Bivalve Response to Estuarine Eutrophication: The Balance between Enhanced Food Supply and Habitat Alterations

BIVALVE RESPONSE TO ESTUARINE EUTROPHICATION: THE BALANCE BETWEEN ENHANCED FOOD SUPPLY AND HABITAT ALTERATIONS

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ABSTRACT As a result of insufficient sampling, differences in estuarine attributes, species variation, and poor links to anthropogenic sources, responses of bivalve mollucs to anthropogenic nutrient enrichment of coastal waters remains poorly defined for most systems worldwide. To establish the net effect of nutrient enrichment on bivalves, we compared changes in growth and survival of different bivalve species reported in 5 studies conducted in a representative estuarine system (on Cape Cod, MA) in which effects of eutrophication on food supply and habitat were quantified and related directly to land-derived nitrogen (N) sources. N-stable isotope ratios in suspended particulates and bivalve tissues demonstrated that N derived from anthropogenic wastewater was assimilated into bivalve tissues as N loads increased. Bivalve shell and soft-tissue growth also increased in response to increased chlorophyll *a* concentrations driven by land-derived N loads. Growth was accompanied by increased percent N content of tissues in some species, suggesting a change in tissue composition with N enrichment. In contrast, bivalve survival was lower in years of higher microalgal production, suggesting eutrophic-driven habitat degradation may have contributed to mortality. The net effect of eutrophication on bivalves, therefore, depended on the balance between enhanced food supply and habitat alterations that are mediated by attributes of the receiving estuary, and differences among species, particularly feeding habits, feeding physiology, and tolerance to hypoxia.

KEY WORDS: nitrogen, stable isotope, chlorophyll, growth, survival

INTRODUCTION

Increased nutrient enrichment to coastal waters worldwide (National Research Council 2000, Paerl 2006) has increased algal productivity, stimulated accumulation of organic matter from detritus of algae, and increased nitrogen (N) content of particles in the water and sediment (Zeitzschel 1980, Granéli & Sundbäck 1985, Cloern 2001). The resulting eutrophication of coastal waters ultimately may cause loss of seagrasses, anoxia in near-bottom waters, and lower sediment redox (Paerl et al. 1998, Gray et al. 2002, Hauxwell et al. 2003). Although the susceptibility of a coastal system to these effects depends on physical–chemical attributes of the water body, such as salinity, temperature, mixing, discharge, and flushing rates (Cloern 2001, Paerl 2006), eutrophic-driven changes in water quality have resulted in widespread species loss in many estuaries (Baden et al. 1990, Cloern 2001, Gray et al. 2002).

Because increased primary production often translates to increased food quantity and quality for primary consumers such as bivalves (e.g., Bayne & Widdows 1978, Newell et al. 1982, Smaal & Van Stralen 1990, Fegley et al. 1992, Carmichael et al. 2004), there may be corresponding increases in growth and abundance of consumers in nutrient-enriched estuaries (Nixon & Buckley 2002, Kirby & Miller 2005). The extent to which these potentially positive effects of enrichment are detectable in coastal food webs, however, is not well established (Micheli 1999). The notion that nutrient enrichment may stimulate production of consumers has been largely overlooked in favor of efforts to identify, diagnose, and remediate the negative effects of eutrophication (Micheli 1999, Fluharty 2000, Nixon & Buckley 2002, Verdelhos et al. 2005).

The bulk of evidence supporting eutrophic-driven secondary production comes from fertilization experiments in Scottish sea lochs more than 60 y ago (Orr 1947, Raymont 1947), and to a lesser degree from more recent studies in the Baltic and North Seas, the Kattegat, and Cape Cod estuaries (Tober et al. 2000, Nixon & Buckley 2002). These studies show increases in abundance or biomass of finfish through time or across locations as N and/or phosphorus (P) inputs to water bodies increased. If enrichment-driven secondary production can be detected in some finfish, which tend to be migratory and herbivorous, then production in other primary consumers, particularly sedentary bivalves, should be at least equally coupled to nutrient enrichment and quantifiable (Tober et al. 2000, Carmichael 2004).

BIVALVE RESPONSES TO NUTRIENT ENRICHMENT

Previous studies suggest the effects of nutrient enrichment on bivalves may be positive or negative, depending on whether enrichment affected primarily food resources or habitat (Table 1). Positive effects of nutrient enrichment on bivalves have included increased abundance, biomass, and assimilation efficiency, largely attributed to increased food supply, whereas negative effects included increased mortality, reduced biomass, and lower recruitment, resulting from habitat loss or degradation (Table 1, Fig. 1). Some studies reported a combination of enrichment-related effects (Feinstein et al. 1996, Josefson & Rasmussen 2000, Kirby & Miller 2005, Verdelhos et al. 2005), suggesting that the response of bivalves to nutrient enrichment may be more complex than a simple positive or negative response.

Until recently, however, most studies regarding the effects of eutrophication on bivalves relied on circumstantial evidence. For example, the Scottish loch studies reported increased abundance among bivalves as they did for finfish, but did not similarly detail the effects on bivalves (Orr 1947, Raymont 1947). Until 2001, no studies provided direct links between bivalve responses and a specific source of nutrient enrichment across sites, and only 25% of the reported bivalve responses were substantiated by measuring a potential mechanism of

TABLE 1.

Historically reported bivalve responses to nutrient enrichment, and mechanisms of effect (eutrophic-driven changes in food supply or habitat) across different species, locations, and enrichment types.

