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Response of Growth and Density of a Population of *Geukensia demissa* to Land-Derived Nitrogen Loading, in Waquoit Bay, Massachusetts

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Nutrient enrichment is a widespread phenomenon affecting coastal waters, including salt marshes. As land-derived nitrogen loading in estuarine waters increases, chlorophyll concentrations in the water also increase. We hypothesized that such increases might increase growth of the food-limited population of *Geukensia demissa*, which is a dominant component of salt marshes. To test this, we conducted a regional scale experiment in three estuaries of Waquoit Bay, Massachusetts that receive different nitrogen loading rates. A stable isotope experiment on mussel tissues and on particulate organic matter (POM) showed that mussels within an estuary fed on POM characteristic of that estuary, demonstrating the direct linkage between POM and mussels within an estuary. In addition, we measured age-specific shell growth rates of mussel populations using two different methods: indirectly, shell growth of mussels indicated by internal shell-lines was measured by fitting the data to the von Bertalanffy equation, and directly, mussels were transplanted from one estuary to the other two, and their actual shell growth rates after 80 days were measured. Growth rates of mussels in the Waquoit Bay estuaries varied with age of the mussel, tidal elevation, and with mean concentration of chlorophyll in the water. Mussels grew best in the lower intertidal zone, at the marsh banks. Young mussels grew faster than older mussels. Growth rates increased in response to presumed greater food supply across the estuaries, only for younger mussels. The significant differences we found among the mussels from different estuaries indicate a response to higher concentrations of food particles available in estuaries subject to higher nitrogen loads.

Keywords: growth rates; mussels; nitrogen; loading; Cape Cod; Massachusetts

Introduction

Nutrient enrichment of coastal waters is one of the most pervasive agents of change in the structure and function of coastal aquatic communities (Nixon *et al.*, 1986; Valiela *et al.*, 1992; Valiela, 1995). Such changes have been reported worldwide, as a result of many kinds of human activities, such as increased urbanization, deforestation and agricultural land uses (Valiela *et al.*, 1992, 1997*a*, *b*). Increased nitrogen loading is important because low nitrogen often limits production by plants and algae in coastal waters (Valiela, 1995). Hence, increases in nitrogen supply lead to increased primary production by phytoplankton, increased concentration of particulate organic matter (POM) in the water column, increased abundance of nuisance algae, reduced oxygen content of the water, and decimated shell and finfish populations (Cambridge & McComb, 1984; Valiela *et al.*, 1990, 1992; Sfriso *et al.*, 1992; D'Avanzo & Kremer, 1994).

Ecosystems exposed to the effects of increased nitrogen delivery include salt marshes. One of the dominant components of salt marsh communities is the ribbed mussel, *Geukensia demissa* (Kuenzler, 1961; Jordan & Valiela, 1982; Bertness & Grosholz, 1985; Stiven & Gardner, 1992). *G. demissa* is found in dense aggregations living in the intertidal zone of salt-marshes of the Atlantic coast of North America to the Gulf of Mexico (Bertness, 1980; Brousseau, 1984; Franz, 1996, 1997). The ribbed mussel is a suspension-feeding bivalve that feeds directly on phytoplankton (Yelenik *et al.*, 1996), or phytoplankton and *Spartina alterniflora* detritus, depending on its location in the marsh (Jordan, pers. comm.; Peterson *et al.*, 1985, 1986; Kreeger *et al.*, 1988, 1990; Langdon & Newell, 1990). Bacteria also comprise a small portion of the mussel's diet (Wright *et al.*, 1982; Langdon & Newell, 1990; Kemp *et al.*, 1990).

Growth of *G. demissa* may be affected by differences in food supply related to the mussel's position in the intertidal range (Stiven & Kuenzler, 1979; Lutz & Castagna, 1980; Brousseau, 1984; Borrero & Hillbish, 1988; Lin, 1989*b*; Franz & Tanacredi, 1993; Franz, 1993, 1997). Food supplies may be limiting especially

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for young mussels and growth is density-dependent, since field manipulations showed that increases in density lead to decreases of growth rates (Stiven & Kuenzler, 1979; Bertness & Grosholz, 1985; Lin, 1989*a*; Stiven & Gardner, 1992). Mussels grow best lower in the intertidal, near the marsh edge (Kuenzler, 1961; Gillmor, 1982; Jordan & Valiela, 1982; Bertness & Grosholz, 1985; Hardwick-Witman, 1985; Franz, 1993). Tidal elevation may be important for two reasons: first, lower positions in the intertidal may allow a more prolonged feeding period. Secondly, mussels located higher in the intertidal may have lower food supplies available, because of prefiltration of flooding tidal waters by mussels lower in the intertidal range (Franz, 1996).

As land-derived nitrogen loading rates to estuarine waters increase, chlorophyll *a* concentrations in the water also increase (Valiela *et al.*, 1992; Foreman *et al.*, submitted). Our hypothesis is that as nitrogen loading to saltmarsh estuaries increases, phytoplankton concentrations and chlorophyll *a* concentrations also increase (Valiela *et al.*, submitted; Foreman *et al.*, submitted). Such increases may then lead to concomitant increases in growth rates of the food-limited populations of *G. demissa*.

In this study, we assess the degree of linkage between a bottom-up control factor in an estuary (land-derived nitrogen loading), and growth rate of a consumer (*G. demissa*) that lives in that estuary (Carpenter *et al.*, 1985; Nixon *et al.*, 1986). Such a relationship must be mediated by an intermediate link, in this case the supply of phytoplankton or POM, serving as food for the mussels. The nitrogen input derived from the estuary's watershed should reflect the mix of land uses of the watershed emptying into the estuary (Valiela *et al.*, 1997b).

To test whether increased nitrogen loading rates increase shell growth rates of *G. demissa,* by means of a larger food supply from increased organic matter production, we measured age-specific growth rates of mussel populations growing in three estuaries of Waquoit Bay, Massachusetts that receive different nitrogen loading rates, and where phytoplankton reach different mean concentrations (Nixon *et al.*, 1986; Valiela *et al.*, 1992, 1997*a*, submitted; Foreman *et al.*, submitted). The effect of nitrogen loading on mussel growth was measured in two ways. First, mussels were sampled from three estuaries of Waquoit Bay, Massachusetts (Childs River, Quashnet River, and Sage Lot Pond), from different tidal elevations, and growth rates based on internal shell growth lines were measured. Second, in a field experiment, small mussels were transplanted from Childs River to the other two estuaries, and growth of the transplanted mussels was measured directly after 80 days in the estuaries.

To test our initial assumption that mussel populations fed on phytoplankton and POM from their own estuaries, rather than on a mixture of phytoplankton and POM that was transported into estuaries by tidal waters, we collected mussels and measured the $\delta^{15}N$ signature of their tissues and that of POM from each estuary. The $\delta^{15}N$ signature of consumers is set by the values in their food, as well as by their position in the food web. As urbanization of a watershed increases, nitrogen loading derived from wastewater inputs to the receiving estuaries also increases (Valiela *et al.*, 1997*b*). Wastewater-derived nitrogen has elevated signatures of $\delta^{15}N$. Signatures established in a given estuary by wastewater input are then reflected in producers and POM within the estuaries (McClelland *et al.*, 1997; McClelland & Valiela, 1998). McClelland *et al.* (1997) reported that in Waquoit Bay increases in wastewater contribution to N loads can be identified even at relatively low loading rates, and that groundwater with an elevated isotopic signature acts as a ^{15}N-enriched tracer in the water column and in various producers. Because of the fractionation that characteristically accompanies trophic steps in food webs, mussel tissues should be 2 to 4‰ enriched in heavier isotopes relative to the isotopic signature of their diet (Fry, 1988; Michener & Schell, 1994; Yelenik *et al.*, 1996; McClelland *et al.*, 1997).

