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GRAZING ON *CAULERPA RACEMOSA* VAR. *CYLINDRACEA* (CAULERPALES, CHLOROPHYTA) IN THE MEDITERRANEAN SEA BY HERBIVOROUS FISHES AND SEA URCHINS

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INTRODUCED SPECIES
CAULERPA RACEMOSA
MEDITERRANEAN SEA
GRAZING
FISH
BOOPS
SARPA
SEA URCHIN
PARACENTROTUS
SPHAERECHINUS

ABSTRACT. – The grazing on the invasive *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman *et* Boudouresque has been studied in the Gulf of Marseilles. After three years of field observations, we have determined that the grazing began at the end of summer and increased in autumn when the extent of *C. racemosa* meadows was at a maximum. The Mediterranean herbivorous fish, *Boops boops* and *Sarpa salpa*, essentially grazed on *Caulerpa racemosa* in late summer and early autumn. The regular sea urchins *Paracentrotus lividus* and *Sphaerechinus granularis* also consumed *C. racemosa*. The feeding behaviour of *S. granularis* was generalist with 31.2% ± 2.9 of *C. racemosa* in gut contents. The consumption of *C. racemosa* by the more selective sea urchin *P. lividus* was lower (9.8% ± 2.5 of *C. racemosa* in gut contents). Grazing activity was very limited in space and in time (end of summer and autumn) and quickly compensated by the enhancement of the stolon ramification of *C. racemosa*, so the consumers identified at Marseilles do not seem able to limit the spread of this introduced species.

INTRODUCTION

Since its recent introduction into the Mediterranean Sea, *Caulerpa racemosa* var. *cylindracea* (Sonder) Verlaque, Huisman *et* Boudouresque (hereafter: *C. racemosa*) has spread rapidly in the Mediterranean and the neighbouring areas of the Atlantic (Verlaque *et al.* 2000, 2003, 2004). Various factors may explain the success of the species, such as high growth rate (Piazzi *et al.* 1997, Piazzi & Cinelli 1999, Ruitton *et al.* 2005) and strong spread capacity by sexual reproduction (Panayotidis & Žuljević 2001), cutting (*i.e.* dispersal through vegetative fragmentation) (Ceccherelli & Piazzi 2001) and propagule production (Renoncourt & Meinesz 2002), which allow the plant to rapidly recover its extent and even to progress after a more or less drastic decline during the cold season (Piazzi *et al.* 2001, Ruitton *et al.* 2005). The rapid spread of *C. racemosa* suggests that it is not of interest to many consumers. *Caulerpa* species contain secondary metabolites. Caulerpenyne is the most abundant cytotoxic sesquiterpenoid (Lemée *et al.* 1993, Amade & Lemée 1998). Dumay *et al.* (2002) measured 35 to 80 times less caulerpenyne in *C. racemosa* than in *C. taxifolia* (Vahl) C. Agardh. However, Jung *et al.* (2002) by using a more efficient extraction method obtained a caulerpenyne concentration only twice lower than *C. taxifolia*. The secondary metabolites are usually considered to play a protective role against biological attacks (pathogens, parasites, competitors, epiphytes and herbivores) (Stachowicz & Lindquist 2000, Schnitzler *et al.* 2001, Koh *et al.* 2002, Lindquist 2002). In the Mediterranean Sea, *C. taxifolia* is usually avoided by herbivores except for Sacoglossan molluscs (Lemée *et al.* 1996, Thibaut & Meinesz 2000, Thibaut *et al.* 2001, Žuljević *et al.* 2001). The lack of herbivorous pressure could represent one of the causes of *C. racemosa* invasion success. Indeed, in the present study, we report observations on the consumption of *C. racemosa* by herbivorous fish and sea urchins at the northwest limit of its Mediterranean range. So the knowledge of the grazing activity on this invasive species could be important in order to evaluate the possible biological control of the spread and discuss the possible impact of this grazing on the dynamics of *C. racemosa* meadows.

