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Feeding the Larvae of the Sea Urchin *Strongylocentrotus intermedius* on a Red-Tide Dinoflagellate *Cochlodinium polykrikoides*

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This study is the first attempt to understand the feeding physiology of a sea-urchin larva on a red-tide dinoflagellate. Fifteen day old larvae of *S. intermedius* capture *C. polykrikoides* cells by localized reversal of ciliary beats. No failure to transporte the algal cells from theciliated band to mouth and no rejection at the mouth suggest that *C. polykrikoides* has no feeding deterrence to *S. intermedius* larvae. The trend obtained for the clearance rate of *S. intermedius* larvae is similar to that of other sea urchin larvae. Thus, the clearance rate decreased as the algal concentration increased. Maximum clearance rate of *S. intermedius* on *C. polykrikoides* was 17.7 μl/larva/hr. Ingestion rate rapidly increased at lower algal concentrations and saturated at higher concentrations. There was no inhibition in ingestion rate at the highest prey concentration of ca. 3000 cells/ml. Maximum ingestion rate of *S. intermedius* on *C. polykrikoides* was 131 ngC/larva/d, which is higher than that reported for the larvae of the mussel *Mytilus galloprovincialis*, but lower than that of the ciliate *Strombidinopsis* sp. The grazing rate, calculated by combining the field data on algal abundances with experimental data on ingestion rate, suggests that due to its low abundance, sea urchin larva has no significant grazing impact on *C. polykrikoides* population.

Key words: *Strongylocentrotus intermedius*, Larvae, *Cochlodinium polykrikoides*, Algal density, Clearance rate, Ingestion rate

Introduction

Larvae of commercially important sea urchins of Korea are planktotrophic. Hence, they have to feed on suspended organic particles in water column during larval period. Nutritional quality of these particles is crucial to the survival, growth, morphology and metamorphosis of larvae, and post-metamorphic growth of juveniles (Boidron-Metairon, 1988; Pearce and Scheibling, 1991; Fenaux et al., 1994). Therefore, feeding and nutrition during larval period can critically affect the population structure after metamorphosis (López et al., 1998). *Strongylocentrotus intermedius* A. Agassiz is a common sea urchin and is harvested commercially in Korea as an important source of roe. There was a study on growth efficiency of *S. intermedius* larvae feeding on different algal species of diatom and microflagellates (Lee and Baik, 1995). However, feeding physiology and/or ecological function of *S. intermedius* larvae as a component of plankton community are not understood yet.

Planktonic algae in seawater are important food for filter-feeding animals. In most cases, high algal production is beneficial for aquaculture and fisheries management. However, some algal blooms, especially dominated by dinoflagellates, are harmful (so called red tide), causing great losses to fisheries. Recently, the frequency and scale of red tides around the Korean coast have substantially increased (Kim et al., 1997). Among the red-tide dinoflagellates, *Cochlodinium poly-*

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krikoides is known as the most harmful species. *C. polykrikoides* is a naked, chain-forming dinoflagellate, with diameter of 19~22 ㎛. A number of studies were made on different aspects of *C. polykrikoides*, such as biological and ecological characteristics (Na et al., 1997; Park and Park, 1999; Cho et al., 2000), toxicity (Lee, 1996; Kim et al., 2000), removal by chemicals (Ryu et al., 1998), clays (Choi et al., 1998), micro-organisms (Jeong et al., 2000) and so on. Most of these studies respect on the harmful effect of *C. polykrikoides*. Kim et al. (2000) found the lethal level of *C. polykrikoides* to flounder (*Paralichthys olivaceus*) and red sea bream (*Pagrus major*) at relatively high concentration of 3000 cells/ml. Lee (1996) reported that extracts from *C. polykrikoides* cells showed no toxicity to fishes and mice, and no toxins were detected by HPLC analyses. These evidences imply that the harmful effect of *C. polykrikoides* is not by the toxicity from cellular metabolites but by the side effects of high concentration itself, e.g. clogging in gills or oxygen depletion. In other words, *C. polykrikoides* can play a positive role in the ecosystem, if the concentration is not extremely high. The object of this study is to address on the positive role of *C. polykrikoides* as a food source for larvae of sea urchin, *S. intermedius*. Dinoflagellates as a food source for sea urchin larvae have not been studied comprehensively.

