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The effect of nitrogen loading on the growth rates of quahogs (*Mercenaria mercenaria*) and soft-shell clams (*Mya arenaria*) through changes in food supply

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Abstract

Development of coastal areas in Cape Cod has increased nitrogen (N) loading to the region's estuaries. Nitrogen supply limits phytoplankton, the major food source of many filter-feeding bivalves living in the estuaries, including quahogs (*Mercenaria mercenaria*) and soft-shell clams (*Mya arenaria*). N enrichment may therefore affect growth rates of these shellfish by altering their food supply in the water column. In this study, food quantity, as measured by chlorophyll *a* as a proxy for phytoplankton, was found to be higher in estuaries subject to higher N load. The food quality in these estuaries, measured by the ratio of C to N, remained constant. Results of growth rate experiments on quahogs and soft-shell clams planted in three estuaries of different N load revealed that the shellfish grew fastest in estuaries where phytoplankton abundance was highest. Nitrogen stable isotope analysis confirmed that shellfish were consuming food from within their own estuaries, rather than food from an outside source. Therefore, it appears N load affected the growth rates of the shellfish primarily through causing changes in the quantity, rather than the quality, of the food supply.

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Keywords: Nitrogen loading; Growth; *Mercenaria*; *Mya*

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1. Introduction

Nutrient enrichment of coastal waters has been increasing in recent years, due to human activities such as urbanization, agriculture, and deforestation (Valiela et al., 1992, 1997a,b). This nutrient loading has resulted in many changes to aquatic community structure and function, including increased abundance of nuisance algae, lowered oxygen concentrations, and lowered shell and finfish populations (Valiela et al., 1992). In addition, increased loads of nitrogen stimulate primary production in coastal waters (Valiela, 1995), leading to the eutrophication of the estuaries (Nixon, 1986).

Eutrophication may have important impacts on the growth of organisms that inhabit estuarine waters, such as suspension feeding bivalves, by causing changes in their food supply. For example, eutrophication increases phytoplankton concentrations, a major food source of bivalves. This could potentially increase food supply, resulting in enhanced growth. On the other hand, eutrophication may change the composition of the phytoplankton, altering the quality of the food supply and making it less palatable to the shellfish (Walne, 1970; Mitchell-Innes, 1973; Bass et al., 1990; Duarte, 1995). Also, anoxic conditions associated with eutrophied waters (Valiela et al., 1992) may serve to depress growth rates.

The land use patterns on a watershed strongly influence the rate of nitrogen loading that reaches a receiving estuary. Evidence for this comes from nitrogen stable isotope analysis. Nitrogen occurs as the stable isotopes ^{14}N and ^{15}N in fixed proportions depending on the source (Peterson and Fry, 1987). Isotope data are typically reported as the $\delta^{15}\text{N}$, which is the ratio of ^{15}N to ^{14}N in a sample relative to the ratio of ^{15}N to ^{14}N in atmospheric N_2 . Different sources of N to estuaries (wastewater, fertilizer, or atmosphere) have distinct $\delta^{15}\text{N}$ signatures (Kreitler et al., 1978; McClelland et al., 1997). Wastewater has a signal that is enriched in $\delta^{15}\text{N}$ (McClelland et al., 1997; McClelland and Valiela, 1998) and the amount of N derived from wastewater increases as the watershed becomes more urbanized (Valiela et al., 1997b). More urbanized watersheds, therefore, have heavier $\delta^{15}\text{N}$ signatures (McClelland et al., 1997; Evgenidou, 2000). The enriched signal can be found in primary producers, and is transferred to consumers (Minagawa and Wada, 1984; McClelland et al., 1997; Evgenidou, 2000). Thus, stable isotope signatures found in bivalves can be used to determine whether the bivalves are consuming particles from the specific estuary in which they are found or foreign particles carried by tidal currents into the estuary. Evgenidou (2000) showed that mussels in Waquoit Bay estuaries appeared to feed on particles characteristic of the estuaries in which they were collected since the watersheds that were more urbanized produced heavier signals in the N exported to the estuaries and these heavier signals were found in the mussels.

Quahogs (*Mercenaria mercenaria*) and soft-shell clams (*Mya arenaria*) are two commercially harvested species of bivalves that are common in shallow waters along the east coast of the United States (Belding, 1912; Stanley and DeWitt, 1983; Abraham and Dillon, 1986). It is important to understand how growth rates of these organisms may be affected by N loading to better manage them as valuable economic and ecological resources. Abundant in estuaries of Cape Cod, these shellfish are infaunal suspension feeders that rely on phytoplankton and organic matter in the water column as their main source of food (Chestnut, 1951; Eaton, 1981; Abraham and Dillon, 1986; Newell and

Hidu, 1986). Many studies conclude that food supply controls the growth of bivalves (Pratt and Campbell, 1956; Bricelj et al., 1984; Brown, 1988; Smaal and van Stralen, 1990; Beukema and Cadée, 1991; Coutteau et al., 1994). Where potential food supply has increased owing to N enrichment, growth rates of these bivalves may therefore increase.

In terms of food quantity, Pratt and Campbell (1956) found that growth rates of quahogs increased with phytoplankton concentrations, and Smaal and van Stralen (1990) and van Stralen and Dijkema (1994) reported similar responses in mussels. In the experiments by Coutteau et al. (1994), juvenile quahogs grew significantly faster when fed higher algal rations, and Bayne and Newell (1983) illustrated that growth rates of shellfish increase logarithmically to a maximum rate as food rations increase. Quality of the food supply, however, must also be considered when evaluating how changes in food supply may alter growth of bivalve shellfish. Higher quantities of food may not necessarily result in higher growth rates if the quality of the food is reduced. Studies by Brown (1988) and Beukema and Cadée (1991) suggest that growth rates in bivalves are sometimes better correlated to specific components of phytoplankton than to total concentrations of chlorophyll or particulate organic matter (POM). This suggests that food concentration alone may not always be the best predictor of growth. The ratio of C to N in particulate matter can be used as an indicator of food quality. N supply is an important control of growth in bivalves (Jordan and Valiela, 1982). Russell-Hunter (1970) proposed that animals require the C to N ratio of their food supply to be approximately 17:1, and food rations with higher ratios may be deficient in N. Phytoplankton have a low C to N ratio, while detritus and vascular plant debris tend to have higher values (Valiela, 1995; Iglesias et al., 1996). Therefore, the ratio of C to N may be used to establish the general make-up of particulate matter, which can then help determine food quality.