MATERIALS AND METHODS

Study area and sampling: Field observations and sampling were carried out in the Gulf of Marseilles (France), at Saména (43°13.84'N, 5°20.76'E), which presented dead matte of *Posidonia oceanica* (Linnaeus) Delile (matte: complex of rhizomes, roots and sediment, which persists even after *P. oceanica* has died) densely colonized by *Caulerpa racemosa*. From October 2001 to

September 2004, field observations were conducted at a rate of 1 dive per month during the *Caulerpa racemosa* withdrawal period from January to April and 4 dives per month during the growth season of *C. racemosa* from May to December. Each dive has lasted about 50 minutes and has consisted in a random route in the *C. racemosa* meadows area. Field observations had allowed to identify the consumers and determine the grazing period in the year. Sampling of fish faeces and sea-urchins was carried out between 10 and 20 m depth, from 2001 to 2004, between August and January when *C. racemosa* meadows were developed.

Faeces of Sparidae fish, *Boops boops* (Linnaeus, 1758) and *Sarpa salpa* (Linnaeus, 1758) were collected in the water column, just below the fish schools (*B. boops*: 3 faeces in November 2003; *S. salpa*: 5 faeces in October 2001; 12 in September 2003, 21 in August 2004 and 10 in September 2004). The total length (TL) of the individuals was visually estimated during sampling. No quantitative data on fish density are available.

Regular sea urchins, *Paracentrotus lividus* (Lamarck, 1816) and *Sphaerechinus granularis* (Lamarck, 1816), were collected in the *Caulerpa racemosa* meadows (*P. lividus*: 4 individuals in December 2002 and 21 in October 2003; *S. granularis*: 2 individuals in December 2002 and 19 in October 2003). The horizontal diameter without spines (HD) of the individuals was measured in the laboratory.

Analysis of fish faeces: Analysis of fish faeces by the contact method (Jones 1968, Nédelec 1982) was performed under stereoscopic and light microscope to species or genus level. For each individual a sub-sample of faeces was mounted on a slide; the slide was placed under light microscope equipped with reticulated eyepiece and moved at random. The item placed under the centre of the reticule was identified as one contact. If two items were superimposed under the centre of the reticule, they were both counted. The frequency of an item in a faeces is the percentage of contacts for this item. Ten slides were prepared per gut content and ten contacts were made per slide (total = 100 contacts per individual).

Analysis of gut content of sea urchins: Gut contents were removed and preserved in buffered 4% formaldehyde-seawater. Analysis of gut contents was performed under light microscope. The identification of the food items was conducted as far as possible at a species or genus level. Gut contents of small sea urchins (< 25 mm in diameter) were mounted on a slide and analysed in their entirety. Abundance of each item was expressed in terms of percentage of gut content according to its cover on the slide. For sea urchins larger than 25 mm, the contact method was used (see above). Gut contents were dried at 60°C to constant weight to obtain the dry weight. The ashless weight was obtained after 4 h of combustion at 550°C. The repletion index (dry weight of the gut content divided by the horizontal diameter cubed; Nédelec 1983) was measured.

Data analysis: Statistical differences between the items in the gut content of the two sea urchins species were sought with unilateral t test (t). Cochran test was used to test the homogeneity of variance. When the homogeneity of the variance of the data was not observed, log transformation of variables was applied to data (Zar 1999). Statistical analyses were carried out using the CCS-Statistica microcomputer program (Version 6.1, ®StatSoft).

Principal Component Analyses (PCA) on data collected in October 2003 were performed to described the diet composition of *Paracentrotus lividus* and *Sphaerechinus granularis*.

RESULTS

Field observations

Since 1997, *Caulerpa racemosa* has spread rapidly in the region and, by the end of 2003, it was common on *Posidonia oceanica* dead matte and less frequent on rocky substrate, from a few meters to 35 m depth. In shallow water, *C. racemosa* was rare probably due to its vulnerability in the face of the violent hydrodynamism conditions. At Saména, dense *C. racemosa* meadows colonized the *P. oceanica* dead matte and coarse sediments from 7 m to 30-35 m depth. At Marseilles, as is also the case in other western Mediterranean localities, the development of *C. racemosa* was very seasonal. The growth period began slowly in April, when some stolons with small erect axes appeared on the substrate. At Saména, four consumers of *C. racemosa* were identified, the Sparidae fish *Boops boops* and *Sarpa salpa* and the sea urchins *Sphaerechinus granularis* and *Paracentrotus lividus*.

