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Utilization of *Phaeocystis globosa* colonies by young *Mytilus edulis*

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Abstract

The nutritional value of the bloom-forming alga, *Phaeocystis globosa* (Prymnesiophyceae) for the mussel *Mytilus edulis* was evaluated in laboratory experiments. Young mussels (20 mm shell length) were fed *P. globosa* single cells and colonies, *Phaeodactylum tricornutum*, *Dunaliella salina* and *P. tricornutum* with cell-free medium of dense *P. globosa* colony cultures. After 40 days the mussels showed significant higher meat weight when fed with *P. globosa* colonies and *D. salina* in comparison to the other feeding conditions. When percentage weight increase is correlated with the amount of algal carbon available per mussel, *P. tricornutum* becomes the most efficient food. *P. globosa* colonies were utilized more effectively than *P. globosa* single cells. The effective utilization of *P. globosa* colonies contradicts the hypothesis of negative effects of dense *P. globosa* blooms on the growth of *Mytilus* in the Wadden Sea.

Kurzfassung

Verwertung von *Phaeocystis-globosa*-Kolonien durch junge Miesmuscheln (*Mytilus edulis*)

Im Laborexperiment wurde der Nahrungswert von *Phaeocystis globosa* (Prymnesiophyceae) für die Miesmuschel *Mytilus edulis* evaluiert. Junge *Mytilus* (20 mm Schalenlänge) wurden mit folgenden Algensuspensionen gefüttert: *Phaeocystis globosa* in Kolonieform, *P. globosa* Einzelzellen, *Dunaliella salina* (Chlorophyceae), *Phaeodactylum tricornutum* (Diatomeae) und *P. tricornutum* in Medium aus einer dichten Kultur von *P. globosa* in Kolonieform. Nach 40 Tagen führten die Versuchsansätze mit Fütterung von *P. globosa* Kolonien und *D. salina*, im Vergleich zu den anderen Futterbedingungen, zu einem signifikant höheren Fleischgewicht der Muscheln. Die Relation der prozentualen Gewichtsveränderung der Tiere zum Kohlenstoffangebot der Futteralgen zeigte, daß *P. tricornutum* am effektivsten zum Aufbau von Biomasse genutzt werden konnte. *P. globosa* Kolonien konnten besser verwertet werden *als P. globosa* Einzelzellen. Die effektive Verwertung von *P. globosa* in Kolonieform widerspricht der Hypothese negativer Effekte dichter *P. globosa* Blüten auf das Wachstum von *Mytilus* im Wattenmeer.

Resumen

Utilización de colonias de *Phaeocystis globosa* por juveniles de mejillón (*Mytilus edulis*)

El valor nutricional del alga *Phaeocystis globosa* (Prymnesiophyceae) para el mejillón *Mytilus edulis*, se ha evaluado en experimentos de laboratorio. Mejillones jóvenes (20mm longitud de la

concha), fueron alimentados con células individuales y colonias de *Phaeocystis globosa* y *Dunaliella salina* (Chlorophyceae). Además fueron alimentados con *Phaeodactylum tricornutum*. (Diatomea), tanto sólo como en un medio de cultivo denso, libre de células individuales, de *Phaeocystis globosa*. Cuarenta días después, los mejillones presentaban un aumento del peso de su carne significativamente mayor cuando eran alimentados con colonias de *P. globosa* y de *Dunaliella salina*, en comparación con las otras condiciones de alimentación. Cuando el porcentaje de peso aumenta lo hace en relación con la cantidad de carbono del alga accesible para el mejillón, *P. tricornutum* resulta entonces el alimento más eficiente. Las colonias de *P. globosa* son utilizadas de forma más eficiente que las células individuales. La eficacia de la utilización de las colonias de *P. globosa* contradice la hipótesis de los efectos negativos que producirían los afloramientos de *P.globosa* en el crecimiento de *Mytilus* en las marismas del Mar del Norte.

