Seagrass (*Zostera marina* L.) bed recolonisation after anoxia-induced full mortality

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Abstract

Recolonisation of *Zostera marina*, following complete destruction caused by an anoxic crisis, was studied in the Thau lagoon (French Mediterranean Sea) from February 1998 to September 1999. The recolonisation took place surprisingly rapidly as biomasses similar to those from untouched areas were reached only nine months after seed germination. The recolonisation success was partly due to a high seedling survival rate as well as a rapid vegetative recruitment (ranging from 0.012 to 0.042 per day). Two phases of recovery could be observed: a rapid multiplication of shoots during the first 3 months was followed by an increase in biomass due to elongation of leaves. During the first year of recolonisation no flowering shoot was observed whilst reproductive effort was considerable during the second year. In case of two consecutive anoxic crises at the same site, the recovery would have probably been much slower, since the annual seedbank would have been depleted.
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1. Introduction

Anoxic events are known to be one of the major disturbances in coastal waters and can lead to important benthic life and fish mortality (Segar and Berberian, 1976; Kemp et al., 1992; Viaroli et al., 2001). These episodes are generally transient and come to their end when the oxygen demand due to organic matter mineralization decreases and the wind-induced turbulence becomes sufficient to re-oxygenate the water column (Chapelle et al., 1994). Recolonisation by benthic communities then becomes possible.

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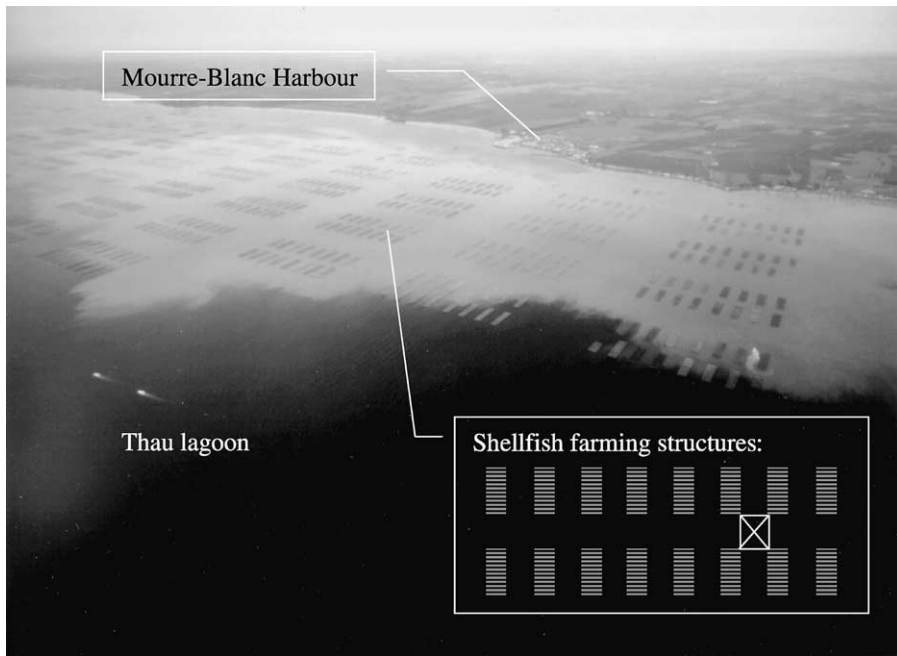*E-mail address:* martin.plus@ifremer.fr (M. Plus).

Fig. 1. Aerial photograph taken on 27 August 1997 (J.-M. Deslous-Paoli, personal communication), during the anoxic crisis in the Thau lagoon. The white waters denote presence of anaerobic bacteria, thus delimiting the affected zone. The study site ($\boxtimes$) is reported at its exact position.

Recolonisation by seagrasses after various causes of disturbance has been extensively studied such as: the "big wasting disease" (Den Hartog, 1970; De Jonge and Ruiter, 1996), increasing eutrophication (Burdick et al., 1994; Duarte, 1995; Harwell and Orth, 2002), fluctuating salinity (Grillas et al., 2000), storms (Patriquin, 1975; Preen et al., 1995; Short and Wyllie-Echeverria, 1996), sand dredging (Penn, 1981), anchor damage (Creed and Amado Filho, 1999) or oil spills (Jacobs, 1980; Zieman et al., 1984) but, as far as we know, little has been reported on the process of recolonisation after an anoxic event.

