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Can low sea urchin densities control macro-epiphytic biomass in a north-east Atlantic maerl bed ecosystem (Bay of Brest, Brittany, France)?

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The distribution, abundance and feeding behaviour of sea urchins (*Paracentrotus lividus, Psammechinus miliaris, Sphaerechinus granularis*) and the macro-algal biomass were assessed in two maerl beds within a north-east Atlantic coastal ecosystem (Bay of Brest, Brittany, France). To study the possible control of herbivorous sea urchins on the macrophytic algae, one maerl bed under the influence of urban sewage (northern site) was compared to one less influenced by urban and industrial outlets (southern site). Macrophytic biomass in the northern site was estimated as 40-fold higher than in the southern site where sea urchins were, on average, 38-times more numerous. Preliminary results support the hypothesis that grazing of sea urchin, even in low densities, can be a factor regulating the macrophytic biomass on maerl beds except in too nutrient enriched environments. So in the northern basin of the Bay, data pointed out the role of anthropogenic impacts on macrophytic biomass increase which was concomitant with the progressive disappearance of sensitive herbivorous species like sea urchins, both processes result in change in the ecosystem.

INTRODUCTION

Sea urchins are important grazers; they can regulate the abundance of macroalgae in many subtidal macrophyte habitats and their role in the functioning of benthic subtidal communities has been studied extensively (reviews by Lawrence, 1975; Harrold & Pearse, 1987; Chapman & Johnson, 1990; Hagen, 1995). The sea urchin effect has been described in kelp forest communities where their activity leads to barren grounds (reviewed by Palacín et al., 1998). Overgrazing has also been reported in more diversified algal habitats, such as Mediterranean communities where sea urchins can decimate the soft upstanding algae (Verlaque, 1984, 1987). In these communities *Paracentrotus lividus* was the 'key' species and its density was generally high (up to 100 ind m^{-2}). Kitching & Ebling (1961) and Verlaque (1987) estimated that a minimum sea urchin density of 15 to 20 ind m^{-2} was necessary to inhibit algal development. However, Palacín et al. (1998) have recently demonstrated that in the western Mediterranean a density of less than 5 ind m^{-2} can be sufficient to exert a significant influence on the dynamics of the algal assemblages where sea urchins were actively moving.

Maerl beds constitute a favourable substratum to macrophyte development (Maggs, 1983; Hily et al., 1991; Grall & Glémarec, 1997a,b). In the Bay of Brest ecosystem, the sea urchins *Psammechinus miliaris* (Gmelin), *Paracentrotus lividus* (Lamarck), and *Sphaerechinus granularis* (Lamarck), are the dominant biomass grazers of the maerl community (BIOMAERL, 1999), although their density are actually low, less than 1 ind m^{-2}, in comparison with other north-east Atlantic urchin-dominated habitats such as intertidal maerl beds (Keegan, 1974) or coastal lagoon as Lough Hyne in Ireland before 1983 (Kitching & Thain, 1983; Barnes et al., 2002) or Urbinu in Corsica (Fernandez et al., in press). In the Bay of Brest, two sites in a contrasting situation were regularly surveyed during the Biomaerl EC programme by a multidisciplinary team aiming to better understand the yet poorly known function of the maerl beds, particularly biodiversity, functional structure and anthropogenic impacts (BIOMAERL, 1999). These sites were used in the present study. Site A situated in the north of the Bay in the vicinity of the harbour can be considered as a nutrient enriched site compared with Site B situated in the south part far from the urban and industrial disturbances (Grall & Glémarec, 1997a). Macrophytic cover was much higher in Site A compared with Site B while the herbivorous sea urchins, the dominant grazers in the two sites, were much less numerous.

The macrophytic biomass in the northern part of the Bay appears to have increased during the last ten years (Hily et al., 1992) while the sea urchin number has drastically decreased (Lumingas, 1994). The inverse relationship between sea urchin densities and the abundance of maerl-associated epiflora raises the question of the determinant role of these herbivorous species in macroalgae regulation. A possible regulation of the macrophytic production by macrograzers like sea urchins in a similar manner that benthic suspension feeders limits by grazing the summer phytoplanctonic populations of the nitrogen-enriched Bay of Brest (Hily, 1991; Jean, 1994; Chauvaud et al., 2000), can be envisaged.

The purpose of this study is to compare concomitantly the algal biomass and the sea urchin abundance in the two different nutrient enriched habitats over a one year cycle, in order to define if the sea urchin grazing in the southern beds was sufficient to prevent an increase in algal biomass such as in the northern area. Such an approach required assessment of the sea urchin dynamics in the studied areas. An estimation of the sea urchin grazing (in quality and quantity) was made through the analysis of the algal biomass ingested by the different species along with its seasonal variations. The sea urchin ingestion rate was assessed in experimental control close to the environmental conditions. These data should confirm if the hypothesis of macrophyte regulation by the sea urchin is tenable and if an *in situ* experimental study to quantify this grazing pressure should be undertaken.

MATERIALS AND METHODS

The study area

This study took place in the Bay of Brest, western Brittany, France (Figure 1) between November 1996 and September 1998. It is a semi-enclosed ecosystem (Delmas, 1981) with water-exchange with the open sea through a channel. The waters are well mixed by tides and regular wind-generated swell. Two rivers (Aulne and Elorn) fertilize the bay leading to an eutrophic ecosystem with an annual phytoplanctonic primary production of 255 to 280 g C m^{-2} y^{-1} (Tréguer & Quéguiner, 1989; Del Amo, 1996).

