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RESPONSES OF INTERTIDAL AND SUBTIDAL COMMUNITIES OF THE MACROBENTHOS TO ORGANIC LOAD AND OXYGEN DEPLETION IN THE SETO INLAND SEA, JAPAN.

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Key words: macrobenthos, organic matter, acid volatile sulfide, tidal estuary

Abstact: The physico-chemical characteristics of ebbing tidal creek and emerged sediments along a transect line set between the LWL (low water level) and the ELWL (extreme low water level) were monitored monthly for a year. At the sampling stations, the seasonal changes of the macrobenthic communities were investigated simultaneously. A similar survey on the chemical characteristics of the sediments and the macrobenthic communities was carried out on an adjacent subtidal station (water depth *ca.* eight metres, at low tide). In spring and summer, both primary and secondary production on the intertidal flat were extremely high. Minimum ammonium concentrations and oversaturated oxygen concentrations in the water column related to the development of a conspicuous biomass of the macroalgae *Ulva* sp., which covered large areas of the tidal flat. During the same period, the biomass of two dominant bivalves, *Ruditapes philippinarum* and *Musculista senhousia*, increased sharply from 60.1 ± 34.9 gWW m^{-2} (April 1994) to 1032 ± 189 gWW m^{-2} (August 1994). However in early autumn, the rapid decomposition of the macroalgae, enhanced by the deterioration of meteorological conditions, led to a distrophic crisis. A sharp increase of ammonium, pheopigments and particulate organic carbon (POC) in the ebbing water, and pheopigments, total organic carbon (TOC) and acid-volatile sulfide (AVS) at the surface sediments coincided with the catastrophic mortality of *R. philippinarum*. The biomass of this bivalve species crashed from 563 ± 163 gWW m^{-2} (September 1994) to 77.0 ± 61.2 g WW m^{-2} (October 1994). In contrast, Polychaeta profited from the increased amount of dead organic materials and increased both in density and biomass through the next months. At the adjacent subtidal station, the organic load from the intertidal zone simultaneously caused anoxia at the bottom sediments. Unfavourable benthic conditions had deleterious and similar effects on the subtidal macrobenthic communities. Polychaeta increased in density, while Bivalves did not survive and the total biomass drastically declined from 179 gWW m^{-2} (July 1994) to 11.1 gWW m^{-2} (October 1994). This work represents the first documented case of how intertidal and subtidal communities of the macrobenthos in a tidal estuary of the Seto Inland sea are affected by the drastic shift from an hypertrophic to a distrophic period.

RÉPONSES DES COMMUNAUTÉS MACROBENTHIQUES INTERTIDALES ET SUBTIDALES À UNE CHARGE ORGANIQUE ET À UNE DÉSOXYGENATION DANS LA MER INTÉRIEURE DE L'ÎLE DE SETO, JAPAN

Mots clés : *macrobenthos, matière organique, sulfure d'hydrogène, estuaire tidal*

Résumé : *Le long d'un transect compris entre les bas niveaux de marée moyenne (LWL) et de vives eaux (ELWL), les caractéristiques physico-chimiques de sédiments émergés et ceux d'un chenal de jusant furent enregistrés mensuellement pendant une année. Aux stations étudiées, les changements saisonniers des communautés macrobenthiques furent suivis. Il en a été de même pour les caractéristiques chimiques des sédiments et les communautés benthiques d'une station subtidale adjacente (profondeur huit mètres à basse mer). Au printemps et en été, les productions primaires et secondaires de la zone intertidale furent extrêmement fortes. Dans la colonne d'eau, les concentrations minimales d'ammonium et les sursaturations d'oxygène purent être reliées au développement d'une forte biomasse de la macroalgue* Ulva sp. *qui couvrait de grandes surfaces sur l'estran. Pendant la même période, la biomasse des deux Bivalves dominants,* Ruditapes philippinarum *et* Musculista senhousia, *augmenta brusquement de 60.1 ± 34.9 gWW m^{-2} (avril 1994) à 1032 ± 189 gWW m^{-2} (août 1994). Cependant, au début de l'automne, en raison de la détérioration des conditions climatiques, la rapide décomposition des macroalgues conduisit à une crise distrophique. En même temps que la mortalité catastrophique de* R. philippinarum, *il se produisit une forte augmentation de l'ammonium, des phéopigments et du carbone organique particulaire (POC) dans l'eau de reflux, et celle de phéopigments, du carbone organique total (TOC) et du sulfure d'hydrogène (AVS) à la surface des sédiments. La biomasse de ce Bivalve chuta de 563 ± 163 gWW m^{-2} (septembre 1994) à 77.0 ± 61.2 g WW m^{-2} (octobre 1994). A l'opposé, les Polychètes profitèrent de cet apport de matériel organique mort et augmentèrent à la fois en densité et en biomasse les mois suivants. A la station subtidale adjacente, la charge organique issue de la zone intertidale provoqua simultanément l'anoxie des sédiments. De telles conditions benthiques défavorables eurent un effet similaire sur les communautés macrobenthiques subtidales. Les Polychètes augmentèrent en densité alors que les Bivalves ne survécurent pas et, de ce fait, la biomasse totale déclina brutalement de 179 gWW m^{-2} (juin 1994) à 11.1 gWW m^{-2} (octobre 1994). Dans un estuaire de la mer intérieure de Seto, ce travail est la première étude d'un cas de fluctuations des communautés intertidales du macrobenthos en liaison avec le passage brutal d'une période hypertrophique à une période distrophique.*

INTRODUCTION

Over the last few decades, estuarine and coastal areas throughout Japan have become seriously endangered by drastic biogeochemical changes caused by an excessive exploitation of land for human activities (Murakawa, 1987), deposition of terrigenous materials (Hoshika *et al.*, 1991) and tidal flat reclamation (Abe, 1981). An increasing or altered (as a ratio) load of nutrients (Ukita & Nakanishi, 1986 ; Nakanishi *et al.*, 1991, 1992) and organic matter (Montani *et al.*, 1991; Ogawa & Ogura, 1997) from the inland have weakened the self-purifying and self-buffering potential of the intertidal zones and accelerated the processes of benthic metabolism (Yamada *et al.*, 1993).

Worldwide, many studies have shown that the structure of the macrobenthic communities is strongly affected by both the vicinity of a source of organic enrichment (Rhoads, 1974; Pearson & Rosenberg, 1978) and long periods of eutrophication (Beukema, 1991, 1992). In organically polluted sediments, annelids should be the dominant *taxa* (Tsutsumi *et al.*, 1991; Beukema, 1992), even shifting to small size deposit-feeding and resistant species in the case of further organic enrichment (Pearson & Rosenberg, 1978), while in less stressed environments the numerical proportion of worms is expected to decrease in favour of molluscs and crustaceans (Beukema, 1991; Tsutsumi & Inoue, 1996).

Extreme consequences of an excessive organic load are oxygen depletion in the near bottom waters and at the bottom sediments (Diaz & Rosenberg, 1995) and production of toxic hydrogen sulfide (Roden & Tuttle, 1992), which will cause massive benthic mortality (Tsutsumi & Kikuchi, 1983; Friligos & Zenetos, 1988; Llansó, 1992; Tsutsumi & Inoue, 1996).

