

**DENSITY-DEPENDENT GROWTH AND GRAZING EFFECTS OF
JUVENILE QUEEN CONCH *Strombus gigas* L. IN
A TROPICAL SEAGRASS MEADOW**

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DENSITY-DEPENDENT GROWTH AND THE GRAZING EFFECTS
OF JUVENILE QUEEN CONCH (STROMBUS GIGAS LINNE)
IN A TROPICAL SEAGRASS MEADOW

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Running Head: Growth and effects of queen conch

ABSTRACT

Field experiments with one-year old queen conch, Strombus gigas, in a seagrass meadow of the Exuma Cays, Bahamas, indicated that growth rates and mortality were density-dependent and related to food limitation. Juvenile queen conch are probably more important consumers of detritus than previously known. Enclosure/exclosure treatments showed that natural field densities of conch ($2.0/\text{m}^2$) reduce significantly the standing crop of senescent seagrass blades and macrodetritus, but not living seagrass biomass. Sediment grain size, organic content, and chlorophyll were not influenced by juvenile conch, but removal of seagrass detritus may have a major influence on other benthic invertebrates.

Key words: Density-dependent; Growth; Seagrass; Herbivory; Strombus gigas

INTRODUCTION

The queen conch (Strombus gigas Linnaeus) is a large gastropod mollusc of commercial significance found throughout the Bahama Islands, Caribbean Sea, Bermuda, and southeastern Florida in the United States (Abbott, 1974). Population biology has been studied in a variety of localities including the Berry Islands, Bahamas (Iversen et al., 1986), the Caicos Islands (Hesse, 1979), the Virgin Islands (Randall, 1964), Puerto Rico (Appeldoorn, 1987a, b), Martinique (Rathier, 1985), and Venezuela (Weil & Laughlin, 1984).

The first year of life is poorly understood for S. gigas, but at approximately one year of age, juveniles emerge from the sediment to feed and grow in habitats providing adequate algal and detrital foods (Randall, 1964). After emerging, juveniles can be found in high abundance in seagrass meadows, with reports of densities commonly between one and two animals/m² in shallow seagrass meadows (Alcolado, 1976; Hesse, 1979; Wood & Olsen, 1983; Weil & Laughlin, 1984; Iversen et al., 1986). In some cases, abundance of juveniles in certain locations is observed repeatedly over many years (Wicklund et al., 1988). Densities as high as 350 conch/m² were observed recently for newly emergent queen conch undergoing mass migration in the central Bahamas (Stoner et al., 1988).

Because of rapidly declining queen conch populations throughout the northwest Atlantic (Gibson et al., 1983; Goodwin, 1983; Appeldoorn et al., 1987), interest in supplementing wild stocks with hatchery reared juveniles has risen. Although density-dependent effects are known for the species in the

laboratory (Siddall, 1984) and in culture (Appeldoorn & Sanders, 1984), little is known about the carrying capacity of natural conch habitats. Knowledge of such density-dependent effects will be important for understanding wild populations as well as for supplementing dwindling stocks. In this report, the effects of juvenile conch densities on survival and growth rates are examined. Concurrent investigation of conch growth, diets, and the benthic habitat helps to elucidate mechanisms related to the carrying capacity of the habitat and the potential role of juvenile queen conch in the benthic environment.

METHODS

The experiment was conducted in the Exuma Cays, Bahamas, at a site approximately 1.5 km west of Children's Bay Cay (23°45'N, 76°05'W), in a seagrass meadow of Thalassia testudinum König. The particular seagrass bed characteristically contains high densities of juvenile queen conch, Strombus gigas Linne (Wicklund et al., 1988). The experimental site has a mean depth of 3.5 m, with a tidal amplitude of 1.0 m, and is subject to strong tidal currents (to approx. 50 cm s⁻¹).

Field Methods

Experimental animals were recently emerged, one-year old S. gigas collected from a mass migration of juveniles which occurred near the test site between April and June 1987 (Stoner et al., 1988). All animals at the beginning of the experiment were approximately one year old, between 82 and 105 mm total shell length. Animals introduced after the beginning of the experiment to replace lost or killed individuals were of a size similar to the mean conch size in a particular treatment on the date of replacement. All animals were individually marked with either vinyl spaghetti tags (Floy Co.) tied to the shell or small plastic numbers attached with narrow cable ties around the shell spire.

Field enclosure/exclosures were constructed of 1.9 cm black plastic mesh forming circular walls 40 cm in height and 5.0 m in diameter. The topless pens were held upright by as many as 15 vertical pieces of 13 mm diameter reinforcement bar driven into the sediment and wired to the plastic mesh. The enclosures were pushed into the sediment approximately 3 cm. Repairs to the pens were made throughout the experimental period using cable ties.

A random-block design was employed to examine the effects of

animal density on growth rates and effects of the animals on the benthic environment. Five treatments, replicated in three blocks, included: 1) uncaged sites open to the movements and grazing effects of juvenile queen conch and other large macroinvertebrates, marked with a 50 cm high PVC pole about which a 2.5 m radius could be examined, 2) enclosures - pens with all S. gigas and other readily detected and epibenthic macroinvertebrates, 3) enclosures with 40 juvenile queen conch per pen (equivalent to 1.0 times the natural density of juveniles in the seagrass meadow surrounding the pens in May 1987, 4) enclosures with 80 conch per pen (2.0 times natural density), and 5) enclosures with 160 conch per pen (4.0 times natural density). Animal densities in the 4.0 X treatment were high, equivalent to 8 conch m⁻², but much lower than the density potential in aggregations of juveniles observed during the experimental period near the test site (to > 300 conch m⁻² (Stoner et al., 1988).