For many years, the Thau lagoon (south Mediterranean coast of France) has been suffering anoxic events (locally called "malaïgues", Baleux and Sinègre, 1984; Frisoni and Cejpa, 1989) that occasionally were responsible for genuine disasters in shellfish farming activities. During the period 23–27 August 1997, an anoxic crisis started near the little harbour called Mourre-Blanc and quickly extended across the shellfish cultivation structures (Fig. 1) killing about 3500 tonnes of oysters and mussels. The triggering factor was the degradation of green algae and probably organic matter coming from aquaculture, accelerated by high temperatures (Souchu et al., 1998; Chapelle et al., 2001). Moreover, the expansion of the event was favoured by a period of very calm winds. Proportional oxygen saturation decreased to 0% in bottom waters during the episode, and toxic sulphuric compounds were released by the sediment (Souchu et al., 1998; Chapelle et al., 2001). Subsequently, benthic vegetation which had been previously described as dense within the shellfish cultivation

structures (*Zostera marina* meadows mixed with *Gracilaria* spp., *Alsidium corallinum* and *Codium fragile* populations, according Lauret, 1990), totally disappeared. In the beginning of September 1997, oxic conditions re-occurred in the water column thanks to stronger winds (above $4 \, \mathrm{m \, s^{-1}}$) and the discovery of numerous seagrass seedlings led to the present study.

The aim of this study was to follow the recolonisation characteristics (recruitment, mortality, biomass and meadow morphology) of a *Z. marina* meadow, and thus to assess the impact, over the short- or medium-term, of an anoxic episode on seagrass beds in the Thau lagoon.

2. Study site, material and methods

The study site is a $20 \, \mathrm{m} \times 25 \, \mathrm{m}$ rectangle well delimited by four shellfish farming structures (called conchological tables), located at $4.2 \, \mathrm{m}$ depth, in the middle of a perpetually submerged area which had been affected by the anoxia (Fig. 1). Twenty PVC cylinders (31 cm diameter and 25 cm height) were gently pushed into the sediment in order to isolate some recently germinated *Zostera* seedlings (five at maximum), as well as their below-ground organs. Each cylinder had been numbered previously and marked with notches, which allowed identification in case of low underwater visibility (light extinction coefficient in the Thau lagoon ranges 0.4–$0.9 \, \mathrm{m^{-1}}$, according to Deslous-Paoli, 1995).

Each month, from February 1998 to September 1999, the number of shoots in each cylinder was recorded, as well as the density and biomass of shoots in the study area but outside the cylinders (10 successive random samples with a $0.15 \, \mathrm{m^2}$ quadrat). Thirty shoots were also sampled at random and brought back to the laboratory. The material was sieved, well rinsed and carefully washed to remove epiphytes, before separation into leaves, below-ground organs (rhizomes and roots) and inflorescences. Leaf length and width as well as number of leaves by shoot were measured in order to calculate the leaf area index (LAI, total leaf surface per unit ground surface). Dry biomass was then determined by drying all plant material in an oven at $80 \, ^{\circ}\mathrm{C}$ for 48 h. Afterwards, the leaf and rhizomes/roots carbon and nitrogen contents were determined on three sub-samples using a LECO 800 CHN autoanalyser (elementary thermoanalysis method).

In addition, every 3 months, all shoots present in three randomly selected cylinders were sampled carefully including all below-ground organs, and rhizome diameter, horizontal internode lengths as well as number of horizontal branches were recorded.

Water temperature and salinity were measured during the whole of the observation period and the Météo-France station in Fréjorgues Airport (20 km from study site) provided solar radiation data.

2.1. Recruitment and mortality rates calculation

Recruitment and mortality rates (respectively, β and δ, expressed in per day) were calculated using typical equations of population dynamics, considering that appearance and disappearance of shoots is a continuous rather than discrete process (Duarte et al., 1994):

$$\beta = \ln\left(\frac{N_t}{N_t - n}\right) \times \frac{1}{t} \tag{1}$$

$$\delta = \ln\left(\frac{N_0}{N_t - n}\right) \times \frac{1}{t} \tag{2}$$

where N_0, the initial number of shoots, N_t, the number of shoots at time t and n, the number of newly produced shoots during the time t, were deduced from the number of internodes present on the rhizomes. Recruitment and mortality rates were calculated for each 3-month period.

2.2. Rhizome elongation

The first rhizome internodes on an established seedling are morphologically distinct: it is thinner and curved like a hook (Setchell, 1929; Den Hartog, 1970). We used this to find the initial origin of a spreading rhizome. The elongation rate was deduced from the total number of internodes between the scorpioïd extremity and the last shoot, and the length of each internode. Calculations of the age-reconstruction proposed by Duarte et al. (1994) and of the plastochrone interval were not necessary because the age of the rhizome was known. Calculation of the elongation rates has therefore been made each time a rhizome has been found complete, from the scorpioïd extremity to the youngest shoot.

