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When intraspecific exceeds interspecific variance: Effects of phytoplankton morphology and growth phase on copepod feeding and fitness

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Abstract

When different growth phases (exponential or stationary) or forms (solitary cells or colonies) of a single clone of *Phaeocystis globosa* were fed to three copepods, grazing, measured indirectly by fecal-pellet production, on different types of *P. globosa* differed by nearly two orders of magnitude, with differences on this clone sometimes exceeding differences between different phytoplankton species. The copepods *Pseudodiaptomus pelagicus* and *Eucalanus pileatus* fed more on colonies than solitary cells, with *P. pelagicus* also feeding more on exponential than on stationary cultures. Feeding by *Acartia tonsa* was complex and dramatically more variable. *A. tonsa* consumed 16–92 times more *P. globosa* when feeding on stationary-phase colonies than on any other *P. globosa* cell type. It fed five times more on stationary-phase colonies of *P. globosa* than on the palatable *Rhodomonas baltica*, but fed more on *R. baltica* than on other stages of *P. globosa.* Diet effects on copepod fitness were not related to amounts of foods consumed. Survivorship of *A. tonsa* and *E. pileatus* did not differ on any of the *P. globosa* cell types, but survivorship of *P. pelagicus* was suppressed on colonies (which they consumed more of) versus solitary cells. *A. tonsa* consumed 30 times more stationary-phase colonies than exponential-phase solitary cells, but produced two times more eggs on the lesser consumed food. Dramatic consumption of stationary-phase colonies may occur because this is a low-quality food and *A. tonsa* attempts to compensate by consuming more. The limited consumption of other *P. globosa* types is suggestive of chemical defenses that may be compromised when colonies enter stationary phase.

Phytoplankton, seaweeds, higher plants, and invertebrates exhibit intraspecific variance in morphology and chemistry that alters how consumers use these resources as foods (Butler et al. 1989; Karban and Baldwin 1997; Tollrian and Harvell 1999). While many studies emphasize interspecific differences among plants and the effects of this variance on herbivore feeding and fitness, recent studies suggest that intraspecific variation within plants may be equally important to plant–herbivore interactions (Lawrence et al. 2003). Intraspecific variance in plant traits can strongly determine herbivore preference (Jones 1962) as well as herbivore growth, survivorship, and fitness (Barrett and Agrawal 2004). This intraspecific variance can lead to significant differences in natural rates of herbivory (Lawrence et al. 2003), herbivore population densities (Ylioja et al. 1999), and even community structure and ecosystem function (Bailey et al. 2004). Although relatively well described for terrestrial plants and a few seaweeds, the effects of variable phytoplankton traits on zooplankton herbivores are understudied despite the potential for cascading affects of this variance on food webs and energy flow in pelagic ecosystems (Hay and Kubanek 2002).

Phytoplankton encounter diverse environmental conditions on ecological and evolutionary timescales that create or maintain genetic and phenotypic variability in traits, such as physiological status and morphology (Taroncher-Oldenburg et al. 1997). Some phytoplankton are even capable of rapidly altering morphology as an induced defense against planktonic consumers (Tang 2003; Long 2004). Despite substantial intraspecific variance in how some phytoplankton are utilized by consumers (Houde and Roman 1987; Sterner and Hessen 1994), previous studies frequently ignored this variance (Huntley et al. 1986). This has led to the common use of adjectives such as palatable or toxic, defended or undefended, and good or bad to describe the food quality of a given phytoplankton species to herbivores (Koski et al. 1999). This focus on the Latin binomial as an adequate descriptor of the prey being studied will be useful if interspecific variance of phytoplankton predictably exceeds intraspecific variance in how these prey are treated by consumers. However, if intraspecific variance equals, or exceeds, interspecific variance, then appreciating such variance will be critical for our understanding of food-web dynamics and community structure in pelagic communities—as it has been for terrestrial (Karban and Baldwin 1997) and benthic marine systems (Hay 1996).

There are seemingly conflicting outcomes of studies regarding whether particular phytoplankton species are readily consumed by, or avoided by, zooplankton (reviewed in Weisse et al. 1994). For example, some studies report that copepods readily feed on *Phaeocystis pouchetii* (Huntley et al. 1987; Tande and Båmstedt 1987; Turner et al. 2002), while other studies report that copepods feed only reluctantly and at low rates on this alga (Verity and Smayda 1989). If

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the species name alone is an adequate descriptor of *P. pouchetii* food value, then these studies conflict. However, grazing zooplankton, like other herbivores, ''do not eat Latin binomials'' (Janzen 1979) but instead encounter individual phytoplankton cells whose histories, nutritional status, defensive traits, and thus values as foods may vary (Jonasdottir 1994). This variability can affect copepod feeding selectivity (Butler et al. 1989), growth (Koski et al. 1998), and reproductive success (Jonasdottir 1994). If a single phytoplankton species can vary enough to occupy both palatable and unpalatable ends of the food spectrum, then these apparently conflicting reports could be explained by an unappreciated role of intraspecific variance in traits affecting utilization by zooplankton.

