

2000

Aspects of Growth for the Northern Quahog, *Mercenaria mercenaria*

Craig Lawrence Appleyard
University of Rhode Island

Follow this and additional works at: <https://digitalcommons.uri.edu/theses>

Terms of Use

All rights reserved under copyright.

Recommended Citation

Appleyard, Craig Lawrence, "Aspects of Growth for the Northern Quahog, *Mercenaria mercenaria*" (2000).
Open Access Master's Theses. Paper 1370.
<https://digitalcommons.uri.edu/theses/1370>

This Thesis is brought to you by the University of Rhode Island. It has been accepted for inclusion in Open Access Master's Theses by an authorized administrator of DigitalCommons@URI. For more information, please contact digitalcommons-group@uri.edu. For permission to reuse copyrighted content, contact the author directly.

ASPECTS OF GROWTH FOR THE NORTHERN QUAHOG, *MERCENARIA*

MERCENARIA

BY

CRAIG LAWRENCE APLEYARD

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE

REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

IN

FISHERIES, ANIMAL, AND VETERINARY SCIENCE

UNIVERSITY OF RHODE ISLAND

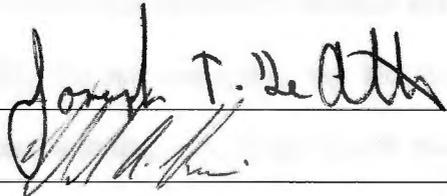
2000

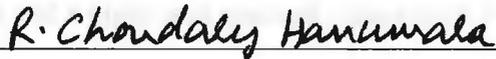
MASTER OF SCIENCE THESIS
OF
CRAIG LAWRENCE APLEYARD

APPROVED:

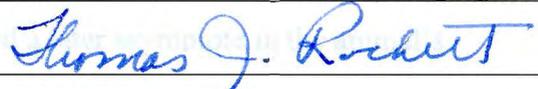
Thesis Committee

Major Professor









DEAN OF THE GRADUATE SCHOOL

UNIVERSITY OF RHODE ISLAND

2000

ABSTRACT

The growth of the northern quahog, *Mercenaria mercenaria*, has been mathematically modeled over both the nursery stage and the complete life so as to develop expectations of growth as a function of environmental suitability. Then, the growth of northern quahogs in an experimental nursery upweller was evaluated as a function of system operating parameters (flow rate and stocking density) and other environmental parameters to determine the limiting factors in this critical phase of shellfish aquaculture.

The von Bertalanffy growth equation was used to predict increases in shell length (millimeters), weight (grams), and the relative growth rate (% increase per day) at various instantaneous growth coefficients (K). The relative growth rate (RGR) was also determined over a number of time intervals, including 1, 4, 7, 14, and 28 days. The age at which the maximum shell length and weight was reached varied with K . A higher K (0.30) resulted in rapid growth and an earlier asymptote, while a lower K (0.20 and 0.10) resulted in slower growth and a later asymptote in the animal's maximum shell length and weight. The RGR averaged over an annual time interval (annual RGR), as predicted by von Bertalanffy, decreased rapidly as the northern quahog aged, approaching 0.5 % increase/day after age 2. Annual RGR at different K values was similar, indicating that RGR was insensitive to changes in K . During the first growing season (210 days in the northeast), the increase in shell length predicted by von Bertalanffy was linear with a slope determined by K , that is, a greater slope results in a higher K . A similar relationship was apparent with weight. The RGR,

however, varied greatly during the first growing season. Specifically, the RGR was 11 % increase/day at 90 days after spawning and 2 % increase/day at 210 days after spawning. The RGR at different K values was also insensitive to changes in K . There were no detectable differences between RGR determinations at a K of 0.10, 0.20, and 0.30 with varying time intervals (T); however, the value of RGR at a given point in time varied substantially with the time interval used to calculate RGR. The larger the growth interval, the larger the RGR. The a and b coefficients estimated for the weight-length relationship from the adult and nursery stage northern quahogs differed from each other and published measures from Narragansett Bay northern quahogs. This suggests that researchers should use data collected from northern quahogs in a size range similar to that being modeled when estimating biomass from length and abundance data. Predicted shell lengths and RGRs were compared to observed shell lengths and RGRs from a field experiment growing northern quahogs in an experimental-scale upweller (nursery stage). The northern quahogs grew at a K of 0.25 indicating favorable conditions for growth. Early in the experiment (between 70 and 100 days after spawning), the experimental RGR differed markedly from the predicted measure; however, after 100 days post spawning the experimental RGR was higher than expected and followed the general trend of decreasing RGR over time.

Northern quahog seed were grown from ~2 (longest axis) to ~13 mm in an experimental-scale floating upweller from June 21 to August 19, 1999 in Point Judith Pond, Wakefield, Rhode Island. Flow rates and stocking densities were varied in order to produce a chlorophyll- a effective flow rate range of 360 to 1,500 μg per minute per liter of northern quahog volume ($\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$), and growth and

environmental parameters were measured semiweekly. During the first two-week experiment (June 21 to July 7) an asymptotic relationship was observed between growth (% increase/day) and chlorophyll-a effective flow rate. A significant difference in growth was found between the treatments. The difference in the functional relationship between experiments 1 and 3 was possibly related to lower initial DO values, which reduced differential growth in experiment 3. In experiment 1, the low-biomass treatments grew faster than the high-biomass treatments. A significant difference in growth between treatments was also observed in experiment 3, although the asymptotic relationship was less pronounced. In experiment 3, the high-biomass replicates grew faster than the low-biomass replicates. Experiments 1 and 3 both experienced similar environmental conditions; however, experiment 1 encountered higher initial morning dissolved oxygen (DO) levels. In addition, the within experiment variability in experiment 3 was much less than the variability in experiment 1; therefore, accentuating growth differences in experiment 3. In both experiments 1 and 3, maximum growth occurred near treatment 2 in a range of chlorophyll-a effective flow rates of 550 to 650 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$. In experiments 2 and 4, there were no significant differences in growth between treatments.

Growth appeared to be limited by environmental conditions. In order to eliminate the effect of food limitation on growth, the upper third of the replicates (fastest growing animals) were used to calculate the RGR during the two-month experiment. Growth was linearly correlated with morning-dissolved oxygen ($R^2 = 0.42$) and with chlorophyll-a ($R^2 = 0.35$). The critical DO threshold for growth in upwellers appears to be 5 ppm, below which growth is adversely affected. During this

study, morning DO levels were less than 50 % saturated, indicating the potential for DO levels to be increased. Future research should investigate methods for elevating DO levels in upwellers.

ACKNOWLEDGEMENTS

Financial support for this research was provided by the Rhode Island Sea Grant Program. There are a number of people that made this research possible. I wish to thank my advisor, Dr. Joseph DeAlteris, whose support, patience, and insight made this a true learning experience. I wish to thank my committee members Drs. Robert Rheault, Michael Rice, and R. Choudary Hanumara for their comments and input.

Special thanks go to Kurt Schmidt and his staff for their assistance and generosity during my experiment. Thanks also to David Beutel, Glenn Hovermale, and Jeff Kosiorek for their daily assistance in design, construction, and maintenance of the upweller. I would also like to thank the staff at the Fisheries Center, especially Laura Skrobe, for their friendship, enthusiasm, and assistance during my research.

I am especially grateful to my parents, Norman and Barbara Appleyard, for their support.

PREFACE

This thesis was prepared in the manuscript format in accordance with the University of Rhode Island guidelines for thesis preparation. Two manuscripts address growth of the northern quahog, *Mercenaria mercenaria*, in an experimental-scale upweller (nursery stage). The first manuscript focuses on the theoretical growth of the northern quahog over the bivalve's life span as well as during the first growing season in the northeast. The second manuscript presents the results of a study on growth of the northern quahog in an experimental-scale upweller. Appendix I includes the mean and standard error for chlorophyll-a data as well as for all averages used during the analysis. Appendix II includes means and standard errors for the RGR of the upper 1/3 of treatment replicates used to quantify environmental influences on growth during the two-month experiment.

TABLE OF CONTENTS

	Page
Abstract.....	ii
Acknowledgements.....	v
Preface.....	vii
Table of Contents.....	viii
List of Tables.....	x
List of Figures.....	xi

MODELING GROWTH OF THE NORTHERN QUAHOG, *MERCENARIA*

MERCENARIA

Abstract.....	2
Introduction.....	4
Methods.....	8
Results.....	12
Discussion.....	16
References.....	41

GROWTH OF THE NORTHERN QUAHOG, *MERCENARIA MERCENARIA*, IN AN EXPERIMENTAL-SCALE UPWELLER

Abstract.....	45
Introduction.....	47
Methods.....	51
Results.....	58

Discussion.....	64
Summary and conclusions.....	72
References.....	109
Appendix I.....	113
Appendix II.....	119
Bibliography.....	121

LIST OF TABLES

MODELING GROWTH OF THE NORTHERN QUAHOG, *MERCENARIA* *MERCENARIA*

	Page
Table 1. Parameters used to model growth of the northern quahog in Rhode Island waters.....	20

GROWTH OF THE NORTHERN QUAHOG, *MERCENARIA MERCENARIA*, IN AN EXPERIMENTAL-SCALE UPWELLER

	Page
Table 1. Chlorophyll-a effective flow rates and their corresponding treatment.....	73
Table 2. Sample calculations of initial chlorophyll-a effective flow rates for the first growth interval (June 21 to June 24) in experiment 1. The average chlorophyll-a concentration during the time period was $11.70 \pm 2.06 \mu\text{g/l}$ (S.E.).....	75

LIST OF FIGURES

MODELING GROWTH OF THE NORTHERN QUAHOG, *MERCENARIA*

MERCENARIA

		Page
Figure 1.	Length (A) and weight (B) at time for K values of 0.10, 0.20, and 0.30 over the life span of the northern quahog in Rhode Island waters.....	21
Figure 2.	Daily relative growth rate (A) and specific growth rate (B) averaged on an annual basis at K values of 0.10, 0.20, and 0.30.....	23
Figure 3.	Length (A) and weight (B) at time for K values of 0.10, 0.20, and 0.30 during the northern quahog's first growing season.....	25
Figure 4.	The relative growth rate (A) and specific growth rate (B) expressed as % increase/day at K values of 0.10, 0.20, and 0.30 during the northern quahog's first growing season in Rhode Island waters (calculated over a 1-day time interval).....	27
Figure 5.	The relative growth rate (% increase/day) over time at varying K calculated over: 4-day time interval (A); 7-day time interval (B); 14-day time interval (C); and,	

	28-day-time interval (D).....	29
Figure 6.	The relative growth rate (% increase/day) over time at varying time intervals for a single <i>K</i> value of 0.20.....	31
Figure 7.	Linear regression of the natural log (LN) of weight (kg) and natural log (LN) of length (cm) of adult northern quahogs sampled from Narragansett Bay (A) and of juvenile northern quahogs sampled from an experiment in Point Judith Pond (B).....	33
Figure 8.	Linear regression of length (mm) with time (number of days after spawning) used to estimate <i>t</i> ₀ from juvenile northern quahogs sampled during the summer 1999 used to estimate	35
Figure 9.	Observed shell length during the summer 1999 along with the predicted shell length at a <i>K</i> of 0.25 during the northern quahog's first growing season in Rhode Island waters.....	37
Figure 10.	The predicted RGR versus the experimental RGR during the first growing season on the northern quahog.....	39

GROWTH OF THE NORTHERN QUAHOG, *MERCENARIA MERCENARIA*, IN AN
EXPERIMENTAL-SCALE UPWELLER

Figure 1.	Growth (% increase/day) of northern quahogs as a function of chlorophyll-a effective flow rate re-plotted from Manzi <i>et al.</i> , (1986).....	77
Figure 2.	Location of the experimental scale-upweller at Ram Point Marina, Point Judith Pond, Wakefield, Rhode Island.....	79
Figure 3.	Photograph of the experimental-scale floating upweller.....	81
Figure 4.	Growth (% increase/day) as a function of chlorophyll-a effective flow rate for experiment 1 (June 21 to July 7, 1999). The average chlorophyll-a concentration during the time period was $16.42 \pm 2.25 \mu\text{g/l}$ (S.E.).....	83
Figure 5.	Growth (% increase/day) as a function of chlorophyll-a effective flow rate for experiment 2 (July 7 to July 22, 1999). The average chlorophyll-a concentration during the time period was $11.83 \pm 1.16 \mu\text{g/l}$ (S.E.).....	85
Figure 6.	Growth (% increase/day) as a function of chlorophyll-a effective flow rate for experiment 3 (July 22 to August 5, 1999). The average	

	chlorophyll-a concentration during the time period was $18.55 \pm 2.12 \mu\text{g/l}$ (S.E.).....	87
Figure 7.	Growth (% increase/day) as a function of chlorophyll-a effective flow rate for experiment 4 (August 5 to August 19, 1999). The average chlorophyll-a concentration during the time period was $17.91 \pm 3.17 \mu\text{g/l}$ (S.E.).....	89
Figure 8.	Relative growth rate (% increase/day) for the upper third of replicates from June 21 through August 19, 1999.....	91
Figure 9.	Relative growth rate (% increase/day) for the upper third of replicates with morning temperature ($^{\circ}\text{C}$) from June 21 through August 19, 1999.....	93
Figure 10.	Relative growth rate (% increase/day) for the upper third of replicates with morning salinity (‰) from June 21 through August 19, 1999.....	95
Figure 11.	Relative growth rate (% increase/day) for the upper third of replicates with morning chlorophyll-a ($\mu\text{g/l}$) from June 21 through August 19, 1999.....	97
Figure 12.	Linear regression of the relative growth rate (% increase/day) for the upper third of replicates versus chlorophyll-a ($\mu\text{g/l}$) from June 21 through August 19, 1999.....	99

Figure 13.	Relative growth rate (% increase/day) for the upper third of replicates with morning-dissolved oxygen (ppm) from June 21 through August 19, 1999.....	101
Figure 14.	Linear regression of the relative growth rate (% increase/day) for the upper third of replicates versus morning dissolved oxygen (ppm) from June 21 through August 19, 1999.....	103
Figure 15.	Morning dissolved oxygen (ppm) with morning-dissolved oxygen (% saturation) from June 21 through August 19, 1999.....	105
Figure 16.	Chlorophyll-a ($\mu\text{g/l}$) with morning dissolved oxygen (ppm) from June 21 through August 19, 1999.....	107

MODELING GROWTH OF THE NORTHERN QUAHOG, *MERCENARIA*

MERCENARIA

growth of the quahog, *Mercenaria mercenaria*, was modeled using a von Bertalanffy growth curve. The von Bertalanffy growth curve is a mathematical model that describes the growth of an organism over time. The model is based on the assumption that the growth rate of an organism decreases as it approaches a maximum size. The von Bertalanffy growth curve is defined by the following equation:

$$L_t = L_{\infty} (1 - e^{-k(t-t_0)})$$

where L_t is the length of the organism at time t , L_{∞} is the maximum length of the organism, k is the growth rate coefficient, and t_0 is the theoretical age at which the organism would have zero length. The von Bertalanffy growth curve was fitted to the length-at-age data for the quahog, and the parameters of the model were estimated using nonlinear least squares regression. The maximum length of the quahog was estimated to be 110 mm, and the growth rate coefficient was estimated to be 0.15 yr⁻¹. The theoretical age at which the quahog would have zero length was estimated to be -1.5 years. The von Bertalanffy growth curve was used to predict the length of the quahog at any given age, and to estimate the age of the quahog from its length.

The relative growth rate (RGR) of the quahog was also modeled using a von Bertalanffy growth curve. The RGR is defined as the change in length of the organism divided by the length of the organism and the time interval over which the change occurred. The RGR of the quahog was estimated to be 0.15 yr⁻¹, which is the same as the growth rate coefficient of the von Bertalanffy growth curve. The RGR of the quahog was used to estimate the age of the quahog from its length, and to predict the length of the quahog at any given age.

The von Bertalanffy growth curve was also used to estimate the age of the quahog from its length. The age of the quahog was estimated to be 1.5 years for a quahog that was 100 mm long. The von Bertalanffy growth curve was used to estimate the age of the quahog from its length, and to predict the length of the quahog at any given age.

ABSTRACT

Growth of the northern quahog, *Mercenaria mercenaria*, was deterministically modeled over the life span of the bivalve as well as during its first growing season (nursery stage) in Rhode Island waters. Specifically, the von Bertalanffy growth equation was used to predict increases in shell length (millimeters), weight (grams), and the relative growth rate (% increase per day) at various instantaneous growth coefficients (K). The relative growth rate (RGR) was also determined over a number of time intervals, including 1, 4, 7, 14, and 28 days. The age at which the maximum shell length and weight was reached varied with K . A higher K (0.30) resulted in rapid growth and an earlier asymptote, while a lower K (0.20 and 0.10) resulted in slower growth and a later asymptote in the animal's maximum shell length and weight. RGR averaged over an annual time interval (annual RGR) decreased rapidly as the northern quahog aged, approaching 0.5 % increase/day after age 2. The annual RGR at different K values was similar, indicating that RGR was insensitive to changes in K . During the first growing season (210 days in the northeast), the increase in shell length predicted by von Bertalanffy was linear with a slope determined by K , that is, a greater slope results in a higher K . RGR, however, varied greatly during the first growing season. Specifically, the RGR was 11 % increase/day at 90 days after spawning and 2 % increase/day at 210 days after spawning. A similar relationship was observed with weight. The RGR at different K values was also insensitive to changes in K . There were no detectible differences between RGR determinations at a K of 0.10, 0.20, and 0.30 with varying time intervals (T); however, the value of RGR at a specific time

varied with the time interval used to calculate RGR. The a and b coefficients estimated for the weight-length relationship from the adult and nursery stage northern quahogs differed from each other and published measures from Narragansett Bay northern quahogs. This suggests that researchers should use data collected from northern quahogs in a size range similar to that being modeled when estimating biomass from length and abundance data. Predicted lengths and RGRs were compared to observed lengths and RGRs from a field experiment growing northern quahogs in an experimental-scale upweller (nursery stage). The northern quahogs grew at a K of 0.25 indicating favorable conditions for growth. Early in the experiment (between 70 and 100 days after spawning), the experimental RGR differed markedly from the predicted measure; however, after 100 days post spawning the experimental RGR was higher than predicted and followed the general trend of decreasing RGR over time.

INTRODUCTION

The success of a shellfish aquaculture operation depends on optimizing production, specifically, on maximizing growth and survival. Growth is defined as an increase in the size of an individual or the mean increase in the size of a population (Malouf and Bricelj, 1989). Growth is usually expressed as a change in shell length, weight, or volume. The particular method employed to quantify clam growth depends on the life stage of the animal, the application of the measurement, as well as the resources available.

The change in size (shell length, weight, or volume) per unit time is defined as the growth rate. The growth rate is usually expressed as an absolute growth rate, a relative growth rate, or an instantaneous (specific) growth rate (Ricker, 1975). The absolute growth rate describes an increase in size (shell length, weight, or volume) over a specific time interval, usually a month or year. The absolute growth rate does not account for differences in the initial size of the animal. Two northern quahogs may have the same absolute growth rate, but different initial sizes; therefore, the smaller northern quahog is growing more relative to its initial size than the larger northern quahog. To incorporate the effect of initial size on growth, the relative growth rate or specific growth rate are commonly employed. The relative growth rate measures the change in size of the animal relative to its initial size. The specific growth rate is a special case of the relative growth rate that uses a log or natural log transformation (Jobling, 1994).

A number of growth models are utilized in the literature; however, the von Bertalanffy model is the standard for marine species (King, 1995) and has been successfully applied to the northern quahog (Jones *et al.*, 1989). Traditionally, northern quahog growth studies have focused on aging northern quahogs in the natural environment based on sclerochronology or shell growth rings (Kennish and Loveland, 1980, Peterson *et al.*, 1984, Jones *et al.*, 1989, Rice *et al.* 1989, Arnold *et al.*, 1991, Slattery *et al.*, 1991). These studies have documented the effect of environmental conditions (Ansell, 1968, Jones *et al.*, 1989), habitat (Peterson *et al.*, 1984, Slattery *et al.*, 1991), and fishing pressure (Rice *et al.* 1989) on the growth history of the animal. In aquaculture research, sclerochronological measurements are not required for documenting growth because the age is based on time from spawning or settlement.

Growth of the northern quahog varies both temporally and spatially. Ansell (1968) documented growth of the northern quahog over its natural geographic range. Jones *et al.* (1989) compared Ansell's data to their own and found that northern quahogs from Narragansett Bay grow exceptionally fast during the first 2 years of life. They also reported that growth varied widely throughout the bay. They found that the von Bertalanffy estimates of the maximum shell length (L_{∞}) varied from 67 to 100 mm, the growth coefficient (K) varied from 0.16 to 0.30, and the time at zero length (t_0) varied from -0.05 to -0.81. The authors report that *Mercenaria mercenaria* have been known to live as long as 40 years, although only 10 % of the clams from Narragansett Bay lived longer than 30 years. Rice *et al.* (1989) also documented differences in growth throughout the bay. Northern quahogs sampled from Greenwich cove exhibited an L_{∞} of 87 mm and a K of 0.09, while northern quahogs from the West

Passage exhibited an L_{∞} of 111 mm and a K of 0.10. There are a variety of factors that could account for these differences including fishing pressure (density), environmental conditions (temperature, salinity, oxygen, and food availability), sediment type, food concentration and quality, nutrient loading, and current speed.

The diversity of growth estimates used in shellfish aquaculture research is daunting. Malinowski (1988) described growth as an increase in shell length (mm) over the number of days from spawning, an increase in microns per day, as well as a percent weekly increase in packed volume. Manzi *et al.* (1984) defined growth in terms of increases in shell length and settled volume (biomass). Since the time intervals varied between measurements, the authors converted biomass increases into an equivalent monthly relative growth rate. Similarly, a number of studies have transformed biomass increases into daily, weekly, and monthly growth rates (Manzi *et al.*, 1986, Malinowski and Siddall, 1989, Hadley *et al.*, 1999).

The variability present in the above experiments and in others makes it extremely difficult to compare growth between studies. In addition, because growth is being expressed during different time periods and over varying sizes, the validity of growth comparisons is questionable. Furthermore, investigators have not predicted or modeled growth under optimal conditions. Without an estimate or expectation of growth, researchers lack a baseline for comparison. In other words, observed differences in growth due to experimental treatments could be confounded by differences in the predictable growth of the animal depending on the measure used.

The purpose of this research was to:

- I. Develop a set of expectations for northern quahog growth over both a time-line and the first season of growth based on units of shell length, weight, and volume;
- II. Investigate the sensitivity of RGR to changes in the growth coefficient (K) and the time averaging period over which RGR was measured; and
- III. To finely apply the theoretical growth models to observations from the field and from a nursery upweller.

Growth of the northern quahog, *Mercenaria mercenaria*, was modeled over the course of the animal's life span and during the first growing season (nursery stage).

Comparisons were made with different growth coefficients (K) as well as during different time periods. Finally, predicted growth was compared to observed growth in an experimental-scale upweller.

