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Growth, condition, reproductive potential, and mortality of bay scallops, *Argopecten irradians*, in response to eutrophic-driven changes in food resources

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Abstract

Anthropogenic nutrient enrichment of coastal waters is changing the habitat and food resources of bay scallops, *Argopecten irradians*. As land-derived nitrogen (N) enters estuaries, phytoplankton abundance, particulate organic matter, and nitrogen content of seston may increase, providing a higher quantity and quality of food. Understanding these changes is important for monitoring declining populations or developing field aquaculture systems. To examine if changes in food resources due to nutrient enrichment will affect growth, condition, reproductive potential, and mortality, we conducted a field experiment in seven estuaries each having a different land-derived N load. We placed juvenile bay scallops within these estuaries for approximately 12 weeks while monitoring food quantity and quality. Stable isotopic signatures suggested that scallops assimilated food from the specific estuaries in which we placed them. Growth rates were relatively high and did not increase with higher phytoplankton concentrations, suggesting that at the densities we deployed, ambient phytoplankton concentrations were in excess of consumption ability. Growth rates decreased at sites with lower salinities, and where high densities of competitors (barnacles and slipper shells) fortuitously settled on the scallops. Condition index significantly increased with higher growth rates. Gonad index and mortality were not related to food resources, but mortality increased with lower salinities. Land-derived N load seems unlikely to directly alter condition, reproductive potential, or mortality. These results suggest that estuaries undergoing anthropogenic nutrient additions may provide food concentrations above the maximum ration assimilable, resulting in high bay scallop growth rates.

Keywords: Aquaculture; Chlorophyll *a*; Epibionts; Food quantity and quality; N loading; Salinity

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1. Introduction

Increased anthropogenic nutrient additions to coastal waters due to urbanization, agriculture, and atmospheric deposition is one of the leading problems altering the environmental quality of coastal waters today (GESAMP, 1990; Goldberg, 1995; Valiela et al., 1992, 1997a,b). Nutrient loading, especially of nitrogen (N), has changed aquatic community structure and function, including increased abundance of nuisance macroalgae, lowered oxygen concentrations, and has caused the reduction of eelgrass beds (Valiela et al., 1992). The effects of increased nitrogen loading to coastal waters are important to understand because N limits phytoplankton production, and in excess may lead to eutrophication (Nixon et al., 1986; Valiela, 1995), thereby changing food resources of suspension feeders.

Bay scallop, *Argopecten irradians*, populations have been declining due to declining eelgrass habitat and coastal eutrophication (Stauffer, 1937; Dreyer and Castle, 1941; Stewart et al., 1981; Leavitt and Karney, 2001). Eelgrass (*Zostera marina*) meadows are the main habitat for bay scallops, and are rapidly disappearing as shallow estuaries become eutrophied (Belding, 1910b; Gutsell, 1930; Stauffer, 1937; Dreyer and Castle, 1941; Valiela et al., 1992; Duarte, 1995; Short and Burdick, 1996; Valiela and Cole, 2002). Much attention has been focused on eutrophication driven loss of eelgrass beds, the key habitat for bay scallops, but little on other effects of coastal eutrophication on bay scallops through changes in food resources.

Increased land-derived nitrogen entering an estuary could alter food resources for suspension-feeding bivalves. Since nitrogen is the major limiting nutrient of coastal waters, increases in phytoplankton abundance, particulate organic matter and N content of seston are likely to increase as land-derived N load increases (Ryther and Dunstan, 1971; Howarth, 1988; Valiela, 1995). These changes may change the quantity and quality of food. Food quantity can be assessed as the abundance of phytoplankton and particulate organic matter. Food quality can be defined in part as the carbon to nitrogen ratio of seston and the ratio of particulate inorganic to organic matter (Vahl, 1980; Valiela, 1995; Cranford et al., 1998), where high inorganic content is nutritionally poor and may lower assimilation efficiency (Dyer, 1975; Vahl, 1980; Valiela, 1995).

Differences in food quantity and quality may alter growth, condition, reproductive potential, and mortality. First, growth rates of bay scallops may increase with increasing phytoplankton concentrations (Kirby-Smith, 1970, 1972; Kirby-Smith and Barber, 1974; Cahalan et al., 1989). Thus, nitrogen enrichment may be, in part, beneficial to natural or aquacultural populations of bay scallops by increasing growth rates.

Second, food resources may alter scallop condition index (shell to tissue weight ratio). Condition index is a measure of the physiological state of a bivalve at a given moment (Lucas and Beninger, 1985). Rheault and Rice (1996) found a positive correlation between condition index in bay scallops and average chlorophyll ration consumed. Therefore, nutrient enrichment leading to increased food availability may increase condition index.

Third, altered food resources may affect gametogenesis and gonad development. Gonad index (the ratio of gonad weight to tissue weight) increases with food concentrations (Sastry, 1966, 1968). Gonad weights can provide an ecologically meaningful estimate of gamete production or reproductive output (Thompson and MacDonald, 1991). Thus, increased food quantity or quality may increase gonad development and reproductive potential.

Fourth, food resources may alter mortality. Low concentrations of food in estuaries may not provide enough nourishment to sustain a population of scallops at high densities, an important consideration in aquacultural practices (Duggan, 1973; Widman and Rhodes, 1991; Barber and Davis, 1997). Higher concentrations of food in eutrophic estuaries may be able to sustain higher density populations, thereby reducing mortality.