Introduction

The genus *Phaeocystis* (Prymnesiophyceae) frequently dominates the phytoplankton of nutrient-rich temperate and polar seas throughout the world's oceans (Lancelot *et al.* 1994). In the southern North Sea the *Phaeocystis* blooms in spring, following the diatom bloom, are largely dominated by the colonial palmelloid form of the species, with only low densities of free-living motile single cells (Baumann *et al.* 1994). Degradation of the senescent colonies may lead to foam accumulation on the beaches. Duration and density of the blooms have increased in recent decades (Bätje and Michaelis 1986, Rousseau *et al.* 1994). In 1993 a maximum density of 100 000 colonies l^{-1} was recorded in the Wadden Sea, off Norderney (Michaelis and Rahmel 1993).

Dense *Phaeocystis* blooms can lead to very high levels of dimethyl sulfate (DMS) and acrylic acid in the cells and surrounding water (Guillard and Hellebust 1971, Gibson *et al.* 1988, Liss *et al.* 1994), which may affect aquatic animals and even contribute to climatic changes by aerosol formation (see *e.g.* Foley *et al.* 1991). In order to test possible effects of DMS and acrylic acid, *M. edulis* were fed a cell-free medium from dense *Phaeocystis* cultures with *P. tricornutum* as food particles.

The physiology and taxonomy of *Phaeocystis*, as well as the bloom-controlling factors, are insufficiently known (Lancelot *et al.* 1994) and its trophic significance in the marine food web is still under discussion (Weisse *et al.* 1994, p. 76: "Very few experimental investigations have included comparisons of *Phaeocystis* with other phytoplankton, so that it remains uncertain whether, although ingested, *Phaeocystis* represents a nutritionally satisfactory food source.") Especially scarce are quantitative investigations on the trophic relevance of *Phaeocystis* for "one of the most important benthic filter-feeders of coastal waters" (Dankers and Koelemaij 1989), the blue mussel *Mytilus edulis*. Several authors assume that *Phaeocystis* blooms have negative effects on *Mytilus*, such as decreased filtration efficiency or growth deficiencies (Pieters *et al.* 1980, Obert and Michaelis 1989, Wolters 1989), while Asmus *et al.* (1992) recognized qualitatively an intensive uptake of *Phaeocystis globosa* during measurements in a benthic tunnel and flume. A recent paper by Kamermans (1994) stated that single cells of *Phaeocystis* were consumed by *Macoma balthica*, but colonies were rejected. Beukema and Cadée (1991) assumed that growth of *M. balthica* is inhibited during *Phaeocystis* blooms.

Mortality of mussel populations due to the exocellular polysaccharide layer of a non-flagellated member of the chrysophyceae is described by Smayda and Fofonoff (1989) and Tracey (1988). Mussels died of filtration inhibition during an extraordinarily dense brown tide of the picoalga *Aureococcus anophagefferens* in Narragansett Bay, Rhode Island.

During measurements on an artificial mussel bed in a flow-through tank, Prins *et al.* (1994) found reduced clearance rates in the mussels coinciding with a bloom of *Phaeocystis* sp. After a further mesocosm experiment Prins *et al.* (1995) suggested that grazing of mussels may be of minor importance in regulating *Phaeocystis* sp. flagellates, in contrast to changing environmental conditions such as P-limitation.

In the light of these contradictory results *Phaeocystis* was suspected to be one reason for the observed decrease in the mussel population of the Wadden Sea (Lower Saxony) within the last decade (Michaelis pers. comm.; Michaelis *et al.* 1995). This paper investigates possible effects of *P. globosa* blooms on mussel growth.

