

Growth and Grazing Rates of the Heterotrophic Dinoflagellate *Polykrikos kofoidii* on Red-Tide and Toxic Dinoflagellates

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ABSTRACT. We investigated growth rates, grazing rates, and prey selection of *Polykrikos kofoidii* when feeding on several species of red-tide and/or toxic dinoflagellates. *Polykrikos kofoidii* ingested all prey species used in this study, exhibiting positive growth on *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, *Ceratium furca*, *Gymnodinium catenatum*, *Gyrodinium impudicum*, *Prorocentrum micans*, and the toxic dinoflagellate *Amphidinium carterae*, but not on *P. minimum*. Specific growth rates of *P. kofoidii* increased rapidly with increasing density of *L. polyedrum*, *S. trochoidea*, *C. furca*, and *G. catenatum* before saturating between 500–2,000 ng C ml⁻¹. Specific growth rates increased continuously when *P. kofoidii* was fed the other prey species. Maximum specific growth rates of *P. kofoidii* on *G. catenatum* (1.12 d⁻¹), *S. trochoidea* (0.97 d⁻¹), and *L. polyedrum* (0.83 d⁻¹) were higher than those on *C. furca* (0.35 d⁻¹), *A. carterae* (0.10 d⁻¹), *P. micans* (0.06 d⁻¹), *G. impudicum* (0.06 d⁻¹), and *P. minimum* (–0.03 d⁻¹). Threshold prey concentrations (where net growth = 0) were 54–288 ng C ml⁻¹. Maximum ingestion and clearance rates of *P. kofoidii* on these dinoflagellates were 5–24 ng C pseudocolony⁻¹ d⁻¹ and 1.0–5.9 μl pseudocolony⁻¹ h⁻¹, respectively. *Polykrikos kofoidii* strongly selected *L. polyedrum* over *S. trochoidea* in prey mixtures. *Polykrikos kofoidii* exhibited higher maximum growth, ingestion, and clearance rates than previously reported for the mixotrophic dinoflagellate *Fragilidium cf. mexicanum* or the heterotrophic dinoflagellates *Protoperdinium cf. divergens* and *P. crassipes*, when grown on the same prey species. Grazing coefficients calculated by combining field data on abundances of *Polykrikos* spp. and co-occurring red-tide dinoflagellate prey with laboratory data on ingestion rates obtained in the present study suggest that *Polykrikos* spp. sometimes have a considerable grazing impact on prey populations.

Key Words. Feeding, food web, harmful algal bloom, protist, red tides.

DINOFLAGELLATE blooms, often referred to as red tides, can alter the balance of food webs and cause large-scale mortalities of fish and shellfish (ECOHAB 1995). Studies of red-tide formation and persistence suggest that grazing pressure may play an important role in bloom dynamics (Watras et al. 1985). In particular, grazing by microzooplankton is believed to contribute to the decline of red tides (Eppley and Harrison 1975; Holmes, Williams, and Eppley 1967). The heterotrophic dinoflagellates *Polykrikos* spp. are ubiquitous and abundant (reported maximum density = 200 pseudocolonies ml⁻¹) in many coastal waters, in particular, during red tides dominated by *Gymnodinium catenatum*, *Alexandrium tamarense* (previously *Gonyaulax excavata*), *Ceratium furca*, *Scrippsiella trochoidea*, and *Lingulodinium polyedrum* (Carreto et al. 1986; Matsuyama, Miyamoto, and Kotani 1999; Morey-Gaines 1980; Sampayo 1998). Morey-Gaines (1980) reported the maximum growth rate of *Polykrikos kofoidii* on *Scrippsiella trochoidea* and Matsuyama et al. (1999) estimated the ingestion rate of *P. kofoidii* on *Gymnodinium catenatum*. However, few studies have measured growth or grazing rates of *P. kofoidii* as a function of prey concentration and no study has examined threshold prey concentration or prey selection.

To better understand the ecological role of *Polykrikos* spp. in the planktonic community, we established a monoclonal culture of *Polykrikos kofoidii* and conducted experiments to examine its numerical and functional responses when grown on a variety of toxic and/or red tide dinoflagellates (hereafter RTDs). Our goal was to explore the predator-prey relationship between *Polykrikos kofoidii* and RTDs by determining threshold prey concentrations, optimal prey species, and the dinoflagellate's maximum growth, ingestion, and clearance rates. We also estimated grazing coefficients attributable to *Polykrikos* on RTDs spp. using our data for ingestion rates and published accounts of predator and prey abundance in the field.

Maximum growth and grazing rates of *Polykrikos* spp. on unialgal diets are compared to those of mixotrophic or heterotrophic dinoflagellates and ciliates feeding on the same prey

species. Results of the present study provide a basis for understanding the potential of *Polykrikos* spp. 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 (Guillard and Ryther 1962) minus silicate, with continuous illumination of 100 μE m⁻²s⁻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 (Strathmann 1967).

Isolation and culture of *Polykrikos kofoidii*. Plankton samples collected with a 25-cm diameter, 25-μm mesh plankton net were taken from coastal waters off Kunsan, Korea, during October, 1998 (Table 2; Expt. 3–5, 7–10) and May, 2000 (Table 2; Expt. 1, 2, 6, 11, 12) when water temperatures were 18 and 17 °C, respectively. The samples were screened gently through 154-μm Nitex mesh and placed in 1-liter polycarbonate (PC) bottles. A mixture of *Lingulodinium polyedrum* and *Scrippsiella trochoidea* and 50 ml of f/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 50 μE m⁻² s⁻¹ of cool-white fluorescent light. Three 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 *Polykrikos kofoidii* were obtained, they were transferred to 500 or 1,000-ml PC bottles of fresh prey every two or three days. Experiments were conducted when a large volume of *P. kofoidii* culture was available.

Growth and ingestion rates. Experiments 1–9 were designed to measure growth, ingestion, and clearance rates of *Polykrikos kofoidii*, as a function of the prey concentration, when feeding on RTDs (Table 2). In particular, Expt. 2 was designed to further explore feeding of *P. kofoidii* on *Gymnodinium catenatum* because data near threshold prey densities in Expt. 1 showed a high degree of scatter, with data above and below threshold values showing somewhat different relationships between growth rate and ingestion rate.

One or two days before these experiments were conducted, dense cultures of *P. kofoidii* growing on *Scrippsiella trochoidea* were transferred into 1-liter PC bottles containing low concen-

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Table 1. Species of autotrophic or mixotrophic prey and predator used in the present study, listed in order of cell volume. Volume of preserved prey cells (to the nearest hundred) was calculated according to the equation: Volume = $4/3 \pi (ESD/2)^3$. ESD (Mean equivalent spherical diameter) was measured by a PAMAS-SVSS particle counter. Cell volume of the predator being satiated with *Scripsiella trochoidea* and then starved for 1 day. The number of cells measured, n, was >2,000 for prey and >500 for the predator.

Species	Approximate volume (μm^3)
<i>Prorocentrum minimum</i>	1,100
<i>Amphidinium carterae</i>	2,200
<i>Gyrodinium impudicum</i>	6,500
<i>Scripsiella trochoidea</i>	8,300
<i>Prorocentrum micans</i>	9,200
<i>Ceratium furca</i>	12,700
<i>Gymnodinium catenatum</i>	20,600
<i>Lingulodinium polyedrum</i>	28,500
<i>Polykrikos kofoidii</i>	43,000

trations 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. The abundances of *P. kofoidii* and prey were determined by enumerating cells in three 1-ml Sedgwick-Rafter counting chambers (hereafter SRCs).

For Experiments 1 and 3–9, initial concentrations of *Polykrikos kofoidii* and target prey were established using an autopipette to deliver predetermined volumes of known cell concentrations to the bottles. Triplicate 80-ml PC experiment bottles (mixtures of predator and prey) and triplicate control bottles (prey only) were set up at each predator-prey combination. Triplicate control bottles containing only *P. kofoidii* were also established at one predator concentration. Ten ml of f/2 medium were added to all bottles, which were then filled to capacity with freshly filtered seawater and capped. To determine actual predator and prey densities at the beginning of the experiment and after 24, 48, and 72-h incubation, a 5-ml aliquot was removed from each bottle and fixed with 5% Lugol's solution, and all *Polykrikos* pseudocolonies and all or > 200 prey cells in three 1-ml SRCs were enumerated. Prior to taking subsamples, the condition of *P. kofoidii* and its prey was assessed using a dissecting microscope. 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.

For Experiment 2, initial concentrations of *Gymnodinium catenatum* were established using an autopipette as described above, while those for *Polykrikos kofoidii* were obtained by careful individual transfer with a Pasteur micropipette. Triplicate 32-ml PC experiment bottles and triplicate control bottles (prey only) were set up at each predator-prey combination. Triplicate control bottles containing only *P. kofoidii* were also established at one predator concentration. Three ml of f/2 medium were added to all bottles, which were then filled to ca-

Table 2. Design of experiments. Values in prey and predator columns represent initial concentrations (cells ml^{-1}) followed by calculated carbon biomass (ng C ml^{-1}) in parentheses.

