



The impacts of aquacultured oysters, *Crassostrea virginica* (Gmelin, 1791) on water column nitrogen and sedimentation: results of a mesocosm study

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Abstract

To determine effects of aquacultured oysters *Crassostrea virginica* (Gmelin, 1791) on the overlying water column, a mesocosm study was performed at the Marine Ecosystem Research Laboratory (MERL) from June to October, 2000. The MERL facility is located adjacent to Narragansett Bay and consists of fourteen 13,000-l mesocosm tanks designed to simulate the Bay environmental conditions. Two hundred oysters (≈ 35 mm valve height; nominally filtering about 55 l/day/individual) were placed into three mesocosms, and three mesocosms were maintained without oysters as controls. Experiments were run with varying rates of water exchange in the tanks ranging from 0% to 100% per day (13,000 l/day). Parameters that were measured and compared between the two treatments included chlorophyll-*a*, particulate organic and inorganic matter, sedimentation, nitrate, ammonia, selected phytoplankton species and oyster growth rates. Oysters affected phytoplankton species composition and increased rates of sedimentation. Large diatoms were net sampled, and *Nitzschia striata* was predominant in mesocosms with oysters, while *Skeletonema costatum* dominated the control tanks. Ammonia excretion rates were determined for *C. virginica* using the salicylate–hypochlorite method. Ammonia excretion can be described by the allometric equation $E = 50.65w^{0.699}$ when E is the ammonia excretion rate in $\mu\text{g/h}$, and w is the soft tissue dry weight in grams. Based on rates of ammonia excretion by oysters and observed steady states of ammonia and other forms of inorganic nitrogen in mesocosm tanks, it can be hypothesized

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that ammonia generated by oysters is taken up by rapidly regenerating phytoplankton in the water column.

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1. Introduction

In Narragansett Bay, the number of shellfish aquaculture farms has been growing since 1995 (CRMC, 2001), and the question of environmental impacts has been raised. Inevitably, comparisons are drawn between aquacultural practices and other more established uses of the coastal waters. For example, since pre-industrial times urban and coastal development has nearly doubled nitrogen input and caused excess eutrophication (Nixon, 1997). One suggested solution for mitigating of eutrophication is to increase bivalves in Narragansett Bay through aquaculture (Ulanowicz and Tuttle, 1992; Rice, 2000).

Attention has been focused on historical populations of fisheries resources and the historical ecology of coastal ecosystems (e.g. Jackson et al., 2001). As in other estuaries, the oyster population in Narragansett Bay has changed throughout history. In 1911, there were 20,846 acres leased for cultivating oysters or about one-third of the bottom of Narragansett Bay. The landings at that time were 1,394,983 bushels of oysters and an additional 1,331,192 gallons of oyster meats (Rhode Island Commissioners of Shellfisheries, 1912). Assuming 30 kg/bushel live weight, 33% shucked meat weight to live weight ratio, 4 kg/gallon shucked meats, and 20% dry to shucked weight ratio, the 1911 harvest amounted to 57,825 metric tons live weight, 19,275 metric tons shucked weight or 3855 metric tons dry soft tissue weight sold.

Historical records of Rhode Island's oyster industry can be used to draw inferences about the population structure oysters in the Bay. Oyster recruitment in Narragansett Bay has long been known to be very episodic; even at the time of earliest oyster landing records beginning 1865 the natural sets of oysters in Narragansett Bay were rare. For example, there were two "good" natural sets (1897 and 1898) during the decade of the 1890s (Rhode Island Commissioners of Shellfisheries, 1900), then two more over a decade later in 1910 and 1911 (RI Commissioners of Shellfisheries, 1912). Due to fishing pressure, native oyster reefs were no longer intact, so to sustain the industry seed oysters were brought in from Connecticut, New York, and as far away as Virginia (Rhode Island Commissioners of Shellfisheries, 1908). Laws mandated return of cultch materials back to the Bay. Assuming that it took 3 years for oysters to reach market size on the leases, the average standing crop biomass in 1911 would be about 2.5 times the annual harvest or 144,562 metric tons live weight or about 9637 metric tons soft tissue dry weight. In 1999, only 41.9 metric tons, shucked wet weight, which is equivalent to 8.4 metric tons tissue dry weight, were landed (NMFS, 2002). Of that total, 350,000 oysters or about 0.9 metric tons tissue dry weight was produced by aquaculture (Alves, 2000). Thus, over the course

of the 20th century, there has been over a thousand-fold decrease in the oyster fisheries and oyster populations.

