Aquat Ecol (2010) 44:113–119
DOI 10.1007/s10452-009-9264-5

Grazing and growth responses of a marine oligotrichous ciliate fed with two nanoplankton: does food quality matter for micrograzers?

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Received: 16 December 2008 / Accepted: 26 June 2009 / Published online: 9 July 2009

Abstract To investigate whether predator growth and grazing would depend on prey properties besides size, we studied the numerical and functional responses of a marine oligotrichous ciliate isolated in Hong Kong coastal waters, *Strobilidium* sp., on two nanoplanktonic preys of similar size. The growth and ingestion rates of *Strobilidium* sp. could be fit with prey concentrations by hyperbolic curves. *Strobilidium* sp. exhibited higher maximal growth rates and gross growth efficiencies, and lower maximal clearance rates on *Nannochloropsis* sp. than on *Isochrysis galbana*. Our results demonstrate that prey properties presumably food quality can have a considerable effect on predator growth and grazing and implications on phytoplankton community structure and biogeochemical cycling.

Keywords Ciliate · Grazing · Growth · Food quality

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Introduction

It has been widely recognized that microbial food web dominates biogeochemical cycles in the sea since 1980s (Azam et al. 1983). Trophic transfer from pico- and nano-plankton to microzooplankton such as ciliates and dinoflagellates is an important link in the microbial food web (Azam et al. 1983; Sherr and Sherr 1988). Oligotrichous ciliates are an important component of microzooplankton (20–200 μm) that are dominant consumers of phytoplankton and transfer substantial amount of carbon from the microbial loop to higher trophic levels in the sea (Gifford 1991; Pierce and Turner 1992; Liu et al. 2005).

It is of great interest to study the factors affecting the trophic transfer from phytoplankton to herbivores (e.g., Brett and Goldman 1997). Size has been shown to play a pivotal role in determining predator–prey feeding relationships (Hansen et al. 1994), and ingestion and growth rates (Hansen et al. 1997) and as such current nutrient–phytoplankton–zooplankton models containing multiple phytoplankton boxes are often established solely based on size (e.g., Armstrong 1994). However, besides size, the food quality may also be an important factor affecting trophic transfer. For example, the essential fatty acid content such as docosahexaenoic acid (DHA, 22:6($n-3$)) in food may have a significant effect on the egg production and hatching success of a marine calanoid copepod *Temora longicornis* (Evjemo et al. 2008). The limited amounts of eicosapentaenoic acid (EPA, 20:5($n-3$))

have been also considered as the major factor limiting the trophic transfer from lake cyanobacteria to *Daphnia magna* (Muller-Navarra et al. 2000).

The effects of food quality on the feeding and growth of oligotrichous ciliates have been relatively less studied. Selective grazing against inert beads or dead preys has occasionally been shown, although not always, in some marine ciliates (Sherr et al. 1987; Christaki et al. 1998). Many studies used artificial or dead preys to measure grazing rates of flagellates and ciliates, which may bias the real situation (e.g., Ichinotsuka et al. 2006). Whether different food quality will induce grazing selectivity of predators is an open question. Cowles et al. (1988) found that the copepod *Acartia tonsa* selectively fed on fast-growing *Thalassiosira weissflogii* cells that contained greater nitrogen and protein contents than slow-growing cells at the same prey densities. With different algae as preys, however, grazing selection of copepods may depend on food concentration (DeMott 1989). When food concentrations are low, grazing selectivity is low and vice versa.

This study aims to address the effect of food quality on growth and ingestion of an oligotrichous ciliate, *Strobilidium* sp., isolated from Port Shelter (22°20.45′N, 114°17.70′E), Hong Kong. Port Shelter is a mesotrophic bay with an average depth of 20 m affected by China coastal currents and the South China Sea. An investigation in 2007 showed that surface Chl *a* concentration averaged 1.9 μg L^{-1} and oligotrichs including *Strombidium* and *Strobilidium* dominated the ciliate community with a mean concentration of 8.4 ciliates mL^{-1} in the water column of Port Shelter and had a significant grazing impact on phytoplankton (Chen et al. 2009). The isolated ciliate was fed with two nanoplanktonic preys of similar size, *Isochrysis galbana* and *Nannochloropsis* sp., at different concentrations, so that the effect of prey size could be excluded and functional and numerical responses could be obtained for both preys. Our results prove that both functional and numerical behaviors of micrograzers could differ in response to preys with different food quality.

