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Long-term changes in populations of subtidal bivalves (*Abra alba* and *A. prismatica*) from the Bay of Morlaix (Western English Channel)

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Abstract

Two populations of *Abra alba* (Wood) and one of *A. prismatica* (Montagu) (Mollusca: Bivalvia) were studied over a 10 yr period (1977–1987) in two muddy fine-sand subtidal communities of the Bay of Morlaix, France. The survey provided an example of long-term changes in the three *Abra* spp. populations, which displayed synchronized changes, with a regular annual cycle and increasing densities during 1979–1980 related to the higher concentration of organic matter resulting from the "Amoco Cadiz" oil spill in March 1978. *A. alba* rapidly adapts its demographic strategy to eutrophic conditions by increasing its reproductive potential, growth, and abundance. During times of eutrophication, *A. alba* has three spawning periods and three recruitments per year as opposed to two spawning periods and two recruitments per year during oligotrophic conditions. Growth of the juveniles of this species is insignificant until spring for individuals recruited in the autumn, whereas individuals which settle during spring or summer display immediate rapid growth. *A. prismatica* has a low capacity to adapt to eutrophic conditions. It has one annual period of sexual maturation at the end of the summer, with spawning in September–October and settlement beginning in mid-November. Growth of the juveniles after settlement is also insignificant until April. These results enable comparison of the demographic strategies of these two sympatric species.

Introduction

The two bivalves *Abra alba* (Wood) and *A. prismatica* (Montagu) are common species in coastal muddy sand sediments of northwestern Europe.

Abra alba is widely distributed and can be found at any depth down to 80 m (Tebble 1966), and is often the dominant species in shallow-water sandy communities. Dauvin (1986a) gave a chronological account of the numerous studies on *A. alba*. Since then, Cornet (1986a, b) has furnished data for *A. alba* populations in the northern part of the Bay of Biscay, Dauvin et al. (1986) have compared biology and dynamics from English Channel populations, and Webb (1986) has described their post-larval development. *A. alba* is an opportunistic species and an interesting biological indicator of disturbed environments (Hily and Le Bris 1984).

Abra prismatica occurs from the low-water mark to a depth of 200 m in clean fine sands but also may occur in muddy sand (Tebble 1966). Production of a population from the fine-sand community in the Bay of Morlaix was studied by Dauvin (1986b).

The first data on *Abra alba* and *A. prismatica* populations from the fine-sand community at Station "Pierre Noire" comprised basic observations from 1977–1982 by Dauvin (1986a, b). Continuous data covering a period of 10 yr from 1977–1987 are now available for two subtidal communities from the Bay of Morlaix, at Stations Pierre Noire and Rivière de Morlaix. These surveys provide an example of long-term changes in *Abra* spp. populations and allow a comparison of the demographic strategies of two sympatric species, *A. alba* and *A. prismatica,* and of two separate *A. alba* populations. This paper also presents first data on the reproductive cycle of *A. prismatica* and on the early benthic stages of both species.

Materials and methods

Study area

The main characteristics of the two sampling stations have been described by Dauvin (1982, 1984, 1986a).

The station "Pierre Noire" is located in the central part of an *Abra alba* – *Hyalinoecia bilineata* sandy community at 17 m depth. The sediment is fine sand with median particle size between 148 and 184 μm (1% of particles <63 μm) and a low particulate organic carbon content comprising 0.47% of the dry sediment weight (Beslier 1981). The benthic water

Table 1. Main characteristics of sampling techniques

	Macrobenthic survey		Post-larval survey, Pierre Noire (Feb. 1985–Mar. 1986)	
	Pierre Noire (Apr. 1977–Dec. 1987)	Rivière de Morlaix (Aug. 1977–Dec. 1987)		
Sampling gear	0.1 m^2 Smith-McIntyre grab	0.1 m^2 Smith-McIntyre grab	0.1 m^2 Smith-McIntyre grab	0.016 m^2 Reineck box corer
No. of samples per series	10	10	10	5
Total sampling area per series	1 m^2	1 m^2	1 m^2	0.08 m^2
Sieve mesh-size	1 mm, circular	1 mm, circular	0.5 and 1.0 mm, circular	0.5 and 1.0 mm, circular; and 0.18, 0.28, 0.355 mm square-mesh
Sampling frequency	5 to 12 times/yr	4 to 6 times/yr	monthly	fortnightly
Total no. of series	92	52	13	25

temperature varies between 8.8 °C in winter and 15.3 °C in summer, salinity between 34.50‰ in winter and 35.30‰ at the beginning of autumn.

The station "Rivière de Morlaix" lies in the middle of the navigational channel on the eastern border of the Morlaix estuary at 10 m depth, on an *Abra alba – Melinna palmata* muddy community. The sediment there is a mixture of fine sand and mud with median particle size between 77 and 122 μm and a fine fraction of particles <63 μm which comprises between 17.5 and 39% of the total sediment dry weight. This station is rich in organic matter, particulate organic carbon accounting for 1.39% of the dry sediment weight (Beslier 1981). Bottom-water temperatures range from 8 °C in winter to 16 °C in summer, and salinity usually from 34.00‰ in winter to 35.10‰ at the end of the summer.

No major changes in the normal hydrologic conditions at these sites were recorded between 1977 and 1987.

Sampling techniques (Table 1)

Material collected with the Smith-McIntyre grab (macrobenthic survey) was fixed with 10% neutral formalin and sorted twice.

Sediment samples collected with the Reineck box corer were fixed with 5% neutral formalin containing Rose Bengal stain and were sieved using sea water into five size fractions (1.00, 0.500, 0.355, 0.280 and 0.180 mm sieve mesh-sizes). This greatly facilitated the subsequent sorting of post-larval bivalves from the background sediment.

Length measurements

The shell length of small individuals (<3 mm) was measured under a dissecting microscope with an ocular micrometer of 0.08 mm precision, and larger specimens were measured with calipers of 0.1 mm precision. Lengths were pooled into 1.0 mm size classes.

