Journal of Shellfish Research, Vol. 9, No. 2, 299–307, 1990.

GROWTH OF NORTHERN QUAHOGS (*MERCENARIA MERCENARIA* (LINNAEUS, 1758)) FED ON PICOPLANKTON

ANN E. BASS,[1,4] ROBERT E. MALOUF,[2] AND SANDRA E. SHUMWAY[3]

[1]*Marine Sciences Research Center*
State University of New York
Stony Brook, New York, 11794-5000
[2]*New York Sea Grant Institute*
State University of New York
Stony Brook, New York, 11794-5001
[3]*Department of Marine Resources*
West Boothbay Harbor, Maine, 04575

ABSTRACT The growth of hard clams, *Mercenaria mercenaria*, feeding on chlorophyte and cyanobacterial picoplankton (<1–4 μm in diameter) was investigated to determine if these small algae and cyanobacteria, and indirectly nitrogenous wastes from Long Island, NY duck farms, are responsible for poor growth of *M. mercenaria* in certain locations of Great South Bay and Moriches Bay, NY. Preliminary experiments verified that hard clams were capable of clearing "small forms" from suspension. In a six-week growth experiment, clams fed *Nannochloris atomus*, a common "small form" chlorophyte showed no tissue growth, while clams fed another alga, *Pseudoisochrysis paradoxa*, known to support growth in bivalve molluscs, grew well. In subsequent experiments, absorption efficiencies of "small form" chlorophytes and cyanobacteria by clams ranged from 17.6% to 31.1%, in contrast to 86.5% for algal species normally used for clam culture.

KEY WORDS: *Mercenaria mercenaria*, quahog, feeding, growth, picoplankton

INTRODUCTION

The natural phytoplankton population of coastal waters is typically a mixed composition of diatoms, green flagellates, and dinoflagellates (Ryther 1954). Size fractionation studies in North American marine ecosystems on the east coast (Yentsch & Ryther 1959, Bruno et al. 1983) and the west coast (Malone 1971) indicate that, whereas nanoplankton (<20 μm) comprise the most abundant size fractions in terms of measured chlorophyll *a* during most of the year, net plankton (>20 μm) may become dominant during seasonal, winter-spring bloom periods (Bruno et al. 1983). Picoplankton cells (0.2–2.0 μm) have been the major components of many recent blooms from the 1950's to the present and topic of a recent symposium (Cosper et al. 1989). In addition to blooms, they have been found to be present continually in northeastern coastal waters at concentrations of 10^6–10^9 cells l^{-1}, with cyanobacteria (primarily *Synechococcus*) at concentrations of 10^4–10^6 (Hargrave et al. 1989, Tracey et al. 1988). Field studies in the 1950's of the "small form" picoplankton in Great South Bay, Long Island, NY (Ryther 1954) and recent field studies in Narragansett Bay, R.I. (Tracey et al. 1988) have shown both beneficial and detrimental effects of picoplankton on nutrition of bivalves. The studies suggest that picoplankton and its species composition have high potential to influence the nutrition of bivalve molluscs.

Ryther (1954) defined the locally named "small forms" in Great South Bay, Long Island, NY, as "small, unicellular, green organisms 2–4 μ in diameter." Dense blooms of the "small form" chlorophyte species *Nannochloris* and *Stichococcus* induced by the flow of duck wastes into the bay, along with salinity and circulation changes, coincided with the failure of the bay's oyster industry around 1950. Data collected between 1933 and 1950 during summer months show a negative correlation between "small form" densities and oyster meats (Redfield 1951). Although these results are derived from Redfield's 1952 work, the "small form" population was as high in 1981 (E. Carpenter, pers. com.) with peaks of "small form" concentrations during the summer months of 10^9 cells l^{-1}. Approximately 77% of the phytoplankton biomass in Great South Bay through the year consists of the <10 μm fraction as determined by chlorophyl *a* concentration (Lively 1981).

In 1985 and 1986, there was a "brown tide" in Peconic Bay, NY. The effect of the small, "brown tide" alga, *Aureococcus anophagefferens*, (about 2 μm in diameter) on scallops, scallop larvae, and mussels has been described by Tracey (1988), Bricelj and Kuenstner (1989), Gallager et al. (1989), and Ward and Targett (1989). *A. anophagefferens* is retained with low efficiency by the bivalves' gills during particle capture (Cosper et al. 1987, Bricelj & Kuenstner 1989), and feeding rates of scallops and mussels are depressed when fed *A. anophagefferens* at bloom den-

[4]*Current address:* Penobscot Valley Council of Governments, One Cumberland Place, Suite 300, P.O. Box 2579, Bangor, Maine, 04401-8520, USA.

sities (Tracey 1988, Bricelj & Kuenstner 1989). Both bivalves can, however, absorb the ''brown tide'' alga with a maximum efficiency of about 90% (Bricelj & Kuenstner 1989).

Oceanic seawater normally has a nitrogen to phosphorus ratio of 8–17:1 (Redfield 1952). Coastal eutrophication can lower the N:P ratio significantly, to values of 4–6:1 (Redfield 1952) and subsequently alter the phytoplankton assemblage from mixtures containing diatoms such as *Nitzschia closterium,* (40 μm, Newell & Newell 1977) to primarily the smaller cyanobacteria and chlorophytes (2–4 μm) (Ryther 1954). The low N:P ratio in pollutants coupled with the presence of organic nitrogen compounds favor the growth of *Nannochloris* and *Stichococcus* over the more typical estuarine phytoplankton (Ryther 1954). In a critique of the dominance of nanoplankton (2–20 μm) as an indicator of marine pollution, Eppley and Weiler (1979) discussed selective effects of certain pollutants on phytoplankton species assemblages that suggest the smaller forms, (nanoplankton), may persist where larger-celled and chain-forming phytoplankton have been lost as a result of pollution. In the examples they examined, dominance of nanoplankton appeared to be related to habitat features, food web interactions, and eutrophication rather than selective toxicity of pollutants to larger phytoplankton (Eppley & Weiler 1979).

Some ''small-form'' species, e.g., *Chlorella* and *Nannochloris,* have been recommended for oyster culture (Dupuy et al. 1977); however, these same species are also considered unacceptable food for many species of bivalve molluscs, including oysters (Redfield 1951, Ryther 1954), and larvae of angel wing clams, American oysters, and hard clams (Tiu et al. 1989). *Nannochloris* sp. did not support growth in these three larval bivalve species under tropical experimental conditions (30°C) (Tiu et al. 1989).

