

Ingestion, absorption, and growth rates of *Paracentrotus lividus* (Echinodermata: Echinoidea) fed different macrophytes

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ABSTRACT: We recorded ingestion, absorption, total and gonadal growth rates of *Paracentrotus lividus* fed unlimited rations of 12 macrophytes (*Rissoella verruculosa*, *Corallina elongata*, *Asparagopsis armata*, *Cystoseira mediterranea*, *Stypocaulon scoparium*, *Padina pavonica*, *Cystoseira compressa*, *Colpomenia sinuosa*, *Dilophus spiralis*, *Ulva rigida*, *Posidonia oceanica* and *Codium vermilara*) over a 6 mo period. Macrophytes seemed to affect ingestion, absorption, total and gonadal growth rates. This effect was altered by changes in echinoid size and temperature during the length of the experiment. The highest ingestion, total growth and gonadal production were obtained with *R. verruculosa* whereas the lowest rates were obtained with *A. armata* and *D. spiralis*. There was no gonadal growth below a minimal ingestion rate of 3 g organic matter per 6 mo. Above this ingestion rate threshold, the allocation of energy between somatic and gonadal growth was not affected by the offered macrophyte. The highest absorption rates were recorded for *A. armata*. The lowest absorption rates were recorded for *C. elongata* and *S. scoparium*. Ingestion and absorption rates correlated negatively. Overall, individual growth rates positively correlated with rates of ingested organic matter, and even more so for the total time interval of the growth experiment, with absorbed organic matter. Individual monthly growth rates were better correlated with amounts of ingested organic matter than with ingested volume, wet weight, dry weight, or even energy, proteins and essential amino acids. Probably due to high individual variability, coefficients of determination were not significantly higher when using absorbed amounts of organic matter, dry weight, energy and proteins.

INTRODUCTION

The effect of food quality on ingestion and absorption rates of benthic primary consumers is still unclear. Optimal foraging theory postulates that ingestion rates should be positively correlated with food quality (Taghon 1981), but compensatory intake models predict a negative relationship between these 2 variables (Cammen 1980). Empirical testing of these 2 hypotheses is complicated by the difficulty in assessing food quality (Grémare et al. 1988). In fact, 'food quality'

effects often refer to differences in physiological responses (i.e. ingestion, absorption, reproduction or growth rates) of organisms fed on different food sources (Grémare et al. 1988). In practice, organic matter (Cammen 1980), carbon (Grémare et al. 1988), nitrogen (Tenore 1977, 1983, Tenore & Chesney 1985, Grémare et al. 1988), energy (Tenore 1977, 1983, Grémare et al. 1988), and protein (Taghon & Jumars 1984, Taghon & Greene 1990) have been used as indices of food quality. These facts, together with the inclusion of a maximum upper limit on growth or assimilation (Phillips 1984a), may account for the conflictive results concerning the response of deposit-feeders to variation in food concentrations (Cammen 1980, Taghon 1981).

Production of benthic primary consumers may be limited by the availability of macro- (carbon, nitrogen,

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proteins, energy) or micronutrients (amino acids, fatty acids, sterols, vitamins) (Phillips 1984b, Tenore 1988). Some 'essential' amino acids and fatty acids cannot be synthesised *de novo* by primary consumers. The availability of such essential micronutrients in diet may limit the production of benthic primary consumers and may thus constitute a better index of food quality than macronutrient availability. If a specific nutrient limits production, as limiting factor theory postulates, a large component of total variation explained by the linear relationship between food quantity and growth or reproduction rates should be contributed by the supposedly limiting substance. Therefore it may be possible to identify potential specific limiting factors by comparison of the correlation coefficients found in the relationship between production and the quantity of the nutrients supplied.

Previous studies have related components of the bioenergetics of benthic primary consumers (e.g. growth: Tenore 1983, Marsh et al. 1989; or reproduction: Grémare et al. 1988, Grémare et al. 1989a, b) with both quantity and the biochemical composition of the available food. To our knowledge these studies have only been carried out on infauna and there are no data available for grazers. For example, Marsh et al. (1989) compared the ability of macro- and micronutrients contents of different diets to describe growth rates of the deposit-feeding polychaete *Capitella capitata* (type 1). They recorded the best description of growth rates as a function of rations of 2 essential amino acids, histidine and phenylalanine. However, their experiment was not designed to measure ingestion nor absorption. Thus, these data are limited to one factor of the multiple bioenergetics parameters (i.e. ingestion, absorption, etc.), namely food available. Therefore, it still seems useful to collect such data for other benthic primary consumers for a variety of food sources.

Herbivorous echinoids such as *Paracentrotus lividus* Lamarck constitute a good biological model for this kind of study. These echinoids feed preferentially on live macrophytes. Their nutritional ecology has been extensively studied, especially in terms of food preferences (Lawrence 1975, Vadas 1977, Steinberg 1988), feeding (Lawrence 1975, Larson et al. 1980), absorption (Lawrence 1975, Lowe & Lawrence 1976, Vadas 1977), and assimilation rates (Lawrence 1975, Vadas 1977, Larson et al. 1980). In spite of these important efforts, no simultaneous measurements of ingestion, absorption and growth rates of herbivorous echinoids fed a large variety of macrophytes have been made. The objectives of the present study were thus to measure ingestion, absorption, and growth rates of *P. lividus* fed on different benthic macrophytes, and to relate these indices to food biochemical composition, specifi-

cally some macro- and micronutrients (i.e. essential amino acids).

MATERIALS AND METHODS

Macrophytes. Twelve benthic macrophytes were used: Rhodophyta: *Rissoella verruculosa* (Bertoloni) J. Agardh, *Corallina elongata* Ellis & Solander and *Asparagopsis armata* Harvey; Chromophyta: *Cystoseira mediterranea* Sauvageau, *Stypocaulon scoparium* (Linnaeus) Kützinger, *Padina pavonica* (Linnaeus) Thivy, *Cystoseira compressa* (Esper) Gerloff & Nizamuddin, *Colpomenia sinuosa* (Mertens) Derbes & Solier, and *Dilophus spiralis* (Montagne) Hamel; Chlorophyta: *Ulva rigida* C. Agardh, *Posidonia oceanica* (Linnaeus) Delile (Spermatophyta) and *Codium vermilara* (Olivier) Delle Chiaje. These species are among the dominant macrophytes in the upper sublittoral zone of the western Mediterranean Sea. All macrophytes were collected from rocky substrata in the shallow waters (0 to 2 m depth) of the Bay of Banyuls (north-west Mediterranean Sea) between February and August 1990.

Characteristics of macrophytes. The biomass was always measured on a wet weight (WW) basis. Ingestion and absorption rates were then converted, using appropriate conversion factors, into volume, dry weight (DW), organic matter (OM), energy (caloric content), protein, specific amino acids, and carbohydrate.

Volumes were measured by recording (to the nearest 0.1 cm³) a displacement of seawater. Dry weights were measured (to the nearest 1 mg) after spin-drying (600 × *g* for 1 min), freezing, and freeze drying. Organic content was determined by ashing in a muffle furnace for 3.5 h at 500 °C. Caloric contents were measured using a Phillipson microcalorimeter. Proteins were measured using the Lowry procedure as modified by Hartree (1972). Carbohydrates were analyzed using the Dubois procedure (Dubois et al. 1956). Amino acids were analyzed with high performance liquid chromatography of precolumn derivatives after Lindroth & Mopper (1979). Phenolics were analyzed using the Folin-Denis technique (Singleton & Rossi 1966).

Echinoids. We used only small echinoids to facilitate measuring significant growth. Small (14.0 to 16.4 mm test diameter, 1.23 to 2.47 g WW) *Paracentrotus lividus* were collected in February 1990 from the same location as the macrophytes, and held in the laboratory in ambient running seawater.

Experimental design. Echinoids were reared in twelve 14 l plastic tanks filled with running ambient seawater. Each tank was divided into 10 equal compartments using plastic grid (mesh size of 1 cm²). One

individual was placed randomly in each of these 120 compartments.

