Limnol. Oceanogr., 55(5), 2010, 2107–2116
© 2010, by the American Society of Limnology and Oceanography, Inc.
doi:10.4319/lo.2010.55.5.2107

Effects of omnivory and predator–prey elemental stoichiometry on planktonic trophic interactions

Amy N. S. Siuda[1] and Hans G. Dam*

Department of Marine Sciences, University of Connecticut, Groton, Connecticut

Abstract

We used laboratory food chains to experimentally explore the independent and combined effects of omnivory and food quality on planktonic trophic interactions. Omnivory is predicted to dampen indirect (trophic cascade) interactions, whereas availability of a low-quality diet, here defined as predator–prey elemental stoichiometric imbalance, should strengthen both direct (grazing and predation) and indirect interactions. Food chains were constructed with a copepod, *Acartia tonsa*, an aloricate ciliate, *Strombidinopsis* sp., and two centric diatoms of different size, *Thalassiosira weissflogii* (larger) and *Thalassiosira pseudonana* (smaller). Comparing results between food chains with two (copepod and diatoms or ciliate and diatoms) and three (copepod, ciliate, and diatoms) trophic levels tested omnivory effects. Offering grazers phytoplankton grown under nitrogen-replete and nitrogen-limited conditions tested stoichiometric imbalance effects. Carbon ingestion increased by 25% for the copepod and 160% for the ciliate on the nitrogen-limited relative to the nitrogen-replete diatom, demonstrating considerable compensatory feeding by both grazers. On a mixed diet comprised of the nitrogen-limited large diatom and the nitrogen-replete small diatom, the copepod continued to engage in compensatory feeding, but the ciliate did not. Cascading indirect effects of the copepod on phytoplankton via the ciliate were minimal. The decrease in phytoplankton due to direct grazing by the copepod was much greater than any indirect increase resulting from reduced ciliate grazing pressure. Omnivory and compensatory feeding were stronger than positive prey selection for the N-replete intermediate grazer, thus weakening cascading indirect effects of the top predator on phytoplankton.

Trophic interactions in planktonic food webs can be characterized by direct (e.g., arising from grazing and predation) and indirect effects (e.g., arising from trophic cascades), which in turn might be affected by omnivorous feeding behavior and prey nutritional quality. Trophic cascade theory predicts that increases in top consumer abundance will result in positive indirect effects on primary producers in food chains with an odd number of trophic levels and negative indirect effects in food chains with an even number of trophic levels (Carpenter et al. 1985). This theory is predicated on the assumption that omnivory is rare. Yet, omnivory is common among planktonic consumers. For instance, metazoan mesozooplankton consume auto- and heterotrophic prey in both the micro- and nanoplankton (20–200 and 2–20 μm, respectively) range (Gifford and Dagg 1988; Calbet and Saiz 2005). Thus, when the direct (negative) grazing effect of mesozooplankton on large phytoplankton is stronger than the indirect (positive) effect via reduction of a microzooplankton intermediate, indirect cascading effects are not obvious. Hence, omnivory should weaken indirect trophic effects (Hart 2002).

Trophic interactions might also be affected by prey nutritional quality, here defined as the difference between consumer and prey elemental stoichiometry. A comparison of biologically relevant elemental ratios between consumers and their prey is one index of prey nutritional quality (Sterner and Elser 2002; Ventura 2006). Elemental ratios across trophic levels depart from the canonical 106 carbon (C) to 16 nitrogen (N) molar stoichiometry for plankton. C : N typically decreases with increasing trophic level, from producer to herbivore to carnivore (Sterner and Elser 2002; Denno and Fagan 2003). Further, phytoplankton often exhibit a C : N ratio that varies widely in concert with fluctuations of dissolved nutrients. Although the average C : N for marine phytoplankton as a whole is close to 6.6, C : N for individual species ranged from 3 to 17 under nutrient-replete conditions, and this range broadened when nutrients were limiting (reviewed by Geider and LaRoche 2002). In contrast, zooplankton consumers exhibit species-specific homeostatic regulation of elemental composition, with copepod C : N typically between 4 and 6 (Koski 1999; Pertola et al. 2002). The difference between the consumer and the producer elemental ratios is termed the stoichiometric imbalance. In theory, the lower this imbalance, the better the food quality for the consumer (Sterner and Elser 2002).

In order to meet their fixed energy (e.g., C) and nutrient (e.g., N) requirements, zooplankton can adjust physiologically or behaviorally. Zooplankton can, to a certain extent, increase their assimilation efficiency for the limiting dietary component (Hessen 1992). More significantly, zooplankton can select higher quality prey (Kiørboe et al. 1996; Broglio et al. 2004) or increase ingestion (compensatory feeding) of low-quality prey (Plath and Boersma 2001; Augustin and Boersma 2006). In a three-level food web, selection for intermediate trophic level and higher quality prey over low-quality phytoplankton prey relaxes grazing pressure by both consumer groups and the phytoplankton population

* Corresponding author: hans.dam@uconn.edu

[1] Present address: Sea Education Association, Woods Hole, Massachusetts

should increase. Compensatory grazing by organisms in the top trophic level has the opposite effect on low-quality phytoplankton. Therefore, stoichiometric imbalance should strengthen both direct and indirect trophic effects (Plath and Boersma 2001).

We constructed experimental food chains with copepods, ciliates, and diatoms to examine the independent and combined effects of omnivory and stoichiometric imbalance on trophic interactions. We hypothesized that, in the absence of alternate prey, copepods and ciliates would increase ingestion rates of low-quality phytoplankton. If alternate higher quality prey (ciliates or N-replete over N-depleted phytoplankton for copepods or N-replete phytoplankton for ciliates) were available, copepods and ciliates would switch entirely to the high-quality prey or consume a suitable mix. Such responses of both ciliates and copepods to prey availability and quality can shed light on our current understanding of trophic interactions, particularly those that lead to strengthening or weakening of planktonic trophic cascades (Micheli 1999; Shurin et al. 2002; Sipura et al. 2003).

Methods

Species complement of the experimental food chain—The copepod *Acartia tonsa* is common in the Long Island Sound Estuary (LIS) and was the most abundant copepod species in eastern LIS at the time of the experiment (Capriulo et al. 2002, and our own observations). Similarly, centric diatoms dominate the autotrophic biomass of LIS, particularly in winter and early spring (Capriulo et al. 2002). Hence, a large and a small species of *Thalassiosira* were selected as the basal prey. Because culturing of ciliates is an important consideration for experimental work, our choices were limited. The ciliate *Strombidinopsis* sp., unlike *Strobidium* ($\sim$ 30 μm equivalent spherical diameter [ESD]), *Strobilidium* ($\sim$ 40 μm ESD), and *Tinitinnopsis* ($>$ 40 μm ESD), the three most common genera in LIS (Capriulo et al. 2002), was already isolated and successfully cultured by B. Costas at the University of Connecticut.

Culture and collection of study organisms—Semi-continuous cultures of the two centric diatoms, *Thalassiosira weissflogii* (*Tw*-high; National Marine Fisheries Service collection [NMFS] Milford, Connecticut) and *Thalassiosira pseudonana* (*Tp*; Provasoli-Guillard National Center for the Culture of Marine Phytoplankton culture 1335), were grown at 18°C in a walk-in environmental chamber with a 12 : 12 light : dark (LD) schedule. Guillard's F/20 growth medium ($\sim$ 90 μmol L^{-1} NO_3 and 3.5 μmol L^{-1} PO_4) provided a 10-fold nitrogen increase over typical LIS concentrations (Capriulo et al. 2002). A separate N-limited culture of *T. weissflogii* (*Tw*-low) was maintained in medium made with one-fourth of the nitrogen salts required for F/20. Cell diameter (Table 1) and culture concentrations ($\sim 5.0 \times 10^4$ and $\sim 5.0 \times 10^5$ cells mL^{-1} for 2-liter bottles of *Tw* and *Tp*, respectively) were monitored daily with an Elzone 280 PC particle analyzer (Particle Data). Cultures were refreshed weekly with new medium to maintain exponential growth in preparation for the experiments.