Species	Location	Enrichment Type	Bivalve Response to Enrichment	Mechanism of Effect (food supply or habitat metric)	Source
Mytilus edulis *Mya arenaria* *Macoma balthica* *Cardium edule* *Paphia pullastra* *Scrobicularia plana* *Modiolus* spp.	Loch Craiglin, Scotland	P and N fertilization	Increased abundance	Increased food supply (phytoplankton abundance)	Marshall (1947) Raymont (1947)
Mytilus edulis *Mya arenaria* *Macoma balthica* *Cardium* spp.	Baltic Sea	Urbanization: increased P and N (not measured)	Increased abundance and tissue weight (*Mya, Macoma* only)	Presumed increased food supply (not measured)	Cederwal and Elmgren (1980)
Mytilus edulis	Rías Bajas, Spain	Upwelling	Increased tissue weight	Presumed increased food supply (not measured)	Blanton et al. (1987)
Mya arenaria *Cardium edule* *Abra alba* *Arctica islandica* *Corbula gibba*	Kettegat, Sweden	Urbanization: N and P	Mortality among most species	Habitat change: hypoxia (measured oxygen concentrations)	Baden et al. (1990)
Corbula gibba	Adriatic Sea	Urbanization: increased nutrients	Increased abundance	Presumed habitat change: anoxic stress (not measured)	Crema et al. (1991)
Argopecten irradians	Waquoit Bay, USA	Urbanization: increased N	Reduced catch	Habitat change: eelgrass loss (measured) and presumed anoxia (not measured)	Valiela et al. (1992)
Ruditapes decussatus	Ria Formosa, South Portugal	Urbanization (not measured)	Increased respiration, reduced absorption efficiency	Increased organic content (not directly measured)	Costa et al. (1993)
Mya arenaria *Mercenaria mercenaria*	Waquoit Bay, USA	Urbanization: increased N	Increased shell growth (*Mya* only)	Increased food supply (not directly measured)	Chalfoun et al. (1994)
Nucula annulata	Narragansett Bay, USA	Increased organic matter; N, P, and silica fertilization	Increased mortality and recruitment failure	Presumed habitat change: hypoxia, settlement interference (not measured)	Craig (1994)
Katelysia spp.	Princess Royal Harbor, Australia	Urbanization: increased nutrients	Increased mortality and recruitment failure	Presumed habitat change (no specific aspect measured)	Peterson et al. (1994)
Geukensia demissa	Waquoit Bay, USA	Urbanization: increased N	Increased shell growth in juveniles, reduced shell growth in adults	Presumed combination of increased food supply and density (not measured)	Feinstein et al. (1996)

TABLE 1.
continued

Species	Location	Enrichment Type	Bivalve Response to Enrichment	Mechanism of Effect (food supply or habitat metric)	Source
Mytilus edulis *Mya arenaria* *Cardium edule*	Denmark	Freshwater-derived N and P	Increased biomass (to ~350 kg N/ha/y) followed by decreased biomass (>1,000 kg N/ha/y)	Presumed increased food supply (not measured), mediated by estuary flushing rates	Josefson and Rasmussen (2000)
Mytilus edulis *Pecten maximus*	Hopavagen Bay, Norway	N, P, silica fertilization	Increased shell height and tissue weight	Increased food supply (primary production)	Reitan et al. (1999)
Argopecten irradians	Waquoit Bay, USA	Urbanization: increased N	Increased mortality	Presumed habitat change (no specific aspect measured)	Fila et al. (2001)
Geukensia demissa	Waquoit Bay, USA	Urbanization: increased N	Increased shell growth	Presumed increased food supply (not directly measured)	Evgenidou et al. 2002
Mya arenaria *Mercenaria mercenaria*	Cape Cod estuaries, USA	Urbanization: increased N	Increased shell growth	Increased food supply (chlorophyll *a* concentrations)	Weiss et al. 2002
Argopecten irradians	Cape Cod estuaries, USA	Urbanization: increased N	High growth rates in all locations, no change in mortality or condition	Food supply: In excess even at sites receiving lower N loads (chlorophyll *a* concentrations)	Shriver et al. 2002
Mya arenaria *Mercenaria mercenaria*	Cape Cod estuaries, USA	Urbanization: increased N	Increased shell and soft-tissue growth, increased percentage of N in tissues	Increased food supply (chlorophyll *a* concentrations)	Carmichael et al. (2004)
Crassostrea virginica	Cape Cod estuaries, USA	Urbanization: increased N	Increased shell and soft-tissue growth	Increased food supply (chlorophyll *a* concentrations)	Carmichael et al. (unpubl.)
Crassostrea virginica	Chesapeake Bay, USA	Urbanization: increased TOC in sediment cores (from literature)	Increased shell and soft-tissue growth (initially), followed by reduced growth	Presumed increased food supply followed by hypoxia and habitat degradation (not measured)	Kirby and Miller (2005)
Scrobicularia plana	Mondego estuary, Portugal	Increased N and P, coupled with high water residence time	Increased abundance and juvenile recruitment at eutrophic sites, but overall reduced biomass and production	Secondary effects of macroalgal blooms and loss of seagrass (direct mechanism not measured)	Verdelhos et al. (2005)
Crassostrea gigas	Irish Sea, Ireland and Wales	Land use change: increased nutrients and TOC	Increased mortality (field tests) and immune suppression (laboratory tests)	Combination of high nutrient concentrations and high temperature (measured in field and laboratory)	Malham et al. (2009)

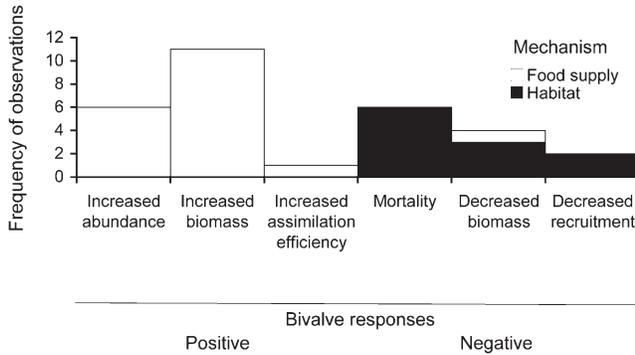N, nitrogen; P, phosphorus; TOC, total organic carbon.