Within the two maerl bed sites (northern site) and (southern site) monitored, sea urchin populations grew on a substratum covered by maerl composed of living thalli of the calcareous red alga *Lithothamnion corallioides* (P. and H. Crouan). This substratum promotes the development of epiphytic macrophytes assemblages dominated by Rhodophyceae (Hily et al., 1992).

The data on physical and biological parameters of the water column were obtained from Chauvaud et al., 1996, Grall, 2002 and from results of the European BIOMAERL programme, 1996–1999 (BIOMAERL, 1999). The water temperature scale in the Bay ranges from 9°C to 18°C. The two sites undergo very similar variations through the year. The salinity of the two sites is under the influence of local rivers. Water salinity usually falls below 30 psu after heavy rainfall and over dry periods it may exceed 35 psu for a few months. The spring phytoplankton bloom in the Bay occurs in April–May with a maximum of 10 μg chlorophyll-a l^{-1} on both sites. The production continues until September. The highest values are maintained longer in the northern site than in the southern one. When large amounts of dead phytoplankton have sedimented onto the bottom, they can cause hypoxia on maerl beds (Grall & Glémarec, 1997b). Seston concentrations varied between one and 14 mg l^{-1} throughout the year. In the southern site, the suspended matter in the bottom water is more stable than over the northern grounds. Photosynthetically available radiation (PAR) at the bottom appeared lower on the northern site than on the southern one at every sampling occasion (Table 1).

The northern site, near the urban and harbour areas, is suffering from anthropogenic pollution compared with the

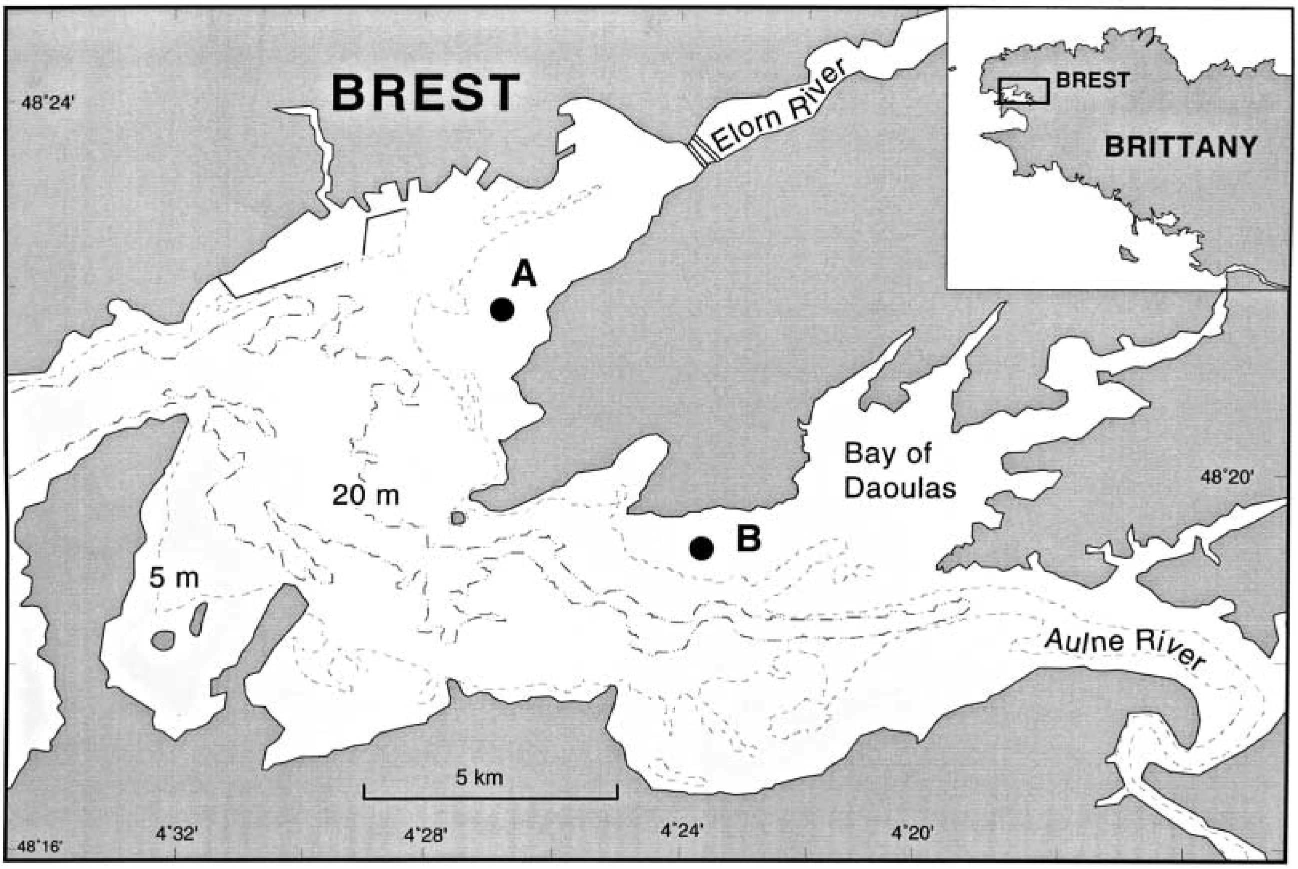

Figure 1. Location of the sea urchin sampling sites on two maerl beds in the Bay of Brest. (A) Northern site; (B) southern site.

