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EFFECTS OF AN ALGAL BLOOM ISOLATE ON GROWTH AND SURVIVAL OF BAY SCALLOP (*ARGOPECTEN IRRADIANS*) LARVAE

CHRISTOPHER L. NELSON AND SCOTT E. SIDDALL
Marine Sciences Research Center
State University of New York
Stony Brook, New York, 11794-5000

ABSTRACT Some aspects of the nutritional value of *Minutocellus polymorphus*, a 2.5–3.5 μm diatom isolated from algal blooms implicated in the devastation of scallop populations of eastern Long Island, New York, were assessed. Growth in shell length, grazing rate, absorption efficiency and survival of bay scallop (*Argopecten irradians*) larvae, were determined in laboratory cultures fed this bloom isolate and the Tahitian strain of *Isochrysis* sp. Absorption efficiency was determined using a dual radiotracer method in which algae were labeled with both ^{51}Cr and ^{14}C. Survival was not significantly affected by algal diets. The type of algal species affected the growth of early larvae while growth of later larvae was affected by algal cell concentration. Early larvae absorbed less carbon from *Minutocellus* than from Tahitian *Isochrysis*. Grazing rates on *Minutocellus* were comparable to those on *Isochrysis* until metamorphosis was completed at which point *Isochrysis* was grazed at a greater rate than *Minutocellus*. The results suggest that a qualitative aspect, possibly a relatively low digestibility, of the *M. polymorphus* diet resulted in larval mortalities and widespread recruitment failure.

KEY WORDS: *Minutocellus polymorphus, Argopecten irradians*, picoplankton, bloom, larvae

INTRODUCTION

The bay scallop, *Argopecten irradians* (Mollusca:Pectinidae) is a suspension-feeding bivalve mollusc indigenous to coastal estuarine waters of North America (Belding 1931, Rehder 1981). In New York, locally important, commercial fishery for the species exists primarily in the Peconic-Gardiners Bays estuary of Long Island. The 1984 bay scallop harvest from the Peconic-Gardiners Bays area was valued at $1.26 million (New York State Department of Environmental Conservation, Fisheries Statistics 1984). Bay scallop population sizes experience a large degree of interannual variability (U.S. Department of the Interior 1981, see also Ingersoll 1886) which is attributed to the species' short life span and semelparous reproductive cycle (Gutsell 1930, Belding 1931). Bay scallops generally spawn only once during their life cycle, this occurring before the end of their first year. Bay scallop populations are thus composed of only one year class; two year old animals are rare exceptions (Belding 1931). The planktotrophic, planktonic larvae remain in the water column for 10–19 days (Castagna and Duggan 1971) and settle, attach and complete metamorphosis on suitable substrates such as eelgrass, *Zostera marina* (Belding 1931). Should conditions be unfavorable for larval recruitment in any year, the following season's scallop harvest, entirely dependent on the previous year class, may be extremely poor.

A phytoplankton bloom is an example of an oceanographic condition which can affect bivalve larval recruitment. The coastal embayments of Long Island have a history of recurrent phytoplankton blooms (Ryther 1954) which may have been one of the primary factors which led to the demise of the once prosperous oyster industry in the area. Plankton samples collected in June, 1985, from Northwest Harbor, Long Island, New York (Figure 1) as part of a New York Sea Grant Institute-funded research program on bay scallop larvae, showed that abundances of bivalve larvae (>150 μm) declined dramatically throughout the summer, concurrent with a picoplankton bloom (Cosper et al. 1987). Spat collectors presenting several substrate types gathered no bivalve postlarvae throughout June–August, 1985; in fact, few fouling organisms of any type were found. This apparent failure of bivalve larval recruitment accompanied by an intense picoplankton bloom (up to 2000 cells · ml^{-1}) presented a unique opportunity to study how such oceanographic phenomena affect the growth and survival of bivalve larvae.

The objective of this study was to assess the effect of a microalgal species isolated from the 1985 Long Island bloom on the growth and survival of bay scallop larvae. Possible mechanisms for effects on growth and survival were investigated by measuring grazing rates and absorption efficiencies of larvae feeding on the isolate.

The degree to which a particular algal diet supports growth in bivalve larvae may be influenced by either the quality of the alga (nutritional contents, cell size and shape, digestibility) or the quantity of algal cells provided. Toxic metabolites produced by the algal cells or the toxicity of the cell contents are also possible factors affecting the value of an algal species as food for bivalve larvae (Bayne 1983).

The fact that some microalgal species are more suitable than others as food for bivalve larvae has been well documented (Davis and Guillard 1958, Walne 1963, Newkirk and Waugh 1980). Pechenik and Fisher (1979) state that the

> "value of an algal species as a food depends upon 1) the ability of the zooplankton organism to ingest it, i.e., on cell size and shape, 2) the accessibility of the cell contents to

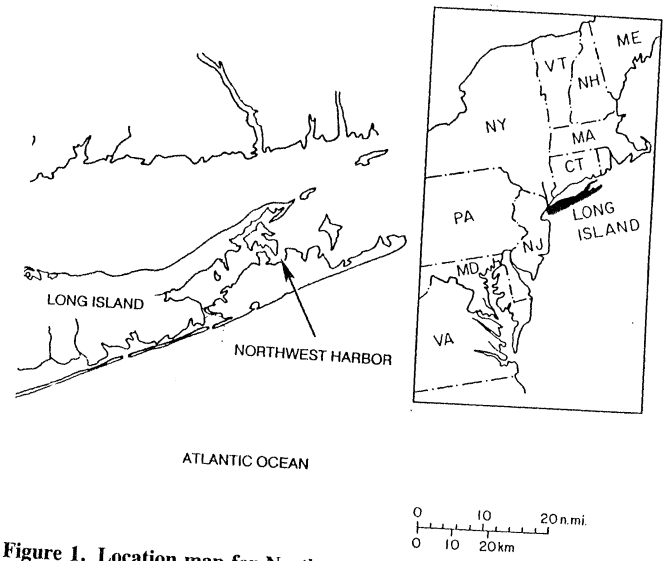

Figure 1. Location map for Northwest Harbor on Long Island, New York.

the herbivore's digestive system, and 3) the ability of the phytoplankton species to provide the organism with nutrients essential for growth and development."

In this study the first two criteria of food value (ability of the organism to ingest and digest the food) are addressed. The role of specific essential nutrients in the nutritional value of certain algal species has been addressed in a number of studies (Waldock and Nasciomento 1979, Langdon and Waldock 1981, Chu et al. 1982, Langdon 1983), however, the biochemical analyses and biochemically defined diets needed for such experimentation were not within the scope of this study.