2.3. Statistical analysis

All means are given with standard errors and comparisons of data sets were performed using analysis of variance when conditions of homoscedasticity and normality of distributions were fulfilled or using non-parametric test (Kruskal–Wallis rank test) when they were not.

3. Results

The Mediterranean climate imposes large seasonal variations of water temperature and salinity in the Thau lagoon (Fig. 2). Strong rainfalls during the winter of 1997–1998 produced lower salinity during this period (33.6 PSU in January 1998). The following winter, however, low salinities were not observed, but water temperature was quite low, with a minimum of 5 °C in February 1999.

Measured biomasses and densities showed a rapid recolonisation (Fig. 3), with values similar to those previously reported for the same area (25–75 g DW m^{-2} in October 1986, according to Gerbal and Verlaque, 1995) being reached about 9 months after seed germination. With the exception of the first samples in February 1998, when all shoots found were still attached to their seeds and no older rhizome was found in the sediment, no other new seedlings were observed during the following seasons.

The number of germinated seeds during the winter following the anoxic crisis was 15.7 ± 13.9 m^{-2}. Maximum shoot density (124 ± 84 shoots m^{-2}) was measured only 3 months later, when leaf biomasses still exhibited low values (3.7 ± 2.5 g DW m^{-2}). Afterwards, a rapid increase in leaf length and width, as well as an increase of the number of leaves by shoot (Fig. 4) led to the increase in biomass. Maximum biomass (39.5 ± 15 g DW m^{-2}) and LAI (1.6 ± 0.3 m^2 m^{-2}) were recorded in late October 1998.
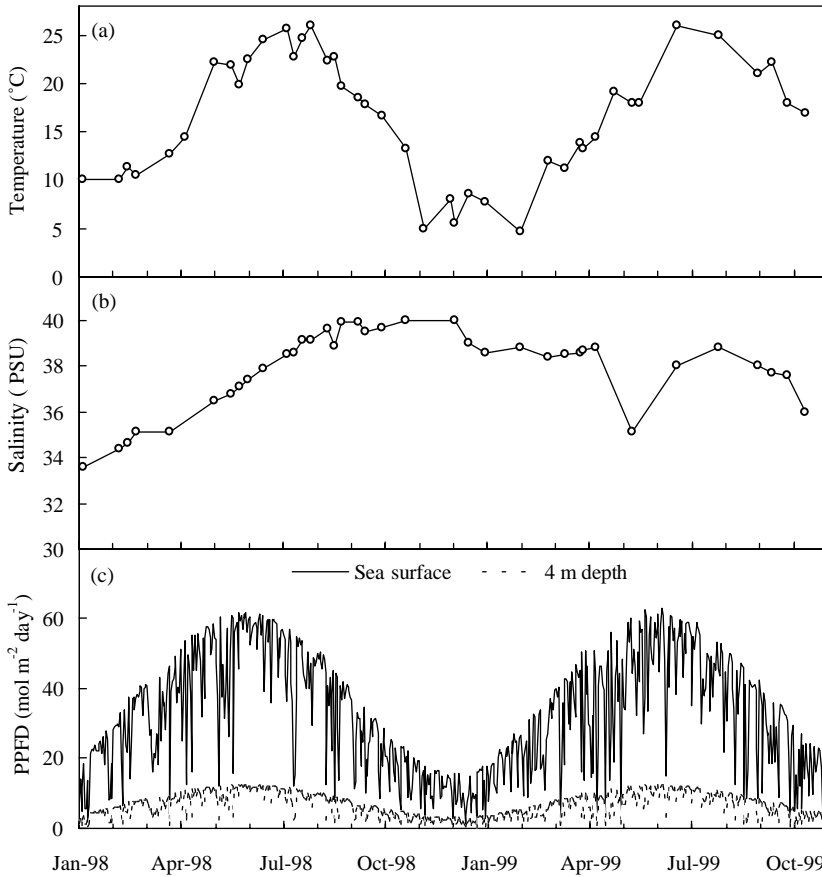
Fig. 2. Water temperature (a); salinity (b); and photosynthetic photon flux density (PPFD) (c) at the sea surface and at 4 m depth (calculated using a water light extinction coefficient of $0.4\,m^{-1}$, following Deslous-Paoli, 1995), recorded during the study period.

