1983

Life history and secondary production of the crustacean gammarus mucronatus say (amphipoda: gammaridae) in warm temperate estuarine habitats, York River, Virginia

Thomas J. Fredette
College of William and Mary - Virginia Institute of Marine Science

Recommended Citation

Fredette, Thomas J., "Life history and secondary production of the crustacean gammarus mucronatus say (amphipoda: gammaridae) in warm temperate estuarine habitats, York River, Virginia" (1983). *Dissertations, Theses, and Masters Projects.* Paper 1539616648.
https://dx.doi.org/doi:10.25773/v5-btmt-g654

INFORMATION TO USERS

This reproduction was made from a copy of a document sent to us for microfilming. While the most advanced technology has been used to photograph and reproduce this document, the quality of the reproduction is heavily dependent upon the quality of the material submitted.

The following explanation of techniques is provided to help clarify markings or notations which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting through an image and duplicating adjacent pages to assure complete continuity.
2. When an image on the film is obliterated with a round black mark, it is an indication of either blurred copy because of movement during exposure, duplicate copy, or copyrighted materials that should not have been filmed. For blurred pages, a good image of the page can be found in the adjacent frame. If copyrighted materials were deleted, a target note will appear listing the pages in the adjacent frame.
3. When a map, drawing or chart, etc., is part of the material being photographed, a definite method of "sectioning" the material has been followed. It is customary to begin filming at the upper left hand corner of a large sheet and to continue from left to right in equal sections with small overlaps. If necessary, sectioning is continued again–beginning below the first row and continuing on until complete.
4. For illustrations that cannot be satisfactorily reproduced by xerographic means, photographic prints can be purchased at additional cost and inserted into your xerographic copy. These prints are available upon request from the Dissertations Customer Services Department.
5. Some pages in any document may have indistinct print. In all cases the best available copy has been filmed.

University
Microfilms
International
300 N. Zeeb Road
Ann Arbor, MI 48106

8407856

Fredette, Thomas Joseph

LIFE HISTORY AND SECONDARY PRODUCTION OF THE CRUSTACEAN GAMMARUS MUCRONATUS SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA

The College of William and Mary in Virginia PH.D. 1983

University
Microfilms
International 300 N. Zeeb Road, Ann Arbor, MI 48106

LIFE HISTORY AND SECONDARY PRODUCTION OF THE CRUSTACEAN *GAMMARUS MUCRONATUS* SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

---

by
Thomas J. Fredette
1983

APPROVAL SHEET

This dissertation is submitted in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy

Author

Approved, August 1983

Robert J. Diaz, Ph.D.

Donald F. Boesch

Donald F. Boesch, Ph.D.

Robert J. Byrne, Ph.D.

Robert J. Orth

Robert J. Orth, Ph.D.

Charles A. Menzie, Ph.D.
EG&G, Consultants
Waltham, Massachusetts

TABLE OF CONTENTS

Page

ACKNOWLEDGEMENTS. v

LIST OF TABLES. vii

LIST OF FIGURES ix

ABSTRACT. xi

INTRODUCTION. 2

LITERATURE CITED. 5

Chapter 1

LIFE HISTORY OF THE CRUSTACEAN _GAMMARUS_ _MUCRONATUS_ SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA 6

ABSTRACT. 7

INTRODUCTION. 8

MATERIALS AND METHODS 11

RESULTS 21

DISCUSSION. 45

LITERATURE CITED. 57

Page

Chapter 2

SECONDARY PRODUCTION OF THE CRUSTACEAN <u>GAMMARUS MUCRONATUS</u> SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA 63

ABSTRACT. 64

INTRODUCTION. 65

MATERIALS AND METHODS 68

RESULTS 77

DISCUSSION. 87

LITERATURE CITED. 95

APPENDIX A. 100

LITERATURE CITED. 113

VITA. 122

ACKNOWLEDGEMENTS

I would like to thank Dr. Robert J. Diaz, my major professor, for first introducing me to the topic of secondary production and providing much valuable advice. The other members of my committee, Dr. Donald F. Boesch, Dr. Robert J. Byrne, Dr. Robert J. Orth and especially Dr. Charles A. Menzie, are thanked for greatly improving the study design and final manuscript.

I am grateful to Drs. Morris H. Roberts, Jr. and Robert J. Orth for loan of laboratory space and equipment. Brian Meehan and Linda Schaffner are thanked for reviewing previous drafts of this document and engaging in productive discussions. Other colleagues to whom I am indebted for field assistance and advice are Larry Gadbois, Eric Koepfler, Deborah Penry, David Stilwell, Elizabeth van Montfrans and Jacques van Montfrans.

Partial support for this study was provided by a College of William and Mary Minor Research Grant.

To my parents, Charles and Josephine Fredette, I express my gratitude for their constant support throughout

my education. I will always be appreciative of their ability to assist with, but not dictate decisions, which allowed those of us who are their children to seek dreams of our own.

A special 'Thank you' to my wife, Julie, for her field assistance, many long hours of laboratory work, constant encouragement, support and love. Without her, this goal could not have been achieved.

LIST OF TABLES

LIFE HISTORY OF THE CRUSTACEAN <u>GAMMARUS</u> <u>MUCRONATUS</u> SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA

Table — Page

1. Numbers of males and females present in each habitat by date. Significant departures from a 1:1 ratio are indicated by an asterisk (*) ($p<0.05$). 22

2. Mean size of individuals at each sample date by sex and total population. Blanks indicate either no samples taken or absence of amphipods. Significant size differences are indicated by an asterisk (*) ($p<0.05$). 23

3. Mean size (mm) (L_{H3}) of 24 individuals per treatment in the food comparison experiment. 28

4. Estimated temperature dependent rate of egg development. 29

5. Comparison of size-frequency distributions between replicates on a given sample date, between successive dates and between habitats (goodness of fit G-test). 36

SECONDARY PRODUCTION OF THE CRUSTACEAN <u>GAMMARUS</u> <u>MUCRONATUS</u> SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA

1. Size-frequency production estimates for male and female subgroups from the seagrass habitat (see text for explanation of terms). 80

2. Production estimates for <u>Gammarus</u> <u>mucronatus</u> from the seagrass habitat for the total fortnightly sample set (26 Dates), the two alternate four week sets (13 Even, 13 Odd), the summation of the separate sexes (M+F) and the instantaneous growth estimate (IGR). Both seasonal and total production are shown. 83

Table		Page
3.	Production estimates for *Gammarus mucronatus* from the algal habitat for the total fortnightly sample set (26 Dates), the summation of the separate sexes (M+F) and the instantaneous growth estimate (IGR).	84
4.	Production/Biomass ratio estimates for *Gammarus mucronatus* based on computation of predictive models.	92

LIST OF FIGURES

LIFE HISTORY OF THE CRUSTACEAN <u>GAMMARUS MUCRONATUS</u> SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA

Figure		Page
1.	Sampling locations in the lower York River, Virginia.	12
2.	Temperature (a) and salinity (b) records during the study period. △ *Zostera marina* site, □ algal site.	13
3.	Mean size (mm) of ovigerous females.	24
4.	Relationship of length of head and first three pereonites to time in growth experiments. △ 5° C, □ 14° C, ○ 23° C.	26
5.	Relationship of brood size to female size (mm).	30
6.	Relationship of eggsize (mm) to time from winter to summer. Regression ± 95% confidence limits.	31
7.	Mean density ($\# \cdot m^{-2}$) of *Gammarus mucronatus* at the seagrass site (a), and mean dry weight biomass ($g \cdot m^{-2}$) of *Zostera marina* (b).	33
8.	Mean density ($\# \cdot m^{-2}$) of *Gammarus mucronatus* at the algal site (a), and mean dry weight biomass ($g \cdot m^{-2}$) of *Enteromorpha*-*Ulva* (b).	34
9.	Size-frequency distributions for the fortnightly samples from the seagrass habitat (0.5 mm length classes, class 1 = 0.5-0.9mm). Cohort I crosshatched, cohort II striped.	39

Figure Page

10. Size-frequency distributions from the March and May intensive sampling, seagrass site. 16 February and 13 April added for reference. Cohort I crosshatched, Cohort II thick diagonal striping, cohort III thin diagonal striping. 40

11. Size-frequency distributions for the algal site, 8 December to 6 July (dates omitted where *Gammarus mucronatus* was absent). 42

12. Mean densities ($\# \cdot m^{-2}$) of juveniles (see text) ⊞ , and ovigerous females △ (exaggerated by a factor of 8) from the seagrass habitat, 8 December to 3 August. 43

13. Temperature dependent egg development rates for *Gammarus pseudolimnaeous* (Marchant and Hynes 1981), *Dogielinotus loquax* (Hughes 1982) and *Gammarus mucronatus* (present study). 51

SECONDARY PRODUCTION OF THE CRUSTACEAN *GAMMARUS MUCRONATUS* SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA

1. Sampling locations in the lower York River, Virginia. 69

2. Size-frequency distributions for the seagrass habitat 8 December to 22 June (0.5 mm length classes, class 1 = 0.5-0.9mm). Cohort I crosshatched, cohort II thick diagonal striping, cohort III thin diagonal striping. 73

3. Amphipod dry weight biomass ($mg \cdot m^{-2}$) during the study period (a) seagrass habitat (b) algal habitat. 79

4. Resultant curves from computation of daily IGR production (a) seagrass habitat (b) algal habitat. 86

ABSTRACT

In order to assess the secondary production potential of the amphipod *Gammarus mucronatus* its life history was examined with laboratory experimentation and field sampling in two warm temperate estuarine habitats in the York River, Virginia. A seagrass (*Zostera marina*) bed and a macroalgae (*Ulva* spp., *Enteromorpha* spp.) fouling community on old pier pilings.

Variations in amphipod abundance between the habitats were not similar. *G. mucronatus* was present in the seagrass habitat during most of the year attaining maximum densities of $1200 \cdot m^{-2}$ in the spring. Presence of *G. mucronatus* in the macroalgae habitat was almost totally restricted to late spring and early summer, but maximum densities as high as $6800 \cdot m^{-2}$ occurred.

Estimates from field and laboratory evidence suggest that *G. mucronatus* produced 6-9 generations over a one year period. Rapid turnover resulted from increased spring and summer growth rates and maturation at smaller sizes during these months. Reduction in size of summer adults is hypothesized to be a co-evolutionary response to predation by which the amphipod population can increase its intrinsic rate of growth (r).

Production calculations were made using four different approaches. The size-frequency method was calculated for 26 fortnightly sample dates, two alternate subsets of the data set (13 sample dates each), and separate calculations for the sexes. The fourth approach utilized a modified instantaneous growth (IGR) equation. The IGR method produced results that were more than 25% greater than the size-frequency estimates which all agreed fairly well. Monthly sampling is sufficient to characterize the population for production estimates, but because of rapid spring and summer growth it is incapable of detecting voltinism.

Production in the algal habitat was $10.2\ g \cdot m^{-2} \cdot yr^{-1}$ with a $P/\bar{B}$ of 60.8, greater than the $5.0\ g \cdot m^{-2} \cdot yr^{-1}$ production and 40.0 $P/\bar{B}$ of the seagrass habitat. The higher algal values are the result of the greater maximum abundance of this habitat coinciding with rapid spring and summer growth.

Of three different predictive models tested, one proposed by Robertson (1979) provides the best agreement with the $P/\bar{B}$ estimates calculated from empirical data.

LIFE HISTORY AND SECONDARY PRODUCTION OF THE CRUSTACEAN *GAMMARUS MUCRONATUS* SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA

Introduction

Primary production, or the synthesis of energy into biological matter, is most commonly associated with the process of photosynthesis. Any autotrophic organism, be it chemoautotrophic bacteria or an oak tree can be properly classified as a primary producer. Those organisms which directly or indirectly through a food web rely on primary producers for their energy are secondary producers. Secondary production is measured as the accumulation of biomass by a heterotrophic organism or group of heterotrophic organisms. A simpler term for expressing this process is growth.

Initially, interest in secondary production estimation of aquatic organisms centered around commercial and sport fish species. In order to manage such fisheries there was a need to know how fast fish grew and replenished their stock. Interest in secondary production estimation of invertebrate organisms is based on a need to determine the potential food resource value of a stream, lake or other aquatic habitat to fish species (Waters 1977).

Adequate methods for the measurement of fish production had been developed by the 1940's (Allen 1949, Ricker 1946). Most commercially important fish have limited breeding seasons and live for several years. Thus, a distinct cohort is produced every year that can be measured or aged to distinguish it from other year classes. On the other hand, many invertebrates have extended breeding seasons and short life spans. Often cohorts can not be distinguished and growth rates are unknown. Adequate calculation methods for secondary production estimation of such populations were not developed until the 1960's (Hynes and Coleman 1968, Hamilton 1969). Thus, production of aquatic invertebrates has only been studied for the brief period of a decade (Waters 1977, Warwick 1980).

Production estimates of entire aquatic invertebrate communities are relatively scarce in comparison to even the meager number of single species studies (Waters 1977) and the majority of these community studies have been in fresh water systems or cold temperate latitudes. In one of the only warm temperate studies, Diaz and Fredette (1982) estimated one of the highest productions per unit area recorded for marine invertebrates. In this study they examined three decapod species, three isopod species, two mollusc species and one species of amphipod with monthly sampling intervals in a Chesapeake Bay seagrass bed. They concluded that this sample frequency was insufficient for tracking cohorts within the isopod and amphipod populations because of rapid growth between sample dates. Without adequate knowledge of the growth rate and voltinism (generation time) of an organism, secondary production can not be estimated with confidence (Waters 1979).

The present study was designed to (1) investigate the life history of the amphipod studied by Diaz and Fredette (1982), *Gammarus mucronatus* and (2) use the life history information as a tool in estimating the secondary production of the species. The details of this study are presented in the two chapters that comprise this text. The first paper involves the life history aspects of *G. mucronatus*; growth, voltinism, reproduction and abundance, the second paper is a report on the secondary production of this species and the effects of different methods of production estimation.

Literature Cited

Allen, K. R. 1949. Some aspects of the production and cropping of fresh waters. Rpt. Sixth Sci. Congr. 1947. Trans R. Soc. N. Z. 77, 222-228.

Diaz, R. J. and T. J. Fredette. 1982. Secondary production of some dominant macroinvertebrate species inhabiting a bed of submerged vegetation in the lower Chesapeake Bay. In, Structural and functional aspects of the biology of submerged aquatic macrophyte communities in the lower Chesapeake Bay, by R. L. Wetzel, K. L. Webb, P. A. Penhale, R. J. Orth, D. F. Boesch, G. W. Boehlert and J. V. Merriner. Final Report EPA/CBP Grant No. R805974.

Hamilton, A. L. 1969. On estimating annual production. Limnol. Oceanogr. 13, 771-782.

Hynes, H. B. N. and Coleman, M. J. 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13, 569-573.

Ricker, W. E. 1946. Production and utilization of fish populations. Ecol. Monogr. 16, 373-391.

Warwick, R. M. 1980. Population dynamics and secondary production of benthos. In, K. R. Tenore and B. C. Coull (Eds.), Marine Benthic Dynamics. Univ. S. Carolina Press, Columbia, S. C. 451pp.

Waters, T. F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 14, 91-164.

Waters, T. F. 1979. The turnover ratio in production ecology of freshwater invertebrates. Am. Nat. 103, 173-185.

LIFE HISTORY OF THE CRUSTACEAN GAMMARUS MUCRONATUS SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA

Abstract

The life history of the amphipod _Gammarus mucronatus_ was examined in two warm temperate estuarine habitats, a seagrass (_Zostera marina_) bed and the macroalgae region (_Ulva_ spp., _Enteromorpha_ spp.) of a fouling community. Amphipod populations were present in the seagrass habitat during most of the entire year ranging from $<50 \cdot m^{-2}$ in late summer to $1200 \cdot m^{-2}$ in June, while the algal habitat was utilized only from late winter to early summer, but with maximum abundances as high as $6800 \cdot m^{-2}$. Based on laboratory growth experiments, observations on field growth rates and recognition of cohorts from size-frequency distributions it is estimated that _G. mucronatus_ is capable of producing approximately 6-9 cohorts per year. Rapid spring and summer growth is accompanied by maturation at smaller size and reduction in brood size, egg size and development time.

Introduction

Gammarus mucronatus is an endemic shallow water amphipod of the estuaries and coasts of the North American Atlantic seaboard and the Gulf of Mexico (Bousfield 1969, Dickinson et al. 1980). This relatively small (Steele and Steele 1975) eurytopic *Gammarus* occurs in diverse habitats such as seagrass beds (Marsh 1973, Nelson 1980a), sponges (Biernbaum 1981), *Spartina* marshes, soft bottoms with shell or cobble (van Maren 1978), oyster bars and open beaches (Watling and Maurer 1972). Salinity tolerance ranges from 4-35‰ (Bousfield 1973).

Gammarus mucronatus has a generalized diet including macroalgae, microalgae, detritus and possibly some macrofauna (Zimmerman et al. 1979). In seagrass beds, this amphipod may function as both a link in the decomposition process, reducing the particle size of detritus by shredding with mouth appendages, and as a grazer of seagrass epiphytes (Howard 1982). *G. mucronatus* is probably important as a prey item for both juvenile and adult fish and large decapod crustaceans (Nelson 1979, 1981, Young et al. 1976, Van Dolah 1978).

Unlike its congener _G_. _palustris_, whose life history characteristics are well known (Gable and Croker 1977, Rees 1975, Van Dolah et al. 1975), the life history of _G_. _mucronatus_ has not been closely examined. Borowsky (1980) examined fecundity, brood size and embryonic period and Van Dolah and Bird (1980) studied egg and brood size. Steele and Steele (1975, and references therein) examined the life history of several _Gammarus_ species but provided little data on _G_. _mucronatus_. However, they do suggest that two or more generations per year may occur south of their Newfoundland study location.

General lack of life history information for _G_. _mucronatus_ was noted by Diaz and Fredette (1982) in a study of secondary production of macrobenthic invertebrates. They examined size-frequency histograms based on monthly samples in a Chesapeake Bay seagrass bed and were unable to distinguish cohorts. They concluded that rapid growth may have precluded tracking cohorts by using only a monthly sampling interval. Therefore, the present study was designed to examine more closely the life cycle, abundance and growth rate of _G_. _mucronatus_ through laboratory experimentation and intensive field sampling. This data will then be used to more precisely calculate secondary production estimates for this organism.

This paper presents the life history aspects of _G. mucronatus_, a second paper (Fredette 1983) examines the secondary production of this species. Among the life history factors examined here that are important for the estimation of secondary production are growth rate, size-class structure, number of generations, abundance and the variability of these in different habitats (Martien and Benke 1977, Waters 1977,1979).

Materials and Methods

Study Sites

Two different habitat types were chosen for the examination of the population dynamics of _G_. _mucronatus_ (Figure 1), a seagrass (_Zostera_ _marina_) bed in the vicinity of Jenkins′ Neck and a hard substrate habitat covered primarily by macroalgae and located on old pier pilings at the Virginia Institute of Marine Science, Gloucester Point, Virginia. These two habitats were chosen for study because (1) from prior investigation amphipod abundances were expected to be high and (2) it would provide an opportunity to compare differences in population characteristics and secondary production of two spatially proximate habitats over the same time period. Both study sites are located in the lower York River, a subestuary of the Chesapeake Bay.

The lower York is generally upper-mesohaline - polyhaline, with a seasonally fluctuating salinity range. Salinity and temperature fluctuations at the two sites exhibited similar trends (Figure 2) with both parameters tending to be somewhat higher at the seagrass bed owing to

Figure 1. Sampling locations in the lower York River, Virginia.

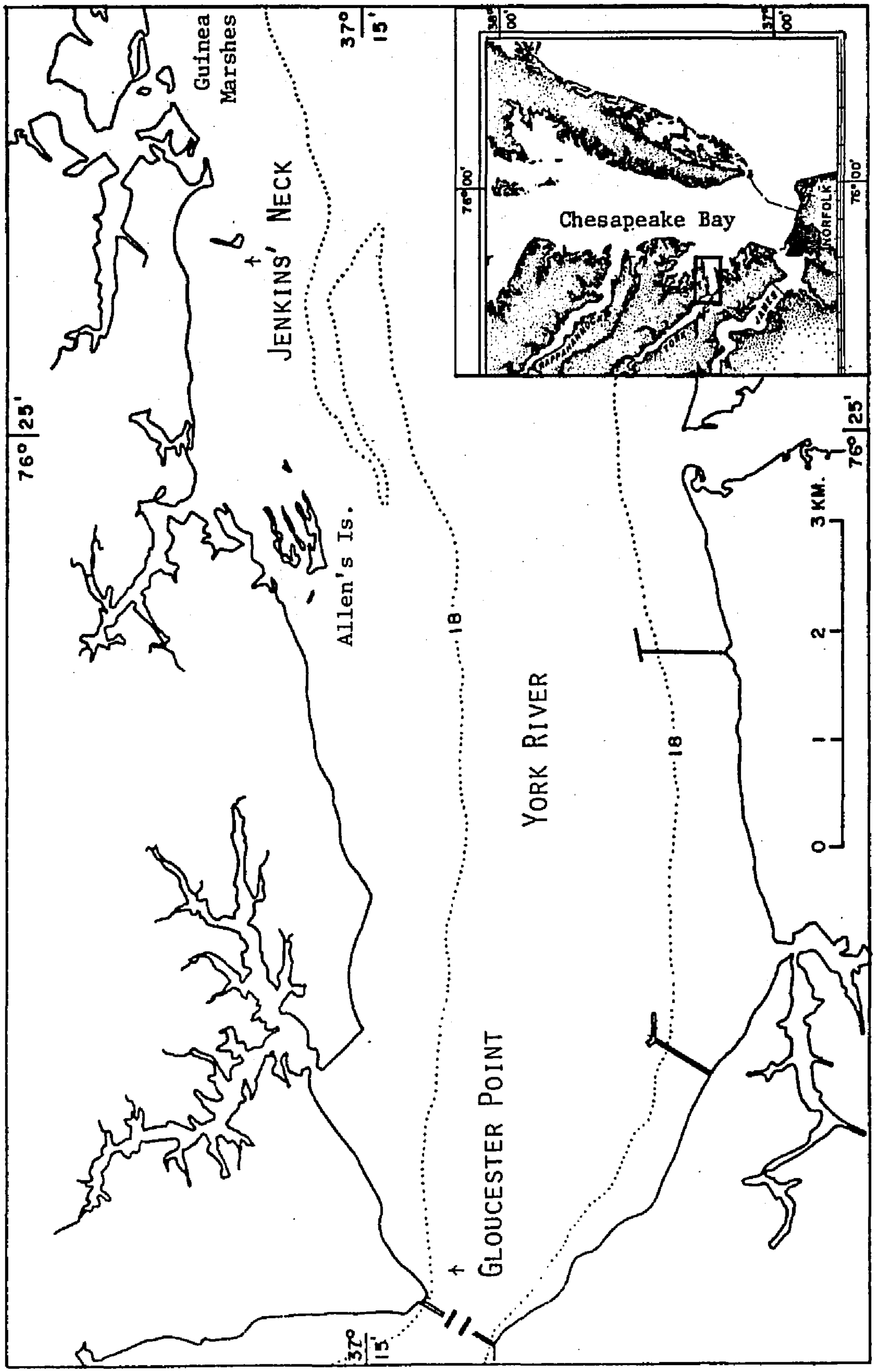
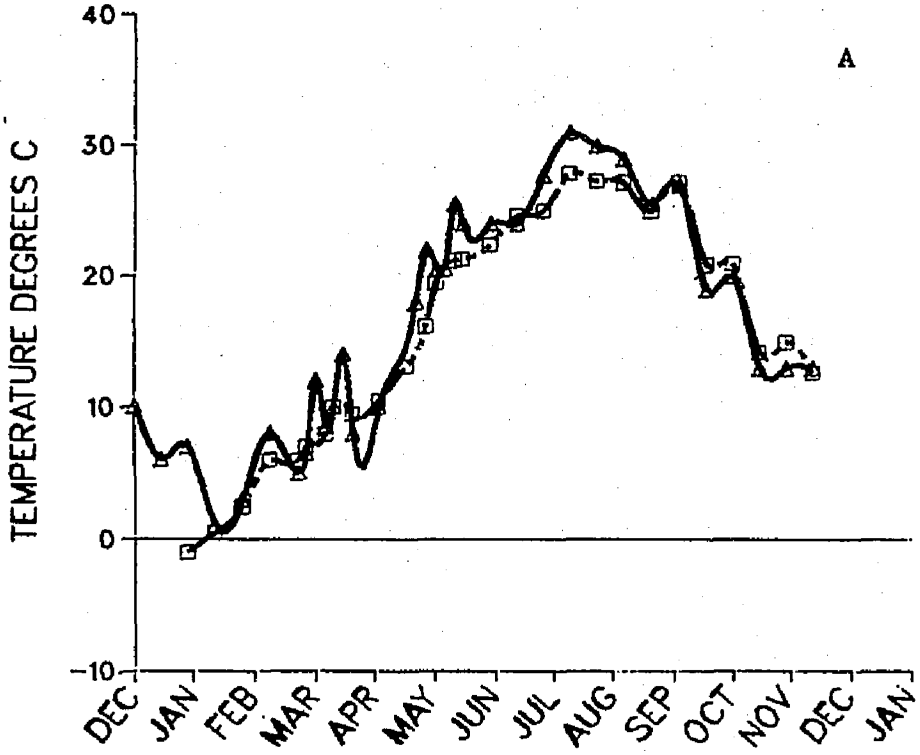
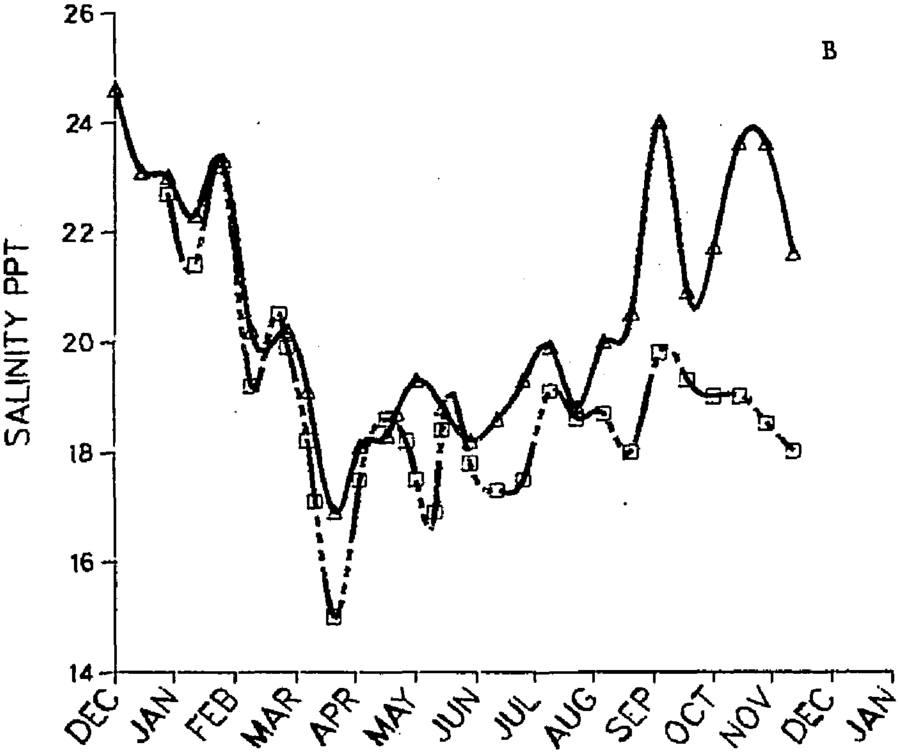

Guinea Marshes
37° 15'
Jenkins' Neck
76° 25'
Allen's Is.
18
York River
18
0
1
2
3 KM.
76° 25'
Gloucester Point
37° 15'
Chesapeake Bay
38° 00'
37° 00'
76° 00'
76° 00'
Norfolk
Rappahannock
York
James

Figure 2. Temperature (a) and salinity (b) records during the study period. △ *Zostera marina* site, □ algal site.