Materials and methods

Study area

Sampling took place in the three estuaries of Waquoit Bay, Massachusetts, and included three sampling sites in each estuary (Figure 1). Childs River, Quashnet River, and Sage Lot Pond are similar in depth, open water area, salinity ranges, tidal excursion, temperature, and residence times (Table 1). The similar values of tidal excursion and residence times in these estuaries imply that flow regimes are similar. However, the three estuaries differ in the degree of urbanization of their watershed (Valiela *et al.*, 1992, 1997*a*). Childs River's watershed is more urbanized than Quashnet River's, which, in turn is more urbanized than Sage Lot Pond's (Valiela *et al.*, 1992). Childs River receives higher nitrogen loading (601 kg ha^{-1} yr^{-1}) than Quashnet River (350 kg ha^{-1} yr^{-1}), and Sage Lot Pond is subject to a relatively low nitrogen loading rate (12 kg ha^{-1} yr^{-1}) (Valiela *et al.*, 1997*b*). Subsequently, these three estuaries differ in mean PON and Chl *a* concentrations in their water column (Table 1).

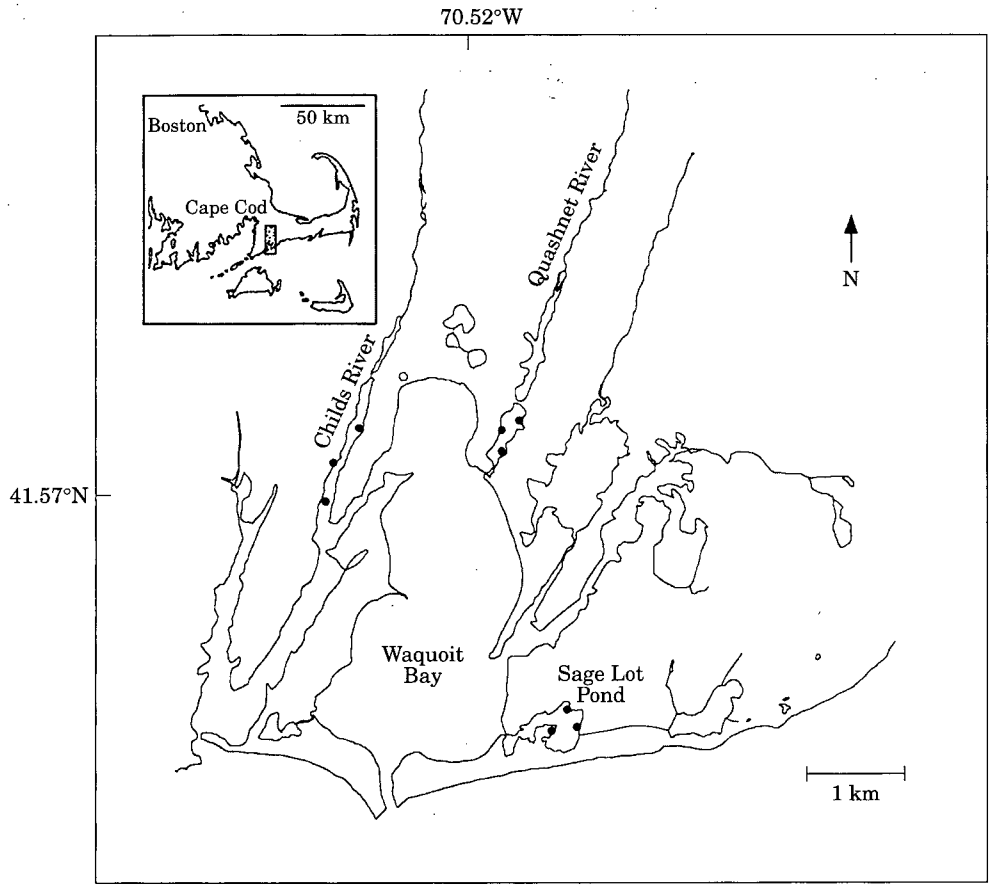

FIGURE 1. The three subestuaries of Waquoit Bay, Massachusetts: Childs River, Quashnet River and Sage Lot Pond. Points mark sites were mussels were sampled for growth measurements.

TABLE 1. Mean depth (m) at mean low water (MLW), residence times (ds), mean (± SE) PON concentrations (mg m^{-3}) and mean chlorophyll *a* (± SE) concentrations (mg m^{-3}) collected from the three estuaries of Waquoit Bay, Mass (data from Valiela *et al.*, submitted; Foreman *et al.*, submitted)

	Mean depth	Residence times	PON	Chl *a*
Childs River	1·4	2·3	222·7 ± 14·6	9·36 ± 0·98
Quashnet River	0·8	1·7	155 ± 11·2	7·49 ± 0·8
Sage Lot Pond	1·3	1·5	86·3 ± 8·2	4·54 ± 1·1

These three watersheds provide a regional-scale experiment (Valiela *et al.*, 1992) of the effects of increased nitrogen loading on growth of *G. demissa*, since most other environmental factors are similar among the three estuaries. Many papers have appeared in which we show that it is possible to interpret the differences among these estuaries as largely being influenced by the rates of land-derived nitrogen loading (Valiela *et al.*, 1992, 1997*a*, 1997*b*; Yelenik *et al.*, 1996; McClelland *et al.*, 1997; McClelland & Valiela, 1998).

Stable isotopes

To examine whether mussels fed on particulate organic matter from the same estuary, we measured the $\delta^{15}N$ signature of particulate organic matter and mussel tissues. δ indicates the enrichment (+) or depletion (−) of the heavy isotope relative to the lighter isotope according to the formula:

$$\delta^{15}N\ (‰) = \frac{\text{Rsample} - \text{Rstandard}}{\text{Rstandard}}\ 10^3,$$

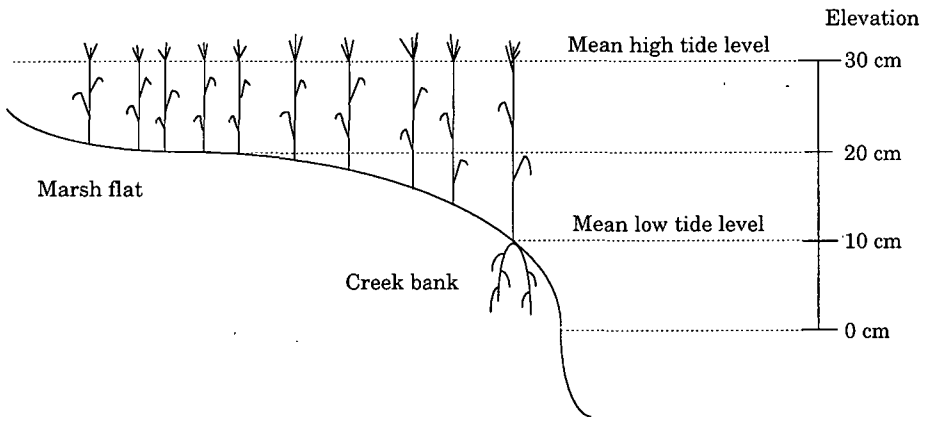

FIGURE 2. Cross-section of the *Spartina alterniflora* marsh, in the three estuaries of Waquoit Bay. Dotted lines indicate the three tidal elevations (0–0, 10–20, 20–30 cm) above MLW from where the mussels were sampled.

where $R = {}^{15}N/{}^{14}N$ of samples and standards (Peterson *et al.*, 1986). Sample values are typically normalized using as a standard atmospheric N_2 (Michener & Schell, 1994; McClelland *et al.*, 1997; McClelland & Valiela, 1998).