Gonad development

Sexual maturity was determined by macroscopic examination of gonads and microscopic observations of gonadal tissue from approximately 20 and 30 individuals of *Abra alba* and *A. prismatica*, respectively. An approximately equal number of specimens were examined in each of four size classes: 7.1 to 10 mm, 10.1 to 12.5 mm, 12.6 to 15 mm and >15 mm for *A. alba* and 5.0 to 7.0 mm, 7.1 to 10.0 mm, 10.1 to 12.5 mm and >12.5 mm for *A. prismatica*.

Six stages (0, 1 a, 1 b, 1 c, 2 a, 2 b) of gonad development, grouped into three degrees of gonad development (spent, developing, spawning), were determined following Dewarumez (1979), Brown (1982) and Dauvin (1986 a);

Stage 0: indeterminate sex, undifferentiated cells, no gametes;

Stage 1 a (onset of development): first stage of spermatogenesis with occasional sperm, small round oocytes present at the periphery of ovarian tubules;

Stage 1 b: gonad increases in size, sperm are now clearly visible occupying approximately 40 to 50% of volume of tubule, pear-shaped oocytes visible, with some ova detached from the walls of follicles;

Stage 1 c: gonad attains maximum size, fully ripe ova and sperm;

Stage 2 a: gonad reduced in size and number of ripe gametes considerably diminished;

Stage 2 b: further reduction in volume of gonad, residual gametes.

Results

Reproductive cycle

Abra alba

At Station Pierre Noire, 165 specimens were examined from December 1984 to March 1986: 47 females and 51 males were identified, giving a sex-ratio of 0.92.

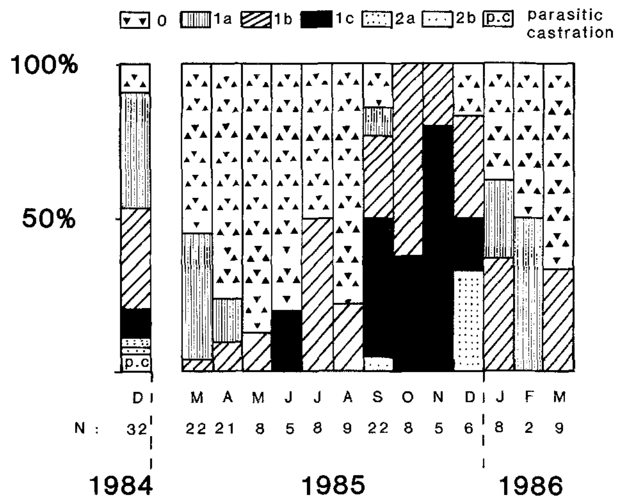

Fig. 1. *Abra alba.* Seasonal pattern of gonad maturity of population at Pierre Noire station, plotted each month from December 1984 to March 1986 in terms of percentage of the six gonadal stages (see "Materials and methods – Gonad development") N: no. of individuals examined

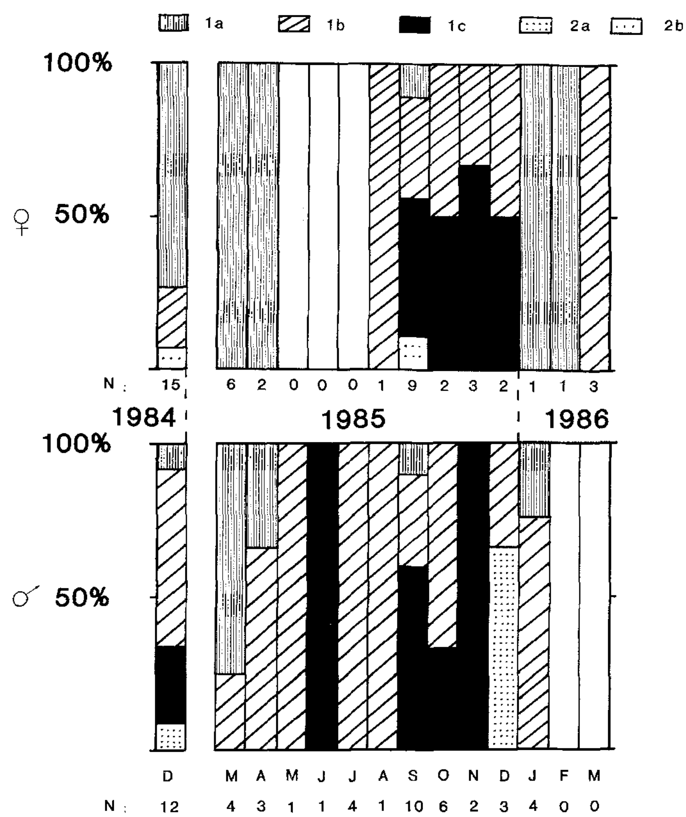

Fig. 2. *Abra alba.* Seasonal pattern of gonadal maturity of sexed females (upper graph) and males (lower graph) of population at Pierre Noire station, plotted each month from December 1984 to March 1986 in terms of percentage of five gonadal stages (1 a, 1 b, 1 c, 2 a, 2 b). N: no. of individuals examined

Fig. 1 shows the reproductive condition of the population during the survey. After the winter, there was a slow progressive maturation of gametes from March to August, with low percentages of Stages 1 b and 1 c present. Rapid maturation then occurred in autumn (100% were in Stages 1 b and 1 c in October and November). Spawning individuals were observed in September and December (Fig. 1).

The percentage of undifferentiated individuals was very high from March to August. Only two parasitically castrated females were observed, in December 1984.

For sexed females, the percentages of Stages 1 b and 1 c (Fig. 2) were high from August to December 1985. The occurrence of Stage 2 b in September indicated an earlier spawning during the summer. A second spawning occurred at the end of the autumn. For sexed males, the percentages of Stages 1 b and 1 c were high and stable except in March. Mature individuals were observed in June and from September to December.

Abra alba displayed two spawning periods during this study: the first was restricted to early summer, and the second and more important spawning occurred during the autumn.

Some departure from results obtained from December 1978 to March 1982 (Dauvin 1986 a) was apparent: (1) the percentage of undifferentiated *Abra alba* was very high during the present study [32% (1984–1986) vs 3% (1978–1982)]; (2) from 1978 to 1982, *A. alba* showed no period of sexual inactivity and three periods of spawning were identified – March–April, June, and October–November; (3) from 1978 to 1982, mature males were observed throughout the year. It is concluded that there was a reduction in the sexual activity of *A. alba* in 1984–1986.