A
TEMPERATURE DEGREES C
40
30
20
10
0
-10
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN


B
SALINITY PPT
26
24
22
20
18
16
14
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN

its shallower, lower estuary location. Temperature ranged from -1.0° C to 33° C and salinity varied less than 15‰ for the year with the lowest values occurring during the spring and summer months. Salinity range was 10 to 24‰ at the seagrass bed and 15 to 24‰ at the algal habitat.

The seagrass bed is part of one of the largest tracts of submerged aquatic vegetation in the lower Chesapeake Bay extending from Allen's Island down estuary to Guinea Marsh (Orth et al. 1979). Algae occurring at the pier site have been previously described by Wulff and Webb (1969). Sampling of the algal site was restricted to those areas dominated by the green algae *Ulva* spp. and *Enteromorpha* spp.

Field Program

To assess population dynamics and seasonal field growth rates a fortnightly (every 14 days) schedule of field sampling was established from December 1981 to November 1982. It was expected that fortnightly sampling would be sufficient to track cohorts in the winter, but a shorter time scale would be needed in the spring and summer if warmer temperatures led to faster growth. To examine this possibility I decided to sample more intensively (every four or five days) in two months, March and May.

Sampling was done at low tide, facilitating access to both sites. Ten 0.0165 m^2 replicate samples were taken randomly from each habitat. Seagrass samples were obtained with an acrylic corer gently placed over the seagrass and pushed through the rhizome and root layer. The corer was designed to reduce escape of organisms. After removal from the bottom, samples were placed into a bucket and thoroughly rinsed. All of the seagrass blades were then removed from the sediment core and placed with the bucket contents into a 0.25 mm mesh bag (based on the size of newly hatched juveniles this mesh should retain all individuals). Samples were transferred to glass jars in the laboratory and preserved in 10% buffered, Rose Bengal stained formalin.

Samples of the algal community were taken with a specially designed piling scraper. The device was made by cutting a crescent of the same curvature of an average piling in the end of a 0.0165 m^2 acrylic tube. This edge was then gasketed with a 3 cm wide strip of neoprene. A 0.25 mm mesh bag with an internally enclosed scraper was attached to the other end of the tube. Sampling was accomplished by pushing the sampler against a piling over the Ulva and Enteromorpha (the gasket sealing most irregularities of the piling and barnacles). The algae was then scraped off the piling surface and the entire sample contained by quickly sweeping upward to the water surface. Samples were preserved as above.

Laboratory Sample Processing and Data Analysis

Amphipods were sorted from the samples with the aid of a dissecting microscope, enumerated, measured with an ocular micrometer to the nearest 0.1 mm and their sex determined. Individuals were measured from the tip of the rostrum to the posterior edge of the third pereonal segment (L_{H3}). In addition, approximately 75 amphipods were measured for head length (L_H) and total length (L_T) to provide conversion to these commonly used measures.

Head length and total length are strongly correlated to the measure of head plus the first three segments and result in the equations

$$L_T(\text{mm}) = 3.74\ L_{H3}(\text{mm}) - 0.42 \qquad (r^2 = 0.98,\ n = 72)$$

and

$$L_H(\text{mm}) = 0.29\ L_{H3}(\text{mm}) + 0.11 \qquad (r^2 = 0.94,\ n = 78)\ .$$

All lengths reported in this paper (including those of other authors) will be the L_{H3} measure. However, total length is approximately 3.3 times greater.

Males were identified by the presence of penial papillae, females by the presence of broods or oostegites. Maturity of non-brooding females was determined by presence of setae on the oostegites. To determine if the sex ratio varied from 1:1, the null hypothesis ($p=k=0.5$) was tested against the binomial distribution. Juveniles were defined as all individuals smaller than 1.0 mm (rostrum to rear border of third segment) plus a few slightly larger individuals on which sex could not be determined. Juvenile amphipods are released from the brood pouch at approximately 0.5 mm.

Field growth rates were determined by tracking recognizable cohorts with size-frequency distributions (0.5 mm length classes) from successive sample dates. Replicate size-frequency distributions (within habitats, by date) were tested for homogeneity of population structure with the G test (Sokal and Rohlf 1981). Successive sample dates within habitats and between habitat comparisons were also examined for homogeneity. Mean size of males, females and total populations were tested for differences between the two habitats on each sample date using t-tests (Nie et al. 1975).

Stoner (1980a) has shown that abundance of many macroinvertebrates in seagrass beds is related to macrophyte density and not simply bottom area. To adjust for this potential bias, seagrass and algae were separated from the samples, dried in an oven at 60° C and weighed to determine biomass. A moving average was then applied to these values to better estimate mean standing stock of the macrophytes. These values were then used to determine areal estimates of amphipod abundance.

Laboratory Program

Growth rates of G. mucronatus were examined under controlled laboratory conditions to assess the effects of temperature and for comparison to field estimates. In March 1982 several dozen adult G. mucronatus were collected at the seagrass bed and brought alive to the laboratory. Several ovigerous females were isolated and their broods allowed to hatch. After release from the brood pouch, juveniles were randomly assigned to one of three compartmented trays. Tray compartments were filled with approximately 50 ml ambient salinity seawater and each contained one amphipod. Each tray was then placed into an incubator set at 5, 14 or 23° C with a 12 hour light and dark cycle. These temperatures were chosen as representative of those G. mucronatus would experience in the field. Amphipod food supply consisted of algae and fresh and detrital seagrass. For this and all laboratory experiments water was changed and fresh food added every 3 or 4 days. Over time amphipods were randomly chosen for preservation and measurement.

The effects of food type and habitat of origin on amphipod growth were tested. Four treatments were established; seagrass amphipods - detrital seagrass food, seagrass amphipods - algae food, algal amphipods - detrital seagrass food, and algal amphipods - algae food. Ovigerous amphipods were obtained from each habitat and newly released juveniles were randomly assigned to each of the two food types, with 10-14 juveniles placed into 16 500 ml culture bowls (4 bowls each treatment). After 21 days six amphipods were chosen randomly from each bowl and preserved for later measurement. It was determined from the previous growth experiment that this design would be sufficient to detect a 15% difference in growth between treatments (α=0.05, β=0.005). A 2 X 2 ANOVA was used to examine the experimental results (Nie et al. 1975).

Reproduction

The length of time from oviposition to brood release was examined at 6° C. This temperature was chosen to complement data from previous studies. Borowsky (1980) has previously estimated development time at 17 and 21° C and Steele and Steele (1975) presented estimates (based on egg size) for 0 and 10° C. Six females in precopula with males were isolated and checked daily. After oviposition females were separated from males and placed into a compartmented tray in an incubator maintained at 6° C, 12 hour light and dark cycle. The embryonic development time was recorded as that time from oviposition to release of juveniles from the brood pouch.

To determine the relation between female size and brood size 97 ovigerous females collected from December to August were measured and the number of eggs recorded. Of these 37 had broods that were at the "A" stage of development, which is defined by Steele and Steele (1969) as eggs recently oviposited. Size of six eggs per brood was determined by the method of Steele and Steele (1969) as the average of the length and width.

Results

Population Structure

Overall sex ratios in each habitat do not appear different than an even distribution. Sex ratios were found to differ ($p<0.05$) from a 1:1 ratio on 6 May in the seagrass habitat, when females out numbered males (2.5:1) (Table 1). On 22 June males were more abundant than females in seagrass (1.6:1) and less abundant than females at the algal habitat (1:2.6). Mature non-ovigerous females were rare with over 90% of all mature females carrying broods.

Mean size of males, females and total populations between habitats does not appear to differ (Table 2). Although there are some significant ($p>0.05$) differences, no general pattern was evident. There may be some evidence for larger females and males at the algal habitat in April and early May with a reversal in late May but it is not very conclusive. Analysis of the size of ovigerous females (Figure 3) indicates a reduction in mean size from approximately 3.5 mm to 1.5 mm from the winter months to

Table 1. Numbers of males and females present in each habitat by date. Significant departures from a 1:1 ratio are indicated by an asterisk (*) ($p<0.05$).

TABLE 1

	Seagrass		Algae	
Date	# Male	# Female	# Male	# Female
8 DEC	4	1		
22 DEC	2	2		
5 JAN	5	6	3	3
19 JAN	8	6		
2 FEB	4	8		
16 FEB	2	6	1	
2 MAR	7	12	2	3
6 MAR	4	5		
11 MAR	17	13		
16 MAR	10	9		1
20 MAR	8	6		
25 MAR	7	6		
30 MAR	8	9		
13 APR	15	15	2	3
27 APR	25	24	12	19
1 MAY	18	20	21	19
6 MAY	11	* 27	52	47
11 MAY	11	17	31	31
16 MAY	20	22	197	181
20 MAY	29	25	314	316
25 MAY	22	23	231	261
8 JUN	43	54	74	81
22 JUN	36	* 22	6	* 16
6 JUL	14	7	5	10
20 JUL	5	1		
3 AUG	9	6		
17 AUG	4	5		
31 AUG	1	1		
14 SEP		1		
28 SEP				
12 OCT				
26 OCT		1		
9 NOV				
23 NOV	1	5		
Total N	350	365	951	991

* $p<0.05$

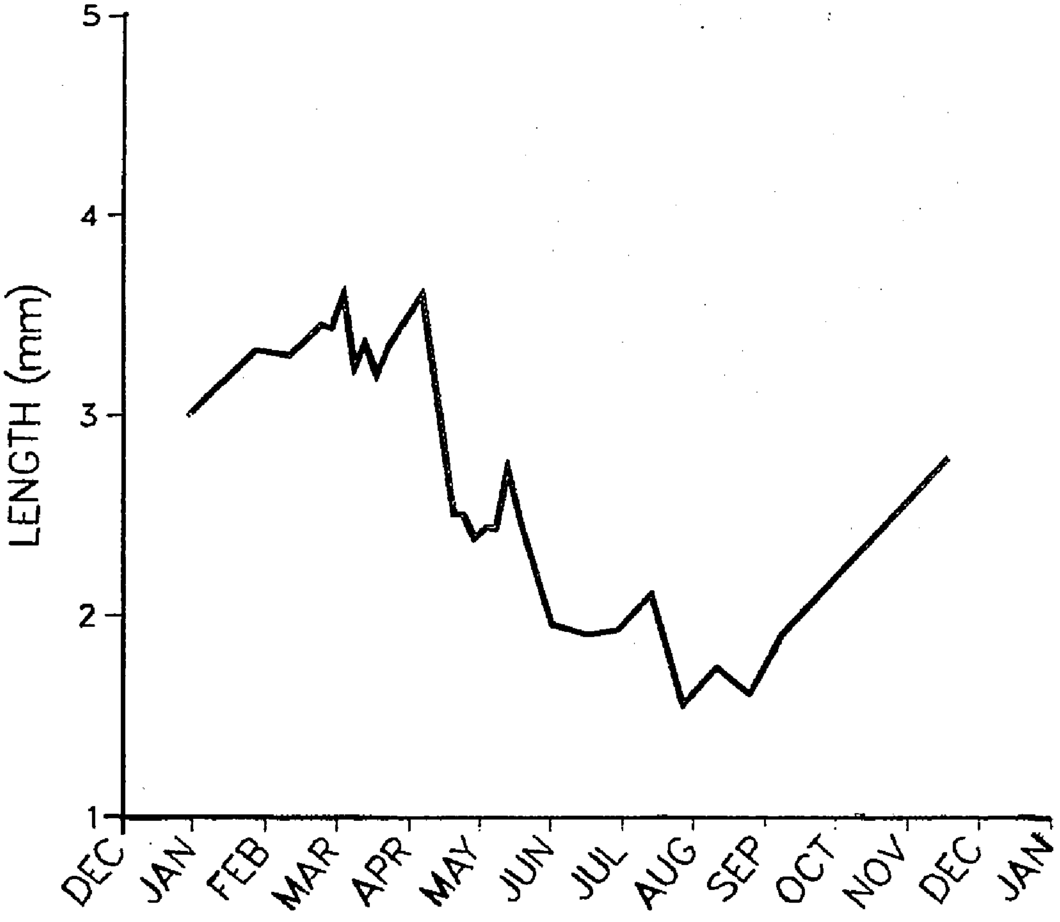
Table 2. Mean size of individuals at each sample date by sex and total population. Blanks indicate either no samples taken or absence of amphipods. Significant size differences are indicated by an asterisk (*) ($p<0.05$).

TABLE 2

	Males		Females		Total Pop.	
Date	Seagrass	Algae	Seagrass	Algae	Seagrass	Algae
8 DEC	2.98	2.73	1.45	2.77	2.68	2.21
22 DEC	2.31		1.91		1.36	
5 JAN	2.66	1.77	2.48	2.38	2.10	1.94
19 JAN	2.18		1.97		1.68	
2 FEB	3.00		2.82		2.57	
16 FEB	3.75	3.20	2.82		1.57	3.20
2 MAR	1.93	1.45	2.41	2.57	1.95	2.12
6 MAR	2.10		2.90		2.07	
11 MAR	2.15		2.22		1.79	
16 MAR	3.11		2.72	4.10	2.02	4.10
20 MAR	2.24		3.27		1.81	
25 MAR	2.37		2.83		1.53	
30 MAR	2.64		3.01		1.01	0.90
13 APR	1.65	2.00	1.31 *	3.27	0.81	1.02
27 APR	1.71	2.31	1.67 *	2.36	1.30	1.42
1 MAY	1.71 *	2.29	1.71 *	2.25	1.27	1.23
5 MAY	1.63	1.70	2.09 *	1.73	1.47 *	1.08
11 MAY	2.31 *	1.58	2.14	1.81	1.14 *	0.89
16 MAY	2.06	1.85	2.19	1.95	1.28	1.17
20 MAY	1.98	1.94	1.85	1.92	0.96 *	1.25
25 MAY	1.68	1.82	1.78	1.69	1.03 *	1.30
8 JUN	1.53	1.48	1.55	1.44	1.10	1.04
22 JUN	1.66	1.72	1.63	1.76	1.32	1.48
6 JUL	1.76	1.26	1.93 *	1.45	1.46 *	0.89
22 JUL	1.66		2.10		1.02	
3 AUG	1.44		1.43		1.08	
17 AUG	1.20		1.54		1.10	
31 AUG	2.10		1.60		1.85	
14 SEP			1.90		0.97	
26 OCT			1.70		0.80	
9 NOV					0.80	
23 NOV	3.40		2.78		2.54	

* $p<0.05$

Figure 3. Mean size (mm) of ovigerous females.


5
4
3
2
1
LENGTH (mm)
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN

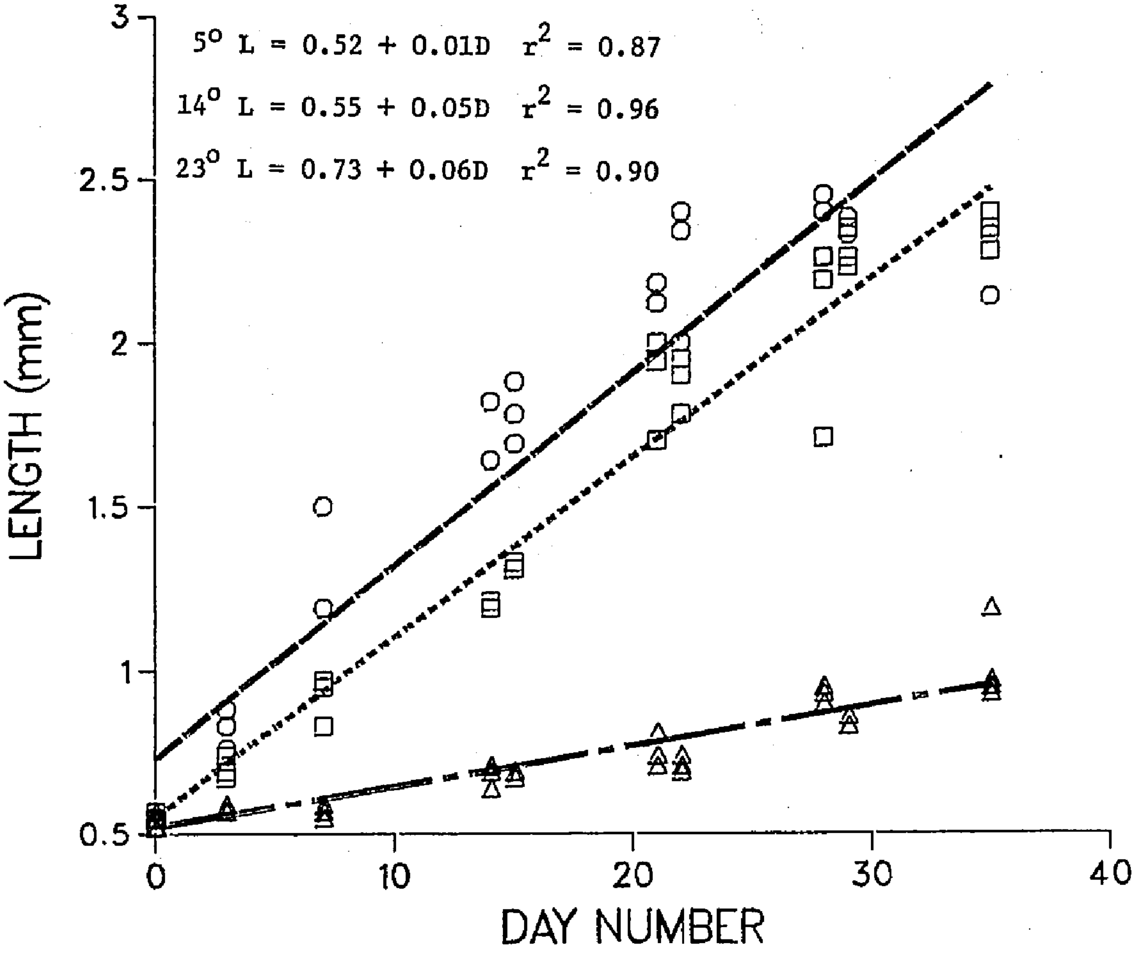
the summer. This reduction in mean size is also paralleled by a reduction in minimum reproductive size.

Growth

Field growth rates were determined from the median size of recognizable cohorts through time. This resulted in a winter growth rate of 0.04 mm/day (L_{H3}) and a spring rate of 0.11 mm/day (L_{H3}). Growth rates of individuals raised in the laboratory were determined from regression analyses (Figure 4). Each data set was tested for agreement with linear, power and exponential curve fits and a linear relationship proved the best descriptor for all three. There is some suggestion that the amphipods in the 23° C treatment may be reaching an asymptotic size but more information is needed to clearly define this trend. Growth at 5° C is determined to be $0.01\ \mathrm{mm} \cdot \mathrm{day}^{-1}$. An increase of nine degrees to 14° C resulted in a $0.05\ \mathrm{mm} \cdot \mathrm{day}^{-1}$ rate while another nine degree increase to 23° C only resulted in a slight increase to $0.06 \cdot \mathrm{mm} \cdot \mathrm{day}^{-1}$. Using these rates minimum ovigerous size (1.1 mm) can be attained in 12 and 10 days and mean ovigerous size (2.3 mm) can be reached in 36 and 30 days at 14 and 23° C respectively.

Food type has a significant effect ($p<0.001$) on the potential growth rate of _G_. _mucronatus_, with the

Figure 4. Relationship of length of head and first three pereonites to time in growth experiment △ 5° C, □ 14° C, ○ 23° C.


5^{o} L = 0.52 + 0.01D r^2 = 0.87
14^{o} L = 0.55 + 0.05D r^2 = 0.96
23^{o} L = 0.73 + 0.06D r^2 = 0.90
LENGTH (mm)
3
2.5
2
1.5
1
0.5
0
10
20
30
40
DAY NUMBER

Ulva-*Enteromorpha* diet resulting in 12.4-29.8% less growth after 21 days than the seagrass diet (Table 3). Two way interactions between food and habitat were not significant ($p>0.05$) and habitat of origin contributed very little to the overall variance ($p>0.4$).

Reproduction

Brood development at 6° C was very consistent among the six individuals examined taking an average of 30.7 days ($s^2 = 1.07$). Most of these females produced second or third broods when they were again paired with males. Combining these data with those of Steele and Steele (1975) and Van Dolsh and Bird (1980) (Table 4) temperature seems to affect development time exponentially as:

$$D = 64.03\ e^{-0.13\ T} \qquad (r^2 = 0.96,\ n = 5)$$

where D is time in days and T is degrees Celsius.

The number of eggs carried by a female varied from 3 to 200 but was highly dependent on female size (Figure 5). A curvilinear relationship provided a slightly better fit to the data than a simple linear regression ($r^2 = 0.77$ vs $r^2 = 0.67$). Egg size varied seasonally decreasing from winter to summer (Figure 6) ($p<0.001$, $r^2 = 0.59$) with a range of 0.308 to 0.532 mm.

Table 3. Mean size (mm) (L_{H3}) of 24 individuals per treatment in the food comparison experiment.

TABLE 3

Habitat of Origin	Food Type	Size after 21 Days mm (L_{H3})	
		$\bar{X}$	s^2
Seagrass	Seagrass	1.27	0.096
Seagrass	Algae	1.13	0.020
Algae	Seagrass	1.35	0.041
Algae	Algae	1.04	0.022

Table 4. Estimated temperature dependent rate of egg development.

TABLE 4

Temperature Celcius	Egg Development Time in Days	Source
0	73.1	Steele and Steele (1975)
6	30.7	present study
10	12.0	Steele and Steele (1975)
17	8.3	Borowsky (1980)
21	4.3	Borowsky (1980)

Figure 5. Relationship of brood size to female size (mm).