Table 1. *Principal physical and biological characteristics of the two study sites (northern site, A; southern site, B).*

	Site A	Site B	References
Water column			
Chlorophyl-*a* (no. of weeks over 5 $\mu g\,l^{-1}$)	18	13	BIOMAERL, 1999; Grall, 2002
Bottom PAR (mean % from surface PAR)	42%	61%	BIOMAERL, 1999; Grall, 2002
Sediment			
Fines particles <63 μm (%)	36	14	Grall & Glémarec, 1997b
Organic matter (%)	24	18	Grall & Glémarec, 1997b
Tributyltin (TBT) ng g^{-1}	197	16	Troadec, 1997
Polycyclic aromatic hydrocarbons (PAHs) ng g^{-1}	6760	<200	Quiniou et al., 1999
Infauna (% of total abundance)			Grall & Glémarec, 1997a,b
Opportunistic species (cirratulid, polychaetes)	32%	9%	
Sensitive species (crustacean, molluscs, sabellid polychaetes)	38%	54%	

PAR, photosynthetically available radiation.

southern site where the only detectable disturbances are agricultural in origin (Troadec, 1997). By the use of biological indicators, Glémarec (1997) describes the northern site as a biologically unbalanced zone and the southern site as normal. The industrial and domestic wastes provide the northern site with a complex set of micro-pollutants such as tributyltin (TBT) and polycyclic aromatic hydrocarbons (PAHs) which are present in the sediment at higher concentration in Site A than in Site B (Troadec, 1997; Quiniou et al., 1999). The two maerl beds consist of mixed sediments with the same proportion of sands and gravel, but the level of fine particles (<63 μm) and organic matter in the sediment are much higher in the northern site compared to the southern site. These organic matter levels are high compared to other sediment in the Bay of Brest with a similar level in fine particles (Grall & Glémarec, 1997b), but this is due to the presence of living maerl thalli in the sediment (Table 1).

At the infaunal level, organic input of urban and industrial origin decreases the species richness in the northern site compared to the southern one. It increases the biomass of opportunistic species (mainly cirratulid polychaetes) and it changes the trophic structure, favouring surface and subsurface deposit feeders (Grall & Glémarec, 1997a,b; BIOMAERL, 1999).

Sampling

Macroalgae biomass

Quantitative samples were collected monthly at about 5 m depth by SCUBA divers between November 1996 and September 1997. The diver-collected samples consisted of the total epiflora and epifauna; they were extracted by suction with a device equipped with a 0.125 m^2 quadrat to sample sediments. All samples were immediately preserved in formalin (7%), then frozen in the laboratory. For each month, three stations per site were randomly defined and analysed. After identification, the macroalgae were drained, dried in blotting paper then weighed to the nearest 0.01 g.

Sea urchin abundance

Concomitantly to macroalgae sampling, total sea urchin abundance was determined by SCUBA divers from December 1996 to September 1998 (southern site) and to July 1998 (northern site), respectively with an interruption due to climatic disturbance and logistics from September 1997 to February 1998. The sampling areas were 10-m diameter circles (78.5 m^2). Divers randomly anchored one end of a 5-m ground line and held the other one while drawing a circle. All the sea urchins present in this 5-m radius were counted and measured to the nearest 0.1 mm at the ambitus without spines using callipers. This procedure was repeated randomly three times at each sampling for the two sites.

Organic material in the gut contents

To follow the seasonal change in the organic material ingested by the sea urchins, an analysis of their gut contents was made. Ten sea urchins of each species were taken monthly from each site between April 1997 and March 1998. As it was not possible to analyse the whole population, they was sampled in the dominant size-class of the population. Sea urchin guts were extracted, opened and washed and the gut content was carefully removed from the gut walls under a dissecting microscope, dried at 60°C and weighed 24 h later. The organic content levels of the total gut contents were determined by ignition in a muffle furnace at 450°C for 4 h 30 min. Weight loss was accurately measured with a precision balance and expressed as percentage.

Ingestion rate

Ingestion rates of *Paracentrotus lividus* and *Psammechinus miliaris* were recorded in the laboratory during one year. Forty sea urchins of both species were collected by SCUBA from the southern site where these species were present in sufficient number and divided into four replicates of each species. As for the organic material calculation, a homogeneous size-class representative of the dominant size-class of each population was chosen. The sea urchins were placed in tanks (60×40×30 cm) filled with seawater at a controlled temperature defined in relation with that daily observed in the natural environment and ranged from 9°C in winter to 18°C in summer. Photoperiod was regularly adjusted by the main of a bank of neon tubes placed over the tanks (one tube of 30 watts for two tanks). The feeding rate of these sea urchins was measured weekly from March to July then from September to March. Each group of ten sea urchins was fed 10 g wet weight (WW) of *Palmaria palmata* (Linné) and 10 g WW of *Laminaria digitata* (Hudson) added simultaneously in the tanks. These are their preferred algae as determined by a preference test before the beginning of this experiment (Guillou & Vachet, personal observation). Food remaining after three days was weighed and the ingested biomass was calculated. Biomasses were measured to the nearest 0.01 g WW after drying in blotting paper. As the experimental food ration was always greater than the ingested biomass, between the experiments sea urchins received the same daily algal biomass as in the experimental process. Tanks were cleaned before each experiment and the introduction of the experimental food ration.

Statistical analysis

Changes vs time in abundance, size, dry weight and organic concentration of the gut contents were tested for each sea urchin species with a one-way analysis of variance (ANOVA) ($P<0.05$) with the least significant difference test once homogeneity of variances had been tested. The analyses were performed with the statistical software STATGRAPHICS.