POM and mussel tissues were sampled in July 1999, from three different sites from Childs River, Quashnet River, and Sage Lot Pond (Figure 1). We sampled particulate organic matter by collecting two replicate samples of seawater in 2-l bottles. Water was taken from 0·5 m below the surface. The seawater was then filtered through ashed Gelman A/E glass fibre filters with a low-pressure vacuum pump. The filters were dried at 60 °C.

We sampled mussels from the lowest tidal elevation (0–10 cm, Figure 2) from each site, and from each estuary. Mussels from each site were grouped into three size categories according to their length: small (<30 mm in length), medium (30–60 mm), and large (>60 mm). Each small, medium, or large mussel sample consisted of 15, 7, or 4 individuals respectively. The mussels were taken to the laboratory and held in filtered seawater for 24 h to allow their guts to clear. Then the mussel tissues were dried at 60 °C, and ground into a homogenous powder. All samples were analysed in the Boston University Stable Isotope Laboratory using a Finnigan Delta-S isotope ratio mass spectrometer. Precision of replicate analyses was ± 0·2‰.

Indirect measurement of shell growth of mussels

Mussels were sampled from three different sites in each estuary (Figure 1). At all sites, sampling took place at three different ranges of tidal elevations 0–10, 10–20 and 20–30 cm above mean low water (MLW) (Figure 2). We measured tidal elevation as height of water in a tube that was connected to a reservoir. The reservoir was placed at the upper part of the marsh, and the tube extended towards the water, till the point of MLW (Figure 2). Then the tube was held upwards, vertical to the water level, and the height of the water in the tube was measured. This was repeated upwards, while the reservoir was held at the same location. The maximum height measured was the tidal range in the estuaries (30 cm), and sampling was grouped into three different tidal elevations corresponding to different microhabitats in the distribution of *G. demissa* (Figure 2). The first 10 cm above MLW spanned the creek banks, where mussels are very densely populated, buried in the mud or attached to each other, and often covered with *Fucus vesiculosus*. Here, the substrate contained high densities of *Spartina alterniflora* roots and rhizomes. The next elevation range (10–20 cm), extended from the creek banks and upwards. At this elevation mussels reach lower densities and are buried in the marsh peat, where shoots of tall *S. alterniflora* grow (Rietsma *et al.*, 1982). The upper-most elevation (20–30 cm) supported shoots of short *S. alterniflora*, where mussels are much less dense and not attached to each other. Mussels were absent at higher elevations.

A 20 × 20 cm quadrat was tossed randomly five to 10 times at each tidal elevation and at each site, and all the mussels contained within each quadrat were collected. In the laboratory, shell length (± 0·1 mm) of all mussels collected was measured with calipers. For aging the mussels, shell length was divided into 10 different size classes (0–10, 10–20, 20–30, . . ., and 90–100 mm in shell length). In each quadrat, and on all sampling dates, we estimated the age of 3 mussels from each of the 10 size classes, whenever 3 mussels were available. To age each of those mussels, one valve was sectioned longitudinally along a plane

through the umbo. The section was then polished, and the internal growth lines were counted (Lutz & Castagna, 1980). Brousseau (1984) found that internal growth lines tend to overestimate age, but in mussels from Waquoit Bay there was no difference in estimates of age between external and internal growth lines. In a pilot study we counted internal and external growth lines for 100 mussels and all points fell on the 1:1 line. We chose internal growth lines since the external were not very clear, because of wear and discoloration.

We sampled sites monthly from April until August of 1999, to collect enough mussels for our statistical analysis (4/25–27, 5/27–29, 6/27–29,7/28–30, 8/22–24). Within each of the estuaries sampled, monthly data were pooled (Evgenidou, pers. comm.). There were also no statistical differences among sampling sites within each estuary, so length-age data from the sites were also pooled together. In the end, our data were organized in nine different groups, representing three different tidal elevations (0–10, 10–20, 20–30 cm) coming from three different estuaries of Waquoit Bay (Childs River, Quashnet River and Sage Lot Pond).

We calculated growth rates of the mussels by using the von Bertalanffy growth equation,

$$L_t = L_\infty\ (1 - e^{-K\ (t - t_o)}) \qquad (1)$$

where L_t=length at time t, L_∞ is an asymptotic length achieved by the species, K is the constant that indicates the rate at which L_∞ is approached, and t_o is the time at which growth starts (Valiela, 1995). This equation produces a decaying exponential curve that approaches L_∞ as a limit (Fabens, 1965; Seed, 1976; Brousseau, 1984), and has been used successfully to describe growth for bivalves (Brousseau, 1979), including *G. demissa* (Brousseau, 1984). Rearranging Equation 1 we arrive at:

$$-Ln\ [1 - (Lt/L_\infty)] = -K\ t_o + K\ t. \qquad (2)$$

We can, therefore, linearize the von Bertalanffy equation if we plot $-Ln\ [1 - (Lt/L_\infty)]$ *vs.* t (which is the age in years). The slope of the curve equals K, and the intersection of the curve with the Y-axis equals $-K\ t_o$. We applied this equation to data obtained from each of the three tidal elevations at each of the three estuaries.

By differentiating equation 1, we obtain,

$$dL_t/dt = L_\infty\ K\ e^{-(t - t_o)\ K} \qquad (3)$$

which expresses the change of length *vs.* change in time (age). We used this term to calculate the age-specific growth rates of the mussels. Because growth is age-dependent, we calculated growth rates for mussels within three different age groups (0–3, 3–10, and >10 years).

Direct measurement of shell growth of mussels

To measure growth directly, mussels 10 to 40 mm in length were collected from the lowest tidal elevation (0–10 cm) of site 1 in Childs River (Figures 1, 2). The edge of each mussel's shell was painted with red enamel and then 15 mussels were placed into mesh bags. The mesh bags were made out of plastic with pore size 0·5 cm. Six replicate bags were then fixed in place with stakes within 0–10 cm above MLW in each of the three estuaries. The bags were placed in the field on 20 August and were recovered on 8 November 1999. Growth in New England populations of *G. demissa* peaks in late summer, mostly August and September (Jordan & Valiela 1982; Hardwick-Witman, 1985; Franz, 1997). The mussels were taken to the laboratory, and final and initial shell length ($\pm$ 0·1 mm) were measured.

Measurement of density

To examine density-dependent differences in growth (Stiven & Kuenzler, 1979), we measured mussel density in the three estuaries of Waquoit Bay. Density (mussels m^{-2}) was measured as number of mussels contained in every quadrat (20 × 20 cm). The quadrat was tossed five to 10 times in the same sites and tidal elevations that growth was measured.

Results and discussion

Stable isotopes

The stable isotopic signature of particulate organic matter in the water of the estuaries was heavier as nitrogen loading to the estuary increased (Figure 3 top), in accordance with previous results (McClelland & Valiela, 1998). The heavier signatures derive from the increasing contribution of wastewater nitrogen as loading rates increase (McClelland *et al.*, 1997; McClelland & Valiela, 1998). The differences in isotopic signatures in the POM from the different estuaries are evidence that the nitrogen from a particular watershed can be traced in the phytoplankton and POM in the water column.