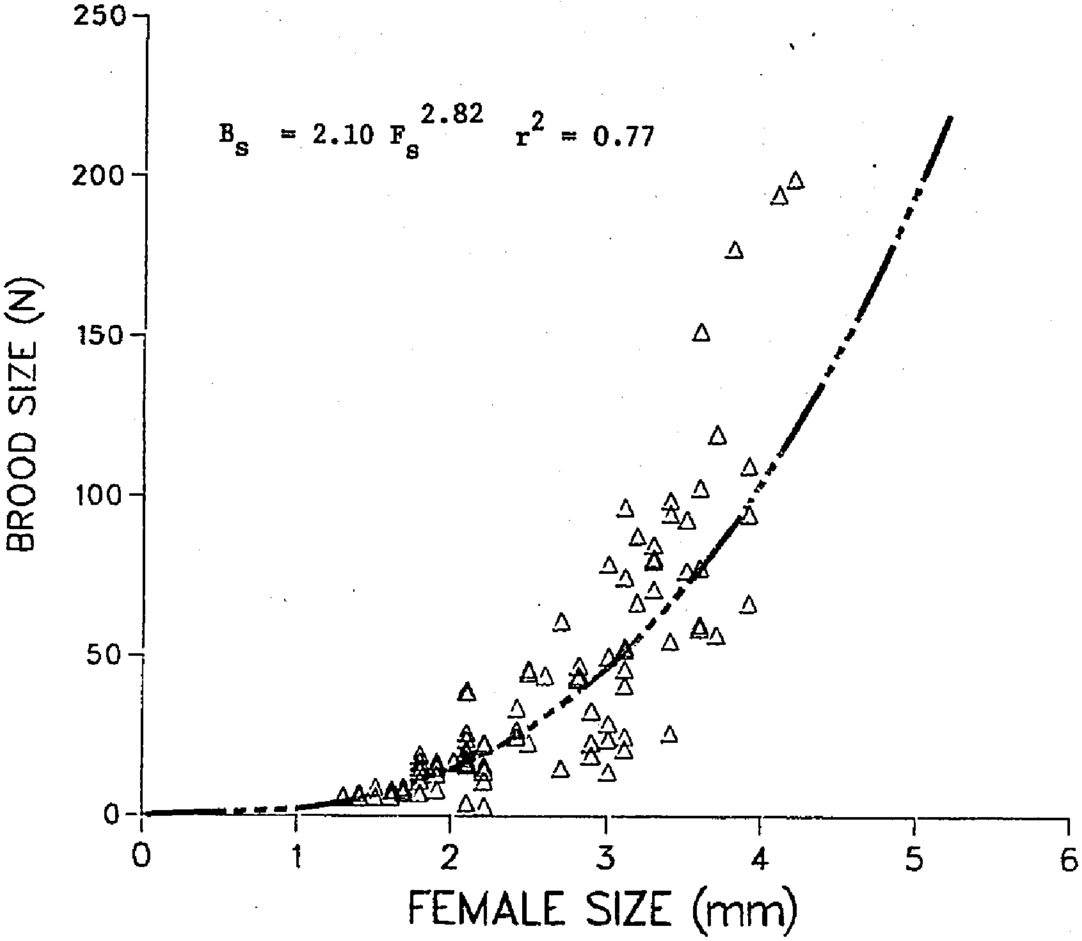
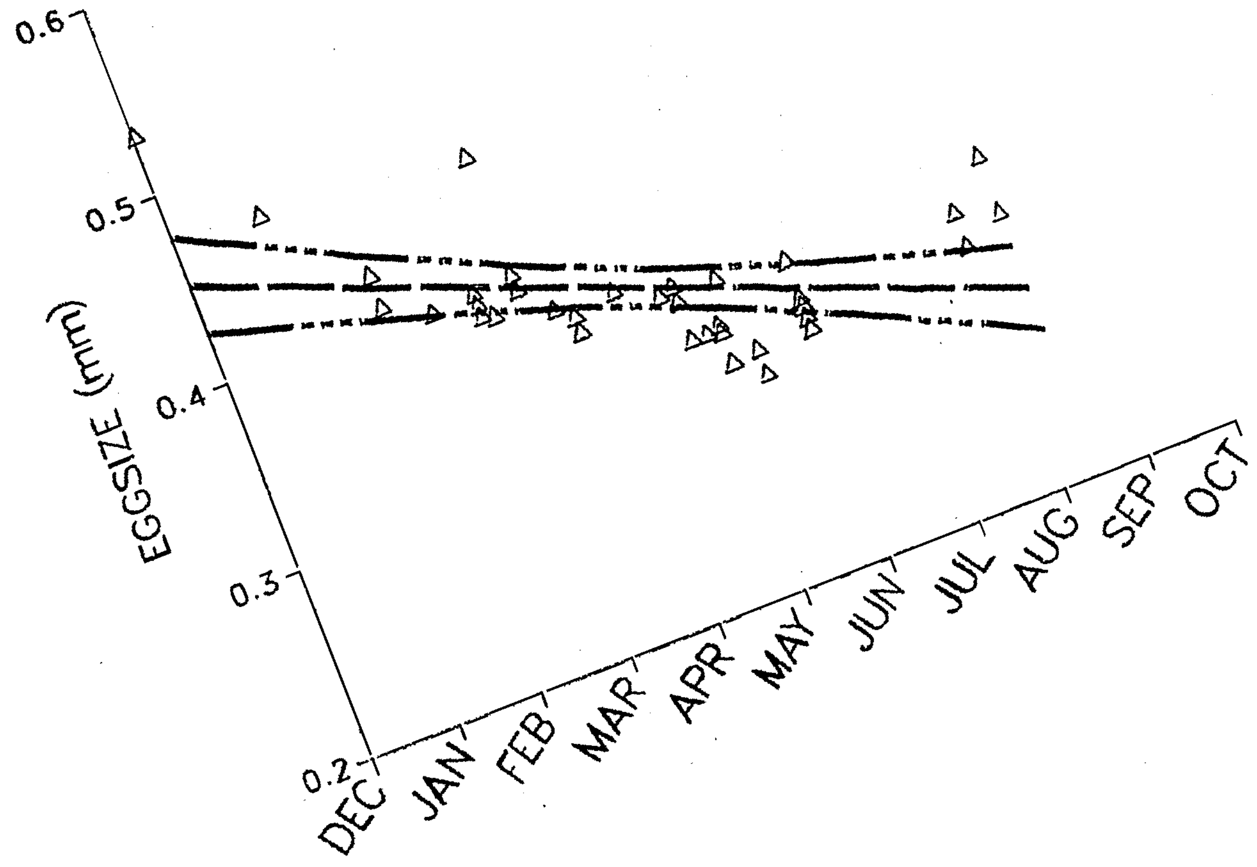

$B_s = 2.10 F_s^{2.82}$ $r^2 = 0.77$
BROOD SIZE (N)
250
200
150
100
50
0
0
1
2
3
4
5
6
FEMALE SIZE (mm)

Figure 6. Relationship of eggsize (mm) to time from winter to summer. Regression ± 95% confidence limits.

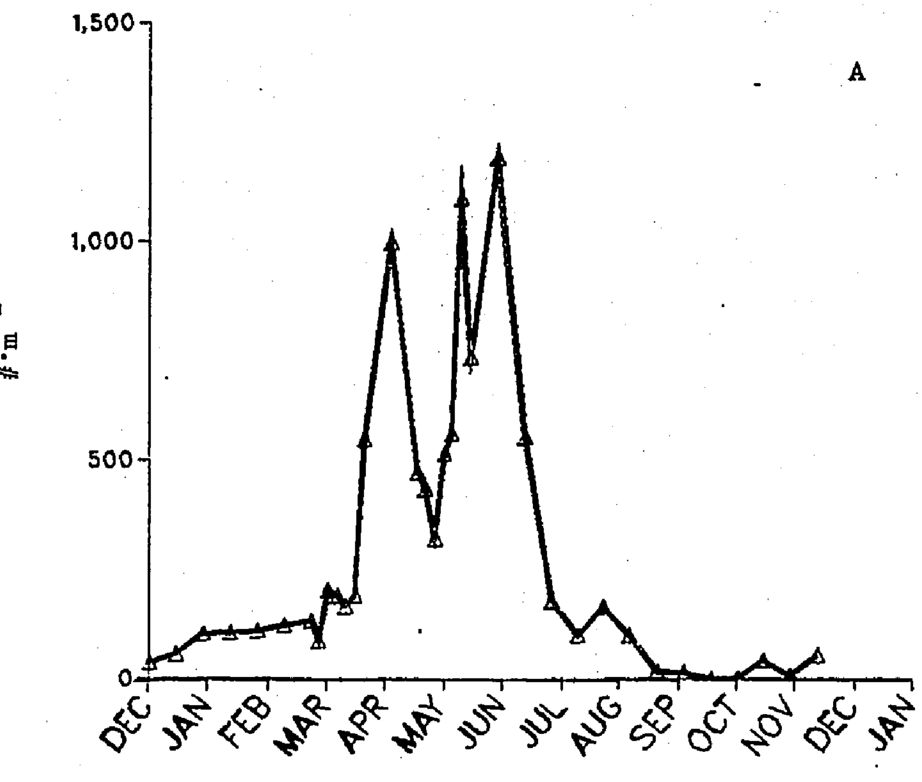

0.6
0.5
0.4
0.3
0.2
EGGSIZE (mm)
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT

Abundance and Size-frequency Distributions

In the seagrass habitat G. mucronatus ranged in density from less than $50 \cdot m^{-2}$ (below limits of detection) in late September and early October to $1190 \cdot m^{-2}$ in late June (Figure 7a). Seagrass biomass seemed to increase somewhat from December to January declining through late winter until growth began in spring (Figure 7b). A maximum mean biomass of 186.1 $g \cdot m^{-2}$ dry weight occurred in late May after which a typical summer decline ensued as has been observed by Orth and Moore (1982).

The abundance of G. mucronatus in the algal community was sporadic and low from 8 December to 30 March, but greatly increased to $6800 \cdot m^{-2}$ on 20 May before rapidly declining to zero on 20 July (Figure 8a). Presence of Enteromorpha spp. and Ulva spp. exhibited a similar pattern of abundance with a maximum biomass of 26.6 $g \cdot m^{-2}$ dry weight occurring on 16 May (Figure 8b). Ice floes in mid-January may have severely affected abundance patterns of both the algae and G. mucronatus by physical removal of the algae and freezing of macrofauna. This was indicated by the total lack of algae from 2 February to 16 March, and the observation that most of the macrofauna present in the samples during this period were in a state of decay.

Figure 7. Mean density (#·m^{-2}) of _Gammarus_ _mucronatus_ at the seagrass site (a), and mean dry weight biomass (g·m^{-2}) of _Zostera_ _marina_ (b).


A
#·m^{-2}
1,500
1,000
500
0
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN

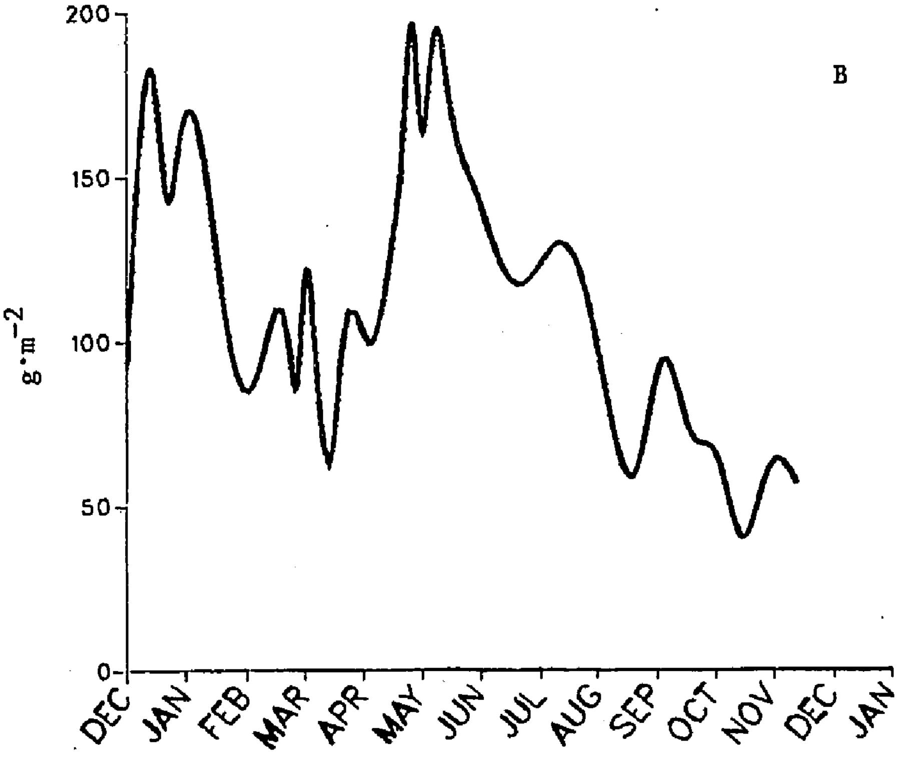
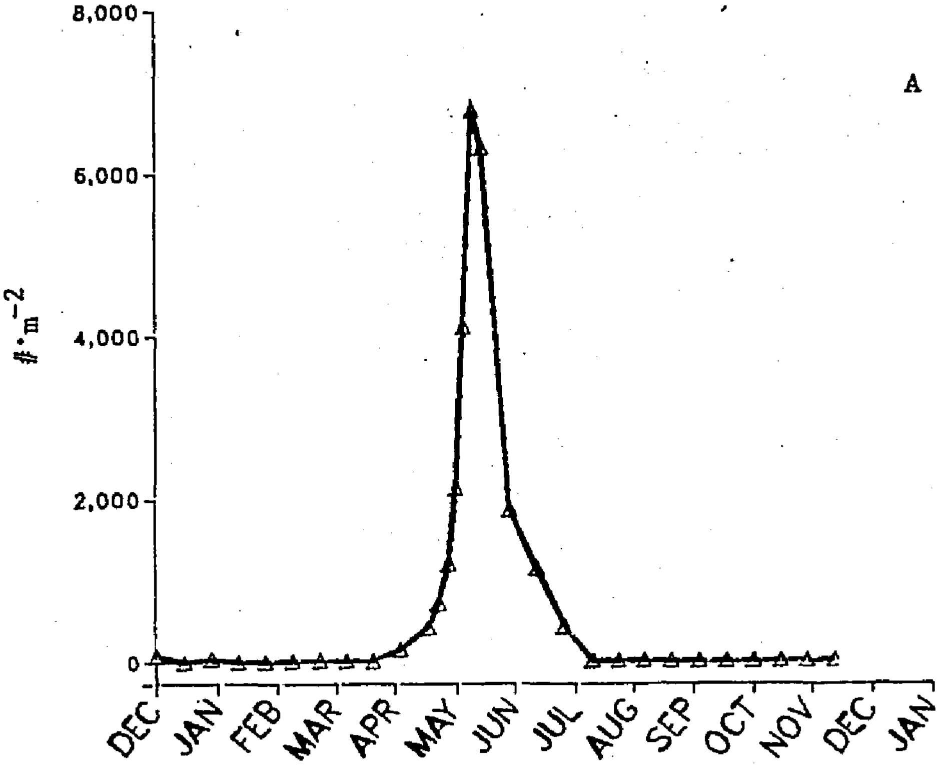
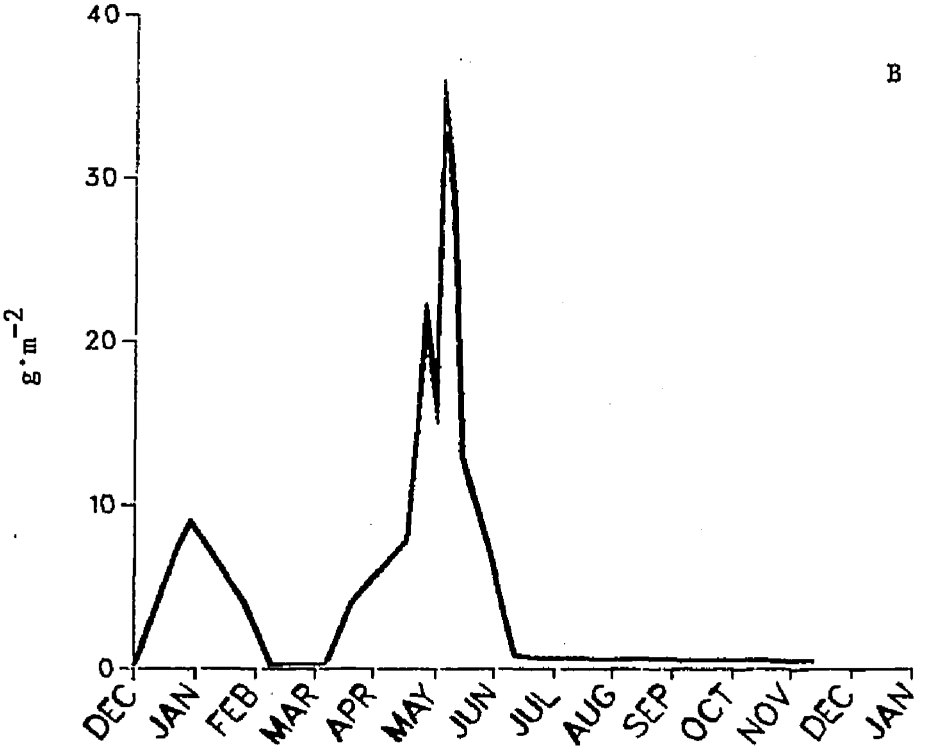

B
g·m^{-2}
200
150
100
50
0
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN

Figure 8. Mean density (#$\cdot$m^{-2}) of _Gammarus mucronatus_ at the algal site (a), and mean dry weight biomass (g$\cdot$m^{-2}) of _Enteromorpha-Ulva_ (b).


A
8,000
6,000
4,000
2,000
0
#·m^{-2}
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN


B
40
30
20
10
0
g·m^{-2}
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN

Size-frequency distributions of _G_. _mucronatus_ within replicate samples collected from the seagrass bed do not differ significantly ($p<0.05$) except on 11 and 20 May (Table 5). For these dates differences are probably due to a preponderance of juveniles in one sample of the set. No differences were detected following removal of these outliers from the analyses. Successive sample dates were usually different except in some cases when either densities were low (winter and summer) or sample dates were close in time (March, May). These results indicate that within the seagrass bed spatial variation is not great, but as expected temporal variations in size-frequency distributions occur as a result of growth and recruitment between successive sampling dates.

Size-frequency distributions of amphipods from the algal habitat show a different pattern than the seagrass bed in that there were differences ($p<0.005$) within sample dates. Differences were found on 16, 20, 25 May and 8 June (Table 5). These differences do not appear to be due to single outlier samples and indicate a greater spatial heterogeneity on the pilings. Differences in the size-frequency distributions between successive sample dates also were different with the same exceptions as noted for the seagrass habitat. Comparisons between habitats indicate that there are significant differences in size-frequency distributions on all dates tested except

Table 5. Comparison of size-frequency distributions between replicates on a given sample date, between successive dates and between habitats (goodness of fit G-test).

TABLE 5

	FORTNIGHTLY SAMPLES				
	Seagrass			Algae	
Date	Within Date	Between Dates	Between Habitats	Within Date	Between Dates
8 DEC	NS#				
		NS			
22 DEC	NS				
		*			
5 JAN	NS				
		NS		Insufficient	
19 JAN	NS				
		*		Data	
2 FEB	NS				
		*			
16 FEB	NS				
		**			
2 MAR	NS				
		**			
16 MAR	NS				
		**			
30 MAR	NS				
		NS			
13 APR	NS		*	NS	
		**			NS
27 APR	NS		**	NS	
		**			**
11 MAY	*		*	NS	
		*			**
25 MAY	NS		**	**	
		*			**
8 JUN	NS		NS	**	
		*			**
22 JUN	NS		NS	NS	
		NS			**
6 JUL	NS		**	NS	
		NS			
20 JUL	NS			Insufficient	
		NS			
3 AUG	NS			Data	
		NS			
17 AUG	NS				

\# NS - no significance $p>0.05$
* - $p<0.05$
** - $p>0.005$

TABLE 5 (continued)

INTENSIVE SAMPLES					
	Seagrass			Algae	
Date	Within Date	Between Dates	Between Habitats	Within Date	Between Dates
2 MAR	NS[#]				
		NS			
6 MAR	NS				
		NS			
11 MAR	NS				
		**			
16 MAR	NS			No Intensive	
		*			
20 MAR	NS			Sampling Done	
		*			
25 MAR	NS				
		NS			
30 MAR	NS				
27 APR	NS		**	NS	
		*			NS
1 MAY	NS		**	NS	
		*			NS
6 MAY	NS		**	NS	
		**			NS
11 MAY	*		*	NS	
		NS			**
16 MAY	NS		*	**	
		**			**
20 MAY	*		**	**	
		NS			**
25 MAY	NS		**	**	

[#] NS - no significance p>0.05
  * - p<0.05
** - p>0.005

8 and 22 June, thus the two habitats may not represent continuous populations.

Size-frequency distributions were further analyzed for recognizable cohorts. The fortnightly size-frequency distributions (Figure 9) from the seagrass habitat reveal two recognizable cohorts. The first cohort (I) recruited in December, matured over the winter and disappeared from the population by 30 March. Cohort II recruited in February, matured in March and disappeared by May. For the remainder of the year additional cohort recognition was impossible. Size-frequency distributions from the short interval March sampling (Figure 10) suggest that the second cohort (II) recognized from the fortnightly samples actually matured and disappeared by 16 March and a third cohort (III) which recruited in early March was responsible for the adults that were present in late March and mid April. This third cohort was very distinct while the second was not clearly expressed.

Recognition of cohorts in the samples from the May data is difficult (Figure 10) even with the aid of the probability paper method of Harding (1949). By 20 May rapid growth combined with continuous reproduction quickly obscured what may have been a distinguishable cohort in early May.

Figure 9. Size-frequency distributions for the fortnightly samples from the seagrass habitat (0.5 mm length classes, class 1 = 0.5-0.9 mm). Cohort I crosshatched, cohort II striped.

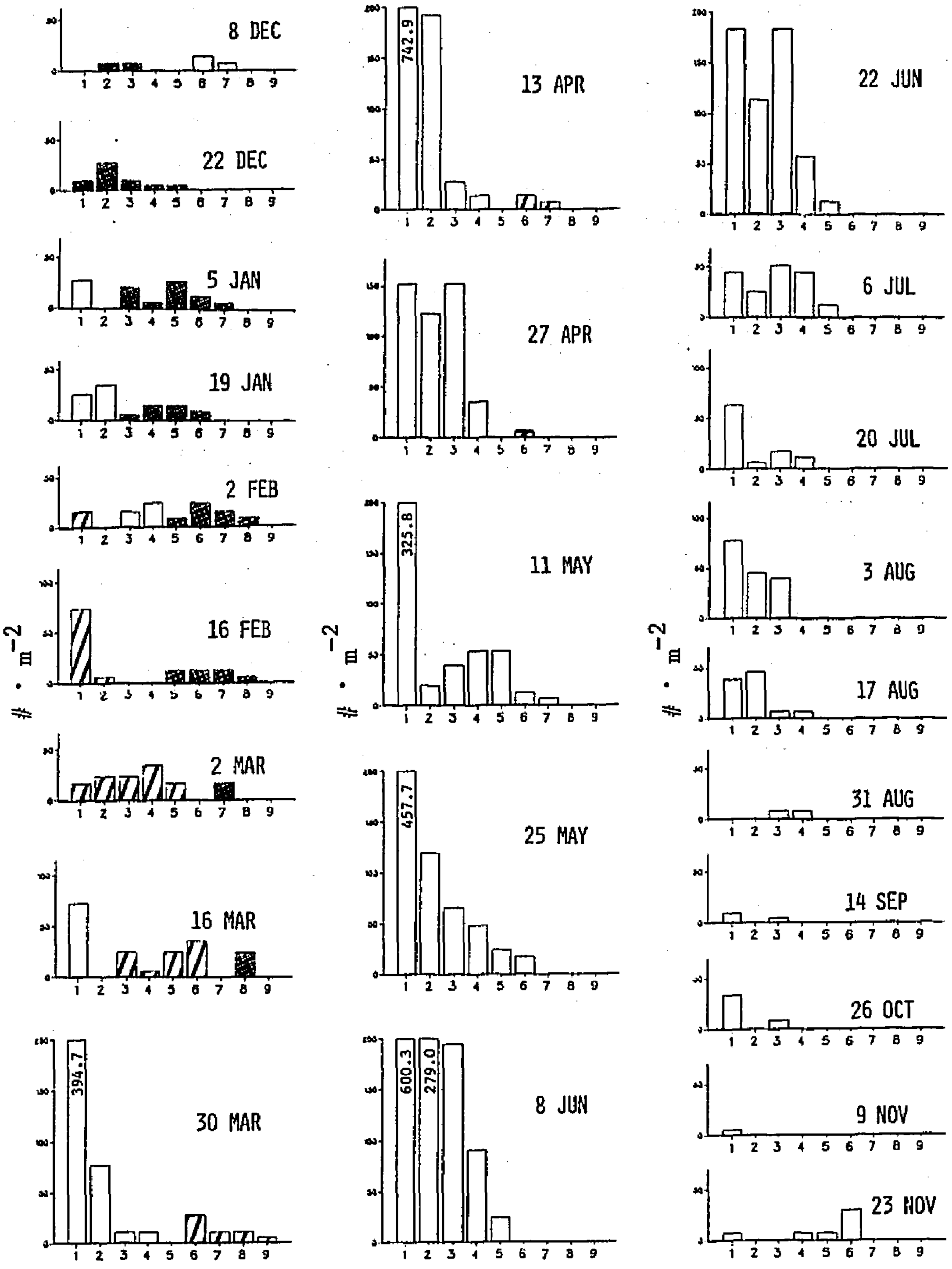
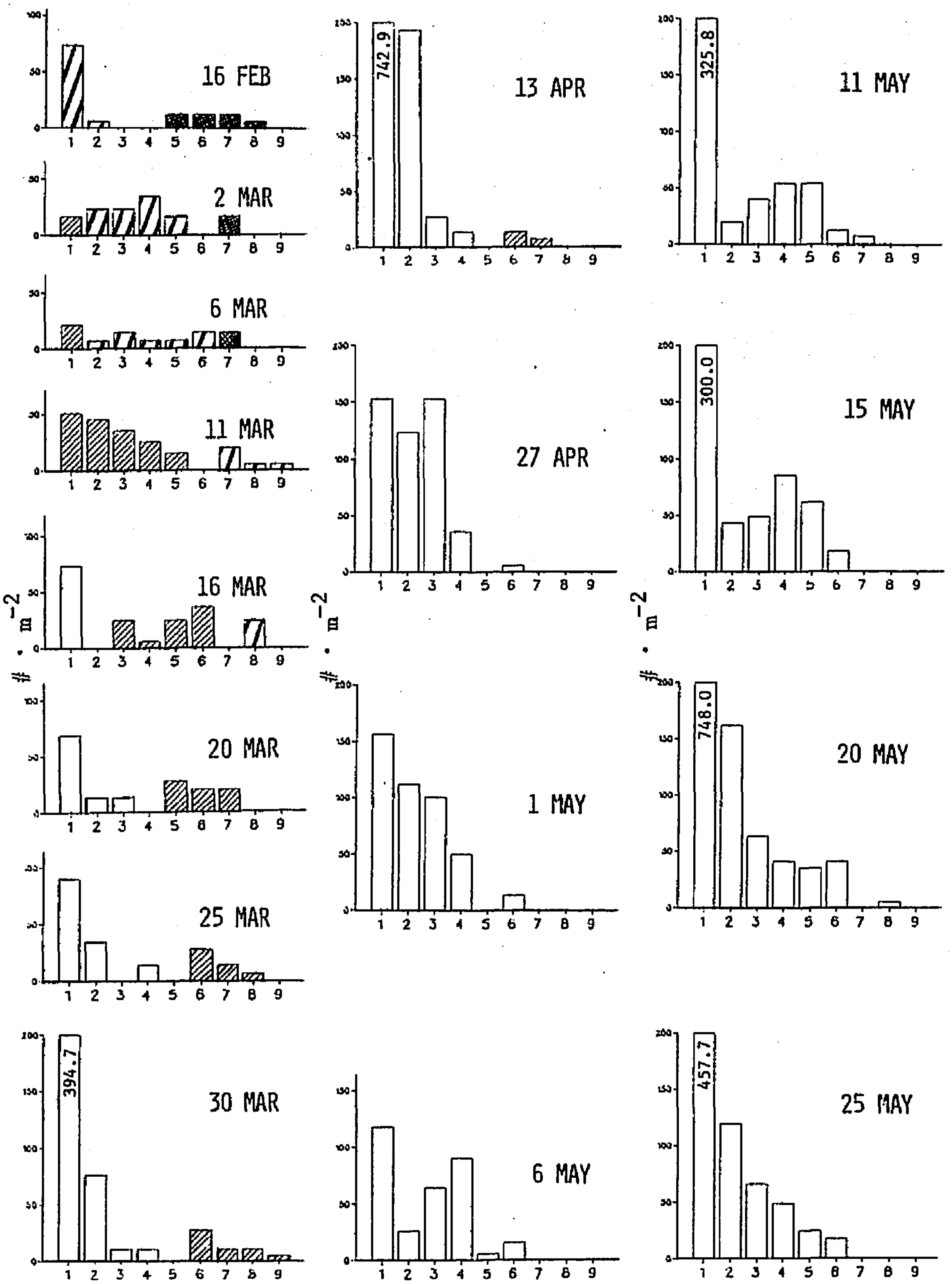

8 DEC
22 DEC
5 JAN
19 JAN
2 FEB
16 FEB
2 MAR
16 MAR
30 MAR
394.7
13 APR
742.9
27 APR
11 MAY
325.8
25 MAY
457.7
8 JUN
600.3
279.0
22 JUN
6 JUL
20 JUL
3 AUG
17 AUG
31 AUG
14 SEP
26 OCT
9 NOV
23 NOV
· m^{-2}
· m^{-2}
· m^{-2}
1 2 3 4 5 6 7 8 9

Figure 10. Size-frequency distributions from the March and May intensive sampling, seagrass site. 16 February and 13 April added for reference. Cohort I crosshatched, Cohort II thick diagonal striping, cohort III thin diagonal striping.