At Station Rivière de Morlaix, individuals with a shell length >7 mm occurred only from August to October, 77% of these individuals had gonads at Stages 1 b and 1 c (50% at Stage 1 b and 27% at Stage 1 c in August, and 22% at Stage 1 b and 55% at Stage 1 c in October).

Abra prismatica

At Station Pierre Noire, 422 specimens were examined from December 1979 to July 1981; these included 149 identified females and 137 identified males, giving a sex-ratio of 1.09. Fig. 3 shows the reproductive condition of the population during the survey. The annual reproductive cycle was characterized by two main phases: (1) from December to June, the majority of individuals was undifferentiated (Stage 0) or with a slightly developed gonad (Stage 1 a); (2) from July to November, the bulk of the individuals was at Stage 1 b (gonad increasing in size) or at Stage 1 c (full gonad). Some individuals at Stage 1 c were also observed during February and May 1980. A large proportion of the females exhibited parasitic castration (39%), especially during winter and spring.

Separate inspection of sexed females (Fig. 4) showed that proliferation of the gonad began in March and sexual maturity was attained between June and September. Spawning probably occurred at the end of the summer, from August to October. For the sexed males (Fig. 4), individuals with gonads in Stage 1 b occurred in varying numbers throughout the study. Mature males (Stage 1 c) were observed in February and from June to October 1980. No

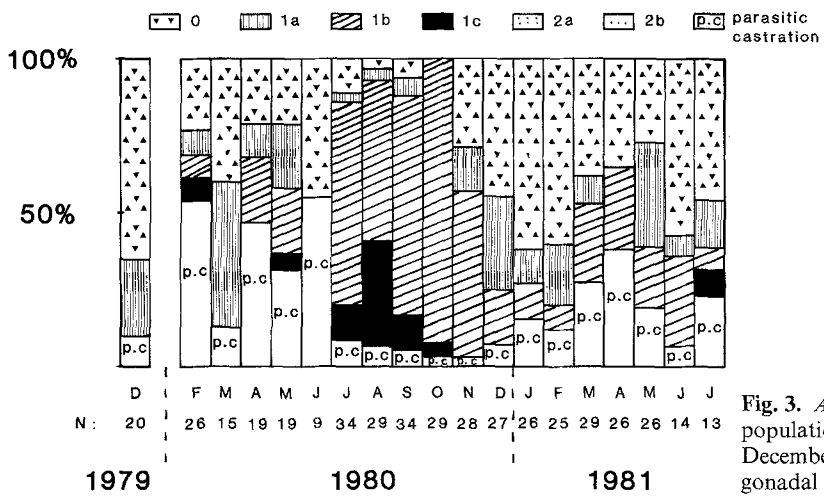

Fig. 3. *Abra prismatica.* Seasonal pattern of gonad maturity of population at Pierre Noire station, plotted each month from December 1979 to July 1981 in terms of percentage of the six gonadal stages. N: no. of individuals examined

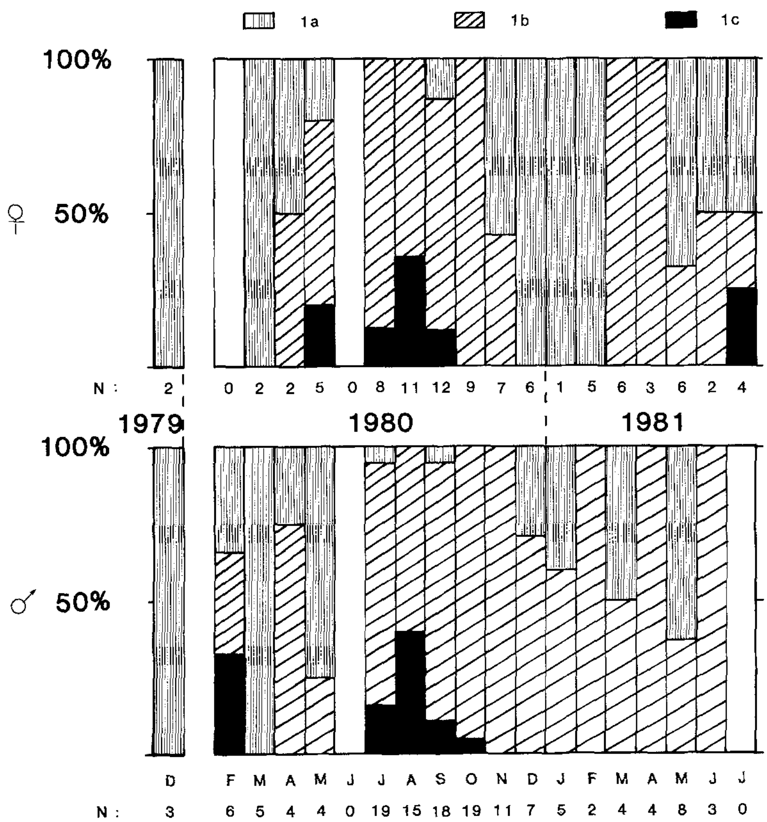

Fig. 4. *Abra prismatica.* Seasonal pattern of gonad maturity of sexed females (upper graph) and males (lower graph) of population at Pierre Noire station, plotted each month from December 1979 to July 1981 in terms of percentage of three gonad stages (1 a, 1 b, 1 c). N: no. of individuals examined

mature females or males were observed between November and June 1981.

In summary, *Abra prismatica* from the Bay of Morlaix showed only one spawning period per year, at the end of summer.

Early stages

The main diagnostic characters used to identify the benthic post-larvae of the two species were (1) the general appearance of the shell, which was more elongated for *Abra prismatica,* and (2) the form of the prodissoconch, which was more globular for *A. prismatica* than for *A. alba* (Webb 1986).

