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Phaeocystis globosa (Prymnesiophyceae) and the planktonic food web: Feeding, growth, and trophic interactions among grazers

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Abstract

The feeding and growth of copepods and heterotrophic protozoans when fed *Phaeocystis globosa* (Prymnesiophyceae) single cells were studied in the laboratory. The calanoid copepod *Acartia tonsa* fed on *P. globosa* at low clearance rates (<20 ml ind^{-1} d^{-1}). *P. globosa* appeared to be a poor diet for *A. tonsa* in terms of fatty acid composition, yielding a low egg production rate (0–4.5 eggs ind^{-1} d^{-1}) and an egg production efficiency (EPE; increase in egg production/increase in ingestion) close to zero, in contrast to an EPE of 35% when *Rhodomonas salina* (Cryptophyceae) was offered as food. Nauplii of *A. tonsa* feeding on *P. globosa* suffered higher mortality and arrested development relative to those feeding on *R. salina.* Among the three ciliates and two dinoflagellates tested, ingestion rates on *P. globosa* single cells increased with the protozoan cell size, and the growth yield in terms of biovolume ranged from 9 to 78%. We studied the trophic interactions among grazers in *P. globosa*-based food chains. *Gyrodinium dominans* (dinoflagellate) growing on *P. globosa* improved the nutritional quality of *P. globosa* by 7.8 times for *A. tonsa,* such that *A. tonsa* feeding on *G. dominans* as an intermediate prey had an EPE of 35%. The ciliate *Mesodinium pulex* also exploited *P. globosa* indirectly by consuming the dinoflagellate *Gymnodinium* sp. as an intermediate prey. Our study showed that the trophic efficiency of a system dominated by *P. globosa* is dependent on the complex food-chain structures within the planktonic food web.

Phaeocystis (Prymnesiophyceae) is a globally distributed phytoplankton genus that often dominates the phytoplankton communities in temperate and polar oceans (reviewed in Lancelot et al. 1998). Frequent and massive blooms of *Phaeocystis* often constitute environmental nuisances in coastal waters (reviewed in Weisse et al. 1994). For any phytoplankton bloom to develop, the accumulation rate of the phytoplankton cells (e.g., due to growth) must exceed the loss rate (e.g., due to grazing). Thus, knowledge of the trophic responses of grazers to *Phaeocystis* is essential to understanding the potential top-down control of *Phaeocystis* bloom development. Past studies have focused on one prey–one predator interactions (e.g., reviewed in Weisse et al. 1994), yet the bloom dynamics of *Phaeocystis* may be affected by complex interactions among different groups of grazers. For example, copepod predation on protozoans could reduce the overall grazing pressure on *Phaeocystis,* thus facilitating bloom development (Hansen et al. 1993). Although grazing on *Phaeocystis* has been studied frequently, little is known about its nutritional value for grazers. Studies thus far have shown that *Phaeocystis* supports low egg production in copepods (Verity and Smayda 1989) and suboptimal growth in heterotrophic protozoans (Hansen et al. 1993). In conjunction with the view of complex trophic interactions within the food web, one needs to consider possible change of food quality along *Phaeocystis*-based food chains. A recent study has shown that protozoans may improve the food quality of algae for higher predators by acting as intermediate prey (Klein Breteler et al. 1999). Thus, it is possible that higher predators may obtain a better nutrition from *Phaeocystis* blooms by feeding on intermediate prey. For grazers such as copepods, whose life cycle involves a drastic change in body size and feeding habit (Berggreen et al. 1988), it is also necessary to consider the impacts of *Phaeocystis* on different life stages of these grazers (e.g., Verity and Smayda 1989; Hansen et al. 1990).

We studied the feeding and growth responses of protozoan and metazoan grazers to *Phaeocystis globosa* single cells. Although the *P. globosa* life cycle involves single-cell and colonial stages, we focused on single cells because this is the dominant form of *P. globosa* at the beginning of a bloom (Rousseau et al. 1994); thus, grazing on single cells could potentially suppress bloom development (Weisse and Scheffel-Möser 1990). The heterotrophic protozoans and copepods used in the experiments represent some of the most common planktonic grazers in temperate coastal waters. The trophic value of *P. globosa* was compared with that of other diets. We also studied the interactions among grazers in differently structured *Phaeocystis*-based food chains. Our goal was to investigate how the food-chain structures affect the trophic significance of *P. globosa* in the planktonic system.

Materials and methods

Phytoplankton—A nonaxenic strain of *P. globosa* (CCMP1528) was obtained from the Bigelow Laboratory in Maine that was originally isolated from the Pacific Coast of South America. *Rhodomonas salina* (Cryptophyceae) and *Isochrysis galbana* (Prymnesiophyceae) were obtained from

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Table 1. Heterotrophic protozoans and prey species used in the present study. ESD = mean equivalent spherical diameter in micrometers, measured by ocular micrometer or *Elzone particle counter. Cell carbon content is estimated according to Strathmann (1967).

	Cell size (ESD±SD)	References on species identification
Predators		
Ciliates		
L. oviformis	17±1	Lynn and Montagnes (1988)
R. conicum	25±3.7	Agatha and Riedel-Lorje (1998)
S. vestitium	19±2	Agatha and Riedel-Lorje (1997)
Naked heterotrophic dinoflagellates		
G. dominans	15±1	Hansen and Larsen (1992)
Gymnodinium sp.	4.5*	Jakobsen and Hansen (1997)
Prey (Prymnesiophytes)		Cell carbon content (pg C cell^{-1})
I. galbana	4.2*	8.2
P. globosa	4.4*	9.3
R. salina	6.9*	29.8

the University of Copenhagen, Denmark. Batch phytoplankton cultures were maintained in exponential growth in L-medium (Guillard and Hargraves 1993) at 19 ± 1°C, 60–100 μE m^{-2} s^{-1}, with a 12-h : 12-h light : dark (LD) cycle. Single cells of *P. globosa* were obtained by gravity filtration of the culture through an 11-μm sieve. Cell size was measured by an Elzone 180 particle counter, and cell abundance was determined by either the particle counter or microscopic count of preserved samples (1–4% Lugol's solution). Cell carbon concentrations were estimated from cell size according to Strathmann (1967).

Grazers—We used the calanoid copepod species, *Acartia tonsa*, that commonly coexists with *Phaeocystis* in coastal waters (e.g., Weisse 1983; Verity and Smayda 1989). The copepods originated from a continuous culture kept at the Danish Institute for Fisheries Research. Protozoans were collected at the Øresund (the strait separating Denmark and Sweden) and were concentrated from seawater by gravity on an 11-μm sieve. Because of the similar size between *I. galbana* and *P. globosa* single cells, small amounts of *I. galbana* were added to the raw seawater to enhance growth of heterotrophs feeding within this particular prey size window. Once growth of protozoans was observed, typically within 1–2 wk, individual cells were isolated and maintained in 0.2 μm filtered 32-psu seawater treated in a microwave oven (Keller et al. 1988) with L-nutrients added (Guillard and Hargraves 1993). Either *I. galbana* or *P. globosa* single cells were added as food. Some of the protozoan species were kindly identified by S. Agatha (Universitaet Salzburg, Austria). The protozoan and prey species used are summarized in Table 1.