Intraspecific variance in bloom-forming phytoplankton could affect how consumers respond to these phytoplankton, and this change could significantly alter food-web structure and energy flow within planktonic ecosystems. For example, *Phaeocystis* spp. can represent over 85% of total phytoplankton biomass during blooms (Davies et al. 1992), and most *Phaeocystis* spp. alternate between solitary cell and colonial forms. Because of size-selective feeding, microzooplankton are assumed to graze solitary cells in preference to colonies and mesozooplankton are assumed to graze preferentially on appropriate-sized colonies (Verity 2000). Although morphological and physiological variability within *Phaeocystis* spp. might affect food webs dominated by this phytoplankton, direct comparisons of grazing on different types of *Phaeocystis* spp. are rare. In the few studies that measured grazing on multiple morphologies, copepods grazed colonies at higher rates than solitary cells (Huntley et al. 1987; Tande and Båmstedt 1987). However, these studies tested only one copepod species, *Calanus hyperboreus,* so it is unclear if copepods in general prefer colonies or if this is a species-specific trait of the copepod that was studied. Similarly, few grazing studies directly controlled the growth phase of *Phaeocystis* spp. (Huntley et al. 1987; Turner et al. 2002), and none of these studies measured grazing on stationary-phase algae. However, growth phase could be a key factor regulating grazing of *Phaeocystis* spp. For example, Estep et al. (1990) observed higher grazing of *P. pouchetii* colonies by *Calanus finmarchicus* during later stages of blooms when colonies appeared less healthy—possibly due to changes in nutrient availability and the resources available for allocation to defenses against consumers. In addition, the potential interactive effects of *Phaeocystis* spp. growth phase and morphology on algal palatability are unknown despite the demonstrated importance of such complex interactions on the susceptibility of seaweeds and terrestrial plants to herbivory (Cruz-Rivera and Hay 2003; Barrett and Agrawal 2004). Considering that *Phaeocystis* spp. can represent the majority of phytoplankton biomass during blooms (Davies et al. 1992) and that these blooms sequester large amounts of carbon (Arrigo et al. 1999), the dynamics of *Phaeocystis*–grazer interactions could affect *Phaeocystis*-dominated communities and the ecosystems in which they occur.

To assess how a phytoplankton's growth phase and morphology affect its value as a food for consumers, we offered three copepod species one of four types of *Phaeocystis globosa* in a two-factor design, with *P. globosa* growth phase (stationary or exponential) and morphology (solitary cells or colonies) as the two factors. We assessed how these different *Phaeocystis* cell types affected copepod survivorship for all three copepods and how the foods affected egg production for *Acartia tonsa.*

Materials and methods

Plankton cultures—P. globosa (CCMP 627), originally isolated from the Gulf of Mexico, was grown xenically in L1-Si medium (CCMP recipe) at 20°C under a light : dark cycle of 14 : 10. Illumination was provided by a combination of cool white and daylight fluorescent bulbs at ~100–150 μmol quanta m^{-2} s^{-1}. Batch cultures of *P. globosa* were transferred each week into fresh media at a 1 : 10 dilution, for a starting concentration of approximately 50,000 cells mL^{-1}. *A. tonsa* and *Pseudodiaptomus pelagicus* were collected in the Wilmington River near the Priest Landing dock (31°57.736′N, 81°00.710′W), Skidaway Island, Savannah, Georgia. *Eucalanus pileatus* were collected on the middle continental shelf off Savannah, Georgia. All animals were collected by slow, oblique tows with a 200-μm-mesh plankton net. Following collection, animals were immediately dispersed in large volumes of surface seawater and placed in a 20°C room. Within 10 h, adult female copepods were sorted into Whatman GF/F (0.7 μm glass fiber) filtered seawater to allow gut evacuation for at least 1 h.

Fecal-pellet production as a measure of feeding on different diets—Copepods can physically disrupt *Phaeocystis* colonies (Hansen et al. 1994) and copepod-associated chemical cues can suppress colony formation (Long 2004). Thus, a change in the density of an algal form (e.g., colony or single-cell density) can result from indirect chemical cues rather than consumption. Additionally, the magnitude of this indirect chemical effect can equal the magnitude of the direct effect of grazing, thus, confounding measures of grazing based on counts of cell types (Long 2004). Under these conditions, measuring grazing on different morphologies needs to rely on methods other than counts of cells or colonies. We estimated grazing by measuring fecal-pellet volume when consumers were confined with different cell types.

We measured fecal-pellet production for each copepod species (*A. tonsa,* first experiment $n = 4$ and second experiment $n = 3$ separate containers; *E. pileatus,* $n = 4$; *P. pelagicus,* $n = 6$) feeding on a monoculture of the four different types of *P. globosa* (exponential-phase solitary cells, exponential-phase colonies, stationary-phase solitary cells, or stationary-phase colonies) as well as on a palatable control food and in a treatment with no food. The first experiment with *A. tonsa* was confounded by time because we first offered copepods exponential-phase algae and then separate *A. tonsa* were offered stationary-phase algae. To remove time as a confounding factor, we conducted a second experiment in which we simultaneously offered either exponential or stationary-phase algae to *A. tonsa.* This second approach was used for all other copepod species as well. Copepods in treatments with food received 22,000 cells mL^{-1} *P. globosa* or an equivalent cellular volume of a control food (5,000 cells mL^{-1} *Rhodomonas baltica* for *A. tonsa* and *P. pelagi-*

cus or 11 cells mL^{-1} *Rhizoselenia* sp. for *E. pileatus*). The cell density for *P. globosa* represents natural concentrations during peak bloom periods (Claustre et al. 1990). For each replicate, several adult female copepods (13 *A. tonsa*, 4 *E. pileatus*, or 10 *P. pelagicus*) were incubated with the test alga in 500-mL jars, systematically interspersed on a plankton wheel (60 cm in diameter) and rotated at ~0.5 revolutions per minute. Grazing was allowed for approximately 24 h, and copepods were removed the next day.