In recent years, the organic load in coastal areas and embayements is often related to the development of high amounts of macroalgal biomass (Fiton & Menesguen, 1992; Viaroli *et al.*, 1992) which represent a multiple threat to the communities of the macrobenthos. Algal coverage acts as a filter of settling larvae (Olafsson, 1988; Bonsdorff *et al.*, 1995) and is not a suitable environment for settlement itself (Bonsdorff *et al.*, 1995). Coverage up to 100 % (Hartlin & Rines, 1993) also significantly reduces light penetration on the surface sediment. This is likely to limit the development of microphytobenthos and therefore will indirectly influence food availability for bivalves feeding on microphytobenthos resuspended by tidal current and wind-driven waves (Numaguchi, 1990; De Jonge & Van Beusekom, 1992). Further, massive die-offs and crashes of benthic populations have been recently shown under natural occurrences of drift algal mats (Norkko & Bonsdorff, 1996a, b). Less information is however available on the effects of decomposing macroalgae on the chemical characteristics of intertidal and subtidal sediments and the parallel responses of the autochthonous communities of the macrobenthos.

This study was carried out in the context of an integrated project which aims at quantifying the dynamics of biophilic elements (i.e. carbon, nitrogen, phosphorus and silicon) in a tidal estuary of the Seto Inland sea, Japan (Magni, 1998; Magni & Montani, 1998; Montani *et al.*, 1998). The roles played by producers (Magni & Montani, 1997) and consumers on the processes are under investigation. This is the first work conducted in the Seto Inland sea which assesses the parallel changes of intertidal and subtidal macrobenthic communities following distrophic events. On the intertidal flat, the heavy growth of the macroalgae *Ulva sp.* and the parallel strong increase in biomass of bivalves *Ruditapes philippinarum* and *Musculista senhousia* indicated a highly productive spring-summer. On the other hand in early autumn, the decomposition of high amounts of the macroalgae caused an exceptional distrophic crisis. A massive mortality of the bivalve *R. philippinarum* on the intertidal flat and a drastic reduction of the macrobenthic biomass on an adjacent subtidal station occurred. The factors which determined such changes are discussed and the inverted responses of different trophic groups of the macrobenthic communities examined.

MATERIAL AND METHODS

Study area and sampling activities

On the intertidal flat, an inner station for water samples (Stn H1) was located in a shallow creek (*ca.* 50 cm depth at low tide) of the river Shin (figure 1). This creek is formed during low-tide, which crosses the emerged tidal flat and runs towards the low-tide shore-line. At Stn H1, salinity (YSI portable salinometer), temperature and dissolved oxygen concentrations (UK 2000 portable D.O. meter) were recorded and duplicate water samples for chemical analyses (ammonium, Chl *a*, pheopigments and particulate organic carbon) were collected within a hour from each other, before the surging tidal flood.

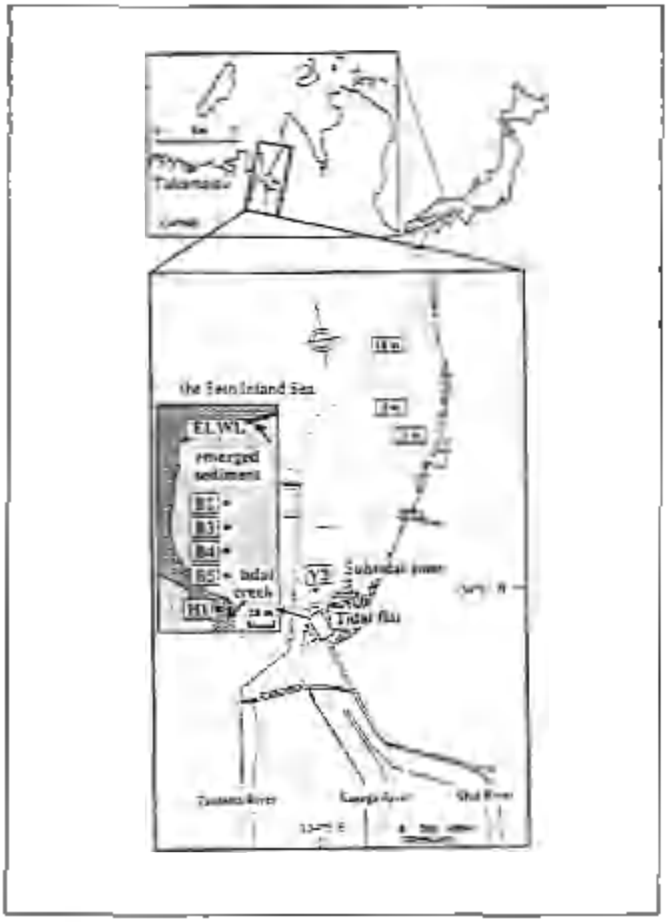


Figure 1. Study area and location of the sampling stations.
Figure 1. Zone d'étude et localisation des stations.

Close to Stn. H1, a transect line of four stations at 25 metre intervals (Stns. B5 to B2) was set between the LTL (low tidal level) and the ELWS (extreme low water spring tide) (figure 1). At these stations, emerged sediment samples from the two uppermost layers (0-0.5 cm and 0.5-2 cm in depth) were collected for chemical analyses (Chl *a*, pheopigments, total organic carbon, acid-volatile sulfide) using acrylic core tubes (3 cm i.d.) (Magni & Montani, 1997). At each station, duplicate sediment samples were taken simultaneously using a 100 cm^2 core and sieved on a mesh size of 1 mm. The residue was fixed in a Rose bengal-formalin solution for the determination of the macrobenthos.

Stn. Y1 was set *ca.* 200 metres from Stn. B2 (figure 1). It was located at the edge between the intertidal and the subtidal zone. As a result of an atypical bathymetry, this station was the deepest site of the local subtidal zone (10 metres at high tide). Sampling was carried out from a boat within a few days from the survey on the tidal flat. Duplicate sediment samples from the uppermost layer (0-1 cm in depth) were collected for chemical analyses (as those for the intertidal sediment samples) using an acrylic resin cylinder (i.d. 4 cm, height 50 cm) fitted to a gravity corer. Further, duplicate sediment samples were simultaneously collected with a 400 cm^2 Ekman-Birge grab sampler and sieved on a mesh size of 1 mm. The residue was fixed in a Rose bengal-formalin solution for the determination of the macrobenthos.

Sampling was carried out monthly from April 1994 to April 1995 on the intertidal flat and in July and October 1994 and January, April, July and October 1995 on the subtidal station.

Daily data of air temperature, rainfall and solar radiation were obtained from the Takamatsu Meteorological Agency Station, close to the estuary under investigation. Data of daily low tide level were obtained from the Maritime Safety Agency.

Water sample treatment and analyses

In the laboratory, water samples were filtered for the analyses of ammonium (NH_4^+-N), photosynthetic pigments (Chl *a* and pheopigments), particulate organic carbon (POC) and for the determination of the total suspended matter (TSM) (Magni & Montani, 1998).

NH_4^+-N concentrations were determined with a Technicon autoanalyzer II, according to Strickland & Parsons (1972). Pigments were extracted using a 90 % acetone solution and extracts were analyzed for Chl *a* and pheopigments by spectrophotometer according to Lorenzen's (1967) method, as described in Parsons *et al.* (1984). POC was analyzed using a CHN analyzer (Yanako, Model MT-3).

