J. Mar. Biol. Ass. U.K. (1998), **78**, 239–248
Printed in Great Britain

IN VITRO CONSUMPTION OF *CAULERPA TAXIFOLIA* (CHLOROPHYTA) BY ACCUSTOMED AND NON-ACCUSTOMED *PARACENTROTUS LIVIDUS* (ECHINOID): SEASONAL VARIATIONS

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In vitro short time experiments (a few weeks) show that daily ingestion by *Paracentrotus lividus* (Echinodermata: Echinoidea) is weak (0–81 mg DW d^{-1} ind^{-1}) for *Caulerpa taxifolia* (Chlorophyta), compared to the data recorded with an almost totally avoided brown alga, *Cystoseira compressa* (24–137 mg DW d^{-1} ind^{-1}) and with a preferred brown alga, *Halopteris scoparia* (79–397 mg DW d^{-1} ind^{-1}). There is no significant difference between spring (when the toxic metabolite content is at its minimum) and summer–autumn (when it is at its maximum). In contrast, the absorption rate of the sea urchin fed on *Caulerpa taxifolia* is significantly weaker in spring than in summer–autumn. Overall, the daily absorbed weight is negative in spring with *C. taxifolia* (compared with 18 mg DW d^{-1} ind^{-1} with *Cystoseira compressa* and 25 mg DW d^{-1} ind^{-1} with *H. scoparia*). It has also been demonstrated that *P. lividus* becomes accustomed to *Caulerpa taxifolia,* at least for short time experiments: the echinoid consumes greater quantities of this alga especially if it is fresh when it has already consumed it previously.

INTRODUCTION

Since 1984, the introduced alga *Caulerpa taxifolia* (Vahl) C. Agardh (Chlorophyta) has steadily spread along the Mediterranean coast of France (Meinesz & Hesse, 1991; Meinesz et al., 1993a,b, 1994, 1995), Italy (Morucci et al., 1994) and Spain (Pou et al., 1993; Ballesteros et al., 1994); the area covered increased annually between 1984 and 1991 by a factor of six (Boudouresque et al., 1992a,b; Boudouresque & Gómez-Garreta, 1992).

Contrary to observations in tropical seas, *C. taxifolia* meadows in the Mediterranean are very dense, and frond length may reach 85 cm (Meinesz & Hesse, 1991; Villèle & Verlaque, 1995). Most substrate types can be colonized: rock, sand, mud, dead rhizomes (or shoots) of *Posidonia oceanica* (Linnaeus) Delile, sea grass meadows (Meinesz et al., 1993), from the surface to 100 m depth (Belsher et al., 1994), with an optimum growth rate between 2·5 and 35 m depth.

Caulerpa taxifolia presents an optimum growth rate between 20 and 30°C (Komatsu et al., 1994). This introduced alga synthesizes several secondary metabolites (particularly caulerpenyne) in greater quantities than in the tropical seas (Guerriero et al., 1992, 1994; Lemée et al., 1993).

The echinoid *Paracentrotus lividus* (Lamarck, 1816) is a major grazer in Mediterranean phytobenthic communities (Verlaque & Nédélec, 1983). Its diet is mainly herbivorous and it presents very algal marked preferences (Traer, 1980; Verlaque & Nédélec, 1983; Verlaque, 1987; Frantzis et al., 1988; Rico, 1989; Frantzis & Grémare, 1992). *In vitro* studies on its feeding behaviour toward *C. taxifolia* show that this alga is not particularly avoided in winter–spring, but is avoided in summer–autumn, at least in long duration (three months) experiments (Lemée et al., 1994a; Boudouresque et al., 1996). At this time, the alga's toxicity is at its highest (Lemée et al. 1993). Moreover, Gobert (1992) has shown *in vitro* that the food ration of *P. lividus*, when it is fed on a preferred alga (*Rissoella verruculosa* (Bertoloni) J. Agardh), decreases in the presence of *C. taxifolia*. This may be due to the leaching of toxic metabolites (or of their degradation products) by this alga. *In situ*, Ruitton & Boudouresque (1994) noted, at Cap Martin (Alpes-Maritimes, France), that the sea urchins moved away from the invaded area, toward not yet invaded substrates. Moreover, previous long term studies have shown that, when *P. lividus* is fed exclusively on *C. taxifolia*, certain of its biotic parameters are affected: decrease of the gonadal growth rate, increase of the righting time (time taken to recover a normal position, mouth down, from being turned over), loss of spines (Lemée et al., 1994b; Boudouresque et al., 1996). Since the area occupied by *C. taxifolia* exceeds 1300 ha between Nice and Menton (Vaugelas et al., 1994), the echinoid populations in the Alpes–Maritimes area might be affected. The antimitotic properties of caulerpenyne on sea urchin eggs have been demonstrated (Lemée et al., 1993).

