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Enhanced growth of a filter-feeding bivalve by a deposit-feeding polychaete by means of nutrient regeneration

by James R. Weinberg¹ and Robert B. Whitlatch¹

ABSTRACT

Sediment reworking and tube irrigation by the deposit-feeding polychaete, *Clymenella torquata*, reduced the quantity of particulate organic matter (POM) at the sediment-water interface and increased concentrations of dissolved nutrients (nitrite, ammonia, silicate, phosphate) in the water overlying laboratory microcosms. To determine the effect of these changes on growth of the filter-feeding bivalve, *Gemma gemma*, clams of the same initial size were grown under different laboratory conditions, representing all combinations of the following three treatments: (a) presence or absence of light, (b) presence or absence of *C. torquata*, and (c) proximity to *C. torquata* (clams living in sediment with worms or in sediment-filled microcosms positioned 1 cm above the worms).

Clams grown in sediment with *C. torquata*, and in light, experienced less POM at the sediment surface than clams elevated in the water column, due to the burial of POM by accumulations of worm-defecated mineral particles. Among clams grown in the same tank, those in sediment with worms grew faster ($p < 0.1$) than those elevated above worms, indicating that worm-induced POM reduction at the sediment surface, or factors correlated with it, were responsible for increased clam growth.

Clams elevated above worms (in light) were exposed to higher concentrations of dissolved nutrients and microflora than control populations in another tank which did not contain *C. torquata*. Elevated clams grew faster ($p < 0.1$) when worms were present in the tank than when worms were absent. Worm activity transported nutrient rich sedimentary pore water into the overlying water, apparently stimulating microfloral populations which supported improved clam growth. The effects of *C. torquata* on *G. gemma* growth may be one mechanism contributing to the common association of these species in New England sand flats.

1. Introduction

Activities of infaunal deposit-feeding organisms affect physical and chemical characteristics at the sediment-water interface (Berner, 1976; Rhoads *et al.*, 1977; Aller, 1978a,b; Aller and Yingst, 1978). Examples of these effects include changes in water turbidity (Rhoads, 1973), fecal pellet accumulation (Rhoads *et al.*, 1977), water content of sediment (Rhoads and Young, 1970; 1971; Gust and Harrison, 1981) and quantity of organic mineral aggregates (Weinberg, 1979). Furthermore, deposit

1. Department of Marine Sciences and Biological Sciences Group, The University of Connecticut, Marine Sciences Institute, Groton, Connecticut, 06340, U.S.A.

feeders and microbial activity can increase remineralization rates of benthic organic matter (Welsh, 1975; Fenchel and Harrison, 1976; Aller and Yingst, 1978) which can increase the flux of dissolved and particulate nutrients from sediments to the overlying water column (Rhoads *et al.*, 1975; Rowe and Smith, 1977; Hartwig, 1976; Nixon *et al.*, 1976; Boynton *et al.*, 1980).

As growth (Coe, 1948; Loosanoff and Tommers, 1948; Pratt and Campbell, 1956; Tenore *et al.*, 1968; Rhoads, 1973; Rhoads *et al.*, 1975) and distributions (Rhoads and Young, 1970) of filter-feeding bivalves are affected by sedimentary characteristics and food availability, it is important to investigate the effects of deposit feeders on the benthic environment to explain characteristics of filter-feeding bivalve populations. The effect of deposit feeders on filter feeders can be either positive or negative. Rhoads and Young (1970), Rhoads (1973) and Rhoads *et al.* (1975) demonstrated that filter-feeding bivalves grew faster while ingesting organic particles which were resuspended by benthic deposit feeders. However, clams could not naturally inhabit this substratum because deposit feeders are capable of destabilizing sediments, which leads to burial of larvae and clogging of eulamellibranch filtering structures. Loosanoff and Tommers (1948), Loosanoff (1962) and Kiorboe *et al.* (1980; 1981) have also shown that filter-feeding bivalve growth can increase or decrease depending on level of resuspended silt and organic matter.