Sediment sample treatment and analyses

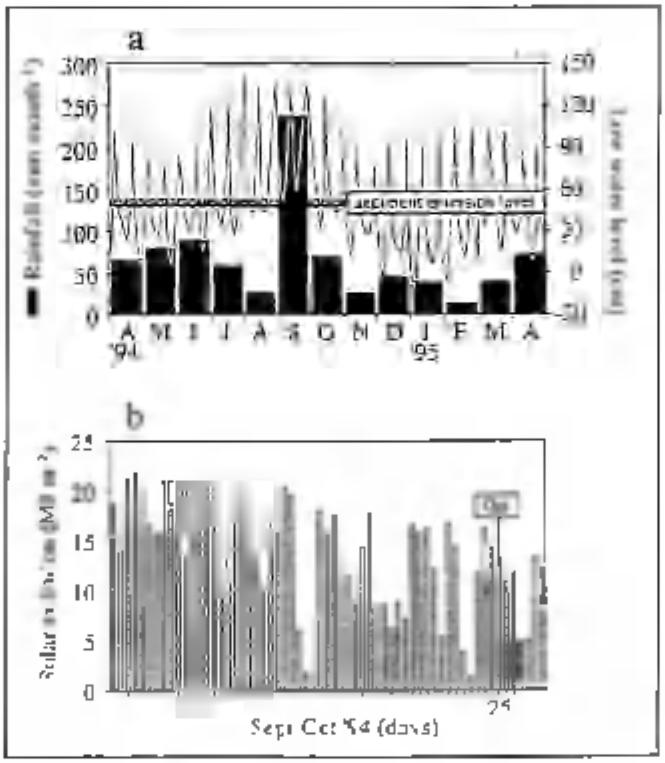
In the laboratory, pigments were extracted from duplicate subsamples of wet sediment (*ca.* 1 g) using a 90 % acetone solution and extracts were spectrophotometrically analyzed for Chl *a* and pheopigments (Magni & Montani, 1997). From the same pool of fresh sediment, acid-volatile sulfide (AVS) content was determined in duplicate subsamples (*ca.* 1 g) with an AVS test column (Gastec, Model 201 L and 201 H) (Magni & Montani, 1997). Total organic carbon (TOC) content was determined using a Yanako and a Fisons NA 1500 CHN analyzers for the intertidal (<250 µm fraction) and the subtidal sediments, respectively.

The benthic animals, previously fixed in a formalin solution, were sorted from the residue and preserved in 75 % ethanol with ethylene glycol. They were sorted and counted under a stereo-microscope (Olympus, Wild M3Z). The wet weight of Polychaeta was determined directly to the nearest 1 mg after being rapidly dried on blotting paper, the soft tissue of Bivalves was calculated as 19 % and 32 % of the total weight (including shells) for *Ruditapes philippinarum* and *Musculista senhousia*, respectively. Percentile values of Bivalves were obtained from a linear regression line of the plots total weight vs wet weight soft tissue (unpublished).

RESULTS

Environmental conditions and physico-chemical parameters of ebbing tidal-creek.

Rainfall was least in February 1995 (13 mm $month^{-1}$), infrequent during the most irradied months of July and August (58.5 mm $month^{-1}$ and 26.0 mm $month^{-1}$, respectively) and highest in September (237 mm $month^{-1}$) (figure 2a). Between late September and October 1994, heavy rainfall (109 mm day^{-1} on September 28th) and a sharp decrease of solar radiation (1.7 MJ m^{-2} and 1.3 MJ m^{-2} on September 29th and October 21st, respectively) occurred before sampling on October 25th (figure 2b).



Figures 2a and 2b. a) Monthly values of rainfall and seasonal variations of the lower low-tide water level. As a mixed semidiurnal type estuary (with pronounced differences between two successive low and high tides), the lower low tide of each day was plotted to represent the seasonal changes of the low water tidal level. b) Variations of daily solar radiation in September (12th) and October (25th).

Figures 2a et 2b. a) Valeurs mensuelles de la pluviosité et variations saisonnières du plus bas niveau de l'eau. b) Variations quotidiennes de l'ensoleillement en septembre et octobre 1994. Sont indiquées les dates d'échantillonnage (12 septembre et 25 octobre).

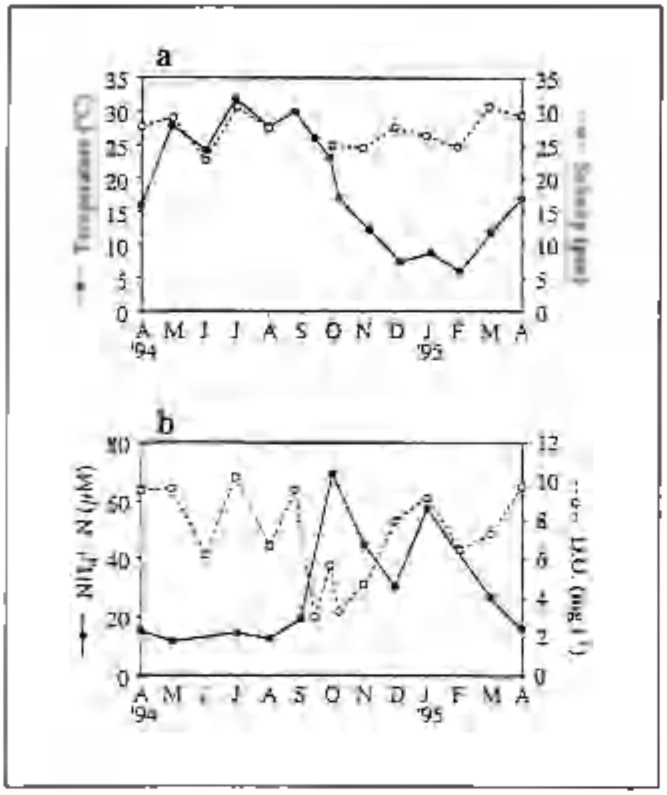
Mean emersion level of the sampling stations was ca. + 50 cm (figure 2a) the local mean sea level) (Takamatsu

Fort). Due to the seasonal changes of the tidal level (figure 2a), several days of no air exposure of the surface sediments occurred between September and October, in coincidence with the deterioration of the meteorological conditions. Differently, emersion of the surface sediments between December and January was more prolonged (figure 2a).

Water temperature of the ebbing tidal creek (Stn. H1) varied from 5.8° C (February) to 32.2° C (July) (figure 3a). Salinity varied from 22.7 psu (June) to 30.7 psu (March) (figure 3a). In September, we expect that the high rainfall (figure 2a) affected salinity, which unfortunately was not measured.

Dissolved oxygen (D.O.) concentrations were generally oversaturated in spring and summer 1994, with a maximum of 10.2 mg l^{-1} (167 % air saturation) in July, but dropped to low levels from late September to October (figure 3b). From November, D.O. concentration increased again up to oversaturation as in April 1995 (figure 3b). Hourly measurements of D.O. concentration carried out the subsequent year in presence of high (May) and low (September) macroalgal biomass indicated the strong effect of *Ulva sp.* mats on the processes of production and respiration, with diurnal fluctuations of D.O. varying from 1.3 mg l^{-1} (17.6 % of air saturation) to 17.4 mg l^{-1} (224 % of air saturation) and from 1.2 mg l^{-1} (15.8 % of air saturation) to 7.9 mg l^{-1} (120 % of air saturation) in May and September, respectively (unpublished).