Each echinoid was fed for 6 mo (from 15 February to 15 August 1990), with each tank receiving 1 of the 12 macrophytes. The main weakness of this experimental design is due to the possible existence of tank effects. Since the treatments are not distributed randomly among tanks, tank and treatment effects may be indistinguishable. This design has been nevertheless retained because it is known that, in echinoids, feeding rates may be significantly affected by dissolved substances produced by benthic macrophytes (Lawrence 1975, Vadas 1977). This important effect would have been ignored by mixing several macrophytes in the same tank. On the other hand, it was impossible to measure absorption in 120 tanks. Care was taken to reduce any potential tank effect. The tanks were all identical (design, material and date of construction), and they were submitted to the same conditions in terms of illumination and water flow (60 l h^{-1}). Moreover, growth rates of *Paracentrotus lividus* are significantly correlated with those of *Abra ovata* fed on the same macrophytes ($n = 12$, $r = 0.706$, $0.01 < p < 0.05$) (Frantzis & Grémare unpubl.), thereby suggesting that if ever present, tank effects are rather limited.

Care was taken to remove epiphytes off the food ration. Only the non-epiphyted green and clean parts of the leaves of *Posidonia oceanica* were offered to echinoids. Food was replaced every 4 to 5 d by newly collected macrophytes and was never limiting. The tanks were cleaned 3 times per month.

The water temperature was recorded daily and varied from 12.3 to 23.5 °C during the 6 mo of the experiment.

Ingestion rates. Ingestion rates of *Paracentrotus lividus* fed unlimited rations of the 12 macrophytes were recorded monthly. For each macrophyte, a given biomass was presented separately to each individual. The offered biomass (ration) ranged between 1 and 5 g WW due to increasing ingestion rates over the 6 mo of the experiment. Ration was equal for all individuals of the same tank. It was at least 1.5 times greater than the ingested biomass. Food remaining after 3 d was weighed and the ingested biomass was calculated by subtraction. Biomasses were measured to the nearest 0.01 g WW after 1 min centrifugation ($600 \times g$) (10 replicates of 5 g WW of *Cystoseira mediterranea* and 5 g WW of *Stypocaulon scoparium* using this method resulted in a coefficient of variation of 1.0 and 0.9 % respectively). For each macrophyte, 10 controls were run to correct for change in macrophyte biomass in the absence of echinoids. Within such controls, biomass changes ranged between -3.1 and +2.3 % of the initial biomass per day (for *Padina pavonica* and *S. scoparium* respectively). Ingestion rates were expressed in terms

of volume, wet and dry weight, organic matter, caloric content, protein, and carbohydrate using the conversion factors presented above.

Absorption rates. Absorption rate, the percentage of ingested material moving across the intestinal wall (Lawrence 1975), was calculated using the following equation:

$$\frac{100 \times (\text{Ingested material} - \text{Egested material})}{\text{Ingested material}} \quad (1)$$

Absorption rates were expressed in terms of dry weight, organic matter, protein, carbohydrate, and caloric content. Average absorption rates of the 10 individuals fed a given macrophyte were measured during the second, fourth, and sixth month of the experiment, 3 d after ingestion measurements and during a 3 d period. Fecal pellets produced during this period by all the echinoids in each tank were collected daily. Fecal pellets were separated from macrophytic fragments, drained several times between 2 filter papers, freeze dried, and then weighed to the nearest 0.1 mg DW. Fecal pellets were analysed for organic matter, protein, and carbohydrate using the procedure described for analysis of macrophytes.

Growth. Growth rates were recorded monthly using total wet weight. For measuring wet weight, individuals were drained on a towel for 5 min before being weighed to the nearest 0.01 g. Ten replicates of 2 individuals (1.55 and 4.43 g WW respectively) resulted in a coefficient of variation of 1.3 and 1.4 % respectively.

The total and gonadal wet weights of 30 individuals, collected simultaneously and having the same size as those used during the experiment were measured at the beginning of the experiment. Their mean gonadal wet weight was subtracted from that at the end of the experiment to measure gonadal growth. Gonadal wet weights were determined to the nearest 0.1 mg after dissection and air drying (on a filter paper for 3 min). Gonad index was computed as the ratio of gonadal to total wet weight. Whenever possible, individuals were sexed by microscopic examination of a small portion of the gonads.

Statistics. The relationships between ingestion, absorption, and growth rates recorded during the first month of the experiment and the main characteristics (i.e. water contents, % organic matter, caloric contents, protein concentrations, carbohydrate concentrations, essential amino acid concentration, non-essential amino acid concentrations, and phenolic contents) of the 12 tested detritus were assessed using a principal component analysis (Himmelman & Nedelec 1990). All of these variables were expressed in (or converted to) dry weight, except water contents which were converted to wet weight.

RESULTS

Composition of macrophytes

The average water contents, % organic matter, caloric contents, protein concentrations, carbohydrate concentrations, and phenolic contents of the macrophytes are presented in Table 1.

Water content ranged from 27.0 (*Corallina elongata*) to 92.0 % (*Colpomenia sinuosa*). Percentage organic matter (i.e. weight of organic matter per 100 g DW) ranged from 21.5 (*C. elongata*) to 78.7 % (*Rissoella verruculosa*). Caloric contents ranged from 2.3 (*C. elongata*) to 14.8 J mg⁻¹ DW (*Posidonia oceanica*, May). Protein concentrations ranged from 4.6 (*C. elongata*) to 20.6 g protein per 100 g DW (*Cystoseira compressa*). Carbohydrate concentrations ranged from 5.1 (*C. elongata*) to 41.7 g carbohydrate per 100 g DW (*Rissoella verruculosa*, July). Large differences among macrophytes were evident in the amino acid profiles (Fig. 1). *Asparagopsis armata* and *Padina pavonica* had the highest and lowest levels of both essential and non-essential amino acids, respectively. There was a strong correlation between the levels of essential and non-essential amino acids recorded for each macrophyte ($n = 12$, $r = 0.91$, $p < 0.001$). Phenolic contents ranged from 0.6 (*A. armata*) to 53.0 mg Tannic acid equivalent g⁻¹ OM (*C. compressa*).

Ingestion

Average ingestion rates are presented in Fig. 2 in terms of volume, wet weight, dry weight, organic matter, energy, and protein. Coefficients of variation of ingestion rates (not shown in Fig. 2) ranged between 20 and 40 %. In terms of volume and wet weight, and

for each month, the highest ingestion rates were recorded for *Colpomenia sinuosa*. The lowest ingestion rates (depending on the month of measurement) were recorded either for *Asparagopsis armata*, *Dilophus spiralis* or *Posidonia oceanica*. In terms of dry weight, the highest ingestion rate (438.0 mg DW d⁻¹) occurred with *Corallina elongata* during the last month of the experiment. The lowest ingestion rates (depending on the month of measurement) were recorded either for *A. armata* or *D. spiralis*. In terms of organic matter and energy, the highest ingestion rates (102.4 mg OM d⁻¹ and 1544 J d⁻¹) occurred during the last month of the experiment for *C. elongata* and *Rissoella verruculosa*, respectively. In both cases, the lowest ingestion rates were recorded for *Codium vermilara* and *A. armata*. In terms of protein, the highest ingestion rate (20.6 mg Prot d⁻¹) occurred with *C. elongata* during the last month of the experiment. The lowest ingestion rates (depending on the month of the experiment) were recorded either for *A. armata* or *C. vermilara*.

Average ingestion rates increased with time. However, as this increase is positively correlated with initial (i.e. recorded during the first month of the experiment) ingestion rates, differences in ingestion rates of poorly and highly consumed macrophytes increased with time.