Expt. No.	Species	Prey		Predator ^a
		Density		<i>Polykrikos kofoidii</i>
1	<i>Gymnodinium catenatum</i>	31 (58), 77 (144), 166 (311), 302 (567), 813 (1528), 1940 (3,647), 3555 (6,682)		7–74
2 ^b	<i>Gymnodinium catenatum</i>	47 (89), 108 (203), 207 (389), 420 (789), 750 (1,411), 2018 (3,794), 3837 (7,215)		2.5–10
3	<i>Scripsiella trochoidea</i>	165 (140), 488 (415), 1378 (1,171), 2985 (2,537), 8836 (7,511), 19043 (16,187)		6–80
4	<i>Lingulodinium polyedrum</i>	56 (140), 191 (478), 522 (1,305), 1259 (3,148), 2412 (6,030), 4043 (10,108)		7–63
5	<i>Ceratium furca</i>	47 (59), 86 (108), 196 (244), 508 (634), 1079 (1,349), 2056 (2,570)		4–74
6	<i>Gyrodinium impudicum</i>	26 (17), 61 (43), 283 (198), 1254 (878), 4620 (3,234)		4–84
7	<i>Prorocentrum micans</i>	40 (38), 123 (116), 635 (597), 1785 (1,678), 4916 (4,621)		6–65
8	<i>Amphidinium carterae</i>	1175 (317), 2734 (738), 11160 (3,013), 34193 (9,232), 70992 (19,168)		11–142
9	<i>Prorocentrum minimum</i>	1446 (217), 3842 (576), 10183 (1,527), 29194 (4,379), 51611 (7,742)		15–64
10	<i>Lingulodinium polyedrum</i> <i>Scripsiella trochoidea</i>	89/4400 (222/3740), 184/3000 (460/2550), 289/2407 (723/2046), 887/7653 (2217/6505), 405/1712 (1013/1455), 540/902 (1350/766)		43–56
11	<i>Lingulodinium polyedrum</i>	1,470 (3,675)		126
	<i>Gymnodinium catenatum</i>	2,040 (3,835)		125
	<i>Scripsiella trochoidea</i>	3,497 (2,972)		165
	<i>Prorocentrum micans</i>	3,447 (3,240)		101
	<i>Gyrodinium impudicum</i>	4,460 (3,122)		97
12	<i>Lingulodinium polyedrum</i>	1,100 (2,750)		1 ^c
	<i>Scripsiella trochoidea</i>	3,100 (2,635)		1
	<i>Prorocentrum micans</i>	4,050 (2,835)		1

^a Densities of *Polykrikos kofoidii* in control bottles were 12–24 pseudocolonies ml^{-1} in Expt. 1 and 3–9 and 2.5 pseudocolonies ml^{-1} in Expt. 2.

^b The volume of incubating bottles in Expt. 2 was 32 ml, while those in Expt. 1 and 3–9 were 80 ml.

^c The number of *Polykrikos kofoidii* in Expt. 12 was one pseudocolony per Petri-dish (see text).

capacity with freshly filtered seawater and capped. To determine actual prey densities at the beginning of the experiment and after 48-h incubation, a 5-ml aliquot was removed from each bottle and fixed with 5% Lugol's solution, and all or > 200 prey cells in three 1-ml SRCs were enumerated. After 48-h incubation, remaining contents of each bottle were transferred to wells of 6 well plate chambers and then all *Polykrikos* pseudocolonies were enumerated by individual transfer with a Pasteur micropipette.

The specific growth rate of *Polykrikos kofoidii*, μ (d⁻¹) was calculated by averaging the instantaneous growth rates (IGR) for each sampling interval, calculated as:

$$\text{IGR} = \frac{\ln(S_{t_2}/S_{t_1})}{t_2 - t_1} \times 24 \quad (1)$$

where S_{t_1} and S_{t_2} = the concentration of *P. kofoidii* at consecutive samplings. The final t_2 for calculation was 48 h, which provided the highest specific growth rate.

Data for *Polykrikos kofoidii* growth rate were fitted to a Michaelis-Menten equation:

$$\mu = \frac{\mu_{\max}(x - x')}{K_{GR} + (x - x')} \quad (2)$$

where μ_{\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_{GR} = the prey concentration sustaining $\frac{1}{2} \mu_{\max}$. Data were iteratively fitted to the model using DeltaGraph[®] (Delta Point).

Ingestion and clearance rates were calculated using the equations of Frost (1972) and Heinbokel (1978). 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:

$$\text{IR} = \frac{I_{\max}(x)}{K_{IR} + (x)} \quad (3)$$

where I_{\max} = the maximum ingestion rate (cells *Polykrikos* pseudocolony⁻¹d⁻¹ or ng C *Polykrikos* pseudocolony⁻¹d⁻¹); x = prey concentration (cells ml⁻¹ or ng C ml⁻¹), K_{IR} = the prey concentration sustaining $\frac{1}{2} I_{\max}$.

Prey selectivity in prey mixtures. Prey selectivity of *Polykrikos kofoidii* was examined using mixtures of *Lingulodinium polyedrum* and *Scrippsiella trochoidea* as food. *Polykrikos kofoidii* grew well on both prey species when the unialgal diets were offered in Expt 3. and 4. *Polykrikos kofoidii* cells growing on mixtures of *L. polyedrum* and *S. trochoidea* were added to 80-ml PC bottles containing different ratios of *L. polyedrum* and *S. trochoidea* (Table 2, Expt. 10). Triplicate experimental (containing both predator and prey) and control bottles (containing only prey) were set up for each predator-prey treatment. Ten ml of f/2 media were added to each bottle. A 5-ml aliquot was removed from each bottle and fixed with Lugol's solution to determine the actual initial concentrations of the predator and prey. The bottles were filled again to capacity with freshly filtered seawater, capped, and placed on rotating wheels using environmental condition described above. After 24-hour incubation, the contents of each bottle were fixed with acidic Lugol's solution, with predator and/or prey concentrations and predator ingestion rates determined as previously described. The carbon ratio for ingestion rate of *P. kofoidii* on *L. polyedrum* to that for *S. trochoidea* was expressed as a function of prey availability (*L. polyedrum* carbon / *S. trochoidea* carbon).

Feeding frequency, attack ratio, and successful capture. Two separate studies were conducted to determine the relative

ease with which *Polykrikos kofoidii* captured and ingested different RTDs. The first study (Table 2, Expt. 11) was designed to determine feeding frequency (FF) of *P. kofoidii* on prey (*Lingulodinium polyedrum*, *Scrippsiella trochoidea*, *Gymnodinium catenatum*, *Gyrodinium impudicum*, and *Prorocentrum micans*) after 10-min incubation. FF is the proportion of *P. kofoidii* cells that feed, as determined from the presence of ingested prey, and was calculated as the percentage of *P. kofoidii* containing one or more target prey cells. The initial concentrations of *Polykrikos kofoidii* and prey were established using an autopipette to deliver a predetermined volume of culture with known cell density to the experimental bottles. Three 32-ml PC bottles (mixtures of predator and prey) were set up for each predator-prey treatment. The bottles were filled to capacity with freshly filtered seawater, capped, and placed on a rotating wheel at 0.9 rpm at 19 °C. All bottles were taken from the rotating wheel after 10 min and the contents of the bottles were fixed with Bouin's solution. The number of prey cells observed inside *P. kofoidii* (i.e. ingested prey) and in the medium and the numbers of *P. kofoidii* with and without ingested prey were determined by observing and counting > 300 prey cells and all predators in three 1-ml Sedgwick-Rafter chambers using a compound microscope.

In the second study (Table 2, Expt. 12), attack ratio (i.e. number attempted captures relative to number of physical contacts between predator and prey) and capture success (i.e. number prey ingested relative to number attempted captures) was determined by monitoring the behavior of *P. kofoidii* in the presence of different RTDs. Attempted captures represented physical contacts where the predator remained associated with the prey for longer than two seconds. Successful captures were attacks that resulted in the prey being attached to the predator by a tow filament and then ingested. Individual *P. kofoidii* cells starved for 1 d were transferred to a Petri-dish (85 mm in diam.) containing unialgal prey (*Lingulodinium polyedrum*, *Scrippsiella trochoidea*, or *Prorocentrum micans*) and each predator was tracked under a dissecting microscope until it successfully engulfed a prey cell or until 1 h had elapsed. For each prey species, the number predator-prey encounters, attempted prey captures, and successful captures were recorded for ten *P. kofoidii* (i.e. 10 replicates).

Grazing impact. With some assumptions (see Table 5), we estimated grazing coefficients attributable to *Polykrikos* on RTDs by combining published field data on abundances of *Polykrikos* and prey with ingestion rates of the predator on the prey obtained in the present study.

Grazing coefficients (g, h⁻¹) were calculated as:

$$g = (1/\Delta t) \{ \ln [C_i / (C_i - C_e)] \}$$

where Δt (h) is a time interval, C_e (cells ml⁻¹) is the number of prey cells eaten by the *Polykrikos* population in 1 ml of seawater in an hour, and C_i (cells ml⁻¹) is the initial prey cell concentration on a given hour. The values of C_e were calculated as:

$$C_e = \text{PIR} \times 1 \text{ hour} = \text{IR} \times G \times 1 \text{ hour}$$

where PIR is the population ingestion rate of *Polykrikos* sp. on a RTD in 1 ml of seawater (prey eaten ml⁻¹h⁻¹), IR is the ingestion rate (prey eaten *Polykrikos* pseudocolony⁻¹hour⁻¹) of *Polykrikos* sp. on a RTD, and G is the abundance (pseudocolonies ml⁻¹) of *Polykrikos* on the same time as C_i .