Cell Size and Shape

Veliger larvae concentrate suspended particles for ingestion using an opposed cilia band system (Strathmann and Leise 1979, Strathmann et al. 1972). Rather than the cilia acting as a sieve, the individual cilia are presumed to intercept the particles, pushing particles faster than the water around them by way of some sort of weak adherence of particle to cilium. There probably is no minimum particle size limit below which particles are too small to be captured by bivalve larvae (Strathmann et al. 1972), however, many investigators do report an optimum range of particles captured with the greatest efficiency (Walne 1965, Wilson 1979, 1980, Riisgard et al. 1980, Fritz et al. 1984, Sprung 1984a).

Digestibility

Other investigators have emphasized the importance of digestibility in assessments of the nutritional value of microalgae in bivalve larval diets (Chu et al. 1982). Interspecific differences in digestibility exist for many species of microalgae. As food for bivalve larvae, naked flagellates have been found to be superior to algae with rigid, cellulose cell walls, the assertion being that cell walls inhibit the digestive capability of the larvae (Walne 1965, Davis and Guillard 1958, Babinchak and Ukeles 1979).

Quantity of Algal Cells

Much work has been done on the important relationship between larval growth rate and algal cell concentration {reviewed by Bayne (1983) and Sprung (1984b)} as well as grazing or clearance rate and algal cell concentration (reviewed by Sprung 1984a). For example, Walne (1965) found that *Ostreas edulis* larvae fed *Isochrysis galbana* grew maximally at algal cell concentrations of 50 cells/μl. During the picoplankton bloom of 1985, bivalve larvae in the waters of the Peconic and Gardiners Bay estuary experienced persistent concentrations of phytoplankton cells in excess of 2000 cells · ml^{-1}. Many investigators have reported that such high algal cell concentrations reduce larval feeding rates and growth (Sprung 1984b, Wilson 1979, Malouf and Breese 1977, Rhodes and Landers 1973, Walne 1966, Loosanoff et al. 1953, 1954).

Toxic metabolites associated with high concentrations of microalgae have been implicated as a possible reason for the depressed growth rates seen at supraoptimal concentrations of food (Davis 1953, Loosanoff and Davis 1963, Rhodes and Landers 1973, Sprung 1984a). Mechanical inhibition of larval feeding due to the excess production of pseudofeces in response to high algal cell concentrations was first reported by Yonge (1926) and has been cited as another possible cause for reduced growth rates at such concentrations (Malouf and Breese 1977, Sprung 1984a). Overloading of the larval digestive system has also been suggested as a possible explanation for the observed low growth rates of larval bivalves fed algae at high cell concentrations (Malouf and Breese 1977).

Little is known of the relationship between food concentration and absorption in bivalve larvae. One potential mechanism of response to an overabundance of food is a reduction in absorption efficiency. However, Walne (1965) found that although total assimilation (absorption–excretion) increased with algal cell concentration, even up to very high concentrations, the assimilation efficiency was relatively constant over a wide range of cell concentrations.

MATERIALS AND METHODS

Isolation and Identification of Picoplankton

Discrete, round, brown, unialgal (although non-axenic) colonies of a small (2.5–3.5 μm diameter) centric diatom (isolated from field samples taken at Jessup's Neck, Long Island New York, during July, 1985) grew well on F/2-enriched agar plates (Guillard and Ryther 1962). These colonies were picked individually and used to inoculate sterile culture tubes of F/2-enriched, filtered seawater. Scanning and transmission electron micrographs of this isolate re-

vealed this species to be *Minutocellus polymorphus* (hereinafter referred to as M-POLY) (Siddall et al. 1986). This identification concurred with an earlier, preliminary identification by Greta Hasle (University of Oslo, Norway; personal communication). Other scanning electron micrographs of this bloom isolate and field samples indicated that M-POLY was at least one of the species of algae present in the Bays during the bloom (Siddall et al. 1986).

Early attempts to produce scanning electron micrographs revealed algal cells which were enveloped in what appeared to be a thick sheath of organic material. Attempts to dissolve this refractory sheath by washing in concentrated hydrochloric acid for up to 24 hr. were unsuccessful. Methanol was the only solvent capable of dissolving this sheath (J. Mitchell pers. comm.).

Culture and Radiolabeling of Algae

Algae were cultured following the methods described by Guillard (1974). The Tahitian strain of *Isochrysis* sp. (referred to as T-ISO) was used in growth experiments as a control diet of known value (Ewart and Epifanio 1981) against which growth of larvae fed the bloom isolate could be evaluated. M-POLY seeemed to grow best under constant agitation and lower intensity light than was given other algae grown in the laboratory. M-POLY grew very well in culture most of the time but was unpredictable in cultures larger than 1.5 L. Large, 15 L cultures of M-POLY sometimes failed to grow after inoculation, however when cultures grew well during the first 24 hrs. invariably dense cultures of algae resulted. To ensure a constant supply of large volumes of isolate, semi-continuous rather than batch culture of M-POLY was used when rearing algae for growth experiments. Both species of algae were harvested during the exponential phase of growth ($2.0–7.0 \times 10^7$ cells $\cdot$ ml^{-1}). Phytoplankton cell counts were made on a Coulter Electronics model TA-II electronic particle counter.

The production of radiolabeled algae for use in absorption efficiency experimentation in general followed the methods described by Bass (1983) and Bricelj et al. (1984). Cultures ranging in volume from 150 to 500 ml were incubated with ^{14}C-bicarbonate radiolabel (0.2 μCi/ml) in tightly capped Ehrlenmeyer flasks for five to six days or until the cultures were sufficiently dense to provide enough labeled algal cells to conduct an absorption efficiency experiment. At least 24 hr. before the ^{14}C-labeled algae was harvested, ^{51}Cr in 0.1 N hydrochloric acid (1 μCi/ml of algae culture) was added. The hydrochloric acid was neutralized with an appropriate volume of 0.1 N sodium hydroxide.

Before each experiment, unincorporated radiolabel was washed from the labeled algae by centrifuging the algae and resuspending the cells in unlabeled, filtered seawater. This process was repeated three times. It was assumed that all of the unincorporated radiolabel was removed by this process.