When pooling data for all macrophytes, and regardless of the index of ingested biomass, ingestion rates were significantly correlated with individuals wet weight. The lowest correlation coefficient ($n = 720$, $r = 0.41$, $p < 0.001$) was obtained for ingested volume, whereas the highest correlation coefficient ($n = 720$, $r = 0.80$, $p < 0.001$) was obtained when using ingested organic matter as the index of the ingested biomass. When used as a second variable in a multiple linear regression model, temperature did not significantly increase the values of these coefficients ($r = 0.47$ and

Table 1. Principal characteristics (mean and SE) of 12 tested macrophytes. Water content: % H₂O per wet weight; organic matter: % OM per dry weight; caloric content: J per mg dry weight; proteins: % prot. per dry weight; carbohydrates: % carb. per dry weight; phenolics: mg tannic acid equivalent per g organic matter

Macrophyte	Water content (n = 15)	Organic matter (n = 9)	Energy content (n = 9)	Proteins (n = 6)	Carbohydrates (n = 6)	Phenolics (n = 2)
<i>Rissoella verruculosa</i>	70.9 (1.4)	78.7 (1.3)	13.7 (0.5)	12.4 (2.6)	41.7 (9.6)	9.8 (0.2)
<i>Cystoseira mediterranea</i>	79.3 (1.4)	70.2 (1.3)	12.5 (0.5)	18.6 (2.0)	20.2 (1.2)	18.2 (0.4)
<i>Corallina elongata</i>	27.0 (2.3)	21.5 (1.9)	2.3 (0.4)	4.6 (0.4)	5.1 (0.8)	2.4 (1.7)
<i>Stypocaulon scoparium</i>	67.0 (3.7)	69.3 (3.1)	11.7 (1.0)	16.3 (3.3)	22.7 (3.3)	3.0 (0.1)
<i>Padina pavonica</i>	78.7 (1.3)	48.7 (5.4)	5.6 (1.4)	12.3 (5.4)	11.7 (1.6)	4.9 (0.4)
<i>Ulva rigida</i>	78.7 (0.9)	68.5 (2.2)	10.2 (0.6)	6.5 (3.8)	37.0 (6.3)	1.0 (0.1)
<i>Cystoseira compressa</i>	82.9 (1.4)	65.1 (0.8)	10.3 (0.5)	20.8 (1.8)	15.2 (1.4)	53.0 (0.1)
<i>Colpomenia sinuosa</i>	92.0 (1.1)	36.6 (5.6)	6.7 (0.8)	13.3 (1.4)	13.7 (2.2)	9.2 (0.1)
<i>Posidonia oceanica</i>	76.4 (3.2)	78.4 (3.2)	14.8 (0.6)	12.4 (2.6)	33.6 (7.2)	24.0 (3.1)
<i>Codium vermilara</i>	91.9 (0.5)	50.5 (2.6)	9.0 (0.6)	9.6 (1.9)	27.7 (1.2)	1.1 (0.0)
<i>Asparagopsis armata</i>	84.2 (1.8)	66.7 (3.2)	10.7 (0.5)	14.3 (2.5)	30.2 (5.4)	0.6 (0.1)
<i>Dilophus spiralis</i>	81.0 (1.1)	70.3 (4.7)	14.3 (0.8)	19.0 (2.7)	16.6 (4.2)	3.4 (0.1)

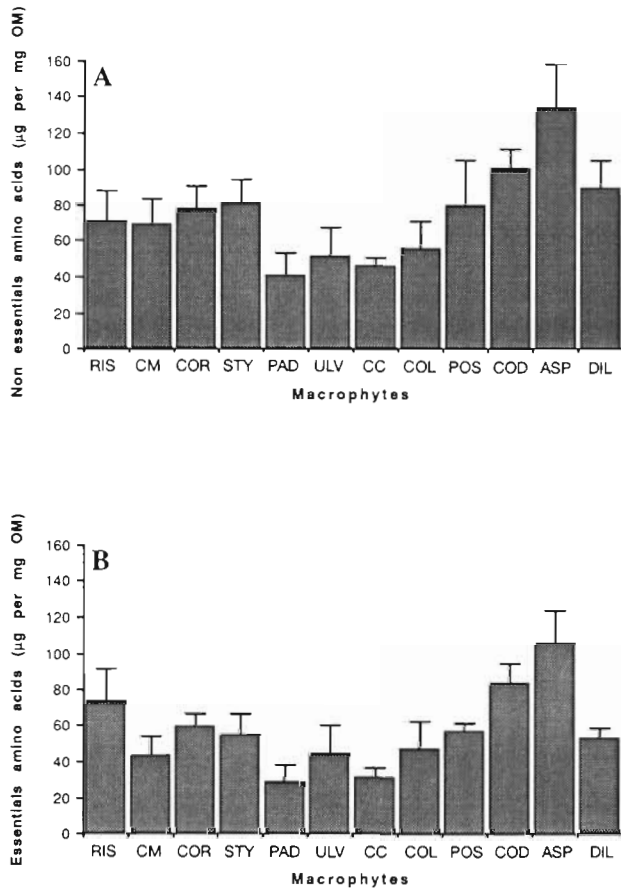


Fig. 1. Profile of total (A) non-essential and (B) essential amino acid levels in each macrophyte. For non-essential amino acids, each bar represents the sum of: asparagine, glutamine, aspartic acid, glutamic acid, serine, glycine, tyrosine and alanine. For essential amino acids, each bar represents the sum of: histidine, threonine, arginine, methionine, valine, phenylalanine, isoleucine, leucine, and lysine. ASP: *Asparagopsis armata*; CC: *Cystoseira compressa*; CM: *Cystoseira mediterranea*; COD: *Codium vermilare*; COL: *Colpomenia sinuosa*; COR: *Corallina elongata*; DIL: *Dilophus spiralis*; PAD: *Padina pavonica*; POS: *Posidonia oceanica*; RIS: *Rissoella verruculosa*; STY: *Stypocaulon scoparium*; ULV: *Ulva rigida*

$r = 0.80$ for ingested volume and ingested organic matter respectively).

Because of this size effect, we compared ingestion rates recorded during the first month of the experiment in order to further assess the effect of macrophyte on ingestion rates. In fact, after 15 d, there was no significant difference among average wet weights of individuals fed different macrophytes (1-way ANOVA, $p = 0.37$). For all the 6 indices of ingestion, there seemed to be significant differences in ingestion due to macrophyte type. However, rankings of macrophytes were highly dependent on the specific index of ingestion. In terms of volume and wet weight, *Colpomenia sinuosa* was ingested most. In terms of dry weight,

Corallina elongata was ingested most. In terms of organic matter, *Rissoella verruculosa*, *Cystoseira mediterranea*, *C. elongata*, and *Stypocaulon scoparium* were the most ingested macrophytes. In terms of energy, *R. verruculosa*, *C. mediterranea* and *S. scoparium* were ingested most. In terms of protein, *C. elongata*, *S. scoparium* and *Padina pavonica* were ingested most.

There was no significant correlation between the concentration of total phenolics and average ingestion rates recorded during the first month of the experiment ($n = 12$, $r = -0.22$, $0.2 < p < 0.5$). There was a significant correlation between organic matter contents and average ingestion rates ($n = 12$, $r = -0.61$, $0.02 < p < 0.05$).

Absorption

Absorption rates recorded during the experiment are presented in Fig. 3. Absorption rates were computed in terms of dry weight, organic matter, protein, and carbohydrate. Absorption rates of carbohydrate were significantly correlated with absorption rates in terms of dry weight and organic matter ($n = 36$, $r = 0.91$ and $r = 0.86$, $p < 0.001$ in both cases). Absorption rates of proteins and carbohydrates were also significantly correlated ($n = 36$, $r = 0.74$, $p < 0.001$).

Temporal changes in absorption rates seemed relatively high at least for some macrophytes. However, among macrophytes, these temporal changes did not follow a similar pattern. Such an absence of trend may be partly due to high individual variability (Lawrence 1975).

There were considerable differences in absorption rates among macrophytes for simultaneous measurements. In terms of organic matter for example, the absorption rate recorded during the second month of the experiment was 2.4 times greater for *Asparagopsis armata* (92 %) than for *Stypocaulon scoparium* (38 %). Similar patterns were found when using dry weight, protein and carbohydrate as the index of absorption.

In terms of organic matter, absorption rate was negatively correlated with ingestion rate ($n = 36$, $r = -0.44$, $0.01 < p < 0.05$) (Fig. 4). Similar results were obtained when considering ingestion rates and absorption rates in terms of dry weight and proteins ($0.001 < p < 0.002$ and $0.02 < p < 0.05$ respectively). The correlation between ingestion rate and absorption rate was not significant in the case of carbohydrate ($0.05 < p < 0.10$).

