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Nutritional value of *Phaeocystis pouchetii* (Prymnesiophyceae) and other phytoplankton for *Acartia* spp. (Copepoda): ingestion, egg production, and growth of nauplii

P. G. Verity [1] **and T. J. Smayda** [2]

[1] **Skidaway Institute of Oceanography, Post Office Box 13687, Savannah, Georgia 31416, USA**

[2] **Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island 02882, USA**

Abstract

Ingestion and egg production by *Acartia hudsonica* (5 °C) and *A. tonsa* (10 °C) from Narragansett Bay, Rhode Island, USA, was measured in the laboratory over a range of concentrations of the prymnesiophyte *Phaeocystis pouchetii* and the diatom *Skeletonema costatum*. Both *Acartia* species reproduced well when fed unialgal diets of *S. costatum*. Egg production by females fed *P. pouchetii*, either as gelatinous colonies (primarily > 200 μm in diameter) or solitary cells (3 to 5 μm), was not significantly different than that of starved females. *Acartia* spp. fed selectively on *S. costatum* in multialgal treatments. The presence of *P. pouchetii* did not reduce ingestion of *S. costatum;* the availability of *S. costatum* did not increase ingestion of *P. pouchetii*. Nauplii of *A. hudsonica* grew equally well on separate diets of *P. pouchetii* and *Isochrysis galbana*, two flagellates of similar size. Adult *Acartia* spp. reproduced poorly when fed these phytoplankton, suggesting that particle size may be more important than food quality in describing the responses. Grazing by *Acartia* spp. does not directly impact the dynamics of *P. pouchetii*, but may indirectly contribute to blooms of this prymnesiophyte by removal of competing phytoplankton.

Introduction

Phaeocystis pouchetii is an enigmatic phytoplankton species. Its life cycle includes both a solitary swarmer of 3 to 7 μm and a colonial aggregation of non-flagellated cells encased in a gelatinous sheath (Kornmann 1955, Kayser 1970). It occurs most prominently in the plankton in this latter stage, in which thousands of cells occur in colonies up to 10 mm in diameter (Gieskes and Kraay 1975, Verity et al. 1988a). Enormous blooms of colonial *P. pouchetii*, exceeding 10^8 colonies per m^3, occur in both coastal and oceanic waters (Kashkin 1963), near the ice edge in both polar regions (Smayda 1958, Palmisano et al. 1986), and exhibit a cross-shelf distributional gradient influenced by frontal and shelf-break dynamics (Iverson et al. 1979a, b).

These blooms often involve the minimal co-occurrence of other phytoplankton species (Smayda 1973, 1980, Chang 1983, Veldhuis et al. 1986, Weiße et al. 1986). Factors hypothesized to account for their monospecific nature include the absence of silicate for competing diatoms (van Bennekom et al. 1975, Verity et al. 1988a), binding and release of trace metals by *Phaeocystis pouchetii* (Morris 1971, Davidson and Marchant 1987), and antagonistic effects of *P. pouchetii* on other phytoplankton (Smayda 1973). Grazing by herbivores may also contribute to the dominance of *P. pouchetii* and the magnitude of its blooms. The life-history alternation between small solitary cells and large gelatinous colonies influences its susceptibility to predators of different size. Several contradictory lines of evidence suggest that *P. pouchetii* may be detrimental to higher trophic levels.

Early studies of gut contents concluded that *Phaeocystis pouchetii* is ingested by copepods, cladocerans, and meroplanktonic larvae (Lebour 1922, Nicholls 1935, Jones and Haq 1963, Fretter and Montgomery 1968) and by certain euphausids, including *Euphausia superba* (Sieburth 1960, Marr 1962). However, oyster larvae showed a 26 to 83% reduction in growth rate relative to controls during *P. pouchetii* blooms (Walne 1970), and *P. pouchetii* is an inadequate food for adult oysters (Gabbott and Walker 1971). *P. pouchetii* blooms in Dutch waters have been implicated in starvation of mussels, resorption of ripe gametes, and subsequent reduction in protein and lipid content of mussels (Pieters et al. 1980).

Among copepods, evidence of grazing on *Phaeocystis pouchetii* is also confused. Although Schnack (1983) reported that suspension-feeding Antarctic species did not prey on colonies, whereas copepods characterized by a "mixed and raptorial feeding mode" did, Huntley et al. (1987) and Tande and Båmstedt (1987) reported that large suspension-feeding copepods did feed on both solitary cells and colo-

nies of *P. pouchetii.* Intermediate-sized copepods, such as *Acartia* spp., were reported to ingest colonies of 50 to 350 μm diam (Weiße 1983). However, this conclusion was based upon decreases in colony number in the presence of copepods that may not have been due to ingestion. Field studies often assume that copepods do not feed on blooms of colonial *P. pouchetii* (e.g. Dagg et al. 1982), perhaps because colony fragments adhere to their appendages (Schnack et al. 1985).

All studies which have shown ingestion of *Phaeocystis pouchetii* by copepods used unialgal cultures. Because other phytoplankton species were not available, it remains unknown whether *P. pouchetii* was a preferred food. The ability of *P. pouchetii* to support long-term copepod cultures or egg production has also not been evaluated. The present study considers prey selection and nutritional value. Two species of *Acartia* were used as test grazers because of their numerical importance in temperate and boreal coastal waters (Turner 1981) and their use in previous studies on *P. pouchetii.* Responses of copepods offered *P. pouchetii* were compared to those fed the chain-forming diatom *Skeletonema costatum,* a known good food source (Deason 1980).

Materials and methods

Clones of *Phaeocystis pouchetii* and *Skeletonema costatum* from Narragansett Bay, Rhode Island, USA, were isolated into unialgal cultures. The *S. costatum* clone was axenic. The *P. pouchetii* clone could not be cleaned entirely of its bacterial population, perhaps because of the localized occurrence of the bacteria on the gelatinous sheaths of its colonies. Healthy colonies of *P. pouchetii* generally have few bacteria attached to their surfaces (Verity et al. 1988 b). Repeated treatments with antibiotics resulted in very low bacteria levels, as determined by visual counts.

