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Growth of the bivalve *Nucula annulata* in nutrient-enriched environments

Nancy I. Craig *

Marine Ecosystem Research Laboratory, Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA

ABSTRACT: Measured changes in shell length and in the oxygen isotopic composition of shell growth bands were used to determine growth rates and season of maximum growth of the bivalve mollusc *Nucula annulata* from unstressed and nutrient-enriched environments in Narragansett Bay (Rhode Island, USA). Clams from unenriched environments grew between 0.55 and 0.9 mm yr^{-1}. Significant growth was limited to temperatures between 10 and 20 °C, in late spring and early fall. Populations in unstressed environments were dominated by high abundances of small clams (< 1 mm in length). Populations from nutrient-enriched environments consisted of fewer, larger clams. Data from a 2.3 yr nutrient gradient experiment and a 2 mo growth experiment suggest the larger individuals are simply older clams rarely found in unenriched environments. $\delta^{18}O$ temperature values from shell growth bands indicated a shift in the season of maximum growth from spring to summer for clams in eutrophic environments. Peak spawning activity of *N. annulata* usually coincides with the summer maxima in temperature (22 °C) in Narragansett Bay. The low numbers of juveniles found in enriched environments coupled with warmer shell growth temperatures imply a decline in successful reproduction and/or recruitment in eutrophic areas. Deteriorating environmental conditions associated with nutrient enrichment, i.e. low water column oxygen levels, may also enhance the survivorship of older, larger *N. annulata* possible through a reduction in predation pressure.

KEY WORDS: *Nucula* · Eutrophication · Growth

INTRODUCTION

The structure of coastal soft-bottom marine benthic communities is governed by 3 basic types of interactions: an organism's responses to the physical and chemical environment, population level responses to changes in the environment and biological interactions both within and between species (Zajac & Whitlatch 1988). Traditional descriptive studies of soft-bottom benthic communities clarify the outcome of such interactions but provide little information on the particulars driving the decline of species within a community (Sanders 1956, 1960, McCall 1976, Rhoads et al. 1978). Detailed accounts of the natural history of the component species are needed to isolate and identify the underlying mechanisms which give rise to shifts in community structure.

Nucula annulata was selected as the study organism because it is a numerically dominant component of mud-bottom benthic communities in temperate estuaries such as Narragansett Bay, Rhode Island, USA. *N. annulata* is a protobranch bivalve generally found in the top few centimeters of silty muds. It is a selective subsurface deposit-feeder favoring fine particles and sediments rich in organics and bacteria. Its major spawning effort coincides with summer maxima in temperature, ~22 °C in Narragansett Bay (Sanders 1956, 1960, Carey 1962, Blake & Jeffries 1971, Hampson 1971, Levinton 1972, McCall 1976, Ritacco 1980, Lopez & Cheng 1983, Nixon et al. 1984, Grassle et al. 1985, Frithsen et al. 1985b, Lopez & Levinton 1987). *Nucula* species are usually associated with unstressed depositional environments though they do persist and have even been described as 'active' during hypoxic and anoxic events (Moore 1931, Rachor 1976, Nixon et al.

* Present address: Marine Science Research Center, State University of New York, Stony Brook, New York 11794-5000, USA

1984). *N. annulata* does not appear to be sensitive to changes in available resources such as increased food or space (McCall 1976, Rhoads et al. 1978, Nixon et al. 1984, Grassle et al. 1985).

The objectives of this study were to quantify shell growth rates and assess the impact, if any, of exposure to conditions associated with nutrient enrichment on shell growth of *Nucula annulata*. Seasonal patterns in shell growth and absolute growth rates were determined from growth experiments and from the ratios of the stable isotopes of oxygen recorded in shell growth bands of clams from unstressed and nutrient-enriched environments. The effect of enrichment on the population structure of *N. annulata* was examined both in the field and in a 2.3 yr nutrient gradient study conducted at the Marine Ecosystem Research, University of Rhode Island.

MATERIAL AND METHODS

Study area. Narragansett Bay is a shallow-water, temperate-zone estuary. It is well mixed with little vertical stratification. Annual water temperatures range from −0.5°C in January to 22°C in August. Salinities range from a low of 20‰ in the Providence River to 32‰ at the mouth of the bay. Mean bay salinity falls between 28 and 32‰. Additional information on the physical, geological and chemical characteristics of Narragansett Bay can be found in Hicks (1959), McMaster (1960), Oviatt et al. (1984) and Pilson (1985a, b).

Molluscs and sediment were collected from 2 stations in Narragansett Bay, Stn 1 (41° 35' N, 71° 22' W) and Stn 2 (41° 38' N, 71° 20' W) (Fig. 1). Both stations are located in about 7 m of water, and their sediments are clayey-silt (McMaster 1960). Stn 1 is a well-studied mid-bay site (Oviatt et al. 1984, Grassle et al. 1985, Nixon et al. 1986, Frithsen 1988, Widbom & Elmgren 1988). The benthic community at this site is numerically dominated by 2 deposit feeders, the capitellid polychaete *Mediomastus ambisita* and the protobranch bivalve *Nucula annulata*. In decades past, the mid-bay benthic community was dominated by *Nephtys incisa* and *Nucula annulata*. This shift in dominants in the mid-bay region may indicate greater nutrient enrichment in this region though no evidence for a long-term increase in phytoplankton biomass or production has been observed (Oviatt et al. 1984, Grassle et al. 1985, Hinga et al. 1988). Stn 2 is located in the more heavily impacted upper-bay region. Gradients in sediment concentrations of hydrocarbons, heavy metals, and pore-water nutrients exist along the north-south axis of Narragansett Bay with Providence River sediments (north end of the gradient) containing the highest levels of these contaminants (Bayne et al. 1979, Olsen et al. 1980, Oviatt et al. 1984). The organic matter per dry weight sediment at Stn 2 was 6.35%, approximately twice that found in Stn 1 sediments (3.2%) (Craig 1989). Organic carbon levels at Stn 1 were 1.8% (Lambert & Oviatt 1986).