Declines in bay scallop populations have prompted increased aquacultural efforts to rear bay scallops for restoring natural populations or for farming for the valuable shucked meat (Leavitt and Karney, 2001). Since most scallop aquaculture is done using field grow-out techniques, possibly in eutrophied bays and estuaries, it is important to understand how possible differences among field sites may affect the bay scallop. Many studies, mostly laboratory-based, have provided information on aquacultural requirements of bay scallops, such as temperature, density, and most importantly, food supply (Kirby-Smith, 1970, 1972; Kirby-Smith and Barber, 1974; Dyer, 1975; Cahalan et al., 1989; Widman and Rhodes, 1991; Rheault and Rice, 1996). In this experiment we examine the effects of eutrophied waters on bay scallop growth, condition, reproductive potential, and mortality through changes in food resources. To measure the effects of land-derived nitrogen enrichment, populations of scallops were allowed to grow in cages placed in estuaries with different land-derived N loads. First, to ascertain if changes in food resources due to anthropogenic nitrogen enrichment are likely to affect bay scallops, we used stable isotopic signatures to make sure the scallops were feeding on food particles produced within the estuary in which were placed. Second, to determine the effects of N load on bay scallops, we compared the differences in food resources among estuaries to the different responses of scallops.

Stable isotopic signatures have been used to link consumers within specific estuaries to the land-derived nitrogen sources entering each estuary from its watershed (McClelland et al., 1997; McClelland and Valiela, 1998; Evgenidou and Valiela, 2002; Weiss et al., 2002). Nitrogen occurs as stable isotopes ^{14}N and ^{15}N in fixed proportions depending on the source and the ratio of isotopes are reported as a $\delta^{15}N$ value (Peterson and Fry, 1987). In Cape Cod estuaries, as urbanization of a watershed increases, nitrogen input to the receiving estuary shifts primarily from atmospheric deposition to primarily wastewater (Valiela et al., 1997b) causing the $\delta^{15}N$ signature to become heavier (McClelland et al., 1997). Therefore, potential food particles within estuaries having different percentages of wastewater input will have recognizably distinct signatures. By comparing the $\delta^{15}N$ signatures of seston to the $\delta^{15}N$ signature of scallop tissue, we can assess whether scallops are feeding on particulates produced by wastewater nitrogen entering the watershed in which they are feeding or on food particles carried in from deeper water by tidal currents. Thus, stable isotopes can assure that changes in growth, condition, reproductive potential, or mortality will be in response to estuary-specific anthropogenic nitrogen loads.

To determine the effects of N load on bay scallops, we first verified that differences in N load changed chlorophyll *a*, total suspended particulate matter (SPM), suspended particulate organic (POM) and inorganic matter (PIM), and the carbon to nitrogen ratio of seston (C/N). We then compared differences in growth rates, condition index, gonad index, and mortality among sites to the differences in food quantity and quality among the estuaries to assess the responses of scallops to eutrophication.

2. Methods

2.1. Study sites

Experimental treatments consisted of seven estuaries, each having a different land-derived N load due to different degrees of urbanization within their watersheds (Table 1) (Costa, 1994; Kroeger et al., 1999; Valiela et al., 2000; Kroeger, in preparation). Four of these estuaries (Childs River, Quashnet River, Jehu Pond, and Sage Lot Pond) are located within the Waquoit Bay National Estuarine Research Reserve, Cape Cod, MA, one is located immediately west (Green Pond), and two (Snug Harbor and Wild Harbor) are located on Buzzards Bay, MA (Fig. 1). Two study sites were chosen within each estuary, in locations with similar depth, flow regimes, and temperature.

2.2. Design of field experiment

Juvenile bay scallops, average size of 33.7 ± 0.10 mm and 6.97 ± 0.06 g whole wet weight, were obtained from Taylor Seafood company, Fairhaven, MA. They were held in unfiltered flow through seawater tables for 1 or 2 weeks until field placement. Immediately

Table 1
N load, chlorophyll *a*, salinity, and initial and final shell height for the two sites in each of the seven estuaries

	Site	N load (kg N ha^{-1} $year^{-1}$)	Chlorophyll *a* (μg l^{-1})	Salinity (‰)	Initial length (mm)	Final length (mm)	Growth (mm $week^{-1}$)
Sage Lot Pond	1	14	10.8	30.1	34.4	56.3	1.9
	2		9.7	29.4	34.0	53.9	1.7
Jehu Pond	1	21	11.5	29.4	33.7	56.3	2.0
	2		12.8	28.8	33.9	55.7	1.9
Wild Harbor	1	65	11.6	24.9	32.6	41.5	0.8
	2		15.4	23.9	32.6	40.9	0.7
Green Pond	1	178	28.77	25.5	33.5	52.0	1.7
	2		16.88	29.0	33.5	53.4	1.7
Snug Harbor	1	236	28.33	18.4	33.5	43.5	0.9
	2		26.5	25.0	33.6	51.5	1.6
Quashnet River	1	353	27.4	21.9	34.8	38.0	0.6
	2		20.6	23.1	33.9	no data	no data
Childs River	1	601	29.6	23.3	34.2	47.8	1.2
	2		23.1	24.5	34.1	47.4	1.2

Growth was calculated as the increase in shell length during the experiment. No data were available on the final size and growth rate for Quashnet River 2 due to 100% mortality at this site.

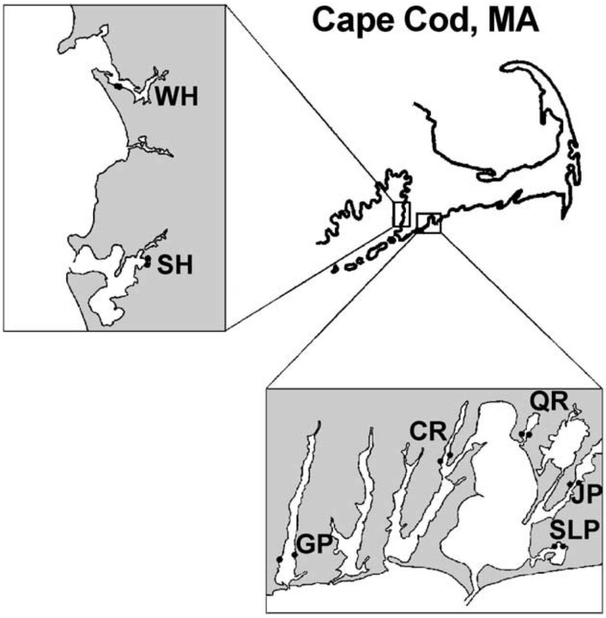

Fig. 1. Map of the seven study estuaries. Dots represent location of sites within estuaries. Lower figure: Childs River (CR), Quashnet River (QR), Green Pond (GP), Jehu Pond (JP), and Sage Lot Pond (SLP). Upper figure: Wild Harbor (WH) and Sung Harbor (SH).

before field placement, each individual was weighed, measured using calipers to the nearest 0.05 mm, and randomly labeled with a plastic numbered tag attached to both shells using a marine underwater patching compound (Pettit Paint, Rockaway, NJ).