Although no significant relationship was found between above-ground biomass and density, above-ground biomass and LAI exhibited a highly significant linear relationship ($r^2 = 0.86$, $P < 0.001$). Leaves were found to be significantly shorter and thinner during the winter than the summer period, the biggest leaves were found during the second year (Table 1). Moreover, the mean leaf number on shoots was found significantly lower during winter than any other seasons, however it did not differ significantly between the two study years (Table 1). Thus, it appears that the morphometric features of the leaves (length and thickness) have a significant impact on the variation of above-ground biomass. For example, during autumn and winter 1998–1999, the seagrass biomass hardly decreased until the beginning of March 1999 (biomass was below $10\,g\,DW\,m^{-2}$). This reduction was not due to a reduction in density, as the number of shoots remained roughly constant during this period (Fig. 3b), but was probably the result of a reduction in leaf mean length and width (Fig. 4a
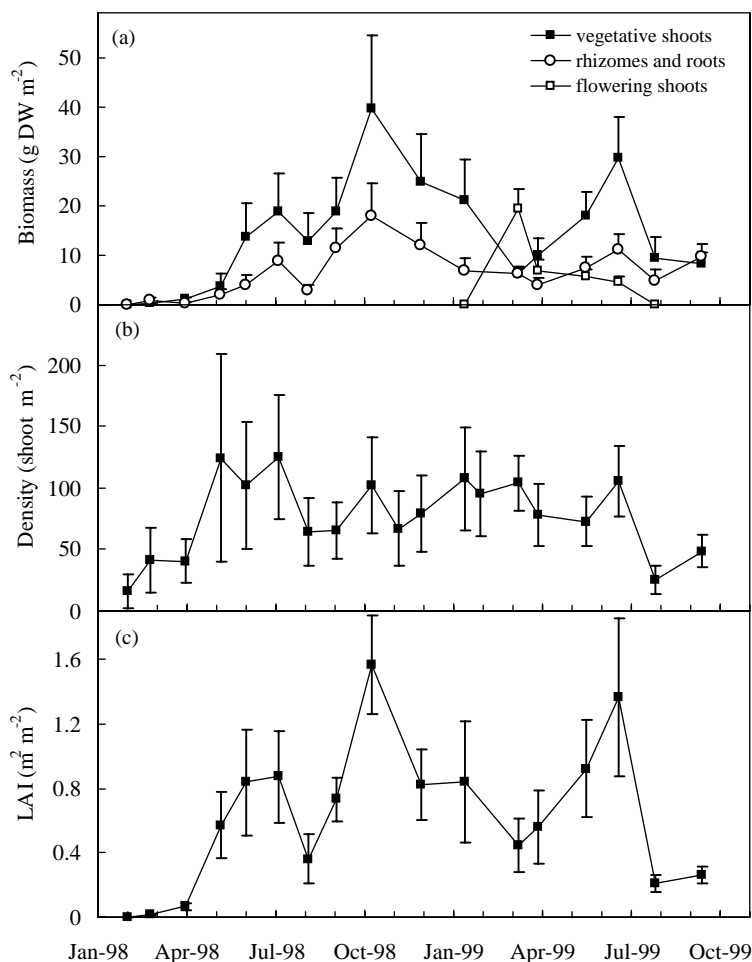
Fig. 3. Seasonal variation of seagrass biomass (a); density of shoots (b); and leaf area index (c) of the *Z. marina* meadow during the recolonisation phase. Standard errors are given as vertical bars.

and b), with the old longer leaves grown in summer 1998 disappearing and being replaced by shorter young leaves.