Stichococcus sp., one of the ''small forms'' in Great South Bay, caused cultures of *Venus* (=*Mercenaria*) *mercenaria* larvae to grow more slowly than those in unfed control cultures and Davis and Guillard (1958) suggested that *Stichococcus* may produce metabolites that are toxic to bivalve larvae. Walne (1973) showed that differences in food supply can alter the protein:carbohydrate ratio in clam tissues and that this ratio is affected by the algal species, the concentrations at which the algae are fed to the clam, and possibly the physiological state of the algal species. The rate of filtration by adult hard clams, *Mercenaria mercenaria,* on ''small form'' algae (*Nannochloris atomus,* 2 μm; *Chlorella,* 4 μm) is much lower than when the same clam filters water containing a diatom species (*Nitzschia* sp., 19 μm × 5 μm; *Nitzschia closterium,* 43 μm × 4 μm) (Rice & Smith 1958). The average filtering rate by the hard clam was higher when diatoms and *Nannochloris* were in mixed suspensions than when the clam was in unialgal suspensions of *Nannochloris* (Rice & Smith 1958). Also, *Chlorella* cells appeared to have an unfavorable effect upon the filtering rate of the clam (Rice & Smith 1958). Thus, although the retention efficiency of cells declines with particle size, these results suggest that there may be more than just size affecting the filtration rate. There is, therefore, some indirect evidence that ''small forms'' may inhibit growth of the hard clam but the question has never been rigorously studied.

The primary objective of this study was to determine whether or not the ''small form'' picoplankton sustain growth in juvenile *Mercenaria mercenaria.* This paper examines the effect of bivalve growth and feeding on Ryther's ''small forms'', specifically the chlorophytes *Nannochloris atomus* GSB and *Stichococcus* sp. (now *Nannochloropsis salina* GSB ~ 17 μm^3; Hibberd 1981), two clones: Say 2 and Say 3 (now both *Nannochloropsis* sp.), and the cyanobacteria *Synechococcus bacillarius* (Syna), and ASN C-3 (*Synechococcus* sp.). The hypothesis tested is that unialgal cultures of these particular ''small forms'' do not support growth in *Mercenaria mercenaria.* To test this, three contingent questions were addressed. First, preliminary experiments were run to verify a previous study (Rice & Smith 1958) which indicated that hard clams are capable of clearing ''small form'' cells from suspension. Additional experiments were designed to answer two questions: can ''small forms'' support growth in *Mercenaria mercenaria* and can the clams efficiently absorb the organic material from the ''small form'' cell.

MATERIALS AND METHODS

Algae were cultured using standard methods (Guillard, 1975) at 17–20°C.

A. Preliminary Filtration Experiments

The objective of these experiments was to determine if the northern quahog, *Mercenaria mercenaria,* removes ''small form'' chlorophyte and cyanobacteria cells from suspension. In each of the three experiments, at least two containers per algal species were examined. One contained approximately 20 juvenile quahog (hard clams) while the other container held no quahogs (control). Experiment I examined hard clam filtration of *Nannochloris atomus* (GSB), a chlorophyte of about 3 μm diameter isolated by Ryther in 1952. The experiment was run in triplicate. Experiment II measured the grazing rate by hard clams of three other green ''small form'' species also about 2–3 μm: *Stichococcus* sp., isolated by Ryther in 1952, (now *Nannochloropsis salina* GSB; Hibberd 1981) and two clones; Say 2 and Say 3, isolated by Guillard in 1965, (now both *Nannochloropsis* sp.). Experiment III examined hard clam filtration of two species of cyanobacteria: Syna (*Synechococcus bacillaris*) less than 1 μm in length and isolated from Long Island Sound by Guillard and Ryther, and ASN C-3 (*Synechococcus* sp.), approximately 1 μm in length, isolated from Great South Bay by Sarokin (1981). Experiments II and III were not replicated.

The hard clams were approximately 30 mm in length and had been conditioned with a diet of mixed "small form" algal species for 4–5 days previous to the experiment. The quahogs were placed on screens approximately 2 cm off the bottom in aerated basins holding 7-liters of 0.22 μm filtered seawater. The basin and screen assemblies were soaked in filtered seawater before use.

The initial cell concentrations in Experiment I were chosen to provide equal particulate organic carbon concentrations to the quahogs. *Pseudoisochrysis paradoxa* (Va 12, 4 μm in equivalent spherical diameter) and GSB *Nannochloris atomus* were sampled during logarithmic growth and analyzed on a CHN analyzer (Hewlett Packard model #185). The carbon in 10^5 cells · ml^{-1} *P. paradoxa* is equivalent to that in 1.62×10^5 cells ml^{-1} *N. atomus*. The ratio for equivalent carbon is 1.00:1.62.

The initial cell concentrations in Experiments II and III were determined by calculating equal volumes (μm^3) of the "small form" species. The cell concentration (cells · ml^{-1}) during logarithmic growth of each algal culture was multiplied by the equivalent spherical volume of the cells. The ratio of equivalent volumes in Exp. II was 0.13 Syn a: 0.58 ASN C-3: 1.00 *P. paradoxa* and in Exp. III the ratio was for all *Stichococcus* clones 0.35:1.00 *P. paradoxa*.

Initial and final concentrations in each container were determined microscopically with a haemocytometer to estimate filtering activity. The experimental temperature was 21 ± 3°C; the salinity was 27 ± 2‰.

B. Growth Experiment

The objective of this experiment was to determine if the "small form" *Nannochloris atomus* can support growth in hard clams. Of the available species, *N. atomus* was selected because it was shown by Ryther (1954) to be one of the dominant "small form" types in Great South Bay. Unfed animals and a group fed on the chrysophyte *Pseudoisochrysis paradoxa* (Va 12) provided a growth comparison to animals fed *N. atomus*. *P. paradoxa* has been shown to be a relatively good food for hard clams (Epifanio et al. 1975). The algal combinations used in the growth experiments were as follows:

1) 100% *P. paradoxa* 0% *N. atomus;*
2) 75% *P. paradoxa* 25% *N. atomus;*
3) 50% *P. paradoxa* 50% *N. atomus;*
4) 25% *P. paradoxa* 75% *N. atomus;*
5) 0% *P. paradoxa* 100% *N. atomus;* and
6) Unfed.

There were three replicates of each treatment.

The basin and screen assemblies were the same as in the filtration experiments. In addition, the containers were rinsed with a mild chlorine wash and tap water every other day to control bacterial growth.

Juvenile hard clams were randomly divided and distributed into 18 growth containers of 100 clams each. Forty randomly selected samples of 10 clams each were frozen to provide an estimate of initial ash-free dry weights. The basins were placed in a circulating water bath at 18–20°C. The 7 L of filtered seawater in the containers were changed daily. Temperature ranged from 19°–21°C. The salinity was 26–27‰.

In determining the food concentration needed per container per day, two boundary conditions were considered. The lower cell concentration boundary was based on the minimum number of cells required per clam for growth. The upper boundary was determined by the cell concentration at which pseudofeces appeared to form.