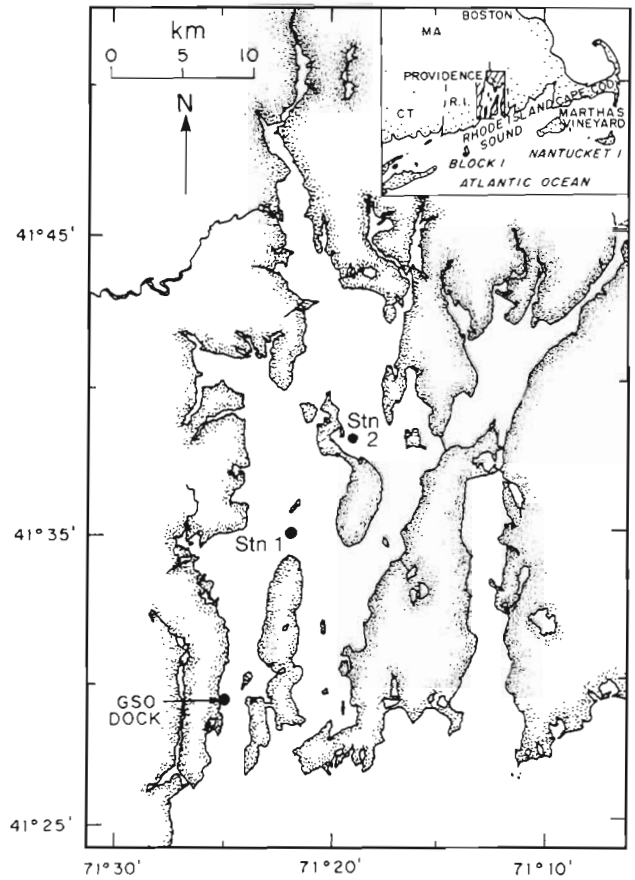

Fig. 1. Narragansett Bay (Rhode Island, USA) showing Stns 1 & 2

Estimates of abundance and size distribution were based on sediment cores collected on a seasonal basis from Stns 1 (unenriched) and 2 (enriched) during 1986 and 1987. Between 5 and 10 cores (20.48 cm^2) were collected from each station on each date. Cores were sectioned in 0 to 2 cm and 2 to 6 cm intervals, sieved through a 300 µm mesh, and *Nucula annulata* were identified and enumerated following procedures modified from Lambert & Oviatt (1986). Clams used in the isotope analysis and growth studies were collected using a Wildco Ponar Grab.

Mesocosms. Various components of this study were conducted in the Marine Ecosystem Research Laboratory (MERL) mesocosms. Previous studies have demonstrated that the mesocosms are representative of a simplified plankton-based coastal ecosystem (Pilson et al. 1979, Nixon et al. 1980, 1986, Oviatt et al. 1986).

Physical parameters are scaled to match natural conditions (temperature, mixing, water column turnover time). Benthic and pelagic community associations within individual mesocosms resemble those occurring in the mid-bay region of Narragansett Bay in terms of magnitude and seasonality of cycles in species abundance and composition, biological rate processes and nutrient and chlorophyll *a* concentrations.

Growth experiments. Absolute growth rates for *Nucula annulata* were determined from 2 mark-recovery growth experiments. Clams and sediment used in both experiments were collected from the mid-bay region (Stn 1). The average initial length of clams used in the 2 experiments did not vary significantly between experiments. Clams ranged in size from 1.50 to 3.16 mm with a mean length of 2.27 ± 0.18 mm. Individual clams were measured and marked with distinct symbols to allow for identification upon recovery at the end of both experiments. The marking process entailed blotting dry the surface of an individual's shell and scraping off a small section of the periostracum using a diamond scribe pen. Symbols were painted on with a thin bristle brush using rapidograph ink. A thin coat of acrylic resin was applied over each mark to reduce the chance of it being rubbed off as *N. annulata* moved through the sediment. Within a few hours of being returned to the sediment most clams had burrowed into the mud and extensive tracks were visible on the sediment surface (Craig 1989). Growth rates were calculated for both experiments as follows:

$$\text{growth rate} = \frac{\text{final shell length (mm)} - \text{initial shell length (mm)}}{\text{time (d)}}$$

Growth Expt 1: Growth Expt 1 ran from July 22 to September 22, 1986 (60 d). The objectives of this experiment were to determine growth rates for *Nucula annulata* during the late summer–early fall and to examine the effect of short-term exposure to conditions associated with nutrient enrichment on shell growth. Approximately 15 *N. annulata* were marked, measured and placed in enclosures in 3 mesocosms, preventing loss of marked clams to the surrounding sediment. Of the 3 mesocosms, 1 served as an unenriched control while the 2 remaining mesocosms had received daily additions of nitrogen, phosphorus and silica corresponding to 8 times (8×) the average daily areal (m^2) input of inorganic nutrients from sewage into Narragansett Bay for 1 yr prior to the start of Growth Expt 1. The mesocosms used in Growth Expt 1 were a part of a larger 1 yr experiment examining interactions between silica, the benthos and eutrophication. Details and results of this experiment can be found in Doering (1989) and Doering et al. (1989a, b). Clams were added to the mesocosms on July 22 and recovered by divers on September 22. Sediment was sieved through a 1 mm sieve and marked clams were sorted from material retained on the sieve and measured. There were no significant differences between 8× treatments and the control so data were pooled for analysis.

Growth Expt 2: The objectives of Growth Expt 2 were to determine (1) the onset of spring growth and (2) growth rates for *Nucula annulata* during the spring and early summer, the expected season of maximum growth. Growth Expt 2 was conducted from March to July 1987 (120 d). The experimental set-up for Expt 2 consisted of a 400 l tank containing sediment collected from Stn 1. The system was attached to a flow-through seawater line and continuously mixed. Temperature was monitored daily and maintained within 2 °C of ambient bay water for the duration of the experiment. Marked clams were added to the system in groups of about 25 on 4 separate dates (Days 1, 22, 48 & 80) by placing them on the sediment surface and allowing them to burrow into the sediment. The experiment ended on Day 120, July 5, 1987. The sediment was sieved through a 1 mm sieve and marked clams were sorted from material retained on the sieve and measured.

Integrated growth temperatures–oxygen isotope analysis. Several recent studies have shown that the isotopic composition recorded in the shells of marine molluscs can provide information on life history and the environment in which shell growth took place (Jones et al. 1983, Krantz et al. 1987, Allard 1988). Molluscs construct their shells out of calcium carbonate as either calcite or aragonite or a combination of both. During this process calcium carbonate becomes enriched in ^{18}O over the ^{16}O by about 3% compared to ambient seawater. The degree of fractionation is dependent on the temperature of the water in which the shell is being accreted. Carbonate $\delta^{18}O$ values increase with decreasing temperature. Variations in the $\delta^{18}O$ content of growth bands can be used to determine seasonality and the temperature of maximum growth (an integrated measure of the temperature over which the animal was growing most rapidly) (Williams et al. 1982, Arthur et al. 1983, Jones et al. 1983, Allard 1988, Krantz et al. 1988). The $\delta^{18}O$ values from shell deposited by clams during Growth Expt 2 were measured and converted to temperature values (°C) to verify that *Nucula annulata* does accrete shell at or near isotopic equilibrium with overlying waters. $\delta^{18}O$ values were converted to temperature values using Grossman & Ku's (1986) equation for biogenic aragonite (Eq. 3: for molluscs only):

$$T\ (°C) = 21.8 - 4.69 \times (\delta^{18}O_{aragonite} - \delta^{18}O_{water})$$

where $\delta^{18}O_{aragonite} = [(^{18}O/^{16}O)_{sample} - (^{18}O/^{16}O)_{std}] / (^{18}O/^{16}O)_{std} \times 1000$. The $\delta^{18}O_{water}$ was estimated using Fairbanks' (1982) salinity (S‰) to $\delta^{18}O_{water}$ relationship following Allard (1988): $\delta^{18}O_{water} = 0.258 \times (S‰) - 9.14$. Salinity was monitored weekly during the experiment.

The $\delta^{18}O$ content of shell-margin samples of clams from the 2 field stations was measured to determine season of growth relative to season of collection. Additional information of the growth history of *Nucula annulata* was obtained by sequential sampling of growth bands within the shell of individuals from Stns 1 & 2 (length = 3.1 mm).