Culture of Larvae

Sexually mature *Argopecten irradians* adults were spawned artificially within two days of collection from the field. Sperm and eggs were collected separately then mixed in a ratio of ~100 sperm cells per egg; on some occasions mass spawning and fertilization was allowed. In such cases, some degree of self-fertilization was inevitable, however, Castagna and Duggan (1971) reported that self-fertilization in bay scallops did not significantly affect the growth or survival of the resultant larvae. Gametes were allowed to commingle for 15–20 min. after which time fertilized embryos were separated from sperm by gently rinsing the embryos with filtered seawater onto a Nitex screen (20 μm mesh). Embryos were reared at 200–300/ml in conically-shaped 15 L polyethylene culture vessels. Veliger larvae were collected on 63 μm Nitex screens and placed in freshly filtered seawater. Except for larvae for growth experiments 1 and 2 which were immediately used in the experiments, larvae were fed 50 T-ISO cells/ml and reared in 15 l cultures (20/ml) or 2 l cultures (2/ml). Cultures were maintained at 22–25°C and 30 ppt. with complete seawater exchanges every 48 hrs.

Grazing Rate Experiments

To determine if the small cell size (2.5–3.5 μm) of M-POLY limited the ability of scallop larvae to capture it, grazing rates of larvae and postlarvae fed M-POLY or T-ISO were measured. Each experiment was conducted with ten 2 L culture vessels: six vessels were stocked at 2 larvae/ml. Four vessels, stocked only with algae, were used as controls to account for algal cell division during the course of the experiment. There were two treatments of algae used in these experiments:

Treatment—50 T-ISO cells/μl
Treatment 2—M-POLY cells/μl

T-ISO (5–7 μm equivalent spherical diameter as reared in our laboratory) is four times as voluminous as M-POLY (2.5–3.5 μm equivalent spherical diameter). On a total cell volume basis, 50 cells/μl T-ISO is equivalent to 200 cells/μl M-POLY. Concentrations providing a total cell volume equivalent to 50 cells/μl T-ISO were considered optimal (10–100 cells/μl according to Sprung 1984b, Gallager and Mann 1980, Walne 1963, 1965, Wilson 1980).

Low larval stocking densities (2/ml) were used to minimize effects on grazing rates observed by other investigators at high larval stocking densities (Fritz et al. 1984, MacDonald in press). There were two controls of each species of algae at the appropriate concentration in seawater during each experiment. These experiments were conducted with larvae and postlarvae from a single spawning of scallops. These animals ranged in shell length

(parallel to the hinge line) from 119 μm larvae to 507.5 μm postlarvae (Table 1). Experiments with veligers and pediveligers lasted from eight to twelve hours; 4.5 to 8 hr. with the postlarvae. Grazing rate determinations were conducted in total darkness to minimize algal cell division.

Triplicate samples of seawater from each culture were taken at initiation and termination of each experiment. Samples were immediately fixed with Lugol's solution and cell concentrations determined using a Coulter Model TA-II electronic particle counter.

The changes in algal cell concentration in experimental cultures were corrected for algal cell divisions observed in control cultures (no larvae). Total numbers of cells grazed per hr. were then calculated from total culture volume. Three estimates were made of age-specific grazing rates for each treatment.

Absorption Efficiency Experiments

The amount of carbon which scallop larvae could absorb from M-POLY or T-ISO relative to the amount of carbon available was determined using the ^{51}Cr:^{14}C dual tracer method for measuring absorption efficiency (Calow and Fletcher 1972). This method was adapted for use with suspension feeding bivalves by Bricelj et al. (1984). Although other methods of directly measuring absorption or assimilation by adult bivalves do exist (see Bricelj et al. 1984), the dual radiotracer method is the most appropriate for bivalve larvae as there is no need to separate feces from food or pseudofeces.

Four 100 ml cultures of scallop larvae (five larvae/ml) were held in 10 cm diameter acrylic chambers with 63 μm mesh Nitex bottoms, placed inside 1500 ml heavy-duty glass beakers. The chambers allowed larvae to be transferred gently to different algal suspensions with minimum disturbance. The chamber was removed from the beaker of algae, gently rinsed of excess algae with filtered seawater, and replaced in a beaker containing a fresh suspension of algae. The suspension was stirred approximately every 30 min. by gently raising and lowering the chamber through the depth of the algal suspension. Larval feces fell or were rinsed through the screen on which the larvae were retained. Larvae used in absorption efficiency experiments were 100 and 121 hr. post-fertilization and 107.6 and 110.9 um in shell length, respectively.

Availability of radiochemicals and difficulties in culturing sufficient quantities of radiolabeled algae, led to variations in experimental concentrations of radiolabeled algae in treatments of the two absorption efficiency experiments. Absorption efficiency experiment 1 was conducted using the following four treatments of dual-labeled algae. The comparative role of each treatment in these experiments (noted in parentheses) is based on Walne's (1965) report that 50 *Isochrysis* sp. cells/μl was "optimal" for *Ostrea edulis* larvae and our own observations of 2000 picoplankton cells/μl in field samples of the 1985 bloom.

Treatment 1 was T-ISO at 50 cells/μl (T-ISO "optimal")
Treatment 2 was T-ISO at 250 cells/μl (low bloom equivalent)
Treatment 3 was M-POLY at 200 cells/μl (T-ISO "optimal" equivalent)
Treatment 4 was M-POLY at 1000 cells/μl (low bloom)

Absorption efficiency experiment 2 was conducted with the following four treatments of dual-labeled algae:

Treatment 1 was T-ISO at 50 cells/μl (T-ISO "optimal")
Treatment 2 was T-ISO at 500 cells/μl (high bloom equivalent)
Treatment 3 was M-POLY at 200 cells/μl (T-ISO "optimal" equivalent)
Treatment 4 was M-POLY at 2000 cells/μl (high bloom)

Preliminary experiments had shown that scallop larvae could pass fluorescent paint particles through their digestive tracts in as little as 30 min. Thus it was assumed that 30 min. was the earliest time at which labeled feces could be collected after larvae were pulse-fed labeled algae.

After actively feeding for 30–35 min. in the labeled algae, the larvae and the chamber were thoroughly rinsed with filtered seawater and placed in a beaker of fresh, filtered seawater stocked with unlabeled algae of the same species and concentration as the labeled treatment. Every 1–2 hr. each chamber of larvae was rinsed and moved to a fresh, unlabeled algal suspension of appropriate cell concentration. Fecal material which passed through the Nitex screen bottom of each chamber was collected by gently filtering the entire volume of algal suspension and associated fecal material onto Nuclepore membrane filters (0.6 μm pore size, 38 mm diameter). Feces were collected over a 7–8 hr. period. A preliminary, 15 hr. dual-tracer experiment demonstrated that 98% of the total recovered non-ab-

TABLE 1.

Description of larvae and postlarvae used in grazing rate determinations.

Experiment	Mean length (μm)	Age (days after fertilization)	Description
1	119	7	veligers
2	168	9	veligers, some pediveligers
3	172	11	onset of metamorphosis
4	189	13	postlarvae, 2–5 ctenidia
5	258	16	2–6 ctenidia
6	361	18	3–6 ctenidia
7	508	24	7–8 ctenidia

sorbed ^{14}C was collected during the first 5 hr. after the larvae were removed from the radiolabeled food.

