

FEEDING BY LARVAE OF THE MUSSEL *MYTILUS GALLOPROVINCIALIS* ON RED-TIDE DINOFLAGELLATES

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ABSTRACT To investigate feeding by the larvae of the mussel *Mytilus galloprovincialis* on red-tide dinoflagellates, we measured grazing rates of *M. galloprovincialis* larvae as a function of larval age and prey concentration when feeding on several species of the red-tide dinoflagellates *Alexandrium affine*, *Cochlodinium polykrikoides*, *Lingulodinium polyedrum*, *Prorocentrum minimum*, *Prorocentrum micans*, and *Scrippsiella trochoidea*, as well as the flagellate *Isochrysis galbana* as a control species. The larvae were able to ingest all dinoflagellates offered in the current study; however, first feeding of the larvae on each species of the dinoflagellates occurred 9–13 days after fertilization, whereas that for *I. galbana* occurred after 5 days. Ingestion rates of the larvae on unialgal diets of the dinoflagellates and *I. galbana* increased with increasing larval age up to 17–21 days, but were saturated or showed a continuous increase thereafter. Ingestion rates of 25-day-old larvae feeding on unialgal diets of the dinoflagellates increased rapidly with increasing prey concentration up to 1000–2200 ng C mL⁻¹, but were saturated at higher prey concentrations. The harmful alga *C. polykrikoides*, which has been responsible for great losses in the aquaculture industry, was the optimal prey. Maximum ingestion and clearance rates of the larvae on these dinoflagellates were 14–69 ng C predator⁻¹ day⁻¹ and 1.5–11.4 μ L predator⁻¹ h⁻¹, respectively. *M. galloprovincialis* larvae, one component of microzooplankters, exhibited higher maximum ingestion and clearance rates than previously reported for other microzooplankters, such as *Fragilidium* cf. *mexicanum* (mixotrophic dinoflagellate), *Proto-peridinium* cf. *divergens*, *Polykrikos kofoidii* (heterotrophic dinoflagellates), or *Tiarina fusus* (small ciliate), but lower rates than *Strombidinopsis* sp. and *Favella* sp. (large ciliates). The results of the current study suggest that dinoflagellates sometimes can be primary prey for the *Mytilus* larvae, and the grazers compete with other microzooplankters for dinoflagellate prey. Also, red-tide dinoflagellates can be used for culturing the *Mytilus* larvae as prey in the aquaculture industry.

KEY WORDS: benthic–pelagic interaction, benthos, bivalve; HAB, mollusca, plankton, *Mytilus*

INTRODUCTION

Bivalves and dinoflagellates are major components of benthos and plankton in marine environments, respectively (Ruppert & Barnes 1994, Steidinger & Tangen 1997). Red tides and/or harmful algal blooms dominated by phototrophic dinoflagellates often have caused large-scale mortality of adult bivalves (e.g., ECOHAB 1995). As a consequence, there have been many studies on interactions between adult bivalves and red-tide dinoflagellates (Widows et al. 1979, Nielsen & Strømgren 1991, Shumway & Cembella 1993, Shumway et al. 1997, Matsuyama et al. 1997, Bricelj & Shumway 1998). Bivalve larvae spend a certain period after hatching as plankton and need to feed on planktonic prey. Red-tide dinoflagellates often dominate phytoplankton assemblages in coastal waters. Thus, there is a high possibility that bivalve larvae frequently encounter red-tide dinoflagellates. While there are some studies on the grazing by bivalve larvae on microflagellates and/or diatoms in the laboratory (Bayne 1965, Riisgård et al. 1980, Sprung 1984a, Sprung 1984b, Leonardos & Lucas 2000), there are a few studies on the interactions between bivalve larvae and red-tide dinoflagellates (Wikfors & Smolowitz 1995, Matsuyama et al. 2001); no data are available for bivalve larvae grazing rates as a function of red-tide dinoflagellate concentration and first feeding age for prey species.

Among bivalves, the genus *Mytilus* has a cosmopolitan distribution (e.g., Seed 1976). Some species are commercially important and cultivated at high densities in many countries (Hickman 1992). *Mytilus galloprovincialis* is a common bivalve in Europe (Moroiño et al. 1998, Tubaro et al. 1998), Asia (Matsuyama et al. 1997,

NFRDI 1999), and Oceania (Gardner 2002) and is spreading to other areas as an invasive species (McQuaid & Phillips 2000).

To investigate interactions between bivalve larvae and red-tide dinoflagellates, we established cultures of *M. galloprovincialis* larvae and conducted experiments to examine their functional response when fed a variety of red-tide dinoflagellates. Our goal was to explore the predator–prey relationship between *M. galloprovincialis* larvae and red-tide dinoflagellates by determining the larval ingestion and clearance rates as functions of prey concentration and larval age.

The maximum ingestion and clearance rates of *M. galloprovincialis* larvae on unialgal diets of red-tide dinoflagellates were compared with those of other microzooplankters (heterotrophic dinoflagellates, and ciliates), which also are potential competitors, when feeding on the same prey species. Results of the current study provide a basis for understanding the interactions between bivalve larvae and red-tide dinoflagellates.

MATERIALS AND METHODS

Culture of Phytoplankton Prey

The dinoflagellates (Table 1) which have formed red tides in many coastal waters (Eppley & Harrison 1975, Jeong 1995, Ismael 2003) were grown at 19°C in enriched *f/2* seawater media (Guillard & Ryther 1962) without silicate, under continuous illumination of 100 μ E m⁻² s⁻¹ provided by cool white fluorescent light. Only cultures in the exponential growth phase detected by cell count were used for the feeding experiments. Carbon contents for red-tide dinoflagellates were estimated from the volume of cells in batch cultures according to Strathmann (Strathmann 1967).

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TABLE 1.

Species of red-tide dinoflagellate prey and a flagellate *Isochrysis galbana* used in the current study, listed in order of cell volume.*

Species	ESD + Standard Error (μm)	Approximate Volume (μm^3)
<i>Isochrysis galbana</i> (IGKC99)	4.8 \pm 0.2	57
<i>Prorocentrum minimum</i> (PMJH99)	12.9 \pm 3.6	1100
<i>Cochlodinium polykrikoides</i> (CPKS00)	23.2 \pm 3.1	6600
<i>Alexandrium affine</i> (AAJM00)	24.0 \pm 1.1	7200
<i>Scrippsiella trochoidea</i> (STKP99)	25.1 \pm 2.8	8300
<i>Prorocentrum micans</i> (PMCJH99)	26.0 \pm 2.3	9200
<i>Lingulodinium polyedrum</i> (LPSD95)	37.9 \pm 4.5	28,500

* Mean equivalent spherical diameter (ESD) was measured by the PAMAS-SVSS particle counter. Volume was calculated according to the equation: Volume = $4/3 \pi (\text{ESD}/2)^3$. The number of cells measured, *n*, was >2000.

Preparation of M. galloprovincialis Larvae

Approximately 300 adults of the blue mussel *M. galloprovincialis* were collected from an aquafarm off Yeosu, Korea, in March 2001 when the seawater temperature was 12°C and the salinity was 33.4 psu. The shell length of the mussels ranged from 45 to 65 mm and gonads of most individuals were at late active or ripe stages. The mussels were transported to the laboratory within 6 h after collection and then acclimated to an experimental temperature (15°C) for two months. During acclimation, the mussels were maintained in two 200-L aquariums where seawater freshly filtered through 5 μm GF/F filters and air from an air pump were supplied. The microflagellate *Isochrysis galbana* (final concentration = approximately 10^3 cells mL^{-1}) was provided as prey every day. The mussels were observed daily to check their condition, and dead mussels were removed immediately after they were found.