RESULTS

Seasonal changes in macroalgae biomass and estimation of algal production

The algal biomass in the northern site (A) grew from 0.16 in January 1997 to 72.7 g dry weight (DW) m^{-2} in July, then dropped to 15.6 g DW m^{-2} in September (Figure 2). It was significantly higher ($P<$ 0.05) than that measured in the southern site (B) which increased from 0.02 in January to 2.2 g DW m^{-2} in July, and dropped to 0.13 g in September.

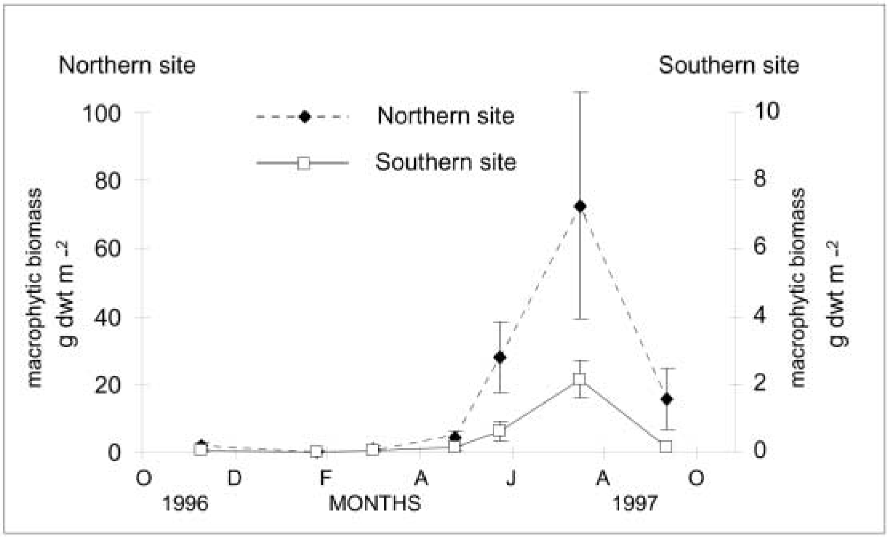

Figure 2. Changes in the macrophytic biomass (mean ±SE) in the two study sites over an annual cycle (November1996 to September 1997).

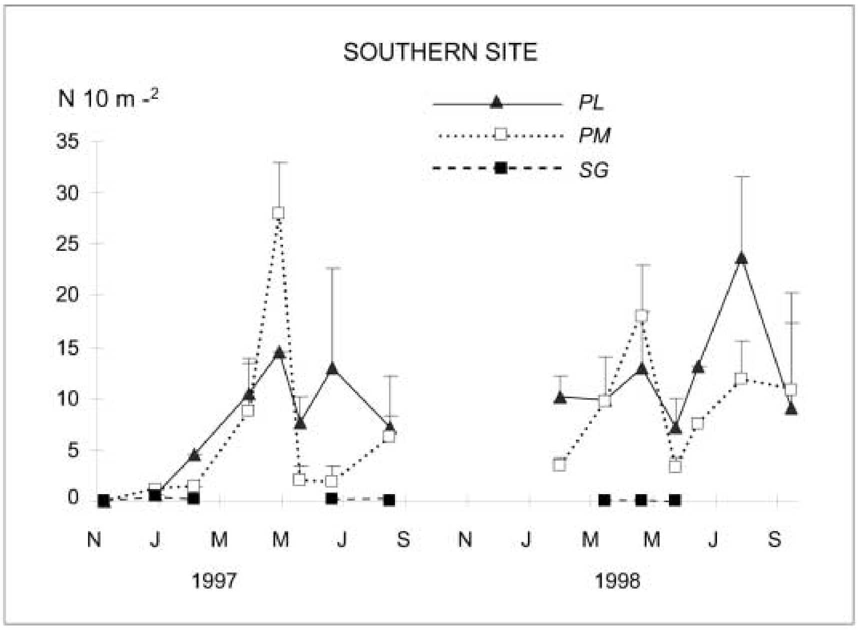

Figure 3. Number of sea urchins per 10 m^2 in the southern site (mean ±SE) from December 1996 to September 1997 and from February 1998 to September 1998.

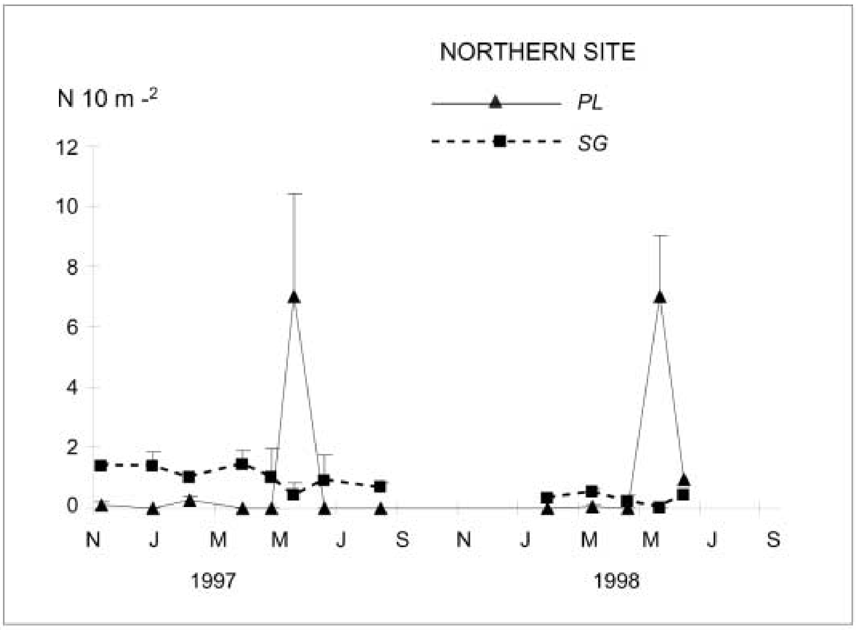

Figure 4. Number of sea urchins per 10 m^2 in the northern site (mean ±SE) from December 1996 to September 1997 and from February 1998 to July 1998.