We hypothesized that increased N loads due to changes in land use support higher concentrations of phytoplankton in estuaries of Waquoit Bay, and the increased phytoplankton provided a larger food supply to support shellfish growth. In this study, we assessed the effects of N load on growth of quahogs and soft-shell clams by experimentally planting shellfish in estuaries subject to different N loads. To verify that the different land-derived N load created differences in food supply for the bivalves, chlorophyll *a*, C, and N concentrations of the particulate matter in the water column were measured. Nitrogen stable isotope analyses were performed to test the assumption that the clams were consuming phytoplankton from the specific estuaries in which they were planted. Finally, growth rates of the shellfish were compared to differences in food supply to determine how N load-mediated changes in food supply affected growth.

2. Materials and methods

2.1. Site selection

The study was conducted in two estuaries of Waquoit Bay, MA, and one adjacent estuary (Fig. 1) The three estuaries (Sage Lot Pond, Green Pond and Childs River) are subject to different N loads resulting from differences in development within the watersheds (Valiela et al., 1992; Kroeger et al., 1999). Sage Lot Pond has little urbanization on

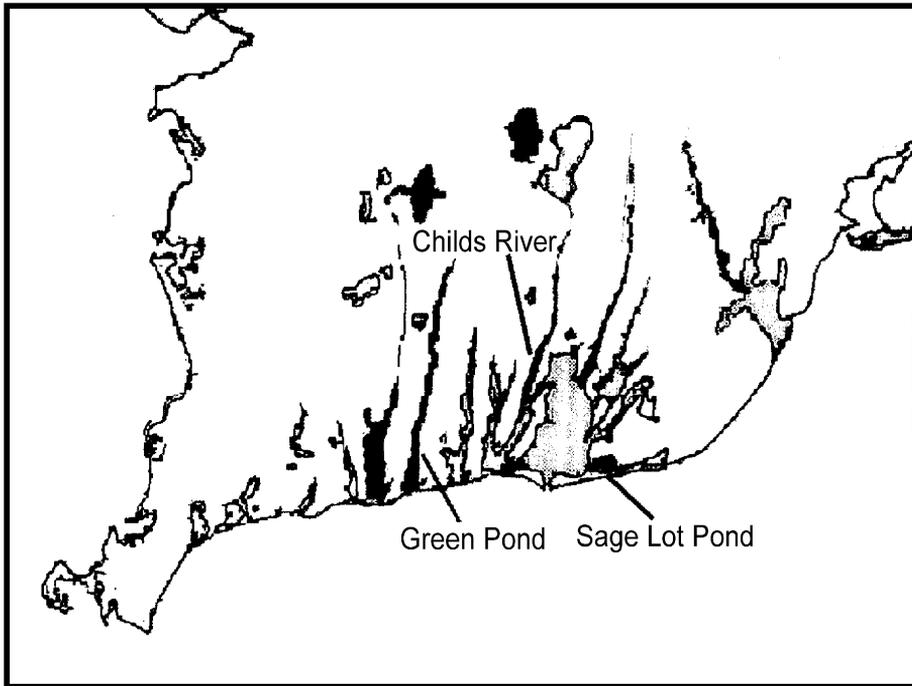


Fig. 1. Map of Cape Cod, showing the three study areas: Sage Lot Pond, Green Pond, and Childs River.

its watershed, which produces low levels of N loads ($14 \text{ kg N ha}^{-1} \text{ year}^{-1}$). Green Pond has intermediate development on its watershed, with intermediate nutrient loading ($137 \text{ kg N ha}^{-1} \text{ year}^{-1}$). Childs River has the most developed watershed, and also produces the highest rate of N loading to its estuary ($601 \text{ kg N ha}^{-1} \text{ year}^{-1}$). Though differing in amount of N delivered to the estuaries, Sage Lot Pond, Green Pond, and Childs River are relatively similar in other aspects such as water residence time, depth, temperature, and salinity.

Six sites in each estuary were selected for the growth rate study, all at 1–1.5 m in depth. To capture the effects of differences in flow, salinity, and temperature within each estuary, the transplantation experiments were located at two sites near the mouth region, two in the middle region, and two in the upper region of the three estuaries.

2.2. Water sampling

Water samples were collected in acid-washed 1-l bottles every 2 weeks for the duration of the study, to determine the concentrations of chlorophyll *a*, particulate C and particulate N. Chlorophyll was measured to serve as an indicator of phytoplankton concentrations, to determine the quantity of food supply in the water column. The quality of food was considered by measuring C and N. Water samples were collected from within 20 cm of the bottom. Samples were stored on ice and in the dark until return to the laboratory, where

they were filtered on ashed GF/F Whatman glass fiber filters (47-mm diameter, 0.7- μm pore size) and stored for further analysis. Chlorophyll samples were frozen prior to acetone extraction and spectrophotometry according to Lorenzen (1967). Filters for C and N analysis were dried in a drying oven at 60 °C for 24 h, and stored in a dessicator. To determine C and N, each filter was cut into quarters and one fourth of the filter was prepared for combustion in a Perkin-Elmer Elemental Analyzer. The remaining three-quarters of the filter were reserved for additional analyses.