Materials and methods

Three nanophytoplankters, *Nannochloropsis* sp., *Rhodomonas* sp., and *Isochrysis galbana*, were maintained in f/2-Si medium and kept in exponential growth phase at 24°C. We isolated *Strobilidium* sp. from Port Shelter on the east coast of Hong Kong in October 2006. Sea water was first screened through a 64-μm mesh to exclude larger metazoans and gently dispensed into three polycarbonate bottles. The three species of algae, *I. galbana*, *Nannochloropsis* sp., and *Rhodomonas* sp., were added into each bottle separately at an appropriate concentration. Our studies on phytoplankton pigments in Port Shelter showed that haptophytes, green algae, and cryptophytes were important components during the summer–autumn period (H. Liu, in preparation). After 2 days of incubation, the bottle enriched by *Nannochloropsis* was dominated by *Strobilidium* sp. Single cell isolation was then conducted, and finally the clonal culture of *Strobilidium* sp. was obtained. *Strobilidium* sp. culture was maintained on the prey of *Nannochloropsis* sp. in the dark and was transferred to fresh algae every 2 or 3 days.

Grazing experiments were conducted in 57 mL polypropylene centrifuge tubes using *Nannochloropsis* sp. and *I. galbana* as prey. Before conducting experiments, *Strobilidium* sp. culture was left unfed for 2 to 3 days to reduce the residual prey concentration in the culture. The initial prey densities were adjusted to 4.4–209.1 $\times$ 10^3 and 6.1–97.9 $\times$ 10^3 mL^{-1} for *Nannochloropsis* sp. and *Isochrysis galbana* in eight density levels, respectively. Control tubes that contained the same densities of prey but no ciliates were also prepared. Both control and experimental tubes were in triplicate and kept in dark at 26°C, the in situ temperature when the ciliate was isolated, for 24 h. At the end of the experiment, a 2–5 mL subsample was fixed by 5% acidic Lugol's solution, and both algae and ciliate abundances were counted under the microscope. The ciliates were counted under an inverted microscope (Olympus IX51) at the magnification of 40×, and the algal cells were counted at 200×.

The biovolume of algae was measured using a Z2 particle counter (Beckman Coulter), while the carbon and nitrogen content was measured using a CHN elemental analyzer (Perkin Elmer) by filtering 30–50 mL algal culture onto precombusted GF/C glass-fiber filters (Whatman). The biovolume of ciliate was calculated by the measurement of the diameter of the preserved cell under the microscope, assuming the ciliate cell was spherical. The biovolume was

converted to carbon using the conversion factor 0.19 pg μm^{-3} according to Putt and Stoecker (1989).

Clearance rate (C, μL ciliate^{-1} h^{-1}) and ingestion rate (I, pg C ciliate^{-1} h^{-1}) of the ciliate were calculated based on Frost (1972). Assuming exponential growth, growth rate (μ, day^{-1}) of the ciliate was calculated as $\ln(n_t/n_0)$, where n_t and n_0 were the ciliate densities at the end and the beginning of the incubation, respectively. Ingestion and growth rates versus mean prey concentrations (x, μg C mL^{-1}) during incubation were fitted to the following equations (Montagnes 1996; Jeong et al. 2004; Gismervik 2005) using the software SigmaPlot 9.0 (Systat Software, Inc.):

$$I = \frac{I_{\max} x}{K_I + x},$$

where $I_{\max}$ was the maximal ingestion rate of the ciliate, and K_I was the "prey concentration sustaining 1/2 $I_{\max}$" (Jeong et al. 2004).

$$\mu = \frac{\mu_{\max}(x - x_0)}{K_G + (x - x_0)},$$

where $\mu_{\max}$ was the maximal growth rate of the ciliate, K_G was the "prey concentration sustaining ½ $\mu_{\max}$" (Jeong et al. 2004), and x_0 was the threshold prey concentration for the ciliate. The maximum biovolume-specific clearance rate (h^{-1}) was calculated by dividing the maximal clearance rate by the biovolume of the ciliate. Gross growth efficiency (GGE) was calculated as the ratio of ciliate growth in terms of carbon over total ingested prey carbon.