A. tonsa and *P. pelagicus* were removed by passing incubation jar contents through a 160-μm mesh. *E. pileatus*, a larger species, were removed individually with a large-bore pipette. Fecal pellets were collected by separately sieving the remaining contents of each container through a 25-μm mesh. Fecal-pellet production rates were corrected for the number of surviving copepods and the size of fecal pellets for each diet. Fecal-pellet counts were multiplied times standard pellet volumes determined from a subset of 20–50 pellets per copepod and per diet.

With the exception of the first experiment with *A. tonsa*, experiments assessing the effects of various foods for a particular copepod species were all run synchronously to prevent confounding treatment effects with temporal effects, but each copepod species was assayed at a different time. Thus, we can rigorously contrast effects of different foods on a copepod species, but we cannot rigorously contrast effects across different copepod species due to time and species being confounded.

The four *P. globosa* types were all from the same clone, but were collected from two stock cultures—one in exponential phase and one in stationary phase. For both cultures, solitary cells were separated from colonies by repeatedly reverse filtering cultures through a 10-μm mesh. Prior to assays, exponential-phase cultures were diluted daily with fresh media to maintain their growth phase. Stationary-phase cultures were inoculated 10 d prior to feeding assays to ensure that they would reach stationary phase by the start of feeding assays. To confirm that this transfer schedule produced stationary-phase cultures, we measured chlorophyll *a* (Chl *a*) concentrations each day in a similarly inoculated culture for 12 d, with the exception of day 8. Chl *a* concentrations of three 10-mL subsamples were measured using the fluorometric method.

Effects of diet on copepod feeding, survivorship, and egg production—Copepods sometimes increase feeding rates when offered the same food for several days because of increasing hunger or because of acclimation to the diet (Price and Paffenhöfer 1984). To determine if copepods changed their feeding rates with increased exposure to particular diets and to assess the effects of *P. globosa* diets on copepod fitness, copepods were transferred to new solutions of the same food type daily for several days (3 d for *E. pileatus*, 4 d for *P. pelagicus*, and 3–7 d for *A. tonsa*). We depleted our stock of stationary-phase colonies after 3 d during the *A. tonsa* assay, so copepods receiving this diet were switched to a diet of exponential-phase colonies on days 4–7 to see how their feeding changed with this change in diet. We measured fecal-pellet production and survivorship each day. For *A. tonsa*, we also measured daily egg production as an additional measure of the fitness effects of feeding on different *P. globosa* diets.

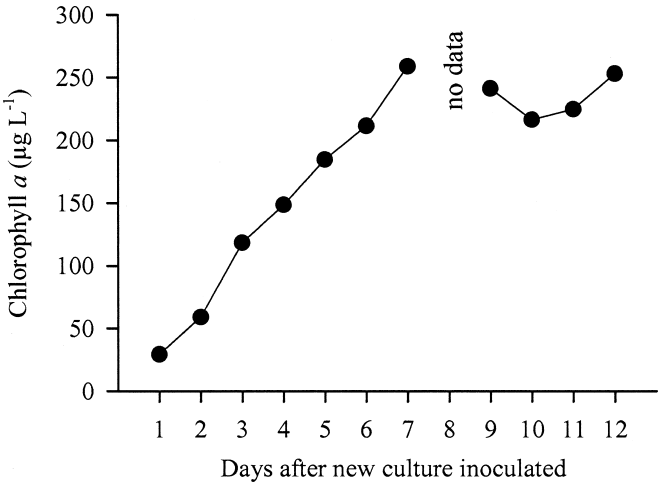

Fig. 1. Growth (measured by Chl *a* concentration) of a *P. globosa* culture grown under experimental conditions.

Data analysis—We used a two-factor analysis of variance (ANOVA), with growth phase and morphology as separate factors, to examine differences in fecal-pellet production across diets on day 1 for each copepod species. Simple linear regression determined whether fecal-pellet production changed with time, an indication of acclimating to diets. Only the first 3 d were included in regression analyses for *A. tonsa* fed stationary colonies because we exhausted all of this food type by the end of day 3. Survivorship for all copepod species was assessed on the last experimental day by comparing transformed percentages using ANOVA. For *A. tonsa*, this was done on day 3 as well because that is when we exhausted our supply of stationary-phase colonies. Post hoc comparisons of survivorship were made with Tukey tests. The total number of *A. tonsa* eggs produced was determined by adding the daily number of eggs produced for each replicate, and these totals were compared using ANOVA followed by Tukey tests. This was done on day 3 for all diets and then on day 7 for all diets but the stationary-phase colonies, for which diet type was changed between day 3 and 4—see above.

Results

P. globosa cultures grew rapidly on days 1–7, but were in stationary phase thereafter (Fig. 1). Thus, the 10-d-old cultures we used in feeding assays were in stationary phase. The change in Chl *a* levels during the rapid-growth phase were linear, rather than exponential, but this likely reflects changes in chlorophyll levels within cells as nutrients become more limiting rather than a lack of exponential growth in biomass or biovolume (Larson and Rees 1996).