At the beginning of the experimental period, mid-May 1987, three blocks of treatments were laid out in a uniform stand of Thalassia testudinum. Five 1.0 m long pieces of PVC pipe were driven into the sediment at 12.5 m intervals in a straight line running perpendicular to the prevailing tidal currents. This process was repeated twice more for the three blocks separated by 60 m.

Within a 2.5 m radius of the 15 stakes, several measurements were taken to establish the similarity of the habitats before construction of the enclosures: 1) All conch were counted and measured for shell length. 2) Four replicate cores of 15.7 mm internal diameter, penetrating 1.0 cm were taken for chlorophyll-a concentration. 3) Two replicate cores of 3.5 cm diameter,

penetrating 5.0 cm were taken for determination of sediment grain-size distribution and organic content. 4) Macrophytes and macroscopic detritus were collected from 25 cm square quadrats into nylon bags with 3.0 mm mesh openings for determination of above-ground biomass. Four replicates were collected from each experimental plot. Sediments for grain size and organic content were frozen whole until analyzed. Sediments for chlorophyll analysis were filtered onto Whatman No. 42 filter paper to remove excess water and frozen until extraction was performed.

Analysis of variance indicated that the blocks and individual plots were not different statistically in terms of either green seagrass biomass ($F = 0.312$, $p > 0.05$; $F = 0.201$, $p > 0.05$; respectively for blocks and individual plots) or macrodetritus ($F = 0.365$, $p > 0.05$; $F = 0.235$, $p > 0.05$; respectively). Treatments were then randomly assigned to each of the three experimental blocks and pens were constructed where required. Four days following the completion of an individual cage, it was cleared of all visible gastropods and other large invertebrates such as urchins, and the specified number of juvenile *S. gigas* were introduced after individual marking and measurement to the nearest 1.0 mm. All cages were loaded by 30 May 1987.

Numbers of conch enclosed in the various treatments were determined on the basis of the 15 estimates of conch density provided in the examination of the treatment sites. During the same period of time, 813 individually tagged and measured juvenile queen conch were released in the vicinity of the enclosures for examination of growth rates in free-ranging individuals. Between June and September 1987, 927 additional one

year old conch were tagged and distributed at the experimental site.

Growth of the conch, both in the wild and in enclosures, was examined by remeasurement at intervals of approximately 28, 57, 91, and 133 days, with exact growth rate determined on the basis of mm d^{-1} . Any missing or dead animals were replaced in enclosures at each of the measurement times and invading invertebrates were recorded and removed. Very low appearance of untagged S. gigas into the enclosures and few unaccounted losses over the experimental period showed that the pens were effective in retaining the test organisms. Hermit crabs were capable of crossing over the enclosure walls; they are known predators of conch in the test area (Marshall, 1988) and were frequently found inside tagged conch shells.

Measurements of sediment chlorophyll and macrophyte biomass were repeated at the mid-point of the experiment in July, and at the termination of the experiment in October. Three conch from each enclosure and representatives of individuals in the wild were collected from each block in July and in October for examination of gut contents. Sediment grain-size and organic content determinations were repeated only at the termination of the experiment. Also at the end of the experiment, 18 to 25 individuals from each treatment were examined for wet weight without shells for a analysis of differences in weight-length relationships.

Laboratory Methods

For determination of macrophyte biomass, individual samples were divided into green Thalassia blades and detritus (senescent blades and macroscopic detrital particles, most of which were

from Thalassia). Other seagrass and algal species were also separated. Below ground parts were discarded. Macrophytes were dried at 80°C to constant mass and biomass was determined by extrapolating values for the individual samples and components to dry weight per square meter.

Sediment organic content was determined by drying a subsample of approximately 100 g wet weight at 80°C to constant mass and incineration at 550°C for four hours. Organic content was quantified as the percent difference between dry weight and ash-free dry weight.

After washing to remove salts and to extract the silt-clay fraction, another sediment subsample of approximately 50 g was analyzed for granulometric properties using standard Ro-Tap procedures. Silt-clay fractions were analyzed using standard pipet procedures (Folk 1966). Product moment statistics were generated for mean grain size and sortedness.

Sediment chlorophyll concentrations were determined by standard fluorometric methods where whole sediment samples were extracted with 85% acetone according to the recommendations of Phinney and Yentsch (1985). First, average porosity of samples was determined for each set of collections, by subtracting wet and dry weights of 6 samples. Water content averaged 60.5%, ranging from 52.7% to 65.8%. For chlorophyll extraction, each sample was weighed wet and photometric grade acetone was added to reach 85% acetone solution. Samples were placed in 40-ml dark extracting bottles, mixed thoroughly, and extracted overnight in a refrigerator. The samples were centrifuged to remove sediment and chlorophyll concentrations in the supernatant were determined with a Turner Design Model 111 Fluorometer, employing the methods

of Strickland and Parsons (1972). Values were compared on the basis of ug chlorophyll-a per sample.