Copepod feeding experiments—Feeding experiments were done with the conventional bottle incubation method (Frost 1972) at 19 ± 1°C, 2 μE m^{-2} s^{-1}, with a 12 : 12 LD cycle. *A. tonsa* females with spermatophores were acclimated to different concentrations of *P. globosa* single cells under the experimental conditions for 24 h, then incubated for another 24 h. At the end of the experiments, eggs and fecal pellets were collected on a submerged 11-μm sieve. Egg carbon content was assumed to be 45.7 ng C egg^{-1} (Kiørboe et al. 1985).

Copepod egg production efficiency experiments—Experiments were conducted to compare the nutritional value of *P. globosa* single cells and *R. salina* for *A. tonsa. Rhodomonas* sp. is known to be a good diet for egg production in *A. tonsa* (Jónasdóttir 1994), and *R. salina* has been used regularly as food for our *A. tonsa* cultures. To eliminate the compounding factors of female age and physiological conditions, the two diets were tested in parallel incubations using *A. tonsa* from the same cohorts (3–5 wk old from hatching). Female individuals were acclimated for 24 h to the experimental diet of either *P. globosa* or *R. salina*, then incubated for another 24 h, and egg and fecal pellet productions were measured. The nutritional values of the two diets were compared based on the egg production efficiency (EPE) of the copepods. EPE is here defined as increase in egg production per unit of increase in ingestion; thus, EPE indicates how efficient the copepods convert the newly ingested materials to egg production and is derived from the slope of linear regression between egg carbon production and food carbon ingestion. The nutritional contents of *P. globosa* and *R. salina* were also compared with respect to their fatty acid compositions. Fatty acids of the phytoplankton cells were extracted with chloroform/methanol and analyzed by gas chromatograph as described in Jónasdóttir (1994).

Nauplii survival and development experiments—Newly hatched *A. tonsa* nauplii were incubated individually at 19 ± 1°C in multiwell plates; each well was filled with either *P. globosa* single cells or *R. salina* at a carbon concentration of 500 μg C L^{-1} for near maximum growth rate (Berggreen et al. 1988). Mortality and development of the nauplii to copepodites were recorded every day. About 80% of the medium in each well was removed daily with a pipette and replaced with fresh medium to replenish the food.

Feeding and growth experiments with heterotrophic protozoans—We compared the feeding and growth of heterotrophic protozoans on *I. galbana* and *P. globosa* single cells at saturating food concentrations (>160 μg C L^{-1}). The protozoans were acclimated to the experimental diets for at least five cell divisions prior to the experiments. Grazing and growth experiments were run in triplicate with parallel prey controls. Incubation was done on a rotating plankton wheel (0.5 rpm) under an irradiance of 20 μE m^{-2} s^{-1}. Samples were taken for cell counts every 24 h at a fixed time of day to eliminate potential diurnal variations in feeding and growth rates of the protozoans. Ingestion rates (U) of the protozoans were estimated from changes in prey cell numbers in treatments compared to prey densities in controls. These calculations were based on an iterative approach described in Jakobsen and Hansen (1997). Briefly, the change in prey (x) and predator (y) concentrations over time t are described by

$$\frac{dx}{dt} = \mu_x x - Uy \quad (1)$$

$$\frac{dy}{dt} = \mu_y y \quad (2)$$

This iterative approach assumes that the concentrations of prey and predator increase exponentially at constant rates μ_x and μ_y, respectively. The prey mortality induced by predators is Uy (where U is per capita ingestion rate) and was calculated iteratively on a computer with steps of 0.01 h. Daily ingestion and growth rates were averaged over 1–2 d. Biovolume of phytoplankton was measured by particle counter. Cell sizes of the protozoans were measured by an inverted microscope equipped with an ocular micrometer. The biovolume of protozoans was calculated from the linear dimensions using appropriate volumetric formulae. Growth yield of the protozoan in terms of biovolume was calculated as

$$\text{Growth yield (\%)} = \frac{\mu_y \times V_y}{U \times V_x} \quad (3)$$

where V_x and V_y are the biovolume of phytoplankton and protozoan, respectively. Expressions of ingestion and growth rates in terms of biovolume allow us to compare our results with literature values (*see* ''Discussion'').

Food-chain structure experiment I—We conducted experiments to compare the EPE of *A. tonsa* feeding on *P. globosa* single cells only and when *Gyrodinium dominans* (heterotrophic dinoflagellate) was present as an intermediate prey. *G. dominans* was grown for >10 divisions with *P. globosa* single cells as food; thus, ~100% of the *G. dominans* cells were presumably derived from *P. globosa* materials. To calculate the carbon intake by *A. tonsa*, we converted the biovolume of *G. dominans* to a cell carbon content of 0.27 ng C cell^{-1} according to Menden-Deuer and Lessard (2000). Copepods were acclimated to the experimental diets for 48 h prior to experiments. Triplicates of 10 *A. tonsa* females were incubated for 24 h with either *P. globosa* single cells (25 μg C L^{-1}) (experimental setup A) or a mixture of *P. globosa* (25 μg C L^{-1}) and *G. dominans* (27 μg C L^{-1}) (experimental setup B). Primary control contained *G. dominans* and *P. globosa* (duplicate), and secondary control contained *P. globosa* only (duplicate). We measured the egg productions by *A. tonsa* in both experimental setups. Ingestion rate of *A. tonsa* on *P. globosa* in experimental setup A was calculated according to Frost (1972). For experimental setup B (mixed diet), ingestion rates on *G. dominans* and *P. globosa* had to be calculated separately. Ingestion rate on *G. dominans* was calculated according to Frost (1972) using the specific growth rate of *G. dominans* from the primary control. *P. globosa* in experimental setup B was subject to grazing by both *A. tonsa* and *G. dominans*, with the latter being preyed upon by *A. tonsa* at the same time. Thus, the ingestion rate of *A. tonsa* on *P. globosa* in setup B was calculated by solving coupled nonlinear equations as explained below.

Changes in *P. globosa* and *G. dominans* concentrations per time t in experimental setup B are described by the following two equations:

$$\frac{dP}{dt} = (\mu_p - g_c CV - g_z Z)P \quad (4)$$

$$\frac{dC}{dt} = (\mu_c - h_z Z)C \quad (5)$$

where P = cell concentration of *P. globosa*, C = cell concentration of *G. dominans*, Z = number of *A. tonsa*, and V = volume of experimental setup. μ_c is specific growth rate of *G. dominans* determined from primary control (time^{-1}), and μ_p is specific growth rate of *P. globosa* determined from secondary control (time^{-1}). h_z is per capita feeding coefficient of *A. tonsa* on *G. dominans* according to Frost (1972) (copepod^{-1} time^{-1}). g_c = per capita feeding coefficient of *G. dominans* on *P. globosa* (dinoflagellate^{-1} time^{-1}), estimated as the difference in *P. globosa* specific growth rates between the primary and secondary controls divided by the average number of *G. dominans* in the primary control. The unknown, g_z, is per capita feeding coefficient of *A. tonsa* on *P. globosa* (copepod^{-1} time^{-1}). Equation 4 describes the time rate of change of *P. globosa* (P) due to growth ($\mu_p P$) and grazing by both *G. dominans* ($-g_c VCP$) and *A. tonsa* ($-g_z ZP$). Coupled to this, Eq. 5 describes the time rate of change of *G. dominans* (C) due to growth ($\mu_c C$) and predation by *A. tonsa* ($-h_z ZC$). The solution to Eqs. 4 and 5 can be written as

$$P(t) = P_0 \exp\left[(\mu_p - g_z Z)t - g_c V \int_0^t C(t)\, dt\right] \quad (6)$$

$$C(t) = C_0 \exp[(\mu_c - h_z Z)t] \quad (7)$$

where P_0 and C_0 are the initial cell concentrations of *P. globosa* and *G. dominans*, respectively, and Z is the number of *A. tonsa* constant during the experiment. Substituting Eq. 7 into the integral term in Eq. 6 gives

$$P(t) = P_0 \exp\left\{(\mu_p - g_z Z)t - \frac{g_c C_0 V}{h_z Z - \mu_c}[1 - \exp((\mu_c - h_z Z)t)]\right\} \quad (8)$$