This study examined the effect of a deposit-feeding polychaete, *Clymenella torquata*, on growth of a filter-feeding bivalve, *Gemma gemma*. Both species often coexist at high densities in New England sandflats (Sanders *et al.*, 1962; Mills, 1967; Dobbs, 1981) and previous studies (Weinberg, 1983) demonstrated that *G. gemma* grew at a faster rate in the presence of *C. torquata*. We performed an experiment to ascertain which mechanisms control *G. gemma's* growth rate. Four hypotheses were tested:

- (1) *G. gemma* has a higher growth rate in sediments occupied by *C. torquata* because the polychaete reduces particulate organic matter (POM) at the sediment-water interface. POM clogs *G. gemma's* filtering structures.
- (2) Bioturbation by *C. torquata* increases the food supply for *G. gemma* through regeneration of nutrients from the sediment to the overlying water.
- (3) *G. gemma* utilizes photosynthetic microorganisms for its growth more than dissolved nutrients.
- (4) Food levels for the bivalves in the overlying water increase with proximity to *C. torquata* and should be reflected by enhanced bivalve growth.

2. Materials and methods

a. Study area. Field collections were made in Little Narragansett Bay, north of the barrier island, Sandy Point, Rhode Island, at the eastern end of Long Island Sound.

The site is a shallow (20–30 cm deep at mean low water) subtidal sandflat consisting of well sorted, medium sized, sand (90% by weight is $\geq 250 \mu\text{m}$; Dobbs, 1981). *G. gemma* and *C. torquata* are common members of the infauna (Dobbs, 1981; Weinberg, 1983). Further descriptions of this area and its benthic fauna can be found in Ehinger *et al.* (1978) and Dobbs (1981).

b. The organisms. *C. torquata* inhabits vertical tubes and ingests sediment from the tube base at depths of 5–30 cm (Mangum, 1964; Rhoads and Stanley, 1965; Aller, 1978b). In addition to pumping water through their tubes for respiration (Mangum, 1964), the worms typically defecate unconsolidated sediment 2–4 times per hour (Dobbs, 1981) into the water column. Defecated material, estimated at 87 liters/m²/yr in Barnstable Harbor (Rhoads and Stanley, 1965), is ejected and rises 1–4 cm above the sediment surface before deposition (personal observation). Other aspects of the biology of this species are given by Newell (1951) and Pilgrim (1960).

G. gemma are small bivalves (adults approximately 3 mm in length) with short (<3 mm) siphons (Sellmer, 1967). Individuals burrow and filter-feed from the sediment-water interface (Bradley and Cooke, 1959). Further descriptions of this species are given in Green and Hobson (1970) and Thompson (1982).

c. Laboratory experiment. A laboratory experiment was conducted (June 26, 1981–August 18, 1981) to study the effects of *C. torquata* on organic content of surface sediments, nutrient concentrations in the overlying sea water and growth of *G. gemma*. The experiment was conducted in four tanks (26 cm deep and 35 cm sides). Each tank represented one of the four combinations of two treatments: (1) Illumination (presence/absence of light), and (2) Biota (presence/absence of *C. torquata* referred to as “Worm” and “no Worm” in microcosms containing sediment. Two adult *C. torquata* (5 cm in length) were added to every microcosm in the two “Worm” tanks on June 27, 1981. There was no *C. torquata* mortality during the experiment. This *C. torquata* density was common at Sandy Point (Dobbs, 1981) and the worm defecation mounds changed the topography of the sediment surface within each microcosm. No worms were added to the other two tanks.

Each tank contained 14 microcosms (5 cm in diameter and 14 cm deep), which had open tops and mesh (300 μm) bottoms. This permitted sea water circulation from above and below each microcosm. Each microcosm contained only azoic sediment from Sandy Point (sieved through a 1 mm mesh and dried) before addition of organisms.

Fresh sea water, added to all tanks every third day, was filtered through a 300 μm net to remove macrofaunal larvae. Water overflowed from the tops of the tanks during water replacement. Currents were present in the tanks only when water was flowing in. Water within tanks was continuously aerated. Every five days detritus was collected from sea water tables at the University of Connecticut’s Marine Research Laboratory and heated to 95°C to kill larvae. It was cooled and added to the microcosms (0.8

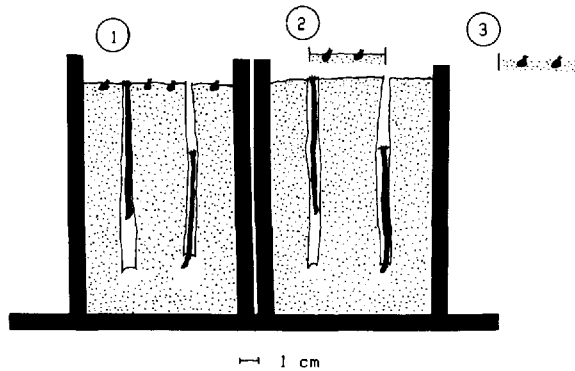


Figure 1. Three clam feeding positions in each of four tanks. Clams are depicted at sediment surface (number of clams depicted should not be used to estimate density; see text). Worms are depicted in their tubes in microcosms which contain sediment (stippled). (Worms were only placed into two of the four tanks.)

ml \pm 0.3 ml, mean \pm 95% C. I. per microcosm) to serve as a food source and bacterial substrate.