The food concentrations needed per container were based on information from the literature on consumption rates of *Pseudoisochrysis paradoxa* by juvenile Pacific oysters at temperatures comparable to those of the present study (Malouf & Breese 1978). *Crassostrea gigas* (mean length 3.2 mm; AFDW ~ 100 μg) filtered between 1×10^3 and 5.5×10^3 cells min^{-1} $oyster^{-1}$ (Malouf & Breese 1978). At 1×10^3 cells min^{-1} and 100 animals, 100×10^3 cells min^{-1} or 14.4×10^7 cells day^{-1} per 7 L container are required as a minimum. The lower boundary cell concentration is 2×10^4 cells ml^{-1}.

As only one feeding per day was feasible during the growth experiment, a range of food concentrations, all greater than the minimum required for growth, were employed: 3×10^3 to 5×10^3 cells ml^{-1}. The initial cell concentration was calculated to be 6.2×10^4 to 10.3×10^4 cells ml^{-1} $basin^{-1}$ day^{-1}.

Although no cell concentration for pseudofeces production in quahogs, *M. mercenaria*, has been determined, our preliminary observations show that little or no production occurred at cell concentrations less than 10^5 cells ml^{-1}. To restrict pseudofeces production, no more than 10^5 cells · ml^{-1} were administered to each container. These estimates were based on experiments using *P. paradoxa*. To supply equivalent organic carbon content to all treatments, the carbon ratio of 1.00 *P. paradoxa:*1.62 *N. atomus* determined in Filtration Exp. I was used. For each algal species, the required cell concentration · $container^{-1}$ was divided by the daily count of cultures (cells ml^{-1}), and the food aliquot (mls) was calculated. The experiment was carried out over a period of 37 days. Growth was determined by the change in ash-free dry weight of tissue between initial and final samples in each treatment following standard methods (Gabbott & Walker 1971). The clams were dried at 95°C, weighed on a Cahn 26 automatic electrobalance, combusted in a muffle furnace at 450°C, and reweighed.

C. Absorption Efficiency Experiments

The objective of these experiments was to determine how efficiently juvenile quahogs absorb organic material from the "small form" algae tested. A dual ^{14}C:^{51}Cr radio-

tracer technique (Calow & Fletcher 1972, Wrightman 1975, Cammen 1977, 1980, Lopez & Cheng 1982, 1983) was adapted for estimating absorption efficiencies of suspension feeders (Bricelj et al. 1984). The technique compared the ^{51}Cr:^{14}C ratio of the food with that of the feces to calculate the absorption efficiencies (AE).

Calow and Fletcher (1972) listed four conditions that must be met before employing the radiotracer technique: 1) that the ^{14}C and ^{51}Cr be evenly distributed throughout the food material, 2) that ^{14}C and ^{51}Cr move along the gut at similar rates, 3) that ^{51}Cr cannot be absorbed to any great extent, and 4) that the non-absorbed indicator is all present in feces (i.e., not readily leached out). Conditions 1, 3, and 4 were shown to be met under the circumstances employed in this study. Preliminary experiments showed, however, that ^{14}C and ^{51}Cr move along the gut at different rates and therefore that quantitative recovery of feces is necessary to obtain accurate estimates of ^{51}Cr (see Bricelj et al. 1984).

Three species of algae and cyanobacteria were used in each experiment: a "small form" chlorophyte, a cyanobacteria, and *Pseudoisochrysis paradoxa* (Va 12). The chlorophyte species used in absorption Experiments I and II were *Nannochloris atomus* (GSB) and *Stichococcus* clone Say II, (now *Nannochloropsis* sp.). Cyanobacterial clones used in Experiments I and II were Syn a and ASN C-3, both *Synechococcus* species.

The quahogs, 29–35 mm in length, were conditioned for five days at warmer seawater temperatures (about 15°C) and fed an increased ration of (*Pseudoisochrysis paradoxa*). The experiments were run at room temperature, approximately 26°C.

Twelve clams were initially fed with food suspensions of 5×10^4 to 1×10^5 cells ml^{-1} in 200 ml of 0.22 μm filtered seawater. The labeled algal volumes delivered were determined by cell counts. The labeled algal aliquots were centrifuged twice at about 8000 rpm for 10–15 min. They were rinsed with filtered seawater and brought up to volume to ensure only cell-incorporated ^{14}C was fed to the clams. Algae were resuspended in filtered seawater, and a 5 ml aliquot was removed and filtered onto a 0.6 μm Nucleopore filter, which was stored in a glass scintillation vial for later analysis. The conditioned quahogs were then introduced and monitored individually, and the time at which they began to filter was recorded. The clams were allowed to feed for 30–45 min, because preliminary work indicated pseudofeces production began after about 45 minutes of active feeding (Bass, 1983). Seven of the twelve clams were transferred to filtered seawater containing unlabeled algae. Unlabeled algae were added at 3×10^4 to 4×10^4 cells ml^{-1} every 1–2 hr for the first 12 hr, the critical period of time for metabolism of the labeled algae. Preliminary work showed that 82% of the ^{14}C passed through the clam within 12 hr of ingestion. The clams were fed periodically for another 36 hr. The clams fed labeled "small forms" did not filter as readily as those fed labeled *Pseudoisochrysis paradoxa*. Therefore, clams initially fed labeled "small form" species were fed an equal, unlabeled mixture of their respective "small form" species and *P. paradoxa*. In this mixture, the clams filtered normally. Feces collection began 2 hr after the initial feeding. Samples of the feces were pipetted onto 0.6 μm Nucleopore filters. The filters were stored individually in glass scintillation vials for later analyses. Collection occurred every 4–5 hr for the first 12 hr and less regularly thereafter until 48 hr after the initial feeding. The samples were analyzed for ^{14}C and ^{51}Cr dpm and the ^{51}Cr to ^{14}C ratio and absorption efficiency were calculated using the following expression (Calow & Fletcher 1972, Bricelj et al. 1984):

$$AE = 100(1 - [\text{dpm } ^{51}Cr/\text{dpm } ^{14}C \text{ (susp.)}]/[\text{dpm } ^{51}Cr/\text{dpm } ^{14}C \text{ (feces)}]) \quad (1)$$

The 95% confidence intervals were calculated for the mean absorption efficiency of each algal species (Sokal & Rohlf 1969). A t-test of difference between means (Sokal & Rohlf 1969) was computed for each combination of means of absorption efficiencies for all species used in both experiments.

RESULTS

Preliminary Filtration Experiments

The results of the preliminary filtration experiments indicate that the hard clam, *M. mercenaria,* is capable of removing "small form" chlorophyte and cyanobacteria cells from suspension (Table 1).

Clams fed a diet of the chlorophyte, *Nannochloris atomus,* removed 56% of the cells in suspension over 7 h. The clams fed diets of the *Stichococcus* clones removed a mean value of 61% of the cells from suspension over 5 h. The clams fed diets of cyanobacteria over 5 h removed

TABLE 1.