Spawning of the mussels was induced from May to June when natural spawning usually occurs in the Korean coastal waters. Approximately 10 individuals were used for each spawning period. Before spawning, the shell surface of the mussels was scraped to remove epibionts and rinsed with freshly filtered seawater. To

induce spawning, the mussels were exposed to air for 1 h, put back into a 10-L aquarium filled with freshly filtered seawater, and then the water temperature was increased gradually to 25°C. Most of these mussels released sperm and eggs within 30 min after the water temperature reached 25°C. As soon as any male first released sperm, the other males were removed to avoid possible polyspermy. One hour after spawning, all mussels were removed, and then aliquots of the water in the aquarium were taken to determine the fertilization rate. During the current study, we induced spawning 10 times, and the fertilization rates were always >95%. The mean diameter of the fertilized eggs was approximately 60 μm . The egg suspension was passed through a 100- μm mesh screen to remove fecal material and other large particles, and a 35- μm mesh screen was used to collect fertilized eggs without excessive numbers of sperm and smaller eggs. The eggs were rinsed three times with 5- μm filtered and autoclaved seawater and were then incubated in a 20-L aquarium at 15°C in darkness without aeration. After 1-day incubation, most eggs had developed to the trochophore larval stage. From the first day after fertilization, *Isochrysis galbana* (final concentration = approximately 5×10^3 cells mL^{-1}) was provided to larvae as prey every day. Incubation water was wholly renewed every day.

Ingestion Rates as a Function of Larval Age

Experiments 1 to 7 were designed to measure ingestion and clearance rates of *M. galloprovincialis* larvae as a function of the larval age (elapsed time after fertilization), when feeding on unialgal diets of 6 red-tide dinoflagellate species and *Isochrysis galbana* as a control species (Table 2). Feeding experiments were conducted when larvae were 1, 5, 9, 13, 17, 21, and 25 days old, because settlement of the larvae had started when they were 27 days old.

One day before these experiments were conducted, cultures of *M. galloprovincialis* larvae unfed (for the 1-day-old larvae) or growing on *Isochrysis galbana* (for the other aged larvae) were sieved through meshes of 80–150 μm , and the larvae retained were transferred into 1-L polycarbonate (PC) bottles. The bottles were filled to capacity with filtered seawater and placed on plankton wheels rotating at 0.9 rpm and incubated at 15°C under continuous

TABLE 2.

Experimental design: Values in prey and predator columns represent actual initial densities (cells mL^{-1} for prey and individuals mL^{-1} for predator) followed by calculated carbon biomass (ng C mL^{-1}) in parentheses.

Experiment No.	Prey		Predator
	Species	Density	Density
1	<i>Isochrysis galbana</i>	72,100–84,067 (865–1009)	3–7
2	<i>Prorocentrum minimum</i>	7227–9976 (1084–1496)	4–9
3	<i>Cochlodinium polykrikoides</i>	1532–1883 (1072–1318)	3–9
4	<i>Alexandrium affine</i>	1103–1560 (838–1185)	4–9
5	<i>Scrippsiella trochoidea</i>	1245–1667 (1058–1417)	3–8
6	<i>Prorocentrum micans</i>	947–1363 (890–1223)	3–5
7	<i>Lingulodinium polyedrum</i>	439–582 (1098–1455)	4–9
8	<i>Prorocentrum minimum</i>	255 (38), 723 (108), 1443 (216), 7638 (1146), 15483 (2322), 32288 (4843)	1–5
9	<i>Cochlodinium polykrikoides</i>	27 (19), 151 (106), 298 (208), 1492 (1044), 3120 (2184), 4147 (5925)	1–5
10	<i>Alexandrium affine</i>	33 (25), 130 (99), 266 (202), 1354 (1029), 2178 (1655), 4423 (3362)	1–7
11	<i>Scrippsiella trochoidea</i>	20 (17), 113 (96), 224 (191), 1126 (957), 2433 (2068), 4930 (4191)	1–7
12	<i>Prorocentrum micans</i>	24 (23), 108 (102), 236 (221), 1159 (1089), 2249 (2114), 4703 (4420)	1–4
13	<i>Lingulodinium polyedrum</i>	10 (25), 43 (107), 93 (234), 417 (1041), 819 (2048), 1629 (4072)	1–4

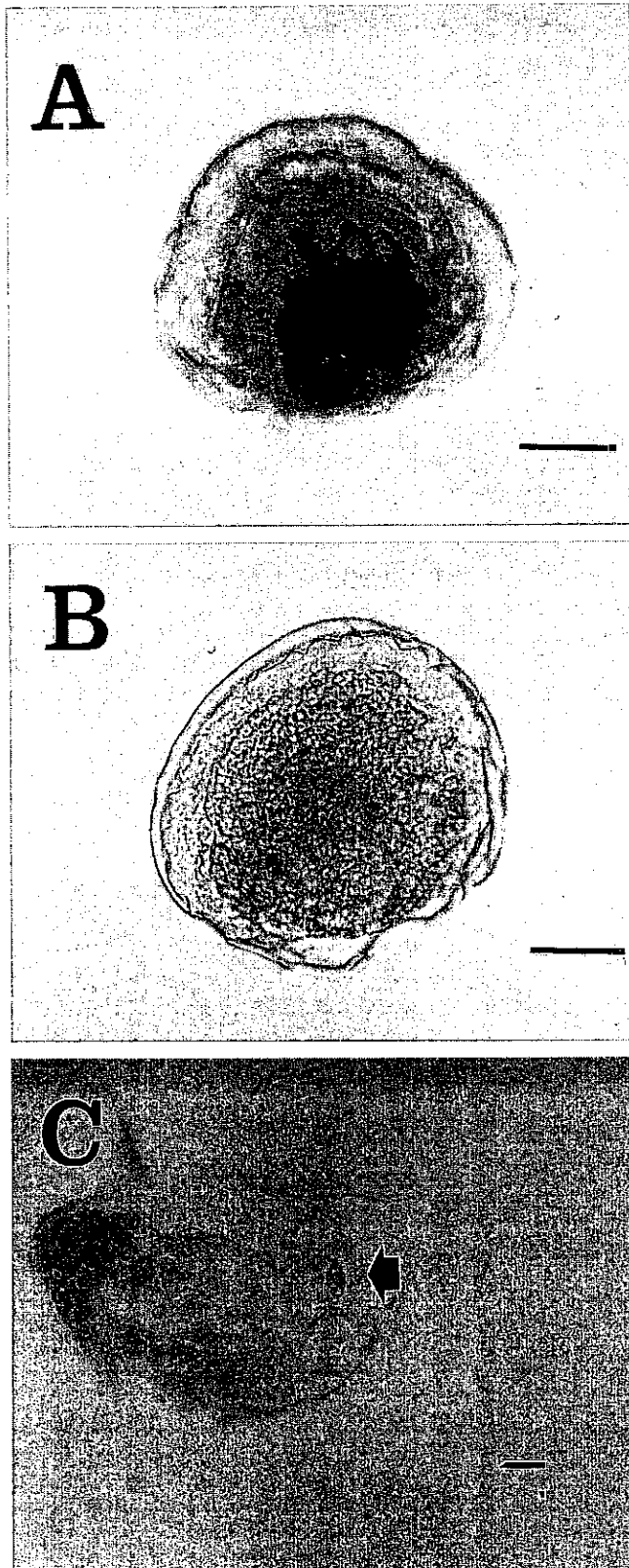


Figure 1. *Mytilus galloprovincialis* larva fed (A) and unfed (B) red-tide dinoflagellates. An undigested *Prorocentrum micans* cell (arrow) from the crushed stomach of a larva (C). Scale bars are 50 μm in (A & B) and 20 μm in (C).

illumination of $50 \mu\text{E m}^{-2} \text{s}^{-1}$ from cool white fluorescent light. One day later, prey inside the stomach of the larvae was almost digested and indiscernible by microscope examination. The abundance of *M. galloprovincialis* larvae was determined by enumerating larvae in three 1-mL Sedgwick-Rafter counting chambers (hereafter SRCs).

Initial densities of *M. galloprovincialis* larvae and target prey were established using an autopipette to deliver predetermined volumes of known densities to the bottles. Triplicate 270-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 *M. galloprovincialis* larvae also were established. Thirty milliliters of f/2 medium were added to each bottle. Each bottle then was filled to capacity with freshly filtered seawater and capped. The bottles were placed on plankton wheels under the environmental conditions described above. To determine actual predator and prey densities at the beginning of the experiment, and after 24, 48, and 72 h incubation, 10-mL aliquots were removed from each bottle and fixed with 5% Lugol's solution, and all larvae and all or >200 prey cells in three 1-mL SRCs were enumerated. Prior to taking subsamples, the condition of *M. galloprovincialis* larvae and prey was assessed by looking through the surface of each capped bottle using a dissecting microscope. The bottles were filled again to capacity with freshly filtered seawater, capped, and placed on plankton wheels as described above. Dilution of the cultures associated with refilling the bottles was considered in calculating ingestion rates.