MATERIALS AND METHODS

The von Bertalanffy growth model was used to characterize growth of the northern quahog in the coastal waters of Rhode Island. The von Bertalanffy equation in terms of shell length is:

$$L_t = L_\infty \left[1 - e^{-K(t-t_0)} \right]$$

where L_t is the shell length at age t , L_∞ is the maximum shell length attained by the animal, K is the growth coefficient, and t_0 is the theoretical age (years) at zero length (King, 1995). Length in centimeters at time t (L_t) was converted to weight in grams at time t (W_t) by using:

$$W_t = aL_t^b$$

where a is a unit conversion factor and b is the volumetric expansion factor. The growth rate was defined as the daily relative growth rate (RGR) and as the specific growth rate (SGR). RGR was calculated as:

$$RGR = \left(\frac{W_{final} - W_{initial}}{W_{initial}} \right) (T^{-1})$$

where W_{final} is the final weight (g) and $W_{initial}$ is the initial weight (g) and T (days) is the intervening time period (Ricker, 1975). The RGR is expressed as a % increase per day. The SGR was calculated as:

$$SGR = \left(\frac{LN(W_{final}) - LN(W_{initial})}{T} \right) (100)$$

where LN is the natural log, W_{final} is the final weight (g), $W_{initial}$ is the initial weight (g), and T (days) is the intervening time period. The SGR is also expressed as a % increase per day

Growth over the lifetime:

The increase in the length and weight of the northern quahog was characterized over the course of the bivalve's lifetime at varying growth coefficients (K) of 0.10, 0.20, and 0.30. The growth coefficients of 0.10, 0.20, and 0.30 were selected to encompass the range observed in Narragansett Bay. The maximum age of the northern quahog was assumed to be 40 years (Jones *et al.*, 1989) and t_0 was assumed to be +0.10 years or 36 days. A value of +0.10 was chosen because the time from spawning to settlement can take anywhere from 3 to 5 weeks depending on water temperature (Rice, 1992). The L_{∞} for the von Bertalanffy and the a and b weight coefficients for the length-weight relationship were based on samples collected in Narragansett Bay (Jones *et al.*, 1989, Rice *et al.*, 1989). The daily RGR and SGR averaged on an annual basis were calculated over the life span of the quahog.

Growth during the first growing season:

To document growth of the northern quahog during the nursery stage (2 to 14 mm) shell length, weight, and RGR were modeled during the first growing season. In Rhode Island waters, the growing season is approximately seven months (210 days) and lasts from mid April to mid November (Ansell, 1968). The model was initiated at

the time of spawning and t_0 , the age that the clams had a size of 0 mm, was assumed to be 36 days to account for the time between spawning and settlement.

The increase in shell length, weight, RGR, and SGR were modeled during the first growing season (36 to 210 days) at K values of 0.10, 0.20, and 0.30. The RGR during the first growing season was further investigated by varying the growth interval (T) between determinations. Specifically, growth intervals of 1, 4, 7, 14, and 28 days were used to calculate RGR (Figure 5).

Application of the growth model to field and experimental data:

The theoretical models for growth over the lifetime and during the nursery stage were applied to northern quahog growth data from Narragansett Bay and Point Judith Pond, Rhode Island. Weight-length data for northern quahogs in the size range of 60 to 140 mm were collected with a dredge in upper Narragansett Bay and analyzed for the a and b coefficients of the weight-length relationship. Data collected during the summer 1999 from an experimental-scale upweller in Point Judith Pond were used to define growth of the northern quahog during its first growing season. Specifically, the growth coefficient (K) was determined by non-linear regression methods (DeAlteris and Skrobe, unpublished); the time at length zero (t_0) was determined from a linear regression of length versus time after spawning; and the length-weight parameters (a and b) were calculated using linear regression of the log transformed length and weight data.

To elucidate differences between the observed growth rate of the northern quahog during the summer 1999 (Appleyard, 2000) and the predicted growth rate,

residuals between the predicted RGR and the experimental RGR were calculated. A linear regression of the residuals and morning-dissolved oxygen (DO) was performed to investigate the influence of environmental conditions on residual growth during the experiment. RGR residuals were also compared to morning temperature and chlorophyll-a concentration.

RESULTS

Growth over the lifetime:

The parameters employed to model growth of the northern quahog in Rhode Island waters are included in Table 1. The increase in shell length over the course of the northern quahog's 40-year life follows the classic asymptotic relationship. The shell length increases steeply during the first couple of years of the animal's life and then increases at a decreasing rate until the asymptote or maximum shell length is attained. The rate that the northern quahog reaches its maximum shell length varies substantially with varying K (Figure 1A). The northern quahog reaches a maximum length of 140 mm in 11 years with a K of 0.30, in 17 years with a K of 0.20, and in 33 years with a K of 0.10. A similar relationship is apparent with weight (g). The northern quahog reaches a maximum weight of 647 grams in 15, 23, and 39 years with a K of 0.30, 0.20, and 0.10, respectively (Figure 1B). As the growth coefficient increases, the time required for the northern quahog to reach its maximum shell length and weight decreases. RGR over an annual time interval decreases from 3.3 % increase/day during the first year to 0.5 % increase/day during the juvenile years (age 1-2) and becomes negligible during the adult years (age 2+) (Figure 2A). Although the same general trend was apparent for the SGR averaged over an annual time interval, the SGR during the juvenile years was about half the RGR (Figure 2B).

Growth during the first growing season:

The parameters in Table 1 were also used to model growth of the northern quahog during the first growing season. The increase in shell length during the first seven-month (210 day) growing season was linear, as would be expected from the von Bertalanffy growth curve. The maximum shell length reached during the first growing season varied considerably with K . The northern quahogs reached a shell length of 27 mm with a K of 0.30, a shell length of 18 mm with a K of 0.20, and a shell length of 9 mm with a K of 0.10 (Figure 3A). A similar relationship was apparent with weight during the first growing season. Specifically, a weight of 6.20 g, 2.20 g, and 0.30 g was reached during the first growing season with K values of 0.3, 0.2, and 0.1, respectively (Figure 3B).

The difference in final shell length and weight observed at K values of 0.10, 0.20, and 0.30 were not apparent when growth was converted to a RGR (Figure 4A). Although there was a considerable change in the RGR during the first growing season, the northern quahogs displayed similar RGRs at varying K values. In particular, at 90 days after spawning, the northern quahogs grew at a rate of 11 % increase/day, while at 150 days after spawning they grew at 3 % increase/day. The relative growth rate was high early in the northern quahogs first growing season, but decreased substantially and leveled off after 180 days after spawning. The SGR during the first growing season mirrored the RGR (Figure 4B).

The relative growth rate was also determined using a variety of growth intervals. There were no detectible differences between RGR determinations at a K of 0.10, 0.20, and 0.30 with varying time intervals (Figures 4A, 4B, 5A, 5B, 5C, and 5D); however, the value of RGR at a specific time varied with the time interval used to

calculate RGR (Figure 6). At 90 days after spawning, the northern quahogs grew at 26 % increase/day during a 28-day growth interval, at 15 % increase/day during a 14-day growth interval, at 13 % increase/day during a 7-day growth interval, at 11 % increase/day during a 4-day growth interval, and at 10 % increase/day during a 1-day growth interval. In other words, the larger the growth interval that RGR was averaged over, the larger the RGR. This relationship becomes less obvious when the northern quahogs reach 120 days after spawning and disappears after the first growing season (Figures 6, 2A, and 2B).

Application of the growth model to field and experimental data:

For adult northern quahogs collected in upper Narragansett Bay, the linear regression of the natural log (LN) of weight (g) versus the natural log (LN) of length (cm) resulted in an R^2 of 0.94 (Figure 7A). From this relationship, the a and b coefficients of the weight-length relationship were determined to be 0.00023 and 3.15, respectively.

For the nursery stage, the northern quahogs were spawned on April 8, 1999 at Bluepoints Company, Inc., West Sayville, New York. The linear regression of shell length versus the number of days after spawning was significant ($F(1, 6) = 132.87$, $p < 0.05$) with an R^2 of 0.96 (Figure 8). From this relationship, t_0 was determined as 63 days after spawning. The linear regression of the natural log (LN) of weight (g) versus the natural log (LN) of length (cm) resulted in an R^2 of 0.99 (Figure 7B). The a and b coefficients of the weight-length relationship were determined to be 0.00027 and 2.81, respectively.

A non-linear regression method estimated K to be 0.25 for the experiment completed during the summer 1999 (Appleyard, 2000) (Figure 8). This is graphically apparent when the experimental lengths are plotted with the predicted length at the empirical K of 0.25 (Figure 9). The predicted RGR was compared to the experimental RGR over a 4-day growth interval (Figure 10). The experimental RGR varies considerably with the predicted RGR during the first 25 days of the experiment; the clams grew slower than expected. At approximately 100 days after spawning, the experimental RGR intersects the predicted curve. After 100 days, the northern quahogs grew faster than expected, but tended to follow the general trend of decreasing RGR over time. The linear regression of RGR residuals versus morning DO, morning temperature and chlorophyll-a concentration were insignificant.

DISCUSSION

Growth over the lifetime:

The results of this growth modeling exercise indicate that the growth rate of the northern quahog over its life span changes considerably (Figure 1A and 1B) as a function of K . In particular, early on growth of the northern quahog is nearly linear and reaches an asymptote as the animal ages. The age that growth reaches an asymptote depends on the particular growth coefficient (K) used. A higher K results in rapid growth and an earlier asymptote in the animal's maximum shell length and weight, while a lower K results in slower growth and a later asymptote; therefore, K is a useful indicator of environmental suitability for growth. RGR averaged over an annual time interval decreases rapidly as the northern quahog ages, approaching 0 % increase/day after age 2. RGR was relatively insensitive to changes in K . SGR closely followed the patterns observed for RGR; however, because of the log or LN transformation, SGR during the juvenile years was about half the RGR.

Growth during the first growing season:

To predict growth during the nursery stage, growth of the northern quahog was investigated during the first growing season (210 days in Rhode Island). The increase in shell length and weight was linear (Figure 3). The final shell length and weight reached during the first growing season varied considerably with K ; however, the RGR at different K values was almost identical. Again, the measure of RGR was relatively insensitive to changes in K . The RGR did vary during the first growing

season. The RGR was extremely high early in the growing season (at 90 days after spawning the predicted RGR was 11 % increase/day), but then decreased substantially and leveled off (at 150 days after spawning the predicted RGR was less than 4 % increase/day).

The RGR was further investigated by altering the time period between RGR determinations. There were no observable differences between RGR at a K of 0.10, 0.20, and 0.30 with varying time intervals of 1, 4, 7, 14, and 28 days (Figures 4, 5A, 5B, 5C, and 5D). In other words, RGR does not detect differences in the instantaneous growth rate (K). This has serious implications for experiments hoping to quantify differences in growth between treatments. The value of RGR at a specific time varied with the time interval used to calculate RGR. Specifically, at 90 days after spawning there was a considerable difference between the RGR calculated over a 28-day interval and the RGR calculated over a 4-day interval (Figure 6).

Application of the growth model to experimental data:

The a and b coefficients estimated for the weight-length relationship from the adults and nursery stage northern quahogs were different from each other and from other values published for Narragansett Bay northern quahogs (Figure 7). This suggests that researchers should always use data collected from locally available northern quahogs in a size range similar to that being modeled when estimating biomass from shell length and abundance data.

The relative growth rate changes considerably during the first growing season. The growth rate depends on the size of the animal as well as the time period between

measurements. Growth studies on upwellers have not taken into account these differences. In addition, the variability between growth measurements has prohibited meaningful comparisons between research studies. Manzi *et al.* (1984) converted their biomass increase to a monthly percent increase because the time interval between volume determinations varied. The investigator's failed to take into account changes in the growth rate at different time intervals. A study completed by Hadley *et al.* (1999) found a relationship between the daily growth rate (DGR) and flow ratio at varying northern quahog shell lengths. In particular, the authors found that the DGR increased as the size of the animal decreased. Based on the results of this modeling exercise, the RGR is expected to increase with decreasing size. The relationship developed by the authors correlates well with predicted growth in the natural environment.

During the experiment completed in the summer 1999 (Appleyard and DeAlteris, 2000) the northern quahogs grew at a K of 0.25 (Figure 7B), indicating favorable conditions for growth. A K of 0.25 approaches the maximum K observed by Jones *et al.* (1989) in Narragansett Bay.

The predicted RGR was compared to the experimental RGR during the study. Early in the experiment, between 70 and 100 days after spawning, the experimental RGR differs markedly from the predicted RGR; however, above 100 days after spawning the experimental RGR was higher than expected and followed the general trend of decreasing RGR over time (Figure 10). To incorporate the influence of anticipated growth on the experiment, the residuals between the predicted and experimental RGR were determined. The residuals were then compared to key

environmental conditions to elucidate their effect on growth. Although there were no clear conclusions, this exercise was important in accounting for anticipated changes in growth over the first year of the northern quahog's life.

Figure 1. Growth of northern quahog in the first year of life. Growth is measured in mm.



Table 1. Parameters used to model growth of the northern quahog in Rhode Island waters.

L_{∞}	=	140 mm
t_0	=	0.10 years (36 days)
a	=	0.0004
b	=	2.80
K	=	0.1, 0.2, and 0.3



Figure 1. Length (A) and weight (B) at time for K values of 0.10, 0.20, and 0.30 over the life span of the northern quahog in Rhode Island waters.



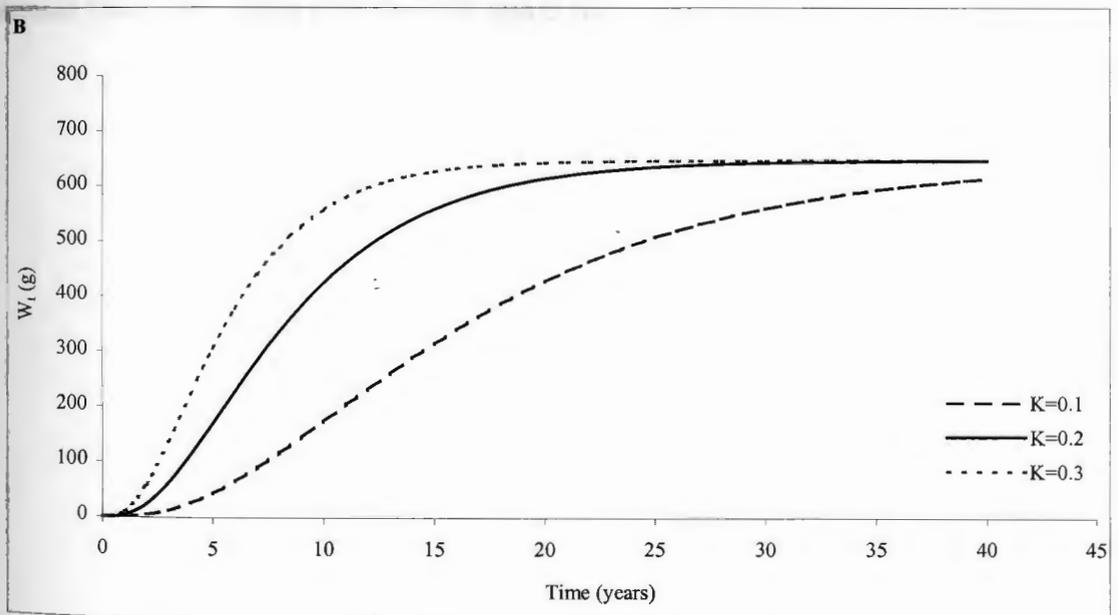
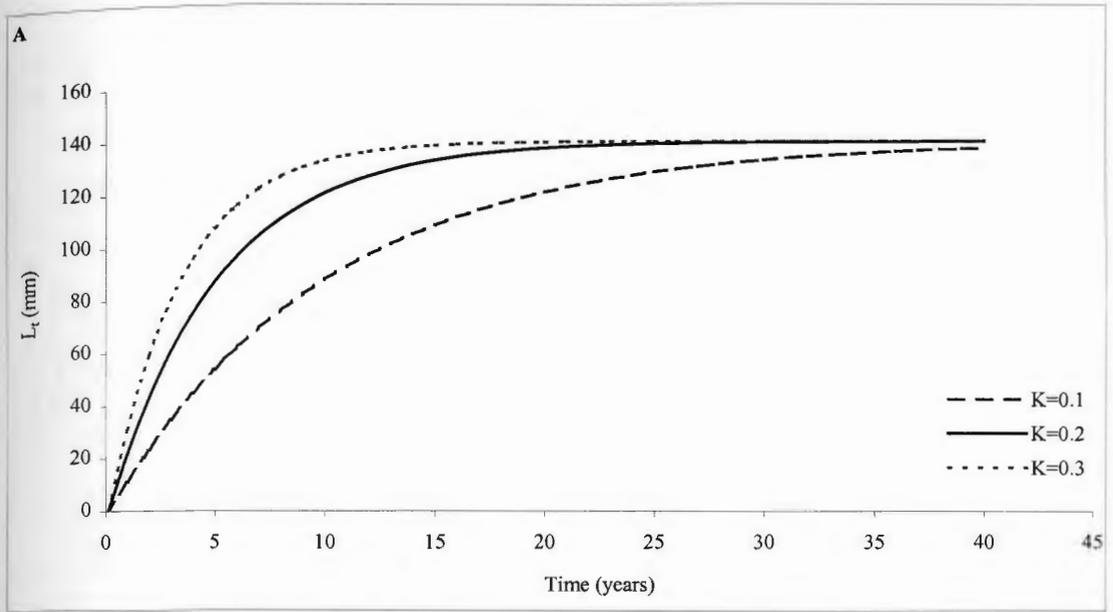




Figure 2. Daily relative growth rate (A) and specific growth rate (B) averaged on an annual basis at K values of 0.10, 0.20, and 0.30.



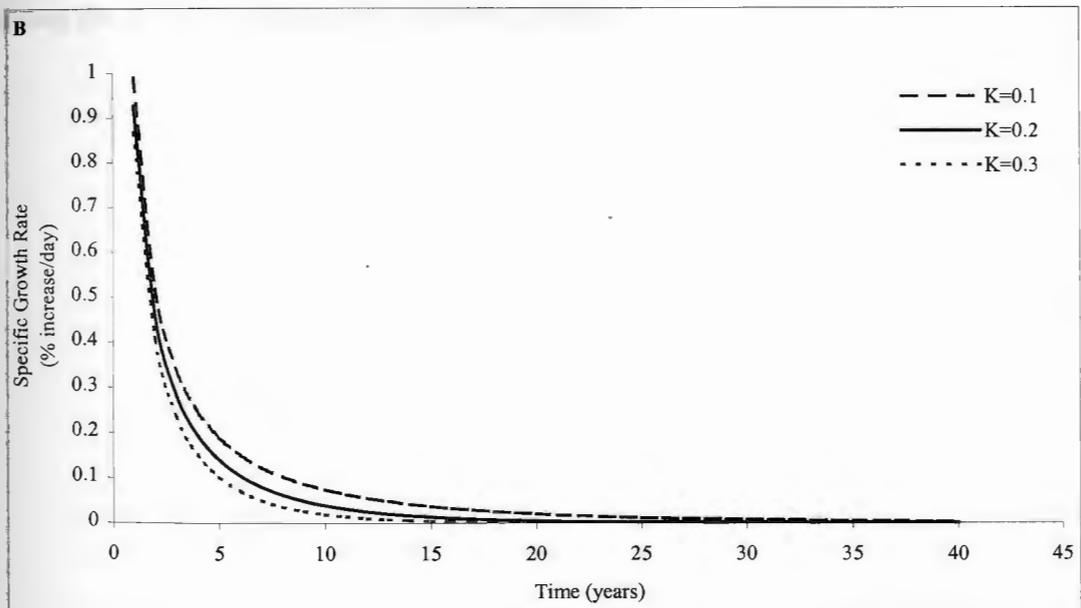
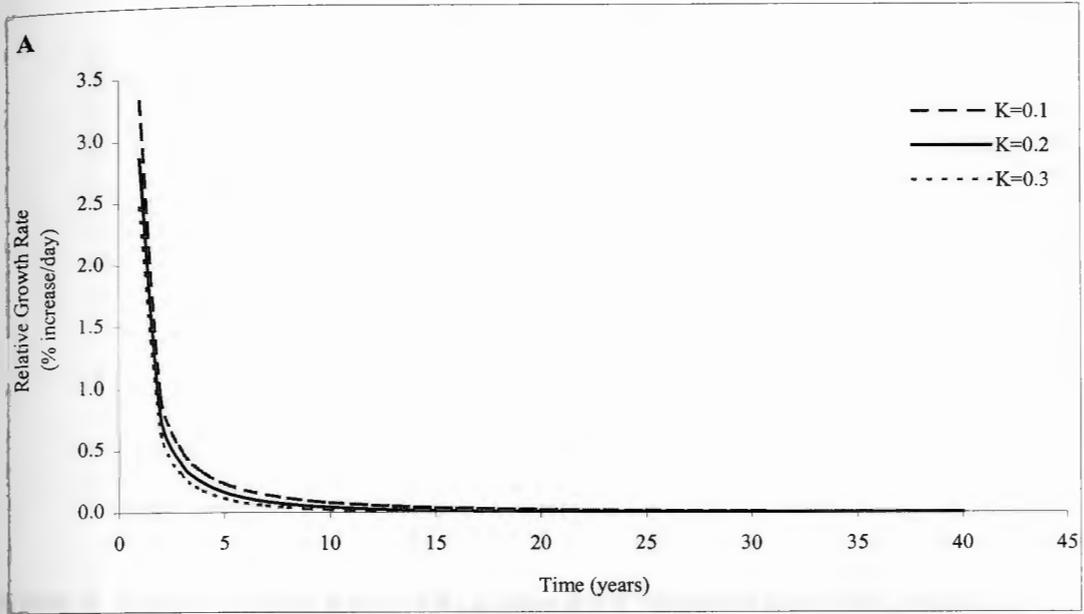




Figure 3. Length (**A**) and weight (**B**) at time for K values of 0.10, 0.20, and 0.30 during the northern quahogs first growing season.



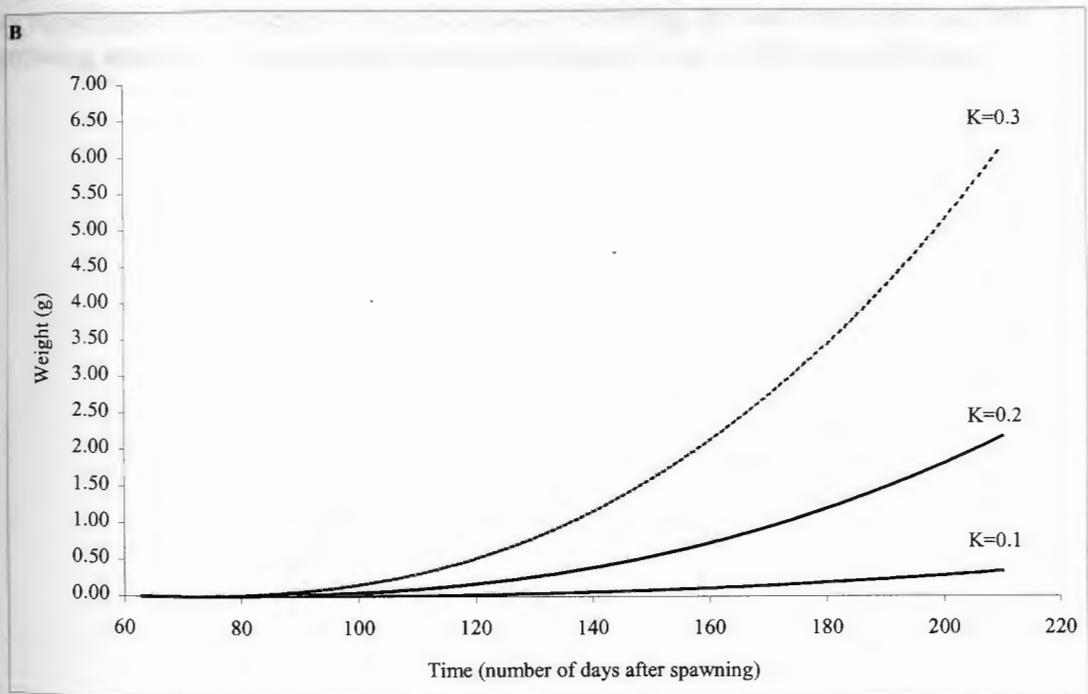
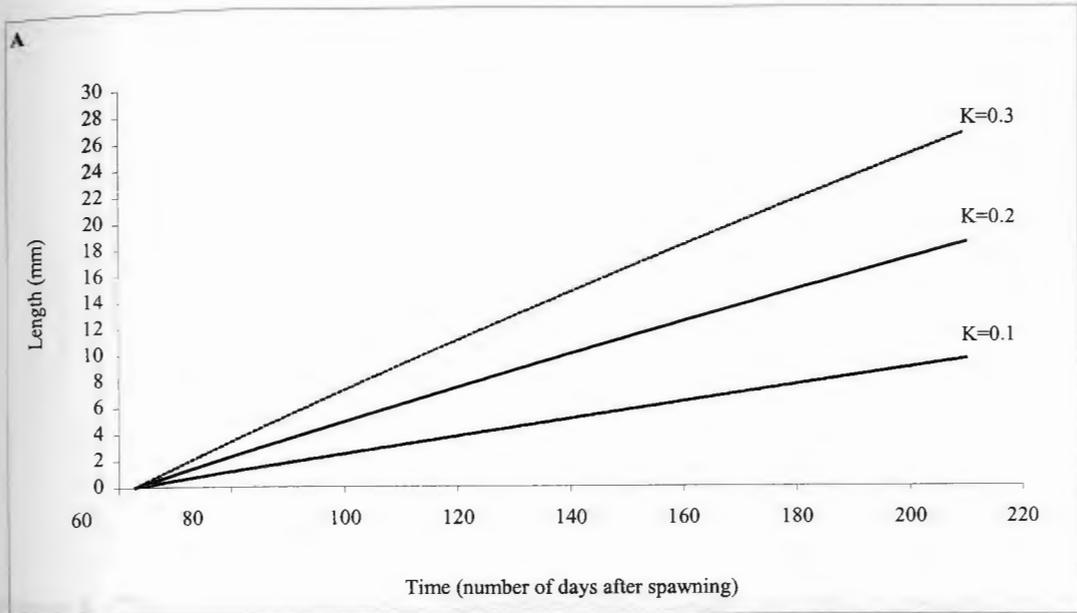


Figure 4. The relative growth rate (A) and specific growth rate (B) expressed as % increase/day at K values of 0.10, 0.20, and 0.30 during the northern quahogs first growing season in Rhode Island waters (calculated over a 1-day time interval).