Growth

Initial average wet weight of the 12 groups of individuals used during this experiment was of $1.87 \pm$

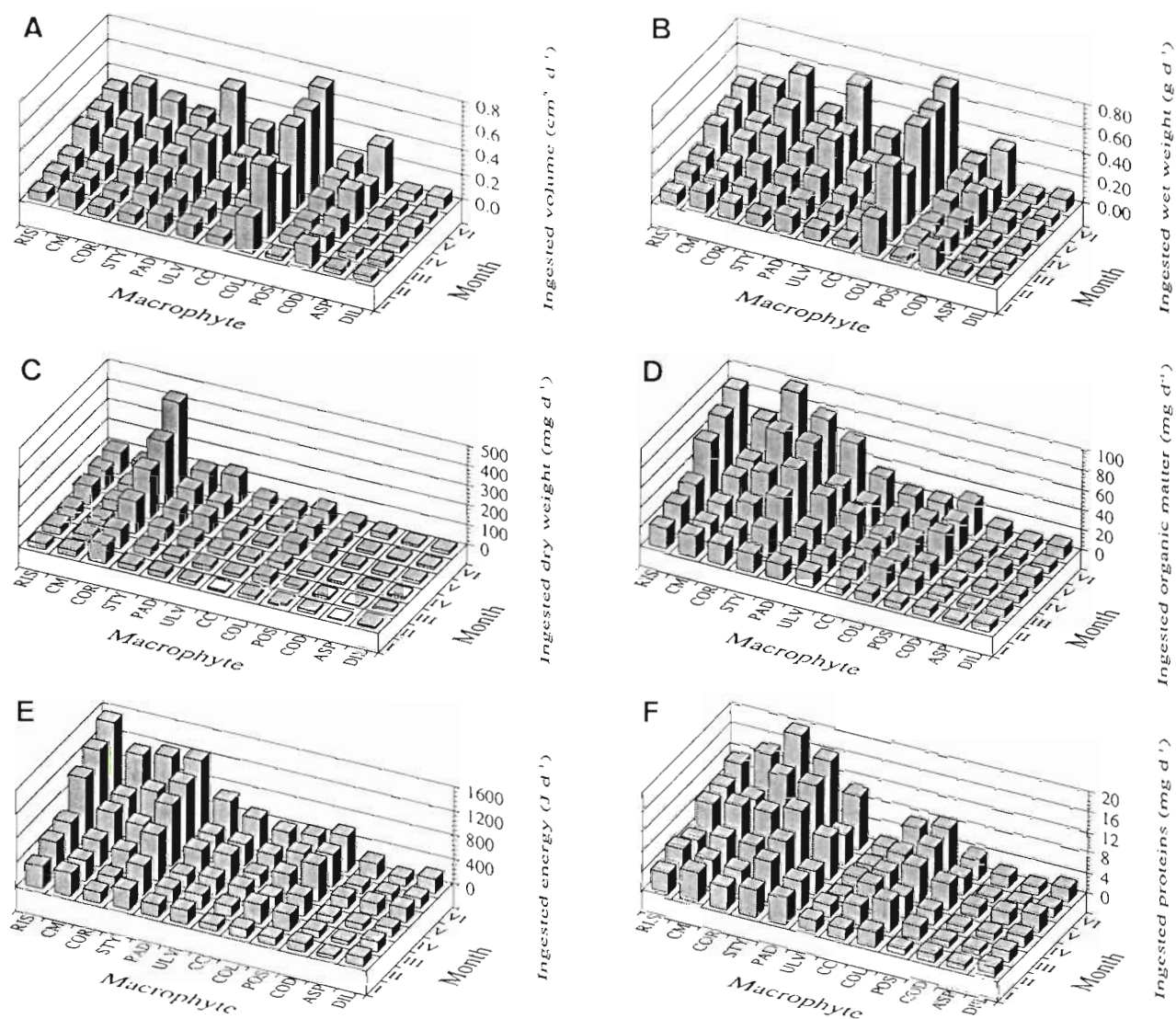


Fig. 2. *Paracentrotus lividus*. Average ingestion rates by for the 12 macrophytes tested. Ingestion rates are expressed in terms of (A) volume, (B) wet weight, (C) dry weight, (D) organic matter, (E) energy, and (F) protein. Species as in Fig. 1

0.04 g WW (95 % confidence limit interval). Cumulated growth rates are presented in Fig. 5A. At the end of the experiment, the highest average wet weight (9.52 g) was recorded for *Rissoella verruculosa*, whereas the lowest average wet weight was recorded for *Dilophus spiralis* (2.35 g).

Average growth rates recorded between 2 successive measurements are presented in Fig. 5B. The highest average growth rate (1.69 g WW mo^{-1}) was recorded for *Rissoella verruculosa* during the fourth and fifth month, whereas the lowest average growth rate was negative (-0.15 g WW mo^{-1}) and recorded for *Posidonia oceanica* during the first month. For all macrophytes, growth rates recorded during the first month of the experiment were lower than almost all those

recorded during the remainder of the experiment. This may be due partly to the adjustment to experimental conditions (including food regime). Results of the 2-way ANOVA assessing the effect of time and macrophyte were not affected when discarding the data corresponding to the first month of the experiment.

Average specific growth rates recorded between 2 successive measurements are presented in Fig. 5C. The highest average specific growth rate (0.44 g WW g^{-1} echinoid WW mo^{-1}) was recorded for *Cystoseira mediterranea* during the second month, whereas the lowest average specific growth rate was negative (-0.10 g WW g^{-1} echinoid WW mo^{-1}) and recorded for *Posidonia oceanica* during the first month. Here again,

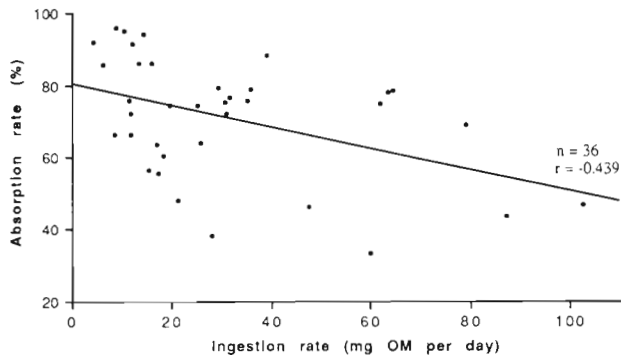


Fig. 3. *Paracentrotus lividus*. Relationship between average ingestion rates and absorption rates. Ingestion and absorption rates are both expressed in terms of organic matter. Data are pooled for all tested macrophytes

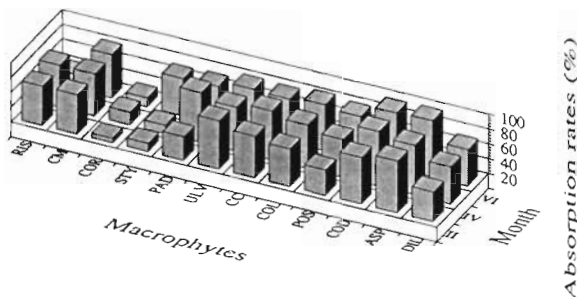
average specific growth rates recorded during the first month were significantly lower than those recorded during the second month of the experiment. For most of the macrophytes, average specific growth rates decreased between the second and the sixth month of the experiment.

When pooling results corresponding to all macrophytes, there was a significant correlation ($r = 0.84$, $n = 120$, $p < 0.0001$) between the amount of ingested organic matter and individual growth rates recorded between the beginning and the end of the experiment (Fig. 6A). This correlation was even better ($r = 0.89$,

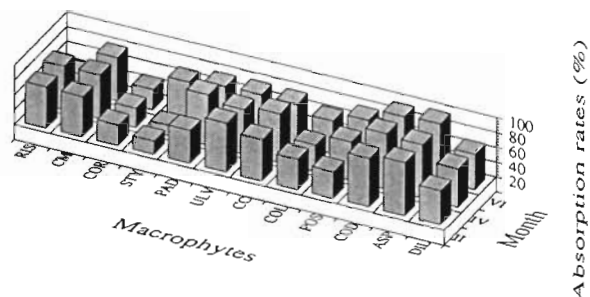
$n = 120$, $p < 0.0001$) when considering the amount of absorbed organic matter instead of amount of ingested matter as the independent variable of the regression model (Fig. 6B).

