Demographics, production, and benthic -pelagic coupling by the suspension feeding polychaete Chaetopterus pergamentaceus in the lower Chesapeake Bay

Michelle Lynne Thompson Neubauer

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DEMOGRAPHICS, PRODUCTION, AND BENTHIC-PELAGIC COUPLING BY THE SUSPENSION FEEDING POLYCHAETE *Chaetopterus pergamentaceus* IN THE LOWER CHESAPEAKE BAY

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 of the Degree of
Doctor of Philosophy

by

Michelle Lynne Thompson Neubauer

2000
Approval Sheet

This dissertation is submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Michelle Lynne Thompson Neubauer

Approved, April 2000

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Dedication

To my family,
my husband Scott and baby Neubauer along with Chaetopterus and Wolftrap
in appreciation of their endless support and love, without which this dissertation
would have never been completed.
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DEMOGRAPHICS, PRODUCTION, AND BENTHIC-PELAGIC COUPLING BY THE SUSPENSION FEEDING POLYCHAETE
Chaetopterus pergamentaceus IN THE LOWER CHESAPEAKE BAY

Abstract

For many shallow water environments, ecosystem function depends on the cycling and flow of materials and energy between benthic and pelagic subsystems. Benthic suspension feeders often are important links between the water column and sediment in coastal ecosystems. Populations of the suspension feeding polychaete Chaetopterus pergamentaceus (previously reported as Chaetopterus variopedatus) are widely distributed along the United States East Coast, ranging from New England to Florida. This species is a structurally and functionally important member of the lower Chesapeake Bay benthic community, where it has maintained stable populations for at least the last 15 years. Little is known regarding the dynamics of this population and its role in benthic-pelagic coupling. For this study, I elucidated demographics, identified the organic matter sources fueling growth and production, determined the in situ behavior, rates and allometry of filtration, and developed an energy budget for this polychaete within the lower Chesapeake Bay estuary.

Chaetopterus pergamentaceus exhibited high seasonal and interannual variability in growth, reproduction, and secondary production. High secondary production was mainly due to the rapid growth and maturation of new recruits during summer. Highly variable interannual production was due to inconsistency in recruitment success. Spatial variations in population processes, concordant with major environmental gradients, may influence the population dynamics. Locally produced organic matter, primarily fresh phytoplankton and secondarily recycled material from microbial sources with minimal to no terrestrial input, was utilized for growth and reproduction. Chaetopterus pergamentaceus has a filtration rate comparable to oysters and has the potential to transfer large quantities of matter from the water column to the benthos. This polychaete may filter a large portion of, or an amount equivalent to, the net water column community production on an annual basis. When considered on a daily basis, the potential carbon flux may be greater than net community production. Thus, this organism plays an important role in benthic-pelagic coupling in the lower Chesapeake Bay.

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SCHOOL OF MARINE SCIENCE
THE COLLEGE OF WILLIAM AND MARY IN VIRGINIA

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DEMOGRAPHICS, PRODUCTION, AND BENTHIC-PELAGIC COUPLING
BY THE SUSPENSION FEEDING POLYCHAETE *Chaetopterus pergamentaceus*
IN THE LOWER CHESAPEAKE BAY
GENERAL INTRODUCTION

In most aquatic systems the structure, biomass, and metabolism of the benthos are strongly related to the rate and nature of organic matter supplied (Hargrave & Peer 1973; Reimers 1988; Jumars & Wheatcroft 1988; Grebmeier et al. 1988, 1989; Grebmeier & McRoy 1989; Johnson & Wiederholm 1992; Fitzgerald & Gardner 1993; Noji et al. 1993). Close coupling between pelagic and benthic subenvironments facilitates the high benthic invertebrate secondary productivity of the coastal zone that ultimately makes its way to commercially valuable species such as fish and crabs (Nixon 1988; Diaz & Schaffner 1990). Furthermore, in shallow systems the benthos may greatly influence both the structure and function of pelagic communities (Doering 1989; Sullivan et al. 1991). Phytoplankton production in the water column and subsequent consumption by the benthos are important driving forces in the carbon and nutrient dynamics within shallow aquatic systems (Capone & Kiene 1988; Seitzinger 1988). Thus, our understanding of major processes governing the structure and function of aquatic ecosystems depends on elucidation of the mechanisms and processes linking pelagic and benthic processes.

Suspension feeding organisms are important links between pelagic and benthic subsystems (Dame et al. 1979; Ward et al. 1990; Jumars 1993; Alldredge & Jackson 1995). Benthic suspension feeders have been shown to retain even the smallest particles with relatively high efficiency (Wooton 1990). For example, suspension feeding sponges can extract greater than 95% of the bacteria from water they filter.
(Pile et al. 1997a & 1997b). Grazing by the benthos has been suggested as a primary mechanism controlling phytoplankton biomass in some estuaries (Cloern 1982; Alpine & Cloern 1992; Cohen et al. 1984). In the open ocean large fast sinking particles, such as the fecal pellets of suspension feeding salps and copepods, are a major mechanism for the transport of organic matter to the deep sea (Wiebe et al. 1979; Fortier et al. 1994). The production of fecal pellets by zooplankton also is important in many coastal systems and lakes (Andersen & Nival 1988; Ward et al. 1990). In coastal systems such as estuaries, where benthic suspension feeders have ready access to material suspended in the water column, due to the shallow depths and physical mixing, the importance of benthic suspension feeders is maximized (Dame 1979).