FILTRATION EXPERIMENTS. Data Summary. Filtration rates of "small form" cells by 30 mm quahogs at 26° C. Duration of Experiment I: 7 h; Experiment II and III: 5 h each.

"small form" Species	With Clams Initial Conc. (×10⁴ cells/ml)	With Clams Final Conc.	% Removal	Controls Without Clams Initial Conc. (×10⁴ cells/ml)	Controls Without Clams Final Conc.
Nannochloris	25	11	56	23	25
Syn a	220	139	27	175	169
ASN C-3	109	22	80	101	96
Mean			53.5		
Stichococcus	46	6	87	41	32
Say 2	44	26	41	48	47
Say 3	44	20	55	41	52
Mean			61		

TABLE 2.

Results of t-test of the differences between mean weights of *M. mercenaria* juveniles fed different diets of *P. paradoxa* and *N. atomus*, plus a no food control (n = 3) (Sokal & Rohlf 1969). * = p < 0.05; ** = p < 0.01; ***p < 0.001; ns = not significant.

Comparison (% *P. paradoxa*/% *N. atomus*)	t_s	Significance Level
100/0 × initial	5.46	**
100/0 × 0/100	8.09	**
100/0 × unfed	10.75	***
0/100 × initial	1.38	ns
0/100 × unfed	6.01	**
initial × unfed	.48	ns
75/25 × initial	4.67	**
100/0 × 75/25	2.13	ns
50/50 × 75/25	.67	ns
75/25 × 25/75	5.34	**
75/25 × 0/100	9.59	***
75/25 × unfed	13.23	***
50/50 × initial	3.96	*
100/0 × 50/50	.61	ns
50/50 × 25/75	2.57	ns
50/50 × 0/100	4.13	*
50/50 × unfed	5.91	**
25/75 × initial	2.96	*
100/0 × 25/75	5.5	**
25/75 × 0/100	6.53	**
25/75 × unfed	11.46	***

fewer of the smaller *Synechococcus* species Syn a (<1 μm) from suspension, 27%, than of the larger species ASN C-3 (1 μm), 80%. In comparison with the control treatments of no clams, where the algal concentrations remained approximately constant, between 78% and 127% of the initial concentrations, results showed that *Mercenaria mercenaria* is capable of removing "small form" cells from suspension.

Only experiment I was run in triplicate, with the means of the replicates given in the summary data table (Table 1). The experiment was analyzed by t-test for statistical differences in the mean concentrations before and after filtration by 30 mm hard clams (n = 3) at 26°C (Sokal & Rohlf 1969). The t_s for the clam filtration experiments was 17.06, a very significant correlation ($p < 0.01$). The t_s for the controls (no clams) was 2.24 and not significant.

B. Growth Experiment

The results of the growth experiments showed that juvenile hard clams, *M. mercenaria,* do not grow significantly on a sole diet of *Nannochloris atomus* (Table 2). The clams fed on intermediate concentrations of the "small form" grew at a slower rate than did those fed the control diet of 100% *Pseudoisochrysis paradoxa* (Fig. 1).

The final mean individual weight of the group of juvenile hard clams fed the 100% "small form" diet (1.37 mg) did not differ from that of the clams in the initial samples (1.23 mg), whereas the clams fed the 100%, 75%, and 50% *P. paradoxa* diet did differ significantly from the initial samples or the unfed control.

Absorption Efficiency Experiments

The absorption efficiencies of chlorophyte and cyanobacterial picoplankton by *M. mercenaria* are relatively low, 17.6% to 31.1%, compared to the absorption efficiencies of *P. paradoxa* by hard clams, 80.3% and 86.5% (Table 3).

Within groups, the absorption efficiencies did not differ; however, between groups the absorption efficiencies of

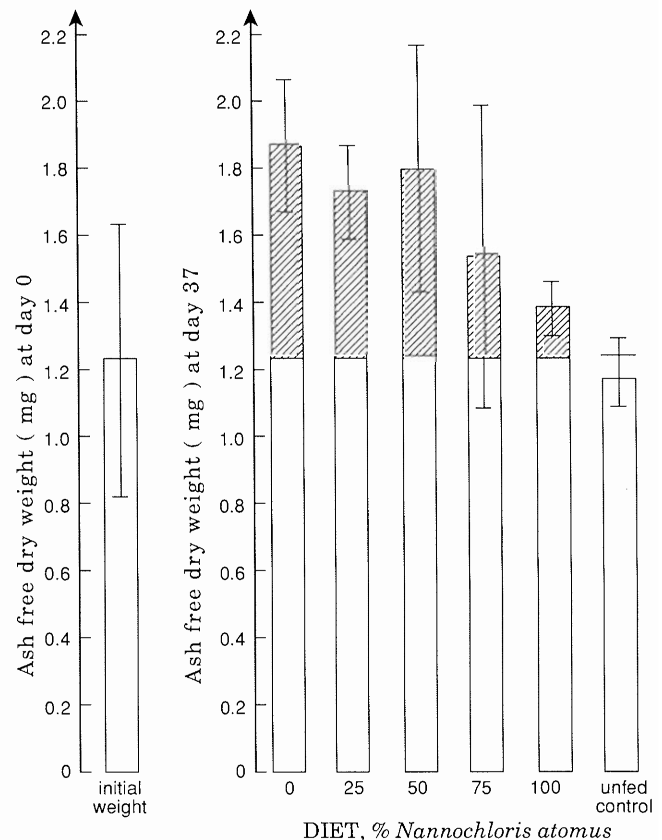

Figure 1. Mean initial weight of clams used for all experiments on the left (n = 100) and the mean final weight on day 37 of the groups of clams from each treatment (n = 48; 3 replicates) on the right. Error bars represent 95% confidence intervals. Dotted line indicates mean initial weight of quahogs. Actual data points as follows:

Algal Diet (% *P. paradoxa*: % *N. atomus*)	Ash-Free Dry Weight (mg) mean (±s.d.) (n = 48)	95% Confidence Intervals
initials	1.23 (±0.21)	0.82–1.64
100/0	1.86 (±0.10)	1.66–2.06
75/25	1.72 (±0.07)	1.58–1.86
50/50	1.79 (±0.19)	1.42–2.16
25/75	1.53 (±0.04)	1.08–1.98
0/100	1.37 (±0.04)	1.29–1.45
no food	1.18 (±0.05)	1.08–1.28

TABLE 3.