Abra alba

The minimum shell length recorded was 0.34 mm (see Table 2 for the different sizes collected with the five mesh-sizes). The early stages were found in the sediment fraction 0.5 mm

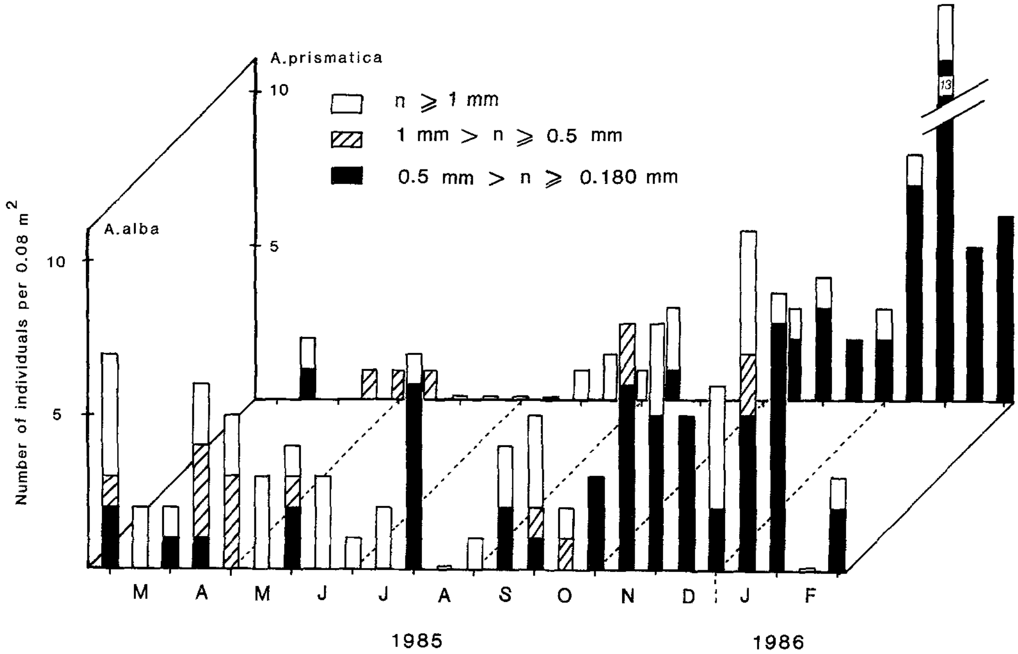

Fig. 5. *Abra alba* and *A. prismatica*. Seasonal pattern of juveniles at Pierre Noire station, plotted for each fortnightly box-corer sampling from February 1985 to March 1986. n: no. of individuals collected as a function of mesh size

Table 2. *Abra alba* and *A. prismatica*. Range of shell length (L) and number of individuals (N) collected with box-corer at Pierre Noire station, as a function of sieve-mesh size

Sieve mesh-size (mm)	*A. alba*		*A. prismatica*	
	L (mm)	N	L (mm)	N
0.18	0.34–0.46	22	0.36–0.46	3
0.28	0.44–0.62	26	0.48–0.60	37
0.355	0.58–1.2	2	0.62–0.70	2
0.5	0.76–1.3	13	0.74–1.4	3
1.0	⩾0.66	43	⩾0.78	14
Total N of individuals		106		59

and were collected through the year (Fig. 5), with two principal maxima. The first peak occurred during the summer at the end of July, reaching a maximum of 6 individuals 0.08 m^{-2}, corresponding to a density of 75 individuals m^{-2}; the second peak occurred during the winter at the beginning of February, with 8 individuals 0.08 m^{-2}, corresponding to a density of 100 individuals m^{-2}. Nevertheless, the period of maximum abundance extended from the beginning of November to the beginning of March; 74% of the early stages were collected during this period. Juveniles were collected on the 0.5 mm-mesh sieve throughout the year (Fig. 5 and Table 3). The proportion of young individuals was maximal during the winter, comprising 72.7% of the population at the end of January and at the beginning of the spring, and 27.7% of the population at the end of March. A second and lower peak of young individuals occurred at the end of July, when they constituted 11.5% of the population.

Abra prismatica

The smallest individuals had a length of 0.36 mm. Table 2 shows the different sizes collected with the five mesh sizes. The early stages were found in the sediment fraction <0.5 mm and occurred from mid-September to mid-March (Fig. 5). Their number was relatively stable during the autumn, then increased rapidly during the winter. At the beginning of February it reached a maximum of 13 individuals per 0.08 m^2, corresponding to a density of 163 juveniles m^{-2}. Some juveniles were also collected on the 0.5 mm-mesh sieve in the spring as well as in the box-corer from mid-April to mid-May (Fig. 5) and in the Smith McIntyre grab from the beginning of March to the end of May (Table 3). Young individuals represented 50% of the population at the end of April.

Macrobenthic phase

Abra alba

Fig. 6 shows the length-frequency histograms of *Abra alba* at Station Pierre Noire from December 1984 to March 1986. Specimens were first retained on a 1 mm-mesh sieve from March to the beginning of September. The number of *A. alba* reached a maximum during the spring, when 15.4 to 48.9% of the individuals collected on the 1 mm sieve had a length <3 mm.

Fig. 7 is a length-frequency histogram of *Abra alba* at Station Rivière de Morlaix from February 1985 to December 1985. In February, all specimens had a length <6 mm.

Table 3. *Abra alba* and *A. prismatica*. Monthly survey at Pierre Noire station. Density (nos. m^{-2}) and percentage of individuals retained by two sizes of screens (circular mesh, in mm) are shown

Date	*Abra alba*				*Abra prismatica*			
	1 mm		0.5 mm		1 mm		0.5 mm	
	Nos. m^{-2}	(%)	Nos. m^{-2}	(%)	Nos. m^{-2}	(%)	Nos. m^{-2}	(%)
1985								
27 Feb.	28	(90.3)	3	(9.7)	5	(100)	0	–
29 Mar.	26	(72.2)	10	(27.7)	3	(75)	1	(25)
29 Apr.	29	(80.5)	7	(19.5)	4	(50)	4	(20)
31 May	47	(87.0)	7	(13.0)	12	(80)	0	–
27 June	52	(92.9)	4	(7.1)	11	(100)	0	–
29 July	23	(88.5)	3	(11.5)	13	(100)	0	–
04 Sep.	35	(92.1)	3	(7.9)	5	(100)	0	–
26 Sep.	10	(91.0)	1	(9.0)	3	(100)	0	–
28 Oct.	5	(100.0)	0	–	1	(100)	0	–
02 Dec.	6	(75.0)	2	(25.0)	6	(100)	0	–
1986								
07 Jan.	10	(62.5)	6	(37.5)	5	(100)	0	–
30 Jan.	3	(27.3)	8	(72.7)	2	(100)	0	–
03 Mar.	11	(91.7)	1	(8.3)	3	(75)	1	(25)