To understand the interactions between *S. intermedius* larvae and *C. polykrikoides*, experiments were made with cultures of these organisms to assess the functional response of *S. intermedius* larvae to the different concentration of *C. polykrikoides*. The feeding process of *S. intermedius* larvae was observed microscopically and described. Rates of clearance and ingestion of *S. intermedius* larvae were calculated by changing the concentration of *C. polykrikoides* before and after incubation. Rates of clearance and ingestion of *S. intermedius* larvae fed on *C. polykrikoides* were compared with those of the larvae of other sea urchin, bivalve and heterotrophic ciliate. Grazing impact of the sea urchin larvae on *C. polykrikoides* during red tide was also assessed using data on ingestion rate obtained from laboratory experiment and data on the algal abundance from literature. This paper is the first attempt to know the feeding physiology of a sea urchin larva on a red-tide dinoflagellate, and will provide a basis for understanding the roles of *S. intermedius* larvae and *C. polykrikoides* as predator and prey in the coastal ecosystems.

Materials and Methods

Test organisms

Approximately 30 individuals of adult *S. intermedius* were collected at a rocky coast near Kangnung by SCUBA diving in October 2001, transported to the laboratory within 12 hrs after collection, and then acclimated to the experimental temperature (20℃) for 48 hrs. During acclimation, the sea urchins were maintained in a 200 L aquarium with 5 ㎛ filtered seawater with strong aeration and fed on the kelp *Laminaria* spp. Spawning of gametes was induced by injecting 2 ml of 0.5-N KCl through peristomial membrane. Fertilization was achieved by mixing sperm and eggs from three pairs of male and female. The diameter of egg was 98.5±2.5㎛ (n = 30) before fertilization, and 121.0±6.4㎛ (n = 30) after fertilization. Fertilization success was more than 95%. Egg suspension was passed through a 150㎛ mesh screen to remove fecal material and other large particles, and the fertilized eggs were collected on a 80㎛ mesh screen, allowing the unused sperm, and smaller eggs to pass through. Eggs were rinsed three times with 5㎛ filtered and autoclaved seawater, and then incubated in a 20 L aquarium at 20℃ in dark place without aeration for 48 hrs. After 48 hrs, most eggs developed to the 2-armed echinopluteus larvae. Seawater was renewed to make larval density of 1 larva/ml. The larvae were reared in 10 L polycarbonate bottles at 20℃ under dim light (20 $\mu E/m^2/sec$) with gentle aeration. They were fed with 10^4 cells/ml of *Isochrysis galbana* every other day. Experiments were conducted with 15-day old larvae (4-armed echinoplutei), of which the length (from the anterior end of the postoral arm rod to the posterior end of the somatic rod) was 405.3±17.1㎛ (n = 30). The strain of *C. polykrikoides* was supplied from the

Red Tide Research Center, Kunsan National University. *C. polykrikoides* was grown at 20℃ in enriched f/2 seawater medium (Guillard and Ryther, 1962) without silicate, with continuous illumination of 100 μ E/m^2/sec provided by cool-white fluorescent lights. Only culture in exponential growth phase was used for experiments. Mean equivalent spherical diameter (ESD) was measured by a PAMAS-SVSS particle counter. The number of measured cells was more than 2000. Volume of cells was calculated according to the equation: Volume = $4/3\,\pi\,(ESD/2)^3$. Carbon content of *C. polykrikoides* (0.7 ngC/cell) was estimated from cell volume, according to Strathmann (1967).