The large, tubiculous, suspension feeding polychaete *Chaetopterus pergamentaceus* (provisional specification Mary Petersen, pers. comm.; Eckberg & Hill, 1996; formally *Chaetopterus variopedatus* e.g. Enders 1909) is an abundant and functionally important species within the soft-sediment, benthic community of coastal and estuarine systems (Schaffner, 1990; reported as *Chaetopterus variopedatus* - Enders 1909; Eckberg & Hill, 1996). This worm is a biomass dominant and has been shown to be important in determining the structure of the soft-bottom benthic community of lower Chesapeake Bay where it has been observed to maintain relatively stable populations for at least the last 15 years (Huggett 1987; Schaffner 1987, 1990). Benthic-pelagic coupling by this species may be an important factor in ecosystem function, but remains largely unresolved. *Chaetopterus pergamentaceus* inhabits a parchment-like semicircular tube, which penetrates up to 15 cm or more.
below the sediment surface. Water pumped through the tube with specialized parapodia is filtered with a mucus net and then formed into a food ball for ingestion (Enders 1909; MacGinitie 1939; Brown 1975; Flood & Fiala-Medioni 1982; Riisgård 1989; and others). Particles as small as 1.2 \( \mu \text{m} \) can be retained with 90% efficiency (Jørgensen et al. 1984) while smaller particles and dissolved organic matter may be retained by physio-chemical attachment to the mucus itself (Wooton 1990). The tubes are well oxygenated, house commensal organisms and are likely to have significant effects on sediment biogeochemistry. The tubes protrude above the sediment surface and with their associated epifauna modify water-sediment interactions, which may, in turn, alter sediment resuspension and transport processes (Wright et al. 1997). The feeding activity of this polychaete alters particle size distributions via pelletization of suspended material, and enhances deposition of organic matter.

In this dissertation I examine the role *C. pergamentaceus* plays in benthic-pelagic coupling in a representative estuarine/coastal environment, the lower Chesapeake Bay. I determined the demographics of *C. pergamentaceus*, the organic matter sources fueling growth and production, and the *in situ* behavior, rates and allometry of filtration within the lower Chesapeake Bay estuary.

In Chapter 1 I discuss the population dynamics of *C. pergamentaceus*, which I investigated over a two year period beginning January 1994 through December of 1995. Demographic parameters including density, population size structure and reproductive activity, and growth rates of this polychaete were determined and used
to calculate secondary production. The role of this polychaete in benthic-pelagic coupling is evaluated based on the demographic results.

In Chapter 2 I discuss the local scale demographics of *C. pergamentaceus* population in the lower Chesapeake Bay and potential links to environmental gradients.

In Chapter 3 I discuss the sources of organic matter available to *C. pergamentaceus*, consider which sources of organic matter fueled reproduction versus growth, and examine the temporal and spatial variations in the source(s) of organic matter. I employed a combination of methods including visual observations (dissecting and epifluorescence microscopy), and measures of chlorophyll *a*, carbon and nitrogen, lipid biomarkers, and stable isotopes for samples collected in 1995. The role of this worm in benthic-pelagic coupling is evaluated based on these results.

Chapter 4 discusses the *in situ* behavior, rates and allometry of filtration of *C. pergamentaceus*. The *in situ* filtration rates were measured during the spring, summer and fall for worms spanning a range of sizes using thermistor flowmeters.

In Chapter 5 I use the results of the population dynamics (Chapter 1), organic matter sources (Chapter 3), filtration rates (Chapter 4), and biodeposition analyses (Schaffner unpub. data) to develop an energy budget for *C. pergamentaceus* within the lower Chesapeake Bay. The role of this polychaete in benthic-pelagic coupling is evaluated based on the results from the energy budget analysis.
Chapter 1

Population biology and secondary production of the suspension feeding polychaete *Chaetopterus pergamentaceus*: Implications for benthic-pelagic coupling in the lower Chesapeake Bay

Will be submitted to Limnology and Oceanography with the following authors: M.L. Thompson and L.C. Schaffner.
The suspension feeding polychaete *Chaetopterus pergamentaceus* is a structurally and functionally important annelid which is widely distributed in marine and estuarine communities along the east coast of the United States including at subtidal depths in the lower, polyhaline Chesapeake Bay estuary where this study was conducted. This polychaete functions as a coupling agent, linking the water column and the benthos. We found high seasonal and interannual variations in growth, reproduction, and secondary production as well as the potential for iteroparous spawning. Recruitment success varied three fold interannually showing a seasonal peak pulse in the summer with limited recruitment throughout the fall. A two cohort model consisting of juveniles and adults exhibiting seasonality best described the data even though more than two age classes were likely present. High secondary production was mainly due to rapid growth and maturation of new recruits, although highly variable interannual production was likely due to inconsistency in recruitment success. We also found that tube production is a significant part of the total worm production and should be included in future studies of this polychaete. General trends of gross primary production and worm production are distinctly similar with between 35 to 100% of the net water column community production in the region necessary to support the secondary production of these worms. Thus, this organism seems to play a strong role benthic-pelagic coupling in the lower Chesapeake Bay.
INTRODUCTION

For many shallow water environments, ecosystem function depends on the cycling and flow of materials and energy between benthic and pelagic subsystems. Numerous studies have now demonstrated that benthic suspension feeders are important links between the water column and sediment in coastal ecosystems (Graf 1992; Heip et al. 1995) where they can exhibit high densities and biomass, (e.g. at times over 1000 animals m$^{-2}$ in the southern and over 2000 animals m$^{-2}$ in northern San Francisco Bay; Cloern 1982; Alpine and Cloern 1992). Benthic suspension feeders increase nutrient regeneration (Doering 1989) partially due to bioturbation and bioirrigation and the resulting indirect effects such as stimulation of microbial processes (Barbanti et al. 1992) and partially as a result of excretion (Kemp et al. 1990), which may increase phytoplankton production (Doering et al. 1986; Prins and Smaal 1990). Yet, suspension feeding can consume more than 50% of the water column production which may result in a reduction of planktonic biomass (Cohen et al. 1984; Loo and Rosenberg 1989; Alpine and Cloern 1992; Gerritesen et al. 1994). Benthic suspension feeders often enhance deposition of material from the water column, influence particle transport potential by pelletization of suspended material, and act as sinks for organic matter (Haven and Morales-Alamo 1970; Tagon et al. 1984; Loo and Rosenberg 1989; Heip et al. 1995; Pile et al. 1997a and b). Thus, benthic-pelagic coupling affects food web dynamics and the cycling of organic matter and nutrients.