Before each experiment, samples were taken of each species of radiolabeled microalgae for analysis of the isotopic ratio of the food. Algal samples were gently filtered onto Nuclepore membrane filters (0.6 μm pore size, 25 mm diameter) and rinsed with filtered seawater. The filters on which the food samples and fecal samples were retained were placed individually in plastic counting tubes and immediately measured for ^{51}Cr counts per min. (cpm) on a gamma counter (Beckman model 8000). After gamma counting, each sample was moistened with 0.1 ml distilled water and digested for at least 24 hr. in 1–2 ml of tissue solubilizer (NCS, Amersham). Twelve ml of scintillation cocktail (Econofluor) were then added and allowed to equilibrate with the NCS in the dark for 24 hr. Carbon-14 decays per min. (dpm) were measured with an LKB liquid scintillation counter which had an internal dual-label counting program. The program incorporated a quench correction curve generated with a series of ^{14}C-hexadecane standards quenched to varying degrees with different concentrations of algal cells. With this quench curve the program automatically estimated ^{14}C dpm from cpm. Computer programs were written to convert ^{51}Cr cpm to ^{51}Cr dpm. The dpm of each isotope were summed for all fecal samples gathered during the course of each experiment to calculate the fecal isotopic ratio of ^{51}Cr:^{14}C. The programs made all necessary decay, energy spectrum interference, and background radiation corrections to data and ultimately computed absorption efficiencies.

Calow and Fletcher (1972) state that one of the assumptions of the dual-label method is that ^{51}Cr is not absorbed to any significant extent. A preliminary experiment showed that ^{51}Cr absorption by bay scallop veligers was negligible (~1%). Absorption efficiency was calculated as

$$AE = 1 \frac{\text{food isotopic ratio}}{\text{fecal isotopic ratio}} \times 100\%$$

Growth and Survival Experiments

To measure the effect of a diet of M-POLY on bay scallop larvae, the following five diets of cultured algae were fed to larvae in each of the four longer-term growth experiments (as for absorption efficiency experiments, the comparative role of each treatment in these experiments is noted in parentheses):

Treatment 0–Unfed control, filtered seawater
Treatment 1–T-ISO at 50 cells/μl (T-ISO "optimal")
Treatment 2–T-ISO at 500 cells/μl (T-ISO bloom equivalent)
Treatment 3–M-POLY at 200 cells/μl (T-ISO "optimal" equivalent)
Treatment 4–M-POLY at 2000 cells/μl (bloom)

M-POLY, cultured to 3–6 × 10^3 cells/μl, was centrifuged and resuspended in filtered seawater to give an algal cell concentration on the order of 1 × 10^5 cells/μl for the preparation of treatments 3 and 4. Each diet was fed to three replicate (2 larvae/ml in 1500 ml of seawater in 21 vessels). Larval cultures were sampled at the beginning of the experiment and at least after every water exchange (every 48 hr.) by slowly thrusting a perforated, acrylic plunger vertically downward seven times through the water column of each culture to suspend the larvae uniformity. Using a graduated plastic syringe (minimum diameter 3 mm), a 30 ml sample of culture water and larvae was removed immediately and placed in a sample tube containing ~2 ml of 30% buffered formalin (final concentration of formalin was ~2%). Larvae were counted and sized to the nearest 6 μm with a dissecting microscope (Wild model M3a) and ocular micrometer.

Larvae used in these experiments varied in age, shell length and feeding history at the beginning of the experiment (Table 2).

An instantaneous growth coefficient (k) was calculated for each larva using the following equation (e.g., Walne 1963, Bayne 1965, Malouf and Breese 1977):

$$k = \frac{\ln(\text{final individual length}) - \ln(\text{initial mean length})}{\text{elapsed time}} \times 100\%$$

Proportional data were arcsine transformed prior to statistical analysis (Zar 1984). Most statistical procedures were conducted using the subprograms of SPSSx on an IBM 3083 computing system. Homoscedastic data sets were analyzed with parametric one-factor and two-factor analyses of variance (ANOVA) and Student-Newman-Keuls (SNK) multiple range tests. Data sets with heterogeneous variances were analyzed with nonparametric Kruskal-Wallis one-factor and two-factor ANOVA as well as with nonparametric multiple comparison tests following the methods of Zar (1984).

TABLE 2.

Larvae used in growth and survival experiments.

Experiment	Age (hr.)	Shell length (μm)	Feeding history
1	52	103	unfed
2	54	94	unfed
3	121	100	unfed for 27 hr. then 50 T-ISO cells/μl for 95 hr.
4	153	117	unfed for 24 hr. then 50 T-ISO cells/μl for 129 hr.

Mortality

An instantaneous coefficient of mortality (Z) was calculated with the following formula:

$$Z = \frac{\ln(\text{initial number of larvae}) - \ln(\text{final number of larvae})}{\text{elapsed time}}$$

Parametric one-factor ANOVA were conducted for mortality coefficients for each experiment. The mortality here is actually a combination of mortality caused by the experimental treatments (experimental mortality) and "sampling mortality". Sampling mortality resulted from repeated sampling of small percentages (2%) of the total volume of a culture of larvae a number of times over the course of an experiment. No compensation for this loss of larvae was attempted.

RESULTS

Grazing Rate Experiments

Figure 2 presents age-specific grazing rates of larvae and postlarvae feeding on each species of algae. One cell of T-ISO was assigned an arbitrary value of one cell volume equivalent (CVE), therefore, based on cell diameter, one cell of M-POLY was equal to 0.25 CVE. Figure 3 presents age-specific grazing rates expressed as CVE/scallop/min.

Grazing rates of larvae peaked at nine days after fertilization and probably continued to increase before the onset of metamorphosis 11 days after fertilization. During the early stages of metamorphosis, grazing rates were negligible. At 13 days after fertilization, postlarval grazing rates on T-ISO were still nearly zero while M-POLY was being removed from suspension at much higher rates. From days 16–18, postlarvae were capturing similar volumes of both species of algae, however, by day 24, the CVE grazing rate for T-ISO was greater than that for M-POLY.

Absorption Efficiency Experiments

Figure 4 presents the results of the absorption efficiency experiments. In these experiments, larvae fed on four different diets of radiolabeled algae. Algal species rather than concentration differences affected the absorption efficiency of the scallop larvae. Larvae were able to absorb more carbon from T-ISO than from M-POLY regardless of cell concentrations. Cell concentration alone had no consistent effect on the absorption efficiency of the larvae (i.e., higher efficiencies on low concentrations in one experiment, lower efficiencies on high concentrations in the other).