Table 1. Size and elemental composition summary for model experimental food web species. Phytoplankton sizes are given as equivalent spherical diameter (ESD). *Strombidinopsis* sp. approximate dimensions are given as length of cone-shaped cell by width of oral opening. *Acartia tonsa* size is the approximate length of the prosome. C : N ratios are geometric means $\pm$ standard error (n = 5). High and low for *Thalassiosira weissflogii* refer to nitrogen-replete and nitrogen-limited growth conditions, respectively.

Species	Size (μm)	Molar C : N
Thalassiosira weissflogii-high	11.9	7.4±0.1
Thalassiosira weissflogii-low	11.7	10.3±0.3
Thalassiosira pseudonana	4.5	9.1±0.1 (n=3)
Strombidinopsis sp.	100×50	3.3±0.02 (n=3)
Acartia tonsa female	1000	3.6±0.05

Microplankton ciliates, *Strombidinopsis* sp., were originally isolated from LIS during the summer of 2004, with additions of new individuals to the culture during the summer of 2005 to maintain genetic diversity of the population. The culture was maintained in Guillard's F/20 solution amended with a phytoplankton monoculture of *Rhodomonas* sp. (NMFS collection, Milford, Connecticut) at a concentration of 10^4 cell mL^{-1}. Cultures were transferred to new medium weekly and maintained at the same temperature and light conditions as the phytoplankton cultures.

In fall 2005, *A. tonsa* copepods were collected from LIS with a 200-μm mesh net equipped with a solid cod end. Within a couple of hours of collection, actively swimming adult females were transferred to 0.2-μm-filtered seawater and allowed to evacuate their digestive tracts for 24 h prior to beginning the experiment.

The particulate C and N content of cultured and net-collected organisms was measured with a Fisions Instruments EA 1108 CHNS Element Analyzer. For phytoplankton cells, approximately 150 mL of each culture was filtered onto a precombusted Whatman GF/F filter. Cell concentrations of each phytoplankton culture were enumerated as described previously to obtain per-cell carbon and nitrogen content. *Strombidinopsis* sp. elemental composition was determined from replicates, each comprised of 2000 starved individuals. Approximately 10 d after transfer to new medium, ciliates were individually picked from a culture depleted of phytoplankton cells and rinsed in 0.2-μm-filtered seawater prior to being carefully placed on precombusted Whatman GF/F filters. Filter blanks were created with an equivalent amount of rinse water. These blanks contained no detectable nitrogen, thus indicating negligible nitrogen enrichment (e.g., *Rhodomonas* sp. contamination) from the residual rinse water. *A. tonsa* females (50 individuals with empty guts) were placed onto precombusted Whatman GF/D filters. Average molar C : N ratios were determined from the geometric mean of three to five samples for each organism.

Experimental design—Triplicate 150-mL high-density polyethylene bottles were prepared for each of 6 controls and 16 treatments. Five phytoplankton controls consisted

of *Tw*-high, *Tw*-low, *Tp*, *Tw*-high supplemented with *Tp*, and *Tw*-low supplemented with *Tp*. Experimental food chains represented all possible two- and three-level combinations of the phytoplankton, ciliate, and copepod: ciliates and copepods were separately offered each of the phytoplankton diets (10 treatments), copepods were offered ciliates alone (one treatment), and copepods were offered ciliates in addition to each of the phytoplankton diets (five treatments). A sixth control, consisting of *Strombidinopsis* sp. alone, accounted for loss of ciliates during transfer and starvation death in the treatment where *Strombidinopsis* sp. was the sole prey item for *A. tonsa*.

Densities of phytoplankton were selected based on the results of functional response preexperiments with *A. tonsa* and measurements of phytoplankton concentrations in natural assemblages. In LIS, large (> 2 μm) phytoplankton concentrations range from 2000 to 8000 cells mL^{-1}, with small bloom concentrations near 4000 cells mL^{-1} (Capriulo et al. 2002). *Tw*-high and *Tw*-low were added at ~ 3000 cells mL^{-1} (~ 250 μg C L^{-1}) and *Tp* was added at ~ 18,000 cells mL^{-1} (~ 200 μg C L^{-1}) to all control and treatment bottles. Hence, treatments with mixed-algal assemblages contained ~ 450 μg diatom C L^{-1}. Phytoplankton cells were suspended in filtered (0.2 μm) F/20 or N-limited F/20 growth medium. Experimental copepod and ciliate concentrations were representative of bloom conditions in LIS (Capriulo et al. 2002). Individually selected and rinsed *Strombidinopsis* sp. were added to experimental bottles at an initial concentration of 1 cell mL^{-1}. Three adult female *A. tonsa* were added to each replicate bottle in the 11 treatments requiring copepods.

Controls and grazing treatments were concurrently prepared. All bottles were filled to capacity to avoid bubbles and placed on slowly rotating plankton wheels (0.6 m diameter; ~ 4 m min^{-1}) for 24 hours in an 18°C walk-in environmental chamber with a 12 : 12 LD schedule. The relatively short experimental duration was designed to minimize nutrient recycling and change in phytoplankton elemental composition, as observed by John and Davidson (2001) over the course of a 10-d experiment.

At the end of the experiment, actively swimming copepods were counted under a dissecting microscope. In the case of copepod death (15% of copepod treatment bottles), pre- and postexperiment concentrations were averaged. A 20-mL sample was removed from each bottle for phytoplankton enumeration. Phytoplankton samples from treatments containing ciliates were reverse-filtered through a 20-μm mesh, thus leaving the ciliates behind. Live phytoplankton concentrations were immediately measured with the Elzone 280 PC, and the remaining water was returned to the experimental bottles. The complete samples were then preserved with acidic Lugol's (5% total concentration) and settled for *Strombidinopsis* sp. enumeration under an inverted microscope.

Data analysis—Phytoplankton growth rates from controls and concurrent ingestion rates from treatments comprised exclusively of copepods and phytoplankton were calculated with the equations of Frost (1972). Because ciliates typically exhibit similar growth rates to phytoplankton, we expected ciliate concentrations to change during the course of the experiment. Hence, modified versions of the Frost (1972) equations were derived to determine ingestion rates for treatments that included *Strombidinopsis* sp.

By substitution, the average number of *Strombidinopsis* sp. ($\overline{S}$) in each 150-mL bottle was estimated:

$$\overline{S} = \frac{(S_f - S_i)}{k_s t} \tag{1}$$

where S_f and S_i are the final and initial counts of *Strombidinopsis* sp., t is the duration (d) of the experiment, and, assuming exponential growth, k_s is the growth rate (d^{-1}) of *Strombidinopsis* sp. (Heinbokel 1978). Thus, for treatments in which *Strombidinopsis* sp. was the sole grazer, phytoplankton clearance rates (F_{sp}, mL ind^{-1} d^{-1}) were determined by using the above estimated average number of *Strombidinopsis* sp. per bottle:

$$F_{sp} = \frac{V g_{sp}}{\overline{S}} \tag{2}$$

where V is the volume (mL) of the experimental bottle and g_{sp} is the *Strombidinopsis* sp. grazing coefficient (d^{-1}) for the phytoplankton prey.