Both phytoplankton species were grown in *f*/20 medium (Guillard 1975); the medium used for *Phaeocystis pouchetii* lacked silicate. The cultures were grown at experimental temperatures of 5 °C (*Acartia hudsonica*), 10 °C (*A. tonsa*), and 12 °C (naupliar growth studies) and a photoperiod of 12 h light : 12 h dark. Stock cultures were grown at saturating irradiances to maintain cells in log-phase growth. Irradiances during each experiment were low (60 to 90 μE m^{-2} s^{-1}) to minimize changes in algal density other than those due to grazing. The photoperiod and temperatures are those experienced by *P. pouchetii, Skeletonema costatum,* and the two *Acartia* species during the winter months in northern temperature waters.

Copepods were collected by 333 μm net tows in lower Narragansett Bay. *Acartia tonsa* were caught in the late fall and early winter before the appearance of *A. hudsonica.* This is the only season when temperatures occur within the tolerances of both *A. tonsa* and *Phaeocystis pouchetii. A. hudsonica* was collected in the early spring when *A. tonsa* was absent [*A. clausi* in northeastern North America was reclassified as *A. hudsonica* (Bradford 1976)]. The contents of the net tows were diluted into larger buckets of unfiltered seawater and returned to the laboratory. Adults were pipette-isolated into two-liter borosilicate glass beakers containing the various experimental combinations and concentrations of phytoplankton, and were held for 18 to 24 h. Collection and incubation temperatures did not differ by more than 3 C°.

Separate treatments to measure the ingestion and egg production of *Acartia* spp. were run concurrently. Similar batches of individuals were transferred into two sets of two-liter beakers. Both sets contained *Phaecystis pouchetii* and/or *Skeletonema costatum* in varying concentrations and ratios (described in following paragraph). Copepods were transferred into the food treatment in which they had been fed. One set of duplicate beakers contained an inner sleeve of PVC with a 153 μm mesh on the bottom. The eggs released by grazing females during the incubation fell through the mesh. The other set of duplicate beakers, with identical contents but lacking the inner sleeves, were placed on a stirring device similar to that described by Frost (1972). The concentration of copepods ranged from 10 to 30 per liter in the various experiments, similar to densities in Narragansett Bay. Beakers lacking copepods were used to correct for changes in algal density not due to grazing.

Three types of food treatments were offered to both *Acartia* species: (1) a series of concentrations of unialgal *Phaeocystis pouchetii* and *Skeletonema costatum*; (2) a multi-algal series with differing relative concentrations of these two phytoplankton, but containing the same total number of algal cells; (3) a multi-algal series with a constant abundance of *S. costatum* combined with increasing concentrations of *P. pouchetii.* The first treatment was designed to determine the functional response of each *Acartia* species to each alga, which would serve as bench marks for comparing responses to multi-algal treatments. The second and third treatments were designed to measure the effects of the presence of each alga on ingestion of the other, and the resultant egg production by females. Initial cell concentrations ranging from 0.1 to 10×10^3 cells ml^{-1} were attained by diluting stock cultures with appropriate amounts of fresh medium. These experiments were conducted using cultures of *P. pouchetii* colonies, primarily > 200 μm average diameter, and cultures of solitary cells of *P. pouchetii.* The latter were maintained by frequent transfers into medium of high nutrient concentration (*f*/2).

The grazing and egg production incubations were terminated after 24 h. Triplicate subsamples were taken from each of the grazing experiment beakers to determine changes in phytoplankton abundance. Counts of *Phaeocystis pouchetii* and *Skeletonema costatum* cells were made using Palmer-Maloney chambers or hemocytometers (Guillard 1978, Venrick 1978). The abundance of cells in colonies of *P. pouchetii* was determined using the methods of Verity et al. (1988 a). Results are expressed in cellular units, but can be converted to carbon using the following cell quotas: *P. pouchetii* = 20 pgC, *S. costatum* = 30 pgC.

Ingestion was calculated from end-point measurements using the equations of Frost (1972). Calculations were made using the mean concentration of phytoplankton cells present in the grazing chambers during the course of the incubations rather than the initial concentration (Marin et al. 1986) for two reasons. Grazing of *P. pouchetii* and *S. costatum* occurred at different rates and, presumably, with differing critical concentrations. The variable absolute and relative concentrations of the two phytoplankton would require different optimal incubation times according to Marin's method of calculation. We chose incubation times of 24 h for all treatments to incorporate any diel variability in feeding or egg production under the 12 h light: 12 h dark photoperiod. Calculations using the initial concentration may be inherently more accurate (Marin et al. 1986), but that benefit may be obscured by errors introduced in extrapolating from short-term incubations to daily rates, as demonstrated for *Acartia tonsa* (Stearns 1986, Stearns et al. 1987). Differences in relative food value of two contrasting phytoplankton species are apparent when rates are calculated according to the original formulation (Frost 1972).

The egg production treatments were terminated by adding the vital stain, neutral red, to the experimental vessels (Crippen and Perrier 1974) to stain the living copepods. Mortality during the incubations was rare. Dead copepods were not included in the calculations. Copepods were collected on 153 μm meshes for sex and stage determination, and eggs were collected on 35 μm meshes. The eggs were enumerated using a dissecting microscope. Although we tried to use only adults for grazing and egg-production measurements, post-experiment identifications showed that an occasional late-copepodite stage was included. These were assumed to contribute to grazing of phytoplankton, but not to egg production.

Two laboratory experiments were conducted to investigate whether responses by *Acartia* spp. to solitary cells of *Phaeocystis pouchetii* were due to factors other than cell size, such as nutritional content or "food quality." In one experiment (Table 1) similar in design to those described above, adult *A. hudsonica* were separately offered equal cell concentrations of solitary cells of *P. pouchetii* and of *Isochrysis galbana*, a similarly-sized alga which is a good food source for various planktonic grazers (Sekiguchi et al. 1980, Verity 1985). Grazing and egg production were compared to starved copepods and those fed *Skeletonema costatum*. A second experiment (Table 2) compared the percent egg hatch and rate of stage development of cohorts of nauplii of *A. hudsonica* when parents and nauplii were fed unialgal cultures of these three phytoplankton species. Eggs laid during an 8 h period were pipetted into sets of sterile plastic petri dishes containing the same phytoplankton fed to the parent during the egg-laying period. Triplicate petri dishes were sampled at 48 h intervals for 8 d to determine the abundance and stage distribution of nauplii feeding on *P. pouchetii*, *S. costatum*, and *I. galbana*. Results were compared to starved nauplii which developed from the eggs of parents which were not fed during the egg-laying period.