An examination of counts of unabsorbed ^{14}C and ^{51}Cr in collected fecal material allows for a crude comparison of gut passage time for different diets. The data suggested that larvae feeding on low concentrations of T-ISO retained

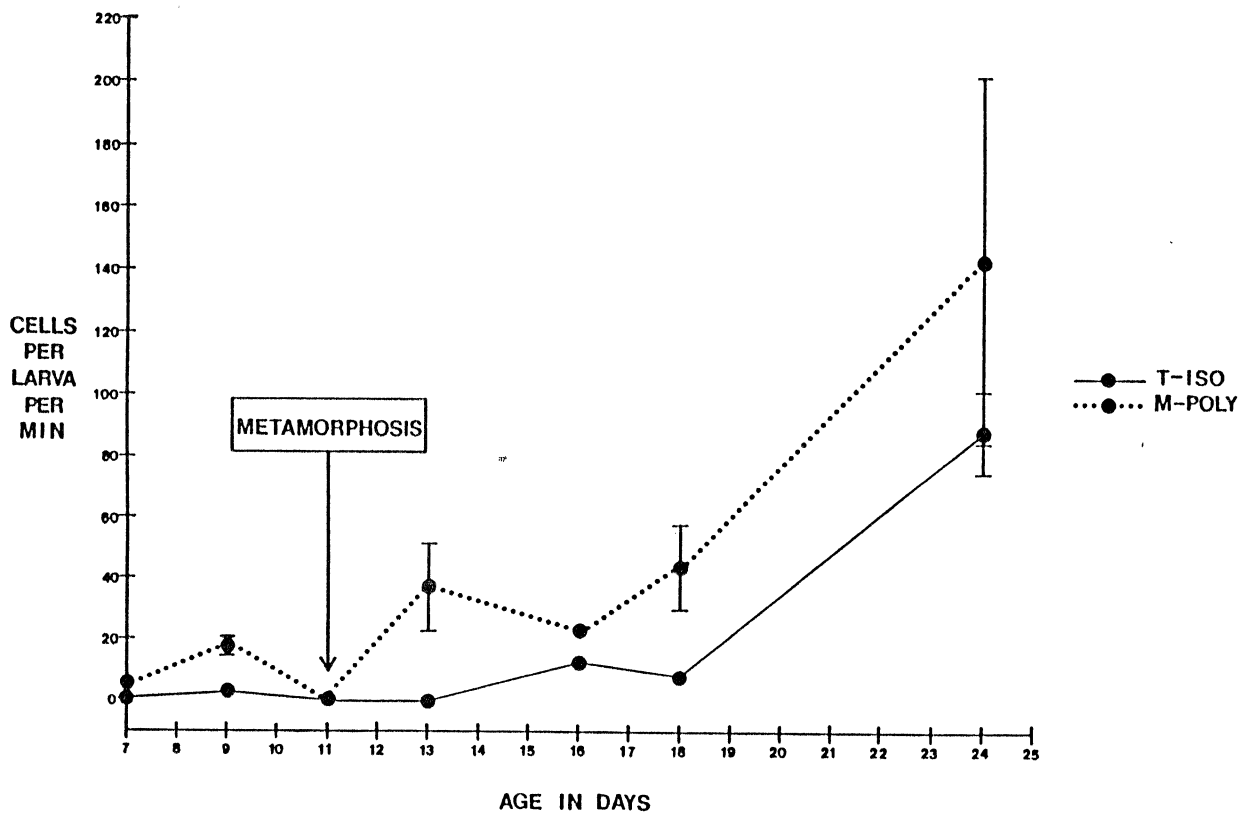

Figure 2. Grazing rates (cells/scallop/minute) of bay scallop veligers or juveniles at seven different ages (days after fertilization) feeding on two different microalgal diets. Error bars are ±S.E.

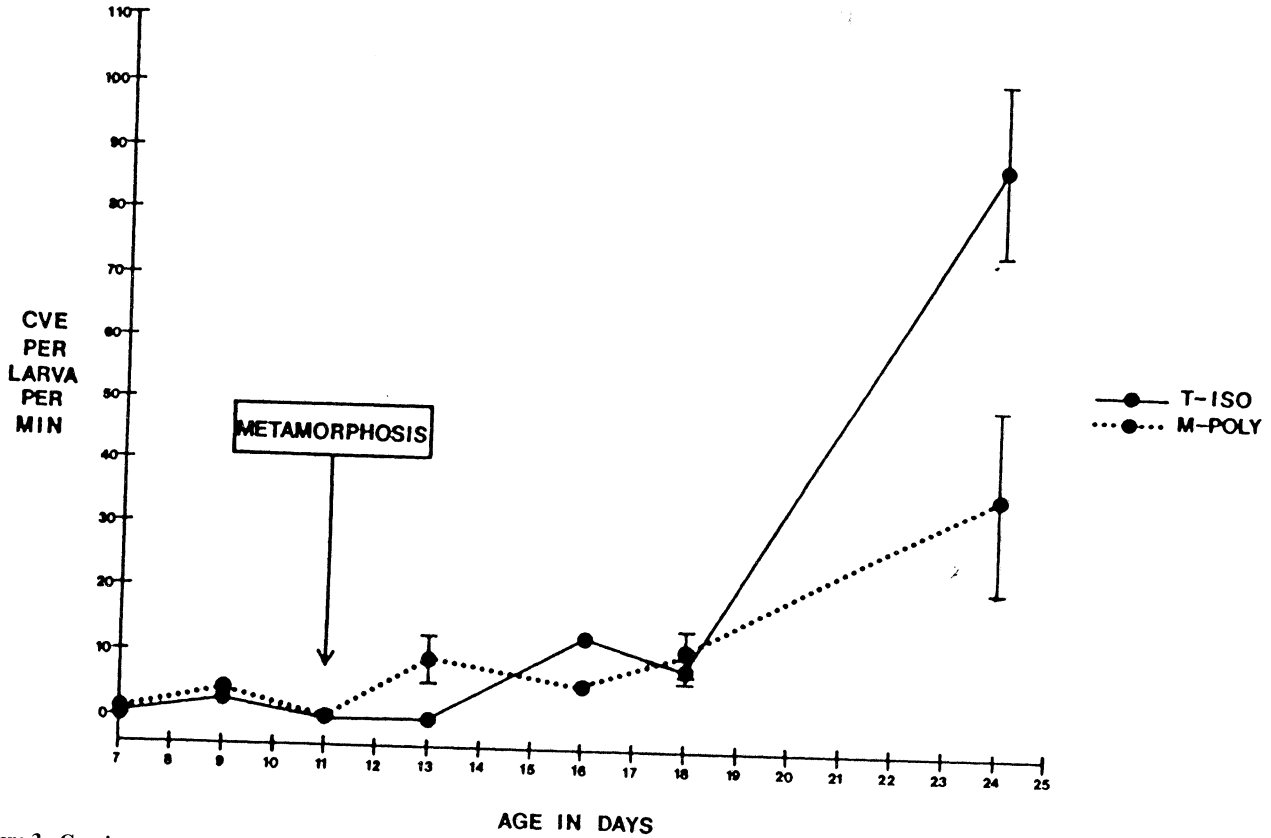

Figure 3. Grazing rates (CVEs/scallop/minute) of bay scallop veligers or juveniles at seven different ages (days after fertilization) feeding on two different microalgal diets. Error bars are ±S.E.