Results

The isolated ciliate was subspherical (Fig. 1) with a diameter approximately 40 μm and carbon content 6.4 ng C cell^{-1}. When observed under the microscope, the ciliates showed a movement with "rotating in one direction then jumping 2–4 body lengths" as described for *Strobilidium spiralis* or *S. neptuni* on the website http://www.liv.ac.uk/ciliate/. The morphology preserved in Lugol's solution was also very similar to *S. spiralis* or *S. neptuni*. Unfortunately, protargol staining was not performed to identify it to species level. The two nanoplanktonic preys were very similar in terms of cell size, cellular carbon, and nitrogen content. Mean (±SD) prey equivalent spherical diameters (ESDs) were 4.7 ± 0.5 μm for *Nannochloropsis* sp. and 4.6 ± 0.5 μm for *I. galbana*. Mean (±SD) cellular carbon and nitrogen contents were 16.5 ± 1.6 pg C cell^{-1} and 2.4 ± 0.3 pg N cell^{-1} for *Nannochloropsis* sp., and 15.4 ± 0.8 pg C cell^{-1} and 2.3 ± 0.1 pg N cell^{-1} for *I. galbana*, respectively. Aloricate oligotrichous ciliates have an optimum predator:prey size ratio of about 8:1 (Jonsson 1986), therefore both preys used in our experiments were suitable for the 40 μm *Strobilidium* sp. based on size alone.

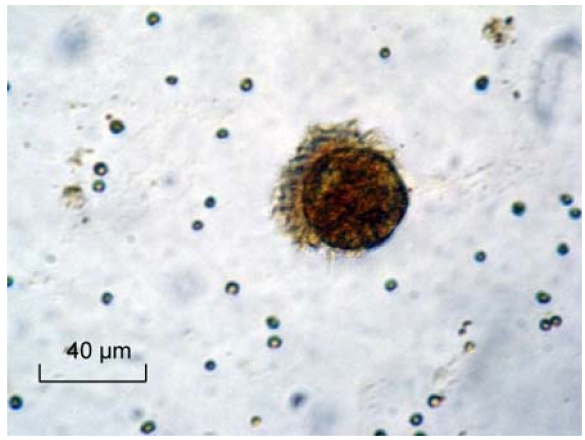

Fig. 1 A photograph of the isolated ciliate, *Strobilidium* sp., fixed in Lugol's solution. Surrounding *small dots* are the prey cells

The relationships between growth rates of *Strobilidium* sp. and mean prey densities could be well fitted by the hyperbolic equation (Fig. 2). $\mu_{\max}$ of *Strobilidium* sp. fed on *I. galbana* was 2.0 day^{-1}, while it was 3.5 day^{-1} on *Nannochloropsis* sp. K_G was 235.4 μg C L^{-1} for *Nannochloropsis* and 50.1 μg C L^{-1} for *I. galbana*, suggesting that the growth of *Strobilidium* sp. was getting saturated at lower carbon concentrations when fed on *I. galbana*. The threshold prey concentration (x_0) was 28.4 μg C L^{-1} for *Nannochloropsis* and 19.6 μg C L^{-1} for *I. galbana*.

