Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

Changes in shell and soft tissue growth, tissue composition, and survival of quahogs, *Mercenaria mercenaria*, and softshell clams, *Mya arenaria*, in response to eutrophic-driven changes in food supply and habitat

R.H. Carmichael[*], Andrea C. Shriver, I. Valiela

Boston University Marine Program, Marine Biological Laboratory, Woods Hole, MA 02543, USA

Abstract

Eutrophic-driven changes in the composition of near-bottom seston and surface sediment potentially affect food resources and habitat of commercially important bivalves like quahogs, *Mercenaria mercenaria*, and softshell clams, *Mya arenaria*. To define how land-derived nitrogen loads and resulting eutrophication affect bivalves, we compared estuarine features to growth and survival of clams across estuaries receiving different N loads. The major effects of nitrogen enrichment on near-bottom seston and surface sediment were to (1) increase microalgal concentrations and reduce carbon to nitrogen ratios, increasing quantity and quality of available foods, and (2) reduce oxygen content in sediments, potentially reducing habitat quality. Shell growth of juvenile and native clams increased with increasing food supply, driven by N enrichment. Growth of soft tissue followed growth of shell, and %N content of soft tissue increased across N loads, providing direct evidence of a link between N loads and growth responses in clams. In some locations, low salinity limited growth and low oxygen concentrations may have reduced survival.

    * Corresponding author. Now at: University of Maine at Machias, 9 O'Brien Avenue, Machias, ME 04654, United States. Tel.: +1 508 289 7515; fax: +1 508 289 7949.

    E-mail address: rherrold@alum.bu.edu (R.H. Carmichael).

Despite these factors, our data indicate the major effect of N enrichment on clams was increased secondary production in terms of shell and soft tissue growth.

1. Introduction

Increased anthropogenic nitrogen (N) addition to coastal waters is a major agent of change among coastal ecosystems worldwide (GESAMP, 1990; Goldberg, 1995; NRC, 2000). In New England and elsewhere, land-derived N loads have increased during the 20th century due primarily to wastewater from residential sprawl (Valiela et al., 1992; Smith et al., 1999; Bowen and Valiela, 2001). These increased deliveries of N have prompted eutrophication in many estuaries (Nixon et al., 1986; Nixon, 1992; Valiela et al., 1992; Valiela et al., 1997; Caraco and Cole, 1999; Valiela et al., 2000), which, in turn, has altered features of receiving estuarine ecosystems (Paerl et al., 1998; Cloern, 2001).

Quahogs (*Mercenaria mercenaria*) and softshell clams (*Mya arenaria*), historically two of the most abundantly harvested and cultured species in U.S. waters (Belding, 1912; Matthiessen, 1992; National Marine Fisheries Service, Annual Commercial Landings Statistics, 2003), are among the most susceptible to effects of eutrophication since they inhabit coastal areas that put them in close proximity to development along the shoreline (Belding, 1912; Stanley and Dewitt, 1985; Abraham and Dillon, 1986; Matthiessen, 1992). Many studies have addressed the variety of factors that may affect bivalve growth and survival (Winter, 1978; Bayne and Newell, 1983; Grant, 1996; Grizzle et al., 2001; and many others), but few have considered how eutrophication might change these observations. Critical reading of the literature reveals there may be both positive and negative responses by bivalves to eutrophication (De Zwaan, 1983; Loo and Rosenberg, 1989; Navarro and Iglesias, 1992; Chalfoun et al., 1994; Everett, 1994; Peterson et al., 1994; Josefson and Rasmussen, 2000; Evgenidou and Valiela, 2002; Shriver et al., 2002; Weiss et al., 2002).

Increased N loads may initially increase food quantity and quality for bivalves in receiving estuaries. N is the major nutrient limiting primary production in coastal waters (Ryther and Dunstan, 1971; Howarth, 1988; Valiela, 1995). As land-derived N loads increase, productivity and N content of phytoplankton and benthic algae also increase (Goldman, 1975; Granéli and Sundbäck, 1985; Sundbäck et al., 1991; Valiela et al., 1992, Cloern, 2001; Carmichael and Valiela, in press). Since bivalves consume microalgae and other particles from the water column and sediment surface (Rasmussen, 1973; Rhoads et al., 1975; Kamermans, 1994; Carmichael et al., unpublished), the initial responses of these bivalves to enhanced N loads might be increased growth and survival (Rask, 1982; Grizzle and Morin, 1989; Cahalan et al., 1989; Rheault and Rice, 1996; Evgenidou and Valiela, 2002; Weiss et al., 2002).

As N loads increase, reduced habitat quality may lower growth and survival of bivalves. First, enriched environments are more subject to depletion of oxygen (Paerl et al., 1998; Cloern, 2001; Gray et al., 2002). In N rich waters, accumulation of organic

matter from detritus of phytoplankton and macroalgae increases organic content of sediments (Zeitzschel, 1980; Cadée, 1984; Zimmerman and Canuel, 2000). This process, in turn, increases microbial biomass (Hargrave, 1980; Koster et al., 1997; Cloern, 2001) and oxygen consumption, leading to anoxic or hypoxic conditions in near-bottom waters and sediments (Hargrave, 1980; Maughan and Oviatt, 1993; D'Avanzo and Kremer, 1994; Paerl et al., 1998). Lower oxygen concentrations associated with N enrichment, therefore, could ultimately lower growth rates and reduce survival among clams (De Zwaan, 1983; Everett, 1994; Thiel et al., 1998; Borsuk et al., 2002).

Second, increased N loads may alter extent and quality of bivalve habitat (Sardá et al., 1996). Increased concentration of fine organic particles may change sediment texture, making habitat less suitable and affecting growth or survival of bivalves (Rhoads and Young, 1970; Pearson and Rosenberg, 1978; Newell and Hidu, 1982). N enrichment also may be associated with increased numbers of grazers that compete with bivalves for food (Novak et al., 2001; Shriver et al., 2002), high concentrations of suspended particulate matter that may slow bivalve feeding rates (Rice and Smith, 1958; Tenore and Dunstan, 1973; Winter, 1978), and lower mean salinity, since land-derived N loads are typically transported to estuaries by freshwater (Valiela et al., 1992). Weiss et al. (2002) speculated lower salinity or high concentrations of suspended particulate matter limited growth in juvenile clams at high N loads. That study, however, did not collect sufficient data to resolve with certainty how these variables interact with increased N loads to affect growth and survival of clams.

Eutrophic-driven changes in food quantity and quality may affect different bivalve species in different ways. First, different species process foods differently and, in turn, assimilate foods at different rates (Tenore and Dunstan, 1973; Kirby-Smith and Barber, 1974; Bayne and Newell, 1983; Bricelj and Malouf, 1984; Bricelj et al., 1984; Grant and Thorpe, 1991; Bacon et al., 1998; MacDonald et al., 1998; Milke and Ward, 2002; Ward et al., 2003). Second, changes in food supply may have varying effects on the biochemical composition of soft tissue in different species (Gabbott and Bayne, 1973; Laing, 1993; Baker and Hornbach, 1999). Third, some bivalves can reallocate assimilated foods to support different types of growth under different conditions. Quahogs and softshell clams, specifically, shift from shell growth to soft tissue growth or among different types of soft tissue (Lewis and Cerrato, 1997; Eversole, 2001). Quahogs and softshell clams, therefore, are good models in which to study effects of N enrichment on bivalves since they live and feed similarly relative to the sediment–water interface (Bayne and Newell, 1983; Kamermans, 1994), but may assimilate foods differently. Comparisons among these relatively similar species allow us to examine the specificity of links between land-derived N loads and the dynamics of bivalve growth and survival.

Shell growth can be measured directly and relatively rapidly in transplanted juveniles (Evgenidou and Valiela, 2002; Shriver et al., 2002; Weiss et al., 2002) and indirectly estimated in native clams using established models such as the von Bertalanffy (1960) growth model. The von Bertalanffy growth model produces a decaying exponential curve that approaches the species-specific maximum growth asymptote (Fabens, 1965). This model provides a quite accurate estimate of growth throughout the life span of bivalves compared to other models (Urban, 2002) and has been successfully applied to assess

growth of quahogs, softshell clams, and other bivalves (Brousseau, 1979; Appledoorn, 1982; Jones et al., 1989; Appleyard and DeAlteris, 2001).

Although shell length is the variable most commonly used to assess bivalve growth (e.g., Belding, 1912; Brousseau, 1979; Newell and Hidu, 1982; Grizzle et al., 2001), soft tissue growth is also important. First, changes in food supply can uncouple shell and soft tissue growth (Lewis and Cerrato, 1997), indicating shell and tissue may respond differently to changes in food quantity and quality. Second, since clams may reallocate resources to support different types of growth under different conditions (Eversole, 2001), changes in soft tissue growth may reflect changes in physiological condition of clams. Third, if management goals include increased stocking of commercially important bivalves, it is important to know whether growth of the valuable soft tissue portion of clams is affected by N enrichment in the same manner as shell growth. These observations suggest both shell and soft tissue growth are important to assessing the effects of N enrichment on clam growth.

In this study, we determined how eutrophic-driven changes in food supply and habitat-affected growth, survival, and tissue composition of two clam species, *M. mercenaria* and *M. arenaria*. To do this, we first determined how differences in N loading rates among estuaries affected (1) chlorophyll *a*, C, and N concentrations in near-bottom seston and surface sediment, (2) dissolved oxygen concentration in near-bottom waters, and (3) reduction–oxidation potential in sediment. We then compared changes in these estuarine features to growth, survival, and %N in tissues of clams across estuaries to determine how N enrichment affected clams.

2. Methods

2.1. Study sites and sampling schedule

Sampling took place in eight Cape Cod estuaries that receive different N loads to their watersheds (Fig. 1; Table 1). These estuaries span most of the range of land-derived N loads common to coastal estuaries (Nixon, 1992; Nixon et al., 2001) and represent N loads as large as can be found in our area (Valiela et al., 1992; D'Avanzo and Kremer, 1994). This study was conducted from early June to mid September at six sites in three estuaries (Sage Lot Pond, Green Pond, and Childs River) in 2000 and two sites in eight estuaries in 2001 (Fig. 1; Table 1). Sampling sites in each estuary had similar depth (~1 m at mean low water), flow regimes, sediment types, and temperatures (Table 1).

2.2. Seston and sediment sampling

To determine how characteristics of the water column and sediments were affected by N loading, we collected seston and sediment every 2 weeks at each site during the study. To collect near-bottom seston, we sampled water ~10 cm from the sediment surface using a Wildco horizontal water sampler and filtered 2 l of sample (200 μm pre-filtered) onto a pre-ashed 0.7-μm Whatman GF/F filter. To collect sediment samples, we used a 1-cm
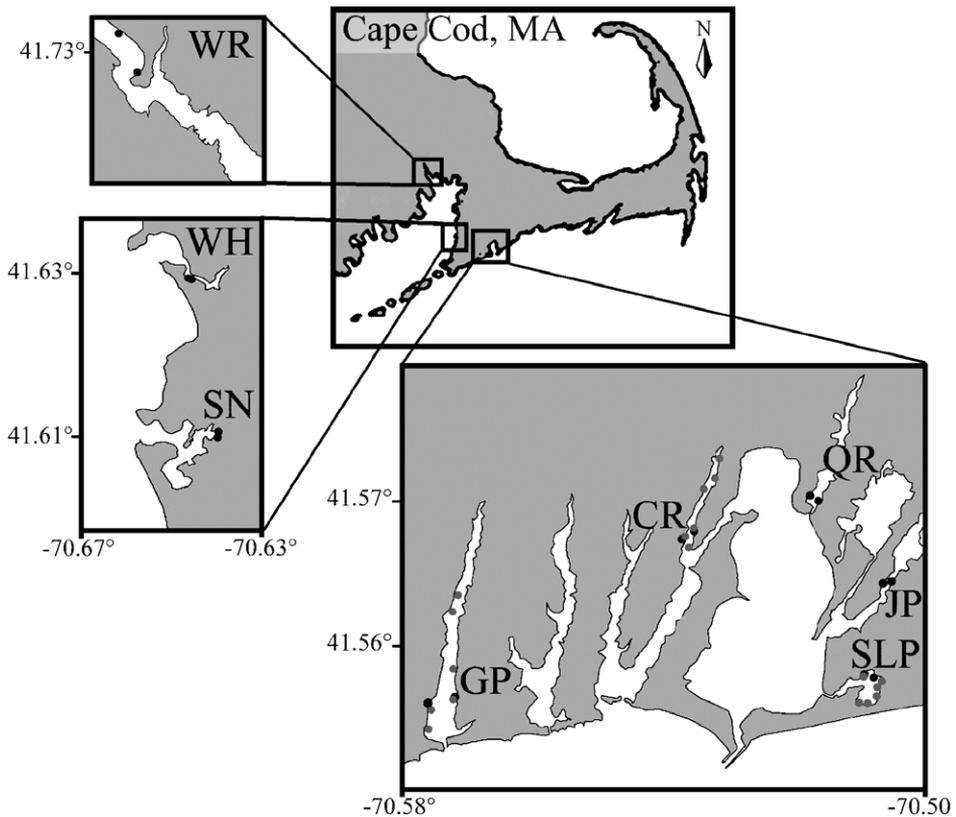
Fig. 1. Locations in eight estuaries of Cape Cod, MA, where juvenile clams were transplanted, native clams were collected, and seston and sediment samples were taken in 2000 (gray dots) and 2001 (black dots). WR=Weweantic River, WH=Wild Harbor, SN=Snug Harbor, GP=Green Pond, CR=Childs River, QR=Quashnet River, JP=Jehu Pond, SLP=Sage Lot Pond.

diameter syringe corer to take the top 3 cm of sediment and pooled sediment from three replicate cores at each sampling site.