Twenty-five scallops were placed in plastic coated wire mesh boxes ($30 \times 30 \times 10$ cm) lined with 4-mm plastic mesh sewn shut to prevent predation by small crabs. Two boxes were placed at each site for a total of 100 scallops per estuary. Sites were a few meters from shore and at approximately 1 m depth at mean low tide. Tidal range was approximately 0.3–1 m. To prevent covering by benthic macroalgae, the boxes were suspended 10 cm off the bottom by stakes attached to the corners of the box, and boxes were cleaned every 2 weeks with a bristled brush. Scallops were allowed to grow in the field for approximately 12 weeks from early June to early September 2001. Since most growth occurs during the 4 or 5 warmest months of the year (Belding, 1910b; Gutsell, 1928) when phytoplankton abundance is highest, seasonality was not a considerable factor in this experiment. At the end of the experiment, all scallops were collected and taken to the lab, where they were drained of mantle water and frozen until analyzed.

2.3. Assessment of potential food

To evaluate the potential food regimes at each site, water samples were collected every 2 weeks at each site during the time scallops were in the field to measure concentrations of chlorophyll *a*, total suspended particulate matter, organic and inorganic matter, and carbon to nitrogen ratio of seston. Two liters of water were collected in acid-washed 1-l plastic bottles in the area and at depth where the scallops were growing. Water samples were kept on ice and in the dark until filtered on ashed GF/F Whatman 47 mm 0.7 μM glass fiber filters (25 mm for C/N analysis). Filters for chlorophyll *a* determination were stored at 4 °C, and filters for C/N and stable isotope analysis were dried at 60 °C overnight and then placed in a dessicator.

Chlorophyll *a* concentration was determined according to Lorenzen (1967) by acetone extraction and spectrophotometery. Total suspended particulate matter was determined by comparison of filter weights before and after filtration of a known amount of water. Ashing filters at 490 °C for 4 h determined the organic vs. inorganic content of SPM. To determine the amount of carbon and nitrogen in the seston, filters were combusted in a Perkin Elemental Analyzer model 2400.

Other estuary characteristics were measured every 2 weeks at the time of water collection. Water temperature and dissolved oxygen (DO) were measured using a YSI 95, and salinity was measured using a refractometer. Since measuring DO at dawn was not always possible, DO measurements vs. the time of day were plotted, and regression was used to convert the original concentration to concentration at sunrise. This number was taken to represent lowest DO concentration at each estuary during the experiment.

2.4. Response measurements

Growth was determined as the difference between initial and final shell length. Shell length was measured as the longest distance from the umbo to the shell edge. Tissue dry weights were used to determine condition index and gonad index. Tissue was separated from the shell, and shell weight was recorded. The gut was separated from the tissue to prevent contamination of $\delta^{15}N$ signatures from unassimilated food in the gut, but kept to be included in whole tissue weights. All tissues were first dried at 60 °C for approximately 72 h, and then tissue and gonads were weighed.

Condition index was calculated as: CI=(tissue dry weight/shell weight) × 100. Gonad index was calculated as: GI=(gonad dry weight/tissue dry weight) × 100. In Massachusetts, gonad growth peaks in July/August while spawning takes place late in August/September (Sastry, 1970). Our gonad index values were determined in September to be sure gonads were active. Percent mortality was calculated as the average number of dead scallops found per site at the end of the field experiment.

2.5. Stable isotopes

To assure that the transplanted scallops were feeding on suspended particulate matter from the estuaries in which they where placed, $\delta^{15}N$ signatures of seston and scallop tissue were measured. Nitrogen isotopic signatures were calculated as $\delta^{15}N$ (‰) $=[(R_{sample}/R_{standard})-1]\times 10^3$ (Peterson and Fry, 1987). Seston samples were filtered on 25 mm 0.7 μM GF/F Whatman glass fiber filters until clogged, to assure enough sample was present to obtain a signal and dried at 60 °C overnight. The dry tissue, guts excluded, of 10 randomly chosen scallops from each site was ground to a powder. Filters and tissue were analyzed in a Finnegan Delta-S isotope ratio mass spectrometer at the Boston University Stable Isotope Facility.

2.6. Statistics

For regression analysis, all independent variables in this study (i.e. food resources and salinity) contained natural variation or error. For comparisons using these variables, a Model II geometric mean regression was used (Sokal and Rohlf, 1995). The only exception was for analysis involving N load and percent wastewater as the independent variable. These were assumed not have variation and therefore a Model I regression was used.

3. Results and discussion

3.1. Food quantity and quality

Food resources available to suspension feeders in the estuaries of this study differed in some aspects but not in others. Chlorophyll *a* concentrations were significantly higher in estuaries receiving larger land-derived N loads (Fig. 2, top). Concentrations of total suspended particulate matter and organic matter were not significantly higher with larger N loads (Fig. 2, middle). The ratio of particulate inorganic matter to organic matter also was not related to N load (Appendix A, Shriver, 2002). The ratio of carbon to nitrogen in particulates decreased significantly as N load increased, suggesting that larger N loads yielded better quality food for suspension feeders (Fig. 2, bottom). These different chlorophyll *a* concentrations and C/N values suggest that higher quantity and better quality food particles were available to scallops in estuaries with higher land-derived N load.