The strength of biologically mediated benthic-pelagic coupling depends on factors such as local hydrodynamic conditions, the quality and quantity of suspended material, and the filtration capacity of a suspension feeding population. Hydrodynamic
conditions influence particle availability by enhancing mixing of the water column, which affects particle delivery to the near-bed region (Wildish and Kristmanson 1984; Fréchette et al. 1989). Further, feeding behavior may change in differing hydrodynamic conditions (Wildish and Kristmanson 1997 and references therein). The filtration capacity of a benthic suspension feeding population is dependent upon intrinsic factors. Feeding mechanisms vary markedly among benthic suspension feeders, which often use mucus as a trap (e.g. mucus net in polychaetes and ascidians) or beating cilia, flagella or setae (e.g. sponges, barnacles), and may involve particle selection (Wildish and Kristmanson 1997). Differential particle size retention efficiencies are important in determining the type, quantity, and quality of material filtered from the water column, thereby influencing the organism-mediated flux of material to the benthos. In general, particles larger than 2 μm are effectively filtered by most macrobenthic suspension feeders. Smaller particles may be efficiently removed by sponges (Pile 1996), some bivalves (Wright et al. 1982; Jørgensen et al. 1984) and some polychaetes (Flood and Fiala-Médioni 1982). Encounter rates are of equal importance to retention efficiencies when calculating particle fluxes; a high encounter rate may offset a low retention efficiency (Shimeta and Jumars 1991). Further, the filtration capacity of the population may be dependent upon the population size structure. A higher density results in greater grazing pressure which leads to increased benthic-pelagic coupling (Doering et al. 1986). Also, organism size has been shown to affect filtration rate with larger organisms having increased gross filtration rates (i.e. Mohnenberg and Riisgård 1979).

Other demographic parameters may affect the flow of matter and energy through
an ecosystem. Life span affects the turnover time for carbon and other nutrients (Fortier et al. 1994). Organisms with longer life spans (e.g. some bivalves) sequester carbon, and nutrients within their tissues for longer periods of time than short-lived animals such as jellyfish or hydroids. Organism growth rates can have an important impact, with faster growing animals sequestering nutrients and essential dietary compounds rendering them unavailable to other organisms. Further, size affects the filtration rate (see above), so growth rate can affect filtration capacity. By virtue of their size, large bivalves and other macrofauna serve as greater storage reservoirs compared to smaller organisms. Seasonal dynamics of organisms play an integral part in the timing of growth and storage. Thus, elucidating the population dynamics and secondary production of benthic suspension feeders will lead to a better understanding of the function of aquatic ecosystems.

The large, tubiculous, suspension feeding polychaete *Chaetopterus pergamentaceus* (provisional specification Mary Petersen, pers. comm.; Eckberg and Hill, 1996; formally *Chaetopterus variopedatus* e.g. Enders 1909) is an important component of the soft sediment benthic community of lower Chesapeake Bay where it has been present since at least 1951 (Klingel). This polychaete has been observed from the bay mouth region as far north as the Rappahannock River including the York River as well as the Piankatank River, while maximum abundances occur within the central basin of lower Chesapeake Bay (Wass 1972; Schaffner 1987; personal observation). Relatively stable populations of this worm in the lower bay have been noted for at least the last 15 years, with densities of ≥100 individuals m\(^{-2}\) for the region between Wolf Trap Light and the York Spit Channel are known from the
1980s (Huggett 1987; Schaffner 1987, 1990). This polychaete has been reported in other marine and estuarine communities along much of the east coast of the United States between New England and Florida (reported as *Chaetopterus variopedatus* - Enders 1909; Eckberg and Hill, 1996). Benthic-pelagic coupling by this species may be an important factor in ecosystem function, but remains largely unresolved. A previous investigation demonstrated positive effects of *C. pergamentaceus* on the density and diversity of the benthic community within the lower Chesapeake Bay (Schaffner 1990). This polychaete inhabits a parchment-like semicircular tube that can penetrate over 15 cm below the sediment surface. Water, which is pumped through the tube with specialized parapodia, is filtered with a mucus net and then formed into a food ball for ingestion (Enders 1909; MacGinitie 1939; Brown 1975; Flood and Fiala-Medioni 1982; Riisgård 1989). Particles as small as 1.2 μm can be retained with 90% efficiency (Jørgensen *et al.* 1984). The tubes are well oxygenated, house commensal organisms and are likely to have significant effects on sediment biogeochemistry. The tubes and associated epifauna modify water-sediment interactions and thus alter sediment resuspension and transport processes (Wright *et al.* 1997).

Some aspects of the ecology of *C. pergamentaceus* are known. McNulty and Lopez (1969) reported year-round recruitment of *C. variopedatus* in Florida, while in North Carolina recruitment occurs in early summer with rapid growth to adulthood by the end of summer (Enders 1909). Within Chesapeake Bay, this polychaete: 1) demonstrated a strong inverse relationship between juvenile growth rates and density when data from a low and high recruitment year were considered and 2) exhibited
spatial patterns in juvenile density and ash free dry weight concordant with environmental gradients within a high recruitment year (Chapter 2 which is Thompson and Schaffner 2000). The role of specific gradients requires further investigation (Chapter 2).

This study investigated the population dynamics of the large infaunal benthic suspension feeder, *C. pergamentaceus*, within the lower Chesapeake Bay over two consecutive years. Demographic parameters including density, age structure, reproductive activity, and growth rates were measured because they reflect the potential for B-P coupling. Secondary production was calculated since it reflects a throughput component. Information was gathered through field studies in 1994 and 1995 with subsequent laboratory analysis.

**METHODS**

SITE – The study region is located within lower Chesapeake Bay encompassing approximately 54 km² (Figure 1-1). This region has water depths of 10 - 15 m, bottom water salinities of 20-27 ppt and a annual range in bottom water temperature of 4-25°C. The mean tidal range in this region is 60 cm with maximum tidally-induced current speeds of 20-40 cm s⁻¹ at 1 m above the bed. Sediments are primarily silts (40 - 50%) and fine sands (40 - 50%) (Schaffner et al. 2000). The study region does not suffer hypoxia or anoxia during the summer as occurs further north in the bay. The benthic fauna consists of a diverse assemblage of suspension and deposit feeders with *Chaetopterus pergamentaceus* often being the biomass dominant (Schaffner 1990; Wright et al. 1997). On the western edge of the study region is the Wolf Trap
Figure 1-1. Study site within the lower Chesapeake Bay.
(WT) site which has been extensively studied, providing historical biological, geological, and physical information on the lower estuary (Schaffner 1990; Wright et al. 1992). In the southern area of the study region is the Cherrystone (CS) site where concurrent investigations of the biology, geology, and physics of the region were conducted (Wright et al. 1997; Schaffner et al. 2000).