Since temperature and size of test organisms changed with time in the course of the experiment, monthly growth rates taken in February are under different constraints (i.e. small size and low temperature) than those taken in August (various sizes and high temperature). To account for such confounding effects, we *a posteriori* decided to split our data set in 6 sub-groups based on temperature (i.e. $< 16^\circ\text{C}$ and $> 16^\circ\text{C}$) and individual size (i.e. small < 5.40 g WW; 5.40 g WW $<$ medium < 9.65 g WW; and 9.65 g WW $<$ large) (Tenore & Chesney 1985). In practice, this process resulted in the identification of 4 groups since no large individuals and only 2 medium individuals were present at low (i.e. $< 16^\circ\text{C}$) temperature. In small echinoids, description of growth rates by the ingested or absorbed amounts of food was assessed using simple linear regression models (Grémare et al. 1988). Relationships between the amounts of ingested organic matter and individual monthly growth rates are presented in Fig. 6. The analysis of these relationships confirms the effect of temperature. In fact, the slope of the regression is significantly higher for low temperature (i.e. $< 16^\circ\text{C}$, slope = 0.90 ± 0.24 , 95 % confidence limit interval) than for high temperature (i.e. $> 16^\circ\text{C}$, slope = 0.58 ± 0.08 , 95 % confidence limit

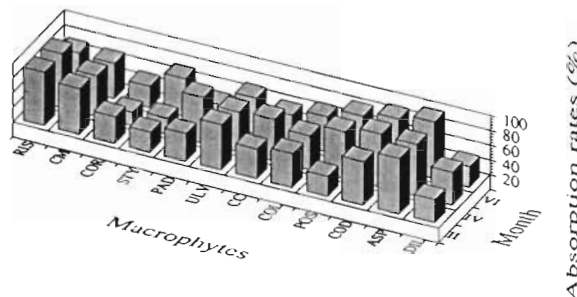
DRY WEIGHT



ORGANIC MATTER



PROTEINS



CARBOHYDRATES

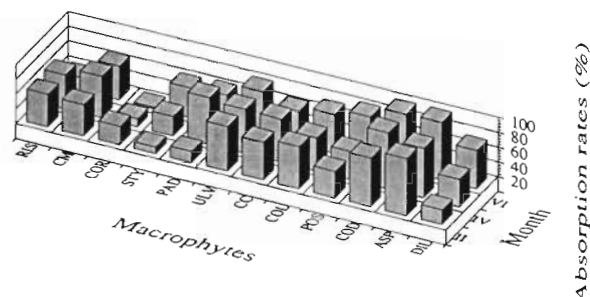


Fig. 4. *Paracentrotus lividus*. Absorption rates (%) recorded for the 12 tested macrophytes. Absorption rates are expressed in terms of dry weight, organic matter, protein and carbohydrate. Species as in Fig. 1

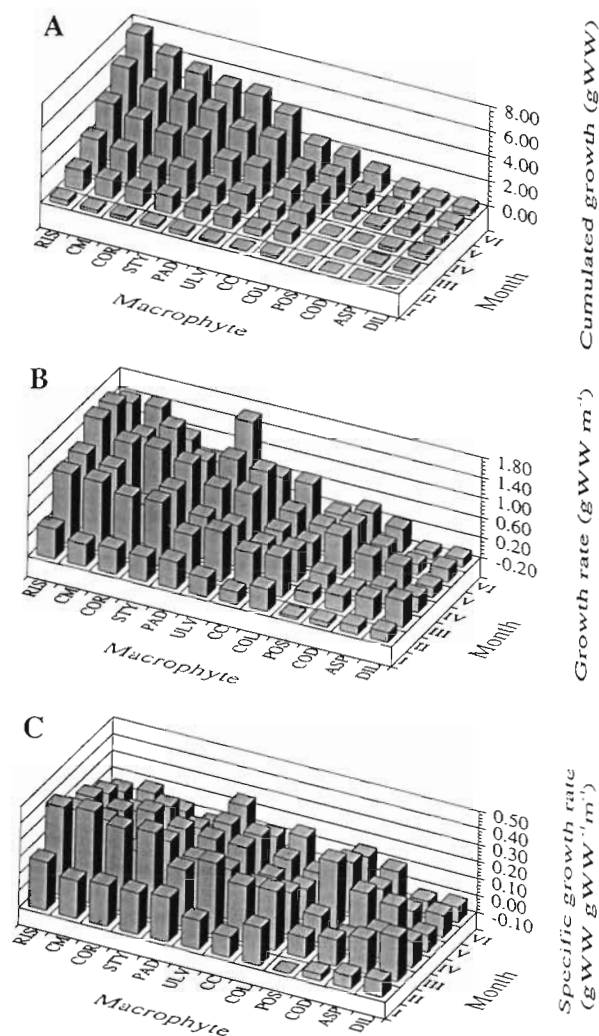


Fig. 5. *Paracentrotus lividus*. (A) Cumulated growth rates, (B) average growth rates, and (C) average specific growth rates recorded for 12 tested macrophytes. Species as in Fig. 1

interval), reflecting the increase in metabolism due to temperature rise.

At either low or high temperature, individual monthly growth rates were better described when using total amounts of ingested organic matter rather than ingested volume, wet weight, dry weight, or even energy, proteins, and essential amino acids (Table 2). The description of individual monthly growth rates was not improved when using ingested amounts of essential amino acids or absorbed amounts of organic matter, dry weight, and proteins.

Gonadal growth

Average gonadal wet weights (Fig. 8A) recorded for the 12 macrophytes at the end of the experiment

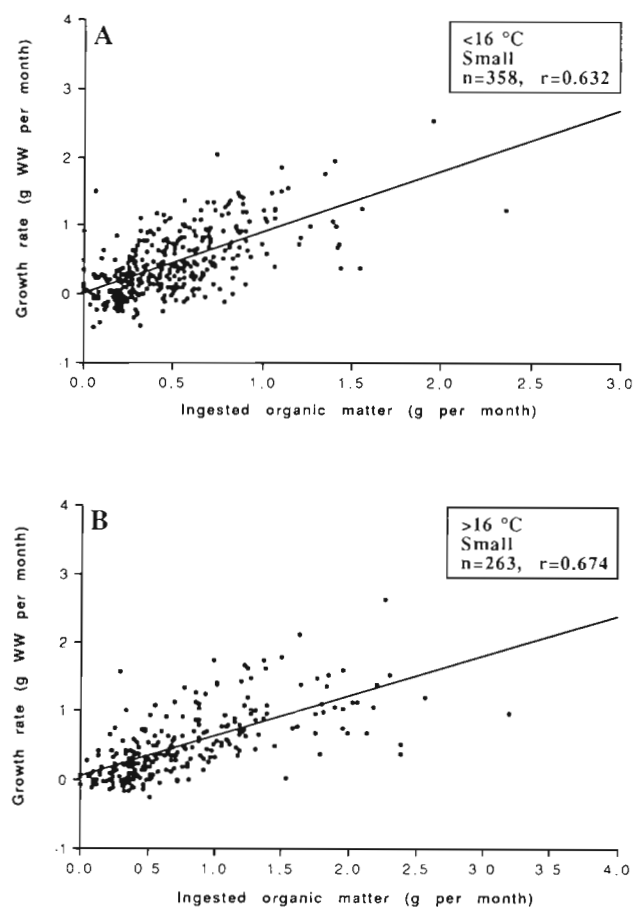


Fig. 6. *Paracentrotus lividus*. Relationship between cumulated growth and the amount of (A) ingested and (B) absorbed organic matter during the whole experiment. Data are pooled for all tested macrophytes

seemed to be significantly affected by the offered macrophyte. The highest average gonadal wet weight (0.553 g) was recorded for *Rissoella verruculosa* whereas the lowest average gonadal wet weight (0.001 g) was recorded for *Asparagopsis armata* and *Dilophus spiralis*. The corresponding gonad indices are presented in Fig. 8B. Here again, the highest gonad index was observed for *R. verruculosa* (60.2) whereas the lowest gonadal index (0.5) was observed for *A. armata*. The relationship between gonadal growth and ingestion of organic matter is presented in Fig. 9. Below a threshold value of ingestion (3 g OM per 6 mo⁻¹), gonadal growth was not significantly different from 0. Above this threshold, the relationship between gonadal growth and ingested organic matter was well described when using a log-log regression model ($n = 74$, $r = 0.84$, $p < 0.001$). The same pattern was found when assessing the relationship between the amount of absorbed organic matter and gonadal growth ($n = 74$, $r = 0.81$, $p < 0.001$).

