Growth and Grazing Rates of the Marine Planktonic Ciliate Strombidinopsis sp. on Red-Tide and Toxic Dinoflagellates

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ABSTRACT: We investigated growth and grazing rates of Strombidinopsis sp. when feeding on several species of red-tide and/or toxic dinoflagellates. Strombidinopsis sp., one of the largest aloricate choerocithids so far reported, grew well on Lingulodinium polyedrum, Gymnodinium sanguineum, Scrippsia trochoidea, Cochlodinium polykrikoides, and Procentrum minimum, but failed to grow on Amphidinium carterae. Specific growth rates of Strombidinopsis sp. increased rapidly with increasing prey density up to ca. 100 ng C ml⁻¹, but were saturated or increased slightly at higher concentrations. Maximum specific growth rates of Strombidinopsis sp. on various prey species were 1.38 day⁻¹ for C. polykrikoides, 1.27 for G. sanguineum, 1.06 for P. minimum, 0.83 for L. polyedrum, and 0.67 for S. trochoidea. Threshold prey concentrations (where net growth = 0) were 12-32 ng C ml⁻¹. Maximum ingestion and clearance rates of Strombidinopsis sp. were 355 ng C grazer⁻¹ day⁻¹ and 111 ng C grazer⁻¹ h⁻¹, respectively. Strombidinopsis sp. exhibited higher maximum growth, ingestion, and clearance rates than the mixotrophic dinoflagellate Fragilidium cf. mexicanum or the heterotrophic dinoflagellate Protoperidinium cf. divergens and P. crassipes, when grown on the same prey species. In addition, the sequence of prey species arranged according to growth response of Strombidinopsis sp. differed considerably from those of Fragilidium cf. mexicanum, Protoperidinium cf. divergens, and P. crassipes.

Supplementary key words: Choerocithrichia, feeding, protist, red tide.

DINOFLAGELLATE blooms, often referred to as red tides, can alter the balance of food webs and cause large-scale mortalities of fish and shellfish [2]. Studies of red-tide formation and persistence suggest that grazing pressure may play an important role in bloom dynamics [38]. In particular, grazing by microzooplankton is believed to contribute to the decline of red tides [3, 11]. While several studies have considered feeding by tintinnid ciliates on red-tide dinoflagellates (RTDs) [8, 16, 28, 30, 31, 36], fewer studies have addressed grazing by aloricate choerocithrichid or oligotrich ciliates on red-tide species [5, 29, 33], even though these ciliates can be abundant during dinoflagellate blooms [25, 29]. Although species of Strombidinopsis (Order Choerocithrichida) often occur in many coastal waters [7, 17, 20, 26], few studies have determined growth [1, 5, 18, 33] or grazing [7, 23, 34] rates for members of this genus. Only one of these studies has examined ingestion and/or clearance rates as a function of prey concentration [33].

During recent examination of natural water samples collected at the mouth of an estuary near Kunsan, Korea, we found a large Strombidinopsis species (hereafter, Strombidinopsis sp.) that frequently contained cells of the red-tide dinoflagellate Gymnodinium sanguineum. To better understand the ecological role of this ciliate, we established a monoculture of Strombidinopsis sp. and conducted experiments to examine its numerical and functional responses when grown on a variety of toxic and/or RTDs. Our goal was to explore the predator-prey relationship between Strombidinopsis sp. and RTDs by determining threshold prey concentrations, optimal prey species, relative nutritional value of different dinoflagellate prey, and the ciliate’s maximum growth, ingestion, and clearance rates.

For prey, we chose to study the RTDs Gymnodinium sanguineum, Cochlodinium polykrikoides, and Lingulodinium polyedrum and the toxic, but non-red-tide species Amphidinium carterae. These dinoflagellates are common to many coastal areas and represent prey species of diverse sizes, shapes, and swimming speeds. They also appear to differ in susceptibility to microbial predation. Gymnodinium sanguineum is a less-preferred prey of mixotrophic and heterotrophic dinoflagellates (e.g. Protoperidinium spp., Noctiluca scintillans, Fragilidium spp.), with few other protists reported to feed on this red-tide species [14, 15] (Jeong, H. J. 1995. The interactions between microzooplankton grazers and dinoflagellates causing red tides in the open coastal waters off southern California. Dissertation. University of California, San Diego). Only a few species of ciliates (e.g. Pavella sp., Tintinnopsis fusus) are known to feed effectively on L. polyedrum [28] (Jeong, unpubl. data). (Jeong, 1995. Dissertation). Perhaps reflecting a need of a large or flexible cytoplasm to ingest this large RTD, few heterotrophic protists are known to feed on the toxic species A. carterae and none effectively consume C. polykrikoides, which may use its rapid swimming speed (up to 1.45 mm sec⁻¹) to avoid microbial predators [15, 22, 28] (Blackburn, D. J. 1974. The feeding biology of tintinnid protozoa and some other inshore microzooplankton. Dissertation. University of British Columbia). Prey used in the current study also represent a sequence in prey quality for supporting the growth of grazers. For example, Protoperidinium spp., N. scintillans, and Fragilidium spp. had higher growth rates and/or feeding frequencies on L. polyedrum than on Gymnodinium sanguineum, while Pavella sp., a copepod, and a larval fish had higher growth or development rates on the latter prey than on the former [12, 13, 24] (Jeong, 1995. Dissertation).