Ingestion rates of *Strobilidium* sp. on these two preys also followed the hyperbolic function. $I_{\max}$ of *Strobilidium* sp. on *I. galbana* was 8,440 pg C ciliate^{-1} h^{-1}, while $I_{\max}$ on *Nannochloropsis* sp. was 6,960 pg C ciliate^{-1} h^{-1}. It is noteworthy that the ingestion rates of *Strobilidium* sp. declined at the highest density of *Nannochloropsis* compared with the second highest prey density. However, when

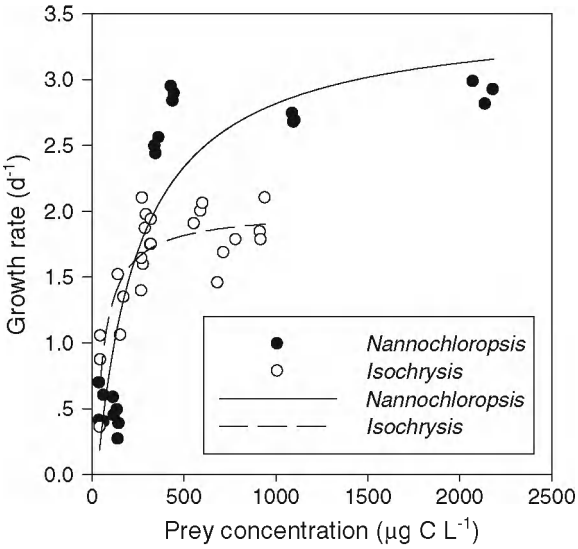

Fig. 2 Growth rates (μ, day^{-1}) of *Strobilidium* sp. on *Isochrysis galbana* and *Nannochloropsis* sp. as a function of mean prey concentration (x, µg C L^{-1}). The fitted equations were $\mu = 2.0\{(x - 19.6)/[50.1 + (x - 19.6)]\}$ for *I. galbana* ($r^2 = 0.72$) and $\mu = 3.5\{(x - 28.4)/[235.4 + (x - 28.4)]\}$ for *Nannochloropsis* sp. ($r^2 = 0.82$)

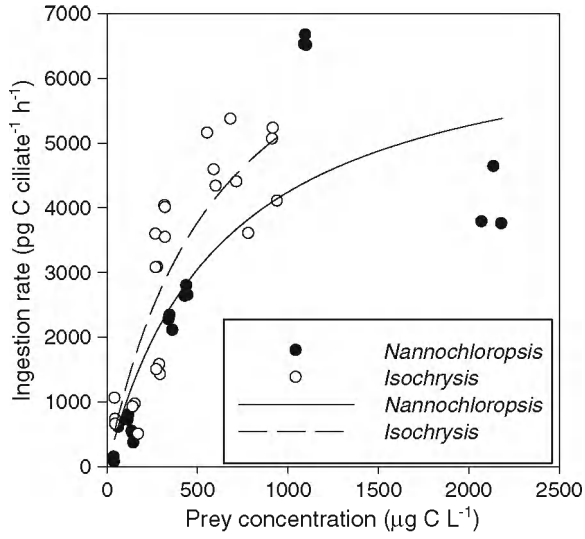

Fig. 3 Ingestion rates (I, pg C ciliate^{-1} h^{-1}) of *Strobilidium* sp. on *Isochrysis galbana* and *Nannochloropsis* sp. as a function of mean prey concentration (x, µg C L^{-1}). The fitted equations were $I = 8{,}440\ [x/(619 + x)]$ for *I. galbana* ($r^2 = 0.75$) and $I = 6{,}960\ [x/(641 + x)]$ for *Nannochloropsis* sp. ($r^2 = 0.77$)

fitted with the hyperbolic curve, the highest ingestion rates measured appeared to be an outlier (Fig. 3). K_I was 641 µg C L^{-1} for *Nannochloropsis* sp. and 619 µg C L^{-1} for *I. galbana*.