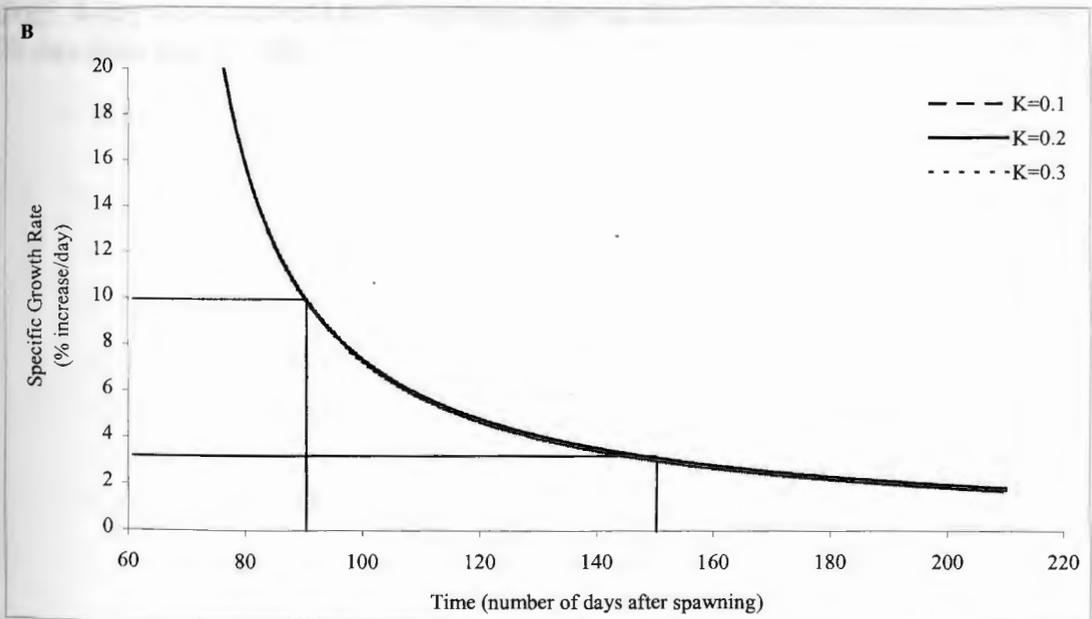
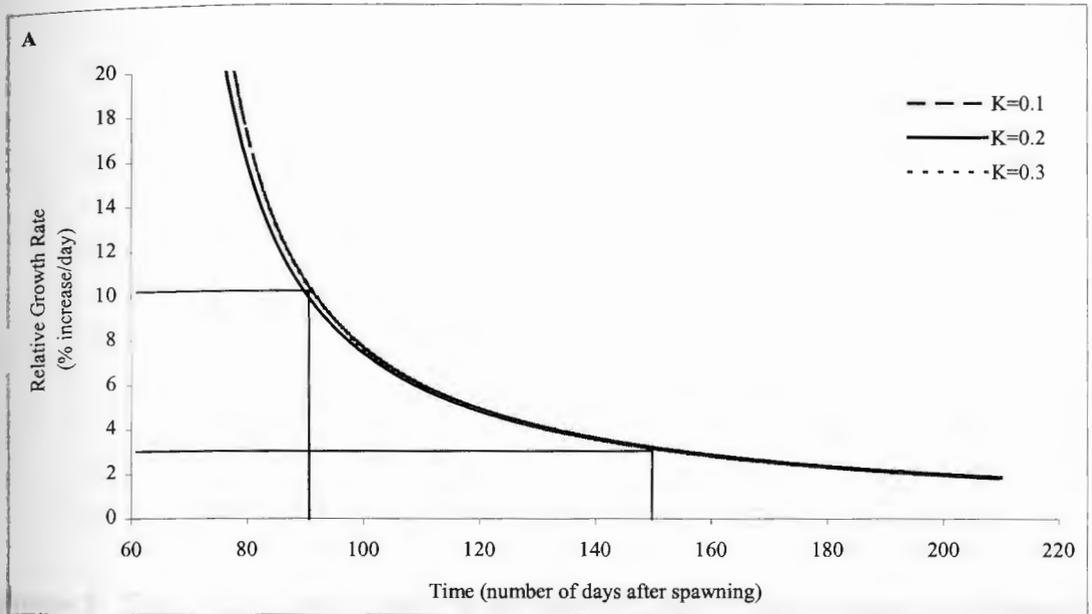


Figure 5. The relative growth rate (% increase/day) over time at varying K calculated over: 4-day time interval (A); 7-day time interval (B); 14-day time interval (C); and, 28-day-time interval (D).

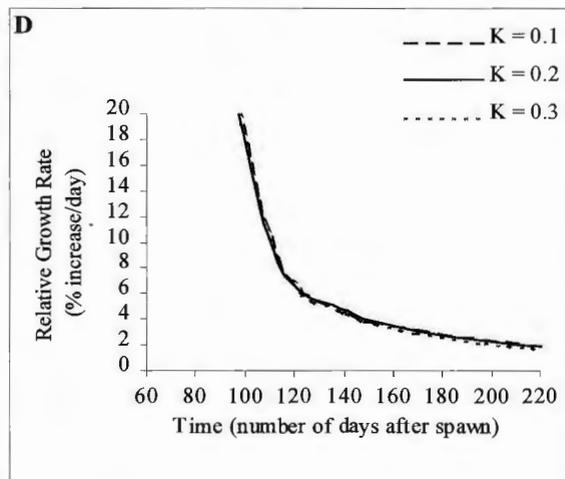
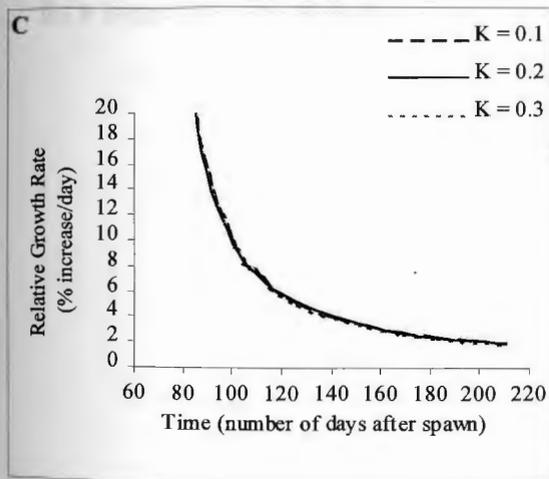
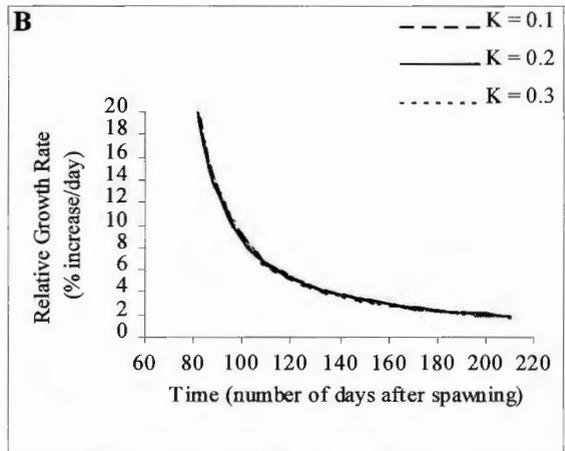
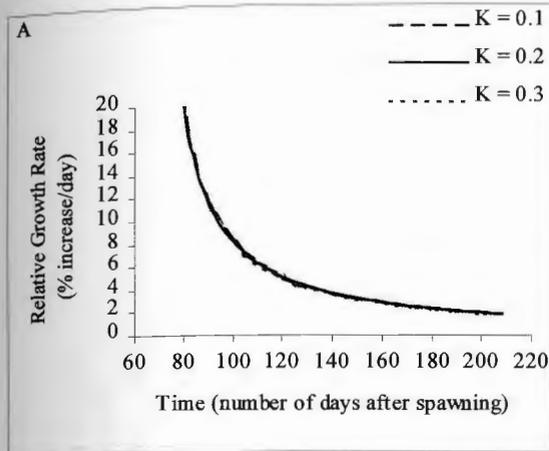


Figure 6. The relative growth rate (% increase/day) over time at varying time intervals for a single K value of 0.20.

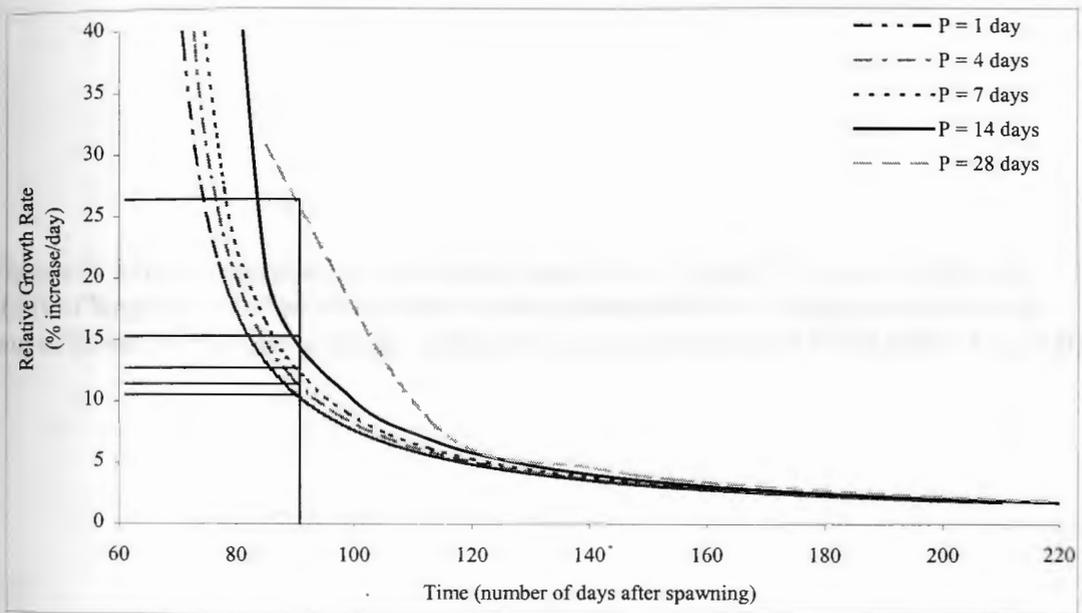




Figure 7. Linear regression of the natural log (LN) of weight (kg) and natural log (LN) of length (cm) of adult northern quahogs sampled from Narragansett Bay (A) and of juvenile northern quahogs sample from an experiment in Point Judith Pond (B).



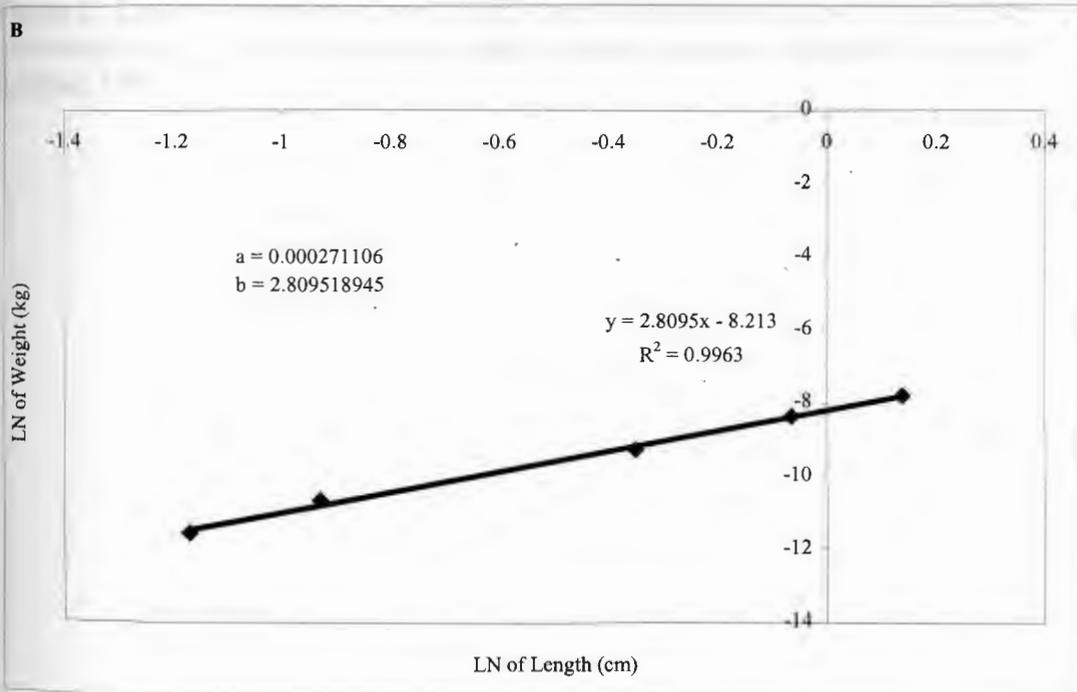
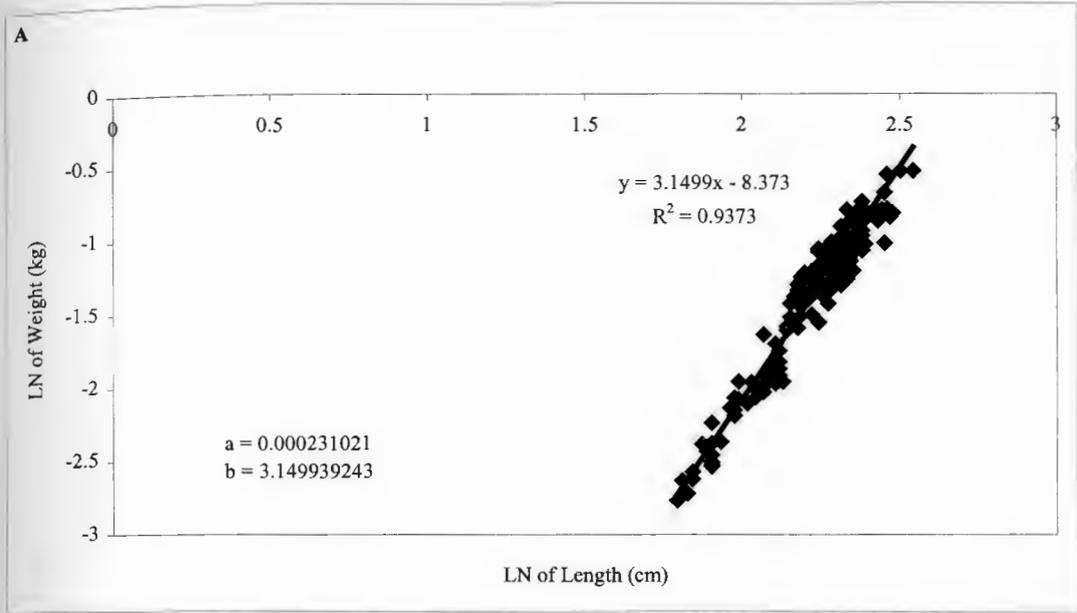


Figure 8. Linear regression of shell length (mm) with time (number of days after spawning) used to estimate t_0 from juvenile northern quahogs sampled during the summer 1999.

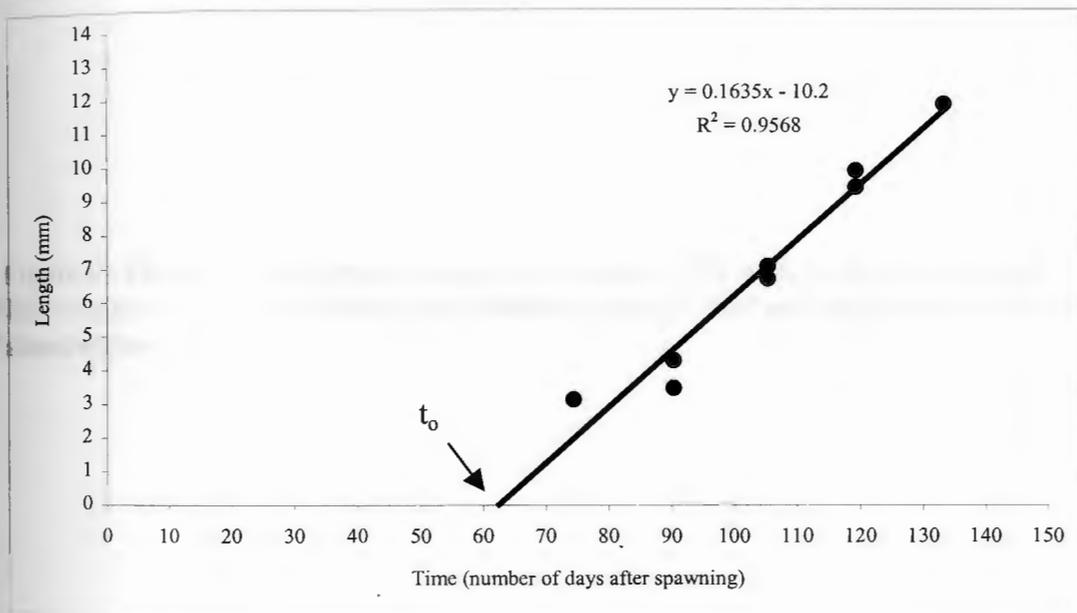


Figure 9. Observed shell length during the summer 1999 along with the predicted shell length at a K of 0.25 during the northern quahog's first growing season in Rhode Island waters.

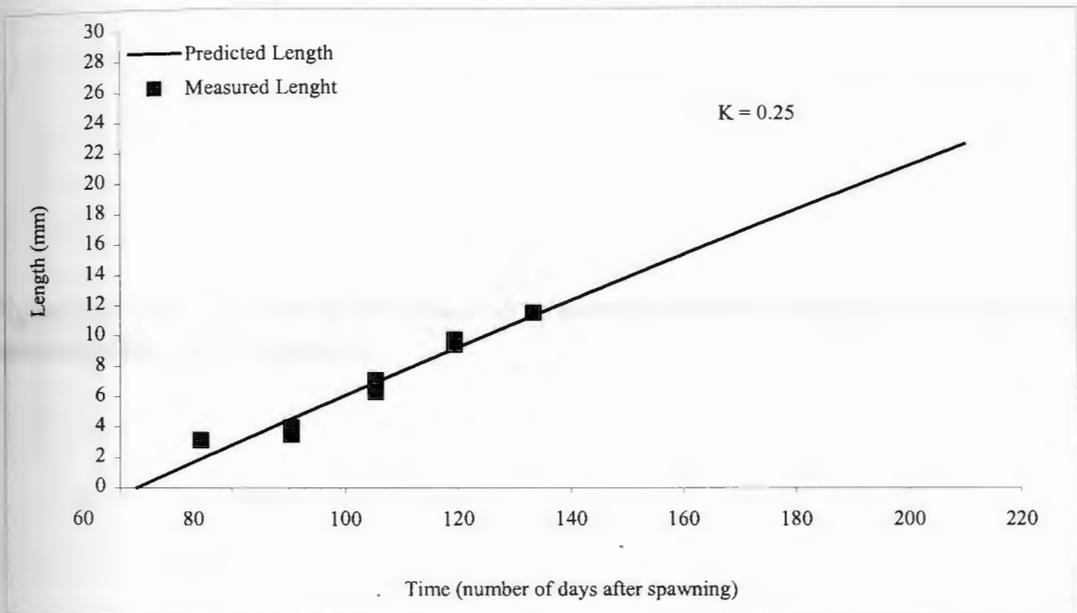
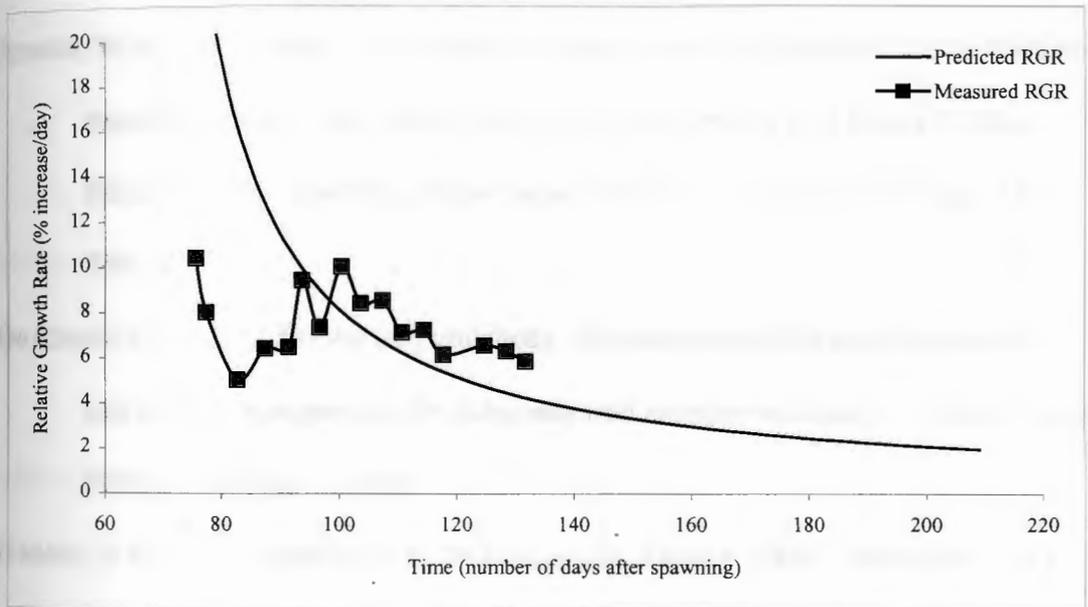


Figure 10. The predicted RGR versus the experimental RGR during the first growing season on the northern quahog.