2.3. Assessment of potential food supply

To determine the quantity and quality of organic particles in seston and sediment, we measured chlorophyll *a* (chl *a*), carbon (C), and nitrogen (N) concentrations, and C/N ratios in both seston and sediment as well as total suspended (SPM) and organic (POM) particulate matter in seston. To measure chl *a* concentration in seston and sediment, we extracted filters and bulk sediments with acetone and analyzed by spectrophotometry (Lorenzen, 1967; Moss, 1971). To determine C and N concentrations, we combusted filters and sediment in a Perkin-Elmer 2400 CHN elemental analyzer. Prior to combustion, sediments were acidified overnight by fuming with concentrated HCl to remove carbonates. To determine total and organic particulate

Table 1
N loading rate, mean water temperature, seston and sediment characteristics, and % survival of quahogs and softshell clams in eight Cape Cod estuaries (c.f. Fig. 1)

Estuary	N load (kg N ha^{-1} year^{-1})	Temperature (°C)	Salinity (‰)	Seston				Sediment			Survival (%)			
				SPM (mg l^{-1})	POM (mg l^{-1})	C (mg l^{-1})		Snails (No. m^{-2})	Silt+clay (%)	Sand (%)	Quahogs		Softshell clams	
						2000	2001				2000	2001	2000	2001
Sage Lot Pond	14	25±0.1	28.2±1.5	19±2	5.0±1.1	1.2	1.5	0	6±4	94±3	98±1	48±48	91±4	6±2
Jehu Pond	21	25±1.0	29.1±0.3	26±1	5.3±0.2	–	1.1	0	5±1	95±1	–	68±16	–	0
Wild Harbor	65	25±0.5	24.4±0.5	33±4	6.7±0.9	–	1.9	0	1±0	86±3	–	94±6	–	62±34
Green Pond	178	25±0.3	27.6±0.4	33±10	7.1±1.5	2.2	2.6	347±14	10±2	85±1	100	92	83±5	64
Snug Harbor	236	25±0.5	21.7±3.3	43±16	7.9±1.1	–	3.2	0	11±3	80±2	–	52±12	–	52±12
Weweantic River	339	25±0.1	18.0±0.3	34±1	7.7±0.4	–	1.7	246±88	3±0	96±2	–	84	–	20±12
Quashnet River	353	24±0.4	22.5±0.6	16±2	5.5±0.3	–	1.5	0	3±2	97±1	–	0	–	0
Childs River	601	24±1.0	23.9±0.1	27±1	6.4±0.2	2.0	1.7	78±26	12±3	89±3	99±1	0	89±5	0

Seston characteristics include total suspended (SPM) and organic (POM) particulate matter and C composition, and sediment characteristics include density of snails (N. obsoletus), and % by weight of silt+clay (<63 μm) and sand (63 μm–2 mm). N loading rates from Valiela et al. (1997), except Wild Harbor and Weweantic River for which values were modified from Costa (1994), according to Valiela et al. (2000).

matter, we quantified weight of seston per volume of water filtered and ashed filters at 490 °C for 4 h.

2.4. Assessment of habitat

To assess the physical features of each estuary during this study, we measured a variety of water column and sediment characteristics. Salinity was measured by refractometer, and water temperature was determined using a YSI 95 digital meter. To measure oxygen content of bottom waters and in sediment porewater, we measured dissolved oxygen (D.O.) in the water column and reduction–oxidation potential (Eh) in sediments in situ. To sample D.O., we used a YSI 95 digital meter suspended within 10 cm of the sediment surface. It was not possible to simultaneously measure D.O. at dawn in each estuary. Hence, we measured D.O. at various times of day, plotted D.O. vs. the time of day when measurements were taken, and used the best-fit significant regression through these data to calculate mean D.O. at sunrise for each estuary during this study. This approach provided an estimate of lowest mean D.O. concentration in each estuary during our sampling period. To determine Eh in sediments, at least two replicate measurements were taken using a platinum electrode (Bohn, 1971; Faulkner et al., 1989) mounted to a graduated 1.5 m wooden stake and inserted into the sediment to a depth of 1 cm at each site. We used a Ag–AgCl reference electrode, and Eh measurements were normalized to temperature and differences from a quinhydrone standard (Jones, 1966). Eh measurements were taken in mid September, at the end of our sampling period. To determine sediment grain size, we sieved subsamples of wet sediment from each site (Mudroch and Azcue, 1995), sorting sediments into three categories: clay+silt (<63 μm), sand (63 μm–2 mm) and gravel (>2 mm) (Wentworth, 1922). Each particle size fraction was dried and weighed to determine the percentage of composition.

2.5. Growth and survival of juvenile clams

To directly measure growth of quahogs and softshell clams, we transplanted 8–12 mm hatchery-reared clams into each estuary. We used hatchery-reared juvenile clams because they were likely to grow quickly and allowed us to compare changes in growth among animals that originated from the same seed stock. Juvenile quahogs were obtained from the Aquaculture Research Corporation in Dennis, MA, and juvenile softshell clams from the Beals Island Shellfish Hatchery in Beals, ME. Before transplanting, clams were marked at the outer edge with waterproof ink. Clams were then planted into plastic-coated wire mesh aquaculture cages measuring 30×30 cm and 10-cm deep. Cages were lined on the inside with 6-mm plastic mesh and filled with sediment from the estuary into which they were transplanted. A total of four cages were transplanted at each sampling site, two containing quahogs and two containing softshell clams. Clams were removed from each estuary after at least 42 days in 2000 and 84 days in 2001. On retrieval, we recorded the longest length of each clam to the nearest 0.1 mm at the ink mark and at the outer edge of the shell. We calculated shell growth as the difference between initial and final shell length. To determine the percentage of survival, we counted the number of living clams in transplant cages, divided by the total number planted, and multiplied by 100. To determine

whether survival was affected by the presence of predators or competitors, we also identified and counted other species in transplant cages at the end of the study.

2.6. Growth and soft tissue composition of native clams

To determine how N loads affected growth of native quahogs and softshell clams, we collected native clams from each estuary and measured shell length, height, and width, to the nearest 0.1 mm using calipers. To sample quahogs and softshell clams throughout their life span, we needed to collect clams of the broadest range of sizes in each estuary. To feel confident that we reliably sampled this range and to account for potential changes in size frequency distributions across estuaries, we first collected at least 100 clams of each species, where possible, from a low (Sage Lot Pond), intermediate (Green Pond), and high (Childs River) N loaded estuary. From these size frequency distributions (Carmichael, 2004, Appendices A and B), we determined approximate minimum and maximum sizes of clams likely to be found among the estuaries we sampled. We then selected ~40 individuals representing the full range of clam sizes to generate initial length-at-age relationships. In the remaining estuaries, we collected the number of clams needed to obtain length-at-age relationships that were significant and equally predictive compared to the three estuaries initially sampled. To age these clams, we radially sectioned one valve of the shell using a Buehler ISOMET low-speed saw with a diamond wafer blade. To prevent shattering smaller shells while sectioning, clams <25 mm in length were embedded in acrylic resin before sectioning (Meltzer, 2002). Sections were then polished and internal growth lines counted (MacDonald and Thomas, 1980; Grizzle and Lutz, 1988; Jones et al., 1990).

To estimate growth rates of native clams, we applied the von Bertalanffy growth model (VBGF), $L_t = L_\infty [1 - e^{-k(t-t_0)}]$, where L_t = shell length at age t, L_∞ = the maximum shell length achieved by the species, k is a growth coefficient describing the rate at which L_∞ is approached, and t_0 = time at which growth starts (von Bertalanffy, 1960; Brousseau, 1979). We then used k values as a proxy for growth rate throughout the life of native clams (Brousseau, 1979; Appleyard and DeAlteris, 2001; Urban, 2002). To solve for k, we linearized VBGF by plotting $-Ln[1 - (L_t/L_\infty)]$ vs. t (the estimated age of each clam in years). The slope of the resulting regression is k and the y-intercept is $-kt_0$ (Evgenidou and Valiela, 2002). We then solved for L_t and generated a best-fit regression line to our length-at-age data. To determine how N enrichment affected soft tissue growth and composition, we separated soft tissue from shell and dried it to a constant weight at 60 °C. To determine whether changes in shell growth were reflected in soft tissue mass, we then plotted soft tissue dry weight (DW) vs. shell length. N content of soft tissue was determined by mass spectrometry.

3. Results and discussion

3.1. Effects of N enrichment on food quantity

Chlorophyll a concentrations in near-bottom seston and surface sediment increased as N load increased across estuaries (Fig. 2). Highest chl a concentrations in seston were
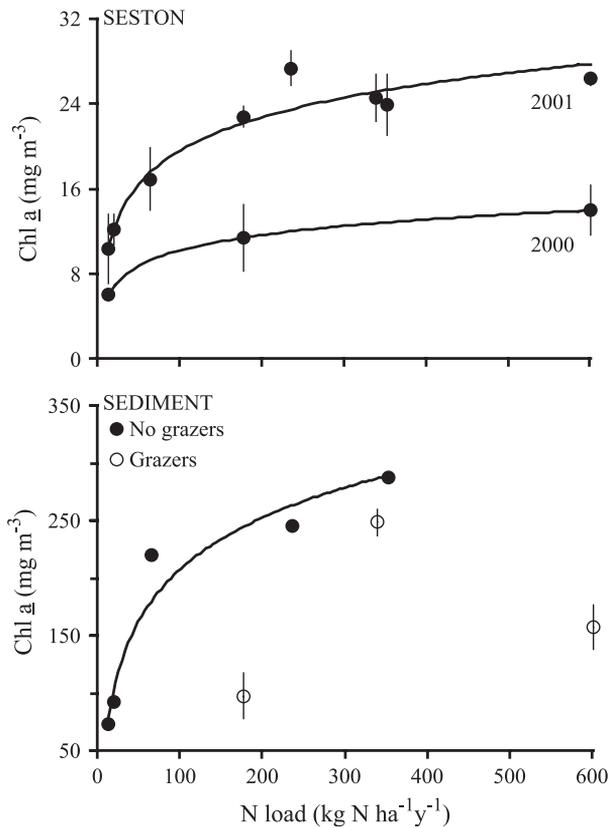
Fig. 2. Mean (±standard error) chlorophyll *a* concentration in near-bottom seston (top) and surface sediment (bottom) compared to N loads to Cape Cod estuaries. Sediment chl *a* was sampled in 2001, and sites with grazers (*N. obsoletus*) were not included in the regression. [seston 2000: $y=2.12 \ln(x)+0.40$, $R^2=0.99$, $F_2=6265.22$, $P<0.001$; seston 2001: $y=4.58 \ln(x)-1.56$, $R^2=0.90$, $F_7=51.97$, $P<0.001$; sediment: $y=64.99 \ln(x)-92.04$, $R^2=0.94$, $F_4=46.92$, $P<0.01$]. Sediment chl *a* concentration was converted from m^{-2} to m^{-3} by multiplying each concentration by the mean depth of the water column over each sampling site. Since mean depth was 1 m, sediment chl *a* values did not change in this conversion.

found in Childs River (30 ± 4 mg m^{-3}, Fig. 2, top), and in sediment in Quashnet River (386 ± 58 mg m^{-2}, Fig. 2, bottom), the two estuaries receiving the highest N loads to their watersheds (Table 1). There was considerable variation in chl *a* concentration in seston between years and in sediment among estuaries (Fig. 2). In seston, chl *a* concentrations and the rate of chl *a* increase across estuaries in response to increasing N loads were higher in 2001 than 2000 (test for homogeneity of slopes: $F_1=6.53$, $P=0.04$) (Fig. 2, top). This relatively greater response to increased N loads in 2001 was likely due to external factors such as the number of favorable days that may have stimulated production (Valiela, 1995). Chl *a* concentrations in surface sediment were lower at sites with higher concentrations of the grazer, *Nassarius obsoletus* (Table 1), suggesting most of the variation in sediment chl *a* among sites may be explained by reduction of benthic microalgal biomass by grazers (Fig. 2, bottom) (Pace et al., 1979; Novak et al., 2001).

