55: 865–878.

Glémarec, M., 1978. Problèmes d'écologie dynamique et de succession en baie de Concarneau. Vie Milieu 28–29: 1–20.

Holland, A. F., 1985. Long-term variation of macrobenthos in a mesohaline region of Chesapeake Bay. Estuaries 8: 93–113.

Hummel, H., 1985a. Food intake of *Macoma balthica* (Mollusca) in relation to seasonal changes in its potential food on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res. 19: 52–76.

Hummel, H., 1985b. An energy budget for a *Macoma balthica* (Mollusca) population living on a tidal flat in the Dutch Wadden Sea. Neth. J. Sea Res. 19: 84–92.

Jørgensen, C. B., 1946. Reproduction and larval development of Danish marine bottom invertebrates. 9. Lamellibranchia. Medd. Komm. Havundersøg., Kbh Ser. d, Plankton 4: 277–311.

Lammens, J. J., 1967. Growth and reproduction in a tidal flat population of *Macoma balthica* (L.). Neth. J. Sea Res. 3: 315–382.

Luckenbach, M. W., 1984. Settlement and early post-settlement survival in the recruitment of *Mulinia lateralis* (Bivalvia). Mar. Ecol. Prog. Ser. 17: 245–250.

Nichols, F. H., 1985. Abundance fluctuations among benthic invertebrates in two Pacific estuaries. Estuaries 8: 136–144.

Nichols, F. H. & J. K. Thompson, 1982. Seasonal growth in the bivalve *Macoma balthica* near the southern limit of its range. Estuaries 5: 110–120.

Persson, L. E., 1983. Temporal and spatial variation in coastal macrobenthic community structure, Hanö Bay (Southern Baltic). J. exp. mar. Biol. Ecol. 68: 277–293.

Peterson, C. H. & S. V. Andre, 1980. An experimental analysis of interspecific competition among marine filter feeders in a soft-sediment environment. Ecology 61: 129–139.

Powell, E. N., H. Cummins, R. J. Stanton Jr. & G. Staff, 1984. Estimation of the size of molluscan larval settlement using the death assemblage. Estuar. coast. shelf. Sci. 18: 367–384.

Rasmussen, E., 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). Ophelia 11: 1–507.

Shaw, W. N., 1965. Seasonal setting patterns of five species of bivalves in the Tred Avon River, Maryland. Chesapeake Sci. 6: 33–37.

Sullivan, C. M., 1948. Bivalve larvae of Malpeque Bay, P.E.I. Bull. Fish. Res. Bd Can. 77: 1–36.

Vahl, O., 1982. Long-term variations in recruitment of the Iceland scallop, *Chlamys islandica*, from northern Norway. Neth. J. Sea Res. 16: 80–87.

Weinberg, J. R., 1985. Factors regulating population dynamics of the marine bivalve *Gemma gemma*: intraspecific competition and salinity. Mar. Biol. 86: 173–182.

Williams, J. G., 1980. The influence of adults on the settlement of spat of the clam, *Tapes japonica*. J. mar. Res. 38: 729–741.

Woodin, S. A., 1976. Adult-larval interactions in dense infaunal assemblages: patterns of abundance. J. mar. Res. 34: 25–41.

Fluctuations naturelles et évolution artificielle des biocénoses macrozoobenthiques intertidales de trois estuaires des côtes françaises de la Manche

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Abstract

The study of the intertidal benthic population dynamics in three estuaries of the English Channel (Baie des Veys, Seine estuary, Baie de Somme:France) brings to light two types of species:
– key-species which directly respond to the local disturbance of the environmental conditions in their densities (Spionidae, Capitellidae) and in their growth rates (*Cerastoderma edule*);
– target-species such as *Macoma balthica* which can endure brief changes in the environmental factors and shows no sign of long-lasting consequences on its population dynamics; yet, it fully integrates long-term changes through its numbers and productivity.

The parallel between such a regular study of the seasonal variations on selected sites and various base line surveys allows the authors to discuss the COST 647 sampling programm in order to select natural fluctuations (storms, range of temperature) from human disturbances (embankments, chemical pollution, eutrophication).

Diverse hypothesis are suggested which bring about several research topics to be developed within a european cooperation.

Introduction

Les études portant sur la cinétique et la dynamique des populations du macrozoobenthos intertidal des principaux estuaires de la Manche centrale et orientale n'ont démarré que dans les années 1970–1972 pour la Baie des Veys (Sylvand, 1986), 1978 pour l'estuaire de la Seine (Desprez, 1981) et la Baie de Somme (Simon *et al.*, 1981). La constitution du Groupe d'Etude des Milieux Estuariens et Littoraux remonte à 1981, année de lancement du programme européen COST 647. En compilant les données acquises de façon discontinue sur l'ensemble de ces trois écosystèmes estuariens jusqu'en 1985 et sur quelques stations-pilotes retenues dans le cadre du COST, il est maintenant possible de s'adonner à la comparaison de l'évolution de ces embouchures macrotidales mais aussi de comprendre leur évolution en la confrontant à celle d'autres

estuaires européens ou d'un vaste ensemble intertidal comme la Mer des Wadden où le suivi du benthos couvre près d'un siècle: Van Der Baan *et al.* (1958) aux Pays-Bas, Mobius (1893) et Wolhenberg (1937) en Allemagne, Thamdrup (1935) au Danemark. Nos travaux s'inspirent d'ailleurs largement des recherches menées plus récemment par Beukema (1974, 1979, 1982, 1985), Michaelis (1976) et Madsen (1984), et ont bénéficié des conseils précieux de ces auteurs.

Présentation des sites

Les trois sites estuariens étudiés, les plus importants des côtes françaises de la Manche centrale et orientale, sont régulièrement distribués d'ouest en est (Fig. 1):
– la *Baie des Veys* est le seul site à présenter une