16 FEB
2 MAR
6 MAR
11 MAR
16 MAR
20 MAR
25 MAR
30 MAR
394.7
13 APR
742.9
27 APR
1 MAY
6 MAY
11 MAY
325.8
15 MAY
300.0
20 MAY
748.0
25 MAY
457.7
• m^{-2}
1 2 3 4 5 6 7 8 9

Size-frequency distributions of amphipods from the algal habitat (Figure 11) do not provide any evidence for separation of cohorts. Abundances of ovigerous females and juvenile amphipods both paralleled the general population trend which was seen in figure 8a.

Population Dynamics

Examination of the dynamics of ovigerous females and juveniles from the seagrass habitat (Figure 12) supports the overall interpretation of the size-frequency data. The cohort which matured over winter (I) produced a peak of ovigerous females on 2 March which was then followed by some mortality of adults. Before dying these females produced the small recruitment present on 16 March (cohort II) and the juveniles responsible for the third cohort (III). Cohort II and cohort III both contributed to the formation of the next peak of ovigerous females (16-30 March) which spawned the large peak of juveniles on 13 April. Mortality of adults again led to the reduction in ovigerous females observed on this day. With the warmer spring temperatures maturation of these juveniles occurred 23 to 32 days later on 6 to 16 May. The subsequent juvenile maxima (20 May) again matured quickly in 19 days and resulted in the maxima of 127 mature females$\cdot m^{-2}$ on 8 June. The entire population then experienced fairly rapid declines into the summer months.

Figure 11. Size-frequency distributions for the algal site, 8 December to 6 July (dates omitted where *Gammarus mucronatus* was absent).

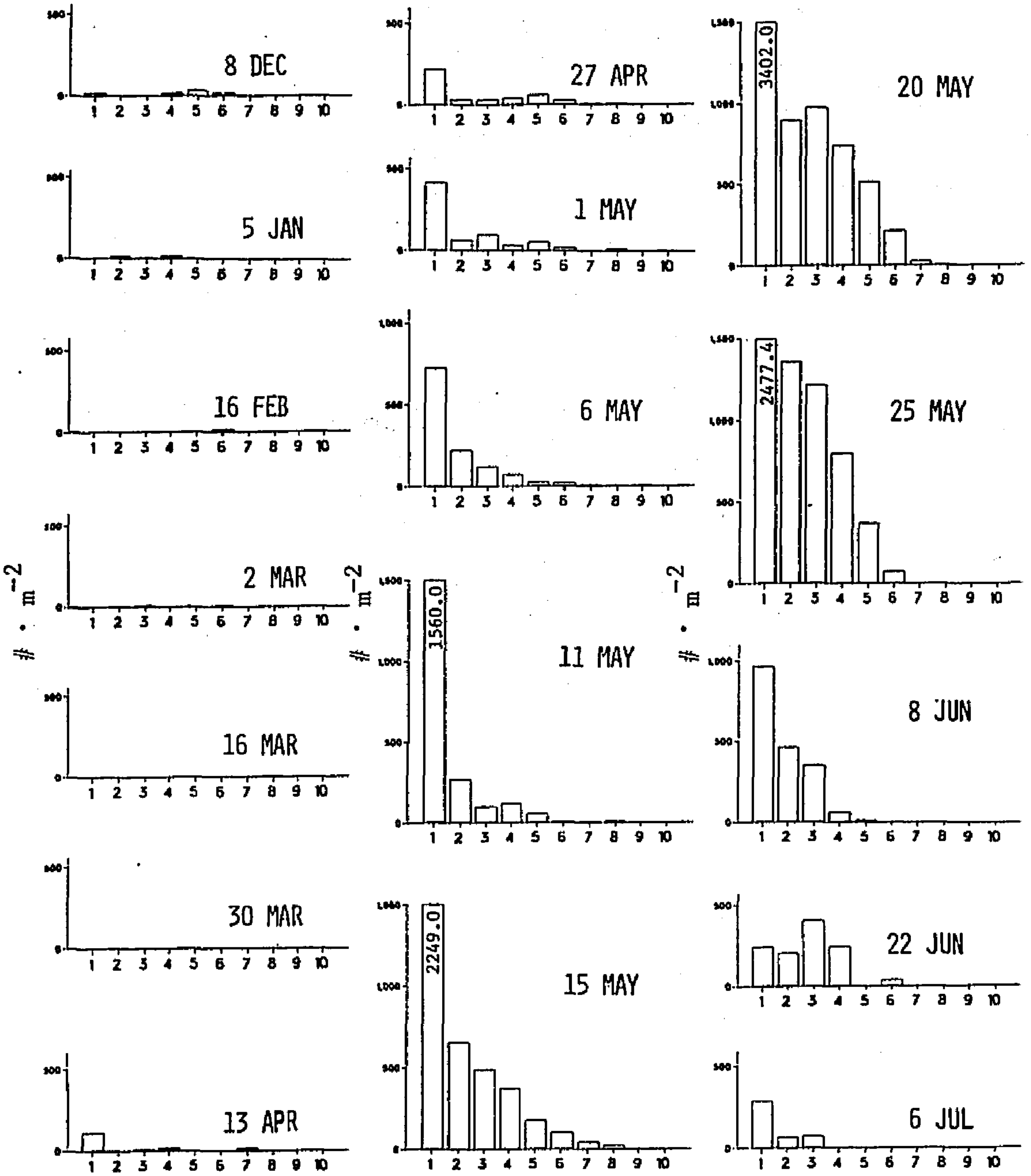
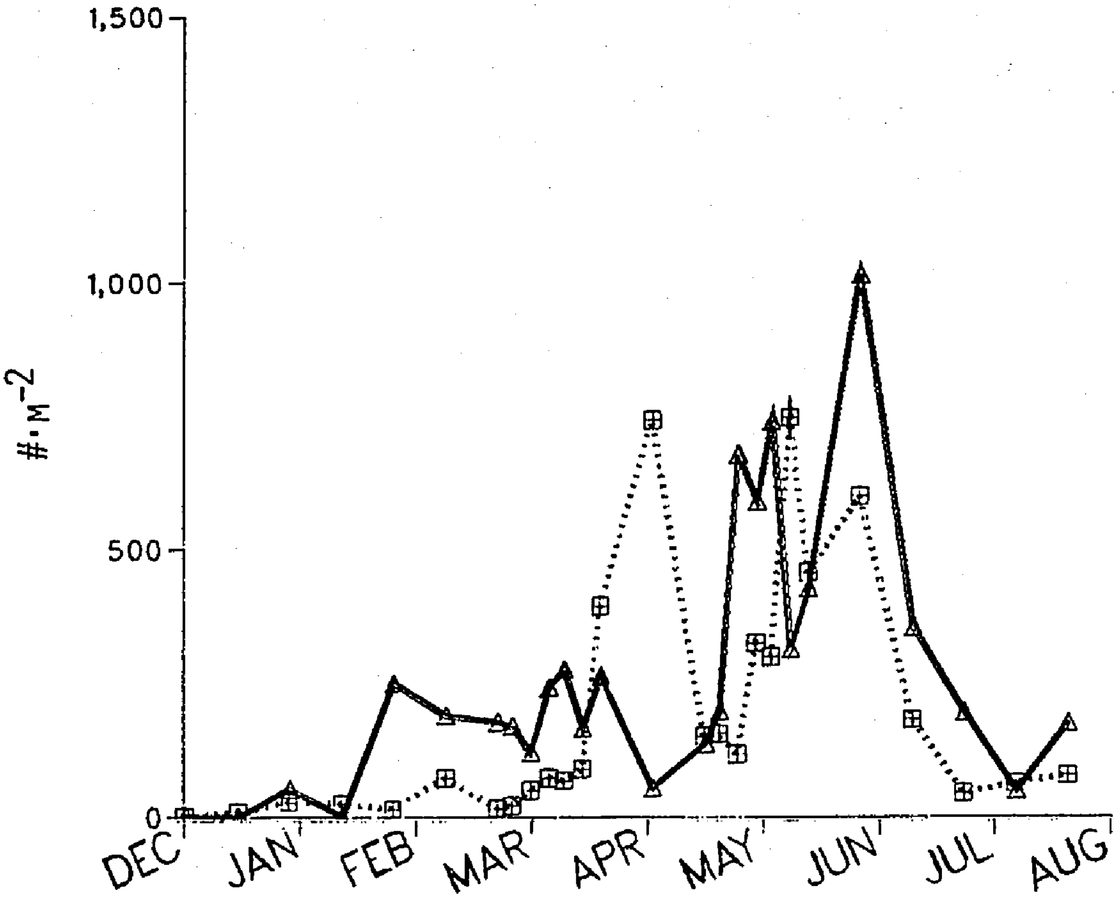

8 DEC
5 JAN
16 FEB
2 MAR
16 MAR
30 MAR
13 APR
27 APR
1 MAY
6 MAY
11 MAY
1560.0
15 MAY
2249.0
20 MAY
3402.0
25 MAY
2477.4
8 JUN
22 JUN
6 JUL
• m^{-2}
• m^{-2}
• m^{-2}
500
1,000
1,500
0
1 2 3 4 5 6 7 8 9 10

Figure 12. Mean densities ($\# \cdot m^{-2}$) of juveniles (see text) ⊞ , and ovigerous females △ (exaggerated by a factor of 8) from the seagrass habitat, 8 December to 3 August.


1,500
1,000
500
0
#·M^{-2}
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG

The numbers of juveniles produced by each peak of mature females were not proportionally similar. The first and second peak which were of similar magnitude resulted in very different quantities of juveniles. The third and fourth peaks in mature females were 3-4 times greater than the first and second and yet only yielded juvenile abundances as great as or less than the second peak. The differences between the first two may be a result of poor survival of eggs and juveniles at cold ambient temperatures. Differences between the second peak and the last two probably result from the general reduction in female maturation size and the concomitant reduction in brood size occurring in these later populations.

Discussion

Growth

Evidence from both the field data and laboratory data indicate that G. mucronatus has a great potential for growth. Length increases appear to be linear over the short time period examined in laboratory experiments (35 days), though they probably decrease with maturity as has been found for other amphipods (Nair and Anger 1979, Vassallo and Steele 1980, Savage 1982). Field derived growth rates from the seagrass habitat are much greater than would be predicted from laboratory experiments at similar temperatures. This discrepancy may result from (1) the field temperature record, taken every two weeks (and often in the morning) did not detect daily warming of the water over the shallow seagrass bed (where field growth rates were determined) and (2) the probable lack of ideal laboratory conditions for growth experiments. Since periods of warmer water temperature could have led to faster growth it is difficult to project field growth rates from laboratory data without an accurate record of field temperatures. Consequently, the field growth rates were considered to be more reliable and thus were used to estimate the number of cohort production intervals (CPI) occurring during the year.

Benke (1979) defined the CPI as the time period necessary for growth of an individual from recruitment to the largest size class. It is a term that is only equivalent to generation time when reproduction coincides with attainment of maximum size. Thus G. mucronatus would be capable of a greater number of generations than CPI's. CPI has been chosen as the unit of measure expressing longevity since it is subsequently used in an examination of the production of this amphipod (Fredette 1983).

There are two clearly recognizable cohorts present from December to the end of March (I and III) (Figure 9,10), cohort II being somewhat indistinct. Based on the estimated growth rate of the March cohort and the suggestion of a quickly growing cohort in May it is conservatively estimated that approximately three cohorts (3.25) occurred from December to the end of May. From June to November growth is conservatively estimated to be equal to the March field estimate since there is not evidence to determine summer growth rate. Because in the summer maximum size is much less than in winter, rapid growth leads to very short CPI's and an estimate of 5.6 cohorts results. Based on these estimates a minimum of 8.8 non-overlapping cohorts could have occurred in the year with the number of generations certainly exceeding 10 since reproductive maturity is attained before maximum size. The possibility also exists that high summer temperatures actually inhibit growth so that the number of cohorts may be less than 8.8. Because of this uncertainty I estimate that approximately 6 cohorts could have developed before high (>25° C) summer temperatures occurred.

The majority of prior amphipod life history studies have been in cold temperate or boreal regions (Wildish 1982). The populations under study usually have one or two generations per year (Gable and Croker 1977, Goedmakers 1981, Klien et al. 1975, Waters and Hokenstrom 1980) while a few studies in tropical or warm temperate regions reported more than two. Omori et al. (1982) estimated that Corophium volutator may produce four of more generations. For C. insidiosum, Birklund (1977) found a generation time of 4-5 weeks and states that Casabianca (1975) found 5-6.5 generations in a Mediterranean population. Steele (1973) examined the tropical amphipod, Parahyalella pietschmanni, and determined that generation time was 4-5 weeks and reproduction was continuous throughout the year. Venables (1981) studied an extremely productive population of talitrids and found that reproductive maturity was reached in 3-4 weeks and maximum size in 8 weeks. There is also a growing body of laboratory evidence which shows rapid growth and maturation of amphipods (Cooper 1965, Doyle and Hunte 1981, Krishnan and John 1974, Macko et al. 1982). Doyle and Hunte (1981) raised _Gammarus lawrencianus_ at room temperature through 25 generations in approximately 30 months and Macko et al. (1982) raised _Ampithoe valida_ and _Parhyale hawaiensis_ to maturity in 5-6 weeks at 21-23° C. The growth rates measured for _G. mucronatus_ are comparable to these other amphipods as maturation in warmer months may require only 3-5 weeks.

Reproduction

Winter and summer populations of _G. mucronatus_ employ different reproductive strategies. Summer populations have reduced brood size, egg size, development time, size at maturity, maximum size and increased growth rate. The smallest reproductively mature female I observed (1.1 mm) is only slightly larger than the 1.0 mm predicted by Steele and Steele (1975). Females in the observed size range are capable of carrying only 3-10 eggs and further reduction in size may not be possible especially if there is a critical lower limit to egg size.

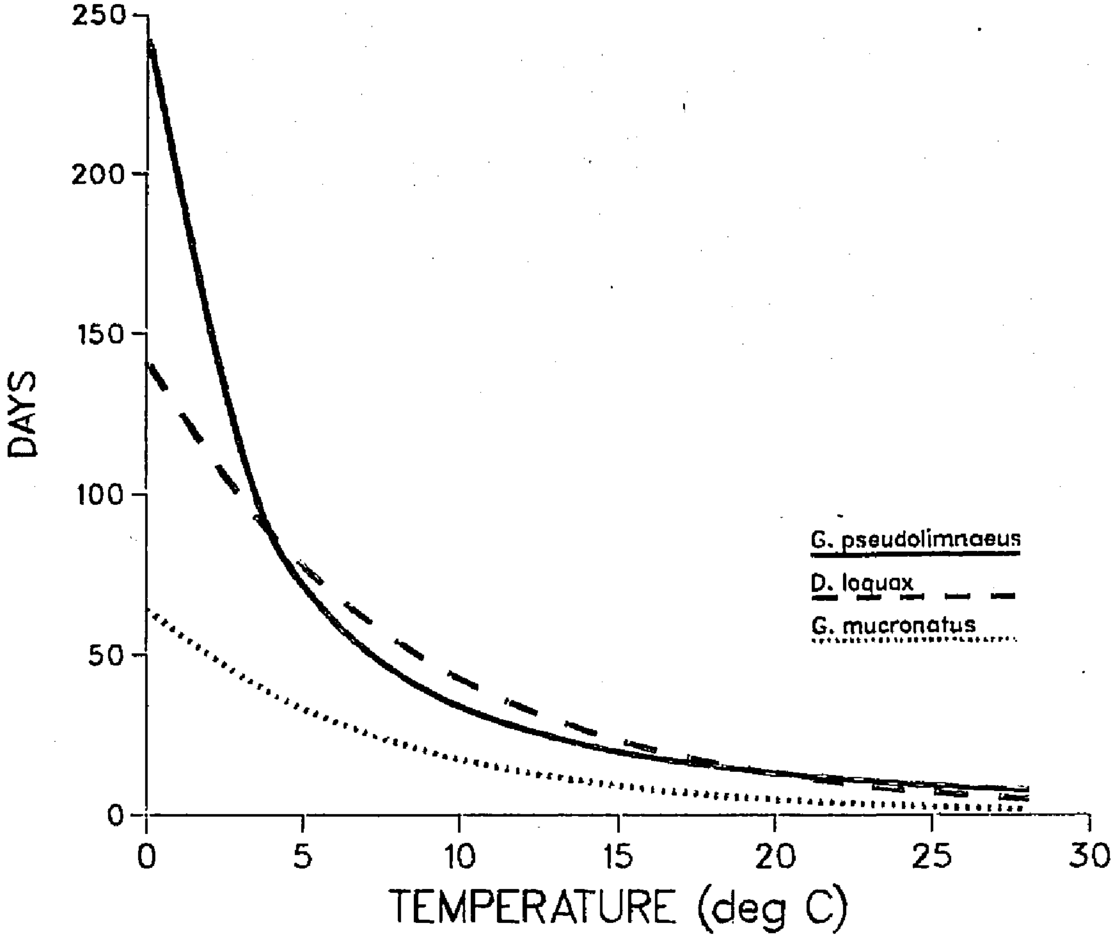
Borowsky (1980) has previously reported on the brood size, egg size and development time in _G. mucronatus_. She found a range in brood size of 1-57, while the present study extends the upper end of the range to 200. This is largely due to the wider range of female sizes used here. Based on the largest sized female she examined I would predict an average brood size of 39, a fair estimate considering that the mean for that size is probably somewhat below 57. The largest female _G. mucronatus_ examined by Steele and Steele (1975) carried 18 eggs and I would predict 15.

Steele and Steele (1975) and Van Dolah and Bird (1980) have provided linear regression equations relating brood size to female size for _G. mucronatus_. As suggested by Van Dolah and Bird (1980), I employed a larger data set than theirs and found that a curvilinear function provided a better fit. Van Dolah et al. (1975) reported similar results for _G. palustris_. Intuitively, this is an expected relation since available brood space should increase as a power function of size.

Van Dolah and Bird (1980) report that northern populations of _G. mucronatus_ have larger eggs than southern populations. Heeding the caution of Steele and Steele (1975) that egg size varies with season (also shown by my data) comparisons are made within season. Such comparisons are valid only if it can be assumed that southern populations experience similar environmental temperatures as northern counterparts, temporal equivalence is not sufficient since egg size is probably more closely tied to temperature than season. I found egg size to vary in the range of 0.308-0.532 mm depending on season while Steele and Steele (1975) report an average of 0.355 mm. Van Dolah and Bird (1980) report a range of 0.276-0.378 mm for eggs of females from several locations along the Atlantic Coast. Those values smaller than my minimum are from more southerly populations but as emphasized earlier latitudinal comparisons need to be considered more carefully.

Brood development time in amphipods seems to be clearly related to temperature (Borowsky 1980). Comparison of my equation to those of Marchant and Hynes (1981) and Hughes (1982) (Figure 13) indicate that _G_. _mucronatus_ develops more rapidly than either _G_. _pseudolimnaeus_ or _Dogielinotus_ _loquax_, especially at lower temperatures, but the general trend is similar. Steele and Steele (1973) have reported similar development rates in other species of _Gammarus_. Brood development time and brood number may also be affected by seasonal egg size. It has been clearly shown that smaller egg sizes develop more quickly (Clarke 1982). Experiments performed on winter eggs at summer temperatures will probably underestimate actual summer potential. It should also be expected that like sized females in different seasons may

Figure 13. Temperature dependent egg development rates for *Gammarus pseudolimnaeous* (Marchant and Hynes 1981), *Dogielinotus loquax* (Hughes 1982) and *Gammarus mucronatus* (present study).


250
200
150
100
50
0
DAYS
0
5
10
15
20
25
30
TEMPERATURE (deg C)
G. pseudolimnaeus
D. loquax
G. mucronatus

have different egg carrying capacities as a result of varying egg sizes.

Population Dynamics

Temporal variation of *G. mucronatus* populations in the seagrass and algal habitats were quite different. The presence of algae on the pilings is ephemeral, but when present this habitat is rapidly and densely populated by *G. mucronatus*. Conversely, the relatively permanent seagrass habitat appears to be utilized throughout the year with peak amphipod densities occurring in spring and summer months.

The ephemeral algal habitat which occurs the length of the pier may actually be an extension of a more constant algal habitat occurring in very shallow water during most of the year. This habitat includes drift algae, as well as algae attached to hard substrates (rubble) along the shore and a few of the innermost pilings. This more permanent habitat may serve as a source of colonizing amphipods when algae does grow on all of the pilings. This potential source of recruits is supported by the fact that *G. mucronatus* is commonly observed in estuarine shallow water meroplankton samples (Williams and Bynum 1972). In addition, Meyer (1982) has shown that juvenile *G. mucronatus* may be a common component of the plankton over seagrass beds. Despite the propensity for drift by _G. mucronatus_, the analyses of size-frequency distributions between habitats (Table 5) indicates that drift is not of sufficient magnitude to obscure population size class differences.

The variations in _G. mucronatus_ population density in the seagrass habitat do not seem to be closely tied to the availability of substrate (Figure 7) as was found in the algal habitat (Figure 8). It could be hypothesized that the population decline of _G. mucronatus_ in the seagrass bed results from the arrival of migratory predators in the spring and summer. Predation is often invoked as a major factor in amphipod population regulation (Nelson 1979), though Krebs (1978) argues that many populations may be self regulating. Chesapeake Bay seagrass beds have abundant predatory populations of fish and decapod crustaceans (Heck and Orth 1980, Orth and Heck 1980). Though, Stoner (1980b) has shown that not all amphipod populations in seagrass beds decrease in periods of high predator abundance, as some attain their highest densities during these times. General observation of population trends of other amphipods and isopods collected in my study support his contention.