RESULTS

Feeding process. *Polykrikos kofoidii* was observed to capture prey cells by deploying a tow filament. Approximately ten seconds later the length of the tow filament was shortened and

Table 3. Growth and grazing data for *Polykrikos kofoidii*. Parameters are for numerical and functional response from Eqs. (2) & (3) as presented in Fig. 1–14. μ_{\max} (maximum growth rate, d^{-1}), K_{GR} (prey concentration sustaining $0.5 \mu_{\max}$, $ng\ C\ ml^{-1}$), x' (threshold prey concentration, $ng\ C\ ml^{-1}$), I_{\max} (maximum ingestion rate, $ng\ C\ Polykrikos\ pseudocolony^{-1}\ d^{-1}$), K_{IR} (prey concentration sustaining $0.5 I_{\max}$, $ng\ C\ ml^{-1}$).

Figures	Species	μ_{\max}	K_{GR}	x'	r^2	I_{\max}	K_{IR}	r^2
1 & 9	<i>Gymnodinium catenatum</i>	1.12	847	288	0.73	17.1	240	0.56
2 & 10	<i>Scrippsiella trochoidea</i>	0.966	652	54	0.81	16.6	345	0.79
3 & 11	<i>Lingulodinium polyedrum</i>	0.826	493	64	0.78	24.4	184	0.75
4 & 12	<i>Ceratium furca</i>	0.354	128	113	0.81	9.8	55	0.45
5	<i>Amphidinium carterae</i>	0.101*						
6 & 13	<i>Prorocentrum micans</i>	0.062*				4.6	33	0.19
7 & 14	<i>Gyrodinium impudicum</i>	0.055*				5.4*		
8	<i>Prorocentrum minimum</i>	-0.03*						

* The maximum value among the mean growth or ingestion rates measured at the given prey concentrations.

the prey cell was attached to the posterior flagellar pore of *P. kofoidii*. Within 10 sec the prey was engulfed. Once the predator attached a tow filament to a prey cell, it succeeded in engulfing the prey.

Growth rates. *Polykrikos kofoidii* grew on *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, *Ceratium furca*, *Gymnodinium catenatum*, *Gyrodinium impudicum*, *Prorocentrum micans*, and a toxic dinoflagellate, *Amphidinium carterae*, but failed to grow on *P. minimum*, even though the species was ingested.

The specific growth rates of *Polykrikos kofoidii* feeding on unialgal diets of *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, *Ceratium furca*, and *Gymnodinium catenatum*, increased with increasing mean prey concentration less than ca. 500–2,000 $ng\ C\ ml^{-1}$, but were saturated or showed only a slight increase at higher prey concentrations (Fig. 1–4). When the data were fitted to Eq. (2), the maximum specific growth rates (μ_{\max}) of *Polykrikos kofoidii* were $1.12\ day^{-1}$ for *G. catenatum* diet, 0.97 for *S. trochoidea*, 0.83 for *L. polyedrum*, 0.35 for *Ceratium furca* (Table 3). The specific growth rates of *Polykrikos kofoidii* feeding on unialgal diets of *Amphidinium carterae*, *Prorocentrum micans*, *Gyrodinium impudicum*, and *P. minimum* increased almost linearly with increasing mean prey concentration with the maximum specific mean growth rate of 0.10, 0.06, 0.06, and $-0.03\ day^{-1}$, respectively, at the given prey concentrations (Fig. 5–8). Threshold prey concentrations (where net growth = 0) were 54 (22), 64 (75), 113 (90), and $288\ ng\ C\ ml^{-1}$ (153 cells ml^{-1}) for *L. polyedrum*, *S. trochoidea*, *C. furca*, and *G. catenatum*, respectively (Table 3).

Ingestion and clearance rates. The ingestion rates of *Polykrikos kofoidii* on unialgal diets of *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, *Ceratium furca*, *Gymnodinium catenatum*, and *Prorocentrum micans* increased rapidly with increasing mean prey concentrations up to ca. 500–1,000 $ng\ C\ ml^{-1}$,

but were saturated or showed only a slight increase at higher prey concentrations (Fig. 9–13). When the data were fitted to Eq. (3), the maximum ingestion rates of *P. kofoidii* in $ng\ C\ Polykrikos\ pseudocolony^{-1}\ day^{-1}$ and (prey cells pseudocolony $^{-1}\ d^{-1}$) were 24.4 (9.8), 17.1 (9.1), 16.6 (19.5), 9.8 (7.8), and 4.6 (4.9) for *L. polyedrum*, *G. catenatum*, *S. trochoidea*, *C. furca*, and *P. micans*, respectively. Ingestion rates for *G. impudicum* increased more linearly (Fig. 14), the maximum mean ingestion rate measured at a give prey concentration being $5.4\ ng\ C\ pseudocolony^{-1}\ d^{-1}$ (7.7 prey cells pseudocolony $^{-1}\ d^{-1}$) (Table 3).

Maximum clearance rates of *Polykrikos kofoidii* were $5.9\ \mu l\ grazer^{-1}\ h^{-1}$ for *L. polyedrum*, 4.6 for *G. catenatum*, 3.7 for *C. furca*, and 2.3 for *P. micans*, 1.3 for *G. impudicum*, and 1.1 for *S. trochoidea*.

Prey selectivity in prey mixtures. The ability of *Polykrikos kofoidii* to show a dietary preference was examined in feeding experiments using *Lingulodinium polyedrum* and *Scrippsiella trochoidea* in combined and at different ratios of the mean prey concentrations (Table 2, Expt. 10). When *P. kofoidii* ingestion rates for *L. polyedrum* were expressed as a ratio relative to ingestion rates for *S. trochoidea* and plotted as a function of the ratios for mean prey concentration (Fig. 15), all data points fell above the 1:1 line (line of no preference), indicating that *P. kofoidii* strongly preferred *L. polyedrum* to *S. trochoidea*.

Feeding frequency, attack ratio, and successful capture. *Polykrikos kofoidii* had a significantly higher feeding frequency on *Lingulodinium polyedrum* (mean \pm S.E., $39.2 \pm 1.4\%$) than on *Gymnodinium catenatum* ($24.3 \pm 0.8\%$) (one tailed *t*-test, $p < 0.01$), but not significantly higher than on *Scrippsiella trochoidea* ($34.1 \pm 1.9\%$) ($p > 0.05$) after 10-min incubation (Fig. 16). *Polykrikos kofoidii* did not have a significantly higher feeding frequency on *Gyrodinium impudicum* ($8.9 \pm 2.2\%$) than on *Prorocentrum micans* ($4.7 \pm 1.6\%$) (one tailed *t*-test, $p > 0.05$).

Table 4. Comparison of growth, ingestion and clearance rates of *Polykrikos kofoidii* and other protists on the same red-tide dinoflagellate prey. Rates are corrected to 19 °C using $Q_{10} = 2.8$ (Hansen, Bjørnsen and Hansen 1997). PV (Predators' volume as $\times 10^5\ \mu m^3$); μ_{\max} (maximum growth rate in d^{-1}); I_{\max} (maximum ingestion rate in $ng\ C\ predator^{-1}\ d^{-1}$); C_{\max} (maximum clearance rate as $\mu l\ predator^{-1}\ h^{-1}$); NC (naked ciliate); TC (tintinnid ciliate); HD (heterotrophic dinoflagellate); MD (mixotrophic dinoflagellate).

Prey species	Predator	PV	μ_{\max}	I_{\max}	C_{\max}	Reference
<i>Lingulodinium polyedrum</i>	<i>Polykrikos kofoidii</i> (HTD)	43	0.83	24	5.9	this study
	<i>Protoperdinium cf. divergens</i> (HD)	119	0.48	12	0.7	Jeong and Latz (1994)
	<i>Protoperdinium crassipes</i> (HD)	204	0.31	5	0.5	Jeong and Latz (1994)
	<i>Fragilidium cf. mexicanum</i> (MD)	85	0.26	7	4	Jeong et al. (1999a)
	<i>Strombidinopsis</i> sp. (NC)	560	0.83	222	110	Jeong et al. (1999b)
<i>Scrippsiella trochoidea</i>	<i>Polykrikos kofoidii</i> (NC)	43	0.97	17	1.1	this study
	<i>Strombidinopsis</i> sp. (NC)	560	0.67	207	41	Jeong et al. (1999b)
	<i>Favella</i> sp. (TC)			237	43	Steocker, Guillard, Kavee (1981)

Table 5. Estimation of grazing impact by a *Polykrikos* population on a RTD population using the equations in Fig. 9–14 and the abundances of *Polykrikos* spp. and RTDs. PIR = Population ingestion rate (prey eaten ml⁻¹ h⁻¹); g = grazing coefficient (h⁻¹).