Preparation of samples for mass spectrometer analysis was similar to procedures used by Jones et al. (1983). The periostracum and other debris were carefully removed from shells. Carbonate samples were collected by drilling off individual growth bands using a Dremel drill. It was necessary to grind away the entire growth band on both valves of an individual to obtain sufficient material for analysis. Samples were roasted at 400°C under vacuum for 1 h and then reacted in 100% orthophosphoric acid at 50°C. The resultant CO_2 gas was analyzed on a V. G. Micromass 602-D isotope ratio mass spectrometer. The $\delta^{18}O$ values are reported in the standard delta (δ) notation relative to PeeDee Belemite (PDB) reference standard. The analytical precision of the oxygen isotope data was ± 0.1‰.

Nutrient gradient experiment. The effect of long-term exposure to elevated nutrient concentrations on the growth of *Nucula annulata* was assessed as a part of a larger 2.3 yr experiment examining the impact of eutrophication on a coupled benthic-pelagic system (Jun 1981 to Sep 1983) (Nixon et al. 1984, 1986, Kelly et al. 1985, Oviatt et al. 1986, Widom & Elmgren 1988, Sampou & Oviatt 1991). The nutrient gradient experiment was conducted in the large outdoor experimental mesocosms at MERL. The experimental gradient consisted of 6 mesocosms receiving different levels of nutrient loading along a geometric sequence from 1× to 32×. The range in nitrogen input corresponds to the range of nutrient loadings found in natural systems (Nixon et al. 1986). The lowest level of nutrient loading, the 1× treatment (7.57 N, 0.591 P, 0.54 Si mmol $tank^{-1}$ d^{-1}) is the estimated average daily areal input of dissolved inorganic nutrients into Narragansett Bay from sewage and runoff. The 32× level is similar to the level of loading in the heavily impacted lower Hudson River estuary. Solutions of NH_4Cl, $KHPO_4$ and $NaSiO_3 \cdot 9H_2O$ were added to each treatment daily in the molar ratio characteristic of sewage entering Narragansett Bay over an annual cycle (12.8 N : 1.00 P : 0.91 Si) (Nixon et al. 1984, 1986). Data on the size and abundance of macrofauna were collected bimonthly and processed following procedures outlined in Lambert & Oviatt (1986). At the end of the experiment, the sediment from each mesocosm was sieved through a 3.1 mm sieve and large macrofauna were identified and enumerated (Frithsen et al. 1985b). Shell length (anterior to posterior margin) and axis of growth (maximum dimension between the umbo and growing edge of the shell) of 100 clams from 2 unenriched controls and the 4×, 8×, 16× and 32× nutrient treatments were measured using a stereo microscope (± 20 µm). The outcome of statistical analyses was the same for both measurements so only the length data is presented. Additional results from the nutrient gradient experiment were presented by Nixon et al. (1984), Frithsen et al. (1985a, b), Kelly et al. (1985), Oviatt et al. (1986) and Sampou & Oviatt (1991).

Statistical analysis. Observed differences in size, abundance and isotopic content of *Nucula annulata* were assessed using analysis of variance and the Student-Newman-Keuls (SNK) test. Significance levels of the tests were 0.05 unless otherwise noted.

RESULTS

Growth experiments

In Expt 1, July 22 to September 22, 1986, there were no significant differences in shell growth between clams in the control and in the two 8× nutrient treatments; so data from the treatments were pooled (Table 1). *Nucula annulata* deposited an average of 188 µm ± 118 µm (SD) of shell over the 60 d of the experiment (Table 1). Short-term (60 d) exposure to eutrophic conditions in Growth Expt 1 had no apparent effect on shell growth in *N. annulata*.

In Growth Expt 2, differences in total shell accumulation and in growth rates were used to determine the approximate start date of spring growth. Clams added prior to the onset of fast growth would have the highest total accumulation of shell but the lowest growth rates. Clams introduced after initiation of growth would have higher growth rates but a lower total accumulation of shell. As seen in Table 1, Groups 1 through 3 (those added between March and late April) deposited 331 ± 128 (SD), 370 ± 154 and 397 ± 127 µm of shell respectively. Length differences between these groups were not significant. Individuals from Group 4 (added on May 26) deposited on average only 240 ± 93 µm of shell, suggesting that the onset of fast spring growth had already occurred by the time Group 4 clams were added to the experiment. Differences in growth rates also suggest a similar timing of events. *Nucula annulata* from Groups 3 & 4 grew an average of 5.1 ± 1.6 and 6 ± 2.3 µm d^{-1} whereas Group 1 & 2 clams grew at comparatively slower rates of only 2.8 ± 1.1 and

Table 1. *Nucula annulata*. Data from Growth Expts 1 & 2. Means with the same letter are not significantly different from each other as judged by the SNK test

Expt	Treatment	Dates	Duration (d)	n	Change in length (μm ± SD)	Growth rate (μm d^{-1} ± SD)
1	Control	Jul 22–Sep 22, 1986	60	11	207 ± 76 (A)	3.5 ± 1.3 (A)
	8×, a	Jul 22–Sep 22, 1986	60	13	224 ± 142 (A)	3.5 ± 2.2 (A)
	8×, b	Jul 22–Sep 22, 1986	60	11	137 ± 116 (A)	2.1 ± 1.8 (A)
2	Group 1	Mar 5–Jul 5, 1987	120	26	331 ± 128 (B)	2.8 ± 1.1 (B)
	Group 2	Mar 28–Jul 5, 1987	98	21	370 ± 154 (B)	3.6 ± 1.5 (B)
	Group 3	Apr 28–Jul 5, 1987	72	25	397 ± 127 (B)	5.1 ± 1.6 (C)
	Group 4	May 26–Jul 5, 1987	40	28	240 ± 93 (C)	6.0 ± 2.3 (C)

3.6 ± 1.5 μm d^{-1} (Table 1). Initiation of shell growth occurred in early May at water temperatures between 8 and 10 °C (Fig. 2). *N. annulata* deposited on average 357 ± 22 μm of shell during the experiment. The amount of shell deposited was not dependent on the initial length of clams over the size range used in the experiment (1.5 to 3 mm) (Craig 1989).

The results of these 2 experiment indicate that measurable shell growth occurs in both the late spring (357 ± 22 μm) and in the late summer–early fall (188 ± 118 μm). While experimental set-ups were not identical, differences were not thought to significantly affect the results. The addition of marked clams represented < 1 % of the population of *Nucula annulata* in the mesocosms of Expt 1 and < 4 % of the population in Expt 2 (Doering 1989a, Craig unpubl.). *N. annulata* used in both experiments were similar in size (Craig 1989). Molluscs and sediment were collected from Stn 1 for both experiments. During the 180 calendar days covered by Expts 1 & 2, *N. annulata* deposited approximately 545 μm of shell (357 + 188 = 545 μm). If *N. annulata* only deposited shell during the time of year covered by these 2 experiments than this value could be used as a estimate of yearly shell growth. It seems more reasonable however, to use 545 μm as a minimum estimate of yearly shell growth. An upper limit of 0.9 mm yr^{-1} was calculated assuming that clams grew 6 μm d^{-1}, the fastest growth rate from Expt 2, and that clams deposited shell between 10 and 20 °C. The lower limit of 10 °C was chosen based on results from Growth Expt 2; 20 °C was chosen as an upper limit because *N. annulata* spawns in the summer at 22 °C, and it is likely that some reallocation of resources towards reproduction occurs in the weeks leading up to spawning (Ritacco 1980). Narragansett Bay waters fall within the 10 to 20 °C range approximately 5 mo of the year (Frithsen et al. 1985a). Based on these assumptions, *N. annulata* may grow as much as 0.9 mm yr^{-1}.