The questions addressed in this study are:

(1) Is there any variation of daily ingestion and absorption rate, in short duration experiments, when *P. lividus* is fed on *C. taxifolia*, between spring (when the alga synthesizes few secondary metabolites) and summer–autumn (when secondary metabolite content is maximum)?

(2) If *C. taxifolia* is maintained for a long time in aquaria, is its ingestion rate altered (at equal temperatures) as compared to the freshly collected alga?

(3) Do sea urchins become accustomed to *C. taxifolia*, and/or do they react to the repellent effect of *C. taxifolia*?

MATERIALS AND METHODS

Experimental closed circuit aquaria contained 20 dm^3 of artificial sea-water. They were equipped with an air pump, a filter and a plastic grid bottom to avoid faeces ingestion. They were situated in a culture room with controlled temperature and exposed to natural light. The artificial sea-water (38 g dm^{-3} of aquarium salt Ocean®, Aquarium Systems) was totally renewed every three days. During transport and during the experiments, the temperature was adjusted to the sea temperature at the time of collection of the *Caulerpa taxifolia* (sea-water temperature in spring: 13–17°C; in summer–autumn: 19–25°C).

The sea urchins *Paracentrotus lividus*, with a test diameter between 4 and 6 cm (measured at the ambitus, without spines) were collected at Saména (Marseilles, Bouches-du-Rhône, France) between 2 and 3 m depth, in an overgrazed zone where the trophic resource is a limiting factor. The sea urchins were replaced at the beginning of each experiment ('non-accustomed echinoids': NAE) except in experiments 8 and 11 to 14 (Table 1), where the same sea urchins were kept from one experiment to another, in order to determine in summer–autumn a possible ability to become accustomed to *C. taxifolia* ('accustomed echinoids': AE).

The green alga *C. taxifolia* was collected at Cap Martin (Alpes-Maritimes, France) at 6 m depth. The whole thallus of this alga (fronds, stolons, rhizoids) was used in each experiment. The brown alga *Cystoseira compressa* (Esper) Gerloff & Nizamuddin came from Cap Martin and Sausset-les-Pins (Bouches-du-Rhône, France). The brown alga *Halopteris scoparia* (Linneaus) Sauvageau was collected at Saména (Marseilles, Bouches-du-Rhône, France) at 5 m depth. These last two algae, the first almost totally avoided, the second preferred (Frantzis & Grémare 1992), were taken as controls (experiments 17–27 and 28–39).

In order to verify whether *C. taxifolia* becomes more appetizing after a long period in the aquarium, experiments were performed with *C. taxifolia* in two different states: one referred to as 'old' (O), maintained at least one week in aquaria before the beginning of the experiment (experiments 5, 6, 8, 10, 12), the other referred to as 'fresh' (F) collected less than a week previously (experiments 1–4, 7, 9, 11, 13–16).

For each experiment, ten sea urchins were placed in each aquarium, without fasting. The fresh alga provided was weighed and completed to 50 g (strained wet weight) every day. The control aquaria containing 50 g of alga alone served to determine the possible growth or degeneration of the three species. Before each weighing, a standardized straining protocol was carried out: rough straining, centrifugation (2500 rpm for 1 min; rotor diameter Jouan E82® 14·5 cm), then weighing of the fresh weight (at least 0·1 g). For *H. scoparia*, manual centrifugation at 420 rpm for 1 min was carried out before centrifugation at 2500 rpm.

The ingested wet weight was calculated as follows:

$$\text{Ingested wet weight} = Wexp_0 - Wexp_1 - (Wt_0 - Wt_1) \quad (1)$$

where: $Wexp_0$ is the weight of alga at time 0 in the experimental aquarium; $Wexp_1$ the weight of alga at time 1 in the experimental aquarium; Wt_0, weight of alga at time 0 in the control aquarium; Wt_1, weight of alga at time 1 in the control aquarium.