Ingestion and clearance rates of *M. galloprovincialis* larvae on RTDs were calculated using the equations of Frost (1972). The incubation time for calculating ingestion and clearance rates was 48 h.

To examine the occurrence of ingestion by *M. galloprovincialis* larvae on each prey species, 2-mL aliquots from each experimental and control bottle, preserved with Lugol's solution after 48 h incubation, were transferred into wells of 12-well plate chambers. Subsequently, 0.3 mL thiosulfate ($\text{Na}_2\text{S}_2\text{O}_3$) of a 10^5 mg L^{-1} con-

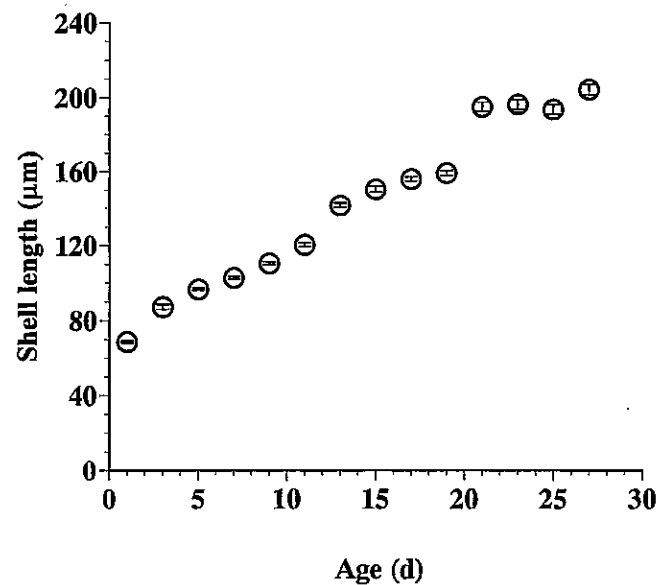


Figure 2. Shell length of *Mytilus galloprovincialis* larvae used for Experiments 1 to 7 as a function of larval age. Symbols represent treatment means ± 1 SE. $n = 37\text{--}403$ for each larval age.

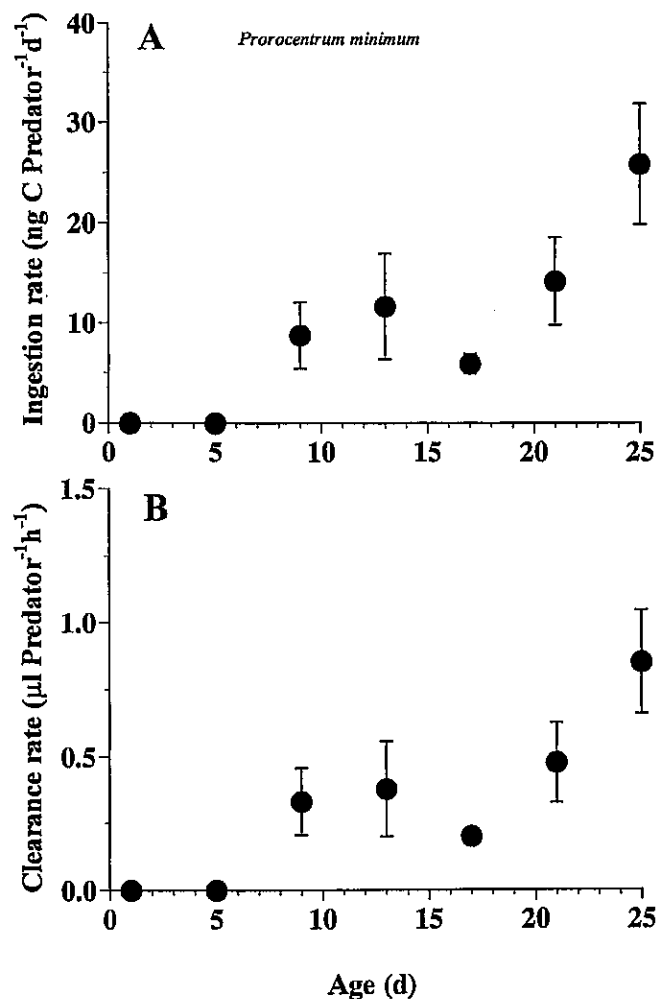


Figure 3. Ingestion (A) and clearance rates (B) of *Mytilus galloprovincialis* larvae on *Prorocentrum minimum* as a function of larval age. Symbols represent treatment means \pm 1 SE.

centration was added into each well to decolorize. One day later, the stomachs of the larvae were examined at 40–200 \times using Olympus compound and dissecting microscopes, and photographs were taken. Also, to find any undigested prey cells inside the stomachs of the larvae, approximately 20 *M. galloprovincialis* larvae fed on *Prorocentrum micans* were rinsed and carefully crushed using a very thin needle. We chose *P. micans* because it has an easily discernible shape. Photographs of the contents from the stomach were taken.

The shell lengths of *M. galloprovincialis* larvae at the beginning of each experiment and after 48 h incubation were measured using an image analyzing system; each individual larva was observed at a magnification of 20 \times , and its image was recorded using a Toshiba Model IK-642K CCD camera attached to a stereo-zoom microscope (Nikon, SMZ-U). Measurements of the shell length (the distance between the anterior and posterior ends of a shell) were conducted using the UTHSCSA Image Tool program. The shell lengths of 30 larvae at each age were measured.

Ingestion Rates as a Function of Prey Concentration

Experiments 8 to 13 were designed to measure ingestion and clearance rates of 25-day-old *M. galloprovincialis* larvae, as a

function of prey concentration, when feeding on unialgal diets of the red-tide dinoflagellates (Table 2).

The procedures for setting-up experiments, measuring predator and prey densities, and calculating ingestion and clearance rates were the same as described above, except that 80-mL PC bottles were used, 10 mL of *f/2* medium were added into each bottle, and 5-mL aliquots were removed from each bottle and fixed with 5% Lugol's solution.

Ingestion rate data were fitted to a Michaelis–Menten equation:

$$IR = I_{max}(x)/[K_{IR} + (x)] \quad (1)$$

where I_{max} = the maximum ingestion rate (cells predator⁻¹ day⁻¹ or ng C predator⁻¹ day⁻¹); x = prey concentration (cells mL⁻¹ or ng C mL⁻¹), and K_{IR} = the prey concentration sustaining $\frac{1}{2} I_{max}$.

RESULTS

Feeding and Shell Length of *Mytilus* Larvae

M. galloprovincialis larvae were able to ingest all red-tide dinoflagellates offered in the current study. The larvae fed on RTD in feeding currents produced by the ciliated velum. The stomach areas of *M. galloprovincialis* fed red-tide dinoflagellates were 20–

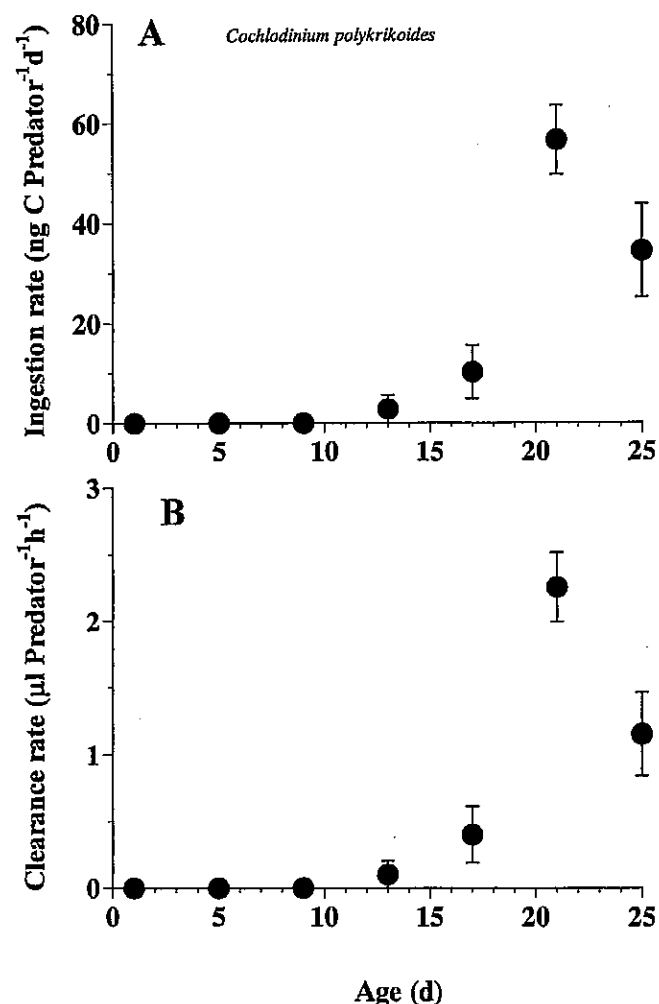


Figure 4. Ingestion (A) and clearance rates (B) of *Mytilus galloprovincialis* larvae on *Cochlodinium polykrikoides* as a function of larval age. Symbols represent treatment means \pm 1 SE.