Predator (<i>Polykrikos</i>)	Prey species	Predator density (pseudo- colonies/ ml)	Prey density (cells/ml)	PIR	g	Reference
<i>P. kofoidii</i>	<i>Lingulodinium polyedra</i>	4.6	8.3	0.2	0.010	Morey-Gaines (1980)
	<i>Prorocentrum micans</i>	4.6	41.0	0.5	0.013	Morey-Gaines (1980)
	<i>Ceratium</i> spp. ^a	4.6	20.2	0.4	0.020	Morey-Gaines (1980)
<i>P. schwartzii</i> ^b	<i>Gonyaulax excavata</i> ^c (= <i>Alexandrium tamarens</i>)	7.2	1850.0	2.6	0.001	Carreto et al. (1986)
	<i>Gonyaulax excavata</i> ^c	38.4	34.6	2.4	0.073	Carreto et al. (1986)
<i>P. kofoidii</i>	<i>Gymnodinium catenatum</i>	9.3	627.0	2.5	0.004	Matsuyama et al. (1999)

Ceratium spp.^a: assuming that the ingestion rate of *Polykrikos kofoidii* on the other *Ceratium* species is the same as that on *Ceratium furca*. *P. schwartzii*^b: assuming that the ingestion rates of *P. schwartzii* on red-tide dinoflagellates is the same as that for *P. kofoidii*. *Gonyaulax excavata*^c: assuming that the ingestion rate of *P. kofoidii* on *Gonyaulax excavata* is the same as that on *Lingulodinium polyedra*.

After this short incubation period, some *Polykrikos* colonies contained two *L. polyedrum*, *S. trochoidea*, or *G. catenatum* cells in their protoplasm, but none contained two *P. micans* cells.

Polykrikos kofoidii had a significantly higher attack ratio on *Lingulodinium polyedrum* (mean \pm S.E., 61 \pm 16%) than on *Prorocentrum micans* (13 \pm 3%) (one tailed *t*-test $p < 0.01$), but not significantly higher than on *Scrippsiella trochoidea* (39 \pm 11%) ($p > 0.1$) (Fig. 17A). Attack ratio on *S. trochoidea* was significantly higher than on *P. micans* ($p < 0.05$). Similarly, successful capture on *L. polyedrum* (100%) was significantly higher than on *P. micans* (50 \pm 16%) (one tailed *t*-test, $p < 0.01$), but not significantly higher than that on *S. trochoidea* (90 \pm 7%) ($p > 0.1$) (Fig. 17B). Successful capture on *S. trochoidea* was also significantly higher than on *P. micans* ($p <$

0.05). In particular, *P. kofoidii* was almost 100% successful in capturing motionless *P. micans* cells, but had only a 10% success rate when attacking actively moving cells.

DISCUSSION

The present study shows that *Polykrikos kofoidii* exhibits positive growth when feeding on RTDs belonging to several genera. Among the unialgal diets of eight dinoflagellate species offered as prey in the present study, only *Prorocentrum minimum* failed to support population growth of *P. kofoidii*. Data also show that growth and ingestion rates of *P. kofoidii* on RTDs were significantly affected by prey species and prey concentration.

Prey species. *Polykrikos kofoidii* had wide ranges of growth rates, ingestion rates, and feeding frequencies when feeding on unialgal diets (Table 3 and Fig. 16). Data from this study show that maximum growth and ingestion rates of *P. kofoidii* are positively correlated with prey cell volume (Fig. 18A, B). This relationship suggests that prey cell volume generally has a

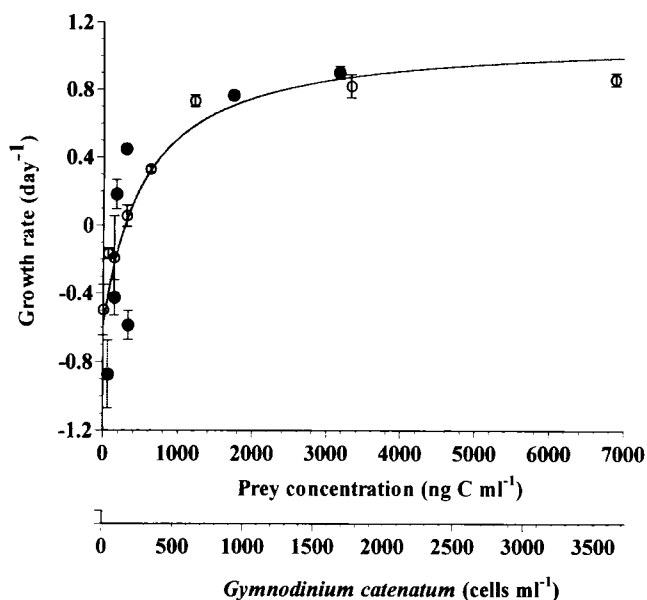


Fig. 1. Specific growth rates of *Polykrikos kofoidii* on *Gymnodinium catenatum* as a function of mean prey concentration. Symbols represent treatment means \pm 1 S.E. The volume of incubating bottles in Expt. 1 (●) and Expt. 2 (○) were 80 and 32 ml, respectively. The equation of the regression line was obtained by pooling all treatments from Expt. 1 and 2. The curves are fitted by a Michaelis-Menten equation [Eq. (2)] (see Table 3).

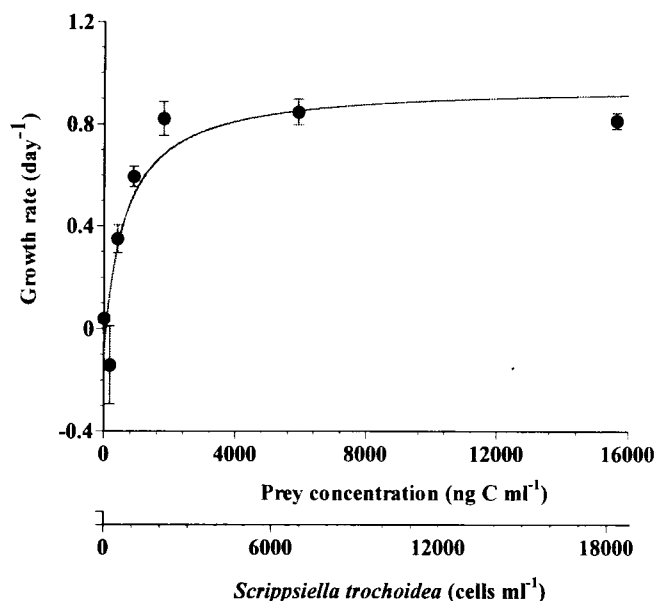


Fig. 2. Specific growth rates of *Polykrikos kofoidii* on *Scrippsiella trochoidea* as a function of mean prey concentration. Symbols represent treatment means \pm 1 S.E. The curves are fitted as Fig. 1.

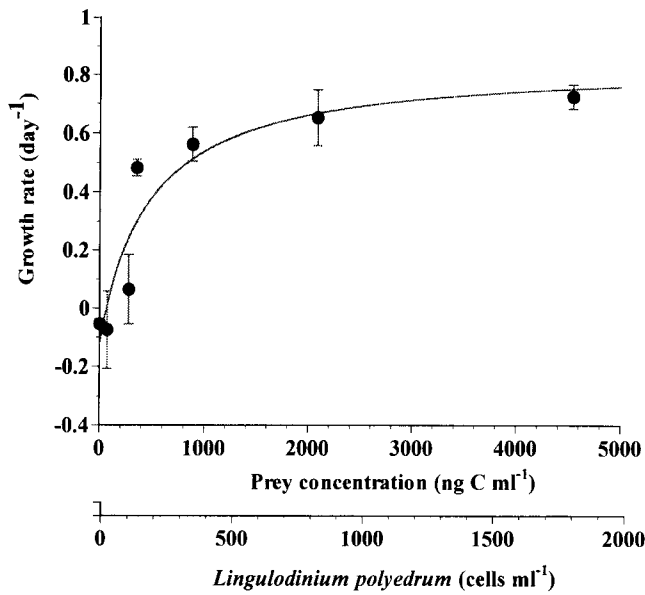


Fig. 3. Specific growth rates of *Polykrikos kofoidii* on *Lingulodinium polyedrum* as a function of mean prey concentration. Symbols represent treatment means \pm 1 S.E. The curves are fitted as Fig. 1.

