

# Green urchin as a significant source of fecal particulate organic matter within nearshore benthic ecosystems

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## Abstract

The role of green sea urchin *Strongylocentrotus droebachiensis* as a source of fecal particulate organic matter (POM) for the benthic nearshore ecosystems has been studied over a 3.5-month period. Three macroalgae were tested as food sources: *Alaria esculenta*, *Laminaria longicruris* and *Ulvaria obscura*. Urchins were fed ad libitum with either a single alga species or a mixture of all three algae. Consumption and defecation rates were determined as well as the feces/alga ratio in term of biomass and biochemical composition. Consumption rate increased exponentially with urchin size and also varied with alga species. In the single alga trial, consumption rate was higher for both brown algae (*Laminaria* and *Alaria*) compared to *Ulvaria*. Urchins feeding on the mixture of algae maintained their total ingestion rate (sum of the three algae) at the same level to those feeding on a single alga diet. The mixed algae trial showed that urchins clearly preferred *Laminaria* (72% of total ingestion) over *Alaria* (22%) and *Ulvaria* (6%). The defecation rate was tightly correlated with the food consumption rate and thus increased with urchin size. On average, 75% of the ingested algal biomass was released as fecal POM. The percentage of food defecated changed with alga species, with the highest value for *Alaria* (81%) and the lowest for *Laminaria* (67%). The percentage of food defecated by urchins feeding on the mixture of algae was generally comparable to those feeding on single alga diet. Biochemical composition (in soluble carbohydrates, proteins and lipids) of urchin fecal POM reflected that of the algae content. From 40% to 80% of macronutrients in algal food persisted in fecal matter. This proportion varied with the alga species and macronutrient considered. This study shows that the green sea urchin plays a significant role in the production of POM within nearshore benthic ecosystems, and it is a potentially nutritious food source for detritivores.

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## 1. Introduction

Marine macroalgae play a pivotal role within nearshore benthic ecosystems, as they represent the

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predominant source of particulate organic matter (POM) (Bustamante and Branch, 1996). Macroalgae POM are formed mainly through fronds fragmentation and decomposition that are favoured by the physical action of waves and currents (Mann, 1988). There is also POM formation during the feeding of benthic grazers that may transform a great part of the consumed macroalgae (up to 70%) to detrital fecal matter (Vadas, 1977; Larson et al., 1980; Koike et al., 1987; Frantzis and Grémare, 1992; Lison de Loma et al., 2000; Mills et al., 2000). In the latter case, benthic grazers may form a trophic link between macroalgae production and the feeding of detritivores in the same habitat. As many food chains start with feces, the urchin fecal wastes may constitute a source of fresh POM for the nearshore benthic ecosystems, formed by tissues of almost intact cells, containing much more macro- and micronutrients than POM from dead algae (Lawrence, 1976; Tenore et al., 1984; Koike et al., 1987; Cabral de Oliveira, 1991; Wotton, 1994; Lawrence and Klinger, 2001; Wotton and Malmqvist, 2001; Levinton et al., 2002).

Sea urchins are often the dominant grazers in nearshore benthic ecosystems as they have a broad distribution, dense population and high grazing activity (Lawrence, 1975, 2001). Their role as secondary producers of benthic POM has been pointed out by Mukai and Nojima (1985) and Koike et al. (1987) for the sea urchin *Tripneustes gratilla* that grazes on seagrass. It was observed that 65% of the caloric content of seagrass remained in fecal matter, and there is a higher persistence of nitrogen and phosphorous in comparison to carbon (Koike et al., 1987). No previous study has specifically focused on the generation of POM by the feeding activity of urchins on macroalgae. Their fecal POM may have a high potential of energy transfer to the upper level of the trophic chain. Vascular plant POM (derived from seagrass and eelgrass) are loaded in indigestible components (cellulose, waxes and lignin) that alter food assimilation while macroalgae POM, rich in nitrogen compounds and poor in refractory matter, are considered as good food sources for detritus feeders. Studies showed that fresh macroalgae POM greatly stimulate the growth of several nearshore invertebrates including deposit-feeder benthic worms and mudsnails (Tenore, 1977; Tenore and Hanson, 1980; Levinton, 1985) and filter-feeder oysters and mussels (Duggins and Eckman, 1997; Levinton et al., 2002).

In contrast with previous studies that compare the gross chemical composition (C, N, P and caloric content) between seagrass leaves and fecal matter (Mukai and Nojima, 1985; Koike et al., 1987), more recent reports on the contribution of benthic herbivores to POM production focus on macronutrient contents such as soluble carbohydrates, total proteins and lipids which provide much more specific information about the nutritional quality of the fecal POM (Fabiano et al., 1993; Chiantore et al., 1998; Lison de Loma et al., 2000; Mills et al., 2000).

Our principal objective was to quantify the transformation of macroalgae into fecal POM by the grazing activity of the green sea urchin *Strongylocentrotus droebachiensis*, Müller 1776. This species is one of the most ubiquitous urchins in northern benthic ecosystems (Scheibling and Hatcher, 2001). It usually heavily grazes on erect algae (Foreman, 1977; Hagen, 1983; Keats, 1991; Keats et al., 1991) and may form in kelp beds at a density of up to 450 ind./m<sup>2</sup> (Himmelman et al., 1983), suggesting a high generation of fecal POM from the field population. Consequently, this species may act as a significant secondary source of POM within the nearshore benthic ecosystems. More specifically, we highlight the importance of the POM production by green urchin in term of biomass and nutritional quality, in relation with the type of food and urchin size.