The grazing on *Caulerpa racemosa* by *Boops boops* was only observed in October and November. The grazing on *C. racemosa* by *Sarpa salpa* was less restricted in space and time. It began at the end of summer and increased to reach a maximum intensity in autumn. The schools of *S. salpa* moved from place to place above the *C. racemosa* meadows and grazed small areas (some m^2).

Juveniles of *Sphaerechinus granularis* and *Paracentrotus lividus* were only found under small rocky blocs scattered in *C. racemosa* meadows. Adults of *Paracentrotus lividus* were present in small densities in the *C. racemosa* meadows developed on *Posidonia oceanica* dead matte and under rocky blocs whereas adults of *S. granularis* were exposed on *C. racemosa* meadows. The consumption of *C. racemosa* by sea urchins was attested by the composition of the gut content.

Faeces of fish

The grazing of *Caulerpa racemosa* by *Boops boops* in November was confirmed by the examination of faeces of 3 individuals (in mean 90% of *C. racemosa* and 10% of *Dictyota* spp.). The percentage of *C. racemosa* in faeces of *S. salpa* ranged from 3 ± 1% in summer to 20 ± 11 - 78 ± 5% in

Table I. – Mean frequency ± SE of items in the faeces of *Sarpa salpa*, collected at Saména, 10-20 m depth. n: number of individuals. -: absent.

	Oct-2001	Sep-2003	Aug-04	Sep-04
n	5	12	21	10
TL (mm)	150-250	200-250	150-200	200-250
Phaeophyceae				
Cladostephus spongiosus	7.0 ± 4.4	-	-	2.9 ± 2.8
Colpomenia sinuosa	-	-	0.1 ± 0.1	-
Cystoseira amentacea var. *stricta*	-	15.0 ± 5.4	1.9 ± 1.9	-
Dictyota spp.	47.0 ± 10.3	12.0 ± 4.1	19.5 ± 3.7	13.8 ± 3.8
Ectocarpaceae	-	0.3 ± 0.1	-	-
Halopteris spp.	5.0 ± 2.8	-	8.3 ± 1.7	0.3 ± 0.2
Kuckuckia spinosa	-	-	-	0.7 ± 0.5
Nereia filiformis	-	-	0.2 ± 0.2	-
Padina pavonica	-	-	3.1 ± 0.9	-
Sphacelaria spp.	3.4 ± 0.9	0.1 ± 0.1	8.2 ± 1.2	0.6 ± 0.4
Rhodophyceae				
Antithamnion sp.	-	-	0.4 ± 0.2	-
Boergeseniella fruticulosa	-	-	0.3 ± 0.2	-
Ceramium spp.	0.3 ± 0.2	-	4.9 ± 0.9	-
Ceramiaceae	-	-	0.7 ± 0.2	-
Chondracanthus acicularis	-	-	0.2 ± 0.2	-
Chondria spp.	-	0.5 ± 0.4	0.3 ± 0.1	-
Corallinaceae epiphyte	-	-	1.1 ± 0.4	-
Corallina elongata	8.9 ± 5.0	-	3.5 ± 1.0	0.2 ± 0.1
Delesseriaceae	-	-	0.4 ± 0.3	-
Feldmannophycus rayssiae	-	-	1.5 ± 0.6	-
Gelidiella sp.	-	-	0.1 ± 0.1	-
Gelidium spp.	7.0 ± 3.9	-	6.6 ± 1.2	0.2 ± 0.1
Spermothamnion flabellatum	-	-	0.5 ± 0.3	-
Spermothamnion irregulare	-	-	0.5 ± 0.3	-
Herposiphonia spp.	-	-	3.5 ± 0.7	0.1 ± 0.1
Hypnea sp.	-	-	0.1 ± 0.1	-
Jania sp.	-	-	0.6 ± 0.3	-
Laurencia microcladia	-	0.1 ± 0.1	4.3 ± 0.9	-
Osmundea truncata	-	-	0.1 ± 0.1	-
Peyssonnelia spp.	-	-	5.0 ± 1.8	-
Polysiphonia spp.	-	7.8 ± 7.1	2.5 ± 0.6	-
Ptilothamnion pluma	-	-	0.1 ± 0.1	-
Rhodophyllis divaricata	0.3 ± 0.3	-	1.0 ± 0.4	-
Rhodymenia ardissonei	-	-	1.5 ± 0.9	-
Sphaerococcus coronopifolius	-	-	0.4 ± 0.4	-
Womersleyella setacea	-	-	1.1 ± 0.5	-
Chlorophyceae				
Bryopsis sp.	-	-	0.2 ± 0.2	-
Caulerpa racemosa	20.0 ± 11.3	61.8 ± 8.0	2.5 ± 1.3	78.0 ± 4.7
Cladophora spp.	-	-	7.5 ± 1.1	0.3 ± 0.2
Codium sp.	0.2 ± 0.2	-	-	-
Derbesia tenuissima	0.2 ± 0.2	-	-	-
Pseudochlorodesmis furcellata	0.1 ± 0.1	-	2.7 ± 1.0	-
Magnoliophyta				
Posidonia oceanica	0.6 ± 0.5	1.7 ± 1.2	0.6 ± 0.4	2.7 ± 1.9
Cyanobacteria	-	0.2 ± 0.2	0.6 ± 0.3	-
Fauna				
Bryozoa	-	-	0.3 ± 0.3	0.1 ± 0.1
Crustacea exuvia	-	0.4 ± 0.4	0.1 ± 0.1	-
Hydroid	-	0.1 ± 0.1	0.8 ± 0.3	-
Mollusk	-	-	0.3 ± 0.1	-
Ostracod	-	-	0.1 ± 0.1	0.1 ± 0.1
Undetermined items	-	-	1.8 ± 0.5	-

