

1991

Population Biology of the polychaete *Loimia medusa* (Savigny) on a Tidal Sand Flat of the York River, Chesapeake Bay

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**POPULATION BIOLOGY OF THE POLYCHAETE LOIMIA MEDUSA (SAVIGNY)
ON A TIDAL SAND FLAT OF THE YORK RIVER, CHESAPEAKE BAY**

A Thesis

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
Master of Arts

by

Rochelle Diane Seitz

1991

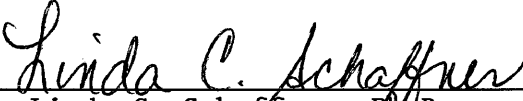
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Master of Arts

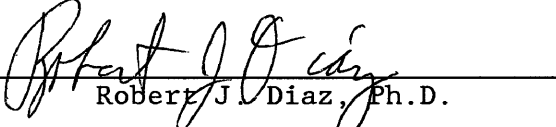


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Approved, August 1991



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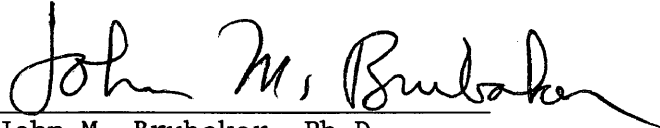
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DEDICATION

To my parents, Roger and Janet

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ACKNOWLEDGEMENTS

I wish to thank all of those who helped make this thesis a reality. I am grateful to my advisor, Linda Schaffner, who provided support and continually pushed me to do my best. I also wish to express my gratitude to the members of my thesis committee Bob Diaz, Mark Luckenbach, Roger Mann and John Brubaker for their review of this thesis as well as for their guidance and constructive input.

I would like to thank those who generously helped me with field collections, especially Marty Cavalluzzi, Joe Neubauer and Stephanie Leyland. Thanks also to the staff and students in the Benthic Ecology department who helped me along the way, and to Gary Anderson in the computer center and Billy Jenkins in the photo lab. I am also grateful to Marilyn Mayer for her helpful review of this thesis and a shared enthusiasm for *Loimia*.

Thanks to my parents for their patience, encouragement and interest in my endeavors.

I wish to give special thanks to Marty who not only helped me in the field and reviewed this manuscript, but who also was a constant source of optimism, companionship, and energy during my graduate studies.

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ABSTRACT

The terebellid polychaete *Loimia medusa* (Savigny) is a prominent, relatively large member of many soft bottom communities in Chesapeake Bay as well as other temperate waters. This study quantifies its population ecology on a tidal flat of the York River, Virginia. Monthly sampling over a year revealed average densities of 3 to 60 individuals m^{-2} . Abundances were highest in August through September when settlement occurred. Two cohorts recruited to the population in summer. Growth was temporally variable; in winter, growth was approximately 0.10 mm in head width per month (with a mean change in weight of 0.01 g in 4 months), and in summer immediately after settlement, growth of a new cohort was approximately 2 mm in head width (mean change in weight of 0.01 g) per month. Adults were reproductively active May through October. Larvae were released to the water column and spent less than one month in the plankton. New recruits attained sexual maturity within two months of settlement. Fecundity was high with the number of oocytes per segment ranging from 201 to 15,840. Secondary production was high at 3.3 g AFDW $m^{-2} yr^{-1}$ and the P/B ratio was 3.0. *Loimia medusa* appears to have a life span of approximately one year. It shows properties of both opportunistic and equilibrium species. It can recruit in relatively large numbers (compared with the adult population), grow rapidly, and exhibit high secondary production, as an opportunist does. It also exhibits characteristics typical of equilibrium species such as relatively few reproductive cycles per year, a life span of one year, and large body size. The suite of life history characteristics displayed by *Loimia medusa* render it well adapted for estuarine existence. Rapid growth of juveniles may provide a survival advantage as animals can exploit existing conditions. Numerous settlement events during a single summer and early fall provide multiple opportunities to recruit to benthic habitats, including those disturbed by low oxygen stress. Fast growth, combined with adult tolerance to hypoxia may lead to *Loimia medusa*'s dominance throughout Chesapeake Bay.

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INTRODUCTION

Community dynamics are driven by the fluctuations of resident species, interactions among species, as well as environmental changes (Menge and Sutherland 1987). An important aspect of this is the demographics of individual species and their life histories (Whittaker and Goodman 1979, Sousa 1980, Zajac and Whitlatch 1989). A life history tactic, defined by Stearns (1976) as "a set of coadapted traits designed, by natural selection, to solve particular ecological problems", can reveal a great deal about an organism's relationship with its environment.

Depending on its life history tactic, a species can be classified along a continuum between opportunistic and equilibrium (Grassle and Grassle 1974, McCall 1977, Pearson and Rosenberg 1978). Opportunistic species are those that respond quickly to disturbance; they usually are small, short-lived (i.e. months) and reproduce frequently (Grassle and Grassle 1974). Equilibrium species are those that represent the climax community; they tend to be found in fairly predictable environments and are typically large, long-lived (i.e. years) species with slower development and annual reproductive cycles (Pianka 1970, McCall 1977).

Polychaetes are the dominant taxa in most marine and estuarine soft-bottom communities, thus, the demography of field populations of polychaetes will aid in our understanding of community ecology. Polychaete life history involves a series of distinct events, as

described by Fauchald (1983): spawning and fertilization, pre-release development, the larval stage (planktonic or not), metamorphosis, establishment in the adult habitat, growth, gamete maturation, spawning, and finally death. Strategies for these events differ depending on the species and may vary between populations of the same species.

Capitella capitata and *Streblospio benedicti* are classic examples of opportunistic species. They both exhibit small body size (1-10 mm in length), short generation time, early reproduction, and brood protection (Grassle and Grassle 1974, Levin 1984). Individual *C. capitata* can produce one or several broods, in contrast to most opportunists which have a single reproductive effort each generation (Pianka 1970). Opportunistic species typically have a high rate of increase in abundance followed by a sharp decline, and show high mortality. They are usually temporally and spatially patchy since they are common in disturbed areas (Pearson and Rosenberg 1978).

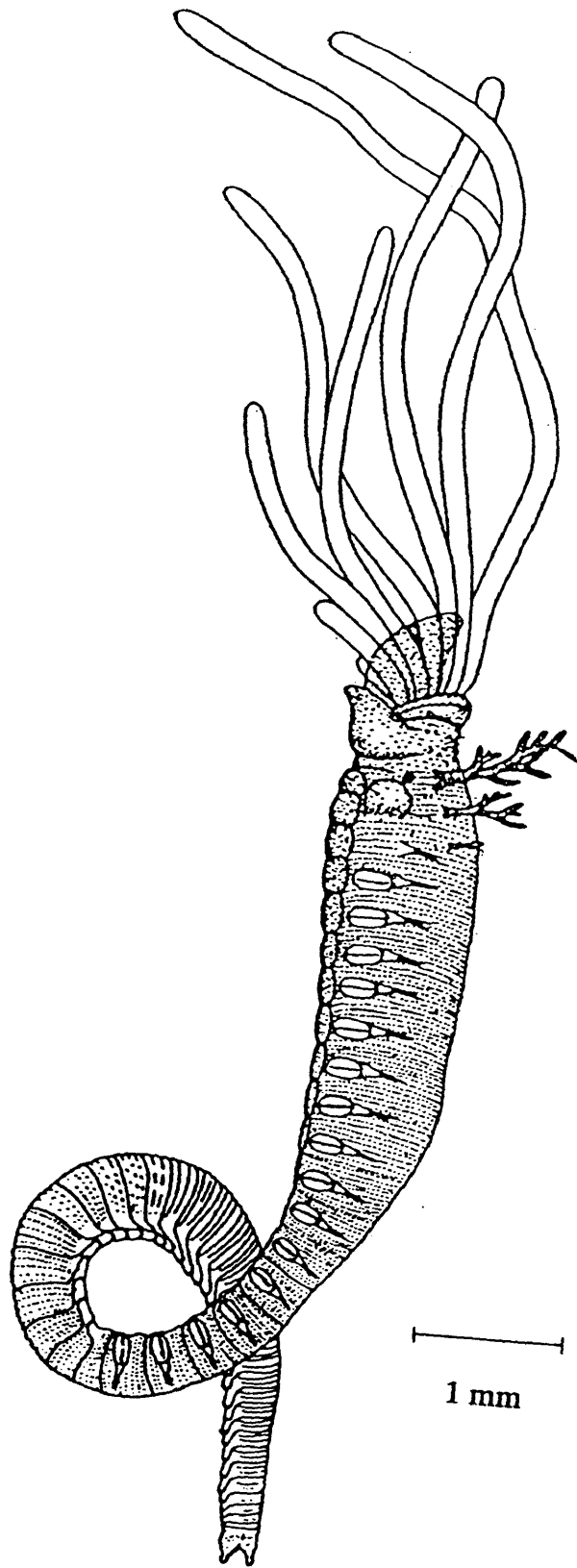
In contrast, other species such as the pectinarid *Pectinaria californiensis* (Nichols 1975), the nephtids *Nephtys hombergii* and *N. caeca* (Olive 1977, Zajac and Whitlatch 1989), the ampharetid *Ampharete acutifrons* and the terebellid *Amaena occidentalis* (Fauchald 1983) are annual breeders. Following the general pattern of annual breeders, these species exhibit large reproductive efforts, produce moderately large eggs, and release planktotrophic larvae (Guillou and Hily 1983). In the harbor of Brest, France, the ampharetid, *Melinna palmata* is an annual spawner that has an extended spawning period (August through October) with larval settlement in fall and early winter (Guillou and Hily 1983). The terebellid *Nicolea zostericola*, reproduces

annually from mid-April, after a rise in seawater temperature, to early July (Eckelbarger 1974).

Other characteristics of equilibrium species such as long life, multiple spawning, and delayed breeding are also displayed by some of these polychaetes. For example, *Nephtys hombergii* and *N. caeca* survive to 5 and 7 years of age respectively (Olive 1977). A single generation of nephtids may release larvae into the water column for three consecutive years. *Pectinaria californiensis* survives to 4 years of age (Nichols 1975). In the terebellid *Eupolyornia nebulosa*, there is a long period of immaturity, and breeding is delayed until the second year of life (Bhaud 1988a).

The terebellid polychaete *Loimia medusa* (Savigny) is common and abundant in Chesapeake Bay (Holland et al. 1986, Dauer et al. 1989, Schaffner 1990) as well as other temperate to tropical oceans worldwide (Wilson 1928, Day 1967), yet, little is known of its demographics. *L. medusa* is a large polychaete with adults reaching approximately 10 cm in length (Fig. 1). It is a sedentary tube-dweller which surface deposit feeds by extending numerous buccal tentacles up to 30 cm across the sediment surface (Llanos 1990). The adults actively irrigate U-shaped tubes which penetrate down to 15 cm in the sediment. The tubes are well-oxygenated and have a significant effect on sediment chemistry (M. Mayer personal communication). These tubes also house commensal organisms (personal observation) similar to *Chaetopterus* (Schaffner 1990). Therefore *Loimia medusa* has the potential to affect both the structure and function of the surrounding community.

Figure 1. Juvenile *Loimia medusa* approximately 10 mm in length
(adapted from Wilson 1928).

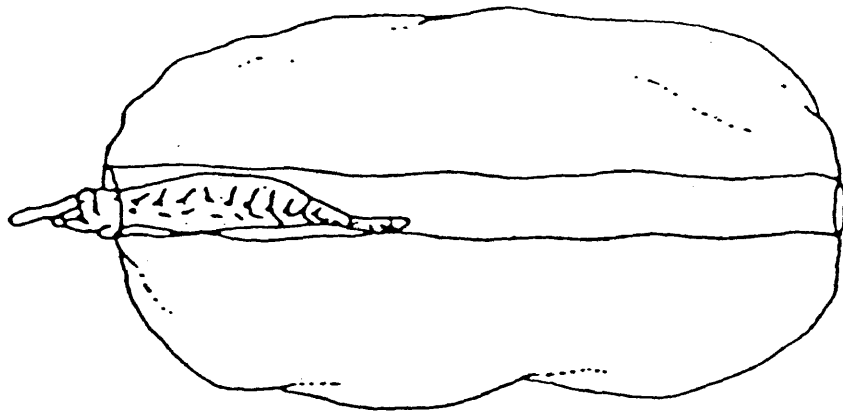


Wilson (1928) first recognized *L. medusa* larvae in gelatinous cases (Fig. 2) in spring plankton tows from British waters near Plymouth. Based on morphological similarity to *Lanice conchilega*, Bhaud (1988b) proposed that there are two planktonic stages in the life cycle of *L. medusa*. The first of these is a trochophore-metatrochophore stage with a following short-lived intermediate benthic stage. Then there is a second planktonic stage, an aulophore (which settles after approximately 60 days), which is similar in morphology to the late benthic stage in other terebellids such as *Eupolyornia nebulosa* (Bhaud 1988b). The form described by Wilson (the relatively large larva in the gelatinous case) corresponds to the aulophore, the second planktonic stage in the scheme proposed by Bhaud. Both genera *Lanice* and *Loimia* possess statocysts and therefore are expected to have long planktonic stages (Thorson 1946).

According to Wilson's study (1928), the larva leaves the gelatinous case and settles when it reaches approximately 7.5 mm total length (including the longest tentacle). In Wilson's laboratory experiments, larvae settled after three months, however, he suggested that in the field the development may be quicker. Upon settlement, the worms immediately begin to build a sandy tube. Other aspects of the population biology of *L. medusa* are poorly studied.

Closely related species often share life history characteristics, thus, the features of one species' life history may be used to predict that of a related species (Spight et al. 1974). The family Terebellidae, however, exhibits large variability in spawning behavior, larval ecology, and reproductive morphology (Smith 1989). *Eupolyornia*

Figure 2. Planktonic larval *Loimia medusa* approximately 1 mm in length inside gelatinous case (adapted from Wilson 1928).



1 mm

nebulosa exhibits several peaks in spawning activity each spring and has continuous iteroparous production (Bhaud and Gremare 1991). The larvae have a short planktonic or mainly benthic existence. In a Nahant, Massachusetts population of *Nicolea zostericola*, annual spawning occurs over a three month period and eggs are deposited in cocoons, where development occurs. Somatic growth is slow in fall and winter but there is a large increase one month before spawning (Eckelbarger 1974). Conversely, a related terebellid, *Lanice conchilega* has a planktonic larva and a juvenile which develops in a tube. The juveniles in a population from French waters show a minor peak in abundance in June and a major occurrence in August-September (Bhaud 1988a). The features of the life histories of other terebellids are so varied, that they provide little insight for *Loimia medusa*.

The specific objectives of this study were to quantify population characteristics including density, age-structure, reproductive activity, growth, and production for the polychaete *Loimia medusa* at a site in the York River, a sub-estuary of Chesapeake Bay, Virginia. This work results in a greater understanding of the life history, ecology, distribution and abundance of this species and its role in estuarine communities of Chesapeake Bay.