The isotopic signature of the mussels follows the signature in POM, allowing for the 2–4‰ enrichment that typically accompanies a trophic step (Michener & Schell, 1994). Even though the estuaries in the

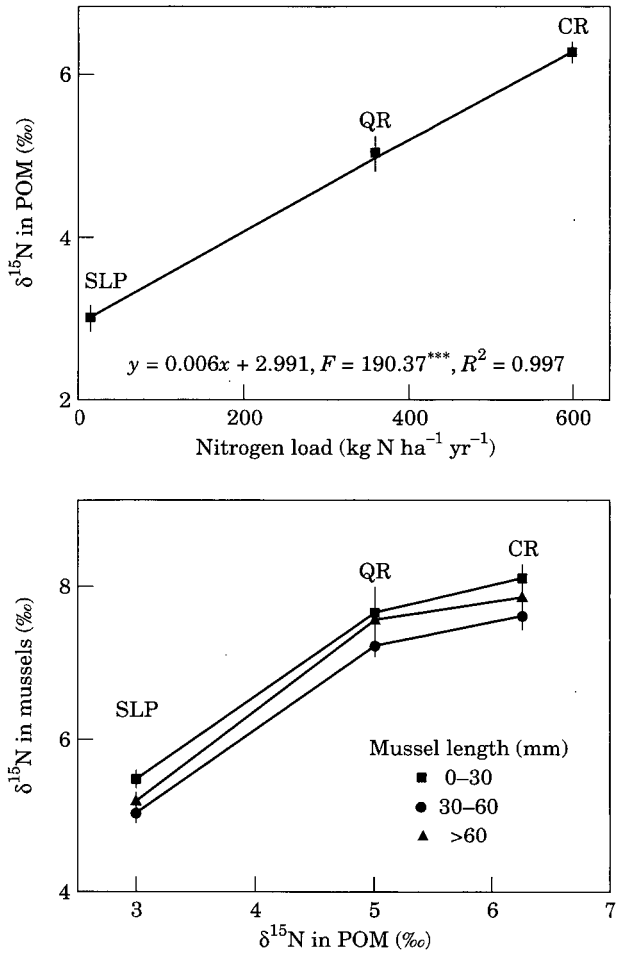

FIGURE 3. Top: δ^{15}N in particulate organic matter (POM) plotted vs. nitrogen loading rates of Sage Lot Pond (SLP), Quashnet River (QR) and Childs River (CR). Points with error bars represent the average ± standard error for δ^{15}N of POM sampled from different sites of the estuaries. Bottom: δ^{15}N in mussels plotted vs. δ^{15}N in particulate organic matter (POM), from Sage Lot Pond (SLP), Quashnet River (QR) and Childs River (CR). Squares, circles and triangles represent small: mussels <30 mm in length, medium: mussels 30–60 mm in length, and large: mussels >60 mm in length, respectively. Points with error bars represent the average ± standard error for δ^{15}N of mussels sampled from different sites from the three estuaries.

Waquoit Bay system have brief water residence times (Table 1), the particulate matter assimilated by *G. demissa* seems native to that particular estuary, rather than by a mix of POM brought into the estuary by tidal exchange. We conclude that *G. demissa* consumed POM from the estuary they were in, because isotopic signatures in the mussels reflect the POM signatures within that estuary (Figure 3 bottom).

Mussels showed heavier isotopic signature as mussel size increased (Tables 2, 3). The reason for size-related responses are not very clear. Peterson *et al.*

TABLE 2. δ^{15}N signatures of mussels (average ± SE) for Childs River, Quashnet River, and Sage Lot Pond (values represent averages from three different sites of each estuary)

	Length of mussels (mm)		
Estuary	Small (<30)	Medium (30–60)	Large (>60)
Childs River	7·6 ± 0·2	7·9 ± 0·1	8·1 ± 0·2
Quashnet River	7·2 ± 0·1	7·6 ± 0·4	7·7 ± 0·1
Sage Lot Pond	5·1 ± 0·1	5·2 ± 0·1	5·5 ± 0·1

(1986) observed only slight seasonal differences in the isotopic composition of small *G. demissa*, when compared to older conspecifics, and he attributed these findings to more rapid tissue turnover times and large changes in the diet of young mussels. Fry (1988) argued that there were no differences in the stable isotopic signatures in scallops (*Placopecten magellanicus*) 2 and 9-years-old.

Mussels within an estuary then evidently feed on POM characteristic of that estuary, demonstrating the direct linkage between a watershed, POM in the receiving estuary, and consumers within that estuary (McClelland *et al.*, 1997). Given that there are differences in food supply among the three estuaries we studied (Valiela *et al.*, 1992, submitted), we therefore would expect that growth rates of a food-limited consumer, such as the ribbed mussel, might also increase in enriched estuaries.

Indirect measurement of shell growth of mussels

The number and length of mussels found at different elevations in the three estuaries differed greatly (Figure 4). In general, the majority of the mussels were low in the intertidal (left panels of Figure 4), with fewer at higher intertidal ranges (right panels of Figure 4). Mussel length, in all estuaries, ranged from 2·5 to 110 mm. The population consisted of many cohorts, with median lengths that were similar in all estuaries (Figure 4).

We calculated growth rates from data on the length and age of individual mussels (Figures 5, 6) using the von Bertalanffy approach. This was repeated for each data set for the three elevation ranges within each estuary. The length-age curves (Figure 5) resembled typical growth curves (Brousseau, 1984), with a high rate of increase in shell-length at early ages, and a subsequent decrease at older stages. In all estuaries, the ages of mussels ranged from <1 to 20 years, but most mussels ranged from 1 to 10 years in age.

To calculate growth rates, we linearized (Figure 6) the von Bertalanffy's equation, and estimated

TABLE 3. Analysis of variance in a split plot design of $\delta^{15}N$ signature of mussels under the effects of size and estuary

	DF	SS	MS	F
Site within estuary	2	0·89	0·445	
Estuary	2	35·26	17·63	182·7***
Estuary by site	4	0·39	0·09	
Size	2	0·9	0·458	9·862**
Estuary × size	4	0·04	0·009	0·199 ns
Sizes and sites within estuaries	12	0·56	0·05	