Maximum growth and grazing rates of Strombidinopsis sp. on unicellular algae are compared to those of other ciliates and to mixotrophic and heterotrophic dinoflagellates feeding on the same prey species. Data are also used to evaluate a sequence in prey quality for supporting growth of Strombidinopsis sp. The species of Strombidinopsis examined here is one of the largest aloricate choerocithrichid ciliates for which growth and/or grazing rates have been measured [see 9, 21]. Therefore, results of the present study provide data useful to understanding the relationship between ciliate growth or grazing rate and cell volume. They also provide a basis for understanding the potential of large non-lerucite ciliates to influence the population dynamics of RTDs.

MATERIALS AND METHODS

Culture of phytoplankton prey. RTDs (Table 1) were grown at 19°C in enriched f/2 seawater media [6] without silicate, with continuous illumination of 100 μE m⁻² s⁻¹ provided by cool-white fluorescent lights. Only cultures in exponential growth phase were used for feeding experiments. Carbon contents for dinoflagellates were estimated from cell volume according to Strathmann [32].
Table 1. Species of autotrophic or mixotrophic prey and predator listed in order of size. Volume of preserved prey cells (to the nearest hundred) was calculated according to the equation: Volume = 4/3 π (ESD/2). ESD (Mean equivalent spherical diameter) was measured by a PAMAS-SVSS particle counter. The number of cells measured was >2,000 for prey and >500 for the predator.

<table>
<thead>
<tr>
<th>Species</th>
<th>Approximate volume (µm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey</td>
<td></td>
</tr>
<tr>
<td>Procorcentrum minimum</td>
<td>1,100</td>
</tr>
<tr>
<td>Amphidinium carterae</td>
<td>2,200</td>
</tr>
<tr>
<td>Cocchlidium polykrikoides</td>
<td>6,600</td>
</tr>
<tr>
<td>Scrippsiella trochoidea</td>
<td>8,300</td>
</tr>
<tr>
<td>Gymnodinium sanguineum</td>
<td>25,000</td>
</tr>
<tr>
<td>Lingulodinium polyedrum</td>
<td>28,500</td>
</tr>
<tr>
<td>Predator</td>
<td></td>
</tr>
<tr>
<td>Strombidinopsis sp.</td>
<td>560,000</td>
</tr>
</tbody>
</table>

Isolation and culture of Strombidinopsis sp. Plankton samples collected with a 25-cm diam., 25-µm mesh plankton net were taken from the mouth of Man-kyeong Estuary, Kunsan, Korea, during August, 1997, when water temperature was 22°C. The samples were screened gently through 154-µm Nitex mesh and placed in 1-L polycarbonate (PC) bottles. A mixture of L. polyedrum and G. sanguineum (500–700 cells ml⁻¹ for each prey) and 50 ml of 0.2% media were added as food. Bottles were placed on plankton wheels rotating at 0.9 rpm and incubated at 19°C under continuous illumination of 20 µE m⁻² s⁻¹ of cool-white fluorescent light. Two days later, aliquots of the enriched water were transferred to 6-well tissue culture plates and a monoclonal culture was established by two serial single cell isolations. Once dense cultures of Strombidinopsis sp. were obtained, they were transferred to 500- or 1,000-ml PC bottles of fresh prey every one or two days. Experiments were conducted when a large volume of Strombidinopsis sp. culture was available.

Taxonomic authorities used to identify Strombidinopsis sp. were Lynn et al., Montagnes & Taylor, and Snyder & Ohman [17, 20, 26]. Morphological features used to characterize this ciliate included size and shape, number of polykinetids in the external oral polykinetid zone (EPK's in the EPZ), number of polykinetids in the inner oral polykinetid zone (IPK's in the IPZ), number of somatic kineties (SKs), and number of macronuclei. Microscopic observations were made using living ciliates or specimens fixed with 5% (final conc.) Bouin’s solution and subsequently stained by the Quantitative Protargol Stain method (QPS) [19].