METHODS

Study Area

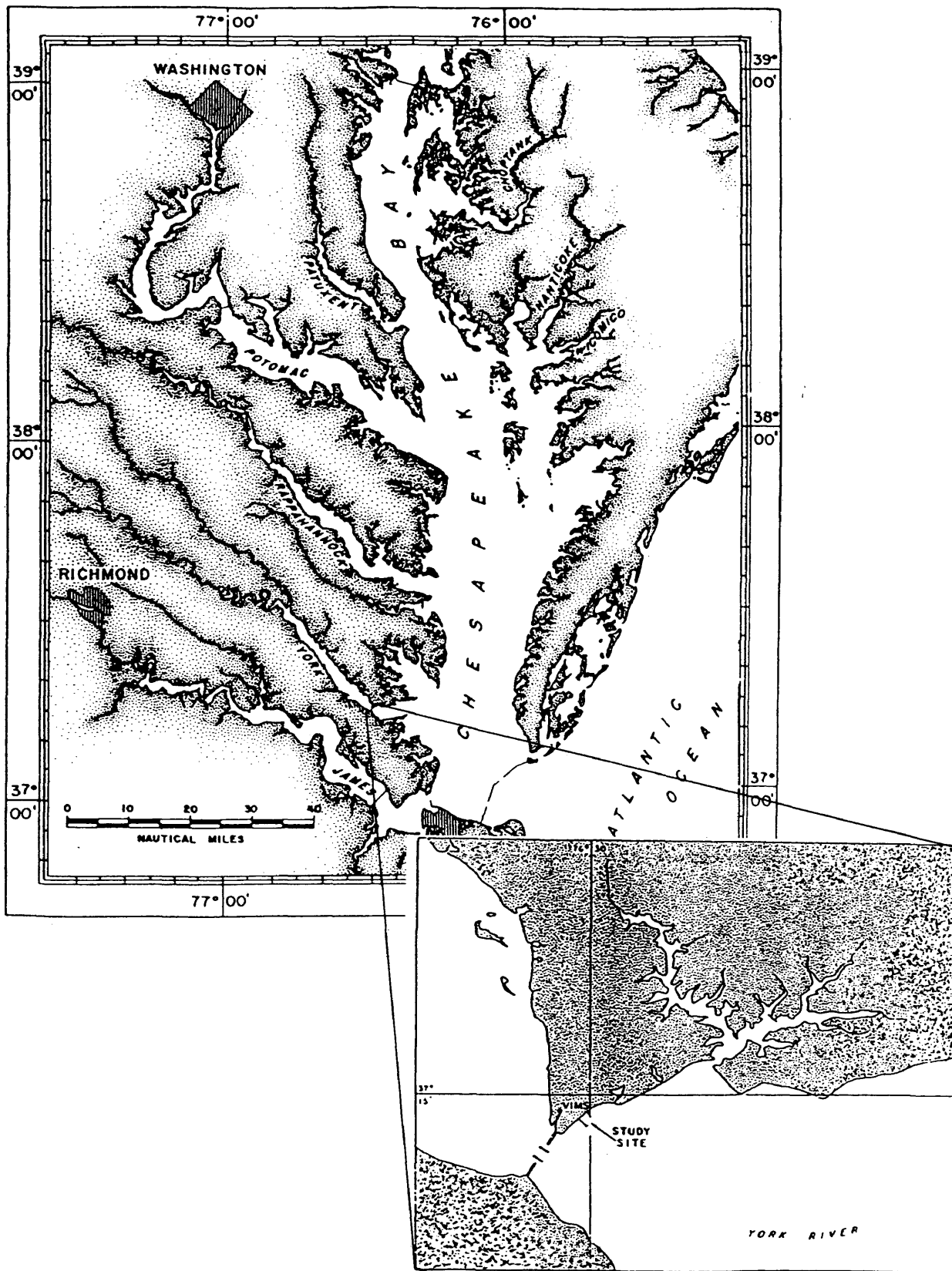
Field studies were conducted on an intertidal to shallow subtidal (0-1.4 m at mean low water) sand flat in the York River, a sub-estuary of Chesapeake Bay (Virnstein 1977) (Fig. 3). Salinity typically ranges from 17 to 25 ppt and temperatures range from 0 to 30°C (Virnstein 1976). Sediments are fine to medium sands (Skrabal 1987). The semidiurnal tide has a range of approximately 0.7 m at mean tide (United States Department of Commerce 1990). The benthic fauna is dominated by polychaetes, and *Loimia medusa* is prominent in this community (Virnstein 1976, L. Schaffner personal communication).

Studies of larvae

To determine the initiation of spawning, plankton was sampled at 2-7 day intervals from June 1989 to December 1990, following the method of Luckenbach (1984). Plankton samples were taken with a 125 μm mesh plankton net fitted to a steel ring 50 cm in diameter. The net was deployed from a pier at the north end of the flat for 3-4 hour periods over flood or ebb tide during daytime hours.

Plankton samples were washed into dishes and examined live for the presence of *Loimia medusa* larvae. Each larva, placed into a small dish that contained filtered seawater and sieved and sterilized

Figure 3. Location of study site on the York River, Chesapeake Bay, Virginia. Enlargement shows location of sand flat at the Virginia Institute of Marine Science.



sediment, was then maintained in an incubator at 20°C. Unfiltered seawater was added to each dish to allow larvae to feed on other plankton. A slurry of fine sediment and water, on which larvae could feed after settlement, was also added. Water was changed daily.

Larvae were removed from the incubator once a week and measured for total length and maximum head width using a dissecting microscope fitted with an ocular micrometer. These measurements were used to calculate growth. In addition, the number of tentacles present, date of initial branchiae development, duration of time in gelatinous case and date of initiation of tube building were recorded.

The remaining material from plankton samples was saved and preserved with 10% buffered formalin with added Rose Bengal stain. To estimate the efficiency of the live examination method, preserved and stained samples for 21 sampling dates were reexamined. These counts showed that, on average, the live examination method was 50% (SD = 24%) effective in detecting *L. medusa* larvae, thus, all live counts were doubled except those for which preserved samples were directly enumerated.

Larval abundance differences between lunar quarters were compared with a one-way analysis of variance (ANOVA) (Ryan et al. 1985) and a Tukey multiple comparison test (Zar 1984, van Montfrans et al. 1990). For the purposes of this analysis, lunar quarters were defined as new moon (date of new moon and 3 days before and after), first quarter (date of first quarter and 3 days before and after), full moon (date of full moon and 3 days before and after), and last quarter (date of last quarter and 3 days before and after).

Infaunal Sampling

In October 1989, quantitative infaunal sampling began and 12 random subtidal samples were taken each month (except for October and November 1989, see below) until October 1990. The subtidal sampling consisted of three 30-meter shore-perpendicular transects layed out at random locations along-shore on the subtidal flat (one transect was sampled in October 1989, two in November 1989, and three in subsequent months). Along each transect, four random distances from the base (at approximately MLW) were chosen for extracting a benthic faunal sample of 0.1 m² in area to a sediment depth of 20 cm. This was accomplished using a small suction dredge with a 500 μm mesh bag fitted to the outflow. Material retained in each sample bag was fixed in 10% buffered formalin with added Rose Bengal stain.

The sample size needed to determine the mean population width to a known precision was estimated by iteration of the equation:

$$N = \frac{SD^2 \times t^2_{\alpha=.05(2)(n-1)} \times F_{\beta=.10(1)(n-1),v}}{d^2}$$

(Zar 1984) (SD = standard deviation of sample obtained from initial sampling in October, d = minimum detectible difference in width, α = alpha, β = beta, v = n - k, k = number of treatments, n = number of samples) which resulted in a sample size (N) of 12. After November 1989, changes in the population of *L. medusa* were followed by taking twelve random samples each month until October 1990. No sampling was conducted in December 1989.

To further assess patterns of small-scale distribution, two transects were visually inspected by free diving on November 14, 1989 and *L. medusa* tubes observed within 10 cm to either side of the transects were counted. The number of tube tops observed within each meter of transect were delineated. Using Morisita's Index of Dispersion (Elliott 1977), the number of tube tops per meter was compared to the average number that each meter would contain if each had the same number of tube tops. The index would equal one for a random distribution, would be greater than one for a contagious distribution, and would be less than one for a regular distribution.

Because of the limitations of the suction dredge (it cannot be used in areas with less than approximately 20 cm of water), each month, beginning in January 1990, two additional 30 m shore-parallel transects used to position additional collections (intertidal samples). These transects were placed at random locations 10 m or less below approximately mean water level in the intertidal area. *L. medusa* sighted within 10 cm to either side along each transect were removed with a hand-held can-core of 0.02 m² area and individually fixed as described above.

In the laboratory, samples were processed to obtain data on abundance, population size-structure and reproductive condition of *L. medusa*. Length from the head to the 17th thoracic setiger, width of the third setiger, and maximum head width of each *L. medusa* was measured using a dissecting microscope equipped with an ocular micrometer. Width measurements were chosen as the most reliable indication of size because length measurements of polychaetes are often inaccurate due to

elasticity of the animals or breakage (Warwick and Price 1975, Duchene 1976, Olive 1977, Guillou and Hily 1983).

Maximum head widths were used to construct size-frequency histograms for each sampling period. From these histograms, cohort composition of the population, mean cohort growth, and mortality were estimated for subtidal animals. Animals were also examined to determine the presence or absence of eggs. Animals from intertidal samples were also counted, measured, and examined as above to obtain estimates of population abundance, size structure and reproductive condition. Mortality and life span of *L. medusa* was estimated by monitoring the adult population to see when sharp decreases in abundance occurred during the year, and by examination of size-frequency histograms.

As an additional measure of growth, in June 1990, 12 adult *L. medusa* were excavated from the sand flat using a can-core, measured, and allowed to reburrow in sediment cores in the laboratory. These cores were replanted in the field with their surfaces flush with the natural sediment surface. Four months later the cores were re-excavated and the worms re-measured to compare their relative growth with that determined by other procedures.

Fecundity Estimates

Female fecundity was determined by removing two oovigerous segments from the mid-section (segments 17 and 18) of adult *L. medusa* and extracting all mature oocytes, following the procedure of Zajac and Whitlatch (1988). Following dilution and mixing of oocytes with 20 ml water, 1 ml aliquots were removed and oocytes were enumerated. The

number of oocytes per segment was estimated from four counts for each preparation. The maximum head width of each individual was also measured.

The mean diameter of oocytes within the coelom at each monthly sampling was estimated by measuring oocyte diameter from two individuals from each sampling period (only one in June); thirty oocytes per individual were measured. This information was used to determine time of oocyte release (Guillou and Hily 1983).

Production Estimates

For subtidal animals, formalin-preserved ash free dry weights (AFDW) were obtained for a selection of animals from each size class to be used in length-weight, and width-weight regressions. Regressions were performed using Minitab (Ryan et al. 1985). Secondary production estimates were made using the regression of *L. medusa* maximum head width versus AFDW ($\ln \text{width} = 0.242 \ln \text{AFDW} + 2.38$), as this relation provided the best estimate of AFDW (the highest r^2). Delineation of cohorts was based on visual inspection of size-frequency histograms; cohorts were separated based on modes in the size distribution. Production was calculated using the increment summation method (Downing and Rigler 1984). In this method the production is the product of the average number of individuals between two sampling intervals and difference in mean weight between the two sampling intervals. This is then summed over n time periods, as in the following equation:

$$P = ((N_1 + N_2)/2)(w_2 - w_1) + ((N_2 + N_3)/2)(w_3 - w_2) + \dots \\ \dots + ((N_{n-1} + N_n)/2)(w_n - w_{n-1})$$

which results in $P = g \text{ AFDW m}^{-2} \text{ yr}^{-1}$ for 12 monthly sampling intervals. For cohort 3, which appeared on the last sampling date, production was estimated as the standing stock biomass (Waters and Crawford 1973).

The contribution from eggs released into the water column was estimated using mean size of the eggs for each particular month to obtain volume. Egg AFDW in grams was estimated using the density of protoplasm (1.2 g cm^{-2}) (H. Kator, personal communication), and the conversions: 0.167 (wet weight to dry weight) and 0.9 (dry weight to AFDW) from Waters (1977). The number of eggs per segment was estimated from Figure 12, then multiplied by 80 oovigerous segments per worm, then multiplied by the number of worms per square meter (Fig. 5), resulting in the number of eggs per square meter. The number of eggs per square meter was then multiplied by g AFDW per egg, resulting in g AFDW per square meter.

RESULTS

Physical Conditions

Trends in water temperature for 1989 and 1990 were similar, with a steady increase from 16°C in May to a maximum of approximately 28°C in August, and then a steady decrease after September (Fig 4a). In 1989, May and June temperatures were slightly higher than those in 1990. In 1990, July and August temperatures were higher than those recorded in 1989. Salinities ranged between a high of 24 ppt in late January 1989 and a low of 15 ppt in April 1990 (Fig. 4b).

Patterns of Abundance

Loimia medusa was present at many sampling locations at the study site (Appendix I). During the one year sampling period, average monthly subtidal densities ranged from 0.3 to 6 individuals per 0.1 m² (Fig. 5). *L. medusa* showed a general trend of declining abundances between November 1989 and July 1990, when the adults from cohort 1 appeared to suffer post-spawning mortality; there were slight increases in April and July. The variability was high due to the patchiness of the species. In August and October 1990, mean abundance increased following the settlement of juveniles in cohort 2 and 3 (see below). There was no settlement in September 1990.

During November 1989, the small-scale (1 m) spatial distribution pattern of the adult population based on Morisita's Index was aggregated

Figure 4. a. Mean weekly York River water temperature ($^{\circ}\text{C}$) for 1989 and 1990 determined 1 m from the bottom at the VIMS Ferry Pier (source: VIMS Computer Center).

b. Mean weekly York River salinity (ppt) for 1989 and 1990 determined 1 m from the bottom at the VIMS Ferry Pier (source: VIMS Computer Center).