Table 2. *Size-frequency distribution of the three sea urchin species in the two study sites with monthly data for each size group: mean ±SE and sea urchin percentage (%).*

		1996	1997							1998						
		Dec	Jan	Mar	Apr	May	Jun	Jul	Sep	Feb	Mar	Apr	May	Jun	Aug	Oct
Site B							*Psammechinus miliaris*									
<13 mm	Mean															11.6
	SE															1.5
	N (%)															4
13–25 mm	Mean				23				23.6	19.8	20.2	20.5	21.7	22.2		24.3
	SE				1.1				0.9	3.3	3.2	3.3	2.2	1.6		1.8
	N (%)				2				2	17	15	25	17	34		15
>25 mm	Mean			31.7	30.4	30.9	32.7	34.2	31.3	29.7	31.3	30.9	31.9	32.4	32.9	31.5
	SE			2.4	2.4	2.3	2.7	3.2	2.2	2.4	2.3	2.6	2.5	2.8	3	2.7
	N (%)			100	98	100	100	100	98	83	85	75	83	66	100	81
Site B							*Paracentrotus lividus*									
<30 mm	Mean								22						22	26.1
	SE								1						2	3.4
	N (%)								1						3	25
>30 mm	Mean			40.1	43.9	44.3	44	47.5	45.2	46	42	43.5	46.4	47.2	49.5	47.1
	SE			5.7	5.8	5.9	4.9	6.3	4.7	4.8	4.4	5.2	4.2	3.9	5.3	3.9
	N (%)			100	245	100	100	100	99	100	100	100	100	100	97	75
Site A							*Paracentrotus lividus*									
<45 mm	Mean						31.8							33.6		
	SE						6							5.4		
	N (%)						22							31		
>45 mm	Mean						61.6							59.2		
	SE						7							6.3		
	N (%)						78							69		
Site A							*Sphaerechinus granularis*									
>90 mm	Mean	101.8	106.3	105.6	98.3	98.9	106.5	102	100.6	102.9	105.7	104.5	102.5			
	SE	7.6	5.7	4.6	7.4	5	5.7	5.9	5.1	6.6	6.1	5.4	6			
	N (%)	22	33	8	34	24	10	21	16	12	20	10	15			

An estimation of the algal production was made between January when the biomass was zero (or very low) and July when the biomass was maximal at both sites. The mean production per six months without taking in account the sea urchin grazing should be 72.5 g DW m^{-2} or 680 g WW m^{-2} in the northern site and 2.2 g DW m^{-2} or 20 g WW m^{-2} in the southern one.

Sea urchin abundance

Sea urchin distribution depended on the station considered: two species, *Psammechinus miliaris* and *Paracentrotus lividus*, were dominant in the southern site (Figure 3). From March 1997 to June 1998, the density of *P. lividus* was constantly fluctuating between 5 and 15 ind 10 m^{-2}, with a low, but insignificant, annual increase in May; then, in August 1998 the population temporarily grew to 24 ind 10 m^{-2}. The yearly increase in May was much more noticeable in *Psammechinus miliaris*. A sharp and significant variation was detected in this species in April–May with maxima of 18 and 28 ind 10 m^{-2} in 1997 and 1998, respectively, before a sudden drop to 2 or 3 ind in June. The northern site was characterized by the almost exclusive presence of *Sphaerechinus granularis* (Figure 4). Its density was low, (1.3 ±0.2 ind m^{-2}) at the beginning of this study, between December 1996 and April 1997; it progressively dropped to 0.3 ind m^{-2} in June 1998. Indeed, there were two decreases observed in June 1997 and February 1998, respectively. One should note that, every year in June, about 8 ind 10 m^{-2} *Paracentrotus lividus* were temporarily present at this site while this species was almost completely absent during the rest of the year.

Size–frequency distributions

The biometrical analysis of *Paracentrotus lividus* collected from the southern station showed homogeneity in size-distribution over the study period (Table 2). Apart from October 1998 when juveniles below 30 mm in diameter were noticeably recorded in the site, most of the population-size was within 35 and 55 mm (mean size: 44.8 ±2.8 mm) without possible distinction among year-classes. The lack of juveniles was not due to the sampling method since small individuals below 30 mm were recorded with the same method at the northern site. At this station the size-distribution of *P. lividus* was significantly different ($P<0.05$); there, indeed, most of the population laid within 45 and 70 mm and constituted a modal component with a mean size of 60.4 ±6.6 mm. The individuals below 45 mm were fewer in number and had a mean size of 32.7 ±5.7 mm.