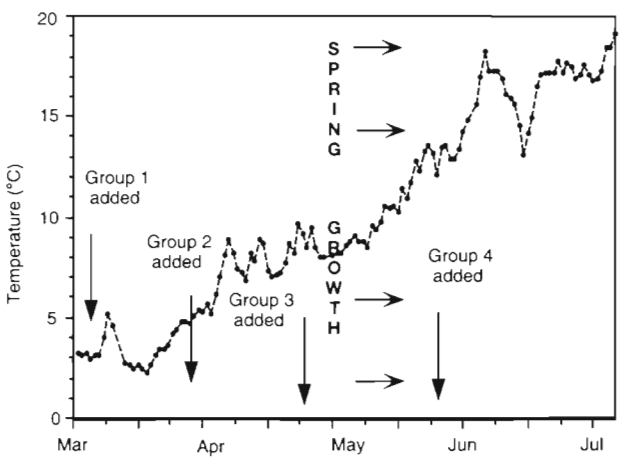

Fig. 2. Measured water temperature over the course of Growth Expt 2 in 1987, showing dates of additions and the approximate start of spring growth

Integrated growth temperatures ($\delta^{18}O$ values)

The $\delta^{18}O$ values of shell deposited by clams during Growth Expt 2 provides an integrated measure of the temperature over which the clams were growing most rapidly. Differences between groups were not significant and clams recorded comparable $\delta^{18}O$ values regardless of when they were added to the experiment. The mean $\delta^{18}O$ temperatures for each group fell between 15 and 19 °C with an average value of 17.1 ± 1.3 °C. Growth temperatures were not significantly different from the average water temperature (16.6 ± 0.3 °C) during the time in which shell growth was thought to have occurred (Fig. 3). *Nucula annulata* appears to accrete shell in or near isotopic equilibrium with overlying waters.

Population dynamics – Stn 1 vs Stn 2

Clams at Stn 2 were over 1 mm larger, but an order of magnitude less abundant than those at undisturbed

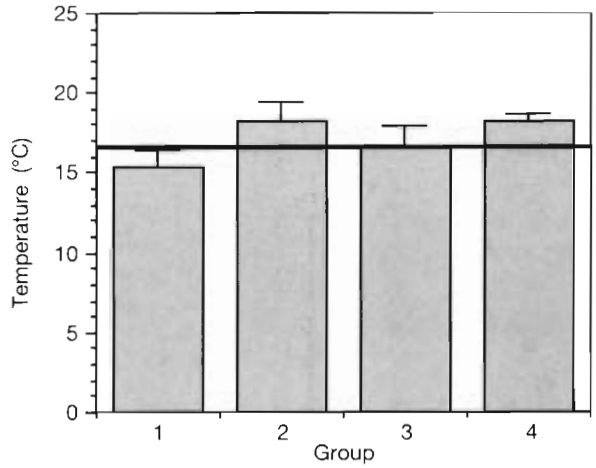

Fig. 3. *Nucula annulata*. Mean (+ SD) $\delta^{18}O$ growth temperatures of Groups 1 through 4 from Growth Expt 2. Values were not significantly different from the average water temperature (16.6 ± 0.3 °C, solid line) during the period April 28 to July 5, 1987, when shell deposition is thought to have occurred; see Table 1. Mean $\delta^{18}O$ growth temperature of all 4 groups: 17.1 ± 1.3 °C

Stn 1 (Fig. 4a, b). The population at Stn 1 maintained a mean density of 6728 ± 720 ind. m^{-2} with an average length of 1.42 ± 0.06 mm. Mean shell length of *Nucula annulata* at Stn 2 (enriched site) was 3.11 ± 0.29 mm with an average population density of 720 ± 528 ind. m^{-2}. Analysis of log-transformed abundance data indicate that differences between stations were significant on all sample dates. Differences in mean size of *N. annulata* between the 2 stations were also significant on 4 out of 5 of the dates sampled.

An attempt to identify age classes using length-frequency distributions yielded ambiguous results. Stn 1 data did not show any clear patterns in age distribution over the sampling period, and low densities of *Nucula annulata* at Stn 2 precluded any detailed assessment of the population structure in that area, so data from all 5 sample dates for each station were pooled (Fig. 5). Small clams (<1 mm) accounted for approximately 50% of the total population of *N. annulata* at Stn 1 while at Stn 2 this group represented less than 20% of the total number of clams found there. Individuals >3 mm accounted for only 10% of the Stn 1 population while this fraction represented approximately 50% of the clams at Stn 2.

Season of maximum growth – Stn 1 vs Stn 2

The purpose behind measuring the $\delta^{18}O$ composition of the newest growth band deposited by clams was to

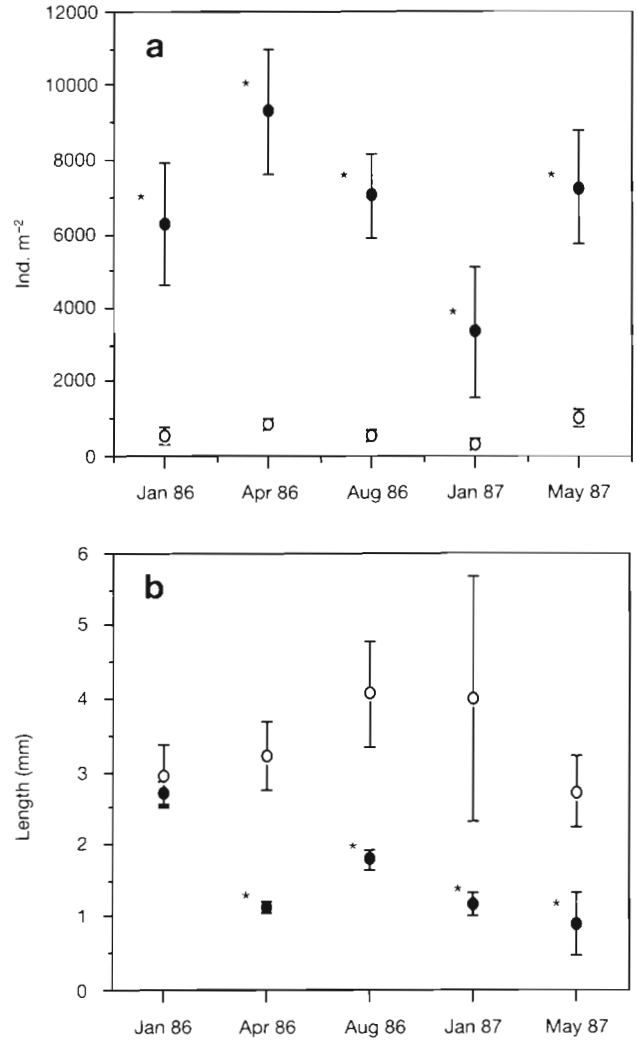

Fig. 4. *Nucula annulata*. Average (± SE) (a) densities and (b) lengths of clams collected at (●) Stn 1 and (○) Stn 2. (★) Dates on which differences between stations were significant (SNK test)