Feeding rates on the different diets—During the first day of feeding, *E. pileatus* and *P. pelagicus* fed more on colonies of *P. globosa* than on solitary cells (Fig. 2; $F_{1,12} = 4.65$, p

= 0.052 and $F_{1,20}$ = 4.35, p = 0.050, respectively). *P. pelagicus* also fed more on exponential than on stationary-phase cells ($F_{1,20}$ = 7.18, p = 0.014), while *E. pileatus* did not differentiate as a function of growth phase ($F_{1,12}$ = 0.30, p = 0.592). Feeding by *A. tonsa* was more complex, but despite this complexity, patterns were similar for both experiments (Fig. 2A,B). In both experiments, *A. tonsa* feeding rates on the different *P. globosa* diets completely bracketed feeding on the positive control diet (Fig. 2A,B), and there was a significant interaction between *P. globosa* growth phase and morphology (Fig. 2A, $F_{1,12}$ = 81.85, $p < 0.001$; Fig. 2B, $F_{1,8}$ = 240.55, $p < 0.001$). This copepod fed 16 (Fig. 2A) to 92 times (Fig. 2B) more rapidly on colonies that were in stationary phase than on colonies of the same clone that were in exponential phase. When *P. globosa* was undergoing exponential growth, *A. tonsa* fed more on solitary cells than on colonies, but when *P. globosa* reached stationary phase, *A. tonsa* feeding rates reversed and the copepods fed much more heavily on colonies. *A. tonsa* feeding patterns seen during day 1 were consistent over longer time periods; feeding was consistently much higher on stationary-phase colonies of *P. globosa* than on any other food (Fig. 3A during the first 3 days while receiving stationary-phase colonies). Fecal-pellet production by *A. tonsa* was 3.5–5 times higher on stationary-phase colonies compared with *R. baltica* diets for the 3 d that we offered both algae to *A. tonsa* (Fig. 3A). When *A. tonsa* confined with stationary-phase colonies were switched to a diet of exponential-phase colonies on day 4, fecal-pellet production immediately decreased by about 95% and remained low for the next 4 d of the experiment (Fig. 3A, dashed portion of the line).

Both *E. pileatus* and *P. pelagicus* fed more on the positive control foods than on any of the *P. globosa* diets. In contrast, *A. tonsa* confined with stationary-phase colonies consumed about five times as much *P. globosa* as control food, but when feeding on the other three types of *P. globosa* cells, consumption was much less than for the control food. Thus, *A. tonsa* recognized the intraspecific differences within one clone of *P. globosa* as more dramatic than the interspecific differences between *Rhodomonas* and *P. globosa.*

Temporal patterns of feeding—Because three copepod species were each offered either a positive control food or each of four *P. globosa* types, we measured fecal-pellet production for a total of 15 copepod–food combinations. Long-term fecal-pellet production of *A. tonsa* on stationary-phase colonies could be assessed for only 3 d because of limited food supply. Fecal-pellet production decreased through time for 1 of our 15 combinations (*E. pileatus* feeding on stationary-phase colonies; R^2 = 0.462, p = 0.015; Fig. 3), increased with time for four combinations (*A. tonsa* feeding on the positive control food (R^2 = 0.411, p = 0.002) and on exponential-phase solitary cells (R^2 = 0.295, p = 0.011), and *P. pelagicus* feeding on exponential-phase colonies (R^2 = 0.163, p = 0.050) and stationary-phase solitary cells (R^2 = 0.400, p = 0.001)), and did not change with time for 10 of the copepod-by-food-type combinations. Given that most copepods were consuming minimal amounts of the *P. globosa* diets, one might expect increasing hunger to increase feeding over time. However, fecal-pellet production re-