In treatments that contained both ciliate and copepod grazers, the predatory effect of *A. tonsa* on *Strombidinopsis* sp. (e.g., *Strombidinopsis* sp. net growth rates, *A. tonsa* grazing coefficients for *Strombidinopsis* sp., and *A. tonsa* ingestion rates for *Strombidinopsis* sp.) was determined prior to resolving the effects of both on the phytoplankton prey. In order to separate the simultaneous phytoplankton grazing effects of ciliates from those of copepods, a new treatment-specific *Strombidinopsis* sp. grazing coefficient for phytoplankton (g^*_{sp}, d^{-1}) was estimated:

$$g^*_{sp} = \frac{\overline{F_{sp}} \times \overline{S}}{V} \tag{3}$$

where $\overline{F_{sp}}$ is the average *Strombidinopsis* sp. clearance rate for phytoplankton from bottles in the treatment without copepods (Gismervik 2006). The *A. tonsa* grazing coefficient for phytoplankton (g^*_{cp}, d^{-1}) was then calculated as a difference:

$$g^*_{cp} = G_T - g^*_{sp} \tag{4}$$

where G_T is the total grazing coefficient (d^{-1}) calculated according to Frost (1972). Treatment-specific clearance and ingestion rates for phytoplankton by *A. tonsa* and *Strombidinopsis* sp. were estimated by substituting the new grazing coefficients, g^*_{sp} and g^*_{cp}, into the original equations of Frost (1972). Student's *t*-tests were employed to determine statistical differences between calculated ingestion rates.

Results

Phytoplankton populations reached exponential growth phase within 4 d of nutrient addition, with specific growth rates of ~ 0.5 d^{-1} (Fig. 1). Phytoplankton size and C : N

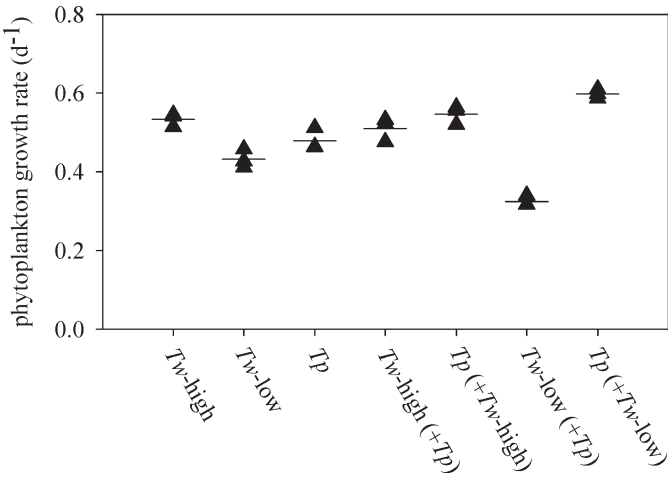

Fig. 1. Growth rates for phytoplankton species in control bottles. Horizontal bars indicate the mean of triplicates for each control. Phytoplankton suspension composition is indicated along the *x*-axis. *Tw* = *Thalassiosira weissflogii*; *Tp* = *Thalassiosira pseudonana*. High and low refer to nitrogen-replete and nitrogen-limited growth conditions, respectively. Growth rates for each species in mixed-algal controls are presented separately. For example, *Tw*-high (+ *Tp*) is the growth rate of *Tw*-high in suspension with *Tp*.

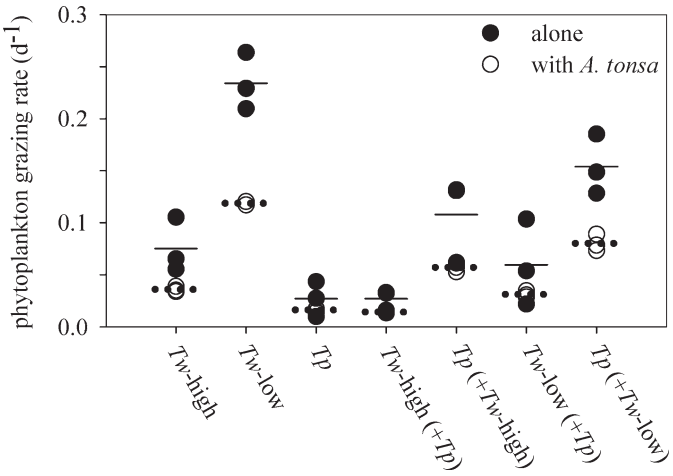

Fig. 2. Phytoplankton grazing rates by the ciliate *Strombidinopsis* sp., with (open circles) or without (closed circles) the copepod *Acartia tonsa* present. Phytoplankton diet is indicated along the *x*-axis. As in Fig. 1, grazing rates for each species in mixed-algal diets are presented separately. Horizontal bars indicate the mean of triplicates for each treatment with (dotted lines) or without (solid lines) the copepod present.

composition for each culture are presented in Table 1. At the time of the experiment, ESD measurements for *Tw*-high and *Tw*-low were not significantly different ($p > 0.05$): 11.9 and 11.7 μm, respectively. The mean cellular carbon contents of the *Tw* cultures were also equivalent (0.09 ng C cell^{-1}; $\pm$ 0.005 SE for *Tw*-high and $\pm$ 0.003 SE for *Tw*-low; $n = 5$). In contrast, the molar C : N of the nutrient replete culture was 7.4 ($\pm$ 0.1 SE; $n = 5$), which was significantly lower ($p < 0.05$) than that of the nitrogen-limited *Tw*-low culture (10.3; $\pm$ 0.3 SE; $n = 5$). The ESD for *Tp* was 4.5 μm, the mean cellular carbon content was 0.009 ng C cell^{-1} ($\pm$ 0.0002; $n = 3$), and the molar C : N was intermediate at 9.1 ($\pm$ 0.1 SE; $n = 3$).

Ciliates and copepods exhibited significantly lower ($p < 0.05$) molar C : N ratios than the phytoplankton (Table 1). The *Strombidinopsis* sp. molar C : N was 3.3 ($\pm$ 0.02 SE; $n = 3$). Although this value is seemingly low, recall that N values were obtained after subtraction of rinse-water-saturated blanks, which precluded overestimation of nitrogen content of the ciliate. In addition, the measured carbon content (mean = 13.7 ng C cell^{-1}; $\pm$ 0.7 SE; $n = 3$) was similar to the 12 ng C cell^{-1} for *Strombidinopsis* sp. estimated from the carbon-to-volume ratio for marine oligotrich ciliates (Putt and Stoecker 1989). *A. tonsa* adult females with empty guts had a molar C : N of 3.6 ($\pm$ 0.05 SE; $n = 3$), which was similar to previous estimates (Ambler 1985).

Phytoplankton grazing rates by ciliates and copepods in the experimental treatments summarize the general feeding behavior of the two heterotrophs. Maximum grazing rates by ciliates occurred on the nutrient-limited (*Tw*-low) monoculture diet, whereas minimum rates were observed on the *Tp* monoculture diet (Fig. 2). As part of a mixed diet, grazing rates for *Tp* increased and those for *T. weissflogii* decreased (Fig. 2). Grazing of *A. tonsa* on *Tp*, however, remained low regardless of diet composition (Fig. 3). Ciliate grazing rates on phytoplankton consistently decreased when *A. tonsa* was present (Fig. 2). This effect was not entirely reciprocal; for example, the presence of ciliates only decreased ($p < 0.05$) copepod grazing of *T. weissflogii* in mixed-phytoplankton diets (Fig. 3). There were no significant differences ($p > 0.05$) in grazing rates between *A. tonsa* and *A. tonsa* + *Strombidinopsis* sp. grazer treatments when *Tw* was the sole food (Fig. 3).