This paper concentrates on laboratory experiments on the growth of young mussels utilizing different food algae (*P. globosa* colonies, *P. globosa* single cells, the diatom *Phaeodactylum tricornutum*, the green alga *Dunaliella salina*, and artificial food). It is part of a study into the relevance of *Phaeocystis globosa* as a food source for *M. edulis* (Petri *et al.* 1995). The study includes measurements of shell growth of marked mussels in the field, laboratory evaluation of clearance rates with *P. globosa* and other algae as the food source and investigations into the influence of *P. globosa* colonies on morphological structures (gills and labial palps) of the mussels.

Materials and methods

Mussels

Young mussels, originating from the spatfall in early summer 1994, were collected in October of the same year from a natural mussel bed at Janssand (tidal inlet on Langeoog). The mean shell length at the start of the experiment was 19.6 mm (sd = 1.5). Prior to the experiments the animals were acclimatized to laboratory conditions for three weeks in ventilated 30-l tanks (closed system) with unfiltered natural sea water and artificial food TETRA AZ 400. Water was changed every week.

Algae

Dunaliella salina (CCAP 19/3) and *Phaeodactylum tricornutum* (CCAP 1052/1a) were taken from batch cultures in artificial seawater at a temperature of 22 °C and under continuous light, according to the method used by Janssen (1981). *Phaeocystis* colonies were isolated from a natural bloom near Norderney in April 1994, *Phaeocystis* single cell cultures originated from a strain cultured at NIOZ, Texel; both were cultured in non axenic batches in natural seawater (0.2 m filtered) without aeration, shaken by orbital movements at about 70 rounds per min., at a temperature of 11 ± 1 °C and a light : dark regime of 12 h : 12 h. Culture conditions correspond to the method used by Stosch and Drebes (1964), as modified by Baumann (pers. comm.) and Jahnke and Baumann (1987).

Experimental design

Experiments were carried out in 1-l beakers with 800 ml 0.7 m filtered sea water (ph 7.5 to 8.0; salinity 27.5 to 29.2 %; temperature 11 ± 1 °C; light intensity at the surface of the beakers 6 to 9 µE $m^{-2}s^{-1}$; dark:light regime 12h:12h). Ventilation was achieved by bubbling air through a Pasteur pipette fixed just above the bottom of the beaker. This, together with the ventilation current of the mussels, caused sufficient water movement to prevent sedimentation of the food algae.

Seven different feeding conditions (experimental units) were tested, each with 3 replicates (*sensu* Hurlbert 1984):

1. control: no food, starvation (0.7 m filtered natural sea water only)
2. Tetra AZ 400 (weaning food for marine fish)
3. *Dunaliella salina*
4. *Phaeodactylum tricornutum*
5. *Phaeocystis globosa* colonies
6. *Phaeocystis globosa* single cells
7. *Phaeodactylum tricornutum* + cell-free filtrate from dense cultures of *P. globosa* in colony form

Each of the 21 beakers was stocked with 15 mussels, chosen at random from the acclimatization tanks. After measurements of length and weight they were placed on grid nets with a mesh-size of 1 mm, positioned about 1 cm above the bottom of the beakers. The animals readily attached themselves to the nets and it was not necessary to destroy their byssus threads in order to change the water; sedimenting faeces or pseudofaeces did not reach the filtration range of the animals. Water was changed and beakers cleaned every 3 days to prevent bacterial growth.

In order to standardize feeding conditions, experimental units 3 to 7 were given the same number of cells per feeding (final concentration 4×10^4 cells ml^{-1}). Complete uptake of cells added was confirmed by filtration experiments (Petri *et al.* 1995, unpubl.). Food was added twice a day. Continuous feeding would have required elaborate equipment and would not have been feasible for feeding intact *P. globosa* colonies. In experimental unit 7, 25 ml of cell-free filtrate (0.2 m filter) from dense batch cultures of *P. globosa* colonies (about 200 000 colonies l^{-1}) were added, simulating the concentration of dissolved organic compounds of about 10 000 *Phaeocystis* colonies l^{-1}, a concentration typical of a dense-bloom in the Wadden Sea. Dimethyl sulfide (DMS) and acrylic acid concentrations could not be quantified with our facilities available; but the presence of these substances was confirmed by olfactory tests. In experimental unit 2, 10 mg of Tetra AZ 400 was added twice a day. Cell densities and volumes of single cells were measured with a particle counting device (Cellanalyser CASY, Schärfe System, Reutlingen).