Natural populations of bivalves are known to control phytoplankton blooms, reduce total suspended solids through filter feeding (Cloern, 1982; Officer et al., 1982; Haamer, 1996; Soto and Mena, 1999) and recycle and remove organic nutrients in the water column (Doering and Oviatt, 1986; Rice, 1999). However, there is little information on the impacts aquacultured bivalves have on the environment except for a few studies on mussels and the northern quahog (Dahlback and Gunnarsson, 1981; Kaspar et al., 1985; Mojica and Nelson, 1993; Haamer, 1996; Grant et al., 1995; Kaiser et al., 1996, 1998). In some of these studies, particularly in the case of off-bottom intensive mussel culture in areas with low tidal flushing, the result was bottom hypoxia caused by feces and pseudofeces accumulation on the sediment. The primary purpose of the present study is to evaluate the environmental impacts of bivalve aquaculture on chlorophyll levels, total organic carbon, particulate organic matter, sedimentation rates, phytoplankton species composition, nitrate and ammonia concentrations.

2. Materials and methods

The experiments were conducted at the Marine Ecosystem Research Laboratory (MERL), Narragansett, RI, from late June to early October, 2000 using six 13,000-l mesocosms that simulate the environmental conditions of a shallow, unstratified coastal ecosystem. During the experiment, tank agitators (3 rpm and periodically reversing direction to minimize vortex formation), were used to prevent stratification in the tanks. The mesocosms closely resemble Narragansett Bay with respect to primary production (Oviatt et al., 1981), nutrient concentration and dynamics (Pilson et al., 1980), temperature and mixing (Nixon et al., 1980) and phytoplankton population structure (Vargo et al., 1982), so they provide a good means for conducting well-constrained experiments mimicking coastal environments (Sanford, 1997). In the experiment, three mesocosms were stocked with oysters (treatment) and three were not stocked with oysters (control). In the treatment mesocosms, oyster cages (1 × 1 × 1 m wire-mesh with three shelves to hold 61 × 61 × 5 cm, 12-mm mesh plastic mesh bags described by Rheault and Rice, 1995) were stocked with two hundred 35-mm oysters each. With a nominal filtration rate of 55 l/individual/day (based upon average daily filtration rates in Haven and Morales-Alamo, 1970; Riisgard, 1988), population filtration approximates the entire mesocosm volume per day. However, according to Powell et al. (1992), the 55 l/day filtration rates by oysters in the size range we used are in the high range of reported literature values, if we were to use their alternative lower estimate, the oysters may be filtering at about 15 l/individual/day, thus increasing the tank filtration turnover time to about 3 days. Measurements of the longest axis of all oysters were taken weekly with vernier calipers to the nearest millimeter to determine growth. Mortalities were noted. Water quality measurements including dissolved oxygen, temperature and salinity were measured (usually at 9:00 AM) 3 to 5 times per week with an YSI Environmental Monitoring System 610-D. Walls of the tanks were cleaned twice per week with an apparatus that had scrub pads attached to a hoist. This helped to remove any fouling that had occurred.

Comparisons made between treatment and control mesocosms at different water exchange rates. The parameters measured were chlorophyll, particulate organic matter (POM), particulate inorganic matter (PIM), ammonia, nitrate, sedimentation rate, phytoplankton species composition and total particulate matter. Chlorophyll-*a* samples were taken twice a week, 3 times a day at 6 AM, 11 AM and 4 PM from each of the tanks. Chlorophyll was determined by fluorometry after extraction in acetone (Yentsch and Menzel, 1963) and read on a Turner Designs Model 10 Fluorometer. To determine PIM and POM, triplicate 1-l seston samples from the water column were taken twice a week, were filtered on to a pre-weighed, pre-combusted (450 °C) glass fiber filter (Whatman GF/C) and rinsed with 500 mM ammonium formate. This was dried at 60 °C for 48 h and then weighed to the nearest milligram. The filter was then ashed in a muffle furnace at 450 °C for at least 2 h (Conover, 1966). To determine sedimentation rates, two sedimentation traps (20 cm² collection area, 10 cm in height) were lowered to the bottom of each tank alongside the oyster cages or in the center of control tanks for 24 h and the samples collected on a filter, ammonium formate rinsed, and ashed. Total particulate matter residual in the mesocosm tanks was determined at the end of the experiment. Tanks were drained to 0.5 m and were stirred manually with a canoe paddle until a homogenous mixture was formed, then the tanks were sub-sampled. The total volume was determined and three sub-samples (3 l each) were taken manually and filtered on to a 20- μ m nylon filter. The particulate matter was rinsed in 500 mM ammonium formate, then placed in an aluminum container dried at 100 °C overnight, dry weights taken, and the samples were ashed at 450 °C according to methods of Gross (1972).