Results

Acartia hudsonica at 5 °C actively fed on *Skeletonema costatum* in unialgal treatments (Fig. 1). Ingestion increased with cell concentration and appeared to saturate above $\sim 5 \times 10^3$ cells ml^{-1}. Egg production by *A. hudsonica* females exhibited a functional response to abundance of *S. costatum* similar to that observed for ingestion, with a maximum of 8 to 9 eggs female^{-1} d^{-1}. In contrast, *A. hudsonica* showed significantly less ($p < 0.01$) feeding on unialgal cultures of colonies of *Phaeocystis pouchetii* (Fig. 1). Ingestion was significantly greater than zero only at concentrations of 2.5 and 5.0×10^3 cells ml^{-1}. Females offered colonies of *P. pouchetii* did not lay significantly more eggs ($p < 0.05$) than starved copepods, irrespective of algal abundance.

Acartia hudsonica fed mixtures of colonies of *Phaeocystis pouchetii* and *Skeletonema costatum* ingested the diatoms at rates proportional to their abundance, but ingested *P. pouchetii* at rates that were low or not significantly different from zero (Fig. 2). Females in these mixtures produced fewer eggs as the concentration of *Skeletonema costatum* decreased and that of *P. pouchetii* increased. As in the previous unialgal treatments, *A. hudsonica* fed 10^4 cells ml^{-1} of *S. costatum* produced ca. 9 to 10 eggs female^{-1} d^{-1}, compared to ca. 1 egg female^{-1} d^{-1} by copepods fed equivalent concentrations of *P. pouchetii*. *A. hud-*

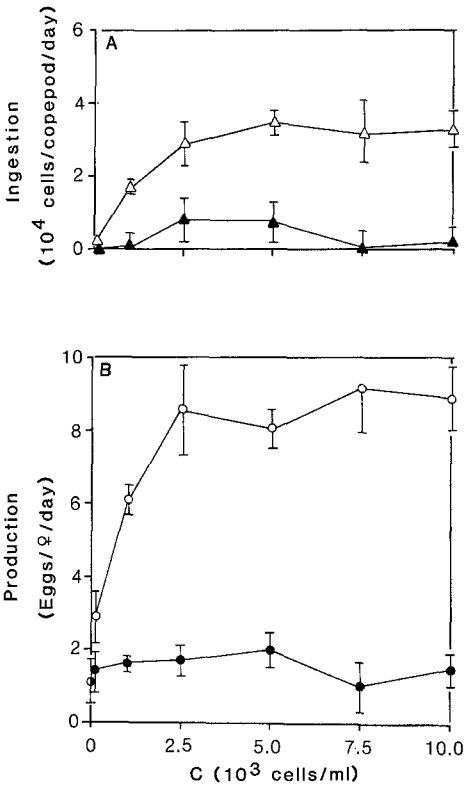

Fig. 1. *Acartia hudsonica*. Ingestion (A) and egg production (B) of copepods fed various concentrations, C, of colonies of *Phaeocystis pouchetii* (filled symbols) and *Skeletonema costatum* (open symbols), in unialgal treatments (5 °C). Error bars indicate ±1 SD

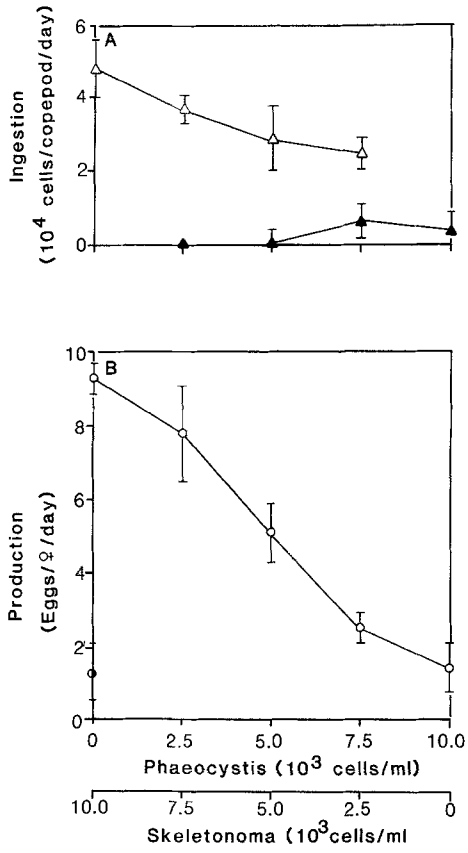

Fig. 2. *Acartia hudsonica.* Ingestion (A) and egg production (B) of copepods fed mixtures of colonies of *Phaeocystis pouchetii* and *Skeletonema costatum.* Total cells initially available in all treatments was 10^4 cells ml^{-1}. Symbols as in Fig. 1

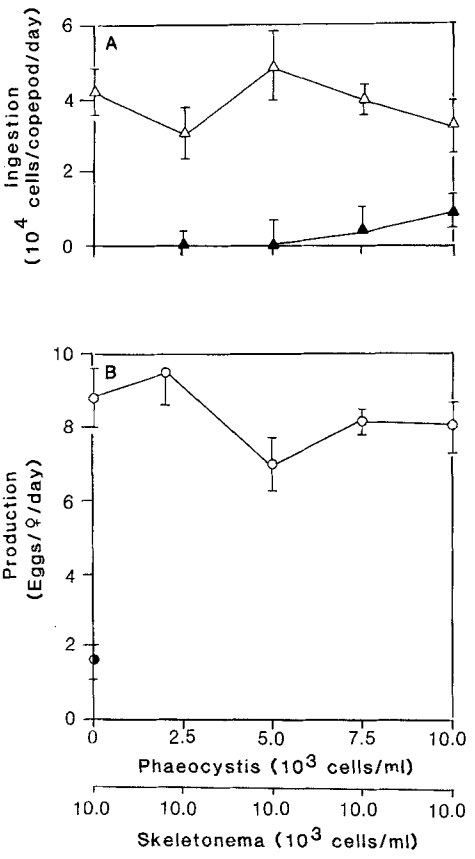

Fig. 3. *Acartia hudsonica.* Ingestion (A) and egg production (B) of copepods fed mixtures of colonies of *Phaeocystis pouchetii* and *Skeletonema costatum.* Total cells initially available ranged from 1 to 2×10^4 cells ml^{-1}. Symbols as in Fig. 1