After addition of the food suspension, the animals usually started feeding at once. Production of pseudo-faeces was not observed. No mortality was recorded during the experiment.

The Tetra dry food (experimental group 2) in suspension mainly consisted of particles between 3 and 15 m in diameter (measured by CASY system). Part of this food was lost for ingestion due to sedimentation, which was not the case in the algal suspensions. *Dunaliella* (experimental group 3) was used for bivalve filtration investigations by Winter (1969, 1973), although the nutritional value for *Mytilus* is in doubt (Janssen, pers. comm.). *P. tricornutum* (experimental group 4), a diatom characterized by a shell containing little silicate, has been repeatedly proven to be an ideal food for *Mytilus* (*e.g.* Wolters 1989, Winter 1978).

Phaeocystis colonies (experimental group 5) have not previously been used for feeding experiments with benthic filter feeders, but Kamermans (1994) showed that *Macoma balthica* can utilize single-celled *Phaeocystis* (experimental group 6). In treatment 5 the size of the colonies differed throughout the experimental period, according to the different growth phases of the stock cultures. Consequently the food suspensions contained a mix of size classes. Colony densities in the feeding suspensions were between 20 000 and 40 000 colonies l^{-1}, corresponding to dense *Phaeocystis* blooms in the Wadden Sea. In the feeding suspensions 50 to 70 % of the total number of cells were colonies (determined by 30 m reverse filtration). Uptake of live, intact *P. globosa* colonies by the mussels was proven by measuring a percentage decrease in colonies in the feeding suspension. Densities and size classes (< 300 m; 300 to 600 m; > 600 m) of colonies were counted by an image analyzing system (SIS, Soft Imaging Software GmbH, Münster) up to 30 minutes after adding feeding suspension.

Carbon content of algal cells was calculated from cell volumes according to Montagnes *et al.* (1994):

$$C = 0.109 \times V^{0.991} \qquad \text{(Equation 1)}$$

where C = C $cell^{-1}$ [pg], and V = cell volume [μm^3]

For shell measurements the mussels were fixed horizontally with plasticine (right valve down). Length (longest horizontal distance between umbo and posterior shell edge) and surface area of the left valve were measured by projection via digitized pictures under a binocular microscope using an image analysing system (SIS). During the experiments the fresh weight of live mussels was measured every two weeks, after the animals had been placed on tissue paper to remove surface moisture. For the determination of the ash-free dry weight the animals were first boiled in sea water for about 2 minutes, in order to facilitate the removal of the soft body. This procedure does not influence the weight of the soft body (Zwarts 1991). The shells and soft body were then dried at 60 °C to weight constancy and incinerated at 540 °C for 4 hours for dry and ash weight measurements (precision scale Sartorius Research RC 210 P; accuracy 0.01 mg).

Shell measurements were made on 10 or 15 individuals (3 replicates each) at days 0, 20 and 40. Meat weight measurements were made at days 20 and 40 by taking 3 replicates of pooled samples of 5 or 10 individuals.

Statistics

For statistical evaluations BMDP 88 (IBM PC/DOS, program 7D, Dixon 1988) was used. First, global null hypotheses (equality of means) were tested by classical ANOVA

(assuming equality of variances). This test was selected after testing the equality of variances by the Levene Test. Null hypotheses were rejected at 95 % significance level ($p < 0.05$). Secondly, heterogeneity of means was analysed in more detail using the Student-Newman-Keuls Multiple Range Test ($\alpha = 0.05$). This robust test procedure involves an adjusted significance level for each group of ordered means (Dixon *et al.* 1988, p. 541). BMDP outputs do not include values for the test statistics, but provide corresponding graphical information (that is, means which do not differ significantly are joined in groups by vertical bars, see Table 2). The advantage of this procedure is that results are readily available, in contrast, for example, to outputs of paired t-tests (adjusted to multiple comparisons), which would have been adequate too. We have found no contradictions in our study for the test procedures mentioned above.