***P<0·001; **P<0·01; ns=not significant.

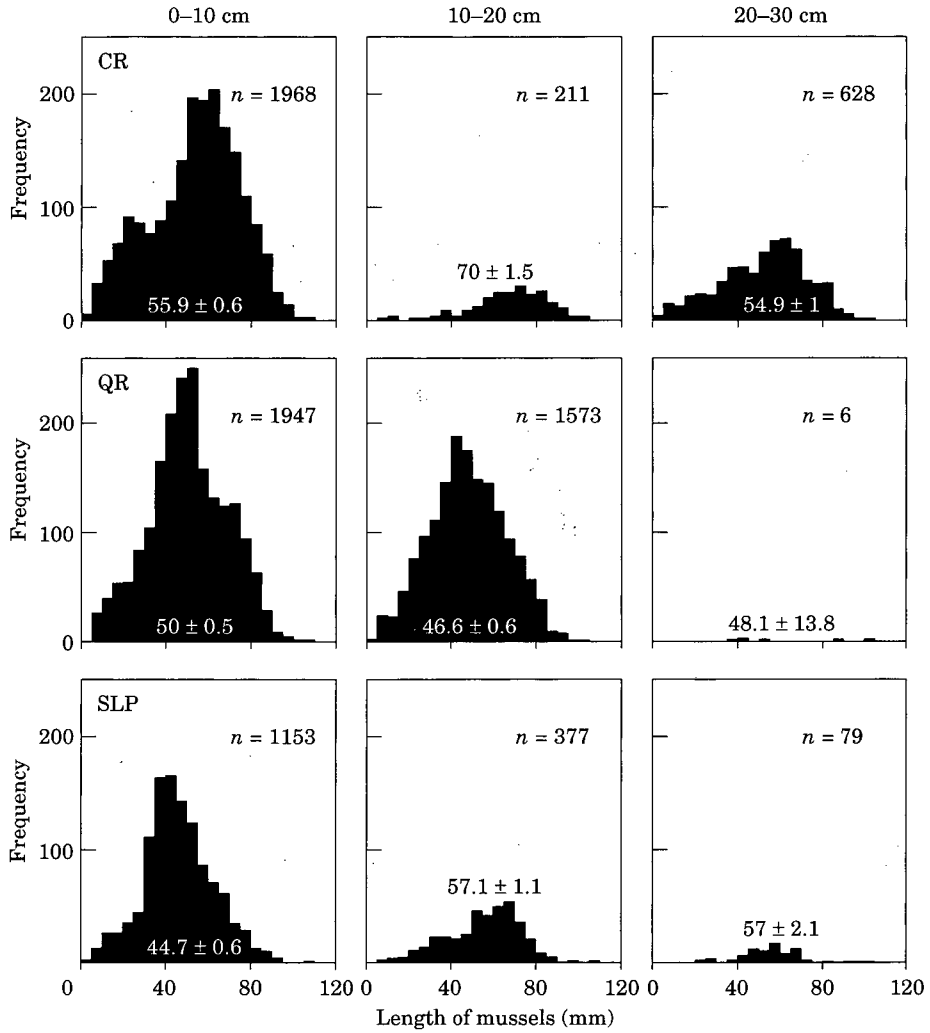

FIGURE 4. Frequency distributions of length (mm) of all the mussels sampled from the three estuaries of Waquoit Bay. The three top, the three middle, and the three bottom histograms correspond to mussels from Childs River (CR), Quashnet River (QR), and Sage Lot Pond (SLP) respectively. The first column corresponds to the lowest tidal elevation sampled (0–10 cm above MLW), the second column to the middle tidal elevation sampled (10–20 cm above MLW) and the third column to the upper tidal elevation sampled (20–30 cm above MLW). In each histogram the number of mussels sampled (n), and the median (± SE med) is given.

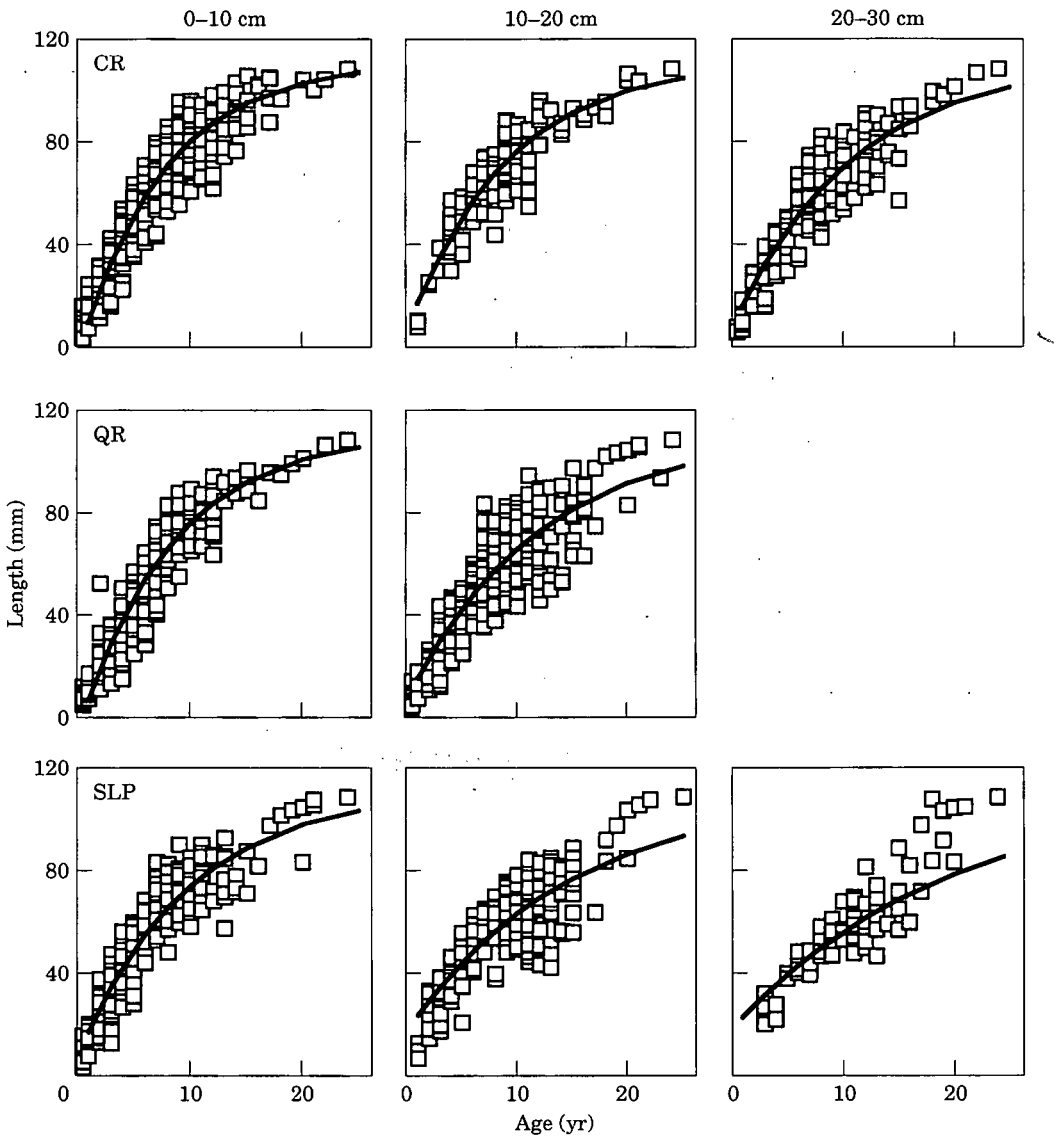

FIGURE 5. Length (mm) *vs.* age (years) of the mussels sampled from Childs River (three top graphs), Quashnet River (three middle graphs) and Sage Lot Pond (three bottom) with the fitted von Bertalanffy curves. The first column corresponds to the lowest tidal elevation sampled (0–10 cm above MLW), the second column to the middle tidal elevation sampled (10–20 cm above MLW) and the third column to the upper tidal elevation sampled (20–30 cm above MLW).

parameters for every tidal elevation and every estuary (Table 4). The parameter K in the von Bertalanffy equation is the growth coefficient (its units are in time^{-1}); it is not a growth rate. As an indication of growth, K expresses how fast the mussels are reaching L_∞. K was highest in Childs, and lowest in Sage Lot Pond, in every elevation (t-test Childs-Quashnet: $P<0{\cdot}05$, t-test Childs-Sage Lot Pond: $P<0{\cdot}05$, for every elevation). K decreased as tidal elevation increased in each estuary.