REFERENCES

- Ansell, A.D. 1968. The rate of growth of the hard clam *Mercenaria mercenaria* throughout the geographical range. *Journal du Conseil International pour l'Exploration de la Mer*, 31: 346-409.
- Appleyard, C.A. 2000. Aspects of growth for the northern quahog, *Mercenaria mercenaria*. Masters Thesis. University of Rhode Island, Kingston. 123 pp.
- Arnold, W.S., D.C. Marelli, T.M. Bert, D.S. Jones, and I.R. Quitmyer. 1991. Habitat-specific growth of hard clams *Mercenaria mercenaria* (L.) from the Indian River, Florida. *Journal of Experimental Marine Biology and Ecology*, 147: 245-265.
- DeAlteris, J.T. and L. Skrobe (unpublished). *Introduction to fish stock assessment and fishery management for fishermen and resource managers*. Atlantic States Marine Fisheries Council.
- Hadley, N.H., R.B. Baldwin, M.R. DeVoe, and R. Rhodes. 1999. Performance of a tidal-powered upwelling nursery system for northern quahogs (hard clams) (*Mercenaria mercenaria*) in South Carolina. *Journal of Shellfish Research*, 18(2): 555-560.
- Jobling, M. 1994. *Fish Bioenergetics*. Chapman & Hall, London. 309 pp.
- Jones, D.S., M.A. Arthur and D.J. Allard. 1989. Sclerochronological records of temperature and growth from shells of *Mercenaria mercenaria* from Narragansett Bay, Rhode Island. *Marine Biology*, 102: 225-234.

- Kennish, M.J. and R.E. Loveland. 1980. Growth models of the northern quahog, *Mercenaria mercenaria* (Linné). *Proceedings of the National Shellfisheries Association*, 70: 230-239.
- King, M. 1995. *Fisheries biology, assessment and management*. Fishing News Books, Oxford. 341 pp.
- Malinowski, S.M. 1988. Variable growth rates of seed clams, *Mercenaria mercenaria* (Linné) in an upflow nursery system and the economics of culling slow growing animals. *Journal of Shellfish Research*, 7(3): 359-365.
- Malinowski, S.M. and S.E. Siddall. 1989. Passive water reuse in a commercial-scale hard clam, *Mercenaria mercenaria*, upflow nursery system. *Journal of Shellfish Research*, 8(1): 241-248.
- Malouf, R.E. and V.M. Bricelj. 1989. Comparative biology of clams: environmental tolerances, feeding, and growth. Pages 23-74. In Manzi, J.J. & Castagna (eds.), *Clam Mariculture in North America*. Elsevier, New York, 461 pp.
- Manzi, J.J., N.H. Hadley, C. Battey, R. Haggerty, R. Hamilton, and M. Carter. 1984. Culture of the northern hard clam *Mercenaria mercenaria* (Linné), in a commercial-scale, upflow, nursery system. *Journal of Shellfish Research*, 4(2): 119-124.
- Manzi, J.J., N.H. Hadley, and M.B. Maddox. 1986. Seed clam, *Mercenaria mercenaria*, culture in an experimental-scale upflow nursery system. *Aquaculture*, 54: 301-311.
- Peterson, C.H., H.C. Summerson, and P.B. Duncan. 1984. The influence of seagrass cover on population structure and individual growth rate of a suspension-

- feeding bivalve, *Mercenaria mercenaria*. *Journal of Marine Research*, 42: 123-138.
- Rice, M.A. 1992. *The northern quahog: the biology of Mercenaria mercenaria*. Rhode Island Sea Grant, University of Rhode Island, Narragansett. 60 pp.
- Rice, M.A., C. Hickox, and I. Zehra. 1989. Effects of intensive fishing effort on the population structure of quahogs, *Mercenaria mercenaria* (L., 1758), in Narragansett Bay. *Journal of Shellfish Research*, 8(2): 345-354.
- Ricker, W.E. 1975. *Computation and interpretation of biological statistics of fish populations*. Bulletin of the Fisheries Research Board of Canada. Bulletin 191, Ottawa, Canada. 382 pp.
- Slattery, J.P., R.C. Vrijenhoek, and R.A. Lutz. 1991. Heterozygosity, growth, and survival of the hard clam, *Mercenaria mercenaria*, in seagrass vs. sandflat habitats. *Marine Biology*, 111: 335-342.

GROWTH OF THE NORTHERN QUAHOG, *MERCENARIA MERCENARIA*, IN AN
EXPERIMENTAL-SCALE UPWELLER

ABSTRACT

Upwellers have proved to be extremely effective as bivalve nursery units, and their use is steadily increasing in North America. The re-analysis of previous work by others suggested an asymptotic relationship between growth (% volume increase per day) and chlorophyll-a effective flow rate (the amount food flowing past a unit biomass of northern quahogs, μg per minute per liter of northern quahog volume). The purpose of this study was to define the relationship between flow rate, stocking density, and growth in order to determine the flow rate and density that optimizes growth. Furthermore, this study was designed to investigate other significant environmental parameters influencing bivalve growth in an experimental-scale upweller system. Northern quahog, *Mercenaria mercenaria*, seed were grown from ~2 (longest axis) to ~13 mm in an experimental-scale floating upweller from June 21 to August 19, 1999 in Point Judith Pond, Wakefield, Rhode Island. Flow rates and stocking densities were varied in order to produce a chlorophyll-a effective flow rate range of 360 to 1,500 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$, and growth and environmental parameters were measured semiweekly. During the first two-week experiment (June 21 to July 7) an asymptotic relationship was observed between growth (% increase/day) and chlorophyll-a effective flow rate. A significant difference in growth was found between the treatments. The difference in the functional relationship between experiments 1 and 3 was possibly related to lower DO values, which reduced differential growth in experiment 3. In experiment 1, the low-biomass treatments grew faster than the high-biomass treatments. A significant difference in growth between treatments was also observed in experiment 3, although the asymptotic

relationship was less pronounced. In experiment 3, the high-biomass replicates grew faster than the low-biomass replicates. Experiments 1 and 3 both experienced similar environmental conditions; however, experiment 1 encountered higher morning dissolved oxygen (DO) levels. In addition, the within experiment variability in experiment 3 was much less than the variability in experiment 1; therefore, accentuating growth differences in experiment 3. In both experiments 1 and 3 maximum growth occurred near treatment 2 in a range of chlorophyll-a effective flow rates of 550 to 650 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$. In experiments 2 and 4 there were no significant differences in growth between treatments.

Growth appeared to be limited by low oxygen. In order to eliminate the effect of food limitation on growth, the upper third of the replicates (the fastest growing animals) were used to calculate the relative growth rate (RGR) during the two-month experiment. Growth was linearly correlated with morning-dissolved oxygen ($R^2 = 0.42$) and with chlorophyll-a ($R^2 = 0.35$). The critical DO threshold for growth in upwellers appears to be 5 ppm, below which growth is adversely affected. During this study, morning DO levels were less than 50 % saturated, indicating the potential for DO levels to be increased. Future research should investigate methods for elevating DO levels in upwellers.

INTRODUCTION

Over the past decade the use of upwellers as bivalve nursery units has increased dramatically in North America (Manzi and Castagna, 1989). A number of studies have explored the relationships between flow rate, stocking density, and growth in upwellers (Hadley *et al.*, 1999, Baldwin *et al.*, 1995, Malinowski and Siddall, 1989, Malinowski, 1988, Manzi and Hadley, 1988, Manzi *et al.*, 1986, Manzi, 1985, Hadley and Manzi, 1984, Manzi *et al.*, 1984, Bayes, 1981, Claus, 1981, Manzi and Whetstone, 1981, Rodhouse and O'Kelly, 1981). The majority of research on upwellers has focused on the northern quahog, *Mercenaria mercenaria*, because of its significant aquaculture potential. In particular, the northern quahog grows well at high densities, has adapted to a variety of geographic sites along the northeast coast, and has a lucrative market.

Manzi *et al.* (1986) described a qualitative relationship between flow rate, stocking density, and growth in an experimental-scale upweller. In their experiment, stocking densities were varied while flow rates were held constant. The flow rate was converted to an effective flow rate by multiplying the amount of food ($\mu\text{g}/\text{l}$ of chlorophyll-a) by the flow rate (l/min). The amount of food passing by a unit biomass of clams was defined as the chlorophyll-a effective flow rate ($\mu\text{g}\cdot\text{min}^{-1}\cdot\text{kg}^{-1}$). During a period of optimal northern quahog growth in the fall 1982 the authors found that a maximum biomass increase of 267 % (over 30 days) occurred at the highest chlorophyll-a effective flow rate of $1,929 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{kg}^{-1}$ and the most efficient growth (213 %) occurred at an intermediate chlorophyll-a effective flow rate of $476 \mu\text{g}\cdot\text{min}^{-1}$

$l \cdot kg^{-1}$. If growth (% increase/day) is plotted as a function of chlorophyll-a effective flow rate, the data is represented by an asymptotic relationship; in particular, as the chlorophyll-a effective flow rate increases, growth increases steeply and then levels off with increasing chlorophyll-a effective flow rates (Figure 1). Efficiency in this upweller system refers to economically optimizing both upweller space (density) and pumping capacity (flow). Theoretically, growth will be optimized at some percentage of the maximum growth rate; as indicated in Figure 1, 80 to 90% of the maximum growth rate equates to a chlorophyll-a effective flow rate range of 470 to 700 $\mu g \cdot min^{-1} \cdot kg^{-1}$.

Manzi *et al.* (1986) concluded that food supply was the primary limitation in their upweller system. Their data suggests that to obtain unlimited growth, northern quahog seed needed to remove approximately 150 $\mu g \cdot min^{-1} \cdot kg^{-1}$. The investigators deduce that northern quahog growth was reduced if more than 20 % of the ambient chlorophyll-a concentration ($\mu g/l$) was removed as water passed by the bivalves.

Consequently, to supply the necessary ration of 150 $\mu g \cdot min^{-1} \cdot kg^{-1}$ without exceeding 20 % removal, food must be supplied to the bivalves at a rate of 750 $\mu g \cdot min^{-1} \cdot kg^{-1}$.

Malinowski and Siddall (1989) confirmed that ambient chlorophyll-a concentrations were reduced by ~20% through an initial silo of northern quahogs at similar stocking densities. However, they found that after water passed through an initial group of northern quahogs it could then support an additional equivalent biomass of northern quahogs at the same growth rate. They conclude that to achieve maximum growth of northern quahogs in an upweller it is necessary to pass more water through the animals than can actually be filtered; therefore, the low rate of chlorophyll-a removal reported

by Manzi *et al.* (1986) may reflect a large amount of unused water through the system. The authors hypothesize that this surplus water may be a physical requirement of the system where minimum flow rates are required to create uniform flows through the seedbed, remove waste products, maintain water quality, and maintain a minimum concentration of chlorophyll-a.

Manzi *et al.* (1986) found that food was the primary limitation in their upweller system, while Malinowski and Siddall (1989) concluded that flow rate was the primary limitation. Malinowski and Siddall (1989) also speculate on the importance of environmental conditions, specifically water quality, but they fail to characterize these parameters in their system. Growth and survival of the northern quahog is clearly influenced by the surrounding environment. Northern quahog adults and juveniles can survive in water temperatures from 1 to 33 °C, but grow optimally at 23 °C (Stanley, 1985, Stanley and Dewitt, 1983). Northern quahogs can tolerate salinities between 10 and 35 ‰ (Stanley and Dewitt, 1983) for short periods, but prefer to inhabit waters greater than 20 ‰ (Castagna and Kraeuter, 1981). Northern quahogs have been known to endure oxygen concentrations below 1 mg O₂/l (Stanley and Dewitt, 1983) for more than three weeks; however, growth is significantly reduced and an oxygen debt is incurred when oxygen concentrations fall below 5 mg O₂/l (Stanley and Dewitt, 1983, Hamwi, 1969).

Although there is a general disagreement as to the limiting parameter for growth in upwellers, in the literature growth is clearly related to both system operating parameters (flow rate and stocking density) and environmental conditions at the site (temperature).

Given the environmental conditions in the study area, the objectives of this study were to:

- I. Develop a relationship between flow rate, stocking density, and growth so as to determine the chlorophyll-a effective flow rate that optimizes growth; and
- II. Determine the most significant limiting parameter for bivalve growth in the upweller system.

The experiment monitored growth of northern quahog seed in an experimental-scale floating upweller at three ranges of nominal chlorophyll-a effective flow rates of 350, 600 and 1,400 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$. In addition, environmental conditions were monitored at the site.

MATERIALS AND METHODS

Experimental Design

Growth of northern quahog seed was studied over an 8-week period in an experimental-scale floating upweller system located in a nutrient-rich estuary. At the beginning of the experiment the ambient chlorophyll-a concentration ($\mu\text{g/l}$) was measured at the site, and flow rates and stocking densities were adjusted to achieve three nominal ranges of chlorophyll-a effective flow rates, including a low ($\sim 350 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$), medium ($\sim 600 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$), and high range ($\sim 1,200 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$). Each combination of effective flow rate ($\mu\text{g}/\text{min}$) and northern quahog biomass (l) or chlorophyll-a effective flow rate ($\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$) represents a treatment, as shown in Table 1. A sample calculation of initial chlorophyll-a effective flow rates for the first growth interval (June 21 to June 24, 1999) is illustrated in Table 2. The average chlorophyll-a concentration during the time period was $11.70 \pm 2.06 \mu\text{g/l}$ (S.E.) and the flow rates were set at 4 l/min, 6 l/min, and 8 l/min resulting in three effective flow rates of 38.36 $\mu\text{g}/\text{min}$, 57.84 $\mu\text{g}/\text{min}$, and 77.12 $\mu\text{g}/\text{min}$. The northern quahog seed were initially stocked at a biomass of 0.055 l (density of $0.3 \text{ l}/\text{cm}^2$) and 0.109 l (density of $0.6 \text{ l}/\text{cm}^2$) resulting in the desired range of chlorophyll-a effective flow rates. The experiment was a two (density) by three (effective flow rate) factorial design with six treatments of chlorophyll-a effective flow rates. Each treatment was replicated in triplicate resulting in a total of 18 observations (silos).

Site Location

The experiment was conducted at Ram Point Marina, Inc., at the head of Point Judith Pond, Wakefield, Rhode Island (41°25.57'N; 71°29.87'W) (Figure 2). Ram Point Marina, Inc. is located on a spit between Silver Spring Cove and the Upper Pond. The site was selected to take advantage of the relatively high and consistent phytoplankton biomass (chlorophyll-a concentrations >10 µg/l, Rheault, 1995) during the summer months. The experimental-scale floating upweller was situated at the northernmost corner of the marina to ensure a water depth > 1.4 meters at mean low tide.

Upweller System

An experimental-scale floating upweller was designed and constructed so as to ensure the control of flow through each silo (Figure 3). The upweller unit was 4.27 m long, 1.22 m wide, and 1.35 m deep. Two 25 cm inside diameter (ID) polyvinyl chloride (PVC) pipes were positioned at the base and ran the length of the unit forming a manifold. Ten 15 cm (ID) silos were plumbed into the top of each manifold. Flow was provided by a ½ horsepower axial flow pump (Ice Eater, Power House) mounted in each manifold. Water was pumped along the manifold, flowed up each 15 cm silo, and exited through an 8 cm (ID) ball valve plumbed into the top of each silo. The seed were placed on a Nytex screen 0.5 m above the silo's base. When the unit was in operation, each ball valve lay approximately 8 cm above the water line. Flow through each silo was manipulated with the ball valve and was measured volumetrically with a graduated cylinder and a stopwatch.

Northern quahog seed (300,000 at 0.6 mm) were purchased from Bluepoints Company, Inc., West Sayville, New York. The seed were held in the upweller until they reached > 2 mm (longest axis).

Data Collection

At the beginning of each experiment the seed were pulled from the unit, sieved, and randomly distributed throughout the 18 replicates at a biomass of 0.055 l (wet volume) and 0.109 l. In addition, the valve length of a random sample ($n = 75$) of seed was measured to the nearest 0.01 mm with vernier calipers. Five sub-samples of northern quahogs were also taken to develop a relationship between wet volume (l) and wet weight (kg). Each experiment was terminated when the biomass in the slowest growing replicate doubled. This occurred approximately every two weeks during the summer. At the termination of each two-week experiment, the valve length of a random sample ($n = 25$) of northern quahogs from each replicate was determined. Four two-week experiments were completed during the summer 1999.

The change in volume of each silo was measured semiweekly resulting in 3 to 4 day growth intervals. Semiweekly flow rates to each silo were also measured in the morning or late at night to minimize wave activity. Care was taken to ensure that the upweller unit was not altered during measurements and flows were adjusted accordingly.

Chlorophyll-a (Chl-a), particulate organic matter (POM), temperature, salinity, and dissolved oxygen (DO) were measured semiweekly from an empty silo. With the start of the second two-week experiment (July 7) all environmental parameters were

taken in the morning, midday, and evening to quantify daily fluctuations at the site. Discrete chlorophyll-a samples ($n = 3$) were taken with a syringe. Samples were pre-filtered with a $150\ \mu\text{m}$ Nyltex screen to remove particulates that bivalves are unable to filter (Defosseze and Hawkins, 1997). Samples (10 ml) were forced through a 25 mm diameter Whatman GF/F filter contained in a 25 mm Swinnex filter holder. The procedure for chlorophyll-a analysis is slightly modified from the standard procedure outlined in Strickland and Parsons (1972). Filters were dissolved in acetone for 24 hours and read on a Turner Designs fluorometer (Model 10-005R, Turner Designs, Inc., Sunnyvale, CA). All samples were corrected for phaeophytin-a. One-liter samples were also taken ($n = 2$) for POM analysis. The samples were pre-filtered on a $150\ \mu\text{m}$ Nyltex screen and later analyzed in the laboratory. In the laboratory, samples were vacuum pumped through a pre-ashed 47 mm Whatman GF/F filter (normal pore size $0.1\ \mu\text{m}$), rinsed with isotonic ammonium formate, and dried in an oven at $110\ ^\circ\text{C}$ for 24 to 48 hours. Filters were then ashed for > 6 hours at $450\ ^\circ\text{C}$ in a muffle furnace. Filters were weighed on an Ohaus electronic balance (Model AS120) to the nearest 0.1 mg. Temperature and salinity were measured with an YSI (Model 30) probe and oxygen was measured with an YSI (Model 55) probe. The oxygen probe was calibrated prior to each measurement.

When measuring the change in volume of northern quahog seed, each silo and screen were cleaned with freshwater. Once a week the remainder of the upweller manifold was cleaned by a diver to ensure consistent flow through the system.

Approximately 10 days into each of the experiments a feeding rate experiment was completed to quantify the amount of ambient chlorophyll-a removed by the

northern quahogs, expressed as % clearance. Samples ($n = 2$) of 50 ml were taken from the empty silo as well as from each replicate. Sampling was conducted in the early afternoon of a clear day and was completed within a 10-minute window. Samples were vacuum filtered in the laboratory through a 25 mm Whatman GF/F filter within 2 hours of sampling. Chlorophyll-a analysis was completed as previously outlined.

Data Analysis:

The chlorophyll-a effective flow rate ($\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$) for each replicate was calculated as the product of the average chlorophyll-a concentration ($\mu\text{g/l}$) during the period and the flow rate (l/min) to the replicate all divided by the average biomass (l) of the replicate during the same period. This study characterized growth as the relative growth rate (RGR) and was calculated as:

$$\text{RGR} = \{[(\text{Volume}_{(\text{final})} - \text{Volume}_{(\text{initial})}) / \text{Volume}_{(\text{initial})}] \times 100\} / \# \text{ of days}$$

where volume is measured in liters. RGR is expressed as an % increase per day (% increase/day). POM (mg/l) was calculated as the difference between total suspended particulate matter (SPM) and particulate inorganic matter (PIM). Percent chlorophyll-a removed (% clearance) was calculated as:

$$\% \text{ Chlorophyll-a Removed} = [\text{Chl-a}_{(\text{ambient})} - \text{Chl-a}_{(\text{outflow})}] / \text{Chl-a}_{(\text{ambient})}$$

where $\text{Chl-a}_{(\text{ambient})}$ is the Chl-a concentration of incoming seawater and $\text{Chl-a}_{(\text{outflow})}$ is the Chl-a concentration of outgoing seawater from each replicate.

The effect of food limitation on growth

To elucidate differences in growth between treatments the total RGR (% volume increase) was divided by the largest time period available, the length of each experiment. Since the RGR (% increase/day) measures the change in volume over each two-week experiment, the average chlorophyll-a concentration and average treatment biomass during the time period was used to calculate treatment chlorophyll-a effective flow rates. Prior to ANOVA analysis, the RGR (% increase/day) was arcsine transformed (Sokal and Rohlf, 1995). Within each experiment, one-way ANOVAs were performed for each two-week experiment with the average RGR (% increase/day) as the dependent variable and treatment as the independent variable. Differences between treatment means were elucidated with the Tukey Honestly Significant Difference (HSD) test. When the one-way ANOVA proved significant, a within experiment two-way ANOVA was performed to further investigate the effective flow rate and density as independent variables. Again, the Tukey HSD test was used to verify differences in means. The strength of the relationship was characterized by the standard omega-squared (ω^2), when appropriate. The ω^2 was calculated as

$$\omega^2 = [SS_{\text{Effect}} - df_{S/A} (MS_{S/A})] / SS_T + MS_{S/A}$$

where SS_{Effect} is the sum of squares of the effect, $df_{S/A}$ is the degrees of freedom for the error term, $MS_{S/A}$ is the mean squares for the error term, and SS_T is the sum of squares total.

A between experiment one-way ANOVA was performed to elucidate growth differences between the two-week experiments. The Tukey HSD test quantified differences between means.

The effect of environmental characteristics on growth

In order to illustrate the effect of environmental parameters on northern quahog growth, growth was characterized at the finest possible scale. In particular, RGR was calculated for each 3 to 4 day period (growth interval) between semiweekly volume determinations. The daily value of each environmental parameter was averaged over the concurrent growth interval.

To eliminate the effect of food limitation on growth, RGR of the upper third of the replicates (upper 1/3 RGR) was calculated. A linear regression analysis (SAS Institute, Inc.) of the upper 1/3 RGR was performed with temperature, salinity, chlorophyll-a, and dissolved oxygen to determine which independent variables were significant in determining growth. Dissolved oxygen concentrations were converted to percent saturation based on temperature and salinity measurements (Benson and Krause, 1984). A step-wise linear regression analysis was also performed to elucidate the most significant parameter(s) for predicting growth in the experiment.

RESULTS

The effect of food limitation on growth

There were no observed mortalities during the course of the two-month experiment. Calculated mortalities were extremely variable in experiments 1 and 2 because counts per ml were not replicated. In addition, counts were not made before and after sieving. In experiments 3 and 4, counts per ml were replicated ($n = 3$) and counts were made before and after sieving. Mortality was calculated to be $111 \pm 3\%$ (S.E.) and $99 \pm 2\%$ (S.E.) respectively.