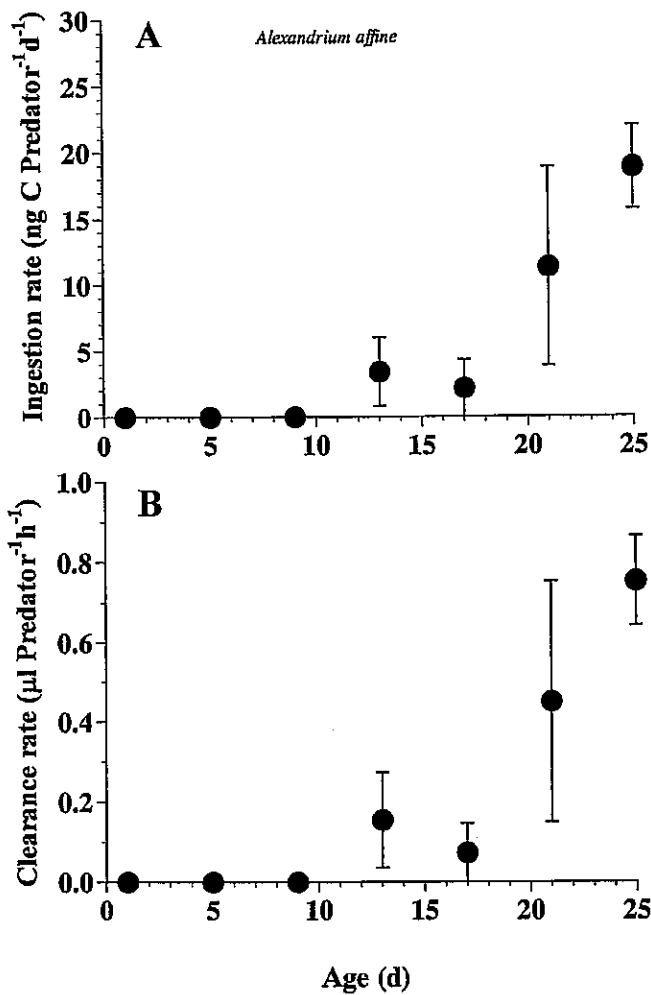


Figure 5. Ingestion (A) and clearance rates (B) of *Mytilus galloprovincialis* larvae on *Alexandrium affine* as a function of larval age. Symbols represent treatment means ± 1 SE.

30% larger than those starved in the control bottles, and the color of the stomachs of fed larvae became dark brown, whereas that of unfed larvae was almost transparent (Figs. 1A and 1B). Undigested *Prorocentrum micans* cells from the crushed stomachs of the larvae also ascertained the ingestion of the prey species (Fig. 1C).

With increasing larval age (elapsed time after fertilization), the mean shell length of *M. galloprovincialis* larvae almost linearly increased from 69 to 204 μm (Fig. 2).

Ingestion and Clearance Rates as a Function of Larval Age

The first feeding by *M. galloprovincialis* larvae on each red-tide dinoflagellate species occurred when the larvae were approximately 9–13 days old (Figs. 3–8); whereas that for *Isochrysis galbana* occurred at the larval age of 5 days (Fig. 9).

The ingestion rates of *M. galloprovincialis* larvae on *P. minimum* were undetectable when the larvae were 1–5 days old. However, they increased to 6–14 ng C predator⁻¹ day⁻¹ at the larval age of 9–21 days and reached 26 at 25 days (Fig. 3A). The clearance rates were 0.2–0.5 $\mu\text{L predator}^{-1} \text{h}^{-1}$ at the age of 9–21 days and reached 0.9 at 25 days (Fig. 3B).

The ingestion rates of *M. galloprovincialis* larvae on *Cochlodinium polykrikoides* were undetectable or very low when the larvae were 1–13 days old, but they rapidly increased to 34–56 ng C predator⁻¹ day⁻¹ at the larval age of 21–25 days (Fig. 4A). The clearance rates also were undetectable or very low at the larval age of 1–13 days, but increased to 1.3–2.3 $\mu\text{L predator}^{-1} \text{h}^{-1}$ at the larval age of 21–25 days (Fig. 4B).

The ingestion rates of *M. galloprovincialis* larvae on *Alexandrium affine* were undetectable or very low when the larvae were 1–17 days old, but they rapidly increased to 19 ng C predator⁻¹ day⁻¹ at the age of 25 days (Fig. 5A). The clearance rates also were undetectable or very low at the larval age of 1–17 days, but increased to 0.8 $\mu\text{L predator}^{-1} \text{h}^{-1}$ at the larval age of 25 days (Fig. 5B).

The ingestion rates of *M. galloprovincialis* larvae on *Scrippsiella trochoidea* were undetectable or very low when the larvae were 1–13 days old, but they increased rapidly to 19–20 ng C predator⁻¹ day⁻¹ at the age of 21–25 days (Fig. 6A). The clearance rates also were undetectable or very low at the larval age of 1–13 days, but increased to 0.3–0.7 $\mu\text{L predator}^{-1} \text{h}^{-1}$ at the larval age of 21–25 days (Fig. 6B).

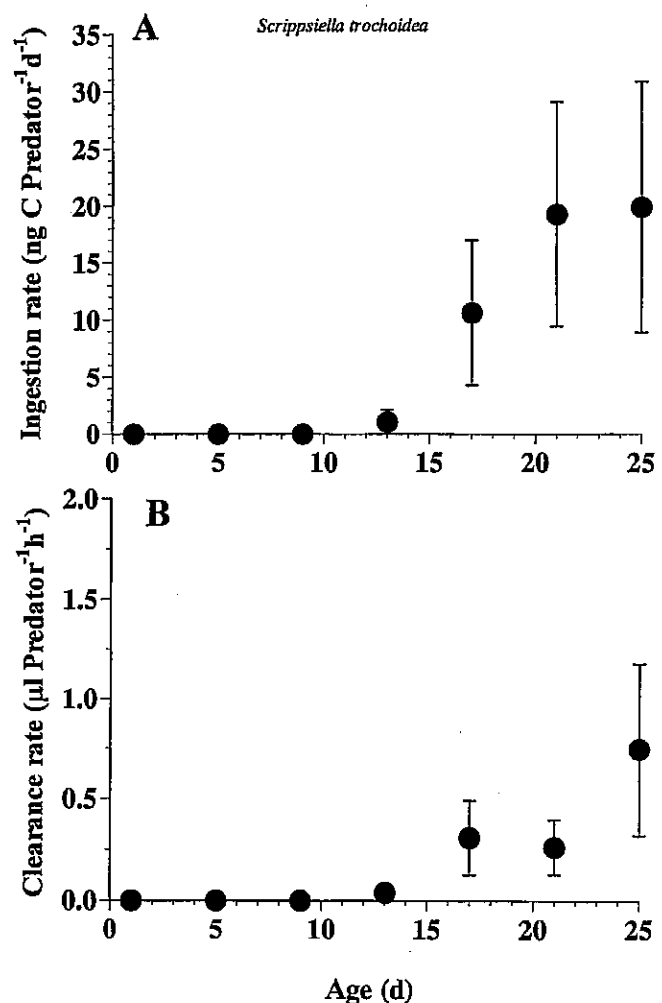


Figure 6. Ingestion (A) and clearance rates (B) of *Mytilus galloprovincialis* larvae on *Scrippsiella trochoidea* as a function of larval age. Symbols represent treatment means ± 1 SE.