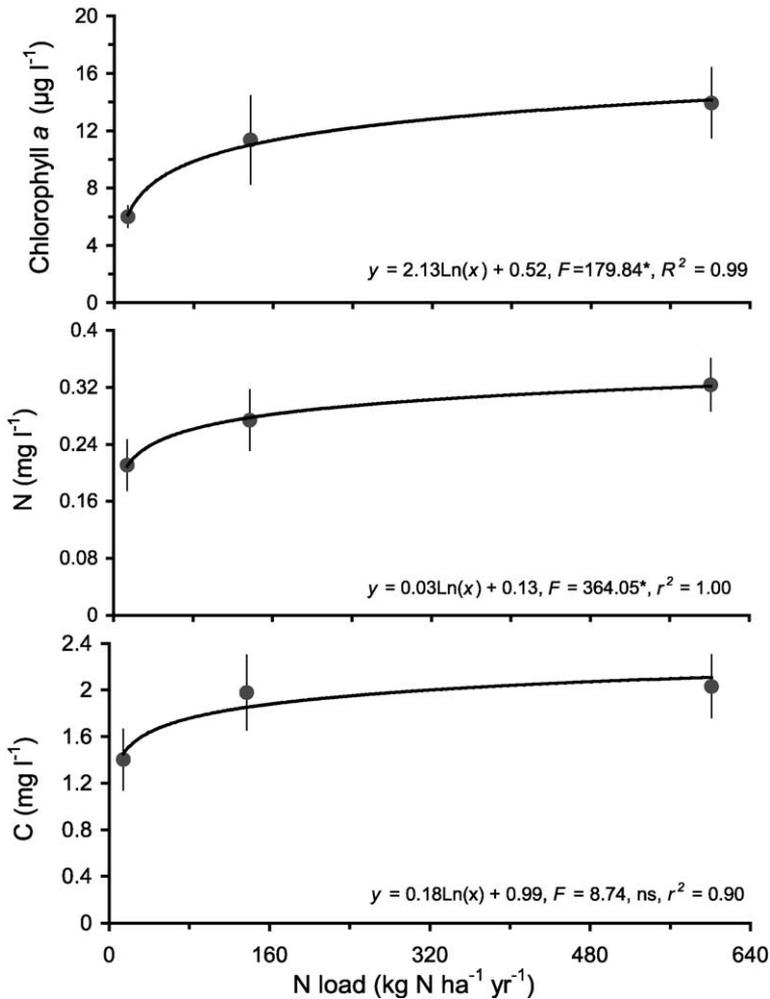


Fig. 2. N load ($\text{kg N ha}^{-1} \text{ year}^{-1}$) plotted vs. chlorophyll *a* ($\mu\text{g l}^{-1}$) (top), C (mg l^{-1}) (middle) and N (mg l^{-1}) (bottom). Points correspond to Sage Lot Pond, Green Pond, and Childs River and are means (\pm S.E.) of all samples taken throughout the study.

2.3. Growth rate study

Juvenile quahogs and soft-shell clams (8–12 mm) were obtained from the Aquaculture Research Center in Chatham, MA and Beals Island Shellfish Hatchery on Beals Island, ME, respectively. Shellfish were measured and labeled with black permanent marker and stored in unfiltered flow-through seawater tanks for 24 h before being placed in the estuaries.

Shellfish were planted in the estuaries in plastic coated wire-mesh boxes (30×30×10 cm). The boxes were lined with 1/4-in. plastic mesh to prevent shellfish and sediment from falling out. To prevent any potential effects of differences in sediment type on growth rate, all boxes were filled with clean sand from the mouth of Sage Lot Pond. Twenty quahogs or 20 soft-shell clams were added to each box, resulting in a shellfish density of approximately 200 m⁻².

To test whether quahogs and soft-shell clams responded to the changes in food supply, we conducted a growth rate experiment in which juvenile clams were transplanted to the three estuaries and growth of the transplanted quahogs and soft-shell clams was measured after periods of approximately 6, 8, or 10 weeks. At each of the six sites in the three estuaries, one box of quahogs and one box of soft-shell clams were planted. The boxes were introduced to the estuaries the week of June 20, 2000. After approximately 6 weeks, boxes were removed from the two sites in the middle reaches of each estuary. After approximately 8 weeks, the two sets of boxes from the upper regions were removed, and after about 10 weeks, the final two sets from the mouth regions were removed. All shellfish were measured and growth rates per week were calculated.

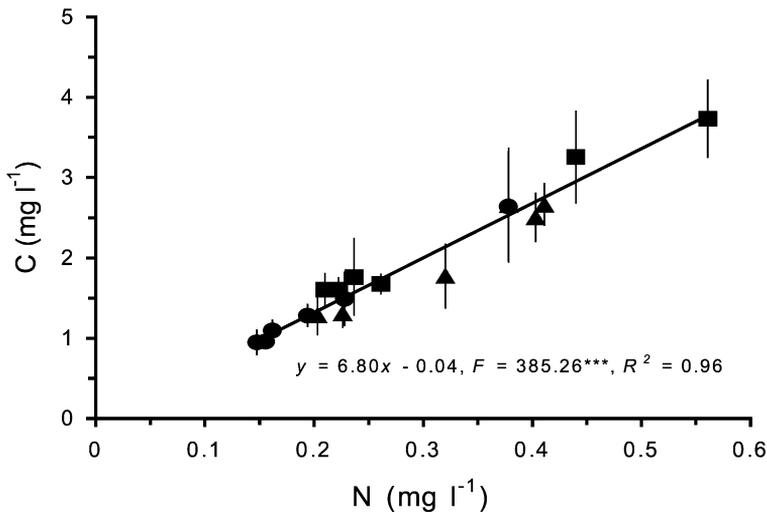


Fig. 3. The relationship between C (mg l⁻¹) and N (mg l⁻¹). The relationship between C and N. C values are means of samples at each site. N values are means (±S.E.) of samples for each site. ●=Sage Lot Pond, ■=Green Pond, ▲=Childs River. Regression analyses: Sage Lot Pond: $y=0.14 \times +0.02^{***}$, $r^2=1.00$, Green Pond: $y=0.15 \times -0.02^{***}$, $r^2=0.98$, Childs River: $y=0.13 \times +0.05^{**}$, $r^2=0.94$. Regression lines are statistically similar to each other. The slope of line indicates the C to N ratio.

2.4. Stable isotope analysis

The $\delta^{15}\text{N}$ signature of particulate organic matter (POM) and transplanted shellfish meats was measured in order to test the assumption that the clams were feeding on the POM from their estuaries. The enrichment or depletion of $^{15}\text{N}/^{14}\text{N}$ was calculated using the following equation:

$$\delta^{15}\text{N} (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where $R=^{15}\text{N}/^{14}\text{N}$ for samples and standards (Peterson and Fry, 1987).

Shellfish meats for N stable isotope analysis were removed from their shells. Guts were separated, and the meats were dried for 24 h in a drying oven at 60 °C and then ground to a fine powder. Samples were analyzed in a Finnegan Delta-S isotope ratio mass spectrometer at the Boston University Stable Isotope Laboratory.