## 2. Materials and methods

### 2.1. Experimental design

Green urchins were collected by SCUBA diving at about 6 m in depth from a rocky shore population near Métis lighthouse (southern St. Lawrence Estuary, eastern Canada). Afterward, urchins were acclimated to laboratory conditions during 4 weeks. They were kept in a flow through system supplied with natural unfiltered seawater. During this period urchins were fed ad libitum with freshly collected macroalgae.

We fed urchins with macroalgae over a 3.5-month period (30 June to 12 October 2002) and collected regularly their fecal matter to determine consumption and defecation rates. There were 12 treatments in the experimental design: 3 classes of urchin size  $\times$  4 types of food. The feeding trials involved urchins in post-

metamorphic phase including young animals (~1 year old) of 10 mm in test diameter (TD) until the older ones of TD>50 mm (>14 years; Pelletier et al., 2001). To evaluate the variation in consumption and defecation rates as a function of size, urchins were separated in three classes: small (<20 mm TD), medium-sized (20–30 mm) and large (>40 mm). Previous studies indicated that the natural diet of *S. droebachiensis* may consist of several species of common macroalgae although it can be a highly selective feeder (Vadas, 1977; Larson et al., 1980; Himmelman, 1984; Himmelman and Nédélec, 1990). Three of the potential food sources of green urchin that are abundant along the St. Lawrence Estuary shores were supplied as foods: *Alaria esculenta* (L.) Greville Chromobionta, *Laminaria longicuris* De la Pylaie Chromobionta and *Ulvaria obscura* (Kütz.) Gayral Chlorobionta (Lavergne and Himmelman, 1984; Cardinal, 1990; Himmelman and Nédélec, 1990). Urchins were fed ad libitum with either a single alga species or a mixture of all three algae (same wet weight for each alga).

The experiment was conducted in duplicate with 10 urchins in each tank for a total of 24 tanks. All tanks were supplied with natural seawater at a rate of 1.5–2 renewals per hour. Water temperature was  $8.6 \pm 0.4$  °C at the beginning of the experiment (30 June 2002), reached the maximum of  $10.7 \pm 0.6$  °C in mid-July/August and decreased to  $7.2 \pm 0.2$  °C at the end of experiment (12 October 2002). The experiment was conducted under light conditions mimicking the natural photoperiod by modifying the light cycle in the experiment room bi-weekly.

### 2.1. Consumption and defecation of algal foods

Every 3 days, freshly collected algae were cleaned of all epiphytes, cut into fragments (5–20 cm length), spin-dried, weighed and supplied in excess to the urchins. The remaining algae from the previous feeding were removed, spin-dried and weighed. The supplied quantity and the remaining of three algae in the mixed food were separately weighted. Fecal matter produced by urchins within each 3-day interval was collected daily by suction. It was then separated from the seawater by filtration, cleaned of algae debris and freeze-dried over 96 h.

Algal biomass consumed by urchins within the 3-day time interval was calculated as the weight difference between the supplied and remaining algae. Biomass of consumed algae was converted to dry weight using dry matter content of each alga: 16.1% for *Alaria*, 11.2% for *Laminaria* and 19.8% for *Ulvaria*. Defecation rate was also expressed on a dry weight basis. Percentage of food defecated was determined as follow:

Percentage of defecation (%)

$$= (\text{defecated biomass} / \text{ingested biomass}) \times 100 \quad (1)$$

The absorption efficiency usually reported in literature can be easily obtained with the following equation:

Absorption efficiency (%)

$$= 100 - \text{Percentage of defecation} (\%) \quad (2)$$

### 2.3. Macronutrient contents

Soluble carbohydrates (CHO), proteins (PRT) and lipids (LIP) were determined for macroalgae and urchin fecal matter. Freeze-dried samples of algae and fecal matter were finely ground, and kept frozen (–80 °C) before the analysis. Soluble carbohydrate was extracted in 5% trichloroacetic acid and the concentration was estimated by the phenol–sulfuric acid method (Dubois et al., 1956). Optical density was measured at 490 nm, and glycogen (reagent grade) was used as a standard. Soluble protein was extracted in 1 N NaOH and the concentration was estimated by the Bradford dye binding method (Bradford, 1976), measuring the optical density at 595 nm and using bovine serum albumin as a standard. Total lipids were extracted in dichloromethane–methanol (2:1 v/v), and the concentration was estimated by the gravimetric method (Bligh and Dyer, 1959).

For urchins feeding the mixture of algae, the concentrations of CHO, PRT and LIP in fecal matter were obtained directly by biochemical analysis of that fecal matter. However, the biochemical composition of food was determined indirectly using the relative proportion of each algae (% in d.w.) ingested when

urchins were fed mixed diets (obtained from this study) and the biochemical composition of each alga. Macronutrient contents are reported on a dry weight basis. Percentage of defecation was determined with Eq. (1) by replacing the biomass by macronutrient content.