Equation 8 describes the time variation of *P. globosa* due to growth and ingestion by both *G. dominans* and *A. tonsa*. The exponential term within the exponential represents the change in concentration of *G. dominans* due to growth and predation and the subsequent effect of its grazing on *P. globosa*. The only unknown in the equation is the coefficient g_z of *A. tonsa* feeding on *P. globosa*. If the duration of the experiment is T, and the observed concentration of *P. globosa* after that time is P_T, then g_z can be calculated from

$$g_z = \frac{\ln(P_0) - \ln(P_T) + \mu_p T}{ZT} - \frac{g_c C_0 V}{ZT(h_z Z - \mu_z)}\{1 - \exp[(\mu_c - h_z Z)T]\} \quad (9)$$

The calculated g_z can then be used to evaluate Eq. 4, and the net per capita ingestion rate (I_{pz}) of *A. tonsa* on *P. globosa* during the entire experiment can be determined by in-

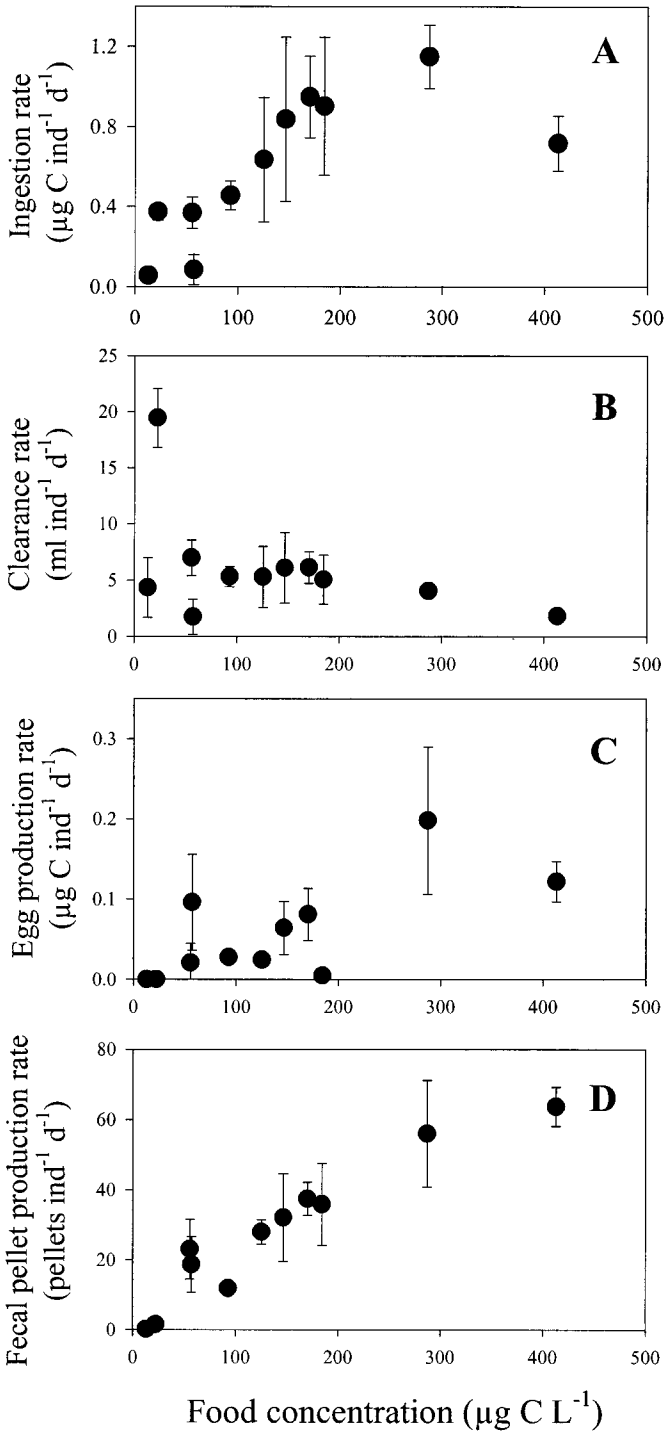

Fig. 1. Trophic responses of *A. tonsa* to *P. globosa* single cells as functions of food concentration. (A) Ingestion rate; (B) clearance rate; (C) egg production rate; and (D) fecal pellet production rate. Error bars are standard deviations of triplicates.

tegrating the instantaneous ingestion rate (third term on the right-hand side of Eq. 4).

$$I_{pz} = \frac{Vg_z}{T} \int_0^T P(t)\, dt \qquad (10)$$

Unfortunately, there is no general analytic solution to this integral given the form of $P(t)$ in Eq. 8, and Eq. 10 has to be solved by numerical integration. In cases where the difference between P_0 and P_T is small, Eq. 10 can be simplified to $I_{pz} \approx Vg_z(P_0 + P_T)/2$.

Food-chain structure experiment II—The common coastal ciliate *Mesodinium pulex* (ESD = 14.9 µm) was used as predator and was acclimated to the experimental diets for >48 h prior to experiments. *M. pulex* (20 ml^{-1}) was incubated (triplicate) for 24 h with either *P. globosa* single cells (2×10^4 cells ml^{-1}) or a mixture of *P. globosa* single cells (2×10^4 cells ml^{-1}) and the dinoflagellate *Gymnodinium* sp. (3,000 cells ml^{-1}). The dinoflagellate had been growing on *P. globosa* for more than five divisions before the experiments. Triplicate controls with *P. globosa* only and triplicate controls with *Gymnodinium* sp. and *P. globosa* were run at the same time. Ingestion and growth of *M. pulex* were calculated as explained in Eqs. 1–3.

Results

Trophic responses of A. tonsa—The ingestion rate of *A. tonsa* on *P. globosa* single cells increased up to a concentration of 300 µg C L^{-1} (Fig. 1). The maximum ingestion rate was 1.2 µg C ind^{-1} d^{-1}. The clearance rate of the copepods remained mostly <10 ml ind^{-1} d^{-1}. Egg production rate was low, at 0–4.3 eggs ind^{-1} d^{-1}, equivalent to 0–0.2 µg C ind^{-1} d^{-1}. Fecal pellet production increased almost linearly with food concentration, up to about 65 pellets ind^{-1} d^{-1} (Fig. 1).