Despite the negative effect of grazers on benthic microalgal biomass, sediment chl *a* concentrations were at least four times higher than chl *a* in seston (Fig. 2).

Chl *a* concentrations in seston and sediment measured during this study were high compared to those in other coastal areas (Lukatelich and McComb, 1986; Valiela et al., 1992; Cebrián and Valiela, 1999; Shriver et al., 2002). Increased N loads, however, were not related to total suspended (SPM) or organic (POM) particulate matter concentrations (Table 1), which were comparable to measurements in other areas (Essink and Bos, 1985; Grizzle and Morin, 1989; Fegley et al., 1992). Hence, although phytoplankton biomass was high among our estuaries, it comprised a relatively small portion of bulk seston, and increased N loads did not measurably affect other particles in bulk seston. The overall positive effect of N enrichment on microalgae biomass, however, suggests land-derived N enrichment increased food supply available to clams in these estuaries (Evgenidou and Valiela, 2002; Shriver et al., 2002; Weiss et al., 2002).

3.2. Effects of N enrichment on food quality

The mean C/N in near-bottom seston and surface sediment decreased with increasing N load (Fig. 3). Ratios of C to N in sediment were higher than in seston, particularly in low N
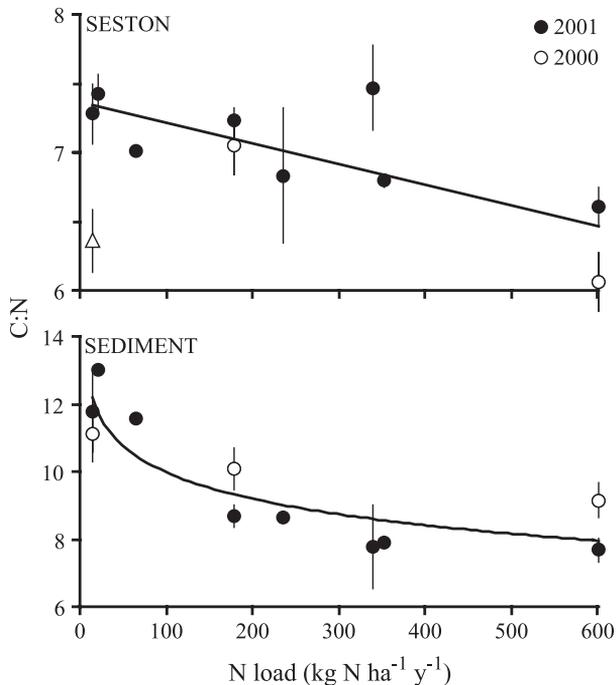

Fig. 3. C/N in near-bottom seston (top) and sediment (bottom) sampled in 2000 and 2001, compared to N loading rate to each estuary. Triangle (top) shows outlier (Sokal and Rohlf, 1981) not included in the regression [seston: $y = -0.002x + 7.37$, $R^2 = 0.58$, $F_9 = 10.95$, $P = 0.01$; sediment: $y = -1.13 \ln(x) + 15.18$, $R^2 = 0.77$, $F_{10} = 30.37$, $P < 0.001$].

load estuaries (Fig. 3). Relationships between mean C/N and N load varied between years, with the greatest change in C/N across estuaries in 2001 (Fig. 3), when chl *a* concentrations were higher (Fig. 2). There was also more variation in C/N in seston than in sediment, possibly resulting from greater stability of sediments compared to seston in these estuaries with relatively short flushing times (Carmichael and Valiela, in press). The overall pattern of decreasing C/N with increasing N loads implies N enrichment improved the quality of food available to clams, affecting the greatest change in sediment. Lower mean C/N in seston, however, suggests this source ultimately may provide a higher quality food source for clams.

3.3. Effects of N enrichment on habitat quality

Larger N loads were associated with more reduced conditions in surface sediments (Fig. 4, top), with the highest mean Eh at −139 mV, indicating surface sediments even in the most pristine estuaries were likely anoxic (Fig. 4, top). In near-bottom water, D.O. concentrations were rather low in general (Fig. 4, bottom). In all estuaries, D.O. values at dawn dropped near or below levels associated with deleterious effects on benthic species (NRC, 2000) (Fig. 4, bottom, light-gray shaded area), and in some, particularly QR, mean D.O. concentrations were remarkably low, suggesting hypoxia (Fig. 4, bottom, dark-gray shaded area). These findings indicate low oxygen conditions occurred at the sediment–water interface where clams live, particularly at higher N loads. Increased N loads did not measurably change other habitat variables we measured (Table 1).

The eutrophic-driven changes in food supply and habitat we measured are consistent with the notion that increased N loads may have positive and negative effects on bivalves. These data suggest N enrichment increased quantity and quality of foods available to clams, but potentially reduced habitat quality through reduced surface sediments and low oxygen concentrations in near-bottom waters. Inter-annual variation in these changes may further affect clam responses. To establish the net result of these potentially conflicting effects of eutrophication, we need to compare these data to empirical measurements of growth and survival of quahogs and softshell clams living in the estuaries.

3.4. Direct measurement of juvenile shell growth

Shell growth rates of transplanted juvenile clams ranged from 0.3 to 1.4 mm week^{-1} among quahogs and 0.3–1.8 mm week^{-1} among softshell clams, with growth increasing significantly as chl *a* concentrations in seston increased (Fig. 5, left panels). Relationships between shell growth and benthic chl *a* concentration, however, could not be defined (Fig. 5, right panels). The rate at which shell growth increased with N load was similar between species, demonstrated by homogeneity of slopes (F_{13}=1.14, P=0.31) and intercepts (ANCOVA: F_{14}=3.30, P=0.10) of the regressions in Fig. 5. Shell growth among juveniles was not related to C/N in seston or sediment, D.O. or Eh. These findings suggest juvenile clams primarily responded to increased microalgal biomass in seston, stimulated by N enrichment.
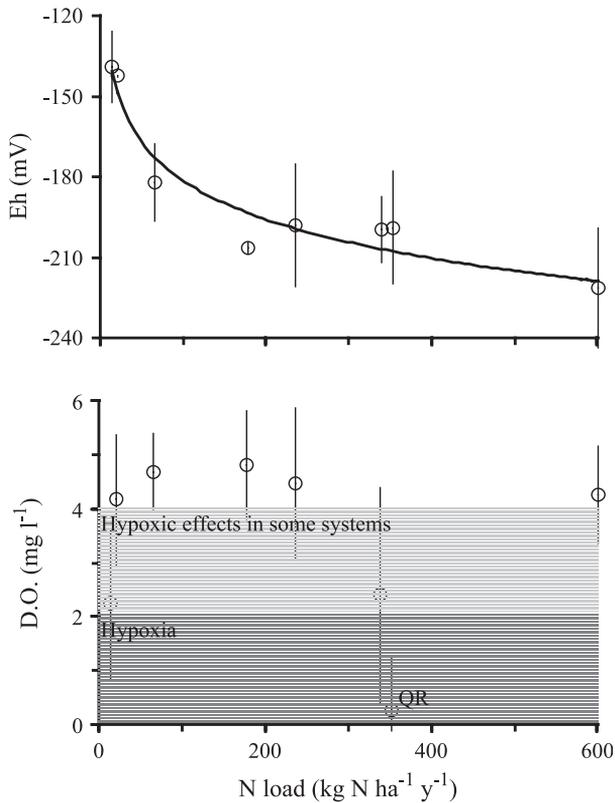
Fig. 4. Mean (± standard error) redox potential (Eh) in the top 1 cm of sediment (top) and estimated dissolved oxygen (D.O.) in bottom waters at sunrise (bottom) compared to N loading rate to watersheds of 8 Cape Cod estuaries [Eh: $y = -20.78 \ln(x) + 85.82$, $R^2 = 0.93$, $F_7 = 77.32$, $P < 0.001$]. Shaded areas in bottom panel show the reported range of D.O. concentrations at which survival of benthic species may decline (light gray) and coastal waters are defined as hypoxic (dark gray) (NRC, 2000). Standard error of D.O. was propagated from the standard errors of the slope and intercept of the regression used to calculate D.O. at dawn for each estuary. QR=Quashnet River.

Mean shell growth rates of quahogs and softshell clams transplanted in Weweantic River (WR) and Snug Harbor (SN) were lower than expected given the relatively high chl *a* concentrations in these estuaries and relationships between growth rate and chl *a* concentration in the other estuaries (Fig. 5, left panels). Data from these estuaries were outliers (Sokal and Rohlf, 1981) to the regressions in Fig. 5 (open symbols), and were not included in the regression analyses. These data suggest some factor moderated the growth-enhancing effects of increased food supply in WR and SN.

Before assessing why shell growth was relatively depressed in WR and SN, we first wanted to know whether relationships between shell growth and eutrophic-driven changes in food quantity and quality were maintained throughout life among native clams. This approach allowed us, in turn, to discern whether the factor limiting
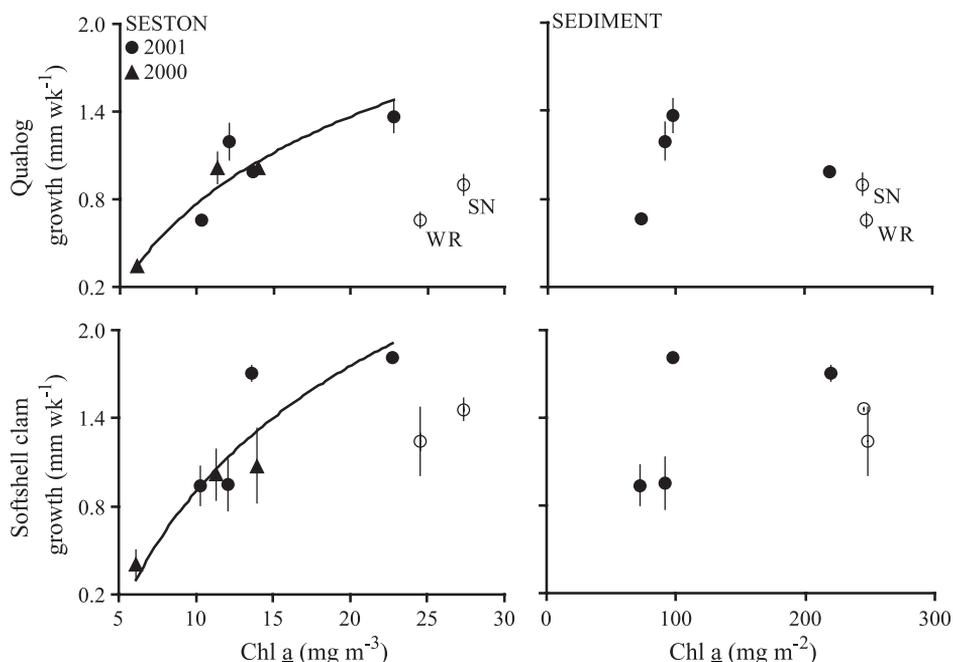
Fig. 5. Mean growth rates (±standard error) of transplanted juvenile quahogs (top panels) and softshell clams (bottom panels) compared to chl a concentrations in near-bottom seston (left panels) and surface sediment (right panels). SN=Snug Harbor and WR=Weweantic River, sites not included in regression analyses [type II regression yielded best-fit lines: quahogs: $y=0.86\ \ln(x)-1.21$, $R^2=0.84$, $F_6=25.62$, $P=0.004$; softshell clams: $y=1.23\ \ln(x)-1.93$, $R^2=0.80$, $F_6=20.54$, $P=0.01$].

growth in WR and SN was a consistent feature of these estuaries or a short-term effect that may have occurred only during the 2001 season when we directly measured shell growth in these estuaries.