POM samples were prepared from the dried filters used for the CHN analysis. Twelve samples from each estuary (two per site) were selected for analysis. Precision and accuracy decrease sharply when samples contain less than 20 $\mu\text{g N}$. Therefore, only filters with

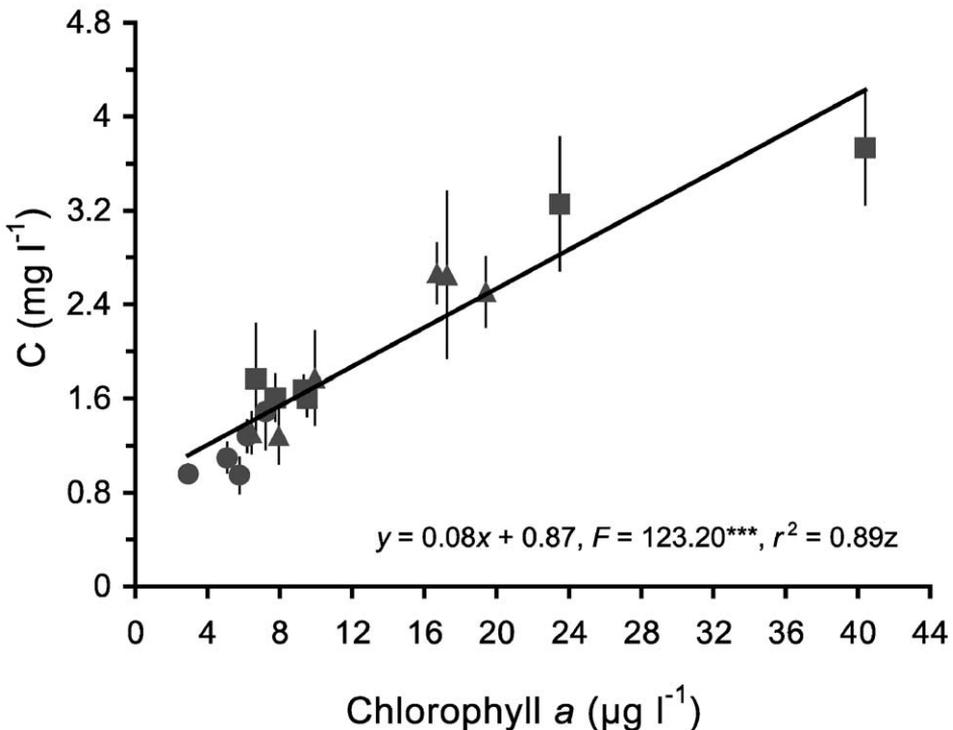


Fig. 4. C (mg l^{-1}) plotted vs. chlorophyll a ($\mu\text{g l}^{-1}$). Points are means (\pm S.E.) of samples from each of the six sites in the three estuaries. The ratio of C to chlorophyll a is about 83, the slope of the regression line of C and chlorophyll was plotted with the same units.

amounts greater than 20 µg N (as determined from the CHN analysis) were submitted. Samples were sent to University of California, Davis Stable Isotope Facility for analysis in a Europa Scientific Hydra 20/20 three isotope ratio mass spectrometer.

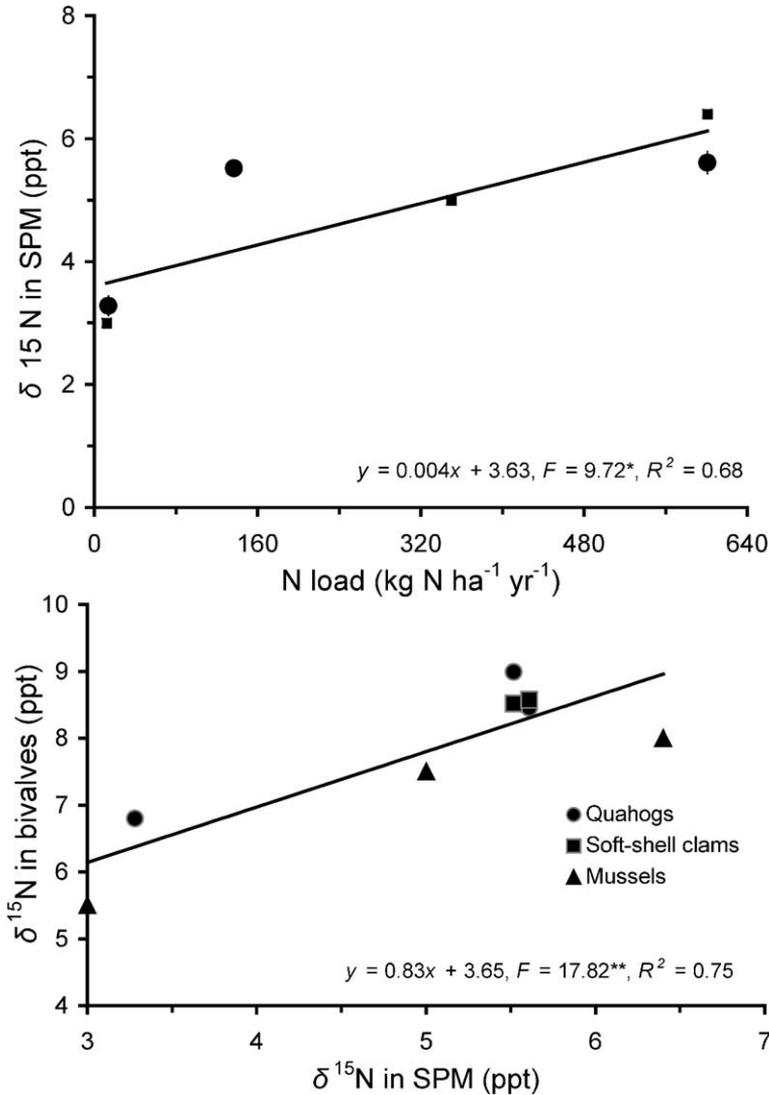


Fig. 5. Top: δ¹⁵N in SPM (ppt) plotted vs. N load (kg N ha⁻¹ year⁻¹). Results from Evgenidou (2000) (■) are included with results from this study (●), which are means (±S.E.) of shellfish tissues from each estuary. Points for (●) correspond to Sage Lot Pond, Green Pond, and Childs River. Points for (■) correspond to Sage Lot Pond, Quashnet River, and Childs River. Bottom: δ¹⁵N in bivalves plotted vs. δ¹⁵N in SPM. Results for quahogs (●) and soft-shell clams (■) are means (±S.E.) of shellfish tissues from each estuary. Also included are results of δ¹⁵N in mussels (▲) from Evgenidou (2000).