sonica offered constant concentrations of *S. costatum* combined with increasing numbers of colonies of *P. pouchetii* preyed on the diatoms at rates which did not vary significantly ($p < 0.05$) with algal abundance (Fig. 3). Ingestion of *P. pouchetii* increased with abundance, but it was significantly lower than that of *S. costatum* when both species were present together at similar concentrations (10^4 cells ml^{-1}). Females in these mixtures produced eggs at daily rates (7 to 9 eggs $female^{-1}$) which were not significantly correlated with the abundance of colonies of *P. pouchetii.* High combined concentrations of *P. pouchetii* and *S. costatum* supported rapid egg production, in contrast to high unialgal concentrations of *P. pouchetii.*

Acartia tonsa fed unialgal cultures of colonies of *Phaeocystis pouchetii* and *Skeletonema costatum* at 10 °C (Fig. 4) exhibited responses similar to those of *A. hudsonica.* Ingestion of the diatom increased with concentration, with little evidence of saturation even at 10^4 cells ml^{-1}. Egg production also increased with concentration of *S. costatum* concentration, up to a maximum of 19 eggs $female^{-1}$ d^{-1}. In contrast, *A. tonsa* ingested significantly fewer *Phaeocystis pouchetii,* and egg production was not significantly greater than by starved females.

The functional response of *Acartia tonsa* to various mixtures of *Skeletonema costatum* and *Phaeocystis pouchetii* differing in relative and absolute concentrations (Figs. 5 and 6) was also similar to that of *A. hudsonica* (Figs. 2 and 3). Copepods ingested diatoms at rates proportional to their abundance, while feeding on co-occurring colonies of *P. pouchetii* was negligible or not significantly different from zero ($p < 0.05$). Egg production followed trends similar to those of ingestion. The presence of diatoms did not result in significant increases in feeding on colonies of *P. pouchetii,* and the occurrence of the colonies did not substantially interfere with predation on diatoms.

Acartia hudsonica did not acquire much more nutrition while feeding on solitary cells of *Phaeocystis pouchetii* (Fig. 7) than it did feeding on colonies (Fig. 1). Ingestion increased slightly with concentration of *P. pouchetii,* but variability obscured possible significant differences. Egg production of females fed solitary cells increased with food concentration, but was only significantly different from starved copepods at 7.5×10^3 cells ml^{-1} ($p < 0.05$). In contrast, copepods isolated from the same net tow actively fed and reproduced on a unialgal diet of *Skeletonema costatum.*

In mixtures of diatoms and solitary cells of *Phaeocystis pouchetii* (Figs. 8 and 9), *Acartia hudsonica* ingested significantly more *Skeletonema costatum,* even when *P. pouchetii* was more abundant. As in unialgal treatments, the cope-

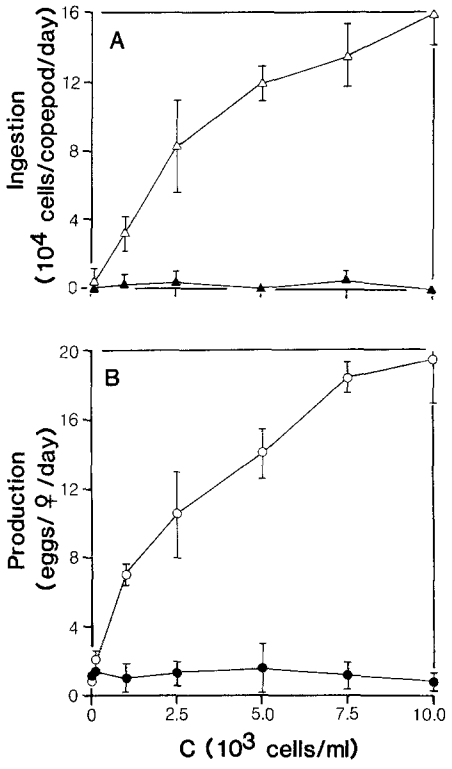

Fig. 4. *Acartia tonsa.* Ingestion (A) and egg production (B) of copepods fed various concentrations, C, of colonies of *Phaeocystis pouchetii* (filled symbols) and *Skeletonema costatum* (open symbols), in unialgal treatments (10 °C). Error bars indicate ±1 SD

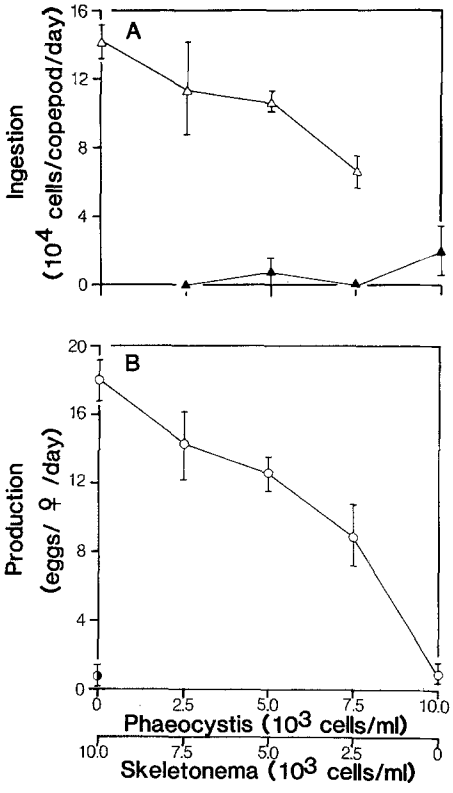

Fig. 5. *Acartia tonsa.* Ingestion (A) and egg production (B) of copepods fed mixtures of colonies of *Phaeocystis pouchetii* and *Skeletonema costatum.* Total cells initially available in all treatments was 10^4 cells ml^{-1}. Symbols as in Fig. 4