Figure 1. Frequency distribution of positive and negative bivalve responses to increased nutrient enrichment reported in Table 1. Results are separated by the reported mechanism of effect (changes in food supply or habitat conditions). Positive responses include increased abundance, biomass, and assimilation efficiency. Negative responses include mortality and decreased biomass and recruitment.
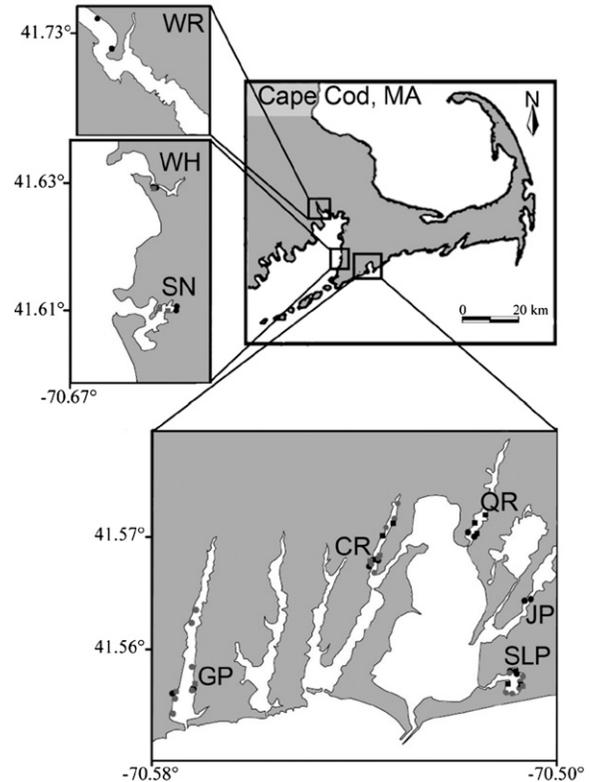

Figure 2. Estuaries of Cape Cod, MA, where bivalve responses to nutrient enrichment were studied. Study locations in each estuary are shown for Carmichael et al. (2004) and Shriver et al. (2002) (black dots), Weiss et al. (2002) (gray dots), Evgenidou and Valiela (2002) (black squares), and Carmichael et al. (unpubl.) (gray squares). CR, Childs River; GP, Green Pond; JP, Jehu Pond; QR, Quashnet River; SLP, Sage Lot Pond; SN, Snug Harbor; WH, Wild Harbor; WR, Weweantic River.

change (such as enrichment-driven increased food supply or changes in habitat; Table 1). Hence, there has been insufficient data to define clearly the underlying mechanisms by which eutrophication may affect bivalve growth or survival.

Physiological differences among bivalve species further confuse interpretation of the net effects of nutrient enrichment on bivalves. Past studies have considered a variety of different species across different locations (Table 1). These species process and assimilate foods differently (Tenore & Dunstan 1973, Bayne & Newell 1983). They also have different tolerances to hypoxia, particle loads, and estuary-specific attributes, such as salinity (Tenore & Dunstan 1973, Bayne & Newell 1983, Marsden 2004). Hence, nutrient enrichment may affect different species in different ways across locations, altering growth, survival, or having no apparent effect (Table 1). The extent to which species differences may mediate responses of bivalves to nutrient enrichment across locations has not been addressed clearly.

These data suggest that it is not sufficient to monitor individual bivalve responses under different enrichment conditions to establish the net effect of eutrophication on bivalves. Instead, we must define the underlying mechanisms of effect by comparing changes in growth and survival of different species across a common set of estuaries in which eutrophic-related changes in food supply and habitat are quantified and related directly to land-derived sources of enrichment. Here we review and assimilate data from 5 studies conducted on Cape Cod, MA, that meet these criteria and provide case studies to define more completely the mechanisms by which eutrophication affects bivalves.

CAPE COD CASE STUDIES

Five studies in Cape Cod estuaries have linked land-derived sources of nutrient enrichment to specific symptoms of eutrophication that, in turn, affected growth and survival of different bivalve species (Table 1, Fig. 2) (Evgenidou & Valiela 2002, Shriver et al. 2002, Weiss et al. 2002, Carmichael et al. 2004, Carmichael et al. unpubl.). To define these linkages, the studies first used N-stable isotopes to trace N from sources on land to suspended particles in the water column (food sources) and

ultimately to tissues of bivalves feeding in each estuary. To define the associated mechanism of bivalve response, the studies directly compared growth and survival of transplanted or native bivalves to eutrophic-driven changes in food supply and habitat conditions.

Results of the 5 Cape Cod case studies have implications for understanding eutrophic-driven mechanisms that affect bivalve production or survival in other coastal systems. The estuaries are largely enriched by wastewater associated with increased watershed urbanization (Valiela et al. 1992, Valiela et al. 1997), a common source of estuarine enrichment (Table 1 (Cloern 2001)). The estuaries receive N loads that span most of the range of land-derived N loads to coastal waters (Table 2) (Nixon 1992, Nixon et al. 2001). The bivalves studied—Atlantic bay scallop (*Argopecten irradians*, Lamarck), Northern quahogs = hard clam (*Mercenaria mercenaria*, Linnaeus), soft-shell clam (*Mya arenaria*, Linnaeus), ribbed mussel (*Geukensia demissa*, Dillwyn), and Eastern oyster (*Crassostrea virginica*, Gmelin)—include species that are among the most valuable and abundantly harvested from coastal estuaries in the United States (Valiela et al. 1992, Carmichael 2004, Lellis-Dibble et al. 2008), and represent a range of feeding strategies based on lifestyle (e.g., epifaunal or infaunal, sedentary or motile) and physiological capabilities, including differences in rates and efficiencies of particle capture, selection,

TABLE 2.

Flushing times and N loading rates for Cape Cod estuaries shown in Figure 2.