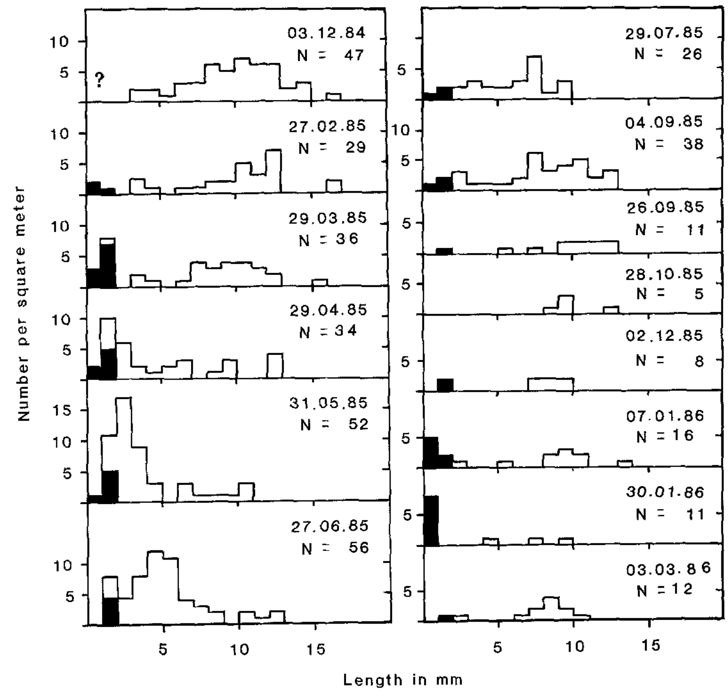

Fig. 6. *Abra alba*. Length-frequency histograms of shells of individuals at Pierre Noire station, plotted each month from December 1984 to March 1986. Date and no. of individuals collected (N), are given for each sampling date. Filled histograms indicate individuals collected only on 0.5 mm-mesh sieve

The May samples revealed an important spring recruitment. New juveniles were again observed at the end of July. All of the individuals recruited in spring died before the winter. The total mortality of these individuals appears to be connected with their late autumn reproduction.

Abra alba collected at Station Rivière de Morlaix in July were slightly larger than those collected at Pierre Noire: mean lengths of 8.25 vs 5.7 mm (Kolmogorov-Smirnov test: $P<0.001$). In May and September no significant difference in length was detected ($P>0.05$). The spring growth appeared to be more rapid at Rivière de Morlaix.

Abra prismatica

Macrobenthic recruitment (retained on the 1.0 mm-mesh sieve) first occurred in March–April and finished in May 1985 (Dauvin 1986b and Table 3 of present paper). As the densities were low during this sampling period, the length-frequency histograms have not been graphed.

Long-term changes in the three populations

Densities of individuals in the three populations displayed an annual cycle, reaching a maximum in summer after the

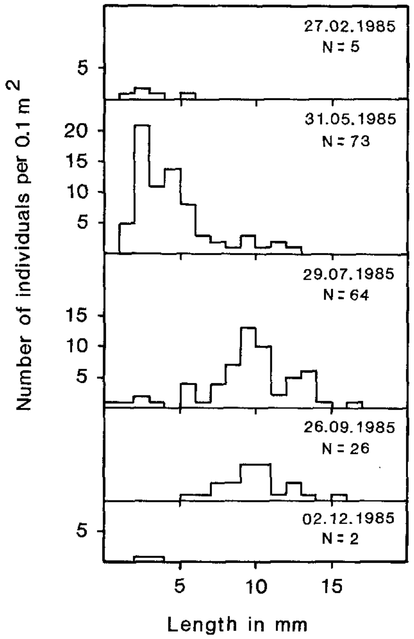

Fig. 7. *Abra alba.* Length-frequency histograms of shells of individuals at Rivière de Morlaix station, plotted from February to December 1985. Date and no. of individuals collected (N), are given for each sampling date

spring recruitment (judged by recruitment on 1 mm-mesh sieves) and a minimum in winter (Fig. 8). This pattern was clear at Rivière de Morlaix, where the population of *Abra alba* disappeared each year at the end of autumn. The three populations showed synchronized long-term changes. In 1979 and 1980 increased densities were related to the higher concentration of organic matter resulting from the "Amoco Cadiz" oil spill (Boucher et al. 1984). During these years, the increase in the *A. alba* population at Pierre Noire was greatest, with a maximum density about three times higher than the *A. prismatica* population at the same place and the *A. alba* population at Rívière de Morlaix. After this 2 yr period of stimulation, the populations displayed moderate pluriannual fluctuations, although the *A. prismatica* population increased during both 1986 and 1987.