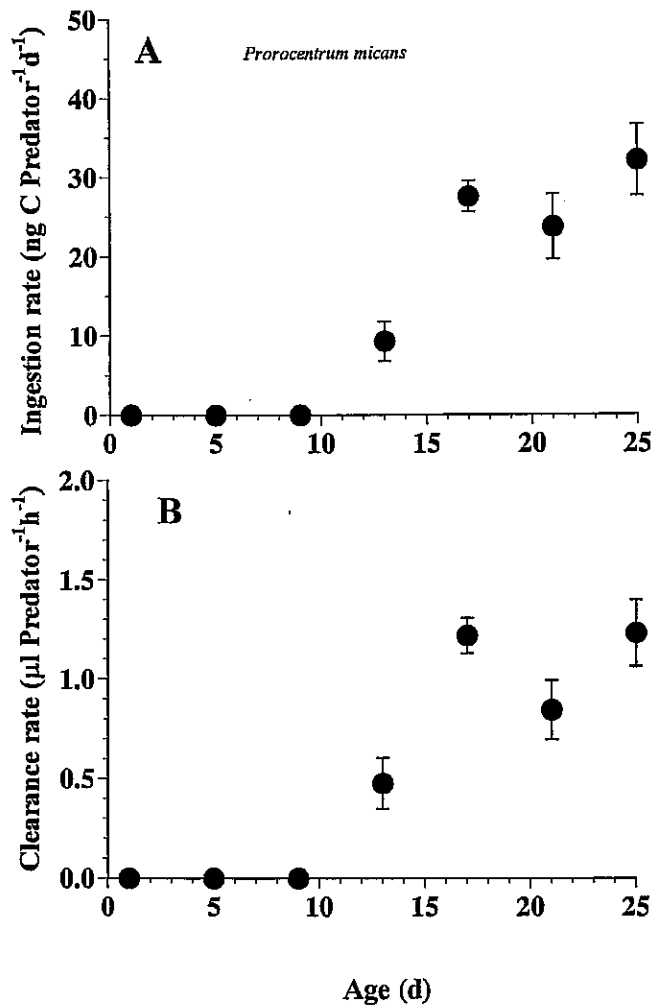


Figure 7. Ingestion (A) and clearance rates (B) of *Mytilus galloprovincialis* larvae on *Prorocentrum micans* as a function of larval age. Symbols represent treatment means \pm 1 SE.

The ingestion rates of *M. galloprovincialis* larvae on *Prorocentrum micans* were undetectable when the larvae were 1–9 days old, but they increased rapidly to 27–32 ng C predator⁻¹ day⁻¹ at the age of 17–25 days (Fig. 7A). The clearance rates were also undetectable or very low at the larval age of 1–9 days, but increased to 0.8–1.2 μ L predator⁻¹ h⁻¹ at the larval age of 17–25 days (Fig. 7B).

The ingestion rates of *M. galloprovincialis* larvae on *Lingulodinium polyedrum* were undetectable when the larvae were 1–9 days old, but they were 10–11 ng C predator⁻¹ day⁻¹ at the age of 13–21 days (Fig. 8A). The rates reached a maximum of 27 ng C predator⁻¹ day⁻¹ at the age of 25 days. The clearance rates were also undetectable when the larvae were 1–9 days old, but they were 0.1–0.4 μ L predator⁻¹ h⁻¹ at the age of 13–21 days (Fig. 8B). The rate reached a maximum of 1.1 μ L predator⁻¹ h⁻¹ at the age of 25 days.

The ingestion rates of *M. galloprovincialis* larvae on *Isochrysis galbana* were undetectable when the larvae were 1 day old, but they were 19–32 ng C predator⁻¹ day⁻¹ at the age of 5–17 days (Fig. 9A). The rates reached maximum of 111 ng C predator⁻¹ day⁻¹ at the age of 21 days. The clearance rates were also undetectable when the larvae were 1 day old, but they were 1.0–1.7 μ L preda-

tor⁻¹ h⁻¹ at the age of 5–17 days (Fig. 9B). The rate reached a maximum of 7.8 μ L predator⁻¹ h⁻¹ at the age of 25 days.

No dead *M. galloprovincialis* larvae were found upon examination with a dissecting microscope prior to taking subsamples in these experiments.

Ingestion and Clearance Rates as a Function of Prey Concentration

In Experiments 8 to 13, the ingestion rates of 25-day-old *M. galloprovincialis* larvae on unialgal diets of *P. minimum*, *C. polykrikoides*, *A. affine*, *S. trochoidea*, *P. micans*, and *L. polyedrum* increased rapidly with increasing prey concentration up to 1000–2200 ng C mL⁻¹, but were almost saturated at higher prey concentration (Figs. 10–15). When the data were fitted to Eq. 1, the maximum ingestion rates of *M. galloprovincialis* larvae in ng C predator⁻¹ day⁻¹ and (prey cells predator⁻¹ day⁻¹) were 69 (99) for *C. polykrikoides*, 56 (60) for *P. micans*, 45 (18) for *L. polyedrum*, 26 (173) for *P. minimum*, 21 (25) for *S. trochoidea*, and 14 (18) for *A. affine* (Table 3). Maximum clearance rates of *M. galloprovincialis* larvae were 11.4 μ L predator⁻¹ h⁻¹ for *L. polyedrum*, 8.4 for *P. micans*, 3.8 for *A. affine*, 3.5 for *S. trochoidea*, 2.8 for *C. polykrikoides*, and 1.5 for *P. minimum*.

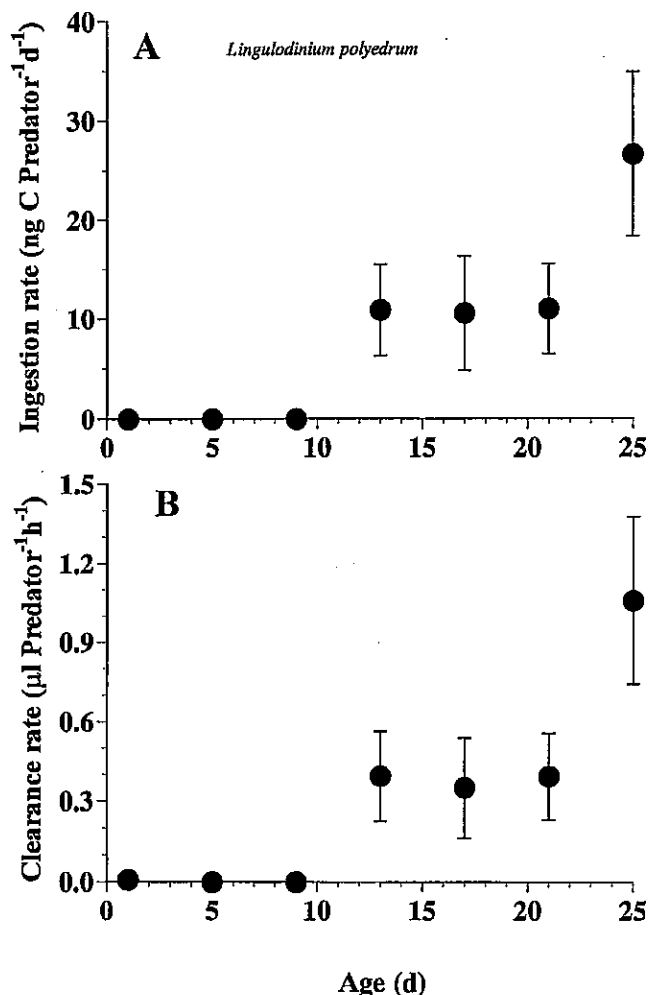


Figure 8. Ingestion (A) and clearance rates (B) of *Mytilus galloprovincialis* larvae on *Lingulodinium polyedrum* as a function of larval age. Symbols represent treatment means \pm 1 SE.