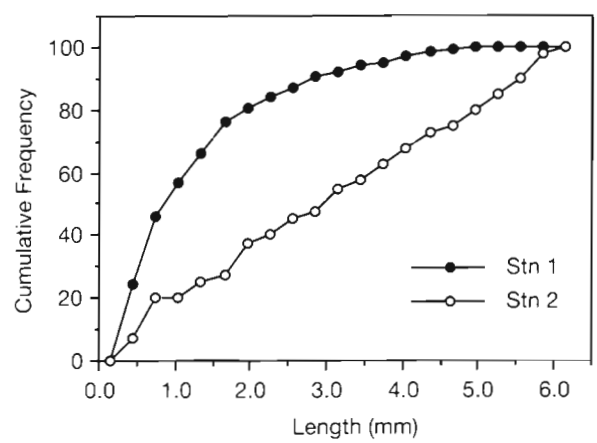

Fig. 5. *Nucula annulata*. Cumulative frequency distribution of pooled length data from Stns 1 & 2

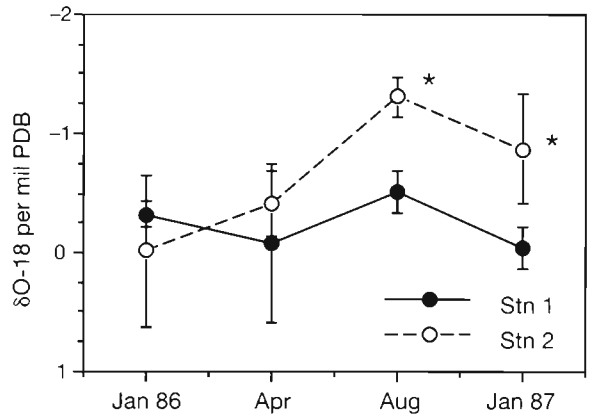

Fig. 6. *Nucula annulata*. Mean (± SD) $\delta^{18}O$ values (relative to PDB) of shell-margin samples collected on a seasonal basis from Stns 1 & 2, January 1986 to January 1987. (*) Dates when between-station differences were significant

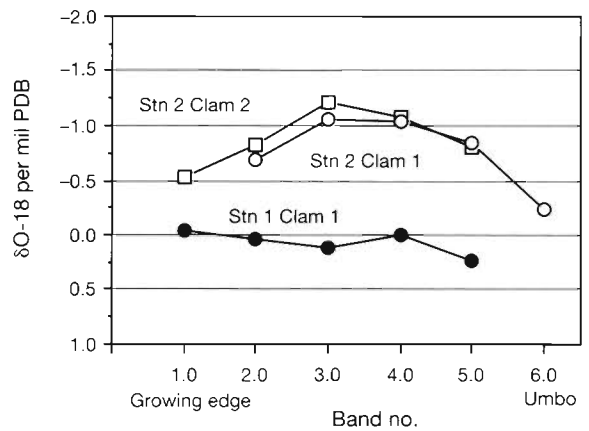

Fig. 7. *Nucula annulata*. $\delta^{18}O$ values (relative to PDB) from individual growth bands within shells collected from Stns 1 & 2 in May 1987. Differences within stations were not significant; differences between stations were significant

determine if growth was synchronous at the 2 field sites. Between-site differences were significant on 2 of 4 sample dates, August 1986 and January 1987 (Fig. 6). The lighter $\delta^{18}O$ values indicate Stn 2 individuals deposited more shell at warmer temperatures, relative to Stn 1 clams. The $\delta^{18}O$ values from Stn 1 ranged from −0.78‰ to + 1.11‰, with a mean value of −0.21 ± 0.41‰ (SD). Stn 2 values ranged from −1.40 to +1.02‰ with a mean of −0.57 ± 0.69‰. Serial sampling of growth bands within the shells of individual clams also indicated that there was a shift in the season of maximum growth from spring to summer in Stn 2 clams (Fig. 7). $\delta^{18}O$ values from Stn 2 shell growth bands were consistently depleted relative to Stn 1 (−0.92 ± 0.42‰ vs 0.07 ± 0.11‰).

Nutrient gradient experiment

An examination of the abundance of juvenile *Nucula annulata* (<1 mm) showed that numbers of small clams declined over the 3 summers of the experiment as a consequence of conditions associated with nutrient enrichment in the MERL mesocosms (Fig. 8). Mean densities of *N. annulata* (<1 mm) were comparable in the controls and nutrient treatments during the first 2

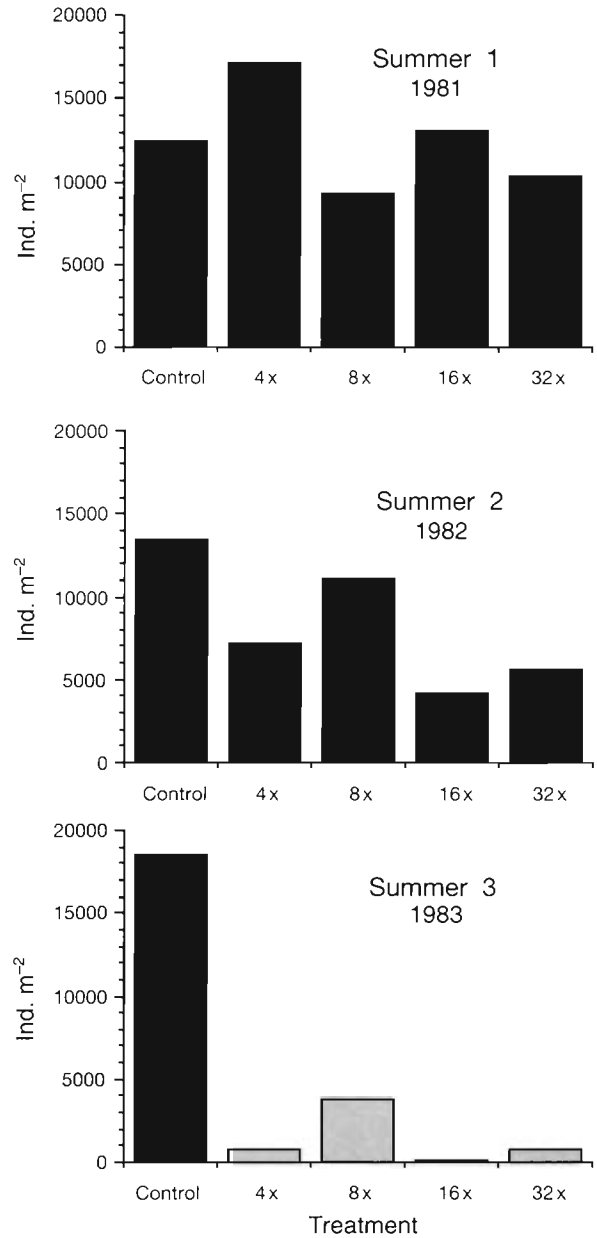

Fig. 8. *Nucula annulata*. Average densities of juveniles (i.e. clams <1 mm in length) for the 3 summers of the nutrient gradient experiment (1981 to 1983). Bars with the same shading are not statistically different

Table 2. *Nucula annulata*. Mean lengths and relative growth rates of clams collected at the end of the nutrient gradient experiment, September 1983. Means with the same letter are not significantly different from each other

Treatment	Average length (mm ± 95% CI)	Relative growth rates (mm yr^{-1})
Control	3.85 ± 0.07 (A)	0
4×	4.01 ± 0.09 (A)	0.07
8×	4.95 ± 0.12 (B)	0.49
16×	5.15 ± 0.12 (B)	0.58
32×	5.67 ± 0.16 (C)	0.81

summers of the nutrient gradient experiment (1981–1982). However, by the third and final summer of the experiment (1983) the average abundance of small *N. annulata* (<1 mm) in the nutrient treatments was significantly less than what was found in the control during that summer and the nutrient treatments during the previous 2 summers. Initial abundances of *Nucula annulata* in all treatments ranged from 9200 to 17 200 ind. m^{-2}. By the third summer of the experiment densities of juvenile *N. annulata* had dropped to 98 ± 98 and 789 ± 394 ind. m^{-2} in the 16× and 32× treatments respectively. The mean density of small *N. annulata* in the controls did not vary significantly between the 3 summers of the experiment.