Predation, when size selective, can also be implicated as a mechanism for reducing the size range of summer individuals. However, reduction in maturation size may preclude the need to grow larger. Similar early maturity has been noted for amphipods by Birklund (1977), Cooper (1965), Nelson (1980b) and Nair and Anger (1979), for cladocerans by Vijverberg and Richter (1982) and is well demonstrated for copepods (Uye 1982). It is conceivable that size selective predation occurs, but it is also possible that the process of size reduction is physiological. Early maturation, if physiologically controlled, could be a co-evolutionary response with predators, because if the dominant predators (which arrive in the spring) crop only large individuals then it would be advantageous for the prey species to program early maturation during these periods. Southwood (1976) has demonstrated that the intrinsic rate of population growth (r) is more easily maximized by reduction of generation time (T_c) than an increase of fecundity (R_o) as:

$$r \simeq \frac{\ln R_o}{T_c}$$

Thus, if _G_. _mucronatus_ decreases generation time between seasons by a third (90 to 30 days) by growing faster and maturing at smaller sizes, fecundity, as measured by the number of eggs per brood, must be reduced. Even if the number of eggs per brood is reduced by an order of magnitude (200 to 10), "r" is increased (0.059 to 0.077). Thus, summer populations of _G_. _mucronatus_ can increase at a faster rate than winter populations, possibly to balance the higher rates of predation. Ultimately, predation pressure may be responsible for the evolution of reduced size of summer adults, but on an ecological time scale the process may be inevitably tied to physiology such that even in the absence of predators (i.e. with caging) it would occur.

One possible mediating factor in the physiological expression of maturity at small sizes may be temperature. However, seasonally changing food resources may also be involved. My results and those of Vassallo and Steele (1980) have shown that growth of amphipods occurs at different rates on different diets. Vassallo and Steele (1980) further demonstrated that those diets producing rapid growth also led to maturity at smaller sizes given identical temperature conditions. Thus early maturity may be related to a seasonally changing suite of food resources, rate of growth, temperature or these and other factors in combination.

Even though regulation of adult size at maturity and population density of amphipods appear from circumstantial evidence to be predator controlled, rigorous testing is necessary. The observed population decline in the summer may be an inevitable response to factors other than predation. The populations of this amphipod may be tracking a seasonally abundant, preferred food source or substrate (as was seen in the algal habitat). Or perhaps high summer temperatures are actually an inhibition to growth and survival. The relationship between predation, as a regulating mechanism, and the life history strategy of G. mucronatus warrants further study.

Gammarus mucronatus exhibits a very flexible life history that may be related to its eurytopic abilities and wide latitudinal range. Such a life history is probably not unique suggesting a need for closer examination of other pericaridean and decapod crustacean species. Recently Alon and Stancyk (1982) have shown that the decapod shrimp Palaemontes pugio exhibits both a summer and winter generation in a South Carolina estuarine environment. For adequate estimates of such phenomena both laboratory and field growth studies should consider short time scales (days-weeks) before assuming that longer intervals provide adequate characterization. I expect that such evaluations of life cycles of other shallow, warm water species will support the findings of this study. Such evidence will require that we reevaluate our assessment of such habitats as they may prove to be of a much more dynamic and productive nature than previously thought.

Literature Cited

Alon, N. C. and S. E. Stancyk. 1982. Variation in life-history of the grass shrimp Palaemonetes pugio in two South Carolina estuarine systems. Mar. Biol. 68, 265-276.

Benke, A. C. 1979. A modification of the method for estimating secondary production with particular significance for multivoltine populations. Limnol. Oceanogr. 24, 168-171.

Biernbaum, C. K. 1981. Seasonal changes in the amphipod fauna of Microciona prolifera (Ellis and Solander) (Porifera: Demospongia) and associated sponges in a shallow salt-marsh creek. Estuaries 4, 85-96.

Birklund, J. 1977. Biomass, growth and production of the amphipod Corophium insidiosum Crawford, and preliminary notes on Corophium volutator (Pallas). Ophelia 16, 187-203.

Borowsky, B. 1980. Reproductive patterns of three intertidal salt-marsh gammaridean amphipods. Mar. Biol. 55, 327-334.

Bousfield, E. L. 1969. New records of Gammarus (Crustacea: Amphipoda) from the middle Atlantic region. Ches. Sci. 10, 1-17.

Bousfield, E. L. 1973. Shallow-water Gammaridean Amphipoda of New England. Cornell Univ. Press, Ithaca, N.Y. 312pp.

Casabianca, M. -L., de. 1975. Methode de calcul de la production par estimation de la mortalite. Application a une population a structure complexe du crustace Corophium insidiosum Crawford (Lagune de Biguglia, Corse). -C. r. Hebd. Seanc. Acad. Sci., Paris 280, 1139-1142.

Clarke, A. 1982. Temperature and embryonic development in polar marine invertebrates. Int. J. Invert. Repro. 5, 71-82.

Cooper, W. E. 1965. Dynamics and production of a natural population of a fresh water amphipod, Hyalella azteca. Ecol. Monogr. 35, 377-394.

Diaz, R. J. and T. J. Fredette. 1982. Secondary production of some dominant macroinvertebrate species inhabiting a bed of submerged vegetation in the lower Chesapeake Bay. In, Structural and functional aspects of the biology of submerged aquatic macrophyte communities in the lower Chesapeake Bay, by R. L. Wetzel, K. L. Webb, P. A. Penhale, R. J. Orth, D. F. Boesch, G. W. Boehlert and J. V. Merriner. Final Report EPA/CBP Grant No. R805974.

Dickinson, J. J., R. L. Wigley, R. D. Brodeur and S. Brown-Leger. 1980. Distribution of gammaridean amphipoda (Crustacea) in the Middle Atlantic Bight region. U.S. Dept. of Commerce. NOAA Tecnical Report NMFS SSRF-741, 46 pp.

Doyle, R. W. and W. Hunte. 1981. Genetic changes in "fitness" and yield of a crustacean population in a controlled environment. J. Exp. Mar. Biol. Ecol. 52, 147-156.

Fredette, T. J. 1983. Chapter 2. In, Life history and secondary production of the crustacean Gammarus mucronatus Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats. Ph.D. dissertation. The College of William and Mary, Williamsburg, Va.

Gable, M. F. and R. A. Croker. 1977. The salt marsh amphipod, Gammarus palustris Bousfield, 1969 at the northern limit of its distribution. I. Ecology and life cycle. Estuar. Coastal Mar. Sci. 5, 123-134.

Goedmakers, A. 1981. Population dynamics of three gammarid species (Crustacea, Amphipoda) in a French chalk stream. Part II. Standing crop. Bijdr. Dierk. 51, 31-69.

Harding, J. P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc., U.K. 28, 141-153.

Heck, K. L., Jr. and R. J. Orth. 1980. Structural components of eelgrass (Zostera marina) meadows in the lower Chesapeake Bay - Decapod Crustacea. Estuaries 3, 289-295.

Howard, R. K. 1982. Impact of feeding activities of epibenthic amphipods on surface-fouling of eelgrass leaves. Aquat. Bot. 14, 91-97.

Hughes, J. E. 1982. Life histoey of the sandy-beach amphipod Dogielinotus loquax (Crustacea: Dogielinotidae) from the outer coast of Washington, USA. Mar. Biol. 71, 167-175.

Klein, G., E. Rachor and S. A. Gerlach. 1975. Dynamics and productivity of two populations of the benthic tube-dwelling amphipod Ampelisca brevicornis (Costa) in Helgoland Bight. Ophelia 14, 139-159.

Krebs, C. J. 1978. A review of the Chitty Hypothesis of population regulation. Can. J. Zool. 56, 2463-2480.

Krishnan, L. and P. A. John. 1974. Observations on the breeding biology of Melita zeylanica Stebbing, a brackish water amphipod. Hydrobiol. 44, 413-430.

Macko, S. A., W. Y. Lee and P. L. Parker, 1982. Nitrogen and carbon isotope fractionation by two species of marine amphipods: laboratory and field studies. J. Exp. Mar. Biol. Ecol. 63, 145-149.

Marchant, R. and H. B. N. Hynes. 1981. The distribution and production of Gammarus pseudolimnaeus (Crustacea: Amphipoda) along a reach of the Credit River, Ontario. Fresh. Biol. 11, 169-182.

Marsh, G. A. 1973. The Zostera epifaunal community in the York River, Virginia. Ches. Sci. 14, 87-97.

Martien, R. F. and A. C. Benke. 1977. Distribution and production of two crustaceans in a wetland pond. American Midl. Natur. 98, 162-175.

Meyer, C. E. 1982. Zooplankton communities in Chesapeake Bay seagrass systems. M.A. thesis. The College of William and Mary, Williamsburg, Virginia. 96 pp.

Nair, K. K. C. and K. Anger. 1979. Experimental studies on the life of Jassa falcata (Crustacea, Amphipoda). Helgo. Wiss. Meeres. 32, 444-452.

Nelson, W. G. 1979. An analysis of structural pattern in an eelgrass (Zostera marina L.) amphipod community. J. Exp. Mar. Biol. Ecol. 39, 231-264.

Nelson, W. G. 1980a. A comparative study of amphipods in seagrasses from Florida to Nova Scotia. Bull. Mar. Sci. 30, 80-89.

Nelson, W. G. 1980b. Reproductive patterns of gammaridean amphipods. Sarsia 65, 61-71.

Nelson, W. G. 1981. Experimental studies of decapod and fish predation on seagrass macrobenthos. Mar. Ecol. Prog. Ser. 5, 141-149.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent. 1975. Statistical Package for the Social Sciences. McGraw-Hill, Inc. N.Y., N.Y. 675pp.

Omori, K., M. Tanaka and T. Kikuchi. 1982. Seasonal changes of short-term reproductive cycle in Corophium volutator (Crustacea: Amphipoda). - Semi-lunar or lunar cycle? Publ. Amakusa Mar. Biol. Lab. 6, 105-117.

Orth, R. J., K. A. Moore and H. H. Gordon. 1979. Distribution and abundance of submerged aquatic vegetation in the lower Chesapeake Bay, Va. E.P.A. Rep. No. 600/8-79/029/SAV 1.

Orth, R. J. and K. L. Heck, Jr. 1980. Structural components of eelgrass (Zostera marina) meadows in the lower Chesapeake Bay--Fishes. Estuaries 3, 278-288.

Orth, R. J. and K. A. Moore. 1982. The biology and propagation of Zostera marina, eelgrass, in the Chesapeake Bay, Virginia. Virginia Institute of Marine Science, Special Report 265, Applied Marine Science and Ocean Engineering. 187 pp.

Rees, C. P. 1975. Life cycle of the amphipod Gammarus palustris Bousfield. Estuar. Coastal Mar. Sci. 3, 413-419.

Savage, A. A. 1982. The survival and growth of Gammarus tigrinus Sexton (Crustacea: Amphipoda) in relation to salinity and temperature. Hydrobiol. 94, 201-212.

Sokal R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co. San Franciso. 859pp.

Southwood, T. R. E. 1976. Bionomic strategies and population parameters. In, R. M. May (Ed), Theoretical Ecology, W. B. Saunders Co., Philadelphia, p. 26-48.

Steele, D. H. 1973. The biology of Parhyalella pietschmanni Schellenberg, 1938 (Amphipoda, Hyalellidae) at Nosy Be, Madagascar. Crustaceana 25, 276-280.

Steele, D. H. and V. J. Steele. 1969. The biology of Gammarus (Crustacea, Amphipoda) in the northwestern Atlantic. I. Gammarus duebeni Lillj. Can. J. Zool. 47, 235-244.

Steele, D. H. and V. J. Steele. 1973. The biology of Gammarus (Crustacea, Amphipoda) in the northwestern Atlantic. VII. The duration of embryonic development in five species at various temperatures. Can J. Zool. 51, 995-999.

Steele, D. H. and V. J. Steele. 1975. The biology of Gammarus (Crustacea, Amphipoda) in the northwestern Atlantic. XI. Comparison and discussion. Can. J. Zool. 53, 1116-1126.

Stoner, A. W. 1980a. Abundance, reproductive seasonality and habitat preferences of amphipod crustaceans in seagrass meadows of Apalachee Bay, Florida. Contrib. Mar. Sci. 23, 63-77.

Stoner, A. W. 1980b. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. Bull. Mar. Sci. 30, 537-551.

Uye, S. 1982. Population dynamics of Acartia clausi Giesbrecht (Copepoda: Calanoida) in inlet waters. J. Exp. Mar. Biol. Ecol. 57, 55-83.

Van Dolah, R. F. 1978. Factors regulating the distrubution and population dynamics of the amphipod Gammarus palustris in an intertidal salt marsh community. Ecol. Monogr. 48, 191-217.

Van Dolah, R. F. and E. Bird. 1980. A comparison of reproductive patterns in epifaunal and infaunal gammaridean amphipods. Estuar. Coastal Mar. Sci. 11, 593-604.

Van Dolah, R. F., L. E. Shapiro and C. P. Rees. 1975. Analysis of an intertidal population of the amphipod Gammarus palustris using a modified version of the egg-ratio method. Mar. Biol. 33, 323-330.

van Maren, M. J. 1978. Distribution and ecology of Gammarus tigrinus Sexton, 1939 and some other amphipod crustacea near Beaufort (North Carolina, U.S.A.). Bijdr. Dierk. 48, 46-56.

Vassallo, L. and D. H. Steele. 1980. Survival and growth of young Gammarus lawrencianus Bousfield, 1956, on different diets. Crustaceana Suppl. 6, 118-125.

Venables, B. J. 1981. Aspects of the population biology of a Venezuelan beach amphipod, Talorchestia margaritae (Talitridae), including estimates of biomass and daily production, and respiration rates. Crustaceana 41, 271-285.

Vijverberg, J. and A. F. Richter. 1982. Population dynamics and production of Daphnia hyalina Leydig and Daphnia cucullata Sars in Tjeukemeer. Hydrobiol. 95, 235-259.

Waters, T. F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 14, 91-164.

Waters, T. F. 1979. Influence of benthos life history upon the estimation of secondary production. J. Fish. Res. Board Can. 36, 1425-1430.

Waters, T. F. and J. C. Hokenstrom. 1980. Annual production and drift of the stream amphipod Gammarus pseudolimnaeus in Valley Creek, Minnesota. Limnol. Oceanogr. 25, 700-710.

Watling, L. and D. Maurer. 1972. Marine shallow water amphipods of the Delaware Bay area, U.S.A. Crustaceana Suppl. 3, 251-266.

Wildish, D. J. 1982. Evolutionary ecology of reproduction in gammaridean Amphipoda. Int. J. Invert. Repro. 5, 1-19.

Williams, A. B. and K. H. Bynum. 1972. A ten-year study of meroplankton in North Carolina estuaries: amphipods. Ches. Sci. 13, 175-192.

Wulff, B. L. and K. L. Webb. 1969. Intertidal zonation of marine algae at Gloucester Point, Virginia. Ches. Sci. 10, 29-35.

Young, D. K., M. A. Buzas and M. W. Young. 1976. Species densities of macrobenthos associated with seagrass: A field experimental study of predation. J. Mar. Res. 34, 577-592.

Zimmerman, R., R. Gibson and J. Harrington. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Mar. Biol. 54, 41-47.

SECONDARY PRODUCTION OF THE CRUSTACEAN <u>GAMMARUS</u> <u>MUCRONATUS</u> SAY (AMPHIPODA: GAMMARIDAE) IN WARM TEMPERATE ESTUARINE HABITATS, YORK RIVER, VIRGINIA

Abstract

Secondary production of the amphipod _Gammarus mucronatus_ was studied in a seagrass (_Zostera marina_) habitat and a macroalgal fouling community on old pier pilings. _G. mucronatus_ populations were present in the macroalgal habitat during only 4 months of the year but production was 10.2-12.9 $g \cdot m^{-2} \cdot yr^{-1}$ dry weight compared with 5.0-6.5 $g \cdot m^{-2} \cdot yr^{-1}$ dry weight in the seagrass habitat where populations were maintained throughout the year. Rapid turnover rates result in short cohort production intervals (CPI) with annual production to biomass ratios ($P/\overline{B}$) ranging from 36.8-76.8 .

A modified instantaneous growth rate method gave production estimates that were approximately 25% higher than estimates of the size-frequency method. Production estimates of four different variations of the size-frequency method produced results that were similar to one another. The sum of size-frequency estimates when males and females are considered separately results in slightly lower production values than combined calculations since dimorphic size biases are excluded.

Calculation of $P/\overline{B}$ with proposed models shows fair agreement with that of Robertson (1979) while severe underestimates are made by those of Banse and Mosher (1980) and Mann (1969).

Introduction

Estuaries are described as among the most productive of marine habitats, with the Chesapeake Bay estuary often being used as a prime example. The Chesapeake Bay serves as nursery ground for many species of fish and each year yields large harvests of shellfish, crabs and fish to commercial and sport fishermen. As the driving force at the base of this harvest of secondary production is the primary production of the plankton and higher plants in and around the bay. The process of conversion from plants to a commercially harvestable product often requires several levels of transfer through the food web as one organism serves as food for another. Contrasted against the large number of production studies on commercially important organisms (see Ricker 1968) there are few studies on the production potential of those species that serve as their food resources (Waters 1979a).

Estimates of secondary production provide useful information for evaluating habitat resource value. One common food resource for fish and decapod crustaceans in many aquatic communities are amphipods (Nelson 1979a, 1981, Stoner 1979, Van Dolah 1978, Young et al. 1976) which are among the most productive organisms studied (Humphreys 1979, McNeill and Lawton 1970, Venables 1981). However, most studies of amphipod production have involved either fresh water (Cooper 1965, Dessaix and Roux 1980, Goedmakers 1981, Marchant and Hynes 1981, Martien and Benke 1977, Waters and Hokenstrom 1980) or cold temperate-boreal marine populations (Hastings 1981, Klein et al. 1975, Wildish and Peer 1981). There appear to be only two investigations of warm climate marine populations (Diaz and Fredette 1982, Venables 1981). The present study was designed to examine the production of populations of the shallow water amphipod _Gammarus mucronatus_ in warm temperate estuarine habitats of the York River, Virginia, a subestuary of the Chesapeake Bay.

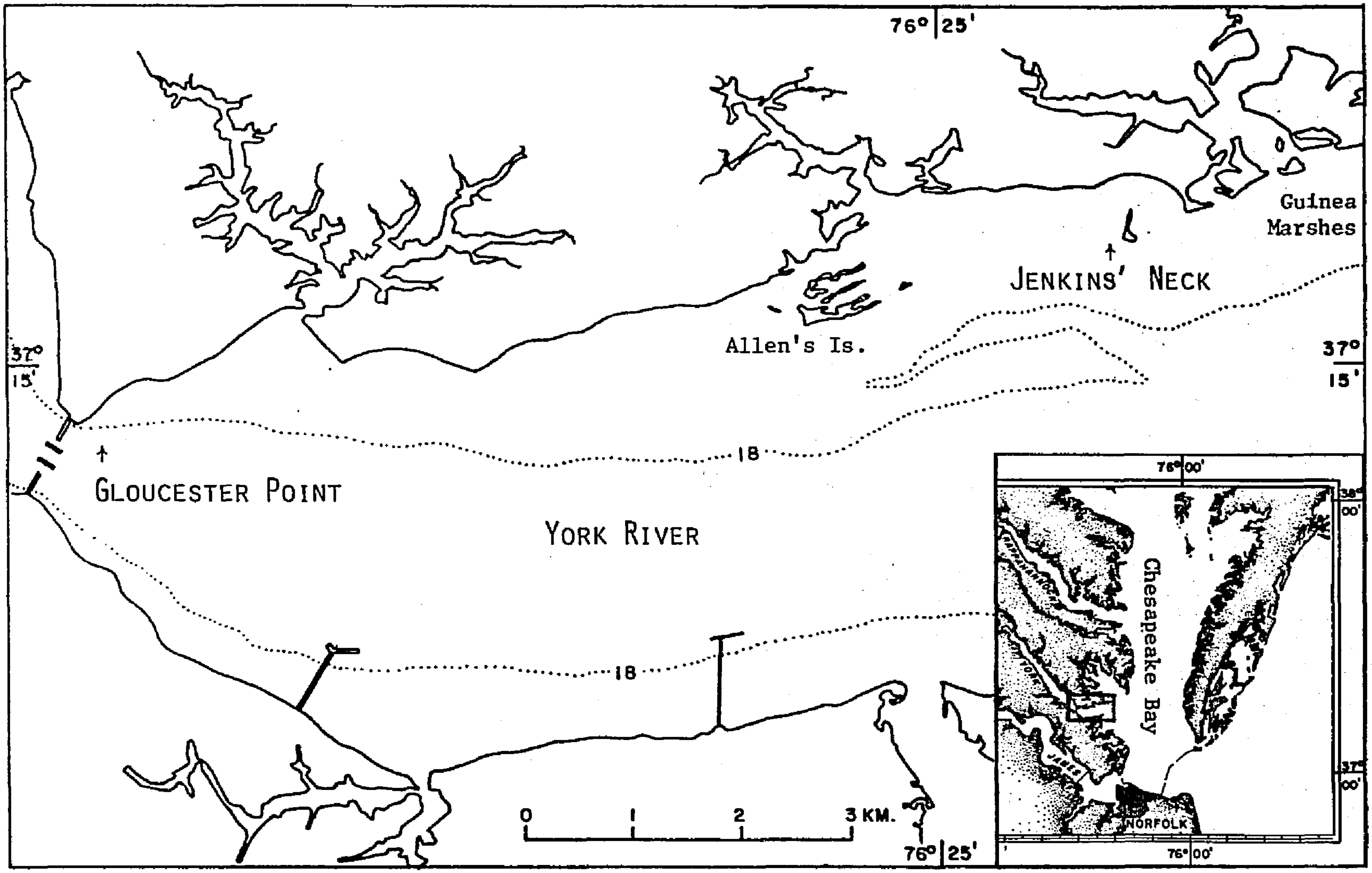
Among the factors that are important for the estimation of secondary production are the habitat examined (Martien and Benke 1977), an organism's voltinism (number of generations), abundance and size-class structure (Waters 1977,1979b). Fredette (1983) has previously examined these and other life history characteristics of _G. mucronatus_ in two spatially proximate habitats from December 1981 to November 1982. In this prior study it was found that population fluctuations and maximum abundance were quite different between habitats. Fredette (1983) also determined that growth in the spring and summer could be very rapid resulting in approximately 6-9 cohorts per year.

Another factor influencing estimates of production is the method of calculation employed. In the present paper I estimate production with the size-frequency calculation method (Hamilton 1969, Menzie 1980) using four different subsets of data and compare these to a fifth estimate based on an instantaneous growth rate (IGR) calculation. Results of the estimates are also used to examine the utility of three different predictive production models.

Material and Methods

The two sites chosen for study were a *Zostera marina* seagrass bed and a fouling community present on old pier pilings dominated by the green algae *Ulva* spp. and *Enteromorpha* spp. (Figure 1). In a previous study of Chesapeake Bay seagrass beds, Diaz and Fredette (1982) concluded that monthly sampling was insufficient for tracking cohorts of amphipods and isopods because of their rapid growth. In order to more clearly define voltinism and field growth rates I sampled more frequently in this study on a fortnightly (every 14 days) basis for a period of one year between December 1981 and November 1982. Because I anticipated that fortnightly sampling might have been insufficient to determine field growth rates in the warmer months due to more rapid growth, a more intensive sampling frequency (every four or five days) was established for the months of March and May 1982. Additional data obtained from these samples included amphipod biomass, abundance and size-frequency distributions. Descriptions of sample sites and sample processing methods are reported in more detail by Fredette (1983).

Figure 1. Sampling locations in the lower York River, Virginia.


76° 25'
Guinea
Marshes
JENKINS' NECK
Allen's Is.
37° 15'
37° 15'
GLOUCESTER POINT
YORK RIVER
18
18
0
1
2
3 KM.
76° 25'
76° 00'
38° 00'
37° 00'
Chesapeake Bay
NORFOLK
YORK
JAMES
76° 00'

Length-weight regressions were determined for each sex (non-ovigerous females only) from both habitats. Amphipods were dried at 60° C for a minimum of 72 hours, cooled in a desiccator and weighed to the nearest 0.1 mg. Small amphipods were pooled to obtain measurable values. Differences in the resultant regressions were compared using covariance analysis (Snedecor and Cochran 1976). All lengths reported in this paper were determined by measuring the distance from the rostrum to the posterior edge of the third pereonal segment. Total length is approximately 3.3 times greater than this measure.

In addition to production through growth, amphipods periodically shed their exoskeletons (exuviae). To examine the amount of exuviae lost during growth 16 newly hatched amphipods were isolated in individual containers and raised in the laboratory at 23° C. Containers were checked daily for presence of molted exoskeletons which were collected and preserved in 10% formalin. At the end of 42 days all amphipods were collected and preserved. Both the exuviae and amphipods were then dried as above and weighed.