Estimates of growth rates (dL_t/dt) of mussels in the Waquoit Bay estuaries were related to age of the mussel, elevation within the intertidal range, and to mean concentration of chlorophyll in the water (Figure 7). Young mussels (Figure 7 top) grew faster than older mussels (Figure 7 middle and bottom). Mussels located lower in the intertidal grew faster than those found at higher elevations, but this elevation effect was more prominent for younger mussels. The effect of increased food supply (as represented by the concentrations of chlorophyll *a* in the water) on shell growth was significant for young mussels at all elevations (significant regression of young mussels at all elevations, Figure 7 top), but not for larger

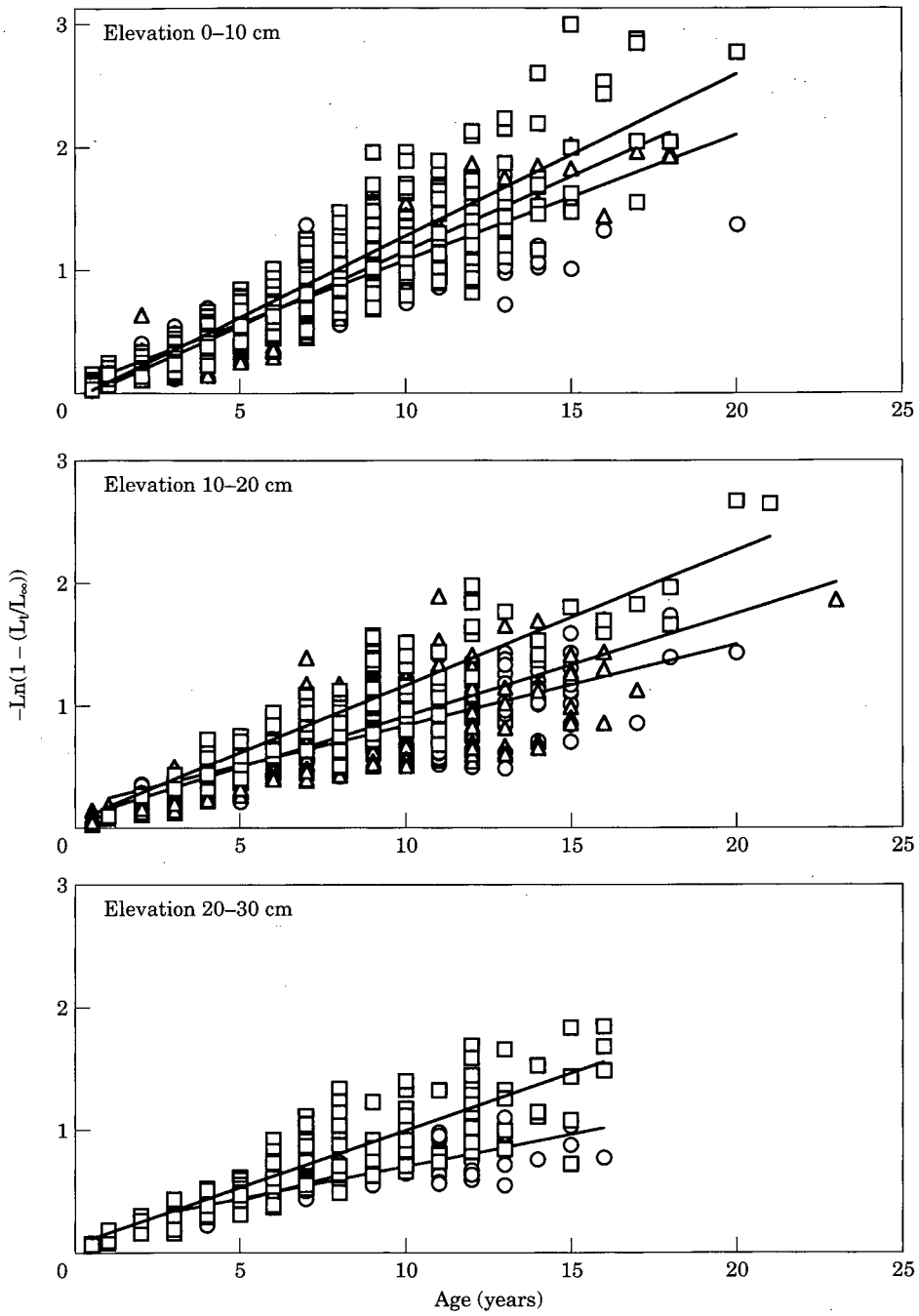

FIGURE 6. The factor $-Ln\,(1-(L_t/L_\infty))$ calculated for mussels coming from each estuary, and plotted *vs.* the age (years) of each mussel. The slope of each curve corresponds to the K of von Bertalanffy's equation, and the X intercept of each curve is equal to $-K\,t_o$. Squares, triangles and circles correspond to data collected from Childs River, Quashnet River, and Sage Lot Pond respectively. Top: Data collected from the first tidal elevation (0–10 cm above MLW), regression analyses: $y=0{\cdot}132x-0{\cdot}039^{**}$, $R^2=0{\cdot}86$ (Childs River), $y=0{\cdot}121x-0{\cdot}051^{**}$, $R^2=0{\cdot}88$ (Quashnet River), $y=0{\cdot}102x+0{\cdot}066^{**}$, $R^2=0{\cdot}82$ (Sage Lot Pond), Middle: second tidal elevation (10–20 cm), regression analyses: $y=0{\cdot}11x+0{\cdot}063^{**}$, $R^2=0{\cdot}79$ (Childs River), $y=0{\cdot}083x+0{\cdot}072^{**}$, $R^2=0{\cdot}7$ (Quashnet River), $y=0{\cdot}066x+0{\cdot}177^{**}$, $R^2=0{\cdot}68$ (Sage Lot Pond), and Bottom: third tidal elevation (20–30 cm), regression analyses: $y=0{\cdot}093x+0{\cdot}064^{**}$, $R^2=0{\cdot}77$ (Childs River), $y=0{\cdot}07x+0{\cdot}073$, $R^2=0{\cdot}95$ (Quashnet River), $y=0{\cdot}052x+0{\cdot}179^{**}$, $R^2=0{\cdot}57$ (Sage Lot Pond), ($^{**}=P<0{\cdot}01$).

TABLE 4. Estimated K and t_o for von Bertalanffy's equations for Childs River, Quashnet River, and Sage Lot Pond. The parameters are calculated separately for every tidal elevation (0–10, 10–20, 20–30 cm)

	Tidal elevation (cm)					
	0–10		10–20		20–30	
	K	t_o	K	t_o	K	t_o
Childs River	0·132	0·295	0·11	−0·527	0·093	−0·688
Quashnet River	0·121	0·421	0·083	−0·867	0·07	−1·04
Sage Lot Pond	0·102	−0·647	0·066	−2·68	0·052	−3·44

mussels (no significant regression, Figure 7 middle and bottom). Moreover, growth rates of young mussels (<3 years old) at all three elevations responded to increased food supply similarly, because the slopes of the regressions were not different (t-test: $P>0·05$). Figure 7 shows that as chlorophyll concentrations increase across the estuaries, shell growth of young mussels increases at all elevations. These results indicate that young mussels may be food-limited, and any increases in food supply (chlorophyll *a*) result in increases of shell growth rates. Older mussels, while being probably food-limited, do not show differences in shell growth among estuaries, because they may be investing their energy for other purposes (Franz, 1996).