Experimental design

Experiments were designed to measure the rates of clearance and ingestion of unialgal diet of the red-tide dinoflagellate *C. polykrikoides* by *S. intermedius* larva as a function of algal concentration. Two days before the experiment, cultures of *S. intermedius* larvae growing on *I. galbana* were transferred into 1 L polycarbonate bottles containing low concentration of *C. polykrikoides*. This was done to acclimate the sea urchin larvae to the target alga. The bottles were filled to capacity with 5 μm filtered seawater and placed on wheels rotating at 0.9 rpm and incubated at 20℃ under continuous illumination of 50 μ E/m2/sec of cool-white fluorescent lights. For feeding experiments, initial densities of *C. polykrikoides* and *S. intermedius* larvae were set up as 80, 160, 350, 1,370, 2,620, and 3,150 cells/ml for the prey and 1, 2, 3, 4, and 5 larvae/ml for the predator. For each experimental set, the initial densities of alga and larva were achieved using an autopipette to deliver predetermined volumes of culture with known densities to the bottles. Triplicate 55 ml polystyrene experimental bottles (mixtures of predator and prey) and triplicate control bottles (prey only) were set up at each predator-prey combination. The control was used to check changes in algal concentration due to growth, death, or attachment of the cells to the bottle. Five ml of f/2 medium were added to all bottles, which were then filled to capacity with freshly filtered and autoclaved seawater, and capped. To determine actual densities of predator and prey at the beginning of experiment, 10 ml were removed from each bottle, and fixed with 5% Lugol's solution. The bottles were filled again to capacity with freshly filtered and autoclaved seawater, capped, and placed on rotating wheels under conditions described above. Dilution of the cultures associated with refilling the bottles was considered in calculating rates of clearance and ingestion. After 96 hrs, 10 ml aliquots were taken from each bottle and fixed with 5% Lugol's solution for enumeration of prey and predator. The abundance of prey and predator was determined by counting all or more than 400 cells in triple 1 ml Sedgwick-Rafter counting chambers.

To know whether *S. intermedius* larvae actually feed on *C. polykrikoides* or not, microscopic observations were conducted. At the beginning of feeding experiment, approximately 30 larvae were separately transferred to a well of 6-well plate with 10 ml of filtered seawater to which ca. 1000 cells/ml of *C. polykrikoides* were added, and then feeding behavior of *S. intermedius* larvae was observed under either a stereo-zoom (Olympus, SZH10) or a epifluorescence (Olympus, BX50) microscope for 1 hr.

Clearance rate (CR) and ingestion rate (IR)

The clearance rate (CR, $\mu\ell$/larva/hr) was calculated as:

$$CR = V\,[\,\ln\,(C^*_t / C^*_0) - \ln\,(C_t / C_0)\,] / N_t \qquad (1)$$

where V = volume ($\mu\ell$); C^*_0 and C^*_t = the initial and final concentrations (cells/ml) of *C. polykrikoides* in control bottles; C_0 and C_t = the initial and final concentrations of *C. polykrikoides* in experimental bottles; N = the total number (ind.) of *S. intermedius* larvae in each experimental bottle; t = incubation time (hrs). The ingestion rate (IR, cells/larva/d) was calculated as:

$$IR = \langle C \rangle\ CR24 \qquad (2)$$

where $\langle C \rangle$ = average concentration (cells/ml) of *C. polykrikoides* in experimental bottles during incubation period (Frost 1972). Ingestion rate was converted to

the carbon equivalent and expressed in ngC/larva/d.

To determine the functional response of *S. intermedius* to the concentration of *C. polykrikoides*, data on ingestion rate were fitted to a Michaelis- Menten equation:

$$IR = I_{max}\ C\ /\ [\ K_{IR} + C\ ] \quad (3)$$

where I_{max} = the maximum ingestion rate (ngC/larva/d); C = concentration of *C. polykrikoides* (cells/ml), K_{IR} = the prey concentration sustaining 50% of I_{max}.

Statistical analyses

Rates of clearance and ingestion of *S. intermedius* at different concentrations of *C. polykrikoides* were compared by one-way analysis of variance (ANOVA) on SPSS program. Multiple comparisons were made using Tukey test (Zar, 1984). Prior to statistical analyses, data on rates of clearance and ingestion were tested for normality (Shapiro-Wilk's test) and homogeneity of variance (Bartlett's test). If at least one of the above ANOVA requirements was not met, the data were $\log_{10}$ transformed, and then ANOVA was repeated. For all analyses, a significance level of $\alpha = 0.05$ was used.