Production was determined using two methods. The first is the size-frequency method refined by Menzie (1980):

$$P = \sum_{j=1}^{i} (N_j - N_{j+1}) \cdot (W_j \cdot W_{j+1})^{1/2}$$

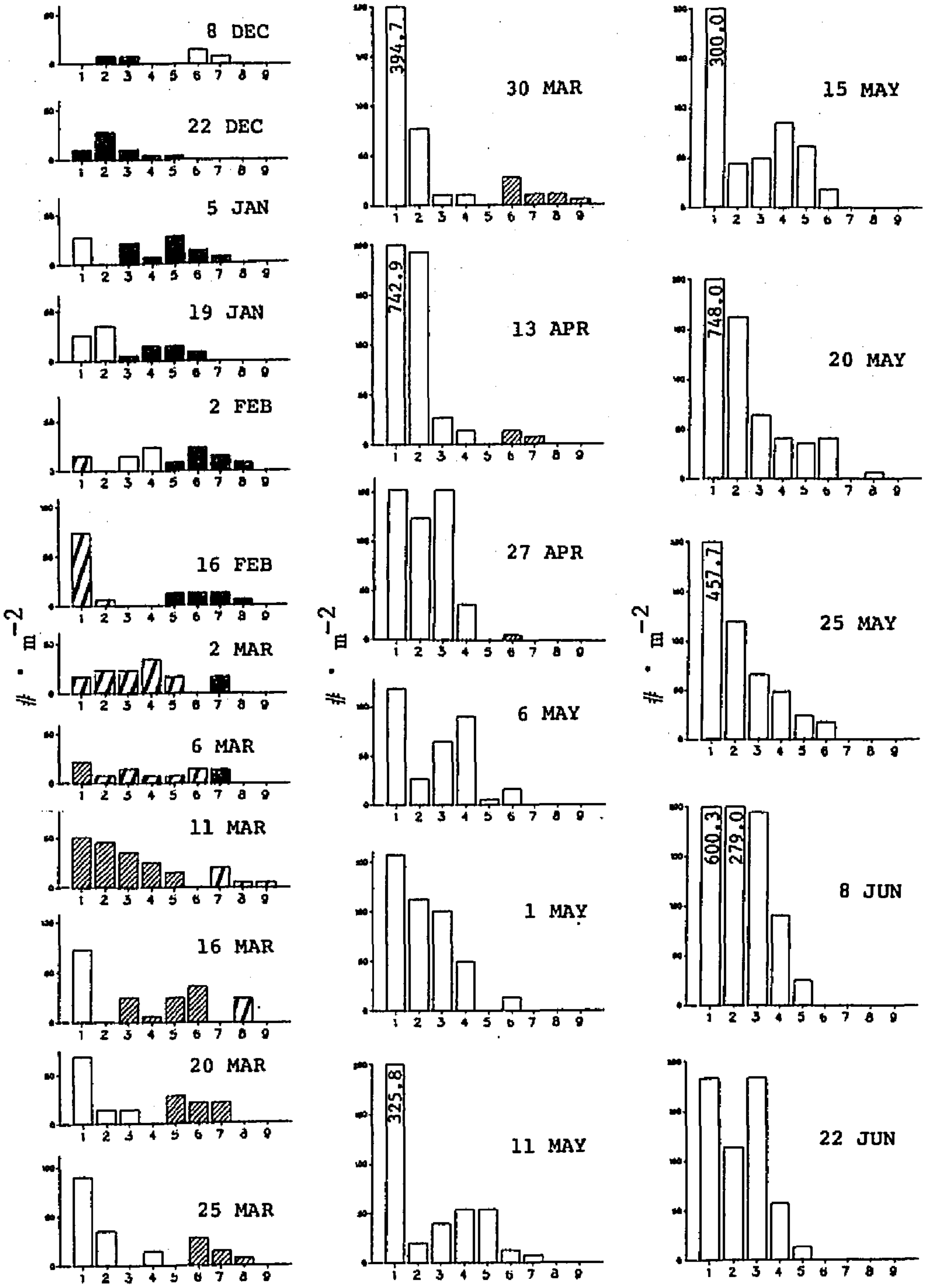
where P is production, i is the number of size classes, N_j is the number of individuals that developed into a given size category over the time interval considered and W_j is the mean weight of an individual in the jth size class. The value of N_j is determined as:

$$N_j = \bar{n}_j \cdot \frac{P_e}{P_a} \cdot \frac{D}{CPI} \cdot C$$

where D is the number of days over which production occurs, n_j is the mean number of individuals that developed into a given size class during time period D, P_e is the estimated time spent in a size class, P_a is the actual time for growth through a size class, CPI is the cohort production interval in days and C is the number of size classes present during time D. The cohort production interval (CPI) is the time required for growth from recruitment to the largest size class (Benke 1979). Growth is considered to be linear for *G. mucronatus* (Fredette 1983) so $P_e/P_a = 1$. This calculation method includes improvements made by Hamilton (1969) to the original Hynes method (Hynes 1961, Hynes and Coleman 1968) and the recommended use of the geometric mean between size classes for weight at loss (W_j) (Krueger and Martin 1980).

To determine production with this method size-frequency distributions were constructed using 0.5 mm length classes. Amphipods were measured from the rostrum to the rear border of the third pereonal segment. Corresponding weights were generated using the regression equations. As previously shown in an examination of the life history of G. mucronatus (Fredette 1983) growth rates are temperature dependent and are best described by a linear function. Based on growth rates determined from three cohorts recognized with size-frequency distributions (Figure 2), G. mucronatus is capable of producing approximately 6-9 cohorts during a year. In addition, during the summer there is a reduction in the maximum size attained by adults which in turn, results in fewer size classes (Figure 2). For these reasons I divided the year into three segments and total annual production was estimated by summing the production estimates for each segment. The CPI was seasonally adjusted for this purpose. The time period from December to the end of February (82 days) was characterized by a cohort production interval of 100 days and eight size classes. From March to May (91 days) there were nine size classes represented in the population and in response to the warmer spring temperatures cohort growth was estimated to take 36 days. From June to November (183 days) only five size classes were represented and growth to the largest size class was more rapid (32 days). Without such

Figure 2. Size-frequency distributions for the seagrass habitat, 8 December to 22 June (0.5 mm length classes, class 1 = 0.5-0.9 mm). Cohort I crosshatched, cohort II thick diagonal striping, cohort III thin diagonal striping.


8 DEC
22 DEC
5 JAN
19 JAN
2 FEB
16 FEB
2 MAR
6 MAR
11 MAR
16 MAR
20 MAR
25 MAR
394.7
30 MAR
742.9
13 APR
27 APR
6 MAY
1 MAY
325.8
11 MAY
300.0
15 MAY
748.0
20 MAY
457.7
25 MAY
600.3
279.0
8 JUN
22 JUN
$\# \cdot m^{-2}$
$\# \cdot m^{-2}$
$\# \cdot m^{-2}$
1 2 3 4 5 6 7 8 9

seasonal segmentation there are serious errors which are introduced into the computation. Two major errors that would occur are application of a uniform size class factor (C) and CPI to production calculated on the entire data set. Both of these would lead to an overestimate of production since summer populations do not have as many size classes and winter populations grow at a slower rate, i.e. have a longer CPI.

The second method used is a modification of the instantaneous growth rate method (IGR) where a daily production value was obtained for each of the sample dates. Daily production was estimated by multiplying the abundance of G. mucronatus in a given size class on a sample date by a seasonally adjusted size specific instantaneous growth rate. Growth rates were estimated and seasonally adjusted from the same data used to estimate CPI. These daily production values were then plotted against time and a curve was drawn between points. The area under the curve was integrated to obtain production. The equation used was:

$$P = \int_{1}^{m} \sum_{j=1}^{i} \frac{w_j \cdot N_j}{T_j}$$

where P is production, T_j is the time period over which growth is considered (i.e. one day), w_j is the instantaneous daily growth rate for the jth size class, i is the number of size classes and m is the number of sample dates in the study period. This method is similar to those described in Edmondson and Winberg (1971) and Venables (1981).

The effects of sampling frequency and separation of sexes were examined for the size-frequency method. Effects of sampling frequency were examined by making separate calculations of production using all 26 fortnightly sample dates and each of the alternate four week subsets of this data (i.e. every odd and every even sample). The effect of combining sexes was studied by separating sexes into two subgroups (juveniles split evenly since a 1:1 sex ratio exists (Fredette 1983)) and estimating production for each. These separate subgroup estimates were combined and compared to the estimate calculated for the population as a whole.

Production to biomass ($P/\bar{B}$) ratios from the above analyses were compared with those predicted from the generalized mathematical models of Mann (1969), Robertson (1979) and Banse and Mosher (1980). Mann (1969) expresses the relationship between production and biomass for organisms with life spans less than one year as:

$$\log_{10} P = 0.411 + 1.237 \log_{10} \bar{B}$$

where P and $\bar{B}$ are in terms of $\text{kcal}\cdot\text{m}^{-2}$. Robertson (1979) includes a term based on life span such that:

$$\log_{10}P/\bar{B} = 0.660(\pm 0.089) - 0.726(\pm 0.147)\log_{10}L$$

where L is mean life span in years. Banse and Mosher (1980) relate $P/\bar{B}$ to mean adult size at maturity (M_s) for organisms living at annual mean environmental temperatures between 5 and 20° C as:

$$P/\bar{B} = 0.65\, M_s^{-0.37} .$$

Solutions to the production models were obtained assuming (1) mean life span (L) in years to be 0.113, based on 8.85 cohorts per year, (2) mean size at maturity to be the mean size of all ovigerous females collected (2.3 mm) converted to a caloric value of 4.55×10^{-3} kcal and (3) a mean biomass of 125.3 $mg \cdot m^{-2}$ converted to 20.2 $kcal \cdot m^{-2}$. The caloric values were estimated from the mean energy content value of 4050 $cal \cdot g^{-1}$ reported for the family Gammaridae by Cummins and Wuycheck (1971). The Robertson (1979) model was calculated using the upper limits provided in the equation which produce the maximum $P/\bar{B}$ prediction for a given set of parameters.

Results

Length-weight regressions for each sex in each habitat were found not to differ on the basis of covariance ($p<0.05$) so the entire data set was combined to provide a single regression expressed as

$$W = 0.0943 \, L^{3.03} \, .$$

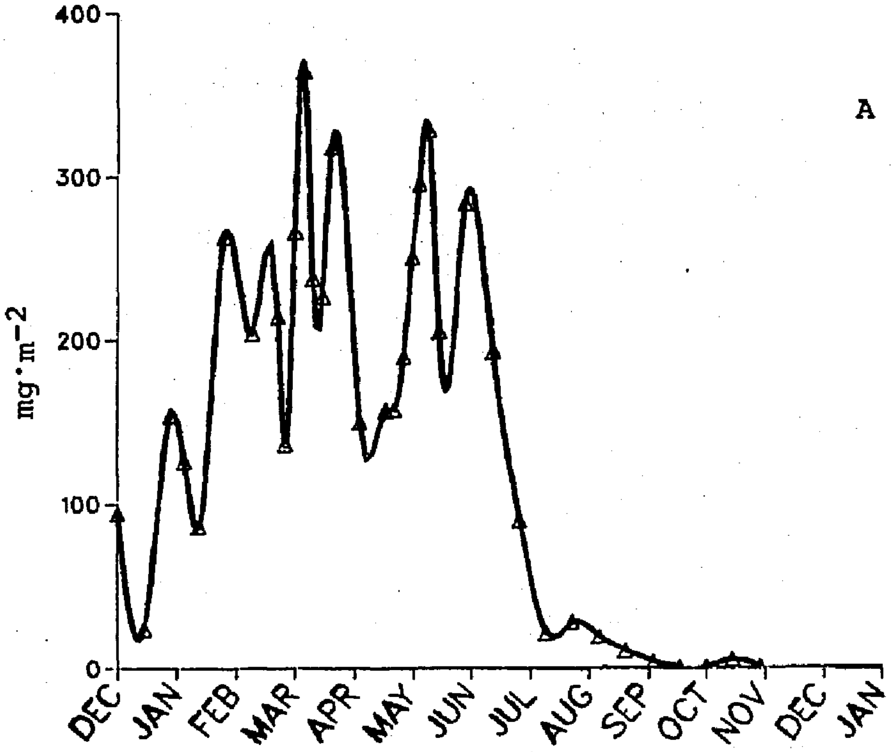
where W is weight in mg and L is length of head and first three pereonites in mm.

Amphipods grown for exuviae collection molted 5-10 times over the 42 day period. Some individuals may have molted more frequently than observed due to reingestion of the exoskeleton. Certain individuals seemed to have greater tendencies for partial reingestion of exuviae than others. Total biomass of exuviae collected was 2.1 mg dry weight while biomass of the amphipods was 5.4 mg dry weight. This exuviae loss thus represents 39% of the amphipod dry weight biomass accumulated by the end of the experimental period.

Fredette (1983) has previously reported that maximum densities of G. mucronatus were approximately $1200 \cdot m^{-2}$ in the seagrass habitat and $6800 \cdot m^{-2}$ in the algal habitat. This habitat difference is reflected in the standing stock dry weight biomass of the two habitats (Figure 3) as there is an order of magnitude difference between them. In the algal habitat (Figure 3b) biomass was extremely high during the brief period from 16-25 May with more moderate values prevailing during the remainder to the time when _G. mucronatus_ was present on the pilings.

The method used to calculate the size-frequency estimates are shown for the separate male and female subgroups from the seagrass habitat in Table 1. Males grew to larger maximum size than females, thus the size class factor (C) is larger, contributing to greater production for males. The production estimate for the entire population (26 Dates) (Table 2) of 5243.5 $mg \cdot m^{-2} \cdot yr^{-1}$ is approximately 5% greater than the 5016 $mg \cdot m^{-2} \cdot yr^{-1}$ of the sum of the sex subgroups (M+F) in the seagrass habitat, but the algal M+F estimate of 10293.4 $mg \cdot m^{-2} \cdot yr^{-1}$ is slightly (<1%) greater than the 10247.4 $mg \cdot m^{-2} \cdot yr^{-1}$ 26 Date value in that habitat (Table 3). This illustrates the effect that a dimorphic difference in growth can have on the estimate since unlike the seagrass habitat males and females in the algal habitat reached similar sizes.

Figure 3. Amphipod dry weight biomass ($mg \cdot m^{-2}$) during the study period (a) seagrass habitat (b) algal habitat.


A
400
300
200
100
0
mg·m⁻²
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN

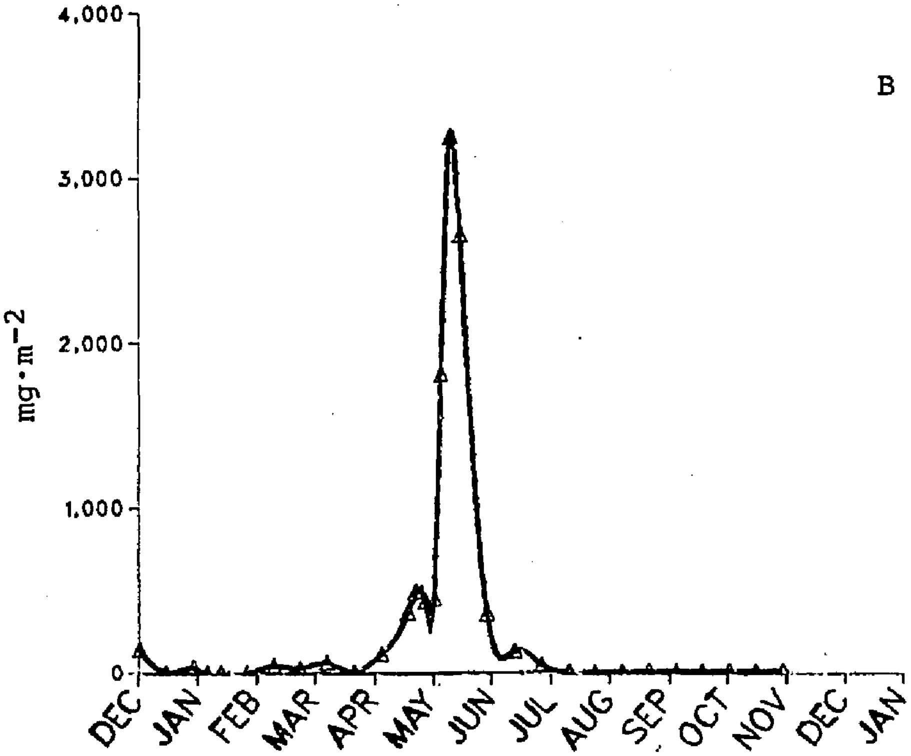

B
4,000
3,000
2,000
1,000
0
mg·m⁻²
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN

Table 1. Size-frequency production estimates for male and female subgroups from the seagrass habitat (see text for explanation of terms).

TABLE 1

SEAGRASS—MALES

8 DEC to 16 FEB

Class	$\bar{n}_j$ (#·m^{-2})	P_e/P_a	C	Adjustment factor (growth period/CPI)	N_j	Loss between classes (#·m^{-2})	W_j (mg)	P (mg·m^{-2})
1	12.5	1.0	8	0.75	75.0			
2	5.6	1.0	8	0.75	33.6	41.4	0.08	3.3
3	5.5	1.0	8	0.75	33.0	0.6	0.28	0.2
4	2.2	1.0	8	0.75	13.2	19.8	0.70	13.9
5	2.2	1.0	8	0.75	13.2	0.0	1.41	0.0
6	7.0	1.0	8	0.75	42.0	-28.8	2.48	-71.4
7	3.7	1.0	8	0.75	22.2	19.8	4.00	79.2
8	2.3	1.0	8	0.75	13.8	8.4	6.04	50.7
						13.8	8.68	119.8
Total P mg dry weight·m^{-2}								195.7

2 MAR to 25 MAY

Class	$\bar{n}_j$ (#·m^{-2})	P_e/P_a	C	Adjustment factor (growth period/CPI)	N_j	Loss between classes (#·m^{-2})	Weight at loss (mg)	P (mg·m^{-2})
1	154.5	1.0	9	2.5	3474.0			
2	37.1	1.0	9	2.5	834.7	2639.3	0.08	211.1
3	24.1	1.0	9	2.5	542.2	292.5	0.28	81.9
4	15.5	1.0	9	2.5	348.7	193.5	0.70	135.4
5	7.1	1.0	9	2.5	159.7	189.0	1.41	266.5
6	6.3	1.0	9	2.5	141.7	18.0	2.48	44.6
7	1.0	1.0	9	2.5	22.5	119.2	4.00	476.8
8	4.1	1.0	9	2.5	92.2	-69.7	6.04	-421.0
9	0.8	1.0	9	2.5	18.0	74.2	8.68	644.1
						18.0	11.99	215.8
Total P mg dry weight·m^{-2}								1655.3

TABLE 1 (continued)

8 JUN to 23 NOV

Class	$\bar{n}_j$ (#·m^{-2})	P_e/P_a	C^*	Adjustment factor (growth period/CPI)	N_j	Loss between classes (#·m^{-2})	Weight at loss (mg)	P (mg·m^{-2})
1	40.9	1.0	5	5.6	1145.2			
2	21.2	1.0	5	5.6	593.6	551.6	0.08	44.1
3	20.7	1.0	5	5.6	579.6	14.0	0.28	3.9
4	8.6	1.0	5	5.6	240.8	339.0	0.70	237.3
5	2.4	1.0	5	5.6	67.2	173.6	1.41	244.8
6	0.6	1.0	5	5.6	16.8	50.4	2.48	125.0
						16.8	4.00	67.2
Total P mg dry weight·m^{-2}								722.3

SEAGRASS--FEMALES

8 DEC to 16 FEB

Class	$\bar{n}_j$ (#·m^{-2})	P_e/P_a	C	Adjustment factor (growth period/CPI)	N_j	Loss between classes (#·m^{-2})	Weight at loss (mg)	P (mg·m^{-2})
1	12.5	1.0	7	0.75	65.6			
2	7.0	1.0	7	0.75	36.7	28.9	0.08	2.3
3	4.0	1.0	7	0.75	21.0	15.7	0.28	4.4
4	5.8	1.0	7	0.75	30.4	-9.4	0.70	-6.6
5	8.9	1.0	7	0.75	46.7	-16.3	1.41	-23.0
6	4.8	1.0	7	0.75	25.2	21.5	2.48	53.3
7	3.4	1.0	7	0.75	17.8	7.4	4.00	29.6
						17.8	6.04	107.5
Total P mg dry weight·m^{-2}								167.5

TABLE 1 (continued)

2 MAR to 25 MAY

Class	$\bar{n}_j$ (#·m^{-2})	P_e/P_a	C	Adjustment factor (growth period/CPI)	N_j	Loss between classes (#·m^{-2})	Weight at loss (mg)	P (mg·m^{-2})
1	154.5	1.0	8	2.5	3090.0			
2	41.7	1.0	8	2.5	834.0	2256.0	0.08	180.5
3	24.9	1.0	8	2.5	498.0	336.0	0.28	94.1
4	12.9	1.0	8	2.5	258.0	240.0	0.70	168.0
5	9.7	1.0	8	2.5	194.0	64.0	1.41	90.2
6	10.0	1.0	8	2.5	200.0	-6.0	2.48	-14.9
7	4.9	1.0	8	2.5	98.0	102.0	4.00	408.0
8	0.8	1.0	8	2.5	16.0	82.0	6.04	495.3
						16.0	8.68	138.9
Total P mg dry weight·m^{-2}								1560.1

8 JUN to 23 NOV

Class	$\bar{n}_j$ (#·m^{-2})	P_e/P_a	C^*	Adjustment factor (growth period/CPI)	N_j	Loss between classes (#·m^{-2})	Weight at loss (mg)	P (mg·m^{-2})
1	40.9	1.0	5	5.6	1145.2			
2	18.3	1.0	5	5.6	512.4	632.8	0.08	50.6
3	18.6	1.0	5	5.6	520.8	-8.4	0.28	-2.3
4	8.7	1.0	5	5.6	243.6	277.2	0.70	194.0
5	1.9	1.0	5	5.6	53.2	190.4	1.41	268.5
6	1.7	1.0	5	5.6	47.6	5.6	2.48	13.9
						47.6	4.00	190.4
Total P mg dry weight·m^{-2}								715.1

* 5 was used for C instead of the number of size classes (6) because the last size class was represented only on the last day of the time period.

Table 2. Production estimates for _Gammarus_ _mucronatus_ from the seagrass habitat for the total fortnightly sample set (26 Dates), the two alternate four week sets (13 Even, 13 Odd), the summation of the separate sexes (M+F) and the instantaneous growth estimate (IGR). Both seasonal and total production are shown.

TABLE 2

Secondary Production--Seagrass Habitat

	Size Frequency				IGR
	26 Dates	13 Even	13 Odd	M+F	
DEC-FEB	389.4	481.2	296.7	363.2	350.0
MAR-MAY	3412.5	3168.1	3308.9	3215.4	4305.0
JUN-NOV	1441.6	992.8	1829.9	1437.4	1802.5
P ($mg \cdot m^{-2} \cdot yr^{-1}$)	5243.5	4642.1	5435.5	5016.0	6475.5
$\bar{B}$ ($mg \cdot m^{-2}$)	125.3	126.1	124.5	125.3	125.3
$P/\bar{B}$	41.8	36.8	43.7	40.0	51.7

Table 3. Production estimates for _Gammarus_ _mucronatus_ from the algal habitat for the total fortnightly sample set (26 Dates), the summation of the separate sexes (M+F) and the instantaneous growth estimate (IGR).

TABLE 3

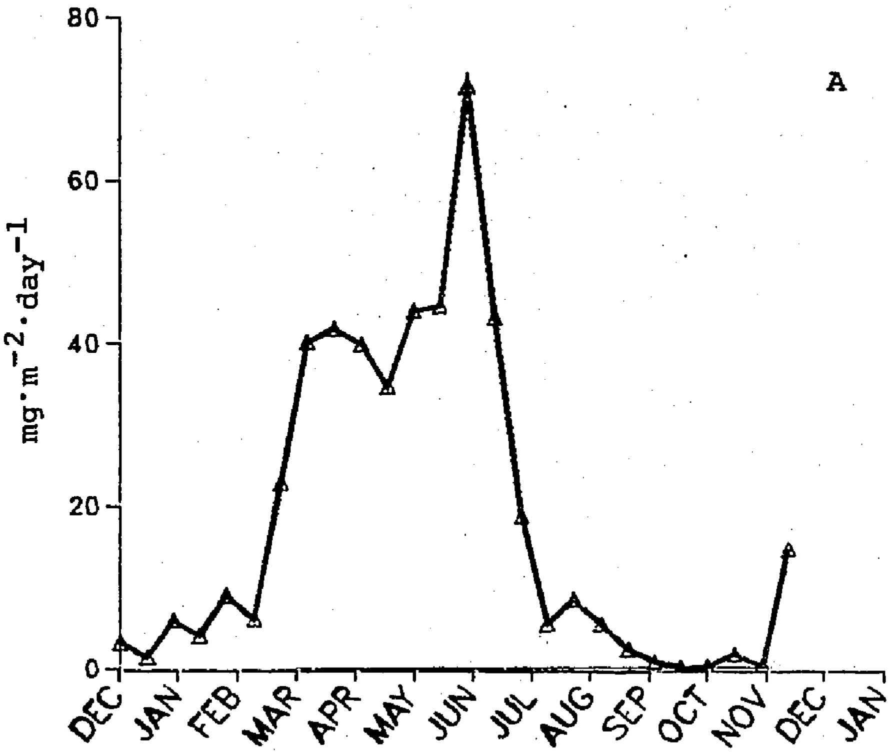
Secondary Production--Algal Habitat

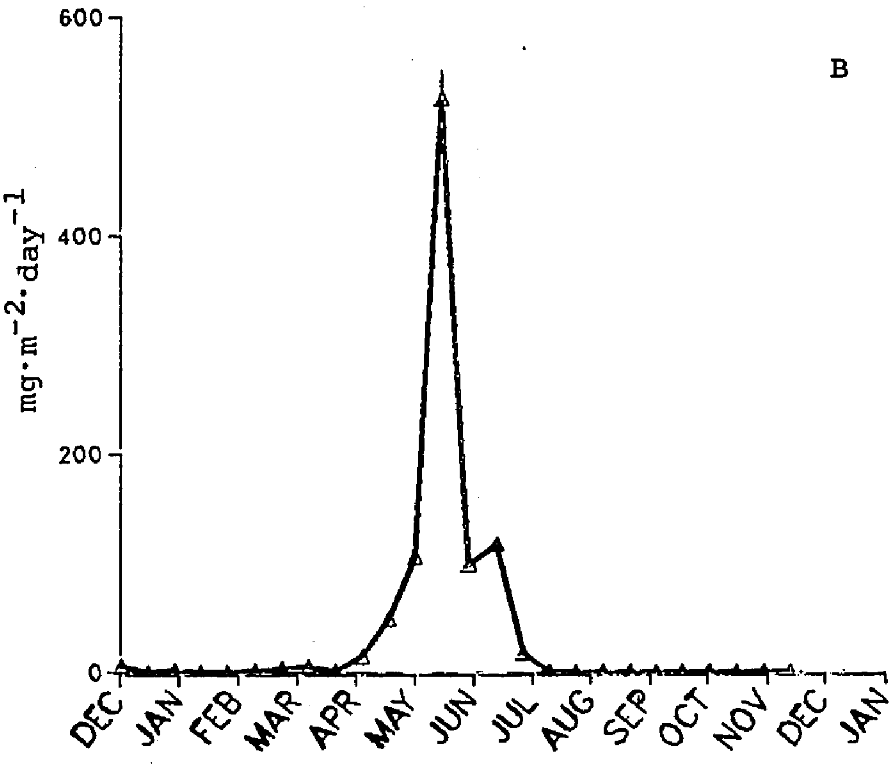
	Size Frequency		IGR
	26 Dates	M+F	
P $(\mathrm{mg \cdot m^{-2} \cdot yr^{-1}})$	10247.4	10293.4	12950.0
$\bar{B}$ $(\mathrm{mg \cdot m^{-2}})$	168.5	168.5	168.5
$P/\bar{B}$	60.8	61.1	76.8

Size-frequency estimates based on an increase of sampling interval from two to four weeks (13 even, 13 odd) result in the Even sample set estimating 12% less production and the Odd set estimating 4% greater production than the 26 Date set. Thus, if variations in estimates of approximately 10% are acceptable for a halving of sample effort, monthly samples would be adequate for estimating production.