#### 2.4. Statistical treatments

All statistical treatments were performed using SigmaStat® software (Jandel Scientific) at 5% significance error level. Preliminary treatments using *t*-test showed no influence of tank on the consumption and defecation rates or on the relative proportion of each one of three algae in mixed food total ingestion. For each sampling date, the average from replicated tanks was then used for statistical treatments. Between-groups comparisons were performed using one-way ANOVA or *t*-test. When differences were detected we performed post hoc comparisons using Student–Newman–Keuls (SNK) test (Zar, 1999).

### 3. Results

#### 3.1. Consumption and defecation of algal foods

Preliminary treatment on bi-weekly gathered data showed both consumption and defecation of algal foods did not change during the experiment period (one-way ANOVA;  $F_{0.05,6,23}=3.023\text{--}3.431$ ,  $p=0.312\text{--}0.479$ ; Figs. 1 and 2). The two other factors, urchin size and alga species, generally influenced the consumption and defecation rate. Also, there was no significant interaction between these two factors (two-way ANOVA). Consumption rate increased with urchin size (Fig. 1). Small urchins ingested on average 20 mg d.w./ind./day (overall mean) while medium-sized and large urchins ingested macroalgae at a rate of 60 and 178 mg d.w./ind./day, respectively. Consumption rate changed with alga species (one-way ANOVA,  $F_{0.05,3,36}=1.423\text{--}1.901$ ,  $p<0.001$ ). In single alga trials, the consumption rate of urchins when feeding on the two brown algae (*Laminaria* and *Alaria*) was higher than when feeding on *Ulvaria* (SNK,  $p<0.05$ ). For small and medium-sized urchins, the consumption rate of *Laminaria* was higher than on *Alaria* (SNK,  $p<0.05$ ). Consumption rates were

comparable in large urchins feeding on these two algae (SNK,  $p=0.054$ ). Urchins feeding on the mixture of algae maintained their total consumption rate (sum of the three algae) in the same range that for urchins feeding on single alga diets (Fig. 1). For small and medium-sized urchins, the consumption rate of the mixture of algae was similar to that on *Alaria* alone (SNK,  $p=0.79$  for small urchins;  $p=0.83$  for medium-sized urchins) but higher than on *Ulvaria* alone (SNK,  $p<0.05$  for small urchins;  $p<0.001$  for medium-sized urchins). It was lower than the feeding rate on *Laminaria* for small urchins (SNK,  $p<0.05$ ) while it was similar to the rate on *Laminaria* for medium-sized urchins (SNK,  $p=0.088$ ). For large urchins, the consumption rate on the mixture of algae was lower than on *Alaria* alone (SNK,  $p=0.001$ ) but comparable to that on *Laminaria* or *Ulvaria* alone (SNK,  $p=0.054\text{--}0.189$ ).

Of the three algae in the mixed food, urchins clearly preferred *Laminaria* over *Alaria* and *Ulvaria* (Table 1). The ingestion of urchins feeding on the mixture of algae was mainly dominated by *Laminaria* (72% in d.w.; mean for all size classes). *Alaria* formed 22% of the ingestion and *Ulvaria* only 6%. Urchin size had no effect on the relative proportion of ingested alga (one-way ANOVA,  $F_{0.05,2,157}=0.243$ ,  $p=0.79$  for *Alaria*;  $F_{0.05,2,157}=0.972$ ,  $p=0.38$  for *Laminaria*;  $F_{0.05,2,157}=2.363$ ,  $p=0.097$  for *Ulvaria*).

The defecation rate was strongly correlated with the food consumption rate (Spearman rank order correlation,  $r=0.96$  for *Alaria*;  $r=0.97$  for *Laminaria*;  $r=0.95$  for *Ulvaria*;  $r=0.95$  for the mixture of algae). It increased with urchin size (Fig. 2). Small urchins defecated in average 16 mg d.w./ind./day (overall mean) while the defecation rate for medium-sized and large urchins was 44 and 144 mg d.w./ind./day, respectively. In general, defecation rate did not change with the type of food (one-way ANOVA). However, one exception was found for large urchins feeding on *Ulvaria*, for which the defecation rate was significantly lower than for urchins feeding on the two other algae or the mixture of the three algae (SNK,  $p=0.002\text{--}0.005$ ).

On average, 75% of the ingested algae biomass (overall mean) was later released by urchins as fecal matter (Table 2), suggesting that urchins absorbed only 25% of ingested algae biomass. For each type of food, percentage of defecation did not change with urchin