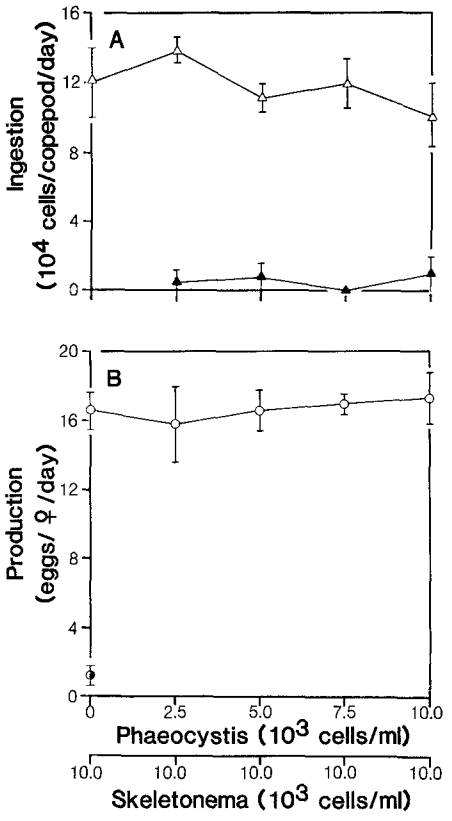

Fig. 6. *Acartia tonsa.* Ingestion (A) and egg production (B) of copepods fed mixtures of colonies of *Phaeocystis pouchetii* and *Skeletonema costatum.* Total cells initially available ranged from 1 to 2×10^4 cells ml^{-1}. Symbols as in Fig. 4

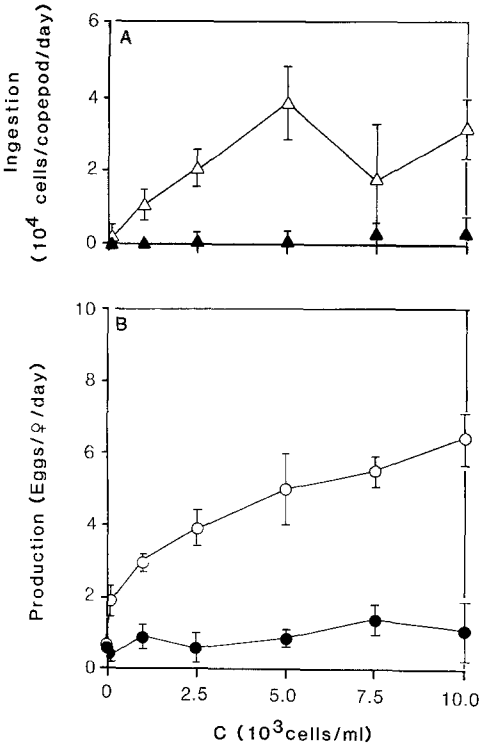

Fig. 7. *Acartia hudsonica.* Ingestion (A) and egg production (B) of copepods fed various concentrations, C, of solitary cells of *Phaeocystis pouchetii* (filled symbols) and *Skeletonema costatum* (open symbols), in unialgal treatments. Error bars indicate ±1 SD

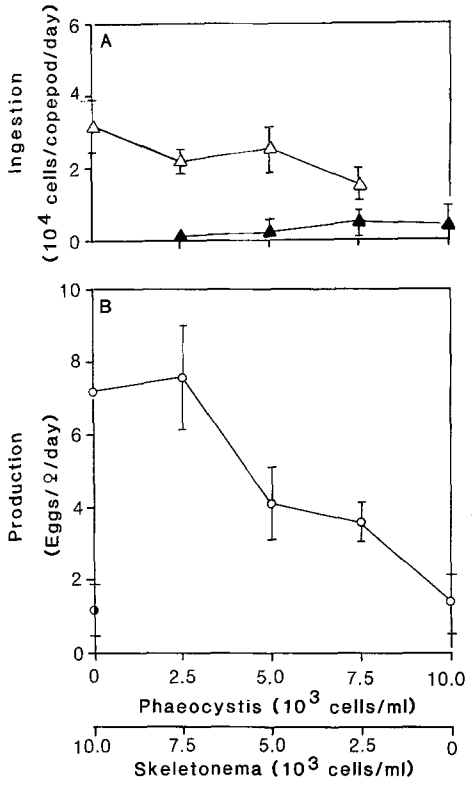

Fig. 8. *Acartia hudsonica.* Ingestion (A) and egg production (B) of copepods fed mixtures of solitary cells of *Phaeocystis pouchetii* and *Skeletonema costatum.* Total cells initially available in all treatments was 10^4 cells ml^{-1}. Symbols as in Fig. 7

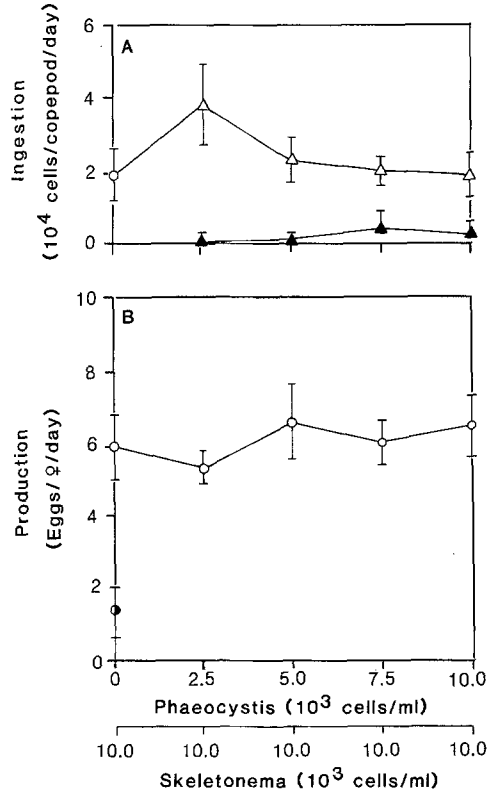

Fig. 9. *Acartia hudsonica.* Ingestion (A) and egg production (B) of copepods fed mixtures of solitary cells of *Phaeocystis pouchetii* and *Skeletonema costatum.* Total cells initially available ranged from 1 to 2×10^4 cells ml^{-1}, Symbols as in Fig. 7