A conversion factor ingested dry weight/ingested wet weight was calculated for the three species. This factor is 0·11 for *C. taxifolia*, 0·16 for *Cystoseira compressa* and 0·29 for *H. scoparia*.

When new sea urchins are used ('non-accustomed echinoids'), the first three days of experiment are not taken into account. During this time, sea urchins in fact egest algae ingested before the experiments; according to Kempf (1962) and Powis de Tenbossche (1978), the intestinal transit lasts from about one day and a half to three days, respectively.

Table 1. *Characteristics and results of the experiments (daily ingested and egested weight, absorption rate and daily absorbed weight: mean ± SD).*

Experiment	Months	Number of days	State of alga	Number of echinoids	Echinoid	Daily ingested weight (mg DW d^{-1} ind^{-1})	Daily egested weight (mg DW d^{-1} ind^{-1})	Absorption rate (%)	Daily absorbed weight (mg DW d^{-1} ind^{-1})
Caulerpa taxifolia									
1	Mar–Apr	10	F	10*	NAE	8 (6)	25 (7)	-212	-17
2	Apr	12	F	10*	NAE	13 (19)	16 (11)	-23	-3
3	Apr–May	30	F	10	NAE	41 (32)	40 (18)	2	1
4	May	14	F	10*	NAE	42 (38)	39 (18)	7	3
5	Jul	8	O	10	NAE	61 (md)	50 (md)	17	11
6	Jul	7	O	10	NAE	63 (md)	32 (md)	49	31
7	Jul	7	F	10	NAE	0 (md)	16 (md)	–	-16
8	Aug	16	O	10	AE	36 (40)	19 (10)	46	17
9	Aug	5	F	10	NAE	12 (9)	0 (0)	100	12
10	Sept	10	O	10	NAE	28 (24)	31 (9)	-12	-3
11	Aug	5	F	10	AE	62 (36)	23 (22)	64	39
12	Sept	10	O	10	AE	18 (19)	36 (14)	-99	-18
13	End Sept	7	F	10	AE	39 (20)	35 (21)	11	4
14	End Sept	7	F	10	AE	81 (18)	35 (14)	57	46
15	End Sept	7	F	10	NAE	33 (25)	5 (9)	85	28
16	End Sept	7	F	10	NAE	25 (9)	17 (106)	33	8
Cystoseira compressa									
17	Mar–Apr	15	F	10	NAE	46 (45)	37 (18)	20	9
18	Apr	14	F	10	NAE	84 (42)	43 (21)	49	41
19	May	24	F	10	NAE	117 (51)	78 (25)	33	39
20	Apr	24	F	10	NAE	89 (55)	59 (37)	34	30
21	Apr	9	F	10	NAE	24 (15)	27 (6)	-12	-3
22	May	21	F	10	NAE	74 (45)	69 (26)	7	5
23	Apr–May	30	F	10	NAE	59 (45)	55 (29)	7	4
24	Jul	7	F	10	NAE	27 (md)	25 (md)	6	2
25	Jul	7	F	10	NAE	71 (md)	49 (md)	30	21
26	Aug	15	F	10*	NAE	137 (91)	114 (42)	17	23
27	Sept	16	F	10	NAE	88 (90)	79 (39)	10	9
Halopteris									
28	Mar–Apr	32	F	10	NAE	85 (73)	51 (31)	40	34
29	May	21	F	10	NAE	213 (78)	182 (63)	14	31
30	Mar–Apr	55	F	10	NAE	134 (96)	103 (78)	23	31
31	Apr	9	F	10	NAE	79 (57)	55 (29)	30	24
32	May	21	F	10	NAE	138 (77)	125 (41)	9	13
33	Apr–May	30	F	10	NAE	121 (77)	105 (50)	13	16
34	Jul	8	F	10	NAE	136 (md)	100 (md)	26	36
35	Jul	8	F	10	NAE	156 (md)	116 (md)	26	40
36	Jul	7	F	10	NAE	119 (md)	86 (md)	28	33
37	Jul	7	F	10	NAE	132 (md)	88 (md)	33	43
38	Aug	15	F	10	NAE	397 (134)	267 (77)	33	130
39	Sept	16	F	10	NAE	343 (146)	289 (86)	16	54

F, fresh alga; O, old alga; AE, accustomed echinoids; NAE, non-accustomed echinoids; md, missing data; *, a part of the sea urchins died before the end of experiments. Calculations take into account only the number of individuals present each day.