Results

Feeding process by *S. intermedius* larvae on *C. polykrikoides*

Feeding by *S. intermedius* larvae on *C. polykrikoides* was detected by microscopic observations. Since the transparent *S. intermedius* larvae swam slowly, the feeding process could easily be observed under the stereo-zoom microscope. Most of larvae oriented with their arms upward in water column. Ciliated bands were observed along the arms. When cells of *C. polykrikoides* approached the ciliated band, cilia adjacent to *C. polykrikoides* changed the direction of beat (reverse direction). As a consequence of this localized reversal, *C. polykrikoides* cells were transported to the mouth of larvae. No failure to transport the algal cells from ciliated band to mouth was observed. All the algal cells arriving at the mouth came into the body. No rejection of alga at the mouth was observed. Ingested cells of *C. polykrikoides* were found in the stomach of larvae (Fig. 1A). When larvae were observed under epifluorescence microscope, ingested cells could easily be distinguished by bright color (Fig. 1B).

Clearance rate (CR)

Clearance rate of *S. intermedius* larvae fed on unialgal diet of *C. polykrikoides* ranged from 2.3 to 17.7 $\mu\ell$/larva/hr. One-way ANOVA showed that there were significant differences in clearance rate of the larvae fed on different algal concentrations ($F = 89.89$, $P < 0.001$). Clearance rate was the highest (17.7$\mu\ell$/larva/hr) when the concentration was the lowest (44 cells/ml). It decreased rapidly ($P < 0.001$) at the concentration of ca. 300 cells/ml; subsequently, it slowly but progressively decreased with increasing concentration (Fig. 2). It was lowest (2.3 $\mu\ell$/larva/hr) at the highest concentration (2,720 cells/ml). Multiple comparisons showed that there were no significant differences in clearance rate at the concentrations between 44 and 90 cells/ml ($P = 0.127$) and between 294 and 655 cells/ml ($P = 0.994$).

Ingestion rate (IR)

Ingestion rate of *S. intermedius* larvae fed on unialgal diet of *C. polykrikoides* ranged from 13.1 to 121.6 ngC/larva/d. One-way ANOVA showed that there were significant differences in ingestion rate of the larva fed at different algal concentrations ($F = 144.95$, $P < 0.001$). Ingestion rate was the lowest (13.1 ngC/larva/d/) at the lowest algal concentration was lowest (44 cells/ml). The increase in the ingestion rate was rapid ($P < 0.001$) until the algal concentration attained the density of ca. 600 cells/ml, but became gradual at higher concentrations (Fig. 3). The highest ingestion rate (121.6 ngC/larva/d) occurred at the concentration of 1,767 cells/ml. Multiple comparisons showed that there were no significant differences in ingestion rate at the algal concentration between 655

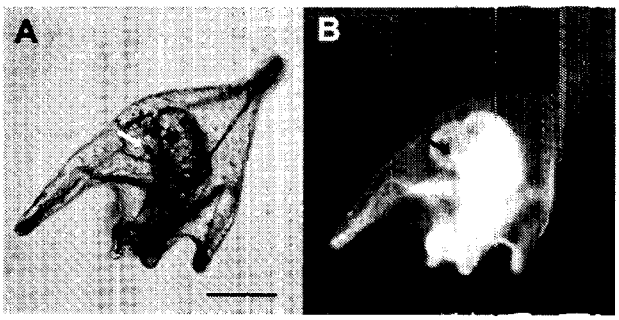

Fig. 1. *Strongylocentrotus intermedius* larva feeding on *Cochlodinium polykrikoides* observed under light (A) and epifluoresscene (B) microscope. Scale bar = 100 um.