autumn (Table I). The upper part of erect axes and stolon apices were preferentially consumed. The other major prey (frequencies in faeces ≥ 7%) were the Phaeophyceae (*Cladostephus spongiosus, Cystoseira amentacea* var. *stricta, Dictyota* spp., *Halopteris* spp. and *Sphacelaria* spp.) and the Rhodophyceae (*Corallina elongata, Gelidium* spp. and *Polysiphonia* spp.) (Table I).

Gut content of sea urchins

Caulerpa racemosa represented the major item in the gut content of juveniles of *Paracentrotus lividus* and *Sphaerechinus granularis* in December 2002 (81.2 ± 3.7% and 100 ± 0.0% of gut contents, respectively) (Table II). In 2003, the study of adults showed a lesser consumption of *C. racemosa*, with consumption significantly higher in *S. granularis* than in *P. lividus*: 9.8 ± 2.5% and 31.2 ± 2.9% of the gut content, respectively (t test: t = 5.16, p<0.001, df = 38, Table III). In contrast to young individuals, the consumption of *Posidonia oceanica* leaves was high: 41.5 ± 5.6% and 25.5 ± 2.1% in the gut content, respectively (no significant difference, t test: t = 0.77, p = 0.449, df = 38, Table III). *C. racemosa* was the third macrophyte ingested by *P. lividus*, after *Posidonia oceanica* and *Dictyota* spp., whereas it was the major item ingested by *S. granularis* after *P. oceanica* and *Rhodomelaceae* (*Herposiphonia* spp., *Polysiphonia* spp. and *Womersleyella setacea* (Hollenberg) R.E. Norris) (Table III).

A first PCA analysis using all items ingested by adult sea urchins did not highlight clearly defined factors. So, a second PCA analysis was performed after removal of items contributing to less than 0.1% of the gut content or present in only one individual. The first two axes of the second PCA explained 35% of total variance. The third axis (eingenvalue: 2.21, 10% of total variance) did not provide information of any further explanatory factor (Fig. 1). The two sea urchin species were well separated from each other along the axis 1 according to their feeding behaviour (Fig. 1, Top). Axis 1 highlighted the major items in the gut content of both sea urchin species. On the contrary, the axis 2 did not separate the two sea urchin species but showed the range of their feeding behaviour. Individuals of *P. lividus* were more grouped than individuals of *S. granularis* (Fig. 1, Bottom).

The dry weight of gut content of *Sphaerechinus granularis* was greater than that of *Paracentrotus lividus* (Table IV), taking into account the difference of individual size. The total repletion index was significantly higher for *S. granularis* than for *P. lividus* (t test: = 3.21, p = 0.002, df = 38), but the repletion index of organic matter was higher for *P. lividus* (t test: t = 6.18; p<0.001, df = 38, Table IV). For *S. granularis*, the repletion index of organic matter was 5 times lower than the repletion index of inorganic matter, whereas it was 1.5 times higher for *P. lividus* (Table IV).