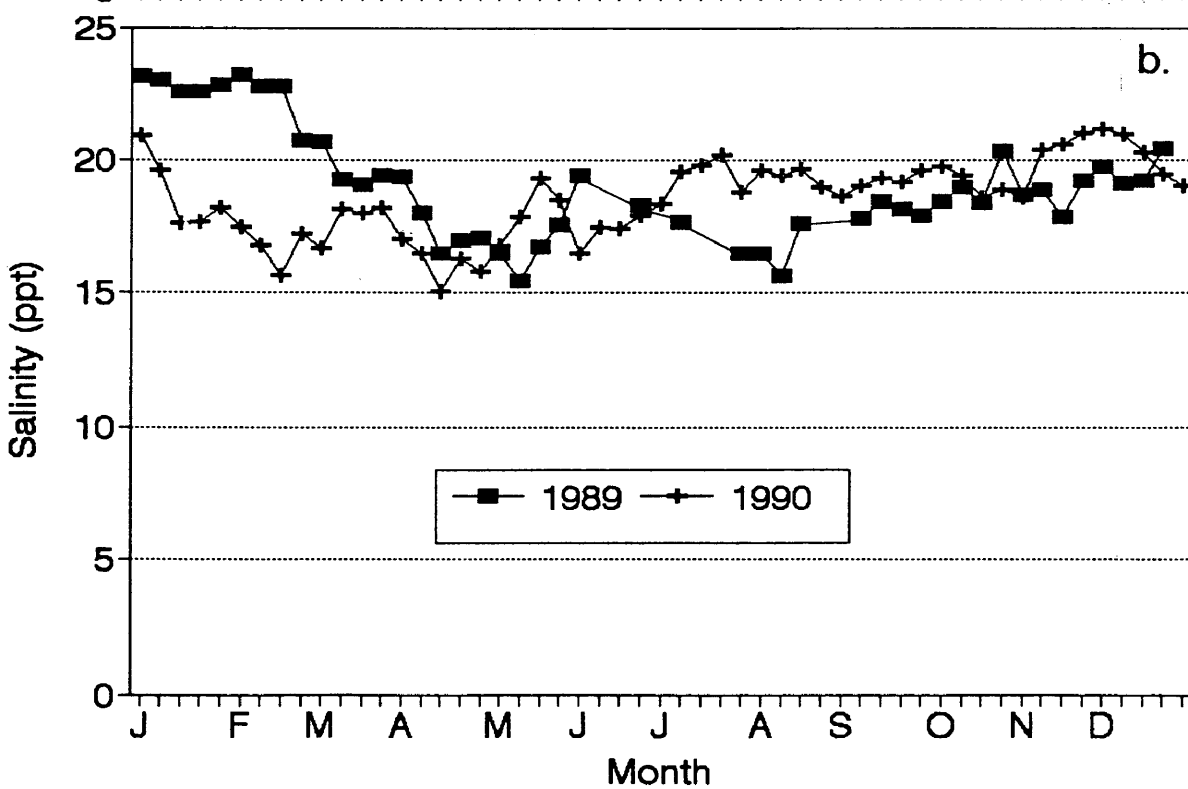
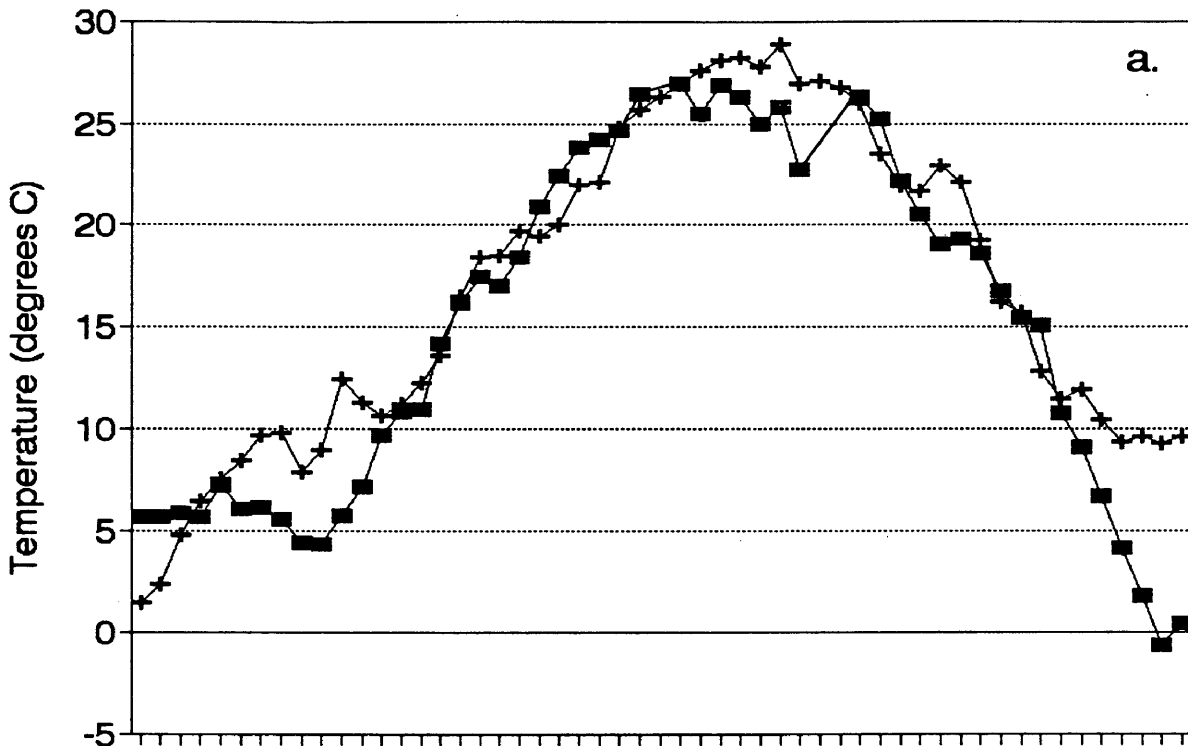
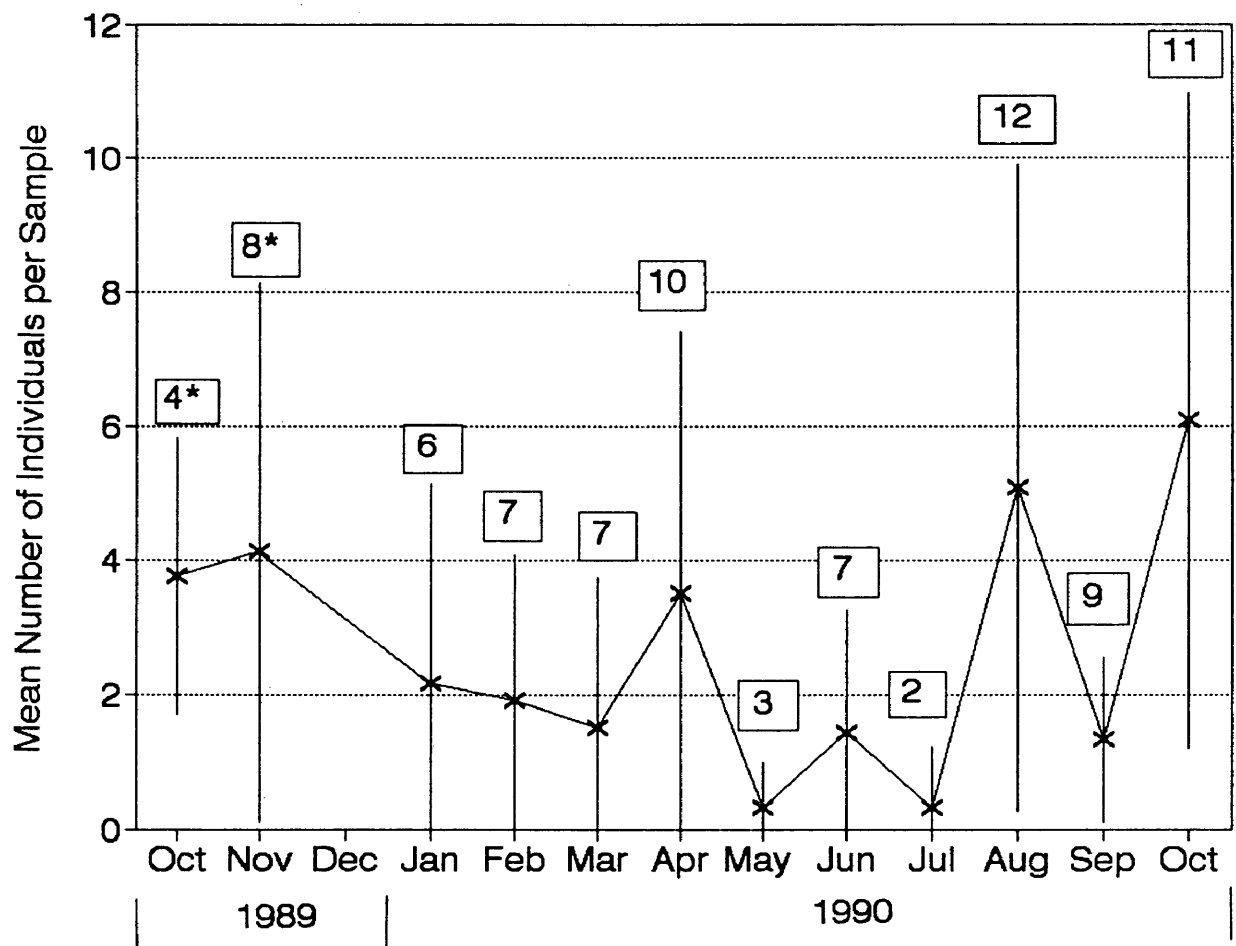


Figure 5. *Loimia medusa*. Mean number of individuals per subtidal sample (0.1 m²) with standard deviations. Total number of samples containing *Loimia medusa* given in box (out of 12 possible unless denoted with *).



(two transects: chi-square = 345.0 and 547.7, df = 15 and 19, $p < 0.0001$ for both). Two subtidal transects were examined, and for both transects surveyed, the Index of Dispersion (I) was above unity.

On a larger scale, following settlement periods, individuals were abundant and widely distributed throughout the subtidal region, being present in 100% and 92% of the samples for August and October, respectively (Fig. 5). Conversely, individuals were rarer during the late spring to early summer period when adults were spawning (*L. medusa* was present in 17-58% of samples for the period May to July).

Ecology of Larvae

Plankton samples were collected from June 1989 through December 1990; the two years showed considerable variation though the sampling effort for the two years was similar (Appendix II). Very few larval *L. medusa* were present in plankton samples in 1989 (Fig. 6). The first larva appeared in June, followed by a small peak in July; none were collected after September. In 1990, considerably more *L. medusa* larvae were collected. No *L. medusa* larvae were found in plankton samples in June, but there were large peaks of larvae in July, August and September. The number of larvae in the water column declined from August to October, and none were collected after October.

Abundances of larvae coincided well with lunar stages (Fig. 7). Most larvae were collected on July 20 and July 23, as well as on August 20 and August 22, sampling dates coincident with new moon periods on July 22 and August 20. During new and full moon periods, there are corresponding spring tides and increased tidal currents (but less than

Figure 6. *Loimia medusa*. Total abundance of larvae present in plankton samples per month for 1989 and 1990.

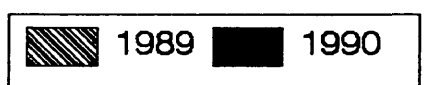
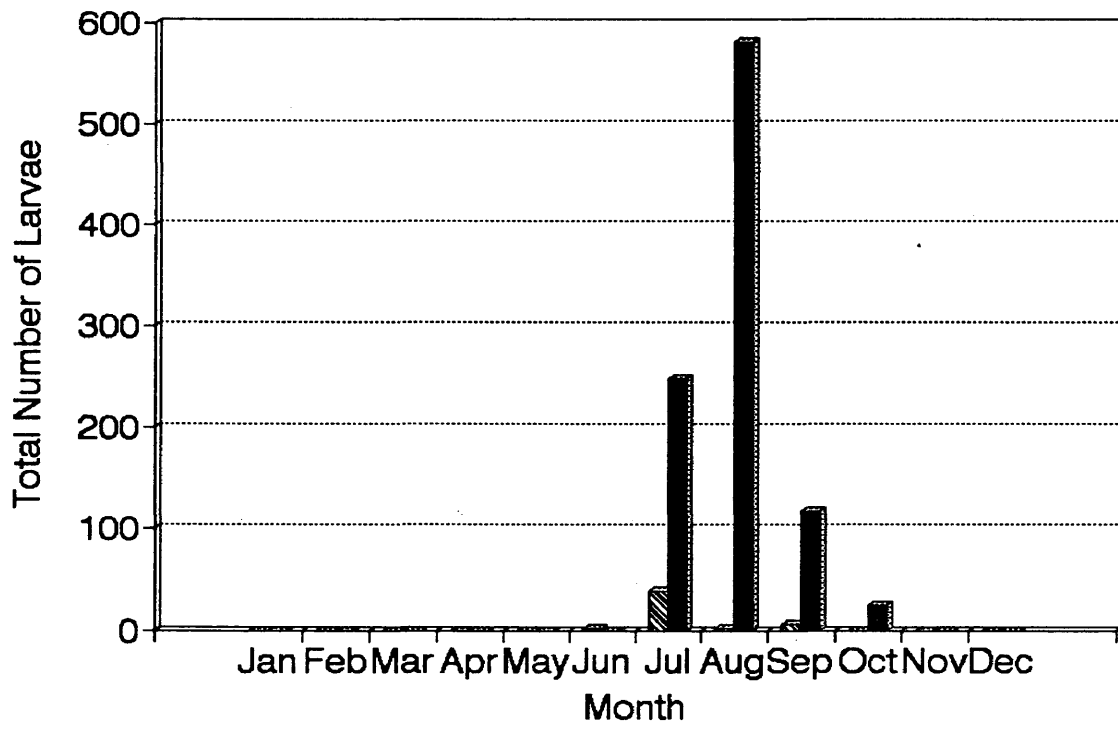
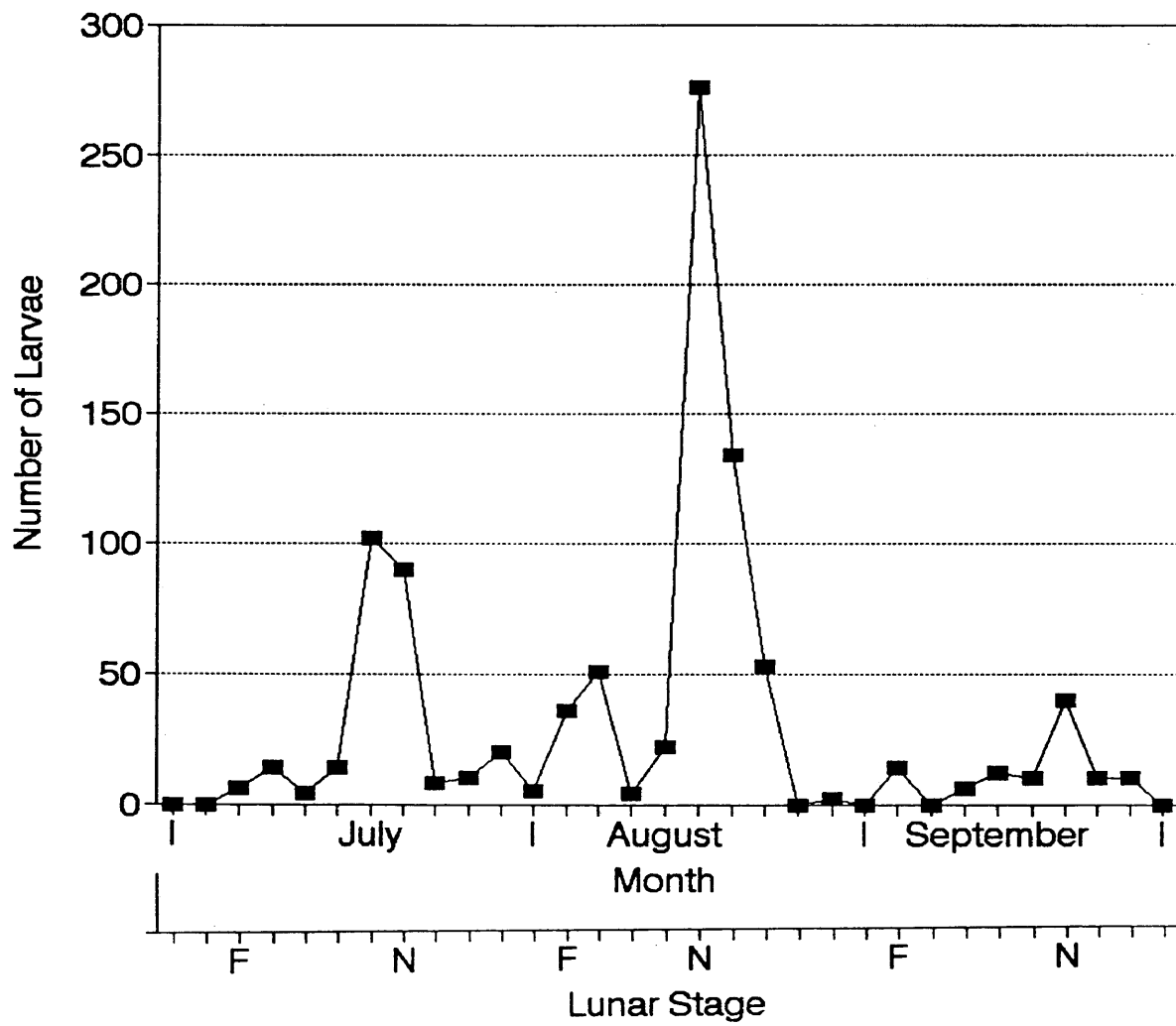


Figure 7. *Loimia medusa*. Number of larvae collected per 3 day interval and lunar stage for summer 1990 (from 7/1 to 9/31).
N = new moon, F = full moon.