3.2. Stable nitrogen isotopes

The δ^{15}N of suspended particulate matter increased significantly as the percentage of total N contributed by wastewater to the estuary increased (Fig. 3, top). This result suggests that the watersheds of the different estuaries impose a distinctive signature on the phytoplankton (or SPM) in each estuary. The δ^{15}N signatures in scallop tissue parallel the differences in δ^{15}N values of suspended particulate matter (Fig. 3, bottom), suggesting that scallops obtained food particles largely from the estuary in which they were placed. Most of the δ^{15}N in scallop tissue fall within a range 2–4‰ higher than the corresponding value of SPM in each estuary, a fractionation characteristic of a trophic level shift from producers to consumers (Peterson and Fry, 1987; McClelland et al., 1997).

These results link the nitrogen in the scallops and suspended particulate matter to the specific watershed and estuary in which scallops were grown, and not to food sources carried in from deeper water by tidal currents. These data, taken together, strongly suggest a close coupling of watershed derived nitrogen into food (SPM) and scallop assimilation of this nitrogen into tissue.

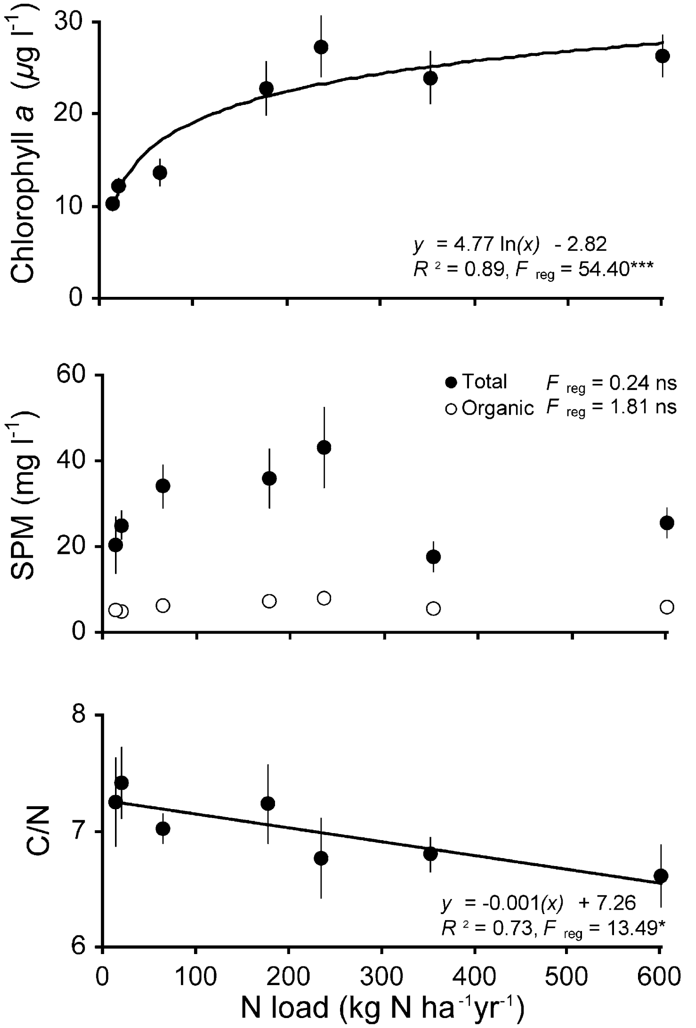

Fig. 2. Mean concentrations of chlorophyll *a* ± standard error (top), suspended particulate matter ± standard error (middle), and the carbon to nitrogen ratio ± standard error (bottom) vs. N load entering the estuaries. *: $p<0.05$, ***: $p<0.001$.

3.3. Growth response to food resources

Bay scallop shell growth differed among all estuaries and ranged from 0.6 to 2.0 mm week^{-1} (Table 1). Growth of the scallops did not respond to the differences in food quantity or quality supplied in these estuaries. Growth rate was not significantly related to land-derived N load (Fig. 4, top), chlorophyll *a* concentration (Fig. 4, middle), particulate organic matter (Fig. 4, bottom), or to the ratio of particulate inorganic matter to organic matter (Shriver, 2002). Growth did significantly increase with C/N of suspended

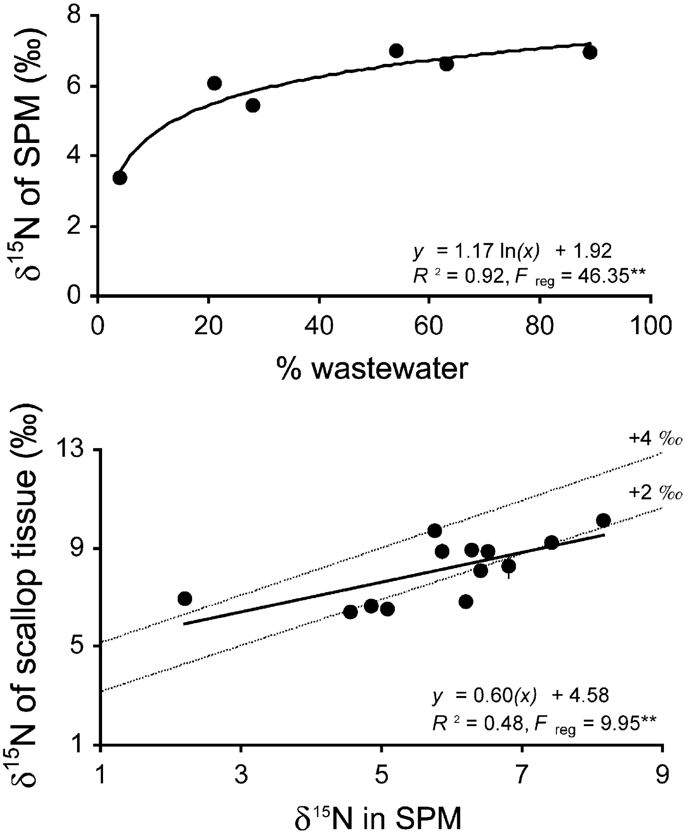

Fig. 3. $\delta^{15}N$ of SPM vs. the percent wastewater contribution to each estuary (top). $\delta^{15}N$ of tissue vs. $\delta^{15}N$ of SPM (bottom). Dashed lines represent a 2–4‰ trophic shift. Wastewater percentages from McClelland and Valiela (1998), Kroeger (1999), Kroeger et al. (in preparation), and modified from Costa (1994). Where there is no visible standard error bar, the value is smaller than the symbol. **: $p < 0.01$.

particulates (Fig. 5). This response is unexpected (and discussed further in salinity section) since most other sources suggest that growth increases among bivalves consuming food with low C/N values (Jordan and Valiela, 1982; Valiela, 1995; Cranford et al., 1998;).