Growth and ingestion rates. Experiments 1 to 6 were designed to measure growth, ingestion, and clearance rates of Strombidinopsis sp. as a function of the prey concentration, when feeding on RTDs (Table 2). One or two days before these experiments were conducted, dense cultures of Strombidinopsis sp. growing on G. sanguineum were transferred into 1-L PC bottles containing low concentrations of the target prey. This was done to acclimate the grazer to the target prey and minimize possible residual growth resulting from ingestion of prey during batch culture. The bottles were filled to capacity with filtered seawater and placed on rotating wheels to incubate as above, except that illumination was provided on 12 h:12 h light–dark cycle. To monitor the condition of and interaction between predator and prey species, cultures were periodically removed from the rotating wheels, examined by looking through the surface of capped bottles using a dissecting microscope, and then returned to the rotating wheels. Preliminary experiments indicated that some dinoflagellates remaining after pre-incubation with Strombidinopsis sp. were in poor physiological condition and subject to mortality without being grazed. To avoid concerns about prey mortality that were not associated with predation, we chose to wait until target prey were eliminated before starting experiments. Once target prey were undetectable, the abundance of Strombidinopsis sp. was determined by transferring 10-ml aliquots of culture to 6-well tissue culture plates, and then counting all ciliates by removing them individually from each well using a Pasteur micropipette.

For each experiment, initial concentrations of Strombidinopsis sp. and target prey were established using an autotipette to deliver predetermined volumes of known cell concentrations to the bottles. Triplicate 270-ml PC experiment bottles (mixtures of predator and prey) and triplicate control bottles (prey only)

Table 2. Initial concentrations (cells ml⁻¹) followed calculated carbon content (µg C ml⁻¹) in parentheses for six species of dinoflagellate prey fed to the ciliestrich ciliate Strombidinopsis sp. to determine growth and ingestion rates.

<table>
<thead>
<tr>
<th>Expt No.</th>
<th>Species</th>
<th>Density</th>
<th>Predatora Strombidinopsis sp.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Gymnodinium sanguineum</td>
<td>11 (24), 53 (119), 366 (816), 755 (1,665), 1060 (3,720), 2500 (5,124)</td>
<td>1.6–6.5</td>
</tr>
<tr>
<td>2</td>
<td>Cocchlidium polykrikoides</td>
<td>12 (8), 42 (30), 897 (628), 2850 (1,995), 6471 (4,530)</td>
<td>1.3–6.4</td>
</tr>
<tr>
<td>3</td>
<td>Lingulodinium polyedrum</td>
<td>11 (26), 49 (121), 98 (244), 444 (1,111), 1264 (3,160), 2452 (6,130)</td>
<td>1.1–7.2</td>
</tr>
<tr>
<td>4</td>
<td>Scrippsiella trochoidea</td>
<td>50 (43), 89 (76), 754 (641), 1725 (1,466), 4549 (3,867), 8756 (7,442)</td>
<td>1.0–5.9</td>
</tr>
<tr>
<td>5</td>
<td>Procorcentrum minimum</td>
<td>128 (19), 658 (99), 2441 (366), 10442 (1,566), 67340 (10,100)</td>
<td>1.0–5.4</td>
</tr>
<tr>
<td>6</td>
<td>Amphidinium carterae</td>
<td>226 (61), 1469 (397), 3542 (956), 5133 (1,380), 12870 (3,745), 28300 (7,641)</td>
<td>1.1–5.3</td>
</tr>
</tbody>
</table>

a Densities of Strombidinopsis sp. in control bottles were 2–5.5 cells ml⁻¹.
were set up at each predator-prey combination. Triplicate control bottles containing only *Strombidinopsis* sp. were also established at one predator concentration. Thirty ml of 1/2 medium were added to all bottles, which were then filled to capacity with freshly filtered seawater and capped. To determine actual predator densities at the beginning of the experiment, 10 ml were removed from each bottle and all *Strombidinopsis* sp. cells present in the aliquot were counted as previously described. An additional 10-ml aliquot was removed from each bottle, fixed with 5% Lugol’s solution and examined with a compound microscope to determine prey abundance by enumerating cells in a 1-ml Sedgewick-Rafter counting chamber (SRC). The bottles were filled again to capacity with freshly filtered seawater, capped, and placed on rotating wheels using environmental conditions described above. Dilution of the cultures associated with refilling the bottles was considered in calculating growth and ingestion rates.