Estimated elemental ingestion rates provide critical information for interpretation of ciliate and copepod feeding behavior. In treatments with only *T. weissflogii* as food, *Strombidinopsis* sp. carbon ingestion rates for *Tw*-low (81 ng C ciliate^{-1} d^{-1}) were approximately 160% greater ($p < 0.01$) than those for the nutrient replete *Tw*-high (Fig. 4a). Hence, the ciliates ingested nitrogen twice as fast (9.5 vs. 4.6 ng N ciliate^{-1} d^{-1}) on the nitrogen-limited than on the nitrogen-rich *T. weissflogii* diet (Fig. 4b). With *Tp* as an additional food source, carbon ingestion of both *Tw*-high and *Tw*-low decreased to $\sim$ 10 ng C ciliate^{-1} d^{-1} (Fig. 4a), and was independent of culture nitrogen content. Ingestion of *Tp* accounted for roughly 3 ng N ciliate^{-1} d^{-1}, and increased the total nitrogen ingestion rate in both treatments to match the nitrogen ingestion rate ($\sim$ 5 ng N ciliate^{-1} d^{-1}) estimated for ciliates grazing on *Tw*-high alone (Fig. 4b). When *T. weissflogii* was offered as a sole food to *A. tonsa*, the carbon ingestion rate of *Tw*-low was also significantly greater ($p < 0.01$) than that for *Tw*-high (Fig. 5a). The ingestion rate of *Tw*-high was $\sim$ 5900 ng C copepod^{-1} d^{-1}, compared to $\sim$ 7400 ng C copepod^{-1} d^{-1} for *Tw*-low. *A. tonsa* ingested *Tp* poorly; *Tp* growth rates were mostly greater than grazing rates, resulting in ingestion rates that were negative or nearly zero in *Tp* monoculture treatments. Ingestion rates of *Tp* did not increase even when this smaller diatom was offered along

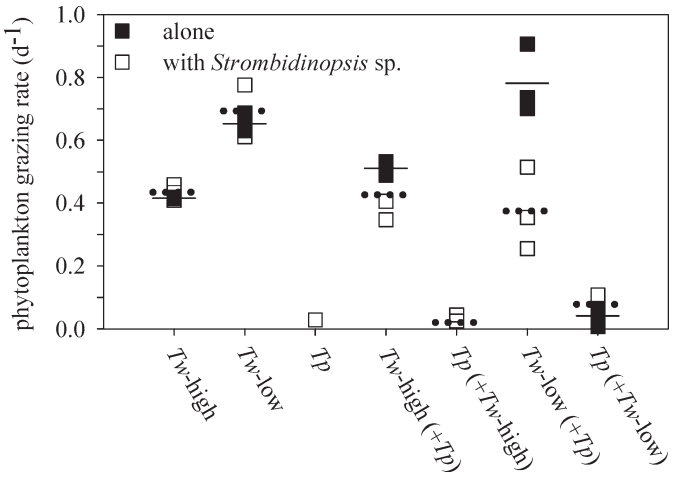

Fig. 3. Phytoplankton grazing rates by the copepod *Acartia tonsa*, with (open squares) or without (closed squares) the ciliate *Strombidinopsis* sp. present. Phytoplankton diet is indicated along the *x*-axis. As in Fig. 1, grazing rates for each species in mixed-algal diets are presented separately. Horizontal bars indicate the mean of triplicates for each treatment with (dotted lines) or without (solid lines) the ciliate present.

with *T. weissflogii* (Fig. 5a). In the presence of *Tp*, carbon ingestion rates of both *Tw*-high and *Tw*-low increased significantly ($p < 0.05$) by 20–25%. As a result, nitrogen ingestion rates did not significantly differ ($p > 0.05$) between *Tw*-high and *Tw*-low treatments containing mixed diets (Fig. 5b).

In treatments comprised of *Tw* alone, ciliates and copepods, *A. tonsa* ingested *Tw*-high at a similar rate ($p > 0.05$) to that observed in the two-trophic-level treatments (Fig. 5a). The *A. tonsa* ingestion rate for *Tw*-low, in the presence of *Strombidinopsis* sp., was slightly greater, but not significantly different from the two-level system. In both cases, copepods ingested *Strombidinopsis* sp. at a rate of ~ 160 ng C copepod^{-1} d^{-1} (~ 90 ng N copepod^{-1} d^{-1}), a much smaller portion of total C ingestion than that contributed by phytoplankton (Fig. 6).

In all treatments, ingestion of *Strombidinopsis* sp. by *A. tonsa* remained low. Unexpectedly, the ciliate ingestion rate for a ciliate-only diet was only just significantly lower ($p < 0.05$) than in a mixed (large diatom and ciliate) diet (Fig. 6). When the small diatom, *Tp*, was offered as part of a mixed diet with ciliates, the ingestion rate did not significantly ($p > 0.05$) differ from the treatment with *Strombidinopsis* sp. alone.

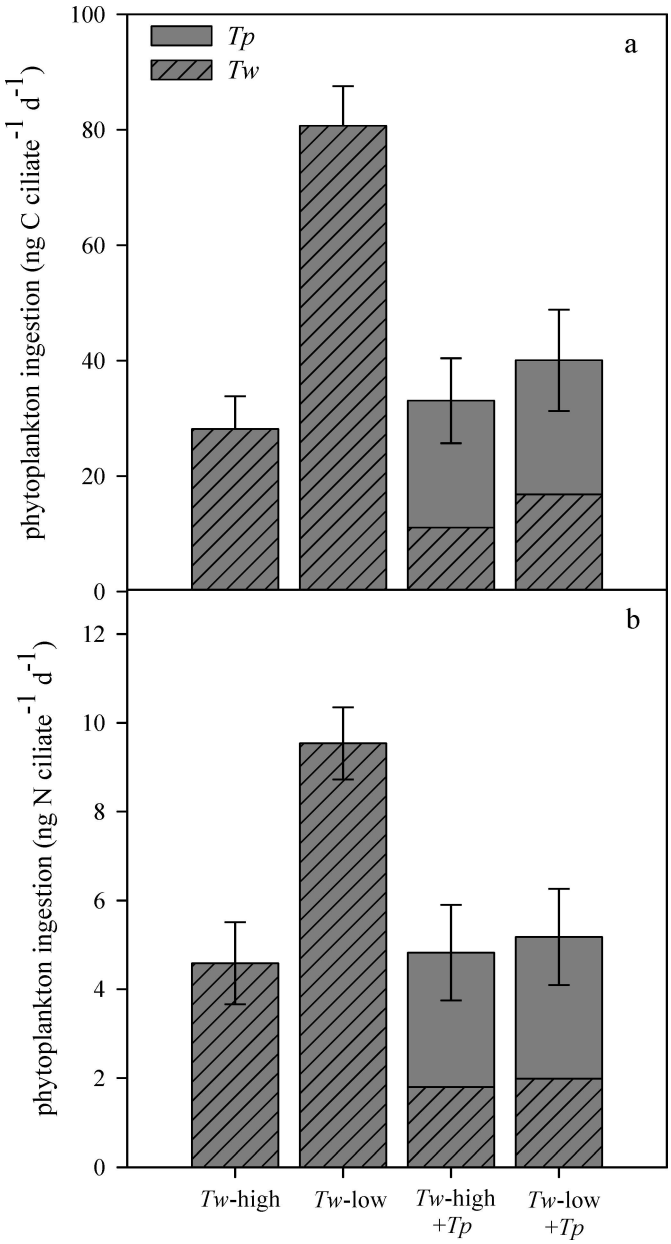

Fig. 4. Total phytoplankton (a) carbon and (b) nitrogen ingestion rates by the ciliate *Strombidinopsis* sp. Phytoplankton diet (monoculture or mixed) is indicated along the *x*-axis. Portion of total ingestion contributed by *Thalassiosira pseudonana* is indicated by solid shading. Error bars denote standard error of the mean ($n = 3$).