Chlorophyll *a* concentrations were high in the seven estuaries studied compared to those reported in other studies relating chlorophyll *a* concentration to the growth of bay scallops (Fig. 6). Other studies have shown that scallop growth rates increased as chlorophyll concentrations increased (Fig. 7) (Kirby-Smith, 1970, 1972), but these measurements were conducted at relatively lower concentrations of chlorophyll (< 15 $\mu g\ l^{-1}$). Kirby-Smith and Barber (1974) suggest that maximum growth rates of scallops could be achieved at chlorophyll concentrations of about 5 $\mu g\ l^{-1}$ or less. Such concentrations were exceeded in all of the sites in this study (Fig. 2, top). If chlorophyll *a* concentrations in the estuaries of this study exceeded those upper thresholds of concentrations, we might expect growth rates to be high in all of the estuaries. Growth rates were indeed among the highest previously reported (Table 2).

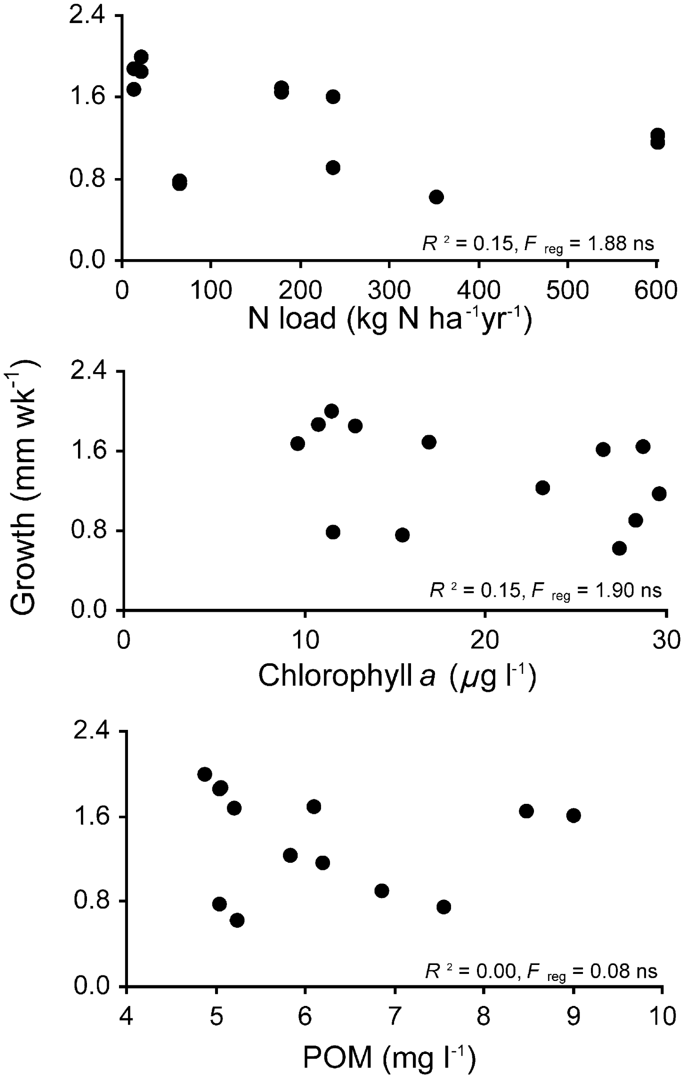

Fig. 4. Mean growth rate (mm week^{-1}) vs. N load (top), chlorophyll *a* concentration (middle) and particulate organic matter (bottom). Where there is no visible standard error bar, the value is smaller than the symbol.

In general, bivalve growth rates have been described as a logarithmic function of food ration (Bayne and Newell, 1983). We fitted such a curve to published and present data on bay scallop growth (Fig. 7) to approximately define the response to food supply. All the values of this study (black circles) lie beyond the 5 μg l^{-1} suggested as the minimum chlorophyll concentration where maximum growth can be achieved. The line in Fig. 7 begins to level off at 5 μg l^{-1}. Our results suggest that the estuaries in this study provided particulate foods in excess of what might be consumed and assimilated by the bay scallops

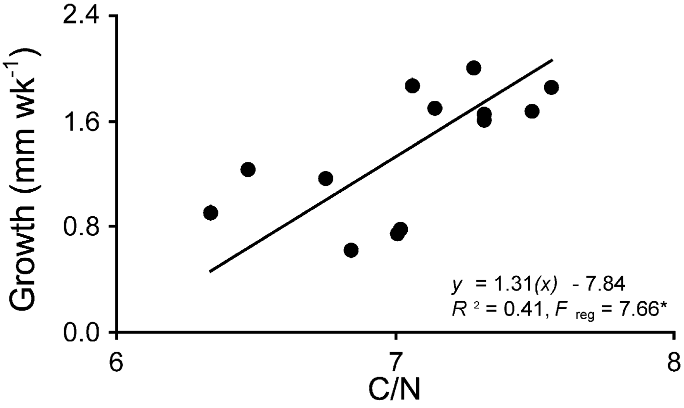

Fig. 5. Mean growth rates (mm week^{-1}) vs. carbon to nitrogen ratio of seston. Where there is no visible standard error bar, the value is smaller than the symbol. *: $p < 0.05$.

at the densities we established in the experimental cages. The scallops in these cages were not food limited, and may have assimilated as much food as was possible.