Ammonia was sampled weekly at several times per day according to the same schedule as the chlorophyll measurements. Five-milliliter samples were taken in triplicate and analyzed by the salicylate–hypochlorite method (Bower and Holm-Hansen, 1980). Concentrations were determined by plotting the sampled values against a standard dilution series of ammonium sulfate. Nitrate was sampled weekly by using a commercial test kit (LaMotte Chemical, Chestertown, MD, USA), which is a manganese-sulfanilamide reduction technique, that we modified for colorimetric readings to be performed using a Spectronic 20 spectrophotometer at an absorbance wavelength of 560 nm to increase measurement precision. Concentrations of nitrate in test samples were determined by plotting the values against a standard using a dilution series of sodium nitrate, with a coefficient of variance of <5% in the 0.1 to 0.5 mg/l range.

Large cell and chain-forming phytoplankton species composition was determined by quantitative tow sampling from bottom to top of the height of the mesocosms with a 20- μ m mesh phytoplankton net with a 0.13-m diameter opening. One-milliliter sub-samples were taken of the phytoplankton collected from the plankton net collection bottle after it was inverted 150 times and preserved in 1% Utermohl's solution (Smayda and Boleyn, 1966). Triplicate sub-samples of phytoplankton was placed in a Sedgwick Rafter cell and species were identified under a compound microscope using phytoplankton guides and references to known species in Narragansett Bay (Karentz and Smayda, 1984, 1998). The total numbers of large cell and chain forming phytoplankton such as the genera *Skeletonema* and *Nitzschia* were recorded per 1-ml volume.

Flow rates of raw influent water pumped by diaphragm pump (to keep plankton intact and alive) into the mesocosms from the adjacent West Passage of Narragansett Bay were

adjusted weekly to 100% (a complete water exchange or 13,100 l/day) 35–50%, 15–25%, and 0%, or static, with no water exchange. Each flow rate was replicated for at least three continuous weeks (Table 1). The various paired control and treatment experiments were run sequentially at the different flow rates according to the schedule in Table 1.

The different parameter results between treatment tanks and controls were statistically analyzed with *t*-tests to determine significance since only experimental and control tanks at any given water exchange rate were to be compared. Since various flow tests were not run simultaneously, detailed inferences among the various exchange regimes would be tenuous, thus more detailed ANOVA analyses are not reported. The data was sorted and compiled using Microsoft Excel and was analyzed using SPSS (Chicago, IL, USA) version 10.0 statistical package software for Microsoft Windows.

Baseline ammonia excretion rates by *Crassostrea virginica* were determined in the lab to update measurements from past studies (Srna and Baggaley, 1976; Hammen et al., 1966) with the more sensitive salicylate–hypochlorite method (Bower and Holm-Hansen, 1980). The newer method was used for ammonia monitoring in the mesocosms. Excretion rates were measured by determining an hourly rate rather than a daily rate to minimize ammonia being lost from the experimental vessel by volatilizing, chemical transformation or metabolic product interference from bacteria in the test vessels. Thirty variously sized oysters ranging from 1.3 to 5.5 g dry tissue weight (approximately 25 to 80 mm valve height) were placed individually into aerated fresh 1- μ m filtered seawater in 2-l static plastic containers after being starved for 24 h. Plastic containers without oysters but holding an equal volume of aerated filtered seawater served as the controls. Temperature, pH, and salinity were monitored (and deviated little from 21 °C, 27 ppt, 7.8 pH), as they are important determinants of speciation between dissolved volatile ammonia and the ammonium ion (Emerson et al., 1975). Samples (5 ml each) were read on a Milton Roy Spectronic 20+ spectrophotometer at a wavelength of 640 nm, calibrated with an ammonium formate standard to determine the total ammonia nitrogen (TAN = NH₃-N).

Table 1
Schedule of different flow rates throughout the experimental mesocosms during the summer/fall of 2000

Flow rates (%)	l/day	Dates
100	13,000	July 5th–July 12th July 12th–July 19th July 19th–July 26th July 26th–August 4th
35–50	4500–6500	September 8th–September 16th September 16th–September 22nd September 29th–October 6th
15–25	1950–3250	August 4th–August 11th September 1st–September 8th September 22nd–September 29th
0	0	August 11th–August 18th August 18th–August 25th August 25th–September 1st

Raw seawater was pumped into mesocosm tanks from the adjacent West Passage of Narragansett Bay at the daily exchange rates indicated.

Table 2

Means and standard errors of the mean of treatments (three tanks each) with and without oysters and their *P*-values for parameters including nitrate, chlorophyll, ammonia, particulate inorganic matter in the water column, particulate organic matter in the water column, as well as total particulate organic matter and total particulate inorganic matter on the tank bottoms at the end of the experiment