3. Results

3.1. Chlorophyll *a*, particulate C and N in the water column

Concentrations of chlorophyll *a* in the water column differed between the three estuaries. Concentrations were lowest in Sage Lot Pond, and higher in Green Pond and Childs River (Fig. 2, top). This is consistent with the previous results that demonstrate a positive relationship between N load and chlorophyll *a* concentrations (Valiela et al., 1992; Evgenidou, 2000).

Concentrations of N, but not of C, increased significantly with N load (Fig. 2, middle and bottom). There was a strong positive relationship between C and N concentrations (Fig. 3), with the slope of 6.8 representing the ratio of C to N. Regression lines were statistically similar among the three estuaries, suggesting that the quality of the food, expressed as C/N, was similar in each of the three estuaries.

The ratio of C to chlorophyll can also be used to estimate phytoplankton abundance (Valiela, 1992). Previous studies have reported ratios of C to chlorophyll ranging from about 10 to 150 (Tett et al., 1975; Dagg and Turner, 1982; Marra et al., 1987). The C/chl in

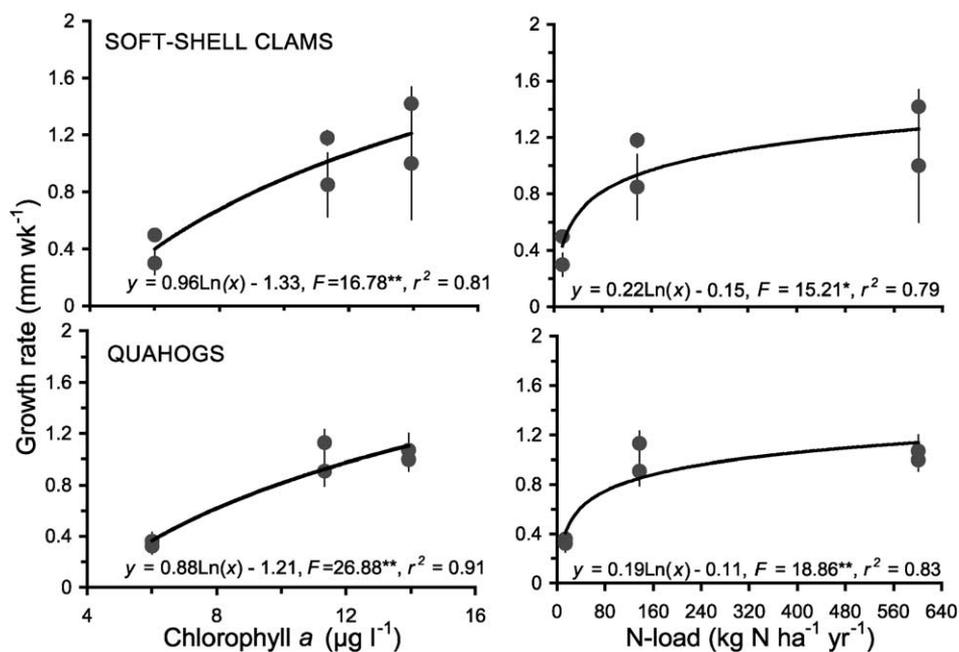


Fig. 6. Left: top and bottom: Growth rate (mm week⁻¹) plotted vs. chlorophyll *a* concentrations (μg l⁻¹). Chlorophyll *a* values are means of all samples taken throughout the experiment. Points correspond to Sage Lot Pond, Green Pond, and Childs River. Growth rates are means (±S.E.) of all shellfish recovered and measurable from each estuary. Statistical analysis indicated that there was no difference in growth rates between the six sites within each estuary or between shellfish taken from the estuaries after different time periods. Right: top and bottom: Growth rate (mm week⁻¹) plotted vs. N load (kg N ha⁻¹ year⁻¹). Additional explanations from above apply.

this study averaged 83 (Fig. 4). It is possible that C from non-phytoplankton sources served to raise the ratio above the strict algal C to chlorophyll ratio since total particulate C was measured. The ratio of C to chlorophyll is relatively constant across all chlorophyll values ($r^2=0.89$), however, indicating that even if non-phytoplankton C was measured, it occurred in the same proportion throughout the area of the study.

3.2. Stable nitrogen isotopes

The nitrogen stable isotope signatures were heavier in the estuaries of higher N load (Fig. 5, top). These data are in accordance with the previous results from McClelland et al. (1997) and Evgenidou (2000), and reflect the greater contribution of wastewater to the total N load in Green Pond and Childs River as compared to Sage Lot Pond.

The $\delta^{15}\text{N}$ signals of the shellfish soft-tissue were 2–4‰ higher than the SPM, typical of trophic level shifts from producers to consumers (McClelland et al., 1997; Peterson and Fry, 1987) (Fig. 5, bottom).

3.3. Growth rates

Growth rates of quahogs and soft-shell clams were positively related to chlorophyll *a* concentrations (Fig. 6, left top and bottom). Chlorophyll *a* concentrations were signifi-