The first experiment began on June 21 and ended on July 7, 1999 (16 days) and the northern quahogs grew from 3.11 ± 0.06 mm (S.E.) to 3.95 ± 0.05 mm (S.E.). The average chlorophyll-a concentration was 16.42 ± 2.25 $\mu\text{g/l}$ (S.E.) and the average treatment biomass ranged from 165.8 to 85.5 ml. The chlorophyll-a effective flow rate ranged from 420 to 1,445 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$ roughly correlating with a RGR from 4.76 to 9.32 % increase/day. As the chlorophyll-a effective flow rate increased, the RGR increased until ~ 650 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$ at which point growth leveled off (Figure 4). Growth, as measured by RGR, was subjected to a one-way ANOVA with six levels of treatment. This was found to be statistically significant ($F(5, 11) = 5.48, p < 0.05$). The strength of the relationship was 0.57 as indexed by the standard omega-squared (ω^2). The Tukey HSD test indicated that the mean RGR for treatment 1 ($\underline{M} = 5.54$) was significantly lower than the means for treatment 4 ($\underline{M} = 8.14$), 5 ($\underline{M} = 8.41$), and 6 ($\underline{M} = 9.26$). To investigate the effect of effective flow rate and biomass on growth, a two-way ANOVA was performed with three levels of seston flux and two levels of

volume. Both effective flow rate ($F(2, 11) = 5.13, p < 0.05$) and biomass ($F(1, 11) = 13.36, p < 0.05$) were statistically significant. The strength of the relationship (ω^2) was 0.21 and 0.31, respectively. The interaction between effective flow rate and biomass was found to be ordinal; therefore, the main effects were examined by the Tukey HSD test. The Tukey HSD test indicated that the low-biomass treatments ($M = 8.60$) grew faster than the high-biomass treatments ($M = 6.99$).

The second experiment began on July 7 and ended on July 22, 1999 (15 days) and the northern quahogs grew from 3.46 ± 0.11 mm (S.E.) to 6.28 ± 0.07 mm (S.E.). The average chlorophyll-a concentration was 11.83 ± 1.16 $\mu\text{g/l}$ (S.E.) and the average treatment biomass ranged from 205.6 ml to 91.6 ml. The chlorophyll-a effective flow rate ranged from 231 to 977 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$ roughly correlating with a RGR from 9.58 to 12.73 % increase/day (Figure 5). RGR was consistently high within the chlorophyll-a effective flow rate range specified. RGR was subjected to a one-way ANOVA and there was no statistical difference between treatments ($F(5, 11) = 1.48, p > 0.05$).

The third experiment began on July 22 and ended on August 5, 1999 (14 days) and the northern quahogs grew from 7.04 ± 0.11 mm (S.E.) to 9.96 ± 0.07 mm (S.E.). The average chlorophyll-a concentration was 18.55 ± 2.12 $\mu\text{g/l}$ (S.E.) and the average treatment biomass ranged from 184.8 to 84.6 ml. The chlorophyll-a effective flow rate ranged from 411 to 1,720 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$ roughly corresponding to a RGR from 7.79 to 10.09 % increase/day (Figure 6). The RGR increased slightly with an increase in the chlorophyll-a effective flow rate until ~ 610 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$, at which point growth decreased and leveled off. RGR was subjected to a one-way ANOVA and was found to be statistically significant ($F(5, 11) = 7.13, p < 0.05$). The strength of the

relationship was 0.64 as indexed by the ω^2 . The Tukey HSD test indicated that the mean RGR for treatment 2 ($\bar{M} = 9.76$) was significantly higher than the means for treatment 4 ($\bar{M} = 7.97$), 5 ($\bar{M} = 8.62$), and 6 ($\bar{M} = 8.38$). In addition, the mean RGR for treatment 4 ($\bar{M} = 7.97$) was significantly lower than the mean for treatment 3 ($\bar{M} = 9.20$). A two-way ANOVA found both effective flow rate ($F(2, 11) = 5.99, p < 0.05$) and biomass ($F(1, 11) = 22.33, p < 0.05$) were statistically significant. The strength of the relationship (ω^2) was 0.21 and 0.45, respectively. The interaction between effective flow rate and biomass was found to be ordinal; therefore, the main effects were examined by the Tukey HSD test. The Tukey HSD test indicated that the high-biomass treatments ($\bar{M} = 9.25$) grew faster than the low-biomass treatments ($\bar{M} = 8.32$). The Tukey HSD test also found that the replicates with an effective flow rate of 111.3 $\mu\text{g}/\text{min}$ ($\bar{M} = 9.19$) grew faster than the replicates with an effective flow rate of 74.2 $\mu\text{g}/\text{min}$ ($\bar{M} = 8.87$).

The fourth experiment began on August 5 and ended on August 19, 1999 (14 days) and the northern quahogs grew from 9.37 ± 0.12 mm (S.E.) to 11.47 ± 0.08 mm (S.E.). The average chlorophyll-a concentration was 17.91 ± 3.17 $\mu\text{g}/\text{l}$ (S.E.) and the average treatment biomass ranged from 147.4 to 73.4 ml. The chlorophyll-a effective flow rate ranged from 491 to 1,905 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$ roughly corresponding to a RGR from 4.98 to 5.96 % increase/day (Figure 7). RGR was consistently low within the chlorophyll-a effective flow rate range specified. RGR was subjected to a one-way ANOVA and there was no statistical difference between treatments ($F(5, 11) = 0.76, p > 0.05$).

A one-way ANOVA was performed to compare the RGR between the two-week experiments. This was found to be statistically significant ($F(3, 64) = 135.34, p < 0.05$) with an ω^2 of 0.80. The Tukey HSD test indicated that there was a significant difference between all the mean RGRs, with growth highest in experiment 2 ($\bar{M} = 11.89$) and decreasing in experiments 3 ($\bar{M} = 8.81$), 1 ($\bar{M} = 7.71$), and 4 ($\bar{M} = 5.57$).

The effect of environmental characteristics on growth

The upper 1/3 RGR varied considerably during the course of the experiment from a high of 10.37 ± 0.43 % increase/day (S.E.) on June 22 to a low of 5.03 ± 0.41 % increase/day (S.E.) on June 29 (Figure 8). During the course of the two-month experiment, RGR decreased sharply (June 22-June 29), then increased (June 29-July 17), and then gradually decreased (July 17-August 19).

Temperature during the experiment varied from 21.4 to 27.3 °C (Figure 9). Other than a brief drop in temperature in mid July due to a rainstorm, temperature was fairly consistent during the experiment. A linear regression analysis indicated that temperature was not significant in determining growth as indicated by the upper 1/3 RGR ($F(1, 15) = 0.58, p > 0.05$). Similarly, salinity during the experiment was relatively consistent ranging from 21.4 to 29.9 ‰ (Figure 10). Linear regression analysis determined that salinity was not significant in predicting the upper 1/3 RGR ($F(1, 15) = 0.70, p > 0.05$). The seston concentration, as indexed by the chlorophyll-a concentration, varied substantially during the course of the experiment from peaks of 21.2 ± 1.23 µg/l (S.E.) on June 28 and 22.8 ± 0.86 µg/l (S.E.) on July 3, to a nadir of 9.5 ± 0.09 µg/l (S.E.) on July 13 (Figure 11). Generally, as chlorophyll-a

concentrations increased growth decreased. Similarly, as chlorophyll-a concentrations decreased growth increased. Linear regression analysis indicated that this trend was significant ($F(1, 15) = 7.46, p < 0.05$) with a correlation coefficient (R^2) of 0.35 (Figure 12). There was a minimal amount of variability between chlorophyll-a measurements as exemplified by the low standard errors between measurements. The chlorophyll-a concentration during the day, however, varied considerably as indicated by the high standard errors between morning, midday, and evening chlorophyll-a determinations (appendix I). Morning DO was used to quantify the effect of limiting dissolved oxygen on growth as morning DO values were consistently the lowest oxygen values experienced by the northern quahogs. Morning DO values ranged from a high of 8.00 ppm on June 22 to a low of 3.37 ppm on July 8 (Figure 13). Morning DO values correlate with the upper 1/3 RGR during the two-month experiment. As morning DO values decreased growth decreased; conversely, as morning DO values increased growth increased (Figure 13). A linear regression analysis indicated that this trend was significant ($F(1, 15) = 10.13, p < 0.05$) with a correlation coefficient (R^2) of 0.42 (Figure 14). Morning dissolved oxygen (ppm) tracked the morning percent saturation of DO (Figure 15). During periods of low morning DO (4 to 3 ppm), % saturation approached 50 %.

Growth was best characterized with morning DO and chlorophyll-a ($F(2, 15) = 8.22, p < 0.05$) resulting in an R^2 of 0.56. As the chlorophyll-a concentration increased morning DO decreased and as the chlorophyll-a concentration decreased morning DO increased (Figure 16).

Clearance rate experiments

A separate clearance rate experiment was performed during each two-week experiment. Clearance rate experiments took place on July 2 (experiment 1), July 22 (experiment 2), August 3 (experiment 3), and August 17 (experiment 4). On July 22 and August 17, more than half of the percent clearance determinations were negative. In other words, the amount of incoming chlorophyll-a was less than the amount leaving. In the remaining clearance rate experiments there was no detectable trend.

DISCUSSION

The effect of food limitation on growth

The one-way ANOVAs found significant differences in growth between treatments in experiments 1 and 3, but none in experiments 2 and 4. Experiments 1 and 3 were characterized by relatively high morning DO values, while experiments 2 and 4 experienced relatively low morning DO values. According to the re-evaluation of the data (Figure 1) presented in Manzi *et al.* (1986), growth as a function of the chlorophyll-a effective flow rate (the amount of food passing by a unit biomass of clams) should follow an asymptotic function. Specifically, growth should increase from the origin (zero growth and zero chlorophyll-a effective flow rate) with increasing chlorophyll-a effective flow rates until a particular point where growth asymptotes or even decreases.

In the first experiment, growth (% increase/day) followed the relationship presented in Figure 1. Growth increased as the chlorophyll-a effective flow rate increased until $\sim 650 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$ at which point growth reached an asymptote. The one-way ANOVA found a significant difference in growth between the treatments with a relatively strong relationship as indexed by the standard omega-squared ($\omega^2 = 0.57$). Furthermore, treatment 1 grew significantly slower than treatments 4, 5, and 6. Treatments 4, 5, and 6 represent the asymptote of the function where growth asymptotes regardless of an increase in the chlorophyll-a effective flow rate. In addition, treatments 4, 5, and 6 were those with a low initial stocking density of $0.3 \text{ l}/\text{cm}^2$. In order to further investigate the effect of effective flow rate and biomass on

growth a two-way ANOVA was performed. There were significant differences between growth with the levels of effective flow rate and biomass. In particular, the low-biomass replicates (treatments 4, 5, and 6) grew faster than the high-biomass replicates (treatments 1, 2, and 3).

In the third experiment, the one-way ANOVA also indicated a significant difference in growth between the treatments with an even stronger relationship ($\omega^2 = 0.64$). The functional relationship between growth and chlorophyll-a effective flow rate was different than that postulated in Figure 1. Growth increased slightly with increasing chlorophyll-a effective flow rate, but then decreased slightly, reaching an asymptote above $1,000 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$. This trend is supported by the Tukey HSD test, which indicated that treatment 2 grew significantly faster than treatments 4, 5, and 6. In addition, treatment 3 grew significantly faster than treatment 4. Since treatment 3 and treatment 4 have nearly the same chlorophyll-a effective flow rate, a significant difference in growth indicates an effect of biomass on growth, with the higher biomass treatment growing faster than the lower biomass treatment. The two-way ANOVA also found a significant effect of biomass on growth with the high-biomass replicates growing faster than the low-biomass replicates. The two-way ANOVA also indicated a significant effect of seston flux on growth with the replicates with the intermediate effective flow rate of $111.3 \mu\text{g}/\text{min}$ growing faster than the replicates with the lower effective flow rate of $74.2 \mu\text{g}/\text{min}$.

Experiments 1 and 3 both experienced initially high morning DO values that decreased during the course of the experiment. Experiment 1 had higher initial morning DO values (8 to 7 ppm) than experiment 3 (5.5 to 6 ppm). The chlorophyll-a

concentration also increased substantially during both experiments, with values peaking at $21.19 \pm 1.23 \mu\text{g/l}$ (S.E.) in experiment 1 and $22.83 \pm 0.86 \mu\text{g/l}$ (S.E.) in experiment 3. In addition, both experiments experienced the same range of chlorophyll-a effective flow rates. The difference in the relationship between growth and chlorophyll-a effective flow rate in experiment 1 and experiment 3 is probably the result of a number of factors. First, since experiment 3 did not experience the initially high morning DO levels observed in experiment 1, the treatments might not have had a chance to separate or grow differentially. Second, the spread in replicates in experiment 3 was considerably smaller than that in experiment 1; therefore, small growth differences between treatments in experiment 3 are essentially accentuated. In other words, the statistical difference between treatments in experiment 3 is a result of the relatively small within replicate variability. In both experiments 1 and 3, maximum growth occurred near treatment 2 in a range of chlorophyll-a effective flow rates of 550 to 650 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$. In order to verify this result, growth should be investigated within the chlorophyll-a effective flow rate range of 0 to 500 $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$.

The benefit of defining a relationship between growth and the amount of food passing by a unit biomass of animals (chlorophyll-a effective flow rate) is apparent in the application to other growers. The relationship can be easily applied to upwellers in a variety of locations, provided optimal environmental conditions persist. An aquaculture extension agent could characterize the water conditions at a site to determine that the minimum water quality standards are met, such as temperature, salinity, and dissolved oxygen. The agent could then measure the amount of chlorophyll-a and estimate the average food concentration at the site. With this

estimate, the grower could determine the biomass and effective flow rate needed to optimize growth in the upweller.

The effect of environmental characteristics on growth

When environmental conditions were suitable for northern quahog growth, especially in the beginning of experiment 1, the effect of food limitation on growth was apparent. When environmental conditions were less than optimal, as in experiments 2 and 4, growth appears constant over a wide range of chlorophyll-a effective flow rates. In other words, growth was not controlled by food limitation, but some other factor. To quantify the effect of environmental conditions on growth, the upper 1/3 of replicates, the fastest growing northern quahogs, were used to determine growth. By eliminating the slowest 2/3 replicates, the effect of food limitation on growth was minimized; therefore, differences in growth were constrained by the environmental conditions at the time.

Manzi *et al.* (1986) concluded that food limited growth in their experimental-scale upweller. Although there were signs of food limitation on growth in experiments 1 and 3, growth in experiments 2 and 4 were controlled by other factors. Malinowski and Siddall (1989) determined that the flow rate limited growth in their upweller system. They surmise that flow through the upweller had to be above a critical threshold in order to create a uniform flow (distribute food evenly among the clam seed), maintain water quality, remove wastes, and provide a sufficient chlorophyll-a concentration to the northern quahogs. Although Malinowski and

Siddall (1989) were unable to quantify the effect of water quality on growth, they eluded to the importance of environmental conditions on growth.

Over the course of the two-month experiment, growth was positively correlated with morning DO and negatively correlated with chlorophyll-a. In late June and early July, the experimental site in Point Judith Pond experienced a pronounced algae bloom. The bloom was evident as an increase and peak in the chlorophyll-a concentration (Figure 11). There was a clear relationship between chlorophyll-a and morning DO, specifically as the chlorophyll-a concentration increased, morning DO levels decreased (Figure 16). The decrease in morning DO was a result of a combination of algae decomposition and algae respiration. At night, the algae were constantly respiring, converting captured energy into simple sugars, an oxygen consuming and carbon dioxide producing process. The algae were also continually dying off and decomposing, again an oxygen consuming process. A second algae bloom in the upper pond was apparent in mid August. Again, the same relationship between chlorophyll-a and morning DO was apparent. In late July, the chlorophyll-a concentration decreased substantially and morning DO levels increased. This decrease in chlorophyll-a was most likely a result of zooplankton grazing described by Bengtson (1982). Alternatively, the decrease in chlorophyll-a could have been caused by a crash or die off of a particular species of algae. The cyclic pattern of algae in the upper pond could be further verified by quantifying the species of algae present as well as the amount of zooplankton at the study site.

Regardless of the specific controlling mechanisms, an increase in algae biomass caused a distinct decrease in morning DO (< 5 ppm) resulting in depressed

clam growth. Hamwi (1969) determined that *Mercenaria mercenaria* were able to maintain a constant rate of respiration with decreasing oxygen levels until 5 ppm. The northern quahog is a classic oxygen regulator (Hamwi, 1969). As the oxygen concentration decreases, bivalves can increase their rate of oxygen consumption through two mechanisms: 1) increasing their pumping rate; or 2) increasing their percentage of oxygen utilization. Hamwi (1969) determined that the pumping rate of northern quahogs remained constant with decreasing oxygen concentrations; however, northern quahogs were able to regulate O₂ consumption by increasing the percentage of oxygen utilized. When oxygen levels reached 5 ppm or below, Hamwi (1969) found that oxygen uptake in northern quahogs decreased continuously and an oxygen debt was incurred. Once conditions were favorable, the oxygen debt was rapidly repaid in a matter of hours and northern quahogs were able to function normally.

Although juvenile northern quahogs can survive in oxygen concentrations below 1 ppm for up to three weeks (Stanley and Dewitt, 1989), 5 ppm is the critical threshold for northern quahog growth. There have been a number of studies that have investigated the effect of low oxygen levels on survival and tolerance, yet none have investigated the effect of low oxygen levels on growth. Based on the work completed by Hamwi (1969), 5 ppm is the critical threshold for northern quahog growth. When oxygen concentrations fall below 5 ppm, the northern quahogs cannot maintain sufficient oxygen uptake and incur an oxygen debt. In essence, the northern quahogs shut down and stop growing until oxygen levels rise above this critical threshold.

The results of this study stress the importance of sufficient oxygen concentrations for northern quahog growth in upweller systems. A number of

methods could be used to ensure optimal oxygen levels in an upweller. The upweller could be moved to a site that experiences lower chlorophyll-a values and higher morning DO values, but food for the northern quahog would be compromised. Alternatively, the oxygen concentration in the upweller could be increased. During periods of low morning DO (< 4 ppm), the % saturation was below 60 (Figure 15); therefore, during periods of low morning DO, oxygen concentrations have the potential of being increased. Future research should investigate the most cost effective and efficient method of increasing dissolved oxygen levels in this upweller as well as in the more traditional passive flow upwellers. With optimal DO levels, the effect of food limitation on growth can be further defined and replicated.

Clearance rate experiments

Manzi *et al.* (1986) postulated that the growth rate of northern quahogs was consistently reduced when % clearance of ambient chlorophyll-a was above 20 %, regardless of the overall amount of chlorophyll-a removed. This result suggests a threshold feeding response. Rheault and Rice (1996) found that scallop clearance rates were significantly reduced when chlorophyll concentrations fell below 12 % of ambient concentrations. Malinowski and Siddall (1989) also found that approximately 17 % of the ambient chlorophyll-a concentration was removed after the first pass through a silo of seed northern quahogs. The water was then passed through a second series of upwellers and the percentage of chlorophyll-a removed ranged from 36 to 73 %. They concluded that factors other than food limited growth of seed northern quahogs in an upweller silo.

The four discrete clearance rate experiments completed during the two-month experiment were inconclusive. Even if the clearance rate experiments proved successful, it would be nearly impossible to compare % clearance, a discrete measurement determined over the course of 20 minutes, to growth, which occurs over a much longer time period. A controlled laboratory experiment would be a more accurate method of quantifying the effect of % clearance on growth. In the laboratory, environmental conditions could be controlled and % clearance could be accurately extrapolated over a longer time period. Another method would be to place a continuous measuring device at the site to document the variability of environmental conditions and % clearance. Ideally, % clearance should be determined continuously by placing a measuring device in the inflow of the upweller as well as in each silo's outflow. Obviously this is not practically or economically feasible. Rheault and Rice (1996) developed a more economical method for measuring food depletion in the field. They measured food depletion in an experimental flume with a continuous flow Turner Designs fluorometer. By allowing the fluorometer readings to stabilize for at least one minute they were able to reduce the variability associated with discrete sampling.

SUMMARY AND CONCLUSIONS

The hypothesized relationship between growth and chlorophyll-a effective flow rate was only apparent during the first two-week experiment (experiment 1). Although there were significant differences in growth between treatments in the third two-week experiment (experiment 3), these differences were most likely the result of small within sample variability. For the remainder of the experiment, northern quahog growth was limited by environmental conditions. Specifically, the relative growth rate of the upper one-third of the replicates was positively correlated with morning-dissolved oxygen ($R^2 = 0.42$) and negatively correlated with chlorophyll-a ($R^2 = 0.35$). The critical dissolved oxygen threshold for northern quahog growth in the experimental-scale upweller appeared to be 5 ppm, below which growth was adversely affected. Future research should investigate the most effective method for elevating DO levels in commercial upwellers.

Table 1. Chlorophyll-a effective flow rates and their corresponding treatment.

Medium	Treatment
High	Treatment 1
Low	Treatment 2

Effective Flow Rate ($\mu\text{g}/\text{min}$)	Initial Stocking Biomass (liters)	
	Low	High
Low	Treatment 4	Treatment 1
Medium	Treatment 5	Treatment 2
High	Treatment 6	Treatment 3

Table 2. Sample calculations of initial chlorophyll-a effective flow rates for the first growth interval (June 21 to June 24) in experiment 1. The average chlorophyll-a concentration during the time period was $11.70 \pm 2.06 \mu\text{g/l}$ (S.E.).

Effective Flow Rate ($\mu\text{g}/\text{min}$)	Initial Stocking Biomass (l)	
	0.055	0.109
38.56	$701 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$	$354 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$
57.84	$1,052 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$	$531 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$
77.12	$1,402 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$	$708 \mu\text{g}\cdot\text{min}^{-1}\cdot\text{l}^{-1}$

Figure 1. Growth (% increase/day) of northern quahogs as a function of chlorophyll-a effective flow rate re-plotted from Manzi *et al.* (1986).