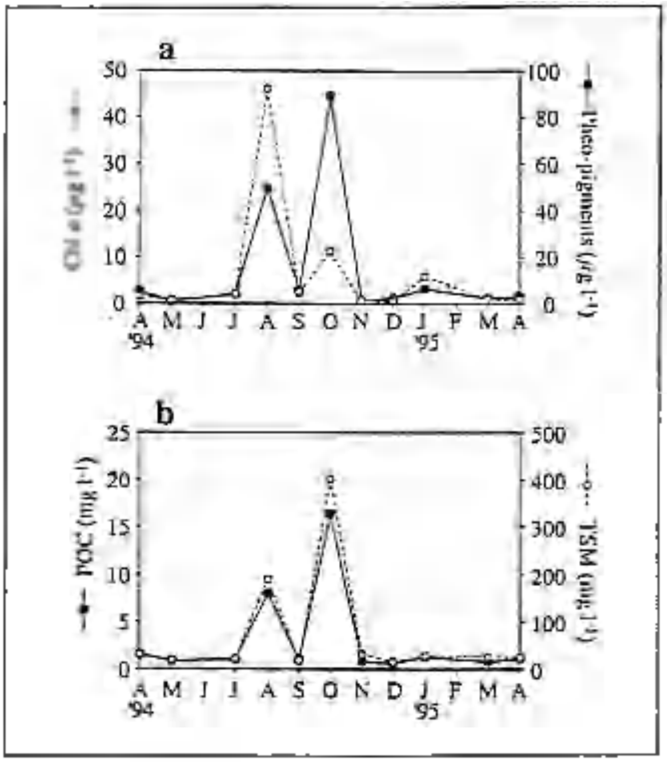
The seasonal pattern of ammonium ($NH4^+$ -N) contrasted with that of D.O.: $NH4^+$ -N concentrations were low in spring-summer and high in autumn-winter. The highest peak of $NH4^+$ -N was in October (69.2 µM), when D.O. concentration was lowest (figure 3b).



Figures 3a and 3b. Monthly variations of temperature and salinity (a), and ammonium (NH_4^+-N) and dissolved oxygen (D.O.) concentrations (b) in ebbing-tidal-creek at Stn. H1.

Figures 3a et 3b : Variations mensuelles a) de température et de salinité et b) de concentrations d'ammonium (NH_4^+-N) et d'oxygène dissous (D.O.) dans le chenal de jusant (station H1).

Figures 4a and b show the seasonal variations of particulate compounds at Stn. H1. Photosynthetic pigments (pheopigments and chlorophyll *a*, figure 4a), particulate organic carbon (POC) and total suspended matter (TSM) (figure 4b) had two significant peaks in August and October. However, while Chl *a* was higher in August than in October, pheopigments, POC and TSM were highest in October. This pattern resulted in a good correlation of POC with pheopigments (r^2 = 0.993, n = 11; plots not shown), but not with Chl *a* (r^2 = 0.273, n = 11; plots not shown).



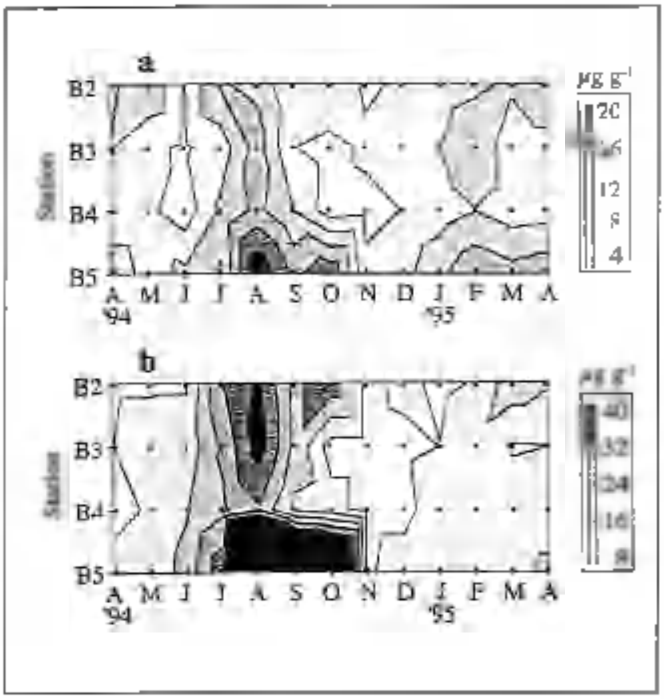
Figures 4a and 4b. Monthly variations of pheopigments and chlorophyll *a* (a), and particulate organic carbon (POC) and total suspended matter (TSM) (b) in ebbing tidal-creek at Stn. H1.

Figures 4a et 4b : Variations mensuelles a) des pheopigments et de la chlorophylle a et b) du carbone organique particulaire (POC) et des matières en suspension totales (TMS) dans le chenal de jusant (station H1).

Chemical characteristics of intertidal and subtidal sediments.

On the intertidal flat, surface sediment Chl *a* content (figure 5a) was low in June (minimum of 1.6 µg g^{-1}, at Stn. B4), October and November (mean of 4.4 ± 3.2 µg g^{-1} and 4.0 ± 1.2 µg g^{-1}, respectively), and high in August (maximum of 24.1 µg^{-1} at Stn. B5, mean of 15.6 ± 5.8 µg g^{-1}). A late-winter bloom occurred in February (mean of 10.4 ± 3.8 µg g^{-1}) (figure 5a). A different distributional pattern was found for pheopigments (figure 5b). Pheopigment content was constantly higher than that of Chl *a* and significantly increased from April 1994 (mean of 8.8 ± 1.9 µg g-1) to July (mean of 29.6 ± 7.2 µg g^{-1}). As for Chl *a*, the highest peak was found in August (mean of 63.5 ± 49.7 µg g^{-1}), with a maximum value of 138 µg g^{-1} at Stn. B5. At all stations, the pheopigment content remained high in September, up to 57.6 µg g^{-1} at Stn. B5, and showed very remarkable differences between stations in October (4.7 µg g^{-1} and 87.5 µg g^{-1} at Stns. B3 and B5, respectively). In November it was low and distributed rather uniformously along the transect line.

Throughout the next months, the pheopigment content did not significantly increase. As a result of the seasonal differences between Chl *a* and pheopigment distributional patterns (figures 5a and 5b), the pheopigment/Chl *a* ratio (not shown) was lowest in spring and winter (mean of 1.0 ± 0.1 and 1.6 ± 0.1 in April 1994 and February 1995, respectively) and significantly higher in late summer and early autumn (mean of 4.5 ± 2.0 and 3.5 ± 1.6 in September 1994 and October 1994, respectively).



Figures 5a and 5b: Monthly variations of chlorophyll *a* (a) and pheopigments (b) content at the surface sediments (0-0.5 cm) of the intertidal stations (Stns. B5 to B2).

Figures 5a et 5b : Variations mensuelles des teneurs en chlorophylle a (a) et en phéopigments (b) des sédiments superficiels (0-0.5 cm) des stations intertidales (B5 à B2).