FIELD SAMPLING – Within the study region WT, CS, and 10 randomly selected stations were sampled beginning January 1994 and ending December 1995 (Figure 1-1). Worms were collected using a Ocean Instruments spade box core (20 x 30 x 30 cm deep) with one and two core sample(s) per station collected in years 1 and 2, respectively. The sampling interval was monthly during winter/spring and semi-monthly during the summer/fall periods of recruitment and rapid growth. Some scheduled 1995 sampling dates were missed due to extreme weather and loss of a boat engine. Three methods were utilized to ensure complete removal of C. pergamentaceus from the sediment. First, a 5 cm diameter by 5 cm deep core was collected and fixed intact to ensure capture of fragile new recruits. Second, surface sediment from the 0 to 2 cm depth interval of the entire box core was removed and elutriated through a 125 μm screen to collect very small worms that are easily damaged. Last, larger worms were dissected directly from the sediment. All C. pergamentaceus removed from the cores were fixed immediately in 10% formalin and subsequently stored in 2% formalin until analysis.

Sediment temperature was measured in the top 0.5 cm. Bottom water samples (1 m above sediment) for salinity (refractometer) and dissolved oxygen content
(Winkler titration by the Analytical Services Center at the Virginia Institute of Marine Science) were collected by Niskin Bottle.

For this study, labile organic matter input to the study region is estimated from sediment photosynthetic pigments (chl-a and phaeopigments), which provide an indication of food availability for benthic animals (Josefson and Conely 1997). From each of three box cores collected at the CS and WT sites on each sampling date a 2.7 cm diameter by 0.5 cm deep subcore was collected for spectrophotometric chl-a analysis (Lorenzen 1967; as modified by Pinckney et al. 1994).

**Population Structure** — Density, population size structure and reproductive condition of *C. pergamentaceus* were determined for each sample. Length of body region A and width at setiger 4 (hereafter referred to as head area; Figure 1-2), as well as overall length (when possible) were measured to the nearest 0.1 mm using a dissecting microscope equipped with an ocular micrometer for smaller specimens and Vernier calipers for larger specimens. Comparisons of $r^2$ values from regressions of each measurement versus ash-free dry weight (AFDW) were used to determine the most reliable indicator of size (the largest $r^2$).

Size frequency histograms relating head area (most reliable indicator of size, see Results) to number of individuals were constructed for each sampling period. New recruits in the population were delineated based on distinct modes in the size distribution; however, once adult size is reached cohorts could not be separated. The software package MULTIFAN, a log likelihood-based method that simultaneously analyzes multiple length frequency data sets, was used to estimate parameters of the
Figure 1-2. Schematic of *Chaetopterus pergamentaceus* indicating body regions (adapted from Gilbert 1984). HW is width of Region ‘A’ at setiger 4; HL is length of region ‘A’.
von Bertalanffy growth function from head area-frequency data using all sampling dates (Fournier et al. 1990; Baelde 1994). Use of MULTIFAN assumes individual growth rates fit a von Bertalanffy function in which size increases at a rate proportional to the distance from the maximum size (Barry and Tegner 1989). We chose this model because the von Bertalanffy growth model is the most commonly used model to describe growth of fishes (Pauly 1982), bivalves (Brousseau 1978; numerous references within Dame 1996), crustaceans (Fournier et al. 1991) and has been used to model deep-sea macrobenthos (Gage 1995). The von Bertalanffy model for individual growth is favored by many researchers for its generality and derivation from allometric and metabolic relationships; hence it should be useful to model worm growth. A generalized form of this function is

\[ S_t = S_{\infty} (1 - be^{-\rho (t+a)}) \]

where \( S_t \) is the size of an individual at time \( t \), \( S_{\infty} \) is the theoretical maximum size, \( b \) is a scaling factor to account for a size at recruitment larger than 0, and \( \rho \) is the Brody growth coefficient (higher values of which result in a more rapid approach to asymptotic size) (Barry and Tegner 1989). The Brody growth coefficient is used to estimate the von Bertalanffy growth constant, \( K \) (\( K = -\ln \rho \)). This growth function is characterized by exponentially decaying change in size, with no lag in early life.

**Fecundity Estimates** - Female fecundity was determined by removing the first ovigerous segment in the tail region, hereafter referred to as Segment C-1 (body region C segment number 1; Figure 1-2), and extracting all oocytes. Since many
worms were broken during sampling, all females in which an intact Segment C-1 could be accurately identified were used for analysis. Data are presented as oocytes per segment rather than oocytes per individual because only Segment C-1 was analyzed. Following dilution and mixing of oocytes with Milli-Q water, 50 μl aliquots were viewed using an image analysis system (Image Pro Plus 2.0) connected to a stereozoom dissection scope (30x) interfaced with a Hitachi color video camera. Eggs in nine fields were enumerated and measured (generally equated to several hundred eggs, but occasionally fewer). Regressions were used to investigate relationships between worm size, egg size, number of eggs per segment C-1, egg diameter and time.

**Production Estimates** - Production (g AFDW m⁻² yr⁻¹) for the sampling period was estimated using the increment summation method (Downing and Rigler 1984). Calculations were completed assuming two cohorts (adults and juveniles) during the summer months with a melding into one adult cohort in the fall (see results) using the following equation:

\[
P = \bar{N}_{1,2} (\bar{m}_2 - \bar{m}_1) + \bar{N}_{2,3} (\bar{m}_3 - \bar{m}_2) + ... + \bar{N}_{(k-1),k} (\bar{m}_k - \bar{m}_{(k-1)})
\]

where \(\bar{N}_{1,2}\) is the average population density over the interval between sampling date 1 and sampling date 2; \(\bar{m}_1\) is the average mass (AFDW) of an individual on sampling date 1, and \(k\) is the number of sampling dates included in the time period for which production is being calculated. These secondary production estimates were made using AFDWs calculated from the best fit regression, a weighted least squares regression (see results) relating organism size (head area) to AFDW. The regression
relating AFDW to worm size was based on male and female worms ranging from juveniles to fully gravid to partially and totally spent individuals. As worms age, energy is diverted from somatic growth to gamete production until a dominant proportion of production is reproduction in adults. Hence production due to egg release into the water column was calculated separately from adult production.