An inventory of *Nucula annulata* collected on a 3.1 mm sieve at the end of the experiment revealed a trend of increasing length with increased levels of nutrient loading (Table 2). *N. annulata* in the controls and 4× treatment were approximately 4.0 mm in length. Clams in the 8× and 16× treatments were about 1 mm larger, at 4.95 ± 0.12 and 5.15 ± 0.12 mm respectively. The 32× treatment contained the largest *N. annulata*, averaging 5.7 ± 0.08 mm in length. The data suggest either enhanced survivorship of older and therefore larger animals, or an accelerated growth rate due to some factor associated with nutrient enrichment (i.e. changing densities as it effects competition for food, space and oxygen). Relative growth rates of *N. annulata* in the 3 highest nutrient treatments indicate that clams in these treatments would have had to deposit an additional 0.5 to 0.8 mm of shell yr^{-1} relative to the controls to reach the observed sizes found in those treatments at the end of the experiment (Table 2).

DISCUSSION

Changes in the availability of resources or shifting environmental conditions can enhance the survivorship of one species while bringing about the decline of another species. The purpose of this study was to examine how the shifting mosaic of interactions associated with nutrient enrichment impacted on the growth and population structure of *Nucula annulata*. Nutrient enrichment was chosen as the specific perturbation in this study because it is a common problem in many coastal environments.

Growth in unstressed environments

Growth experiments and analysis of the oxygen isotopic composition of growth bands were carried out to determine growth rates and seasonality of shell growth in *Nucula annulata* from an unenriched site in Narragansett Bay. Results from 2 growth experiments showed that significant shell growth occurred in the late spring through early fall with initiation of rapid growth at approximately 10 °C in the spring (Table 1). $\delta^{18}O$ growth temperatures indicate that clams in Expt 2 grew most rapidly between 15 and 19 °C (Fig. 3).

The $\delta^{18}O$ content of shell margin bands from Stn 1 clams (the unenriched site) collected between January 1986 and May 1987 provided a means of checking on the seasonality of shell growth in the field. $\delta^{18}O$ values varied between −0.78 to +1.1‰ with a mean value of −0.21‰ and a total range of 1.88‰ (Craig 1989). Allard (1988) predicted that molluscs precipitating aragonite shell year round in Narragansett Bay would record $\delta^{18}O$ values between −1.0 to + 4.0‰ with the total range equal to 4.8‰. *Nucula annulata* recorded $\delta^{18}O$ values over a much smaller range that was skewed towards the more negative end of the scale (warmer temperatures). Both Growth Expt 2 and the oxygen isotope data show that *N. annulata* does not deposit significant amounts of shell during the colder winter months. A slowdown or cessation of activity during winter appears to be a consistent characteristic of *Nucula* species. Cheng & Lopez (1991) noted that *N. proxima* stopped feeding at temperatures below 6 °C. Rachor & Salzwedel (1975) and Rachor (1976) found that for *N. nitidosa*, growth was faster in the summer and slowed down during the winter months. Metabolic studies of *N. proxima* in Long Island Sound showed that maximum growth occurred when respiration was highest around 14 °C and noted a drop in respiration at temperatures below 10 °C (winter) and greater than 19 °C (August–September) (Carey 1962). A drop in metabolic activity during warmer temperatures has been correlated with spawning in *Nucula* species (Carey 1962, Ansell 1974, Rachor 1976, Ansell et al. 1978, Ritacco 1980).

Combining the average change in shell length of animals from the 2 growth experiments gives a minimum estimate of 0.55 mm of shell growth yr^{-1}. An upper limit of 0.9 mm yr^{-1} was calculated assuming

that clams grew 6 µm d^{-1}, the fastest growth rate from Expt 2, and that clams deposited shell between 10 and 20°C. Narragansett Bay waters fall within that range approximately 5 mo of the year (Frithsen et al. 1985a). Shell growth during the warmest part of the summer was thought to be somewhat limited because the major spawning effort of *N. annulata* usually coincides with the warmest part of the summer, ~22°C in Narragansett Bay (Ritacco 1980). It is likely that some reallocation of energy from shell growth towards reproduction is occurring during the time leading up to spawning because of the high energetic costs associated with lecithotrophic larval development in *Nucula* species (i.e. high lipid content and large size of the egg) (Rachor 1976, Ritacco 1980, Davis & Wilson 1985). Studies by Rachor (1976) and Trevallion (1965) as cited by Davis & Wilson (1985) estimated that 50% of total production was allocated to reproductive output in *N. nitidosa* and *N. sulcata*.

The 0.55 to 0.9 mm yr^{-1} estimate from this study falls within the range of literature estimates of growth rates for *Nucula* species (Table 3). Allen (1953, 1954) identified distinct age classes from length-frequency histograms for 5 British species of *Nucula* and reported growth rates of 0.94 to 1.01 mm yr^{-1} regardless of species or age. Blake & Jeffries (1971) reported somewhat higher growth rates of 2 mm yr^{-1} for *N. proxima*, between 1 and 4 mm in length and 1 mm yr^{-1} for larger clams (>5 mm), again based on frequency distributions. Rachor (1976) estimated that *N. nitidosa* had an annual growth rate of 3.5 mm yr^{-1} during Year 1 while older clams grew more slowly at a rate of 1 mm or less yr^{-1}. Both Blake & Jeffries (1971) and Rachor (1976) found a difference in growth rates based on size and presumably age of the animals. In Growth Expt 2 there was no discernible relationship between the amount of shell deposited and the shell length of the clams used in the experiment (Craig 1989). Clams ranged in size from 1.5 to 3.15 mm. Sanders (1956) estimated that *N. proxima* in Long Island Sound grew at a rate of 0.57 to 0.63 mm yr^{-1}. Carey (1962) calculated a lower rate of 0.38 mm yr^{-1}. Both Long Island Sound estimates were based on ring counts. Values obtained by both Sanders (1956) and Carey (1962) for *N. proxima* are fairly close to estimates made in this study for *N. annulata*. It is possible that they were looking at *N. annulata* and not *N. proxima*. A distinction between the 2 species was not made until Hampson (1971). Both species are found in Long Island Sound with *N. annulata* more common in muddy areas while *N. proxima* is usually found at sandier sites (Hampson 1971, Levinton 1972).