When compared to the M+F size-frequency estimates the IGR estimates (Figure 4, Tables 2,3) were 26% and 29% greater in the algal habitat and seagrass habitat, respectively. The majority of the production in the seagrass habitat occurs within the three month period from March to May while June to November contributes the next greatest amount (Table 2, Figure 4a). In addition to production at the algal habitat being twice the seagrass values, $P/\overline{B}$ ratios are also greater with the IGR estimate (76.8) being more than double the lowest estimate from the seagrass habitat. The majority of the production occurs from 13 April to 6 July (Figure 4b) paralleling the presence of _G_. _mucronatus_ in this habitat.

Figure 4. Resultant curves from computation of daily IGR production (a) seagrass habitat (b) algal habitat.


A
mg·m^{-2}·day^{-1}
80
60
40
20
0
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN


B
mg·m^{-2}·day^{-1}
600
400
200
0
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN

Discussion

Production of 5-10 $g \cdot m^{-2} \cdot yr^{-1}$ by Gammarus mucronatus populations in the two habitats studied is moderate in comparison to other amphipod species (Waters 1977). Values of 27.1 $g \cdot m^{-2} \cdot yr^{-1}$ have been reported for Gammarus pseudolimnaeus (Waters and Hokenstrom 1980) and 150-1100 $g \cdot m^{-2} \cdot yr^{-1}$ for Talorchestia margaritae (Venables 1981). However, my estimated $P/\bar{B}$ ratios are among the highest reported in the literature. The high production of G. pseudolimnaeus and T. margaritae are largely due to high standing stocks as the mean $P/\bar{B}$'s are 6.0 and 0.08, respectively. High annual $P/\bar{B}$'s have been reported for amphipods such as 12-19.5 for Corophium insidiosum (Casabianca 1975) and 23.6 for G. mucronatus (Diaz and Fredette 1982). Waters (1977) has reported most $P/\bar{B}$ ratios of univoltine zoobenthos are approximately 5 and for multivoltine species with 2-3 generations per year they are around 10. This implies a cohort $P/\bar{B}$ of approximately 4-5. Thus with approximately 9 cohorts per year, a $P/\bar{B}$ of 40 for G. mucronatus should be expected. Even if the lower estimate of 6 cohorts is considered by reducing the number of summer cohorts by 3, production is estimated to be 4.3 $g \cdot m^{-2} \cdot yr^{-1}$ and the 34.2 annual $P/\bar{B}$ is still very high. High $P/\overline{B}$'s are characteristic of short lived organisms such as zooplankton and some aquatic insects. Menzie (1981) reported a $P/\overline{B}$ of 21.0 for the chironomid *Cricotopus sylvestris* and suggested that the $P/\overline{B}$ may actually have been twice that.

G. mucronatus is only one of several amphipod and isopod species present in the habitats studied. Many of these species are more abundant than *G. mucronatus*. Those that maintain high population densities over the summer could prove to be extremely productive. Amphipod densities in shallow marine habitats of $1x10^4$ are common and can be greater than $1x10^5$ (Birklund 1977, Moller and Rosenberg 1982, Nelson 1979b, Venables 1981). As in the algal habitat studied here, even when high densities are present during only a brief period, large production values can result if coupled with rapid growth. The production potential of tropical and warm temperate shallow water habitats are not well studied. In such habitats where standing stock biomass is low production may be greater than expected due to high turnover ($P/\overline{B}$) rates. Shallow water cold temperate habitats also need to to examined more closely, especially in embayments where temperatures are likely to increase during the summer. Such areas can often warm to greater than 14° C, a temperature at which *G. mucronatus* can grow quite rapidly (Fredette 1983).

In addition to the biomass accumulated during growth, crustaceans periodically cast off exuvial materials which are not a trivial proportion of total production. The dry weight biomass lost by G. mucronatus (39%) during the molting process seems to be quite significant, but is similar to that reported by Strong and Daborn (1979) for the isopod Idotea baltica. Converting their energy content values to milligrams we find that during growth female isopods lose 31% of actual accumulated body mass to exuviae and males lose 37%. When these values are considered in terms of energy the loss is not so severe, but still substantial being 20% for females and 24% for males. Actual percent energy loss by G. mucronatus is also probably less than the biomass loss since the exuviae are likely to have a lower energy to mass content than the entire body.

The variation in estimated production of the different computation methods was not very large with the exception of the IGR estimate. In both habitats the IGR method estimates production to be at least 25% greater than the M+F size-frequency estimate (26% algal, 29% seagrass). This higher estimate may be partially due to the assumption of linear growth for all amphipods when determining size specific instantaneous growth rates. In reality large amphipods probably have reduced growth rates, thus their production is overestimated. Vassallo and Steele (1980), Savage (1982), and Nair and Anger (1979) have all demonstrated that growth of amphipods (in length) tends to be linear until maturation, after which the rate decreases.

Within the seagrass habitat the four size-frequency estimates are fairly close. The production estimates generated by excluding every alternate sample date indicate that with only half the sampling effort (monthly samples) the estimates of production were only 4-12% different than the entire 26 fortnightly sample data set. Because secondary production estimation is not precise, such a trade off is acceptable. Lapchin and Neveu (1980) have reported similar calculation differences for three of four aquatic insect species when sampling frequency was decreased. The most accurate value of the four seagrass habitat size-frequency estimates is probably that obtained from the sum of the male and female subgroups (M+F) since any bias due to dimorphic size differences are eliminated. However, the dimorphic size difference was only one size class and resulted in a minor change in the production estimate. Waters and Hokenstrom (1980) have suggested that in populations where sexes grow to different maximum sizes the size class factor (C) might be reduced to C-1. Using that procedure in this study would lead to an estimate that is 10% lower than actual separation of sexes for the seagrass habitat.

Between habitat comparisons show that despite the relatively brief presence of *G. mucronatus* in the algae habitat, production was more than double that observed in the seagrass bed. This higher production reflects the very high amphipod densities as compared to those observed in the seagrass habitat. The higher $P/\bar{B}$'s of the algal habitat probably result from these high densities coinciding with favorable growth conditions. One of the only other studies which has examined amphipod production in two habitats (Martien and Benke 1977) also reported $P/\bar{B}$ differences between habitats of 6.8 and 8.1 for the amphipod *Crangonyx gracilis* sp. They attributed the differences to inadequate knowledge of the life history and behavior of this amphipod. Food quality is a factor that could result in different growth rates, thus different $P/\bar{B}$'s. Growth of *G. mucronatus* is slower on an algal diet than on a seagrass diet (Fredette 1983). Based on this result I would have expected a lower $P/\bar{B}$ in the algal habitat. Among the factors that may have led to this discrepancy is the greater range of food sources present in the field as compared to the laboratory experiment.

The $P/\bar{B}$'s predicted from the models vary from 2.2-37.6 (Table 4). The Robertson (1979) model produces the closest estimate to my values, presumably because it accounts for life span. The other two models (Mann 1969,

Table 4. Production/Biomass ratio estimates for _Gammarus mucronatus_ based on computation of predictive models.

TABLE 4

Model Predictions

Model	Predicted $P/\bar{B}$
Mann (1969)	2.2
Banse and Mosher (1980)	4.8
Robertson (1979)	37.6

Banse and Mosher 1980) ignore factors which may be affected by how quickly an organism grows. Simply multiplying these latter estimates by the number of cohorts would provide closer agreement (19.5 and 42.3 respectively) and may be a reasonable modification particularly for the Banse and Mosher (1980) model. The Robertson (1979) model may prove to be useful as a management tool, but it is dependent on obtaining a good estimate of life span and should be tested with other data sets before general application.

Instead of comparison of $P/\bar{B}$ values, which may exhibit a fair degree of variation, Waters (1977) has recommended the possible use of the term P/B_{max}, where the production is divided by the maximum biomass observed over the year. He reported that some studies show this value to be consistently close to 1.5, but stresses that more empirical evidence is needed. I concur with this cautionary note as P/B_{max} values of 13.8 for the seagrass habitat and 3.9 for the algal habitat are estimated.

It was previously concluded that monthly sampling provided a reasonable estimate of the production of *G. mucronatus*. However, I was able to determine voltinism only through laboratory experimentation and with field sampling intervals on a time scale of days (Fredette 1983). Future investigations of secondary production must clearly establish the voltinism of the organism under study. The assumption that an organism has an annual life history when in fact there is at least one summer cohort can result in a production estimate half as great as the actual value. If I had asumed one generation per year for G. mucronatus, the seagrass habitat production would have been estimated at 0.7 $g \cdot m^{-2} \cdot yr^{-1}$, 15% of the estimated (M+F) value.

There is a clear need for more study of the production dynamics of warm shallow marine habitats. It is unlikely that most invertebrate groups will exhibit the short generation times some amphipods are capable of in these habitats, but those species that do can be very important in total community production. Shallow marine and estuarine areas are likely to receive greater impact from man's activities relative to deeper areas and must be well understood if we are to evaluate their importance in the marine ecosystem.

Literature Cited

Banse, K. and S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. 50, 355-379.

Benke, A. C. 1979. A modification of the method for estimating secondary production with particular significance for multivoltine populations. Limnol. Oceanogr. 24, 168-171.

Birklund, J. 1977. Biomass, growth and production of the amphipod _Corophium insidiosum_ Crawford, and preliminary notes on _Corophium volutator_ (Pallas). Ophelia 16, 187-203.

Casabianca, M. -L., de. 1975. Methode de calcul de la production par estimation de la mortalite. Application a une population a structure complexe du crustace _Corophium insidiosum_ Crawford (Lagune de Biguglia, Corse). -C. r. Hebd. Seanc. Acad. Sci., Paris 280, 1139-1142.

Cooper, W. E. 1965. Dynamics and production of a natural population of a fresh water amphipod, _Hyalella azteca_. Ecol. Monogr. 35, 377-394.

Cummins, K. W. and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. int. Ver. Limnol. 18, 1-158.

Dessaix, J. and A. L. Roux. 1980. Structure and dynamics of the French upper Rhone ecosystems. X. An estimate of the secondary production of gammarids in the main stream. Crustaceana Suppl. 6, 242-252.

Diaz, R. J. and T. J. Fredette. 1982. Secondary production of some dominant macroinvertebrate species inhabiting a bed of submerged vegetation in the lower Chesapeake Bay. In, Structural and functional aspects of the biology of submerged aquatic macrophyte communities in the lower Chesapeake Bay, by R. L. Wetzel, K. L. Webb, P. A. Penhale, R. J. Orth, D. F. Boesch, G. W. Boehlert and J. V. Merriner. Final Report EPA/CBP Grant No. R805974.

Edmondson, W. T. and G. G. Winberg (Eds). 1971. A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. IBP Handbook No 17, Blackwell Sci. Publ., Oxford, England.

Fredette, T. J. 1983. Chapter 1. In, Life history and secondary production of the crustacean _Gammarus mucronatus_ Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats. Ph.D. dissertation. The College of William and Mary, Williamsburg, Va.

Goedmakers, A. 1981. Population dynamics of three gammarid species (Crustacea, Amphipoda) in a French chalk stream. Part II. Standing crop. Bijdr. Dierk. 51, 31-69.

Hamilton, A. L. 1969. On estimating annual production. Limnol. Oceanogr. 13, 771-782.

Hastings, M. H. 1981. The life cycle and productivity of an intertidal population of the amphipod _Ampelisca brevicornis_. Estuar. Coastal Shelf Sci. 12, 665-667.

Humphreys, W. F. 1979. Production and respiration in animal populations. J. Anim. Ecol. 48, 427-453.

Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 57, 344-388.

Hynes, H. B. N. and Coleman, M. J. 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13, 569-573.

Klein, G., E. Rachor and S. A. Gerlach. 1975. Dynamics and productivity of two populations of the benthic tube-dwelling amphipod _Ampelisca brevicornis_ (Costa) in Helgoland Bight. Ophelia 14, 139-159.

Krueger, C. C. and F. B. Martin. 1980. Computation of confidence intervals for the size-frequency (Hynes) method of estimating secondary production. Limnol. Oceanogr. 25, 773-777.

Lapchin, L. and A. Neveu. 1980. The production of benthic invertebrates: comparison of different methods. II - Application to the benthos of the Nivelle River (Pyrenees-Atlantiques, France). Ecol. Gener. 1, 359-372.

Mann, K. H. 1969. The dynamics of aquatic ecosystems. Adv. Ecol. Res. 6, 1-81.

Marchant, R. and H. B. N. Hynes. 1981. The distribution and production of Gammarus pseudolimnaeus (Crustacea: Amphipoda) along a reach of the Credit River, Ontario. Fresh. Biol. 11, 169-182.

Martien, R. F. and A. C. Benke. 1977. Distribution and production of two crustaceans in a wetland pond. American Midl. Natur. 98, 162-175.

McNeill, S. and J. H. Lawton. 1970. Annual production and respiration in animal populations. Nature, London 255, 472-474.

Menzie, C. A. 1980. A note on the Hynes method of estimating secondary production. Limnol. Oceanogr. 25, 770-773.

Menzie C. A. 1981. Production ecology of Cricotopus sylvestris (Fabricius) (Diptera: Chironomidae) in a shallow estuarine cove. Limnol. Oceanogr. 26, 467-481.

Moller, P. and R. Rosenberg. 1982. Production and abundance of the amphipod Corophium volutator on the west coast of Sweden. Neth. J. Sea Res. 16, 127-140.

Nair, K. K. C. and K. Anger. 1979. Experimental studies on the life of Jassa falcata (Crustacea, Amphipoda). Helgo. Wiss. Meeres. 32, 444-452.

Nelson, W. G. 1979a. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. J. Exp. Mar. Biol. Ecol. 38, 225-245.

Nelson, W. G. 1979b. An analysis of structural pattern in an eelgrass (Zostera marina L.) amphipod community. J. Exp. Mar. Biol. Ecol. 39, 231-264.

Nelson, W. G. 1981. Experimental studies of decapod and fish predation on seagrass macrobenthos. Mar. Ecol. Prog. Ser. 5, 141-149.

Ricker, W. E. 1968. Methods for Assessment of Fish Production in Fresh Waters. IBP Handbook No. 3, Blackwell Sci. Publ. Oxford, England.

Robertson, A. I. 1979. The relationship between annual production: biomass ratios and lifespans for marine macrobenthos. Oecologia 38, 193-202.

Savage, A. A. 1982. The survival and growth of Gammarus tigrinus Sexton (Crustacea: Amphipoda) in relation to salinity and temperature. Hydrobiol. 94, 201-212.

Snedecor, G. W. and W. G. Cochran. 1976. Statistical Methods. The Iowa State University Press, Ames, Iowa. 593pp.

Stoner, A. W. 1979. Species specific predation on amphipod crustacea by pinfish (Lagadon rhomboides): Mediation by macrophyte standing crop. Mar. Biol. 55, 210-207.

Strong, K. W. and G. R. Daborn. 1979. Growth and energy utilisation of the intertidal isopod Idotea baltica (Pallas) (Crustacea: Isopoda). J. Exp. Mar. Biol. Ecol. 41, 101-123.

Van Dolah, R. F. 1978. Factors regulating the distribution and population dynamics of the amphipod Gammarus palustris in an intertidal salt marsh community. Ecol. Monogr. 48, 191-217.

Vassallo, L. and D. H. Steele. 1980. Survival and growth of young Gammarus lawrencianus Bousfield, 1956, on different diets. Crustaceana Suppl. 6, 118-125.

Venables, B. J. 1981. Aspects of the population biology of a Venezuelan beach amphipod, Talorchestia margaritae (Talitridae), including estimates of biomass and daily production, and respiration rates. Crustaceana 41, 271-285.

Waters, T. F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 14, 91-164.

Waters, T. F. 1979a. The turnover ratio in production ecology of freshwater invertebrates. Am. Nat. 103, 173-185.

Waters, T. F. 1979b. Influence of benthos life history upon the estimation of secondary production. J. Fish. Res. Board Can. 36, 1425-1430.

Waters, T. F. and J. C. Hokenstrom. 1980. Annual production and drift of the stream amphipod Gammarus pseudolimnaeus in Valley Creek, Minnesota. Limnol. Oceanogr. 25, 700-710.

Wildish. D. J. and D. Peer. 1981. Methods for estimating secondary production in marine Amphipoda. Can. J. Fish. Aquat. Sci. 38, 1019-1026.

Young, D. K., M. A. Buzas and M. W. Young. 1976. Species densities of macrobenthos associated with seagrass: A field experimental study of predation. J. Mar. Res. 34, 577-592.

APPENDIX A

Size-Frequency Estimate Production Calculations

Seagrass—8 DEC TO 16 FEB

CLASS	8 DEC	22 DEC	5 JAN	19 JAN	2 FEB	16 FEB	SUM
1		9.7	27.5	25.3	15.1	73.3	150.9
2	7.7	27.6		34.7		5.7	75.7
3	7.7	9.7	21.0	5.3	15.1		58.8
4		4.1	6.5	14.7	23.3		48.6
5		4.1	27.5	14.7	8.1	12.4	66.8
6	14.3		12.9	9.3	23.3	12.4	72.2
7	7.7		6.5		15.1	12.4	41.7
8					8.1	5.7	13.8

$\bar{n}_j$ $(n\cdot m^{-2})$	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P $(mg\cdot m^{-2})$
25.2	12.6	0.08	1.01	8.1
12.6	2.8	0.28	0.78	6.3
9.8	1.7	0.70	1.19	9.5
8.1	-3.0	1.41	-4.23	-33.8
11.1	-0.9	2.48	-2.23	-17.9
12.0	5.1	4.00	20.40	163.2
6.9	4.6	6.04	27.78	222.3
2.3	2.3	8.68	19.96	159.7

$517.3 \times 0.75^{*} = 389.4\ mg\cdot m^{-2}$

* cohort adjustment factor

Seagrass—2 MAR TO 25 MAY

CLASS	2 MAR	16 MAR	30 MAR	13 APR	27 APR	11 MAY	25 MAY	SUM
1	16.7	72.8	394.7	742.9	152.6	325.8	457.7	2163.2
2	23.2		76.6	192.8	123.4	19.8	119.2	555.0
3	23.2	24.6	10.7	27.0	152.6	39.6	65.6	343.3
4	34.3	5.7	10.7	13.5	35.8	54.0	48.4	202.4
5	16.7	24.6				54.0	24.2	119.5
6		35.9	27.6	13.5	5.3	12.6	17.3	112.2
7	16.7		10.7	6.8		7.2		41.4
8		24.6	10.7					35.3
9			5.4					5.4

$\bar{n}_j$ ($n \cdot m^{-2}$)	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P ($mg \cdot m^{-2}$)
309.0	230.0	0.08	18.40	165.6
79.3	30.3	0.28	8.48	76.4
49.0	20.1	0.70	14.07	126.6
28.9	11.8	1.41	16.64	149.7
17.1	1.1	2.48	2.73	24.6
16.0	10.1	4.00	40.40	363.6
5.9	0.9	6.04	5.44	48.9
5.0	4.2	8.68	36.46	328.1
0.8	0.8	11.99	9.59	86.3

1369.8 x 2.5^{*}= 3412.5 $mg \cdot m^{-2}$

* cohort adjustment factor

Seagrass--8 JUN TO 23 NOV

CLASS	8 JUN	22 JUN	6 JUL	20 JUL	3 AUG	17 AUG	31 AUG
1	600.3	183.3	44.3	63.4	77.9	39.0	
2	279.0	113.3	24.6	6.1	45.0	45.9	
3	194.3	183.3	50.4	17.1	39.5	6.9	7.8
4	90.6	57.3	44.3	11.0		6.9	7.8
5	24.8	12.7	12.3				

CLASS	14 SEP	28 SEP	12 OCT	26 OCT	9 NOV	23 NOV	SUM
1	9.8			33.6	5.3	7.7	1056.9
2							513.9
3	4.5			8.3			512.1
4						7.7	217.9
5						7.7	49.6
6						30.0	30.3

$\bar{n}_j$ $(n \cdot m^{-2})$	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P $(mg \cdot m^{-2})$
81.9	42.4	0.08	3.39	17.0
39.5	0.1	0.28	0.03	0.1
39.4	22.1	0.70	15.47	77.3
17.3	12.9	1.41	18.19	90.9
4.4	2.1	2.48	5.21	26.0
2.3	2.3	4.00	9.20	46.0

$257.4 \times 5.6^{*} = 1441.6 \ mg \cdot m^{-2}$

* cohort adjustment factor

Females--Seagrass--8 DEC TO 16 FEB

CLASS	8 DEC	22 DEC	5 JAN	19 JAN	2 FEB	16 FEB	SUM
1		4.8	13.7	12.6	7.5	36.6	75.2
2	7.7	13.8		14.6		5.7	41.8
3		4.1	6.5	5.3	8.1		24.0
4		4.1	6.5	9.3	15.1		35.0
5			27.5	5.3	8.1	12.4	53.3
6					23.3	5.7	29.0
7					8.1	12.4	20.5

$\bar{n}_j$ $(n \cdot m^{-2})$	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P $(mg \cdot m^{-2})$
12.5	5.5	0.08	0.44	3.1
7.0	3.0	0.28	0.84	5.8
4.0	-1.8	0.70	-1.26	-8.8
5.8	-3.1	1.41	-4.37	-30.6
8.9	4.1	2.48	10.17	71.2
4.8	1.4	4.00	5.60	39.2
3.4	3.4	6.04	20.54	143.7

$223.7 \times 0.75^{*} = 167.7 \ mg \cdot m^{-2}$

* cohort adjustment factor

Females--Seagrass--2 MAR TO 25 MAY

CLASS	2 MAR	16 MAR	30 MAR	13 APR	27 APR	11 MAY	25 MAY	SUM
1	8.3	36.4	197.3	371.4	76.3	162.9	228.8	1081.4
2	5.6		30.3	113.3	67.7	12.6	62.2	291.7
3	23.2	12.3	10.7	6.8	70.3	27.0	24.2	174.5
4	11.1	5.7			11.9	32.4	29.4	90.5
5	11.1	12.3				32.4	12.1	67.9
6		18.0	27.6		5.3	7.2	12.1	70.2
7	16.7		10.7	6.8				34.2
8		5.7						5.7

$\bar{n}_j$ $(n \cdot m^{-2})$	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P $(mg \cdot m^{-2})$
154.5	112.8	0.08	9.02	72.2
41.7	16.8	0.28	4.70	37.6
24.9	12.0	0.70	8.40	67.2
12.9	3.2	1.41	4.51	36.1
9.7	-0.3	2.48	-0.74	-5.9
10.0	5.1	4.00	20.40	163.2
4.9	4.1	6.04	24.76	198.1
0.8	0.8	8.68	6.94	55.5

624.0 x 2.5* = 1560.1 $mg \cdot m^{-2}$

* cohort adjustment factor

Females--Seagrass--8 JUN TO 23 NOV

CLASS	8 JUN	22 JUN	6 JUL	20 JUL	3 AUG	17 AUG	31 AUG
1	300.1	91.6	22.1	31.7	38.9	19.5	
2	157.7	38.2	6.1		16.5	19.9	
3	109.5	76.4	12.3		16.5	6.9	7.8
4	42.4	25.4	24.6	6.1		6.9	
5	17.5						

CLASS	14 SEP	28 SEP	12 OCT	26 OCT	9 NOV	23 NOV	SUM
1	4.9			16.8	2.6	3.8	532.0
2							238.4
3	4.5			8.3			242.2
4						7.7	113.1
5						7.7	25.2
6						22.3	22.3

$\bar{n}_j$ ($n \cdot m^{-2}$)	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P ($mg \cdot m^{-2}$)
40.9	22.6	0.08	1.81	9.0
18.3	-0.3	0.28	-0.08	-0.4
18.6	9.9	0.70	6.93	34.6
8.7	6.8	1.41	9.59	47.9
1.9	0.2	2.48	0.50	2.5
1.7	1.7	4.00	6.80	34.0