Tube production was estimated separately using two separate best fit regressions that related tube AFDW to worm AFDW (see results). Tubes were rinsed with a variable high pressure hose such that as much adhering sediment could be removed as possible without loss of worm produced tube material. Tubes were then dried and ashed at 450°C for 4 hours.

Egg production was estimated using egg diameter to obtain egg volume which was then converted to wet weight using the density of protoplasm (1.2 g cm$^{-3}$) (Seitz and Schaffner 1995). The conversion 0.9 AFDW / 6.0 wet weight (Seitz and Schaffner 1995; Waters 1977) was used to estimate AFDW. The number of eggs per Segment C-1 was estimated, then multiplied by the number of ovigerous segments per adult ($\# \text{ of segments} = 7.469 \times \text{head area}^{0.25} - 5.55; p < 0.001, r^2 = 0.83$), then divided by 2 since the number of eggs per segment decreases toward the tail thus resulting in a conservative estimate of the number of eggs per female. This result was multiplied by the number of females per unit area (0.5 x the number of adults), yielding the number of eggs m$^{-2}$ which was then multiplied by g AFDW egg$^{-1}$, resulting in g AFDW m$^{-2}$. The contribution of sperm may also be important but was not estimated.

STATISTICAL METHODS – Sokal and Rohlf (1981), Neter et al. (1990),
Underwood (1997), Agresti (1990) and Dr. R. Diaz (personal comm.) were used as guides for the statistical analyses. Most data were analyzed using the SAS program on a UNIX system. However, multiple analysis of variance (MANOVA) was analyzed in MINITAB for the PC and some regressions were computed with Deltagraph 4.0. Analysis of variance (ANOVA), analysis of covariance (ANCOVA), and multiple analysis of variance (MANOVA) were used to investigate spatial and temporal differences. Normality of the data and homogeneity of variances were tested prior to all statistical procedures. Whenever possible, parametric tests were performed.

RESULTS

PHYSICAL CONDITIONS – According to the USGS database, river runoff from the Susquehanna at Conowingo, MD in 1994 was almost double that of 1995 with a low spring and late summer run off in 1995. However, at our site in the lower bay, trends in sediment temperature, bottom water dissolved oxygen, and salinity were similar for 1994 and 1995 (Figure 1-3). Using Wilks’ Lambda in a MANOVA analysis (F = 0.363; DF = 3, 4; p = 0.78) no significant differences in these physical parameters between years were detected.

ANOVA analysis of labile organic matter (Chl-a plus degradation products such as phaeopigments) indicates that there were more pigments at CS than at WT (F = 14.82; DF = 1; p = 0.001) and there was more in 1994 compared to 1995 (F = 56.21; DF = 1; p = 0.001; Figure 1-4; data were homoscedastic Cochran’s C = 0.24; k = 8; DF = 1; p > 0.05).
Figure 1-3. Physical parameters of the water mass in 1994 (squares) and 1995 (circles). Each point represents an average of two points.
Figure 1.4. Chlorophyll a and phaeopigments through time.
Figure 1-5. Population parameters of *Chaetopterus pergamentaceus* in 1994 and 1995. Bars are standard error. Growth rates (± standard deviation) in mg AFDW per day are denoted adjacent to juveniles cohorts (gray markers). Dotted line represents an estimate based on the previous years data.
Figure 1-6. Size (head area) histograms for each sampling date. All sampling dates occurred at the end of every month except where noted. In 1994 one box core was taken at each of 12 stations on every sampling date. In 1995 two box cores were taken at each of 12 stations on each sampling date. Note Y-axis scale changes.
POPULATION STRUCTURE—Visual inspection of size frequency histograms indicate that *C. pergamentaceus* recruited in late July/early August in 1994 and in late June/July in 1995 (Figures 1-5 and 1-6). Growth occurred throughout the summer and fall with rapid growth of juveniles into adult size by the fall. In 1995, recruitment was nearly three fold that of 1994. Average densities of *C. pergamentaceus* ranged from 30 to over 250 individuals m\(^{-2}\) (Figure 1-5). Aside from a short recruitment peak exceeding 1000 individuals m\(^{-2}\), densities were comparable to those reported previously for the central basin of the lower bay (Diaz *et al.* 1985; Huggett 1987; Schaffner 1990) but are much higher than those of intertidal/shallower water sites such as \(-1\) m\(^{-2}\) in North Carolina (Enders 1909), <1 m\(^{-2}\) in South Carolina (Michael Grove, pers com.), or \(-25\) m\(^{-2}\) for all polychaetes including *C. variopedatus* in Florida (McNulty and Lopez, 1969). Densities were highest in the late summer following juvenile recruitment.

The Cochran-Mantel-Haenszel statistic, a type of \(X^2\), \((X^2 = 5.626; \text{DF} = 1; p = 0.02)\) indicated that on any given date the male:female ratio varied; however, the ratio was 50:50 averaged over the entire study period. The size data were not normally distributed (Shapiro-Wilks test, \(p < 0.0001\)) due to bimodality arising from the convergence of two cohorts, yet were homoscedastic (Cochran's \(C = 0.51; k = 2, \text{DF} = 286; p > 0.05;\) Underwood 1997). The Kruskal-Wallis test of analysis of variance by ranks showed that the mean size of males and females did not differ \((X^2 = 0.20; \text{DF} = 1; p = 0.65)\).

MULTIFAN length-frequency analysis yielded a two-cohort model that best described the length-frequency data with a 9923.0 log likelihood of best fit. Values
(± SD) for the theoretical mean asymptotic size (head area) if the worms were to grow indefinitely are $S_\infty = 168 \text{ mm}^3 ± 17$ and the von Bertalanffy $K = 0.81 \text{ year}^{-1} ± 0.01$, higher values of which result in a more rapid approach to asymptotic size. It should be kept in mind that while $S_\infty$ is the average asymptotic size estimated for the population, the asymptote may be greater or smaller for the individual. It is not uncommon to find a few older individuals that are considerably larger than the estimated asymptote (Ricker 1979), as was the case in this study.