1.3X neap tidal current velocities) which may have affected collection rates of larvae. Changes in tidal currents alone do not, however, appear to be sufficient to explain the large increases (e.g. greater than 13X) in the number of larvae collected. Abundances of larvae were significantly affected by lunar period (ANOVA; $p < 0.001$) with increased abundances during the new moon quarter.

Eight *L. medusa* larvae were monitored for growth and settlement in laboratory conditions. Three of these individuals settled and built tubes in laboratory dishes. The mean duration until settlement was 53 (SD = 4) days after capture. Animals in laboratory conditions grew slowly (at 20°C). Most individuals did not show any growth in head width in one week, and the fastest growing individual grew 0.1 mm in head width in one week (Table 1).

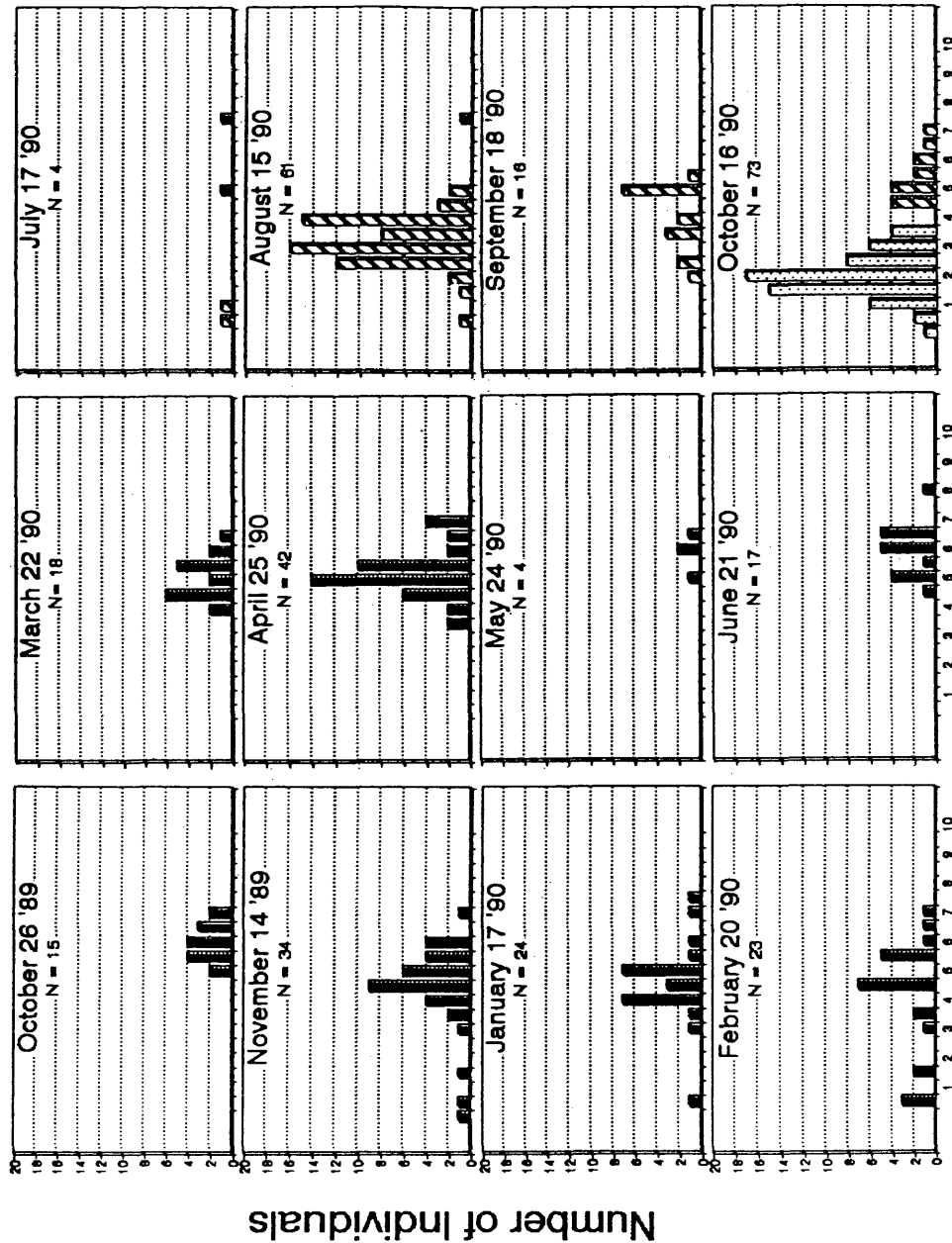
Population Structure

Because of the different collection and preservation techniques for the subtidal and intertidal samples, the two sets of samples could not be pooled. For subtidal samples, three cohorts were delineated by visual inspection of the size-frequency histograms (Fig. 8). The first cohort consisted of the adults present from October 1989 (mean head width 6.19 mm, mean weight 0.10 g) to August 1990 (mean head width 7.88 mm, mean weight 0.27 g). A second cohort was first collected in July 1990 (mean width 1.07 mm, SD 0.17), grew to a mean width of 3.5 mm (SD = 0.9, mean weight 0.01 g) by August, and 5.6 mm (SD = 0.8, mean weight 0.07 g) by the October sampling. A third cohort with a mean width of 2.2 (SD = 0.8, mean weight 0.001 g) was detected in October.

Table 1. Loimia medusa. Growth in head width of larvae in the laboratory.

Date	Growth (mm)							
	# 1	# 2	# 3	# 4	# 5	# 6	# 7	# 8
Width	1.07	1.64	3.64	1.67	2.42	1.67	3.27	1.31
7/26-8/1	0.071	0.095	0.190	0.095	0.024	0.047	0.024	0.023
8/1-8/8	0.000	0.000	0.000	0.119	0.095	0.000	0.000	0.000
8/8-8/15	0.000	0.048	-0.095	0.000	0.000	0.000	0.000	0.024
8/15-8/25	0.048	0.047	0.047	0.048	died	died	died	died
8/25-8/30	0.000	0.024	0.480	settled				
8/30-9/13	0.059	0.119	settled					
9/13-9/21	0.095	settled						
9/21-10/7	-0.073							
10/7-14	0.073							

Figure 8. *Loimia medusa*. Width size-frequency histograms for 12 subtidal sampling dates with cohorts indicated. Total number of individuals collected is given.



Maximum Head Width (mm)

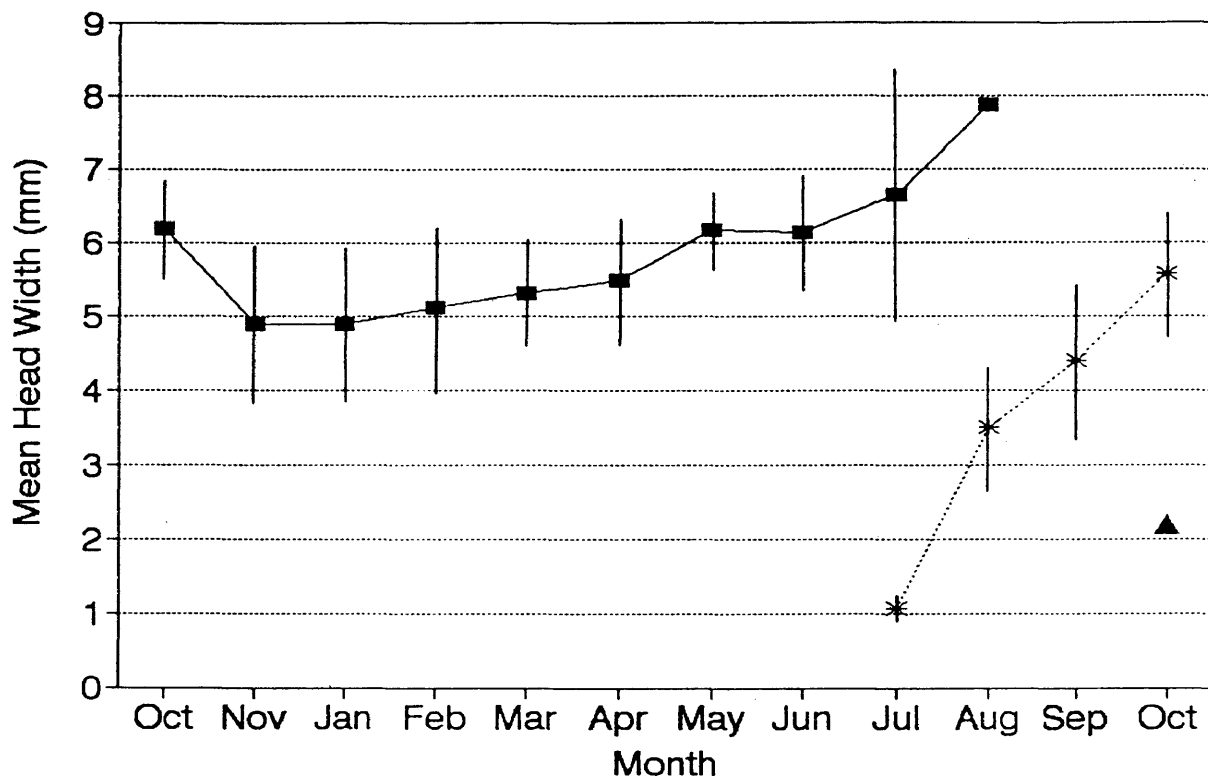


No settlement of small individuals was apparent in the September samples, thus, October recruits probably settled after September 18.

From November 1989 through March 1990, worms in cohort 1 grew slowly, at a rate of 0.1 mm per month (with a change in weight of 0.01 g in 4 months) (Fig. 9). Growth was more than twice as rapid (0.3 mm per month, change in weight of 0.08 g in 4 months) during the March to July period. In July, cohort 2 first appeared in the smaller size-fractions and grew very quickly during the next two months. This cohort grew 2.4 mm mo^{-1} (change in weight of 0.01 g) for the period July 17 to August 15, and 0.9 mm mo^{-1} (change in weight of 0.02 g) for the period August 15 to September 18). Settlement of small individuals (2.2 mm width, SD = 0.8) of a third cohort occurred between September 19 and October 16. Their subsequent growth was not followed since this sampling date was at the end of the study. Adults in cohort 1 were scarce or absent in August, September and October samples.

Similar trends in population dynamics as seen in subtidal samples were observed in the intertidal samples (Fig. 10). By August 18, the adults in cohort 1 were not apparent in the population and cohort 2 individuals were 3-5 mm in width. As in the subtidal samples, there was no settlement of cohort 3 detected in September. By October, the size distribution was bimodal, with cohort 3 present in the 3-5 mm size fraction. The mean sizes of individuals collected in the intertidal were generally larger than those from the subtidal samples; this may have been a function of collection or preservation techniques.

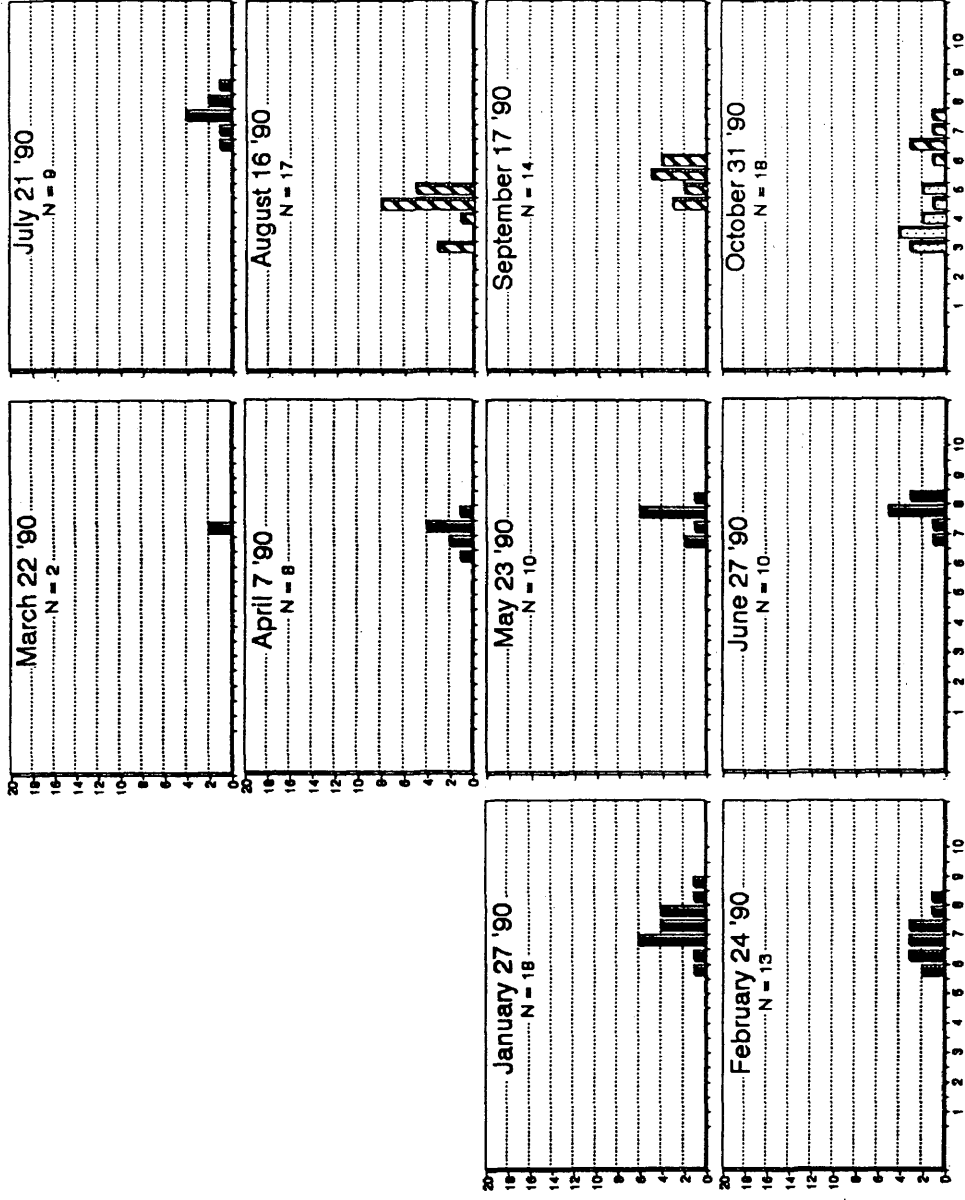
Figure 9. *Loimia medusa*. Mean monthly maximum head width (with standard deviations) for each of three cohorts from subtidal samples.