The spring of the second year of recolonisation was characterised by the appearance of the first flowering shoots. Their presence was recorded from March 1999 to August 1999, with a maximum in March 1999, then accounting for 75% of total above-ground biomass (Table 2). Vegetative growth was resumed during spring and summer 1999, reaching a maximum biomass in July ($30 \pm 8 \, \text{g DW m}^{-2}$). Vegetative biomasses in summer 1999 remained lower than in summer 1998, however, total vegetative plus flowering biomass reached values similar to those reported for the previous year ($34 \pm 9 \, \text{g DW m}^{-2}$). Neither variation in temperature (ANOVA, $P = 0.90$) nor that in light intensity ($P = 0.06$) could explain biomass variance over the whole period.
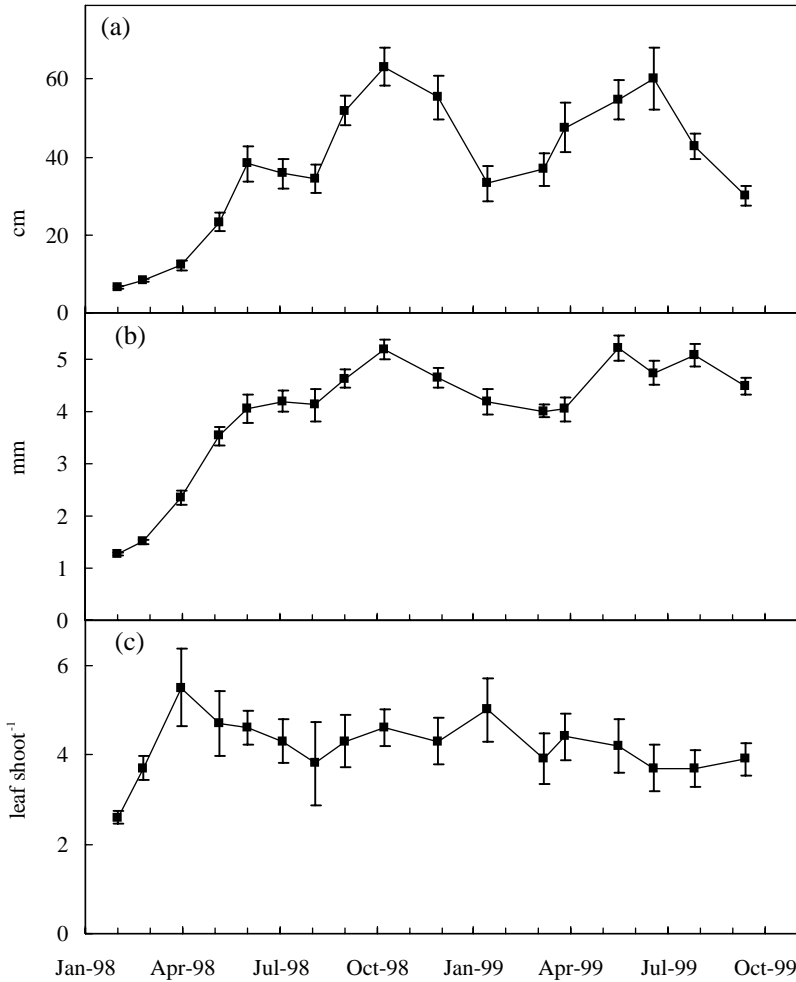
Fig. 4. Leaf length (a); width (b); and leaf number per shoot (c) measured on the *Z. marina* meadow during the recolonisation phase. Standard errors are given as vertical bars.

Seasonal variation of below-ground biomass roughly followed the same unimodal pattern as the above-ground biomass. The amplitude of variation was lower, with a smaller decrease in biomass during winter 1998–1999 (Fig. 3a). The mean above-ground:below-ground biomass ratio was 2.6 ± 0.5 during the whole period with higher values (maximum 4.6) in spring and summer, and minima during autumn (0.8 by the end of September 1999).

In general, nitrogen content was more variable than carbon content (Fig. 5). However, the carbon content in leaves showed a significant ($P = 0.015$), though slight, decrease over the whole period. This tendency was not observed in rhizomes and roots carbon contents. Leaf nitrogen content tended to decrease during spring and summer, and to increase during autumn and winter. Nitrogen and carbon content were found to be significantly higher

Table 1

Effect of season and year of recolonisation on the shoot morphological characteristics: leaf length, width and number of leaves by shoot

	Length (cm)	Width (mm)	Number of leaves
Mean ± S. E. (*n*)	37.3 ± 3.8 (1356)	4.0 ± 0.2 (1356)	4.2 ± 0.5 (352)
Season			
d.f.	1	1	1
%SS	30.9	45.3	11.5
F-value	291.0	666.0	16.5
P-value	<0.001	<0.001	<0.001
Year			
d.f.	3	3	3
%SS	8.8	16.7	0.6
F-value	249.6	738.9	2.4
P-value	<0.001	<0.001	0.12
Season × year			
d.f.	3	3	3
%SS	12.6	8.8	12.7
F-value	118.5	130.1	18.3
P-value	<0.001	<0.001	<0.001

Two-way ANOVA (%SS = factor sum of squares/total sum of squares × 100).

($P < 0.001$) in leaves and reproductive shoots than in rhizomes and roots, but no differences were found between vegetative and reproductive leaves. As a consequence, the above-ground C:N ratio varied from 10.3 (April 1998) to 36.4 (August 1999); the low nitrogen contents of summer 1999 being responsible for this maximum. The below-ground C:N ratio ranged from 21.6 (April 1998) to 56.6 (February 1999).