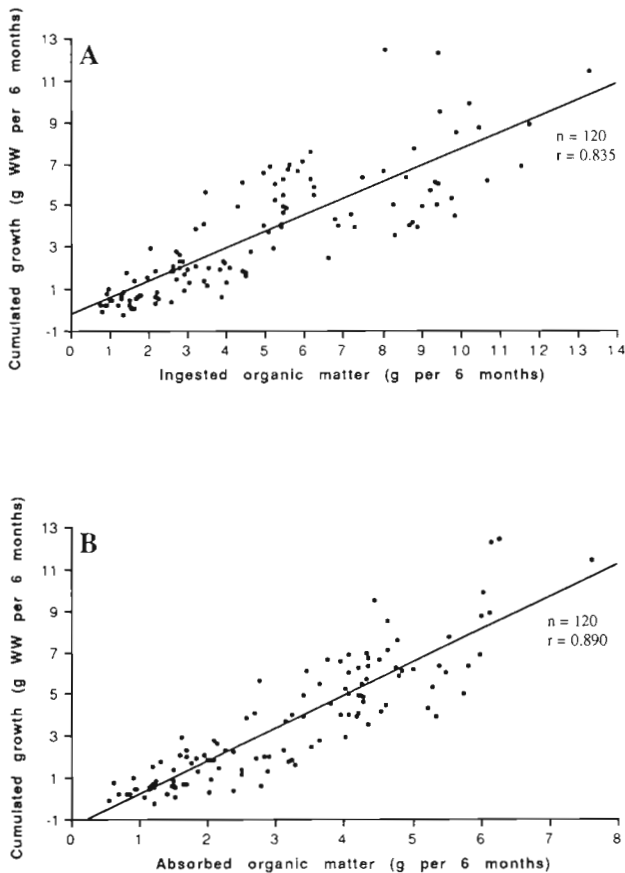


Fig. 7. *Paracentrotus lividus*. Relationships between individual monthly growth rates and amounts of ingested organic matter. (A) Small individuals, temperature $< 16^{\circ}\text{C}$. (B) Small individuals, temperature $> 16^{\circ}\text{C}$.

Principal component analysis

The results of the principal component analysis are presented in Fig. 10. The first 3 axes accounted respectively for 45.2, 19.7 and 15.6 % of the total variance. These axes accounted for 82.0, 78.2 and 39.2 % of the variances of ingestion, absorption and growth rates respectively.

The first axis was mainly defined by the concentrations of essential and non-essential amino acids, % organic matter, carbohydrate concentrations and caloric contents. The 2 macrophytes which were best described by this axis are *Corallina elongata* and *Padina pavonica* (which are characterized by a low % of organic matter). This axis accounted for only 7.1, 33.0 and 28.6 % of the variances of ingestion, absorption and growth rates respectively.

The second axis was mainly defined by water and phenolic contents. It only accounted for 29.1, 16.9 and 9.6 % of the variances of ingestion, absorption, and growth rates respectively.

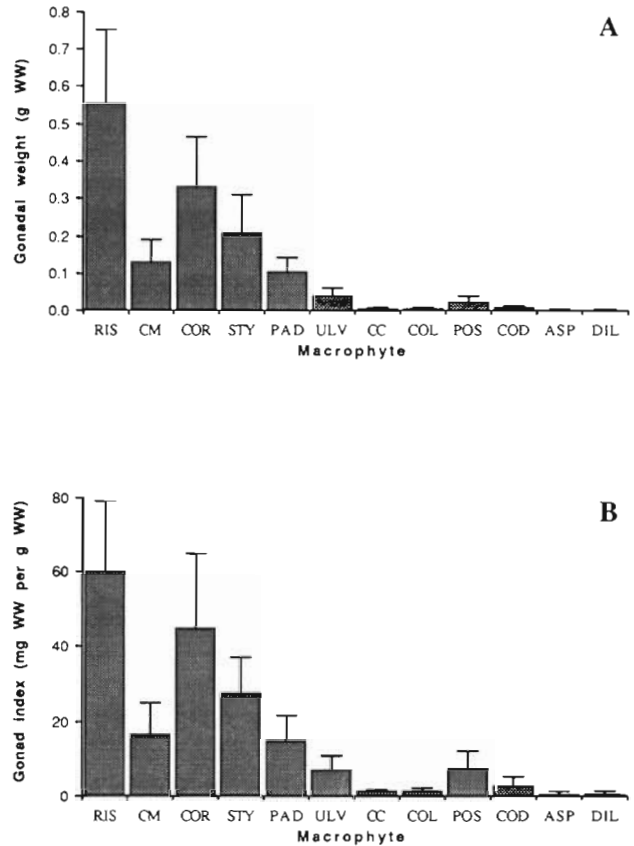


Fig. 8. *Paracentrotus lividus*. (A) Average gonadal wet weight and (B) average gonad index recorded at the end of the experiment for 12 tested macrophytes. Species as in Fig. 1.

The third axis was mainly defined by protein concentrations, phenolic contents, ingestion, and absorption rates. It accounted for 45.7, 28.3 and 1.0 % of ingestion, absorption, and growth rates respectively. This axis suggested a negative effect of protein concentrations and phenolic contents on ingestion rates.

DISCUSSION

Ingestion

Feeding rates recorded during the present study are significantly correlated (Spearman rank correlation coefficient = 0.79, $0.02 < p < 0.05$) with the food preferences of *Paracentrotus lividus* for 7 (*Cystoseira mediterranea*, *Stypocaulon scoparium*, *Dilophus spiralis*, *Ulva rigida*, *Corallina elongata*, *Posidonia oceanica*, *Asparagopsis armata*) of the 12 tested macrophytes (Rico 1989). Such correlations are frequent in echinoids (Vadas 1977, Larson et al. 1980) suggesting, together with other evidences already presented in the 'Materials and methods' that tank effects were rather limited during the present experiment.

Table 2. Correlation coefficients between ingested biomass and monthly growth rate. Data are pooled for all tested macrophytes

Descriptor of growth	Correlation coefficient	
	< 16°C (n = 358)	> 16°C (n = 264)
Ingested volume	0.197	0.122
Ingested wet weight	0.243	0.182
Ingested dry weight	0.356	0.495
Ingested organic matter	0.639	0.674
Ingested energy	0.623	0.608
Ingested proteins	0.601	0.525
Ingested carbohydrates	0.571	0.551
Ingested histidine	0.524	0.519
Ingested threonine	0.553	0.553
Ingested arginine	0.491	0.541
Ingested methionine	0.587	0.495
Ingested valine	0.552	0.574
Ingested phenylalanine	0.550	0.552
Ingested isoleucine	0.550	0.555
Ingested leucine	0.552	0.567
Ingested lysine	0.512	0.579
Absorbed dry weight	0.445	0.530
Absorbed organic matter	0.607	0.635
Absorbed proteins	0.628	0.489
Absorbed carbohydrates	0.498	0.436

Our results suggested the existence of significant differences among feeding rates recorded for *Paracentrotus lividus* fed different macrophytes. This observation is consistent with what has been reported for other echinoids such as *Strongylocentrotus droebachiensis* (Himmelman & Nedelec 1990), *S. franciscanus* (Vadas 1977), *S. purpuratus* (Vadas 1977), *Lytechinus variegatus* (Klinger & Lawrence 1985), and *Parechinus angulosus* (Anderson & Velimirov 1982). These differences may result from the characteristics of the consumed macrophytes.

Our results showed a lower correlation coefficient between echinoid wet weight and ingested volume than between echinoid wet weight and ingested

organic matter. In echinoids, the amount of water in the gut varies inversely with the amount of pellets (Buchanan 1969). Water circulation through the gut seems primarily related to the maintenance of a constant gut volume (Buchanan 1969). Echinoid maximal ingestion rates may thus be limited by physical constraints (i.e. gut section). In this case, and because of the existence of an allometric relationship between total wet weight and gut section, the correlation coefficients between total wet weights and feeding rates recorded for different foods should be maximal when feeding rates are expressed in terms of ingested volumes (i.e. the potential limiting factor of ingestion). This was not the case during the present study. Therefore, it seems that differences among ingestion rates of *Paracentrotus lividus* fed different macrophytes did not result from physical constraints acting on the gut. This result supports the fact that feeding rates of continuously feeding echinoids are not maximal (Bonsdorff 1983, but see Klinger &

Lawrence 1985). However, it should be pointed out that the points which are characterized by a high ingested volume relative to echinoid wet weight mostly correspond to echinoids fed on *Colpomenia sinuosa*. This macrophyte is characterized by a high water content which is likely to be affected (i.e. diminished) by dilaceration during ingestion by echinoids. Since computation of ingested volumes were based on measurements carried out on non-ingested macrophytes, potential differences in compaction among macrophytes were not taken into account, and may thus contribute to explain the low correlation coefficient between echinoid wet weight and ingested volume.