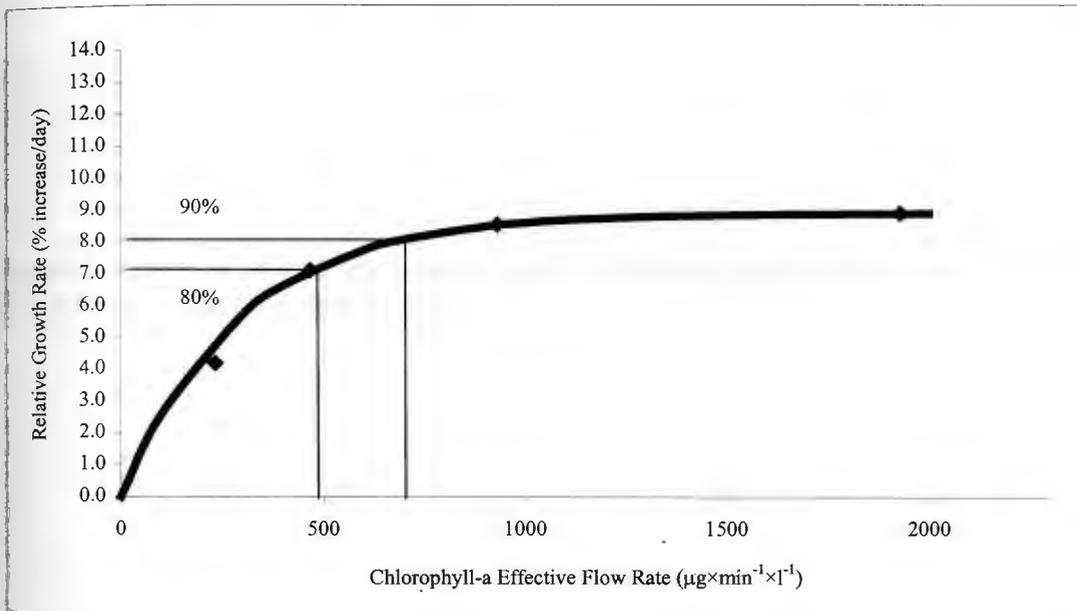
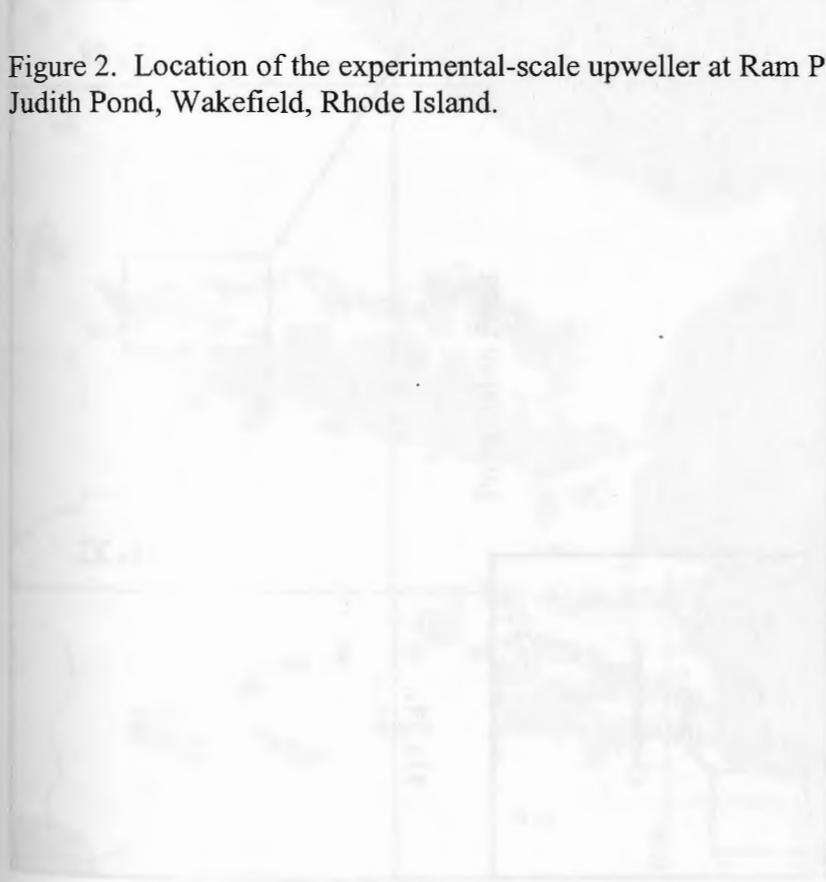
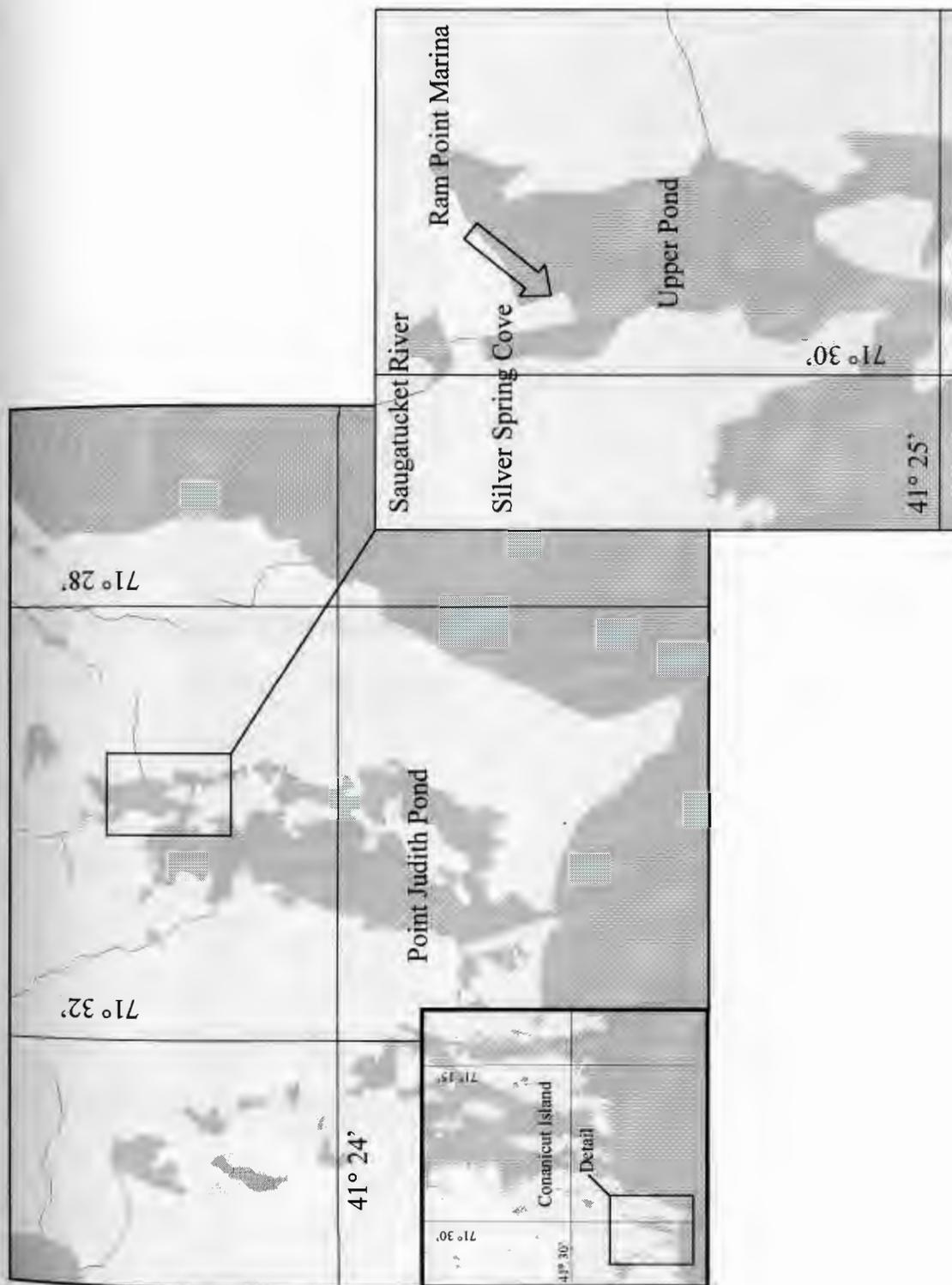




Figure 2. Location of the experimental-scale upweller at Ram Point Marina, Point Judith Pond, Wakefield, Rhode Island.





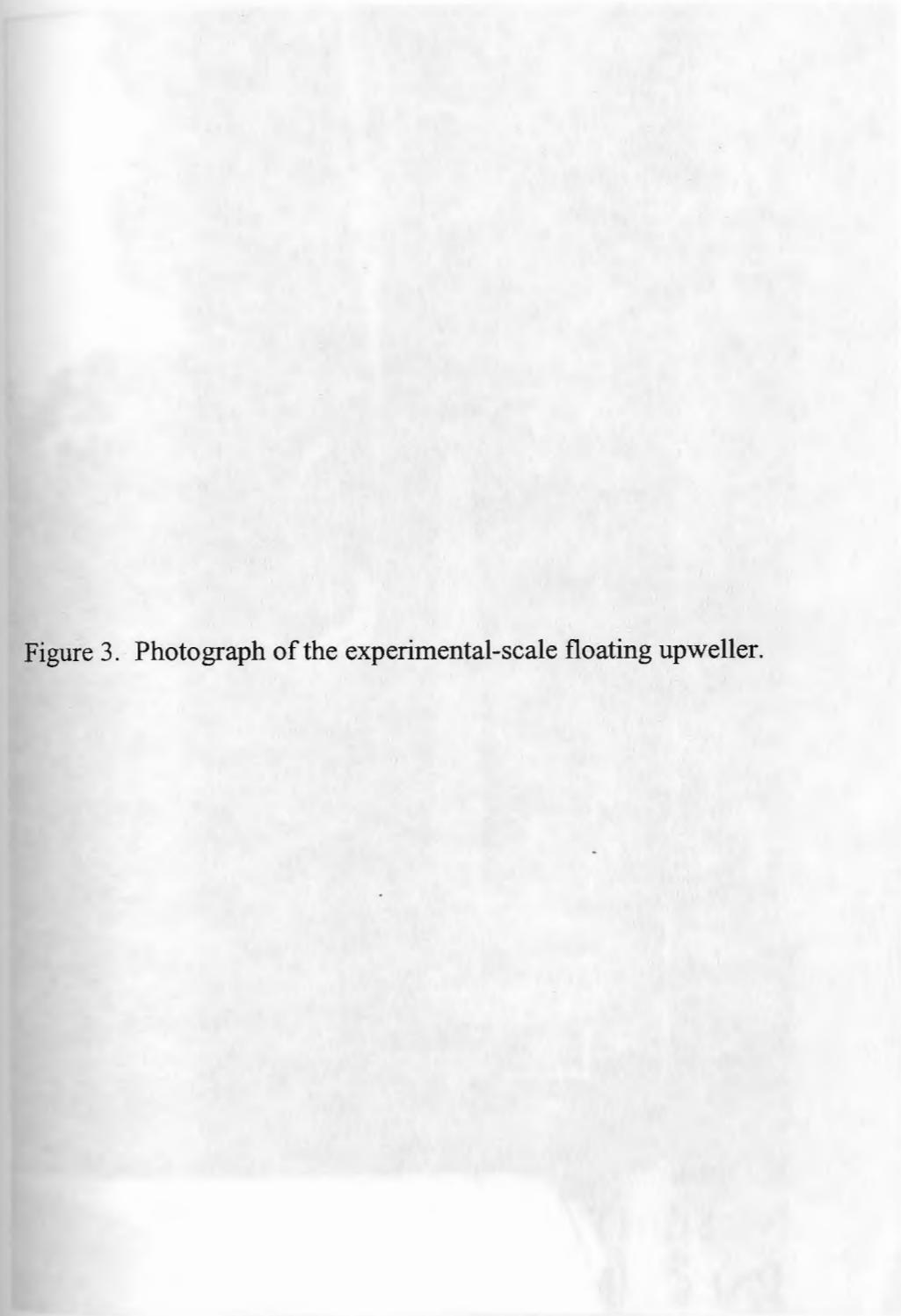


Figure 3. Photograph of the experimental-scale floating upweller.

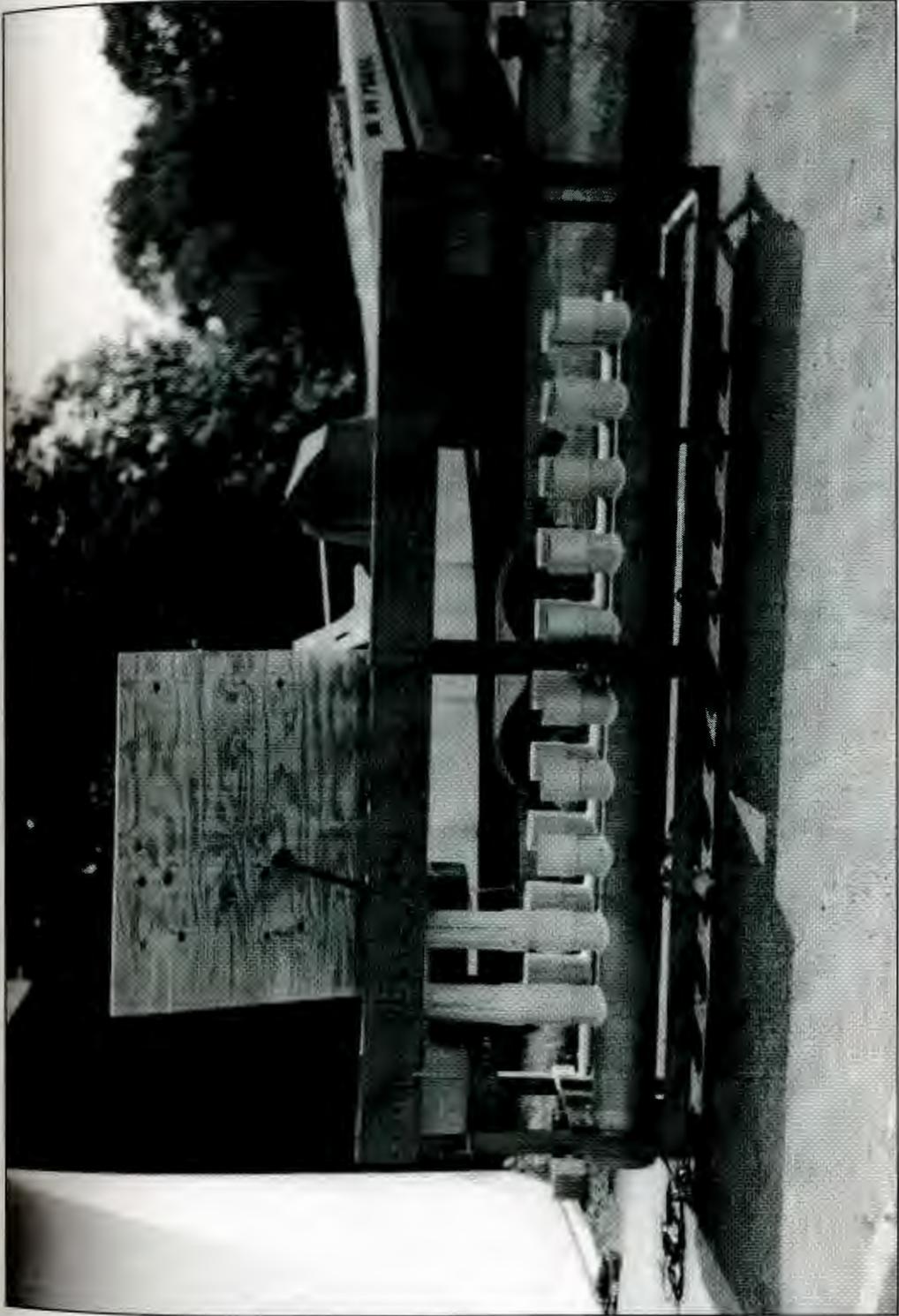


Figure 4. Growth (% increase/day) as a function of chlorophyll-a effective flow rate for experiment 1 (June 21 to July 7, 1999). The average chlorophyll-a concentration during the time period was $16.42 \pm 2.25 \mu\text{g/l}$ (S.E.).

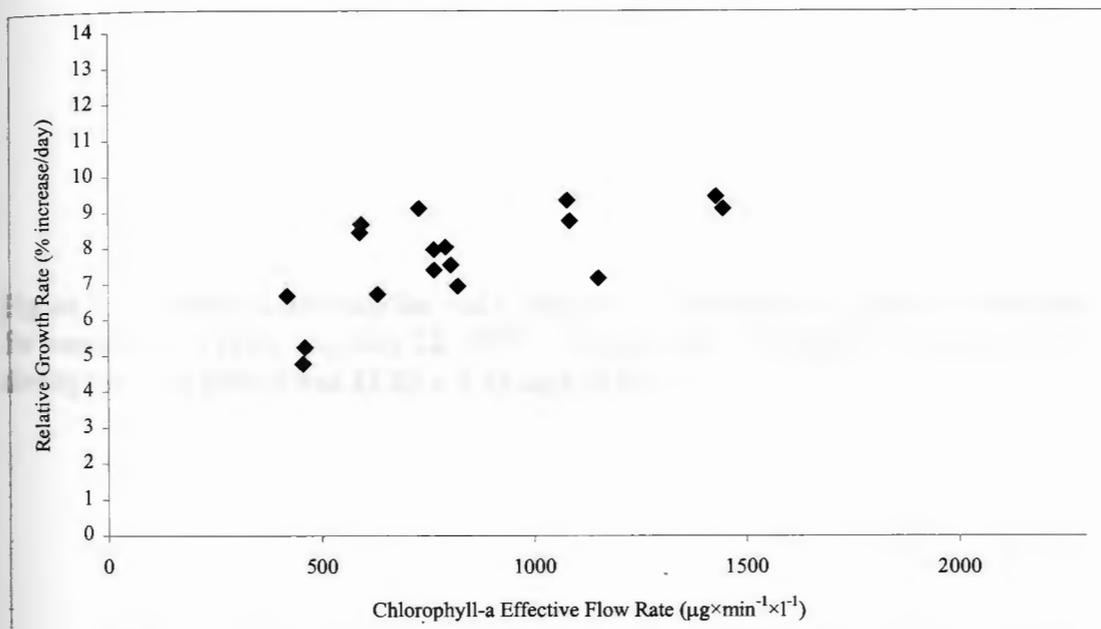


Figure 5. Growth (% increase/day) as a function of chlorophyll-a effective flow rate for experiment 2 (July 7 to July 22, 1999). The average chlorophyll-a concentration during the time period was $11.83 \pm 1.16 \mu\text{g/l}$ (S.E.).

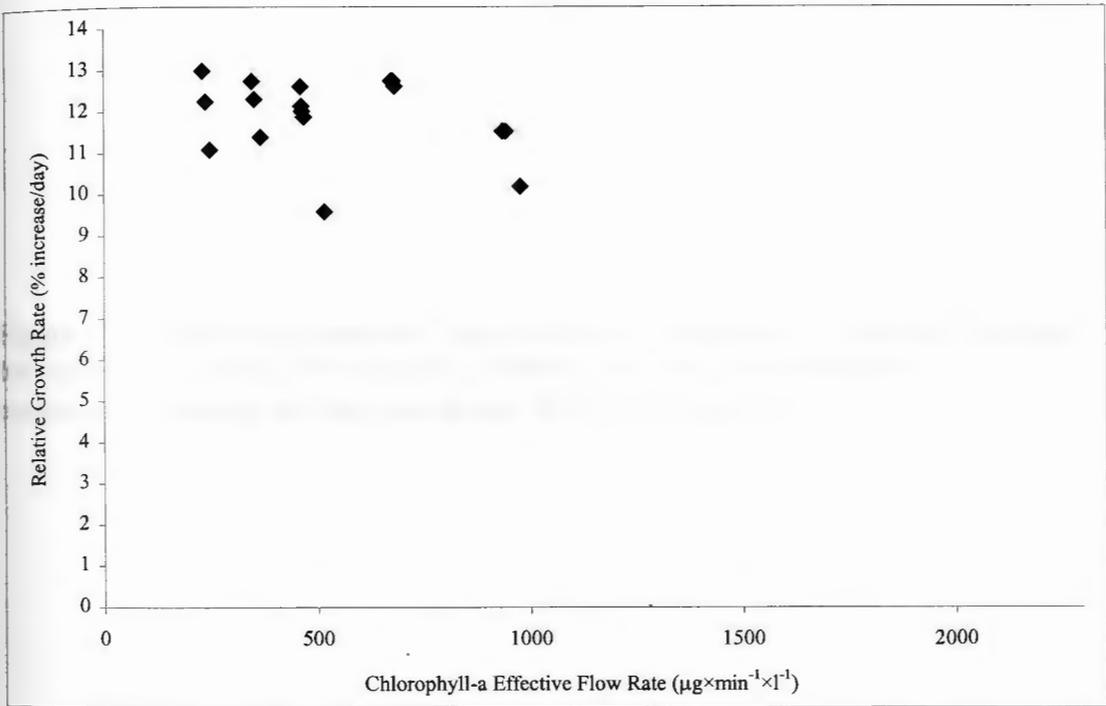


Figure 6. Growth (% increase/day) as a function of chlorophyll-a effective flow rate for experiment 3 (July 22 to August 5, 1999). The average chlorophyll-a concentration during the time period was $18.55 \pm 2.12 \mu\text{g/l}$ (S.E.).

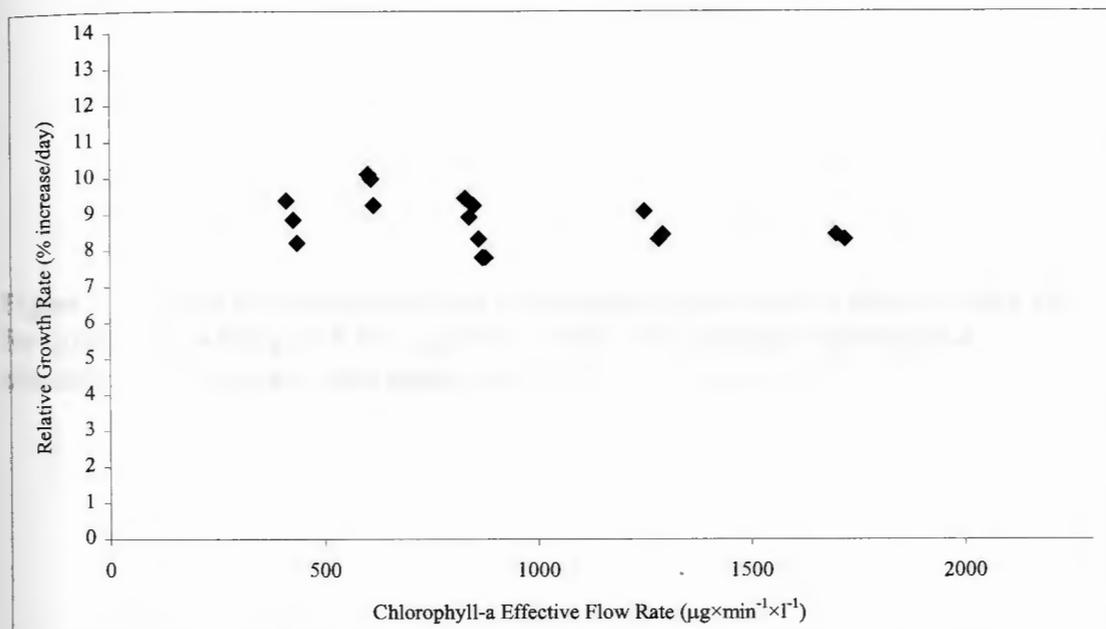


Figure 7. Growth (% increase/day) as a function of chlorophyll-a effective flow rate for experiment 4 (August 5 to August 19, 1999). The average chlorophyll-a concentration during the time period was $17.91 \pm 3.17 \mu\text{g/l}$ (S.E.).

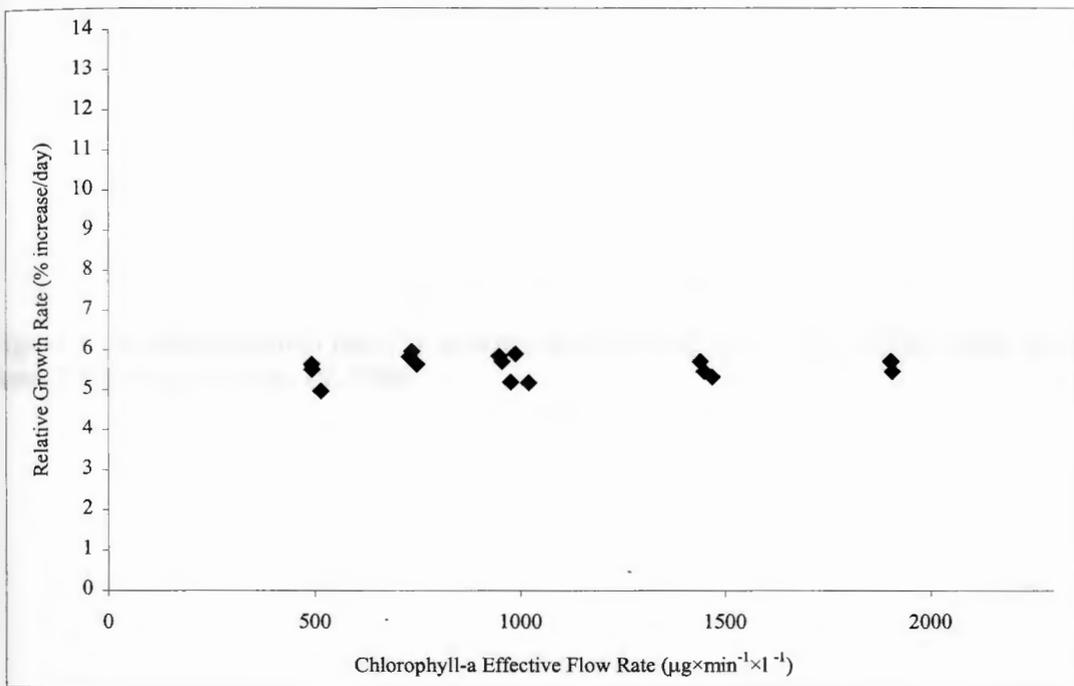


Figure 8. Relative growth rate (% increase/day) for the upper third of replicates from June 21 through August 19, 1999.