Discussion

An experimental approach with laboratory food chains was used to examine the influence of food quality (predator–prey stoichiometric imbalance) and omnivory on cascading planktonic trophic interactions. Two main results were evident. First, we found strong evidence of compensatory grazing of phytoplankton by the ciliate and, to a lesser extent, by the copepod in response to insufficient (i.e., N-limited) phytoplankton quality. Furthermore, the copepod, but not the ciliate, continued to engage in compensatory grazing of N-limited phytoplankton when an alternate higher quality phytoplankton was simultaneously offered. Second, cascading indirect effects of the copepod on phytoplankton via the ciliate were minor. Although the copepod exhibited omnivory when a mixture of ciliates and low-quality phytoplankton was offered, the decrease in phytoplankton concentration due to direct grazing by the copepod was much greater than any indirect increase resulting from reduced ciliate grazing pressure.

Compensatory feeding (Plath and Boersma 2001; Augustin and Boersma 2006) and prey selection (Kiørboe et

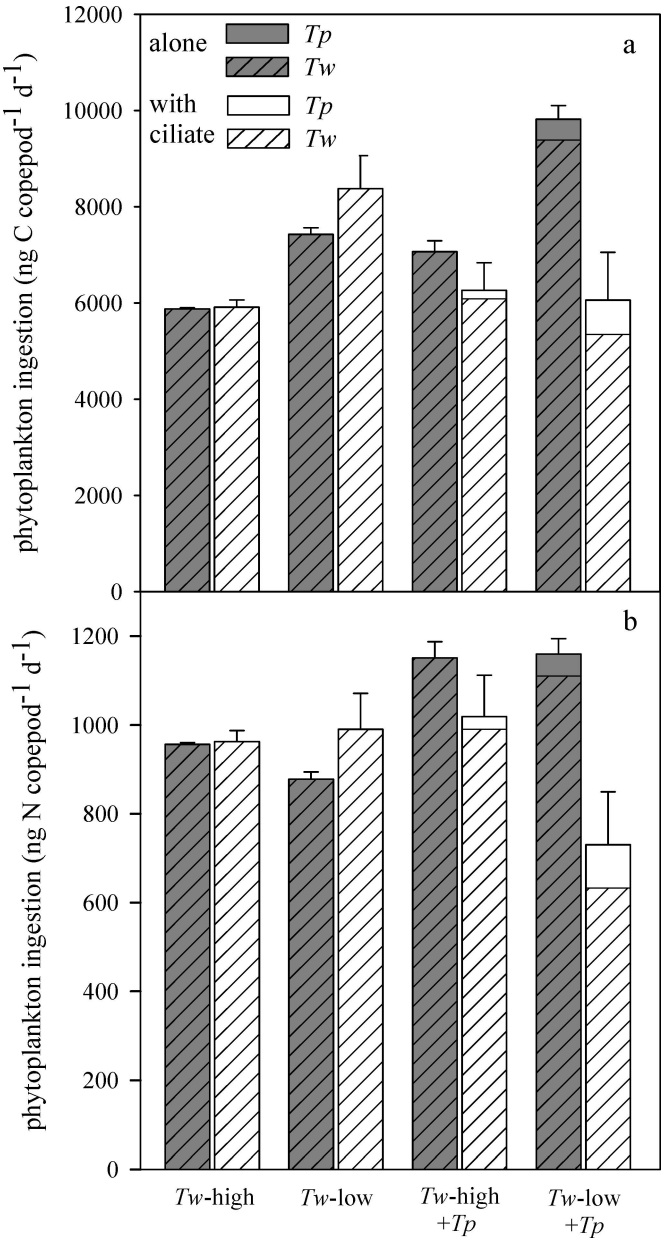

Fig. 5. Total phytoplankton (a) carbon and (b) nitrogen ingestion rates by the copepod *Acartia tonsa*, with or without the ciliate *Strombidinopsis* sp. present. Phytoplankton diet (monoculture or mixed) is indicated along the *x*-axis. As in Fig. 4, portion of total ingestion contributed by each species in a mixed diet is indicated by shading. Error bars denote standard error of the mean (n = 3).

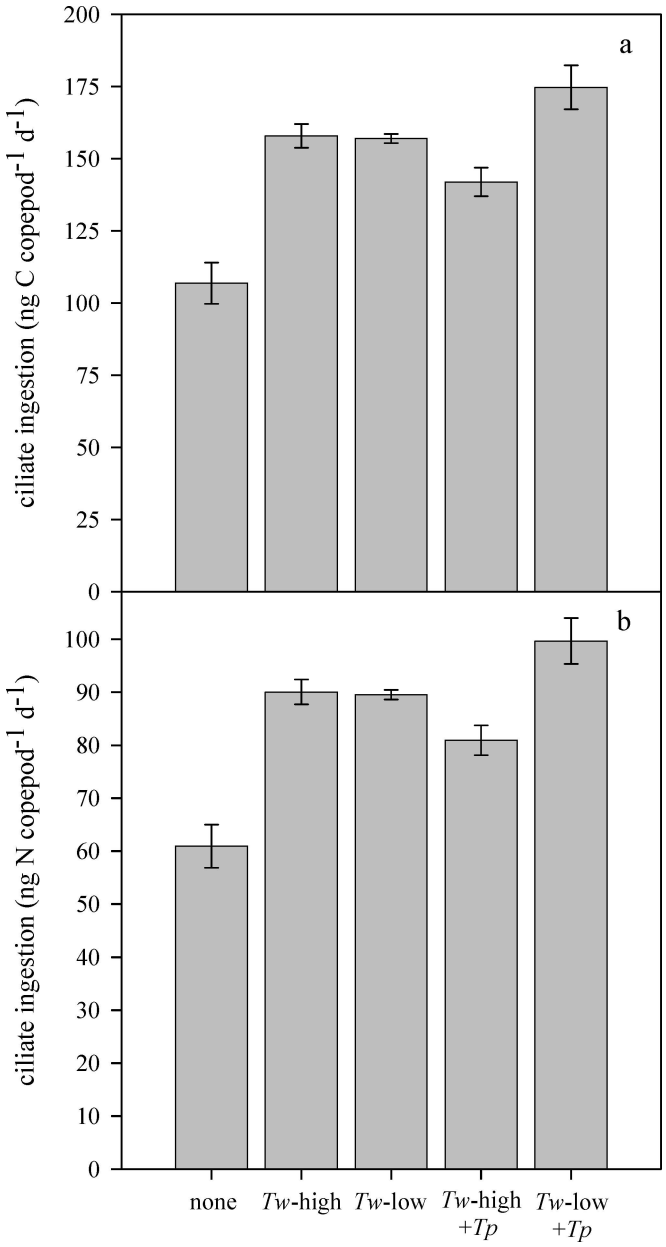

Fig. 6. (a) Carbon and (b) nitrogen ingestion rates of the ciliate *Strombidinopsis* sp. by the copepod *Acartia tonsa*. Accompanying phytoplankton diet (monoculture or mixed) is indicated along the *x*-axis. Error bars denote standard error of the mean (n = 3).

al. 1996; Broglio et al. 2004) are distinct mechanisms by which consumers attempt to overcome energy (carbon) or nutrient (e.g., nitrogen) limitation, and each is hypothesized to have a different effect on cascading trophic interactions. For instance, in a three-level food chain with copepods, ciliates, and diatoms, compensatory grazing activity is predicted to strengthen the direct effect (the copepod reduces diatom concentration) and prey selection is predicted to strengthen the indirect effect (the copepod reduces N-rich ciliate concentration relaxing grazing by the ciliate and increasing diatom concentration) of the top predator on the basal prey.