Our data suggest a negative relationship between macrophyte organic contents and echinoid feeding rates. This result is confirmed by the opposition between ingestion rates and protein concentrations found on the third axis of the principal component analysis. However, it should be pointed out that a linear regression model linking these 2 variables accounts for only 38 % of the variance of feeding rates, thereby suggesting that organic content is not the only factor involved in controlling echinoid feeding rates. Nevertheless, this result is interesting since Cammen (1980) reported a similar correlation between ingestion rate by deposit-feeding invertebrates and the organic contents of their foods. This negative relationship is probably due to the fact that food was available in excess during the present experiment. In fact Phillips (1984a) showed that the incorporation of an upper limit

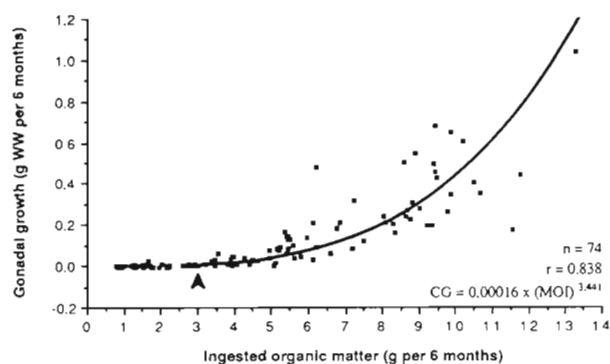


Fig. 9. *Paracentrotus lividus*. Relationship between total amount of ingested organic matter and total gonadal growth. Data are pooled for all tested macrophytes

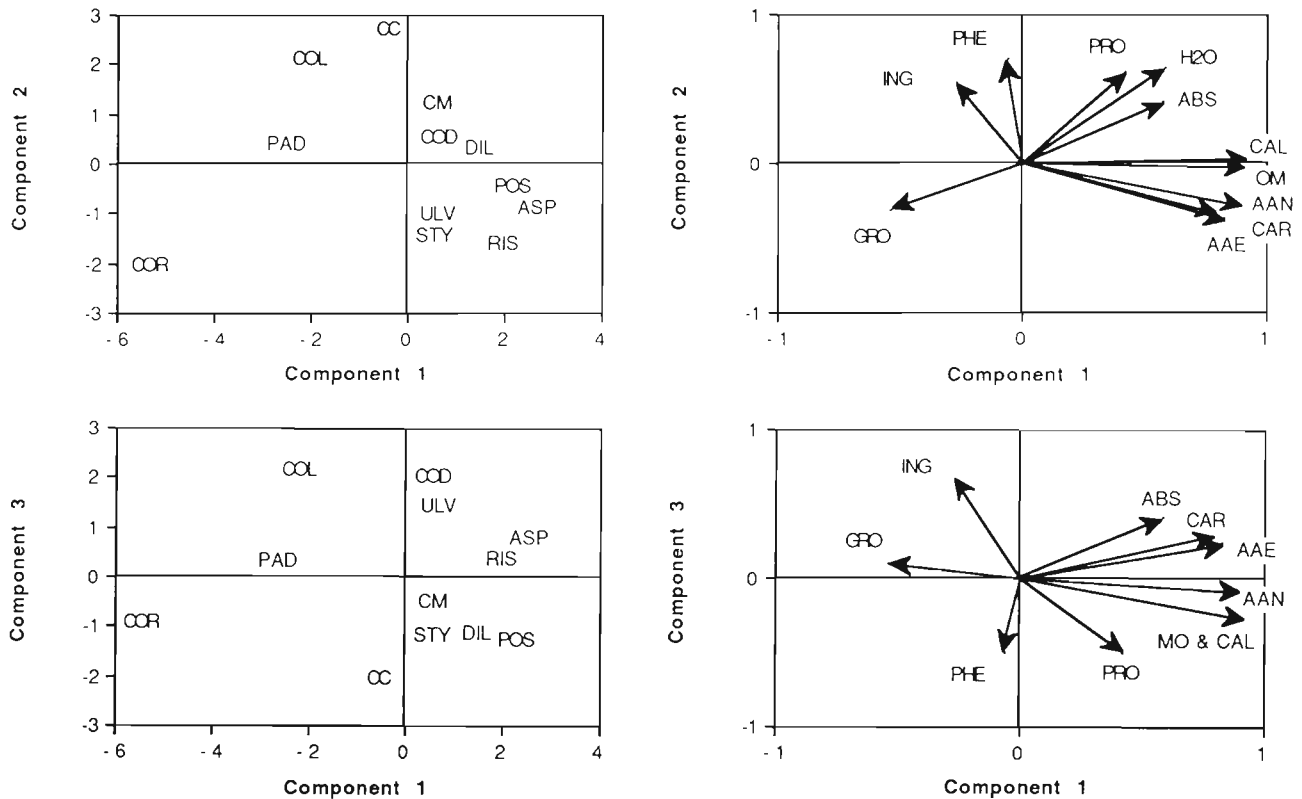


Fig. 10. Principal component analysis based on the values of the following parameters: ingestion (ING), absorption (ABS) and growth (GRO) rates recorded during the first month of the experiment; water contents (H_2O), % organic matter (OM), caloric contents (ENE), protein (PRO) and carbohydrate (CAR) concentrations; phenolic contents (PHE); and essential (AAE) and non-essential (AAN) amino acid concentrations. Relative positions of the 12 macrophytes on Axes 1 and 2 (above), and Axes 1 and 3 (below). The graphs to the right show the position of the descriptors on the same axes. Species as in Fig. 1

to energy gain in optimal foraging model (Taghon 1981) results in a positive correlation between percentage of organic matter and feeding rates when food is scarce, and a negative correlation between these 2 variables when food is abundant. Thus it would be interesting to compare bioenergetics of echinoids fed on several rations of each macrophyte.

Our data showed no significant correlation between phenolic contents and ingestion rates of *Paracentrotus lividus*. This result confirms the observations of Himmelman & Nedelec (1990) concerning *Strongylocentrotus droebachiensis*. It should however be pointed out that the third axis of the principal component analysis suggested a negative effect of phenolic contents on ingestion rates. Thus, beside covariation effects among macrophyte characteristics, the lack of correlation between total phenolics and ingestion may result from 2 different causes. First, herbivores belonging to different taxa and/or exhibiting different life histories differ in their ability to handle chemical defenses (Nicotri 1980, Hay et al. 1987). For example, Steinberg (1988) suggested that echinoids would probably be more apt than gastropods to modify their food regime

when preferred macrophytes are rare or absent. This may have been the case during our long-term no-choice feeding experiment. Second, phenolics are not the only substances involved in chemical defenses. Sulfuric acid is present in the thallus of some Phaeophyta (Anderson & Velimirov 1982). Non-phenolic halogenate compounds and terpenoids contribute to chemical defenses in Rhodophyta, and in Chlorophyta and Phaeophyta, respectively (Ragan & Craigie 1978, Norris & Fenical 1982, Hay et al. 1988). These compounds were not considered during the present study and their potential influence may explain the lack of significant correlation between total phenolics and ingestion rates.

Moreover, echinoid ingestion rates may be related to the interaction between several characteristics of the considered macrophyte. Such interactions may be detected by using multivariate methods (Himmelman & Nedelec 1990, Neighbors & Horn 1991). Results of the principal component analysis showed no clear relationship between ingestion rates and the main characteristics of the 12 tested macrophytes, thereby suggesting that the ingestion rates of *Paracentrotus lividus*

were not solely set by the interaction between macrophyte characteristics measured during the present study. Obviously, other macrophyte characteristics have to be examined in order to explain differences in echinoid feeding rates (see also Neighbors & Horn 1991). For example, it would be especially interesting to include the analysis of other secondary compounds (such as those listed in the preceding paragraph) produced by tested macrophytes. On the other hand, Neighbors & Horn (1991) also stressed the need for an extensive study of attractants produced by macrophytes. The best way to assess these problems may involve the use of artificial diets (Lawrence et al. 1989) since they allow for experimental manipulations of food composition.