Five ml aliquots were taken from each bottle at 6, 18, 24, 30, and 42 h, and the abundances of *Strombidinopsis* sp. were determined as above. An additional 10-ml aliquot from each bottle was fixed with 5% Lugol’s solution and the abundance of target prey determined by counting all or > 300 cells in five 1-ml SRCs. *Strombidinopsis* sp. present in these 1-ml SRC were recorded on video tape and the images of well-preserved specimens analyzed to determine cell length, maximum width, and oral diameter. Prior to taking subsamples, the condition of *Strombidinopsis* sp. and its prey was assessed using a dissecting microscope as described above. After subsampling, bottles were again filled to capacity with freshly filtered seawater and placed back on the rotating wheels.

The specific growth rate of *Strombidinopsis* sp., \( \mu(d^{-1}) \), was calculated by averaging the instantaneous growth rates (IGR) for each sampling interval, calculated as:

\[
IGR = \frac{\ln(S_2/S_1)}{t_2 - t_1} \times 24
\]

where \( S_1 \) and \( S_2 \) = the concentration of *Strombidinopsis* sp. at consecutive samplings. The final \( t_1 \) for calculation was 18 or 24 h, whichever provided the highest specific growth rate. In most experiments, *Strombidinopsis* sp. populations either decreased rapidly after 18 or 24 h due to starvation, or showed significantly reduced growth rate due to reduction of prey concentrations.

Data for *Strombidinopsis* sp. growth rate were fitted to a Michaelis-Menten equation:

\[
\mu = \frac{\mu_{max}(x - X)}{K_G + (x - X)}
\]

where \( \mu_{max} \) = the maximum growth rate (d\(^{-1}\)); \( x \) = prey concentration (cells ml\(^{-1}\) or ng C ml\(^{-1}\)); \( x^* \) = threshold prey concentration (the prey concentration where \( \mu = 0 \)). \( K_G \) = the prey concentration sustaining 1/2 \( \mu_{max} \). Data were iteratively fitted to the model using DeltaGraph\(^{\text{®}}\) (Delphi Point).

Ingestion and clearance rates were calculated using the equations of Frost [4] and Heinbokel [10]. Incubation time for calculating ingestion and clearance rates was the same as for estimating growth rate. Ingestion rate data were fitted to a Michaelis-Menten equation:

\[
IR = \frac{I_{max}(x)}{K_I + (x)}
\]

where \( I_{max} \) = the maximum ingestion rate (cells grazer\(^{-1}\) d\(^{-1}\) or ng C grazer\(^{-1}\) d\(^{-1}\)); \( x \) = prey concentration (cells ml\(^{-1}\) or ng C ml\(^{-1}\)). \( K_I \) = the prey concentration sustaining 1/2 \( I_{max} \).

**Cell volume**. Cell length, maximum width, and oral diameter of the well-preserved *Strombidinopsis* sp. were measured by analyzing video images as described above. The shape of *Strombidinopsis* sp. was estimated as a cone (bottom half of the cell) connected to a truncated cone (top half of the cell). The two cones joined at the cell equator (maximum width of the cell), with the top of the truncated cone being the oral area. Cell volume was then calculated according to the equation: volume = \( \frac{1}{3} \) (cross-sectional area at the oral opening + cross-sectional area at equator) (cell length) + (1/3)(cross-sectional area at equator) (cell length).

**Swimming speed**. The swimming speed of *Strombidinopsis* sp. was measured using a video analyzing system. All aliquots from a dense culture of *Strombidinopsis* sp. were added to wells of a 6-well tissue culture plate containing only freshly filtered seawater. After a 30 min acclimation period, swimming was observed at a magnification of 10–40X and video-recorded using a Water camera (Wat 202B) attached to an Olympus dissecting microscope. Samples were maintained at 19°C while making video records. Only linear paths of fast-swimming cells were analyzed during single-frame playback to obtain mean and maximum values for swimming speed. Average swimming speed was calculated from linear displacement in 1 s using 11 *Strombidinopsis* sp. cells of different sizes.

**RESULTS**

**Characteristics of *Strombidinopsis* sp.** The length, maximum width, and oral diameter of living *Strombidinopsis* sp. cells (mean ± standard deviation, \( n = 30 \)) were 198 ± 34.7 \( \mu \)m (range, 121–242), 100 ± 19.0 \( \mu \)m (66–143), and 73.7 ± 12.3 \( \mu \)m (55–110), respectively, while those of cells fixed with 5% (final conc.) Lugol’s solution (mean ± standard deviation, \( n = 550 \)) were 164 ± 35 \( \mu \)m (range, 75–255 \( \mu \)m), 80 ± 16 \( \mu \)m (43–133 \( \mu \)m), and 62 ± 10 \( \mu \)m (32–97 \( \mu \)m), respectively. The number of EPK, IPK, SK, and macronuclei were 16, 5, 24–27, and 2, respectively. SKs formed of dikinetids were equally spaced around the cell and extended the entire length of the cilium. The species closest to *Strombidinopsis* sp. is S. multilarius [20]. However, *Strombidinopsis* sp. is larger than S. multilarius, and the numbers of the EPKs and SKs are slightly different from those of S. multilarius.