Results and discussion

Table 1 gives results of the growth experiments. Means of shell measurements yielded no significant differences between feeding conditions, while meat weight measurements showed signifcant heterogeneity of means after 40 days. For comparison, Figure 1 shows percentage changes of means within the experiments.

Shell lengths and surface areas increased under all feeding conditions (4 to 14 % resp. 12 to 32 %), even without food. For shell length, no significant differences of means occurred between the experimental units 1 to 7 within 20 or 40 days ($p > 0.05$). In contrast, the two weight variables yielded significant differences ($p < 0.05$) for different feeding conditions after 40 days. Dry weight and ash-free dry weight increased or decreased during the experiment (–9 to +46 % resp. –12 to +45 %). Feeding on *P. globosa* colonies, *D. salina* and *P. tricornutum* resulted in a positive growth rate for all variables. By far the highest increase in dry weight was achieved by feeding with *D. salina* (46 % dry weight increase), followed by *P. globosa* colonies (10 % dry weight increase).

In contrast, *P. globosa* single cells caused a 4 % decrease in body dry weight, though length and surface area of the shells had increased by 9 and 12 %, respectively. Feeding with *P.tricornutum* + medium yielded similar patterns (Figure 1).

When food supply is insufficient, *M. edulis* tends to cease soft body growth, but shell growth persists (Figure 1). Similar results have been reported by Riisgård and Randløv (1981), Bricelj *et al.* (1993), Aldrich and Crowley (1986), Franz (1993) and Hilbish (1986) from field observations and laboratory experiments. Predation risk is reduced for bigger mussels (Reise 1985). This behaviour could therefore be interpreted as a trade-off strategy: *Mytilus* give up the benefits of body growth (resulting in reproductive advantages) in favour of shell growth (resulting in a better protection against predators). This is in contrast to the behaviour of *Macoma balthica*, which ceased shell growth when fed with *Phaeocystis* single cells, though it increased in body weight (Kamermans 1994). Kamermans suggested that this might be a seasonal effect due to the time of the experiments. However, since *M. balthica* burrows in the sand, a bigger size might be of less advantage where predators are concerned. Therefore *M. balthica* displays an opposite trade-off strategy: *M. balthica* resigns the profits of shell increase in favour of the advantages of body growth.

Table 1: Test for equality of means (ANOVA) between feeding conditions. ANOVA p = probability of error (equality of means of the variable at the corresponding time by classical variance analysis ANOVA, assuming equality of variances (Levene Test); level of significance $\alpha = 0.05$; null-hypotheses are to be rejected if $p < 0.050$)

	duration of experiment [days]	ANOVA p	range of means (all feeding conditions)
shell length [mm]	0	0.777	19.3 - 19.8
	20	0.533	20.3 - 21.0
	40	0.071	20.5 - 21.9
shell surface area [mm^2]	0	0.215	161 - 174
	20	0.110	183 - 197
	40	0.020	190 - 213
meat dry weight [mg]	20	0.273	30.2 - 39.3
	40	0.000	27.4 - 57.3
meat ash free dry weight [mg]	20	0.359	28.4 - 35.8
	40	0.000	25.0 - 51.9