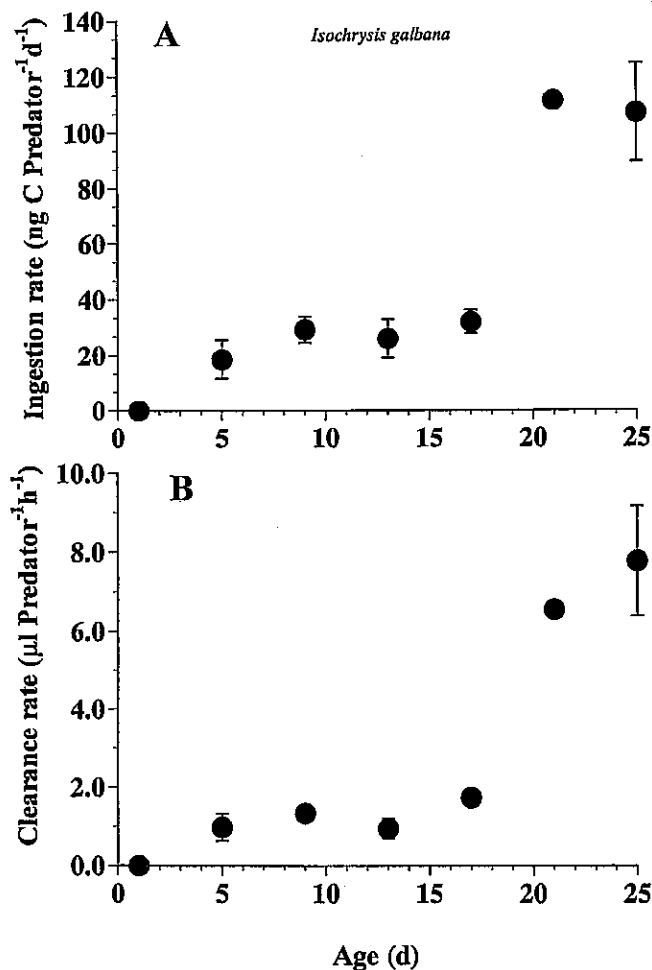


Figure 9. Ingestion (A) and clearance rates (B) of *Mytilus galloprovincialis* larvae on *Isochrysis galbana* as a function of larval age. Symbols represent treatment means \pm 1 SE.

DISCUSSION

Prey Species and Feeding Rates as a Function of Larval Age

There has been no report on the feeding by larvae in the genus *Mytilus* on red-tide dinoflagellates. *M. galloprovincialis* larvae were able to feed on all red-tide dinoflagellate prey offered in the current study. Thus, *M. galloprovincialis* larvae have diverse prey species. In the phylum mollusca, larvae of the oyster *Crassostrea virginica* have been shown to feed on the dinoflagellate *P. minimum* (Wikfors & Smolowitz, 1995), and larvae of the gastropod *Philine aperta* feed on the dinoflagellates *Heterocapsa triquetra* and *Scrippsiella faroense* (Hansen 1991). Further studies on feeding by other molluscan larvae on diverse red-tide dinoflagellates are necessary to better understand their interactions.

Mytilus edulis larvae have been known to ingest particles of 1–9 μm (Riisgård et al. 1980, Sprung 1984b). However, *M. galloprovincialis* larvae are able to ingest red-tide dinoflagellates whose ESDs are 12–38 μm (Table 1). The change in color of the stomachs of the larvae and undigested prey cells found in the crushed stomachs indicated their ingestion (Fig. 1). The mouths of the larvae may be very flexible for ingesting large prey cells or different species in the genus *Mytilus* may have different prey size limitations.

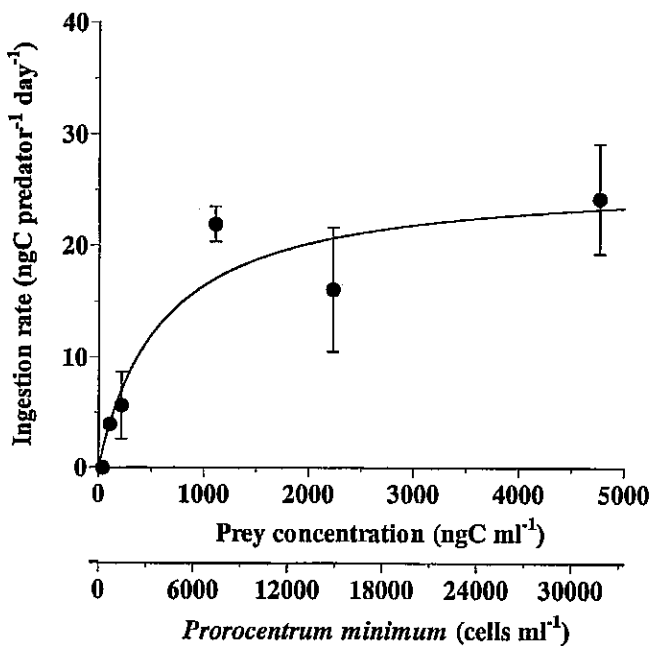


Figure 10. Ingestion rates of 25-day-old *Mytilus galloprovincialis* larvae on *Prorocentrum minimum* as a function of mean prey concentration. Symbols represent treatment means \pm 1 SE. The curves are fitted by a Michaelis-Menten equation (Eq. 1) using all treatments (see Table 3).

The first feeding by *M. galloprovincialis* larvae on each red-tide dinoflagellate species occurred when the larvae were approximately 9–13 days old (Figs. 3–8), whereas that for *I. galbana* occurred at the larval age of 5 days (Fig. 9). Much larger size of red-tide dinoflagellates might delay the larval first feeding.

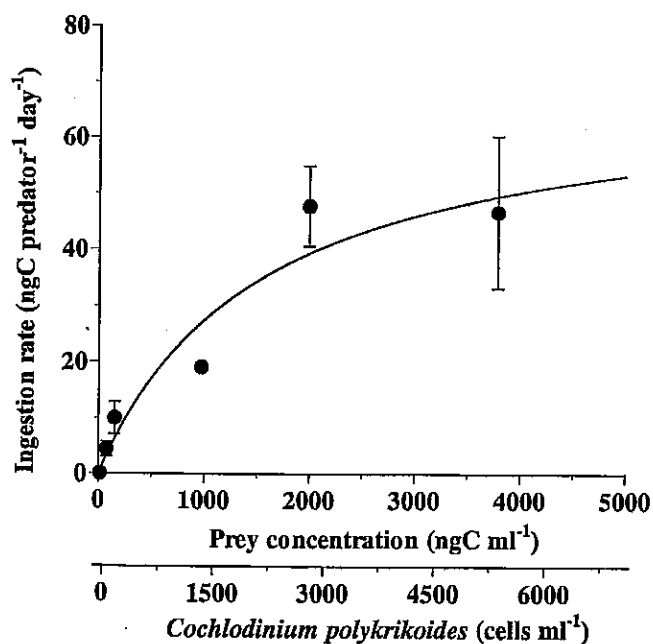


Figure 11. Ingestion rates of 25-day-old *Mytilus galloprovincialis* larvae on *Cochlodinium polykrikoides* as a function of mean prey concentration. Symbols represent treatment means \pm 1 SE. The curves are fitted as in Fig. 10.

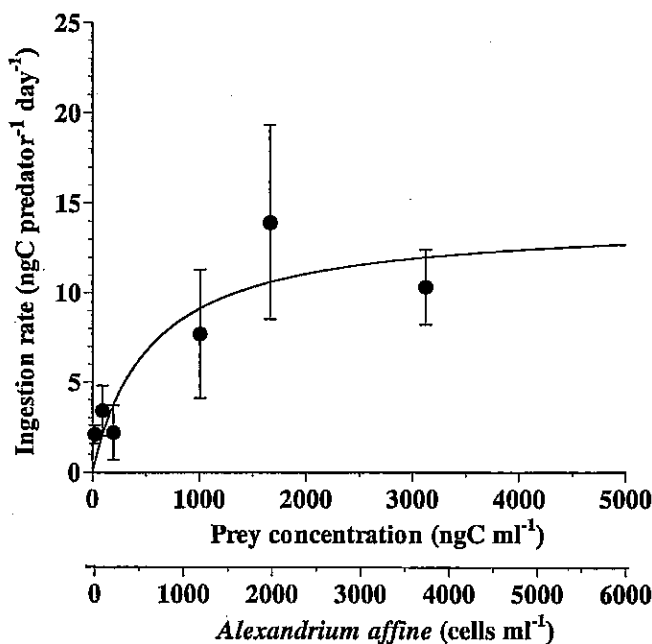


Figure 12. Ingestion rates of 25-day-old *Mytilus galloprovincialis* larvae on *Alexandrium affine* as a function of mean prey concentration. Symbols represent treatment means \pm 1 SE. The curves are fitted as in Fig. 10.