Soft tissue weight of individual conch were determined by carefully drawing the animal from its shell after freezing and subsequent thawing. Weights were used only where the entire animal was removed from the shell. Wet weights were determined after washing away feces and light blotting of the tissues.

Stomachs of conch extracted from shells in the way described above were dissected from the rest of the soft tissues. The stomachs were opened and the contents rinsed with 70% ethanol into containers with a dilute solution of rose bengal. Stomachs from individual enclosures and the from the unenclosed natural population were pooled as separated treatments.

Diets were examined using the gravimetric sieve-fractionation method of Carr and Adams (1972) developed for use with juvenile fishes. Stomach contents were washed through a series of six sieves of decreasing mesh size (2.0, 0.85, 0.425, 0.25, 0.15, and 0.075 mm) and each sieve fraction was examined with the aid of a dissecting microscope. Detrital particles that could be clearly identified as being derived from Thalassia were identified as such. All other food materials were placed in mutually exclusive categories for general interpretation. Where animal or plant materials could be identified to lower taxonomic level, this information was recorded. Because all of the items in a particular sieve fraction were of approximately equal size, the relative proportion of the gut contents made up of each food type was measured directly by counting. After examination, each fraction was dried overnight at 80°C and the total contribution of each food type to total dry weight was calculated.

RESULTS

Animal Mortality

Mortality in the experimental enclosures was examined for each of the four periods between measurements for growth (Fig. 1). In the first 28 days of the experiment, mortality was less than 2.0% of the population in all treatments. Mortality remained low where there were 40 conch per enclosure (1X treatment), but accelerated in both the 2X and 4X treatments. During the last growth period (111 to 133), an average of 17.9% of the population in the 4X treatment died or was killed by predators, despite the fact that 9.2% of the population had been replaced at the beginning of the period. Over the entire experiment 37.9% of the population in the 4X treatment died. Highest mortality in the 2X treatment was 4.2% during period IV, with total mortality at 7.9%. Total mortality in the 1X treatment was 1.6%. Two-way analysis of variance showed significant interaction between treatment and period of measurement (Table 1), but period I was excluded from the analysis. treatment effects were highly significant, with no period, interaction, or block effects.

Growth Rates and Body Condition

Growth rates were a function of animal density and decreased with time in all of the enclosures and in the wild population (Fig. 2). Analysis of variance for growth rates in the three experimental treatments showed no significant block effects ($F = 2.719$, $p > 0.05$); therefore, the blocks were combined and compared with growth rates in the untagged individuals (Table 2). A significant interaction term resulted between treatment and

growth period; this was a function of similarity of growth rates in the 1X treatment and the wild population in the second growth period, but differences in the first, third, and fourth periods. One-way ANOVA and Newman-Keuls multiple range tests run individually for the four growth periods showed that all other combinations of treatments yielded significantly different growth rates ($p < 0.05$).

Growth rates in animals held at high density were low relative to those held at 2.0 animals m^{-2} or in the wild population, with those in the 4X treatment showing zero growth after the second period and negative shell growth by the last growth period. Negative growth appeared to be associated with deterioration and rapid erosion of shells.

Significant differences in the physical condition of animals of various treatments were reflected in the ratio of tissue weight to shell length (here called Condition Factor) at the end of the experiment (ANOVA, $F = 39.79$; $p < 0.001$). Unenclosed animals and animals in the 1X treatment had statistically similar condition factors (0.243 (S.D. = 0.051, $n = 20$) and 0.254 (S.D. = 0.025, $n = 23$), respectively), while conch held in the 2-X treatment had condition factors averaging 0.196 (S.D. = 0.027, $n = 25$), and those in the 4-X treatment averaged 0.146 (S.D. = 0.034, $n = 18$). The latter two values were different from each other and different from values for unenclosed animals and those in the 1-X treatment (Newman-Keuls test, $p < 0.05$).

Animal Diets

Stomach contents of all conch examined were comprised primarily of detritus and sand (Table 3). A large portion of the detrital particles could be identified as Thalassia and it is

likely that most of the unidentified detritus was from the same source as few other macrophytic sources of detritus were present in the study site. In all treatments including the wild population, between 57 and 67% of the diets were comprised of detritus and there was no notable variation in the diets among treatments or between dates.

Gut fullness (Table 3) was a function of treatment ($F = 8.367$, $p < 0.001$). Newman-Keuls test indicated that in June, gut fullness was similar in unenclosed animals those in the 1-X treatment and those in the 2-X treatment. Fullness was also similar in the 2-X and 4-X treatments ($p < 0.05$). In October, unenclosed animals and those in the 1-X treatment had similar gut fullness. Those in 1-X and 2-X were similar, and conch held in the 4-X treatment had lowest gut fullness indices. It seems likely, therefore, that low growth rates in the high density treatments were related to low food intake and not qualitative differences in foods.

Effects of Conch on the Benthic Environment

Given the fact that juvenile conch used in the experiment did not consume green Thalassia blades, it is not surprising that the animals had little influence on the biomass of living seagrass (Fig. 3). After 2-way ANOVA showed no significant block effect for green seagrass ($F = 2.746$, $p > 0.05$), the blocks were combined and the five experimental treatments were compared by individual date. In July, the 4-X treatment had lower biomass of green Thalassia than the other treatments, while there was no significant effect of treatment in October (Table 4).