Comparison of P. globosa *and* R. salina—*A. tonsa* ingested *R. salina* at a higher rate, which translates into a higher carbon intake rate (Fig. 2A,B). Egg production rate of *A. tonsa* was 0.02–0.15 µg C ind^{-1} d^{-1} with *P. globosa* and 0.16–2.7 µg C ind^{-1} d^{-1} with *R. salina* (Fig. 2C,D). Fecal pellet production rate was 1–18.5 pellets ind^{-1} d^{-1} with *P. globosa* and 26–90 pellets ind^{-1} d^{-1} with *R. salina* (Fig. 2E,F). EPE of the copepods, derived as the slope of the regression line between egg production and ingestion, was not different from zero with *P. globosa* ($p > 0.05$) and 35% with *R. salina* ($p < 0.05$) (Fig. 2C,D). When we pooled data from all the *P. globosa* experiments, which include ingestion rates up to 1.4 µg C ind^{-1} d^{-1}, the overall EPE was still not different from zero (Fig. 3). The fatty acid compositions of the two diets are shown in Table 2. The relative concentrations of saturated, monounsaturated, and polyunsaturated fatty acids were similar between the two diets. However, *R. salina* was relatively rich in ω3 polyunsaturated fatty acids and had a higher 22 : 20 ratio.

Copepod nauplii survival and development—In the *R. salina* treatment, nauplii began to molt to copepodites on day 5, and most of the surviving nauplii developed to copepodites within 7 d (Fig. 4). After 13 d, a total of 63% of the nauplii in the *R. salina* treatment had survived and developed to copepodites. In contrast, no nauplii in the *P. globosa* treatment developed past the naupliar stages, and a mortality of 98% was recorded within 13 d (Fig. 4).

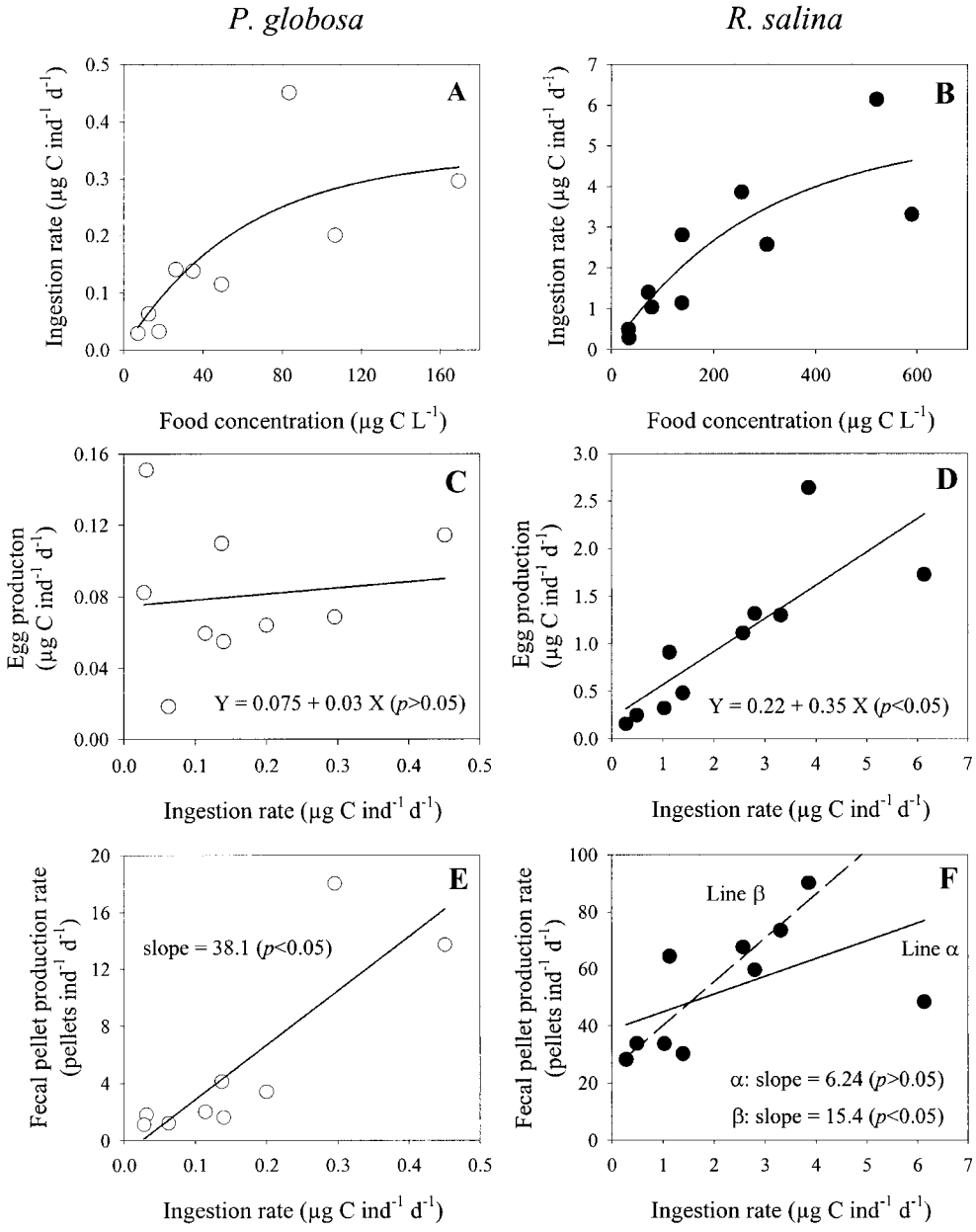

Fig. 2. Comparative study of *P. globosa* single cells and *R. salina* for *A. tonsa.* (A and B) Ingestion rate as functions of food concentrations. Data are fitted to the exponential function $y = a(1 - e^{-b}x)$ at $p < 0.05$. (C and D) Egg production as functions of ingestion rates. Data are fitted to linear regressions. (E and F) Fecal pellet production rate as functions of ingestion rates. Data are fitted to linear regressions.

Feeding and growth of protozoans—There were large variations among the tested species in their responses to the two diets (Fig. 5). *Lohmanniella oviformis* had higher ingestion and growth rates on *I. galbana* than on *P. globosa.* Despite the significantly higher feeding rate of *Rimostrobidium conicum* on *P. globosa,* most of the ingested material was not transformed into new biomass, and the growth yield was <10%. In contrast, *R. conicum* grew efficiently on *I. galbana,* with a growth yield of 40%. *Strombidium vestitum* ingested and grew at higher rates on *P. globosa* than on *I. galbana,* but the growth yield was equally low for both diets, at <20%. *G. dominans* ingested *P. globosa* at a higher rate than *I. galbana* but grew at a similar rate on both diets (0.7 d^{-1}), resulting in a lower growth yield with the *P. globosa* diet. Note that the growth yield of *G. dominans* with *I. galbana* exceeded 100%, and the growth yield with *P. globosa* was also abnormally high (78%). Since the growth yield was calculated based on cell volume, the apparent growth yield would be inflated by a low carbon-to-volume ratio of the cells, which is not uncommon among naked heterotrophic dinoflagellates (Menden-Deuer and Lessard 2000). Nevertheless, these results indicate that *G. dominans* could trans-

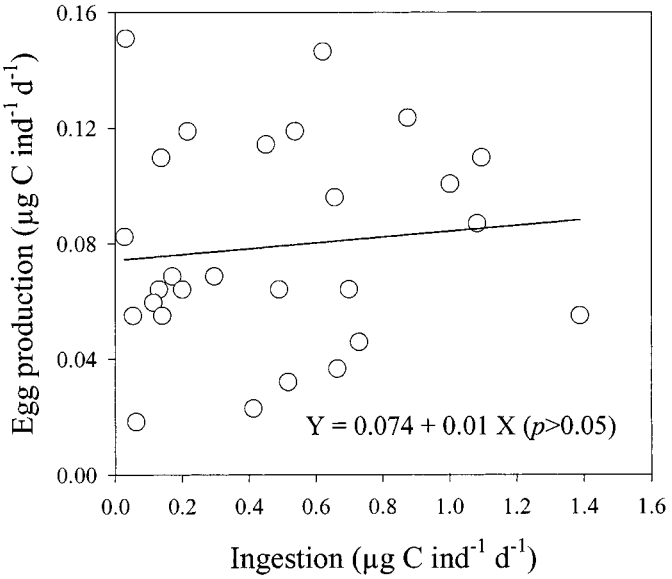

Fig. 3. Egg production of *A. tonsa* as a function of ingestion rate for all experiments with *P. globosa* single cells. Data are fitted to linear regression.