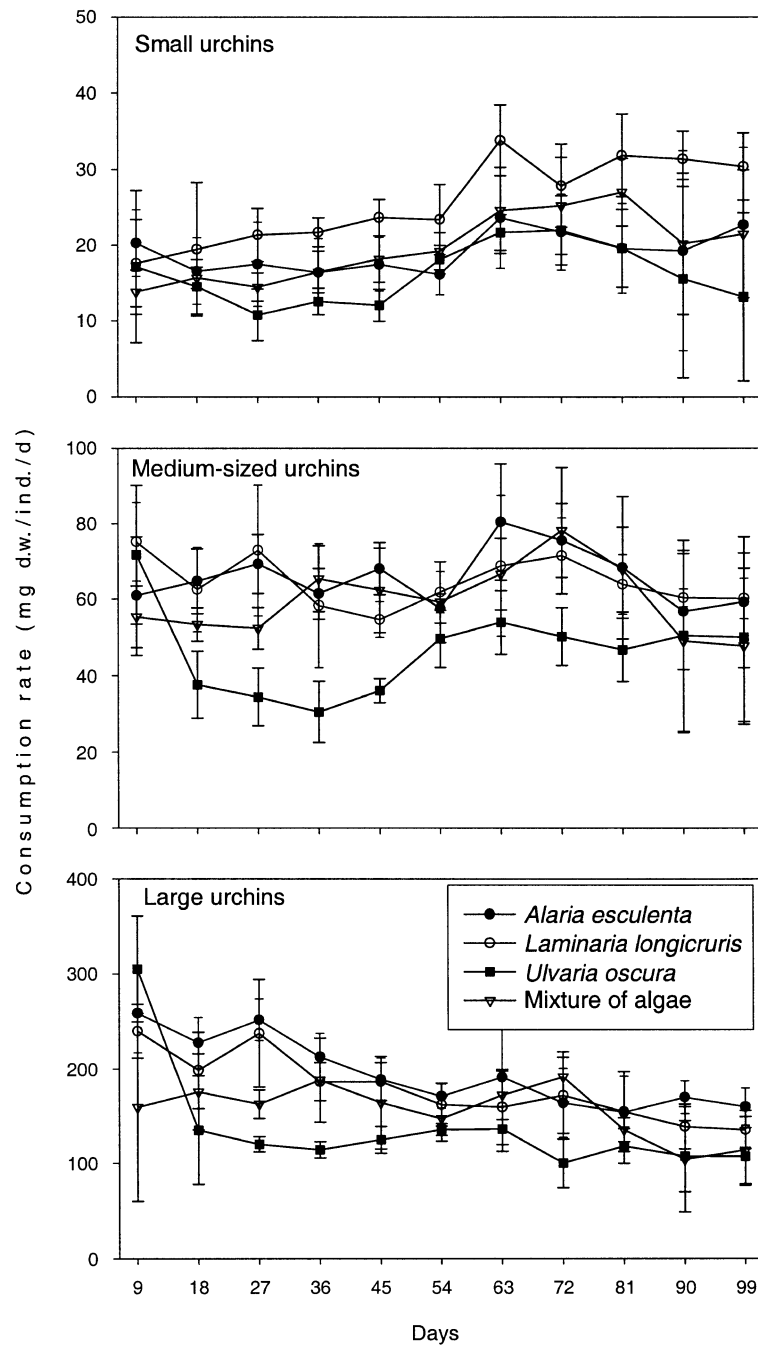


Fig. 1. Rate of consumption of macroalgal food (mean±S.D.) by urchins in three size classes during the 3.5-month period of feeding experiment. Note the change in the left scale.

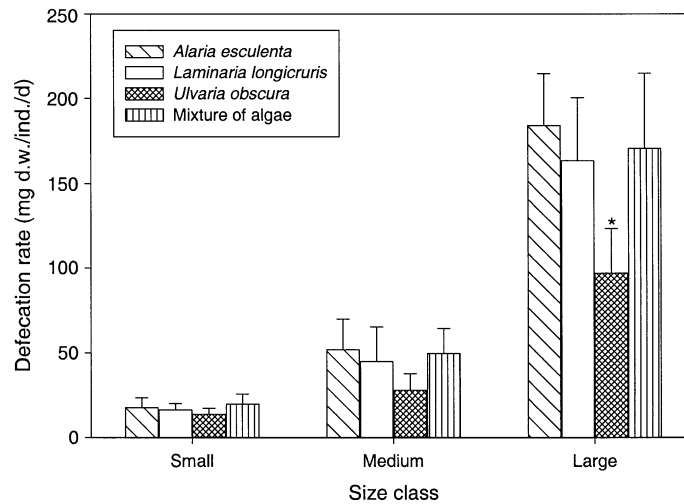


Fig. 2. Rate of defecation of the ingested macroalgae by urchins during the 3.5-month period of feeding experiment.

size (one-way ANOVA;  $p=0.167$  for *Alaria*,  $p=0.39$  for *Laminaria*,  $p=0.069$  for *Ulvaria* and  $p=0.088$  for the mixture of algae). The percentage of defecation changed with the type of food (one-way ANOVA,  $F_{0.05,3,58}=3.355$ ,  $p=0.025$ ). Among the four types of food (the three algae and their mixture), proportion of ingested food defecated was the highest in urchins feeding on *Alaria* (81%; mean for all size classes) and the lowest for urchins feeding on *Laminaria* (67%). The difference in proportion of ingested food defecated between individuals feeding on these two algae was significant (SNK;  $p=0.013$ ). However, difference between individuals feeding on *Alaria* and those feeding on *Ulvaria* was not significant (SNK;  $p=0.21$ ). It was the same between urchins feeding on *Laminaria* and those feeding on *Ulvaria* (SNK;  $p=0.164$ ). Proportion of ingested food defecated by urchins feeding on the mixture of algae was generally comparable to those feeding on single alga diets.