The size-distribution of *Psammechinus miliaris* population did not fluctuate in 1997; it was characterized between March and September by a modal component within 22 to 37 mm with a mean size of 32 ±2.5 mm. A new cohort of lower size individuals, i.e. below 20 mm, was noticeably recorded in February 1998 and its density was increasing till June; its mean size increased from 19.9 mm in February to 22.2 mm in June. In 1998 the size of the adult component was not significantly different from the 1997 cohort. As for *Paracentrotus lividus*, some juveniles with a mean size of 11.6 ±1.5 mm occurred in October 1998.

In the northern site the *Sphaerechinus granularis* population was mainly composed of old individuals above 90 cm in diameter, which according to Lumingas & Guillou (1994) corresponds to a population older than six years. In spring 1997 first, then in February 1998 a high mortality rate was detected through a significant decrease in density ($P<0.05$) concomitant with the presence of spineless dead sea urchins in a greater number than alive individuals (M.G., personal observation).

Organic matter level in gut contents

According to the size-distribution results, the size-classes of the samples were 100–110 mm for *Sphaerechinus granularis*, 40–50 mm for *Paracentrotus lividus* and 30–40 mm

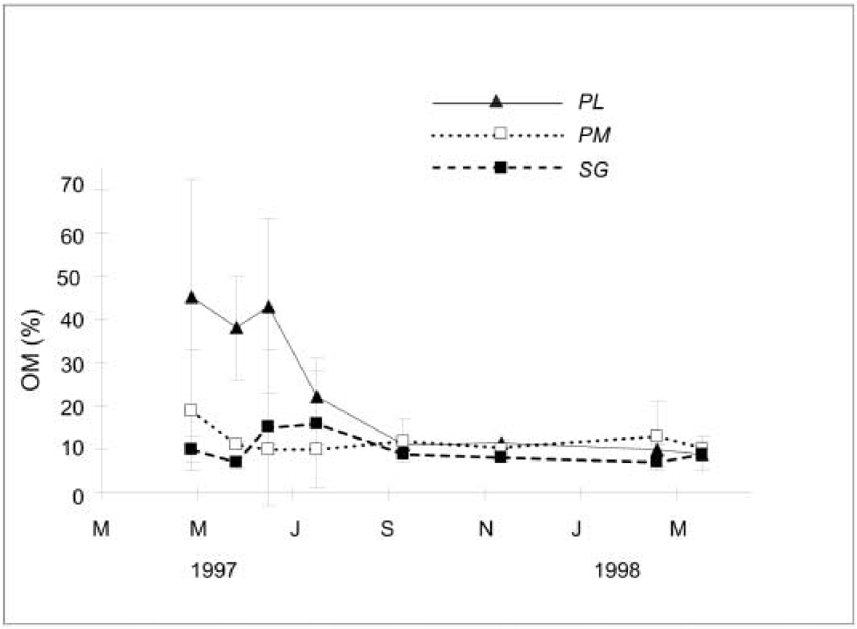

Figure 5. Changes in the percentage of organic matter (mean ±SE) in the gut contents of the three sea urchin species.

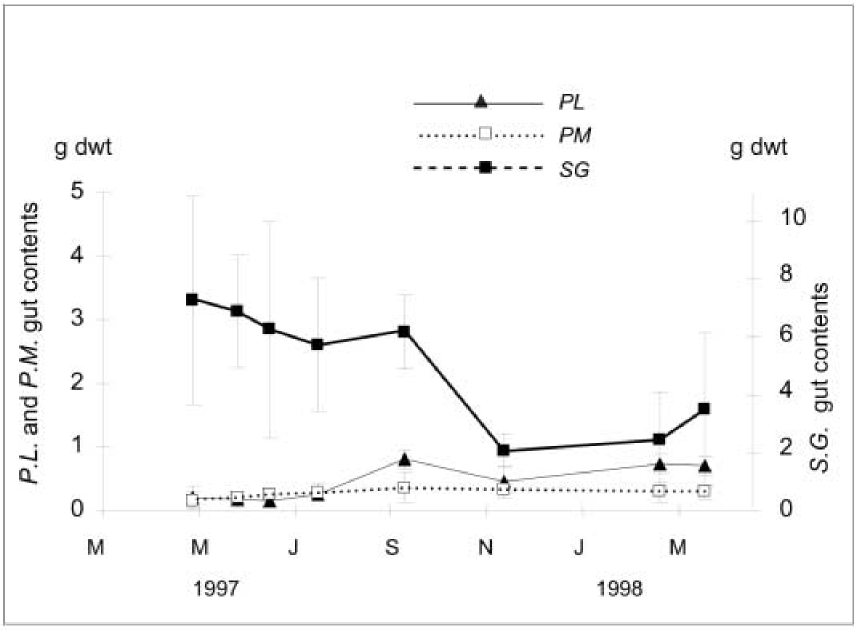

Figure 6. Changes in the gut content weight (in g DW) (mean ±SE) of the three sea urchin species over one year (April 1994–March 1998).