Table 2. Fatty acid composition of *P. globosa* single cells and *R. salina* expressed as % total (average of four measurements). SAFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; 22:20 is the ratio between 22:6 (ω3) and 20:5 (ω3); ω3 (%) is the percentage of ω3 polyunsaturated fatty acids.

	Relative concentration	
Fatty acid	*P. globosa*	*R. salina*
13:0	0	0.442
14:0	6.9	8.96
14:1?	0.17	0
15:0	1.32	1.05
16:0	14.20	15.27
16:1(ω9)	3.82	2.87
16:1(ω7)	6.56	7.96
Unknown unsaturated C_{16}	0	2.21
16:2	0.57	0.54
Unknown	7.42	2.13
18:0	6.43	4.83
18:1(ω9)	16.55	7.69
18:1(ω7)	0.87	3.31
18:2(ω6)	23.23	3.91
18:3(ω3)	1.03	10.09
18:4(ω3)	5.06	14.00
20:0	0	1.52
20:1(ω9)	0.41	0.60
20:2(ω6)	4.28	5.00
20:4(ω3)	0	0.69
20:5(ω3)	1.16	5.77
22:6(ω3)	0	1.18
Total	100	100
SAFA	28.85	32.05
MUFA	28.39	22.43
PUFA	35.33	40.48
22:20	0	0.20
ω3(%)	7.25	31.72

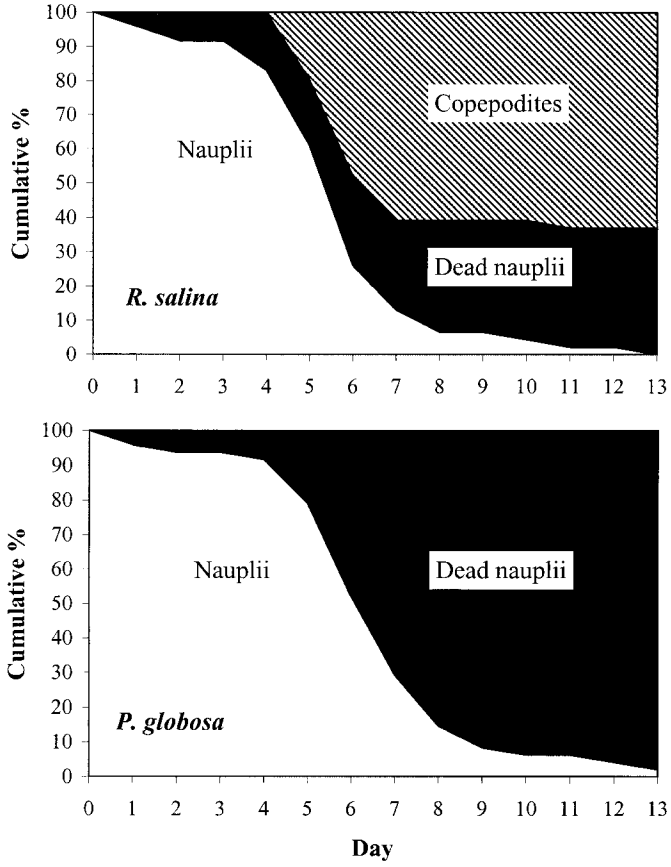

Fig. 4. Cumulative percentages of *A. tonsa* nauplii (white area), dead nauplii (black area), and copepodites (stripped area) in *R. salina* (upper panel) and *P. globosa* (lower panel).

form ingested *I. galbana* and *P. globosa* to cellular material quite efficiently. The small dinoflagellate *Gymnodinium* sp. fed slightly more efficiently on *I. galbana* than on *P. globosa*, although the difference was not significant. The ingestion rate (1–3 cells ind^{-1} d^{-1}) was consistent with previous results for this particular *Gymnodinium* sp. (Jakobsen and Hansen 1997). *Gymnodinium* sp. grew faster in *I. galbana* than in *P. globosa*, but the growth yield was not different, at about 44–48%.

Food-chain structure experiment I—In the direct-grazing food chain, *A. tonsa* grazed on *P. globosa* single cells at a rate of 1.6 µg C ind^{-1} d^{-1} (Fig. 6B), comparable to prior experiments (Fig. 1). When *G. dominans* was present as intermediate prey, *A. tonsa* fed predominantly on *G. dominans*, whereas direct grazing on *P. globosa* was reduced (Fig. 6A). Despite the lower total ingestion in the mixed-prey treatment, egg production rate of *A. tonsa* was significantly higher (Student's *t*-test, $p < 0.05$; Fig. 6C,D). To compute the EPE for *A. tonsa*, we first corrected the egg carbon production for background based on the y-intercept of the regression equation from previous experiments (Fig. 3), then calculated the EPE as corrected egg carbon production divided by carbon ingestion. The EPE of *A. tonsa* was 4.5% for the direct-grazing food chain (Fig. 6F), close to the EPE derived from the larger data sets (slope of regression lines in Figs.