Estuary	Flushing Time (day)	N load (kg N/ha/y)	Source
Sage Lot Pond	1.50‡	14	Valiela et al. (2000)
Jehu Pond	1.10§	21	Valiela et al. (2000)
Wild Harbor	1.80	65	Costa (1994)*
Green Pond	1.40†	178	Kroeger et al. (1999)
Snug Harbor	1.80	236	Kroeger et al. (2006)
Weweantic River	1.14	339	Costa (1994)*
Quashnet River	1.70‡	353	Valiela et al. (2000)
Childs River	2.00‡§	601	Valiela et al. (2000)

* Modified according to Valiela et al. (2002). Estuary flushing times are based on tidal prism methods from
† Howes and Ramsey (unpubl.), ‡Kremer (unpubl.), and §Isaji (unpubl.).

Figure 3. (A, B) $\delta^{15}N$ in suspended particulate matter (SPM) compared with N load (A) and percent contribution of wastewater with total N load (B) for Cape Cod estuaries sampled during 1999, 2000, 2001, and 2003. (A) $y = 0.73 \ln(x) + 2.16$, $R^2 = 0.58$, $F_{27} = 35.94$, $P < 0.001$. (B) $y = 1.04 \ln(x) + 2.13$, $R^2 = 0.70$, $F_4 = 61.04$, $P < 0.001$. N-stable isotopic ratios in SPM were determined by isotope ratio mass spectrometry at either Boston University or University of California, Davis Stable Isotope Facility.

sorting, and assimilation (Jørgensen 1966, Bayne & Newell 1983, Kamermans 1994, Ward & Shumway 2004).

Linking Land-Derived N Loads to N in Bivalves

In Cape Cod estuaries, N-stable isotope ratios provided explicit links among land use, estuarine food resources, and N assimilated by bivalves. N sources have shifted from primarily atmospheric deposition to primarily wastewater as urbanization has increased on Cape Cod watersheds (Valiela et al. 1992, McClelland & Valiela 1998, Mayer et al. 2002). Because N-stable isotope ratios increase with increasing wastewater inputs to these estuaries, this change in land use can be traced as N loads increase (McClelland & Valiela 1998). Accordingly, $\delta^{15}N$ in suspended particulate matter (SPM) from near-bottom waters (where bivalves live and feed) increased with increasing N load (Fig. 3A) and with increasing percent contribution of wastewater to total N load across Cape Cod estuaries (Fig. 3B).

These relationships indicate that N in food particles available to bivalves in each estuary acquired estuary-specific $\delta^{15}N$ values relative to land cover on the receiving watersheds. $\delta^{15}N$ values in SPM did not vary significantly from year to year (ANOVA, $F_{3,29} = 1.74$, $P = 0.18$), suggesting the combination of N sources contributing to the N loads to each estuary did not change substantially from 1999 to 2003, when the Cape Cod studies were conducted. These data also confirm that particles available to bivalves in the water column had sufficient time to assimilate N within each estuary, despite relatively short flushing times (Table 2).

$\delta^{15}N$ ratios in bivalve tissues, in turn, increased with increasing $\delta^{15}N$ in SPM from each estuary (Fig. 4), demonstrating that bivalves assimilated N from SPM and also acquired estuary-specific $\delta^{15}N$ values relative to land-derived sources. Relationships between $\delta^{15}N$ in bivalves and $\delta^{15}N$ in SPM were similar among species (test for homogeneity of slopes, $F_{4,38} = 0.55$, $P = 0.70$; Fig. 4) and decreased ~2–5‰ above the 1:1 line (Fig. 4), consistent with expected N isotopic fractionation for a single trophic step (Peterson & Fry 1987). These data show that N available to, and ultimately assimilated by, bivalves in the Cape Cod estuaries was derived from land rather than from open-ocean sources, providing an unambiguous link from
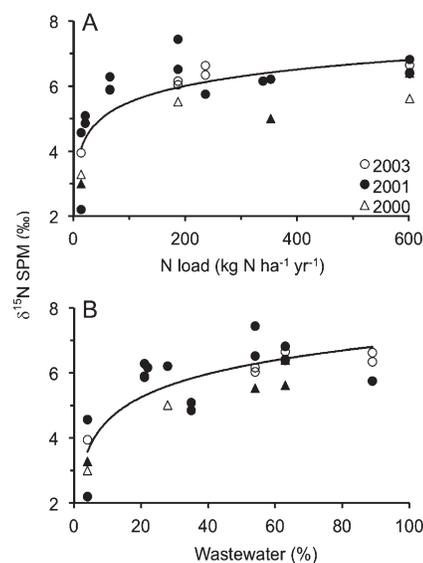
bivalves to their food supply and ultimately to land-derived sources of nutrient enrichment.

Nutrient Enrichment and Bivalve Growth

Shell Growth

From 1999 to 2003, bivalves transplanted in Cape Cod estuaries showed increased shell growth as N loads increased across estuaries (Fig. 5A). Increased growth rates were related to increased chlorophyll a concentrations (Fig. 5B), which also increased with N load across estuaries in each year (Fig. 6). All Cape Cod estuaries had relatively high chlorophyll a concentrations compared with
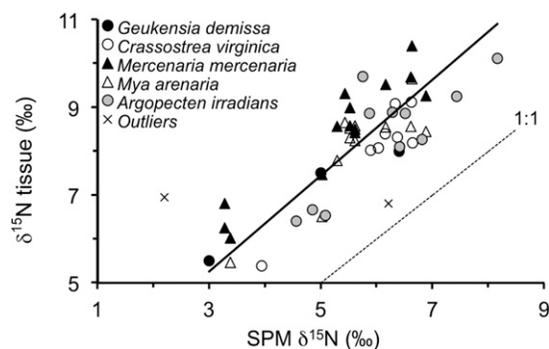