**Growth rates.** *Strombidinopsis* sp. grew well on unialgal diets of G. sanguineum, C. polykrikoides, P. minimum, L. polyedra, and S. trochoidea, but not on A. carterae. The specific growth rates of *Strombidinopsis* sp. feeding on unialgal diets of the RTDs increased with increasing mean prey concentration less than ca. 100 ng C \(^{-1}\), but were saturated or showed only a slight increase at higher prey concentrations (Fig. 1–3). When the data were fitted to Eq. (2), the maximum specific growth rates (\( \mu_{max} \)) of *Strombidinopsis* sp. on these prey species were 1.38 day \(^{-1}\) for C. polykrikoides, 1.27 for G. sanguineum, 1.06 for P. minimum, 0.83 for L. polyedra, and 0.67 for S. trochoidea (Table 3). Statistical analysis of all data above the saturation level showed no significant difference in \( \mu_{max} \) between C. polykrikoides and G. sanguineum diets or between L. polyedra and S. trochoidea diets (t-test, \( p > 0.1 \)). However, \( \mu_{max} \) on G. sanguineum was significantly higher than that on P. minimum (t-test, \( p < 0.01 \)).

The growth rates of *Strombidinopsis* sp. in the control bottles incubated without added prey were between –0.35 and –0.8 day \(^{-1}\). The threshold prey concentrations (where net growth = 0) were between 12 and 36 ng C ml \(^{-1}\) (Table 3).

**Ingestion and clearance rates.** The ingestion rates of *Strombidinopsis* sp. was:

\[
\text{IR} = \frac{I_{max}(x)}{K_I + (x)}
\]

where \( I_{max} \) = the maximum ingestion rate (cells grazer\(^{-1}\) d\(^{-1}\) or ng C grazer\(^{-1}\) d\(^{-1}\}); \( x \) = prey concentration (cells ml\(^{-1}\) or ng C ml\(^{-1}\)). \( K_I \) = the prey concentration sustaining 1/2 \( I_{max} \).
Fig. 1. Specific growth rates of Strombidinopsis sp. as a function of mean prey concentration when fed on Gymnodinium sanguineum (○) and Coccolithus polykrikoides (●). Inset shows data points at low prey concentrations (ng C l⁻¹) using an expanded scale for the abscissa. Symbols represent treatment means ± 1 S.E. The curves are fitted by a Michaelis-Menten equation [Eq. (2)] using all treatments in each experiment (see Table 3).

with increasing mean prey concentration below ca. 500 ng C ml⁻¹ and slowly, but continuously, increased at higher prey concentrations (Fig. 1). When the data were fitted to Eq. (2), the maximum ingestion rates of Strombidinopsis sp. were 353 ng C grazer⁻¹ day⁻¹ for C. polykrikoides (504 prey cells grazer⁻¹ d⁻¹), 343 for G. sanguineum (156), 267 for P. minimum (1,780), 222 for L. polyedrum (89), and 207 for S. trochoidea (244). The maximum clearance rate of Strombidinopsis sp. was 85 µl grazer⁻¹ h⁻¹ for G. sanguineum, 50 for C. polykrikoides, 41 for P. minimum and L. polyedrum, and 41 for S. trochoidea.

Effect of prey concentration on the grazer's cell volume. In general, cell volume of Strombidinopsis sp. did not change markedly with increasing prey concentration < ca. 100 ng C ml⁻¹, but cell volume increased rapidly at higher prey concentrations (Fig. 7–9). Increases in cell volume were caused by increases in cell length and width, with little change in oral diameter. Strombidinopsis sp. appeared to ingest as many prey cells as possible, with > 20 G. sanguineum cells occurring in the protoplasm of some specimens within 2 h of adding high concentrations of the prey. Accumulation of undigested prey in Strombidinopsis sp. appeared to cause an increase in ciliate length and width. When starved, cell volume of Strombidinopsis sp. decreased with increasing incubation time (Fig. 10), reducing by ca. 40% after 42 h starvation. Oral diameter showed little change during starvation. Thus, the shape of Strombidinopsis sp. changed depending on prey concentrations, being almost cylindrical but still posteriorly tapered when prey were depleted, or bulging broadly in the middle of the body when prey were plentiful.