Since food concentration in our estuaries may be saturated, we would expect that growth rates could reach a uniform maximum across all sites, but there was much variation in shell growth rates. The observed variation may be attributable to several factors, including competition for food with epibionts (Belding, 1910a; Sinderman, 1971; Allen and Costello, 1972; Broom, 1976; Motet, 1979), differences in salinity, temperature (Kirby-Smith and Barber, 1974; Tettelbach and Rhodes, 1981; Barber and Blake, 1983; Barber and Davis, 1997), and concentration of dissolved oxygen (Van Dam, 1954). We used additional observations and measurements collected at the field sites to see if we could identify factors that could have been responsible for the variation in growth rates.

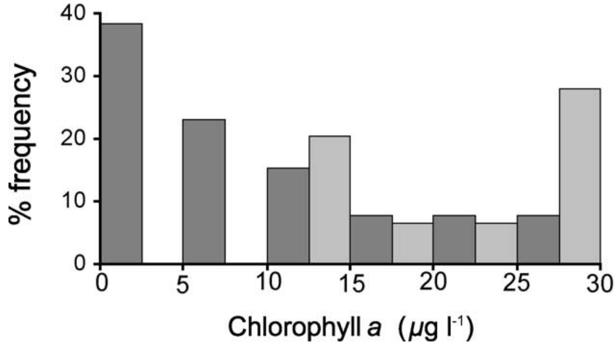

Fig. 6. Comparison of percent frequency of average chlorophyll *a* concentrations from this experiment (light grey box), and natural concentrations used in experiments of the growth response of *A. irradians* (dark grey box) (Rheault and Rice, 1996; Leverone, 1995; Kirby-Smith and Barber, 1974; Kirby-Smith, 1970, 1972).

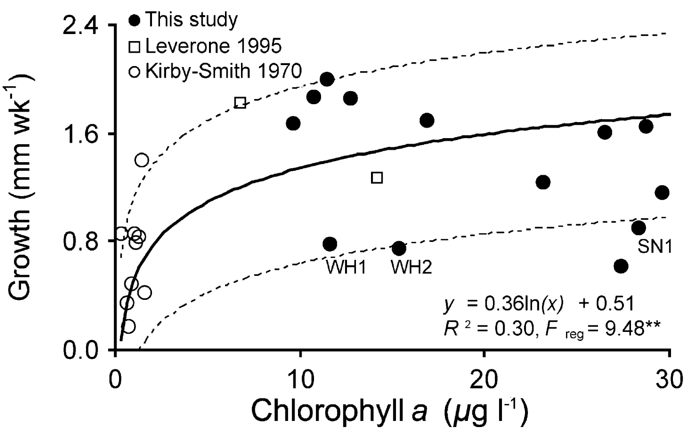

Fig. 7. Mean growth rates (mm $week^{-1}$) vs. chlorophyll *a* concentrations for this study, Leverone (1995), and Kirby-Smith (1970) (field experiment only). Model II regression for all points (—). Upper dashed line represents postulated growth without the effect of salinity. Lower dashed line represents postulated growth with epibionts causing food competition. WH1, WH2, and SN1 represent those sites with epibionts. **: $p < 0.01$.

3.4. Growth response to competition with epibionts

Suspension feeders that settle on scallop shells may compete for food with their host scallop (Belding, 1910a; Sinderman, 1971; Allen and Costello, 1972; Broom, 1976; Motet, 1979). These colonizers are suspension feeders that could have reduced phytoplankton concentrations below the amount at which food was no longer limiting, possibly reducing growth rates of the scallops.

Food competition by epibionts may have reduced growth rates in some sites where there was a fortuitous settlement of barnacles (*Chthamalus fragilis*) and slipper shells (*Crepidula fornicata*) on the scallop shells (Fig. 7). In three sites (Wild Harbor 1, Wild

Table 2
Reported rates of maximum *A. irradians* growth (mm $week^{-1}$), including the results of this study

Maximum growth rate (mm $week^{-1}$)	Source
1.26	Belding (1910a)
1.26	Barber and Davis (1997)
1.30	Barber and Blake (1983)
1.30	Heffernan et al. (1988)
1.40	Kirby-Smith (1970) (field data only)
1.47	Irlandi et al. (1999)
1.68	Cahalan et al. (1989)
1.75	Castagna and Duggan (1971)
1.82	Leverone (1995)
2.0	This study
2.50	Tettelbach (1987)

Harbor 2, and Snug Harbor 1), the shells of scallops became completely colonized by these epibionts. The scallops in the other sites had very little or no colonization. Scallops that were colonized grew significantly less and had a lower condition index than non-colonized scallops (Table 3). The presence of these potential food competitors possibly reduced growth rates to rates achieved at much lower chlorophyll concentrations, below the threshold suggested by Kirby-Smith and Barber (1974) (less than 5 μg l^{-1}). Competition, therefore, could have lowered the growth curve to the levels of the lower dashed line in Fig. 7. It seems reasonable to conclude that part of the variation in growth rate among our sites was related to differences in food supply caused by competition with epibionts.

3.5. Growth response to temperature, dissolved oxygen, and salinity

Many studies have shown that differences in temperature, dissolved oxygen, and salinity affect growth rates (Kirby-Smith and Barber, 1974; Tettelbach and Rhodes, 1981; Barber and Blake, 1983; Barber and Davis, 1997). To check whether these factors could have contributed to the variation among growth, we first ascertained if there were significant differences in these variables among sites. There were no differences in

Table 3
Comparison of growth (mm $week^{-1}$) ± standard error, condition index (tissue dry weight/shell weight) × 100 ± standard error, and gonad index (gonad dry weight/tissue dry weight) × 100 ± standard error between *A. irradians* among sites and with or without epibionts