Figure 4. $\delta^{15}N$ in bivalve tissues compared with $\delta^{15}N$ in suspended particulate matter (SPM), separated by species (ribbed mussels (*Geukensia demissa*), oysters (*Crassostrea virginica*), quahogs (*Mercenaria mercenaria*), soft-shell clams (*Mya arenaria*), scallops (*Argopecten irradians*)). Type II regression yielded a best-fit line to the combined data: $y = 1.10x + 1.97$, $R^2 = 0.69$, $F_{47} = 103.67$, $P < 0.001$. Outliers (Sokal & Rohlf 1981) were not included in the regression analysis. N-stable isotopic ratios in bivalve tissues were determined by isotope ratio mass spectrometry.
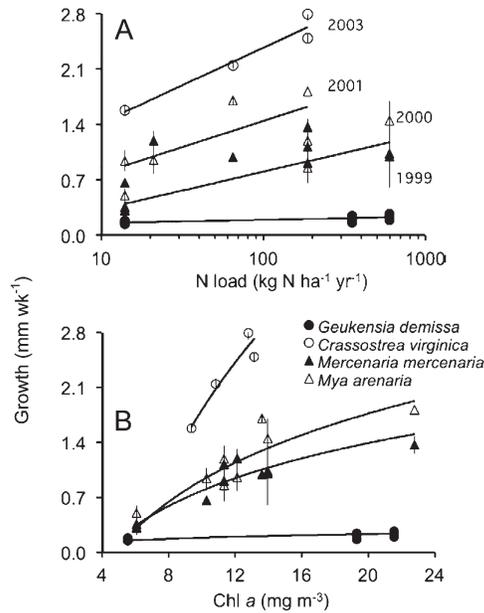
Figure 5. (A, B) Mean (±SE) growth rates in terms of bivalve shell length compared with mean chlorophyll *a* (Chl *a*) concentration (A) for *G. demissa* ($y = 0.64 \ln(x) + 0.03$, $R^2 = 0.55$, $F_8 = 8.42$, $P = 0.02$), *C. virginica* ($y = 3.33 \ln(x) - 5.86$, $R^2 = 0.90$, $F_3 = 17.13$, $P = 0.05$), *M. mercenaria* ($y = 0.88 \ln(x) - 1.24$, $R^2 = 0.85$, $F_9 = 46.42$, $P < 0.001$), and *M. arenaria* ($y = 1.23 \ln(x) - 1.92$, $R^2 = 0.80$, $F_9 = 32.29$, $P < 0.001$), and compared with N loading rate (B) with each estuary for each year bivalves were studied (1999: $y = 0.02x + 0.11$, $R^2 = 0.56$, $F_8 = 9.02$, $P = 0.02$; 2000: $y = 0.21 \ln(x) - 0.15$, $R^2 = 0.81$, $F_8 = 43.60$, $P < 0.001$; 2001: $y = 0.29 \ln(x) + 0.02$, $R^2 = 0.60$, $F_7 = 8.96$, $P = 0.02$; 2003: $y = 0.41 \ln(x) + 0.47$, $R^2 = 0.94$, $F_3 = 30.56$, $P = 0.03$). Type II regression was used to relate growth to chlorophyll *a* concentration (A). Data are from hatchery-reared juveniles transplanted during the peak growing season, except for *G. demissa*, which were obtained from native stocks. Green Pond growth data from Weiss et al. (2002) were compared with an updated N loading rate (Table 2).

Figure 6. Mean (±SE) chlorophyll *a* (Chl *a*) concentration in near-bottom water at bivalve transplant locations 1998 to 2003 compared with N loading rates for Cape Cod estuaries. No bivalves were transplanted in 2002. For clarity, data originally reported by site were combined to yield an estuary mean for transplant sites in each year. Data for 1998 to 2000 are a 3-y average, calculated to represent conditions in Evgenidou and Valiela (2002), who reported only historical Chl *a* concentrations. Data from Shriver et al. (2002) and Carmichael et al. (2004) for 2001 were not significantly different ($t = -99$, $df = 6$, $P = 0.18$), and were combined for simplicity. 2003: $y = 1.86 \ln(x) + 3.99$, $R^2 = 0.91$, $F_4 = 30.84$, $P = 0.01$, data from Carmichael et al. (unpubl.); 2001: $y = 5.00 \ln(x) + 3.62$, $R^2 = 0.90$, $F_7 = 55.36$, $P < 0.001$, data from Carmichael et al. (2004) and Shriver et al. (2002); 2000: $y = 2.08 \ln(x) + 0.56$, $R^2 = 0.99$, $F_2 = 1,357.40$, $P = 0.02$, data from Weiss et al. (2002); 1998 to 2000: $y = 4.26 \ln(x) + 5.70$, $R^2 = 0.99$, $F_2 = 65,659,515.89$, $P < 0.001$, data from Valiela et al. (unpubl.).

other estuaries worldwide (Fig. 6) (Valiela et al. 1992, Cebrián & Valiela 1999, Shriver et al. 2002), and bivalves in Cape Cod estuaries showed maximum growth rates accordingly that were among the highest measured anywhere (Fig. 5) (Carmichael 2004). The bay scallop *A. irradians* was the only species that did not show a change in growth with increasing N load among Cape Cod estuaries, but still had growth rates among the highest reported for this species (Shriver et al. 2002, data not shown). Because chlorophyll *a* concentration is a reasonable proxy for microalgal biomass, these findings suggest that N enrichment increased growth of bivalves in Cape Cod estuaries by increasing the quantity of available food. This finding is consistent with circumstantial reports from the Baltic Sea, Rías Bajas Spain, and Danish estuaries (Table 1).