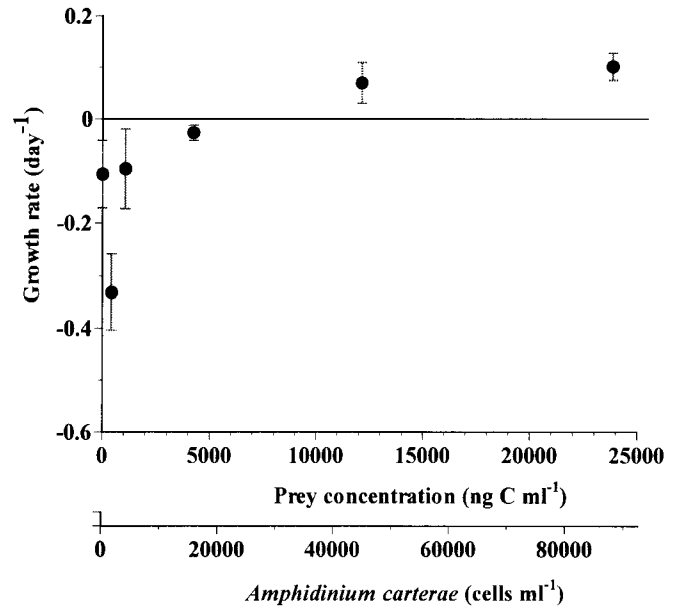


Fig. 5. Specific growth rates of *Polykrikos kofoidii* on *Amphidinium carterae* as a function of mean prey concentration. Symbols represent treatment means \pm 1 S.E.

marked effect on growth and ingestion of *P. kofoidii* on RTDs. However, growth rates, ingestion rates, and feeding frequency of *P. kofoidii* on *Scrippsiella trochoidea* were much higher than those for *Prorocentrum micans*, even though these prey are similar in cell volume. Thus, factors other than prey size may in some cases be important to the feeding activity of *P. kofoidii*. Interestingly, *P. kofoidii* had a significantly higher attack ratio, (number attempted captures)/(number of physical contacts), and greater capture success, (number prey ingested)/(number of attempted captures), when feeding on *S. trochoidea* than when feeding on *P. micans*. These observations suggest that *S. trochoidea* may be more attractive to *P. kofoidii* as prey than *P.*

micans, and/or that *P. kofoidii* may have more difficulty attaching a tow filament to the flattened cells of *P. micans* than to the more spherical cells of *S. trochoidea*.

The ratio of the growth rates relative to the ingestion rate (RGI) of *Polykrikos kofoidii* on *Scrippsiella trochoidea* was markedly higher than that on *Lingulodinium polyedrum* (Fig. 19). Three explanations are possible for this phenomenon; (1) the food quality of *S. trochoidea* as prey for the predator might be higher than that for *L. polyedrum*; (2) conversion factor from volume to carbon for *L. polyedrum* might be higher than that for *S. trochoidea*; (3) accumulation of undigested *L. polyedrum* cells in the predator might be greater than that of *S. trochoidea*.

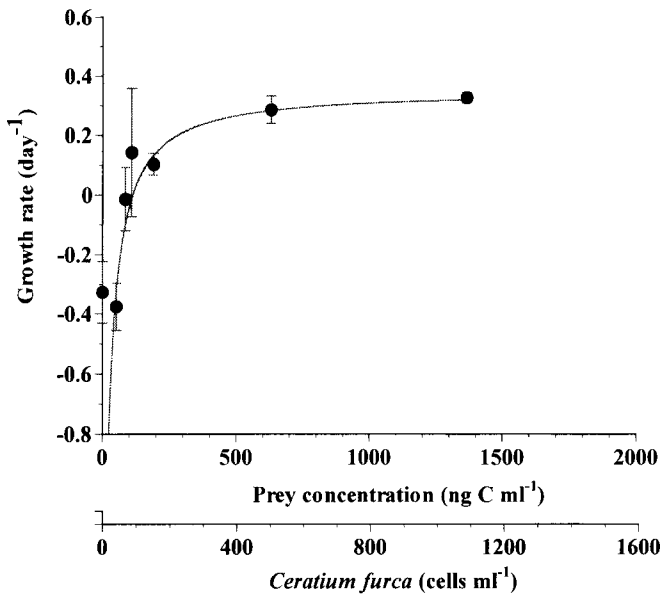


Fig. 4. Specific growth rates of *Polykrikos kofoidii* on *Ceratium furca* as a function of mean prey concentration. Symbols represent treatment means \pm 1 S.E. The curves are fitted as Fig. 1.

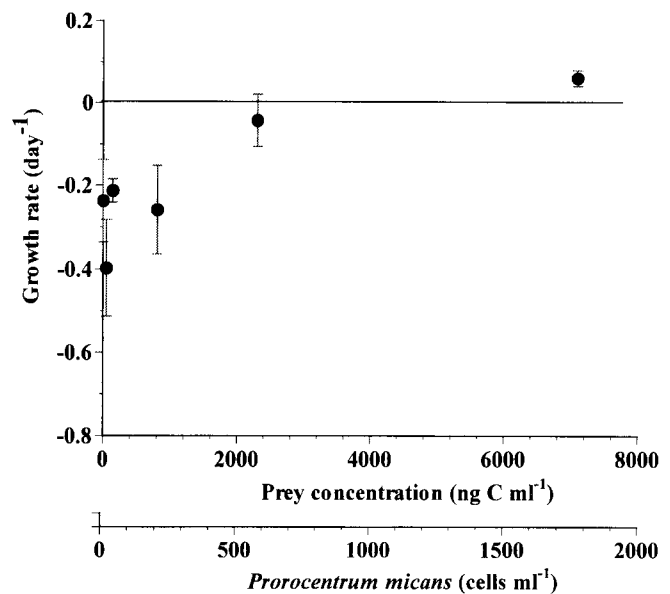


Fig. 6. Specific growth rates of *Polykrikos kofoidii* on *Prorocentrum micans* as a function of mean prey concentration. Symbols represent treatment means \pm 1 S.E.

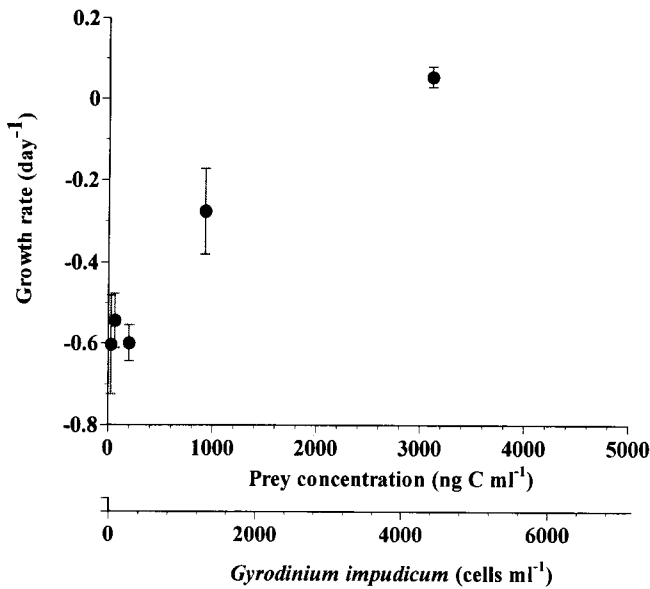


Fig. 7. Specific growth rates of *Polykrikos kofoidii* on *Gyrodinium impudicum* as a function of mean prey concentration. Symbols represent treatment means ± 1 S.E.

In RGI of *P. kofoidii* on *Gymnodinium catenatum* in Expt. 1, the positive growth rates fall along one line, similar to those of *S. trochoidea*, while the negative growth rates fall along another line (*G. catenatum* I-1 and I-2 of Fig. 19, respectively). Also, growth rates varied widely with the prey density near threshold *G. catenatum* densities, while ingestion rate did not. A similar pattern was observed in Expt. 2 (*G. catenatum* II of Fig. 19), even though the degree of scatter in growth rate near threshold *G. catenatum* densities was smaller than that in Expt. 1. These results are difficult to interpret, but this unusual pattern may be related to the fact that the food is packaged as chains, usually with 4 cells/chain. The predators have lower encounter rate with

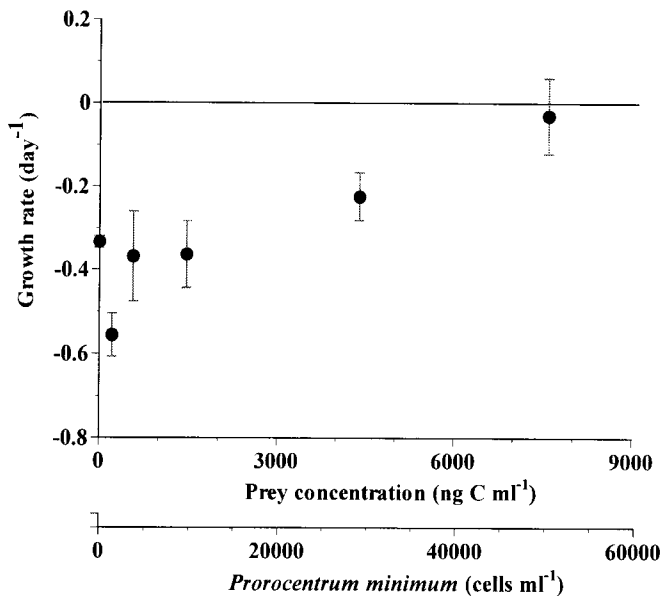


Fig. 8. Specific growth rates of *Polykrikos kofoidii* on *Prorocentrum minimum* as a function of mean prey concentration. Symbols represent treatment means ± 1 S.E.