—■— Cohort 1 ···*··· Cohort 2 -▲- Cohort 3

Figure 10. *Loimia medusa*. Width size-frequency histograms for 10 intertidal sampling dates with cohorts indicated. Total number of individuals collected is given.

Number of Individuals



Maximum Head Width (mm)



Adult Growth

Adults outplanted in the field grew slowly. On average, there was no growth in width measured in the 12 adults outplanted for the period June 18 to November 15, 1990 (Table 2). The smallest animals at the beginning of the experiment were the ones that showed some growth (as much as 0.7 mm head width in 4 months). The majority of animals were nearly full-grown at the time of replanting. These data show that adults grow very slowly after they have reached approximately 7 mm in head width.

Fecundity Estimates

The percentage of gravid *L. medusa* adults for the intertidal population increased from 29% in May to a maximum of 67% in July (Fig. 11). In August, the percentage dropped to 28% gravid adults, as the first cohort spawned and died and the second cohort contained many small, pre-reproductive individuals. The mean size of gravid individuals decreased as individuals from cohort 2 became reproductively active. Thus, in the early summer, animals from cohort 1 became gravid at 6 mm or greater head width (weight = 0.1 g). Later in the summer, individuals in cohort 2 became gravid when they attained 4 mm head width (weight = 0.05 g). Gravid adults were absent after spawning in September.

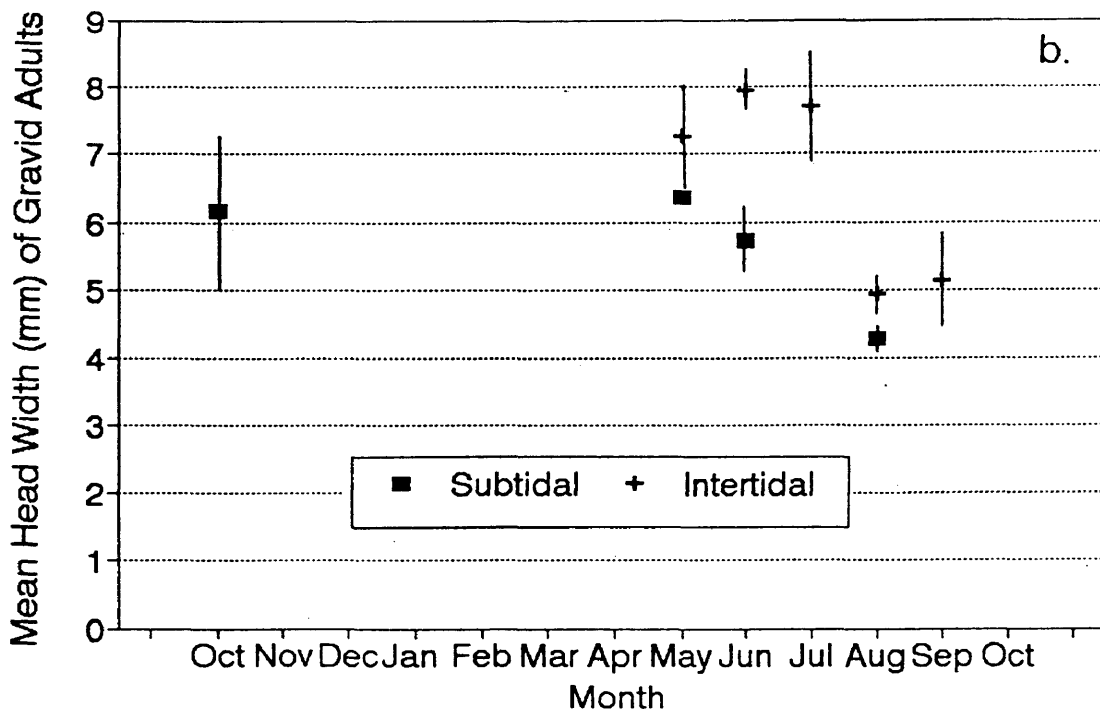
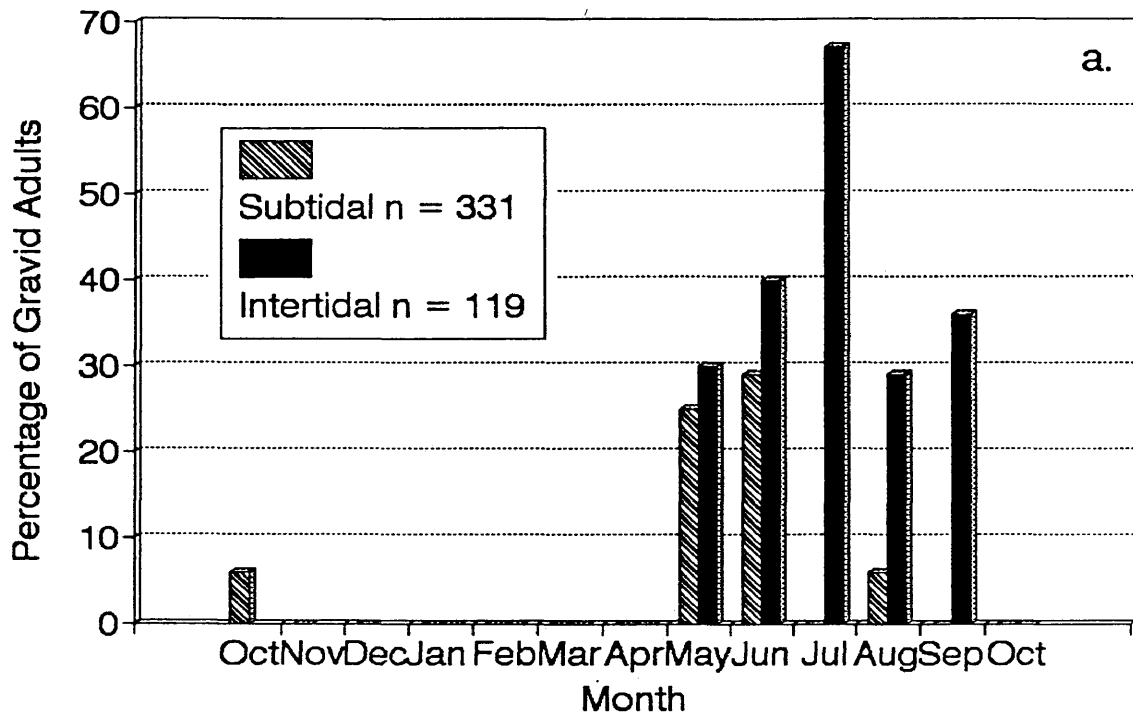
Females from the intertidal samples were well preserved and could be used for fecundity estimates; animals from subtidal samples were usually broken or poorly preserved, making fecundity estimates impossible. Twenty females from the intertidal samples had intact

Table 2. Growth of adult Loimia medusa outplanted from 6/18/90 to 11/15/90. Measurements are in mm maximum head width.

Individual	Beginning Width	Ending Width	Growth (mm)	Change in Biomass (g)
# 1	8.89	8.89	0	0
# 2	8.89	not recovered	-	-
# 3	7.4	7.4	0	0
# 4	8.14	7.4	-0.74	0.1
# 5	8.89	not recovered	-	-
# 6	8.89	7.4	-1.49	-0.24
# 7	9.63	7.4	-1.49	-0.34
# 8	6.66	7.4	0.74	0.07
# 9	8.14	8.89	0.75	0.14
# 10	9.62	8.89	-0.73	-0.17
# 11	6.66	7.4	0.74	0.07
# 12	7.4	8.14	0.74	0.07

Figure 11. a. *Loimia medusa*. Percentage of gravid adults per month for subtidal and intertidal samples.

b. *Loimia medusa*. Mean size of gravid adults (with standard deviations) for subtidal and intertidal samples.

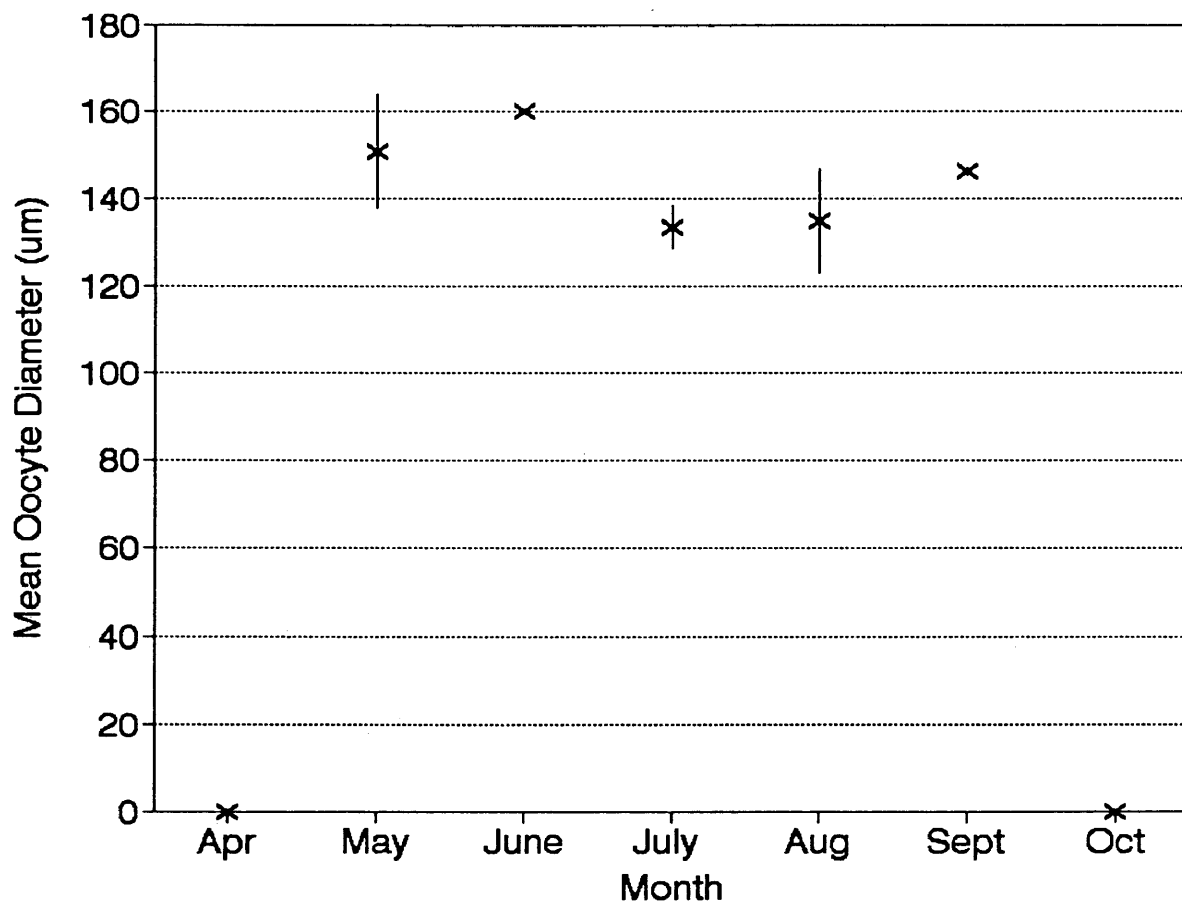


oocytes in the coelom. Of these, 17 were measured and analyzed for oocyte size and number. The three other females contained oocytes, but counts could not be made due to worm breakage.

Fecundity and egg diameter measurements of *L. medusa* were useful in interpreting patterns of spawning and reproduction. There was little change in mean oocyte size during the five months when ovigerous females were present (Fig. 12). Oocyte size, however, decreased somewhat in July after spawning and the release of large oocytes. Largest mature oocytes are presumably released at spawning, thus, the mean diameter of oocytes remaining in the coelom is smallest at spawning. At the time of spawning in July, the mean diameter of oocytes in the coelom was 134 μm . Mature oocytes present from May to September were 134 μm to 160 μm in diameter. After September, no oocytes were apparent in females. Spawning oocytes appeared to be reduced in diameter as the cells changed from flat to spherical at spawning (personal observation), similar to that reported for the terebellid *Lanice conchilega* (Smith 1989) and *N. zostericola* (Eckelbarger 1974).

A quadratic regression was used to describe the relationship between female size and fecundity and was found to be significant at a probability of < 0.0001 and an r^2 of 0.71. This relationship appears to be strongly influenced by a single large individual that exhibited high fecundity. The regression equation was eggs per segment = $41269 - 13557 \text{ head width} + 1151 (\text{head width})^2$. The number of oocytes per segment increased with size of the individual from 201-4530 oocytes per segment for individuals $< 7 \text{ mm}$ in width (from August and September samples) to 422-15840 oocytes per segment for larger females

Figure 12. *Loimia medusa*. Mean monthly coelomic oocyte diameter (with standard deviations) for intertidal animals. Diameter of zero denotes no visible oocytes.



(from May, June, and July samples) (Fig. 13). Even small individuals (4 mm width and greater) were fecund.