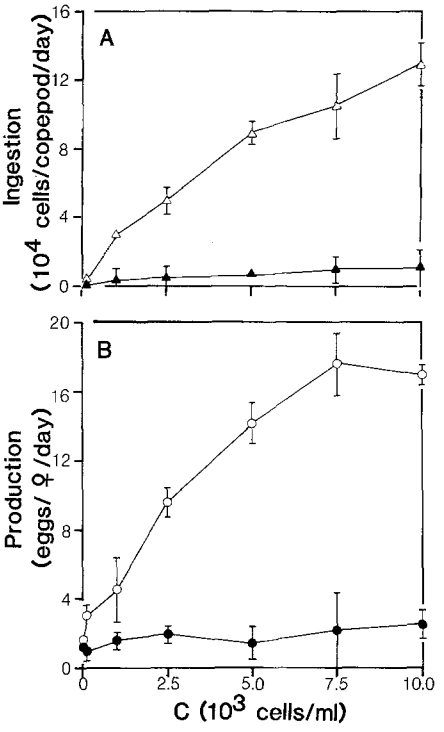

Fig. 10. *Acartia tonsa.* Ingestion (A) and egg production (B) of copepods fed various concentrations, C, of solitary cells of *Phaeocystis pouchetii* (filled symbols) and *Skeletonema costatum* (open symbols) in unialgal treatments. Error bars indicate ± 1 SD

pods appeared to eat more *P. pouchetii* cells at higher concentrations, but rates were seldom significantly greater than zero. Egg production was low (1 to 2 eggs $female^{-1}$ d^{-1}) in the absence of diatoms, and was not significantly different from that of starved females ($p < 0.05$). Increased *S. costatum* abundance was associated with substantial elevations in productivity of *A. hudsonica* (Fig. 8). When diatom concentrations were high and constant (Fig. 9), egg production increased slightly with added numbers of solitary *Phaeocystis pouchetii* cells, but variability obscured the possible significance of this trend.

Acartia tonsa at 10 °C showed similar responses to those of *A. hudsonica* at 5 °C, although ingestion and egg production was considerably higher. Copepods fed unialgal cultures of solitary cells of *Phaeocystis pouchetii* removed only small quantities, which supported low egg-production rates (Fig. 10). In contrast, copepods previously fed *Skeletonema costatum* ingested this diatom at rates exceeding 10^5 cells $copepod^{-1}$ d^{-1} while producing 16 to 17 eggs $female^{-1}$. Copepods offered mixtures of diatoms and solitary cells of *P. pouchetii* ingested measurable quantities of *P. pouchetii* when the abundance of *S. costatum* was high (Figs. 11 and 12), but these rates were not significantly greater than those of copepods fed unialgal cultures (Fig. 10). Ingestion of diatoms decreased as *P. pouchetii* abundance increased (Fig. 12 A), but the decrease was not significant ($p < 0.05$). Egg production was not enhanced by the presence or concentration of solitary cells of *P. pouchetii.*

Acartia hudsonica were fed equivalent concentrations of unialgal cultures of solitary cells of *Phaeocystis pouchetii*

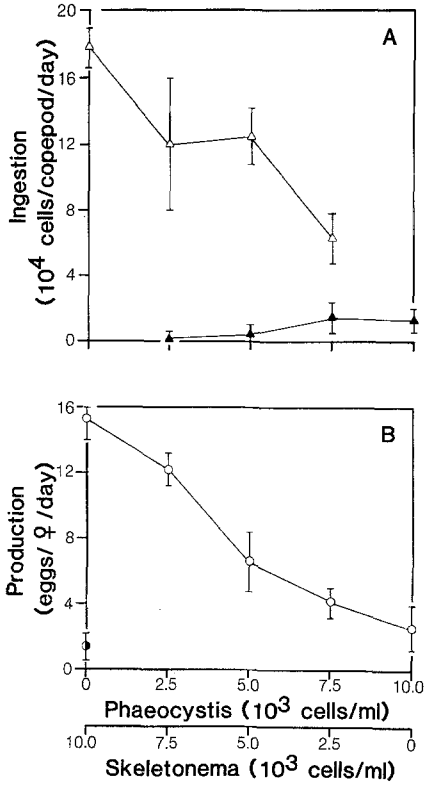

Fig. 11. *Acartia tonsa.* Ingestion (A) and egg production (B) of copepods fed mixtures of solitary cells of *Phaeocystis pouchetii* and *Skeletonema costatum.* Total cells initially available in all treatments was 10^4 cells ml^{-1}. Symbols as in Fig. 10

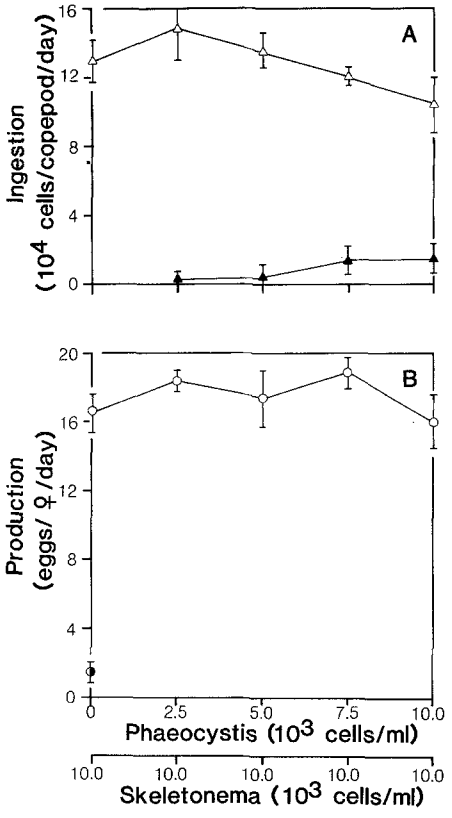

Fig. 12. *Acartia tonsa.* Ingestion (A) and egg production (B) of copepods fed mixtures of solitary cells of *Phaeocystis pouchetii* and *Skeletonema costatum.* Total cells initially available ranged from 1 to 2×10^4 cells ml^{-1}. Symbols as in Fig. 10