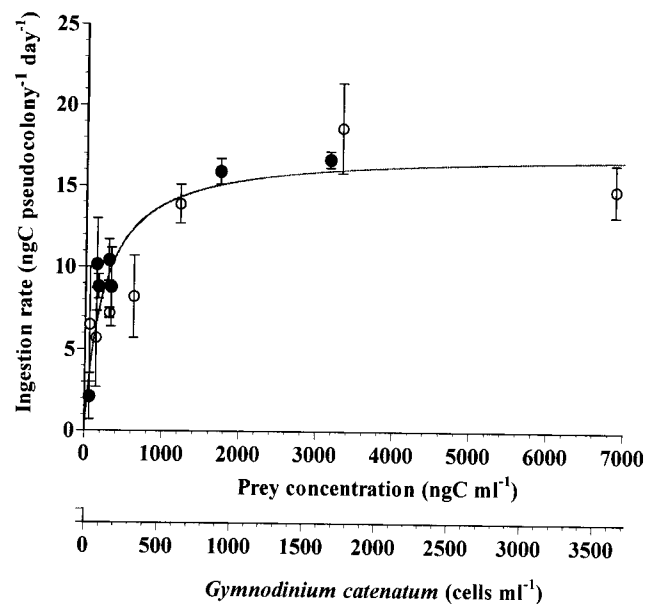


Fig. 9. Ingestion rates of *Polykrikos kofoidii* on *Gymnodinium catenatum* as a function of mean prey concentration. Symbols represent treatment means ± 1 S.E. The volume of incubating bottles in Expt. 1 (●) and Expt. 2 (○) were 80 and 32 ml, respectively. The equation of the regression line was obtained by pooling all treatments from Expt. 1 and 2. The curves are fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments (see Table 3).

prey packaged as chains than with single (i.e. non-chain) prey items at the same prey concentration and must expend more energy to find and capture the former prey relative to the latter prey. At near threshold prey densities, due to possible high variation in expending energy, growth rates may vary widely with the prey density, while ingestion rates are similar. However, to find the exact cause of this pattern, further study is necessary.

Unlike *Favella ehrenbergii*, *Strombidinopsis* sp., and *Fragil-*

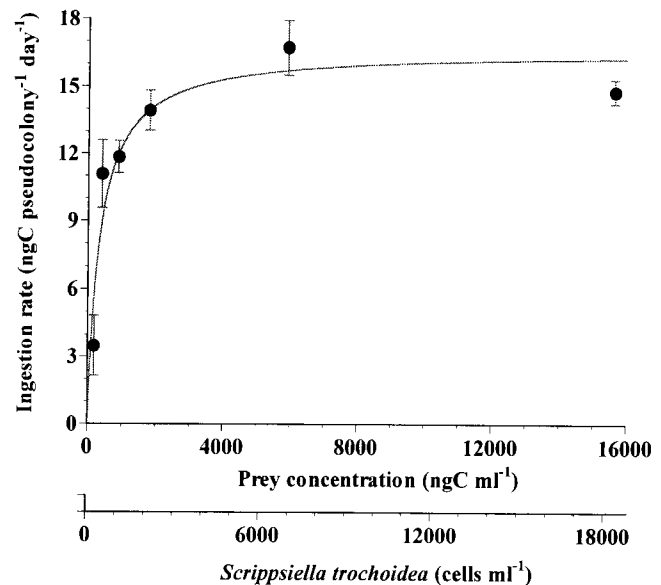


Fig. 10. Ingestion rates of *Polykrikos kofoidii* on *Scrippsiella trochoidea* as a function of mean prey concentration. Symbols represent treatment means ± 1 S.E. The curves are fitted as Fig. 9.

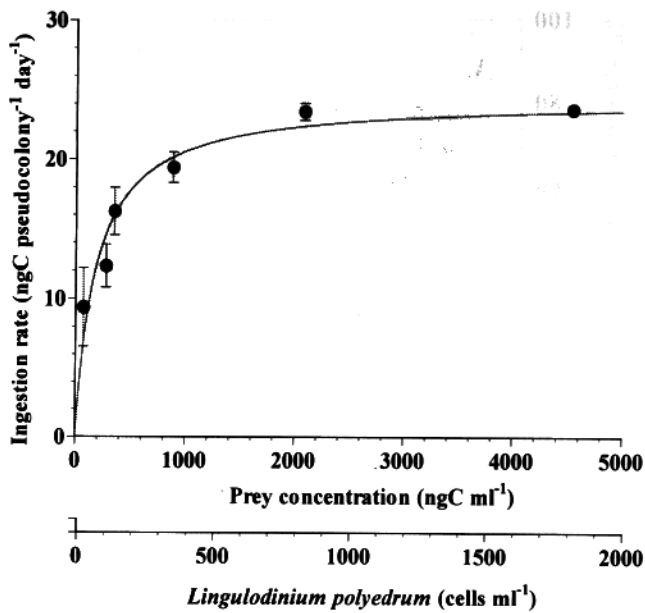


Fig. 11. Ingestion rates of *Polykrikos kofoidii* on *Lingulodinium polyedrum* as a function of mean prey concentration. Symbols represent treatment means \pm 1 S.E. The curves are fitted as Fig. 9.

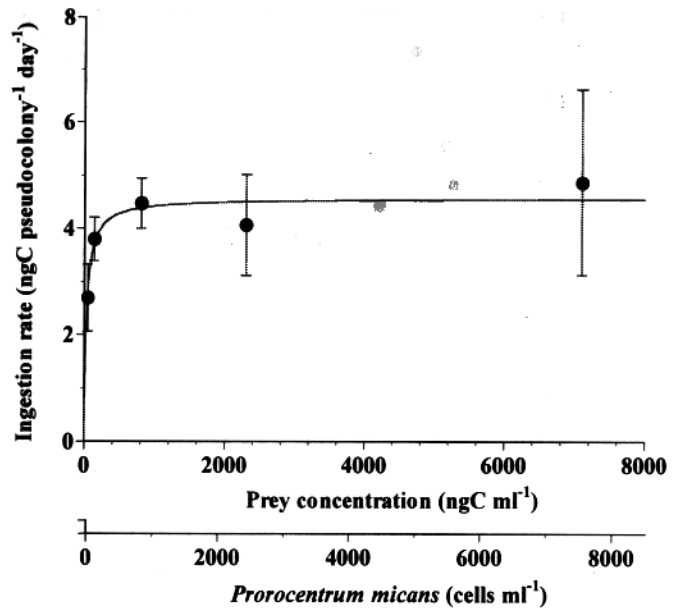


Fig. 13. Ingestion rates of *Polykrikos kofoidii* on *Prorocentrum micans* as a function of mean prey concentration. Symbols represent treatment means \pm 1 S.E. The curves are fitted as Fig. 9.

idium cf. *mexicanum* (Stoecker, Guillard, and Kavee 1981; Jeong et al. 1999a and b), *Polykrikos kofoidii* was able to prey on *Amphidinium carterae*, which is known to be toxic (Steidinger and Tangen 1996). The ability to feed and grow on *A. carterae* suggests that *Polykrikos kofoidii* might be insensitive to the toxin present in this dinoflagellate or may be able to detoxify the toxin.

Growth. *Polykrikos kofoidii* has a higher maximum growth rate (μ) on *Scrippsiella trochoidea* (0.97 day^{-1}) than does *Strombidinopsis* sp. (0.67 d^{-1}) or *Protoperidinium* cf. *divergens* (0) on the same prey at the same temperature (Jeong and Latz

1994; Jeong et al. 1999b) (Table 4). The maximum growth rate of *P. kofoidii* on *Lingulodinium polyedrum* (0.83 d^{-1}) is also higher than that of *Protoperidinium* cf. *divergens* (0.48 d^{-1}), *P. crassipes* (0.31), *Fragilidium* cf. *mexicanum* (0.26) on the same prey, but is the same as *Strombidinopsis* sp. (Jeong and Latz 1994; Jeong et al. 1999a and b), when corrected to 19°C using $Q_{10} = 2.8$ (Hansen, Bjørnsen, and Hansen 1997).

The threshold prey concentration of *Polykrikos kofoidii*, 64 ng C ml^{-1} for *Lingulodinium polyedrum*, was lower than that of *Protoperidinium* cf. *divergens* on the same prey (ca. 200 ng C ml^{-1}), but higher than that of *Strombidinopsis* sp. (20 ng C ml^{-1}). Threshold prey concentration for *S. trochoidea* (54 ng C

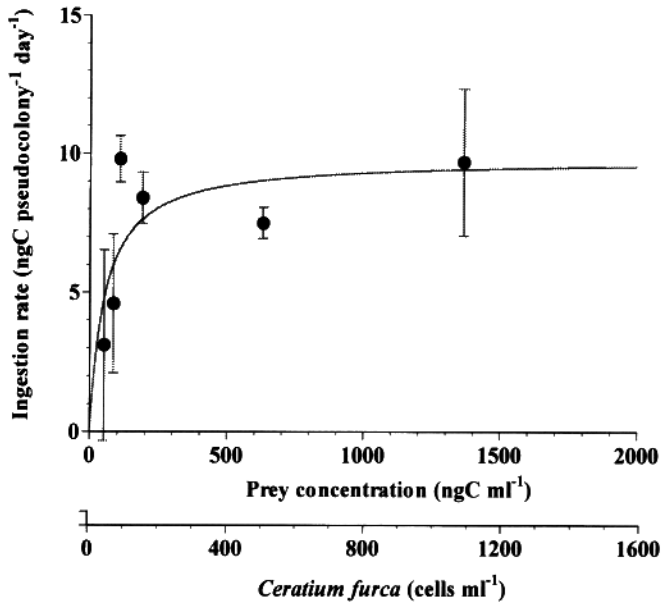


Fig. 12. Ingestion rates of *Polykrikos kofoidii* on *Ceratium furca* as a function of mean prey concentration. Symbols represent treatment means \pm 1 S.E. The curves are fitted as Fig. 9.