DISCUSSION

Caulerpa species contain secondary metabolites. Caulerpenyne is the most abundant cytotoxic sesquiterpenoid (Lemée *et al.* 1993, Amade & Lemée 1998). Dumay *et al.* (2002) measured 35 to 80 times less caulerpenyne in *C. racemosa* than in *C. taxifolia* (Vahl) C. Agardh. However, Jung *et al.* (2002) by using a more efficient extraction method obtained a Caulerpenyne concentration only twice lower than *C. taxifolia*. The secondary metabolites are usually considered to play a protective role against biological attacks (pathogens, parasites,

Table II. Mean frequency ± SE of items in the gut contents of young *Paracentrotus lividus* and *Sphaerechinus granularis* collected at Saména in December 2002, 15-20 m depth. n: number of individuals. -: absent.

	Paracentrotus lividus	*Sphaerechinus granularis*
n	4	2
HD (mm)	10-12	10
Phaeophyceae		
"*Aglaozonia* sp." life-history phase	0.1 ± 0.1	-
Dictyota spp.	3.7 ± 1.1	-
Halopteris spp.	2.5 ± 2.2	-
Sphacelaria spp.	1.3 ± 1.1	-
Rhodophyceae		
Jania sp.	0.1 ± 0.1	-
Pterosiphonia ardreana	0.1 ± 0.1	-
Womersleyella setacea	0.1 ± 0.1	-
Chlorophyceae		
Caulerpa racemosa	81.2 ± 3.7	100 ± 0.0
Magniolophyta		
Posidonia oceanica	3.8 ± 1.1	-
Cyanobacteria	0.1 ± 0.1	-
Undetermined items	7.0 ± 3.6	-

Table III. – Mean frequency ± SE of items in the gut contents of *Paracentrotus lividus* and *Sphaerechinus granularis*, collected in October 2003. Abbreviations correspond to those used in the principal component analysis. T test (t) results testing the differences of items consumption among the sea urchin species. p: level of signification. n: number of individuals. "-": absent.