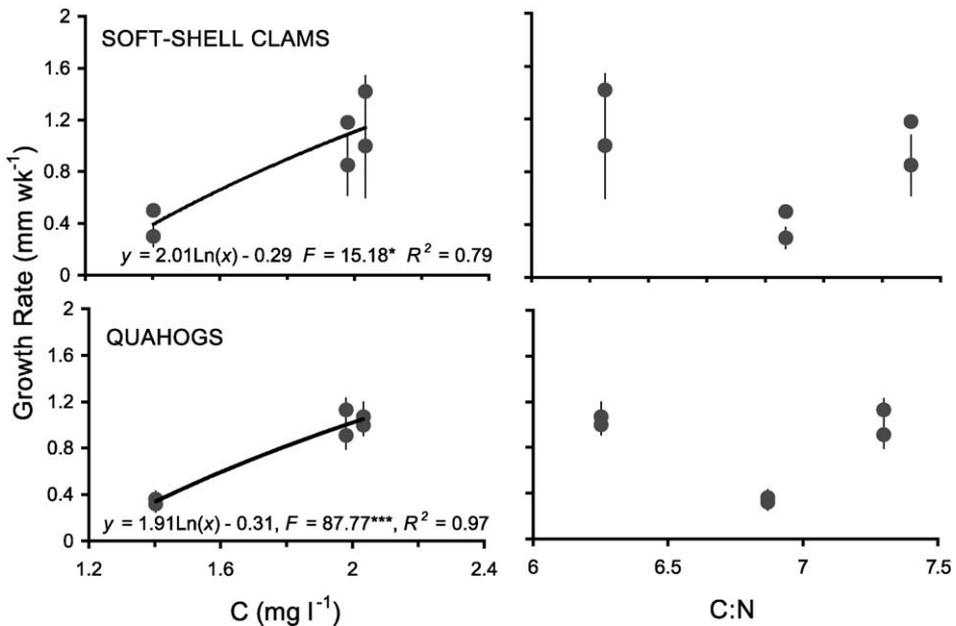


Fig. 7. Left: top and bottom: Growth rates (mm week⁻¹) plotted vs. C (mg l⁻¹). C values are means of all samples. Points correspond to Sage Lot Pond, Green Pond, and Childs River. Growth rates are means (\pm S.E.) of all recovered and measurable shellfish. Right: top and bottom: Growth rates (mm week⁻¹) plotted vs. C/N. Explanation above applies.

cantly higher in Green Pond and Childs River than in Sage Lot Pond. Likewise, growth rates of both shellfish were higher in Green Pond and Childs River. Growth rates were also significantly related to N load (Fig. 6, right top and bottom).

The close relationship between C and chlorophyll *a* forecasts the relationship between growth rates and C (Fig. 7, left top and bottom), since growth rates increased with chlorophyll *a* concentrations. C/N was not related to growth rates of either quahogs or soft-shell clams (Fig. 7, right top and bottom).

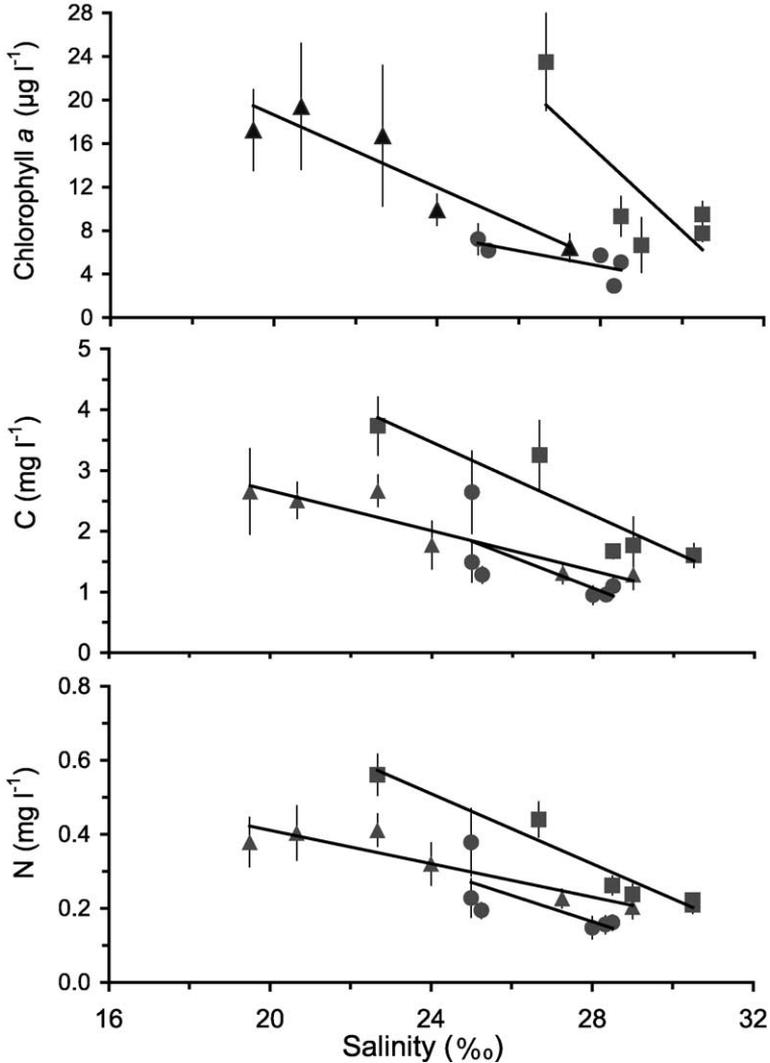


Fig. 8. Top: Chlorophyll *a* (µg l⁻¹) (top), C (mg l⁻¹) (middle) and N (mg l⁻¹) (bottom) plotted vs. salinity (ppt) for the three estuaries. ●=Sage Lot Pond, ■=Green Pond, ▲=Childs River. Chlorophyll concentrations are means (±S.E.) of all samples.

Growth rates of quahogs and soft-shell clams are inversely correlated to size; as size increases, growth rates slow (Stanley and DeWitt, 1983; Abraham and Dillon, 1986). It was therefore a possibility that as the shellfish in this study grew larger, their growth would slow, and growth rates of those removed late in the season would be lower than growth rates of those removed earlier. There were, however, no significant differences between length of stay and growth. For this reason, the average growth rates of the shellfish from all boxes within an estuary were used to obtain mean values for each estuary.

3.4. *Within estuary changes in water column characteristics and effects on growth*

Study sites were chosen at different locations within the estuaries to account for differences in flow, temperature, dissolved O₂ concentration, and salinity, which may affect the growth rates of the quahogs and soft-shell clams (Turner, 1953; Stanley and DeWitt, 1983; Abraham and Dillon, 1986; Grizzle and Lutz, 1989; Grizzle and Morin, 1989). Salinity was measured at each site, and results indicate that salinity was lowest in the upper regions of the estuaries, where fresh groundwater is likely to be entering the systems. Groundwater is considered the primary source of land-derived nitrogen in the Waquoit Bay system (Valiela et al., 1992). As a result, the relationship between salinity and water column factors was investigated.

Concentrations of chlorophyll *a*, C and N all decreased with increasing salinity (Fig. 8). Where nitrogen is entering the system, as determined by salinity measurements, concentrations of chlorophyll *a*, C and N are highest. If phytoplankton drives growth rates, then higher growth rates might be expected in the upper regions, where food supply is greatest. Growth rates, however, did not appear to be related to changes in salinity.