### 3.2. Macronutrient contents

For the three algae, soluble carbohydrates (CHO) were a more important component of dry mass than proteins (PRT) and lipids (LIP) (Fig. 3). An exception was *Alaria* where the concentration of PRT and CHO were comparable ( $t$ -test). The three algae differed in their CHO, PRT, and LIP contents; values were the highest for *Ulvaria* (and markedly greater for CHO). The calculated concentration of these three macronutrients in the mixture of algae reflected the proportion of ingested algae (Fig. 3).

Biochemical composition of fecal matter reflected the food content in these macronutrients. There was much more CHO than PRT and LIP in urchin fecal matter (Fig. 3). For each type of food, the composition of fecal matter did not change with urchin size (one-way ANOVA). However, one exception was for

Table 1

Composition (% in dry weight) of total ingestion of the three algae species (*A. esculenta*, *L. longicruris*, *U. obscura*) when the urchins were fed on the mixed diets during the 3.5-month experiment

Size class	<i>Alaria</i>	<i>Laminaria</i>	<i>Ulvaria</i>
Small	21.3±14.6	71.7±17.8	7.0±7.9
Medium	21.6±13.9	73.5±14.2	4.9±4.7
Large	23.1±14.0	69.3±14.2	7.6±7.0

Values are means±S.D. of the ratio between mass of each alga ingested to total ingestion ( $n=34$ ).

Table 2

Proportion of ingested food defecated by urchins (% in dry weight) in single and mixed diets during the 3.5-month experiment

Size class	<i>Alaria</i>	<i>Laminaria</i>	<i>Ulvaria</i>	Mixture of algae
Small	82.8±5.7	64.8±11.0	81.7±5.9	71.4±14.9
Medium	77.2±11.7	63.2±17.4	70.2±19.4	87.2±9.8
Large	81.7±16.5	74.0±13.7	67.7±15.0	66.0±11.6

Values are means±S.D. of the biomass feces/algal food ratio between the dry mass of fecal matter toward the amount of ingested food ( $n=17$ ).



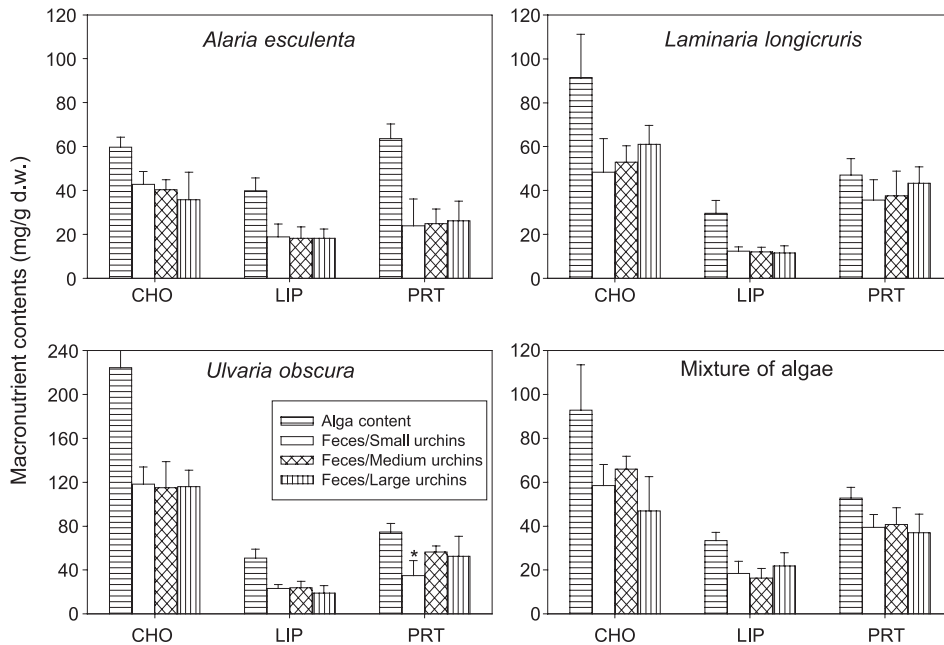


Fig. 3. Rate of defecation of macronutrients ingested with macroalgae by urchins in three size classes during the 3.5-month period of feeding experiment.

animals feeding on *Ulvaria* where fecal matter of small urchins contained much lower PRT than the fecal matter of medium-sized and large urchins (one-way ANOVA,  $F_{0.05,2,17}=5.255$ ,  $p=0.017$ ; SNK,  $p=0.019$ – $0.028$ ).

Feces/algal food ratios in macronutrients showed that 40–80% of food content (overall average) persisted in fecal matter (Table 3). So, urchins absorbed from 20% to 60% of the alga macronutrients. Urchin size did not affect this feces/algal food ratios in macronutrients (one-way ANOVA). However, the percentage of PRT in fecal matter of individuals feeding on *Ulvaria* was lower in small urchins than in medium-sized and large urchins (SNK,  $p<0.05$ ). Defecation of LIP in individuals feeding on the mixture of algae was lower in medium-sized than large urchins (SNK,  $p=0.039$ ). CHO and PRT defecation changed with the type of food (one-way ANOVA,  $F_{0.05,3,63}=9.169$ ,  $p<0.001$  for CHO;  $F_{0.05,3,69}=19.714$ ,  $p<0.001$  for PRT). There was a higher CHO defecation in urchins feeding on *Alaria* or on the mixture of algae than in urchins feeding on *Laminaria* and *Ulvaria* (SNK,  $p<0.001$ ). Defecation of PRT was lower in urchins feeding on *Alaria* than urchins feeding on *Laminaria*, *Ulvaria* or the mixture

of algae (SNK,  $p<0.001$ ). Defecation of LIP was quite similar for all four diets (one-way ANOVA,  $F_{0.05,3,7}=0.565$ ,  $p=0.61$ ).