It is likely that more than two age classes of worms exist at any one time since tagging of individual worms in a population in South Carolina has shown that $C. pergamentaceus$ can live over three years (Michael Grove, pers. comm.). Only about 25% of the tagged individuals in the intertidal survived through the summer, with slightly less mortality in the subtidal (Michael Grove, pers. comm.). Thus, the proportion of individuals in age class 2 or greater for the present study is likely to be small. Further, MULTIFAN yielded a mortality rate of 2.7 year$^{-1}$ for our data indicating the annual survival rate was around 7%. However, this modeled rate appears to be highly influenced by the 1995 recruitment data and the actual survival rate between years among adults would seem to be somewhat higher (Figure 1-5). An assumption of two cohorts, juveniles and adults, seems a reasonable approximation.

Modeling of worm growth using MULTIFAN showed the seasonal growth amplitude was $0.950 ± 0.008$ (on a scale of 0, no seasonal oscillation in growth, to 1, no growth during some seasons) indicating intense seasonal oscillations in growth. This seasonal growth can be seen in the remarkably similar trends within cohorts.
between years indicating that age was an important factor in growth (Figure 1-5). High growth rates occurred in the late summer among new recruits and juveniles while the mean size of adult worms decreased throughout the winter into late spring.

An ANCOVA showed no significant differences between the slopes of the regression lines within the adult cohort indicating head area decreased at the same rate in both years (F = 3.89; DF = 1, 14; P > 0.05). The ANCOVA indicated that head area was significantly larger in 1994 compared to 1995 (F = 4.54, DF = 1, 15; p < 0.001). This suggests that the rate of decline in the adult population is not dependent on the average size of individuals in the overwintering population.

An ANCOVA between the juvenile cohorts showed a significant difference in slopes of regressions of head area through time (July through September) between 1994 and 1995 (F = 5.84; DF = 1, 11; p < 0.05). This indicates that the juvenile cohort grew faster in 1994 (head area = 0.87 * day + -178.9; n = 77; r² = 0.73; p = 0.0001) compared to 1995 (head area = 0.50 * day + -85.5; n = 82; r² = 0.74; p = 0.0004). Slower growth of the 1995 cohort may be related to their spawning behavior. In 1995 individuals invested energy into reproduction; a phenomenon not seen in 1994 (see discussion). The 1995 juvenile cohort showed limited somatic growth in the last couple of weeks in August yielding a lower production value for the cohort with a corresponding increase in oocyte production when nearly all the adult cohort had disappeared (Table 1-1). Also, given higher worm densities in combination with lower labile organic matter (Figure 1-4), a slower growth rate in 1995 might be expected since growth rates were found to be density-dependent (Thompson and Schaffner 2000).
Table 1-I. Secondary production estimates of *Chaetopterus pergamentaceus* from the Lower Chesapeake Bay. Data are in g AFDW $^{-1}$ sampling interval$^{-1}$ except data in brackets [ ] which are in g C m$^{-2}$ sampling interval$^{-1}$.

<table>
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<th>Year</th>
<th>Month</th>
<th>Adults</th>
<th>Cohort 1</th>
<th>Cohort 2</th>
<th>Oocytes</th>
<th>Worm Tubes Total</th>
<th>Grand Total</th>
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</table>

$^1$Back calculated from 1994 data due to missing data.
**FECUNDITY** - Gravid females were found from May 1994 throughout most of the remainder of the study. However, the percentage gravid could not be determined since sex was determined by the presence of eggs or sperm and completely spent small individuals could not be differentiated from juveniles. Spawning was not synchronous among individuals or absolute within an individual. Most female worms appeared to be partially spent at all times. In both years, gravid females were abundant by May. Fecundity was high, ranging from 150,000 to greater than 1 million eggs per female which is comparable to other large infaunal polychaetes including *Loimia medusa* (Seitz and Schaffner 1995 and references therein) and to what has been observed in laboratory experiments with *C. pergamentaceus* (Eckberg and Hill 1996).

Observations of gravid females and recruitment data indicate that spawning took place either continuously or at several times during the summer through fall. No statistical relationships were noted among egg diameter vs. time, number of eggs in segment C-1 vs. time, egg diameter vs. number of eggs in segment C-1, number of eggs in segment C-1 vs. female size, nor egg diameter vs female size. By virtue of their larger size, which equates to more ovigerous segments, larger females will produce more eggs; but there were not more eggs per segment nor were the eggs larger. Further, larval development time could not be determined from this study since spawning was not epidemic and larvae may have been imported from other areas. However, assuming all new recruits were spawned within the Chesapeake Bay, then larval development time could be equal to or less than one or two months.

**SECONDARY PRODUCTION** – Head area was significantly related to AFDW and
can be described by the equation \( \text{AFDW} = [(0.0224 \times \text{length}) + (0.0303 \times \text{width})]^3 \) \( (N = 40, r^2 = 0.93, p < 0.001; \) due to heteroscedasticity, observations were weighted by \( 1/\text{variance} \)). Estimates of secondary production were based upon this regression. Conversion from AFDW to carbon were made using 0.9 g AFDW = 0.5 g carbon (C) (Table 1-I; Waters 1977). Due to their high growth rate, production for the juvenile cohorts was generally positive. In contrast, adult production was usually negative due to declines in size and density, except in late 1994 when the juvenile and adult cohort became indistinguishable resulting in positive production for the adult cohort.

Production estimates for the adult cohort in 1994 vary dramatically between sampling dates and are likely due to the combined effects of spawning, growth and patchiness (Table 1-I). Worm size and density declined throughout the winter resulting in negative production in February and March. In April, worm size and density increased suggesting growth and/or patchiness resulted in positive production estimate. Production remained positive in May, despite a decrease in density, suggesting that positive production in this period was mainly due to worm growth. Negative production in June may have been due to spawning; as density and worm size declined, but oocyte production was high. Thus, it is likely that energy was diverted into reproduction rather than growth and potentially some post spawning mortality occurred. In mid-July a few large polychaetes were collected (due to patchiness or rapid growth of individuals) resulting in a large positive production. Two weeks later, these worms were not collected (due to patchiness or post spawning mortality of larger older individuals) and a negative production estimate was obtained. Neither density, worm size, nor oocyte production changed appreciably from the end
of June to the end of July resulting in near zero production. Variable adult production from mid-August to mid-September is due to worm growth, decreased energy toward reproduction, and a loss of larger worms which is likely post spawning mortality. Rapid growth of the juveniles into the adult cohort with continued growth through the fall resulted in positive production for the population for the remainder of the year.