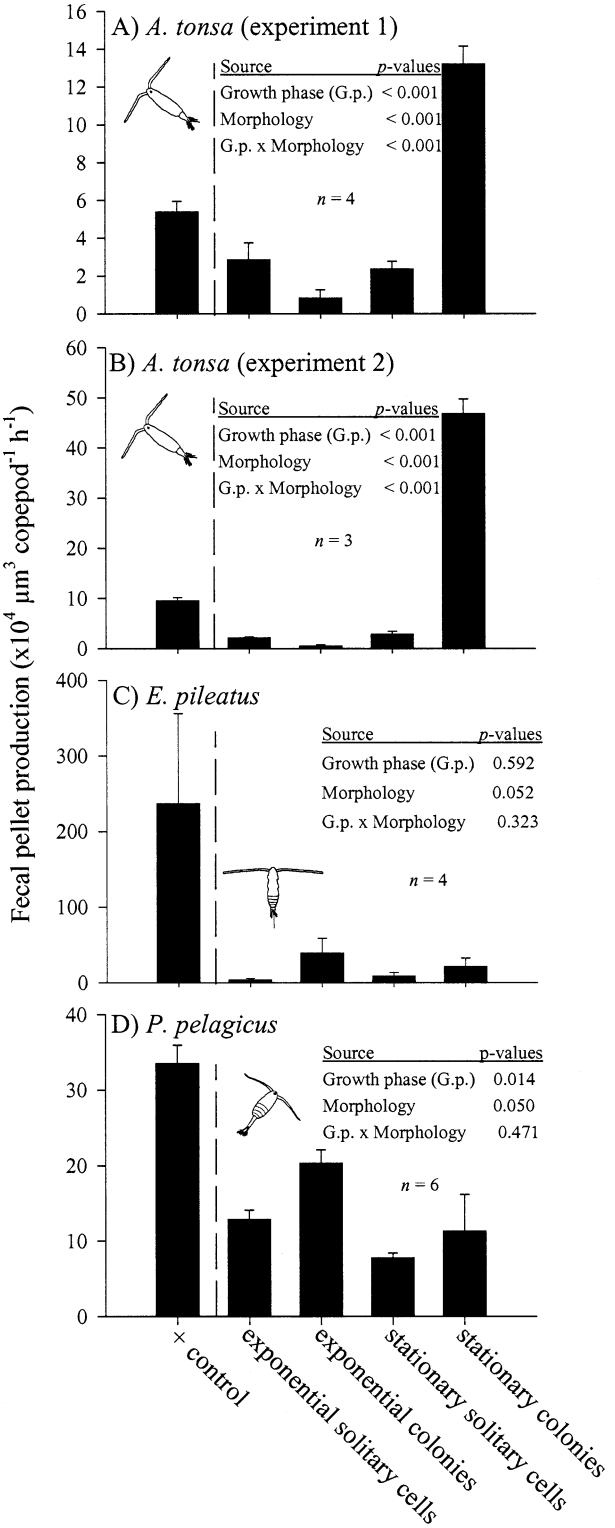

Fig. 2. Fecal-pellet production of (A) *A. tonsa* (first experiment), (B) *A. tonsa* (second experiment), (C) *E. pileatus*, and (D) *P. pelagicus* on day 1 when confined with an equivalent cellular volume of the four different types of *P. globosa* or with a positive control phytoplankton. Values are means + 1 SEM.

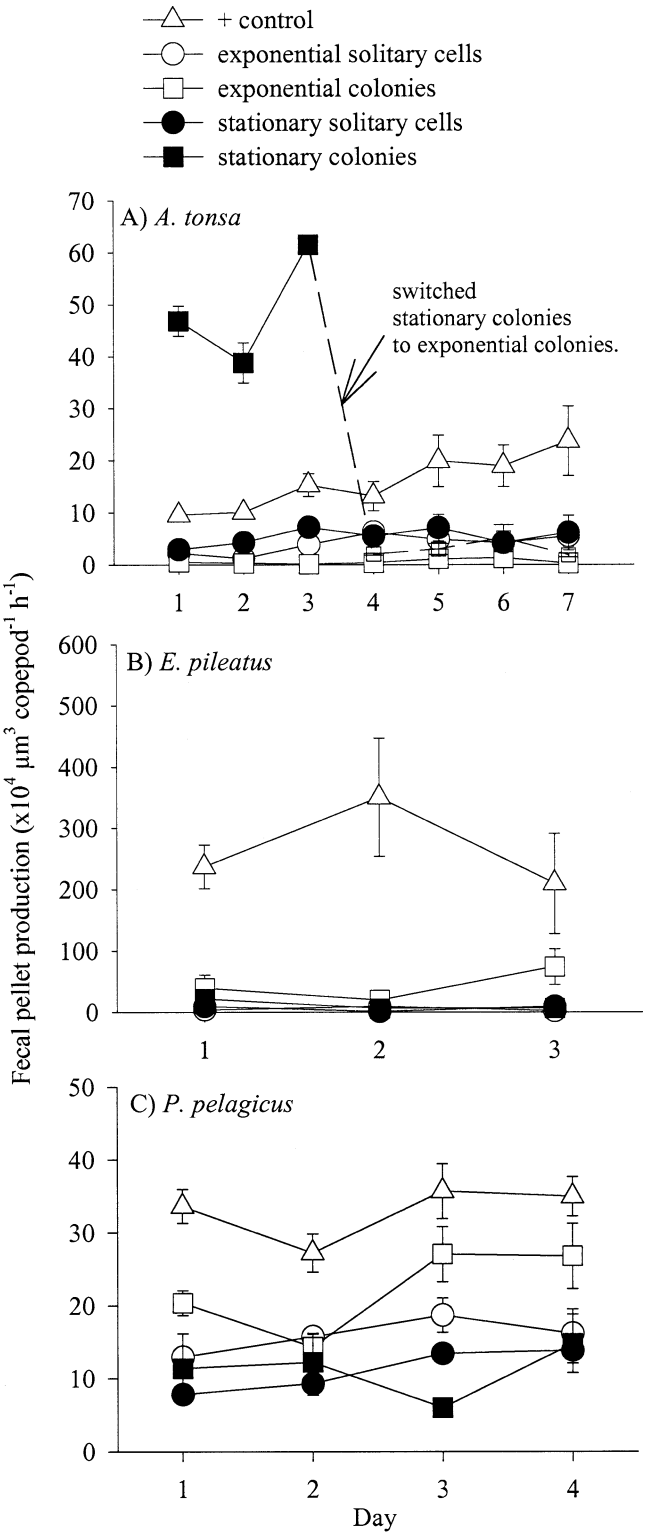

Fig. 3. Fecal-pellet production of (A) *A. tonsa*, (B) *E. pileatus*, and (C) *P. pelagicus* during several days of feeding on equivalent cellular volumes of the four types of *P. globosa* or a positive control phytoplankton. Values are means ± 1 SEM. Note that, after day 3, the *A. tonsa* that had been feeding on stationary-phase colonies were switched to a diet of exponential-phase colonies for days 4–7. The dashed line indicates feeding after this switch.

mained low for most copepods feeding on *P. globosa*, even for those combinations where feeding increased with time.