Absorption efficiency of organic matter by hard clams fed various picoplankton species. Variance of a quotient was estimated as = $(u_x/u_y)^2$ $(var[x]/u_x^2 + var[y]/u_y^2)$. For all treatments, n = 7. 95% confidence intervals calculated as: y ± (1.96)s where s = $\sqrt{\text{variance of quotient}}$ (Sokel and Rohlf, 1969)

Species. (Exp. #)	Mean[a] Absorption Efficiency (%)	95% Confidence Intervals
P. paradoxa (I)	80.3	68.5–92.1
P. paradoxa (II)	86.5	71.2–101.8
N. atomus (I)	23.8	10.9–58.5
Say II (II)	17.6	−49.3–84.4
ASN C-3 (I)	29.4	11.5–47.2
Syn a (II)	31.1	−23.6–85.8

[a] See Equation 1.

each "small form" species differed from that of *P. paradoxa* (Table 4).

DISCUSSION

The hypothesis tested in this study examined whether "small forms" in unialgal systems could support growth in quahogs, *M. mercenaria*. Preliminary experiments indicated that hard clams are capable of clearing "small form" cells from suspension; however, the results of the growth experiment indicated that hard clams do not grow on *Nannochloris atomus*. The results also suggest that when juvenile hard clams feed on a diet of "small forms" in combination with a good food source, they grow in some relation to the percent contribution of the good food source to the diet. One explanation for the lack of growth in hard clams is the inability of *M. mercenaria* to absorb carbon from the algae and cyanobacteria. The results of the double-labeling radiotracer experiments revealed very low absorption efficiencies by hard clams of the "small form" cells tested, whereas they have a high carbon absorption efficiency when fed *Pseudoisochrysis paradoxa*. The absorption efficiencies of the "small form" cells appear to be too low to support significant growth in *M. mercenaria* under unialgal conditions.

Several hypotheses have been suggested to explain the observed differences in food value of algal species (Lackey 1951, Ryther 1954, Claus 1969, Epifanio 1976, Langdon & Waldock 1980, Bayne 1983, Nelson & Siddall 1988). The algal cells may be so small that they are not efficiently retained by the gills of the bivalves. They may produce toxic metabolites which inhibit the filtering mechanism of the clam, be indigestible, or not provide essential nutrients if digested.

The results from the present study, showing that *M. mercenaria* absorbed very little organic matter (<31%) from any of the four "small form" species tested suggest that these cells may be indigestible. The relative digestibility of various algal species due to their chemical composition is also a possible explanation (Epifanio 1979). The theca of both *Carteria chui* and *Platymonas suecica* is nonrigid and composed of complex polysaccharides (not cellulose) and proteins (Lewin 1958,, Roberts et al. 1972). Digestion of this material may be an extracellular process (Owen 1974). Epifanio (1979) proposed that if hard clams and oysters could only accomplish complete extracellular digestion of the theca with some difficulty, digestion of a given volume of *P. suecica* would take longer than digestion of a similar volume of *I. galbana* or *T. pseudonana*. He also pointed out that if the rate of ingestion of *P. suecica* were relatively low, i.e., low food ration, the rate of extracellular digestion might be sufficient to allow complete assimilation of the ration. If the ration were high, however, the rate of ingestion might be such that the stomach would reach maximum capacity and become clogged. One response to such a situation is to shunt partially digested food to the midgut without its entering the digestive diverticula (Winter 1974).

In the preliminary tests of assumptions for the absorption efficiency experiments, ^{14}C and ^{51}Cr were found to have a significantly different gut passage time when hard clams, *M. mercenaria,* were fed labeled *P. paradoxa,* a highly digestible food source (Bricelj et al. 1984). A possible explanation is that the two isotopes follow different pathways through the gut after initial breakdown of cells in the stomach (Bricelj et al. 1984). The ^{51}Cr, absorbed onto the fragmented cell wall which may be less digestible than the cell contents, may be shunted directly to the intestine; whereas the ^{14}C, which is incorporated intracellularly by

TABLE 4.

Results of t-test of the differences in the mean absorption efficiencies of hard clams, *M. mercenaria* (28–35 mm in shell length) fed diets of *P. paradoxa* (Va 12) and several "small form" species: chlorophytes, *N. atomus* (GSB), *Stichococcus* clones, Say II and Say III, and cyanobacteria *Synechococcus* clones, Syn a and ASN C-3, n = 7 (t-test: Sokal and Rohlf, 1979). Symbols as in Table 2.

Test	t_s	Significance
Va 12 × Va 12	1.45	ns
GSB × Va 12	7.85	***
ASN C-3 × Va 12	9.46	***
Say 2 × Va 12	5.84	***
Syn a × Va 12	5.47	***
GSB × Va 12	9.35	***
ASN C-3 × Va 12	12.40	***
Say 2 × Va 12	6.49	***
Syn a × Va 12	6.29	***
Say 2 × Syn a	1.09	ns
GSB × ASN C-3	1.00	ns
Say 2 × GSB	1.12	ns
GSB × Syn a	0.13	ns
Say 2 × ASN C-3	1.81	ns
ASN C-3 × Syn a	0.58	ns

the algae, would pass directly into the digestive gland, before egestion or absorption (Bricelj et al. 1984).

On the other hand, the ability of the bivalve to digest specific proteins may determine its growth (Walne 1973). A low level of a good food such as *Isochrysis galbana* produced the same accumulation of carbohydrate and high nitrogen:glucose ratio in tissue as did all levels of a relatively poor diet (Walne 1973). Walne suggested that the assimilation of nitrogen (protein) may regulate growth, whereas there was much variation in the accumulation of carbohydrate. The proteins differ between species and vary with culture conditions (Walne 1973). Walne (1974) also suggested that bivalves may be unable to digest the cytoplasmic boundaries of some algae.

The assimilation of *P. suecica* by juvenile oysters, *Crassostrea virginica* has been shown to be relatively low, (A.E. = 6.5%) (Romberger & Epifanio 1980). This suggests that the alga was relatively indigestible and inhibited growth (Romberger & Epifanio 1980). The assimilation of a mixed diet of *P. suecica* and *I. galbana* by the oysters appeared to be additive while growth appeared to be non-additive. Ingestion of the combined algal diet was higher than ingestion of either algal species singly, so that although *P. suecica* still presented digestive problems, the increased ingestion of the diet apparently resulted in non-additive growth (Romberger & Epifanio 1980).