Production trends in 1995 were far less variable, yet generally similar to 1994. Density and worm size declined throughout the winter and spring resulting in negative production. Since more samples were collected on each sampling date and the density of worms was greater in 1995, any effects of patchiness that may have influenced the 1994 production calculations were removed in 1995. The juvenile cohort production in 1995 was greater in magnitude on nearly all sampling dates due in part to the much higher densities observed in 1995. A very large estimate of production for mid-August 1995 is due to the presence of a second juvenile cohort that became indistinguishable from the first juvenile cohort in that sampling period.

Excluding tube production, adults accounted for 15% of total worm production in 1994 and -17% in 1995; whereas juveniles accounted for 17% and 105%, respectively. Egg production accounted for 70% and 12% in 1994 and 1995, respectively. For the entire study period, adults resulted in negative production (-10%), juvenile and egg production accounted for most of the production (81% and 28% respectively). On a per capita basis, juveniles were only 50% as productive in 1994 as 1995, excluding any egg production. The exceedingly high production of the second juvenile cohort in 1995, which grew rapidly but only for a very short time,
vanquishes the intuitive conclusion of higher per capita production in the overall faster growing juveniles of 1994.

Tube production was calculated using two regressions relating tube AFDW to worm AFDW, one regression for actively growing worms [tube AFDW = \exp(-0.156) \cdot (\text{worm AFDW}^{0.87}); N = 6; r^2 = 0.77] and another regression including overwintering worms [tube AFDW = \exp(1.817) \cdot (\text{worm AFDW}^{1.37}); (N = 9; r^2 = 0.76)]. Estimates of tube production were based upon these regressions, conversions to carbon (C) were made using 0.9 g AFDW = 0.5 g C (Table 1-1; Waters 1977). Total tube production for the population was estimated to be 20 and 28 g AFDW in 1994 and 1995 respectively.

On an areal basis, and excluding tube production, the estimate of worm secondary production for adults in 1994 was 0.98 g C m\(^{-2}\) compared to -3.17 g C m\(^{-2}\) for 1995 (Table 1-1). The rapidly growing juveniles produced 1.16 g C m\(^{-2}\) in 1994, whereas 18.86 g C m\(^{-2}\) was produced in 1995. Egg production was 4.6 and 2.28 g C m\(^{-2}\) in 1994 and 1995 respectively. Tube production was 11.3 and 15.9 g C m\(^{-2}\) in 1994 and 1995 respectively. Estimates for each cohort, plus the contribution of the eggs and tubes, indicates production of 18.1 and 33.9 g C m\(^{-2}\) in 1994 and 1995 respectively with an average annual production of 26 g C m\(^{-2}\) for the entire period studied.

The ratio of annual production to mean biomass (P/B ratio) was calculated as 2 and 2.4, excluding and including tubes respectively (Table 1-II). However taken on a yearly basis the P/B ratio ranged from 1 to 3.5 and from 1.7 to 3, for 1994 to 1995, excluding or including tubes respectively.
Table 1-II. Production to biomass estimates of *Chaetopterus pergamentaceus* from the Lower Chesapeake Bay.

<table>
<thead>
<tr>
<th></th>
<th>Biomass (g C m(^{-2}))</th>
<th>Production (g C m(^{-2}) yr(^{-1}))</th>
<th>P/B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Excluding 1994</td>
<td>6.7</td>
<td>6.7</td>
<td>1</td>
</tr>
<tr>
<td>Excluding 1995</td>
<td>5.2</td>
<td>18.1</td>
<td>3.5</td>
</tr>
<tr>
<td>Tubes Average</td>
<td>6</td>
<td>12</td>
<td>2</td>
</tr>
<tr>
<td>Including 1994</td>
<td>10.7</td>
<td>18.1</td>
<td>1.7</td>
</tr>
<tr>
<td>Including 1995</td>
<td>11.3</td>
<td>33.9</td>
<td>3</td>
</tr>
<tr>
<td>Tubes Average</td>
<td>11</td>
<td>26</td>
<td>2.4</td>
</tr>
</tbody>
</table>

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DISCUSSION

The population dynamics of *C. pergamentaceus* exhibited high seasonal and interannual variations in growth, reproduction, and secondary production as well as the potential for iteroparous spawning. Recruitment success varied three fold interannually showing a seasonal peak pulse in the summer with limited recruitment throughout the fall. A two cohort model consisting of juveniles and adults exhibiting seasonality best described the data even though more that two age classes were likely present. High secondary production was mainly due to rapid growth and maturation of new recruits, although highly variable interannual production was likely due to inconsistency in recruitment success. We also found that tube production is a significant part of the total worm production and should be included in future studies of this polychaete. The general scheme for this population is that the overwintering population consists of adults and maturing juveniles that spawned the following summer. Spawning is not epidemic among females nor complete within a female since unspent, partially spent and spent females are found throughout the reproductive period. Some, but not all, summer recruits spawn during the same season. Densities are lowest prior to recruitment of juveniles. Since all of the adults did not die in 1994, the life span of *C. pergamentaceus* in lower Chesapeake Bay can exceed one year.

Populations are influenced by a multitude of factors some of which are stabilizing, i.e. recruitment dampening processes (McGorty *et al.* 1990) or density-dependent growth and reproduction (Rothschild 1986), and some of which can be destabilizing, i.e. unpredictatable food supply (Levinton 1972), harvesting the most reproductively valuable species (Brousseau 1978), or variable interannual recruitment (Moller and
Rosenberg 1983; Zajac and Whitlatch 1988). Many estuarine invertebrates, particularly polychaetes, exhibit high interannual variability (Zajac and Whitlatch 1988; Levin and Huggett 1990) often as a result of recruitment variation. Thus, it was not surprising to find high interannual variability due to differential recruitment success in this study. Numerous models have been developed to better understand the impacts of recruitment on the dynamics of benthic species (Roughgarden et al. 1985; Gains and Lafferty 1995) with the end result of macrofauna production that can be high but variable between years (Möller and Rosenberg 1983).