Survivorship and egg production—Growth phase of *P. globosa* did not affect survivorship for any of the three copepod species we investigated (*A. tonsa*, $t = -0.28$, df = 10, $p = 0.789$; *E. pileatus*, $t = 0$, df = 14, $p > 0.999$; *P. pelagicus*, $t = -0.908$, df = 22, $P = 0.374$), so survivorship data for exponential-phase and stationary-phase *P. globosa* were combined so that we could present contrasts of morphologies in Fig. 4. Copepod survivorship did not differ when feeding on colonies versus solitary cells for *A. tonsa* or *E. pileatus*, but survivorship of *P. pelagicus* was twice as high on solitary cells as on colonies (Fig. 4). Survivorship on *P. globosa* diets was higher than on starvation controls for all copepods except *E. pileatus* (Fig. 4, *A. tonsa*, $F_{3,14} = 5.27$, $p = 0.012$, Tukey tests, $p < 0.05$; *E. pileatus*, $F_{3,20} = 0.87$, $p = 0.474$; *P. pelagicus*, $F_{3,32} = 25.51$, $p < 0.001$, Tukey tests, $p < 0.01$). However, both our sample size and experimental duration for *E. pileatus* were low (four replicates with four copepods per replicate, for 3 d), possibly constraining our statistical power and ability to detect differences in survivorship. Survivorship for both *A. tonsa* and *P. pelagicus* was lower on *P. globosa* colonies than on the positive control foods; survivorship on diets of solitary *P. globosa* cells did not differ from survivorship on positive control foods.

After 3 d of feeding, *A. tonsa* females produced only 23–51% as many total eggs when fed *P. globosa* as when fed *R. baltica* (Fig. 5, $F_{5,12} = 49.92$, $p < 0.001$; Tukey tests, $p < 0.05$ for all contrasts). After both 3 and 7 d, egg production was a significant 80–185% higher when *A. tonsa* was feeding on exponential-phase solitary cells than when feeding on any of the other *P. globosa* diets. Although *A. tonsa* ate stationary-phase colonies at about 5–21 times the rate at which it consumed exponential-phase solitary cells (Fig. 2A,B), this increased feeding resulted in significantly fewer, rather than significantly more, eggs (Fig. 5A). A regression of *A. tonsa* fecal-pellet production on day 1 against *A. tonsa* egg production on day 3 indicated no detectable relationship ($R^2 = 0.002$, $p = 0.942$).

Discussion

It is common for prey species to be considered either palatable to, or defended against, a particular consumer. This basic approach underlies general ecological hypotheses or patterns, such as early successional species being more palatable than later successional species (Cates and Orians 1975), tropical species being better defended than temperate species (Bolser and Hay 1996), and spatial escapes from consumers being critical for preventing local extinction of palatable species in areas where consumer activity is high (Lubchenco and Gaines 1981). However, we show here that a single clone of a simple prey species can become up to 92 times more susceptible to consumption by simply growing a few days older and shifting from a solitary to a colonial form (Fig. 2B). The intraspecific variance in palatability of *P. globosa* being grazed by *A. tonsa* exceeded the interspecific difference in palatability between *Rhodomonas* and *P.*