The total organic carbon (TOC) content was low in April 1994 (6.5 ± 1.4 mg g⁻¹), increased in July 1994 (13.1 ± 3.8 mg g⁻¹) and was maximum in October 1994 (18.2 ± 17.9 mg g⁻¹) (figure 6). TOC correlated more strongly with pheopigments (r^2 = 0.827, n = 20; not shown) than with Chl *a* (r^2 = 0.518, n = 20; not shown).

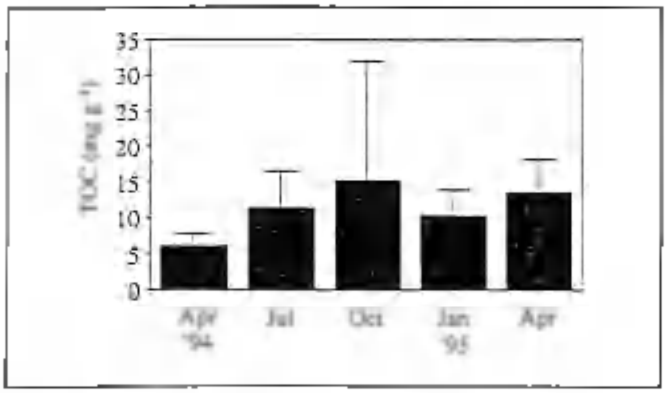
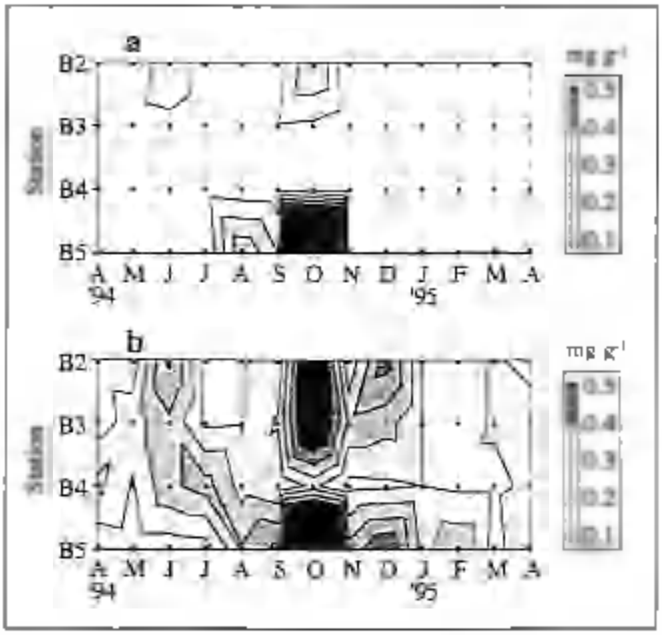


Figure 6: Seasonal variations of total organic carbon (TOC) content at the surface sediments (0-0.5 cm) of the intertidal stations (Stns. B5 to B2).

Figure 6 : Variations saisonnières des teneurs en carbone organique total (TOC) des sédiments superficiels (0-0.5 cm) des stations intertidales (B5 à B2).

In October 1994 the levels of acid-volatile sulfide (AVS) showed a strong peak at the surface sediment at Stns. B5 (1.85 mg g⁻¹) and B2 (figure 7a). Such an increase was more remarkable along the transect line at the sub-surface sediment, with a maximum at Stn. B5 (1.52 mg g⁻¹) (figure 7b). In November 1994 the AVS levels at the surface sediments were again lower than 0.1 mg g⁻¹ at all stations. At the sub-surface, they diminished more gradually through the next few months. Sediment recovery was slower at Stn. B5, where the pheopigment, TOC and AVS levels were highest in October 1994. AVS levels dropped to the lowest values in March 1995 both at the surface (0.01 mg g⁻¹ at all stations) and at the sub-surface (0.09 ± 0.02 mg g⁻¹).



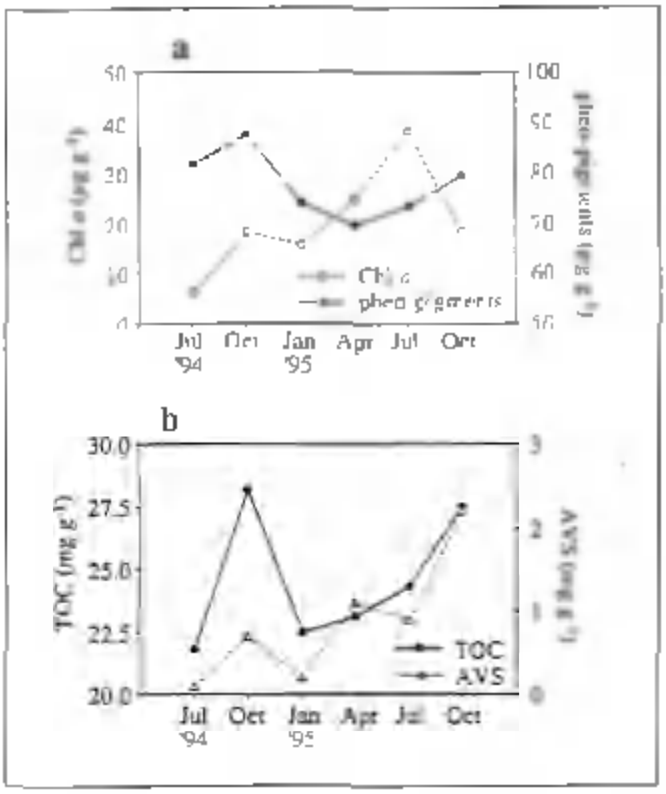
Figures 7a and 7b: Monthly variations of acid-volatile sulfide (AVS) levels in a) the surface (0-0.5 cm) and b) the sub-surface (0.5-2 cm) sediments of the intertidal stations (Stns. B5 to B2).

Figures 7a et 7b : Variations mensuelles des teneurs en sulfure d'hydrogène (AVS) dans les sédiments a) superficiels (0-0.5 cm) et b) sub-superficiels (0.5-2 cm) des stations intertidales (B5 à B2).

On the adjacent subtidal station, the seasonal changes of major chemical parameters of surface sediments (0 -1 cm) coincided with those found on the intertidal zone. In October 1994, both Chl *a* and pheopigment similarly increased, but the pheopigment content was significantly higher than the Chl *a* content (87.7 µg g⁻¹ and 18.2 µg g⁻¹, respectively) (figure 8a). From October 1994 to April 1995, while the Chl *a* content increased up to 25.1 µg g⁻¹, the pheopigment content decreased to a minimum of 69.7 µg g⁻¹. A further increase of Chl *a* content was found in July 1995 with a maximum of 38.3 µg g⁻¹, but a sharp decrease occurred in October 1995 (18.6 µg g⁻¹). Conversely, the pheopigment content increased progressively from April 1995 (69.7 µg g⁻¹) to October 1995 (79.6 µg g⁻¹).

The seasonal variation of TOC content (figure 8b) was rather similar to that of pheopigments (figure 8a). TOC content strongly increased from July 1994 (21.8 mg g⁻¹) to October 1994 (28.2 mg g⁻¹). In January 1995 it was low (22.5 mg g⁻¹), but increased again through the next months up to 27.5 mg g⁻¹ in October 1995. Both in 1994 and in 1995, an increase of pheopigment and TOC contents led to an increase of AVS levels (figure 8b). In

October 1994 surface sediment AVS level was 0.73 mg g^{-1} (2.46 mg g^{-1} at the below 1-2 cm layer, not shown). In October 1995 it peaked 2.19 mg g^{-1} at the surface (figure 8b) and 5.94 mg g^{-1} at the below 1-2 cm layer (not shown).