$127.6 \text{ x } 5.6^{*} = 714.6 \text{ mg} \cdot \text{m}^{-2}$

* cohort adjustment factor

Males--Seagrass--8 DEC to 16 FEB

CLASS	8 DEC	22 DEC	5 JAN	19 JAN	2 FEB	16 FEB	SUM
1		4.8	13.7	12.6	7.5	36.6	75.2
2		13.8		20.0			33.8
3	7.7	4.1	12.9		8.1		32.8
4				5.3	8.1		13.4
5		4.1		9.3			13.4
6	14.3		12.9	9.3		5.7	42.2
7	7.7		6.5		8.1		22.3
8					8.1	5.7	13.8

$\bar{n}_j$ ($n \cdot m^{-2}$)	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P ($mg \cdot m^{-2}$)
12.5	6.9	0.08	0.55	4.4
5.6	0.1	0.28	0.03	0.2
5.5	3.3	0.70	2.31	18.5
2.2	0.0	1.41	0.00	0.0
2.2	-4.8	2.48	-11.90	-95.2
7.0	3.3	4.00	13.20	105.6
3.7	1.4	6.04	8.46	67.6
2.3	2.3	8.68	19.96	159.7

$260.8 \times 0.75^{*} = 195.6 \ mg \cdot m^{-2}$

* cohort adjustment factor

Males—Seagrass—2 MAR to 25 MAY

CLASS	2 MAR	16 MAR	30 MAR	13 APR	27 APR	11 MAY	25 MAY	SUM
1	8.3	36.4	197.3	371.4	76.3	162.9	228.8	1081.4
2	14.3		46.3	79.4	55.7	7.2	57.0	259.9
3		12.3		20.3	82.3	12.6	41.5	169.0
4	23.2		10.7	13.5	23.9	19.8	17.3	108.4
5	5.6	12.3				19.8	12.1	49.8
6		18.0		13.5		7.2	5.2	43.9
7						7.2		7.2
8		18.0	10.7					28.7
9			5.3					5.3

$\bar{n}_j$ $(n \cdot m^{-2})$	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P $(mg \cdot m^{-2})$
154.5	117.4	0.08	9.39	84.5
37.1	13.0	0.28	3.64	32.8
24.1	8.6	0.70	6.02	54.2
15.5	8.4	1.41	11.84	106.6
7.1	0.8	2.48	1.98	17.9
6.3	5.3	4.00	21.20	190.8
1.0	-3.1	6.04	-18.72	-168.5
4.1	3.3	8.68	28.64	257.8
0.8	0.8	11.99	9.59	86.3

$662.3 \times 2.5^{*} = 1655.8 \ mg \cdot m^{-2}$

* cohort adjustment factor

Males—Seagrass—8 JUN TO 23 NOV

CLASS	8 JUN	22 JUN	6 JUL	20 JUL	3 AUG	17 AUG	31 AUG
1	300.1	91.6	22.1	31.7	38.9	19.5	
2	121.2	76.4	18.4	6.1	27.4	26.0	
3	84.7	106.9	38.1	17.1	21.9		
4	48.2	31.8	18.4	6.1			7.8
5	5.8	12.7	12.3				
6							

CLASS	14 SEP	28 SEP	12 OCT	26 OCT	9 NOV	23 NOV	SUM
1	4.9			16.8	2.6	3.8	532.0
2							275.5
3							268.7
4							112.3
5							30.8
6						7.7	7.7

$\bar{n}_j$ ($n \cdot m^{-2}$)	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P ($mg \cdot m^{-2}$)
40.9	19.7	0.08	1.58	7.9
21.2	0.5	0.28	0.14	0.7
20.7	12.1	0.70	8.47	42.3
8.6	6.2	1.41	8.74	43.7
2.4	1.8	2.48	4.46	22.3
0.6	0.6	4.00	2.40	12.0

$129.0 \times 5.6^{*} = 722.2\ mg \cdot m^{-2}$

* cohort adjustment factor

Algae--8 DEC TO 23 NOV**

CLASS	8 DEC	22 DEC	5 JAN	19 JAN	2 FEB	16 FEB	2 MAR	16 MAR	30 MAR
1	16.4								
2			11.7				3.6		5.4
3			5.8				7.2		
4	16.4		17.3						
5	32.6		5.8				3.6		
6	16.4					11.7	3.6		

CLASS	13 APR	27 APR	11 MAY	25 MAY	8 JUN	22 JUN	6 JUL	SUM
1	107.7	215.3	1560.0	2477.4	966.8	242.9	288.0	5874.5
2		32.6	267.5	1358.3	463.3	202.4	63.0	2407.8
3	8.3	32.6	98.2	1219.4	354.6	404.7	72.0	2202.8
4	16.6	39.2	116.0	802.6	62.9	242.9		1313.9
5		58.7	53.4	370.5	11.1			535.7
6		26.1	8.9	77.1		40.5		184.3
7	16.6	6.5	8.9					32.0
8		6.5	8.9					14.4

$\bar{n}_j$ ($n \cdot m^{-2}$)	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P ($mg \cdot m^{-2}$)
225.9	133.3	0.08	10.66	85.3
92.6	7.9	0.28	2.21	17.7
84.7	34.4	0.70	24.08	192.6
50.3	29.7	1.41	41.88	335.0
20.6	13.5	2.48	33.48	267.8
7.1	5.9	4.00	23.60	188.8
1.2	0.6	6.04	3.62	29.0
0.6	0.6	8.68	5.20	41.7

1157.9 x 8.85* = 10247.4 $mg \cdot m^{-2} \cdot yr^{-1}$

* cohort adjustment factor

** _G_. _mucronatus_ not present 20 JUL to 23 NOV

Males--Algae--8 DEC TO 23 NOV**

CLASS	8 DEC	22 DEC	5 JAN	19 JAN	2 FEB	16 FEB	2 MAR	16 MAR	30 MAR
1	8.2								
2			8.8				3.6		2.7
3			5.9				3.6		
4			5.9						
5	16.4								
6						11.7			

CLASS	13 APR	27 APR	11 MAY	25 MAY	8 JUN	22 JUN	6 JUL	SUM
1	53.8	107.6	780.0	1238.5	483.4	121.4	144.0	2937.3
2		26.1	151.5	598.1	205.9	40.5	36.0	1073.2
3	8.3	6.5	44.5	517.0	177.4	81.0	9.0	866.8
4	8.3	6.5	53.4	385.8	28.6	121.6		616.9
5		19.5	8.9	223.8	11.4			287.3
6		13.1	8.9	61.8				95.5
7			8.9					8.9
8		6.5						6.5

$\bar{n}_j$ ($n \cdot m^{-2}$)	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P ($mg \cdot m^{-2}$)
113.0	71.7	0.08	5.7	45.9
41.3	8.5	0.28	2.4	19.0
32.8	9.3	0.70	6.5	52.1
23.5	12.7	1.41	17.9	143.3
10.8	7.1	2.48	17.6	140.9
3.7	3.4	4.00	13.6	108.8
0.3	0.0	6.04	0.00	0.0
0.3	0.3	8.68	2.6	20.8

$530.8 \times 8.85^{*} = 4697.6 \ mg \cdot m^{-2} \cdot yr^{-1}$

* cohort adjustment factor

** _G. mucronatus_ not present 20 JUL to 23 NOV

Females--Algae--8 DEC TO 23 NOV**

CLASS	8 DEC	22 DEC	5 JAN	19 JAN	2 FEB	16 FEB	2 MAR	16 MAR	30 MAR
1	8.2								
2			2.9						2.7
3							3.6		
4	16.4		11.7						
5	16.4		5.8				3.6		
6	16.4						3.6		
7									
8								8.5	

CLASS	13 APR	27 APR	11 MAY	25 MAY	8 JUN	22 JUN	6 JUL	SUM
1	53.8	107.6	780.0	1238.5	483.4	121.4	144.0	2937.3
2		6.5	115.9	760.1	257.4	161.9	27.0	1334.4
3		26.1	53.4	694.5	171.6	323.8	63.0	1336.0
4	8.3	32.6	63.3	409.0	34.3	121.4		697.0
5		39.2	44.5	138.9				248.4
6		13.1		15.5		40.5		89.1
7	16.6	6.5						23.1
8			8.9					17.4

$\bar{n}_j$ $(n \cdot m^{-2})$	# LOST BETWEEN CLASSES	WT. AT LOSS (mg)	WT. LOST (mg)	P $(mg \cdot m^{-2})$
113.0	61.7	0.08	4.9	39.5
51.3	-0.1	0.28	0.0	-0.2
51.4	24.6	0.70	17.2	137.8
26.8	17.2	1.41	24.3	194.0
9.6	6.2	2.48	15.4	123.0
3.4	2.5	4.00	10.0	80.0
0.9	0.2	6.04	1.2	9.7
0.7	0.7	8.68	6.1	48.6

632.3 x 8.85* = 5595.9 $mg \cdot m^{-2} \cdot yr^{-1}$

* cohort adjustment factor

** _G. mucronatus_ not present 20 JUL to 23 NOV

Literature Cited

Allen, K. R. 1949. Some aspects of the production and cropping of fresh waters. Rpt. Sixth Sci. Congr. 1947. Trans. R. Soc. N. Z. 77, 222-228.

Alon, N. C. and S. E. Stancyk. 1982. Variation in life-history of the grass shrimp *Palaemonetes pugio* in two South Carolina estuarine systems. Mar. Biol. 68, 265-276.

Banse, K. and S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. 50, 355-379.

Benke, A. C. 1979. A modification of the method for estimating secondary production with particular significance for multivoltine populations. Limnol. Oceanogr. 24, 168-171.

Biernbaum, C. K. 1981. Seasonal changes in the amphipod fauna of *Microciona prolifera* (Ellis and Solander) (Porifera: Demospongia) and associated sponges in a shallow salt-marsh creek. Estuaries 4, 85-96.

Birklund, J. 1977. Biomass, growth and production of the amphipod *Corophium insidiosum* Crawford, and preliminary notes on *Corophium volutator* (Pallas). Ophelia 16, 187-203.

Borowsky, B. 1980. Reproductive patterns of three intertidal salt-marsh gammaridean amphipods. Mar. Biol. 55, 327-334.

Bousfield, E. L. 1969. New records of *Gammarus* (Crustacea: Amphipoda) from the middle Atlantic region. Ches. Sci. 10, 1-17.

Bousfield, E. L. 1973. Shallow-water Gammaridean Amphipoda of New England. Cornell Univ. Press, Ithaca, N.Y. 312pp.

Casabianca, M. -L., de. 1975. Methode de calcul de la production par estimation de la mortalite. Application a une population a structure complexe du crustace *Corophium insidiosum* Crawford (Lagune de Biguglia, Corse). -C. r. Hebd. Seanc. Acad. Sci., Paris 280, 1139-1142.

Clarke, A. 1982. Temperature and embryonic development in polar marine invertebrates. Int. J. Invert. Repro. 5, 71-82.

Cooper, W. E. 1965. Dynamics and production of a natural population of a fresh water amphipod, Hyalella azteca. Ecol. Monogr. 35, 377-394.

Cummins, K. W. and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. int. Ver. Limnol. 18, 1-158.

Dessaix, J. and A. L. Roux. 1980. Structure and dynamics of the French upper Rhone ecosystems. X. An estimate of the secondary production of gammarids in the main stream. Crustaceana Suppl. 6, 242-252.

Diaz, R. J. and T. J. Fredette. 1982. Secondary production of some dominant macroinvertebrate species inhabiting a bed of submerged vegetation in the lower Chesapeake Bay. In, Structural and functional aspects of the biology of submerged aquatic macrophyte communities in the lower Chesapeake Bay, by R. L. Wetzel, K. L. Webb, P. A. Penhale, R. J. Orth, D. F. Boesch, G. W. Boehlert and J. V. Merriner. Final Report EPA/CBP Grant No. R805974.

Dickinson, J. J., R. L. Wigley, R. D. Brodeur and S. Brown-Leger. 1980. Distribution of gammaridean amphipoda (Crustacea) in the Middle Atlantic Bight region. U.S. Dept. of Commerce. NOAA Tecnical Report NMFS SSRF-741, 46 pp.

Doyle, R. W. and W. Hunte. 1981. Genetic changes in "fitness" and yield of a crustacean population in a controlled environment. J. Exp. Mar. Biol. Ecol. 52, 147-156.

Edmondson, W. T. and G. G. Winberg (Eds). 1971. A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. IBP Handbook No 17, Blackwell Sci. Publ., Oxford, England.

Fredette, T. J. 1983. Chapter 1. In, Life history and secondary production of the crustacean Gammarus mucronatus Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats. Ph.D. dissertation. The College of William and Mary, Williamsburg, Va.

Fredette, T. J. 1983. Chapter 2. In, Life history and secondary production of the crustacean Gammarus mucronatus Say (Amphipoda: Gammaridae) in warm temperate estuarine habitats. Ph.D. dissertation. The College of William and Mary, Williamsburg, Va.

Gable, M. F. and R. A. Croker. 1977. The salt marsh amphipod, Gammarus palustris Bousfield, 1969 at the northern limit of its distribution. I. Ecology and life cycle. Estuar. Coastal Mar. Sci. 5, 123-134.

Goedmakers, A. 1981. Population dynamics of three gammarid species (Crustacea, Amphipoda) in a French chalk stream. Part II. Standing crop. Bijdr. Dierk. 51, 31-69.

Hamilton, A. L. 1969. On estimating annual production. Limnol. Oceanogr. 13, 771-782.

Harding, J. P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. J. Mar. Biol. Assoc., U.K. 28, 141-153.

Hastings, M. H. 1981. The life cycle and productivity of an intertidal population of the amphipod Ampelisca brevicornis. Estuar. Coastal Shelf Sci. 12, 665-667.

Heck, K. L., Jr. and R. J. Orth. 1980. Structural components of eelgrass (Zostera marina) meadows in the lower Chesapeake Bay - Decapod Crustacea. Estuaries 3, 289-295.

Howard, R. K. 1982. Impact of feeding activities of epibenthic amphipods on surface-fouling of eelgrass leaves. Aquat. Bot. 14, 91-97.

Hughes, J. E. 1982. Life histoey of the sandy-beach amphipod Dogielinotus loquax (Crustacea: Dogielinotidae) from the outer coast of Washington, USA. Mar. Biol. 71, 167-175.

Humphreys, W. F. 1979. Production and respiration in animal populations. J. Anim. Ecol. 48, 427-453.

Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 57, 344-388.

Hynes, H. B. N. and Coleman, M. J. 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. 13, 569-573.

Klein, G., E. Rachor and S. A. Gerlach. 1975. Dynamics and productivity of two populations of the benthic tube-dwelling amphipod Ampelisca brevicornis (Costa) in Helgoland Bight. Ophelia 14, 139-159.

Krebs, C. J. 1978. A review of the Chitty Hypothesis of population regulation. Can. J. Zool. 56, 2463-2480.

Krishnan, L. and P. A. John. 1974. Observations on the breeding biology of Melita zeylanica Stebbing, a brackish water amphipod. Hydrobiol. 44, 413-430.

Krueger, C. C. and F. B. Martin. 1980. Computation of confidence intervals for the size-frequency (Hynes) method of estimating secondary production. Limnol. Oceanogr. 25, 773-777.

Lapchin, L. and A. Neveu. 1980. The production of benthic invertebrates: comparison of different methods. II - Application to the benthos of the Nivelle River (Pyrenees-Atlantiques, France). Ecol. Gener. 1, 359-372.

Macko, S. A., W. Y. Lee and P. L. Parker, 1982. Nitrogen and carbon isotope fractionation by two species of marine amphipods: laboratory and field studies. J. Exp. Mar. Biol. Ecol. 63, 145-149.

Mann, K. H. 1969. The dynamics of aquatic ecosystems. Adv. Ecol. Res. 6, 1-81.

Marchant, R. and H. B. N. Hynes. 1981. The distribution and production of Gammarus pseudolimnaeus (Crustacea: Amphipoda) along a reach of the Credit River, Ontario. Fresh. Biol. 11, 169-182.

Marsh, G. A. 1973. The Zostera epifaunal community in the York River, Virginia. Ches. Sci. 14, 87-97.

Martien, R. F. and A. C. Benke. 1977. Distribution and production of two crustaceans in a wetland pond. American Midl. Natur. 98, 162-175.

McNeill, S. and J. H. Lawton. 1970. Annual production and respiration in animal populations. Nature, London 255, 472-474.

Menzie, C. A. 1980. A note on the Hynes method of estimating secondary production. Limnol. Oceanogr. 25, 770-773.

Menzie C. A. 1981. Production ecology of Cricotopus sylvestris (Fabricius) (Diptera: Chironomidae) in a shallow estuarine cove. Limnol. Oceanogr. 26, 467-481.

Meyer, C. E. 1982. Zooplankton communities in Chesapeake Bay seagrass systems. M.A. thesis. The College of William and Mary, Williamsburg, Virginia. 96 pp.

Moller, P. and R. Rosenberg. 1982. Production and abundance of the amphipod Corophium volutator on the west coast of Sweden. Neth. J. Sea Res. 16, 127-140.

Nair, K. K. C. and K. Anger. 1979. Experimental studies on the life of Jassa falcata (Crustacea, Amphipoda). Helgo. Wiss. Meeres. 32, 444-452.

Nelson, W. G. 1979. Experimental studies of selective predation on amphipods: consequences for amphipod distribution and abundance. J. Exp. Mar. Biol. Ecol. 38, 225-245.

Nelson, W. G. 1979. An analysis of structural pattern in an eelgrass (Zostera marina L.) amphipod community. J. Exp. Mar. Biol. Ecol. 39, 231-264.

Nelson, W. G. 1980. A comparative study of amphipods in seagrasses from Florida to Nova Scotia. Bull. Mar. Sci. 30, 80-89.

Nelson, W. G. 1980. Reproductive patterns of gammaridean amphipods. Sarsia 65, 61-71.

Nelson, W. G. 1981. Experimental studies of decapod and fish predation on seagrass macrobenthos. Mar. Ecol. Prog. Ser. 5, 141-149.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent. 1975. Statistical Package for the Social Sciences. McGraw-Hill, Inc. N.Y., N.Y. 675pp.

Omori, K., M. Tanaka and T. Kikuchi. 1982. Seasonal changes of short-term reproductive cycle in Corophium volutator (Crustacea: Amphipoda). - Semi-lunar or lunar cycle? Publ. Amakusa Mar. Biol. Lab. 6, 105-117.

Orth, R. J., K. A. Moore and H. H. Gordon. 1979. Distribution and abundance of submerged aquatic vegetation in the lower Chesapeake Bay, Va. E.P.A. Rep. No. 600/8-79/029/SAV 1.

Orth, R. J. and K. L. Heck, Jr. 1980. Structural components of eelgrass (Zostera marina) meadows in the lower Chesapeake Bay--Fishes. Estuaries 3, 278-288.

Orth, R. J. and K. A. Moore. 1982. The biology and propagation of Zostera marina, eelgrass, in the Chesapeake Bay, Virginia. Virginia Institute of Marine Science, Special Report 265, Applied Marine Science and Ocean Engineering. 187 pp.

Rees, C. P. 1975. Life cycle of the amphipod Gammarus palustris Bousfield. Estuar. Coastal Mar. Sci. 3, 413-419.

Ricker, W. E. 1946. Production and utilization of fish populations. Ecol. Monogr. 16, 373-391.

Ricker, W. E. 1968. Methods for Assessment of Fish Production in Fresh Waters. IBP Handbook No. 3, Blackwell Sci. Publ. Oxford, England.

Robertson, A. I. 1979. The relationship between annual production: biomass ratios and lifespans for marine macrobenthos. Oecologia 38, 193-202.

Savage, A. A. 1982. The survival and growth of Gammarus tigrinus Sexton (Crustacea: Amphipoda) in relation to salinity and temperature. Hydrobiol. 94, 201-212.

Snedecor, G. W. and W. G. Cochran. 1976. Statistical Methods. The Iowa State University Press, Ames, Iowa. 593pp.

Sokal R. R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman and Co. San Franciso. 859pp.

Southwood, T. R. E. 1976. Bionomic strategies and population parameters. In, R. M. May (Ed), Theoretical Ecology, W. B. Saunders Co., Philadelphia, p. 26-48.

Steele, D. H. 1973. The biology of Parhyalella pietschmanni Schellenberg, 1938 (Amphipoda, Hyalellidae) at Nosy Be, Madagascar. Crustaceana 25, 276-280.

Steele, D. H. and V. J. Steele. 1969. The biology of Gammarus (Crustacea, Amphipoda) in the northwestern Atlantic. I. Gammarus duebeni Lillj. Can. J. Zool. 47, 235-244.

Steele, D. H. and V. J. Steele. 1973. The biology of Gammarus (Crustacea, Amphipoda) in the northwestern Atlantic. VII. The duration of embryonic development in five species at various temperatures. Can J. Zool. 51, 995-999.

Steele, D. H. and V. J. Steele. 1975. The biology of Gammarus (Crustacea, Amphipoda) in the northwestern Atlantic. XI. Comparison and discussion. Can. J. Zool. 53, 1116-1126.

Stoner, A. W. 1979. Species specific predation on amphipod crustacea by pinfish (Lagadon rhomboides): Mediation by macrophyte standing crop. Mar. Biol. 55, 210-207.

Stoner, A. W. 1980. Abundance, reproductive seasonality and habitat preferences of amphipod crustaceans in seagrass meadows of Apalachee Bay, Florida. Contrib. Mar. Sci. 23, 63-77.

Stoner, A. W. 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. Bull. Mar. Sci. 30, 537-551.

Strong, K. W. and G. R. Daborn. 1979. Growth and energy utilisation of the intertidal isopod Idotea baltica (Pallas) (Crustacea: Isopoda). J. Exp. Mar. Biol. Ecol. 41, 101-123.

Uye, S. 1982. Population dynamics of Acartia clausi Giesbrecht (Copepoda: Calanoida) in inlet waters. J. Exp. Mar. Biol. Ecol. 57, 55-83.

Van Dolah, R. F. 1978. Factors regulating the distrubution and population dynamics of the amphipod Gammarus palustris in an intertidal salt marsh community. Ecol. Monogr. 48, 191-217.

Van Dolah, R. F. and E. Bird. 1980. A comparison of reproductive patterns in epifaunal and infaunal gammaridean amphipods. Estuar. Coastal Mar. Sci. 11, 593-604.

Van Dolah, R. F., L. E. Shapiro and C. P. Rees. 1975. Analysis of an intertidal population of the amphipod Gammarus palustris using a modified version of the egg-ratio method. Mar. Biol. 33, 323-330.

van Maren, M. J. 1978. Distribution and ecology of Gammarus tigrinus Sexton, 1939 and some other amphipod crustacea near Beaufort (North Carolina, U.S.A.). Bijdr. Dierk. 48, 46-56.

Vassallo, L. and D. H. Steele. 1980. Survival and growth of young Gammarus lawrencianus Bousfield, 1956, on different diets. Crustaceana Suppl. 6, 118-125.

Venables, B. J. 1981. Aspects of the population biology of a Venezuelan beach amphipod, Talorchestia margaritae (Talitridae), including estimates of biomass and daily production, and respiration rates. Crustaceana 41, 271-285.

Vijverberg, J. and A. F. Richter. 1982. Population dynamics and production of Daphnia hyalina Leydig and Daphnia cucullata Sars in Tjeukemeer. Hydrobiol. 95, 235-259.

Warwick, R. M. 1980. Population dynamics and secondary production of benthos. In, K. R. Tenore and B. C. Coull (Eds.), Marine Benthic Dynamics. Univ. S. Carolina Press, Columbia, S. C. 451pp.

Waters, T. F. 1977. Secondary production in inland waters. Adv. Ecol. Res. 14, 91-164.

Waters, T. F. 1979. The turnover ratio in production ecology of freshwater invertebrates. Am. Nat. 103, 173-185.

Waters, T. F. 1979. Influence of benthos life history upon the estimation of secondary production. J. Fish. Res. Board Can. 36, 1425-1430.

Waters, T. F. and J. C. Hokenstrom. 1980. Annual production and drift of the stream amphipod Gammarus pseudolimnaeus in Valley Creek, Minnesota. Limnol. Oceanogr. 25, 700-710.

Watling, L. and D. Maurer. 1972. Marine shallow water amphipods of the Delaware Bay area, U.S.A. Crustaceana Suppl. 3, 251-266.

Wildish, D. J. 1982. Evolutionary ecology of reproduction in gammaridean Amphipoda. Int. J. Invert. Repro. 5, 1-19.

Wildish. D. J. and D. Peer. 1981. Methods for estimating secondary production in marine Amphipoda. Can. J. Fish. Aquat. Sci. 38, 1019-1026.

Williams, A. B. and K. H. Bynum. 1972. A ten-year study of meroplankton in North Carolina estuaries: amphipods. Ches. Sci. 13, 175-192.

Wulff, B. L. and K. L. Webb. 1969. Intertidal zonation of marine algae at Gloucester Point, Virginia. Ches. Sci. 10, 29-35.

Young, D. K., M. A. Buzas and M. W. Young. 1976. Species densities of macrobenthos associated with seagrass: A field experimental study of predation. J. Mar. Res. 34, 577-592.

Zimmerman. R., R. Gibson and J. Harrington. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Mar. Biol. 54, 41-47.

VITA

THOMAS JOSEPH FREDETTE

Born in Gardner, Massachusetts, 18 January 1955. Graduated from Narragansett Regional High School in Baldwinville, Massachusetts in June 1973. Received a B. S. in Marine Biology from Southeastern Massachusetts University, North Dartmouth, Massachusetts, June 1977. Received an M. A. in Marine Science from The College of William and Mary, August 1980. Entered the Ph. D. program in Marine Science at the College of William and Mary, September 1980. Held research and teaching assistantships in the Department of Invertebrate Ecology, Virginia Institute of Marine Science 1978 to present.