Parameters (sampling frequency)	Mean \pm SEM (<i>n</i>) with oysters	Mean \pm SEM (<i>n</i>) without oysters	<i>P</i> -value
Nitrate (weekly)	mg/l	mg/l	
100% Flow rate	0.65 \pm 0.11 (19)	0.56 \pm 0.10 (19)	0.595
35–50% Flow rate	0.36 \pm 0.07 (7)	0.50 \pm 0.13 (7)	0.391
15–25% Flow rate	0.69 \pm 0.18 (7)	0.64 \pm 0.15 (7)	0.916
0% Flow rate	0.85 \pm 0.17 (9)	0.82 \pm 0.16 (9)	0.950
Chlorophyll (semi-weekly)	μ g/l	μ g/l	
100% Flow rate			
6 AM	4.61 \pm 0.56 (27)	5.60 \pm 0.63 (27)	0.150
11 AM	4.93 \pm 0.41 (27)	6.22 \pm 0.78 (27)	0.190
4 PM	6.85 \pm 0.78 (24)	7.62 \pm 0.70 (24)	0.575
35–50% Flow rate			
6 AM	19.89 \pm 5.28 (18)	10.68 \pm 2.77 (18)	0.373
11 AM	11.46 \pm 2.40 (15)	22.16 \pm 9.59 (15)	0.775
4 PM	5.69 \pm 1.74 (18)	4.33 \pm 0.69 (18)	0.623
15–25% Flow rate			
6 AM	15.80 \pm 4.71 (18)	9.00 \pm 2.86 (18)	0.351
11 AM	18.35 \pm 5.91 (18)	15.41 \pm 5.80 (18)	0.719
4 PM	10.30 \pm 1.99 (18)	6.84 \pm 1.26 (18)	0.168
0% Flow rate			
6 AM	6.91 \pm 3.03 (18)	5.59 \pm 2.10 (18)	0.745
11 AM	5.38 \pm 4.62 (18)	3.37 \pm 3.27 (18)	0.448
4 PM	2.67 \pm 1.48 (18)	2.17 \pm 1.27 (18)	0.608
Ammonia (weekly w/ triplicate samples/tank)	μ g/l	μ g/l	
100% Flow rate	60.32 \pm 6.09 (52)	67.01 \pm 12.21 (52)	0.838
35–50% Flow rate	25.15 \pm 1.33 (27)	33.02 \pm 7.63 (27)	0.585
15–25% Flow rate	39.01 \pm 4.05 (32)	42.23 \pm 4.24 (32)	0.890
0% Flow rate	20.42 \pm 1.49 (32)	20.59 \pm 1.79 (32)	0.924
PIM in water column (semi-weekly in triplicate/tank)	mg/l	mg/l	
100% Flow rate	1.79 \pm 0.22 (27)	1.43 \pm 0.23 (27)	0.318
35–50% Flow rate	2.75 \pm 0.46 (18)	2.20 \pm 0.39 (18)	0.415
15–25% Flow rate	1.73 \pm 0.42 (18)	1.87 \pm 0.51 (18)	0.859
0% Flow rate	2.20 \pm 0.33 (18)	1.90 \pm 0.23 (18)	0.192
POM in water column (semi-weekly in triplicate/tank)	mg/l	mg/l	
100% Flow rate	2.49 \pm 0.34 (27)	2.08 \pm 0.28 (27)	0.181
35–50% Flow rate	1.97 \pm 0.62 (18)	2.23 \pm 0.30 (18)	0.688
15–25% Flow rate	1.73 \pm 0.30 (18)	2.30 \pm 0.44 (18)	0.411
0% Flow rate	1.43 \pm 0.19 (18)	1.43 \pm 0.23 (18)	1.00
Total POM sediment (g) in tanks at end of experiment	1606 \pm 345.9 (3)	1168 \pm 126.9 (3)	0.310
Total PIM sediment (g) in tanks at end of experiment	4526 \pm 728.4 (3)	2574.5 \pm 756.7 (3)	0.138

Data include multiple measures in three individual tanks with time, but when duplicate or triplicate samples were taken per tank, the mean measurement value was used as *n* = 1. All data are *P* > 0.05.

Table 3

Calculations of phytoplankton species found from a plankton tows performed in treatment and control tanks

Average # of phytoplankton species/l volume towed

	Mean <i>Nitzchia</i> <i>striata</i> #	SEM (<i>n</i> = 3)	<i>P</i> -value (<i>t</i> -test)	Mean <i>Skeletonema</i> <i>costatum</i> #	SEM (<i>n</i> = 3)	<i>P</i> -value (<i>t</i> -test)
With oysters	186,500	10,001	0.0002	42,750	1645	0.000017
Without oysters	48,450	4353		343,100	12,229	

Data represent mean of single tows taken from three each experimental and control mesocosm tanks in mid-July, 2000.

The hourly rates of total ammonia appearing over an 8-h period for each oyster were averaged and corrected with the control determinations, and the allometric relationship between dry tissue weight and ammonia excretion was determined.