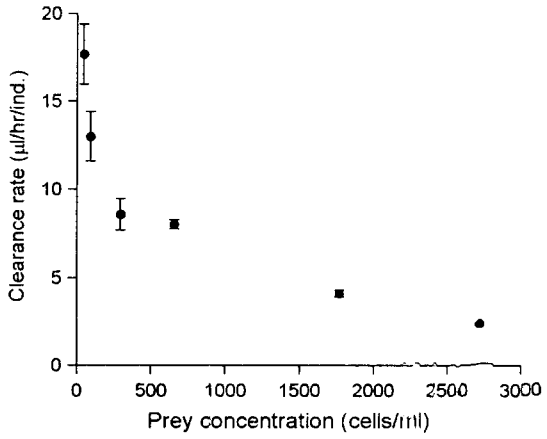

Fig. 2. Effect of unialgal concentration of *Cochlodinium polykrikoides* on clearance rate of (15-days old) *Strongylocentrotus intermedius* larvae. Symbols represent treatment mean 1 SE.

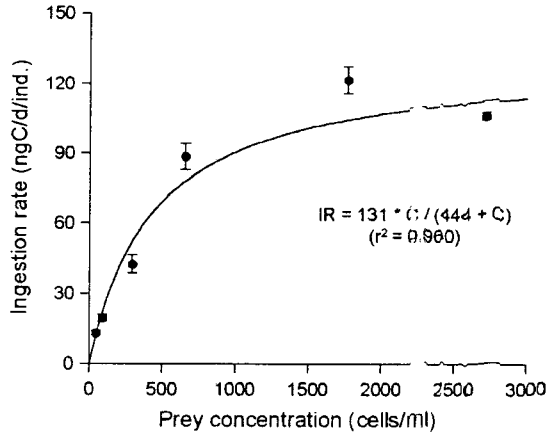

Fig. 3. Effect of unialgal concentration of *Cochlodinium polykrikoides* on ingestion rate of (15-days old) *Strongylocentrotus intermedius* larvae. Symbols represent treatment mean 1 SE. The curve was fitted by a Michaelis-Menten equation [Eq. (3)] using all treatments.

and 2,720 cells/ml ($P = 0.070$). When the data on ingestion rate were fitted to Eq. (3), the maximum ingestion rate (I_{max}) was estimated to be 131 ngC/larva /d and the algal concentration sustaining 50% of the I_{max} (K_{IR}) was 444 cells/ml.

Discussion

The 15-day old larvae of *S. intermedius* readily ingest the red-tide dinoflagellate *C. polykrikoides*. The feeding process with localized reversal of ciliary beat confirms the earlier observation of Strathmann et al. (1972). Significantly, there was no rejection of *C. polykrikoides* cells at the ciliated band and/or mouth of the larvae. Appelmans (1994) reported that the sites of algal selection in sea urchin larvae are the ciliated band, mouth, and esophagus. Selection or rejection of a food particle is related to the size, morphology, and flavor of the algae (Rassoulzadegan et al., 1984; Appelmans, 1994). According to Strathmann (1971), echinopluteus larvae can ingest particles less than 65~86㎛ in diameter and 100~200㎛ in length. The size of *C. polykrikoides* (19~22㎛ in diameter, 75~93㎛ in length: 4-celled chain) is smaller than the upper limit of prey size. Acceptance of *C. polykrikoides* by *S. intermedius* larvae at the ciliated band and mouth indicates that *C. polykrikoides* is a suitable alga for the larvae. Understandably, *C. polykrikoides* cells have no feeding deterrence to *S. intermedius*.

That *S. intermedius* larvae feed on *C. polykrikoides* is highly important from the aquaculture point of view. Though there were many reports on harmful effects of *C. polykrikoides* of fishes (e.g. Kim et al., 2000), *S. intermedius* larvae do not seem to suffer damage. However, it is still questionable whether *C. polykrikoides* is of good nutritional quality to *S. intermedius* larvae, for the efficiencies of assimilation and growth efficiency were not measured in this study. Comparative studies on the nutritional value of *C. polykrikoides* with other planktonic algae (e.g. *Pavlova* sp. and *Isochrysis* sp.) as food sources of *S. intermedius* are necessary.