G. demissa live in an edge habitat. Mussels located lower in the intertidal have more time available to feed, but suffer increased mortality due to predation from crabs (Hardwick-Witman, 1985; Lin, 1989*a*), or due to ice-rafting (Hardwick-Witman, 1985; Bertness & Grosholz, 1985; Stiven & Gardner, 1992). In contrast, mussels located higher in the intertidal have to deal with other mortality factors, such as desiccation (Lent, 1969; Kneib, 1984). Also, at higher elevations the opportunity to feed diminishes; due to shorter submersion time per tidal cycle or of prefiltration of tidal waters by mussels lower in the marsh (Jordan & Valiela, 1982; Peterson & Black, 1988; Lin, 1989*b*; Stiven & Gardner, 1992; Franz, 1993, 1996). Filtration rates do not increase with elevation but with dry weight (Jordan & Valiela, 1982; Riisgard, 1988), but dry weight decreases with elevation (Franz, 1993). Hence, there is less amount of food available for them, and this is reflected to their lower growth rates when compared to conspecifics located lower in the intertidal range (Jordan & Valiela, 1982; Lin, 1989*b*; Stiven & Gardner, 1992; Franz, 1993).

Growth rates increased in response to presumed greater food supply only for younger mussels (0–3 years of age). The fact that small individuals grow faster than larger individuals is well known (Kuenzler, 1961; Jordan & Valiela, 1982; Brousseau, 1979, 1984; Hardwick-Witman, 1985; Bertness & Grosholz, 1985; Borrero & Hilbish, 1988; Feinstein *et al.*, 1996). Growth rates of older mussels (>3 years of age) were not different across the estuaries, in other words, shell growth rates of older mussels did not respond to the elevated food supply. Borrero and Hilbish (1988) showed that in ribbed mussels, shell and body growth occur simultaneously in sexually immature mussels, while in sexually mature mussels, body growth exceeds shell growth. It has been reported that *G. demissa* becomes reproductive after 2 to 4 years (Kuenzler, 1961; Lutz & Castagna, 1980; Hardwick-Witman, 1985; Franz, 1996), hence, in Waquoit Bay, it seems that mussels older than three years deploy their increased resources otherwise than to shell growth, perhaps to reproduction. So, it is possible that increased food supply results in increased shell growth of *G. demissa* before sexual maturity, and in increased reproductive effort afterwards. This reproductive strategy of minimizing somatic production to maximize reproductive output is an adaptive mechanism of this species (Jordan, pers. comm.; Franz, 1997).

In contrast to food quantity, food quality seems to change across the estuaries of Waquoit Bay, as particulate organic nitrogen (PON) concentrations seem to increase from Sage Lot Pond to Childs River (Table 1). Mussels fed upon organic aggregates incorporate five to ten times more nitrogen than when they are fed upon dissolved organic material (DOM) or particulate detritus (Alber & Valiela, 1994). Jordan and Valiela (1982) found that the ribbed mussel assimilates half of the nitrogen it filters, and from the nitrogen assimilated, 20% is invested in growth. As PON concentrations increase across the estuaries, more nitrogen is invested in growth by the mussels. Therefore, food quality must be also playing an important role in growth of the ribbed mussels.

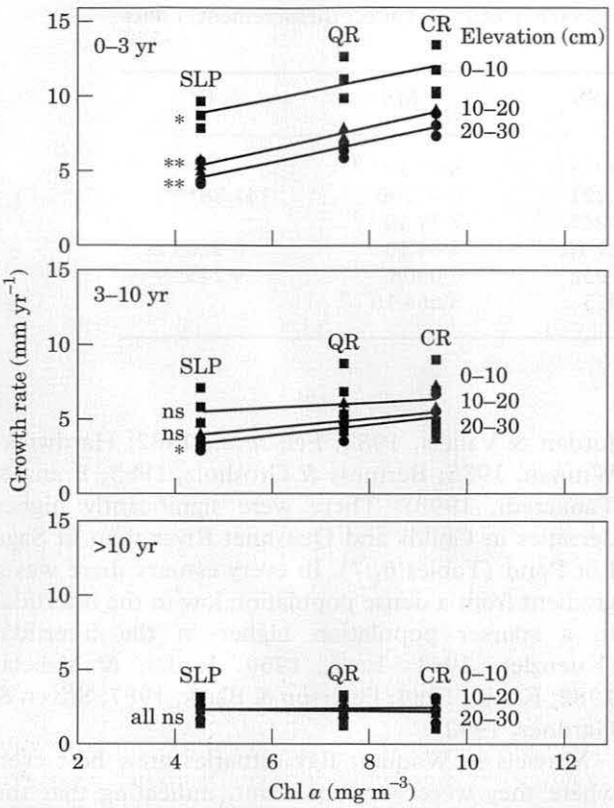

FIGURE 7. Growth rate (dL/dt, in mm yr^{-1}) of mussels plotted vs. chlorophyll *a* concentrations from Childs River (CR), Quashnet River (QR), and Sage Lot Pond (SLP) (data in Table 2). Top, middle and bottom graphs correspond to growth rates of mussels 0–3-years-old, 3–10-years-old, and >10-years-old respectively. Squares, triangles and circles represent mussels collected from tidal elevations 0–10, 10–20 and 20–30 cm above MLW respectively. Top: regression analyses for mussels 0–3-years-old: $y=0{\cdot}664x+50{\cdot}886$*, $R^2=0{\cdot}96$ (tidal elevation 0–10 cm), $y=0{\cdot}77x+0{\cdot}1837$**, $R^2=0{\cdot}985$ (tidal elevation 10–20 cm), $y=0{\cdot}691x+10{\cdot}482$**, $R^2=0{\cdot}974$ (tidal elevation 20–30 cm), Middle: regression analyses for mussels 3–10-years-old: $y=0{\cdot}197x+40{\cdot}586$ ns, $R^2=0{\cdot}802$ (tidal elevation 0–10 cm), $y=0{\cdot}317x+20{\cdot}547$ ns, $R^2=0{\cdot}984$ (tidal elevation 10–20 cm), $y=0{\cdot}374x+10{\cdot}712$*, $R^2=1$(tidal elevation 20–30 cm), Bottom: regression analyses for mussels >10-years-old: $y=-0{\cdot}029x+20{\cdot}44$ ns, $R^2=0{\cdot}529$ (tidal elevation 0–10 cm), $y=-0{\cdot}01x+20{\cdot}356$ ns, $R^2=0{\cdot}03$ (tidal elevation 10–20 cm), $y=0{\cdot}046x+20{\cdot}31$*, $R^2=0{\cdot}5$ (tidal elevation 20–30 cm), (*=$P<0{\cdot}05$, **=$P<0{\cdot}01$, ns indicates F was not significant).

In this study we show that as nitrogen loading, and subsequent chlorophyll *a* concentrations, increase across the estuaries shell growth of the young mussels (0–3 years old) also increases. The differences in nitrogen loading rates between Sage Lot Pond and Childs River were about 50 ×. Because of the several intervening mechanisms that couple land derived nitrogen loading to responses of bivalves, there is a

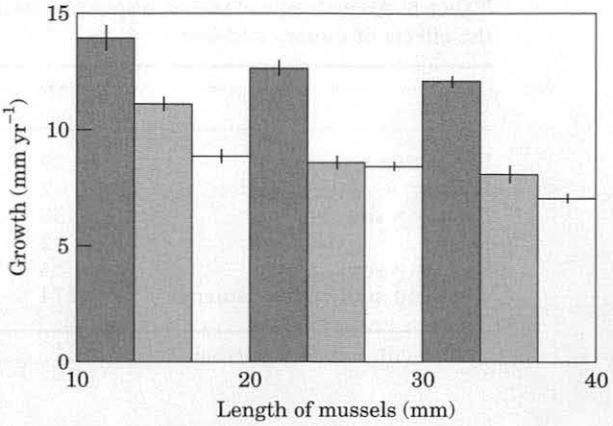

FIGURE 8. Growth of transplanted mussels (mm yr^{-1}) of three different length-classes (10–20, 20–30, 30–40 mm) in Childs River (■), Quashnet River (▨), and Sage Lot Pond (□). Bars with error lines represent mean values ± SE.