algae in their gut longer (mean of recovered fecal ^{14}C = 60.8% of total recovered) than did those larvae feeding on the higher concentration (85.9%). On the same basis, there was a smaller difference in gut retention time between treatments of M-POLY (mean of recovered fecal ^{14}C at the low concentration was 79.0% of total and 83.4% at the high concentration).

Growth and Survival Experiments

Table 3 illustrates differences in effects of treatments on larval growth coefficients. In experiments 1, 2, and 3, growth was affected significantly by algal species (at a = 0.05; parametric two factor ANOVA for experiment 1 and nonparametric Kruskal-Wallis two factor ANOVA for experiments 2 and 3). Generally, larvae fed T-ISO grew faster than larvae fed M-POLY. Statistically significant differences in the growth rates of larvae fed different concentrations of algae did exist, however, those differences were not consistent among any of the first three experiments.

In experiment 4, which used larger more fully developed larvae than the previous three experiments (see Table 2), concentration differences in the algal diets significantly affected growth rate ($p < 0.001$; two-factor parametric ANOVA) whereas effects of algal species were not significant ($p = 0.931$). In experiment 4, larvae fed the higher concentrations of T-ISO or M-POLY grew significantly more slowly ($p < 0.05$; one factor ANOVA and SNK multiple comparisons) than did larvae fed lower concentrations of either species of algae.

In experiment 1, neither algal species nor cell concentration significantly affected growth rates yet there was a significant interaction ($p = 0.049$) between these two factors. A nonparametric, one-tailed multiple comparison (Zar 1984) was conducted to determine if growth rates in the control diet (50 T-ISO cells/μl were greater than those observed in the other treatments. Multiple comparison tests with one-tailed hypotheses allow the detection of a statistically significant difference in only one direction (greater or less than), however, it employs a less conservative critical value for the test statistic Q (Zar 1984). In this analysis, larvae fed the low concentration of T-ISO were found to have grown significantly faster those fed the low concentration of M-POLY ($0.025 < p < 0.05$).

One factor ANOVA revealed no statistically significant difference in survival among treatments for all four experiments (p ranging from 0.121–0.438).

DISCUSSION

Cell Capture by Veligers

The results of the current study do not suggest that M-POLY was too small for scallop larvae to capture, further

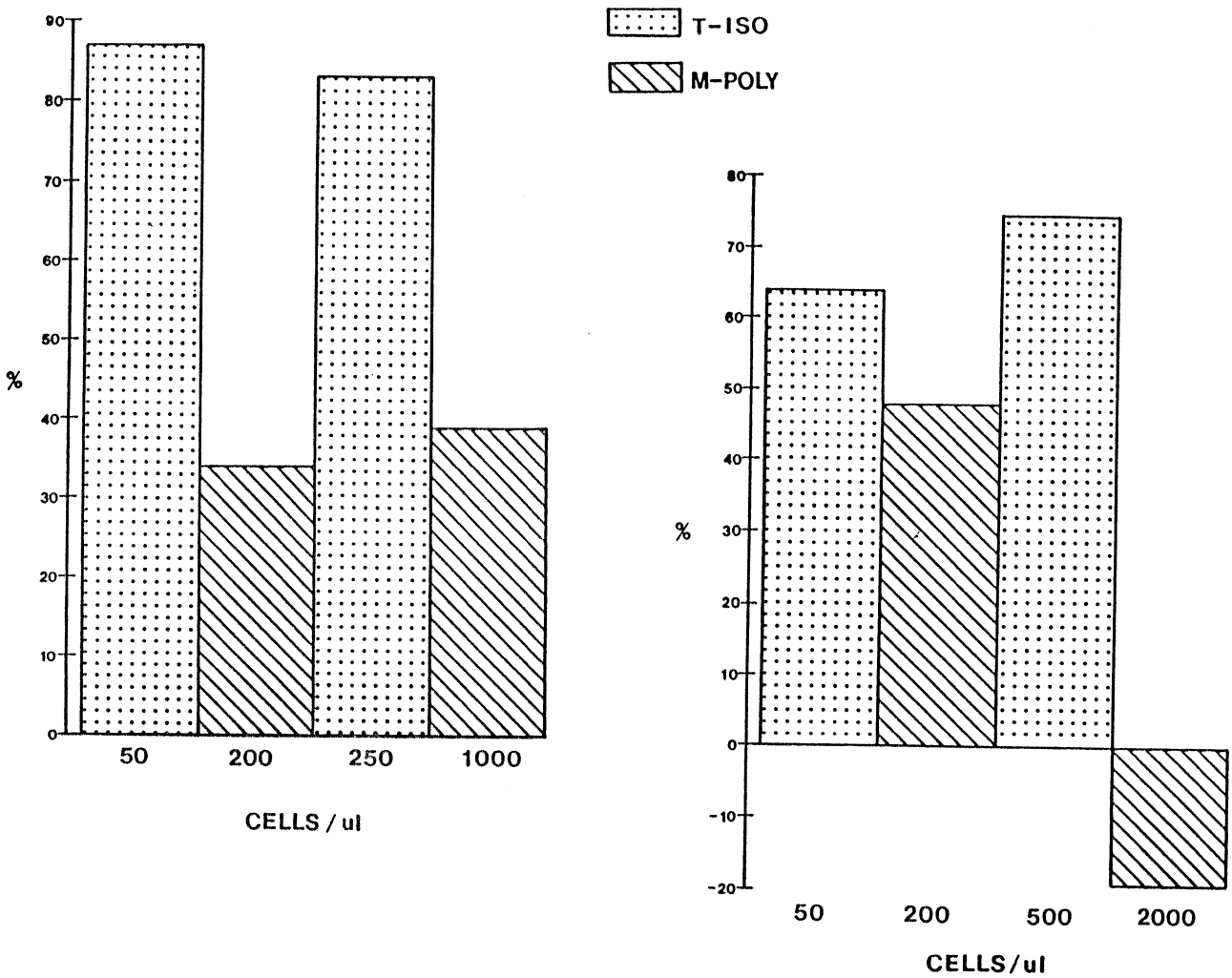

Figure 4. Absorption efficiencies (%) of scallop larvae feeding on different microalgal diets (absorption efficiency experiments 1 and 2).

suggesting that cell size alone was not a factor affecting the growth rate of scallop larvae fed this bloom isolate. In relative terms, the two algae were captured with similar efficiencies. M-POLY cells, which were provided at 4× the concentration of T-ISO cells, were captured by larvae at ~6–12 times the rate of T-ISO cells.