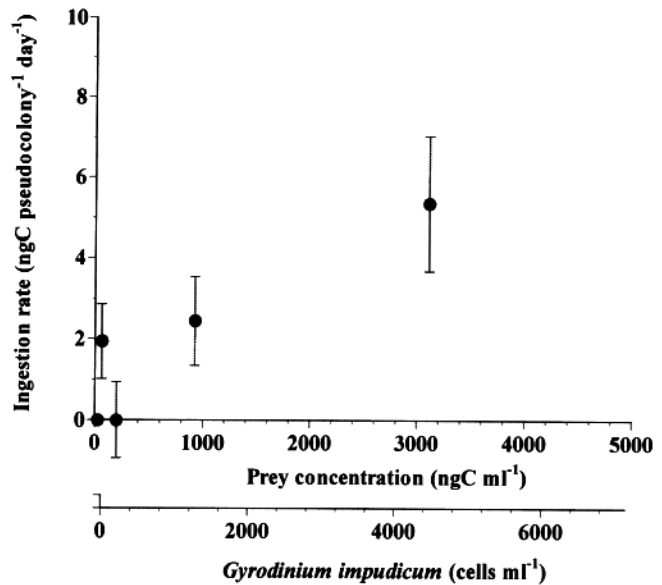


Fig. 14. Ingestion rates of *Polykrikos kofoidii* on *Gyrodinium impudicum* as a function of mean prey concentration. Symbols represent treatment means \pm 1 S.E.

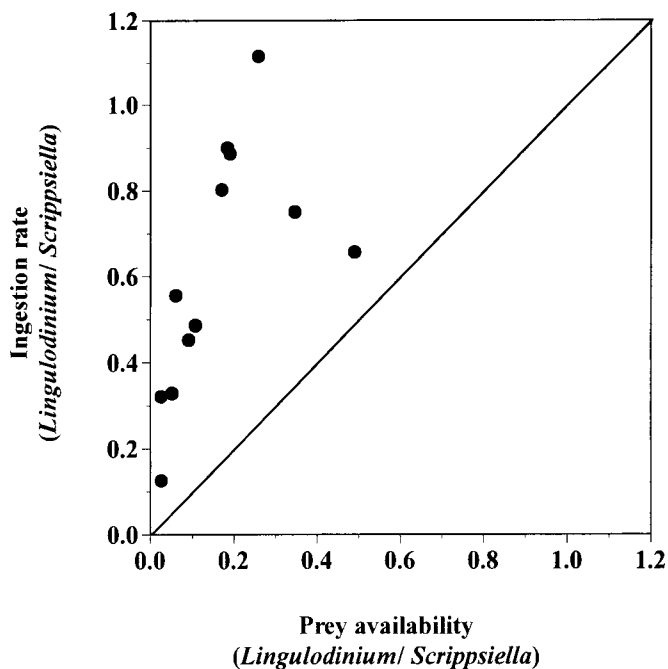


Fig. 15. Prey selection of *Polykrikos kofoidii* on a mixed diet of *Lingulodinium polyedrum* and *Scrippsiella trochoidea*. Each symbol represents the result of a single incubation bottle. The carbon ratio of the ingestion rate of *P. kofoidii* on *L. polyedrum* to that on *S. trochoidea* was expressed as a function of prey availability (*L. polyedrum* carbon / *S. trochoidea* carbon).

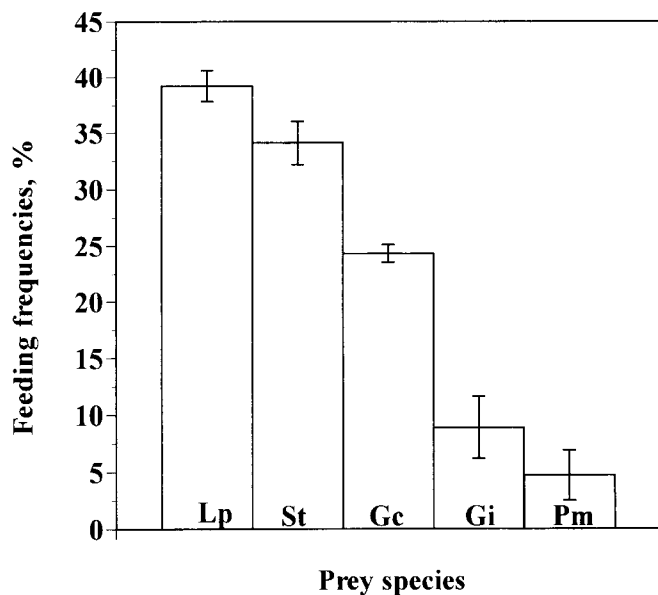


Fig. 16. The feeding frequency (%) of *Polykrikos kofoidii* on *Lingulodinium polyedrum* (Lp), *Scrippsiella trochoidea* (St), *Gymnodinium catenatum* (Gc), *Gyrodinium impudicum* (Gi), and *Prorocentrum micans* (Pm), the proportion of the *P. kofoidii* cells observed to contain prey, measured by calculating the percent ratio of *Polykrikos* containing one or more target prey cells to total *Polykrikos* after 10-min incubation. Symbols represent treatment means \pm 1 S.E.

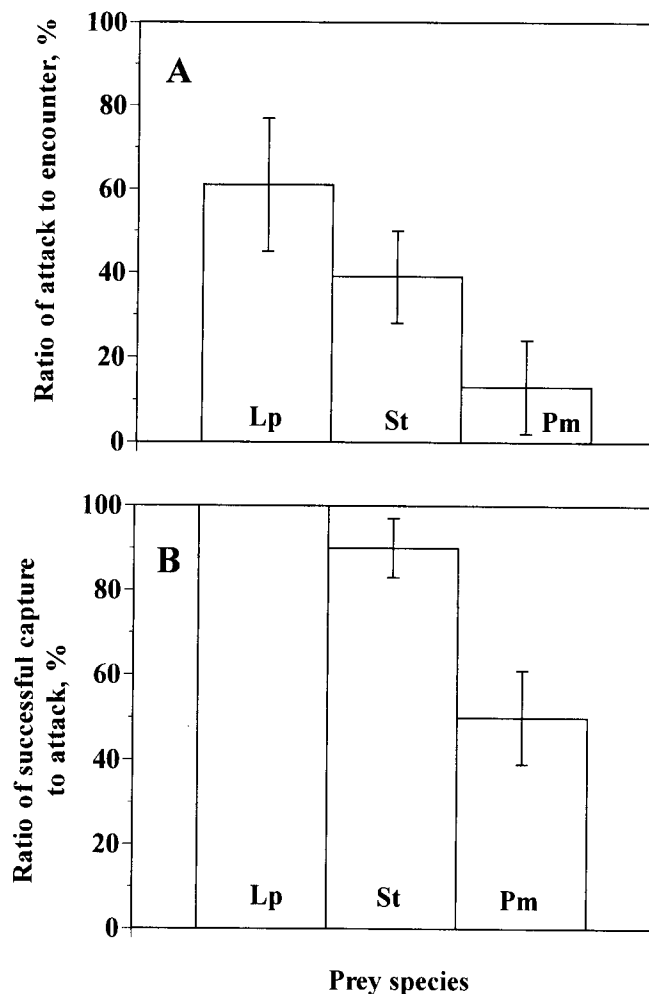


Fig. 17. The ratios of attack by *Polykrikos kofoidii* on *Lingulodinium polyedrum* (Lp), *Scrippsiella trochoidea* (St), and *Prorocentrum micans* (Pm) relative to encounter (A) and of successful capture relative to attack (B). Values are treatment means \pm 1 S.E.

ml⁻¹), was also higher than that of *Strombidinopsis* sp. (29 ng C ml⁻¹). This evidence suggests that engulfing prey captured by a tow filament (*Polykrikos* spp.) is a more effective feeding mechanism at low prey concentrations than is pallium feeding on prey captured by a tow filament (*Protoperidinium* spp.), but less effective than engulfing prey using rows of cilia (*Strombidinopsis* spp.).