Faeces (egested material) were collected daily with a siphon system, sorted (elimination of spines and unconsumed algal fragments that had fallen through the plastic grid) then drained between filter papers before being dried (70°C) for <24 h and weighed to the nearest 0·01 g DW. The egested weight was obtained by the difference between the weight of the dried filter paper with faeces and the initial weight of the dried filter paper.

The absorption rate (AR), the percentage of ingested material moving through the intestinal wall, was calculated using the following equation:

$$AR = \frac{(\text{dried ingested weight-dried egested weight}) \times 100}{\text{dried ingested weight}} \quad (2)$$

The daily absorbed weight is the difference between the dried ingested weight and the dried egested weight.

Non-parametric variance analysis (Kruskal & Wallis test in Conover, 1980) was performed in order to assess whether the food (*C. taxifolia*, *Cystoseira compressa*, *H. scoparia*) might have an influence on the different parameters measured (daily ingested weight, daily egested weight, absorption rate and daily absorbed weight). To assess a possible seasonal influence on absorption rate and daily absorbed weight, a Mann & Whitney non-parametric test was performed (Conover, 1980). In addition, two-way ANOVA, fixed effects (software Statistica) was performed on the ingestion data in order to take into account several factors, such as the state of the plant (fresh or old) or the echinoid ability to become accustomed to *Caulerpa taxifolia* (accustomed echinoid, non-accustomed echinoid), and their interactions with regard to the feeding behaviour of *P. lividus*.

RESULTS AND DISCUSSION

Table 1 presents the results obtained on average daily ingested weight, average daily egested weight, absorption rate and average daily absorbed weight of different echinoid groups, fed on each alga at different seasons, usually during short periods of time (1–3 weeks).

The highest daily ingestions were recorded for *Halopteris scoparia* (from 79 to 397 mg DW d^{-1} ind^{-1}). For *Cystoseira compressa*, the average daily ingestion ranged between 24 and 137 mg DW d^{-1} ind^{-1} and for *Caulerpa taxifolia*, between 0 and 81 mg DW d^{-1} ind^{-1}. These data are higher than or consistent with what has been reported in the literature for *Paracentrotus lividus* kept in aquarium. Mastaller (1974) recorded a Fucophycae ingestion rate ranging from 66 to 146 mg DW d^{-1} ind^{-1}; Frantzis & Grémare (1992) gave for *Cystoseira compressa* from 15 to 70 mg DW d^{-1} ind^{-1}, for *Halopteris scoparia*, between 25 and 100 mg DW d^{-1} ind^{-1}. For *Caulerpa taxifolia*, Lemée et al. (1994a) recorded ingestion rates from 25 mg DW d^{-1} ind^{-1} in winter–spring to 50 mg DW d^{-1} ind^{-1} in summer–autumn (their wet weight values have been transformed with our wet weight/dry weight relation); after three months of experiments, these rates increase up to 100 mg DW d^{-1} ind^{-1} in winter–spring and fall in summer–autumn (<5 mg DW d^{-1} ind^{-1}). Amounts of egested faeces follow the same overall pattern as the ingestion:

from 51 to 289 mg DW d^{-1} ind^{-1} for *H. scoparia*, from 25 to 114 mg DW d^{-1} ind^{-1} for *Cystoseira compressa* and from 0 to 50 mg DW d^{-1} ind^{-1} for *Caulerpa taxifolia*. Results of the Kruskal–Wallis test show that the species of alga given to the sea urchins acts significantly on the daily ingested weight (H=24·98, *P*=0·0001) and on the daily egested weight (H=26·48, *P*=0·0001, 99% confidence limit interval). Thus *P. lividus'* ingestion rate depends on the alga the sea urchin is supplied with. *Halopteris scoparia* is preferred to *Cystoseira compressa*, itself preferred to *Caulerpa taxifolia*. In Fucophycae, chemical defences seem to be linked to the presence of polyphenolic compounds (Lüning, 1990). They form indigestible complexes with proteins in the grazer's gut and thus decrease the digestibility of the ingested material (Feeny, 1976; Rhoade & Cates, 1976). Grazers appear to consume preferentially macrophytes whose content in phenolic compounds is the weakest. The phenol content of *Cystoseira compressa* might explain the behaviour of *P. lividus* toward this alga, which contains a high level of polyphenolic compounds compared to other macrophytes: 22·75 ±5·98% of dry weight for *C. compressa* vs 1·77 ±0·04% for *H. scoparia* (Frantzis & Grémare, 1992). In the Chlorophyta *Caulerpa taxifolia*, the presence of caulerpenyne might act on the feeding behaviour of the sea urchin. Its caulerpenyne content, *in situ* at Cap Martin (Alpes-Maritimes, France), varies over the year, decreasing from 2 mg g^{-1} WW in July to 0·6 mg g^{-1} WW in January, then to 0·2 mg g^{-1} WW at the end of April, according to Guerriero et al. (1994). However, there is no significant seasonal variation of the ingested weight for any of the three algae used in these short duration experiments (Mann–Whitney test with a 95% confidence limit interval: Z=-0·866, *P*=0·386 for *C. taxifolia*; Z=-0·378, *P*=0·705 for *Cystoseira compressa*; and Z=-1·281, *P*=0·200 for *H. scoparia*). The same pattern is observed with the daily egested weight (Mann–Whitney test with a 95% confidence limit interval: Z=-1·888, *P*=0·059) for *Caulerpa taxifolia*; Z=-0·567, *P*=0·571 for *Cystoseira compressa*; Z=-0·641, *P*=0·522 with *H. scoparia*). Calculations have only been made on data obtained with 'fresh' *Caulerpa taxifolia* (F) and 'non-accustomed echinoids' (NAE). A summer drop in *C. taxifolia* short-term consumption rate was described by Lemée et al. (1996), but this is only based on one experiment and is not supported by statistical tests. In the long-term, nevertheless, a similar decline of consumption rate in summer–autumn was well established by Boudouresque et al. (1996).

On the whole, absorption rates measured in our experiments (Table 1) are weak as compared to the data in the literature. Lawrence (1975) gave rates between 60 and 70%; according to this author, absorption affects the inorganic matter as well as the organic matter of the plant. For *P. lividus*, Frantzis (1992) obtained absorption rates between 76 and 86% when the echinoid fed on *Cystoseira compressa*, and between 31 and 70% when it fed on *H. scoparia*. For *Strongylocentrotus franciscanus* (Agassiz, 1863) from California, Vadas (1977) recorded rates ranging from 48 to 91%. The absorption rate of the organic matter ranged, for the Californian *Strongylocentrotus purpuratus* (Stimpson), from 13% (fed on *Cystoseira osmundacea* (Menzics) C. Agardh) to 62% when it is fed on *Macrocystis pyrifera* (Turner) C. Agardh (data from Leighton, 1968 in Lowe & Lawrence, 1976). For *Lytechinus variegatus* (Lamarck, 1816) from the American tropical Atlantic, the absorbtion rate is ~43% fed on *Halimeda incrassata* Ellis, but it is negative (-35%) when the sea urchin is fed on *Eucheuma isiforme* C. Agardh (Lowe &

Lawrence, 1976). So, absorption rate strongly varies according to the ingested plant. On the other hand, in our experiments, the Kruskal–Wallis tests (with a 95% confidence limit interval), performed on parameters of *P. lividus* feeding behaviour, show that, for the three algae, the absorption rate does not significantly differ (H=0·56, *P*=0·756). The difference is significant only for the daily absorbed weight (on average negative for *Caulerpa taxifolia*, 18 mg DW d^{-1} ind^{-1} with *Cystoseira compressa* and 25 mg DW d^{-1} ind^{-1} with *Halopteris scoparia*) with H=12·17 and *P*=0·002. On the other hand, the absorption rate is significantly higher in summer–autumn than in spring for *Caulerpa taxifolia* (Mann–Whitney test with a 95% confidence limit interval, Z=-2·121, *P*=0·034). Thus for this alga, the toxic metabolite content, higher in summer–autumn (Lemée et al., 1993), would not decrease the absorption of ingested material, at least for short duration experiments. As far as the daily absorbed weight is concerned, there is no significant seasonal variation (Z=-1·443, *P*=0·149). In any case, the absorption rate of sea urchins fed on *C. taxifolia* in spring is significantly different from the rate of sea urchins fed on control algae (Z=-1·92, *P*=0·05 for the comparison with *Cystoseira compressa*; Z=-2·57, *P*=0·01 for the comparison with *H. scoparia*). The differences are not significant in summer. During the warm season, in spite of a higher concentration of secondary metabolites of *Caulerpa taxifolia* (caulerpenyne rate suddenly increases when the water temperature exceeds 20°C according to Amade et al., 1996), *P. lividus*' absorption rate is practically the same whatever the ingested alga, during the first weeks of feeding. For *P. lividus*, Frantzis (1992) has not found important seasonal differences, except when the sea urchin was fed on *H. scoparia*: 31% in March and May vs 70% in July. Lawrence (1975), then Frantzis & Grémare (1992), already noted a very high variability of absorption rates, given for different echinoid species, and a seasonal variability of these rates. In our experiments, some rates are even negative, especially when sea urchins are fed on *C. taxifolia* in spring. Lawrence (1975) also showed negative absorption rates when the sea urchins consumed algae containing tannins or alcaloids.