Based on the size of the algal cells, however, this result is not unexpected. Sprung (1984a) reported that *Mytilus*

TABLE 3.

Growth coefficients (k) calculated for bay scallop larvae fed five different diets in experiments 1, 2 and 3.

		Experimental treatment, mean k, (standard deviation)				
Experiment	**N**	**Unfed**	**M-POLY @ 200**	**M-POLY @ 2000**	**T-ISO @ 500**	**T-ISO @ 50**
1	207	0.045 (0.048)	0.107 (0.083)	0.151 (0.079)	0.159 (0.096)	0.175 (0.110)
		Unfed	**M-POLY @ 2000**	**M-POLY @ 200**	**T-ISO @ 50**	**T-ISO @ 500**
2	158	0.009 (0.045)	0.713 (0.035)	0.095 (0.057)	0.132 (0.075)	0.197 (0.069)
		M-POLY @ 2000	**Unfed**	**M-POLY @ 200**	**T-ISO @ 50**	**T-ISO @ 500**
3	452	0.200 (0.063)	0.024 (0.057)	0.036 (0.055)	0.079 (0.082)	0.093 (0.107)

edulis larvae, when fed a wide range of particle sizes, were able to capture 3.5 μm (equivalent spherical diameter) particles with the greatest efficiency. Walne (1965) reported that *Ostrea edulis* larvae efficiently captured algae 3–10 μm in diameter. Wilson (1979, 1980) reported that *O. edulis* larvae were best able to capture algal cells 3–3.5 μm in diameter. Riisgard et al. (1980) reported an optimum size of 2.5–3.5 μm particles for *M. edulis* larvae. Thus, M-POLY (2.5–3.5 μm in diameter) is within a size range for efficient capture by bivalve larvae.

Cell Capture by Postlarvae

Palmer and Williams (1980) reported that the adult pectinid gill has a greatly reduced capture efficiency for particles less than 6–7 μm in diameter. In the current study, postlarvae (12 days after settlement) feeding on T-ISO captured more than twice the number of cell volume equivalents (CVE) per hour than did postlarvae of the same age feeding on M-POLY (Figure 3). This suggested a decrease in the relative efficiency with which the postlarvae were able to capture M-POLY. This result further suggested that the gill of *A. irradians* is functionally complete 12 days after settlement and metamorphosis, or has acquired the particle size-dependent filtration efficiencies characteristic of the adult gill.

Absorption and Growth

The dual-tracer method estimates absorption efficiency as the percentage of carbon ingested which is not egested. This method provides a number of advantages over indirect estimates of absorption efficiency or other radiotracer methods. Most importantly, the accuracy of this method does not depend on knowledge of ingestion rate. In other methods, ingestion rate is often equated with grazing rate, an assumption which is valid only when pseudofecal production is absent (Gallager and Mann 1980). However, as applied in the current study, several sources of error were present in this method, including errors resulting from bacterial respiration, excretion of unabsorbed ^{14}C without proportionate losses of ^{51}Cr, dissolution of feces and algal respiration after food samples were taken. Also, given the fact that ^{14}C moves through the larval gut at a much slower rate than ^{51}Cr failure to allow sufficient time for complete gut evacuation results in an overestimation of absorption efficiency. This last source of error may have been important in these experiments. A preliminary absorption efficiency experiment was conducted to estimate the length of time necessary for the larval gut to release the majority of the unabsorbed ^{14}C and ^{51}Cr, however, only dual-labeled M-POLY was available for this experiment. Estimates of gut retention time indicated that M-POLY was held in the gut for a shorter period of time than T-ISO. Thus the length of time for most of the undigested ^{14}C to be voided from the gut may have been an underestimation of the amount of time needed for most of the unabsorbed ^{14}C from T-ISO to be voided. Consequently, the absorption efficiency of scallop larvae fed T-ISO may have been overestimated by an unknown amount.

Absorption efficiencies were correlated to gut retention times for the two species of microalgae, suggesting that the comparatively greater absorption efficiencies measured for T-ISO are valid results and not artifacts due to incomplete recovery of undigested carbon. Bricelj et al. (1984) found that gut retention time paralleled absorption efficiency in juvenile hard clams (*Mercenaria mercenaria*). Clams experienced a much shorter gut retention time and lower absorption efficiencies when fed the small forms *Stichococcus* and *Nannochloris* than when they were fed *Pseudoisochrysis paradoxa*. Similarly, Pechenik and Fisher (1979) found that assimilation efficiency was correlated with the gut retention time. Indirect estimates of assimilation efficiency at algal cell concentrations similar to the "bloom-like" concentrations used in this study indicated efficiencies of approximately 28% (at 1000 cells/μl; Crisp et al. 1985). Sprung (1984c) estimated assimilation efficiencies of 85.8 and 61.6% at 2 and 40 cells/μl respectively with 150 μm *M. edulis* larvae, results which are comparable to those of our study at low algal cell concentrations. Overestimation of ingestion by ignoring pseudofecal production at high algal cell concentrations may explain the disparity between these indirect estimates and the direct measurements reported in this study.

Effect of Algal Species

Bay scallop larvae were not able to absorb carbon from M-POLY and T-ISO with equivalent efficiencies. Larvae were able to absorb a greater percentage of carbon from T-ISO than from M-POLY (higher growth on T-ISO in growth experiments 1, 2 and 3). Interspecific structural variations such as the presence or absence of a cell wall may explain why one species of algae is absorbed or assimilated more efficiently than another (e.g., Davis and Guillard, 1958, working with *Chlorella*). Similar to the cell wall of *Chlorella,* the organic sheath seen in electron micrographs of M-POLY cells may reduce the availability of algal cell contents for absorption. As noted earlier, this organic sheath was extremely refractory.