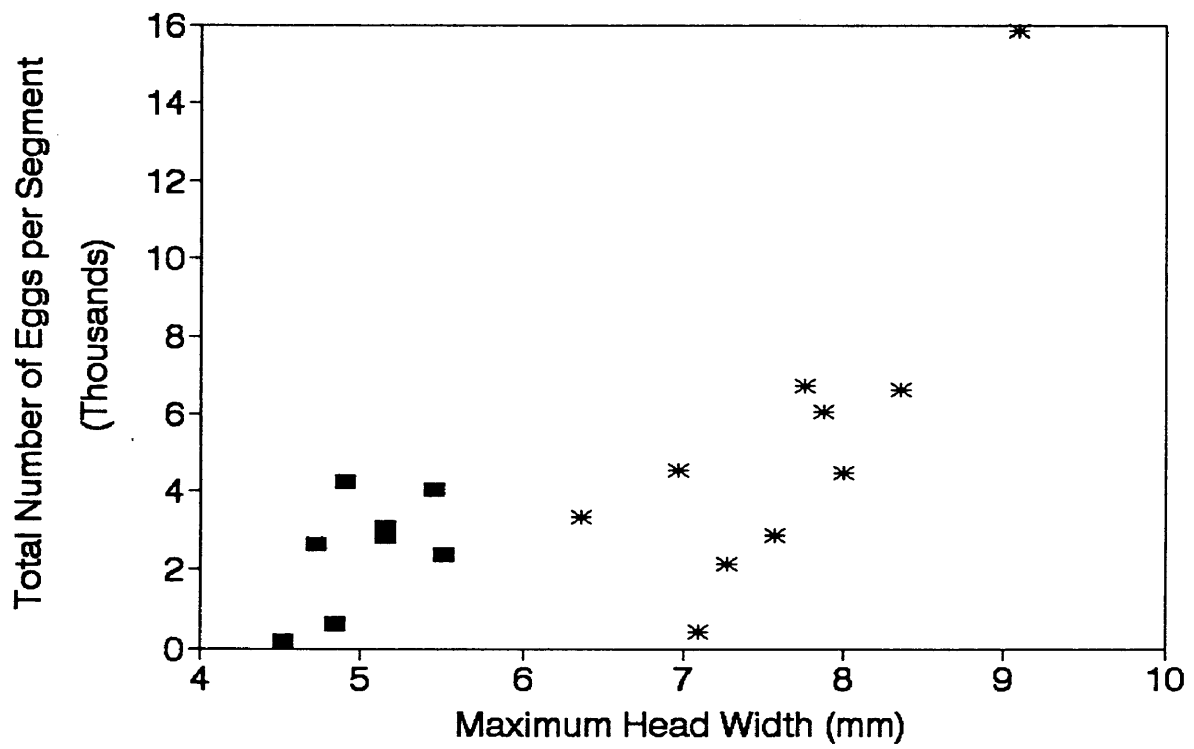
Production Estimates

Size in maximum head width was related to worm weight (AFDW) using the regression $\ln \text{ width} = 0.242 \ln \text{ AFDW} + 2.38$ ($r^2 = 89.1\%$, $df = 20$) for the subtidal samples, and $\ln \text{ width} = 0.293 \ln \text{ AFDW} + 2.41$ ($r^2 = 96.7\%$, $df = 21$) for the intertidal samples. Other measurements (such as body length from the head to the 17th thoracic setiger or width of the third setiger) were less efficient (lower r^2) for describing AFDWs. Due to the paucity of individuals collected from the intertidal sampling, production estimates were only calculated for the subtidal samples.

Based on observed population structure for subtidal individuals (Fig. 8), and the dates of sampling, production was calculated for the period November 1989 through August 1990 for cohort 1, and July 1990 through October 1990 for cohort 2. For cohort 1, the production during the period October 1989 to November 1989 was not included in the total calculation because the October sample consisted of only four replicates and therefore may not have been a good representation of the population. Production for cohort 3, which first appeared on the last sampling date, was calculated as the biomass for the October 1990 sampling date.

The estimate of secondary production for cohort 1 was 1.62 g AFDW m^{-2} for the 9 month period (Table 3). Cohort 2, with a high abundance of juveniles that grew fast, had a higher production estimate of 1.18 g AFDW m^{-2} for the 3 month period. For cohort 3, the production was estimated to be 0.13 g AFDW. During June, egg production was

Figure 13. *Loimia medusa*. Size-specific fecundity of intertidal animals in number of eggs per segment versus maximum head width.



■ Aug & Sept Samp * May, Jun & July Samp

Table 3. Secondary production for 3 cohorts of subtidal Loimia medusa.

Month	PRODUCTION VALUES			Eggs g AFDW/m ²
	Cohort 1 g AFDW/m ²	Cohort 2 g AFDW/m ²	Cohort 3 g AFDW/m ²	
Oct-Nov	-1.830*			
Nov-Jan	-0.008			
Jan-Feb	0.133			
Feb-Mar	0.115			
Mar-Apr	0.182			
Apr-May	0.756			
May-Jun	-0.017			
Jun-Jul	0.296			0.047
Jul-Aug	0.167	0.242		0.005
Aug-Sep		0.469		0.296
Sep-Oct		0.465	0.127	
Total	1.62	1.18	0.127	0.348
Per Month	0.11	0.39		
Per Year	3.32			

*This calculation removed from total because of small sample size in October.

0.05 g AFDW; in July it was 0.005 and in August it was 0.30. Production of *L. medusa* was at its peak between April and May for cohort 1, when the production was 27% of the total population production estimated for the year. For cohort 2, the production was the highest between August and September when 17% of the total population production for the 12 month period occurred. To estimate yearly production, estimates for each cohort plus the contribution of eggs were added together to obtain the total for 12 months; this resulted in a production estimate of 3.3 g AFDW m⁻² year⁻¹. The ratio of annual production to mean biomass (P:B ratio) was calculated as 3.0, with an average biomass of 1.1 g m⁻² for this species.

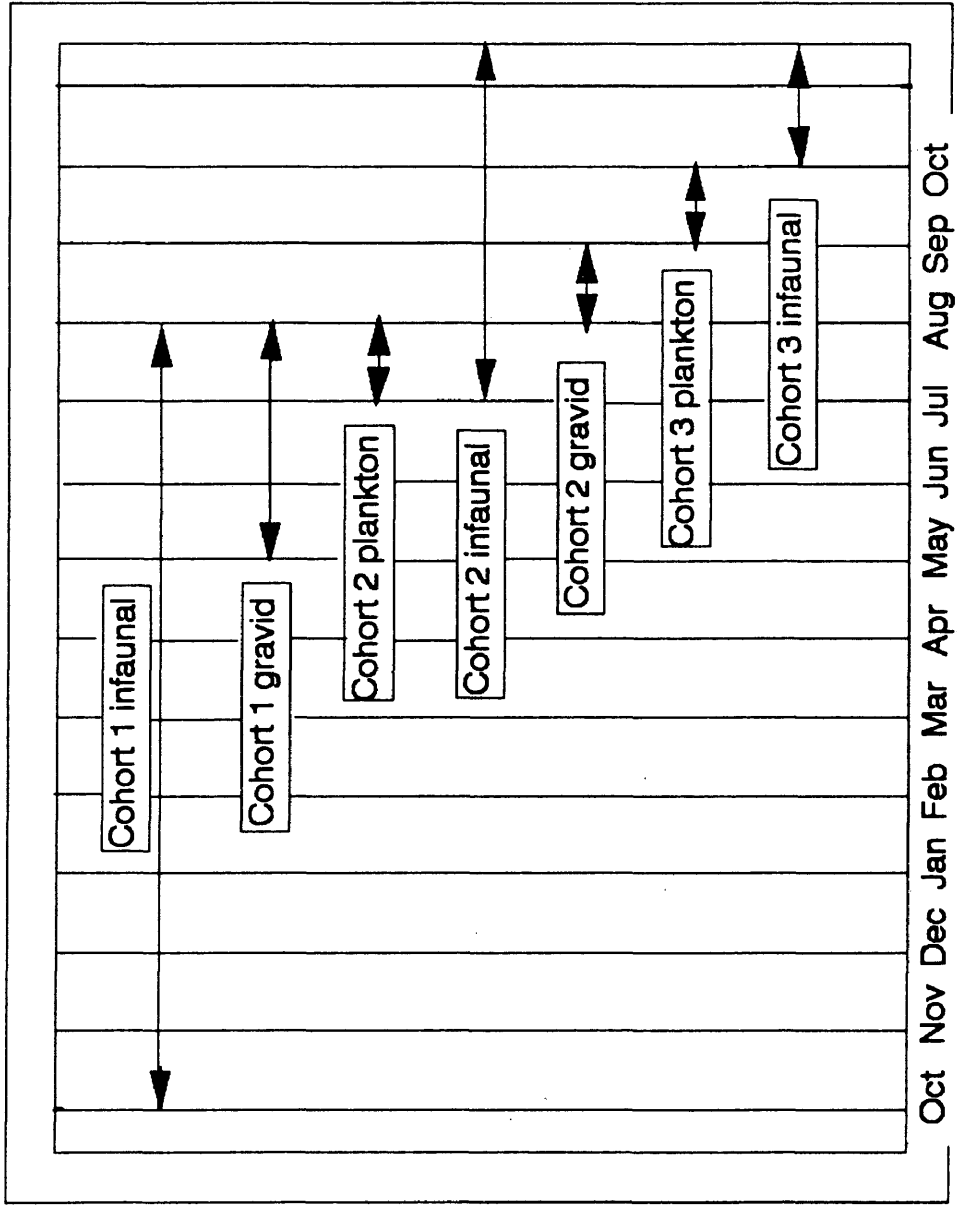
Additional Observations

L. medusa adults were sighted, on occasion, swimming in the water column. This behavior has been observed by other authors (Levin and Greenblatt 1981), and shows that this species may exhibit adult migration and be partially pelagic. This species is able to quickly reburrow (within hours) and may be able to use this swimming behavior to avoid stress. In addition, in several of the *L. medusa* tubes collected, a commensal crab, *Pinnixa chaetopterna* was found. This represents a previously unknown commensal relationship.

DISCUSSION

Densities of *Loimia medusa* found during this study of a tidal flat area (3-60 individuals m^{-2}) were comparable to densities reported for deeper subtidal areas of the Chesapeake Bay (e.g. Rappahannock River, 32 individuals m^{-2} , Dauer et al. 1989; lower Chesapeake Bay, 68 individuals m^{-2} , Schaffner 1990). During October 1989 through October 1990, the population was composed of at least three cohorts (Fig. 14). No more than two cohorts at a time were present in the population. Adults that survived from 1989, cohort 1, became reproductively active in May and June 1990 and apparently released gametes into the water column in late June to early July. Larvae first appeared in the water column in early July. These larvae settled as a second cohort, as a few individuals were detected on July 17, and grew rapidly reaching a mean width of 3.5 mm (SD = 0.85, weight = 0.009 g) by August 15. These larvae, thus, spent less than one month in the plankton. Females in cohort 2 became reproductively active in August and September when they reached a width of greater than 4 mm (0.016 g). A second peak of larvae, the largest observed, was detected in August, but no correspondingly large settlement was observed on the September sample date. A third peak in larvae occurred in September. A third cohort of individuals was apparent in the October infaunal samples. The adults from cohort 1 did not survive into the fall of 1990, thus, *L. medusa* appears to have a life span of 1 year.

Figure 14. Summary of *Loimia medusa* population biology. Arrows indicate presence of animals during dates included.



With regard to the lack of newly settled individuals in September samples, the large number of larvae observed in the plankton in August apparently did not successfully recruit to the benthos in the study area. Since nearly all samples in August and October contained newly recruited individuals, it is unlikely that a larval settlement event was missed in September due to insufficient sampling. It is not possible, given the results of this study, to determine the fate of the larvae that were abundant in August. It may be that they were carried away from the study area and settled elsewhere, they suffered starvation or predation, or suffered mortality by other means.

Previous patterns of spawning and larval release observed for related species are somewhat different than those found for *L. medusa* in this study. In the terebellid *Nicolea zostericola*, females become gravid in March and spawning occurs from mid-April to early July, after seawater temperature rises above 6°C. Only one cohort is produced per year, and individuals live for one year. The larvae produced develop in benthic cocoons, rather than planktonic gelatinous cases, as in *L. medusa* (Eckelbarger 1974). The terebellid *Eupolyornia nebulosa* exhibits several peaks of spawning activity each spring (iteroparous reproduction) and jelly egg masses appear in a period following the full moon (Smith 1989). In addition, the planktonic juvenile of *Lanice* is commonly found off Northumberland (on the North Sea coast of England) with a minor peak in June and a major peak in August (water temperature is 8-10°C) (Romimohtarto 1980), each derived from different cohorts, similar to what occurs in *L. medusa* (present study). Wilson (1928), in

studies of *L. medusa* from Britain (near Plymouth), reported larvae in plankton tows in the spring (water temperatures near 15°C).

During this study there was considerable year to year variation as well as weekly variation in the number of *L. medusa* larvae collected in the water column. In 1989 the number of larvae collected in the plankton was 4% of the total collected in 1990. In addition, researchers at VIMS collected hundreds of *L. medusa* larvae from the water column during summer 1987. This evidence suggests there is substantial year to year variation which is common in highly variable habitats such as estuaries (Orth and van Montfrans 1987), and for recruitment in general (Sale 1990).

The lunar periodicity, as seen here in abundances of *Loimia medusa* larvae, is somewhat common in invertebrates. Another terebellid polychaete, *Eupolymnia nebulosa* lays gelatinous egg masses in the period following the full moon and extending into the fourth quarter (Smith 1989). Settlement of larvae of the blue crab *Callinectes sapidus* is also significantly affected by lunar quarter, with greatest settlement following full moon (van Montfrans et al. 1990). Other decapods, such as *Penaeus duorarum*, settle mainly during new and first quarter lunar periods (Roessler and Rehner 1971). Settlement during the darkest phases of the moon may be advantageous for avoiding predation (van Montfrans et al. 1990).

Temperature appears to be one of many possible environmental factors influencing the onset and cessation of gamete maturation and spawning in *L. medusa*. For both intertidal and subtidal regions, gravid adults first appeared in May when temperatures exceeded 18°C. In both

1989 and 1990, larvae were not collected in the plankton until the temperatures rose above approximately 23°C. An earlier rise in temperature in 1989 coincided with an earlier appearance of larvae (in June) relative to 1990 when larvae did not appear until July. Similarly, all reproductive activity of *L. medusa* ceased in late September and October when water temperatures fell below approximately 23°C. Temperature cues are known to strongly influence the onset of spawning in many other polychaetes (e.g. *Nereis diversicolor* (Dales 1950); *Cirriformia tentaculata* (George 1964); *Scoloplos armiger* (Gibbs 1968); and *Nicolea zostericola* (Eckelbarger 1974)).

Within the *L. medusa* population, growth varied as a function of organism age and temperature. Adults in cohort 1 grew slowly through winter when temperatures were low. Growth increased from April through August as temperatures rose, then mature growth declined or stopped. Large adults outplanted in the field from August to November grew very slowly. Conversely, cohort 2, which settled in July and August, grew quickly at 1-2 mm in width per month. Slow growth of larvae was observed in the laboratory; the fastest growing individual grew 0.1 mm in one week. Growth of larvae in the laboratory may have been limited by relatively low temperature in the laboratory (20°C) relative to field temperatures (> 25°C).