'dilution' of the effects, and the differences between shell growth of young mussels in the two estuaries is much less (~2 ×). The point still remains, though, that the differences are significant although smaller. The 'dilution' might be the result of the several transformations that are interposed between the nitrogen loading from the watershed and the response to the nitrogen load by growth of the mussel.

Direct measurement of shell growth of mussels

Initial mean length of the transplanted young mussels and the range of initial length were similar in all three estuaries (10–35 mm). Transplanted mussels grew during the 80 days of the experiment (Childs River: 23·8 ± 0·9 to 26·7 ± 0·9, Quashnet River: 22·6 ± 1 to 24·7 ± 1, and Sage Lot Pond: 23·8 ± 1 to 25·2 ± 1). We also calculated growth for three different length classes (10–20 mm, 20–30 mm, 30–40 mm) of the mussels of every estuary (Figure 8, Table 5). Growth rates differed in each estuary. Mussels in Childs River grew significantly faster than mussels from Quashnet River and Sage Lot Pond regardless of their size (Figure 8). Growth rates measured in the transplantation experiment were similar to growth rates estimated from the field collections and von Bertalanffy calculations (Figure 9), since the t value for comparing the regression to the 1:1 line is not significant. The results of the transplantation experiment indicates that the differences in growth rates of the mussels across the estuaries of Waquoit Bay, are a response to characteristics of the estuaries themselves, primarily in our view, different food supplies.

TABLE 5. Analysis of variance in a split plot design of growth of mussels (direct measurement) under the effects of estuary and size

	DF	SS	MS	F
Site within estuary	29	0·0025	$8{\cdot}69\ 10^{-5}$	
Estuary	2	0·0221	0·01106	141·88***
Estuary × site	58	0·0045	$7{\cdot}79\ 10^{-5}$	
Size	2	$7{\cdot}29\ 10^{-5}$	$3{\cdot}64\ 10^{-5}$	0·4205 ns
Estuary × size	4	0·0032	0·0008	9·245***
Sizes and sites within estuaries	174	0·015	$8{\cdot}664\ 10^{-5}$	

***$P<0{\cdot}001$; ns=not significant.

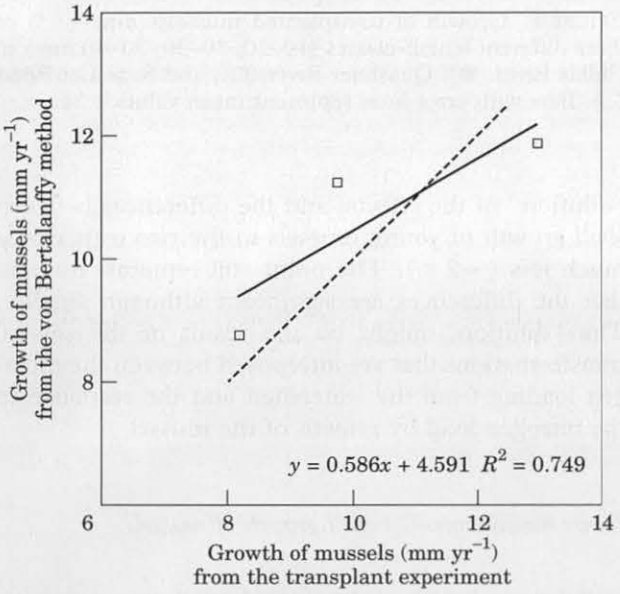

FIGURE 9. Growth (mm yr^{-1}) of mussels calculated with the von Bertalanffy method plotted vs. growth of the transplanted mussels (mm yr^{-1}). The dotted line is the 1:1 line, for comparison. Growth rates compared are only from young mussels (0–3 years of age) and only from the lowest intertidal zone (0–10 cm above MLW).

Measurement of density

Mussel densities in Waquoit Bay lay within the highest range reported from other studies (Kuenzler, 1961; Jordan & Valiela, 1982; Fell *et al.*, 1982; Hardwick-Witman, 1985; Bertness & Grosholz, 1985; Franz & Tanacredi, 1993). There were significantly higher densities in Childs and Quashnet River than in Sage Lot Pond (Tables 6, 7). In every estuary there was a gradient from a dense population low in the intertidal to a sparser population higher in the intertidal (Kuenzler, 1961; Lent, 1969; Jordan & Valiela, 1982; Kneib, 1984; Peterson & Black, 1987; Stiven & Gardner, 1992).

Mussels in Waquoit Bay estuaries grew best even where they were very abundant, indicating that the populations of *Geukensia demissa* in the three estuaries in Waquoit Bay are not density dependent. Our results contradict the density dependence of growth reported in some studies (Stiven & Kuenzler, 1979; Bertness & Grosholz, 1985), but they are in accordance with other reports (Jordan & Valiela, 1982; Fell *et al.*, 1982; Lin, 1989*b*). Growth of *G. demissa* in many places might be not density-dependent, but rather limited by the restricted time window when feeding is possible (Lin, 1989*b*). The significant differences in shell growth that we found among the mussels from different estuaries may be the response to higher concentrations of food particles available in estuaries subject to higher nitrogen loads. Regardless of how much time was available for feeding, growth of young mussels at each elevation, and in each estuary, responded to the ambient food supply. This implies

TABLE 6. Density of mussels (mussels $m^{-2} \pm$ SE) for Childs River, Quashnet River, and Sage Lot Pond, within three different ranges in tidal elevation (0–10, 10–20, and 20–30 cm above MLW). The number of mussels measured for each mean is given in parentheses

	Tidal elevation ranges (cm)		
Estuary	0–10	10–20	20–30
Childs River	2050 ± 249 (n=1968)	251 ± 66 (n=211)	978 ± 288 (n=628)
Quashnet River	2859 ± 257 (n=1947)	896 ± 196 (n=1578)	25 ± 17 (n=6)
Sage Lot Pond	1289 ± 126 (n=1153)	283 ± 39 (n=377)	190 ± 25 (n=79)

TABLE 7. Analysis of variance in a split plot design of density of mussels under the effects of tidal elevation and estuary

	DF	SS	MS	F
Site within estuary	43	26 770 572	622 571	
Estuary	2	52 067 531	26 033 765	51·44***
Estuary × site	86	43 525 739	506 113	
Elevation	2	59 794 108	29 897 054	43·8***
Estuary × elevation	4	7 585 380	1 896 345	2·37*
Elevations and sites within estuaries	258	175 890 488	681 746	

***$P<0.001$; *$P<0.05$.

also that these mussels did not have sufficient time to lower the density of food particles, i.e. this consumer-food link does not seem controlled by top-down processes (Carpenter *et al.*, 1985, 1987) but rather from bottom-up controls.

In most of the shorelines of the world, land-derived nitrogen inputs are increasing and this is accompanied by increases in chlorophyll concentrations (Nixon *et al.*, 1986; Valiela *et al.*, 1992). The results of this paper demonstrate a direct linkage between increased nitrogen delivery from a watershed to an estuary, POM in the receiving estuary, and bivalves within that estuary. Increased phytoplankton production resulting from increased nitrogen loading fosters greater growth of bivalves via bottom-up controls, provided that *Geukensia demissa* is a suitable model for estuarine shellfish. Of course, habitat destruction and hypoxia often accompany eutrophication, but judging from the effects of the food increase as a whole, eutrophication increased growth of suspension-feeding bivalves.

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