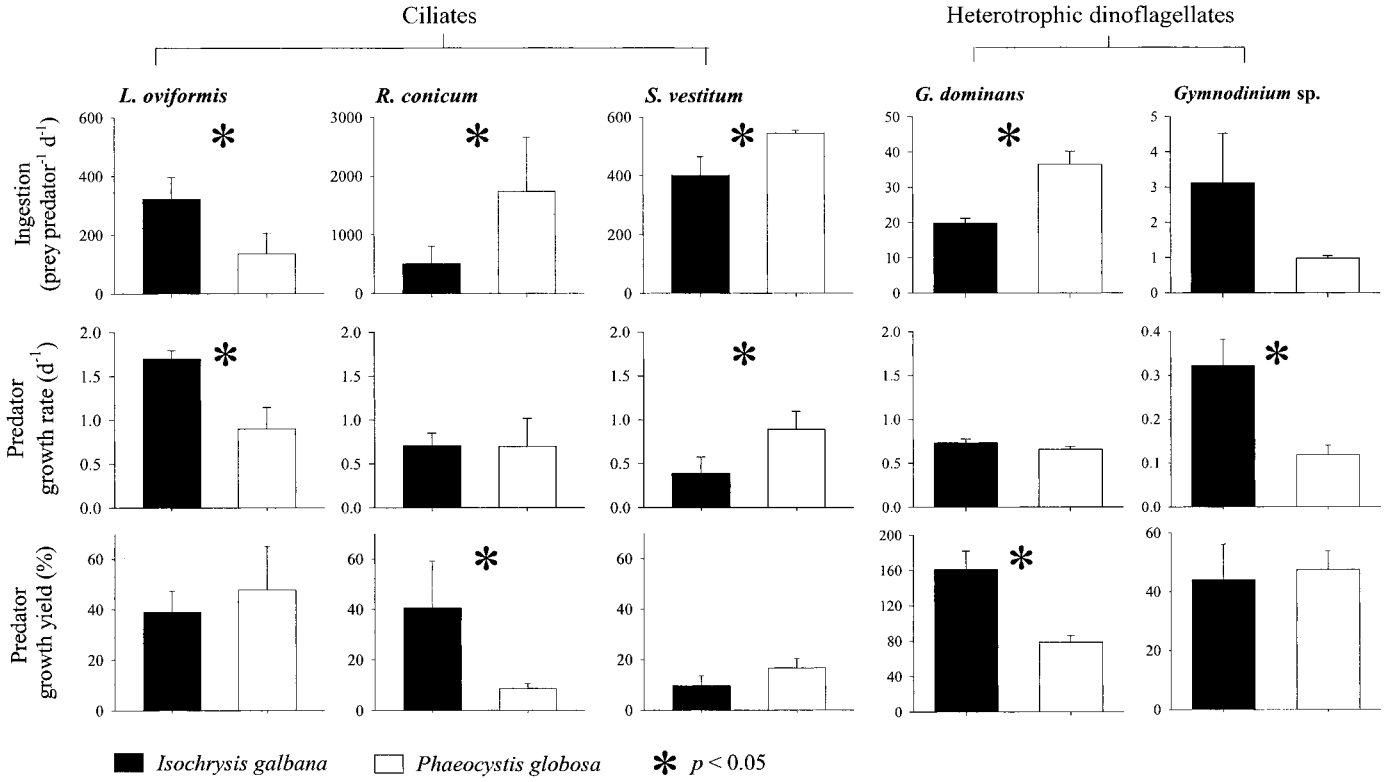

Fig. 5. Ingestion rate, growth rate, and growth yield of heterotrophic protozoans when fed *I. galbana* or *P. globosa* single cells. Error bars are standard deviations of triplicates. *Significant difference between diets was tested with Student's *t*-test or Mann–Whitney rank sum test.

2C, 3). EPE was significantly higher in the mixed-prey treatment, at 35% (Student's *t*-test, $p < 0.05$; Fig. 6E). Note that the regression model of Menden-Deuer and Lessard (2000) tends to overestimate the carbon contents of naked dinoflagellates; thus, our estimate of EPE for *A. tonsa* in the mixed-prey treatment was indeed conservative. Nevertheless, the higher EPE in the mixed-prey treatment indicates that *G. dominans* significantly improved the food quality of *P. globosa* by 35/4.5 or 7.8 times for *A. tonsa.*

Food-chain structure experiment II—M. pulex did not feed on *P. globosa* single cells and had a negative growth (-0.38 d^{-1}), indicating starvation (Table 3). With *Gymnodinium* sp. as intermediate prey, *M. pulex* ingested *Gymnodinium* sp. at a rate of 40 cells ind^{-1} d^{-1}, resulting in a growth rate of 0.63 d^{-1} and a growth yield of 58%.

Discussion

Trophic responses of A. tonsa—In terms of carbon, *A. tonsa* ingested *P. globosa* single cells at <32% of body C d^{-1} (based on 4.60 μg C ind^{-1} for *A. tonsa* from Tang et al. 1999). These feeding rates were lower than the optimal rates of 82 to >100% of body C d^{-1} for *A. tonsa* in the field (Kleppel 1992; Kleppel and Hazzard 2000). Our results are consistent with those of Verity and Smayda (1989), who also reported low ingestion rates of *A. tonsa* and *Acartia hudsonica* feeding on single cells of *Phaeocystis pouchetii.* These low ingestion rates suggest that *Phaeocystis* cells were captured with a low efficiency, although some avoidance of the cells could not be ruled out (*see* Verity and Smayda 1989). Although prey-to-predator size ratio has been suggested as a limiting factor for *A. tonsa* feeding on small phytoplankters (Berggreen et al. 1988), such a relationship is not obvious in the case of other copepods feeding on *Phaeocystis* single cells. For examples, *Calanus finmarchicus* and *Calanus helgolandicus* feed on *Phaeocystis* single cells more efficiently than smaller and larger copepod species (Table 4). Thus, the ingestion rates may depend on the matching between particular copepod and *Phaeocystis* species.

R. salina was more nutritious than *P. globosa* for *A. tonsa,* resulting in a higher EPE of *A. tonsa* when fed *R. salina.* The difference in nutritional content of the two diets was indicated by their fatty acid compositions. In contrast to *R. salina, P. globosa* had a low 22:20 ratio and a low percentage of ω3 polyunsaturated fatty acids, both indicators of poor food quality for copepod egg production (Jónasdóttir 1994; Jónasdóttir and Kiørboe 1996). Our results also corroborate field studies that show *Phaeocystis* sp. to be poor in polyunsaturated fatty acids (Al-Hasan et al. 1990; Claustre et al. 1990). Despite the low ingestion rate of *A. tonsa* on *P. globosa,* the fecal pellet production rate was unexpectedly high and was comparable to *A. tonsa* feeding at a much higher rate on other flagellate species. For example, Besiktepe and Dam (pers. comm.) observed that for a similar fecal

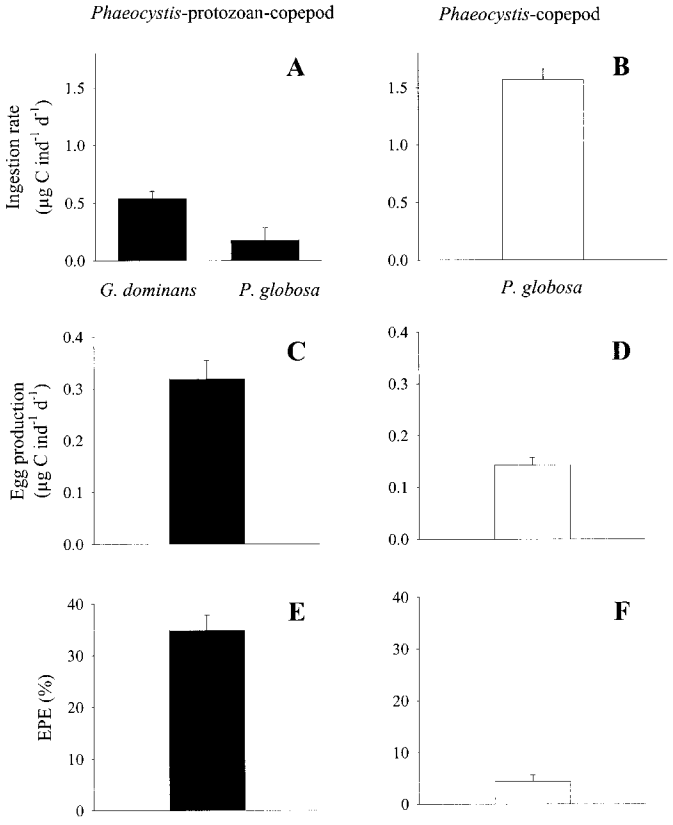

Fig. 6. Comparison two different *Phaeocystis*-based food chains. (A) Ingestion rates of *A. tonsa* on *G. dominans* and *P. globosa* in the mixed-prey treatment (*see Eqs. 4–10*). (B) Ingestion rate of *A. tonsa* on *P. globosa* in the direct-grazing food chain. (C and D) Egg production rates. (E and F) EPEs. Error bars are standard deviations of triplicates.

pellet production rate, *A. tonsa* had to ingest the poor diet *Dunaliella tertiolecta* (Chlorophyceae) >10 times our observed ingestion rate with *P. globosa.* Ingested material can be either rejected as fecal material or assimilated for further use, e.g., egg production. Thus, defecation and assimilation can be viewed as two opposing physiological processes. We used fecal pellet production as a proxy for defecation and egg production as a proxy for assimilation and deduced the relationship among ingestion, defecation, and assimilation for the two diets *P. globosa* and *R. salina*. For the *P. globosa* diet, fecal pellet production rate, but not egg production rate, correlated significantly with ingestion rate (Fig. 2C,E). The opposite was true for *R. salina*: ingestion rate correlated with egg production rate but not fecal pellet production rate (Fig. 2D,F, Line α). Even if we ignored one outlier, the slope of the regression line (Fig. 2F, Line β) was still smaller than that for *P. globosa* (Student's *t*-test, $p < 0.05$). Such a comparison suggests that *A. tonsa* was able to assimilate *R. salina* effectively, and subsequently used the material for egg production. By contrast, *P. globosa* appeared to pass through the copepod's guts with little being assimilated.