Equal densities (1 clam per 1.2 cm²) of *G. gemma* (all 2.4 mm in length) were placed in three positions in each tank on June 28, 1981 (Fig. 1). This density was less than average natural density and was chosen to reduce possible intraspecific competition. Clams in Position 1 occupied the surface sediment of the microcosms (in two tanks, this sediment also contained worms). Clams in Positions 2 and 3 were placed in small translucent containers (3.5 cm diameter and 2 cm deep; open tops and 300 μ m mesh bottoms), filled with sediment (0.5 cm deep), in the water column and 1 cm higher than the microcosms. Clams in Position 2 were directly over the center of a microcosm. Those in Position 3 were laterally displaced 4 cm from the microcosms. Seven replicates of each position were placed evenly within tanks (i.e., every replicate of Position 1 was next to a replicate from Position 2 and 3).

To test each of the worm-clam interaction hypotheses we compared the growth of clams from different treatments. Enhancement of clam growth by worms was tested by comparing clam sizes from tanks with and without worms. Hypotheses 1 and 2 involve the mechanism (e.g., POM reduction at the sediment surface vs. food supply in the overlying water) which causes increased clam growth in the presence of worms. They were tested by comparing clams grown in different positions in tanks with worms. The third and fourth hypotheses relate to the nature of the food which *G. gemma* utilizes (i.e., dissolved nutrients vs. photosynthetically produced particulates). They were tested by comparing clams raised in different illuminations and with or without worms.

Replicate ($n = 2$) sea water samples were collected from each tank and from the sea water system on August 18, 1981 for nutrient analysis. Sampled tank water had been

in tanks for 48 hours without sea water addition. Water was often present in the tanks for this duration during the experiment and we consider these samples to be representative of the relative concentrations of nutrients in the clam's environments during the experiment. Because the experiment had been in progress for seven weeks sediments had time to chemically reach steady state (R. C. Aller, personal communication) and we assume that differences in nutrient concentrations among tanks were due to treatments. Materials used to collect water samples were ultracleaned by acid leaching. Water samples (200 ml) were collected with a hand operated plastic syringe and were filtered through a 0.45 μm Nucleopore membrane by attaching a Luer-lock filtering apparatus to a syringe. Nutrient concentrations were determined colorimetrically with a Technicon Auto-analyzer by methods of Strickland and Parsons (1972). For each nutrient, a two-way (Illumination, Biota) analysis of variance (ANOVA) and *a posteriori* Duncan's tests were performed to compare treatment means.

On August 18, replicate ($n = 3$) cores of sediment (0–2 cm deep, 3.5 cm diameter) were collected from those tanks exposed to light, with and without worms, to measure the effect of worms on the quantity of organic matter at the sediment-water interface. Cores were dried (37°C, 4 days) to constant weight and were reweighed after combustion (450°C, 1 day) in a furnace (clams were picked out of the cores before drying).

After sampling surface POM, all clams were collected from all tanks and were measured. Mortality was less than 5% in all treatments and will not be considered further. The experiment was conducted for seven weeks to allow for measurable growth of clams. Grand mean clam size was estimated from seven replicate means of each position in each tank. Treatment means were compared by three-way ANOVA (Illumination, Biota, Position) and *a priori* Least Significant Difference (LSD) comparisons (Keppel, 1973).

3. Results

a. Physical effect of C. torquata. During the experiment the same quantity of POM was added to all treatment containers (see Methods). After seven weeks, quantity (i.e., grams) of POM in surface sediments with and without worms was 0.148 ± 0.012 and 0.242 ± 0.042 (mean \pm standard deviation), respectively, in tanks exposed to light. The quantity of POM present with worms was less than that without worms (t-test, $p < .05$; data were log transformed to homogenize variances). Although no quantitative samples were collected from the dark tanks, visual inspection indicated that the worms also caused a reduction of POM in the dark.

b. Nutrient regeneration effect of C. torquata. Worms significantly increased concentrations of nitrite, ammonia, silicate and phosphate in overlying sea water either in the presence or absence of light or both (Table 1; Figs. 2 a,c,d,e). Nitrate concentration was not significantly different in the various treatments (Table 1, Fig. 2b).