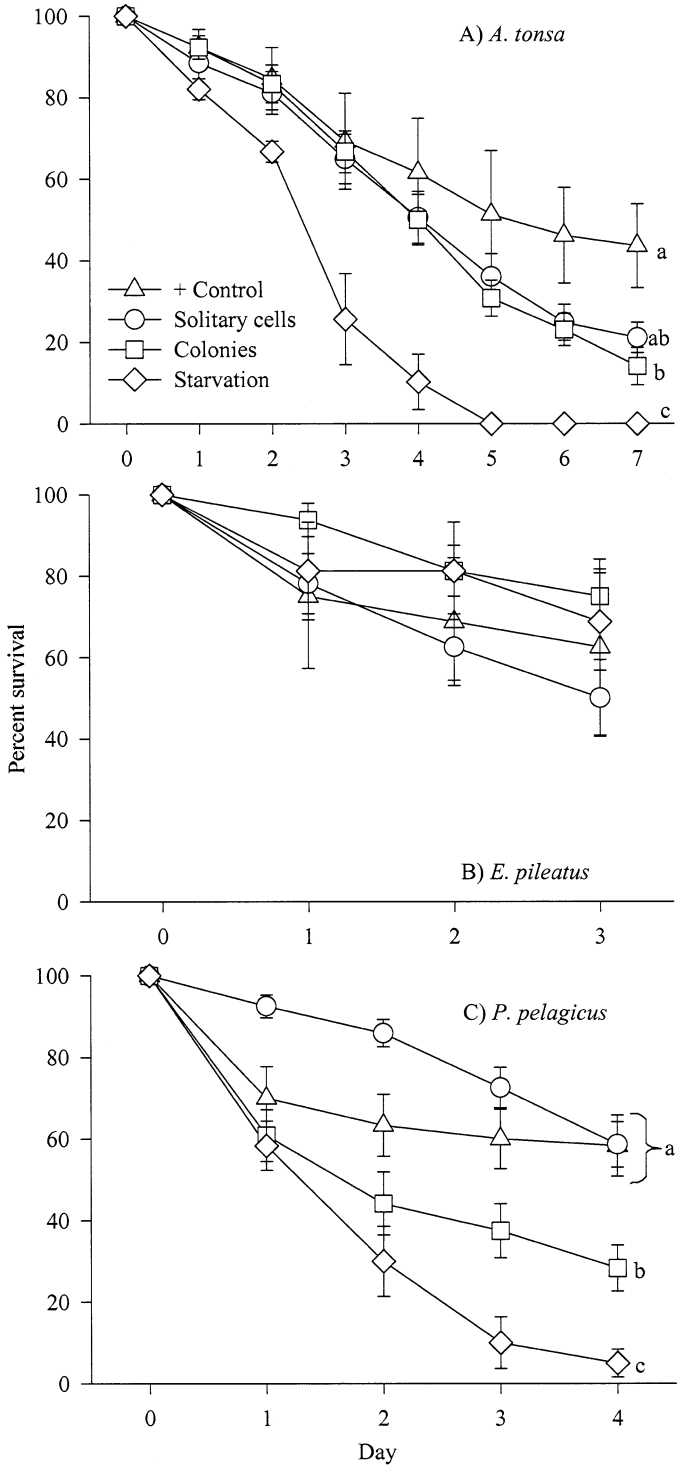

Fig. 4. Survivorship of (A) *A. tonsa,* (B) *E. pileatus,* and (C) *P. pelagicus* during several days of feeding on equivalent cellular volumes of different forms of *P. globosa* or on a positive control phytoplankton. Letters next to values on the last days indicate significant ($p < 0.05$, Tukey) among-treatment differences in survivorship on the last day. Values are means ± 1 SEM.

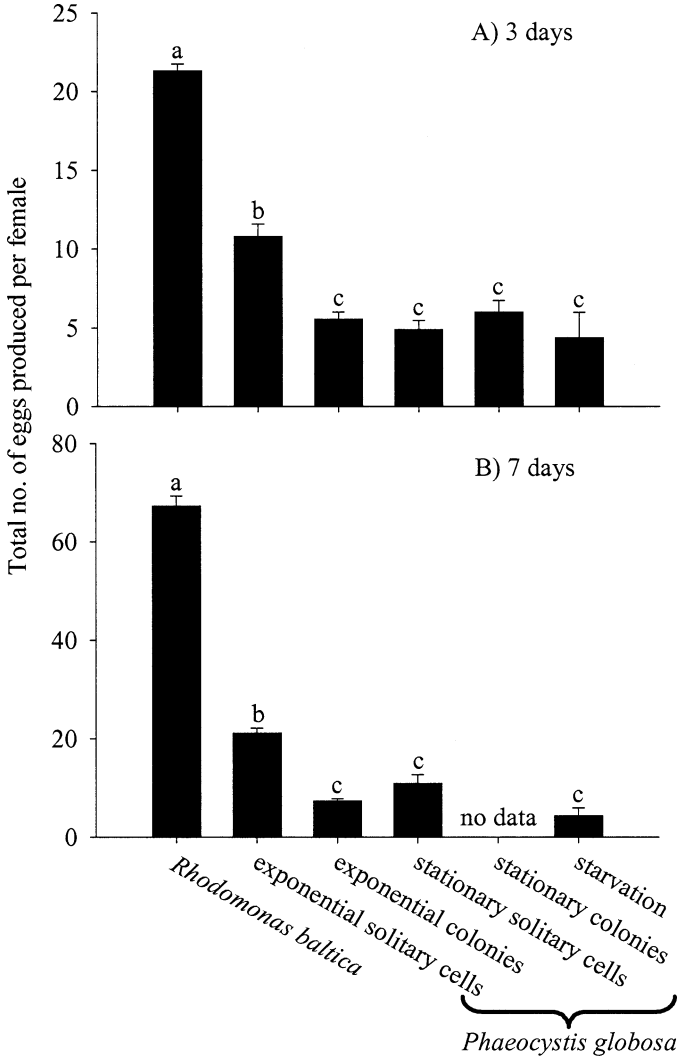

Fig. 5. Total egg production of *A. tonsa* females as a function of diet after (A) 3 days or (B) 7 days. All diet treatments contained equal cell volumes. No data for egg production were collected after 3 d for the diet of stationary colonies. Letters above bars indicate significant ($p < 0.05$, Tukey) among-treatment differences. Values are means + 1 SEM.

globosa. Although the magnitude of this intraspecific difference in grazing seems extreme, the basic finding of intraspecific differences in palatability equaling or exceeding differences among different species also occurs among seaweeds (Bolser and Hay 1996) and terrestrial plants (Lawrence et al. 2003).

Although our findings indicate that *A. tonsa* grazes stationary-phase colonies more readily than exponential-phase colonies, some of the differences in fecal-pellet production could be caused by differences in assimilation efficiency rather than grazing rates. We chose to estimate grazing with fecal-pellet counts because chemical signals from copepod grazing caused transformations between solitary cells and colonies (Long 2004) and because copepods can disrupt colonies and release uneaten solitary cells (Hansen et al. 1994), thereby confounding our ability to assess grazing by changes

in cell-type density. This approach is not novel. Fecal-pellet production frequently is used as a proxy for copepod ingestion rates, including estimates for feeding by *Acartia* (Gaudy 1974; Besiktepe and Dam 2002). A potential cost of estimating grazing rates with fecal-pellet counts is that high fecal-pellet production could be due to other factors, such as low assimilation efficiency or low-density fecal pellets. However, for assimilation efficiency alone to produce the differences seen in Fig. 2B mandates that assimilation efficiency when feeding on the exponential-phase colonies be about 90 times higher than when feeding on the stationary-phase colonies; this magnitude of change is exceedingly unlikely. It is more likely that differences in fecal-pellet production are driven primarily by differences in feeding.