In the current study, the ciliate nearly doubled its N ingestion rate when offered a monospecific diet of the N-limited large diatom (Fig. 4b). Such a behavioral response to detection of low-quality prey is previously undocumented for ciliates. Prior studies focused on the ability of ciliates to select for or against prey from mixed assemblages. Christaki et al. (1998) found that *Uronema* sp. in stationary growth phase removed carboxylate-coated microspheres at higher rates than concurrently available uncoated micro-

spheres. More recently, Hamels et al. (2004) observed benthic ciliates (*Strombidium* sp.) selectively grazing diatoms that enhanced grazer growth rates. No direct contact was necessary for recognition of preferred prey during their experiments; ciliates selected prey based on soluble chemical cues. Prey selection by ciliates was also observed in the present study. When offered large and small diatoms simultaneously, the ciliate decreased ingestion of the N-depleted large diatom by 70% and supplemented its diet with the smaller but N-replete diatom (Fig. 4b). The small diatom provided 60% of the carbon ingested by the ciliate, but represented only 36% of the carbon in the available phytoplankton mixture, indicating positive selection for the smaller diatom. Moreover, total N ingestion rates for mixed diets were not significantly different from each other, nor were they significantly different from N ingestion on the nutrient-replete large-diatom monodiet. Hence, compensatory grazing was no longer necessary for maintenance of homeostatic elemental composition; ciliate N requirements were met by diversifying diet composition.

The copepod increased C ingestion by 25% when fed the N-limited large diatom (Fig. 5). Further, N ingestion on the N-limited large-diatom diet was only 92% of the ingestion on the N-replete large-diatom diet (Fig. 5b), indicating compensatory feeding activity in response to N limitation. Compensatory feeding by copepods has previously been observed. In experiments with *A. tonsa*, Kiørboe (1989) found that the gross growth efficiency for C, but not for N, decreased with the C : N of prey. Also, Augustin and Boersma (2006) observed compensatory grazing by *A. clausii* at high (500 μg C L^{-1}) algal concentrations, but this behavior was absent at an algal concentration similar to that used in the current study. Thus, there seems to be growing evidence that compensatory feeding is a common response by copepods to insufficient food quality. In contrast to the ciliate, the copepod grazed poorly on the small diatom (Fig. 3). Given the size of the small diatom (4.5 μm ESD), this observation is not surprising since particle capture efficiency in *A. tonsa* dramatically decreases for particles smaller than 8 μm (Støttrup and Jensen 1990) and the optimum food particle size is not reached until cells are $>$ 10 μm (Støttrup and Jensen 1990; Besiktepe and Dam 2002). With the two-level experimental food chain, the effect of size constrained acquisition of the higher quality prey. The addition of the small diatom to the diet nonetheless increased the total C ingestion rates over those measured for the large-diatom monodiet, and the copepod continued to engage in compensatory grazing on the mixed-diatom diet (Fig. 5a).

Microzooplankton ciliates are important food for copepods (Sipura et al. 2003; Calbet and Saiz 2005). Furthermore, ingestion of ciliates might improve the dietary value of phytoplankton prey (trophic upgrading) and efficiently link the microbial and classical food webs (Tang et al. 2001). Hence, in accordance with stoichiometric theory, we expected the copepod to preferentially feed on ciliates, or at least to supplement its diet with ciliates, in treatments with phytoplankton of insufficient quality. In fact, the copepod did not positively select for the ciliate. In treatments comprised of copepods, ciliates, and phytoplankton, the ciliate represented $\sim$ 5% of the carbon available for consumption by the copepod, but only 2–3% of the carbon in the copepod diet was derived from ciliate prey (Figs. 5, 6). Consequently, the predicted indirect effect of the copepod on diatoms via the ciliate was minimal.

The weak copepod–ciliate link in this three-level experimental food chain was likely density- rather than size-dependent. Although *Strombidinopsis* sp., at 100 μm in length (50 μm ESD), falls near the upper limits of the *A. tonsa* food size spectrum, recent studies demonstrate that large ciliates can comprise a significant portion of *Acartia* diet in natural communities (Sipura et al. 2003; Rollwagen Bollens and Penry 2003). Ciliates accounted for $>$ 50% of the C consumed by *Acartia* in one sub-estuary of San Francisco Bay and nearly 100% in another (Rollwagen Bollens and Penry 2003). Tiselius (1989) found that *Acartia clausi* achieved maximum clearance for 25-μm ESD ciliates, and continued to clear at the same rate for 50-μm ESD ciliates (the largest size included in his study). For copepods, in general, the clearance rate is $\sim$ 80% of the maximum value at the predator : prey size ratio ($\sim$ 0.1) characteristic of this study (Hansen et al. 1994). Stoecker and Sanders (1985) also measured appreciable *A. tonsa* predation on a different large ciliate, *Favella* sp. (oral lorica diameter $\sim$ 70 μm and length = 100–200 μm; minimum 45-μm ESD), at concentrations of 0.01 to 3.4 individuals mL^{-1}. Moreover, ingestion at 1 *Favella* mL^{-1} was 50 ng C $copepod^{-1}$ h^{-1} (Stoecker and Sanders 1985), nearly 10 times greater than the ingestion rates observed in the present study. Clearly, the copepod used in this experiment is capable of consuming large ciliates with high efficiency. Perhaps relatively high diatom concentrations minimized the importance of the higher quality, but less abundant, ciliate food for the copepod. The large diatom was offered at $\sim$ 250 μg C L^{-1}, equivalent to 18 ciliates mL^{-1}. Because this diatom concentration was not severely limiting for *A. tonsa* (Kiørboe et al. 1996; Besiktepe and Dam 2002), the copepod could readily continue compensatory grazing of the N-limited diatom in order to meet nutritional requirements. Kiørboe et al. (1996) examined selective grazing and found that although *A. tonsa* spent less time on suspension feeding in search of diatom prey as ciliate abundance increased, ciliate clearance rates remained constant across a range of diatom concentrations. Additionally, the functional response for diatom ingestion was depressed only at high ciliate concentrations (12 ciliates mL^{-1}). In the current study, the ciliate was available at a much lower concentration (1 ciliate mL^{-1}), for which the copepod functional response for diatoms was unaffected. Likewise, our results indicate that filter feeding did persist in the presence of the intermediate grazer, and the ciliate losses were probably inadvertent casualties of this nonselective feeding strategy rather than selective preference (Gismervik 2006). Ingestion of ciliates even increased from $\sim$ 26 to 39 ciliates $copepod^{-1}$ d^{-1} when phytoplankton prey were also offered. Although these ingestion rates were below the lower limits (3–21 ciliates $copepod^{-1}$ h^{-1}) reported by Stoecker and Egloff (1987), the rates were well within the range estimated for LIS zooplankton (Lonsdale et al. 1996), and above the 3.3 ng C $copepod^{-1}$ h^{-1} measured for

Acartia feeding on loricate ciliates in San Francisco Bay estuary (Rollwagen Bollens and Penry 2003). Rather than implying an inability to reach a density threshold for efficient capture of motile prey by the copepod, our results suggest instead that omnivory and compensatory grazing were sufficient mechanisms to overcome elemental imbalance, and selection for the ciliate was not essential.

Attempts to identify marine planktonic trophic cascades are common in the literature. Positive identification of cascades in natural assemblages has been restricted to communities with simple food chains or where grazing is limited by prey size and small phytoplankton altogether escape grazing by copepods. For example, Stibor et al. (2004) observed cascades in parallel food chains of different length. Jellyfish decreased calanoid copepod abundance and copepod abundance released ciliates from predation and decreased small phytoplankton concentrations. Similarly, Sundt-Hansen et al. (2006) demonstrated that copepod feeding indirectly controlled picocyanobacteria concentrations via removal of ciliates and appendicularians. Reviews of trophic interactions over a broad range of communities concluded that planktonic cascades are rare and at best weak in marine systems (Micheli 1999; Shurin et al. 2002). Sipura et al. (2003) observed significant removal of ciliates and large phytoplankton during mesocosm experiments, yet no indirect effect on bacteria or nanoflagellates. Thus, the commonly observed weak indirect effects of copepods on phytoplankton beg for mechanistic explanation. The experimental approach of the present study allowed us to isolate and measure the effects of two factors, omnivory and food quality, that may influence cascade strength.