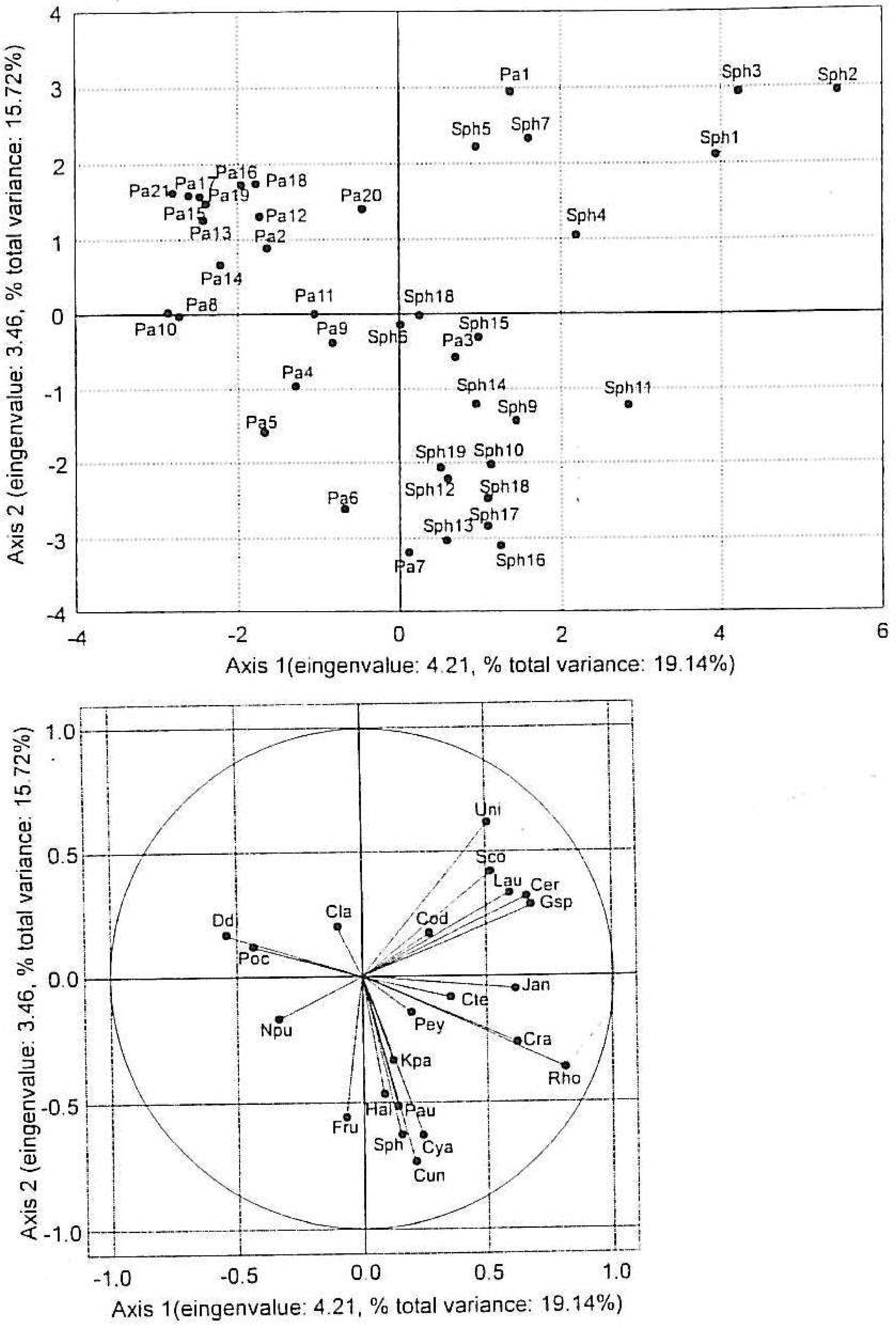
		Paracentrotus lividus	*Sphaerechinus granularis*	T test	
n		21	19		
HD (mm)		12-45	74-94		
	Abbreviation	**mean±SE**	**mean±SE**	**t**	**p**
Phaeophyceae					
Choristocarpus tenellus	Cte	-	0.1 ± 0.1	1.74	0.090
Cladostephus spongiosus	Cla	0.6 ± 0.3	-	1.72	0.093
*Dictyota dichotoma**	Ddi	25.1 ± 4.4	3.6 ± 0.9	6.00	<0.001
Halopteris spp.	Hal	1.3 ± 0.4	0.6 ± 0.2	1.58	0.122
Sphacelaria spp.	Sph	3.7 ± 1.0	2.8 ± 0.6	0.06	0.950
*Taonia atomaria**	Tat	-	0.1 ± 0.1	0.18	0.857
Rhodophyceae					
Antithamnion sp.	Ant	-	-	1.05	0.299
Botryocladia boergesenii	Bbo	-	0.1 ± 0.1	1.05	0.299
Ceramiaceae *	Cun	0.8 ± 0.3	1.2 ± 0.3	0.99	0.299
Ceramium spp.	Cer	0.6 ± 0.2	1.7 ± 0.5	2.20	0.033
Chondria spp.	Cho	-	0.1 ± 0.1	1.05	0.299
"Falkenbergia rufolanosa" life-history phase	Fru	0.4 ± 0.2	0.3 ± 0.1	0.54	0.589
Gelidium spp.	Gsp	1.0 ± 0.7	3.0 ± 0.8	1.95	0.058
Gymnothamnion elegans	Gel	0.1 ± 0.1	-	1.38	0.176
Jania sp.	Jan	2.0 ± 1.0	3.9 ± 0.7	1.61	0.120
Kallymenia patens	Kpa	0.1 ± 0.1	0.4 ± 0.3	1.33	0.190
Laurencia sp.	Lau	-	0.3 ± 0.2	1.90	0.065
Nitophyllum punctatum	Npu	0.4 ± 0.2	-	2.06	0.046
Peyssonnelia spp.	Pey	1.8 ± 0.7	1.4 ± 0.4	0.57	0.572
Plocamium cartilagineum	Pca	0.1 ± 0.1	-	0.95	0.348
Rhodomelaceae	Rho	3.5 ± 0.9	13.7 ± 1.0	7.01	<0.001
Rhodymenia ardissonei	Rar	-	0.3 ± 0.1	1.05	0.299
Spermothamnion irregulare	Sir	-	0.1 ± 0.1	1.89	0.067
Sphaerococcus coronopifolius	Sco	0.4 ± 0.3	0.7 ± 0.2	0.73	0.467
Spyridia filamentosa	Sfi	-	0.3 ± 0.1	1.05	0.299
Chlorophyceae					
*Caulerpa racemosa**	Cra	9.8 ± 2.5	31.2 ± 2.9	5.16	<0.001
*Chaetomorpha aerea**	Cae	0.1 ± 0.1	-	0.95	0.348
Cladophora sp.	Csp	-	-	0.95	0.348
Codium spp.	Cod	-	0.4 ± 0.3	1.65	0.106
Magnoliophyta					
*Posidonia oceanica**	Poc	41.5 ± 5.6	25.5 ± 2.1	0.77	0.449
Cyanobacteria	Cya	1.0 ± 0.4	1.5 ± 0.3	1.30	0.198
Fauna*	Fau	0.3 ± 0.1	0.7 ± 0.2	1.26	0.214
Undetermined items	Uni	5.4 ± 0.9	6.0 ± 0.9	0.50	0.621