3. Results

The physical parameters of salinity, temperature and dissolved oxygen showed little variability among all six tanks between late June to early October. The temperature remained near 20 °C (maximum 24 °C) for most of the experiment, but towards the end (early October) it dropped to 16 °C. The salinity stayed between 30 and 30.5 ppt for the months of June, July, August and early September. The salinity started to increase in mid-September and continued to increase into early October up to 31.5 ppt at the end. Dissolved oxygen stayed at saturation, close to 8 mg/l in all six tanks for most of the experiment, but increased in mid-September and early October to 10 mg/l with lower temperatures.

Table 4

Means of treatments with and without oysters and their *P*-values for particulate organic and inorganic matter in sedimentation traps

Parameter	Mean (mg) ± SEM (<i>n</i> = 9) with oysters	Mean (mg) ± SEM (<i>n</i> = 9) without oysters	<i>P</i> -value
<i>Particulate organic matter in 20-cm² sedimentation traps per day</i>			
100% Flow rate	14.1 ± 7.1	19.4 ± 7.5	0.334
35–50% Flow rate	82.9 ± 28.0	9.8 ± 4.0	0.001
15–25% Flow rate	70.3 ± 21.2	9.3 ± 2.5	0.001
0% Flow rate	39.0 ± 23.2	7.4 ± 3.9	0.036
<i>Particulate inorganic matter in 20-cm² sedimentation traps per day</i>			
100% ± Flow rate	6.0 ± 1.9	6.0 ± 0.9	1.0
35–50% Flow rate	24.8 ± 7.1	5.2 ± 2.1	0.001
15–25% Flow rate	18.1 ± 4.4	3.3 ± 0.6	0.001
0% Flow rate	12.0 ± 6.9	3.0 ± 1.9	0.036

Sediment traps (20 cm² in collection area) were placed in mesocosms for a 24-h period during each of the flow regimes (*n* = mean of duplicate determinations).

Table 5

A comparison of particulate organic matter and inorganic matter on the tank bottom (2.5 m²) expressed as g/m²/day of tank bottom between treatments with oysters and controls without oysters by different measurements being at the end of the experiment versus using mean values obtained from 24-h sedimentation traps (20 cm²) at four different flow rates calculated for duration of experiment (June 29 to Oct. 5)

	End of experiment mean ± SEM (n=3) g/m ² /day	Sediment trap mean ± SEM (n=36) g/m ² /day
POM with oysters	6.51 ± 1.41	25.01 ± 3.96
POM without oysters	4.73 ± 0.53	5.30 ± 0.77
PIM with oysters	18.30 ± 2.95	7.23 ± 1.01
PIM without oysters	10.42 ± 3.07	2.26 ± 0.32

The initial mean size of the oysters (34.3 mm ± 3.4 s.d.) from the beginning of the experiment increased to 45.6 mm ± 5.9 at the end, with no statistical differences among the treatment tanks. During the course of the experiments, 30, 30 and 27 oysters out of the initial 200 oysters in each of the respective mesocosm treatment tanks died.

Parameters that showed no statistical differences between treatment tanks with oysters and the controls ($\alpha=0.05$ when two-tailed *t*-test) were: nitrate, chlorophyll-*a*, ammonia, PIM in the water column, POM in the water column, total POM on the bottom at the end,

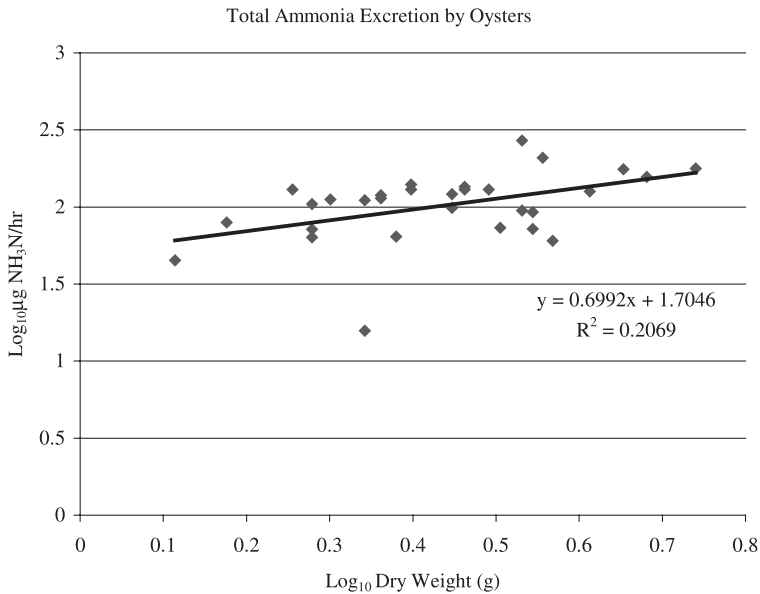


Fig. 1. A regression analysis of ammonia excretion by oysters of different dry weight sizes. Data represent excretion of ammonia by 24-h starved oysters placed in 2 l of fresh seawater with samples taken on an hourly basis for 8 h. Data points refer to ammonia excretion rates of individual oysters as a function of their individual soft tissue dry weights. Regression statistics are as follows: $R^2=0.2069$, y -intercept = 1.7046 ± 0.1120 (s.d.), slope = 0.6992 ± 0.2242 (s.d.), 95% confidence limits on slope = 0.171, 1.172.

and total PIM on the bottom at the end. A listing of the means for each treatment group at different flow rates with their respective standard errors and *P*-values are shown in Table 2.