The cell wall of some "small form" species contains sporopellenin, an indigestible, highly resistant, polymerized carotenoid present in pollen grains and spores (Faegri & Iverson 1964). A strain of *Chlorella*, an organism related to *Nannochloris* (Hargraves et al. 1989), an alga described in Great South Bay and Moriches Bay, a strain of *Scenedesmus*, and two of three strains of *Prototheca* contain sporopollenin in their trilaminar wall component (Atkinson et al. 1972). Sporopollenin has been found in strains of *Nannochloris* (Sarokin 1981). There may be a correlation between the morphological attribute of trilaminar components and the presence of sporopollenin (Atkinson et al. 1972). The indigestibility and possibly the harmful effects of *Chlorella* as food may be attributed to the presence of sporopollenin (Schwimmer & Schwimmer 1964). *Chlorella* cells (clone 211/8) pass through the digestive system of a snail unharmed (Atkinson et al. 1972). Observations during the present study indicate that some of the "small form" species found in Great South Bay and Moriches Bay, NY pass through the digestive system of the hard clam intact. Other occurrences of "small form" species passing through digestive systems intact have been observed in nature and in the laboratory (Shumway, unpublished data). In coastal regions, chroococcoid cyanobacteria (genus *Synechococcus*) have been found intact in both the gut and fecal pellets of calanoid copepods, *Calanus finmarchicus*, without any apparent ultrastructure degradation (Johnson et al. 1983).

Cyanobacteria and a *Chlorella*-like cell have also been found intact in fecal pellets of salps and pteropods and in marine snow (Silver & Bruland 1981, Silver & Alldredge 1981). Some of these small algae contain sporopollenin in their walls and the presence of this inert material is suggested as the main reason these algae are resistant to digestion (Silver & Bruland 1981). This suggestion is in agreement with the hypothesis of the present paper: that sporopollenin in the walls of some cyanobacteria and chlorophyte cells prevent the hard clam, *M. mercenaria*, from efficiently digesting the "small form" cells and utilizing the absorbed carbon for growth.

Several phytoplankton species, besides "small form" species can cause nuisance "tides". Nuisance bloom species can affect growth in bivalves and bivalve larvae in several ways, as described above. Among these is the "brown tide" alga, *Aureococcus anophagefferens*. Recently, dense blooms of this 2 μm chrysophyte occurred in Narragansett Bay, Rhode Island (Sieburth et al. 1988) and Long Island embayments causing extensive damage to the scallop industry in Peconic Bay (Bricelj et al. 1987).

This alga appears to be deleterious to growth in bivalves and bivalve larvae through chronic toxicity at high cell densities (Tracey 1988, Bricelj & Kuenstner 1989, Gallager et al. 1989, Bricelj et al. 1989b, Shumway 1990, Draper et al. 1990). The toxic effects of *A. anophagefferens* on scallop larvae (Gallager et al. 1989) at high cell densities appear to be caused by low capture efficiency of the cells. Results suggest that a cell surface property may interfere with the capture mechanism. In addition, the presence of *A. anophagefferens* cells in a mixed species medium cause the larvae subsequently to reject most cells after capture regardless of nutritional value (Gallager et al. 1989). Draper et al. (1990) suggest that the toxic effects of high cell densities of *A. anophagefferens* on *M. mercenaria* and *M. edulis* are caused by inhibition of the gill cilia resulting in cessation of feeding.

Small cell size and high density of *A. anophagefferens* during "brown tides" may have some detrimental effect on bivalve growth, but it does not appear to be enough to account for the starvation by scallops in the field (Draper et al. 1990). Indigestibility apparently plays no role in the deleterious effects of the "brown tide" alga on mussels and scallops, as both bivalves can absorb the alga with a maximum efficiency of about 90% (Bricelj & Kuenstner 1989). The causes of starvation by scallops in the field exposed to the small, brown tide alga, then, are due to cell contents or cell wall composition, not cell size.

The "small form" algae in the present study, in contrast, do not appear to be toxic. The cells (2–4 μm) are captured, with a range of efficiencies (Table 1). The "small form" cells can be assimilated to some extent: the absorption efficiencies (AE) of the "small forms" by clams ranged from 17.6%–31.1%. This AE level, does not however support growth in hard clams. Results of this study suggest that hard clams are inhibited from using the

carbon in the "small form" cells for growth. This inhibition could be caused by the indigestible polymerized carotenoid, sporopollenin, found in the walls of some cyanobacteria and chlorophyte cells.

The implications of these results extend to laboratory rearing of bivalves as well as the growth of the naturally occurring commercial species. *Nannochloris* and *Synococcus* do not support growth in *M. mercenaria* and should not be used in laboratory rearing of the bivalve. Further, pollution sources which alter the ambient nutrient concentrations and N:P ratio and directly or indirectly promote dominance of the faster-growing cyanobacteria and chlorophytes, should be controlled in areas that support commercially important bivalve fisheries.

ACKNOWLEDGMENTS

We thank G. Lopez for his guidance and assistance with radio-tracer experiments and L. Campbell and R. R. L. Guillard for supplying cultures. We also thank V. M. Bricelj for her continued interest in the research and for critically reading the manuscript and R. R. L. Guillard for thought-provoking discussions. This work is the result of research sponsored by the NOAA National Sea Grant College Program, U.S. Department of Commerce, under Grant NA81AA-d-00027 to the New York Sea Grant Institute. The U.S. Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon.

LITERATURE CITED

Atkinson, A. W., Jr., B. E. S. Gunning & P. C. L. John. 1972. Sporopollenin in the cell wall of Chlorella and other algae: ultrastructure, chemistry, and incorporation of ^{14}C-Acetate, studied in synchronous cultures. *Planta (Berl.)* 107:1–32.

Bass, A. E. 1983. Growth of the hard clams, *Mercenaria mercenaria,* feeding on chlorophyte and cyanobacterial picoplankton. M.S. thesis, Marine Sciences Research Center, State University of New York at Stony Brook, Stony Brook, New York, 66 pp.

Bayne, B. L. 1983. Physiological ecology of marine molluscan larvae. The Mollusca, Vol. 3. In Wilbur, Karl M. (ed.). Academic Press, New York, pp. 299–343.

Bricelj, V. Monica & Susan H. Kuenstner. 1989. Effects of the "Brown Tide" on the Feeding Physiology and Growth of Bay Scallops and Mussels. In "Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms." Cosper, E. M., V. M. Bricelj & E. J. Carpenter (eds.). Coastal and Estuarine Studies. Springer-Verlag. 1989. pp. 491–509.

Bricelj, V. M., A. E. Bass & G. R. Lopez. 1984. Absorption and gut passage time of microalgae in a suspension feeder: an evaluation of the ^{51}Cr:^{14}C twin tracer technique. *Mar. Ecol. Prog. Ser.* 17:57–63.

Bricelj, V. M., J. Epp & R. E. Malouf. 1987. Intraspecific variation in reproductive and somatic growth cycles of the bay scallop, *Argopecten irradians. Mar. Ecol. Prog. Ser.* 36:123–137.

Bricelj, V. M., N. S. Fisher, G. B. Guckert & F.-L. Chu. 1989. Lipid composition and nutritional value of the brown tide alga, *Aureococcus anophagefferens*. In "Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms." Cosper, E. M., V. M. Bricelj & E. J. Carpenter (eds.). Coastal and Estuarine Studies. Springer-Verlag, Berlin, pp. 85–100.