3.5. Indirect measurement of shell growth throughout life

To compare shell growth of native clams across estuaries, we applied the von Bertalanffy growth model (VBGF), which uses length-at-age relationships to estimate the growth coefficient, k time^{-1}. This coefficient is not strictly a growth rate, but rather an expression of how rapidly clams approach their largest size (L_∞). Length-at-age relationships for each species in each estuary (Figs. 6 and 7) were typical of those previously reported (Ansell, 1968; Appledoorn, 1982; Jones et al., 1989; Meltzer, 2002; Urban, 2002), showing growth was rapid among young clams and decreased with age. Shell length of native clams across estuaries ranged from 1.6 to 123.4 mm among quahogs and 1.9 to 96.4 mm among softshell clams (Figs. 6 and 7), suggesting estimated asymptotic lengths (L_∞) of 124 mm for quahogs and 97 mm for softshell clams. Length distributions of clams overlapped extensively across estuaries, with the quahog and softshell clam of longest length found in Green Pond (Figs. 6 and 7).
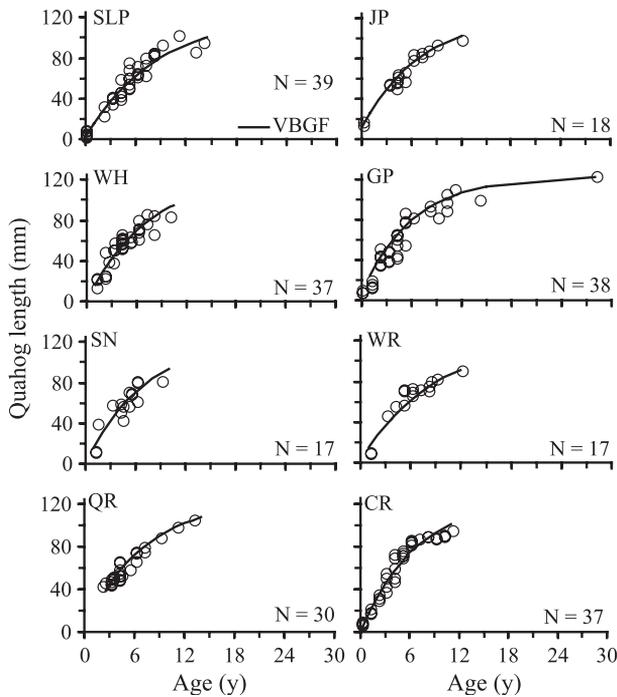
Fig. 6. Length-at-age comparisons and best-fit von Bertalanffy (VBGF) growth curves for quahogs sampled from eight Cape Cod estuaries receiving different N loads. VBGF parameters and regression statistics are shown in Table 2.

Ages of quahogs typically ranged from <1 to 12 years, with one animal from GP estimated at 28 years. Softshell clam ages typically ranged from <1 to 9 years, with one clam in WR reaching 12 years. The shell lengths and ages measured during this study are within the range of sizes and ages typical of quahogs and softshell clams (Brousseau, 1979; Appledoorn, 1982; Jones et al., 1989; Grizzle et al., 2001; Meltzer, 2002). The fit of VBGF to our length-at-age data for each species in each estuary was highly significant (Figs. 6 and 7). Estimated VBGF parameters and regression statistics are shown in Table 2.

For both quahogs and softshell clams, VBGF k values increased with increasing chl a concentration in seston, but not sediment (Fig. 8), indicating clams reached their largest potential size more rapidly in estuaries where more food was available in seston through N enrichment. VBGF k values were consistently higher in softshell clams compared to quahogs (Fig. 8), and the rate at which k increased with food supply was faster among softshell clams (homogeneity of slopes $F_{11}=11.84$, $P=0.01$). As with shell growth in juvenile clams, VBGF k values were lower in WR and SN compared to relationships between k and chl a among other estuaries (Fig. 8, left panels), suggesting shell growth was limited throughout life in clams in these estuaries. VBGF k values were not related to C/N in seston, D.O, or Eh. As found among juvenile
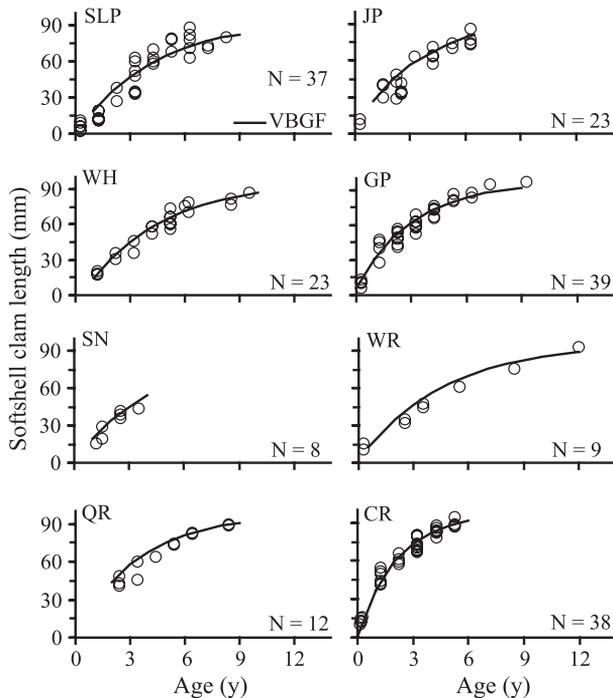
Fig. 7. Length-at-age comparisons and best-fit von Bertalanffy (VBGF) growth curves for softshell clams sampled from eight Cape Cod estuaries receiving different N loads. VBGF parameters and regression statistics are shown in Table 2.

transplants, native clams responded primarily to the N enrichment-stimulated increase in phytoplankton biomass in seston.

Ratios of shell length to height, height to width, and length to width for quahogs and shell length to height for softshell clams were similar across estuaries (Table 3) and consistent with values previously reported in the literature (Newell and Hidu, 1982; Stanley and Dewitt, 1985). Similar shell allometry across sites indicates that N enrichment did not affect any parameter of shell growth more than any other, and shell length was an appropriate measure of shell growth across estuaries. L/H in softshell clams was higher than in quahogs (Table 3), consistent with the oblong shape of softshell clams compared to quahogs. Since quahogs increase more equally in length and height than softshell clams, this difference in shell shape may, in part, explain why softshell clams maintained higher VBGF k values, approaching asymptotic length (L_∞) more rapidly than quahogs when shell growth was measured throughout life (Fig. 8, left panels).

3.6. Soft tissue growth and composition among native clams

Soft tissue dry weight (DW) of quahogs and softshell clams increased significantly as shell length increased (Fig. 9, top panels), indicating that soft tissue growth

Table 2
Estimated growth coefficient (k), theoretical time at which growth started (t_0), and regression statistics for the von Bertalanffy growth model applied to length-at-age relationships (Fig 6 and 7) for quahogs and softshell clams in eight Cape Cod estuaries receiving different N loads

	k	se	t_o	se	R^2	F	P
Quahogs							
Sage Lot Pond	0.117	0.01	−0.20	0.23	0.93	272.05	<0.001
Jehu Pond	0.139	0.01	−0.07	0.08	0.95	191.24	<0.001
Wild Harbor	0.138	0.01	−0.02	0.03	0.87	188.55	<0.001
Green Pond	0.161	0.01	−0.40	0.47	0.92	598.74	<0.001
Snug Harbor	0.117	0.01	−0.01	0.01	0.81	53.75	<0.001
Weweantic River	0.135	0.01	−0.20	0.23	0.92	120.24	<0.001
Quashnet River	0.144	0.01	−0.10	0.12	0.91	610.98	<0.001
Childs River	0.153	0.01	−0.01	0.01	0.95	365.94	<0.001
Softshell clams							
Sage Lot Pond	0.22	0.02	−0.01	0.32	0.93	174.75	<0.001
Jehu Pond	0.27	0.02	−0.20	0.32	0.87	140.04	<0.001
Wild Harbor	0.23	0.02	0.30	0.34	0.95	231.91	<0.001
Green Pond	0.36	0.02	−0.21	0.25	0.92	255.60	<0.001
Snug Harbor	0.20	0.03	−0.13	0.34	0.88	42.23	<0.001
Weweantic River	0.21	0.02	−0.14	0.46	0.97	156.76	<0.001
Quashnet River	0.32	0.02	−0.01	0.25	0.95	348.93	<0.001
Childs River	0.47	0.03	−0.02	0.02	0.96	284.83	<0.001

se=standard error.

accompanied shell growth in response to increased food supply. Regression statistics describing DW-to-length relationships are shown in Table 4. %N in soft tissue of quahogs and softshell clams also increased with increasing N load (Fig. 9, bottom panels), providing a direct link between land-derived N loads and soft tissue composition. Length to DW relationships and the range of %N in soft tissue of clams in this study are consistent with values reported for other Massachusetts water bodies (Leavitt et al., 1990).

Increased %N in soft tissue as N loads increased is consistent with greater food supply at higher N loads. Since bivalves may lose body protein during starvation (Gabbott and Bayne, 1973; Laing, 1993), our results suggest clams were not food-limited and, in fact, were able to build body protein relative to other tissue components (carbohydrates and lipids). This finding is novel since most studies have assessed changes in biochemical composition of bivalve tissue relative to nutritive stress associated with starvation and reproduction (Gabbott, 1983; Laing, 1993; Eversole, 2001). In contrast, we found a biochemical change in clam tissue in response to relatively high concentrations of high-quality food.

Increased %N in soft tissue of clams with increasing N load suggests quahogs and softshell clams consumed (and assimilated into soft tissues) a specific component in seston that also responded to increased N loads. The food accountable for the change in N composition of clam tissue must have comprised a relatively small portion of seston because %N in bulk seston was not significantly related to N load (data not shown). This finding is consistent with our shell growth data, which indicated clams
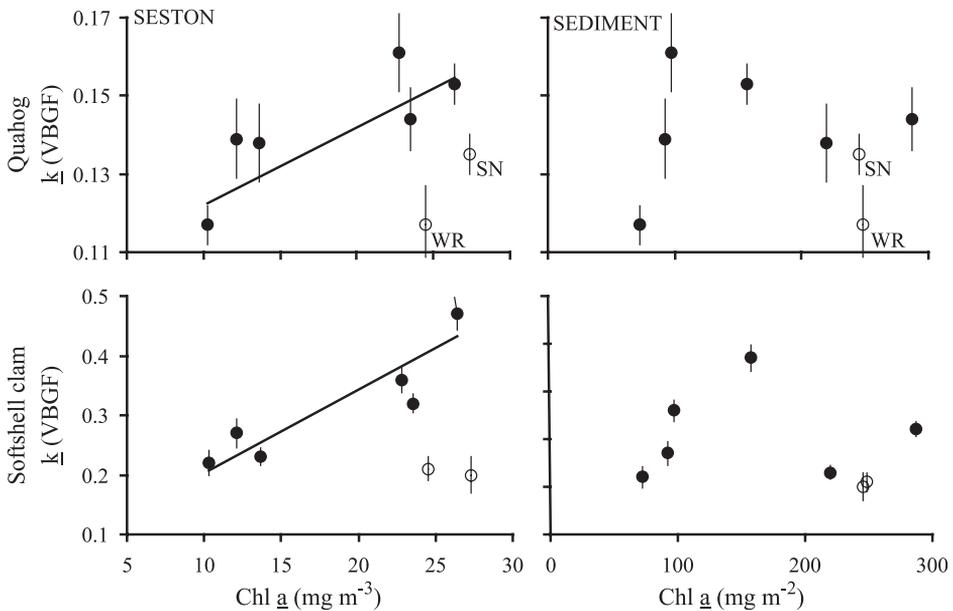
Fig. 8. Mean von Bertalanffy (VBGF) k values ($\pm$standard error) for native quahogs (top panels) and softshell clams (bottom panels) compared to chl a concentrations in near-bottom seston (left panels) and surface sediment (right panels). SN=Snug Harbor and WR=Weweantic River, sites not included in regression analyses [type II regression yielded best-fit lines: quahogs: y=0.002 ln(x)+0.10, R^2=0.66, F_5=7.84, P=0.048; softshell clams: y=0.01 ln(x)+0.06, R^2=0.81, F_6=16.91, P=0.01].

responded specifically to the microalgal portion of bulk seston rather than total SPM or POM, and showed an increase in percentage of organic content in shell with increased N loads (Carmichael, 2004, Appendix D). There is substantial evidence that clams and other bivalves assimilate specific particles from bulk seston and sediment (Canuel et al., 1995; Riera et al., 1999; Davenport and Bax, 2002; Lorrain et al., 2002; Kang et al., 2003; Carmichael, 2004), and our data suggest clams consumed those particles most affected by N enrichment.