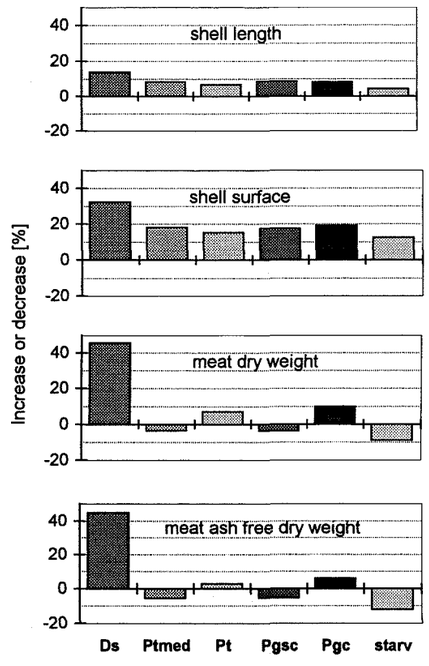

Figure 1: Percent changes (% increase or decrease) in shell length, shell area (day 0 to day 40), meat dry weight and ash-free dry weight (day 20 to day 40) of *M.edulis* held under different feeding regimes. Feeding conditions: starv = starvation, no food; *Ds* = *Dunaliella salina*; *Pt* = *Phaeodactylum tricornutum*; *P*tmed. = *P. tricornutum* + cell-free medium of *P. globosa* colonies, *P*gc = *Phaeocystis globosa* colonies; *P*gsc = *P. globosa* single cells

Table 2: Growth variables of *M. edulis*: Heterogeneity of means between feeding conditions after 40 days of defined algal diet – Student-Newman-Keuls Multiple Range Test (BMDP 7D). Bars indicate groups of means identified by the Student-Newman-Keuls Multiple Range Test (95 % level of significance). range = range of means; n = replicates of pooled samples à 15 or 10 individuals

					groups			
	feeding conditions	mean	range	n	1	2	3	4
shell length	Tetra	20.5	20.2 - 20.7	3				
[mm]	starvation	20.8	20.2 - 21.2	3				
	Phaeodactylum tricornutum	21.1	20.0 - 21.9	3				
	Phaeocystis globosa colonies	21.3	20.6 - 22.0	3				
	Phaeodactylum tricornutum + medium	21.3	21.3 - 21.4	3				
	Phaeocystis globosa single cells	21.4	21.2 - 21.5	3				
	Dunaliella salina	21.9	21.3 - 22.4	3				
shell surface	Tetra	190	184 - 193	3				
[mm^2]	starvation	190	186 - 197	3				
	Phaeodactylum tricornutum	195	181 - 206	3				
	Phaeodactylum tricornutum + medium	199	196 - 203	3				
	Phaeocystis globosa colonies	204	194 - 215	3				
	Phaeocystis globosa single cells	204	202 - 206	3				
	Dunaliella salina	213	204 - 219	3				
meat dry	starvation	27.4	24.8 - 30.0	3				
weight [mg]	*Phaeocystis globosa* single cells	31.7	31.4 - 31.9	3				
	Tetra	32.7	30.1 - 34.5	3				
	Phaeodactylum tricornutum + medium	34.2	32.9 - 35.1	3				
	Phaeodactylum tricornutum	34.7	29.2 - 37.6	3				
	Phaeocystis globosa colonies	41.2	38.5 - 44.7	3				
	Dunaliella salina	57.3	53.7 - 59.8	3				
meat ash free	starvation	25.0	22.6 - 37.4	3				
dry weight	*Phaeocystis globosa* single cells	28.0	27.7 - 28.4	3				
[mg]	Tetra	29.1	26.4 - 31.0	3				
	Phaeodactylum tricornutum + medium	29.9	28.9 - 30.6	3				
	Phaeodactylum tricornutum	30.4	25.3 - 33.3	3				
	Phaeocystis globosa colonies	35.8	33.6 - 38.8	3				
	Dunaliella salina	51.9	48.9 - 54.0	3				

Riisgård and Randløv (1981) used *M. edulis* measuring 16 to 20 mm for 40-day growth experiments with a continuous supply of *P. tricornutum*. Shells increased by 5 to 130 µm day^{-1}. Nielsen and Stromgren (1991) reported a growth rate of 62 µm day^{-1} when *M. edulis* were fed continuously with *Isochrysis galbana* and *Tetraselmis suecica*; however, toxic algae like *Chrysochromulina polylepis* and *Gyrodinium aureolum* inhibited shell growth. Shell growth rates observed in this study of 34 to 68 µm day^{-1} compare favourably with the results cited above and prove that pulse feeding (this study) and continous feeding (Riisgård and Randløv 1981) result in a similar range of growth rates.