Interannual variation in food supply (suggested by variation in chlorophyll *a* concentration) likely contributed to variation in the magnitude of bivalve growth from year to year (Figs. 5A and 6). Variation in chlorophyll *a* can result from differences in the number of favorable days for production across years (Valiela 1995, Holmes 2008) and may, in part, explain why some previous studies have found a relatively weak relationship between chlorophyll *a* concentration and N enrichment through time (Cloern 2001). In Cape Cod estuaries, *M. mercenaria* and
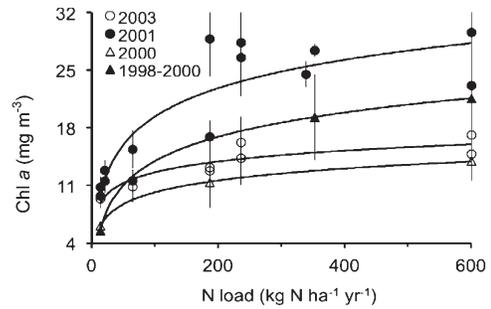
M. arenaria were transplanted serendipitously in the year of highest (2001) and lowest (2000) chlorophyll *a* concentration among these studies (Fig. 6), providing an opportunity to test the effects of interannual variation in food supply on bivalve growth under different N loading regimes. Growth rates of both species were higher in 2001 than 2000 (Fig. 5A), reflecting the higher concentration of food available in 2001. As a result, bivalve growth data sorted out better by year of study than by species when compared with N loading rates (Fig. 5A). Although water temperature was not reported in all studies, it is known to affect primary production seasonally and from year to year (Valiela et al. 1992, Holmes 2008). Temperature did not differ among estuaries during these studies in 2000, 2001, or 2003, indicating that bivalve growth responded to changes in food supply rather than temperature. These findings indicate a tight coupling between bivalve growth and food quantity driven by N enrichment, but also demonstrate that the effects of N enrichment can be mediated by environmental factors.

The differences in magnitude of shell growth among the different bivalve species studied were consistent with established differences in feeding strategies and rates, and efficiencies of particle capture, sorting, and assimilation (e.g., Jørgensen 1966, Tenore & Dunstan 1973, Winter 1978, Gillmor 1982, Bayne & Newell 1983, Kamermans 1994, Ward & Shumway 2004), and were not necessarily related to differences in food quantity. There were significant differences in magnitude of bivalve shell growth among studies (Fig. 5A; test for homogeneity of slopes, $F_{3,25} = 10.37$, $P < 0.001$) that highlight differences among species when growth was compared with chlorophyll *a* (Fig. 5B). The Eastern oyster, *Crassostrea virginica*, which has high feeding and assimilation rates (e.g., Tenore & Dunstan 1973, Palmer & Williams 1980, Bayne & Newell 1983, Ward et al. 1998), showed the highest rates of shell growth (Fig. 5), although food concentrations in the year they were transplanted (2003)

were among the lower concentrations measured across studies (Fig. 6, open circles). The bivalve *A. irradians,* which has a lower feeding capacity than other bivalves studied (Kirby-Smith & Barber 1974, Gillmor 1982), showed no change in shell growth as N loads increased, likely having reached maximum capacity to consume and assimilate food at chlorophyll *a* concentrations in the lowest N-loaded estuaries (Kirby-Smith & Barber 1974, Leverone 1995, Shriver et al. 2002). The lower but increasing shell growth rates of the mussel *G. demissa,* on the other hand, likely resulted from inhabiting tidal marshes where food availability is limited by tidal exposure, potentially curbing growth despite relatively high feeding capacity (Jørgensen 1966, Bayne & Newell 1983). These data indicate that the extent to which eutrophication-enhanced food supply can increase bivalve growth depends, at least in part, on species-specific feeding habits and physiology.

Soft-Tissue Growth and Composition

Eutrophic-driven changes in food supply also altered soft-tissue growth and composition of bivalves in Cape Cod estuaries (Fig. 7). Among studies in which soft-tissue growth was measured, soft-tissue biomass followed shell growth, increasing with increased N load and food supply (Carmichael et al. 2004, Carmichael et al. unpubl.). Furthermore, percent N in soft tissue of *M. mercenaria* and *M. arenaria* increased with increasing N load (Fig. 7A), whereas tissues of *A. irradians* and *C. virginica* did not change (Fig. 7B). On average, percent N content in *M. arenaria* > *A. irradians* > *C. virginica* and *M. mercenaria* (Fig. 7). Increased percent N content in bivalve tissues suggests nutrient enrichment of foods altered the biochemical composition of soft tissues, resulting in a higher proportion of protein compared with lipids and carbohydrates (Gabbott & Bayne 1973, Bayne & Newell 1983, Laing 1993). Changes in tissue composition have implications for commercial shellfish marketing and management

because they may alter flavor or texture of meats. Why changes in N content of tissues were observed in some species but not others is not evident, but may be related to species-specific differences in food selection, N turnover, or food processing (Carmichael 2004).

Changes in N content of bivalve soft tissues suggest a link between N loads and bivalve growth that may result from changes in food quality. Changes in food quality measured as N and carbon (C) content of total SPM, however, did not show consistent trends with increasing N load across the Cape Cod studies (data not shown). Lower C:N with increasing N load was observed only in the year of highest chlorophyll *a* concentration (2001) (Shriver et al. 2002, Carmichael et al. 2004), perhaps because microalgae comprised a relatively larger portion of total SPM and made changes in particle quality more detectable. Relationships between bivalve growth and food quality could not be well established or related to N enrichment across the Cape Cod studies. N enrichment, therefore, appears to have affected growth of bivalves in Cape Cod estuaries primarily via increased food quantity rather than quality.