Discussion

Life-history of *Abra alba*

The *Abra alba* populations from the Bay of Morlaix exhibit several adaptative characteristics in their life cycle in rela-

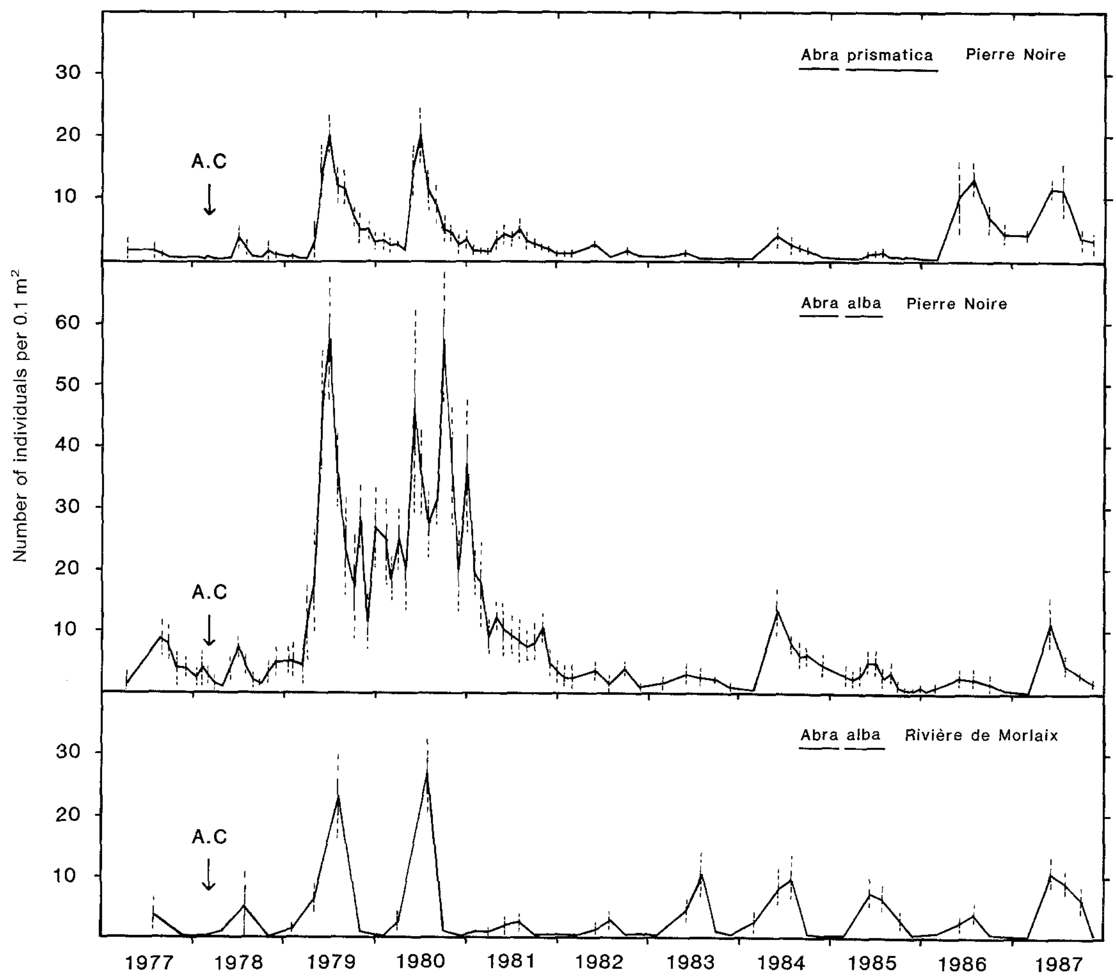

Fig. 8. *Abra alba* and *A. prismatica*. Long-term changes in population densities [nos. ±SEM (short vertical bars) retained per 0.1 m^2 on 1 mm-mesh sieve] at Pierre Noire and Rivière de Morlaix stations; dashed extensions of vertical bars show 95% confidence intervals. "A.C" indicates beginning of hydrocarbon pollution from "Amoco Cadiz oil spill"

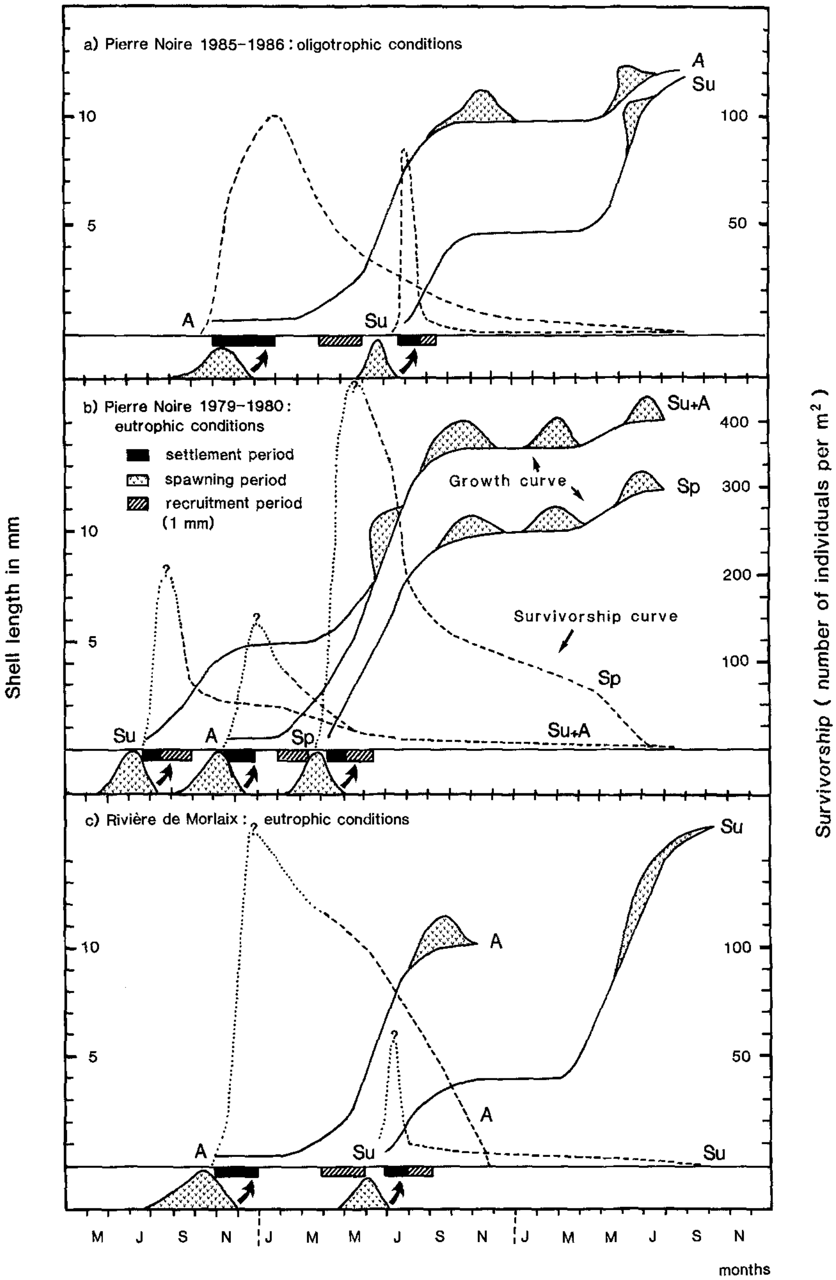

Fig. 9. *Abra alba.* Diagrammatic representation of life cycle at Bay of Morlaix. Sp, Su and A: spring, summer and autumn-recruited cohorts, respectively. Continuous lines: growth curves; dashed lines: observed 1 mm survivorship curves; dotted lines: presumed real survivorship curves

tion to environmental conditions in the two muddy fine-sand communities.