3.7. Food quantity vs. food quality

Although soft tissue growth, shell growth, and VBGF k values responded to eutrophic-driven changes in seston quantity (chl a concentration), growth was not directly related to changes in seston quality in terms of C/N across estuaries. There are several possible explanations for this finding. First, relationships between C/N and N load varied considerably across estuaries and between years (Fig. 3), reducing the chance of a significant relationship between growth and C/N in seston. Second, C/N ratios in seston and sediment in every estuary were less than 17:1, the ratio needed to sustain growth (cf. Fig. 3) (Russell-Hunter, 1970), suggesting food quality was sufficiently high in all estuaries. Third, C/N may not be a universally appropriate measure of food quality among bivalves (Hatcher, 1994). Growth in oysters, for

Table 3
Ratio of shell length (L) to height (H), height to width (W), and length to width for native quahogs and softshell clams measured during this study

Estuary	N	Shell morphometry		
		L/H	H/W	L/W
Quahogs				
Sage Lot Pond	105	1.2	1.6	1.9
Jehu Pond	18	1.3	1.5	1.9
Wild Harbor	37	1.2	1.5	1.9
Green Pond	108	1.3	1.5	1.9
Snug Harbor	17	1.3	1.5	1.9
Weweantic River	17	1.3	1.5	1.9
Quashnet River	31	1.2	1.5	1.9
Childs River	105	1.3	1.6	2.0
Softshell clams				
Sage Lot Pond	39	1.6	–	–
Jehu Pond	29	1.6	–	–
Wild Harbor	32	1.6	–	–
Green Pond	238	1.7	–	–
Snug Harbor	8	1.6	–	–
Weweantic River	9	1.6	–	–
Quashnet River	17	1.7	–	–
Childs River	127	1.6	–	–

N=number of clams sampled. *L*=longest length, *H*=distance from umbo to outer margin, *W*=thickness across the hinge.

example, may be stimulated by high C/N diets (Flaak and Eppifano, 1978). Whatever the reason, our data suggest differences in food quantity rather than quality primarily determined growth rates of clams across estuaries.

3.8. Growth limitation in SN and WR

To discern what factors may have limited growth rates and VBGF k values among quahogs and softshell clams in WR and SN, we compared the features of food supply and habitat in these estuaries with variables defined in the literature as potentially limiting to feeding rates (measured as pumping, clearance, or ingestion rates). Among these variables, only two were consistent with conditions in estuaries sampled during our study; high food concentrations and increased exposure to low salinity.

Most of the chl a concentrations measured in this study were equivalent to phytoplankton carbon (ph C) concentrations within or above the range (600–700 mg C m^{-3}) at which feeding rates of clams reportedly slow (Fig. 10, gray shaded area; Tenore and Dunstan, 1973; Malouf and Bricelj, 1989). Most studies regarding effects of seston composition on feeding rates have been conducted in the laboratory or with cultured algae (Malouf and Bricelj, 1989; Grizzle et al., 2001). Hence, to compare our chl a data to these other studies, we converted chl a concentration measured in each estuary to ph C, assuming a ph C/chl a ratio of 50:1 (Eppley, 1972; Valiela, 1995).
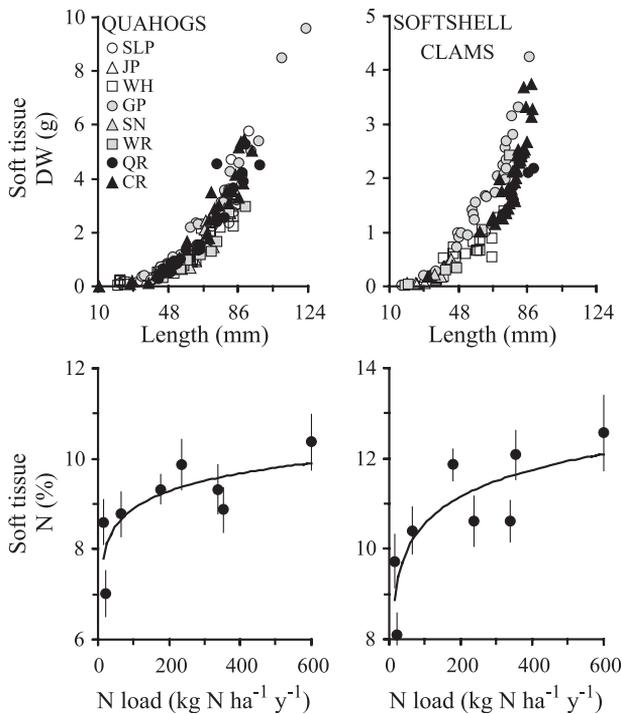
Fig. 9. Dry weight (DW) of soft tissue compared to shell length (top panels) and %N in soft tissue compared to N loading rate (bottom panels) to eight Cape Cod estuaries for quahogs (left panels) and softshell clams (right panels) [%N: quahogs: $y=0.56 \ln(x)+6.31$, $R^2=0.61$, $F_7=9.31$, $P=0.02$; softshell clams: $y=0.86 \ln(x)+6.59$, $R^2=0.69$, $F_7=13.13$, $P=0.01$]. Regression statistics for soft tissue DW to length comparisons are provided in Table 5.

The high concentrations of seston or ph C found among our estuaries, however, did not likely account for lower growth rates in SN and WR. Quahogs and softshell clams in this study fed and grew at ph C concentrations well above the range suggested to slow feeding rates (Fig. 10). Juvenile transplants attained maximum shell growth rates at 1100 mg ph C m^{-3} (Fig. 10, gray arrow, Juveniles) and native clams had maximum k values at 1300 mg ph C m^{-3} (Fig. 10, gray arrow, VBGF). In fact, maximum shell growth rates and VBGF k values of clams measured in this study were among the highest measured anywhere (Table 5), indicating that high ph C in N enriched estuaries either did not slow feeding rates of clams or did not slow feeding rates enough to counter the effects of increased food supply.

Several other caveats corroborate the conclusion that high seston concentrations did not limit growth in SN and WR. First, total SPM and POM concentrations were not particularly high in any of the estuaries we sampled compared to values reported in other studies (Essink and Bos, 1985; Grizzle et al., 1992). Second, SPM, POM, and chl a concentrations were not significantly higher in SN and WR compared to other estuaries in which shell growth increased (Table 1; Figs. 5 and 8). For example, chl a in 2001 did not differ among SN, WR, and CR (ANOVA: $F_{2,44}=0.33$, $P=0.72$), but k

Table 4
Equations and regression statistics for relationships between clam tissue dry weight (DW) and shell length, shown in Fig. 9, for native quahogs and softshell clams from Cape Cod estuaries

Estuary	y	R^2	F	P
Softshell clams				
Sage Lot Pond	$0.002e0.11x$	0.90	28.36	0.01
Jehu Pond	$0.002e0.13x$	0.96	251.24	<0.001
Wild Harbor	$0.016e0.06x$	0.92	192.73	<0.001
Green Pond	$0.116e0.04x$	0.96	549.41	<0.001
Snug Harbor	$0.006e0.10x$	0.84	20.81	0.01
Weweantic River	$0.026e0.06x$	0.99	317.74	<0.001
Quashnet River	$0.010e0.06x$	0.93	25.24	0.04
Childs River	$0.049e0.05x$	0.83	216.29	<0.001
Quahogs				
Sage Lot Pond	$0.03e0.06x$	0.97	1032.56	<0.001
Jehu Pond	$0.05e0.05x$	0.98	352.21	<0.001
Wild Harbor	$0.02e0.07x$	0.84	148.59	<0.001
Green Pond	$0.11e0.04x$	0.94	466.06	<0.001
Snug Harbor	$0.03e0.06x$	0.90	66.12	<0.001
Weweantic River	$0.04e0.05x$	0.95	164.82	<0.001
Quashnet River	$0.07e0.05x$	0.89	184.14	<0.001
Childs River	$0.07e0.05x$	0.95	532.33	<0.001

values in CR were not depressed like those in SN and WR (Fig. 8, left panels). Overall, these data indicate that high concentrations of seston did not account for the relatively depressed growth among clams in SN and WR.

Low mean salinity, on the other hand, may have limited growth in SN and WR since salinity varied among estuaries (Table 1) and dropped below 20‰ more
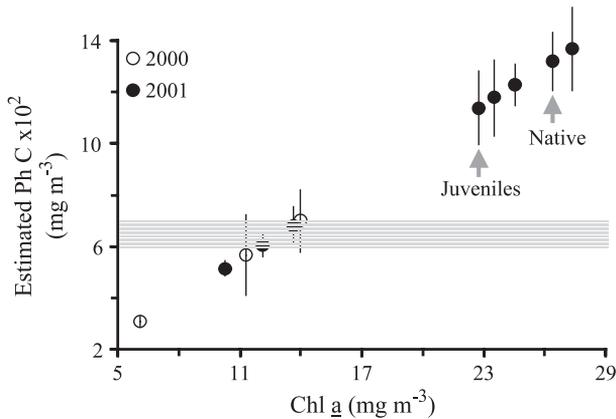

Fig. 10. Estimated phytoplankton C (Ph C) compared to chl *a* in Cape Cod Estuaries in 2000 and 2001. Gray Shaded area shows the range of ph C values at which clam feeding rates slowed during laboratory studies (Tenore and Dunstan, 1973; Malouf and Bricelj, 1989). Gray arrows show data points associated with maximum growth rates in juvenile transplants (Juveniles) and maximum *k* (VBGF) values among Native clams (Native). Error bars show standard error (se) propagated from se of chl *a* concentrations.