Clearance rate decreased significantly with increasing algal concentration (Fig. 2), which is known

as a common trend among suspension feeders (Strathmann, 1971; Bayne et al., 1976; Rassoulzadegan and Fenaux, 1979; Rassoulzadegan et al., 1984; Fenaux et al., 1985). Reduction in clearance rate at high algal concentration may be due to increase in food availability. With abundance of alga, the larva requires less volume of water to be filtered to capture equal number of algal cells. Clearance rate (2.3~17.7$\mu\ell$/larva/hr) of *C. polykrikoides* by *S. intermedius* is within the range reported for the sea urchin larvae (Table 1). The wide inter- and intra-specific variations in clearance rate may be related to the differences in the method of measurement, kind, size, and concentrations of algal particles. Relatively high clearance rates (Strathmann, 1971; Hart, 1991; Appelmans, 1994) are estimated from film or video recording of larval feeding. Clearance rates based on changes in algal concentrations are similar to the results of this study. Therefore, clearance rate of *S. intermedius* on *C. polykrikoides* seems quite normal.

Ingestion rate rapidly increased at lower prey concentration and saturated at higher concentrations (Fig. 3). There was no inhibition at highest concentration of ca. 3000 cells/ml. However, higher concentrations of more than 3000 cells/ml of *C. polykrikoides* were frequently found in water column, when red tides occurred around the Korean coast (Kim et al., 1997). Though there is no rejection at feeding process and no inhibition in ingestion rate, it is not certain with this study alone that the high algal blooms of *C. polykrikoides* over 3000 cells/ml do not have any adverse effect on *S. intermedius* larvae.

Since there is no ingestion rate data available for the sea urchin larvae on *C. polykrikoides*, only comparison with other taxonomic groups is possible. The maximum ingestion rate (I_{max}) of *S. intermedius* on *C. polykrikoides* (131 ngC/larva/d) is higher than 69 ngC/larva/d of mussel larvae *Mytilus galloprovincialis* (Jeong et al., submitted), but lower than 234 ngC/larva/d of ciliate *Strombidinopsis* sp. (Jeong et al., 1999). This suggests that the ciliary upstream-collecting mechanism (c.f. Riisgård and Larsen, 2001) of *S. intermedius* is more effective to trap the alga than the cirral trapping of *M. galloprovincialis*, but less effective than direct engulfing of the prey by ciliary band in the mouth of *Strombidinopsis* sp.

The grazing impact by *S. intermedius* larvae on *C. polykrikoides* is difficult to assess due to inadequate data on the abundance and co-occurrence of other organisms. The natural abundance of sea urchin larvae ranges from 0 to 392 ind./m^3 (Kim, 2001), and that of *C. polykrikoides* from 920 to 8700 cells/ml (Kim et al., 1997). Assuming that the abundances and ingestion rates of the other sea urchin larvae on *C. polykrikoides* are the same as 15-days old *S. intermedius* larvae, the grazing rate is estimated as 8×10^{-5}~8×10^{-4} /d. That is 0.0008~0.008% of *C. polykrikoides* population is removed by sea urchin larvae populations per day when red tides occur. Therefore, the grazing impact of sea urchin larvae on the population of *C. polykrikoides* seems small. For better understanding the ecological role of sea urchin larvae and their interaction with dinoflagellates, more detailed field studies on the abundances of sea urchin larvae and

Table 1. Composition of clearance rates of *Strongylocentrotus intermedius* larvae measured in this study with those of other sea urchin larvae from literatures

Species	Clearance rate ($\mu\ell$/larva/hr)	Reference
Arbacia lixula	0.6~84	Rassoulzadegan and Fenaux (1979)
Dendraster excentricus	12~150	Strathmann (1971)
	0.6~18	Rassoulzadegan et al. (1984)
	60~600	Hart (1991)
	54~426	Appelmans (1994)
Paracentrotus lividus	0.06~3.6	Rassoulzadegan and Fenaux (1979)
	1.2~120	Fenaux et al. (1985)
Strongylocentrotus droebachiensis	42~408	Strathmann (1971)
Strongylocentrotus intermedius	2.3~17.7	This study

dinoflagellates, especially for spawning season, are needed.

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