Clearance rates were generally high but variable when prey densities were low and decreased as prey densities increased (Fig. 4). When fed on *Nannochloropsis* sp., there was a trend that the clearance rates increased from the lowest prey density to an intermediate prey concentration (ca. 500 µg C L^{-1}) and remained nearly constant to the concentration of 1,100 µg C L^{-1} and then decreased at the highest prey density of 2,000 µg C L^{-1} (Fig. 4), similar to the patterns of clearance rates of *Strobilidium spiralis* reported by Gismervik (2005). The maximal clearance rate of *Strobilidium* sp. on *I. galbana* was 16.8 µL ciliate^{-1} h^{-1}, which was also comparable with the maximal clearance rate, 18.3 µL ciliate^{-1} h^{-1}, of *S. spiralis* reported by Gismervik (2005), while the maximal clearance rate on *Nannochloropsis* sp. was 6 µL ciliate^{-1} h^{-1}. The maximal biovolume-specific clearance rate of *Strobilidium* sp. on *I. galbana* was 5.2×10^5 h^{-1}, while the maximal biovolume-specific clearance rate on *Nannochloropsis* sp. was 1.8×10^5 h^{-1}.

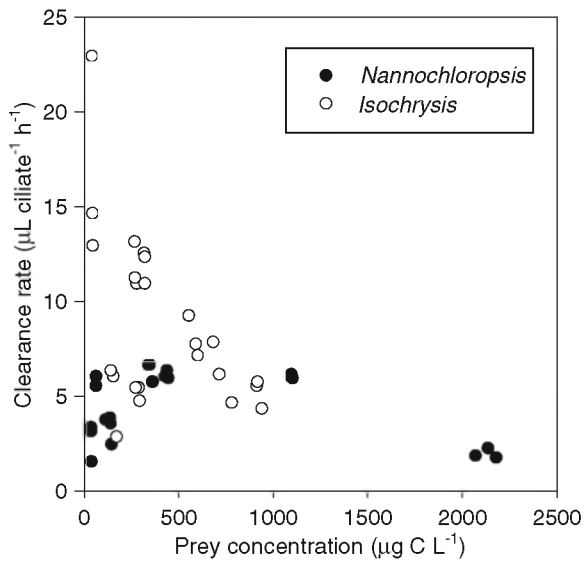

Fig. 4 Clearance rates of (µL ciliate^{-1} h^{-1}) *Strobilidium* sp. on *Isochrysis galbana* and *Nannochloropsis* sp. as a function of prey concentration (µg C L^{-1})

Gross growth efficiency (GGE) of *Strobilidium* sp. was highly variable at low prey concentrations, but it is apparent that GGE of *Strobilidium* sp. was higher on *Nannochloropsis* sp. (20–30%) than on *I. galbana*

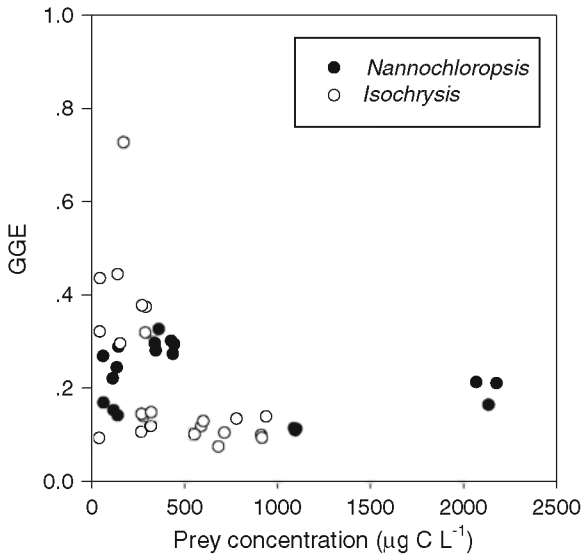

Fig. 5 Gross growth efficiencies (GGE) of *Strobilidium* sp. on *Isochrysis galbana* and *Nannochloropsis* sp. as a function of prey carbon concentration (µg C L^{-1})

(10%) when food was less limiting (Fig. 5). As we did not quantify the volume changes of both prey and predator during the experiment, the calculated GGE should be considered of limited reliability.