Phytoplankton species composition did show a significant difference from a plankton tows taken in July. Treatments were quantitatively dominated by *Nitzschia striata* and controls were dominated by *Skeletonema costatum* (Table 3).

Mean organic matter collected in sedimentation traps for treatments and controls for four different flow rates are compared (Table 4). Significant differences were found at $\alpha=0.05$ for 0%, 15 to 25%, 35 to 50% flow rates when using a two-tailed *t*-test. No significant differences were found at the 100% flow rate. Mean inorganic matter collected in sedimentation traps for treatments and controls for four different flow rates were also compared (Table 4), and significant differences were also found at $\alpha=0.05$ for 0%, 15 to 25%, 35 to 50% flow rates. No significant differences were found at the 100% flow rate. Total organic and inorganic matter are compared between sedimentation traps and on the tank bottoms at the end of the experiment (Table 5). The values obtained for POM and PIM in tanks with oysters and without oysters at the end of the experiment did not show a difference at the $P<0.05$ level. The treatment tanks in all cases always had more particulate matter than the controls.

The laboratory ammonia excretion studies in the laboratory showed an allometric relationship between ammonia excretion and dry weight of the soft tissues with an R^2 value of 0.2069 (Fig. 1). The allometric equation describing the excretion of ammonia as a function of soft tissue dry weight is:

$$E = 50.65w^{0.699}$$

where *E*= ammonia excretion rate ($\mu\text{g/h}$), and *w*= soft tissue dry weight (g).

4. Discussion

Assessing the environmental effects of aquaculture is becoming increasingly more important as the aquaculture industry grows. This research provided information on what impact oysters have on the environment, and whether or not they may aid in combating the problem of eutrophication caused by increased nutrient inputs into coastal estuaries. We measured several parameters in this study, but only a few showed statistically significant differences.

One concern in setting up the design was determining what the carrying capacity should be. The term ‘carrying capacity’ in connection with shellfish aquaculture has been used to mean the stocking density achievable without incurring density-dependent stunting (Incze et al., 1981) or alternatively in the population ecology sense of the maximum stocking density achievable without causing food depletion or population mortalities (Smaal et al., 1998). Aquaculture lease sites are often placed in areas where there is a rapid tidal exchange (Pitcher and Calder, 1998), and stocking densities are often managed such that growth and mortalities are maintained at an economic optimum (e.g. Rheault and Rice, 1996).

Despite our efforts to stock the mesocosm test tanks based upon literature values of filtration rates such that there was a daily population filtration turnover of the water, there

is strong evidence that we did not reach the carrying capacity of the system for oysters. First, all the oysters grew well with comparable growth and mortality rates to oysters in commercial culture nearby in the West Passage of Narragansett Bay (William Geib, personal communication, 2001). Second, in previous flume experiments, depression in growth rates was accompanied by a marked decrease in chl-*a* and particulate organic matter in the water column (Rheault and Rice, 1996), which was not observed in the mesocosms (Table 2). Finally, Tenore and Dunstan (1973) reported that oysters exhibit maximum feeding when food concentration is above 0.25 mg-C/l (or about 0.5 mg/l POM). During the different flow rate treatments, the level of POM in the mesocosm tanks never fell below this level (Table 2).

Due to substantial declines in shellfish populations in the United States, there has been considerable interest establishing shellfish restoration programs (e.g. Mann, 2000; Rice et al., 2000; White et al., 2000). Some information for these programs can be derived from our mesocosm study by extrapolation to estuarine oyster populations. Based on the experimental stocking density, a calculation can be made to determine the amount of oyster biomass Narragansett Bay might be able to sustain. The total volume of Narragansett Bay has been calculated to be $2.724 \times 10^9 \text{ m}^3$ with a complete tidal exchange rate of 25.5 days (Pilson, 1986). On average, this works out to be $1.068 \times 10^8 \text{ m}^3$ of new water/day. In the mesocosms, 200 oysters were in a volume of 13.1 m^3 with water turnover ranging from 100% (the nominal oyster filtration with no physical water exchange) to 200% (the nominal oyster filtration + the 100% physical exchange of water per day) so the proportional number of oysters in Narragansett Bay according to volume would be 1.63×10^9 oysters at 1.3 g dry weight is 2.1×10^{10} g or 21,000 metric tons dry weight (or 315,000 metric tons live weight). This calculated biomass is about twice the estimated 1911 oyster population in Narragansett Bay (144,562 metric tons as previously discussed).