3.1. Recruitment and mortality rates

Shoot vegetative recruitment and mortality rates were calculated over the period of re-colonisation (Table 3). Unfortunately, due to the advanced degradation of the rhizome's oldest parts, plant material sampled in September 1999 did not allow the same calculations. Shoot recruitment rates ranged from 1.2 ± 0.5% per day (autumn 1998) to 4.2 ± 1.2% per day during winter 1998–1999. Shoot mortality rates exhibited the same pattern, with values ranging from 1.2 ± 1.0% per day in autumn to 3.9 ± 1.2% per day during winter. The

Table 2

Morphological characteristics of flowering shoots (mean ± S.E. (*n*)) and estimation of the reproductive effort (calculated as reproductive biomass/total biomass)

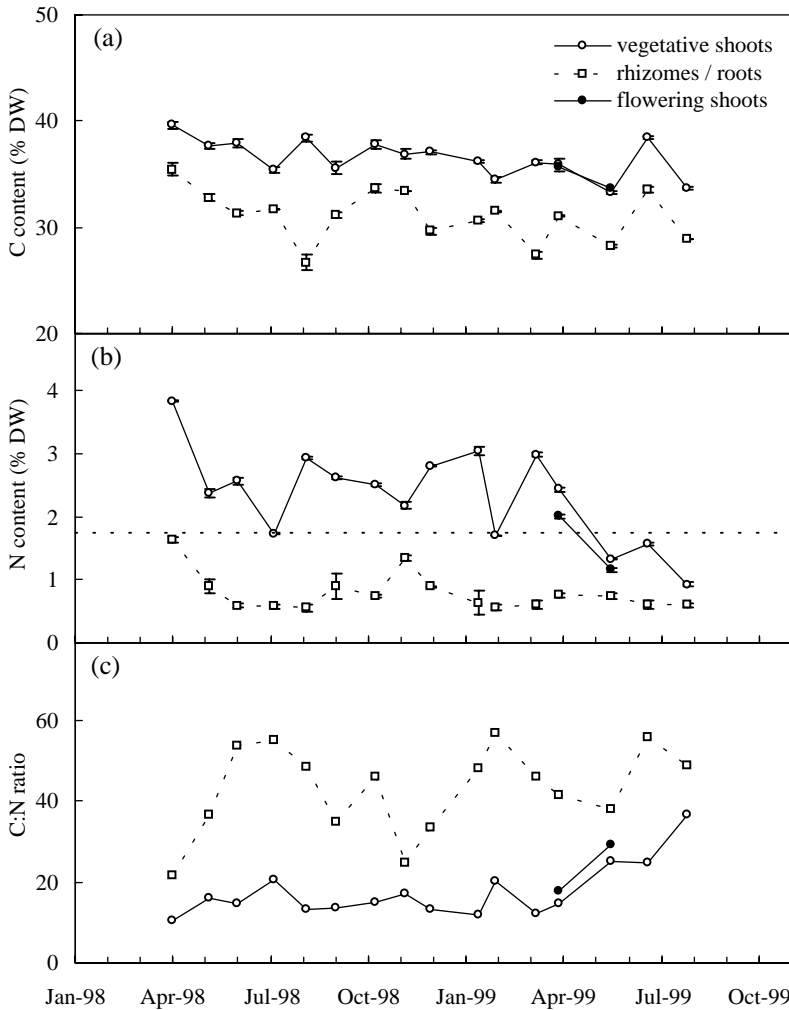| Period	Shoot length (cm)	Number of spathes by shoot	Reproductive effort (%)
March 1999	54.5 ± 6.5 (6)	4.0 ± 0.7 (6)	75.3
April 1999	80.6 ± 11.9 (3)	3.3 ± 2.0 (3)	40.5
June 1999	45.4 ± 5.0 (4)	4.0 ± 1.8 (4)	24.2
July 1999	47.7 ± 10.7 (4)	2.8 ± 0.7 (4)	13.3

Fig. 5. Carbon (a) and nitrogen (b) content (expressed as percentage of the dry biomass) as well as C:N ratios (c) of leaves, flowering shoots and below-ground organs during the recolonisation experiment. Values are means of triplicates and standard errors are given as vertical bars. The 1.8% DW line of Duarte (1990) is indicated in (b).

net result remained positive during the whole first year of recolonisation and was negative between March and June 1999. In August 1998, 79% of initial seedlings were still alive and had developed a rhizome.