Nauplii survival and development—Verity and Smayda (1989) observed that a diet of *P. pouchetii* supported naupliar development to N4 in *A. hudsonica,* although further development to copepodites was not tested. In the present study, 63% of *A. tonsa* nauplii feeding on *R. salina* survived and completed the naupliar development. In contrast, nauplii feeding on *P. globosa* of the same carbon concentration suffered high mortality and did not develop past naupliar stages. Thus, *P. globosa* appeared to be nutritionally insufficient, relative to *R. salina,* to support naupliar survival and development in *A. tonsa.*

Table 3. Results of food-chain structure experiment II: Feeding and growth of *M. pulex* (ciliate) when fed *P. globosa* single cells and *P. globosa* with *Gymnodinium* sp. (dinoflagellate) as intermediate prey. *Gymnodium* sp. had been grown on *P. globosa* for more than five divisions before experiment. Data are mean ± standard deviation of triplicate.

	Ingestion rate (cells ind^{-1})	Growth rate (d^{-1})	Growth yield (%)
P. globosa single cells only	0	−0.38±0.09	0
With *Gymnodium* sp. as intermediate prey	38.5±8.7	0.63±0.10	58±7.1

Feeding and growth of protozoans—Little is known of the trophic significance of *Phaeocystis* for heterotrophic protozoans. While field studies have shown that abundance of heterotrophic protozoans increases in response to *Phaeocystis* blooms (Davidson and Marchant 1992; Stoecker et al. 1995; Rousseau et al. 2000), measurements of ingestion and growth of the protozoans are rare. Weisse and Scheffel-Möser (1990), using the dilution technique to measure the protozoan community-grazing activities, concluded that protozoan grazing on single cells could control *Phaeocystis* bloom development in the North Sea. Unfortunately, the dilution technique does not resolve the differences among different groups of protozoan grazers. To our knowledge, the only previous direct measurements were done by Hansen et al. (1993), who showed that *Phaeocystis* cf. *globosa* single cells were consumed by *Oxyrrhis marina* (heterotrophic dinoflagellate) and *Strombidinopsis acuminatum* (ciliate) but not by *Strombidium elegans* (ciliate). Verity (2000) also showed that *P. globosa* single cells were grazed by a *Strombidium* sp. isolated from the Skidaway River estuary. Our study showed that several common oligotrich ciliates and heterotrophic dinoflagellates could feed on *P. globosa* single cells. It was surprising that most of the tested species fed on *I. galbana* and *P. globosa* at different rates, considering the similar cell size between the two diets. This suggests that ingestion rate of the protozoans is a function of food type in addition to food particle size (cf. Jakobsen and Hansen 1997). Hansen et al. (1997) compiled extensive literature data and deduced relationships between predator size and ingestion and growth rates for ciliates and heterotrophic dinoflagellates feeding on a variety of diets. We used the relationships described by Hansen et al. (1997) as references to examine the feeding and growth responses of protozoans to *Phaeocystis.* When we combined our results with those of Hansen et al. (1993), the ingestion rate on *Phaeocystis*

Table 4. Clearance rates reported for marine copepods feeding on *Phaeocystis* single cells. In studies where food-carbon concentrations were not stated (*), the vales were estimated from chlorophyll concentration or biovolume. B.L., typical body length.

Phaeocystis species	Food conc. (μ C L^{-1})	Copepod species	B.L. (mm)	Clearance rate (ml ind^{-1} d^{-1})	Reference
P. cf. *globosa*	200–250	*Temora longicornis*	1	0.44–3.66	Hansen et al. 1993
P. cf. *globosa*	200*	*T. longicornis*	1	26.1	Hansen 1995
	50*	*T. longicornis* nauplii		0.2	
	18*	*Centropages hamatus*	1.2	17.2	
	10*	*Pseudocalanus elongatus*	1.4	14.4	
	40*	*C. helgolandicus*	3	36.4	
P. pouchetti	0–70*	*A. tonsa*	0.5	0–1.3	Verity and Smayda 1989
	0–70*	*A. hudsonica*	0.5	0–0.4	
P. pouchetti	77	*C. finmarchicus*	4	67.2	Tande and Båmstdet 1987
	230–1,810	*Calanus hyperboreus*	9	9.6–19	
P. pouchetti	965	*C. hyperboreus*	9	7.0–8.4	Huntley et al. 1987
P. globosa	13–410	*A. tonsa*	0.5	1.7–19	This study
	10–185	*T. longicornis*	1	0.6–9.9	Authors' unpubl. data

single cells increased with the protozoan cell size (Fig. 7A). However, while most of the ciliates ingested at close to the expected rates, the heterotrophic dinoflagellate ingestion rates tend to be lower than the expected values. By contrast, the corresponding growth rates of both ciliates and heterotrophic dinoflagellates were lower than the expected predator size-specific growth rates (Fig. 7B), suggesting that *P. globosa* supports poor growth in protozoans. There were notable exceptions to these size-dependent relationships: the ciliates *M. pulex* (this study) and *S. elegans* (Hansen et al. 1993) did not ingest *Phaeocystis* cells, although they fall within the relevant size range. Therefore, in addition to cell size, there may be other species-specific characteristics among protozoans that determine their ability to feed on *Phaeocystis*. A previous study has suggested that ciliates tend to grow two to three times faster than heterotrophic dinoflagellates of similar size under food-saturating conditions (Hansen 1992). However, our present study showed that heterotrophic dinoflagellates and ciliates of comparable size grew at similar rates when fed a saturating amount of *P. globosa* (Fig. 7B); thus, heterotrophic dinoflagellates may be a more important trophic linkage in *P. globosa*-dominated systems than previously thought.

Food-chain structures and nutritional values of P. globosa—Two types of planktonic food chains were investigated, which represented some of the most common trophic structures in the micro- and mesoscales within the planktonic food web: (1) *Phaeocystis*–heterotrophic dinoflagellates–copepods, and (2) *Phaeocystis*–heterotrophic dinoflagellates–ciliates.