* Log transformed data for the homogeneity of variances.

Table IV. – Mean dry weight DW ± SE of gut content (total and organic matter) and repletion index RI ± SE (organic and inorganic matter) of *Paracentrotus lividus* and *Sphaerechinus granularis* collected in October 2003. n: number of individuals.

	Paracentrotus lividus	*Sphaerechinus granularis*
n	21	19
HD (mm)	12-45	74-94
	mean ± SE	**mean ± SE**
Total dry weight (organic + inorganic matter) (g DW)	0.05 ± 0.01	2.12 ± 0.29
Dry weight of organic matter (g DW)	0.03 ± 0.01	0.32 ± 0.02
RI (organic matter) (10^{-7} g DW.mm^{-3})	11.7 ± 0.9	5.2 ± 0.3
RI (inorganic matter) (10^{-7} g DW.mm^{-3})	7.8 ± 1.8	28.1 ± 3.6
Total RI (10^{-7} g DW.mm^{-3})	19.5 ± 2.2	33.3 ± 3.6

Fig. 1. – Top, Principal component analysis. Representation of individuals of sea urchin on axis 1 vs. axis 2. Individuals of sea urchin: Pa: *Paracentrotus lividus*, Sph: *Sphaerechinus granularis*, followed by the number of the individual. Bottom, Principal component analysis. Representation of variables on axis 1 vs. axis 2. Variables: items in the gut content, for abbreviation see table III.



competitors, epiphytes and herbivores) (Stachowicz & Lindquist 2000, Schnitzler *et al.* 2001, Koh *et al.* 2002, Lindquist 2002). In the Mediterranean Sea, *C. taxifolia* is usually avoided by herbivores except for Sacoglossan molluscs (Lemée *et al.* 1996, Thibaut & Meinesz 2000, Thibaut *et al.* 2001, Žuljević *et al.* 2001).

The present study showed that in spite of the presence of caulerpenyne certain Mediterranean herbivores, the fishes *Boops boops* and *Sarpa salpa* and the sea urchins *Paracentrotus lividus* and *Sphaerechinus granularis*, consumed *Caulerpa racemosa*. Other species have already been described as consumers of *C. racemosa* in the Mediterranean Sea: sea slugs (sacoglossa) in Tunisia (Djeloulli *et al.* 2003), in France (Thibaut & Meinesz 2000) the Indo-pacific origin sacoglossa *Elysia tomentosa* (Jensen, 1997) and *Oxynoe viridis* (Pease, 1861) and the native species *Lobiger serradifalci* (Calcara, 1840), *Oxynoe olivacea* Rafinesque 1819 (Cavas *et al.* 2005) and *Ascobulla fragilis* (Jeffreys, 1856) in Turkey and in Croatia (Baki Yokes pers. comm.) and three herbivorous fish, *Siganus luridus* (Rüpel, 1828) and *Siganus rivulatus* (Forsskål, 1775), which are Lessepsian migrants from the Red Sea, in Cyprus

(Eastern Mediterranean) (Lundberg *et al.* 1999) and in Sicily (Central Mediterranean) (Azzurro *et al.* 2004) and *Sarpa salpa* in Turkey (Levent Cavas pers. comm.).