Table 3

Proportion (%) of ingested macronutrients (soluble carbohydrates, total proteins and lipids) defecated by urchins in single and mixed diets during the 3.5-month experiment

Size class	<i>Alaria</i>	<i>Laminaria</i>	<i>Ulvaria</i>	Mixture of algae
<i>Carbohydrates</i>				
Small	76.7±8.6	52.8±16.2	52.7±7.0	63.0±9.7
Medium	67.5±6.9	57.9±8.2	51.2±10.6	71.0±6.0
Large	59.9±18.5	66.8±9.4	51.6±6.8	50.5±15.6
Average	68.0	59.2	51.8	61.5
<i>Proteins</i>				
Small	37.7±19.2	75.6±19.7	47.0±18.3 <sup>a</sup>	74.9±6.8
Medium	39.1±10.5	79.9±23.7	74.9±7.2	77.4±7.5
Large	41.1±14.2	86.7±16.1	70.7±24.4	70.0±8.5
Average	39.3	80.7	64.2	74.1
<i>Lipids</i>				
Small	47.4±17.0	41.6±7.7	45.4±7.8	55.0±5.6
Medium	45.7±15.2	40.5±8.4	44.3±12.5	49.2±4.2 <sup>a</sup>
Large	45.8±12.2	38.7±12.6	37.1±15.1	65.7±5.9
Average	46.3	40.3	42.3	56.6

Values are means±S.D. ( $n=5$ – $8$ ).

<sup>a</sup> Indicates a significantly different value.

#### 4. Discussion

The green urchin is the dominant grazer within the nearshore benthic ecosystem of the St. Lawrence Estuary. Our study shows that its feeding could play a significant role in the generation of POM. The production of fecal POM depends at first on the consumption rate, which varies with the urchin size and with alga species being eaten. The biochemical composition of that fecal POM reflects the composition of the macroalgal food but the levels of macronutrients that are dependent on the percentage of defecation change with alga species. We show that fecal POM from this urchin is a potentially nutritious food source for detritus feeders within the nearshore benthic ecosystems.

The consumption rate increased with urchin size. Similar observations have been reported for the same species and also other herbivore urchins (Larson et al., 1980; Himmelman, 1984; Mukai and Nojima, 1985; Bureau et al., 1997; Barker et al., 1998; Fernandez and Boudouresque, 2000). According to Barker et al. (1998), the higher metabolic demand of larger urchins needs a much higher nutrient uptake compared to the smaller ones. A direct comparison of our results with previous ones obtained for green urchins of eastern coast of Canada is not possible because of a difference in size classification between studies (Himmelman, 1984; Himmelman and Nédélec, 1990). However, when all the data are plotted together (theirs and ours), we observed a clear tendency of consumption rates to increase exponentially with the urchin size ( $r^2=0.83-0.94$ ; Fig. 4). So, it seems reasonable to suggest that urchin consumption rates reported in the present study are comparable to the previously reported ones (Himmelman, 1984; Himmelman and Nédélec, 1990).

Urchins on single alga diets showed similar consumption rates for the two brown algae (*Alaria* and *Laminaria*), both being higher than for *Ulvaria*. This result corroborates previous studies reporting higher consumption rates of green urchins feeding on brown algae than on other macrophytes (Vadas, 1977; Larson et al., 1980; Himmelman, 1984; Himmelman and Nédélec, 1990). The lack of a consistent difference in consumption rates between *Alaria* and *Laminaria* seems to be the result of the opportunistic habit of green urchin that may readily feed on the less

preferred algae in the absence of preferred food sources (Scheibling and Hatcher, 2001). As well demonstrated in the mixed algae trials, the green urchin has a clear preference to feed on *Laminaria* than *Alaria*. This order of preference is the result of the combined effect of two independent parameters: the attractiveness of the algae for the urchin and the palatability of each alga, which together may inform the urchin whether to ingest or avoid ingesting a food source (Nicotri, 1980). The degree of preference may also be affected by food availability (Larson et al., 1980). The abundance of *Alaria* in the field may exceed that of *Laminaria* spp., notably in the *Alaria* fringe (Himmelman et al., 1983; Lavergne and Himmelman, 1984; Himmelman and Nédélec, 1990). Determining the preference of the urchin for macroalgae needs further field studies of its response to other available algae including understory species such as *Devaleraea ramentacea*, *Palmaria palmata* and *Rhodomela conforvoides*, *Spongomorpha arcta*, *Saccorhiza dermatodea* (Himmelman and Nédélec, 1990).