The experimental approach used here has its own limitations that underscore challenges and priorities for future investigations. First, grazing behavior may be altered by culture handling prior to the experiment. Jürgens and Simek (2000) observed decreased grazing rates in experiments with starved freshwater ciliates. In order to ensure minimal *Rhodomonas* sp. contamination during transfer of *Strombidinopsis* sp. to treatments of the present study, ciliates were forced to almost entirely crop phytoplankton in the culture dishes. Perhaps a multiple-stage reverse-filtration and dilution in 0.2-μm-filtered seawater, prior to being individually transferred to experimental medium, would effectively isolate ciliates without depletion of their culture diet. Second, in the three-level experimental food chain, the copepod and the ciliate potentially compete for the phytoplankton resource, but individual effects of competition and predation were not simultaneously measured. To demonstrate competition, a measured reduction of the growth rate of both the copepod and the ciliate would be required. Hence, our results are limited to addressing the effects of grazing alone. Third and most important, trophic interactions will depend upon the available predator and prey species composition (Gismervik 2006), sizes (Tiselius 1989), and concentrations (Kiørboe et al. 1996). Ingestion rates measured for one copepod species consuming a particular ciliate or phytoplankton prey could be entirely different if another prey species is introduced to the existing community. Strom and Morello (1998) measured growth and grazing rates for *Strombidinopsis* sp. on a number of different phytoplankton diets (*T. weissflogii* was not included) and found that the ciliate survived, but did not grow when fed some species. Clearly, repetition of this experiment with ciliates representing a range of sizes and concentrations is a priority to understand the variability in possible outcomes. Nanoplankton concentrations in San Francisco Bay were > 1000 times higher than microplankton concentrations (Rollwagen Bollens and Penry 2003). Kiørboe et al. (1996) conducted experiments to examine prey switching by *A. tonsa* with mixed diets composed of *Strombidium* (1–12 ciliates mL^{-1}) and *Thalassiosira weissflogii* (60–2000 cells mL^{-1}). Although these ratios of phytoplankton to ciliate are not too different from those used in the present study ($\sim 1:1000$), it would be prudent in future studies to use smaller (~ 20 μm ESD) ciliate prey and to increase the ratio of ciliate to phytoplankton ($\sim 1:500$ or $1:100$). Smaller ciliates at higher concentrations might provide the impetus for copepods to switch from compensatory grazing, a likely inefficient mechanism for overcoming energy limitation, to selection for the highest quality prey available.

Questions remain regarding the persistence of the potential top-down control mechanisms induced by prey quality because it is commonly assumed that consumption of low-quality phytoplankton leads to a decrease in the zooplankton numerical response (Jones et al. 2002; Klein Breteler et al. 2005). Plath and Boersma (2001) observed maximum *Daphnia* sp. growth rates at intermediate algal phosphorus concentrations. *A. tonsa* produced fewer eggs, and the resulting nauplii developed slowly, when they were fed N- (Jones et al. 2002) or P (lipid)-limited prey (Klein Breteler et al. 2005). Because both *Strombidinopsis* sp. and *A. tonsa* increased C ingestion rates on the low-N *T. weissflogii* monospecific diet in the current study (Figs. 4a, 5a), and most zooplankton species have very low saturation thresholds for fatty acids (Becker et al. 2004), compensatory grazing could have raised the total lipid intake above such thresholds. Compensatory grazing of N-limited phytoplankton, in the absence of alternative N-replete prey, can moderate the potentially negative effect of a stoichiometric imbalance on individual consumer growth and maintain the numerical response exhibited by the entire population. However, Augustin and Boersma (2006) found that *Acartia* species exhibited higher egg production on an N-limited diet and egg hatching success was unaffected. Their results are in direct contradiction to the findings of Jones et al. (2002), and suggest that N limitation does not automatically result in growth limitation of consumers.

In conclusion, omnivory compounded by compensatory feeding rather than selection for N-replete intermediate grazers induced by predator–prey stoichiometric imbalance had the greatest influence over trophic interactions during the present study. When restricted to a lower quality food, compensatory grazing by both the ciliate and the copepod counteracted the effects of dietary elemental limitation. This compensatory grazing strengthened the direct effect of a consumer on the adjacent trophic level in the food chain. However, when both the copepod and the ciliate were present in the food chain, the continued direct grazing by

the copepod on phytoplankton largely masked the weak indirect (via the ciliate) and positive cascading effects on phytoplankton.

Acknowledgments

We thank B. Costas for providing the *Strombidinopsis* sp. cultures, H. Skelton, G. McManus, and two reviewers for comments on the manuscript, and M. Pace and D. Post for earlier discussions and suggestions. Research was partially supported by grants from the National Science Foundation (International-0086659, Ocean Sciences-0648126), the Environmental Protection Agency (EPA, Research and Development-8317060), and the Research Foundation of the University of Connecticut awarded to HGD, and a Lerner-Gray Grant-in-Aid-of-Research from the American Museum of Natural History awarded to ANSS. This research does not necessarily reflect the views of the EPA, and no EPA endorsement should be inferred. This is contribution #334 of the Ecology and Oceanography of Harmful Algal Bloom (ECOHAB) program.

References

Ambler, J. W. 1985. Seasonal factors affecting egg production and viability of eggs of *Acartia tonsa* Dana from East Lagoon, Galveston, Texas. Estuar. Coast. Shelf Sci. **20:** 743–760, doi:10.1016/0272-7714(85)90030-7

Augustin, C. B., and M. Boersma. 2006. Effects of nitrogen stressed algae on different *Acartia* species. J. Plankton Res. **28:** 429–436, doi:10.1093/plankt/fbi131

Becker, C., H. Feuchtmayr, D. Brepohl, B. Santer, and M. Boersma. 2004. Differential impacts of copepods and cladocerans on lake seston, and resulting effects on zooplankton growth. Hydrobiologia **526:** 197–207, doi:10.1023/B:HYDR.0000041603.41913.95

Besiktepe, S., and H. G. Dam. 2002. Coupling of ingestion and defecation as a function of diet in the calanoid copepod *Acartia tonsa*. Mar. Ecol. Prog. Ser. **229:** 151–164, doi:10.3354/meps229151

Broglio, E., E. Saiz, A. Calbet, I. Trepat, and M. Alcaraz. 2004. Trophic impact and prey selection by crustacean zooplankton on the microbial communities of an oligotrophic coastal area (NW Mediterranean Sea). Aquat. Microb. Ecol. **35:** 65–78, doi:10.3354/ame035065

Calbet, A., and E. Saiz. 2005. The ciliate–copepod link in marine ecosystems. Aquat. Microb. Ecol. **38:** 157–167, doi:10.3354/ame038157

Capriulo, G. M., G. Smith, R. Troy, G. H. Wikfors, J. Pellet, and C. Yarish. 2002. The planktonic food web structure of a temperate zone estuary, and its alteration due to eutrophication. Hydrobiologia **475/476:** 263–333, doi:10.1023/A:1020387325081

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience **35:** 634–639, doi:10.2307/1309989

Christaki, U., J. R. Dolan, S. Pelegri, and F. Rassoulzadegan. 1998. Consumption of picoplankton-size particles by marine ciliates: Effects of physiological state of the ciliate and particle quality. Limnol. Oceanogr. **43:** 458–464, doi:10.4319/lo.1998.43.3.0458

Denno, R. F., and W. F. Fagan. 2003. Might nitrogen limitation promote omnivory among carnivorous arthropods? Ecology **84:** 2522–2531, doi:10.1890/02-0370

Frost, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. **17:** 805–815, doi:10.4319/lo.1972.17.6.0805

Geider, R. J., and J. Laroche. 2002. Redfield ratios revisited: Variability of C : N : P in marine microalgae and its biochemical basis. Eur. J. Phycol. **37:** 1–17, doi:10.1017/S0967026201003456

Gifford, D. J., and M. J. Dagg. 1988. Feeding of the estuarine copepod *Acartia tonsa* Dana: Carnivory vs. herbivory in natural microplankton assemblages. Bull. Mar. Sci. **43:** 458–468.