The ingestion and clearance rates of *M. galloprovincialis* larvae on red-tide dinoflagellates at the larval ages of 21–25 days (14–56 ng C predator⁻¹ day⁻¹ and 0.5–2.3 μ L predator⁻¹ h⁻¹, respectively) measured in Experiments 1 to 7 were lower than those on *I. galbana* (107–111 ng C predator⁻¹ day⁻¹ and 6.5–7.8 μ L predator⁻¹ h⁻¹) (Figs. 3–9). Therefore, red-tide dinoflagellates are less preferred prey for *M. galloprovincialis* larvae than *I. galbana*.

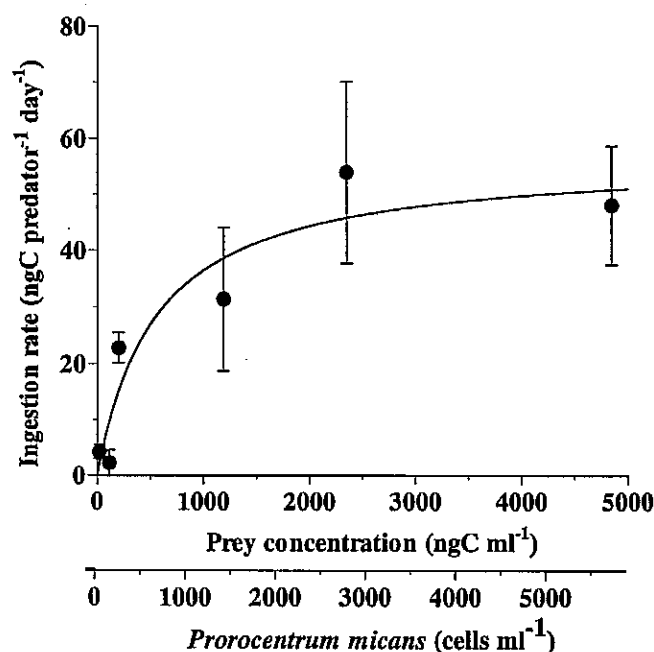


Figure 13. Ingestion rates of 25-day-old *Mytilus galloprovincialis* larvae on *Scrippsiella trochoidea* as a function of mean prey concentration. Symbols represent treatment means \pm 1 SE. The curves are fitted as in Fig. 10.

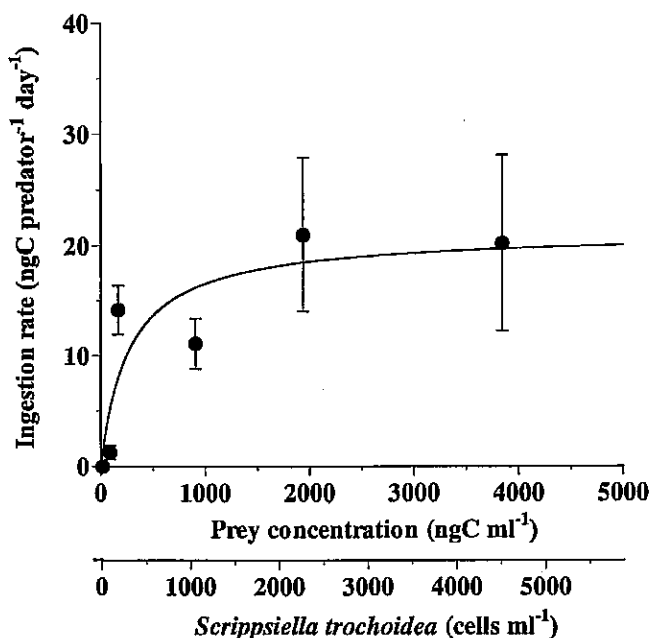


Figure 14. Ingestion rates of 25-day-old *Mytilus galloprovincialis* larvae on *Prorocentrum micans* as a function of mean prey concentration. Symbols represent treatment means \pm 1 SE. The curves are fitted as in Fig. 10.

Ingestion and Clearance

Data from this study show that the maximum ingestion rates of 25-day-old *M. galloprovincialis* larvae on each red-tide dinoflagellate species measured in Experiments 8 to 13 are poorly correlated with prey cell volume (Fig. 16). This relationship suggests that prey cell volume does not have an affect on ingestion by the larvae

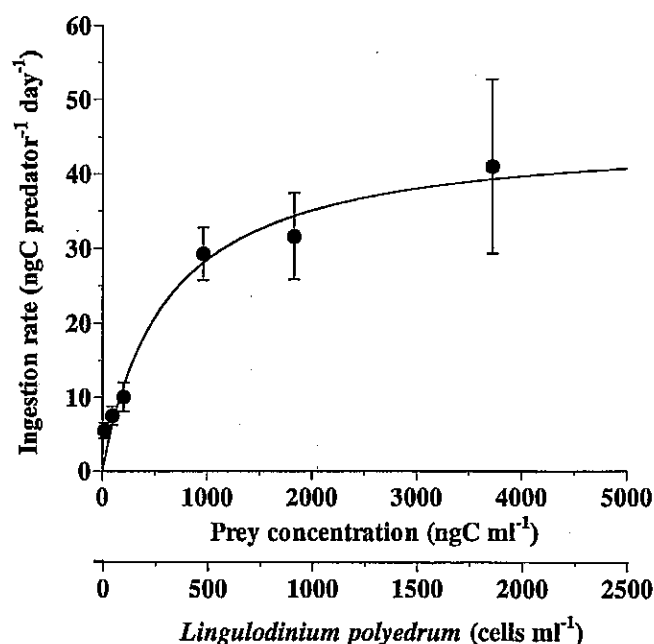


Figure 15. Ingestion rates of 25-day-old *Mytilus galloprovincialis* larvae on *Lingulodinium polyedrum* as a function of mean prey concentration. Symbols represent treatment means \pm 1 SE. The curves are fitted as in Fig. 10.

TABLE 3.
 Grazing data for *Mytilus galloprovincialis* larvae.*

Figures	Species	I_{max}	K_{IR}	r^2
10	<i>Prorocentrum minimum</i>	26	577	0.72
11	<i>Cochlodinium polykrioides</i>	69	1510	0.73
12	<i>Alexandrium affine</i>	14	539	0.48
13	<i>Scrippsiella trochoidea</i>	21	269	0.50
14	<i>Prorocentrum micans</i>	56	538	0.61
15	<i>Lingulodinium polyedrum</i>	45	590	0.73

* Parameters are for functional response from Eq. 1 as presented in Figs. 10–15. I_{max} (maximum ingestion rate, ng C predator⁻¹ day⁻¹), K_{IR} (prey concentration sustaining 0.5 I_{max} , ng C mL⁻¹).

of red-tide dinoflagellates. Thus, factors other than prey cell volume may be important to the feeding activity of the larvae. Maximum ingestion rates of the larvae on *C. polykrioides* and *P. micans* were much higher than those for *S. trochoidea* and *A. affine*, even though these prey species are similar in cell volume. However, these results are difficult to interpret. The C:N ratios of *C. polykrioides* (7.7) and *P. micans* (8.7) are similar to or higher than those for *S. trochoidea* (5.6) and *A. affine* (8.4) (Jeong et al., unpublished data). Thus, nutritional values of prey species may not be responsible for these different maximum ingestion rates. Trochophore larvae of the oyster *Crassostrea gigas* 17 h after fertilization have been shown to be killed when exposed to toxic dinoflagellates (Matsuyama et al. 2001). However, *S. trochoidea* and *A. affine* are nontoxic dinoflagellates (our data). Regarding cell shape, *C. polykrioides* and *P. micans* cells are compressed, whereas *S. trochoidea* and *A. affine* are spherical. Therefore, the compressed cells may be easier for the larvae to ingest than the spherical cells. However, to determine the exact cause of this pattern, further study is necessary.