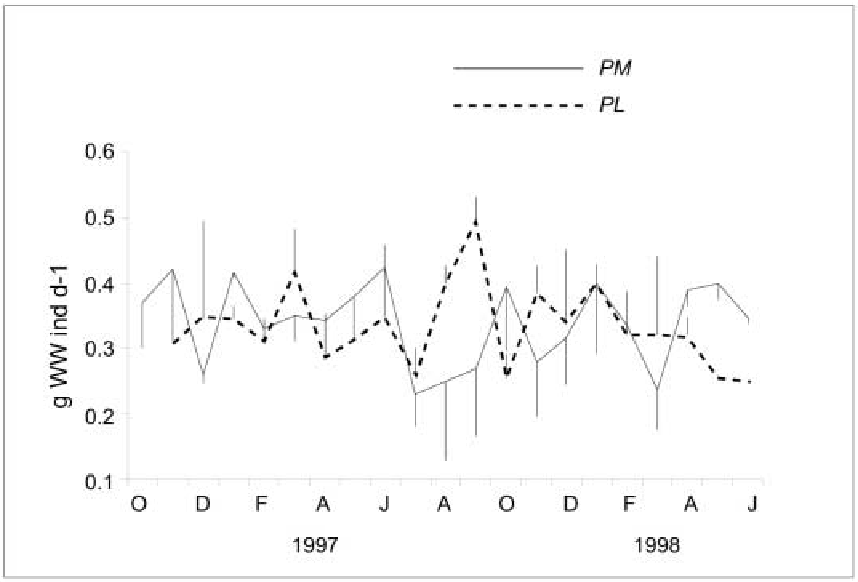

Figure 7. Changes in the daily feeding rate of *Paracentrotus lividus* and *Psammechinus miliaris* when fed on *Laminaria digitata* and *Palamaria palmata* in controlled experimental aquaria.

for *Psammechinus miliaris*. The gut contents of the three species studied contained a mixture of sediments and algal fragments in variable amounts according to the species and season. The animal part, mainly composed of small crustaceans (mysidacea, crab legs) probably ingested by accident while urchins were grazing algae, was very low ($<10\%$ in biomass). As these crustaceans had been removed before drying, one can estimate that the measured organic matter corresponded in a major part to the algal component of the gut contents.

From April to June the proportion of organic matter in gut content was higher in *Paracentrotus lividus* (41.5% ±3.5) than in *Psammechinus miliaris* (13.3% ±4) and *Sphaerechinus granularis*, (10.7% ±3.3) ($P<0.05$) (Figure 5). For *Paracentrotus lividus* gut contents, the maximum organic matter levels fell sharply to 11% in September and remained stable untill March of the following year. The two other echinoid species showed no seasonal changes and no significant differences between the three species ($P>0.05$) were observed from September to March where the mean organic matter level in gut contents was 10 ±1.8%.

In *Paracentrotus lividus*, the lower gut content weight was recorded between April and July when organic matter level was the highest (Figure 6). In *Sphaerechinus granularis*, the gut content weight was significantly higher ($P<0.05$) between April and September than in winter. It was also significantly higher than those of the two other species over the same period. The increase in gut content weight in spring and summer for *S. granularis* and in autumn and winter for *P. lividus* resulted from an ingestion of sand and maerl, both of which are heavier than algae.

Feeding rate

No significant seasonal difference was observed over a one year period in the ingestion rate of *Paracentrotus lividus* and *Psammechinus miliaris* (Figure 7). For both species the ingestion rate varied from 200 to 500 mg WW d^{-1} without any significant trend. The average ingestion over one year was 340 ±80 mg WW d^{-1} for *Paracentrotus lividus* and 350 ±90 mg WW d^{-1} for *Psammechinus miliaris*. During the maximal algal production from April to August it was 310 ±60 and 370 ±90 mg WW d^{-1} for *Paracentrotus lividus* and *Psammechinus miliaris* respectively.

DISCUSSION

The two maerl beds studied in the Bay of Brest display distinct floral and faunal characteristics. In the north of the Bay (Site A), the algal biomass was on average 40 times that of the southern site (Site B) between March and July. On the fauna level, herbivores mainly represented by sea urchins, were far more numerous in the latter site. Two questions were asked to explain such a paradox: (i) was the ecosystem of the northern basin of the Bay too influenced by input of anthropogenic origin which promoted intensive development of primary production in the form of epiphytic algae? (ii) Or was the low macrophytic biomass in Site B the result of herbivore grazing, and the sea urchin abundance decrease in Site A could thus explain the higher algal biomass?

One argument in favour with the first hypothesis is the location of Site A in the vicinity of both the harbour, the town and the Elorn River. These sources of disturbance increase seston concentrations, percentage of fine particles and organic matter on the northern maerl bed compared with the southern site (BIOMAERL, 1999). This anthropogenic input promotes development of primary production in the form of epiphytic algae on the maerl thalli. The comparison of our data with those of Hily et al., 1992 shows a biomass increase from 30 g DW m^{-2} in June 1987 to 72.7 g DW m^{-2} in July 1997 indicating a doubling of the macrophytic biomass within ten years. In the same way, the industrial and domestic wastes provide this site with a complex set of micro-pollutants such as TBT, PAHs which can directly or indirectly disrupt the physiological activities of the most sensitive invertebrates such as echinoderms, molluscs, crustacean or sabellid polychaetes and lead to their progressive disappearance. At the infauna level, Grall & Glémarec (1997a,b) have shown that opportunistic species are replacing the sensitive ones in the macrofaunal assemblages of this area. Ecotoxicological experiments on sea urchins have revealed that the *Sphaerechinus granularis* population from Site A exhibited deficiencies in fertilization and larval development, illustrating the harmful effects of pollutants on this species (Guillou et al., 1997; Quiniou et al., 1998; Guillou et al., 2000). Its density decreased over this study and in comparison with the data of Lumingas (1994), the population was ten times lower in 1997 than in 1992. Moreover few individuals below 80-mm in diameter were recorded in this study. In the southern site, the presence of a cohort of small individuals of *Psammechinus miliaris* are indicative of environmental conditions favourable to sea urchin settlement.