Gravid *L. medusa* collected in August and September 1990 were early maturing individuals from the summer 1990 settlement, thus, animals grow to adult size and sexual maturity in less than two months after settlement and are able to reproduce during the same summer in which they settle. In the harbor of Brest, France, *Melinna palmata*, an

ampharetid, shows growth characteristics similar to *L. medusa* with sharp increases in size from June through August, then a winter growth pause (Guillou and Hily 1983). Other terebellids, such as *Nicolea zostericola*, grow slowly until just before reproduction when growth increases, and do not exhibit immediate growth to sexual maturity as is seen in *L. medusa* (Eckelbarger 1974). Some non-terebellid polychaetes require at least one year of growth before they attain sexual maturity. For example, the sigalionid *Pholoe minuta* requires three years before sexual maturity is attained (Heffernan et al. 1983); *Nephtys hombergii* and *Caulleriella caputesocis* each require one year (Oyenekan 1987).

In comparison with some other species, *L. medusa* shows high fecundity. If the maximum number of oocytes per segment in *L. medusa* is multiplied by the number of oovigerous segments (assuming all segments contain the same number of oocytes), the maximum fecundity would be over a million eggs per worm (range 16,080 to 1,272,640), a high value compared with other large polychaetes. *Nephtys incisa*, for example, shows a fecundity of 50,000 to 450,000 oocytes per worm (Zajac and Whitlatch 1988). The number of eggs laid by the terebellid *Nicolea zostericola* during its spawning period is 44 to 665 (Eckelbarger 1974). Even small *L. medusa* (4 mm in head width) are highly fecund. A large number of eggs released by *L. medusa* may provide the advantage of increased survival of eggs (Grahame and Branch 1985). Similar to *L. medusa*, a positive correlation between size and fecundity has been demonstrated in many polychaetes (i.e. Creaser and Clifford 1982, Levin 1986, and Zajac and Whitlatch 1988).

The measurement of the diameter of coelomic oocytes can be used as an indicator of spawning time as well as an indicator of the amount of parental investment in eggs. When there is a large number of small eggs, pelagic planktotrophic larvae tend to be produced. When parental investment in eggs is great and eggs are larger, a smaller number of eggs are produced (Mileikovski 1971, Vance 1973a,b, Levin and Huggett 1990). Oocytes of 133-160 μm diameter for *L. medusa* are similar to those of *Nephtys hombergii* (Olive 1978), *N. caeca* (Curtis 1977), *Caulleriella caputesocis* (Oyenekan 1987), and *Lanice conchilega* (Smith 1989) which have oocytes of 200 μm , 120-150 μm , 120-160 μm , and 182 μm in diameter respectively. All of these species have planktonic larvae. In a deme of *Streblospio benedicti* with planktonic larvae studied in North Carolina by Levin and Huggett (1990), eggs were 63 μm in diameter.

When eggs are brooded or larvae have direct or lecithotrophic development, oocyte diameter tends to be large. *L. medusa*'s mean oocyte diameter is small when compared to those of polychaetes with non-planktonic larvae. In a North Carolina deme of *S. benedicti* with lecithotrophic larvae, egg size was 152 μm (Levin and Huggett 1990). Other polychaetes which brood or have direct development also show large egg size, such as *Lumbrineris fragilis* (oocyte diameters of 200-250 μm and direct development), *Spio filicornis* (oocytes diameters of 180-300 μm and brooded eggs), *Paraxillella praetermissa* (oocyte diameters of 180-300 μm and brooded eggs), *Scoloplos armiger* (oocyte diameters to 450 μm which develop in cocoons, Curtis 1977), and *Nicolea zostericola* in which eggs develop in a protected benthic cocoon (egg size 220-280 μm) (Eckelbarger 1974, Bhaud 1988b).

When compared with other taxonomic groups, the secondary production for *L. medusa* is high. The value of $3.3 \text{ g AFDW m}^{-2} \text{ yr}^{-1}$ exceeds 87% of the production values calculated for a variety of other taxonomic groups from Chesapeake Bay (Holland et al. 1988). When compared with other production values for polychaetes from a range of habitats worldwide, *L. medusa*'s production is also high (Table 4). Although a large portion of the production comes from the numerous fast-growing juveniles which dominate the population in late summer, the contribution from less abundant *L. medusa* adults is also high.

The large production and relatively low biomass of this species (1.1 g m^{-2}) leads to a relatively high P:B ratio of 3.0 in comparison with a variety of other polychaetes (Table 4). Comparatively, P:B ratios measured for *Terebellides stroemi* and *Nereis virens*, two long-lived polychaetes, are 1.1 and 1.6 respectively (Curtis 1977, Kay and Brafield 1973). Long lived animals tend to have lower P:B ratios (Oyeneke 1987). Rapid growth of juveniles and moderate growth in adults leading to high production can account for the relatively high P:B ratio in *L. medusa*.

The rate of transfer of secondary production from *L. medusa* to higher trophic levels via predation is not well understood. During periods of low dissolved oxygen in the water column, when infaunal species may migrate upwards in the sediment column (Schaffner and Seitz, unpublished ms.), at least some portion of the biomass produced is utilized by benthic predatory fishes such as spot (*Leiostomus xanthurus*), hogchoker (*Trinectes maculatus*) and croaker (*Micropogonias undulatus*) (L. Pihl et al. unpublished ms.).

Table 4. Single-species estimates of annual production (P) ($\text{g m}^{-2} \text{yr}^{-1}$ dry weight unless otherwise stated) and annual P/B ratios for marine polychaetes (adapted from Warwick 1980, and Robertson 1979). ? = aged incorrectly. NA = data not available.

SPECIES	P	P/B	MAX AGE	LOCALITY	REMARKS	REFERENCE
<i>Nephtys australiensis</i>	0.29	0.38	2 + yrs?	Westernport Bay, Australia	Intertidal eelgrass flat	Robertson (in prep.)
<i>Nephtys hombergii</i> I	7.34	1.86	2 + yrs?	Cornwall, England	Intertidal mudflat	Warwick and Price (1975)
<i>Nephtys hombergii</i> II	2.29	2.71	2 + yrs	Southampton Water, England	Sublittoral (mean of 3 stations)	Oyenekan (1986)
<i>Nephtys incisa</i>	9.34	2.16	3 yrs	Long Island Sound, U.S.A.	Subtidal Sandy mud (4-30 m)	Sanders (1956)
<i>Nephtys picata</i>	1.77	4.33	1 + yrs	Lower Chesapeake Bay, U.S.A.	Subtidal (13 m)(mean of 2 sta.)	Huggett (1987)
<i>Cistenoides gouldii</i>	1.70	1.94	2 yrs	Long Island Sound, U.S.A.	Subtidal Sandy mud (4-30 m)	Sanders (1956)
<i>Ampharete acutifrons</i> I	0.12	4.58	1 + yr	"	Subtidal Sandy mud (9-17 m)	Richards and Riley (1967)
<i>Ampharete acutifrons</i> II	2.32	5.45	1 yr	Cornwall, England	Intertidal mudflat	Warwick and Price (1975)
<i>Pectinaria hyperborea</i>	10.6	4.60	2 yrs	Bedford Basin, Nova Scotia	Offshore (60 m)	Peer (1970)
<i>Pectinaria californiensis</i>	3.21	4.32	2 + yrs	Puget Sound, Washington, U.S.A.	Offshore (34-254 m)	Nichols (1975)
<i>Neanthes</i> (= <i>Nereis</i>) <i>virens</i>	9.04	1.60	3 yrs	Thames Estuary, U.K.	Intertidal	Kay and Brafield (1974)
<i>Ammotrypane aulogaster</i>	0.36	2.08	NA	Northumberland, U.K.	Offshore (80 m)	Buchanan and Warwick (1974)
<i>Heteromastix filiformis</i>	0.30	1.01	2 yrs?	"	"	"
<i>Spiophanes kroyeri</i>	0.20	1.40	2 + yrs?	"	"	"
<i>Spiophanes bombyx</i>	3.35	4.86	NA	Carmarthen Bay, South Wales	(13.5 m)	Warwick et al. (1978)
<i>Glycera rouxi</i>	0.19	0.37	5 yrs?	Northumberland, U.K.	Offshore (80 M)	Buchanan and Warwick (1974)
<i>Chaetozone setosa</i>	0.05	1.28	3 yrs	"	"	"
<i>Lumbrineris fragilis</i> I	0.08	1.34	3 yrs	"	"	"
<i>Lumbrineris fragilis</i> II	1.32	0.83	10 + yrs	Oslofjord, Norway	Subtidal (30 m)	Valderhaug (1985)
<i>Arenicola marina</i>	4.99	0.95	3 yrs?	Grevelingen Estuary, Netherlands,	Intertidal & subtidal mudflats	Wolff and de Wolf (1977)
<i>Harmothoe sarsi</i>	0.23	1.99	3 yrs	North Baltic	(64 m)	Cederwall (1977)
<i>Harmothoe sarsi</i>	0.39	2.75	2 + yrs	Gulf of Finland	(33-35 m)(mean of 2 stations)	Sarvala (in press)
<i>Terebellides stromi</i>	3.24	1.09	5 yrs	Disko Bay, West Greenland	Shallow coastal waters	Curtis (1977)
<i>Magelona papillicornis</i>	0.69	1.10	3 yrs	Carmarthen Bay, South Wales	(13.5 m)	Warwick et al. (1978)
<i>Glycera alba</i>	0.28	0.97	3 yrs	"	"	"
<i>Siglion mathildae</i>	0.17	0.44	NA	"	"	"
<i>Tharyx marioni</i>	0.02	0.79	2 yrs	"	"	"
<i>Caulerella caputesocis</i>	2.60	4.50	1 yr	Southampton Water, England	Sublittoral (mean of 3 stations)	Oyenekan (1987)
<i>Macroclymenel = Euclymenelzonalis</i>	3.95	0.40	2 + yrs	Lower Chesapeake Bay, U.S.A.	Subtidal (13 m)(mean of 2 sta.)	Huggett (1987)
<i>Paraprionospio pinnata</i>	0.43	3.50	1 + yr	"	"	"
<i>Chaetopterus veriopodus</i>	20.8	3.46	1 + yr	"	"	"
<i>Melinna palmata</i>	0.43	2.19	2 + yrs	Southampton Water, England	Sublittoral < 60% silt	Oyenekan (1988)
<i>Loimia medusa</i>	2.80	2.54	1 yr	York River, Chesapeake Bay, U.S.A.,	Shallow subtidal	Seitz (present study)

* converted from wet weight to AFDW using conversion factor of 0.15 derived from Waters (1977)

Despite *L. medusa*'s dominance in soft-bottom communities, aspects of its ecology were previously studied only in the 1920's (Wilson 1928). Although only one site was examined for a one year period during this study, interesting characteristics of the *L. medusa* population were apparent. *L. medusa* seems to show properties of both opportunistic and equilibrium species. It can recruit in relatively large numbers (compared with the adult population), grow rapidly and exhibit high production, as an opportunist does. It also exhibits relatively high tolerance to low dissolved oxygen concentrations (0.5 mg l^{-1}) (Llanos 1990). These characteristics suggest that *L. medusa* is well-adapted to survive and colonize disturbed areas, including those affected by oxygen stress, and to grow quickly to dominance. Thus, in the sense of Boesch (1972), it would appear that *L. medusa* has the potential to be both resistant and resilient to some types of disturbance.

L. medusa exhibits other characteristics typical of equilibrium species such as relatively few reproductive cycles per year, a somewhat extended life span, and large body size. Also, females have high fecundity and are able to release many eggs. Planktonic larvae apparently can delay metamorphosis when conditions are unsuitable for settling (laboratory studies).

The suite of life history characteristics displayed by *Loimia medusa* seem to render it well adapted for estuarine existence. Physical conditions change quickly in estuaries and resident species must be able to respond. Rapid growth of juveniles may provide a survival advantage as animals can exploit existing conditions. Numerous settlement events during a single summer and early fall provide multiple

opportunities to recruit to benthic habitats, including those disturbed by low oxygen stress. Fast growth, combined with adult tolerance to hypoxia may lead to *Loimia medusa*'s dominance throughout Chesapeake Bay. Because of its presence in numerous diverse areas in Chesapeake Bay, it would be interesting to determine *Loimia medusa*'s population dynamics and life history strategies in many different localities to evaluate intraspecific differences in life history characteristics correlated with environmental conditions.

Appendix I. Data for Loimia medusa collected in subtidal samples.

Dist = position coordinates for each sample in meters along shore, meters below MLW. Worm measurements are in mm.

Length = length from head to 17th thoracic setiger.

Width = width of the third setiger.

Max W = maximum head width.

Samples which contained no Loimia medusa have zero listed for length.

NO.	ID	DIST.	LENGT	WIDTH	MAX W
SD1	1-1	32,17	27.69	5.03	5.92
10/26/89			Broken	5.63	5.63
			29.32	5.18	5.18
			36.14	5.92	6.22
	1-2	32,9	27.4	5.63	6.66
			21.92	4.59	5.63
			37.02	6.07	6.66
			36.28	6.22	7.4
	1-3	32,14	30.36	5.33	6.52
	1-4	32,18	29.92	5.03	6.22
			25.18	4.74	5.92
			27.69	5.77	5.18
			27.1	5.18	6.07
			30.06	6.52	7.4
			24.44	5.63	6.22

NO.	ID	DIST	LENGT	WIDTH	MAX W
SD2 11/14/89	1-1	45,14	30.67	4.29	4.59
			35.69	6.22	6.22
	1-2	45,15	41.02	7.4	7.26
	1-3	45,21	29.77	5.92	6.37
	1-4	45,28	Broken	5.18	5.92
			25.47	4.44	5.03
			26.36	5.18	5.92
	2-1	59,17	Broken	4.59	4.74
			25.18	4.89	5.48
	2-2	59,20	Broken	3.2	5.03
			2.97	0.476	0.476
			2.14	0.547	0.547
	2-3	59,24	31.25	4.59	4.74
			28.88	5.77	5.92
			17.77	3.26	3.26
			25.62	5.92	6.37
			25.18	4.15	4.59
			25.92	3.7	4.29
			21.47	3.26	3.55
			26.66	3.7	4.29
			17.62	3.7	3.85
			25.62	5.92	5.77
			28.88	4	4.14
	2-4	59,28	23.99	4.29	4.29
			12.29	1.63	1.63
			Broken	4.59	4.59
			20.59	5.18	5.03
			Broken	4.44	4.74
			27.84	4	4.59
			Broken	4.59	4.74
			Broken	4.44	5.18
		31.4	4.74	5.03	
		26.06	5.18	4.88	