Discussion

We observed that both feeding and growth behaviors of the ciliate differed significantly on these two preys of similar size. Because *Strobilidium* sp. attained higher growth rate and GGE when fed on *Nannochloropsis* sp. than on *I. galbana*, it was evident that *Nannochloropsis* sp. was a better prey for *Strobilidium* sp. In contrast, the ciliate did not show higher ingestion rates or clearance rates on *Nannochloropsis* sp. than on *I. galbana*, but on the contrary, the maximal clearance rates were much lower when *Nannochloropsis* sp. was used as prey. The reduced clearance rates at very low prey concentrations may be associated with the threshold feeding behavior (Frost 1975), but it may be also due to difficulties in accurately measuring ingestion rates of ciliates at low prey densities. It was plausible that grazers might need to increase their feeding rate to maximize the uptake of essential elements they need when the prey quality was not optimal, and as a result the GGE was reduced. Therefore, prey food quality affects not only the predator growth, but also the feeding behavior of the predator and may indirectly influence prey community structure in situ. In natural environments where grazing selectivity is shown (Gaul and Antia 2001), it does not necessarily imply that the selected prey is the better food for the grazer. Being a nutritional prey might counterintuitively reduce grazing effect on the prey itself. From a biogeochemical view, *Strobilidium* sp. is supposed to defecate more waste material when feeding on *I. galbana* than on *Nannochloropsis* sp., and thus food quality may also play a role in geochemical cycles.

The issue of food quality to ciliate growth was mostly investigated on prey with potential toxicity. For example, Hansen (1995) observed inhibition of growth of the tintinnid ciliate, *Favella ehrenbergii*, by the red tide dinoflagellate *Gyrodinium aureolum*. Negative growth of *Strombinidinopsis* sp. was also reported by Buskey and Hyatt (1995) when it was exposed to the Texas brown tide alga. However, the two preys used in this study are not species that have been proven to be toxic to grazers. Instead, *I. galbana* was often used as good food for rearing ciliates and in aquaculture (Strom and Morello 1998). Our results suggest that even for *I. galbana* which was believed to be good prey, it may not be the most suitable food for some particular grazers, although it is still unclear what characteristics confers *Nannochloropsis* sp. better food quality. Cellular carbon and nitrogen contents were similar for the two algae. Fatty acid composition may be an important factor in affecting food quality. For example, some *Isochrysis* strains contain negligible amounts of the polyunsaturated fatty acid EPA (20:5($n-3$)) (Volkman et al. 1989). The potential role of fatty acid in affecting trophic transfer from phytoplankton to microzooplankton in marine systems deserves further study.

We are cautious of some limitations in our data. First, all our experiments were conducted in the dark, which differs from natural light–dark cycle. Light may promote the degradation of ingested cells inside protozoan food vacuoles and thus increases ingestion and growth rates of some protists (Strom 2001), but opposite findings have also been reported (Chen and Chang 1999). According to Jakobsen and Strom (2004), our estimates of ingestion and growth rates of *Strobilidium* sp. may be higher than those under natural light–dark cycle. Second, our experiments had limited data points at low prey concentrations (under

starvation), and therefore the estimates of food threshold concentrations could be rough. Oligotrichous ciliates might suffer high mortality under high starvation conditions (Montagnes 1996), which may affect the effects of food concentration on GGE (Fig. 5). However, it can be true that GGE is more constant when food concentration is higher (Gismervik 2005).

Food quality may be an additional factor why in situ ciliate growth rates are lower than theoretical maximal growth rates predicted from temperature and biovolumes only (Macek et al. 1996; Montagnes 1996). Food limitation is ubiquitous for the growth of oligotrichous ciliates in natural waters where ambient nanoplankton prey biomass was often at the same magnitude of or even smaller than the prey threshold concentrations that usually range around 10–100 ng C mL^{-1} (Montagnes 1996). Therefore, this kind of opportunistic growing ciliate might be able to grow fast when encountering rare patches of plenty of food but was not good at exploiting food at low concentrations (Fenchel 1987; Montagnes 1996). The general low in situ growth rates of ciliates, however, may be a consequence of maximizing stability of aquatic food webs (Laws 2008).

Acknowledgments We thank two reviewers and the editor for constructive comments. This study was supported by the Hong Kong Research Grants Council (RGC) research grant HKUST6414/06M provided to H.L. and a Hong Kong University of Science and Technology postgraduate scholarship provided to B.C.

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