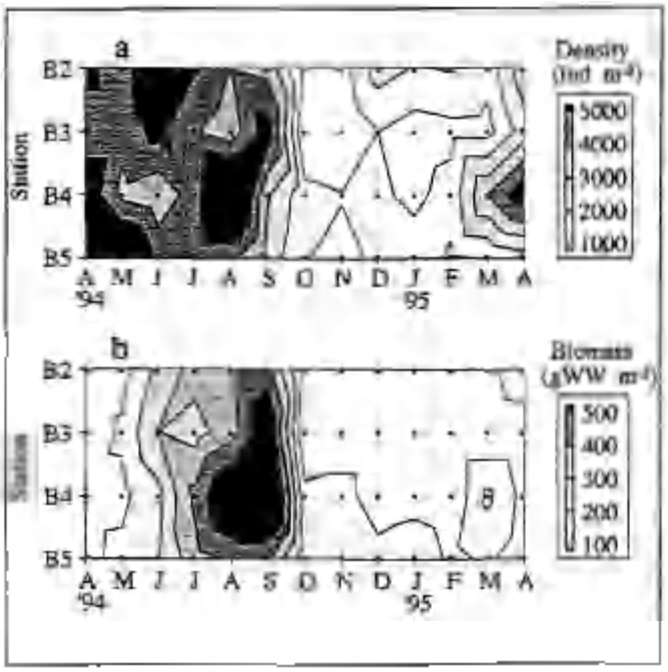


Figures 8a and 8b. Seasonal variations of chlorophyll *a* and pheopigment contents (a), and total organic carbon (TOC) content and acid-volatile sulfide (AVS) levels (b) at the surface sediments (0-1 cm) of the subtidal station (Stn. Y3).

Figures 8a et 8b : Variations saisonnières des teneurs a) en chlorophylle a et phéopigments, et b) en carbone organique total (TOC) et sulfure d'hydrogène (AVS) dans les sédiments superficiels (0-1 cm) de la station subtidale (Y3).

Seasonal changes of intertidal and subtidal macrobenthos

On the intertidal flat, seasonal changes of density and biomass of the bivalve *Ruditapes philippinarum* indicated that this species crashed in October 1994 (figures 9a and 9b). The early-spring recruitment of *R. philippinarum* corresponded to a low biomass in April 1994 (51.7 ± 26.2 gWW m^{-2}) (figure 9b). Most of the individuals were small sized with a mean individual weight (as a rough ratio biomass to density) of 0.009 ± 0.004 gWW ind^{-1}. Throughout the next months, density remained high at all stations (maximum of 7450 ind m^{-2} in August, at Stn. B4), and biomass increased to a maximum of 563 ± 163 gWW m^{-2} in September (mean individual weight of 0.162 ± 0.063 gWW ind^{-1}). In October a visual inspection of the tidal flat during sampling activities revealed that some areas were heavily covered by dead animals of *R. philippinarum*. At this sampling occasion, the sediment was darkish and had smelling. Density (figure 9a) and biomass (figure 9b) of *R. philippinarum* dropped to 763 ± 565 ind m^{-2} and 77.0 ± 61.2 gWW m^{-2}, respectively with no individuals at Stn. B3. During the subsequent months of investigations, the biomass of *R. philippinarum* remained low. Differently, density started to increase again in April 1995 (mean of 2388 ± 1872 ind m^{-2}) as new recruitment occurred in early-spring (figures 9a and 9b). Whereas, density of *R. philippinarum* in April 1995 was lower than that of April 1994 (mean of 5488 ± 862 ind m^{-2}).

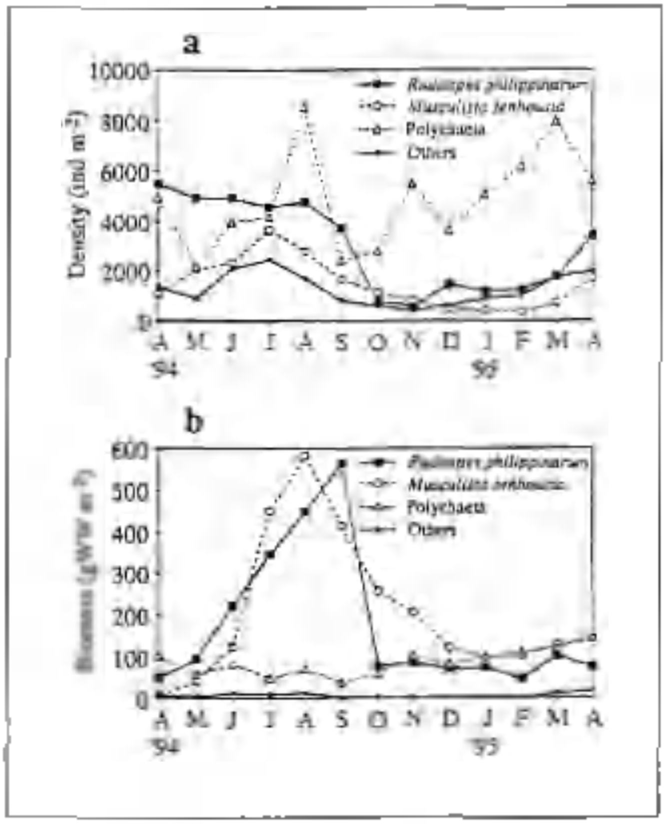


Figures 9a and 9b: Monthly changes in the density (a) and biomass (b) of the bivalve *Ruditapes philippinarum* at the intertidal stations (Stns. B5 to B2).

Figures 9a et 9b : Fluctuations mensuelles de la densité (a) et biomasse (b) du Bivalve Ruditapes philippinarum *aux stations intertidales (B5 à B2).*

With *R. philippinarum*, the bivalve *Musculista senhousia* was dominant on the intertidal flat. The two bivalve species accounted up to 96.1 % of the total biomass (September). From April 1994 through the next few months, *M. senhousia* markedly increased both in density, up to 3638 ± 1987 ind m^{-2} in July 1994 (figure 10a), and in biomass, up to 583 ± 143 gWW ind^{-1} in August 1994 (figure 10b). The mean individual weight increased from 0.006 ± 0.001 gWW ind^{-1} (April 1994) to 0.254 ± 0.013 gWW ind^{-1} (September). Differently from *R. philippinarum*, density and biomass of *M. senhousia* started to decrease from July 1994 and August 1994, respectively. No crash of *M. senhousia* was found in October 1994, but a gradual decrease of its population which reached the minimum values in February 1995 for density (350 ± 381 ind m^{-2}) and in January 1995 for biomass (95.8 ± 108 gWW m^{-2}). Among Polychaeta, *Nereis sp.*, *Cirriformia tentaculata* and *Polydora sp.* were dominant. A sharp peak of Polychaeta density was found in August 1994 (figure 10a). This was due to the sudden appearance of *Polydora sp.* whose density increased from 2000 ± 1134 ind m^{-2} (July) to 4425 ± 2094 ind m^{-2} (August) and rapidly dropped to 200 ± 216 ind m^{-2} in September. On the other hand, no significant changes in the total biomass of Polychaeta occurred (figure 10b), as the small spionidae *Polydora sp.* accounted for only 8.0 ± 5.2 % of the Polychaeta biomass. Whereas, remarkable changes of both density and biomass of Polychaeta occurred between September and November. Density of *Cirriformia tentaculata* increased from 175 ± 104 ind m^{-2} (September) to 1725 ± 1294 ind m^{-2} (November) and biomass of *Nereis sp.* increased from 38.4 ± 15.5 gWW