Urchins released from 67 to 81% of the ingested algal biomass as fecal matter. This corroborates the poor digestion of the ingested macrophytes, previously reported for herbivorous urchins (Vadas, 1977; Larson et al., 1980; Mukai and Nojima, 1985; Frantzis and Grémare, 1992; Agatsuma, 2000). Using absorption efficiency data available from the literature, we estimated the percentage of defecated material (being 100% absorption efficiency) for a number of macrophytes grazers. High proportion of ingested macrophytes defecated by urchins were previously found in *Str. droebachiensis* feeding on *Agarum cribrosum* (60%), *Strongylocentrotus purpuratus* feeding on *Monostroma fuscum* (72%), *Paracentrotus lividus* feeding on *Stypocaulon scoparium* (65%) and on *Corallina elongata* (70%) and *Tr. gratilla* feeding on *Thalassia hemprichii* (85%) (Vadas, 1977; Larson et al., 1980; Mukai and Nojima, 1985; Frantzis and Grémare, 1992). The proportion of ingested macrophytes defecated by urchins depends on the ability of urchin to digest the algal biomass and may vary as a function of both the urchin and alga species (Vadas, 1977; Larson et al., 1980; Frantzis and Grémare, 1992; Agatsuma, 2000). For the green urchin, it may vary from 14% in individuals feeding on *Nereocystis luetkeana* (Vadas,



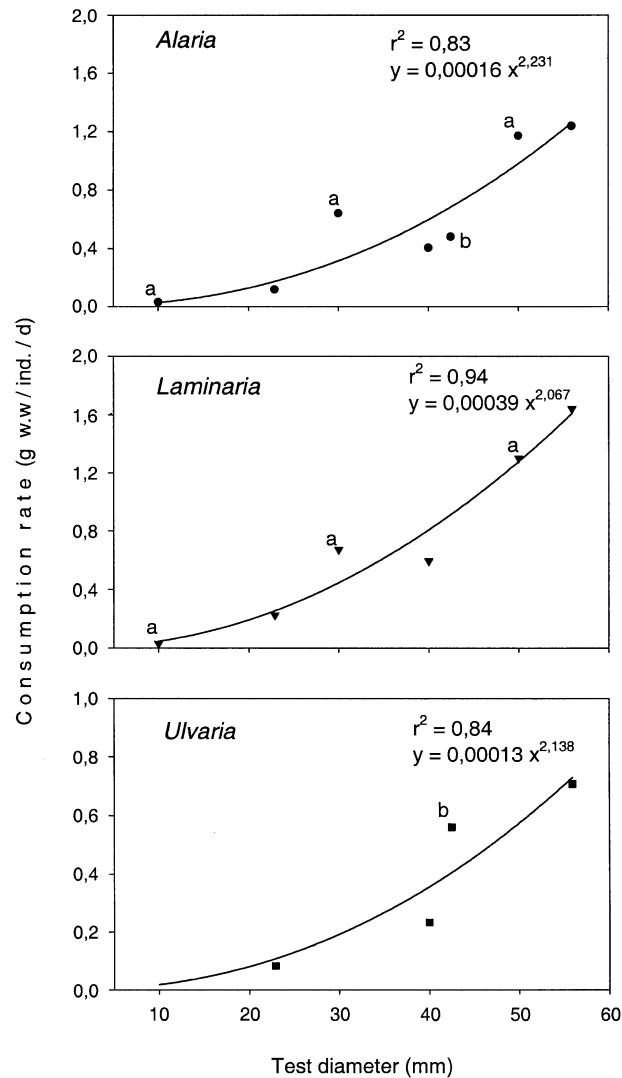


Fig. 4. Relationship between urchin size and the rate of consumption of macroalgae by urchins during the 3.5-month period of feeding experiment. (a) Values from [Himmelman \(1984\)](#); (b) values from [Himmelman and Nédélec \(1990\)](#).

1977) to 81% when feeding on *Al. esculenta* (this study).

In our study, urchins released a smaller proportion of the ingested biomass when feeding on *Laminaria* than for two other algae. This observation corroborates previous studies reporting that green urchin and another related species (*Strongylocentrotus franciscanus*) show a higher absorption efficiency, meaning a lower percentage of defecation, when feeding on preferred or highly consumed algae, including *N. luetkeana*, *Costaria costata*, *Laminaria saccharina*,

*L. longicuris* and *Chondrus crispus* ([Vadas, 1977](#); [Larson et al., 1980](#)). There is a proportionally less bioorganic matter recycled through the defecation process when urchins feed on preferred food sources. However, because of the high consumption rate when feeding on preferred algae, the greatest part of the fecal POM produced in the field is probably derived mainly from preferred algae. This suggest that the level of total organic components as well as the biochemical composition of the field produced fecal POM might vary as a function of the occurrence and

abundance of preferred algae, which in turn will vary with depth, site and geographical region (Vadas, 1977; Himmelman and Nédélec, 1990; Sivertsen, 1997).