4. Discussion

The increased concentrations of chlorophyll *a* suggest that the potential food supply for quahogs and soft-shell clams might have been greater in Green Pond and Childs River than in Sage Lot Pond. Greater amounts of particulate C and N in estuaries of higher N load also suggest that there is more food available for shellfish in these estuaries. The low C/N of 6.8 for all three estuaries is well below Russell-Hunter's (1970) proposed 17:1, suggesting that the quality of the food is relatively high. In addition, the C to N ratios in several types of phytoplankton are generally around 6–6.5 (Valiela, 1995), which is close to the 6.8 ratio of C to N calculated in this study.

The results of the stable isotope study confirmed that the quahogs and soft-shell clams consumed the phytoplankton from their home estuaries, providing a link between growth rates of the shellfish and the food supply in the estuaries in which they were planted. Therefore, the higher chlorophyll *a* in the estuaries where there is a greater N input to stimulate phytoplankton growth are a likely cause of the faster growth rates in estuaries of higher N load. Evidence for this comes from the relationships between growth rates and both chlorophyll *a* and C, which suggest that food quantity is a considerable factor affecting growth. The linear relationship between growth rates and C, as well as chlorophyll *a*, concentrations suggests that concen-

trations of either chlorophyll *a* or C may be used to predict growth rates. Food quality, on the other hand, did not appear to affect growth rates. This result was not surprising as there was no difference in the ratio of C to N between the different estuaries. Though factors other than C/N may affect nutritional value of food, the ratio of C to N is a general measure of food quality. Therefore, since food quantity varied between the three estuaries and C/N remained relatively constant, the differences in growth rates of these shellfish in the three estuaries seem to be due to changes in food quantity rather than quality.

The within estuary differences in water column characteristics may have been expected to affect growth rates. There are two possible explanations for why we did not see changes in growth rates within each estuary. First, the lower salinity in the upper areas of the estuaries may serve to depress growth rates, at least for quahogs. Chanley (1958) found that growth rates in quahogs increased with salinity. Hamwi (1968) also observed lowered pumping rates in quahogs at lower salinities (18‰), with maximum pumping rates at 23–27‰. It is possible that the depression of growth rates due to lowered salinities may have been canceled out by the higher amounts of phytoplankton associated with the areas of low salinity. Therefore, the opposing effects could have counteracted each other, resulting in what appears to be a lack of response of growth to both salinity and food supply.

Soft-shell clams, on the other hand, are able to tolerate a much wider range of salinities and are unaffected by decreases in salinity until concentrations are less than about 10‰ (Matthiessen, 1960). Since none of the salinities measured in this study were below about 19‰, effects of salinity seem insufficient to explain the lack of response of growth rate of soft-shell clams to higher phytoplankton concentrations within each estuary. Several studies suggest that high amounts of suspended matter, especially inorganic sediments, may inhibit growth by decreasing clearance and ingestion rates of bivalves (Rhoads and Panella, 1970; Bricelj and Malouf, 1984; Bricelj et al., 1984). Therefore, it is possible that concentrations of suspended matter were high enough in the upper reaches to depress growth rates enough to mask any effect of increased food supply. Percent organic matter and total suspended particulate matter, however, were not measured in this experiment, so further study is needed to either support or refute this hypothesis.

Overall, however, chlorophyll *a* concentrations increased with N load and growth rates showed a positive relationship with increasing chlorophyll *a* concentrations. Therefore, though within estuary differences in chlorophyll *a* concentrations did not affect growth rates, the overall higher concentrations in chlorophyll *a* in Green Pond and Childs River appear to be sufficient to result in faster growth rates in the estuaries of higher N load.

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References

- Abraham, B.J., Dillon, P.L., 1986. Species profiles: life histories and environmental regulations of coastal fishes and invertebrates (Mid-Atlantic)-Softshell clam. U. S. Fish Wildl. Serv., Biol. Rep. 82, 18 pp.
- Bass, A.E., Malouf, R.E., Shumway, S.E., 1990. Growth of northern quahogs (*Mercenaria mercenaria* (Linnaeus 1758)) fed on picoplankton. J. Shellfish Res. 9, 299–307.
- Bayne, B.L., Newell, R.C., 1983. Physiological energetics of marine molluscs. In: Saleuddin, A.S.M., Wilbur, K.M. (Eds.), The Mollusca, vol. 4. Academic Press, New York, pp. 407–515.
- Belding, D.L., 1912. A Report upon the Quahog and Oyster Fisheries of Massachusetts Wright and Potter Printing, Boston.
- Beukema, J.J., Cadée, G.C., 1991. Growth rates of the bivalve *Macoma balthica* in the Wadden Sea during a period of eutrophication: relationships with concentrations of pelagic diatoms and flagellates. Mar. Ecol.: Prog. Ser. 68, 249–256.
- Bricelj, V.M., Malouf, R.E., 1984. Influence of algal and suspended sediment concentrations on the feeding physiology of the hard clam *Mercenaria mercenaria*. Mar. Biol. 84, 155–165.
- Bricelj, V.M., Malouf, R.E., de Quillfeldt, C., 1984. Growth of juvenile *Mercenaria mercenaria* and the effect of resuspended bottom sediments. Mar. Biol. 84, 167–173.
- Brown, J.R., 1988. Multivariate analyses of the role of environmental factors in seasonal and site-related growth rates of juvenile bay scallops *Argopecten irradians*. J. Exp. Mar. Biol. Ecol. 129, 45–60.
- Chanley, P.E., 1958. Survival of some juvenile bivalves in water of low salinity. Proc. Natl. Shellfish. Assoc. 48, 52–65.
- Chestnut, A.F., 1951. The oyster and other mollusks in North Carolina. In: Taylor, H.F. (Ed.), Survey of Marine Fisheries of North Carolina. University of North Carolina Press, Chapel Hill, pp. 141–190.
- Coutteau, P., Hadley, N.H., Manzi, J.J., Sorgeloos, P., 1994. Effect of algal ration and substitution of algae by manipulated yeast diets on the growth of juvenile *Mercenaria mercenaria*. Aquaculture 120, 135–150.
- Dagg, M.J., Turner, J.T., 1982. Impact of copepod grazing on the phytoplankton of Georges Bank and the New York Bight. Can. J. Fish. Aquat. Sci. 39, 979–990.
- Duarte, C.M., 1995. Submerged vegetation in relation to different nutrient regimes. Ophelia 41, 87–112.
- Eaton, J.S., 1981. Seasonal patterns and discrimination in the feeding behavior of the soft-shell clam: *Mya arenaria*. Proceedings of the 8th Annual Conference of Clam Research, Maine Department of Marine Resources, Boothbay Harbor, pp. 3–14.
- Evgenidou, A., 2000. Response of growth and density of a population of *Geukensia demissa* to land-derived nitrogen loading, in Waquoit Bay, Massachusetts. Masters Thesis, Boston University, 52 pp.
- Grizzle, R.E., Lutz, R.A., 1989. A statistical model relating horizontal seston fluxes and bottom sediment characteristics to growth of *Mercenaria mercenaria*. Mar. Biol. 102, 95–105.
- Grizzle, R.E., Morin, P.J., 1989. Effect of tidal currents, seston, and bottom sediments on growth of *Mercenaria mercenaria*: results of a field experiment. Mar. Biol. 102, 85–93.
- Hamwi, A., 1968. Pumping rate of *Mercenaria mercenaria* as a function of salinity and temperature. Proc. Natl. Shellfish. Assoc. 45, 4.
- Iglesias, J.I.P., Urrutia, M.B., Navarro, E., Alvarez-Jorna, P., Larratxea, X., Bougrier, S., Heral, M., 1996. Variability of feeding processes to changes in seston concentration and composition. J. Exp. Mar. Biol. Ecol. 197, 121–143.
- Jordan, T.E., Valiela, I., 1982. A nitrogen budget for the ribbed mussel *Geukensia demissa* and its significance in energy flow in a New England salt marsh. Limnol. Oceanogr. 27, 75–90.
- Kreitler, C.W., Ragone, S., Katz, B.G., 1978. ¹⁵N/¹⁴N ratios of ground-water nitrate, Long Island, New York. Ground Water 16, 404–409.
- Kroeger, K.D., Bowen, J.L., Corcoran, D., Moorman, J., Michalowski, J., Rose, C., Valiela, I., 1999. Nitrogen