	Site	Growth (mm $week^{-1}$)	Condition index	Gonad index
Scallops without epibionts				
Sage Lot Pond	1	1.9 ± 0.05	23.87 ± 0.47	10.60 ± 0.69
	2	1.7 ± 0.04	22.71 ± 0.40	10.07 ± 0.65
Jehu Pond	1	2.0 ± 0.05	21.09 ± 0.55	15.61 ± 0.97
	2	1.9 ± 0.04	19.60 ± 0.27	16.52 ± 0.99
Green Pond	1	1.7 ± 0.04	20.25 ± 0.77	15.13 ± 0.84
	2	1.7 ± 0.04	18.93 ± 0.44	13.70 ± 0.71
Snug Harbor	2	1.6 ± 0.04	17.95 ± 0.27	8.81 ± 0.38
Quashnet River	1	0.6 ± 0.05	16.51 ± 0.52	18.80 ± 1.10
	2	no data	no data	no data
Childs River	1	1.2 ± 0.04	17.64 ± 0.77	17.35 ± 1.12
	2	1.2 ± 0.04	19.89 ± 0.36	18.20 ± 1.92
		$\bar{X}$ = 1.5 ± 0.04	$\bar{X}$ = 19.84 ± 0.48	$\bar{X}$ = 14.48 ± 0.94
Scallops with epibionts				
Wild Harbor	1	0.8 ± 0.03	15.08 ± 0.21	11.23 ± 0.66
	2	0.7 ± 0.03	13.79 ± 0.30	11.31 ± 0.62
Snug Harbor	1	0.9 ± 0.05	10.69 ± 0.37	12.27 ± 1.01
		$\bar{X}$ = 0.8 ± 0.04	$\bar{X}$ = 13.19 ± 0.29	$\bar{X}$ = 11.60 ± 0.76
		$t = -2.92$	$t = -4.45$	$t = -1.35$
		$P = 0.014$*	$P < 0.001$**	$P = 0.203$ ns

No data available for Quashnet River 2 because of 100% mortality. $\bar{X}$: mean of group. P: probability level of t-test of scallops with and without epibionts; *: $p < 0.05$, **: $p < 0.01$, ns: nonsignificant.

temperature (Kruskal–Wallis test, $P=0.421$) or in DO (Kruskal–Wallis, $P=0.424$), but there were significant differences in salinity among sites (Kruskal–Wallis test, $P<0.001$). We therefore compared growth rates to differences in mean salinity among the sites over the entire study period.

Shell growth among these juvenile bay scallops increased significantly with increasing salinity (Fig. 8). Growth in our populations, so far defined as a saturating function of food supply, may have been affected by salinity, possibly explaining more of the remaining scatter in our populations (Fig. 7). High salinities may physiologically facilitate higher growth rates at any food supply rate. The upper dashed line in Fig. 7 represents an estimate of what growth may have been had salinity not depressed growth. Growth at higher salinity sites to reached rates comparable to the highest reported in Table 2.

Bay scallops are typically found in high salinity estuaries (Belding, 1910b; Gutsell, 1930; Castagna and Chanley, 1973; Duggan, 1975), and authors have speculated that scallops have little tolerance for low or reduced salinities (Marshall, 1960; Kirby-Smith, 1970; Broom, 1976). While a few reports have examined the effects of salinity on the growth of embryonic and larval stage bay scallops (Tettelbach and Rhodes, 1981), the effects of salinity on growth rates have yet to be examined in juvenile and adults stages. In previous reports, beginning with Belding (1910b), salinity was considered not important to growth. The results of this study suggest that salinity may be more important to growth rates of juvenile and adult bay scallops than previously thought, even in estuaries with small salinity ranges.

The effect of salinity on growth also clarified the unlikely relationship between growth and C/N mentioned earlier. In the estuaries we studied, there was a significant coincidental correlation between salinity and C/N ($r=0.75$, $F=14.32$**). Assuming biochemical food value was identical among sites, the unexplained effect of increased growth at higher C/N is most likely an artifact of this positive relationship.

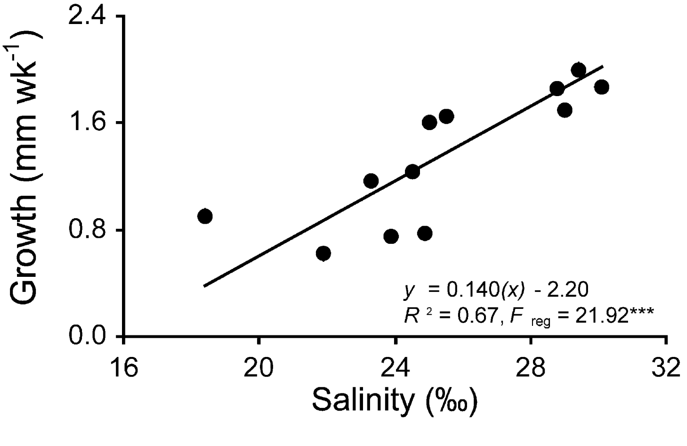

Fig. 8. Mean growth rates (mm week^{-1}) vs. mean salinity. Where there is no visible standard error bar, the value is smaller than the symbol. ***: $p<0.001$.

3.6. Condition index

Our results suggest that differences in food resources due to differences in N load among sites did not affect condition of the animal. Condition index increased significantly with increasing growth (Fig. 9), as would be expected, and with salinity ($r = 0.85$, $F = 28.42$***). There were no significant relationships between condition index and chlorophyll *a*, total suspended particulate matter, or inorganic matter (Appendix B, Shriver, 2002). There was a significant relationship with C/N (Appendix B, Shriver, 2002), most likely because of the correlation between salinity and C/N.