Table 5
Maximum reported growth rates and VBGF k values for quahogs and softshell clams in this study and others

Species	Maximum		Location	Source
	growth rate (mm wk^{-1})	k (VBGF)		
Quahogs	0.45		SC	Eldridge et al. (1979)[a]
	0.48		SC	Hadley and Manzi (1984)[a]
	0.54		Lab	Grizzle et al. (1992)
	0.54		NY	Bricelj (unpublished)[a]
	0.57		Canada	Gionet (unpublished)[a]
	0.62		NY	Flagg and Malouf (1983)[a]
	0.63		Lab	Bricelj et al. (1984)
	0.65		MA	Chalfoun et al. (1994)
	0.73		NJ	Grizzle and Morin (1989)
	0.84		FL	Menzel (1963)[a]
	0.96		NY	Bricelj and Borrero (unpublished)[a]
	1.05		NY	Applemans (1989)[a]
	1.08		GA	Walker and Tenore (1984)[a]
	1.37		MA	This study
	1.45		MA	Weiss et al. (2002)
		0.10	RI	Rice et al. (1989)
		0.16	MA	This study
		0.25	RI	Appleyard and DeAlteris (2001)
Softshell clams	0.79		MA	Brousseau (1979)
	1.03		MA	Weiss et al. (2002)
	1.40		MA	Chalfoun et al. (1994)
	1.50		MA	Matthiessen (1960)
	1.64		Netherlands	Essink and Bos (1985)
	1.80		ME	Newell and Hidu (1982)
	1.82		MA	This study
		0.06	Lab	Emerson (1990)
		0.11	Canada	Newcombe (1935)[b]
		0.17	ME	Spear and Glude (1957)[b]
		0.29	Denmark	Munch-Peterson (1973)[b]
		0.30	Various	Appledoorn (1982)[c]
		0.39	MA	Brousseau (1979)
		0.47	MA	This study
		0.48	MA	Belding (1912)[b]
		0.57	WA	Swan (1952)[b]
		1.48	ME	Meltzer (2002)

[a] In Grizzle et al., 2001.
[b] In Brousseau (1979), converted from mm day^{-1} to mm year^{-1}.
[c] Maximum growth among 20 sites along the Atlantic coast in MA, MD, ME, NJ, RI, and Canada.

frequently in SN and WR than in other estuaries (Fig. 11). Assuming the frequency of sampling days is a proxy for exposure time to different salinities, clams in SN and WR were likely exposed to salinity <20‰ for 36% and 71% of the time of this study, respectively (Fig. 11). Lower pumping rates and reduced shell growth have been found among clams at salinity <20‰ (Matthiessen, 1960; Hamwi and Haskin, 1969; Loesch and Haven, 1973; Walker and Tenore, 1984; Arnold et al., 1996). In fact, growth rates
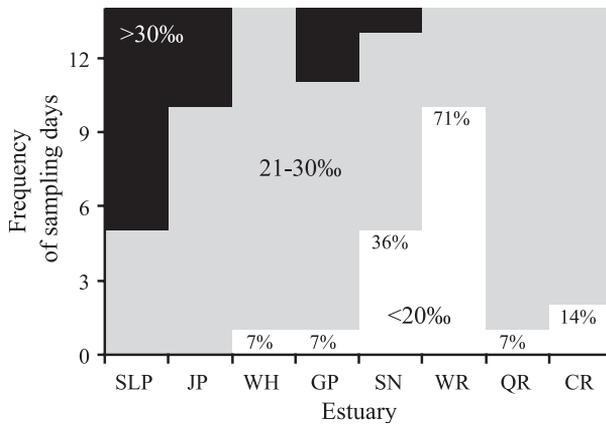
Fig. 11. Frequency distribution of sampling days when salinity in each estuary was <20‰, 21–30‰, and >30‰. Numbers in white columns show approximate percentage of time clams were exposed to salinity <20‰, given the frequency of sampling days at that salinity.

among softshell clams in SN and WR (1.2–1.5 mm week^{-1}, Fig. 5) were nearly identical to growth rates previously measured for softshell clams (1.4 mm week^{-1}) experiencing reduced pumping rates at low salinity (16‰) in other Cape Cod waters (Matthiessen, 1960). It seems likely, therefore, that exposure to lower salinity rather than excess food supply in SN and WR reduced pumping rates and limited shell growth in these estuaries.

It is important to note that even at the relatively lower salinities in SN and WR, shell growth of juvenile transplants in these higher N loaded estuaries was still often higher than shell growth in lower N load estuaries (Fig. 5, left panels), with lower concentrations of food. This fact is particularly noticeable among juvenile softshell clams (Fig. 5, bottom left), perhaps because softshell clams better tolerate lower salinity than quahogs (Matthiessen, 1960; Stanley and Dewitt, 1985; Abraham and Dillon, 1986). Among native clams in SN and WR however, most VBGF k values were as low as k values in estuaries with lower chl a concentrations (Fig. 8, left panels), indicating the growth-limiting effects of low salinity were at least maintained and may have been magnified during the life span of clams in these estuaries. These comparisons suggest that food supply was the primary factor stimulating growth of clams in N enriched estuaries, but exposure to low salinity mediated the magnitude of growth. Similarly, Marsden (2004) found the combination of food quantity and salinity affected growth and condition of transplanted and natural populations of the New Zealand little-neck clam, *Austrovenus stutchburyi*, with lab studies indicating reduced food quantity had a greater effect on soft tissue mass than low salinity.

3.9. Survival

Percent survival of transplanted juvenile quahogs and softshell clams ranged from 0–100% across the 2 years of this study (Table 1). This broad range is consistent with

variation in % survival previously reported for transplanted clams (Hibbert, 1977; Brousseau, 1978; Flagg and Malouf, 1983; Fernandez et al., 1999). In 2000, on average, % survival was higher than in 2001 (Table 1) and did not differ between species (paired, two-tailed *t*-test: $t=3.83$, $P=0.06$, $df=2$). In 2001, survival was 29% higher among quahogs than softshell clams (paired, two-tailed *t*-test: $t=2.97$, $P=0.02$, $df=7$), and neither species transplanted into QR or CR survived.

Relatively low oxygen concentrations at the sediment–water interface may have accounted for the differences in survival we found among estuaries and between species. First, most of the estuaries in which survival was <50% had estimated D.O. concentrations <4 mg l^{-1} at dawn (Fig. 4, bottom and Table 1). Such low D.O. concentrations are associated with reduced survival of benthic species (NRC, 2000; Borsuk et al., 2002; Breitburg, 2002; Gray et al., 2002). Although quahogs and softshell clams are relatively tolerant of hypoxia (Stanley and Dewitt, 1985; Abraham and Dillon, 1986; Gray et al., 2002), low oxygen conditions related to N enrichment have been associated with reduced survival of clams and other bivalves (Craig, 1994; Thiel et al., 1998). Second, ephemeral hypoxic events likely would not have been captured by our sampling regime, but can cause substantial mortality. Even rapid, short-term changes in D.O. concentrations have resulted in high mortality of finfish, crabs, and other benthic species (Breitburg, 1992, 2002; Gray et al., 2002). Third, % survival was not related to any of the other food supply or habitat variables that we measured (Table 1).

The combination of higher food supply and lower D.O. concentrations associated with eutrophication are consistent with the overall increase in clam growth but lower survival we found among juveniles in 2001. Chl *a* concentrations were higher in 2001 than 2000 (Fig. 2), indicating that not only was food supply higher, but low oxygen conditions were more likely to occur since hypoxia is more common in more highly N loaded estuaries where production is high (D'Avanzo and Kremer, 1994; D'Avanzo et al., 1996). If low oxygen conditions in N-enriched estuaries are more extreme or sustained in some years than in others, these conditions could preferentially reduce abundance of young clams, which may be more sensitive to hypoxia (Stanley and Dewitt, 1985; Abraham and Dillon, 1986), but allow larger clams to survive and continue to grow rapidly. Accordingly, Craig (1994) reported fewer but larger sized *Nucula annulata* in nutrient enriched areas and attributed these findings to reduced recruitment and survival due to hypoxia. Although we cannot be certain that low oxygen concentrations were responsible for the differences in % survival we observed because low D.O. conditions were not sustained in the estuaries we sampled, hypoxia at the sediment–water interface seems the most likely explanation.

4. Conclusions

Despite the many potential sources of variation in environmental conditions among different coastal estuaries, we found remarkably consistent positive relationships between increased land-derived N loads and microalgal biomass. These relationships, in turn, were associated with increased secondary production in terms of shell and soft tissue growth in quahogs and softshell clams and resulted in growth rates among the

highest reported anywhere. Exposure to salinity <20‰ was the only environmental factor found to moderate the growth-enhancing effects of increased food supply stimulated by N enrichment, and the effects of low salinity did not completely eliminate growth enhancement of juvenile clams at the highest food concentrations.

Clams measured in this study responded primarily to the quantity of microalgae stimulated by N enrichment. Although juvenile shell growth rates and VBGF k values were primarily related to seston rather than sediment chl a, increased growth may have been stimulated by either phytoplankton or benthic microalgae, since benthic microalgae may be resuspended in seston (Baillie and Welsh, 1980). In fact, Kang et al. (2003) found primary consumers in the water column may feed on equal portions of phytoplankton and resuspended benthic microalgae. Most importantly, since clam growth was not related to total SPM, POM, or C/N in seston, our data suggest microalgal concentration was more important to growth than the quantity or quality of the bulk of available particles in seston.

Low oxygen concentrations at the sediment–water interface may have reduced survival of clams, but reduced survival and N enrichment could not be directly linked in this study. Since increased primary production driven by N enrichment is well-documented to reduce oxygen concentrations in near-bottom waters (Paerl et al., 1998; Cloern, 2001; Breitburg, 2002; Gray et al., 2002), this indirect effect of increased N loading could potentially counter the otherwise seemingly positive effects of N enrichment on quahogs and softshell clams.

Although the major effect of N enrichment on clams in this study was to increase growth, it is possible that negative effects of eutrophication may be realized at higher N loads than those found in the estuaries we studied. Josefson and Rasmussen (2000) found benthic biomass composed primarily of bivalves was depressed at N loading rates much higher than found among Cape Cod estuaries. They could not, however, find a causal link such as low oxygen concentrations to relate depressed biomass to N enrichment. Reduced growth and eventual mortality has been reported among quahogs directly exposed to ammonium and nitrate (Epifanio and Srna, 1975), but such studies are rare and the concentrations required to affect these responses (880 mg NH_4^+ l^{-1} and 2415 mg NO_3^-) were much higher than currently found in the natural environment, even in highly N-enriched estuaries (Nixon et al., 2001; Josefson and Rasmussen, 2000). Since the Cape Cod estuaries we studied represent the range of N loads to most coastal estuaries (Nixon et al., 2001), our results are biologically relevant to assessing ecology and stock management of these commercially important coastal species.

This study and others emphasize that N is an important resource in food webs of coastal estuaries, potentially enhancing primary and secondary production (Reitan et al., 1999; Tober et al., 2000; Evgenidou and Valiela, 2002; Nixon and Buckley, 2002; Shriver et al., 2002; Weiss et al., 2002). Both positive and negative affects of N loading, however, are important to evaluating management strategies for commercial and recreational fisheries, determining sites for aquaculture, assessing trophic interactions, or determining the ecological importance of an estuary to bivalves and other estuarine species, which may show different responses to N enrichment (Valiela et al., 1992; Tober et al., 2000; Evgenidou and Valiela, 2002; Gray et al., 2002; Shriver et al., 2002).

Acknowledgments

References

Abraham, B., Dillon, P., 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)-Softshell Clam. U.S. Fish Wildl. Serv. Biol. Rep. 86, 1–18.

Ansell, A.D., 1968. The rate of growth of the hard clam *Mercenaria mercenaria* (L.) throughout the geographical range. J. Cons.-Cons. Perm. Int. Explor. Mer 31, 364–409.

Appledoorn, R., 1982. Variation in the growth of *Mya arenaria* and its relation to the environment analyzed through principal component analysis and the *W* parameter of the von Bertalanffy equation. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 81, 75–84.

Appleyard, C.L., DeAlteris, J.T., 2001. Modeling growth of the northern quahog, *Mercenaria mercenaria*. J. Shellfish Res. 20, 1117–1125.

Arnold, W.S., Bert, T., Marelli, D., Cruz-Lopez, H., Gill, P., 1996. Genotype-specific growth of hard clams (genus *Mercenaria*) in a hybrid zone: variation among habitats. Mar. Biol. 125, 129–139.

Bacon, G.S., MacDonald, B., Ward, J., 1998. Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicus*) bivalves to variations in the concentration and quality of suspended particles—I. Feeding activity and selection. J. Exp. Mar. Biol. Ecol. 219, 105–125.

Baillie, P.W., Welsh, B.L., 1980. The effect of tidal resuspension on the distribution of intertidal epipelic algae in an estuary. Estuar. Coast. Mar. Sci. 10, 165–180.

Baker, S., Hornbach, D., 1999. Physiological status and biochemical composition of a natural population of unionid mussels (*Amblema plicata*) infested by zebra mussels (*Dreissena polymorpha*). Am. Midl. Nat. 143, 443–452.

Bayne, B.L., Newell, R., 1983. Physiological energetics of marine molluscs. In: Wilbur, K.M. (Ed.), The Mollusca, Physiology, Part I vol. 4. Academic Press, pp. 407–499.

Belding, L., 1912. A Report Upon the Quahog and Oyster Fisheries of Massachusetts. The Commonwealth of Massachusetts.