To answer the second question, it was necessary to know if the difference in algal biomass between the two sites could be correlated with the respective difference in sea urchin grazing impact. This impact depends on sea urchin abundance, mobility, diet and feeding rates. Data for this study showed that in 1997 and 1998 between April and August, during the period of algal production, the densities of *Paracentrotus lividus* and *Psammechinus miliaris* at Site B were significantly greater than the sea urchin densities on Site A even if one note, every year in June, the temporary occurrence of *Paracentrotus lividus* on this latter site. The densities of *P. lividus* and *Psammechinus miliaris* on Site B and *Sphaerechinus granularis* on Site A were 12.4, 10.4 and 0.6 ind 10 m^{-2} respectively.

Sphaerechinus granularis is considered as a grazer which consumes macro-algae and maerl (Guillou & Michel, 1994), dead leaves, rhizomes and scales in sea grass (Campos-Villaca, 1984) and encrusting coralline algae (Verlaque, 1981). It also selectively feeds on detritus (Cornet & Jangoux, 1974; Verlaque, 1981). Adults of *Paracentrotus lividus* feed on macro-algae (Verlaque, 1984) but can behave like detritus feeders and browsers when food becomes limiting (Verlaque, 1987; Fernandez & Boudouresque, 1997). *Psammechinus miliaris* revealed the most diverse diet mainly characterized by ingestion of sand, shell gravel and macro-algae with possible epiphytic animals (Milligan, 1916; Mortensen, 1943; Faller-Fritsch & Emson, 1972 in Lawrence, 1975). Data from this study shows that these three species may ingest available algae (or sediments) over the year. In the gut content, the algal biomass, estimated from the organic matter percentage, was highest from April to July, with highest values observed in *Paracentrotus lividus*. An experimental estimation of the ingestion rate carried out on *P. lividus* and *Psammechinus miliaris* indicated from March to April an average ingestion rate of about 350 mg WW d^{-1} for medium-sized individuals in the two species. For *Paracentrotus lividus*, this value is consistent with the literature which cites estimations from 160 to 560 mg WW d^{-1} dependent upon food (Traer, 1980; Verlaque, 1987; Nédélec et al., 1981; Ménager et al., 1995; Fernandez, 1996). For *Psammechinus miliaris* our values were obviously higher than data reported in the literature when diet is composed of macroalgae or marine plants and which indicated consumption rate between 10 and 20 mg WW d^{-1} (Faller-Fritsch & Emson, 1972 in Lawrence, 1975; Traer, 1980). For *Sphaerechinus granularis*, Guillou & Michel (1994) reported a mean feeding rate of 850 mg WW d^{-1} between April and July for 100-mm diameter individuals feeding upon *Laminaria* in aquaria. These results show that, although the grazing impact of *Paracentrotus lividus* and *Psammechinus miliaris* may be twice as low as *S. granularis* grazing, the respective density of these two spp. over the period of algal production on the Site B was 15- to 20-fold higher than the density of *S. granularis* on Site A. From the experimental ingestion data, and the observed densities during this period, the sea urchin populations could ingest 0.75 g WW $\mathrm{m}^{-2}\ \mathrm{d}^{-1}$ of the algal biomass in Site B and 0.3 g WW $\mathrm{m}^{-2}\ \mathrm{d}^{-1}$ in Site A. Between January and July this grazing would be

135 g WW m^{-2} in Site B and 55 g WW m^{-2} in Site A. Over this seven month period an estimation of the algal production without taking into account the sea urchin grazing would be 680 WW m^{-2} and 20 WW m^{-2} in Sites A and B respectively. These data suggest that the sea urchin density would be sufficient to balance algal production in Site B but not in Site A. Even if on Site A the sea urchin biomass was equal to the biomass estimated in the less-disturbed Site B, the algal biomass in the northern maerl bed of the Bay would still be too high to be regulated by sea urchin grazing alone. The grazing difference between the two sites is insufficient in itself to explain a macrophytic biomass in the northern site 40-fold higher than in the southern site. Other factors which should be considered to explain the high algal biomass in the northern maerl beds include the organic matter enrichment of Site A.

Kitching & Ebling (1961) in Ireland and Verlaque (1987) in the north-western Mediterranean showed that *Paracentrotus lividus* may cause an imbalance between production and consumption and an overexploitation of the algal community at sea urchin densities between 15 and 20 adults m^{-2}. However, more recent studies have stated that the decrease in algal biomass was not proportional to the density of sea urchins (Andrew & Underwood, 1993) and that *P. lividus* grazing activity can exert a significant influence on the structure and dynamics of algal assemblages, even in communities with naturally low sea urchin densities (Palacín et al., 1998). Data obtained in this study from Site B strengthen this assertion with obviously lower sea urchin densities. In the Bay of Brest, sea urchins in a non-eutrophicated environment with densities ranging from 1 to 25 ind 10 m^{-2} (Lumingas, 1994; this study) may thus be a significant structuring force. But they cannot control the algal production in areas submitted to anthropogenic input where toxic pollutants reduce their densities while the increase in organic matter and nutrients loads leads to an increase in algal production.

These results are preliminary; their conclusions are restricted by the measure of ingestion rate in the laboratory, by the use of one size-class of sea urchins only and by food limited to two algal species. But the conclusions are interesting enough to study thoroughly the sea urchin ecological role by *in situ* density manipulations. The quantification of the present assertion answers the need to better understand the insufficiently known interactions betweeen temperate sea urchins and their biotic environment modified by human impact (Boudouresque & Verlaque, 2001).

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