Table 1. Two-way ANOVA and Duncan's test results for nutrient concentrations. Treatments: I (Illumination) = presence/absence of light, B (Biota) = presence/absence of *Clymenella torquata*, I x B = interaction term. Significance: ns. = $p > .05$, * = $.05 > p > .01$, ** = $.01 > p > .001$, *** = $.001 > p$. Duncan's test: lines connect tanks whose nutrient concentrations are not significantly different. Tanks: L = light, no worms, D = dark, no worms, D,W = dark, worms, L,W = light, worms.

Nutrient	Treatment			Duncan's test increasing concentration→
	I	B	I x B	
NO ₃	ns.	ns.	ns.	
NO ₂	ns.	***	ns.	<u>L D</u> <u>D,W L,W</u>
NH ₄	***	***	**	<u>L D</u> <u>L,W D,W</u>
SiO ₂	ns.	**	ns.	<u>L D</u> <u>D,W L,W</u>
PO ₄	ns.	ns.	*	

Tanks containing worms had significantly greater concentrations of nitrite and silicate, independent of light condition (Table 1; I x B not significant; Fig. 2 a,d). In contrast, the two treatments (I, B) interacted and affected the concentrations of phosphate and ammonia (Table 1). In the dark, phosphate concentration was significantly greater when worms were present than when worms were absent (Fig.

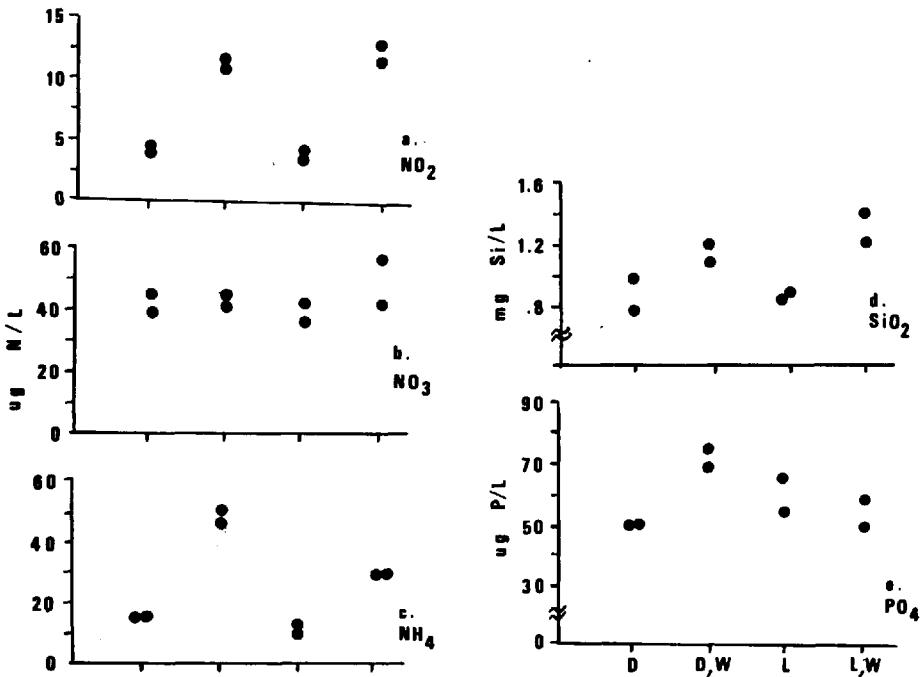


Figure 2. Concentrations of dissolved nitrogen as (a) nitrite, (b) nitrate, and (c) ammonia, silica as (d) silicate, and phosphorus as (e) phosphate, in water overlying microcosms in four tanks (see legend of Table 1 for tank code).

Table 2. Replicate nutrient concentrations in the sea water system at the time when samples were collected from the four experimental tanks.

Nutrient	NO ₂ + NO ₃ μg N/L	NH ₄ μg N/L	SiO ₂ mg Si/L	PO ₄ μg P/L
Concentration	48.16	33.41	0.82	29.40
	42.00	33.25	0.83	28.84

2e). In the light, however, phosphate concentration was independent of the presence of worms. Concentration of ammonia increased due to worm presence to a greater degree in the dark than in the light (Fig. 2c).