Swimming speed. The mean (± standard error, n = 11) and maximum swimming speeds of Strombidinopsis sp. at 19°C were 1,240 (± 90) µm sec⁻¹ and 1,740 µm sec⁻¹ when the mean length of living cells was 176 (± 5.2) µm. The maximum speed...

Fig. 2. Specific growth rates of Strombidinopsis sp. as a function of mean prey concentration when fed on Procentrum minimum. Inset shows data points at low prey concentrations (ng C l⁻¹) using an expanded scale for the abscissa. Symbols represent treatment means ± 1 S.E. The curves are fitted as Fig. 1.

was higher than that of C. polykrikoides (1,450 µm sec⁻¹) and other dinoflagellate prey offered in the present study (<500 µm sec⁻¹) at 22°C [15].

DISCUSSION

The present study shows that Strombidinopsis sp. readily ingests prey and exhibits positive growth when feeding on RTDs...

Fig. 3. Specific growth rates of Strombidinopsis sp. as a function of mean prey concentration when fed on Lingulodinium polyedrum (○) and Scrippsiella trochoidea (●). Inset shows data points at low prey concentrations (ng C l⁻¹) using an expanded scale for the abscissa. Symbols represent treatment means ± 1 S.E. The curves are fitted as Fig. 1.
Table 3. Growth and grazing data for *Strombidinopsis* sp. fed five species of dinoflagellate prey. Parameters are for numerical and functional response from Eqs. (2) & (3) as presented in Fig. 1–6. $\mu_{\text{max}}$ (maximum growth rate, d⁻¹), $K_{\text{ur}}$ (prey concentration sustaining 0.5 $\mu_{\text{max}}$ ng C ml⁻¹), $x^1$ (threshold prey concentration, ng C ml⁻¹), $I_{\text{max}}$ (maximum ingestion rate, ng C grazer⁻¹ d⁻¹), $K_{\text{ir}}$ (prey concentration sustaining 0.5 $I_{\text{max}}$ ng C ml⁻¹).  

<table>
<thead>
<tr>
<th>Figures</th>
<th>Species</th>
<th>$\mu_{\text{max}}$</th>
<th>$K_{\text{ur}}$</th>
<th>$x^1$</th>
<th>$r^2$</th>
<th>$I_{\text{max}}$</th>
<th>$K_{\text{ir}}$</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 &amp; 4</td>
<td><em>Cochlodinium polykrikoides</em></td>
<td>1.378</td>
<td>164</td>
<td>38</td>
<td>0.80</td>
<td>353</td>
<td>161</td>
<td>0.91</td>
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<tr>
<td>2 &amp; 5</td>
<td><em>Gymnodinium sanguineum</em></td>
<td>1.271</td>
<td>58</td>
<td>12</td>
<td>0.94</td>
<td>343</td>
<td>133</td>
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</tr>
<tr>
<td>3 &amp; 6</td>
<td><em>Procentrum minimum</em></td>
<td>1.060</td>
<td>40</td>
<td>15</td>
<td>0.81</td>
<td>267</td>
<td>82</td>
<td>0.79</td>
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<tr>
<td>7</td>
<td><em>Lingulodinium polyedrum</em></td>
<td>0.828</td>
<td>63</td>
<td>20</td>
<td>0.86</td>
<td>222</td>
<td>283</td>
<td>0.86</td>
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<tr>
<td></td>
<td>* Scripsiella trochoidea*</td>
<td>0.671</td>
<td>62</td>
<td>29</td>
<td>0.77</td>
<td>207</td>
<td>135</td>
<td>0.60</td>
</tr>
</tbody>
</table>

belonging to several genera. Among unialgal diets of six dinoflagellate species offered as prey, only *A. carterae* failed to support population growth of *Strombidinopsis* sp. In the presence of abundant, favorable prey, *Strombidinopsis* sp. had high growth rates, but it rapidly starved to death when prey were depleted. Data also show that growth and ingestion rates of *Strombidinopsis* sp. on RTDs were significantly affected by prey species and prey concentration. Thus, in nature, populations of *Strombidinopsis* sp. may change drastically with fluctuations in prey concentration and changes in the species composition of prey assemblages.