Bohn, H.L., 1971. Redox potentials. Soil Sci. 112, 39–45.

Borsuk, M.E., Powers, S.P., Peterson, C.H., 2002. A survival model of the effects of bottom-water hypoxia on the population density of an estuarine clam (*Macoma balthica*). Can. J. Fish. Aquat. Sci. 59, 1266–1274.

Bowen, J., Valiela, I., 2001. The ecological effects of urbanization of coastal watersheds: historical increases in nitrogen loads and eutrophication of Waquoit Bay estuaries. Can. J. Fish. Aquat. Sci. 58, 1489–1500.

Breitburg, D., 1992. Episodic hypoxia in Chesapeake Bay: interacting effects of recruitment, behavior, and physical disturbance. Ecol. Monogr. 62, 525–546.

Breitburg, D., 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries 25, 767–781.

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, R.E., Malouf, C., 1984. Growth of juvenile *Mercenaria mercenaria* and the effect of resuspended bottom sediments. Mar. Biol. 84, 167–173.

Brousseau, D.J., 1978. Population dynamics of the soft-shell clam, *Mya arenaria*. Mar. Biol. 50, 63–71.

Brousseau, D.J., 1979. Analysis of growth rate in *Mya arenaria* using the von Bertalanffy equation. Mar. Biol. 51, 221–227.

Cadée, G., 1984. Has input of organic matter into the western part of the Dutch Wadden Sea increased during the last decades? Publ. Ser.-Neth. Inst. Sea Res. 10, 71–82.

Cahalan, J., Siddall, S., Luckenbach, M., 1989. Effects of flow velocity, food concentration and particle flux on growth rates of juvenile bay scallops *Argopecten irradians*. J. Exp. Mar. Biol. Ecol. 129, 45–60.

Canuel, E.A., Cloern, J.E., Ringelberg, D.B., Gucker, J.B., Rau, G.H., 1995. Molecular and isotopic tracer used to examine sources of organic matter and its incorporation into the food webs of San Francisco Bay. Limnol. Oceanogr. 40, 67–81.

Caraco, N., Cole, J., 1999. Human impact on nitrate export: an analysis using major world rivers. Ambio 28, 167–170.

Carmichael, R., 2004. The Effects of Eutrophication on *Mya Arenaria* and *Mercenaria Mercenaria*: Growth, Survival, and Physiological Responses to Changes in Food Supply and Habitat Across Estuaries Receiving Different N Loads. PhD dissertation, Boston University.

Carmichael, R., Valiela, I., in press. Coupling of near-bottom seston and surface sediment composition: changes with nutrient enrichment and complications for estuarine food supply and biogeochemical processing. Limnol. Oceanogr.

Cebrián, J., Valiela, I., 1999. Seasonal patterns in phytoplankton biomass in coastal ecosystems. J. Plankton Res. 21, 429–444.

Chalfoun, A., McClelland, J., Valiela, I., 1994. The effect of nutrient loading on the growth rate of two species of bivalves, *Mercenaria mercenaria* and *Mya arenaria*, in estuaries of Waquoit Bay, Massachusetts. Biol. Bull. 187, 281.

Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol., Prog. Ser. 210, 223–253.

Costa, J., 1994. A Buzzards Bay embayment subwatershed evaluation: establishing priorities for nitrogen management action. Buzzards Bay Project. EPA.

Craig, N.I., 1994. Growth of the bivalve *Nucula annulata* in nutrient-enriched environments. Mar. Ecol., Prog. Ser. 104, 77–90.

D'Avanzo, C., Kremer, J., 1994. Diel oxygen dynamics and anoxic events in an eutrophic estuary of Waquoit Bay, MA. Estuaries 17, 131–139.

D'Avanzo, C., Kremer, J., Wainright, S., 1996. Ecosystem production and respiration in response to eutrophication in shallow temperate estuaries. Mar. Ecol., Prog. Ser. 141, 263–274.

Davenport, S.R., Bax, N.J., 2002. A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. Can. J. Fish. Aquat. Sci. 59, 514–530.

de Zwaan, A., 1983. Carbohydrate catabolism in bivalves. In: Wilbur, K.M. (Ed.), The Mollusca, Metabolic Biochemistry and Molecular Biomechanics, vol. 1. Academic Press, pp. 138–176.

Emerson, C.W., 1990. Influence of sediment disturbance and water flow on the growth of the soft-shell clam, *Mya arenaria* L. Can. J. Fish. Aquat. Sci. 47, 1655–1663.

Epifanio, C., Srna, R., 1975. Toxicity of ammonia, nitrite ion, nitrate ion, and orthophosphate to *Mercenaria mercenaria* and *Crassostrea virginica*. Mar. Biol. 33, 241–246.

Eppley, R.W., 1972. Temperature and phytoplankton growth in the sea. Fish. Bull. 70, 1063–1085.

Essink, K., Bos, A., 1985. Growth of three bivalve molluscs transplanted along the axis of the EMS estuary. Neth. J. Sea Res. 19, 45–51.

Everett, R.A., 1994. Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages. J. Exp. Mar. Biol. Ecol. 175, 253–274.

Eversole, A.G., 2001. Reproduction in *Mercenaria mercenaria*. In: Kraeuter, J., Castagna, N. (Eds.), Biology of the Hard Clam. Elsevier, pp. 221–260.

Evgenidou, A., Valiela, I., 2002. Response of growth and density of a population of *Geukensia demissa* to land-derived nitrogen loading in Waquoit Bay, MA. Estuar. Coast. Shelf Sci. 55, 125–138.

Fabens, A.J., 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29, 265–289.

Faulkner, S.P., Patrick, W.H., Gambrell, R.P., 1989. Field techniques for measuring wetland soil parameters. Soil Sci. Soc. Am. J. 53, 883–890.

Fegley, S.R., MacDonald, B.A., Jacobsen, T.R., 1992. Short-term variation in the quantity and quality of seston available to benthic suspension feeders. Estuar. Coast. Shelf Sci. 34, 393–412.

Fernandez, E., Lin, J., Scarpa, J., 1999. Culture of *Mercenaria mercenaria* (Linnaeus): effects of density, predator exclusion device, and bag inversion. J. Shellfish Res. 18, 77–83.

Flaak, A.R., Eppifano, C.E., 1978. Dietary protein levels and growth of the oyster *Crassostrea virginica*. Mar. Biol. 45, 157–163.

Flagg, P.J., Malouf, R.E., 1983. Experimental plantings of juveniles of the hard clam, *Mercenaria mercenaria* (Linne.) in the waters of Long Island, New York. J. Shellfish Res. 3, 19–27.

Gabbott, P., 1983. Developmental and seasonal metabolic activities in marine molluscs. In: Hochachka, P. (Ed.), The Mollusca, Environmental Biochemistry and Physiology, vol. 2. Academic Press, pp. 165–217.

Gabbott, P.B., Bayne, B.L., 1973. Biochemical effects of temperature and nutritive stress on *Mytilus edulis* L. J. Mar. Biol. Assoc. U.K. 53, 269–286.

GESAMP, 1990. The State of the Marine Environment. Joint Group of Experts on the Scientific Aspects of Marine Pollution. Rep. and Stud. 39. United Nations Environmental Program.

Goldberg, E., 1995. Emerging problems in the coastal zone for the twenty-first century. Mar. Pollut. Bull. 31, 152–158.

Goldman, J., 1975. Identification of nitrogen as a growth limiting nutrient in wastewaters and coastal marine waters through continuous culture algal assays. Water Res. 10, 97–104.

Granéli, E., Sundbäck, K., 1985. The response of planktonic and microbenthic algal assemblages to nutrient enrichment in shallow coastal waters, southwest Sweden. J. Exp. Mar. Biol. Ecol. 85, 253–268.

Grant, J., 1996. The relationship of bioenergetics and the environment to the field growth of cultured bivalves. J. Exp. Mar. Biol. Ecol. 200, 239–256.

Grant, J., Thorpe, B., 1991. Effects of suspended sediment on growth respiration and excretion of the soft-shell clam (*Mya arenaria*). Can. J. Fish. Aquat. Sci. 48, 1285–1292.

Gray, J., Wu, R., Or, Y., 2002. Effects of hypoxia and organic enrichment on the coastal marine environment. Mar. Ecol., Prog. Ser. 238, 249–279.

Grizzle, R., Lutz, R., 1988. Descriptions of macroscopic banding patterns in sectioned polished shells of *Mercenaria mercenaria* from southern New Jersey. J. Shellfish Res. 7, 367–370.

Grizzle, R., Morin, P., 1989. Effect of tidal currents, seston, and bottom sediments on growth of *Mercenaria mercenaria*: results of a field experiment. Mar. Biol. 102, 85–93.

Grizzle, R.E., Langan, R., Huntting Howell, W., 1992. Growth responses of suspension-feeding bivalve molluscs to changes in water flow: differences between siphonate and nonsiphonate taxa. J. Exp. Mar. Biol. Ecol. 162, 213–228.

Grizzle, R.E., Bricelj, V.M., Shumway, S.E., 2001. Physiological ecology of *Mercenaria mercenaria*. In: Kraeuter, J.N., Castagna, M. (Eds.), Biology of the Hard Clam. Elsevier, pp. 305–382.

Hamwi, A., Haskin, H.H., 1969. Oxygen consumption and pumping rates in the hard clam *Mercenaria mercenaria*: a direct method. Science 163, 823–824.

Hargrave, B.T., 1980. Factors affecting the flux of organic matter to sediments in a marine bay. In: Tenore, D., Coull, B. (Eds.), Marine Benthic Dynamics. University of South Carolina Press, pp. 243–263.

Hatcher, A., 1994. Nitrogen and phosphorus turnover in some benthic marine invertebrates: Implications for the use of C/N ratios to assess food quality. Mar. Biol. 121, 161–166.

Hibbert, C.J., 1977. Energy relations of the bivalve *Mercenaria mercenaria*, on an intertidal mudflat. Mar. Biol. 44, 77–84.

Howarth, R., 1988. Nutrient limitation of net primary production in marine ecosystems. Ann. Rev. Ecolog. Syst. 19, 89–110.

Jones, R.H., 1966. Oxidation–reduction potential measurement. ISA J. November, 40–44.

Jones, D.S., Arthur, M.A., Allard, D.J., 1989. Sclerochronological records of temperature and growth from shells of *Mercenaria mercenaria* from Narragansett Bay, Rhode Island. Mar. Biol. 102, 225–234.

Jones, D., Quitmyer, I., Arnold, W., Marelli, D., 1990. Annual shell banding, age, and growth rate of hard clams (*Mercenaria* spp.) from Florida. J. Shellfish Res. 9, 215–225.

Josefson, A., Rasmussen, B., 2000. Nutrient retention by benthic macrofaunal biomass of Danish estuaries: Importance of nutrient load and residence time. Estuar. Coast. Shelf Sci. 50, 205–216.

Kamermans, P., 1994. Similarity in food source and timing of feeding in deposit- and suspension-feeding bivalves. Mar. Ecol., Prog. Ser. 104, 63–75.

Kang, C., Kim, J., Lee, K., Kim, J., Lee, P., Hong, J., 2003. Trophic importance of benthic microalgae to macrozoobenthos in coastal bay systems in Korea: dual stable C and N isotope analyses. Mar. Ecol., Prog. Ser. 259, 79–92.

Kirby-Smith, W., Barber, R., 1974. Suspension-feeding aquaculture systems: effects of phytoplankton concentration and temperature on growth of the bay scallop. Aquaculture 3, 135–145.

Koster, M., Dahlke, S., Meyer-Reil, L., 1997. Microbiological studies along a gradient of eutrophication in a shallow coastal inlet in the southern Baltic Sea (Nordrügensche Bodden). Mar. Ecol., Prog. Ser. 152, 27–39.

Laing, I., 1993. The response of Manila clam, *Tapes philippinarum*, juveniles to nutritive stress. J. Exp. Mar. Biol. Ecol. 173, 111–121.

Leavitt, D.F., McDowell Capuzzo, J., Smolowitz, R.M., Miosky, D.L., Lancaster, B.A., Reinisch, C.L., 1990. Hematopoietic neoplasia in *Mya arenaria*: prevalence and indices of physiological condition. Mar. Biol. 105, 313–321.