Standing crop of macrodetritus was influenced strongly by the presence of conch and their densities (Fig. 4). In July,

macrodetritus in unenclosed areas had similar biomass to areas enclosed with 2.0 conch m^{-2} , while exclusion of conch resulted in higher macrodetrital biomass. Treatments 2-X and 4-X had similar values for detrital biomass (Table 5). There were no block effects ($F = 0.906$, $p > 0.05$). In October, the trends were similar except that unenclosed areas, 0-X, and 1-X treatments all had statistically similar detritus biomass values. Again, 2-X and 4-X had equal, but lower values (Newman-Keuls test, $p < 0.05$).

Effects of conch density on sedimentary characteristics were not detected in this experiment. Analysis of variance showed no block, treatment, date, or interaction effects with chlorophyll-a or sediment organic content, even while incorporating May, July, and October data in the ANOVA model (Table 6). Chlorophyll values were high and variable, ranging from 2.1 to 15.0 $ug\ cm^{-2}$ (mean = 6.4; S.D. = 2.3; $n = 175$). Organic content of the sediments ranged from 2.70 to 5.55% of dry weight (mean = 3.96; S.D. = 0.53; $n = 90$).

Grain size, probably reflecting a seasonal effect in sediment accumulation, decreased significantly ($p < 0.001$) from an overall mean of 2.125 phi (S.D. = 0.280; $n = 30$) in May to 2.456 phi (S.D. = 0.306; $n = 30$) in October. There were no significant block, treatment, or treatment X date effects for sediment grain size (Table 6).

DISCUSSION

Results of the experiment reported here show that juvenile queen conch are important grazers in seagrass meadows and that densities of animals in nursery habitats such as those near Children's Bay Cay may be limited by abundance of foods. It has been suggested that the foods of Strombus gigas are primarily algal; however, this conclusion may result from the fact that investigations of diets have considered mostly adult or subadult individuals (Robertson, 1961; Randall, 1964; Hesse, 1976). Stomachs filled with macrodetritus, in both wild and enclosed populations, coupled with the removal of senescent seagrass blades and macrodetritus at the experimental site suggests that juvenile conch are more important detritivores than previously known. An analysis of ontogenetic and spatial variation in the feeding of juvenile conch is currently underway; however, examination of animals from 50 to 180 mm shell length has shown that seagrass dwellers feed primarily upon macrodetritus (Stoner, unpubl. data).

Growth rates in unenclosed individuals and those in the 1-X treatment were equivalent throughout the experiment; therefore, the effects of caging on the animals appear to be minimal. Mean growth rates found in the field and in the 1-X treatment ($0.063 - 0.155 \text{ mm d}^{-1}$) were lower than those found for juveniles in Venezuela ($0.13 - 0.50 \text{ mm d}^{-1}$) (Weil) and Laughlin, 1984) and in the Virgin Islands (0.178 mm d^{-1}) (Randall, 1964). This may related to lower water temperature in the Bahamas or limited food. Reduced growth rates in conch enclosed at densities greater than $2.0 \text{ animals m}^{-2}$

suggests that juvenile conch near Children's Bay Cay may have been at densities near the carrying capacity for the habitat in the summer of 1987. Mortality rates were undoubtedly related to the reduction of foods in high density treatments. Low body condition factors and low indices of stomach fullness suggest that the animals at high density were not consuming sufficient food. Mortality in the I-X treatment may have been lower than that for the natural, wild population at the site because of partial protection provided by the enclosures.

Density-dependent survivorship and growth rates have important implications for introducing hatchery-reared conch into the field for stock enhancement. First, each habitat probably has a carrying capacity for juvenile conch, beyond which stocked animals will fail to survive and grow. Second, this value may vary widely with different habitats. Results of a transplant experiment conducted in 1988 suggest that seagrass meadows with similar characteristics of sediments, macrophytes and detritus may yield very different growth characteristics in juvenile conch when held in similar densities (Stoner and Sandt, in preparation). Where there were native stocks of conch, however, growth rates were directly related to macrophyte and detritus standing stocks, suggesting potential food limitation and intraspecific resource competition. Third, the primary emphasis of research related to hatchery enhancement of queen conch stocks has been directed toward losses to predators (e.g., Appeldoorn and Ballantine, 1983; Iversen, et al., 1986) ⁹ ~~Appeldoorn, 1983~~. Predation rates can be very high in certain habitats, but it is now clear that prior to major outplantings of juvenile conch for stock enhancement, preliminary experiments should be conducted to

determine the quality of habitats in the more general sense. It is quite conceivable that habitats that have had historically large juvenile populations are best suited for stock rebuilding.