We show that defecation percentage for each macronutrient varies with alga species. Similar observations have been reported for *P. lividus* and *Lytechinus variegatus* feeding on seaweeds or seagrasses (Lowe and Lawrence, 1976; Frantzis and Grémare, 1992). The most plausible explanation is that the digestion of each gross biochemical component, such as soluble carbohydrates, total lipids and proteins, depends at first on the digestibility of each micronutrient composing those macronutrients, and also on their abundance in different algae (Frantzis and Grémare, 1992). Yano et al. (1993) showed that *Strongylocentrotus intermedius* feeding on the kelp *Laminaria longissima* defecated 51% of ingested laminarian whereas the percentage of defecation of alginate was only 25%. Fernandez and Boudouresque (2000) observed that a slight difference of composition in oil (% of fish and sunflower oils) is sufficient to change the assimilation efficiency of total lipids for *P. lividus* feeding on artificial foods.

According to the theory of nutrient uptake optimization (Vadas, 1977; Himmelman and Nédélec, 1990), it is expected that defecation percentages of macronutrients should be the lowest in the most preferred alga, *Laminaria*. Our results did not consistently support this idea. The highest values of total proteins defecation were observed for urchins feeding on *Laminaria*. This nutrient uptake optimization may be based on high-energy micronutrient absorption rather than on the absorbed amount of macronutrients (Frantzis and Grémare, 1992) since feeding on *Laminaria* spp. usually enhances fitness by favouring both somatic and gonadal growth (Himmelman and Nédélec, 1990; Kennedy et al., 1999; Scheibling and Anthony, 2001). This suggests that urchin feeding on *Laminaria* might have a double advantage for the benthic community dominated by green urchins. First, *Laminaria* should permit a better growth of the urchin (Himmelman and Nédélec, 1990; Kennedy et al., 1999; Scheibling and Anthony, 2001) and further lead to increase production of fecal POM with a level of macronutrients that may rival or exceed the ones derived from less preferred algae.

The green urchin produces neat globular fecal pellets measuring about 1 mm in diameter (Miller and

Mann, 1973). The feces are composed of smaller debris, belonging most probably to the class of the fine POM (<1 mm but >0.45 µm), and several detritivores may use this as a food source (Wotton, 1994). Many of detritivores inhabit the community dominated by green urchins, including sea cucumbers *Cucumaria frondosa* and *Psolus fabricii*, brittle star *Ophiopholus aculeata*, tunicates *Halocynthia pyriformis*, *Boltenia ovifera* and *Ascidia* sp., bivalves *Mytilus edulis* and *Hyatella arctica*, cnidarians *Metridium senile* and *Gersemia rubiformis*, and several sponges (Lavergne and Himmelman, 1984). Previous studies show the presence of undamaged cells (with intact cytoplasmic contents) in fecal matter of herbivorous urchins, and this suggests that urchin fecal POM might be a nutritious food sources for detritivores (Lawrence, 1976; Cabral de Oliveira, 1991). Fresh fecal POM derived from green urchin have the level of macronutrients (CHO=40–120 mg/g d.w.; PRT=20–50 mg/g; LIP=15–20 mg/g) that may rival or exceed other benthic POM such as field total particulate matter, macroalgae and marshgrasses POM, fresh fecal matter of algivorous reef fish and urchin, and biodeposition of mussels with an average content of CHO=20–40 mg/g d.w.; PRT=9–75 mg/g; LIP=8–21 mg/g (Tenore et al., 1984; Chiantore et al., 1998; Lison de Loma et al., 2000; Mills et al., 2000; Wilson, 2002). Using macronutrient data and conversion rate (Brody, 1945) [5.65 cal/mg proteins, 4.10 cal/mg carbohydrates, 9.45 cal/mg lipids] showed that urchin fresh fecal POM may contain from 419 to 963 cal/g d.w. while other benthic POM mentioned above contain from 208 to 786 cal/g d.w.

Using data of urchin density from Himmelman et al. (1983), we estimated the green urchin fecal POM production within the *Alaria* fringe (0–2 m depth) along the southern coast of St. Lawrence Estuary. The density of urchins in this area approximate 150 ind./m<sup>2</sup> with the size-structure corresponding to 99, 28 and 21 ind./m<sup>2</sup> of small, medium-sized and large urchins, respectively. Such a green urchin population within 1 m<sup>2</sup> surface in this area may transform in optimum condition of feeding up to 7.4 g/day of dry algae biomass and produce 5.6 g d.w./day of fecal matter. No similar study has been conducted in St. Lawrence Estuary bivalves, the most studied group of invertebrate in regard to fecal POM production, but it is possible to get a comparison of our results with mussel

biodeposit production using data obtained for blue mussel *M. edulis* in another cold water ecosystem (Kautsky and Evans, 1987). This estimated field production of fecal POM by green urchin is slightly higher than the biodeposit production observed for blue mussels (4.0 g d.w./m<sup>2</sup>/day; Kautsky and Evans, 1987) and evidences the relative importance of urchins in the production of valuable POM. Using caloric contents of urchin fecal matter (above results) and the one of mussel biodeposition (CHO=19 mg/g d.w.; PRT=65 mg/g; LIP=19 mg/g; Energy=625 cal/g d.w.; Chiantore et al., 1998), a comparison of the fecal production of energy by these two groups of benthic animals can be made. It is shown that green urchin of St. Lawrence Estuary may provide to the surrounding detritus feeders up to 5000 cal/day, while the mussels would produce only 625 cal/day.

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