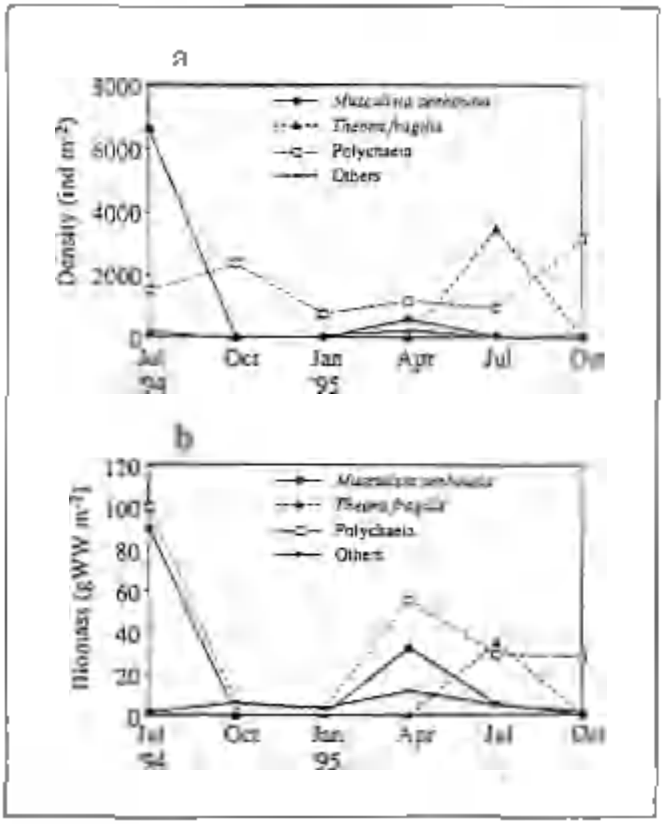
m^{-2} (September) to 82.8 ± 78.5 gWW m^{-2} (November). Figure 10a shows that from October the total density of Polychaeta gradually increased, in spite of a relative decrease in December, and remained constantly higher than that of Bivalves through all the subsequent period of investigations. Also biomass significantly increased up to 144.4 ± 100.9 gWW m^{-2} in April 1995 (figure 10b).



Figures 10a and 10b: Monthly changes in the density (a) and biomass (b) of the intertidal macrobenthic communities at Stns. B1 to B2. Standard deviations are omitted for clarity.

Figures 10a et 10 b : Fluctuations mensuelles de la densité (a) et de la biomasse (b) des communautés macrobenthiques intertidales aux stations B1 à B2.

On the subtidal zone, strong seasonal changes of both density (figure 11a) and biomass (figure 11b) of the macrobenthos were found, which were coincident and rather similar to those that occurred on the intertidal flat. Density and biomass were highest in July 1994 (8488 ind m^{-2} and 179 gWW m^{-2}, respectively) and lowest in January 1995 (813 ind m^{-2} and 5.0 gWW m^{-2}, respectively). In July 1994 *Musculista senhousia* accounted for 77.9 % of the total density (6613 ind m^{-2}). Most of individuals of this Bivalve species were small-sized, with a mean individual weight of 0.014 gWW ind^{-1}. On the other hand in October 1994, no individuals of this Bivalve species were found. Conversely, Polychaeta increased their density to 2250 ind m^{-2} (figure 11a) and accounted for 99.4 % of the total density. Whereas, the biomass of Polychaeta in October 1994 was much lower than that found in July 1994 (figure 11b), as a shift to a small-sized species (*Cossura coasta*) occurred. In April 1995 in spite of a rather low density, the total biomass of the subtidal macrobenthos increased to 99.3 gWW m^{-2}, with a significant contribution of *M. senhousia* (mean individual weight of 0.056 gWW ind^{-1}) (figure 11b). In July 1995, the presence of *M. senhousia* was very limited (38 ind m^{-2}). But the small-sized bivalve *Theora fragilis* overcame the density of Polychaeta (3463 ind m^{-2} and 980 ind m^{-2} respectively) and accounted for 77.6 % of the total density. However, in October 1995 *T. fragilis* was not found. As in October 1994, both Bivalve species were absent and Polychaeta dominated, accounting for 97.3 % and 94.0 % of the total density and biomass, respectively.



Figures 11a and 11b: Monthly changes in the density (a) and biomass (b) of the subtidal macrobenthic communities at Stn. Y3.

Figures 11a et 11b : Fluctuations mensuelles de la densité (a) et de la biomasse (b) des communautés macrobenthiques subtidales à la station Y3.

DISCUSSION

During the period of investigations, major ecological events were related to the development on the intertidal flat of a high amount of the macroalgae *Ulva sp.* in spring and summer and the parallel and fast growth of two bivalves *Ruditapes philippinarum* and *Musculista senhousia*. Whereas, the subsequent decaying of *Ulva sp.* in early autumn, as atmospheric conditions deteriorated, corresponded to an increased amount of detrital organic matter, which enhanced the processes of decomposition and respiration. These events significantly affected the intertidal and subtidal communities of the macrobenthos.

Growth of the macroalgae *Ulva sp.*, depends on several environmental and physico-chemical factors. These include such as light and water temperature (Steffensen, 1976; Lapointe & Tenore, 1981); current velocity, which influences detachment of thalli (Hawes & Smith, 1995); rainfall, which causes flushing away of microphytobenthic assemblages (Magni & Montani, 1998) and most likely macroalgal mat itself; climatic conditions related to the nitrogen loading (Piriou & Menesguen, 1992) and pigment degradation and CO_2 depletion in summer (Frost-Christensen & Sand Jensen, 1990). Besides year to year variations, recurrent seasonal patterns of *Ulva sp.* have been recently reported (Piriou & Menesguen, 1992;

Viaroli *et al.*, 1992; Rivers & Peckol, 1995). In the bay of Saint-Brieuc, northern Brittany (France) a rapid growth of *Ulva sp.* between late May and June and growth cessation at the end of June or early July were observed in 1986, 1988 and 1989 (Piriou & Menesguen, 1992). In Valle di Gorino, a subtidal lagoon in the Po river Delta (Italy), a great development of *Ulva rigida* occurred in spring 1990, leading to oversaturated D.O. concentration, but rapidly decomposed early in July causing complete anoxia (Viaroli *et al.*, 1992). Rivers & Peckol (1995) attributed the summer decline of *U. lactuca* in a New England eutrophic embayement (Waquoit Bay, Massachusetts) to the concomitant effects of carbon imbalance, thermal stress and biological factors (competition and grazing).