Effect of Concentration

Concentration-dependent absorption efficiency was not observed in the absorption efficiency experiments nor were there any consistent effects of concentration on growth rate in the first three growth experiments. From the literature it is unclear how bivalve larvae respond to concentrations of algae such as those seen in the 1985 phytoplankton bloom.

Based on Yonge's (1926) description of the physiology of larval bivalve feeding, Walne (1965) postulated that larvae have two external mechanisms for dealing with an overabundance of food. The larvae must either reduce the rate at which they are capturing particles or increase their

rate of pseudofecal production. An internal mechanism for responding to an overabundance of food could be a decrease in absorption efficiency, however, Walne (1965) found that although total assimilation increased as cell concentration increased, even up to very high concentrations (1000 cells/μl), the assimilation efficiency was relatively constant over a wide range of cell concentrations. Walne (1965) also found that the volume swept free of algal cells per larva (filtration rate) decreased as algal cell concentration increased over a range of 30–371 cells/μl. Since a reduction in assimilation efficiency was not observed as food concentrations increased, Walne (1965) concluded that larvae respond to increased food concentrations either by decreasing feeding activity or by decreasing filtering efficiency (increase pseudofecal production). Either response would maintain a constant rate of ingestion. In concurrence with Walne's (1965) results, Gerdes (1983) found that *Crassostrea gigas* larvae reacted to higher concentrations of food particles by lowering filtration rate to allow ingestion to remain constant at high and low food particle concentrations. Consequently, assimilation also remains relatively constant over a wide range of algal cell concentrations (Gerdes 1983).

In general, growth rates increase with increasing levels of food concentration up to a maximum growth rate at which additional increases in food concentration will not cause further increases in growth rate, yet results are equivocal. Some studies have found that growth rates remain relatively constant at optimal or supraoptimal food concentrations (Davis and Guillard 1958, Newkirk and Waugh 1980, Walne 1965, 1966). Reductions in larval growth rates at high algal concentrations have also been observed. Malouf and Breese (1977) reported reduced growth rates of *Crassostrea gigas* larvae at food concentrations higher than 20–40 cells/μl. (in agreement with Loosanoff et al. 1953, 1954, Rhodes and Landers 1973). Some investigators have suggested that high numbers of food particles alone can affect digestive processes of larvae and result in low growth at high algal cell concentrations. From observations of food movement through the gut of larval *Ostrea edulis,* Millar (1955) reported that there seemed to be no sorting mechanism in the larval gut. He stated that,

> "It is a matter of chance whether material drawn off into the midgut and thence passed to the rectum has been in the stomach for a short or a long time, and therefore to what extent it has been subjected to digestion" (Millar 1955).

Malouf and Breese (1977) cited Millar's (1955) observations as physiological evidence to explain the reduced larval growth rate often recorded at high algal cell concentrations. They hypothesized that a high concentration of food may cause larvae to pass some food particles through their gut relatively undigested. In this way larvae theoretically could eat themselves to death by feeding at a rate which surpassed their ability to digest the material. Energy would be expended toward capturing and ingesting the particles without proportionate energy gain through the digestion and assimilation of nutrients from the particle. Malouf and Breese (1977) also suggested excessive pseudofecal production as another important cause of reduced growth at high algal densities. In addition to the loss of energy through excessive mucus production, larvae may become entrapped in long strands of pseudofecal mucus (Malouf and Breese 1977, R. E. Malouf pers. comm.).

Others have suggested that toxic metabolites associated with high concentrations of algae may cause reduced growth. Toxic metabolites could accumulate (Loosanoff et al. 1954) or be produced as a function of the physiological state of the algal cells (Wilson 1979). The results of the grazing rate experiments suggest that M-POLY does not have associated with it extracellular metabolites which inhibit larval grazing rates as has been reported for other species (Loosanoff et al. 1954, Guillard 1958). We observed no reduction in growth rates of larvae fed the high concentrations of either species of microalgae in experiments 1, 2 and 3. It is possible that the culture vessels provided an environment in which microalgae maintained high rates of photosynthesis and reproduction thereby reducing some negative effects of high algal cell concentrations on larval growth.

There was significant growth rate depression at the higher algal cell concentrations in growth experiment 4, a result which runs counter to those of the other experiments. The reasons for this are not clear, however, a number of investigators who have worked with bivalve larvae (e.g., Malouf and Breese 1977, Babinchak and Ukeles 1979) were unable to explain poor correlation of growth among cultures treated similarly. Larvae of experiment 4 were older than larvae used in the previous three experiments and they reached a more advanced stage of development than did larvae of the other experiments. Several investigators have reported age-specific changes in the ability of bivalve larvae to utilize certain algal species as food.

Survival

The experimental treatments affected larval growth but not survival, however had the experiments been carried through metamorphosis, a critical period during which lipid reserves accumulated through planktotrophy maintain the non-feeding larvae (e.g., Gerdes 1983), it is likely that dietary effects on survival would have been observed.

CONCLUSIONS

The results of these laboratory experiments suggest that one algal isolate of the 1985 picoplankton blooms in the coastal embayments of Long Island cannot support adequate growth of bay scallop larvae. In light of the reproductive strategy (mature quickly and spawn only once) and early life history (planktotrophic larvae) of *Argopecten irradians,* this effect on larval growth was probably the most important impact, both ecological and economic, of the so-

called "brown tide" blooms. The resultant widespread failure of larval recruitment virtually eliminated the bay scallop fishery in New York.

While *Minutocellus polymorphus* is present in these persistent blooms, it is not the dominant phytoplankter; Sieburth et al. (in press) describe a new genus and species, *Aureococcus anophagefferens,* which dominates these widespread and recurring coastal phenomena. Our experimental results with *M. polymorphus* (which is very similar in size to *A. anophageferrens*) suggest that bay scallop larvae can capture such small food particles, but that as larvae complete metamorphosis and begin to feed as juveniles, particle size-dependence becomes apparent and ingestion rates on such small particles decline. Our results suggest that there is no effect of particle concentration on bay scallop veligers. Our absorption efficiency results infer that larval ingestion rates are nearly constant at both bloom and "optimal" particle concentrations. Lower growth was observed in late larvae and postlarvae feeding on high concentrations of *M. polymorphus* and the Tahitian strain of *Isochrysis* sp. Species differences between *M. polymorphus* and Tahitian *Isochrysis* were apparent in the larval growth study; carbon was absorbed less efficiently from *M. polymorphus* than from Tahitian *Isochrysis*. The essential nutritional composition of this bloom isolate remains unknown, however our results suggest that a qualitative aspect of the *M. polymorphus* diet (possibly reduced availability of cell contents of absorption) resulted in poor larval growth and settlement success for bay scallops spawning during recent picoplankton blooms in New York's coastal bays.

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