With regard to the *P. lividus* ability to become accustomed to *C. taxifolia*, the parametric tests (two-way ANOVA) performed on the ingestion data show that whatever the state of the alga (fresh or old), accustomed echinoids consume greater quantities of *C. taxifolia* than non-accustomed ones (*F*=8·29; *P*=0·05). The interaction between the two factors is significant (*F*=6·87; *P*=0·01); the contrast analysis then performed shows that the difference is especially due to the fresh alga (Figure 1). In these summer–autumn *in vitro* experiments (between 7 and 16 d), accustomed echinoids feed more on fresh alga than on old, despite the fact that its toxicity decreases after several days spent in the aquarium (Lemée et al., 1993) and the high caulerpenyne rate in the fresh alga at this season (Amade et al., 1996). This feeding behaviour might show that caulerpenyne degradation products are as toxic as the whole molecule; Amade et al. (1996) observed a toxic effect on urchin eggs due to caulerpenyne degradation products.

This latter result shows that *P. lividus*, accustomed to *C. taxifolia*, can increase its consumption rate, without however reaching the rate obtained with almost totally avoided or preferred algae. Our results might suggest that if such ability to become accustomed also occurred *in situ*, *P. lividus* might become a potential consumer of

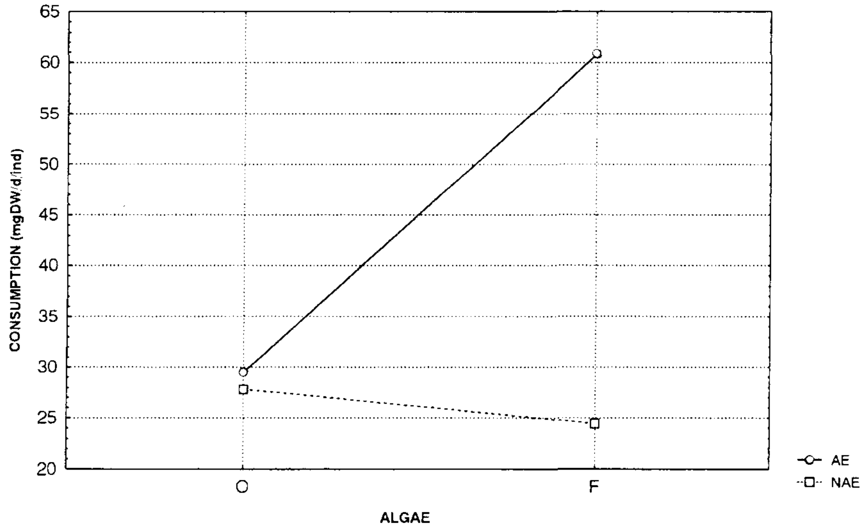

Figure 1. Consumption of *Caulerpa taxifolia* by *Paracentrotus lividus* according to the state of the alga and the echinoids. Algae, *Caulerpa taxifolia*; O, old; F, fresh; AE, accustomed echinoid; NAE, non-accustomed echinoid.

C. taxifolia. Nevertheless, these experiments were performed over a short period, but in the long-term, Lemée et al. (1994b) and Boudouresque et al. (1996) have shown, both in the cold and warm seasons, a significant weakening of the sea urchins, up to death in summer–autumn.

In future experiments, it would be of interest to investigate, on the one hand, what are the mechanisms involved in becoming accustomed in the short term, and on the other hand, what are the factors that offset this trend in the long-term.

This work was supported by the French Ministère de l'Environnement and coordinated by Groupement d'Intèrêt Scientifique (GIS) Posidonie.

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Submitted 16 May 1996. Accepted 18 November 1996.