Effects of nutrient enrichment on growth and population structure

To assess the impact of short-term exposure to conditions typical of nutrient-enriched environs, *Nucula annulata* were placed in MERL mesocosms which had been receiving daily additions of nutrients for 1 yr prior to the start of Growth Expt 1. *N. annulata* did not show a significant growth response to enrichment. Mean shell growth rates of *Nucula annulata* in both 8× treatments were not significantly different from the control (Table 1). Clams in the nutrient treatments did not 'grow faster' than those in the control. *N. annulata* does not appear to be sensitive to increases in the production of organic matter as a consequence of enrichment. Grassle et al. (1985) noted that short-term exposure to organic enrichment (3 mo) had no effect

Table 3. *Nucula* spp. Summary of growth rates

Species	Method	Size range (mm)	Growth rate (mm yr^{-1})	Source
N. turgida	Frequency distributions	–	0.94	Allen (1954)
N. tenuis			0.96	
N. hanleyi			1.01	
N. sulcata			0.96	
N. nucleus			0.94	
N. proxima[a]	Ring counts	–	0.57–0.63	Sanders (1956)
N. proxima[a]	Ring counts	1.54[b]	0.38	Carey (1962)
N. proxima	Frequency distributions	1–4 5	2 1	Blake & Jeffries (1971)
N. nitidosa	Growth experiments and frequency distributions	up to 9	3.5 mm in Year 1 ≤ 1 mm in Years >1	Rachor (1976)
N. annulata	Mark-recovery experiments	1.5–3.15	0.55–0.9	This study

[a]Species may be *N. annulata* rather than *N. proxima*
[b]Mean shell length

on recruitment of *N. annulata*. Densities did not vary between controls and treatments receiving organic additions. Clams were similarly unresponsive when exposed to sewage sludge (Maughan 1986). The lack of a positive response in terms of shell growth and density has been suggested to be in part due to limited availability of organic matter to a subsurface deposit feeder like *N. annulata* (Grassle et al. 1985, Maughan 1986). Wilson & Shelley (1986) also found that there was no clear pattern of distribution of *N. turgida* in relationship with organic content of the sediment over the range of 0 to 2.14% organic matter.

Nucula annulata does show 2 population level responses to long-term exposure to enrichment. First, the low numbers of small *N. annulata* found in the nutrient treatments in the gradient experiment and the overall low densities found in the field suggest that reproduction and/or recruitment were adversely affected by conditions associated with nutrient enrichment (Figs. 4a & 8). Secondly, the percentage of the population greater than 3 mm in length increased in enriched environments (Fig. 5, Table 2). Carey (1962) noted that 99% of the clams from his station in Long Island Sound were lost from the population by the time they reached 3.3 mm in length. Approximately 40% of the population is greater than 3.3 mm at Stn 2 while only 10% of the population is greater than 3.3 mm at Stn 1.

Factors that may influence successful reproduction and/or recruitment include environmentally induced stress, i.e. due to low oxygen conditions or interference in larval settlement due to increases in density of surface feeding species (Rhoads & Young 1970, Ritacco 1980, Maughan 1986, Nixon et al. 1986). Stress in marine molluscs can cause reabsorption of ripe gametes or production of less viable larvae (Sastry 1979, Bayne 1975, Vernberg & Vernberg 1975). Reish & Barnard (1960), as cited by Vernberg & Vernberg (1975), found that *Capitella capitata* did not reproduce at oxygen concentrations less than 3.5 mg l^{-1}. Baker & Mann (1992) noted that larval settlement of juvenile oysters *Crassostrea virginica* was significantly reduced in hypoxic conditions. Rachor (1976) also observed high mortality of juvenile *Nucula nitidosa*, as well as a decrease in maximum size and in growth rates which he attributed in part to suboptimal environmental conditions due to the dumping of sewage sludge in the vicinity of his sample site. Low levels of oxygen were frequently measured in the water columns (< 3.5 mg l^{-1} O_2), of the 8×, 16× and 32× treatments during the second and third summers of the nutrient gradient experiment (Fig. 9). It is likely that sediment oxygen concentrations were even lower and may have resulted in a decline in the reproductive output or recruitment of *N. annulata* (Rachor 1976, Frithsen et al. 1985b, Nixon et al. 1986, Oviatt et al. 1986). Maintenance of populations within the mesocosms is to a large degree dependent on the reproductive success of animals within individual mesocosms because of the relatively short planktonic stage of *N. annulata* (3 d) and the absence any significant populations of *N. annulata* in the vicinity of the seawater intake for the MERL facility (Ritacco 1980). Data from Stn 2 and the nutrient gradient experiment suggest that continued exposure (beyond 2 yr) will first lead to the disappearance of small individuals within a population and eventually result in the complete disappearance of *N. annulata* from the local environment.

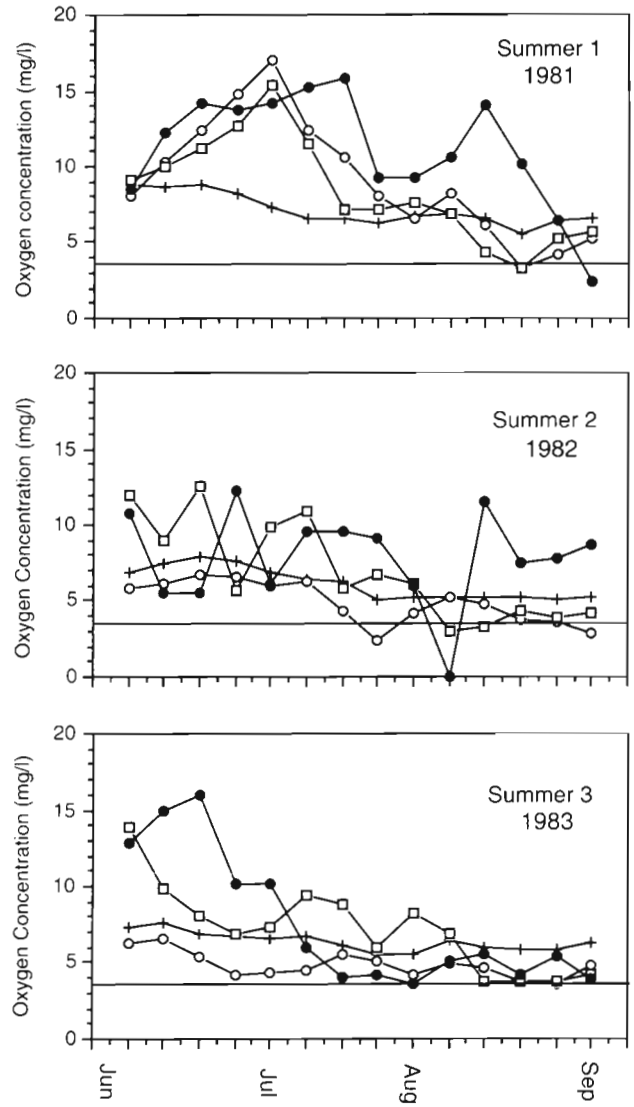

Fig. 9. Weekly water column oxygen concentrations (mg l^{-1}) during the 3 summers (1981-1983) of the nutrient gradient experiment for the (+) control, (○) 8×, (□) 16× and (●) 32× treatments. The horizontal lines indicate 3.5 mg l^{-1} oxygen

The degree to which species interactions impact upon larval settlement is unclear in this experiment since low oxygen concentrations would also adversely affect the survival of many surface feeding species. It is worth noting that *Nucula* species have shown a consistent ability to survive and in some instances remain active in hypoxic/anoxic environments for periods up to several days (Moore 1931, Rachor 1976, Wilson & Davis 1984). *N. annulata* was, in fact, the only bivalve species to persist in the 32× treatment throughout the nutrient gradient experiment (Frithsen et al. 1985b, Nixon et al. 1986). Adult *N. annulata* appear to be able to survive low oxygen conditions but reproduction and/or recruitment may be adversely affected under these conditions.