Juvenile queen conch inhabiting seagrass meadows in densities of one to two animals m^{-2} may play an important ecological role in the benthic community. In a sense, the conch groomed or cultivated the seagrass meadow removing epiphytes and hydroids, and clearing the sediment of senescent seagrass blades and detritus. This could have a significant influence on the benthic community in at least two ways: 1) By keeping seagrasses clear of epiphytes and epizoids, the macrophytes may increase in productivity in the presence of juvenile conch. Similarly, Van Montfrans, et al. (1984) have shown that the small snail Bittium varium clears periphyton and detritus from the surfaces of seagrass; the same is true for certain amphipod grazers (Zimmerman, 1978). Effects on the seagrasses themselves are unknown. 2) Because many benthic invertebrates, such as amphipods, are dependent upon detritus for food or cover (Zimmerman, et al., 1979; Nelson, 1981; Stoner, 1982; Orth, et al., 1984), detritus grazing in seagrass meadows by queen conch may reduce numbers of these smaller consumers. Removal of conch from a seagrass bed would probably result in the increase of the smaller grazers and/or a more rapid accumulation of organic matter in the sediments. The abundance of conch in some seagrass beds, the fullness of their stomachs, and the abundance of conch fecal pellets on the surface of the sediment as opposed to detritus build up where conch were excluded suggests the enormous influence of the gastropods in the benthic community. Future studies in our laboratory will emphasize the role of Strombus

gigas as a grazer and potential competitive interactions with smaller invertebrates.

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Table 1: Results of two-way ANOVA for mortality in the enclosed conch, with and without period I included.

Source	df	MS	F	P
With Period I				
Block	2	1.576	0.106	NS
Treatment	2	284.291	19.180	<0.001
Period	3	65.930	4.448	0.014
Treatment X Period	6	42.913	2.895	0.031
Error	22	14.822		
Without Period I				
Block	2	1.855	0.094	NS
Treatment	2	371.145	18.733	<0.001
Period	2	38.939	1.965	NS
Treatment X Period	4	20.785	1.049	NS
Error	16	19.812		

Table 2: Results of one- and two-way ANOVA for growth rates in the experimental enclosures and the wild population.

Source	df	MS	F	P
Treatment	3	1.852	1014.848	<0.001
Period	3	0.755	413.626	<0.001
Treatment X Period	9	0.037	20.372	<0.001
Error	3818	0.002		
Period I				
Treatment	3	1.023	306.640	<0.001
Error	1114	0.003		
Period II				
Treatment	3	0.545	420.047	<0.001
Error	886	0.001		
Period III				
Treatment	3	0.384	284.307	<0.001
Error	1008	0.001		
Period IV				
Treatment	3	0.286	313.052	<0.001
Error	810	0.001		

Table 3: Stomach contents of conch inside and outside experimental enclosures, June and October, 1987. Values are the percent of total dry weight comprised of the primary food items. All animals were between 90 and 120 mm total shell length. The values for indices of fullness (see text) are mean + standard deviation.

Treatment				
Food	Unenclosed	1-X	2-X	4-X
n for each date	10	9	9	9

June				
<u>Thalassia</u> detritus	15.3	24.8	25.9	22.5
Detritus	46.4	38.8	39.0	37.2
Sand	28.6	27.9	26.2	29.8
Foraminifera	7.4	6.3	7.3	8.7
Miscellaneous	2.3	2.2	1.6	1.8
Index of fullness	3.2 + 0.8	3.3 + 0.5	2.6 + 1.1	2.3 + 1.2

October				
<u>Thalassia</u> detritus	17.4	22.8	16.4	21.4
Detritus	40.0	44.2	49.2	44.8
Sand	23.9	20.7	22.4	20.4
Foraminifera	13.9	7.3	8.6	8.1
Miscellaneous	4.8	5.0	3.4	5.3
Index of fullness	3.8 + 0.4	3.5 + 0.7	2.9 + 1.0	2.1 + 0.8

Table 4: Results of ANOVA for biomass of green Thalassia blades
in five experimental treatments.

Source	df	MS	F	P
July				
Treatment	4	12.024	7.098	<0.001
Error	40	1.694		
October				
Treatment	4	2.364	1.643	NS
Error	40	1.439		

Table 5: Results of ANOVA for Biomass of macrodetritus in five experimental treatments.

Source	df	MS	F	P
July				
Treatment	4	116.439	19.674	<0.001
Error	40	5.919		
October				
Treatment	4	118.224	13.921	<0.001
Error	40	8.493		

Table 6: Results of ANOVA for sediment characteristics.

Source	df	MS	F	P
<u>Chlorophyll-a</u>				
Block	2	5.662	1.121	NS
Treatment	4	10.383	2.056	NS
Date	2	4.375	0.866	NS
Treatment x Date	8	6.028	1.194	NS
Error	163	5.050		
<u>Organics</u>				
Block	2	0.029	0.099	NS
Treatment	4	0.256	0.867	NS
Date	2	0.411	1.393	NS
Treatment x Date	8	0.261	0.844	NS
Error	58	0.295		
<u>Grain Size</u>				
Block	2	0.173	1.990	NS
Treatment	4	0.109	1.259	NS
Date	1	1.646	18.957	< 0.001
Treatment x Date	4	0.054	0.623	NS
Error	48	0.087		

LIST OF FIGURES

- Fig. 1: Percent mortality of conch held at three different densities over the four periods of investigation. Values are mean mortalities per enclosure + S.D. for the three blocks.
- Fig. 2: Growth rates of conch in wild populations and in three experimental treatments of animal density. Values are mean growth rates per day for each of four different growth periods + S.E. where blocks were pooled.
- Fig. 3: Above-ground biomass of green Thalassia blades in open areas (C) and in the four different experimental enclosures/exclosures. Values are means + S.D. for all blocks and samples combined.
- Fig. 4: Biomass of macrodetritus in open areas (C) and in the four different experimental enclosures/exclosures. Values are means + S.D. for all blocks and samples combined.