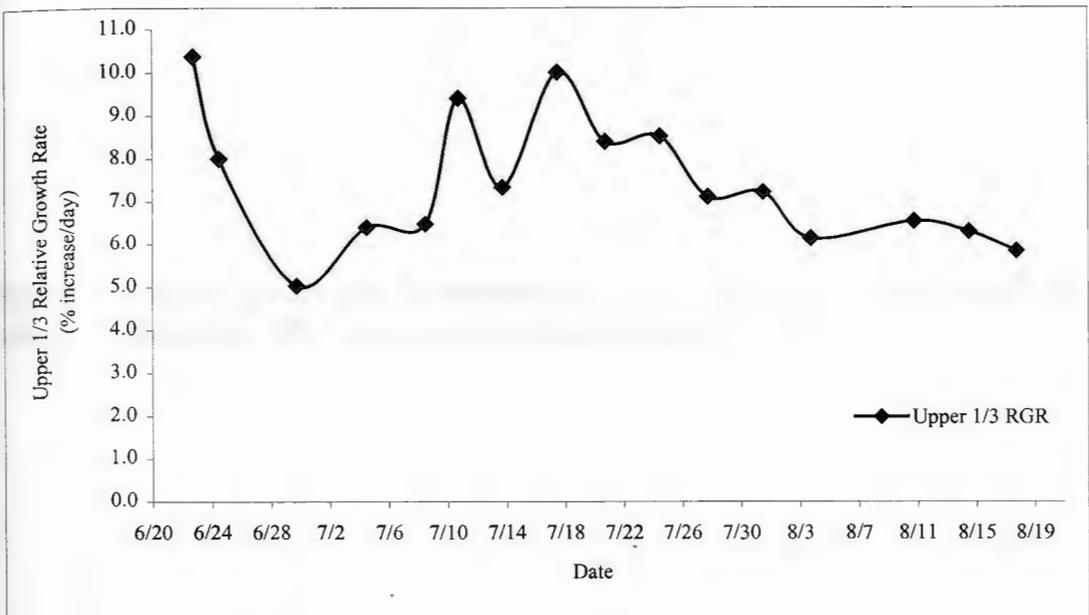


Figure 9. Relative growth rate (% increase/day) for the upper third of replicates with morning temperature ($^{\circ}\text{C}$) from June 21 through August 19, 1999.

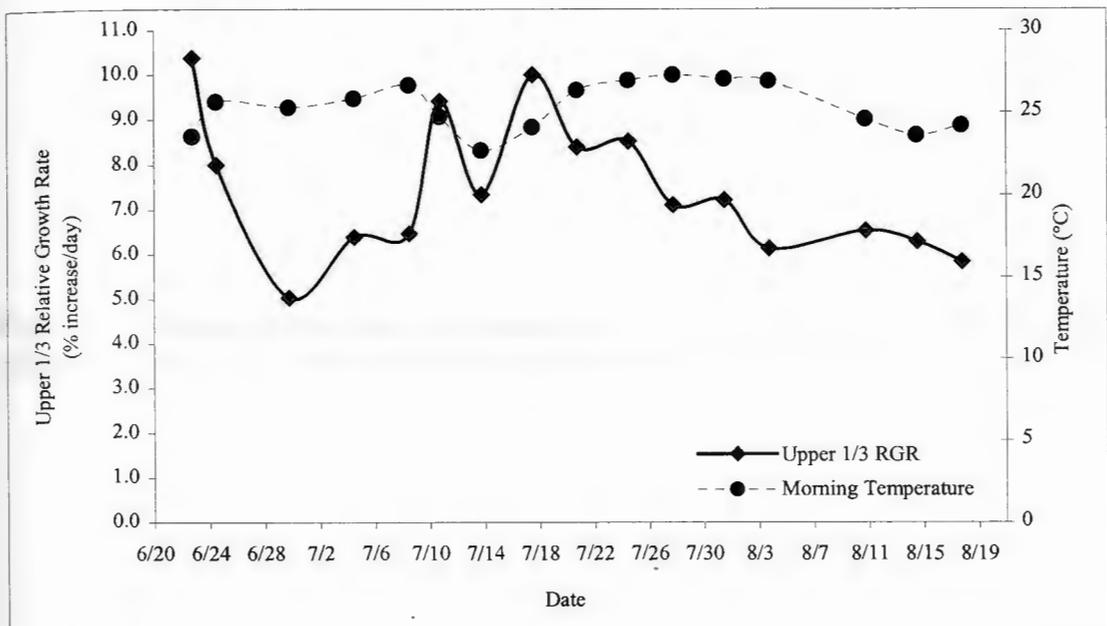


Figure 10. Relative growth rate (% increase/day) for the upper third of replicates with morning salinity (‰) from June 21 through August 19, 1999.

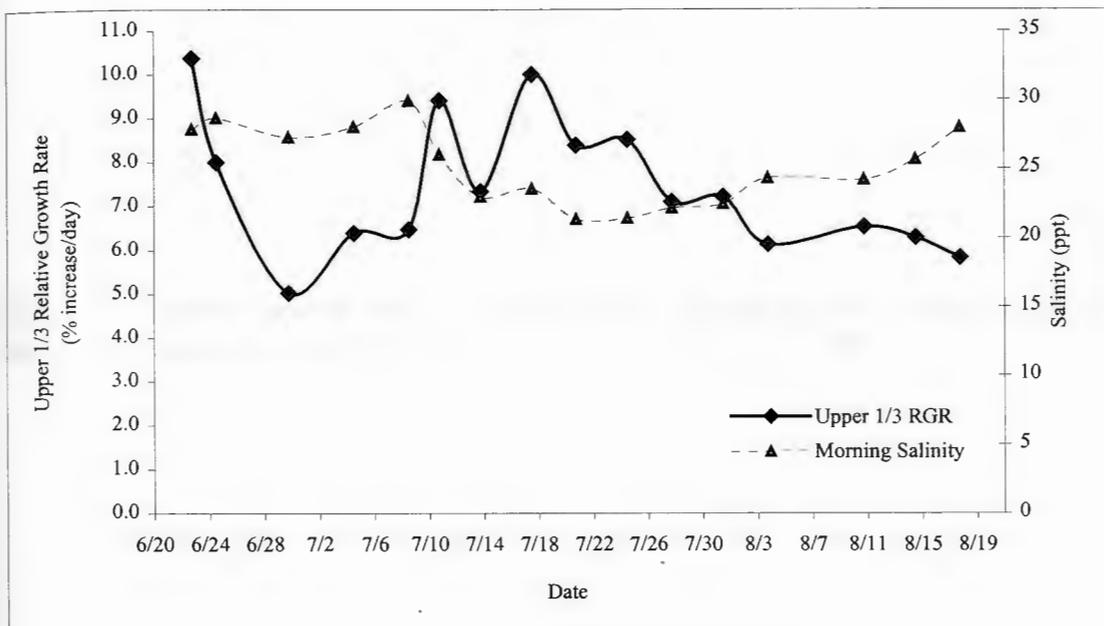


Figure 11. Relative growth rate (% increase/day) for the upper third of replicates with morning chlorophyll-a ($\mu\text{g/l}$) from June 21 through August 19, 1999.

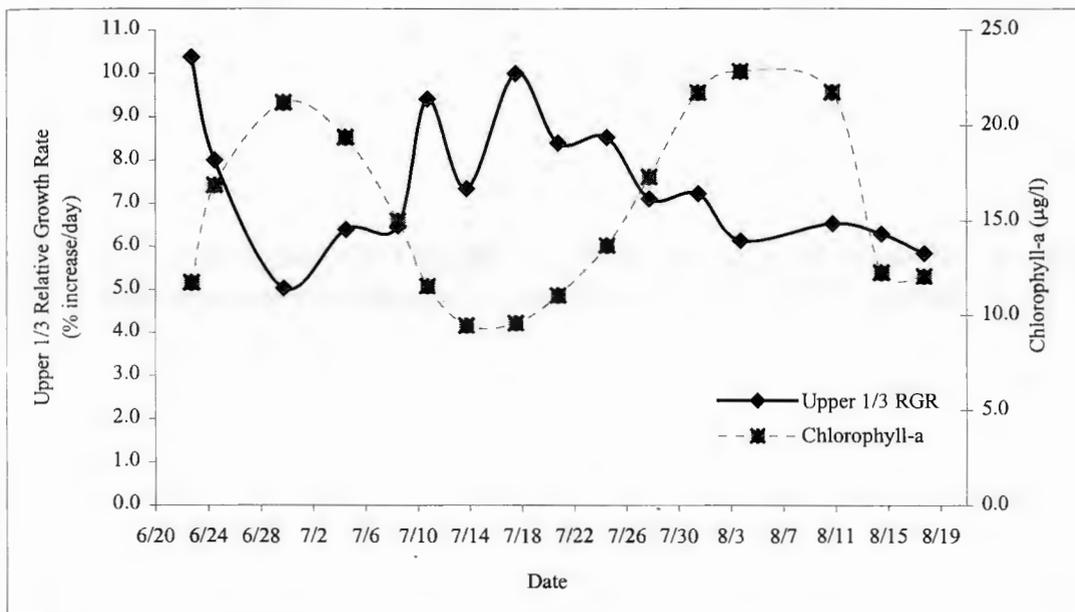




Figure 12. Linear regression of the relative growth rate (% increase/day) for the upper third of replicates versus chlorophyll-a ($\mu\text{g/l}$) from June 21 through August 19, 1999.

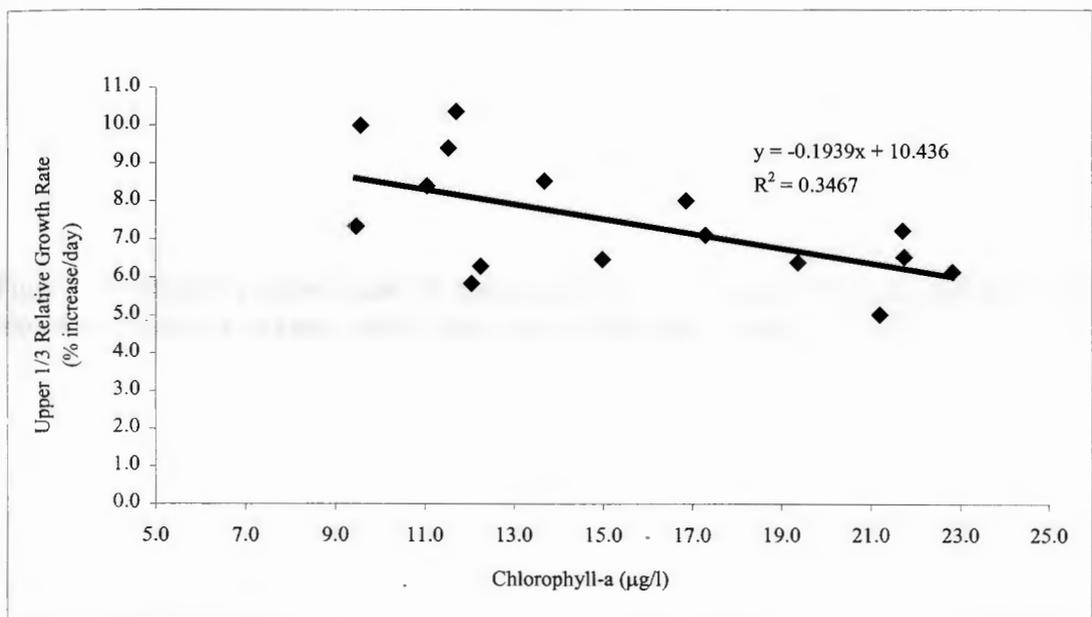




Figure 13. Relative growth rate (% increase/day) for the upper third of replicates with morning dissolved oxygen (ppm) from June 21 through August 19, 1999.

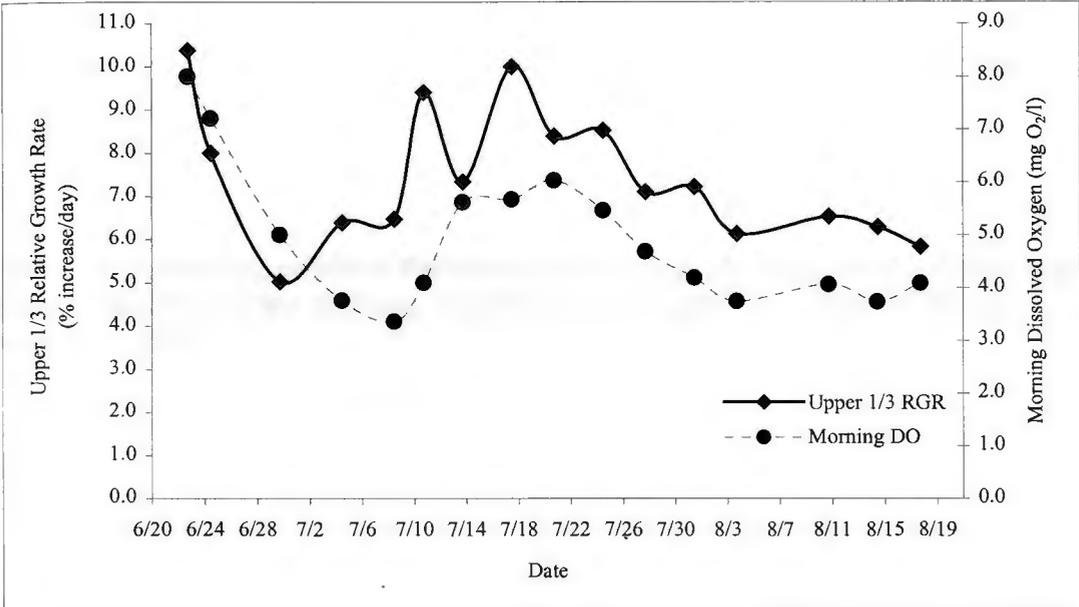




Figure 14. Linear regression of the relative growth rate (% increase/day) for the upper third of replicates versus morning dissolved oxygen (ppm) from June 21 through August 19, 1999.

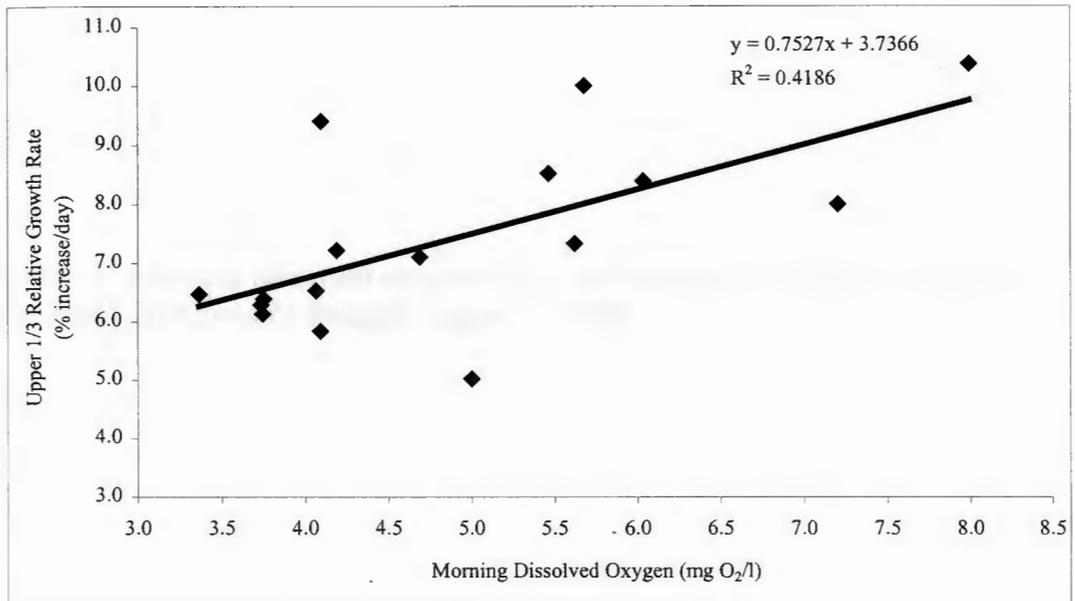


Figure 15. Morning dissolved oxygen (ppm) with morning-dissolved oxygen (% saturation) from June 21 through August 19, 1999.

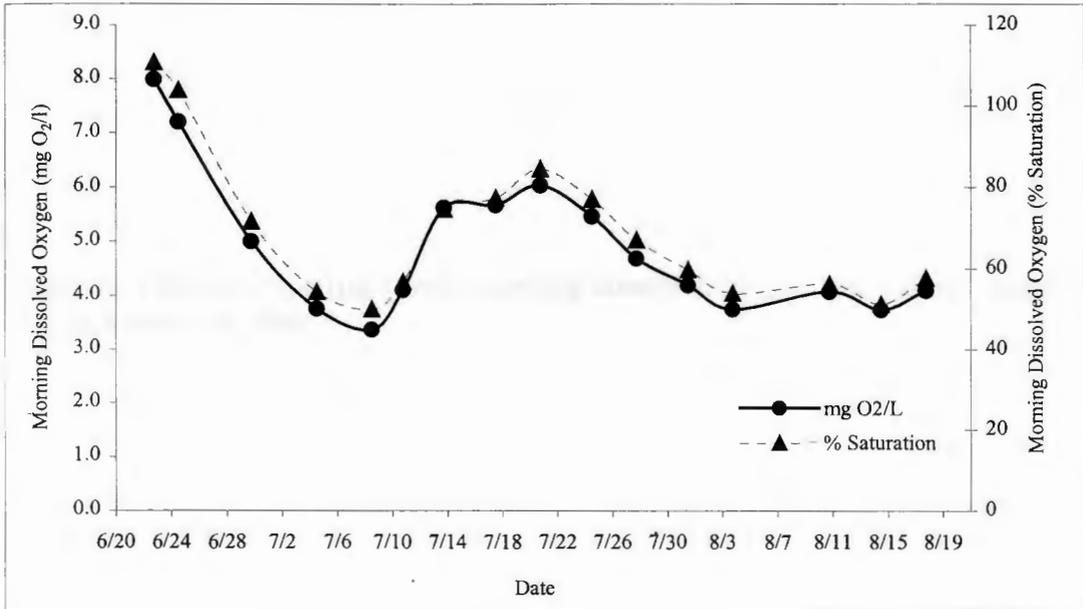
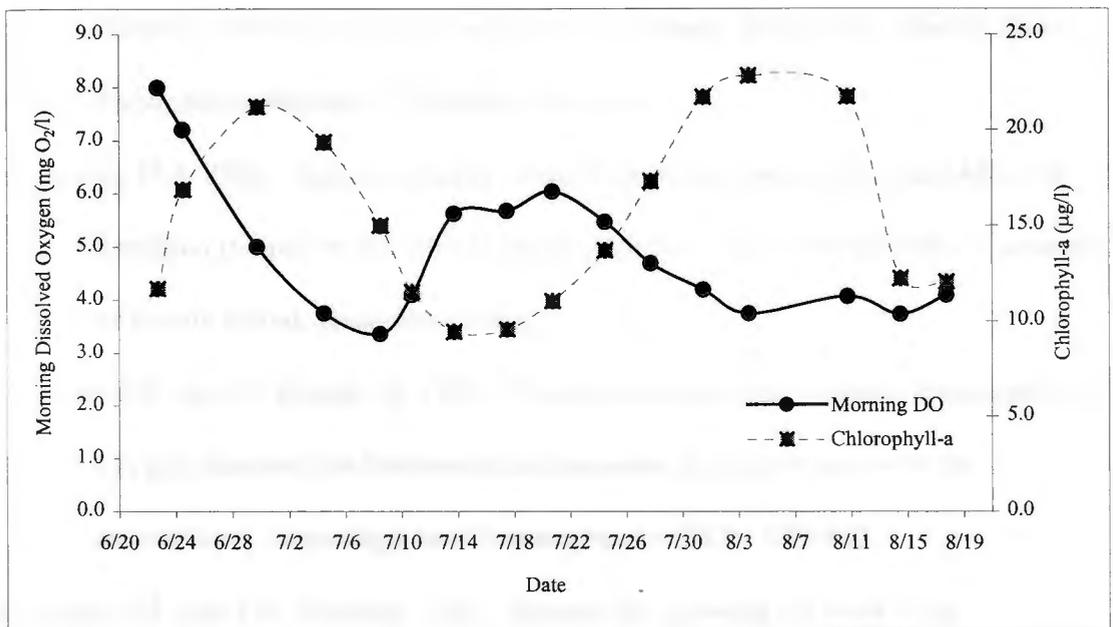


Figure 16. Chlorophyll-a ($\mu\text{g/l}$) with morning dissolved oxygen (ppm) from June 21 through August 19, 1999.



REFERENCES

- Baldwin, R.B., W. Mook, N.H. Hadley, R.J. Rhodes, and M.R. DeVoe. 1995. *Construction and operations manual for a tidal-powered upwelling system*. S.C. Sea Grant Consortium, Charleston, S.C.
- Bayes, J.C. 1981. Forced upwelling nurseries for oysters and clams using impounded water systems. Pages 73-83. In Claus, C., N. DePauw, and E. Jaspers (eds.), *Nursery culturing of bivalve molluscs. European Mariculture Society Special Publication, Number 7.*, Bredene, Belgium.
- Bengtson, D.A. 1982. Resource partitioning by *Menidia menidia* (L.) and *Menidia beryllina* (Cope) in two Rhode Island estuaries. Ph.D. dissertation. University of Rhode Island, Kingston. 214 pp.
- Benson, B.B. and D. Krause, Jr. 1984. The concentration and isotopic fractionation of oxygen dissolved in freshwater and seawater in equilibrium with the atmosphere. *Limnology and Oceanography*, 29(3): 620-632.
- Castagna, M. and J.N. Kraeuter. 1981. *Manual for growing the hard clam, Mercenaria*. Special Report in Applied Marine Science and Ocean Engineering No. 249, Virginia Institute of Marine Science, Gloucester Point, Virginia.
- Claus, C. 1981. Trends in nursery rearing of bivalve molluscs. Pages 1-33. In Claus, C., N. DePauw, and E. Jaspers (eds.), *Nursery culturing of bivalve molluscs. European Mariculture Society Special Publication, Number 7.*, Bredene, Belgium.

- Defosse, J.M. and A.J.S. Hawkins. 1997. Selective feeding in shellfish: size-dependent rejection of large particles within pseudofeces from *Mytilus edulis*, *Ruditapes philippinarum* and *Tapes decussatus*. *Marine Biology*, 129: 139-147.
- Hadley, N.H., R.B. Baldwin, M.R. Devoe, and R. Rhodes. 1999. Performance of a tidal-powered upwelling nursery system for northern quahogs (hard clams) (*Mercenaria mercenaria*) in South Carolina. *Journal of Shellfish Research*, 18(2): 555-560.
- Hadley, N.H. and J.J. Manzi. 1984. Growth of seed clams, *Mercenaria mercenaria*, at various densities in a commercial scale nursery system. *Aquaculture*, 36: 369-378.
- Hamwi, A. 1969. Oxygen consumption and pumping rate of the hard clam *Mercenaria mercenaria* L. Ph.D. dissertation. Rutgers, The State University, New Brunswick, New Jersey. 177 pp.
- Malinowski, S.M. 1988. Variable growth rates of seed clams, *Mercenaria mercenaria* (Linné) in an upflow nursery system and the economics of culling slow growing animals. *Journal of Shellfish Research*, 7(3): 359-365.
- Malinowski, S.M. and S.E. Siddall. 1989. Passive water reuse in a commercial-scale hard clam, *Mercenaria mercenaria*, upflow nursery system. *Journal of Shellfish Research*, 8(1): 241-248.
- Manzi, J.J. 1985. *Clam aquaculture*. Pages 275-310. In Hunter, J.V., and E.E. Brown (eds.), *Crustacean and mollusk aquaculture in the United States*. AVI Publishing Company, Westport, CT.