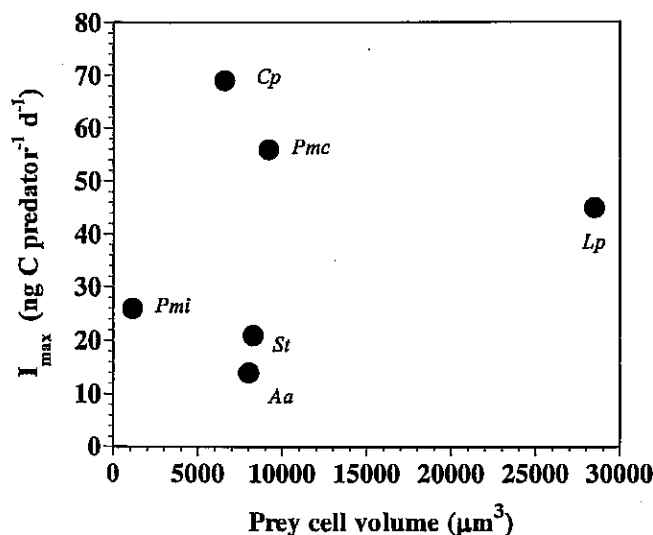


Figure 16. Maximum ingestion rates (I_{max}) of 25-day-old *Mytilus galloprovincialis* larvae on 6 red-tide dinoflagellate species as a function of prey cell volume. Aa: *Alexandrium affine*, Cp: *Cochlodinium polykrioides*, Lp: *Lingulodinium polyedrum*, Pmc: *Prorocentrum micans*, Pmi: *Prorocentrum minimum*, and St: *Scrippsiella trochoidea*.

The maximum ingestion (I_{max}) and clearance rates (C_{max}) of 25-day-old *M. galloprovincialis* larvae on red-tide dinoflagellates obtained in this study (69 ng C predator⁻¹ day⁻¹ and 11.4 μL predator⁻¹ h⁻¹, respectively) are comparable to or lower than those for *M. edulis* larvae on microflagellates (37–160 ng C predator⁻¹ day⁻¹ and 11–88 μL predator⁻¹ h⁻¹, respectively) (Bayne 1965, Riisgård et al. 1980, Riisgård et al. 1981, Jespersen & Olsen 1982, Sprung 1984b), when corrected to 15°C using $Q_{10} = 3.4$ (Hansen et al. 1997). The smaller size of *M. galloprovincialis* larvae (193 μm) with respect to *M. edulis* larvae (250) might be responsible for the former predator's lower C_{max} .

The I_{max} and C_{max} of 25-day-old *M. galloprovincialis* larvae on each red-tide dinoflagellate species are higher than those previously reported for a mixotrophic dinoflagellate, heterotrophic dinoflagellates, or a small ciliate, but much lower than those for large ciliates on the same prey (Table 4). For example, the I_{max} of *M. galloprovincialis* larvae on *Lingulodinium polyedrum* obtained in this study (45 ng C predator⁻¹ day⁻¹) is higher than those of *Polykrikos kofoidii* (16 ng C predator⁻¹ day⁻¹), *Tiarina fusus* (15), *Protoperidinium cf. divergens* (8), *Fragilidium cf. mexicanum* (5), and *Protoperidinium crassipes* (3), but much lower than that of *Strombidinopsis* sp. (147 ng C predator⁻¹ day⁻¹), when corrected to 15°C using $Q_{10} = 2.8$ (Hansen et al. 1997). The C_{max} of *M. galloprovincialis* larvae on *L. polyedrum* (11.4 μL predator⁻¹ h⁻¹) is also higher than those of *P. kofoidii* (3.9), *T. fusus* (3.0), *F. cf. mexicanum* (2.6), *P. cf. divergens* (0.5), and *P. crassipes* (0.3), but much lower than that of *Strombidinopsis* sp. (73). This pattern is maintained in *S. trochoidea*, *C. polykrioides*, *P. minimum*, and *P. mican* prey. This evidence suggests that engulfing prey in the feeding current produced by the ciliated velum near the mouth (*Mytilus* larvae) is a more effective feeding mechanism than engulfing prey captured by a tow filament (*Polykrikos* spp.) or palium feeding on prey captured by a tow filament (*Protoperidinium* spp.), but less effective than engulfing prey using rows of cilia in the mouth (*Strombidinopsis* spp. and *Favella* spp.).

Ecological Importance

In the current study, *M. galloprovincialis* larvae fed on red-tide dinoflagellates without mortality after 72 h exposure to considerable high prey concentrations. Thus, the larvae are able to survive during and/or after red tides dominated by these dinoflagellates. Also, dinoflagellates are one of the most abundant phytoplankters in coastal waters, and thus the bivalve larvae may develop healthily by feeding on commonly distributed dinoflagellates. *M. galloprovincialis* larvae, one component of microzooplankters, exhibited higher maximum ingestion and clearance rates than previously reported for other microzooplankters such as the *Fragilidium cf. mexicanum* (mixotrophic dinoflagellate), the *Protoperidinium cf. divergens*, *Polykrikos kofoidii* (heterotrophic dinoflagellates), or *Tiarina fusus* (small ciliate), but lower rates than *Strombidinopsis* spp. and *Favella* spp. (large ciliates) when fed the same prey species. Thus, *Mytilus* larvae may compete with some microzooplankters for dinoflagellate prey.

ACKNOWLEDGMENTS

The authors thank Kwang Young Kim, Jae Seong Kim, Yeong Du Yoo, and Kyeong A Seong for technical support. This paper was funded by grants from MOST & KOSEF (R12-1999-027-12000-0) and from MOST & KISTEP (M1-0302-00-0068).

TABLE 4.

Comparison of ingestion and clearance rates of *Mytilus galloprovincialis* larvae and protistan predators on the same red-tide algal prey.*

Prey Species	Predator	PV	I_{max}	C_{max}	Reference
<i>Lingulodinium polyedrum</i>	<i>Mytilus galloprovincialis</i> larvae (ML)	4240	45	11.4	This study
	<i>Tiarina fusu</i> (NC)	23	15	3.0	Jeong et al. (2002)
	<i>Polykrikokos kofoidii</i> (HD)	43	16	3.9	Jeong et al. (2001)
	<i>Proto-peridinium</i> cf. <i>divergens</i> (HD)	119	8	0.5	Jeong and Latz (1994)
	<i>Proto-peridinium crassipes</i> (HD)	204	3	0.3	Jeong and Latz (1994)
	<i>Fragilidium</i> cf. <i>mexicanum</i> (MD)	85	5	2.6	Jeong et al. (1999a)
<i>Scrippsiella trochoidea</i>	<i>Strombidinopsis</i> spp. (NC)	560	147	72.9	Jeong et al. (1999b)
	<i>Mytilus galloprovincialis</i> larvae (ML)	4240	21	3.5	This study
	<i>Tiarina fusus</i> (NC)	23	7	0.1	Jeong et al. (2002)
	<i>Polykrikokos kofoidii</i> (HD)	43	11	0.7	Jeong et al. (2001)
	<i>Strombidinopsis</i> spp. (NC)	560	137	27.2	Jeong et al. (1999b)
	<i>Favella</i> spp. (TC)	157	157	28.5	Stoecker et al. (1981)
<i>Cochlodinium polykrikoides</i>	<i>Mytilus galloprovincialis</i> larvae (ML)	4240	69	2.8	This study
	<i>Strombidinopsis</i> spp. (NC)	560	234	33.0	Jeong et al. (1999b)
<i>Prorocentrum minimum</i>	<i>Mytilus galloprovincialis</i> larvae (ML)	4240	26	7.2	This study
	<i>Strombidinopsis</i> spp. (NC)	560	177	73.0	Jeong et al. (1999b)
<i>Prorocentrum micans</i>	<i>Mytilus galloprovincialis</i> larvae (ML)	4240	26	7.2	This study
	<i>Polykrikokos kofoidii</i> (HD)	43	3	1.5	Jeong et al. (2001)

* Rates are corrected to 15°C using $Q_{10} = 2.8$ (Hansen et al. 1997). PV (Predators' volume as $\times 10^3 \mu\text{m}^3$); I_{max} (maximum ingestion rate in $\text{ng C predator}^{-1} \text{day}^{-1}$); C_{max} (maximum clearance rate as $\mu\text{L predator}^{-1} \text{h}^{-1}$); NC (naked ciliate); TC (tintinnid ciliate); HD (heterotrophic dinoflagellate); MD (mixotrophic dinoflagellate); ML (metazoan larvae).

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