Phytoplankton generation times in Narragansett Bay during the warmer spring through fall bloom periods are on the order of 3 to 4 days (Durbin and Durbin, 1981), so regeneration of phytoplankton is likely to be more important to maintaining oyster populations than the 25.5-day water exchange. Newell (1988) estimated the time for oysters to completely filter the volume of Chesapeake Bay had dropped from 3.4 days in the late 19th century to 325 days. Based upon these population filtration estimates alone, he speculated “the decline in the oyster population over the last century may have exacerbated suspended particulate concentrations simply by reducing rates of biodeposition” (Newell, 1988). Actual effects of bivalves on coastal ecosystems are much more complex. Our results show that although there is an increase in biodeposition in treatment tanks, there is no apparent decrease in water column POM and chlorophyll-*a* content although oysters were stocked at a density that would elicit filtration of the entire mesocosm tank volume in 1 to 3 days, a time period corresponding to Newell’s 19th century population filtration rates. The data from our study in no way negates findings that filter feeders in high population numbers can reduce water column turbidity, indeed zebra mussels have demonstrably increased water clarity in the Great Lakes (Budd et al., 2001). Bivalve population filtration rates must exceed phytoplankton regeneration for this to occur and the population filtration of our experimental stocking density approximating historically high populations of oysters in the Narragansett and Chesapeake Bays does not exceed the phytoplankton regeneration rate.

The effects of restoration of oyster reefs or reestablishment of oyster aquaculture to early 20th Century levels on populations of other filter feeders in Narragansett Bay remains an open question. Fishery landing records show that landings of northern quahog (*Mercentaria mercenaria*) grew from about 100 metric tons in 1920 to over 2000 tons per year (shucked meat weight) in the late 1950s as the oyster industry was in decline (NMFS statistics cited in Boyd, 1990). Whether this fishery was based strictly on under exploited stocks of quahogs, or there was a niche replacement by quahogs as oysters declined remains speculative. Anecdotal information from Rhode Island shellfishermen suggests that populations of the slipper shell *Crepidula fornicata* have increased as oyster populations declined. There is some evidence that this filter feeding gastropod may be a niche competitor with oysters (MacKenzie, 1981) but this hypothesis is controversial (DeMontaudouin et al., 1999), and remains an open question.

We determined the rate of ammonia excretion by oysters (Fig. 1). Our data show that ammonia excretion by individual oysters is highly variable, but average ammonia excretion can be described as an allometric function of body weight with an exponent between 0.67 and 0.75. This is within the generally expected of size scaling of metabolic processes (Kleiber, 1961). Based on these rates, two hundred 35-mm oysters would excrete 22.4 $\mu\text{g-N/l/day}$ in the tanks. The data show no differences in ammonia content between tanks with oysters and the control tanks without oysters. In addition the tanks had a much lower ammonia concentration (Table 6) than was calculated from the laboratory study. The ammonia is not lost to nitrification because nitrate levels remain constant between the test and control tanks (Table 2).

Uptake of nitrogen by phytoplankton such as the *Nitzschia striatum* and perhaps unmeasured nanoplankton and picoplankton in the mesocosms may explain these results. For *Nitzschia striatum*, the regeneration rate would be the difference between the populations in the treatment and control tanks or 138,050 cells/l/day. Assuming 5 ng/cell dry weight based on cell dimensions and average organic content of phytoplankton (Durbin and Durbin, 1981), daily biomass production is 0.7 mg/l/day, and 3% dry weight nitrogen content (Durbin and Durbin, 1981) would yield a nitrogen requirement of 20 $\mu\text{g/l/day}$ to regenerate the *Nitzschia striatum*. This is statistically no different than the expected

Table 6
Ammonia in mesocosms

Actual and expected ammonia concentrations in mesocosms				
Exchange rate in mesocosms (m^3/day)	Tanks with oysters ($\mu\text{g/l}$), mean \pm SEM (<i>n</i>)	Tanks without oysters ($\mu\text{g/l}$), mean \pm SEM (<i>n</i>)	<i>P</i>	Expected ammonia in test tanks based on oyster excretion studies ($\mu\text{g/l}$)
13	60.32 \pm 6.09 (52)	67.01 \pm 12.21 (52)	0.838	72
4.5–7.5	25.15 \pm 1.33 (27)	33.02 \pm 7.63 (27)	0.585	123–270
2–3.25	39.01 \pm 4.05 (32)	42.23 \pm 4.24 (32)	0.890	332–392
0	20.42 \pm 1.49 (32)	20.59 \pm 1.79 (32)	0.984	491

Expected daily NH_3 increment above the expected in tanks without oysters based on individual oyster excretion rates = 22.4 $\mu\text{g/l day}$ or 470.4 $\mu\text{g/l}$ during 3-week course of experiment in the static tanks and diluted values based on various water exchange rates. *P* values are result of difference in means between test and control tanks by *t*-test.

daily increment in ammonia concentration (22.4 $\mu\text{g-N/l/day}$). Additional nitrogen may be scavenged by the unmeasured nanoplanktonic flagellates and picoplankton known to be in the mesocosms and adjacent Narragansett Bay (Vargo et al., 1982; Karentz and Smayda, 1998). These results suggest rapid ammonia utilization by phytoplankton, and explain the paradox of increased sedimentation without concomitant reduction of water column particulates.