- Manzi, J.J. and M. Castagna. 1989. Nursery culture of clams in North America. Pages 127-147. In Manzi, J.J. and M. Castagna (eds.), *Clam Mariculture in North America*. Elsevier, New York, 461 pp.
- Manzi, J.J. and J.M. Whetstone. 1981. *Intensive hard clam mariculture: A primer for South Carolina watermen*. South Carolina Sea Grant Consort. Marine Advisory Publication 81-01, Charleston, S.C. 29401.
- Manzi, J.J., N.H. Hadley, C. Battey, R. Haggerty, R. Hamilton, and M. Carter. 1984. Culture of the northern hard clam *Mercenaria mercenaria* (Linne), in a commercial-scale, upflow, nursery system. *Journal of Shellfish Research*, 4(2): 119-124.
- Manzi, J.J., N.H. Hadley, and M.B. Maddox. 1986. Seed clam, *Mercenaria mercenaria*, culture in an experimental-scale upflow nursery system. *Aquaculture*, 54: 301-311.
- Manzi, J.J. and N.H. Hadley. 1988. Recent advances in nursery culture of bivalve mollusks in North America. Pages 41-46. In Sparks, A.K. (ed.), *New and innovative advances in biology/engineering with potential for use in aquaculture*. NOAA Technical Report National Marine Fisheries Service (NMFS) 70, National Marine Fisheries Service, Seattle, WA 98115.
- Rheault, R.B. and M.A. Rice. 1996. Food-limited growth and condition index in the eastern oyster, *Crassostrea virginica* (Gmelin 1791), and the bay scallop, *Argopecten irradians irradians* (Lamarck 1819). *Journal of Shellfish Research*, 15(2): 271-283.

- Rodhouse, P.G., and M. O'Kelly. 1981. Flow requirements of the oysters *Ostrea edulis* and *Crassostrea gigas* Thunbberg. In an upwelling column system of culture. *Aquaculture*, 22: 1-10.
- Sokal, R.R. and F.J. Rohlf. 1995 *Biometry*. W.H. Freeman and Company, New York.
- Stanley, J.G. and R. DeWitt. 1983. *Hard clam. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North America) – hard clam*. U.S. Fish and Wildlife Service. FWS/OBS-82/11.18. U.S. Army Corps of Engineers, TR EL-82-4.
- Stanley, J.G. 1985. *Hard clam. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic) -- hard clam*. Biological Report 82(11.41).
- Strickland, J.D.H. and T.R. Parsons. 1972. A practical handbook of seawater analysis. *Fisheries Research Board of Canada Bulletin*, 167, Second Edition. 310 pp.

average (chlorophyll) = 4 µg/l

Date	Time	Lat	Long	Depth (m)	Temp (°C)	Chlorophyll (µg/l)	Salinity	St. Dev.
1-Jul	7:30	17.18	8.71	1.00	18.40	1.04	34.9	0.1
1-Jul	12:00	17.20	8.67	1.00	18.63	0.12	34.9	0.1
1-Jul	15:30	17.18	8.71	1.00	18.59	0.07	34.9	0.1
1-Jul	17:45	17.18	8.71	1.00	18.04	0.27	34.9	0.1
1-Jul	17:24	17.18	8.71	1.00	18.17	2.08	34.9	0.1
1-Jul	18:15	17.18	8.71	1.00	17.98	2.00	34.9	0.1
1-Jul	19:30	17.18	8.71	1.00	18.37	1.09	34.9	0.1
1-Jul	19:25	17.18	8.71	1.00	18.44	1.22	34.9	0.1
1-Jul	19:45	17.18	8.71	1.00	18.55	2.36	34.9	0.1
1-Jul	20:45	17.18	8.71	1.00	18.90	1.27	34.9	0.1
1-Jul	21:00	17.18	8.71	1.00	19.49	0.98	34.9	0.1
1-Jul	21:20	17.18	8.71	1.00	19.49	0.87	34.9	0.1
1-Jul	8:00	17.18	8.71	1.00	18.94	1.72	34.9	0.1
1-Jul	12:00	17.18	8.71	1.00	18.27	1.27	34.9	0.1
1-Jul	18:00	17.18	8.71	1.00	18.47	1.31	34.9	0.1
1-Jul	18:30	17.18	8.71	1.00	18.43	1.37	34.9	0.1
1-Jul	18:15	17.18	8.71	1.00	18.81	1.45	34.9	0.1
1-Jul	19:15	17.18	8.71	1.00	18.77	1.70	34.9	0.1
1-Jul	19:15	17.18	8.71	1.00	18.74	1.67	34.9	0.1
1-Jul	19:15	17.18	8.71	1.00	18.94	1.16	34.9	0.1
1-Jul	19:15	17.18	8.71	1.00	19.31	1.18	34.9	0.1
1-Jul	19:15	17.18	8.71	1.00	19.63	1.07	34.9	0.1
1-Jul	8:10	17.18	8.71	1.00	18.43	1.37	34.9	0.1
1-Jul	12:15	17.18	8.71	1.00	18.46	1.33	34.9	0.1
1-Jul	18:05	17.18	8.71	1.00	18.34	0.90	34.9	0.1
1-Jul	18:30	17.18	8.71	1.00	18.93	1.40	34.9	0.1
1-Jul	12:15	17.18	8.71	1.00	18.51	1.31	34.9	0.1
1-Jul	18:50	17.18	8.71	1.00	18.69	1.29	34.9	0.1
1-Jul	8:00	17.18	8.71	1.00	18.08	1.14	34.9	0.1
1-Jul	11:05	17.18	8.71	1.00	18.07	1.61	34.9	0.1
1-Jul	18:10	17.18	8.71	1.00	18.04	1.38	34.9	0.1

Appendix I. Chlorophyll-a data.

Sample average chlorophyll-a ($\mu\text{g/l}$)

Date	Time	Anomaly	Chl-a	Chl-a	Chl-a	Chl-a	Chl-a	Mean	Standard Error	Count
22-Jun	7:30		7.55	8.71	8.96			8.40	0.44	3
22-Jun	12:00		8.40	8.65	8.83			8.63	0.12	3
22-Jun	15:30		11.78	11.96	11.90			11.88	0.05	3
24-Jun	7:45	7.50	14.00	13.81	14.74	13.38	13.75	13.94	0.23	5
24-Jun	12:24	1.30	16.35	12.28				14.32	2.04	2
24-Jun	16:15		9.93	14.32	16.78			13.68	2.00	3
28-Jun	8:40		15.37	17.09	15.55			16.00	0.55	3
28-Jun	12:25		19.44	20.30	22.89			20.88	1.04	3
28-Jun	16:45		20.55	23.76	24.68			23.00	1.25	3
1-Jul	8:45		17.90	15.37	13.51			15.59	1.27	3
1-Jul	13:00		20.49	20.98	21.10			20.86	0.19	3
1-Jul	17:20		30.44	29.35	30.93			30.24	0.47	3
7-Jul	8:00		18.90	22.72	19.32			20.31	1.21	3
7-Jul	12:00		21.33	19.32	18.59			19.75	0.82	3
7-Jul	16:00		7.47	7.72	8.51			7.90	0.31	3
9-Jul	8:30		8.43	8.97	8.37			8.59	0.19	3
9-Jul	14:15		22.81	20.46	18.11			20.46	1.36	3
9-Jul	19:05		11.31	9.51	4.39			8.41	2.07	3
12-Jul	9:15		7.04	6.62	7.16			6.94	0.16	3
12-Jul	13:15		9.21	8.30	8.18			8.57	0.32	3
12-Jul	17:15		9.63	11.07	13.96			11.55	1.27	3
15-Jul	8:10		8.43	8.55	8.37			8.45	0.05	3
15-Jul	12:05		12.46	9.27	9.33			10.35	1.05	3
15-Jul	16:05		8.34	9.69	9.34			9.12	0.40	3
19-Jul	8:30	1.23	8.93	5.40				7.16	1.76	2
19-Jul	12:15		12.51	12.21	13.39			12.70	0.35	3
19-Jul	16:30		11.69	11.28	9.57			10.84	0.65	3
22-Jul	8:00		8.05	12.64	13.23			11.31	1.64	3
22-Jul	13:05		13.47	11.92	13.65			13.02	0.55	3
22-Jul	18:30		12.04	13.53	14.01			13.19	0.59	3

26-Jul	8:25		10.31	9.90	9.90		10.03	0.14	3
26-Jul	13:00		12.16	14.61	18.12		14.96	1.73	3
26-Jul	17:30		19.91	19.67	19.14		19.57	0.23	3
29-Jul	8:00	9.90	17.05	19.61			18.33	1.28	2
29-Jul	12:00		24.02	18.54	20.45		21.00	1.61	3
29-Jul	16:00		20.33	25.81	21.94		22.69	1.63	3
2-Aug	8:00		21.58	21.40	22.65		21.88	0.39	3
2-Aug	12:05		28.44	28.79	25.81		27.68	0.94	3
2-Aug	16:10		19.91	21.28	23.31		21.50	0.99	3
5-Aug	8:00		18.48	17.45	19.38		18.44	0.56	3
5-Aug	12:45		21.00	22.21	24.07		22.43	0.89	3
5-Aug	17:15		24.01	26.78	24.31		25.03	0.88	3
9-Aug	8:05		20.28	29.31	26.72		25.44	2.68	3
9-Aug	12:00		25.28	25.22	25.88		25.46	0.21	3
9-Aug	16:20		27.56	29.25	30.21		29.01	0.77	3
12-Aug	7:40		12.74	13.86	13.33		13.31	0.32	3
12-Aug	12:50		12.16	12.68	12.57		12.47	0.16	3
12-Aug	18:00		26.31	26.84	21.02		24.72	1.86	3
16-Aug	8:15		5.64	6.28	5.87		5.93	0.19	3
16-Aug	11:50		7.34	7.16	7.34		7.28	0.06	3
16-Aug	16:00		8.16	10.10	11.04		9.77	0.85	3
19-Aug	8:05	6.28	12.21	14.15			13.18	0.97	2
19-Aug	12:00		19.56	18.26	18.67		18.83	0.38	3
19-Aug	15:55		18.32	17.85	22.61		19.59	1.51	3

Daily average chlorophyll-a ($\mu\text{g/l}$).

Date	Chl-a	Chl-a	Chl-a	Mean	Standard Error	Count
6/22/99	8.41	8.63	11.88	9.64	1.12	3
6/24/99	13.31	14.32	13.68	13.77	0.30	3
6/28/99	16.00	20.88	23.00	19.96	2.07	3
7/1/99	15.59	20.86	30.83	22.43	4.47	3
7/6/99	20.71	20.13	8.05	16.30	4.13	3
7/9/99	8.92	21.27	10.82	13.67	3.84	3
7/12/99	7.21	8.90	12.01	9.37	1.40	3
7/15/99	8.78	10.76	9.12	9.55	0.61	3
7/19/99	5.19	12.70	10.84	9.58	2.26	3
7/22/99	11.31	13.02	13.19	12.51	0.60	3
7/26/99	10.03	14.96	19.57	14.86	2.75	3
7/29/99	15.52	21.00	22.69	19.74	2.17	3
8/2/99	21.88	27.68	21.50	23.69	2.00	3
8/5/99	18.44	22.43	25.03	21.97	1.92	3
8/9/99	25.44	25.46	29.01	26.63	1.19	3
8/12/99	13.31	12.47	24.72	16.83	3.95	3
8/16/99	5.93	7.28	9.77	7.66	1.12	3
8/19/99	10.88	18.83	19.59	16.44	2.79	3

Average chlorophyll-a ($\mu\text{g/l}$) during growth intervals

Growth Interval	Chl-A	Chl-A	Mean	Standard Error	Count
6/21-6/24	9.64	13.77	11.70	2.06	2
6/24-6/28	13.77	19.96	16.86	3.10	2
6/28-7/1	19.96	22.43	21.19	1.23	2
7/1-7/7	22.43	16.30	19.36	3.06	2
7/07-7/9	16.30	13.67	14.98	1.32	2
7/9-7/12	13.67	9.37	11.52	2.15	2
7/12-7/15	9.37	9.55	9.46	0.09	2
7/15-7/19	9.55	9.58	9.57	0.01	2
7/19-7/22	9.58	12.51	11.04	1.46	2
7/22-7/26	12.51	14.86	13.68	1.18	2
7/26-7/29	14.86	19.74	17.30	2.44	2
7/29-8/2	19.74	23.69	21.71	1.97	2
8/2-8/5	23.69	21.97	22.83	0.86	2
8/9-8/12	26.63	16.83	21.73	4.90	2
8/12-8/16	16.83	7.66	12.25	4.59	2
8/16-8/19	7.66	16.44	12.05	4.39	2

Average chlorophyll-a ($\mu\text{g/l}$) during experiments

Experiment	1	2	3	4
Time period	6/22-7/7	7/7-7/22	7/22-8/5	8/5-8/19
	9.64	16.30	12.51	21.97
	13.77	13.67	14.86	26.63
	19.96	9.37	19.74	16.83
	22.43	9.55	23.69	7.66
	16.30	9.58	21.97	16.44
		12.51		
Mean	16.42	11.83	18.55	17.91
Standard Error	2.25	1.16	2.12	3.17
Count	5	6	5	5

Average relative growth rate (RGR) data for the upper 1/3 of treatment replicates.

Date	Mean	Standard Error	Count
6/23/99	14.97	0.41	5
6/24/99	8.98	0.14	5
6/29/99	5.03	0.21	5
7/4/99	6.39	0.15	5
7/8/99	6.47	0.17	5
7/10/99	9.41	0.16	5
7/17/99	7.75	0.11	5
7/17/99	10.70	0.11	5
7/20/99	8.39	0.11	5
7/24/99	8.52	0.11	5
7/27/99	7.10	0.12	5
7/31/99	7.32	0.12	5
8/5/99	8.11	0.11	5
8/10/99	8.21	0.12	5
8/14/99	6.29	0.18	5
8/17/99	5.84	0.17	5

Average relative growth rate (% increase/day) for the upper 1/3 of replicates

Date	Mean	Standard Error	Count
6/22/99	10.37	0.43	6
6/24/99	8.00	0.15	6
6/29/99	5.03	0.41	6
7/4/99	6.39	0.18	6
7/8/99	6.47	0.12	6
7/10/99	9.41	0.14	6
7/13/99	7.34	0.11	6
7/17/99	10.00	0.21	6
7/20/99	8.39	0.11	6
7/24/99	8.52	0.14	6
7/27/99	7.10	0.07	6
7/31/99	7.22	0.22	6
8/3/99	6.13	0.18	6
8/10/99	6.53	0.22	6
8/14/99	6.29	0.16	6
8/17/99	5.84	0.17	6

BIBLIOGRAPHY

- Ansell, A.D. 1968. The rate of growth of the hard clam *Mercenaria mercenaria* throughout the geographical range. *Journal du Conseil International pour l'Exploration de la Mer*, 31: 346-409.
- Appleyard, C.A. 2000. Aspects of growth for the northern quahog, *Mercenaria mercenaria*. Masters Thesis. University of Rhode Island, Kingston. 123 pp.
- Arnold, W.S., D. C. Marelli, T. M. Bert, D. S. Jones, and I. R. Quitmyer. 1991. Habitat-specific growth of hard clams *Mercenaria mercenaria* (L.) from the Indian River, Florida. *Journal of Experimental Marine Biology and Ecology*, 147: 245-265.
- Baldwin, R.B., W. Mook, N.H. Hadley, R.J. Rhodes, and M.R. DeVoe. 1995. *Construction and operations manual for a tidal-powered upwelling system*. S.C. Sea Grant Consortium, Charleston, S.C.
- Bayes, J.C. 1981. Forced upwelling nurseries for oysters and clams using impounded water systems. Pages 73-83. In Claus, C., N. DePauw, and E. Jaspers (eds.), *Nursery culturing of bivalve molluscs*. Special Publication 7, *European Mariculture Society*, Bredene, Belgium.
- Bengtson, D.A. 1982. Resource partitioning by *Menidia menidia* (L.) and *Menidia beryllina* (Cope) in two Rhode Island estuaries. Ph.D. dissertation. University of Rhode Island, Kingston. 214 pp.
- Benson, B.B., and D. Krause, Jr. 1984. The concentration and isotopic fractionation of oxygen dissolved in freshwater and seawater in equilibrium with the atmosphere. *Limnology and Oceanography*, 29(3): 620-632.

- Castagna, M., and J.N. Kraeuter. 1981. *Manual for growing the hard clam, Mercenaria*. Special Report in Applied Marine Science and Ocean Engineering No. 249, Virginia Institute of Marine Science, Gloucester Point, Virginia.
- Claus, C. 1981. Trends in nursery rearing of bivalve molluscs. Pages 1-33. In Claus, C., N. DePauw, and E. Jaspers (eds.), *Nursery culturing of bivalve molluscs. European Mariculture Society Special Publication, Number 7.*, Bredene, Belgium.
- DeAlteris, J.T. and L. Skrobe (unpublished). *Introduction to fish stock assessment and fishery management for fishermen and resource managers*. Atlantic States Marine Fisheries Council.
- Defossez, J.M. and A.J.S. Hawkins. 1997. Selective feeding in shellfish: size-dependent rejection of large particles within pseudofeces from *Mytilus edulis*, *Ruditapes philippinarum* and *Tapes decussatus*. *Marine Biology*, 129: 139-147.
- Hadley, N.H., R.B. Baldwin, M.R. Devoe, and R. Rhodes. 1999. Performance of a tidal-powered upwelling nursery system for northern quahogs (hard clams) (*Mercenaria mercenaria*) in South Carolina. *Journal of Shellfish Research*, 18(2): 555-560.
- Hadley, N.H. and J.J. Manzi. 1984. Growth of seed clams, *Mercenaria mercenaria*, at various densities in a commercial scale nursery system. *Aquaculture*, 36: 369-378.

- Hamwi, A. 1969. Oxygen consumption and pumping rate of the hard clam *Mercenaria mercenaria* L. Ph.D. dissertation. Rutgers, The State University, New Brunswick, New Jersey. 177 pp.
- Jobling, M. 1994. *Fish Bioenergetics*. Chapman & Hall, London. 309 pp.
- Jones, D.S., M.A. Arthur, and D.J. Allard. 1989. Sclerochronological records of temperature and growth from shells of *Mercenaria mercenaria* from Narragansett Bay, Rhode Island. *Marine Biology*, 102: 225-234.
- Kennish, M.J., and R.E. Loveland. 1980. Growth models of the northern quahog, *Mercenaria mercenaria* (Linné). *Proceedings of the National Shellfisheries Association*, 70: 230-239.
- King, M. 1995. *Fisheries biology, assessment and management*. Fishing News Books, Oxford. 341 pp.
- Malinowski, S.M. 1988. Variable growth rates of seed clams, *Mercenaria mercenaria* (Linné) in an upflow nursery system and the economics of culling slow growing animals. *Journal of Shellfish Research*, 7(3): 359-365.
- Malinowski, S.M. and S.E. Siddall. 1989. Passive water reuse in a commercial-scale hard clam, *Mercenaria mercenaria*, upflow nursery system. *Journal of Shellfish Research*, 8(1): 241-248.
- Malouf, R.E. and V.M. Bricelj. 1989. Comparative biology of clams: environmental tolerances, feeding, and growth. Pages 23-74. In Manzi, J.J. & Castagna (eds.), *Clam Mariculture in North America*. Elsevier, New York, 461 pp.

- Manzi, J.J. 1985. *Clam aquaculture*. Pages 275-310. In Hunter, J.V. and E.E. Brown (eds.), *Crustacean and mollusk aquaculture in the United States*. AVI Publishing Company, Westport, CT.
- Manzi, J.J. and Castagna, M. 1989. Nursery culture of clams in North America. Pages 127-147. In Manzi, J.J. & Castagna (eds.), *Clam Mariculture in North America*. Elsevier, New York, 461 pp.
- Manzi, J.J. and J.M. Whetstone. 1981. *Intensive hard clam mariculture: A primer for South Carolina watermen*. South Carolina Sea Grant Consort. Marine Advisory Publication 81-01, Charleston, S. C., 29401.
- Manzi, J.J., N.H. Hadley, C. Battey, R. Haggerty, R. Hamilton, and M. Carter. 1984. Culture of the northern hard clam *Mercenaria mercenaria* (Linné), in a commercial-scale, upflow, nursery system. *Journal of Shellfish Research*, 4(2): 119-124.
- Manzi, J.J., N.H. Hadley, and M.B. Maddox. 1986. Seed clam, *Mercenaria mercenaria*, culture in an experimental-scale upflow nursery system. *Aquaculture*, 54: 301-311.
- Manzi, J.J. and N.H. Hadley. 1988. Recent advances in nursery culture of bivalve mollusks in North America. Pages 41-46. In Sparks, A.K. (ed.), *New and innovative advances in biology/engineering with potential for use in aquaculture*. NOAA Technical Report National Marine Fisheries Service (NMFS) 70, National Marine Fisheries Service, Seattle, WA 98115.
- Peterson, C.H., H.C. Summerson, and P.B. Duncan. 1984. The influence of seagrass cover on population structure and individual growth rate of a suspension-

- feeding bivalve, *Mercenaria mercenaria*. *Journal of Marine Research*, 42: 123-138.
- Rheault, R.B. and M.A. Rice. 1996. Food-limited growth and condition index in the eastern oyster, *Crassostrea virginica* (Gmelin 1791), and the bay scallop, *Argopecten irradians irradians* (Lamarck 1819). *Journal of Shellfish Research*, 15(2): 271-283.
- Rice, M.A. 1992. *The northern quahog: the biology of Mercenaria mercenaria*. Rhode Island Sea Grant, University of Rhode Island, Narragansett. 60 pp.
- Rice, M.A., C. Hickox, and I. Zehra. 1989. Effects of intensive fishing effort on the population structure of quahogs, *Mercenaria mercenaria* (L., 1758), in Narragansett Bay. *Journal of Shellfish Research*, 8(2): 345-354.
- Ricker, W.E. 1975. *Computation and interpretation of biological statistics of fish populations*. Bulletin of the Fisheries Research Board of Canada. Bulletin 191, Ottawa, Canada. 382 pp.
- Rodhouse, P.G. and M. O'Kelly. 1981. Flow requirements of the oysters *Ostrea edulis* and *Crassostrea gigas* Thunbberg. in an upwelling column system of culture. *Aquaculture*, 22: 1-10.
- Slattery, J.P., R.C. Vrijenhoek, and R.A. Lutz. 1991. Heterozygosity, growth, and survival of the hard clam, *Mercenaria mercenaria*, in seagrass vs sandflat habitats. *Marine Biology*, 111: 335-342.
- Sokal, R.R. and F.J. Rohlf. 1995. *Biometry*. W.H. Freeman and Company, New York.

- Stanley, J.G. and R. DeWitt. 1983. *Hard clam. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North America) – hard clam*. U.S. Fish and Wildlife Service. FWS/OBS-82/11.18. U.S. Army Corps of Engineers, TR EL-82-4.
- Stanley, J.G. 1985. *Hard clam. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic) -- hard clam*. Biological Report 82(11.41).
- Strickland, J.D.H. and T.R. Parsons. 1972. A practical handbook of seawater analysis. *Fisheries Research Board of Canada Bulletin*, 167, Second Edition. 310 pp.