No.	ID	DIST.	LENGT	WIDTH	MAX W
SD3	1-1	31,9	0		
1/17/90	1-2	31,12	0		
	1-3	31,15	0		
	1-4	31,30	25.92	4.15	4.29
			Broken	3.41	3.41
			Broken	4.29	5.03
			39.99	4.29	4
			23.25	3.41	3.55
			30.36	3.85	4
	2-1	52,9	Broken	7.7	7.11
	2-2	52,10	35.5	7.11	7.7
	2-3	52,14	30.36	3.7	4
			27.84	4.44	4.89
			Broken	4.44	5.03
			43.24	4.44	4.74
			34.8	4.74	5.18
			26.95	4.74	4.74
			26.66	4.95	5.03
			26.06	5.03	5.47
	2-4	52,19	25.62	4.15	5.03
			25.32	4.44	5.18
			21.77	4.15	4.15
			2.85	0.848	0.848
	3-1	63,8	0		
	3-2	63,12	0		
	3-3	63,15	0		
	3-4	53,23	24.58	5.18	6.07
			Broken	4.15	4.15
			Broken	5.48	5.63
			28.29	3.26	4

NO.	ID	DIST	LENGT	WIDTH	MAX W
SD4 2/20/90	1-1	47,21	26.95	5.21	5.57
			Broken	4.36	4.85
			Broken	3.94	4.78
	1-2	47,15	31.84	6.22	6.96
	1-3	47,13	Broken	5.27	5.57
			27.1	4.91	5.76
			19.7	3.21	3.15
			Broken	5.27	5.7
	1-4	47,9	0		
	2-1	70,9	0		
	2-2	70,14	35.99	6.22	7.4
			16.69	1.69	0.571
	2-3	70,28	9.15	2.12	1.93
			28.58	4.48	4.6
			38.8	3.57	3.76
			34.36	4.54	4.6
			12.54	1.76	1.81
			Broken	4.24	4.54
	2-4	70,29	0		
	3-1	93,23	46.65	3.82	3.82
			23.7	4.79	4.54
			41.62	5.76	5.76
			34.8	5.94	6
		3.14	0.595	0.595	
3-2	93,20	2.82	0.762	0.666	
		23.1	4.6	4.91	
3-3	93,13	0			
3-4	93,7	0			

NO.	ID	DIST	LENGT	WIDTH	MAX W
SD5	1-1	56,21	30.2	4.54	4.85
3/22/90	1-2	56,10	0		
	1-3	56,8	48.13	4.97	4.48
	1-4	56,3	0		
	2-1	68,4	0		
	2-2	68,16	20.03	4.18	4.73
	2-3	68,27	0		
	2-4	68,29	0		
	3-1	87,7	Broken	5.39	5.57
	3-2	87,16	30.36	5.76	6.97
			28.88	4.48	4.85
			24.14	4.36	5.15
			25.18	4.54	4.85
			Broken	5.94	5.94
			27.84	5.45	5.7
			Broken	3.94	4.85
	3-3	87,20	39.84	5.94	6.36
			23.7	5.63	5.63
	3-4	87,22	25.32	5.57	6.06
			28.88	4.36	4.36
			29.03	6.36	5.76
			28.58	4.24	4.54
			Broken	4.6	5.15

NO.	ID	DIST	LENGT	WIDTH	MAX W
SD6	1-1	50,14	26.81	7.09	7.09
4/25/90	1-2	50,17	19.55	4.85	5.15
			31.4	4.06	4.06
			28.88	5.7	6.3
			Broken	5.76	5.82
			Broken	4.54	4.67
			21.77	3.64	4.06
	1-3	50,24	23.25	5.45	5.94
			23.55	4.79	5.45
			27.1	5.45	6.06
			26.51	5.39	5.45
			27.25	4.24	4.79
			26.51	4.85	5.57
			Broken	4.36	5.21
			28	4.85	5.63
			25.92	4.42	5.02
	1-4	50,30	0		
	2-1	19,17	25.18	5.76	6.72
	2-2	19,20	31.84	6.97	7.27
			32.58	7.27	7.39
	2-3	19,24	Broken	4.85	5.45
			Broken	5.09	5.45
	2-4	19,30	29.47	5.45	5.63
	3-1	75,20	36.58	9.4	5.7
	3-2	75,18	37.47	5.45	5.45
			34.36	6.06	5.82
			Broken	5.27	5.57
			22.95	4.54	3.94
			46.65	4.54	4.54
			30.36	3.64	3.94
			19.25	4.85	5.03
			34.65	5.45	6.67
			34.8	6.85	7.27
			27.4	4.54	5.45
			27.4	4.84	5.33
	3-3	75,17	27.99	5.15	5.45
			28.14	5.45	5.88
			22.51	5.03	4.85
			20.73	4.85	5.67
			25.92	3.88	4.6
			23.4	3.94	4.6

4/25/90	3-3	75,17	28.14	4.97	5.39
(cont'd)			Broken	4.54	5.27
	3-4	75,10	0		

NO.	ID	DIST	LENGT	WIDTH	MAX W
SD7	1-1	30,3	0		
5/24/90	1-2	30,10	0		
	1-3	30,23	0		
	1-4	30,29	0		
	2-1	55,13	32.88	6.36	6.36
	2-2	55,17	0		
	2-3	55,23	0		
	2-4	55,30	32.28	5.76	6.67
	3-1	57,10	0		
	3-2	57,16	0		
	3-3	57,21	27.4	6.06	6.24
			Broken	5.15	5.45
	3-4	57,30	0		

NO.	ID	DIST	LENGT	WIDTH	MAX W
SD8	1-1	19,4	0		
6/21/90	1-2	19,16	0		
	1-3	19,27	30.36	5.76	6.67
			31.4	5.76	6.06
	1-4	19,29	39.99	6.36	6.97
	2-1	50,10	0		
	2-2	50,17	0		
	2-3	50,24	Broken	6.67	6.6
			41.47	6.42	6.42
			26.36	6.67	6.24
	2-4	50,26	31.84	5.76	6.36
	3-1	69,3	0		
	3-2	69,7	45.91	8.18	8
	3-3	69,19	23.84	4.67	4.85
			29.32	5.67	5.76
			29.62	6.06	6.06
			22.21	5.94	5.45
			33.32	5.15	5.45
			26.66	4.85	5.15
	3-4	69,22	34.06	6.36	6.67
			36.88	6.36	6.54
			29.62	4.97	6.27

NO.	ID	DIST	LENGT	WIDTH	MAX W
SD9	1-1	19,21	40.43	7.57	7.88
7/18/90	1-2	19,17	0		
	1-3	19,16	0		
	1-4	19,5	0		
	2-1	54,4	0		
	2-2	54,8	0		
	2-3	54,12	0		
	2-4	54,25	Broken	5.45	5.45
			Broken	1.07	0.952
			Broken	1.07	1.19
	3-1	89,22	0		
	3-2	89,15	0		
	3-3	89,4	0		
	3-4	89,2	0		

NO.	ID	DIST	LENGT	WIDTH	MAX W		
SD10 8/15/90	1-1	15,15	25.92	5.15	5.15		
			18.81	3.45	3.82		
			18.07	3.33	3.88		
	1-2	15,16	41.02	7.27	7.88		
			12.42	4.3	2.6		
	1-3	15,20	18.66	4.24	4.48		
			15.11	2.73	3.03		
			14.07	3.51	3.64		
			11.94	1.82	1.94		
			17.47	2.91	3.03		
			11.94	2.3	2.67		
			17.47	3.33	3.51		
			26.66	4.54	4.54		
			14.81	2.42	2.73		
			Broken	2.42	3.33		
	2-1	34,30	Broken	3.03	3.33		
			23.61	2.73	3.03		
			Broken	3.03	3.33		
			Broken	3.64	4.24		
			Broken	2.54	2.73		
			2-2	34,18	17.33	3.33	3.39
					14.07	2.61	3.09
					Broken	3.64	3.64
					19.25	3.15	3.03
					19.99	3.64	4.06
	Broken	2.42			2.73		
	17.03	3.03			3.63		
	14.51	2.54			2.85		
	13.77	2.42			2.73		
	19.55	2.18			2.67		
	2-3	34,5	18.81	3.94	4.36		
			13.92	2.73	3.33		
			15.11	2.85	2.79		
			20.29	2.73	2.91		
			29.03	3.21	4.24		
	2-4	34,21	9.48	2.12	2.42		
			10.37	2.42	4.42		
22.96			3.33	2.79			
		11.4	2.85	2.73			
		18.36	3.64	4.24			
		21.18	3.94	5.03			

8/15/90 (cont'd)	2-4	34,21	23.7	4.54	3.33
			Broken	2.73	4.36
	3-1	44,5	17.48	4.42	4.48
	3-2	44,6	23.7	4.24	4.84
	3-3	44,12	18.66	3.03	3.33
			16.88	3.45	3.33
			25.18	3.03	4.42
			24.44	3.64	4.42
			20.44	3.03	3.64
			Broken	2.42	3.21
			19.25	2.85	4.79
			21.92	4.79	4.54
			28.14	4.85	4.18
			20.44	3.94	4.42
			Broken	2.73	4.42
			26.66	3.64	3.7
			3-4	44,21	Broken
	Broken	1.21			3.33
	Broken	2.61			0.727
	Broken	0.727			3.03

NO.	ID	DIST	LENGT	WIDTH	MAX W
SD11 9/18/90	1-1	35,3	17.03	3.03	3.94
			119.99	3.33	3.94
	1-2	35,5	0		
	1-3	35,6	22.21	5.09	5.39
	1-4	35,29	26.66	3.33	4.24
	2-1	56,6	Broken	5.15	5.94
	2-2	56,7	Broken	2.18	2.42
	2-3	56,19	Broken	5.03	5.15
	2-4	56,28	22.21	4.85	5.27
			15.11	2.73	2.85
			Broken	2.42	2.85
	3-1	75,4	0		
	3-2	75,16	0		
	3-3	75,23	26.66	4.48	5.09
			Broken	3.94	4.24
			Broken	4.54	5.27
			Broken	3.21	3.76
	3-4	75,28	25.92	4.24	5.15
			22.96	5.21	5.21

NO.	ID	DIST	LENGT	WIDTH	MAX W		
SD12 10/16/90	1-1	15,5	Broken	6.06	6.36		
			34.51	5.21	5.63		
			9.63	1.82	2.12		
			Broken	4.85	5.45		
			31.1	5.82	6.36		
			22.66	3.21	3.81		
			1-2	15,18	3.09	0.952	0.952
					18.22	4.61	4.79
					2.17	0.666	0.619
					1.43	0.405	0.405
	6.24	1.9			1.83		
	12.29	2.14			2.24		
	5.09	1.07			1		
	1-3	15,21	7.27	1.67	2.02		
			22.36	4.54	4.85		
			15.55	3.39	3.39		
			7.27	2.12	2.12		
			12.14	2.48	2.97		
			7.15	1.88	1.82		
			13.18	2.42	2.42		
			7.39	1.88	2.18		
			7.82	1.76	1.76		
			5.15	2.42	2.36		
			6.54	4.85	1.78		
			7.7	5.15	2.02		
	1-4	15,24	6.97	1.43	1.5		
			Broken	1.07	1.24		
			25.62	4.06	4.6		
			11.51	2.67	2.73		
			10	2.73	2.97		
			Broken	2.18	2.18		
			Broken	1.82	2		
			Broken	3.33	3.51		
Broken			2.73	2.97			
9.27			2.42	2.85			
2-1	41,6	Broken	1.51	2.06			
		Broken	6.36	7.33			
2-2	41,10	8.48	1.7	1.94			
2-3	41,12	3.6	2.73	1.02			
		Broken	5.15	5.64			
		Broken	5.15	5.15			

10/16/90 (cont'd)	2-4	41,17	10	2.06	2.06
			Broken	4.85	5.27
	3-1	78,5	0		
	3-2	78,19	Broken	1.67	1.9
			6.3	1.55	1.67
			Broken	1.43	1.42
			6.36	1.43	1.71
			Broken	4.85	5.33
			7.57	1.33	1.75
			3.33	1.12	1.07
			Broken	2.3	2.6
			4.18	1.82	1.94
			8.18	1.4	1.66
			Broken	1.07	1.07
	3-3	78,24	15.55	2.73	3.15
			17.48	3.64	3.82
			39.45	7.57	6.67
			15.11	3.64	3.94
			Broken	2.73	3.27
			Broken	2.24	2.54
			Broken	2.73	3.03
			Broken	1.27	1.82
			Broken	2.12	2.3
			Broken	2.06	2.24
			10.37	2.42	2.54
			25.18	3.76	4.73
			Broken	2.42	3.03
			Broken	2	2.42
	3-4	78,27	Broken	1.82	1.82
			Broken	3.03	3.21
			Broken	1.76	1.76
			Broken	2.06	2.18
			Broken	2.12	2.18

Appendix II. Number of Loimia medusa larvae collected in the plankton.

* Indicates samples which were counted for efficiency study.

Moon	Date	No. Larvae	Moon	Date	No.larvae	Moon	Date	No.Larva
New	6/20/89	2	Full	2/9/90	0		8/8/90*	15
	7/6/89	2		2/14/90	0		8/10/90*	51
	7/7/89	0	New	2/23/90	0		8/13/90	4
	7/9/89	0		3/2/90	0	New	8/20/90	276
	7/10/89	0	Full	3/9/90	0		8/22/90	134
	7/11/89	2		3/17/90	0		8/25/90	53
	7/14/89	2	New	3/24/90	0		8/29/90	0
	7/17/89	4		3/28/90	0		8/31/90*	2
Full	7/18/89	10		4/6/90	0	Full	9/6/90*	14
	7/19/89	0	Full	4/12/90	0		9/10/90*	0
	7/21/89	6		4/18/90	0		9/12/90*	6
	7/26/89	2	New	4/26/90	0		9/14/90*	12
New	7/28/89	10		5/6/90	0		9/17/90*	10
	8/8/89	2	Full	5/11/90	0	New	9/20/90*	42
	8/16/89	0		5/17/90	0		9/24/90*	10
Full	8/19/89	0	New	5/25/90	0		9/25/90	4
	8/24/89	0		6/1/90	0		9/26/90	8
New	8/28/89	0	Full	6/8/90	0		9/28/90	10
	9/6/89	0		6/15/90	0		10/2/90	8
Full	9/13/89	0	New	6/21/90	0	Full	10/3/90	8
	9/25/89	6		6/25/90	0		10/9/90	4
New	9/27/89	0		6/27/90	0		10/10/90	2
	10/2/89	0		7/3/90	0		10/12/90	0
	10/7/89	0		7/6/90	0		10/15/90	0
Full	10/18/89	0	Full	7/9/90	6	New	10/17/90	0
New	10/25/89	0		7/10/90*	14		10/19/90	0
	11/7/89	0		7/13/90*	4		10/22/90	0
Full	11/15/89	0		7/18/90*	14		10/24/90	2
New	11/22/89	0		7/20/90*	102		10/27/90	0
	12/4/89	0	New	7/22/90*	40		10/30/90	0
Full	12/15/89	0		7/24/90*	50		11/4/90	0
New	12/22/89	0		7/26/90*	8			
	1/5/90	0		7/30/90*	10			
Full	1/11/90	0		8/1/90*	20			
	1/18/90	0		8/3/90*	5			
New	1/30/90	0	Full	8/6/90*	21			

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