Conflicting findings regarding the suitability and palatability of *Phaeocystis* spp. as a food for zooplankton may be partially resolved by an increased appreciation for the phenotypic plasticity of this genus regarding susceptibility to grazers. Some previous studies considered *Phaeocystis* spp. to be poor foods for zooplankton grazers because grazers fed minimally on this genus or experienced reduced fitness when confined to diets of *Phaeocystis* spp. (Verity and Smayda 1989; Tang et al. 2001). However, there is variability in this assessment, and other studies found *Phaeocystis* spp. to be useful foods for zooplankton grazers (Huntley et al. 1987; Tande and Båmstedt 1987; Turner et al. 2002). Previous studies rarely assessed the importance of intraspecific variability of *Phaeocystis* spp. to copepod–*Phaeocystis* interactions, so we cannot rigorously assess the value of our findings for explaining the variable outcomes of other studies. However, it is clear that copepod feeding (Figs. 2 and 3) and fitness (Figs. 4 and 5) can vary considerably as a function of *Phaeocystis* growth stage or form. If we are to adequately understand consumer–prey interactions and the role of various prey species in affecting food-web dynamics, we will need to appreciate the degree to which intraspecific variance in prey susceptibility to consumers can affect these interactions. For some species, variability among phenotypes may be minimal, but for *P. globosa*, it is appreciable. When feeding on stationary-phase cultures, *A. tonsa* produced 6–15 times more fecal volume on colonial versus solitary cell diets, but when feeding on exponential-phase cultures, feces production on colonies declined to only about 25–29% of production on solitary cells (Fig. 2). These changes are dramatic and could affect community function as well as copepod–*Phaeocystis* interactions.

Intraspecific variance in plant traits can affect community-level and ecosystem-level processes (Bailey et al. 2004). For example, beavers are ecosystem engineers, the behavior of which can fundamentally change local ecosystems—their foraging is determined, in part, by the concentration of condensed tannins in trees and these concentrations vary strongly with tree genotype (Bailey et al. 2004). Similarly, the intraspecific variation in *P. globosa* traits could have broader impacts, including altering food webs and biogeochemical processes. For instance, if *A. tonsa* was the predominant grazer in a *P. globosa* bloom, then grazing by *A. tonsa* would be relatively high if the bloom consisted primarily of colonies in stationary growth phase. Although this grazing would not result in large secondary production of *A. tonsa* eggs, it would lead to high fecal-pellet production that could transport carbon and nutrients from surface to deep waters (Besiktepe and Dam 2002). However, much of the production would escape *A. tonsa* consumption if the bloom consisted of *P. globosa* solitary cells or colonies in exponential phase. In this case, much of the energy and nutrients in *Phaeocystis* might be recycled within the microbial loop.

The significant differences in fecal-pellet production on particular diets frequently failed to predict the effects of those *P. globosa* diets on copepod fitness measured both by survivorship and egg production. Surprisingly, the 250–400% increase in fecal-pellet production on stationary-phase colonies versus *R. baltica* did not affect *A. tonsa* survivorship or egg production and, in fact, both traits were lower on stationary-phase colonies than on *R. baltica*. This may indicate that *A. tonsa* finds stationary-phase colonies of *P. globosa* to be a low quality, but nontoxic, food and thus tries to compensate for the low quality by increasing consumption. Compensatory feeding also occurs among marine amphipods (Cruz-Rivera and Hay 2000, 2003), marine zooplankton (Houde and Roman 1987), and terrestrial megaherbivores (Sinclair and Norton-Griffiths 1979) when they are confined to foods of reduced nutritional quality. Although this behavior is common, it can be an effort of desperation when food quality falls too low; compensatory feeding failed to increase survivorship here, as also occurred for several marine amphipods confined to low-quality foods (Cruz-Rivera and Hay 2000, 2003). Given the very low copepod egg-production rates (Verity and Smayda 1989; this study) and naupliar development to copepodites (Tang et al. 2001) on *Phaeocystis* spp. diets compared with other food sources, it appears that adult copepods will have a more important role than juveniles in deciding the fate of *Phaeocystis* production.

Phaeocystis–copepod interactions are complex and generalizations about the palatability of *Phaeocystis* to copepods will thus describe only a subset of these interactions. In this study, intraspecific variation in copepod feeding on *P. globosa* was dramatic with some growth stages or morphologies being consumed nearly two orders of magnitude more than other growth stages or morphologies. This variation was greater than the between-species variation we measured. It is clear that copepods ''do not eat Latin binomials'' (Janzen 1979); instead, they encounter and choose among individual cells of a certain morphology in a certain growth phase. This underappreciated effect of intraspecific variation could be common for phytoplankton, as many phytoplankton species vary in nutritional quality or defenses both temporally and spatially (Sterner and Hessen 1994). When intraspecific variability in phytoplankton affects susceptibility to grazers, these effects can scale up to alter food webs and biogeochemical cycling but also allow for phenotypic plasticity to be used as a defense against grazers (Long 2004). This variation in palatability, as well as its differential effect on different consumers, needs to be more fully understood if we are to gain adequate insight into the processes and mechanisms creating patterns in planktonic ecosystems.

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