PERIOD I

Fig. 1

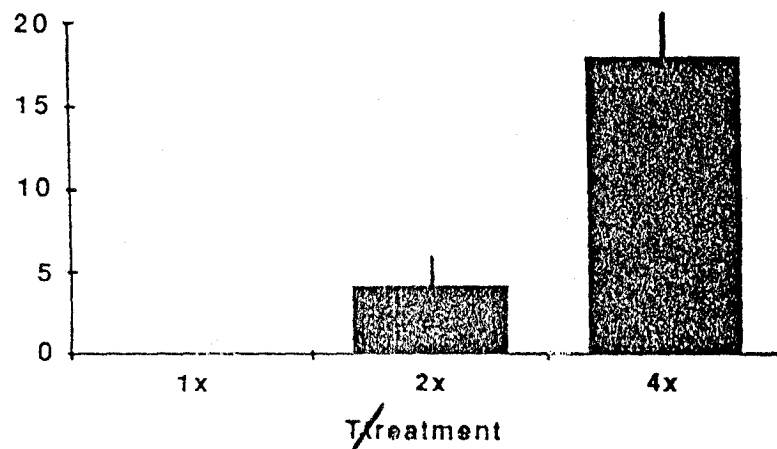
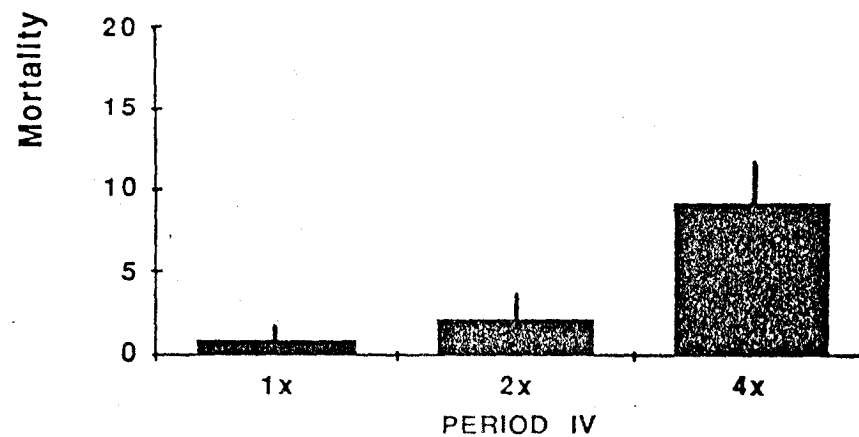
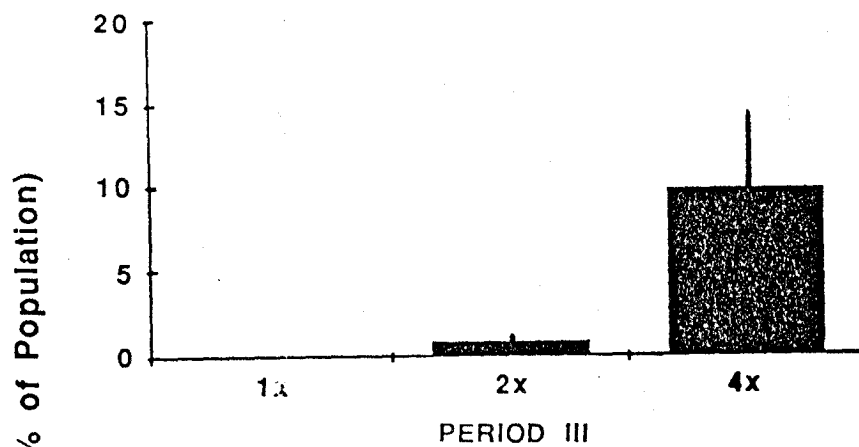