- loading to Green Pond, Falmouth, MA: sources and evaluation of management options. Environ. Cape Cod 2, 15–26.
- Lorenzen, C.J., 1967. Determination of chlorophyll *a* and phaeopigments: spectrophotometric equations. Limnol. Oceanogr. 30, 693–698.
- Marra, J., Wiebe, P.H., Bishop, J.K.B., Stepien, J.C., 1987. Primary production and grazing in the plankton of the Panama Bight. Bull. Mar. Sci. 40, 255–270.
- Matthiessen, G.C., 1960. Observations on the ecology of the soft clam, *Mya arenaria*, in a salt pond. Limnol. Oceanogr. 5, 261–300.
- McClelland, J.W., Valiela, I., 1998. Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. Mar. Ecol.: Prog. Ser. 168, 259–271.
- McClelland, J.W., Valiela, I., Michener, R.H., 1997. Nitrogen-stable isotope signatures in estuarine food webs: a record of increasing urbanization in coastal watersheds. Limnol. Oceanogr. 42, 930–937.
- Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. Geochim. Cosmochim. Acta 48, 1135–1140.
- Mitchell-Innes, B.A., 1973. Ecology of the phytoplankton of Narragansett Bay and uptake of silica by natural populations and the diatoms *Skellatonema costatum* and *Detonula convolvacea*. PhD Dissertation, University of Rhode Island, Kingston, 112 pp.
- Newell, C., Hidu, H., 1986. Species profiles: life histories and environmental regulations of coastal fishes and invertebrates (Mid-Atlantic)-Softshell clam. U. S. Fish Wildl. Serv., Biol. Rep. 86, 17 pp.
- Nixon, S.W., 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. J. Limnol. Soc. South. Afr. 12, 43–71.
- Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. Annu. Rev. Ecol. Syst. 18, 293–320.
- Pratt, D.M., Campbell, D.A., 1956. Environmental factors affecting growth in *Venus mercenaria*. Limnol. Oceanogr. 1, 2–17.
- Rhoads, D.C., Panella, G., 1970. The use of molluscan shell growth patterns in ecology and paleoecology. Lethaia 3, 143–161.
- Russell-Hunter, W.D., 1970. Aquatic Productivity: An Introduction to Some Basic Aspects of Biological Oceanography and Limnology MacMillan, New York, 305 pp.
- Smaal, A.C., van Stralen, M.R., 1990. Average annual growth and condition of mussels as a function of food supply. Hydrobiologia 195, 179–188.
- Stanley, J.G., DeWitt, R., 1983. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic)—hard clam. U. S. Fish Wildl. Serv., Biol. Rep. 82, 19 pp.
- Tett, P., Cottrell, J.C., Trew, D.O., Wood, B.J.B., 1975. Phosphorus quota and the chlorophyll:carbon ratio in marine phytoplankton. Limnol. Oceanogr. 20, 587–603.
- Turner, H.J., 1953. Growth of molluscs in tanks. Sixth Rep. Invest. Shellfish Mass. Dept. Nat. Res., pp. 35–39.
- Valiela, I., 1995. Marine Ecological Processes, 2nd edn. Springer, New York, 686 pp.
- Valiela, I., Foreman, K., LaMontagne, M., Hersh, D., Costa, J., Peckol, P., Demeo-Anderson, B., D'Avanzo, C., Babione, M., Sham, C., Brawley, J., Lajtha, K., 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. Estuaries 15, 443–457.
- Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, J., Foreman, K., 1997a. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol. Oceanogr. 42, 1105–1118.
- Valiela, I., Collins, G., Kremer, J., Lajtha, K., Geist, M., Seely, B., Brawley, J., Sham, C., 1997b. Nitrogen loading from coastal watersheds to receiving estuaries: new method and application. Ecol. App. 7, 358–380.
- van Stralen, M.R., Dijkema, R.D., 1994. Mussel culture in a changing environment: the effects of a coastal engineering project on mussel culture (*Mytilus edulis* L.) in the Oosterschelde estuary (SW Netherlands). Hydrobiologia 283, 359–379.
- Walne, P.R., 1970. Studies of food value of nineteen genera of algae to juvenile bivalves of the genera *Ostrea*, *Crassostrea*, *Mercenaria*, and *Mytilus*. Fishery Investigations, Ministry of Agriculture, Fisheries and Food, London. Series II, 62, 1–62.