Nutrient concentrations of flowing sea water, collected at the same time as samples from tanks, are given in Table 2, for comparison with tank concentrations.

c. *Clam growth response.* Clams grew at different rates (Fig. 3) in response to treatments (I, B) and interactions among treatments (Table 3; I, B, P). Clams grew significantly more in the light than in the absence of light (Fig. 3, Table 3). Three *a priori* comparisons (A, B, C) involving position were made to determine the mechanism by which *C. torquata* increased clam growth (Table 4). None of the comparisons were highly significant statistically although trends did occur (i.e. LSD test, $.05 < p < .1$). Comparison A tested for the effect of *C. torquata* on clam growth due to worm-induced changes in sediment characteristics (e.g., reduction of POM at the surface). Mean clam size in Light, Worm, Position 1 (L, W, 1) was greater (Table 4, comparison A) than clam size in L, W, 2. Comparison B tested for the effect of *C. torquata* on clam growth due to worm-induced changes in overlying water chemistry

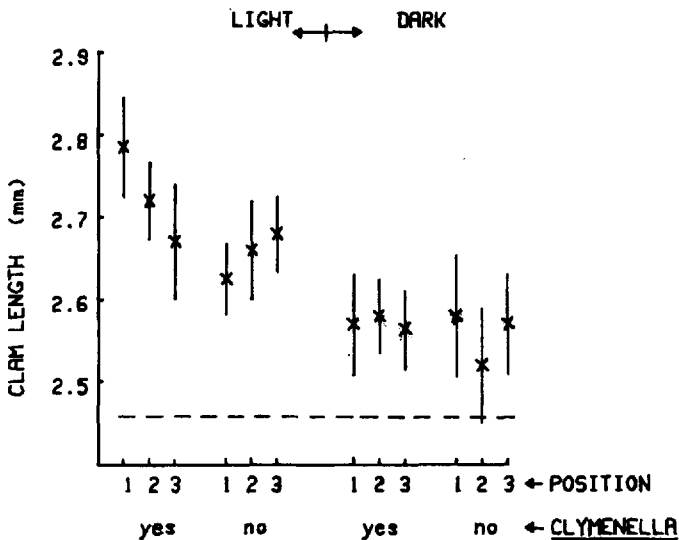


Figure 3. Clam size at end of the experiment (mean \pm 95% confidence interval). There were three treatments (see text for explanation). Dashed line gives size at start of experiment.

Table 3. Three-way ANOVA table of clam size at the end of the experiment (see legend of Table 1 for significance levels).

Source	Significance
Illumination (I)	***
Biota (B)	**
Position (P)	ns.
I × B	*
I × P	ns.
B × P	*
I × B × P	*

(e.g., nutrient concentrations). Mean clam size in L, W, 2 was greater (Table 4, comparison B) than clam size in L, 2 (no worm). Comparison C tested for the effect of proximity of worms among clams held in containers in the water column. Mean clam size in L, W, 2 was not significantly different (Table 4, comparison C) than clam size in L, W, 3, indicating that among positions in the water column proximity to the worm did not affect clam growth (Hypothesis 4).

4. Discussion

Results of our laboratory experiment indicate that *C. torquata* altered the sedimentary environment inhabited by *G. gemma* by reducing the quantity of POM at the sediment surface. This effect was probably more pronounced in the tanks than it is in nature because water currents were not present in the tanks. Organic materials deposited on the sediment surface of the microcosms were buried by *C. torquata* bioturbation. In nature, water movement (e.g., wind-generated waves, tidal currents) would disperse fine-grained material settling on the surface and the effect of *C. torquata* detrital burial would be reduced to some degree. While water movements at Sandy Point are often strong enough to move surficial sediments, *C. torquata* defecation mounds are readily distinguished by differences in their color relative to surrounding sediment. The mounds are often greyish-colored while surrounding sediments tend to be reddish-brown (personal observations), suggesting burial of surface detritus by the polychaete fecal mounds takes place in the field.

In addition to altering sedimentary organic concentrations, *C. torquata* increased concentrations of dissolved nutrients in the overlying water of the laboratory microcosms (Fig. 2). While elevated nutrient concentrations are probably the result of several factors (e.g., decomposition of detrital material, natural levels in sea water added to the tanks, treatment of the sediment used in the experiment, etc.), we consider bioturbational activity by *C. torquata* to be the primary agent responsible for nutrient differences. Other studies (e.g., Aller, 1978b; Aller and Yingst, 1978; Henriksen *et al.*, 1980; Tsuchiya and Kurichara, 1980; Gust and Harrison, 1981) also have demonstrated that biological pumping and/or reworking of sediment increases the exchange

Table 4. Three *a priori* comparisons of clam size at end of experiment. L,W,1 = clams grown in light, with worms, in Position 1; L,W,2 = light, worms, Position 2; L,W,3 = light, worms, Position 3; L,2 = light, no worms, Position 2.