Predicting Growth Responses

These comparisons allow us to identify food concentrations and corresponding N loads at which different species may attain maximum or asymptotic growth in Cape Cod estuaries (Table 3). For example, the bay scallop *A. irradians* likely reached maximum growth rates in the lowest N-loaded estuary, at chlorophyll *a* concentrations less than 10 mg/L and N loads lower than 14 kg/ha/y (Fig. 6) (Shriver et al. 2002). Past studies confirm that *A. irradians* may reach maximum growth at phytoplankton concentrations near 5 mg/L (e.g., Kirby-Smith & Barber 1974, Leverone 1995, Shriver et al. 2002). From the regression lines describing the range of relationships between chlorophyll *a* and N load in Cape Cod estuaries (Fig. 4), we estimate that *A. irradians* would reach maximum growth rates in estuaries receiving ~6–8 kg N/ha/y (Table 3). In years when chlorophyll *a* production is relatively low, most bivalve species would be expected to show increased growth rates in Cape Cod estuaries that are more highly loaded (Tables 2 and 3). During
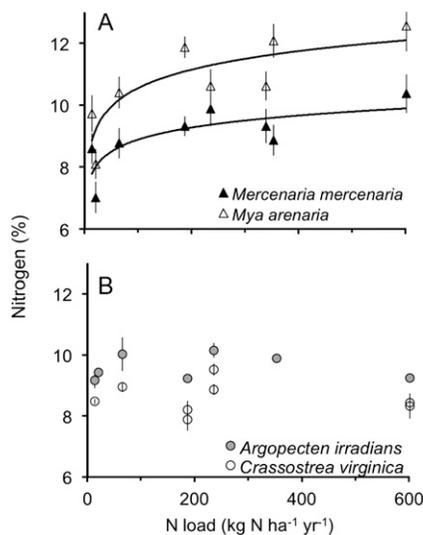

Figure 7. (A, B) Percent N in soft tissue compared with N loading rate for Cape Cod estuaries for *M. mercenaria* and *M. arenaria* (A) and *A. irradians* and *C. virginica* (B) (*M. mercenaria*: $y = 0.56 \ln(x) + 6.31$, $R^2 = 0.61$, $F_7 = 9.31$, $P = 0.02$; *M. arenaria*: $y = 0.86 \ln(x) + 6.59$, $R^2 = 0.69$, $F_7 = 13.13$, $P = 0.01$). No data were available for *G. demissa*. Percent N was determined during mass spectrometry.

TABLE 3.

Estimated chlorophyll *a* (Chl *a*) concentrations and corresponding N loading rates at which maximum growth rates may be achieved by juvenile bivalves in Cape Cod estuaries during years of lower and higher Chl *a* production.

Species	Maximum Growth Rate (mm/wk)	Chl *a* (mg/L)	N load (kg N/ha/y)	
			Lower Production	Higher Production
Argopecten irradians	2.0	5.0	8	6
Crassostrea virginica	2.8	>13.0	>178	>178
Mercenaria mercenaria	1.8	12.0–23.0	>242	22–234
Mya arenaria	1.4	14.0–23.0	>631	34–234
Geukensia demissa	0.3	19.0–22.0	>600	99–179

N loading rates were calculated from the regression lines relating Chl *a* concentration to N load shown in Figure 4 for 2000 (lower production) and 2001 (higher production). Data for maximum growth rates and corresponding Chl *a* concentrations are from Figure 3B and Shriver et al. (2002).

years of high chlorophyll *a* production, however, most bivalve species would reach maximum growth rates in estuaries receiving moderate N loads, ranging from 22–234 kg N/ha/y (Table 3). The oyster *C. virginica* did not appear to reach a maximum growth rate at the measured food concentrations (up to ~13 mg/L) and, therefore, likely would continue to increase growth at chlorophyll *a* concentrations and N loads higher than reported in Table 3.

The extent to which these data may be generalized to predict bivalve growth responses to nutrient enrichment elsewhere may be complicated by factors not related to nutrient enrichment. The Cape Cod studies indicate that physical factors affecting microalgal production from year to year, differences in habitat, or the capacity of individual species to take advantage of increased food supply, in part, mediated bivalve growth (Fig. 5). Species density, the presence of competitors, and lower salinity in some locations also limited bivalve growth in enriched Cape Cod estuaries despite increased food supply (Shriver et al. 2002, Weiss et al. 2002, Carmichael et al. 2004, Carmichael et al. unpubl.). Such variables may explain some of the apparent conflicting responses of bivalves to nutrient enrichment in previous studies (Table 1), and should be considered when assessing the net effects of nutrient enrichment on bivalve growth. It is notable, however, that despite the potential effects of these many variables, the primary response of bivalves to nutrient enrichment in Cape Cod estuaries and in many locations appears to be increased shell and soft-tissue growth (Table 1, Fig. 1).

Nutrient Enrichment and Bivalve Survival

Unlike growth, survival of bivalves did not increase with increasing N load across Cape Cod estuaries (Table 4). Survival was significantly lower, however, in the year chlorophyll *a* concentrations were highest (2001; Table 4, Fig. 6) (ANOVA: $F_{3,30} = 6.29$, $P = 0.002$; Fisher's PLSD: 2001, 2000: $P = 0.02$, 2001, 2002: $P = 0.004$, 2001, 2003: $P = 0.002$). Redox conditions in sediments also decreased significantly with increasing N load in 2001 (Carmichael 2004; data not shown), suggesting that hypoxic conditions in near-bottom waters of Cape Cod estuaries may have accounted for the lower bivalve survival in that year. The results of this study are consistent with observations reported previously, despite the largely circumstantial links between eutrophication, low dissolved oxygen concentrations, and reduced bivalve growth or survival in most studies (Table 1).

There are several possible reasons why it was difficult to link increased N loading rates, hypoxia, and reduced bivalve survival in the Cape Cod studies. First, annual variation in primary production along with salinity, mixing, and flushing rates can uncouple relationships between N load and hypoxia (Cloern 2001, Gray et al. 2002). Cape Cod estuaries are relatively well mixed, have short flushing times (Table 2), and recent studies using radium isotope tracers suggest water mass ages of only 1–2 wk for these estuaries (Holmes 2008). Second, hypoxic events are typically ephemeral or episodic in Cape Cod estuaries (D'Avanzo & Kremer 1994), making them difficult to capture and relate to survival of benthic species. Third, N loads received by Cape Cod estuaries may be too low to generate the sustained hypoxic conditions that affect bivalves substantially. Many bivalves are relatively tolerant to low oxygen concentrations compared with other species (Gray et al. 2002). Established relationships between bivalves and enrichment-driven hypoxia, therefore, are rare in the literature (Table 1). Reported effects, however, range from direct mortality traceable to eutrophication (Baden et al. 1990) to shifts in populations structure (Craig 1994) and speculated predation resulting from shallow burrowing during episodic hypoxia (Long et al. 2008). In fact, tolerance to hypoxia may confer a competitive advantage to bivalves able to survive and benefit from the increased food supply under eutrophic conditions (Breitburg 2002, Gray et al. 2002). Overall, if mortality is the most readily visible sign of stress among these relatively tolerant species in the natural environment, and low oxygen events are ephemeral, then hypoxic conditions may cause substantial mortality, but may dissipate before a relationship to the source of mortality can be established or related further to nutrient enrichment.