Absorption

The present study confirms the existence of large differences in absorption rates of echinoids fed different macrophytes, which has already been reported for other species (Lawrence 1975, Lowe & Lawrence 1976, Vadas 1977, Larson et al. 1980). Our data also confirm the absence of significant correlation between absorption rates and taxonomic grouping (i.e. Rhodophyta, Phaeophyta, Chlorophyta) as observed by Lawrence (1975).

Absorption rates recorded during the present study were high (i.e. often superior to 80 %). These results are in good agreement with the data available in the literature, although the value recorded for *Asparagopsis armata* is the highest presently available. The existence of such high absorption rates in herbivorous echinoids is in slight contradiction with the microscopic examinations of their faeces which often show untouched cells with their cytoplasmic contents intact (Lawrence 1976, Cabral de Oliveira 1991). Two hypotheses may be advanced to explain this contradiction. First, methods used to measure absorption rates do not account for the production of dissolved non-absorbed substances by the gut. The importance of this process in echinoids is still unknown, but it may be high (Miller & Mann 1973), and thus contribute to the overestimation of actual absorption rates. Second, in echinoids, absorption rates are affected by the microflora associated with the gut (Lasker & Giese 1954, Fong & Mann 1980). During long-term monospecific feeding experiment this microflora may become more and more adapted to digest the offered food. This may explain the high absorption rates recorded during the present study.

For almost all the tested macrophytes, absorption rates in terms of dry weight and organic matter were almost equivalent. Due to the percentages of ash in

these macrophytes, this implies a significant absorption of inorganic matter by *Paracentrotus lividus*. A simple computation shows absorption efficiencies of inorganic matter ranging from 20 for *Corallina elongata* (March) to 95 % for *Asparagopsis armata* (July). This result is supported by the fact that echinoids fed on *C. elongata* featured much stronger tests than those fed on other macrophytes (Frantzis pers. obs.), thereby suggesting a significant uptake of carbonate. In any case, if a significant absorption of inorganic matter does occur (Lawrence et al. 1989), then the use of indicator methods based on ash contents (Lowe & Lawrence 1976) would be inappropriate to determine absorption rates of echinoids.

Absorption rates recorded during the present study are almost equivalent when expressed in terms of organic matter, proteins or carbohydrates. This result contradicts the data of Lawrence (1976) who reported that echinoids featured much lower absorption rates for total organic matter than for proteins. This last observation led to the conclusion that echinoids are efficient in digesting proteins and soluble carbohydrates but are incapable of digesting structural polysaccharides (Lawrence 1976, Lowe & Lawrence 1976). Consequently, the relative proportion of protein and carbohydrate of a given macrophyte should affect its digestibility. However, other studies have shown that structural carbohydrates may indeed be digested by echinoids (Fong & Mann 1980, Bedford & Moore 1985). Moreover, in benthic macrophytes, much of the protein fraction is protected by polysaccharidic cell walls. Although some cells will rupture during ingestion by echinoids, (partial) digestion of the cell walls must take place in order to account for high protein absorption rates (Bedford & Moore 1985). Thus, there is a certain dependence between protein and carbohydrate digestion. Our results showed almost equivalent absorption rates for carbohydrates and proteins. Moreover, the measured absorption rates of *Paracentrotus lividus* did not significantly correlate with the main biochemical characteristics (including protein and carbohydrate contents) of the tested macrophytes. These results, together with the lack of correlation between protein concentration in macrophytes and ingestion rates contradict the hypothesis suggesting that echinoids may eat large quantities of plant food in order to satisfy their protein need, defaecating most non-digestible carbohydrates (Lawrence 1975).

Our results showed a negative correlation between ingestion and absorption rates of *Paracentrotus lividus*. Although absorption mechanisms of echinoids are not yet completely understood, the link between ingestion rates and gut residence time seems well established. This dependence results from the poor musculature associated with the gut of echinoids (De Ridder &

Jangoux 1982), thus enhancing the importance of water and newly ingested material in materials progressing through the gut. This explains why starving echinoids have a much longer gut residence time than continuously feeding echinoids (Lasker & Giese 1954, Bedford & Moore 1985). It is assumed that gut residence time and absorption rates of benthic primary consumers are positively correlated (Lopez & Levinton 1987). Therefore, we believe that the negative correlation between ingestion and absorption rates of *P. lividus* recorded during the present study results from: (1) the negative correlation between ingestion rates and gut residence time, and (2) the positive correlation between gut residence time and absorption rates.

There was no significant correlation between absorption and growth rates of echinoids fed on the same macrophyte. For example, echinoids fed *Codium vermilare* or *Asparagopsis armata*, 2 macrophytes which were almost totally absorbed, showed very low or even negative growth rates. On the other hand, despite of low absorption rate, echinoids fed *Corallina elongata* showed high growth rates. The quality of a given food source results from its availability, its biochemical composition, and its level of utilization (Lawrence 1975). Food quality is thus depending on several processes namely: ingestion, digestion, absorption, and assimilation. According to this definition, growth should be the best index of food quality since it accounts for the resultant of all these processes. This point is especially important since on several occasions, absorption rates have been used as an index of food quality (Lopez & Cheng 1982, 1983). The present study confirms that solely looking at absorption rates may result in inaccurate assessments of the nutritional value of benthic macrophytes (Lowe & Lawrence, 1976). The best index of the relative quality of a given food source is the growth rates which are achieved by a test organism fed on this food source, under standard conditions.

Growth

Our results suggest the existence of significant differences among growth rates recorded for *Paracentrotus lividus* fed different macrophytes. This observation is consistent with what has been reported for several other echinoids submitted to similar experimental conditions (Lawrence 1975, Vadas 1977, Larson et al. 1980).

When pooling data corresponding to all macrophytes, there was a highly significant correlation between ingested organic matter and cumulated gonadal growth. Together with the highly significant correlation between ingested organic matter and cumulated growth, this result suggests that, although depending

on the total input, the energy allocation between somatic and gonadic tissues is not dependent on the offered macrophyte. In other words, the qualitative nutrient requirements for somatic and gonadal growth seem to be similar in *Paracentrotus lividus*. This result contradicts previous observations reporting significant differences in energy partitioning between somatic and gonadic tissues among echinoids fed on different macrophytes (Lawrence, 1975).

Correlation coefficients between ingested biomass and growth rates of *Paracentrotus lividus* varied according to the index of food biomass that was used. When considering either monthly or cumulated growth rates, total ingested organic matter described growth rates better than dry weight, energy, proteins or essential amino acids. Therefore, these data do not support the idea that growth rates of echinoids may be more dependent on the amount of ingested protein (Lowe & Lawrence 1976) or essential amino acids than upon the amount of ingested organic matter. Probably due to high individual variability in absorption rates these correlation coefficients were not significantly increased when using absorbed instead of ingested amounts. We believe that the poor description of growth by essential amino acid rations may be related to 3 different causes.

First, echinoids have a well developed digestive tract that is capable of storing nutrient reserve (Klinger et al. 1988). Gonads may also act as a storage organ (Lawrence 1975). Thus, dietary micronutrients may not be as critical in terms of the immediate control of echinoid growth, as they potentially are in opportunistic species such as the polychaete *Capitella capitata* (Marsh et al. 1989). For example, it is possible that the micronutrient reserves in the study animals were sufficient to carry them through the whole experiment. In this case, somatic tissues would have seen a more uniform resource available to them than was initially available in the diet. One of the possible way to further test this hypothesis would be to increase the length of the period of starvation prior to the experiment.

Second, echinoids have a well developed intestinal microflora (mostly bacteria) which can synthesize essential amino acids from cellulose (Fong & Mann 1980). These amino acids may then be efficiently assimilated by echinoids, as demonstrated by the measurements of significant transfers to the gonads (Fong & Mann 1980). The action of this microflora may thus reduce the heterogeneity (relative to amino acids availability) among tested food sources.

Third, the common nature (i.e. living benthic macrophytes) of the tested foods, which is reflected by the similarity in their amino acids profiles, contribute to increase statistical artifacts. Therefore correlation coefficients between different indices of ingested bio-

mass and growth rates are likely to be affected by the number and the nature of the tested food types. In *Capitella capitata* (type 1), for example, Grémare (unpubl.) found that essential amino acids provided a better description of fecundity than macronutrients when considering food types of different origins (i.e. sediment trap material and detritus) whereas macronutrients (i.e. carbon) described fecundity better than micronutrients when restricting the data set to detritic foods. One of the possible way to further test this hypothesis in the case of herbivorous echinoids would be to use artificial diets.

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