Table 1. *Acartia hudsonica.* Comparison of ingestion and egg production by copepods at 15 °C when fed unialgal cultures of three phytoplankton species of similar cell carbon quotas but differing in functional size. *Phaeocystis pouchetii* and *Isochrysis galbana* were present as 3 to 5 μm motile cells; *Skeletonema costatum* was present as chains of varying length, primarily >6 cells $chain^{-1}$

Phytoplankton species	Conc (10^3 cells ml^{-1})	Ingestion (10^4 cells copepods^{-1} d^{-1})	Egg production (eggs $female^{-1}$ d^{-1})
P. pouchetii	11.2	1.6	4.3
I. galbana	9.9	2.0	4.0
S. costatum	9.6	19.0	17.1
Control (no food)	0	–	3.3

and the similarly-sized flagellate *Isochrysis galbana* (Table 1). Copepods fed and reproduced actively on a diet of diatoms, but exhibited very low ingestion of both *P. pouchetii* and *I. galbana.* Egg production of females fed these flagellates was significantly lower ($p < 0.05$) than those fed diatoms, and was not significantly different from that of starved copepods.

Over an 8 d period, there were no significant differences ($p < 0.05$) among the four food treatments in the proportion of eggs which hatched into nauplii (Table 2). However, the rate of development of those nauplii fed similar concentrations of *Skeletonema constatum, Isochrysis galbana,* and solitary cells of *Phaecystis pouchetii* did differ. By Day 8, few starved nauplii had progressed beyond Stage 2 (N2), thought to be the first feeding stage, while approximately three-quarters of the nauplii raised on a diet of diatoms were N4, and the remainder were primarily N3. Nauplii fed *P. pouchetii* and *I. galbana* were also primarily N4 by Day 8. Thus, *P. pouchetii* was as nutritious a food as *I. galbana.*

Discussion

Phaeocystis pouchetii was not as satisfactory a food source as chain-forming diatoms for either *Acartia species.* This was true irrespective of whether *P. pouchetii* was present as gelatinous colonies or as solitary cells alone, or in mixtures with diatoms. Grazing rates on both life-history stages were low, and egg production was seldom significantly greater than that of starved females. These experiments were conducted simulating environmental conditions and using concentrations of phytoplankton and zooplankton species which occur in temperature and boreal waters when *P. pouchetii* is abundant.

The rations obtained by both *Acartia* species in these experiments have been calculated for purposes of comparison with previous studies and interpretation of the egg-production measurements (Table 3). *A. hudsonica* ingested a daily maximum of 2 and 4% of its body carbon when offered solitary cells and colonies of *Phaeocystis pouchetii,* respectively, compared to a maximum of 35% when similar concentrations of *Skeletonema costatum* were offered. *A. tonsa* acquired 6 and 4% of its body carbon when feed-

Table 2. *Acartia hudsonica.* Hatching success and development of nauplii (N) at 12°C when parents and naupliі were fed three phytoplankton species. Eggs laid during 8 h period were isolated into petri dishes, and naupliar stage distribution was recorded at 48 h intervals for 8 d. Hatch is percent of eggs hatched by Day 8. tr: trace; –: zero

Food	Hatch (%)	Time (h)	Stage distribution (%)				
			N1	N2	N3	N4	N5
Phaeocystis pouchetii	75	48	100	–	–	–	–
		96	15	71	14	–	–
		144	–	21	73	6	–
		192	–	3	12	84	1
Isochrysis galbana	71	48	100	–	–	–	–
		96	12	80	8	–	–
		144	–	19	64	17	–
		192	–	1	19	80	–
Skeletonema costatum	78	48	100	–	–	–	–
		96	22	65	13	–	–
		144	–	36	60	4	–
		192	–	4	25	71	tr
Control (no food)	79	48	100	–	–	–	–
		96	23	75	2	–	–
		144	–	95	5	–	–
		192	–	92	8	–	–

Table 3. *Acartia hudsonica* and *A. tonsa.* Range (minimum-maximum) of ingestion by copepods feeding on colonies and solitary cells of *Phaeocystis pouchetii* and on *Skeletonema costatum.* Cellular ingestion was converted to carbon (C) using cell quotas given in "Materials and methods". Carbon-specific rates were converted to daily ration using mean C contents of *A. hudsonica* (5.2 μg) and *A. tonsa* (4.8 g) determined by CHN analyses of copepods and in experiments

Copepod species	10^3 cells copepod^{-1} d^{-1}	μg C copepod^{-1} d^{-1}	% body C d^{-1}
Feeding on colonies			
A. hudsonica	0– 9.4	0–0.19	0–4
A. tonsa	0–10.0	0–0.20	0–4
Feeding on solitary *P. pouchetii*			
A. hudsonica	0– 6.0	0–0.12	0–2
A. tonsa	0–15.9	0–0.32	0–6
Feeding on *S. costatum*			
A. hudsonica	2– 50	0.07–1.8	1– 35
A. tonsa	4–190	0.14–6.7	3–133

ing on solitary cells and colonies of *P. pouchetii,* respectively, while copepods fed diatoms ingested up to 135% daily. The experimental temperatures were in the lower range of the thermal tolerances of both *Acartia* species, but the rations of copepods fed *S. costatum* agree well with studies of *A. hudsonica* grazing on similar concentrations of this diatom (Deason 1980), and *A. tonsa* grazing on natural plankton assemblages (Tester and Turner 1988). The egg production rates of both *Acartia* species fed *S. costatum* also fall within the range observed in other studies at these temperatures (Corkett and Zillioux 1975, Uye 1982), although strict comparisons should be made cautiously because of differences in parental age structure or acclimation conditions (Ambler 1985, Tester 1985, Durbin et al. 1987). The low egg production of copepods fed *P. pouchetii* are probably the result of the low ration they obtained from this alga. Thus, the inverse correlations found in natural waters between the abundance of *P. pouchetii* and that of adults and developmental stages of several *Acartia* species (Smayda 1973, Martens 1981) may have been due to inadequate nutrition and depressed egg production.