The feeding activity of *Boops boops* increases during the post-spawning period (Anato & Ktari 1983). The reproduction period of *B. boops* is the spring and summer (Vidalis 1951, Dieuzeide *et al.* 1955, Tortonèse 1974, Girardin 1978). At Marseilles, the observation on grazing of *C. racemosa* by *B. boops* in November corresponded to its post-spawning period. During this period, the macrophyte communities began to decrease and it is possible that the extended *C. racemosa* meadows provided an alternative food resource for the fish.

Sarpa salpa juveniles are carnivorous but the adults are herbivorous and the rare animals present in the gut content are accidentally ingested (Bini 1968, Anato & Ktari 1983, Velimirov 1984, Bauchot & Hureau 1986, Verlaque 1990). The consumption of another *Caulerpa*, *Caulerpa prolifera* (Forsskål) Lamouroux, by *S. salpa* has been observed in Tunisia (Verlaque 1990), where the fish is considered as toxic or hallucinogenic (Bauchot & Hureau 1986). The consumption of *C. racemosa* had been previously observed in Libya (Nizamuddin 1991). Such abundant macrophytes as *C. racemosa* in autumn represent an easily available food resource for the large schools of *S. salpa* that gather in shallow water and increase their feeding activity during the pre- and post-spawning periods (Bini 1968, Faggianelli & Cook 1981, Anato & Ktari 1983, Bauchot & Hureau 1986, Verlaque 1990). So far, no case of toxic fish has been reported along the French coasts.

Usually, when it has the choice, *Paracentrotus lividus* does not consume either *C. taxifolia*, or *C. prolifera* that contain as much Caulerpenyne as *C. taxifolia* (Boudouresque *et al.* 1994, Ruitton & Boudouresque 1994, Lemée *et al.* 1996, Jung *et al.* 2002). However, even if *C. racemosa* also contains Caulerpenyne, and its concentration is the highest in autumn (Dumay *et al.* 2002, Jung *et al.* 2002), it can be consumed by *P. lividus* and *S. granularis* at this season. Young sea urchins of both species certainly do not move very far, so they consume what they found in the immediate vicinity in the *Caulerpa* meadows of Saména, namely *C. racemosa,* which was by far the major macrophyte resource available. On the other hand, the feeding behaviour of *P. lividus* and *S. granularis* adults differed. *P. lividus* consumed, by order of importance: *Posidonia oceanica* dead leaves, *Dictyota dichotoma* then *Caulerpa racemosa*, whereas *S. granularis* consumed *C. racemosa*, *P. oceanica* dead leaves and Rhodomelaceae (mainly the other introduced species *Womersleyella setacea*). The greater number of macrophytes species and amounts of inorganic material in the diet in *S. granularis* than in *P. lividus* illustrated a more generalist feeding behaviour. In this feeding behaviour pattern, a prey will be consumed according to its availability in the community. This may explain the high frequency of the invasive species, *C. racemosa* and *W. setacea,* in their gut content. As *P. lividus* consumed less *C. racemosa* than *S. granularis*, it seems to be more able to avoid the species because of a more selective feeding behaviour pattern (Verlaque & Nédelec 1983).

Caulerpa racemosa shows great seasonal variations in the north-western Mediterranean area. The depletion of the *Caulerpa* meadows begins in December to reach the minimum of biomass at the end of winter (February - March) (Ruitton *et al.* 2005). The episode of grazing in early autumn was not linked to the seasonal decline of the plant that occurred in early winter. The grazing concerned mainly the apical part of erect axes and to a lesser extent the stolons only, leading to a slight decrease in biomass. Simultaneously, whereas the production of erect axes decreased, the branching of the grazed stolons was significantly enhanced (Ruitton *et al.* 2005). As far as grazing activity is concerned, the phenomenon was very local (small areas) and seasonal (autumn) and was quickly compensated for by the enhancement of the stolon ramification. In the present state of the knowledge, grazing by fish and sea urchins does not seem able to limit the spread of *C. racemosa*. Only experimental survey involving exclosures could allow quantitative assessment of fish and sea urchin grazing of *C. racemosa.*

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