When *G. dominans* and *P. globosa* were present in mixture, *A. tonsa* preferentially fed on *G. dominans*. Such selective feeding would benefit *P. globosa* by reducing the grazing pressure from *G. dominans* (Hansen et al. 1993). *G. dominans* also improved the food quality of *P. globosa*, resulting in a higher EPE of *A. tonsa*. Our fatty acid analysis showed that the poor nutritional value of *P. globosa* could be a result of its low content of certain polyunsaturated fatty acids. A recent study showed that the heterotrophic dinoflagellate *O. marina* could produce polyunsaturated fatty acids that were lacking in the alga *Dunaliella* sp., thus improving the food quality of *Dunaliella* sp. for copepods by acting as an intermediate prey (Klein Breteler et al. 1999). It is therefore possible that *G. dominans* improved the food quality of *P. globosa* by synthesizing polyunsaturated fatty acids required by *A. tonsa*.

Unlike the other protozoans tested, the ciliate *M. pulex* did not directly feed on *P. globosa* single cells. Instead, the small dinoflagellate *Gymnodinium* sp. formed a trophic linkage between *P. globosa* and *M. pulex*. Field studies have demonstrated an increase in protozoan abundance following a *Phaeocystis* bloom, which is viewed as evidence of direct protozoan grazing on *Phaeocystis* (e.g., Weisse and Scheffel-Möser 1990; Stoecker et al. 1995). Our study, however, showed that not only does the ability to graze on *Phaeocystis* cells differ among protozoans, but also certain protozoan species may exploit *Phaeocystis* indirectly by preying on intermediate grazers.

Grazers and trophodynamics in P. globosa*-dominated systems*—The poor trophic value of *P. globosa* single cells for *A. tonsa* can be discerned on three aspects: inefficient feeding, poor assimilation, and low nutritional value. The total reproductive output of the copepod is reduced as a result of low egg production by the adults and low survival and arrested development of the nauplii. Most of the protozoans in the present study ingested *P. globosa* single cells readily, consistent with the high in situ protozoan-grazing rates reported by Weisse and Scheffel-Möser (1990). Thus, frequent blooms of *P. globosa* in coastal waters are unlikely to be a result of the unpalatability of the single cells. Instead, Hansen et al. (1993) suggested that grazing pressure of protozoans may be reduced by top-down predation, an argument also supported by the results of our food-chain structure experiments. In addition, colony formation by *P. globosa* as the bloom progresses could also create a size mismatch problem for the protozoans, leading to reduced grazing (Verity 2000). The trophic significance of *P. globosa* is further complicated by interactions among the grazers. We for the first time demonstrated that an intermediate protozoan prey could significantly improve the trophic value of *P. globosa* for

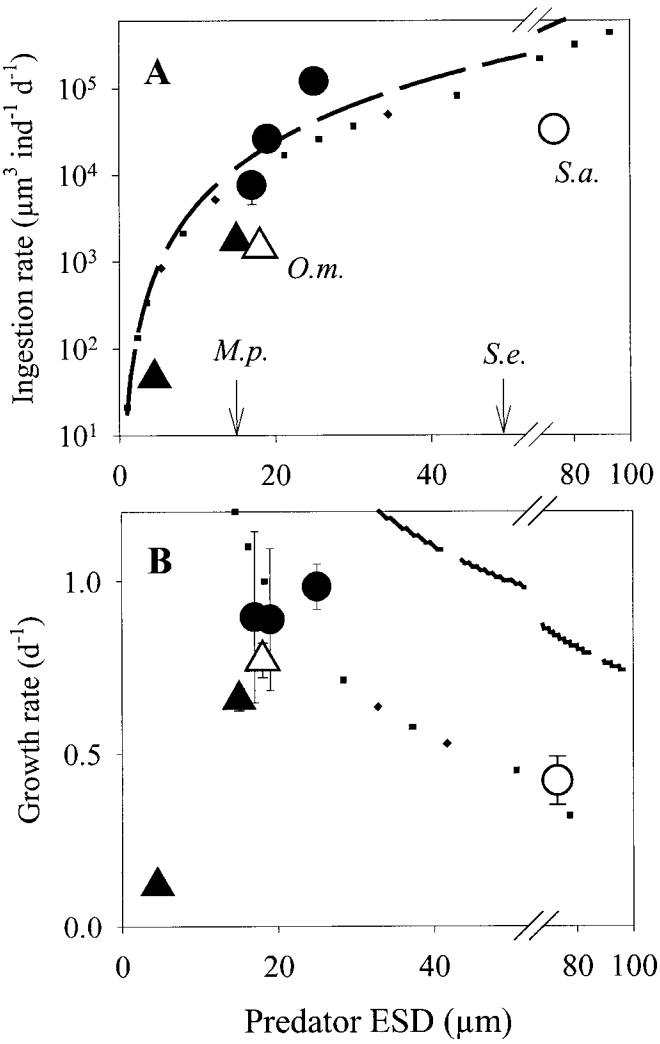

Fig. 7. Relationship between (A) ingestion rate, (B) growth rate, and cell size of heterotrophic dinoflagellates (triangles) and ciliates (circles) for this study (black symbols) and Hansen et al. (1993) (white symbols). Error bars are standard deviations, with some error bars within the symbols. O.m., *O. marina;* S.a., *S. acuminatum.* Arrows on x-axis indicate the size of *M. pulex* (M.p.) and *S. elegans* (S.e.) that did not ingest *Phaeocystis* single cells. Dashed and dotted lines are the expected predator size-specific ingestion rate and growth rate from Hansen et al. (1997) for ciliates and heterotrophic dinoflagellates, respectively.

ciliates and copepods. Thus, species-specific interactions among grazers will be an important consideration when constructing food web models involving *P. globosa* (e.g., Rousseau et al. 2000; Verity 2000). Consider the two different food chains linking *P. globosa* and *A. tonsa* (Fig. 8): A direct linkage between *P. globosa* and *A. tonsa* utilizes only 0–4.5% of the primary production for new biomass production. In contrast, inserting *G. dominans* as an intermediate prey increases the overall efficiency to 27%. In the case of *M. pulex*, absence of an intermediate prey would essentially shut down the grazing food chains. Natural concentrations of heterotrophic protozoans are usually much lower than the concentrations we used in the food-chain structure experiments

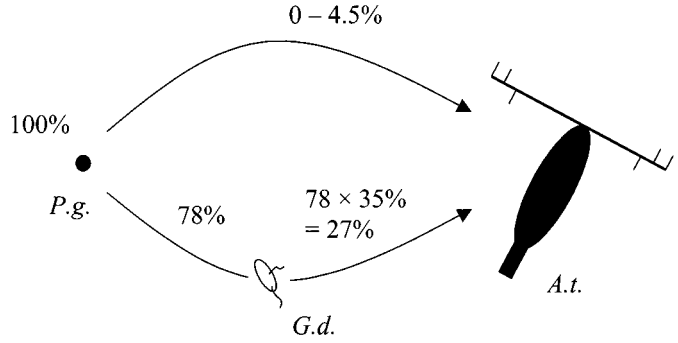

Fig. 8. Different food-chain structures result in different efficiencies in transforming *P. globosa* material to higher production. The upper food chain is based on EPE of *A. tonsa* from Figs. 3, 6F. The lower food chain is based on 78% growth yield of *G. dominans* (Fig. 5) and 35% EPE of *A. tonsa* (Fig. 6E). P.g., *P. globosa* single cells; G.d., *G. dominans;* A.t., *A. tonsa.*

(e.g., Weisse and Scheffel-Möser 1990; Hansen 1991). Thus, despite their ability to improve the trophic value of *P. globosa*, low abundance and low growth rates of protozoans in the field will still limit the total carbon flow from *P. globosa* to higher trophic levels (e.g., Gasparini et al. 2000), leaving most of the primary production to the detrital food chains.

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