The comparatively low feeding rates on *Phaeocystis pouchetii* may reflect a number of causes which are not mutually exclusive. The results were not influenced by stressed or damaged copepods, since copepods collected and isolated at the same time actively grazed on diatoms. It is possible that 18 to 24 h acclimation is insufficient for them to "adjust" to *P. pouchetii,* although this effect was probably minimal, as the metabolism of *Acartia tonsa* closely tracks food availability (Dagg 1977). Higher concentrations of colonies or solitary cells of *P. pouchetii* than we used might result in elevated grazing and egg production. *A. tonsa,* for example, is adapted to high food concentrations (Paffenhöfer and Stearns 1988). However, the maximum concentrations used (10^4 cells ml^{-1}) is equal to or exceeds peak abundances during bloom conditions (Admiraal and Venekamp 1986, Cadee and Hegeman 1986, Verity et al. 1988a). The ecological relevance of higher experimental concentrations is uncertain. Another possibility is that a few copepods may have actively fed on *P. pouchetii* while the majority did little or no feeding. This possibility has some precedence, based on the gut pigment analyses of *Calanus hyperboreus* feeding on *P. pouchetii* in laboratory studies (Huntley et al. 1987) and variability of gut pigment in field-collected *A. tonsa* (Kleppel et al. 1988). However, if such were the case in this study, individual copepods apparently responded differently to the two phytoplankton species, since the high ingestion of diatoms could not have been accomplished by only a small percent-

age of the copepods present in the beakers. In either case, most or all of the copepods responded much differently to *P. pouchetii* than to *Skeletonema costatum.*

Thus, the low grazing rates of *Acartia* spp. on *Phaeocystis pouchetii* are intriguing, as they suggest a preference not to ingest *P. pouchetii,* or an inability to do so. The first hypothesis is indirectly supported by certain physiological traits of this prymnesiophyte and by anecdotal observations. Chemosensory feeders such as crustacean zooplankton (Hamner and Hamner 1977, Poulet and Marsot 1978) might be deterred by three characteristics of *P. pouchetii* colonies: production of dimethylsulfide (Barnard et al. 1984), excretion of acrylic acid (Guillard and Hellebust 1971); and the high mucopolysaccharide content of its gelatinous matrix (Haug et al. 1973, Verity et al. 1988 a). Several studies have concluded that some aspect of the colony gelatin may explain its unpalatability to certain herbivores (Pieters et al. 1980, Martens 1981, Schnack 1983).

Colonies of *Phaeocystis pouchetii* are ingested by some large suspension-feeding copepods, at least in the absence of alternate food (Huntley et al. 1987, Tande and Båmstedt 1987). This implies that colonies are not chemically undesirable to these species, and perhaps not to any. Qualitative observations of ciliates and rotifers plucking individual cells from colonies (Hollowday 1949, Admiraal and Venekamp 1986) support this notion. In the present study, nauplii of *Acartia hudsonica* developed normally at rates comparable to those fed a similarly-sized flagellate of known nutritional quality (*Isochrysis galbana*), although it is possible that nutritional effects might become apparent at later stages (e.g. Huntley et al. 1987). Adult *Acartia* spp. ingested little and reproduced poorly when fed solitary cells of *Phaeocystis pouchetii,* but *I. galbana* was also inadequate at the same concentrations, similar to previous observations (Parrish and Wilson 1978). Thus, their response may reflect an inability to ingest sufficient *P. pouchetii,* rather than a lack of preference. Solitary cells (3 to 5 μm) approach the lower size limit for efficient retention by the feeding mechanism of *Acartia* species (Nival and Nival 1976, Bartram 1981). Colonies, mostly > 200 μm in this study, may simply be too large to collect or may clog the feeding appendages of *Acartia* spp.

These data imply that life cycle alternations by *Phaeocystis pouchetii* may dramatically affect pelagic food webs. Colonies develop from solitary cells and may themselves release solitary cells (Kornmann 1955, Kayser 1970, Verity et al. 1988 a, b). Colonies and solitary cells differ in size by factors of 10^2 to 10^3 in diameter and 10^6 to 10^9 in volume. Solitary cells are susceptible to grazing by developmental stages of copepods and by oligotrich ciliates (Admiraal and Venekamp 1986, Verity unpublished data). Colonies that develop from these cells rapidly grow to a size, and perhaps a chemical composition, which reduce losses to suspension-feeding herbivores of small and intermediate size. While some large suspension-feeding crustacean zooplankton ingest *P. pouchetii,* others apparently do not. Thus, low grazing pressure may partially contribute to the prodigious blooms of colonial *P. pouchetii* noted earlier. Moreover, the presence of *P. pouchetii* in multi-algal treatments did not reduce predation on diatoms, nor did the presence of diatoms increase the removal of *P. pouchetii.* Decreases in clearance of one species as another increases in concentration occurred when *Acartia tonsa* was fed two preferred prey items (Stoecker and Egloff 1987). In the present study, however, both *Acartia* species clearly ingested the diatoms and avoided the gelatinous colonies, suggesting that in nature the selective removal of diatoms may further enhance dominance by *P. pouchetii.*

These data have important implications concerning the fate of blooms of *Phaeocystis pouchetii.* Large calanoid copepods and euphausids may derive nutrition from this alga, but the cold temperatures characteristic of waters in which *P. pouchetii* grows are thought to limit zooplankton reproductive capability (Corkett and McLaren 1970, McLaren 1978). This temperature suppression of zooplankton response time, coupled with changes in susceptibility to grazing due to life-cycle phenomena, may result in a trophic mismatch (e.g. Cushing and Dickon 1976) in which most of the biomass of *P. pouchetii* does not enter planktonic food webs directly. This biomass would be available for export out of the mixed layer. This hypothesis is supported by three years of observations in the Barents Sea of blooms of *P. pouchetii* sedimenting out of the euphotic zone (Wassmann in press). Even then, the trophic fate of *P. pouchetii* remains uncertain, since environmental stresses such as nutrient deprivation or thermal shocks can induce colonies to release solitary flagellated cells (Verity et al. 1988 b).

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