3.2. Rhizomes

A total of 25 intact rhizomes (from the scorpioïd extremity to the youngest shoots) could be analysed from all quarterly samplings (Table 4). Annual mean rhizome diameter was

Table 3
Mean ± S.E. ($n = 3$) daily vegetative shoot recruitment and mortality rates and net recruitment (calculated as recruitment minus mortality) calculated for *Z. marina* shoots during different recolonisation periods

Period	Recruitment rate (percent per day)	Mortality rate (percent per day)	Net recruitment (percent per day)
February–May 1998	2.0 ± 0.9	−1.8 ± 0.4	0.2
June–August 1998	2.4 ± 0.3	−2.2 ± 0.3	0.2
September–November 1998	1.2 ± 0.5	−1.2 ± 1.0	0.0
December 1998–February 1999	4.2 ± 1.2	−3.9 ± 1.2	0.4
March–June 1999	2.2 ± 1.1	−2.5 ± 0.9	−0.3

Table 4
Mean ± S.E. rhizome diameter (RD, in mm), horizontal apical internodes length (HINTL, in mm), horizontal rhizome (principal + branches) elongation rate (HE, in cm per year) and mean horizontal branching frequency (BF, in percent of internodes developing branches) measured in each season

Period	RD	HINTL	HE	BF (%)
May 1998	2.4 ± 0.3 ($n = 9$)	12 ± 2.5 ($n = 14$)	24.5 ± 7.6 ($n = 9$)	7.7
August 1998	2.5 ± 0.2 ($n = 8$)	8.3 ± 1.1 ($n = 17$)	46.1 ± 15.2 ($n = 8$)	7.6
November 1998	2.6 ± 0.3 ($n = 3$)	7.4 ± 2.6 ($n = 7$)	29.1 ± 20 ($n = 3$)	5
February 1999	2.8 ± 0.2 ($n = 5$)	9.6 ± 1.5 ($n = 19$)	20.0 ± 11.4 ($n = 5$)	5.6
P-value	ns	<0.05	ns	

Differences between seasons have been tested using the Kruskal–Wallis rank test (ns, not significant).

2.6 ± 0.1 mm and no significant differences were found among seasons. However, significant differences in apical internode lengths were found between seasons, with minimum lengths measured in November and maximum in May, suggesting an early spring growing season, since longer internodes are associated with periods of intensive growth. Horizontal elongation rates showed high variability from one rhizome to another. Mean annual elongation rate was 31.1 ± 7.6 cm per year. Branching began in May 1998, that is about 90 days after seed germination. Internodes from principal rhizomes were found to be significantly larger than internodes from secondary branches (data not shown, paired *t*-test mean comparison, $P < 0.001$). In summer 1998, all rhizomes were found to have secondary branches and some of them even tertiary branches. In general, the physical separation of principal and secondary rhizomes (disappearance of the junction by rhizome decay) occurred during the following winter but a few rhizomes with tertiary axes could still be found in February 1999 (data not shown). On average 6.5% of internodes developed a branch, during the study period.

4. Discussion

Although the initial recolonisation was by seeds, this study demonstrates that spreading of the *Z. marina* meadow was due to vegetative expansion, with rhizome elongation and branching leading to new shoots. This type of recovery has already been reported for *Z.*

marina (Olesen and Sand-Jensen, 1994b) as well as for other seagrass species (Duarte and Sand Jensen, 1990a,b; Creed and Amado Filho, 1999; Rasheed, 1999). The very high variability of observed densities and biomasses was due to considerable spatial variance and recolonisation by patch expansion, and could probably explain why neither light nor temperature could describe the biomass variance.

The recruiting seeds must have survived not only anoxia, which has been previously reported for *Z. marina* by Churchill (1992) and by Moore et al. (1993), but probably also the toxic hydrogen sulphide linked to anaerobic degradation of organic matter, probably responsible for widespread benthos mortality during summer 1997 (Souchu et al., 1998; Chapelle et al., 2001). Apart from this initial period, no other seed germination was noted during the experimental period. The whole germination process therefore took place between September 1997 and February 1998. We observed a survival rate of young shoots to be near 80% after 6 months, which is much higher than the 10% reported for *Cymodocea nodosa* by Duarte and Sand Jensen (1990a). Buia and Mazella (1991), have studied in vitro young shoots of *Posidonia oceanica*, and reported survival rates of 28% after 8 months. The effect of salinity on seed germination and survival rates is still unclear: some authors noticed a positive effect of low salinity (Hootsmans et al., 1987), whilst others did not detect any effect (McMillan, 1983; Orth and Moore, 1983). In the present study, the salinity always remained above 34 PSU and therefore, seems unlikely to explain the high survival. Nonetheless, our data cannot discount a possible positive effect of these minima on the germination rates during winter 1997–1998. The high survival rates may also be due to the fact that all potentially competing algae were killed during the anoxia, thus allowing a recolonisation on bare surface sediments. Furthermore, it is likely that the benthic invertebrate populations, that play an important role in seedling survival (Wigand and Churchill, 1988; Luckenbach and Orth, 1999), have been affected by the anoxia event, and thus that, e.g. habitual bioturbation and predation processes were reduced.