**Prey species and growth.** *Strombidinopsis* sp. had higher maximum growth rates on *G. sanguineum*, *C. polykrikoides*, and *P. minimum* than on *L. polyedrum* and *S. trochoidea*. By contrast, maximum growth rates and/or feeding frequencies of the mixotrophic dinoflagellate *Fragilidium* cf. *mexicanum* and the heterotrophic dinoflagellates *Proteridinium* cf. *dvergens* and *P. crassipes* are higher for *L. polyedrum* and *S. trochoidea* than for *G. sanguineum*, *C. polykrikoides*, and *P. minimum* [14, 15]. Another heterotrophic dinoflagellate, *N. scintillans*, has much higher growth rates on *L. polyedrum* than on *G. sanguineum* (Jeong, 1993. Dissertation). *Fragilidium* cf. *mexicanum*, *Proteridinium* sp., and *N. scintillans* sometimes have difficulty capturing flat *G. sanguineum* cells or fast swimming *C. polykrikoides* cells (mean and maximum swimming speeds of 1,060 and 1,450 µm sec⁻¹, respectively). However, *Strombidinopsis* sp. had little difficulty capturing these prey. A large tintinnid ciliate, *Favella* sp., also had higher maximum growth on *G. sanguineum* than on *L. polyedrum* (Jeong, 1995. Dissertation). This evidence suggests that the large planktonic ciliates like *Strombidinopsis* sp. and *Favella* sp. may graze blooms of *G. sanguineum* and/or *C. polykrikoides* more effectively than do mixotrophic and heterotrophic dinoflagellates.

*Strombidinopsis* sp. did not prey on the toxic dinoflagellate *A. carterae*, a behavior previously reported for *Favella ehrenbergii* and *Fragilidium* cf. *mexicanum* [15, 31]. The apparent avoidance of *A. carterae* by these grazers may reflect the toxic properties of this species [27]. However, *Diplaplasis lenticula* [22] and *Favella serrata* (Blackbourn, 1974. Dissertation) are known to feed on *A. carterae*. Understanding the extent to which these and other potential grazers exploit toxic dinoflagellates like *A. carterae* merits further study.

The maximum growth rate ($\mu$) of *Strombidinopsis* sp. on *G. sanguineum*, ca. 1.3 day⁻¹, is similar to that of *Favella* sp. on

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**Fig. 4.** Ingestion rates of *Strombidinopsis* sp. as a function of mean prey concentration when fed on *Gymnodinium sanguineum* (*) and *Cochlodinium polykrikoides* (C). Inset shows data points at low prey concentrations (ng C⁻¹) using an expanded scale for the abscissa. Symbols represent treatment means ± 1 S.E. The curves are fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments in each experiment (see Table 3).

**Fig. 5.** Ingestion rates of *Strombidinopsis* sp. as a function of mean prey concentration when fed on *Procentrum minimum*. Inset shows data points at low prey concentrations (ng C⁻¹) using an expanded scale for the abscissa. Symbols represent treatment means ± 1 S.E. The curves are fitted as Fig. 4.
Fig. 6. Ingestion rates of Strombidinopsis sp. as a function of mean prey concentration when fed on Lingulodinium polyedrum (●) and Scrippsiella trochoidea (○). Inset shows data points at low prey concentrations (ng C/ml) using an expanded scale for the abscissa. Symbols represent treatment means ± 1 S.E. The curves are fitted as Fig. 4.

Fig. 7. The cell volume of Strombidinopsis sp. as a function of mean prey concentration when fed on Gymnodinium sanguineum (●) and Ceiithocapsa triquetra (○). Symbols represent treatment means ± 1 S.E.

Fig. 8. The cell volume of Strombidinopsis sp. as a function of mean prey concentration when fed on Prorocentrum minimum. Symbols represent treatment means ± 1 S.E.

The same prey at the same temperature (Jeong, 1995, Dissertation). It is also similar to the maximum growth rate of S. chesilri on a small diatom Thalassiosira pseudonana [21] and of Strombidinopsis cf. acuminatum on the dinoflagellate Heterocapsa triquetra [5], when corrected to 19°C using a Q_{10} of 2.8 [9]. However, the maximum growth rate of Strombidinopsis sp. is approximately 20% higher than would be predicted using the regression equation of Hansen et al. [9]. The threshold prey concentrations, 12–38 ng C ml⁻¹ for all
Table 4. Comparison of ingestion and clearance rates of *Strombidinopsis* sp. and other protists on the same red-tide dinoflagellate prey. Rates are corrected to 19°C using Q_{10} = 2.8 [9]. I_{max} (maximum ingestion rate in ng C predator~l~d~1~); C_{max} (maximum clearance rate as ml predator~1~h~1); NC (naked ciliate); TC (tintinnid ciliate); HD (heterotrophic dinoflagellate); MD (mixotrophic dinoflagellate).