Gismervik, I. 2006. Top-down impact by copepods on ciliate numbers and persistence depends on copepod and ciliate species composition. J. Plankton Res. **28:** 499–507, doi:10.1093/plankt/fbi135

Hamels, I., H. Mussche, K. Sabbe, K. Muylaert, and W. Vyverman. 2004. Evidence for constant and highly specific active food selection by benthic ciliates in mixed diatoms assemblages. Limnol. Oceanogr. **49:** 56–68, doi:10.4319/lo.2004.49.1.0058

Hansen, B., P. K. Bjornsen, and P. J. Hansen. 1994. The size ratio between planktonic predators and their prey. Limnol. Oceanogr. **39:** 395–403, doi:10.4319/lo.1994.39.2.0395

Hart, D. R. 2002. Intraguild predation, invertebrate predators, and trophic cascades in lake food webs. J. Theor. Biol. **218:** 111–128, doi:10.1006/jtbi.2002.3053

Heinbokel, J. F. 1978. Studies on the functional role of tintinnids in the Southern California Bight II. Grazing rates of field populations. Mar. Biol. **47:** 191–197, doi:10.1007/BF00395639

Hessen, D. O. 1992. Nutrient element limitation of zooplankton production. Am. Nat. **140:** 800–813, doi:10.1086/285441

John, E. H., and K. Davidson. 2001. Prey selectivity and the influence of prey carbon : nitrogen ratio on microflagellate grazing. J. Exp. Mar. Biol. Ecol. **260:** 93–111, doi:10.1016/S0022-0981(01)00244-1

Jones, R. H., K. J. Flynn, and T. R. Anderson. 2002. Effect of food quality on carbon and nitrogen growth efficiency in the copepod *Acartia tonsa*. Mar. Ecol. Prog. Ser. **235:** 147–156, doi:10.3354/meps235147

Jürgens, K., and K. Simek. 2000. Functional response and particle size selection of *Halteria* cf. *grandinella*, a common freshwater oligotrichous ciliate. Aquat. Microb. Ecol. **22:** 57–68, doi:10.3354/ame022057

Kiørboe, T. 1989. Phytoplankton growth rate and nitrogen content: Implications for feeding and fecundity in a herbivorous copepod. Mar. Ecol. Prog. Ser. **55:** 229–234, doi:10.3354/meps055229

———, E. Saiz, and M. Viitasalo. 1996. Prey switching behaviour in the planktonic copepod *Acartia tonsa*. Mar. Ecol. Prog. Ser. **143:** 65–75, doi:10.3354/meps143065

Klein Breteler, W. C. M., N. Schogt, and S. Rampen. 2005. Effect of diatom nutrient limitation on copepod development: Role of essential lipids. Mar. Ecol. Prog. Ser. **291:** 125–133, doi:10.3354/meps291125

Koski, M. 1999. Carbon : nitrogen ratios of Baltic Sea copepods—indication of mineral limitation? J. Plankton Res. **21:** 1565–1573, doi:10.1093/plankt/21.8.1565

Lonsdale, D. J., E. M. Cosper, W. K. Kim, M. Doall, A. Divadeenam, and S. H. Jonasdottir. 1996. Food web interactions in the plankton of Long Island bays, with preliminary observations on brown tide effects. Mar. Ecol. Prog. Ser. **134:** 247–263, doi:10.3354/meps134247

Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. Science **285:** 1396–1398, doi:10.1126/science.285.5432.1396

Pertola, S., M. Koski, and M. Viitasalo. 2002. Stoichiometry of mesozooplankton in N- and P-limited areas of the Baltic Sea. Mar. Biol. **140:** 425–434, doi:10.1007/s00227-001-0723-3

Plath, K., and M. Boersma. 2001. Mineral limitation of zooplankton: Stoichiometric constraints and optimal foraging. Ecology **82:** 1260–1269, doi:10.1890/0012-9658(2001)082[1260:MLOZSC]2.0.CO;2

Putt, M., and D. K. Stoecker. 1989. An experimentally determined carbon : volume ratio for marine 'oligotrichous' ciliates from estuarine and coastal waters. Limnol. Oceanogr. **34:** 1097–1103, doi:10.4319/lo.1989.34.6.1097

Rollwagen Bollens, G. C., and D. L. Penry. 2003. Feeding dynamics of *Acartia* spp. copepods in a large, temperate estuary (San Francisco Bay, CA). Mar. Ecol. Prog. Ser. **257:** 139–158, doi:10.3354/meps257139

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecol. Lett. **5:** 785–791, doi:10.1046/j.1461-0248.2002.00381.x

Sipura, J., E. Lores, and R. A. Snyder. 2003. Effect of copepods on estuarine microbial plankton in short-term microcosms. Aquat. Microb. Ecol. **33:** 181–190, doi:10.3354/ame033181

Sterner, R. W., and J. J. Elser. 2002. Ecological stoichiometry: The biology of elements from molecules to the biosphere, 1st ed. Princeton Univ. Press.

Stibor, H., O. Vadstein, S. Diehl, A. Gelzleichter, T. Hansen, F. Hantzsche, A. Katechakis, B. Lippert, K. Løseth, C. Peters, W. Roederer, M. Sandow, L. Sundt-Hansen, and Y. Olsen. 2004. Copepods act as a switch between alternative trophic cascades in marine pelagic food webs. Ecol. Lett. **7:** 321–328, doi:10.1111/j.1461-0248.2004.00580.x

Stoecker, D. K., and D. A. Egloff. 1987. Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. J. Exp. Mar. Biol. Ecol. **110:** 53–68, doi:10.1016/0022-0981(87)90066-9

———, and N. K. Sanders. 1985. Differential grazing by *Acartia tonsa* on a dinoflagellate and a tintinid. J. Plankton Res. **7:** 85–100, doi:10.1093/plankt/7.1.85

Støttrup, J. G., and J. Jensen. 1990. Influence of algal diet on feeding and egg-production of the calanoid copepod *Acartia tonsa* Dana. J. Exp. Mar. Biol. Ecol. **141:** 87–105, doi:10.1016/0022-0981(90)90216-Y

Strom, S. L., and T. A. Morello. 1998. Comparative growth rates and yields of ciliates and heterotrophic dinoflagellates. J. Plankton Res. **20:** 571–584, doi:10.1093/plankt/20.3.571

Sundt-Hansen, L., Y. Olsen, H. Stibor, M. Heldal, and O. Vadstein. 2006. Trophic cascades mediated by copepods, not nutrient supply rate, determine the development of picocyanobacteria. Aquat. Microb. Ecol. **45:** 207–218, doi:10.3354/ame045207

Tang, K. W., H. H. Jakobsen, and A. W. Visser. 2001. *Phaeocystis globosa* (Prymnesiophyceae) and the planktonic food web: Feeding, growth, and trophic interactions among grazers. Limnol. Oceanogr. **46:** 1860–1870, doi:10.4319/lo.2001.46.8.1860

Tiselius, P. 1989. Contribution of aloricate ciliates to the diet of *Acartia clausi* and *Centropages hamatus* in coastal waters. Mar. Ecol. Prog. Ser. **56:** 49–56, doi:10.3354/meps056049

Ventura, M. 2006. Linking biochemical and elemental composition in freshwater and marine crustacean zooplankton. Mar. Ecol. Prog. Ser. **327:** 233–246, doi:10.3354/meps327233

Associate editor: Robert W. Sterner

Received: 26 October 2009
Accepted: 26 May 2010
Amended: 14 June 2010