Feeding on *D. salina* and *P. tricornutum* resulted in numerous living algal cells occurring in the mussel faeces during the first days of the experiments. After one week, however, the faeces were found to be virtually cell free; obviously all cells were now being digested. In the case of *D. salina*, within one week the faeces turned from greenish (intact cells) to brown (only digested cells). When feeding on *P. globosa*, no intact cells were observed in the faeces throughout the experiment. These observations agreed closely with results reported by Stromgren and Cary (1984) about the adaptability of *Mytilus* to varying feeding conditions.

Concerning the uptake of *P. globosa* colonies, image analysis showed that > 80 % of the colonies of all size classes were taken up by the mussels within 30 minutes after adding feeding suspensions (5000 to 100 000 colonies l^{-1}, n = 13).

In order to show which feeding conditions contributed to the results of ANOVA after 40 days of experiment (Table 1), the Student-Newman-Keuls-Test was used for group-formation of means. Groups of means considered to be equal are indicated by bars (Table 2).

Regarding shell length, all feeding conditions form a single group, while shell surface area comprises two strongly overlapping groups: one group of all feeding conditions except *D. salina*, and an alternative group of all values except starvation and Tetra. As for soft body dry weight and ash-free dry weight, four and three groups were identified respectively. In both cases *P. globosa* colonies and *D. salina* have the highest means and constitute separate groups. In contrast to shell measurements, soft body weight seems a suitable indicator for the varying nutritional values of different food items.

In contrast to *P. globosa* single cells, colonies resulted in body weight increase. The colonies were either filtered more effectively, or the mucus from the colonies is of additional nutritional value to the mussels. This view is in contradiction to Lancelot and Mathot (1985) and Veldhuis *et al.* (1986), who supposed the mucus cover to be of low nutritional value to consumers.

Figure 1 shows that *P. tricornutum* yielded an increase in soft body weight. However, if medium from dense *P. globosa* cultures was added to the *P. tricornutum* solution, increase in meat weight was inhibited. This was possibly due to DMS and acrylic acid emitted by the *P. globosa* colonies. However, no growth inhibition was observed when the food was *P. globosa* colonies. Results from filtration-rate experiments (Petri *et al.* 1995) suggest a tentative explanation for this apparent contradiction: In both experimental units the same limited number of *P. tricornutum* cells was available. When *P. globosa* medium was added to the *P. tricornutum* suspension, this triggered a higher feeding activity (reflected in a significantly higher clearance rate; Petri *et al.* 1995), but without

Table 3: Total amount of algal cells and estimated sum of carbon available per mussel within 40 days of investigation. * Montagnes *et al.* 1994, see material and methods for equation; a = Weisse and Scheffel-Möser 1990; b = Rousseau *et al.* 1990; c = Montagnes *et al.* 1994; d = Prins and Smaal 1989; ind. = individual mussel

Algae species	Cell volume [μm^3]	C cell^{-1} [pg] (calculated*)	C cell^{-1} [pg] (literature data)	Σ cells x 10^9 ind.$^{-1}$	Σ C ind.$^{-1}$ [mg]
P. globosa colonies	101.7 ± 16.5	11	9.5[a]	1.29	14.2
P. globosa single cells	105.6 ± 7.4	11	9.5[a] 10.8 – 14.2[b]	1.42	15.6
D. salina	644.8 ± 47.7	70	30 – 63[c]	1.33	93.1
P. tricornutum and *P.t.* + med.	54.5 ± 3.4	6	6.1 ± 0.5[d]	1.72	10.3