Bruno, S. F., R. D. Staker, G. D. Sharma & J. T. Turner. 1983. Primary productivity and phytoplankton size fraction dominance in a temperate north Atlantic estuary. *Estuaries* 6:200–211.

Calow, P. & C. R. Fletcher. 1972. A new radiotracer technique involving ^{14}C and ^{51}Cr for estimating the assimilation efficiency of aquatic primary producers. *Oecologia (Berl.)* 9:155–170.

Cammen, L. M. 1977. On the use of liquid scintillation counting of ^{51}Cr and ^{14}C in the twin tracer method of measuring assimilation efficiency. *Oecologia (Berl.)* 30:249–251.

Cammen, L. M. 1980. The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Neireis succi*. *Mar. Biol.* 61:9–20.

Claus, G. 1969. Life and pollution in Great South Bay. *Underwater Naturalist* 7(1):11–16.

Cosper, E. M., W. C. Dennison, E. J. Carpenter, V. M. Bricelj, J. G. Mitchell, S. H. Kuenstner, D. Colflesh & M. Dewey. 1987. Recurrent and persistent "brown tide" blooms perturb coastal marine ecosystems. *Estuaries* 10:284–290.

Cosper, E. M., V. M. Bricelj & E. J. Carpenter (eds.). 1989. Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms. Coastal and Estuarine Studies. Springer-Verlag, Berlin. 800 pp.

Dahl, E., O. Lindahl, E. Paashe & J. Throndsen. 1989. The *Crysochromulina polylepis* bloom in Scandanavian waters during spring 1988. In "Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms." Cosper, E. M., V. M. Bricelj & E. J. Carpenter (eds.). Coastal and Estuarine Studies. Springer-Verlag. 1989. pp. 381–405.

Draper,C., L. F. Gainey, S. E. Shumway & L. Shapiro. 1990. Effects of *Aureococcus anophagefferens* ("Brown Tide") on the lateral cilia of 5 species of bivalve molluscs. In "Toxic Marine Phytoplankton." E. Graneli, B. Sundström, L. Edler & D. M. Anderson (eds.). Elsevier Science Publishing Co., Inc. pp. 128–131.

Davis, H. C. & R. R. L. Guillard. 1958. Relative value of ten genera of micro-organisms as food for oyster and clam larvae. *U.S. Fish. Wildl. Serv. Fish. Bull.* 58:293–304.

Dupuy, J. L., N. T. Windsor & C. E. Sutton. 1977. Manual for design and operation of an oyster seed hatchery for the American oyster, *Crassostrea virginica*. Special Report No. 142 in Applied Marine Science and Ocean Engineering of The Virginia Institute of Marine Science, Cloucester Point, Virginia. June, 1977. 111 pp.

Epifanio, C. E. 1976. Culture and bivalve molluscs in recirculating systems, nutrition. In Proceedings First International Conference on Aquaculture Nutrition (K. S. Price, W. N. Shaw & K. S. Danberg, eds.) pp. 173–194.

Epifanio, C. E. 1979. Growth in bivalve molluscs: Nutritional effects of two or more species of algae in diets fed to the American oyster *Crassostrea virginica* (Gmelin) and the hard clam *Mercenaria mercenaria* (L.). Aquaculture 18:1–12.

Epifanio, C. E., C. M. Logan & C. Turk. 1975. Culture of six species of bivalves in a re-circulating seawater system. *Proc. Euro. Mar. Biol. Symp.* 10:97–108.

Eppley, R. W. & C. S. Weiler. 1979. The dominance of nanoplankton as an indicator of marine pollution: a critique. *Oceanol. Acta.* 2(2):241–245.

Faegri, K. & J. Iverson. 1964. Textbook of Pollen Analysis. Copenhagen: Munksgaard.

Gabbott, P. A. & A. J. M. Walker. 1971. Changes in the condition index and biochemical content of adult oysters (*Ostrea edulis* (L.)) maintained under hatchery conditions. *J. Int. Explor. Mer.* 34(1):99–106.

Gallager, S. M., D. K. Stoecker & V. M. Bricelj. 1989. Effects of the brown tide alga on growth, feeding physiology and locomotory behavior of scallop larvae (*Argopecten irradians*). In "Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms." Cosper, E. M., V. M. Bricelj & E. J. Carpenter (eds.). Coastal and Estuarine Studies. Springer-Verlag. 1989. pp. 510–541.

Graneli, E., P. Carlsson, P. Olsson, B. Sundström, W. Graneli & O. Lindahl. 1989. From anoxia to fish poisoning: The last ten years of phytoplankton blooms in swedish marine waters. In "Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms." Cosper, E. M., V. M. Bricelj & E. J. Carpenter (eds.). Coastal and Estuarine Studies. Springer-Verlag, 1989. pp. 407–427.

Guillard, R. R. L. 1975. Culture of phytoplankton for feeding marine invertebrates. In Culture of Marine Invertebrate Animals. Ed. W. L. Smith & M. H. Chanley, Plenum Pub. Corp. NY. pp. 29–59.

Hargrave, P. E., R. D. Vaillancourt & G. A. Jolly. 1989. Autotrophic picoplankton in Narragansett Bay and their interaction with microplankton. In "Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms." Cosper, E. M., V. M. Bricelj & E. J. Carpenter (eds.). Coastal and Estuarine Studies. Springer-Verlag, 1989. pp. 23–38.

Hibberd, D. J. 1981. Notes on the taxomony and nomenclature of the algal classes Eustigmatrophyceae and Tribophyceae (synonym Xanthophyceae). *Bot. J. Lin. Soc.* 82:93–119.

Johnson, P. W., Huai-Shu Xu & J. McN. Sieburth. 1982. The utilization of chroococcoid cyanobacteria by marine phytoplankters but not by calanoid copepods. *Annales de L'Institut Oceanographique.* 58:297–388.

Lackey, J. B. 1951. The rehabilitation of Great South Bay. Consultant. Science Ed., The Blackiston Co., Philadelphia, PA. 25 pp.

Langdon, C. J. & M. J. Waldock. 1981. The algal and artificial diets on growth and fatty acid composition of *Crassostrea gigas* spat. *J. Mar. Biol. Ass. U.K.* 61:431–448.

Lewin, R. A. 1958. The cell wall of *Platymonas. J. Gen. Microbiol.* 19:87–90.

Lively, J. S. 1981. Primary production and abundance of phytoplankton in a barrier island estuary. M.S. Thesis. State University of New York at Stony Brook. 63 pp.

Lopez, G. R. & I-J. Cheng. 1982. Ingestion selectivity of sedimentary organic matter by the deposit-feeder *Nucula annulata* (Bivalva: Nuculidae). *Mar. Ecol. Prog. Ser.* 8:279–282.