These studies suggest hypoxia may account for many of the different negative effects reportedly associated with eutrophication (Table 1), including those for which a mechanism has not been defined (e.g., Peterson et al. 1994, Josefson & Rasmussen

TABLE 4.

Percent survival (± SE) of *M. mercenaria*, *M. arenaria*, *A. irradians*, and *C. virginica* transplanted during 2000, 2001, and 2003 in estuaries receiving different N loads.

	Percent Survival					
	Mercenaria mercenaria		*Mya arenaria*		*Argopecten irradians*	*Crassostrea virginica*
N load (kg N/ha/y)	2000*	2001†	2000*	2001†	2001‡	2003§
14	89 ± 9	48 ± 48	48 ± 43	6 ± 2	100	93 ± 3
21	—	68 ± 16	—	0	93 ± 3	—
65	—	94 ± 6	—	62 ± 34	84 ± 3	82 ± 5
178	90 ± 10	92	67 ± 33	64	93 ± 3	97 ± 2
236	—	52 ± 12	—	52 ± 12	90 ± 18	92 ± 6
339	—	84	—	20 ± 12	—	—
353	—	0	—	0	21 ± 21	—
601	86 ± 13	0	70 ± 29	0	89 ± 4	97 ± 1
Mean	88 ± 6	55 ± 13	62 ± 20	26 ± 10	81 ± 10	92 ± 3

* Survival of *M. mercenaria* and *M. arenaria* during 2000 was calculated by averaging data from Weiss et al. (2002) and Carmichael et al. (2004). Other data are from † Carmichael et al. (2004),‡ Shriver et al. (2002), and § Carmichael et al. (unpubl.). —, data not collected.

2000). Aside from eelgrass loss, few other enrichment-related factors have been implicated to negatively affect bivalve growth or survival (Table 1). Several studies have suggested initial increases in bivalve biomass or changes in population structure that maintain biomass, followed by reduced growth or mortality (Craig 1994, Josefson & Rasmussen 2000, Kirby & Miller 2005. Verdelhos et al. 2005). This pattern is consistent with an initial increase in food supply, followed by habitat degradation, including hypoxia. A eutrophic estuary, therefore, could have similar or greater bivalve biomass than a relatively pristine estuary, depending on the balance between enhanced growth and reduced survival. Studies reporting only changes in bivalve biomass or production may miss negative effects of eutrophication on habitat, particularly hypoxia. Although low oxygen may have a variety of effects on bivalve population structure and biomass, these findings suggest that the effects on survival may be the primary negative factor mediating the benefits of food supply enhanced by eutrophication.

CONCLUSIONS

Review of previous studies, including 5 case studies in Cape Cod estuaries (Table 1), revealed that as N loads to coastal estuaries increase, there are explicit changes in food supply and habitat for bivalves that, in turn, potentially affect bivalve secondary production or survival. First, nutrient enrichment increases microalgal production, increasing food supply for many bivalves and, in turn, increasing bivalve secondary production in terms of shell and soft-tissue growth. Changes in food quality related to nutrient enrichment may also change soft-tissue composition among some species, but food quantity rather than quality appears to have the greatest effect on bivalve growth under eutrophic conditions. Second, increased algal production can shade seagrasses that provide essential habitat for bivalves such as the bay scallop *A. irradians*, reducing their numbers in some areas (Valiela et al. 1992, Hauxwell et al. 2003). The potentially positive effect of increased food supply may not compensate for habitat loss for bivalves like *A. irradians,* which are low-capacity feeders and primarily benefit from increased food supply when competition for food is high (Shriver et al. 2002). Third, as N loads increase further, accumulation of organic matter may lead to low oxygen concentrations in near-bottom waters (Cloern 2001, Breitburg 2002, Paerl 2006). Studies in Cape Cod waters and elsewhere suggest that eutrophic-driven hypoxia may be the primary mechanism by which nutrient enrichment affects bivalves negatively—a finding consistent with data for other benthic species (Breitburg 2002). Eutrophic-driven hypoxia, therefore, may counter some of the positive effects of increased food supply, depending on the physical–chemical attributes of receiving estuaries and tolerance of individual bivalve species to hypoxia.

These data confirm that the net effect of nutrient enrichment on bivalve secondary production depends on the balance between positive and negative effects of eutrophication on the system and resident species. Species with high feeding and assimilation rates as well as high tolerance to hypoxia, such as oysters, may be most successful in enriched waters because they are able to take advantage of the abundant food supply and maintain survival better under eutrophic conditions. Such species may be the most successful for shellfish restoration or propagation efforts in urbanized estuaries. There is some evidence that bivalves also may remediate local effects of eutrophication by grazing down phytoplankton abundance and, if harvested, could remove N from an estuary via assimilation of N into tissues (Cloern 2001, Higgins et al. 2011). Although these interactions have not been fully resolved (Burkholder & Shumway 2011, Carmichael et al. unpubl.), the data presented here suggest bivalves that fare well under enriched conditions will also be best suited to potentially remediate the effects of eutrophication. Defining the balance between increased growth and reduced survival for bivalves under nutrient-enriched conditions is critical to conserve and restore the attributes of habitat required to sustain bivalves (and other estuarine species) that provide food, income, and ecological services to coastal communities.

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