The seagrass bed studied showed a unimodal pattern of biomass variation, as previously described for *Z. marina* beds in the Thau lagoon (Laugier et al., 1999) and elsewhere (Sand-Jensen, 1975; Jacobs, 1979; Pedersen and Borum, 1993). Furthermore, it seems that the development of leaf biomass showed two consecutive steps. Firstly, we found a rapid increase in density due to seed germination and recruitment of new shoots, the recolonisation properly speaking, where after an increase in leaf surface area was observed (bigger leaves and greater number of leaves on one shoot). This "two-steps" process is similar to those reported for *Cymodocea nodosa* (Duarte and Sand Jensen, 1990a) and for *Zostera capricorni* (Rasheed, 1999). Maximum densities and biomass remained low when compared to other *Z. marina* beds (Jacobs, 1979; Nienhuis and De Bree, 1980; Olesen and Sand-Jensen, 1994a,b; Laugier et al., 1999) but at the same time leaf lengths were found quite high. The somewhat high depth of the study site (at 4 m depth, the annual mean light intensity was 6.2 mol m^{-2} per day) could explain this morphological aspect (Dennison and Alberte, 1982). Indeed, high shoot density with short leaves would have resulted in high shading effect and thus even lower light availability.

Reproductive shoots accounted for about 75% of total biomass in spring 1999. The energy allocated to sexual reproduction was thus remarkable when compared with other studies (Sand Jensen, 1975; Silberhorn et al., 1983; Marbà et al., 1996; Laugier et al., 1999). Previous studies (Jacobs, 1982; Van Lent and Verschuure, 1994) have shown that *Z. marina*

has to rely on a high generative reproduction effort in order to survive in highly disturbed environments. Thus, the physical disturbance induced by anoxia in the Thau lagoon, could explain the relatively high number of observed flowering shoots.

Carbon and nitrogen contents were found to be similar to those measured for *Z. marina* beds located on the north border of the Thau lagoon (Laugier, 1998). The comparison of the observed leaf nitrogen content with the 1.8% DW threshold suggested for nitrogen limitation by Duarte (1990), leads to the conclusion that the seagrasses were strongly limited during summer 1999, whilst this did not occur during year 1998. This could also explain the success of the first year recolonisation.

The mean rhizome elongation rate reported here remains similar to the ranges published by Marbà and Duarte (1998: 22–31 cm per year) or Olesen and Sand-Jensen (1994a,b: up to 45 cm per year). The measured horizontal rhizome branching rate (6.5% of internodes developing branches) is close to the value found for the same species by Marbà and Duarte (1998: 5.22%) and, as already noticed for the species *Zostera noltii* by Vermaat and Verhagen (1996), maximum branching was recorded in summer. However, contrary to this latter study, some rhizomes were found with tertiary axes in winter. This is probably due to the lower physical disturbance in our study site (for example, no tidal currents) and also to larger rhizome diameters for *Z. marina*.

The seagrass recolonisation after the July 1997 anoxic crisis took place with a surprising rapidity. About 9 months were sufficient to the *Z. marina* bed to reach biomasses similar to those previously reported for the same site. The Thau lagoon is subjected to chronic anoxic outbreaks: since 1975, when a major "malaïgue" affected the whole lagoon, anoxic events took place in 1982, 1983, 1987, 1990 and 1997 with variable amplitudes (Chapelle et al., 2001). These events have a harmful short-term effect on seagrass beds, sometimes leading to complete destruction, but the capacity of *Z. marina* to couple both sexual reproduction and high vegetative growth rates allowed rapid recovery. Nonetheless, recolonisation remains dependent on seed germination, and thus on the sexual reproduction. Since no flowering shoots have been observed during the first year of recolonisation, it is likely that two consecutive anoxic crises at the same site, would deplete the seed bank, thus limiting recovery potential to seed dispersal from elsewhere.

Acknowledgements

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