Lopez, G. R. & I-J Cheng. 1983. Synoptic measurements of ingestion selectivity, and absorption efficiency of natural foods in the deposit-feeding molluscs *Nucula annulata* (Vivalvia) and *Hydrobia totteni* (Gastropoda). *Mar. Ecol.* 2:55–62.

Malone, T. C. 1971. The relative importance of nanoplankton and net-plankton as primary producers in the California Current System. *Fish. Bull.* 69:799–820.

Malouf, R. E. & W. P. Breese. 1978. Intensive culture of the Pacific oyster, *Crassostrea gigas* (Thunberg), in heated effluents. Oregon State Univ. Sea Grant College Program. Publication no. ORESU-T-78-803. 41 pp.

Nielsen, M. V. & Strømgren. 1989. Shell length growth of mussels (*Mytilus edulis*) as a bioassay for toxic algae. Abstract only. Fourth International Conference on Toxic Marine Phytoplankton, Lund, Sweden, June 26–30, 1989.

Nelson, C. L. & S. E. Siddall. 1988. Effects of an algal bloom isolate on growth and survival of bay scallop (*Argopecten irradians*) larvae. *J. Shellfish Res.* 7:683–694.

Newell, G. E. & R. C. Newell. 1977. Marine Plankton, A Practical Guide (5th ed.). Hutchinson of London. 244 pp.

Owen, G. 1974. Feeding and digestion in the bivalvia. In O. Lowenstein (ed.). Advances in comparative physiology and biochemistry. V. 5 Academic Press, New York, NY pp 1–35.

Redfield, A. C. 1951. Report on a survey of the hydrography of Great South Bay made during the summer of 1950 for the town of Islip, NY. Technical Report from Woods Hole Oceanographic Institution. 30 pp. Unpublished manuscript.

Redfield, A. C. 1952. Report to the towns of Brookhaven and Islip, NY on the hydrography of Great South Bay and Moriches Bay. Unpublished manuscript. Reference no. 52-26. Oceanographic Institution, Woods Hole, MA. 16 pp.

Rice, T. R. & R. J. Smith. 1958. Filtering rates of the hard clam, *Venus mercenaria* determined with radioactive phytoplankton. *Fish. Bull.* 58:73–82.

Roberts, K., M. Gurney-Smith & G. L. Hills. 1972. Structure, composition, and morphogenesis of the cell wall of *Chlamydomanas reinhardii*. I. Ultrastructure and preliminary chemical analyses. *J. Ultrastruct. Res.* 40:599–613.

Romberger, H. P. & C. E. Epifanio. 1981. Comparative effects of diets consisting of one or two algal species upon assimilation efficiencies and growth of juvenile oysters, *Crassostrea virginica* (Gmelin). *Aquaculture* 25:77–87.

Ryther, J. H. 1954. The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, New York. *Biol. Bull.* 106:198–209.

Sarokin, D. J. 1981. Ultrastructure and taxomony of the genus *Nannochloris* (Chlorophyceae). M.S. Thesis. State Univ. of NY at Stony Brook, 53 pp.

Schwimmer, D. & M. Schwimmer. 1964. Algae and medicine. In Algae and Man. D. F. Jackson, ed. p. 368–412. New York: Plenum Press.

Shumway, S. E. 1990. A Review of the Effects of Algal Blooms on Shellfish and Aquaculture. *J. World Aquac. Soc.* 21:65–104.

Sieburth, J. McN., P. W. Johnson & P. E. Hargraves. 1988. Ultrastructure and ecology of *Aureococcos anophagefferens* gen. et. sp. nov. (Chrysophyceae): the dominant picoplankter during a bloom in Narragansett Bay, Rhode Island, Summer 1985. *J. Phycol.* 24:416–425.

Silver, M. W. & A. L. Alldredge. 1981. Bathypelagic marine snow: deep-sea algal and detrital community. *J. Mar. Res.* 39:501–530.

Silver, N. W. & K. W. Bruland. 1981. Differential feeding and fecal pellet composition of salps and pteropods, and the possible origin of deep-water flora and olive-green "cells". *Mar. Biol.* 62:263–273.

Sokal, R. R. & F. J. Rohlf. 1969. Biometry. W. H. Freeman and Company, San Francisco. 776 pp.

Tester, P. A., P. K. Fowler & J. T. Turner. 1989. Gulf Stream transport of the toxic red tide dinoflagellate *Ptychodiscus brevis* from Florida to North Carolina. In "Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms. Cosper, E. M., V. M. Bricelj & E. J. Carpenter (eds.). Coastal and Estuarine Studies. Springer-Verlag. 1989. pp. 349–358.

Tiu, T. A., D. Vaughan, T. Chiles & K. Bird. 1989. Food value of euryptopic microalgae to larvae of *Cyrtopleura costata* (Linnaeus, 1758), *Crassostrea virginica* (Gmelin, 1791) and *Mercenaria mercenaria* (Linnaeus, 1758). *J. Shellfish Res.* 8:399–405.

Tracey, G. A., P. W. Johnson, R. L. Steele, P. E. Hargraves & J. McN. Sieburth. 1988. A shift in photosynthetic picoplankton composition and its effect on bivalve mollusk nutrition: the 1958 "brown tide" in Narragansett Bay, Rhode Island. *J. Shellfish. Res.* 7:671–675.

Tracey, G. A. 1988. Feeding reduction, reproductive failure, and mortality in *Mytilus edulis* during the 1985 "brown tide" in Narragansett Bay, Rhode Island. *Mar. Ecol. Prog. Ser.* 50:73–81.

Walne, P. R. 1973. Growth rates and nitrogen and carbohydrate contents of juvenile clams, *Saxidomus giganteus,* fed three species of algae. *J. Fish. Res. Board Can.* 30:1825–1830.

Walne, P. R. 1974. Culture of bivalve molluscs 50 years experience at Conwy. Fishing News (Books) Ltd., Surrey. 137 pp.

Ward, J. E. & N. M. Targett. 1989. Are metabolites from the brown tide alga, *Aureococcus anophagefferens,* deleterious to mussel feeding behavior? In "Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms." Cosper, E. M., V. M. Bricelj & E. J. Carpenter (eds.). Coastal and Estuarine Studies. Springer-Verlag. 1989. pp. 543–556.

Wrightman, J. A. 1975. An improved technique for measuring assimilation efficiency by the ^{51}Cr and ^{14}C twin tracer method. *Oecologia (Berl.)* 19:273–284.

Winter, J. E. 1974. Growth in *Mytilus edulis* using different types of food. *Ber. Dtsch. Wiss. Komm. Meeresforsch.* 23:360–375.

Yentsch, C. S. & J. H. Ryther. 1959. Relative significance of the net phytoplankton and nanoplankton in the waters of Vineyard Sound. *J. Cons. Perm. Int. Explor. Mer.* 24:231–238.