The second effect of nutrient enrichment was a shift in size of *Nucula annulata* towards large individuals in eutrophic environments (Table 2, Fig. 5). The maximum size *N. annulata* at Stn 1 was 3.54 ± 0.85 mm. The average maximum size of Stn 2 clams was approximately 2 mm larger, 5.56 ± 0.74 mm (Craig 1989). Larger clams found in the eutrophic environments may represent older age classes not seen in unenriched areas or reflect a change in the growth patterns of *N. annulata*, either an accelerated growth rate or a shift and/or extension in the length of the growing season. Data from Growth Expt 1 does not support an increase in growth rates of *N. annulata* when exposed to conditions associated with nutrient enrichment and may in fact result in a decrease in growth rates though differences between treatments were not significant (8×, a vs 8×, b) (Table 1). Sedimentary carbon data from June 1982 to the end of the nutrient gradient experiment (Table 4, modified from Widbom & Elmgren 1988) show that the 32× treatment was the only treatment to have noticeably higher sedimentary carbon values than the average value determined for the controls. The only clear enrichment in carbon of the sediment, and presumably food, occurred in the 32× treatment, yet significant increases in mean lengths of clams collected at the end of the experiment occurred in the 8× and 16× treatments as well (Table 2). The availability of food as indicated by the organic content of the sediment does not appear to be the factor controlling size distribution of *N. annulata* at least in this experiment.

Clams in eutrophic environments may have a slightly extended growing season. The lighter $\delta^{18}O$ values of individuals from Stn 2 indicate warmer growth temperatures relative to Stn 1 clams (Figs. 6 & 7). Allard (1988) noted a similar trend of depleted $\delta^{18}O$ values of *Nucula* from the nutrient gradient experiment (Table 5). But, it is unlikely that summer growth could account for the larger than expected clams found in these environments. The relative growth rates for *N. annulata* in the 8× to 32× treatments from the nutrient gradient experiment indicate that these clams needed to deposit an additional 0.5 to 0.8 mm yr^{-1} of shell for each year of the experiment, relative to controls, in order to reach observed sizes at the end of the experiment (Table 2). Under the best conditions, assuming *Nucula* in the 8× to 32× treatments grew throughout the summer at a growth rate of 6 µm d^{-1} (highest rate

Table 4. *Nucula annulata*. Sedimentary carbon data from the nutrient gradient experiment (June 1982 to September 1983) (from Widbom & Elmgren 1988, Table 1)

Load	Sediment carbon (% of DW)
June 1982	
Control	2.2
4×	2.1
8×	2.3
16×	–
32×	3.1
September 1982	
Control	2.1
4×	1.9
8×	2.2
16×	2.0
32×	–
April 1983	
Control	2.0
4×	2.3
8×	2.5
16×	3.0
32×	3.5
June 1983	
Control	2.3
4×	2.3
8×	2.4
16×	2.7
32×	5.0
September 1983	
Control	2.1
4×	2.2
8×	2.3
16×	2.4
32×	3.7

Table 5. *Nucula annulata*. Isotope data from Stns 1 & 2 (this study) and the nutrient gradient experiment (Allard 1988)

Sample	n	$\delta^{18}O$ (‰ ± 95% CI)
Stn 1	19	−0.21 ± 0.19
Stn 2	13	−0.57 ± 0.36
Control	13	−0.33 ± 0.17
8×	11	−0.57 ± 0.17
16×	12	−0.89 ± 0.16
32×	10	−0.84 ± 0.2

from the second growth experiment), clams would have deposited only an additional 0.36 mm of shell yr^{-1}. This is still not enough to account for individuals found in the 16× and 32× treatments at the end of the experiment and conditions were far from ideal in those treatments given the frequent occurrences of low water column oxygen concentrations in those treatments (Fig. 9).

It is more likely that the larger clams found in the nutrient enriched environments are simply older individuals not typically observed in unenriched areas. Measured growth rates of *Nucula annulata* from unenriched areas ranged from 0.55 to 0.9 mm yr^{-1} which fortuitously approximates the calculated relative growth rates of *N. annulata* from the nutrient treatments, (0.5 to 0.80 mm yr^{-1}). The factors influencing the increased survivorship of the larger, older individuals at Stn 2 and in the nutrient treatments remain unclear but may include a reduction in the numbers of predators such as gastropods, bottom fish and crabs, due to decreased oxygen levels. Wilson (1988) found that older year classes of *Nucula turgida* were selectively preyed on by the boring gastropod *Natica* sp.

There is an apparent strong negative correlation between numbers of ind. m^{-2} and size in eutrophic environments (Fig. 4a, b). However, changes in density are thought to be controlled by factors distinct from those influencing maximum attainable size of individuals within a population in eutrophic environments. The decrease in numbers of clams indicates a negative response to conditions associated with nutrient enrichment – a decline in the reproductive success of populations during major spawning periods, possibly due to low levels of oxygen. The shift in maximum size is though to be a positive effect related to a relaxation in predation on larger individuals and not enhanced growth rates due a decrease in competition for resources. Data indicates the larger clams are simply older individuals not more rapidly growing clams. Rachor (1976) found *Nucula nitidosa* grew more slowly and maximum size decreased under suboptimal conditions and noted other researchers had found larger individuals in populations living under more favorable conditions.

CONCLUSIONS

Nucula annulata grew between 0.55 and 0.9 mm yr^{-1} based on measured changes in shell length and the $\delta^{18}O$ composition of shell growth bands. Significant shell growth occurred during the spring through early fall. Initiation of spring growth occurred in early May with maximum growth occurring between 15 and 19 °C. Growth temperatures based on $\delta^{18}O$ values indicated that clams did not deposit significant amounts of shell during the winter.

Nutrient enrichment appears to influence the growth and reproductive patterns as well as survivorship of this species. Numbers of small clams declined while the maximum attainable size increased with increased levels of nutrient enrichment in both the field and in the nutrient gradient experiment. The oxygen isotope data indicated a shift in the apparent season of maximum growth from spring and fall temperatures to warmer summer values for individuals in nutrient-enhanced environments. The shift in the season of maximum growth taken in conjunction with the low numbers of clams suggest that *Nucula annulata* experienced limited reproductive success during the summer in the nutrient-enriched environments. It is likely than that long-term exposure (on the order of years) would eventually result in the disappearance of *N. annulata* from the affected area. Changing environmental conditions also appear to influence factors impacting upon the survival rate of older, larger individuals in the upper nutrient treatments and Stn 2 in a positive way by increasing survivorship of these larger clams. These older age classes were not frequently observed at Stn 1 or in the unenriched nutrient treatments of the nutrient gradient experiment. The specific factors determining the survivorship of these individuals remain unknown but may involve changes in predation pressures.

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