Lewis, D.E., Cerrato, R.M., 1997. Growth uncoupling and the relationship between shell growth and metabolism in the softshell clam *Mya arenaria*. Mar. Ecol., Prog. Ser. 158, 177–189.

Loesch, J., Haven, D., 1973. Estimated growth functions and size–age relationships of the hard clam, *Mercenaria mercenaria*, in York River, Virginia. Veliger 16, 76–81.

Loo, L., Rosenberg, R., 1989. Bivalve suspension-feeding dynamics and benthic–pelagic coupling in an eutrophicated marine bay. J. Exp. Mar. Biol. Ecol. 130, 253–276.

Lorenzen, C.J., 1967. Determination of chlorophyll and pheo-pigments: spectrophotometric equations. Limnol. Oceanogr. 12, 343–346.

Lorrain, A., Paulet, Y., Chauvaud, L., Savoye, N., Donval, A., Saout, C., 2002. Differential δ^{13}C and δ^{15}N signatures among scallop tissues: implications for ecology and physiology. J. Exp. Mar. Biol. Ecol. 275, 47–61.

Lukatelich, R.J., McComb, A.J., 1986. Distribution and abundance of benthic microalgae in a shallow southwestern Australian estuarine system. Mar. Ecol., Prog. Ser. 27, 287–297.

MacDonald, B., Thomas, M., 1980. Age determination of the soft-shell clam *Mya arenaria* using shell internal growth lines. Mar. Biol. 58, 105–109.

MacDonald, B., Bacon, G., Ward, J., 1998. Physiological responses of infaunal (*Mya arenaria*) and epifaunal (*Placopecten magellanicaus*) bivalves to variations in the concentration and quality of suspended particles— II. Absorption efficiency and scope for growth. J. Exp. Mar. Biol. Ecol. 219, 127–141.

Malouf, R.E., Bricelj, V.M., 1989. Comparative biology of clams: environmental tolerances, feeding, and growth. In: Manzi, J.J., Castagna, M. (Eds.), Clam Mariculture in North America. Elsevier, pp. 23–73.

Marsden, I., 2004. Effects of reduced salinity and seston availability on growth of the New Zealand little-neck clam *Austrovenus stutchburyi*. Mar. Ecol., Prog. Ser. 266, 157–171.

Matthiessen, G.C., 1960. Observations on the ecology of the soft clam, *Mya arenaria*, in a salt pond. Limnol. Oceanogr. 5, 291–300.

Matthiessen, G., 1992. Perspective on Shellfisheries in Southern New England. The Sounds Conservancy, vol. 4. Coastal Publication.

Maughan, J., Oviatt, C., 1993. Sediment and benthic response to wastewater solids in a marine mesocosm. Water Environ. Res. 65, 879–889.

Meltzer, K.R., 2002. Interannual Growth Rate Variation in the Soft-shelled Clam, Mya arenaria, and its Relationship to Interannual Temperature Differences and Habitat at Maquoit Bay, Maine. M.A. thesis. Bates College.

Milke, L.M., Ward, J.E., 2002. Influence of diet on pre-ingestive particle processing in bivalves II. Residence time in the pallial cavity and handling time on the labial palps. J. Exp. Mar. Biol. Ecol. 293, 151–172.

Moss, B., 1971. Phytobenthos sampling. In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for Study of Marine Benthos. IBP Handbook. Blackwell Scientific Publications, pp. 183–185.

Mudroch, A., Azcue, J.M., 1995. Manual of Aquatic Sediment Sampling. Lewis Publishers.

National Marine Fisheries Service, Annual Commercial Landings Statistics, 2003. http://www.st.nmfr.gov/st1/Commercial/landings/annual_landings.html.

Navarro, E., Iglesias, J., 1992. Infaunal filter-feeding bivalves and the physiological response to sort-term fluctuations in food availability and composition. In: Dame, R. (Ed.), Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes. Springer-Verlag, pp. 25–56.

Newell, C., Hidu, H., 1982. The effects of sediment type on growth rate and shell allometry in the soft shelled clam *Mya arenaria* L. J. Exp. Mar. Biol. Ecol. 65, 285–295.

Nixon, S., 1992. Quantifying the relationship between nitrogen input and the productivity of marine ecosystems. Proc. Adv. Mar. Tech. Conf. 5, 57–83.

Nixon, S., Buckley, B.A., 2002. "A strikingly rich zone"—Nutrient enrichment and secondary production in coastal marine ecosystems. Estuaries 25, 782–796.

Nixon, S., Oviatt, C., Frithsen, J., Sullivan, B., 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. J. Limnol. Soc. South .Afr. 12, 43–71.

Nixon, S., Buckley, B., Granger, S., Bintz, J., 2001. Responses of very shallow marine ecosystems to nutrient enrichment. Hum. Ecol. Risk Assess. 7, 1457–1481.

Novak, M., Lever, M., Valiela, I., 2001. Top-down vs. bottom-up controls of microphytobenthic standing crop: role of mud snails and nitrogen supply in the littoral of Waquoit Bay estuaries. Biol. Bull. 201, 292–294.

NRC. National Research Council, 2000. Clean Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution. National Academics Press, Washington, DC, pp. 165–176.

Pace, M.L., Shimmel, S., Darley, W.M., 1979. The effect of grazing by a gastropod, *Nassarius obsoletus*, on the benthic microbial community of a salt marsh mudflat. Estuar. Coast. Mar. Sci. 9, 121–134.

Paerl, H.W., Pinckney, J.L., Fear, J.M., Peierls, B.L., 1998. Ecosystem responses to internal and watershed organic matter loading: Consequences for hypoxia in the eutrophying Neuse River Estuary, North Carolina, USA. Mar. Ecol., Prog. Ser. 166, 17–25.

Pearson, T., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev. 16, 229–311.

Peterson, C.H., Irlandi, E., Black, R., 1994. The crash in suspension-feeding bivalve populations in Princess Royal Harbour: an unexpected consequence of eutrophication. J. Exp. Mar. Biol. Ecol. 176, 39–52.

Rask, H., 1982. Growth enhancement of *Mya arenaria* (Linne.) and *Mercenaria mercenaria* (Linne.) by marine macroalgae. J. Shellfish Res. 3, 99–100.

Rasmussen, E., 1973. Systematics and ecology of the Isefjord marine fauna, Denmark. Ophelia 11, 313–315.

Reitan, K., Vadstein, O., Olsen, Y., Reinertsen, H., 1999. Enhanced nutrient supply to Norwegian coastal waters: effects on growth of scallops and blue mussels. U.S.–Japan Cooperative Program in Natural Resources, Aquaculture Panel Proceedings, 28th Meeting.

Rheault, R., Rice, M., 1996. Food-limited growth and condition index in the eastern oyster *Crassostrea virginica* (Gmelin 1791), and the bay scallop, *Argopecten irradians* (Lamarck 1891). J. Shellfish Res. 15, 271–283.

Rhoads, D., Young, D., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. J. Mar. Res. 28, 150–177.

Rhoads, D., Tenore, K., Browne, M., 1975. The role of resuspended bottom mud in nutrient cycles of shallow embayments. In: Cronin, L.E. (Ed.), Estuarine Research, Chemistry, Biology, and the Estuarine System, vol. 1. Academic Press, New York, pp. 565–579.

Rice, T.R., Smith, R.J., 1958. Filtering rates of the hard clam (*Venus mercenaria*) determined with radioactive phytoplankton. Fish. Bull. 58, 71–82.

Rice, M.A., Hickox, C., Zehra, I., 1989. Effects of intensive fishing effort on the population structure of quahogs, *Mercenaria mercenaria* (Linnaeus 1758), in Narragansett Bay. J. Shellfish Res. 8, 345–354.

Riera, P., Stal, L.J., Nieuwenhuize, J., Richard, P., Blanchard, G., Gentil, F., 1999. Determination of food sources for benthic invertebrates in a salt marsh (Aiguillon Bay, France) by carbon and nitrogen stable isotopes: importance of locally produced sources. Mar. Ecol., Prog. Ser. 187, 301–307.

Russell-Hunter, W.D., 1970. Aquatic Productivity. MacMillan, New York.

Ryther, J., Dunstan, W., 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science 171, 1008–1013.

Sardá, R., Valiela, I., Foreman, K., 1996. Decadal shifts in a salt marsh macroinfaunal community in response to sustained long-term experimental nutrient enrichment. J. Exp. Mar. Biol. Ecol. 205, 63–81.

Shriver, A.C., Carmichael, R.H., Valiela, I., 2002. Growth, condition, reproductive potential, and mortality of bay scallops, *Argopecten irradians*, in response to eutrophic-driven changes in food resources. J. Exp. Mar. Biol. Ecol. 279, 1–2.

Smith, V., Tilman, G., Nekola, J., 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environ. Pollut. 100, 179–196.

Sokal, R.R., Rohlf, F.J., 1981. Biometry. W.H. Freeman and Company.

Stanley, J., Dewitt, J., 1985. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)-Hard Clam. U.S. Fish Wildl. Serv. Biol. Rep. 82, 1–24.

Sundbäck, K.V., Enoksson, W., Granéli, K., Pettersson, K., 1991. Influence of sublittoral microphytobenthos on the oxygen and nutrient flux between sediment and water: a laboratory continuous flow study. Mar. Ecol., Prog. Ser. 74, 263–279.

Tenore, K.R., Dunstan, W.M., 1973. Comparison of feeding and biodeposition of three bivalves at different food levels. Mar. Biol. 21, 190–195.

Thiel, M., Stearns, L.M., Wattling, L., 1998. Effects of green algal mats on bivalves in a New England mud flat. Helgol. Meeresunters. 52, 15–28.

Tober, J., Griffin, M., Valiela, I., 2000. Growth and abundance of *Fundulus heteroclitus* and *Menidia menidia* in estuaries of Waquoit Bay, Massachusetts exposed to different rates of nitrogen loading. Aquat. Ecol. 34, 299–306.

Urban, H.J., 2002. Modeling growth of different developmental stages in bivalves. Mar. Ecol., Prog. Ser. 238, 109–114.

Valiela, I., 1995. Marine Ecological Processes, 2nd ed. Springer-Verlag.

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., Collins, G., Kremer, J., Lajtha, K., Geist, M., Seely, B., Brawley, J., Sham, C., 1997. Nitrogen loading from coastal watersheds to receiving estuaries: new method and application. Ecol. Appl. 7, 358–380.

Valiela, I., Geist, M., McClelland, J., Tomasky, G., 2000. Nitrogen loading from watersheds to estuaries: verification of the Waquoit Bay nitrogen loading model. Biogeochemistry 49, 277–293.

von Bertalanffy, L., 1960. Principles and theory of growth. In: Nowinski, W.W. (Ed.), Fundamental Aspects of Normal and Malignant Growth. Elsevier, Amsterdam, pp. 137–259.

Walker, R., Tenore, K., 1984. The distribution and production of the hard clam, *Mercenaria mercenaria*, in Wassaw Sound, Georgia. Estuaries 7, 19–27.

Ward, J.E., Levinton, J.S., Shumway, S.E., 2003. Influence of diet on pre-ingestive particle processing in bivalves I: transport velocities on the ctenidium. J. Exp. Mar. Biol. Ecol. 293, 129–149.

Weiss, E.T., Carmichael, R.H., Valiela, I., 2002. The effect of nitrogen loading on growth rates of quahogs (*Mercenaria mercenaria*) and softshell clams (*Mya arenaria*) through changes in food supply. Aquaculture 211, 275–289.

Wentworth, C.K., 1922. A scale of grade class terms for clastic sediments. J. Geol. 30, 377–392.

Winter, J.E., 1978. A review of the knowledge of suspension-feeding in lamellibranchiate bivalves, with special reference to artificial aquaculture systems. Aquaculture 13, 1–33.

Zeitzschel, B., 1980. Sediment–water interactions in nutrient dynamics. In: Tenore, D., Coull, B. (Eds.), Marine Benthic Dynamics. University of South Carolina Press, pp. 195–218.

Zimmerman, A., Canuel, E., 2000. A geochemical record of eutrophication and anoxia in Chesapeake Bay sediments: anthropogenic influence on organic matter composition. Mar. Chem. 69, 117–137.