Ingestion and clearance. Maximum ingestion (I_{\max}) and clearance rates (C_{\max}) of *Polykrikos kofoidii* on RTDs obtained in this study are comparable to or higher than those previously reported for a mixotrophic dinoflagellate and other heterotrophic dinoflagellates on the same prey (see Table 4). For example, the I_{\max} of *P. kofoidii* on *Lingulodinium polyedrum* (24 ng C *Polykrikos* pseudocolony⁻¹ d⁻¹) is higher than that of *Fragilidium* cf. *mexicanum* (7 ng C grazer⁻¹ d⁻¹) or *Protoperidinium* cf. *divergens* (12), but much lower than that of *Strombidinopsis* sp. (222 ng C grazer⁻¹ d⁻¹), when corrected to 19 °C using $Q_{10} = 2.8$ (Hansen, Bjørnsen, and Hansen 1997). C_{\max} of *P. kofoidii* on *L. polyedrum* (5.9 μ l *Polykrikos kofoidii*⁻¹ h⁻¹) is higher than that of *F. cf. mexicanum* (4 μ l grazer⁻¹ h⁻¹) and *Protoperidinium* spp. (0.6–0.9) on the same prey. I_{\max} and C_{\max} of *P. kofoidii* on *Scrippsiella trochoidea* are much lower than those of *Strombidinopsis* sp. and *Favella* sp.

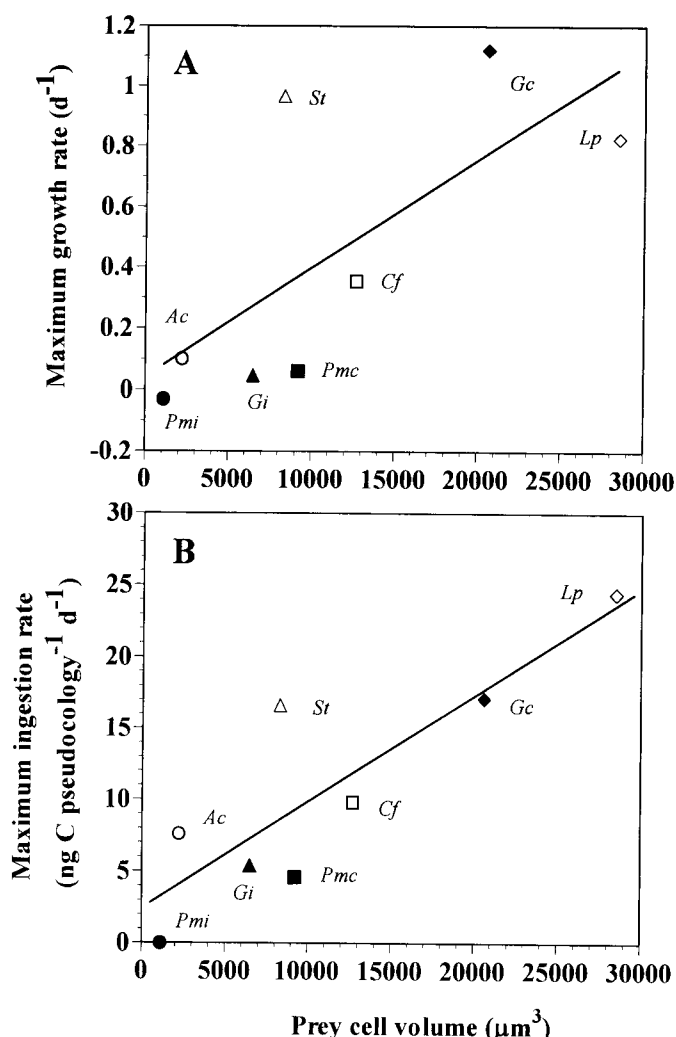


Fig. 18. Maximum growth (μ_{max} , A) and ingestion (I_{max} , B) rates of *Polykrikos kofoidii* on 8 dinoflagellate species as a function of prey cell volume (pcv). The equations of the linear regression were μ_{max} (d^{-1}) = 3.6×10^{-5} (pcv) + 3.1×10^{-2} , $R^2 = 0.513$ (A) and I_{max} ($ng\ C\ pseudocolony\ d^{-1}$) = 7.4×10^{-4} (pcv) + 2.4, $R^2 = 0.741$ (B). Ac: *Amphidinium carterae*, Cf: *Ceratium furca*, Gc: *Gymnodinium catenatum*, Gi: *Gyrodinium impudicum*, Lp: *Lingulodinium polyedrum*, Pmc: *Procerentrum micans*, Pmi: *P. minimum*, and St: *Scrippsiella trochoidea*.

Prey selectivity. The present study shows that *Polykrikos kofoidii* has the ability to feed selectively when offered a mixture of red-tide dinoflagellates as prey and strongly prefers *Lingulodinium polyedrum* to *Scrippsiella trochoidea* (Fig. 15). Prey selection by dinoflagellates in mixtures of prey species appears common, as *Fragilidium cf. mexicanum* strongly preferred *L. polyedrum* to *S. trochoidea* (Jeong et al. 1999a), while *Protoperdinium cf. divergens* strongly selected *L. polyedrum* over *G. sanguineum* (Jeong and Latz 1994), but preferred round copepod eggs with a smooth surface over *L. polyedrum* (Jeong 1996). *Oxyrrhis marina* also has the ability to select prey among different-sized nanophytoplankton (Hansen, Witte, and Passarge 1996). This differential feeding in mixtures of prey may affect the population dynamics of RTDs when favorable conditions for their growth are provided in nature.

Grazing impact. The estimated grazing coefficients attributable to *Polykrikos* sp. on a co-occurring dominant RTD are 0.001–0.073 h^{-1} (i.e. 0.1–7 % of RTD populations were re-

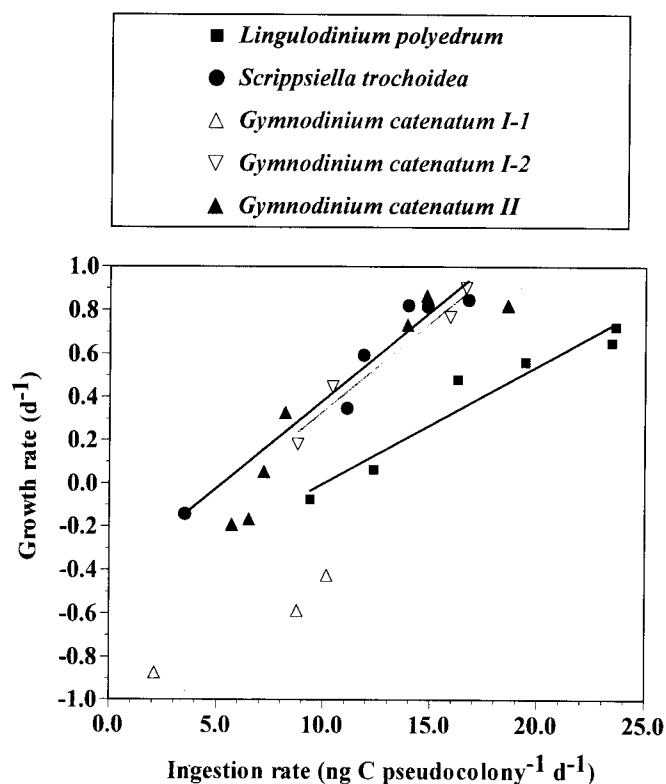


Fig. 19. Growth rates (μ , d^{-1}) of *Polykrikos kofoidii* on *Lingulodinium polyedrum*, *Scrippsiella trochoidea*, and *Gymnodinium catenatum* (*Gymnodinium catenatum* I-1 for negative growth rates, I-2 for positive growth rates in Expt. 1 and *G. catenatum* II for Expt. 2) as a function of ingestion rates (IR, $ng\ C\ pseudocolony\ d^{-1}$). The data pointed were obtained from Fig. 1, 2, 3, 9, 10, and 11. The equations of the linear regression were $\mu = 0.05$ (IR) - 0.55 ($R^2 = 0.94$) for *L. polyedrum*; $\mu = 0.08$ (IR) - 0.43 ($R^2 = 0.95$) for *S. trochoidea*; $\mu = 0.05$ (IR) - 0.99 ($R^2 = 0.96$) for *G. catenatum* I-1; $\mu = 0.08$ (IR) - 0.48 ($R^2 = 0.96$) for *G. catenatum* I-2.

moved by a *Polykrikos* population per hour) (Table 5). The grazing coefficients in the non-bloom periods (0.01–0.073 h^{-1}) are higher than those in the bloom periods (0.001–0.004 h^{-1}). Therefore, *Polykrikos* spp. sometimes have a considerable grazing impact on RTD populations. These grazing coefficients in the bloom periods are very similar to the maximum grazing coefficients of *Protoperdinium* spp. on *Lingulodinium polyedrum* (0.004 and 0.001 h^{-1}) in the coastal waters off La Jolla, CA, USA, in 1992 and 1993, respectively (Jeong 1995). The ciliate *Strombidinopsis* sp. also feeds on *L. polyedrum* (Jeong et al. 1999b), however, its grazing impact is difficult to assess due to the lack of data on the abundance of this grazer in coastal waters of Korea. Nonetheless, ingestion rates of *Strombidinopsis* sp. feeding on *L. polyedrum* (Table 4 and 5; Jeong et al. 1999b) indicate that a *Strombidinopsis* sp. density of 0.75 cells ml^{-1} would be necessary to have the same grazing impact (0.01 h^{-1}) on *L. polyedrum* (8.3 cells ml^{-1}) as *P. kofoidii* (4.6 pseudocolonies ml^{-1}).

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