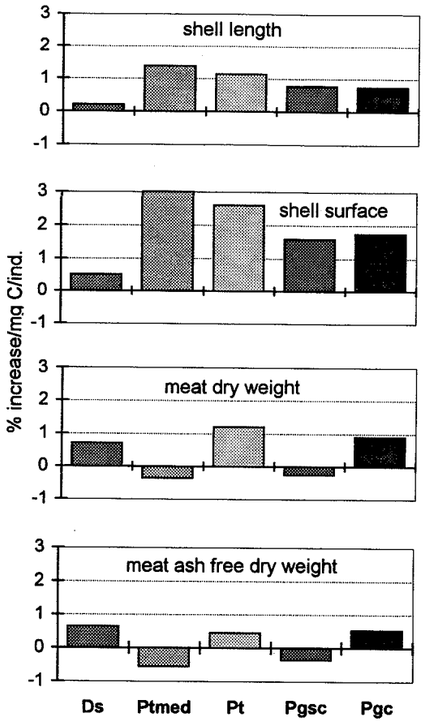

Figure 2: Utilization of different algal species by *M. edulis* during a feeding experiment: Increase in shell measurements and body weight per mg carbon content of algal cells available per individual mussel within 40 days (% increase/mg C/ind.) (see Figure 1 for details of feeding conditions)

the possibility of providing more algal cells. Therefore feeding on *P. tricornutum* + medium resulted in higher energy cost without higher energy yield for the mussels. This might result in an unfavourable energy balance, leading to weight loss. Targett and Ward (1991) stated that extracellular microalgal metabolites can significantly affect both filtration rates and particle selection in the bivalve *Mytilus edulis*. The degree and type of response observed depend upon the microalgal species and the nature and concentration of the bioactive metabolites. Similarly, stimulatory effects of soluble metabolites of *Chaetoceros muelleri* on clearance rates of *Plactopecten magellanicus* were reported by Ward and Cassell (1991).

To summarise, we can state that young *M. edulis* (ca. 20 mm shell length) are able to use colonies of *P. globosa*, as well as *P. tricornutum* and *D. salina* to build up biomass. The same amount of motile single cells of *P. globosa* does not cause an increase in soft body weight. Though *P. globosa* is suspected to have negative effects on filter feeders (Pieters *et al.* 1980, Obert and Michaelis 1989), neither *P. globosa* colonies nor single cells have an inhibitory effect; in contrast, *P. globosa* colonies are a suitable food source for *M. edulis*. These results support the findings of Prins *et al.* (1994), who measured an experimental mussel bed in a tank. They found the fastest increase in ash-free dry weight of mussels during a bloom of *Phaeocystis* sp., whereas they recorded reduced clearance rates at the same time. This result supports the suitability of *Phaeocystis* colonies for mussel feeding.

Table 3 gives the volume and specific carbon content of the algae, along with the sum of carbon available to each individual mussel during the 40-day feeding experiment (Σ C ind^{-1} [mg]). The percent weight increase per mg carbon available (Figure 2) suggests effective utilization of *P. globosa* colonies and *P. tricornutum*. *D. salina* was utilized less effectively. This might be caused to some extent, by the high cellulose content of these cells.

The results of the present investigation require a new appraisal of the digestibility and utilization of *P. globosa* (especially in the colonial form dominant in blooms) by a common filter-feeder, like *M. edulis*. Therefore, existing models concerning the fate of *Phaeocystis* blooms (Lancelot *et al.* 1989, Thingstad and Billen 1994, Wassmann 1994) have to be extended to the compartment of filter-feeding macrozoobenthos, *e.g. M. edulis*. Further investigations are necessary to evaluate energy expediture in the uptake of *P. globosa* by filtering organisms, including *Mytilus* in the field.

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