The study of the benthic stages of this species living at the Pierre Noire station during the 1985–1986 period provided data for oligotrophic conditions in contrast to the earlier studies under the eutrophic conditions that resulted from the "Amoco Cadiz" oil spill (Dauvin 1986a).

Oligotrophic conditions

In oligotrophic conditions, *Abra alba* had two main periods of sexual maturity: in June, and from October to December. Spawning probably occurred both in July and in the autumn. The autumn spawning affected all mature individuals.

The earliest benthic stages, with a minimum shell length of 0.34 mm, were regularly collected during two distinct periods: November to late winter (Line "A" in Fig. 9a) and August–September (Line "Su" in Fig. 9a). It is concluded that the pelagic larval development of *Abra alba* lasts about 1 mo, and is therefore shorter than that of *A. prismatica.*

According to the season of settlement, newly settled individuals differed in terms of growth and potential life span:

(i) Autumn-settled individuals (A) displayed insignificant growth until April (Fig. 9a). Their recruitment on 1 mm-mesh sieve occurred from April to June, 5 to 7 mo after settlement. These individuals had a maximal life span of 21 mo and could produce two spawnings.

(ii) Summer-settled individuals (Su) displayed very rapid growth and were retained one 1 mm-mesh sieve only 1 mo after settlement. They lived about 1 yr, spawning only once. Mortality of the early benthic stages seemed heavier during the summer than in winter (Fig. 9a). For the two cohorts (A and Su) the main growth was restricted to the spring period. Their mean maximum length was slightly greater than 12 mm.

Eutrophic conditions

The "Amoco Cadiz" oil spill in March 1978 introduced a vast, accidental disturbance to the fine-sand communities of the Bay of Morlaix (Dauvin 1982, 1984).

At the Pierre Noire station, there were drastic qualitative and quantitative changes after the spill. The number of species in the community, density and biomass decreased by about 25, 80, and 40%, respectively. The *Ampelisca* spp. (amphipod) populations dominant before the pollution were completely destroyed, and have not yet fully recovered 10 yr later. No subsequent compensatory proliferation has been observed (Dauvin 1984). On the muddy fine-sand community at the Rivière de Morlaix station, the pollution impact has been more limited (Dauvin 1982).

Pierre Noire station. Boucher et al. (1984) observed an eutrophication of the sediments at Pierre Noire in 1979. The *Abra alba* population existed in such eutrophic conditions from 1979–1980 in a disturbed community with vacant ecological niches. During this period, only the macrobenthic stages of the life cycle of *A. alba* were sampled (Dauvin 1986b). *A. alba* displayed three periods of sexual maturation: February–March, April–June, August–October and three spawning periods in March–April, June–July and October–November. Only the autumn spawning affected all mature females. Three periods of recruitment have been identified each year (Fig. 9b): (1) autumn, a weak winter recruitment (February–March) resulting from the autumnal spawning after a pelagic larval development and benthic juvenile development of 5 to 6 mo; (2) spring, a large spring recruitment from April to June resulted from the first annual spawning period (March–April); (3) summer, a weak summer and autumnal recruitment (August to October) resulting from the second annual spawning period (June–July). The combined pelagic larval development and benthic juvenile development of Recruitments Periods 2 and 3 had a duration of 2 to 3 mo.

Growth was rapid during spring and moderate during summer and the beginning of the autumn. The mean maximum length of individuals from the summer (Su) and autumnal (A) cohorts was 15 mm for a maximum life span of 2 yr. The recruits from these cohorts were able to spawn four times. The mean maximum length of individuals from the spring cohort was 12 mm for a maximum life span of 18 mo.

In summary, during the eutrophication phase, *Abra alba* showed (1) a marked sexual activity with three spawning periods, (2) three recruitments per year with a very important spring recruitment (more than 350 individuals m^{-2} on 1 mm-mesh sieve), (3) increased growth rate for the summer and autumn recruits, resulting in greater shell length (15 mm at the end of life, as opposed to 12 mm in oligotrophic conditions).

Rivière de Morlaix station. The *Abra alba – Melinna palmata* community located near the mouth of the Rivière de Morlaix estuary lives in an environment rich in nutrients and in which polychaetes are very numerous. The dominant polychaete species, *Chaetozone setosa* Malmgren, was recognized as an opportunistic species by Hily (1987). The hydrocarbon pollution from the "Amoco Cadiz" modified this benthic eutrophic ecosystem (Dauvin 1982). During the first annual cycle after the oil spill some species were very abundant, e.g. the opportunistic polychaete *C. setosa* and other polychaetes (*Mediomastus fragilis* and *Tharyx marioni*) which had been rare in natural conditions in the Bay of Morlaix. *A. alba* also showed an increase in its summer maxima in 1979 and 1980, related to an increase in organic matter. Nevertheless, in this eutrophic community, *A. alba* showed no modification of its demographic strategy.

Only the macrobenthic stages of the biological cycle have been observed at this station. Some specimens were sexually mature in June. The proportion of mature specimens increased from August to October. The species had probably spawned twice, both in July and in the autumn from September to November. The population had two regular recruitments each year, in April–May (A) and in July–August (Su). Recruits on the 1 mm mesh sieve probably resulted from the two spawning periods in autumn and at the end of the spring (Fig. 9c). This pattern is consistent with the results obtained at the Pierre Noire station and in a similar community in the harbour of Brest (Hily and Le Bris 1984).