Clam comparison	Significance
A. Organic matter effect of worm L,W,1 vs. L,W,2	.05 < p < .1
B. Water column effect of worm L,W,2 vs. L,2	.05 < p < .1
C. Effect of position in water with worm below L,W,2 vs. L,W,3	p > .1

flux of pore water solutes with overlying water. In the absence of benthic organisms only interstitial diffusion and advective currents at the sediment-water interface would affect upward movement of pore-water (Bricker and Troup, 1975). Although *C. torquata* did not feed when Aller (1978b) conducted an experiment similar to that reported here, Aller reported that the worm increased flux of iron, manganese, phosphate and ammonia from the sediment due to worm tube formation and maintenance of a respiratory current (described by Magnum, 1964).

One of the more perplexing results of the data shown in Figure 2 is the difference in nutrient concentrations found in light and dark tanks. Assuming worm behavior was unaffected by illumination (for a subsurface deposit-feeder this seems reasonable) we hypothesize the light-dark tank nutrient concentration differences were the result of increased photosynthetic activities of microflora in the lighted tanks. Several studies have noted that sediment regenerated nutrients can be quickly utilized by diatoms (Redfield, 1958; Peterson *et al.*, 1975; Butler *et al.*, 1979), and Zeitzschel (1980) recently suggested that 30–100% of the nutrient requirements of shallow-water phytoplankton growth comes from the sediment.

Benthic nutrient regeneration has been commonly documented on sand- and mudflats in nature (Rittenberg *et al.*, 1955; Rowe *et al.*, 1975; Hartwig, 1976; Nixon *et al.*, 1976; Rowe and Smith, 1977; Loder and Gilbert, 1980) as well as in experimental sandflats in the laboratory (e.g., Aller, 1978b). Although many investigators have attempted to determine the degree to which coupling occurs between benthic and pelagic biological processes (Furnas *et al.*, 1976; Nixon *et al.*, 1976; Boynton *et al.*, 1980), few studies have investigated the effect of benthic nutrient regeneration on benthic filter feeders (e.g., Rhoads, 1973).

While our experiment did not directly test all aspects of the four hypotheses (e.g., food levels or clogging of bivalve filtering structures), our results suggest mechanisms by which *C. torquata* increased *G. gemma* growth. We speculate that, in the light, the higher accumulation rate of POM (Hypothesis 1) at the sediment surface in microcosms not containing *C. torquata* caused the clams to have lower growth rates relative to microcosms containing the worms (Table 4; comparison A). High levels of silt and organic aggregates have a negative effect on filter-feeding bivalves by affecting

burrowing behavior and clogging feeding structures (Loosanoff and Tommers, 1948; Pratt and Campbell, 1956; Loosanoff, 1962; Tenore *et al.*, 1968; Rhoads and Young, 1970). In addition, Pratt and Campbell (1956) hypothesized that high levels of silt and organic aggregates were harmful to filter feeders because organic decomposition resulted in local depletion of oxygen and accumulation of harmful decomposition products. However, low concentrations of resuspended organic matter and silt particles can serve as food for filter-feeding bivalves (Tenore *et al.*, 1968; Kiorboe *et al.*, 1980; 1981), and increase growth rates. Additional research is needed to clarify the effect of POM composition and concentration on the growth of filter feeders.

C. torquata's effect on overlying nutrient concentrations (Hypothesis 2) also seems to have increased clam growth (Table 4, comparison B). We hypothesize *G. gemma* could not utilize dissolved nutrients for growth because clams did not grow in tank "D, W" any faster than those in "D," even though the former tank had significantly more nutrients. Apparently, *G. gemma* required photosynthetic organisms to convert dissolved nutrients into usable particulate food (Hypothesis 3). This result supports the view that uptake of dissolved compounds for growth is primarily a bacterial and plant process (Sepers, 1977), but opposes another view (see Stewart, 1979, for a review), that dissolved nutrients constitute an important food source to bivalves.

Results of this laboratory experiment demonstrate that the tubicolous, deposit-feeding polychaete, *C. torquata* changed characteristics of sediment and water. These changes caused the growth rate of the filter-feeding bivalve, *G. gemma* to increase (laboratory growth rates were lower than those occurring at Sandy Point during the same period (Weinberg, 1983)). The positive effect of this worm on the clam may be one factor contributing to the association of these species in nature.

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