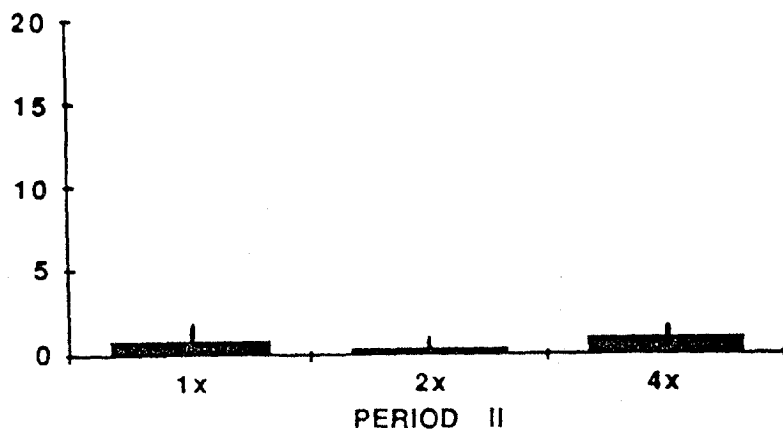
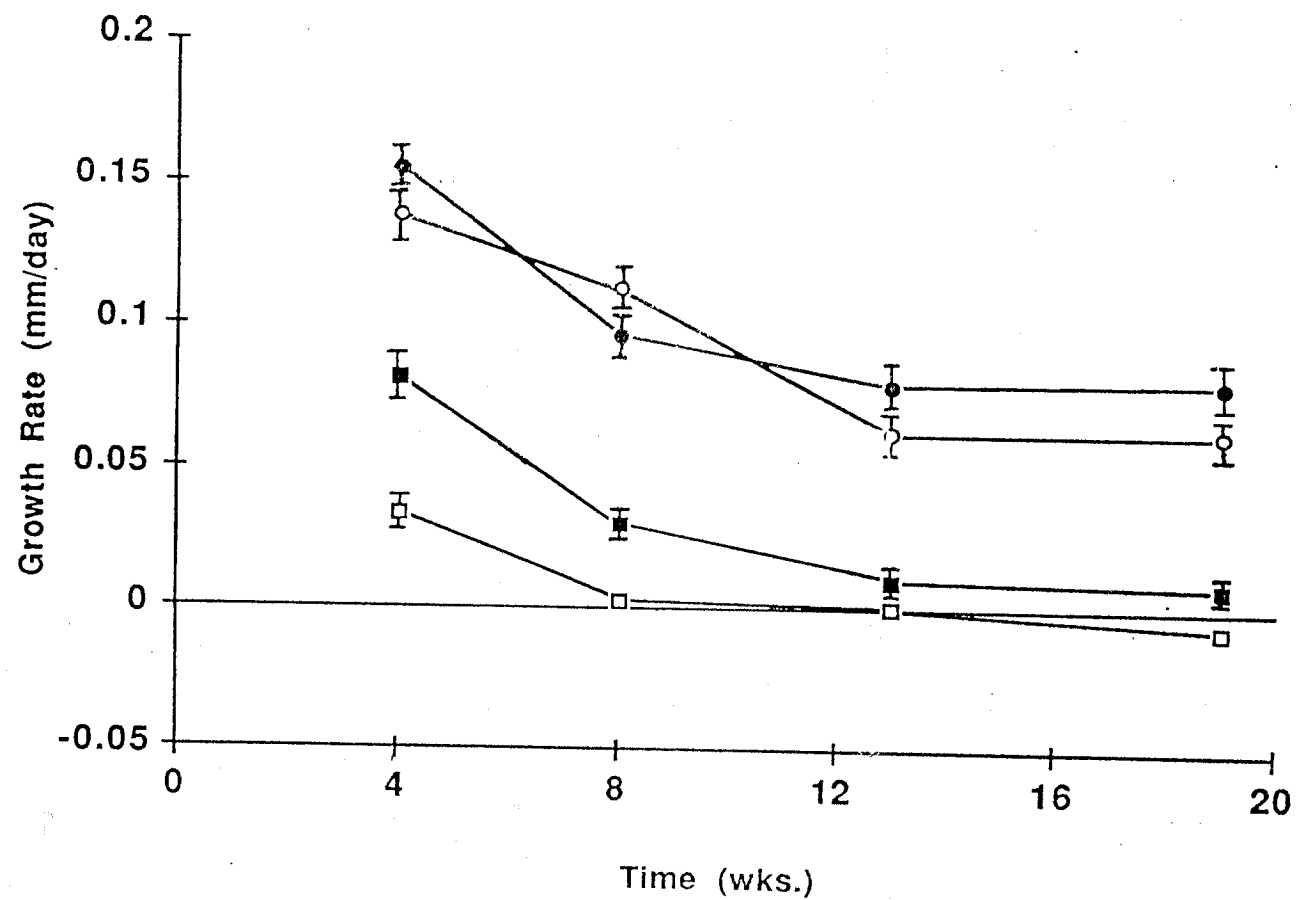
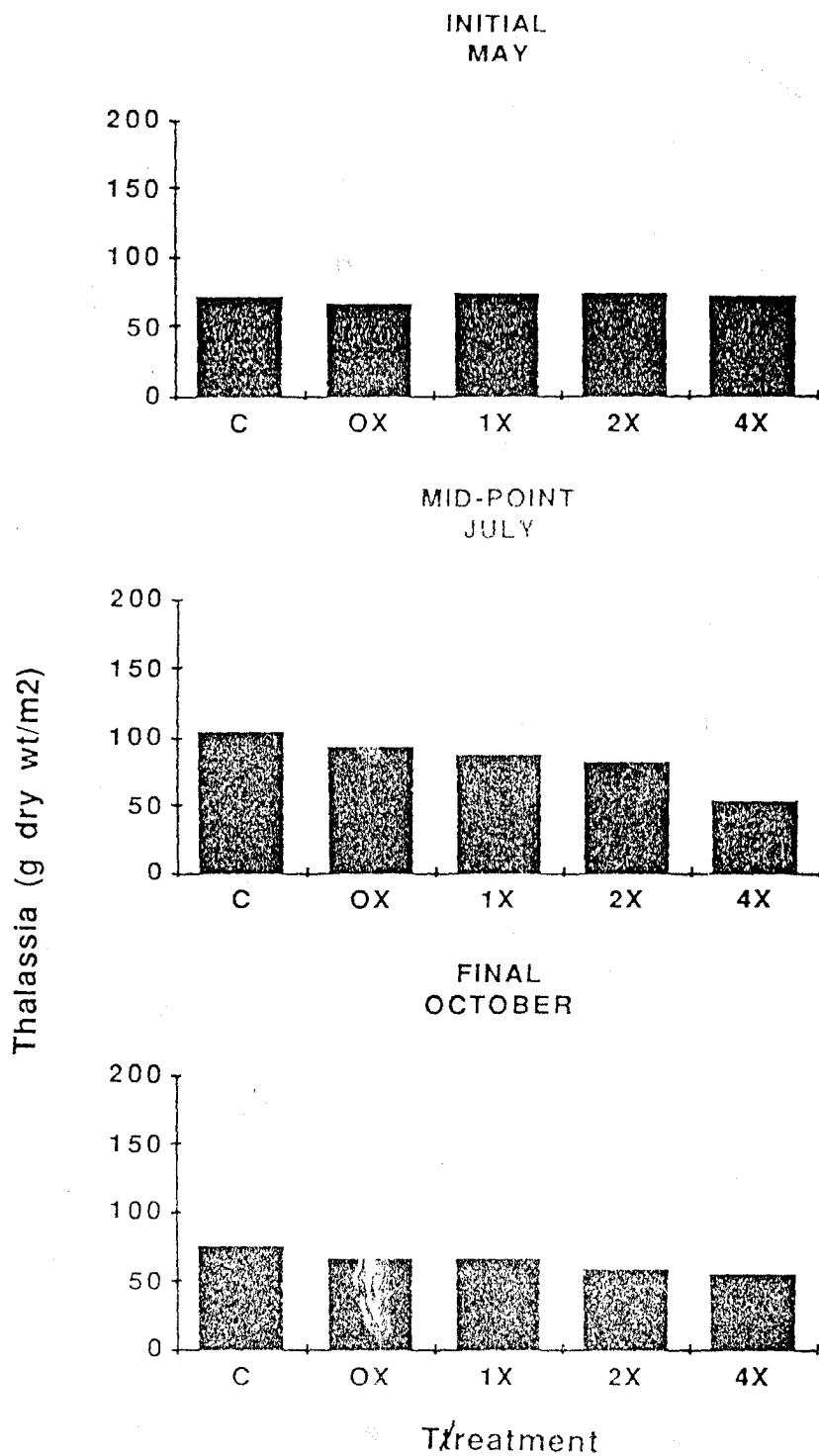