Studies have also suggested that benthic bivalves are important facilitators of regenerating inorganic nutrients (e.g. Doering et al., 1986, 1987; Dame et al., 1991; Dame and Libes, 1993). Recently, Souchu et al. (2001) found that oysters were not food-limited during the summer due to the regenerated primary production enhanced by benthic nutrient fluxes from oyster beds in Thau lagoon, located in southern France. One immediate conclusion that might be drawn from these previous and the recycling of ammonia suggested in this study is that shellfish restoration efforts may be less effective in reducing estuarine eutrophication than has been suggested by Cloern (1982), Officer et al. (1982), Newell (1988) and Rice (2000), who drew their conclusions primarily from filtration rate modeling and/or continual harvest of shellfish by fisheries and aquaculture operations. The question about the efficacy of bivalves in reducing estuarine eutrophication remains open largely due to the unquantified relationship between rates of remineralization and rates of denitrification in the sediments in proximity to the bivalves, and due to unquantified scaling effects that are important in estuarine processes. In the current study, we focused upon recycling of nitrogen, mostly ammonia in the water column, and largely ignored benthic processes attendant to processing sedimentation materials from the bivalves. Denitrification is stimulated in sediments beneath bivalve aquaculture operations, including New Zealand mussels (Kaspar et al., 1985), and oysters in the south of France (Gilbert et al., 1997). This line of inquiry deserves renewed attention. Recent evidence by Newell et al. (2002) have shown that *C. virginica* in shallow water may be increasing rates of denitrification by showing denitrification rates in sediment cores with added phytoplankton cell slurries as an experimental analog for oyster feces and pseudofeces. The degree to which bivalves act to release nutrients during the summer that sustain phytoplankton blooms months after the major spring blooms in the northern hemisphere (e.g. Chapelle et al., 2000) remains a key question. The role of bivalve assemblages to reduce eutrophication by stimulation of secondary productivity in higher trophic levels, including nekton, also remains unknown.

There is a discrepancy between the values obtained for particulate organic matter and inorganic matter between the sediment traps and the amount collected at the end of the study (Table 5). This may be explained as an artifact of the sediment traps, their location in relation to the oyster cages, or currents established by the tank agitator. Amounts of POM and PIM were both higher in tanks containing oysters compared to the control tanks. The largest discrepancy between the sediment traps and the sediment accumulated at end of experiment was between the expected POM in the tanks with oysters (25 $\text{g/m}^2/\text{day}$) and the measured (6 $\text{g/m}^2/\text{day}$). This may be due to oxidation of organic matter. Rudnick and Oviatt (1986) examined the seasonal lags between organic carbon deposition and mineralization in marine sediments. During summer, maximum benthic metabolism occurs at a higher rate as compared to winter and spring. Sedimentation also varies because of changes in phytoplankton size structure, pelagic and benthic grazing, and microbial

activity in the water column (Rudnick and Oviatt, 1986). Since our experiment was conducted during a time when oyster filtration was high and the metabolic activity of decomposing bacteria is maximal, this may explain the differences in organic matter.

Modification of phytoplankton assemblages in constructed oyster fattening ponds has been long studied in France (e.g. Dupuy et al., 1999). Similarly, our data show a shifting of large phytoplankton species dominance between tanks with oysters and controls. Oysters rapidly deplete the chain-forming diatom *S. costatum* (Table 3), and the rapidly growing pennate diatom *Nitzschia striatum* replaces these organisms. These data suggest that oysters are selectively feeding on *S. costatum*, a good food for adult oysters (Walne, 1974; Soletchnik et al., 2001).

At the densities and exchange rates studied, aquacultured oysters had little effect on several environmental parameters, but they did affect the phytoplankton species composition and sedimentation. The phytoplankton species dominance shifted from *S. costatum* to *N. striata* species in mesocosms containing the oysters. The sedimentation rates based on the sediment traps in the tanks with oysters were significantly greater than the tanks without oysters. Sediment in mesocosms at the end of the experiment was greater in treatment mesocosms with oysters, but these contained less organic material than was expected based upon 24-h sedimentation studies using sediment traps. This is probably possibly due to organic decomposition in the benthos. The ammonia concentration in the mesocosms was less than expected based on laboratory excretion measurements, suggesting uptake by rapidly regenerating phytoplankton.

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