Also on the intertidal flat of the present study, *Ulva sp.* shows recurrent seasonal patterns, growing heavily in spring and summer and decomposing in late summer-early autumn. From the spring to summer period of 1994, favourable atmospheric conditions (e.g. low rainfall, high solar radiation and high temperature in July and August 1994, figures 2a and 3a) favoured the heavy growth of *Ulva sp.* The macroalgal mats did not initially affect the growth of two bivalves *Ruditapes philippinarum* and *Musculista senhousia* (figures 10a and 10b). Besides, the ammonium released by the excretory activity of Bivalves (up to 35.6 mM m^{-2} day^{-1} in August 1994, unpublished) may have represented an important nitrogen source for the growth of the macroalgae itself. Whereas, the efficient nitrogen uptake by the macroalgae resulted in low ammonium concentrations in the ebbing tidal-creek from April to September 1994 (figure 3b). As a result of the conspicuous macroalgal biomass, oversaturated dissolved oxygen concentrations occurred in spring and summer (figure 3b). During this period, a relatively high Chl *a* content both in the ebbingtidal-creek (e.g. August 1994, figure 4a) and on the intertidal surface sediments (e.g. August 1994, figure 5a) was an evidence of a high fraction of living algal material (corresponding to a low pheopigment/Chl *a* ratio), as a result of algal primary production. Further, we found a significant decrease of the Chl *a* content at the surface sediment in June and, conversely, a peak in February (figure 5a). We suggest that microphytobenthic biomass and primary production are significantly affected in spring by the development of macroalgal mats reducing penetration of solar radiation to the surface sediments and by the parallel grazing pressure of filtering-feeder *R. philippinarum* and *M. senhousia* on resuspended sediment (Numaguchi, 1990; De Jonge & Van Beusekom, 1992). In contrast, microphytobenthic production is enhanced in late winter, when *Ulva sp.* is almost absent, air exposure of the sediments is longer and macro-zoobenthic biomass is much lower. These processes might be described as an adaptational seasonal antagonism between primary producers.

However, after a warm and highly irradied summer, a drastic deterioration of the meteorological conditions occurred from late September. A marked drop of solar radiation and temperature and an increased rainfall (figures 2a, 2b and 3a) caused the rapid decomposition of the macroalgae (very abundant in early September, visual observations). As a result, an increased fraction of detrital algal material was found both in the particulate and the sedimentary organic carbon standing stock. In the ebbing tidal-creek, this was indicated by a good correlation of POC with pheopigments, both highest in October, but not with Chl *a*. At the sediment level, it was highlighted by the parallel peaks of pheopigment and TOC contents and an increased pheopigment/Chl *a* ratio.

Subsequently, an increased load of refractory and decomposing algal materials enhanced the processes of respiration and anaerobic decomposition. A drop in dissolved oxygen concentrations and a peak in acid-volatile sulfide levels accordingly occurred in October. Coincidentally between September and October, the extent of the self-purifying potential of the intertidal zone, which is promoted by the sediment emersion during low tide, was limited by a high LWL (low tide water level) which kept the sampling stations submerged for longer (figure 3a). Such circumstances most likely prolonged the residence time on the tidal flat of water mass at low D.O. concentration and enhanced the toxic effect of hydrogen sulphide. Although the distrophic events may have started in early October 1994 (visual observations), the submersion of sampling stations prevented us from sampling until October 25th. Whereas, while the AVS levels at the surface sediments might have partially recovered faster, the AVS levels at the subsurface sediments were still significantly higher than those found during the previous months.

Among the intertidal communities of the macrobenthos, *R. philippinarum* was the species most affected by the distrophic events. Parallel to a reduction of *ca.* 60 % of intertidal flats mainly due to human reclamation, a drastic fall in the abundance of *R. philippinarum* has been observed over the last ten years in Japan. In the Prefecture of Kumamoto (southern Japan) the catch has declined in the last fifteen years from 70 000 tons $year^{-1}$ (total weight) to *ca.* 3 000 tons $year^{-1}$ (Tsutsumi, personal communication). An excessive organic load, including detrital algal materials, and subsequent oxygen depletion, as we describe here, appear to be major causes of such changes, with important economical implications due to the commercial relevance of *R. philippinarum*.

Among the other macrobenthic species inhabiting the intertidal flat, *M. senhousia*, a thin-shelled mytilid native to Asia, was not significantly affected by the events of October, but displayed similar life-history characteristics as reported for other intertidal and subtidal soft sediments of bays and estuaries in various parts of the world (Crooks, 1996 and herein cited references). In accord with the yearly high mortality values reported for Japanese embayments (Tanaka & Kikuchi, 1978), also on the intertidal flat under investigation, *M. senhousia* grew quickly in spring-early summer and gradually decreased its population from summer to the subsequent winter.

In contrast to the crash of *R. philippinarum*, the two Polychaeta *Nereis sp.* and *Cirriformia tentaculata* (accounting for *ca.* 60 % and 50 % of the total density and biomass of Polychaeta, respectively) increased significantly both in density and in biomass from October thoughout the next few months. Polychaeta species were not endangered by the increase of AVS levels but possible benefited from a higher amount of detrital organic matter which accumulated on the tidal flat, as a suitable environment for their growth. Although further studies on the population dynamics of *Nereis sp.* and *Cirriformia tentaculata* are required to the analyze in detail their seasonal changes, it can be suggested from the results of the present work an inverted response of different trophic groups (suspension-feeder bivalves *vs.* deposit-feeder

Polychaeta), following the distrophic events occurred between September and October 1994.

Significant changes of the chemical characteristics of the sediments and the macrobenthic communities were also found in October 1994 at the adjacent subtidal station. Between late September and October 1994, decomposing macroalgal detritus was moved backwards into the estuary and/or transported toward the subtidal zone according to the tidal cycle. Thus, it partly deposited on the intertidal flat and partly sunk into the bottom sediments of the subtidal station. This corresponded to the highest peaks of pheopigment (figure 8a) and TOC (figure 8c) contents at this subtidal station. As on the intertidal flat, these events led to enhancement of decomposition processes and oxygen depletion at the bottom sediments, with a subsequent increase of the AVS levels (figure 8b). Bivalves did not survive to such a stressed environment. It can be noted that in July 1994 small-sized individuals of *M. senhousia* were more abundant on the subtidal station (total density: 6613 ind m^{-2}, figure 11a; mean individual weight: 0.014 gWW ind^{-1}) than on the intertidal flat (3638 ± 1987 ind m^{-2}, figure 10a; mean individual weight: 0.130 ± 0.015 gWW ind^{-1}). Whereas, a mass mortality occurred to *M. senhousia* in October 1994 on the subtidal station but not on the intertidal flat. It is likely that more severe anoxic conditions at the subtidal station (e.g. at the subsurface sediments) prevent Bivalves (e.g. *M. senhousia* in 1994 and *Theora fragilis* in 1995) from a successful settlement. Whereas, a substantially more oxidized environment on the intertidal zone allows *M. senhousia* settlement and colonization. Differently from Bivalves, Polychaeta increased in density in October of both 1994 and 1995. We will discuss more in detail in a subsequent study the occurrence of species succession among Polychaeta, which seasonally occurs at the most organically polluted station of the local subtidal zone.

In conclusion, this work represents the first documented case in a tidal estuary of the Seto Inland Sea of how intertidal and subtidal communities of the macrobenthos are affected by distrophic events following the decomposition of macroalgal mats and the enhancement of respiration processes. Drastic changes in macrobenthic species composition and mass mortality of sensitive species, like *R. philippinarum*, is a warning that indispensable countermeasures are necessary for a sustainable use of this tidal estuary, such as reduction of nutrient import from land and control of macroalgal development in shallow waters.

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