Growth of the autumnal cohort (A) was very rapid during the spring. These recruits spawned in the autumn and then died; their life span was about 1 yr. Growth of the summer cohort (Su) was only high during the spring after settlement. These specimens had attained >15 mm in shell length by the end of the summer. They spawned from June to October and then died afterwards. Their life span was about 14 mo.

In summary, in the eutrophic conditions at the Rivière de Morlaix station, *Abra alba* showed (1) a maximum length greater than that of *A. alba* in oligotrophic conditions at the Pierre Noire station, but similar to that of this species in eutrophic conditions at the Pierre Noire station, and (2) a shorter life span than the specimens observed at the Pierre Noire station.

Life-history of *Abra prismatica*

This study furnishes complete data on the life-cycle and the benthic stages of *Abra prismatica,* for which there has previously been very little information. The single annual period of sexual maturation occurs from July to September, with a spawning between September and October. The earliest benthic stages, with a minimum shell length of 0.36 mm, were collected from mid-November (Fig. 10), indicating a pelagic larval development of about 2 mo.

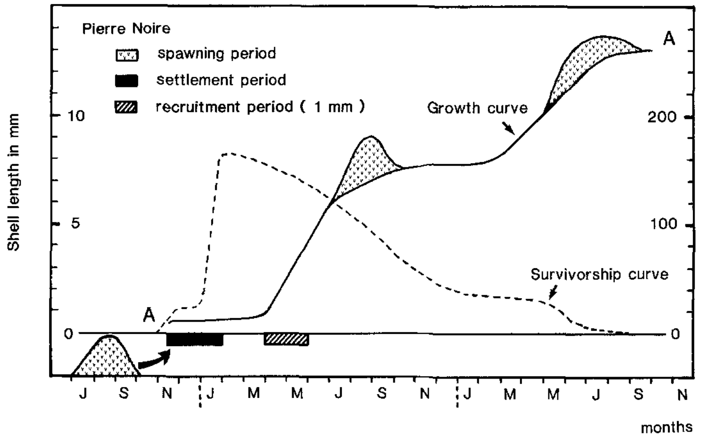

Fig. 10. *Abra prismatica.* Diagrammatic representation of life cycle of autumn-recruited cohort (A) at Pierre Noire station

Growth of individuals after settlement is insignificant until April, but is then very rapid in the spring before again slowing down. Recruitment, as judged by retention on 1 mm-mesh sieves, occurs during the spring. These individuals first spawn after about 1 yr of benthic life. Growth starts again during spring for some over-wintered individuals that can spawn a second time and die afterwards. For these specimens the life span can reach 22 mo.

Comparison of demographic strategies

The life cycles of the two sympatric species, *Abra alba* and *A. prismatica,* were similar.

(1) Both species have a long pelagic larval stage. The larvae suffer important numerical loss due to dispersion by tidal currents in a megatidal regime. The sublittoral muddy-sand benthic communities in the western part of the English Channel have a discontinuous distribution, occurring in isolated patches that are localized in estuaries and bays (Cabioch et al. 1982). The pelagic dispersion of larvae is a favourable factor for colonization of these isolated communities, but unfavourable for mass settlement. These conditions may explain the observed moderate densities of early stages. On the other hand, mortality of the early stages appeared to be moderate (Figs. 9 and 10), except for the summer recruitment of *Abra alba.*

(2) Growth of the juveniles which settled during the autumn was insignificant until the following spring. These recruits initially experienced decreasing temperature and poor trophic conditions. Muus (1973) observed very slow growth rate during the first year after settlement for *Abra alba* in the Öresund, perhaps due to unfavourable abiotic and biotic factors, specimens attaining a length of 1 mm one year after settlement. Two other species of the genus *Abra, A. ovata* and *A. tenuis* also displayed slow growth rates following an autumnal recruitment (Bachelet 1987, Bachelet et al. 1987). Spring and summer recruits have the advantage of being capable of immediate rapid growth under favourable temperature and feeding conditions.

(3) The length of the smallest individuals collected on a 0.180 mm-mesh sieve was very similar: 0.34 mm in *Abra alba* and 0.36 mm in *A. prismatica.* In the case of *A. alba,* this minimum length is within the range observed by different authors for the same species under natural conditions elsewhere: 0.3 to 0.32 mm in Helgoland (Kändler 1926), 0.35 mm in Danish waters (Jörgensen 1946), 0.3 to 0.4 mm in the Öresund (Muus 1973), 0.26 to 0.31 mm in the Bristol Channel, UK (Webb 1986) and 0.2 to 0.4 mm in the bay of Arcachon, France (Bachelet 1987).

(4) Except for the case of the summer recruitment of *Abra alba,* the survivorship curves (Figs. 9 and 10) correspond to the Type II curves of Slobodkin (1962), whereby a constant number of individuals dies per unit of time. There was no selective mortality in this environment which corresponded to slight annual and multiannual variations in the hydrologic conditions and moderate predation by fishes (Dauvin 1984). The survivorship of the *A. alba* summer cohort corresponds to the Type IV curve of Slobodkin, whereby mortality affects most heavily the young stages. Such recruitment occurs during the period of maximum density and consequently during the time of maximum interspecific competition.

During the eutrophication of the environment following the "Amoco Cadiz" oil spill, *Abra alba* rapidly adapted its demographic strategy by increasing its reproductive potential, growth, and abundance. This adaptative strategy explains the variability of the biological cycle of *A. alba* in relation to local conditions. Therefore "demographic polymorphism" (Bachelet et al. 1987) characterizes *A. alba,* which is adapted to rapidly colonize a disturbed community as an "*r*"-strategy species according to Glémarec (1978) and Hily and Le Bris (1984). Thus, this 10 yr survey of the *A. alba* populations from the Bay of Morlaix demonstrates the capacity for adaptation of this species to changes in environmental conditions. On the other hand, during the eutrophication phase, *A. prismatica* showed only a moderate increase in its abundance in relation to a more successful settlement. *A. prismatica* seems to be a "*K*"-strategy species, with reduced capacity for adaptation.

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