Fig. 2



●- WILD ○- 1X ■- 2X □- 4X

Fig. 3

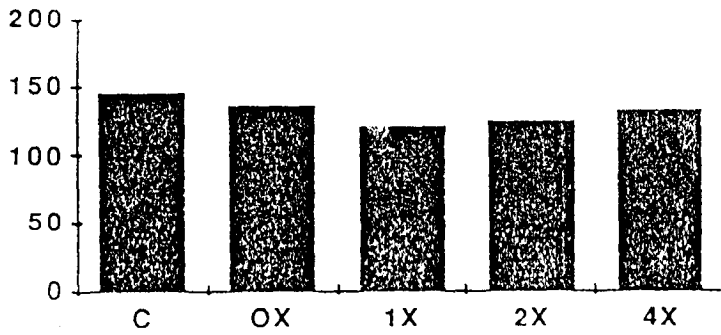


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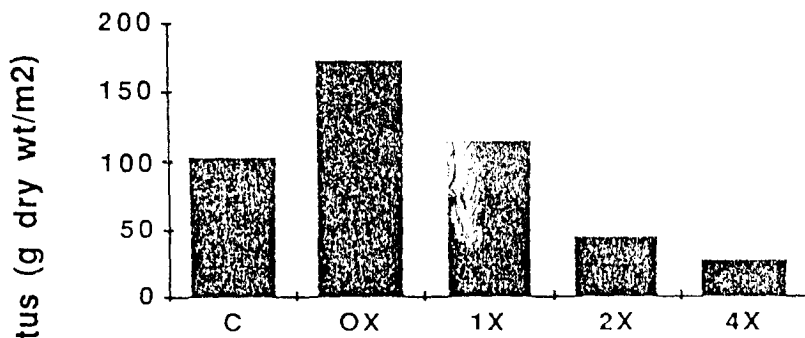
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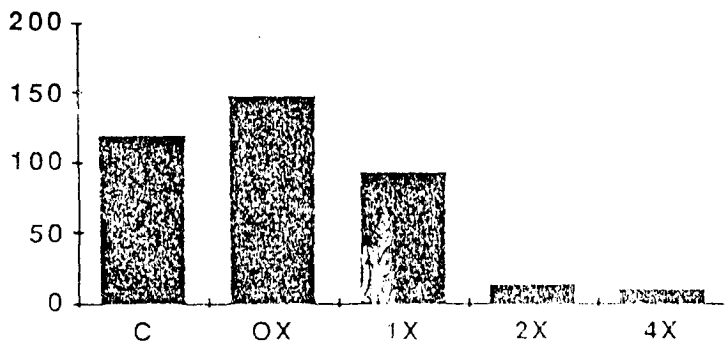
INITIAL
MAY



MID-POINT
JULY



FINAL
OCTOBER



Treatment

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