3.7. Gonad index

Gonad index was not significantly related to food quantity, quality, or growth (Appendix C, Shriver, 2002; Fig. 9). Reproductive potential in these populations did not change with growth rate, condition of the animal, or food resources. Other studies

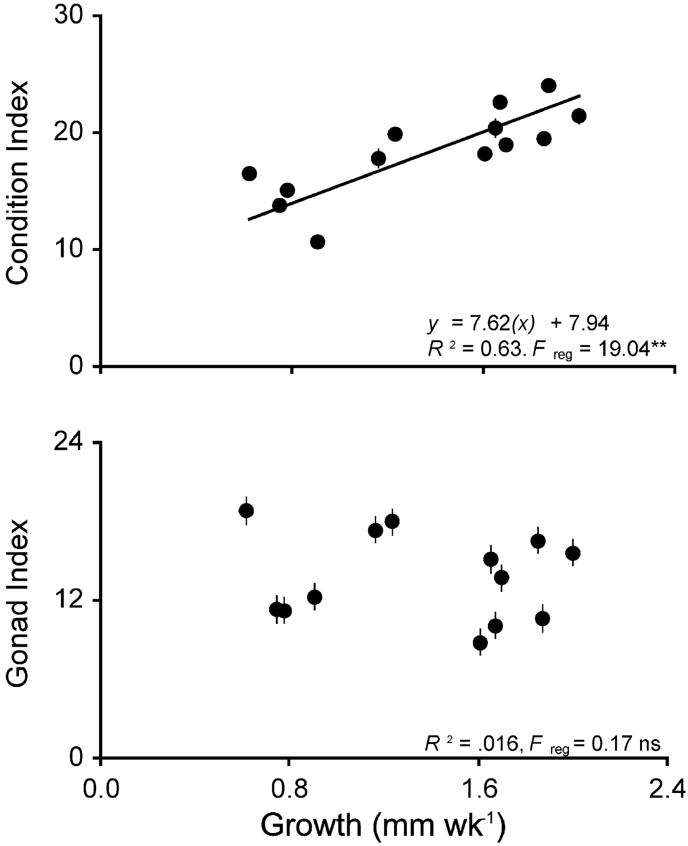

Fig. 9. Mean condition index (top) and gonad index (bottom) vs. growth rates at each site. Where there is no visible standard error bar, the value is smaller than the symbol. **: $p < 0.01$.

found that gonad growth increased with food supply and temperature (Sastry, 1968; Sastry and Blake, 1971). There may not be any significant trends in reproductive potential and gametogenesis in this population because of excess food supply, or the lack of significant temperature differences among sites.

3.8. Mortality

Differences in food quantity or quality did not significantly influence mortality in these populations (Appendix D, Shriver, 2002). This result suggests that these estuaries supplied enough food to support scallops growing at near maximum rates at densities of approximately 280 m^{-2}. Duggan (1973) and Widman and Rhodes (1991) showed experimentally that scallops up to 28 mm in length survived well above densities of 300 m^{-2}. The scallops in our estuaries reached lengths above 28 mm while still having low mortality in most sites. Scallops are commercially grown at densities of about 160 m^{-2} (Leavitt, personal communication). Our results suggest that scallops can be grown in eutrophied estuaries, because of increased food availability, at much higher densities with no negative effect on growth rates and mortality.

The mortality data of this study were scattered, but it is clear that low mortality occurred at salinities higher than 23 ‰ (Fig. 10). Increased scallop mortality has also been reported in other studies in conjunction with lower salinities (Tettelbach and Rhodes, 1981; Mercaldo and Rhodes, 1982). Just as salinity depressed growth in these bay scallop populations, it also depressed survival. These results suggest that bay scallop aquaculture efforts should be restricted to estuaries with salinities above 23 ‰.

3.9. Conclusions

Relationships between growth and food resources in eutrophied estuaries have been demonstrated in other bivalve species such as quahogs (*Mercenaria mercenaria*), softshell

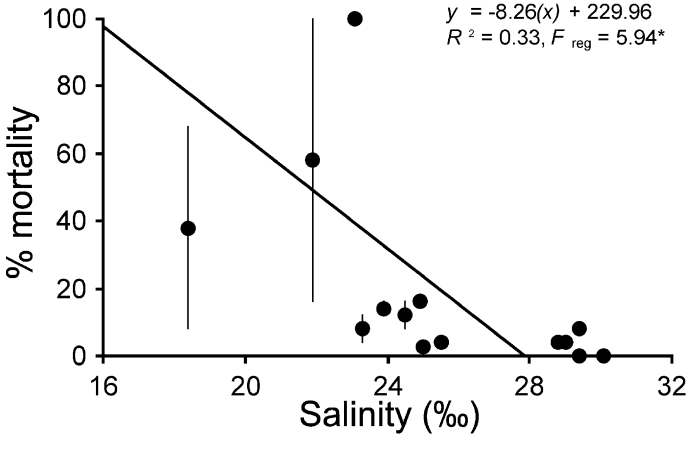

Fig. 10. Percent mortality vs. salinity at each site. Only four of the sites had standard error. *: $p < 0.05$.

clams (*Mya arenaria*), and ribbed mussels (*Geukensia demissa*) (Carmichael, in preparation; Evgenidou and Valiela, 2002; Weiss et al., 2002). The growth rates of all these species were higher where phytoplankton abundance increased due to higher land-derived N loads. For quahogs and softshell clams, growth did not reach a maximum even at chlorophyll *a* concentrations of 14 μg l^{-1} (Weiss et al., 2002). Bay scallops in this study responded differently to increased food supply because they may feed more efficiently and maximally at lower concentrations of food than these other species.

Coastal bodies of water subject to increased nitrogen input may provide greater amounts of food for suspension feeders, allowing for an increase in their densities. Greater amounts of phytoplankton may cause natural or cultured bay scallop populations to be food-saturated. In addition to caged populations, our results suggest that natural populations of bay scallops, usually at densities less than 20 m^{-2} (Thayer and Stuart, 1974; Bricelj et al., 1987), living in estuaries with chlorophyll *a* concentrations above 5 μg l^{-1} would also be under food-saturated conditions.

While land-derived N load seems unlikely to directly alter condition, reproductive potential, or mortality, there may be an effect on shell growth. In eutrophic bays and estuaries, saturating quantities of food may be able to increase the growth rate of *A. irradians* to a maximum unless growth is influenced by other factors such as salinity or competition with epibionts. This response to saturating concentrations of food is important to managers attempting to sustain natural stocks, and aquaculturists deploying juvenile caged bay scallops in field locations for aquaculture, restoration, or conservation programs.

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