<table>
<thead>
<tr>
<th>Prey species</th>
<th>Predator</th>
<th>I_{max}</th>
<th>C_{max}</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lingulodinium polyedrum</td>
<td><em>Strombidinopsis</em> sp. (NC)</td>
<td>222</td>
<td>110</td>
<td>this study</td>
</tr>
<tr>
<td></td>
<td><em>Proteropidium cf. divergens</em> (HD)</td>
<td>11</td>
<td>0.7</td>
<td>[14]</td>
</tr>
<tr>
<td></td>
<td><em>Proteropidium crassipes</em> (HD)</td>
<td>5</td>
<td>0.5</td>
<td>[14]</td>
</tr>
<tr>
<td></td>
<td><em>Fragilidium cf. mexicanum</em> (MD)</td>
<td>7</td>
<td>4</td>
<td>[15]</td>
</tr>
<tr>
<td>Prorocentrum minimum</td>
<td><em>Strombidinopsis</em> sp. (NC)</td>
<td>267</td>
<td>110</td>
<td>this study</td>
</tr>
<tr>
<td></td>
<td><em>Favella taraikaensis</em> (TC)</td>
<td>210</td>
<td>18</td>
<td>[35]</td>
</tr>
<tr>
<td>Scrippsilla trochoidea</td>
<td><em>Strombidinopsis</em> sp. (NC)</td>
<td>207</td>
<td>41</td>
<td>this study</td>
</tr>
<tr>
<td></td>
<td><em>Favella</em> sp. (TC)</td>
<td>237</td>
<td>42</td>
<td>[31]</td>
</tr>
</tbody>
</table>

diets, were similar to those of the smaller ciliates *Strobilidium cf. spiralis* [37], *Strombidium siculum* [18], *Strombidinopsis chestiari* [21], and *Strombidinopsis acuminatum* [33].

**Ingestion and clearance.** The maximum ingestion (I_{max}) and clearance rates (C_{max}) of *Strombidinopsis* sp. obtained in this study are higher than or comparable to those reported for other chlorellich ciliates, mixotrophic dinoflagellates, and heterotrophic dinoflagellates when feeding on the same species of RTDs (see Table 4). The I_{max} of *Strombidinopsis* sp. on *L. polyedrum* is over 20 times higher than that of *Fragilidium cf. mexicanum* or *Proteropidium cf. divergens*, while C_{max} of *Strombidinopsis* sp. on *L. polyedrum* is 22 and 160 times higher than that of *Fragilidium cf. mexicanum* and *Proteropidium sp.*, respectively. The maximum specific clearance rate of *Strombidinopsis* sp. on *L. polyedrum* (2 × 10^{-4} body volumes h^{-1}) is 2.5 and 33 times higher than that of *Fragilidium cf. mexicanum* (0.8 × 10^{-6}) and *Proteropidium cf. divergens* (0.06 × 10^{-6}), respectively. The I_{max} of *Favella* sp. on *P. minimum* is comparable to that of *Favella taraikaensis*, but C_{max} of the former is higher than that of the latter. The I_{max} and C_{max} of *Strombidinopsis* sp. on *S. trochoidea* are comparable to those by *Favella* sp.

In general, ingestion rates of *Strombidinopsis* sp. increased continuously up to and beyond prey concentrations where growth rates were saturated (see Fig. 1–6; K_{max}’s were higher than K_{max}’s in Table 3). Cell volume of *Strombidinopsis* sp. also showed a similar increase relative to prey density (Fig. 7–9). *Strombidinopsis* sp. appeared to ingest as many prey cells as possible when prey were plentiful, raising the possibility that rapid ingestion coupled with slow digestion/assimilation of prey may have contributed to observed patterns in cell volume.

At present, it is impossible to accurately estimate the grazing impact imposed by *Strombidinopsis* sp. on natural populations of RTDs, due to the lack of quantitative data on the abundance of this ciliate in situ. However, results presented here suggest that moderate densities of *Strombidinopsis* sp. may have considerable impact on dinoflagellate red tides, during the decline stage of the bloom (i.e., specific growth rate < 0 or = 0). For example, assuming no prey growth, a starting density of 0.7 *Strombidinopsis* sp. ml^{-1}, and predator feeding and growth rates obtained in the present study, grazing by *Strombidinopsis* sp. would reduce a monospecific bloom of *G. sanguiulatum* at 1,000 cells ml^{-1} by 20% during one day. Clearly, additional studies that provide information on predator and prey densities in the field are needed to elucidate the role of *Strombidinopsis* sp. in the population dynamics of red-tide dinoflagellates.

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**Literature Cited**


![Figure 10](Image) The cell volume of *Strombidinopsis* sp. without added prey as a function of incubation time. Symbols represent treatment means ± 1 S.E.
grazing and growth; scaling within the 2–2,000-μm body size range. *Limnol. Oceanogr.*, 42:687–704.


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