For *C. pergamentaceus*, age was an important factor in growth and production with the highest growth and production rates occurring in the late summer among new recruits and juveniles, while a decline occurred in the overwintering adult population. The scenario of early summer recruitment followed by rapid growth and development during summer and fall to maturity may be common for many annual to long-lived invertebrates, including some bivalves, in temperate estuaries (Seitz and Schaffner 1995). This contrasts with the common strategy of very short-lived estuarine opportunists which tend to reproduce in early spring (Grassle and Grassle 1974) a pattern previously observed for many macrobenthic species in Chesapeake Bay and other coastal systems (Christensen and Kanneworff, 1985; Thompson and Nichols, 1988; Marsh and Tenore, 1990).

The overwintering population of *C. pergamentaceus* began to grow and exhibit positive production in early spring, a time when gross primary production in lower Chesapeake Bay reaches a seasonal submaximal peak (Kemp *et al.* 1997; Figure 1-7).
Figure 1-7. Trends in gross plankton community production (adapted from Kemp et al. 1997) and *Chaetopterus pergamentaceus* through time.
Also during this time, labile organic matter, as estimated from sediment chlorophyll and phaeopigments, reached a peak (Figure 1-4). We found negative worm production during early summer, a time when planktonic respiration is at its maximum while gross primary productivity dips between two peaks (Kemp et al. 1997). An interesting point is that the period of rapid growth for new recruits was during summer and therefore not coincident with the timing of the spring phytoplankton (diatom) bloom. Rather, periods of maximum individual growth coincided with times when small phytoplankton and microbes are thought to dominate production in the overlying water column (Marshall and Lacouture 1986; Malone et al. 1991). The timing of this rapid growth is coincident with a seasonally maximal peak in gross primary production (Kemp et al. 1997) and in net plankton community production (Smith and Kemp 1995).

Recent evidence indicates that patches of high particle concentrations exist within the Chesapeake Bay which may provide a constant and high food concentration (Hood et al. 1998). One such patch, the result of a residual circulation eddy, is located in the vicinity of our study site. This eddy has associated upwelling and downwelling zones, strongly influences plankton distributions, and may induce phytoplankton growth (Hood et al. 1998). This circulation pattern may result in high phytoplankton production resembling a mini-spring bloom condition in which the large phytoplankton such as diatoms may exist (as per Kiørboe 1993). In any case, as a generality, worm secondary production reflects gross primary production, as determined by Kemp et al. (1997), for the lower bay (Figure 1-7). Positive production in worms is generally coincident with high primary production. This
underscores the strength of the benthic-pelagic coupling within the lower Chesapeake Bay.

The average secondary production estimate of 12 g C m\(^{-2}\) yr\(^{-1}\) (ranging from 6.7 to 18, excluding tube production) for *C. pergamentaceus* lies within the upper range of production values for many estuarine and marine species as reported by Robertson (1979), Warwick (1980), and Howe *et al.* (1988). It is particularly high when compared to other polychaetes (conversion to g C m\(^{-2}\) yr\(^{-1}\) using Waters 1977; e.g. *Nephrys incisa* 4.7 (Warwick 1980), *Loimia medusa* 1.67 (Seitz and Schaffner 1985)), but comparable to other suspension feeders such as bivalves (e.g. *Tagelus divisus* 10.5 g C m\(^{-2}\) yr\(^{-1}\), 7 g C m\(^{-2}\) yr\(^{-1}\) for *Mercenaria mercenaria* in intertidal Southampton U.K. (Warwick 1980)). Our secondary production estimates for *C. pergamentaceus* are comparable to previous estimates obtained by Huggett (1987) in a limited study of a region which slightly overlaps the northern portion of our study region.

Taken collectively over the two year study period adult, juvenile, and egg production were -10%, 81%, and 28% respectively of the total worm production (excluding tube production). These data are in contrast to another relatively large, estuarine, tubiculous polychaete *Loimia medusa* in which almost half the production came from adults, only about a third of production came from juveniles and 15% came from egg production (Seitz and Schaffner 1995).

Tube production may represent an important sink for organic matter. Kristensen *et al.* (1991) found that the tubes of the sea anemone *Ceriantheopsis americanus* accounted for 9% of the average particulate carbon and 12% of the nitrogen flux to
the benthos. The composition of *C. pergamentaceus* tubes has not been thoroughly examined. The tube consists of a secretion from the anterior region of the worm, the nature of which may be mucoproteins, mucopolysaccarides, collagen, etc (Barnes, 1965; Brown and McGee-Russell, 1971), with adhering sediments. In this study, tube production was estimated to account for approximately half of the total production. Thus, production of this nature is clearly important and should be included in future studies.

The P/B ratio was lower in 1994 compared to 1995 which not surprising since this ratio is sensitive to size distributions with smaller, fast-growing organisms having higher ratios while larger, older size classes have lower ratios (Griffith and King 1979). The P/B ratio is comparable to other large suspension feeders such as the oyster *Crassostrea virginica* and falls within a range of 0.3 to 4.1 known for molluscs (Dame 1976).

Comparing our worm tissue production values of 6.6 to 18 g C m\(^{-2}\) yr\(^{-1}\) to water column net community production of 237 g C m\(^{-2}\) yr\(^{-1}\) (Smith and Kemp 1995; Kemp *et al.* 1997) then 15% to 75 % of the net plankton community production in the lower Chesapeake Bay is needed to support one benthic species, assuming ecological trophic transfer efficiencies of 10 to 20%. If we incorporate our estimate of tube production, then between 35 and over 100% of the net plankton community production is required for one benthic species. Similar percentages have been found in northern European waters involving filter feeding populations in association with strong benthic-pelagic coupling (Graf 1992; Heip *et al.* 1995; Josefson and Conley 1997). Heip *et al.* (1995) state that suspension feeders can be responsible for large
fluxes of organic matter to the benthos that exceed water column production. Their reasoning is that suspension feeders are patchily distributed and on a systemwide basis the water column productivity limits the suspension feeders; yet the needs of local patches of suspension feeders may exceed local water column production. Grizzle and Morin (1989), Graf (1992) and Loo and Rosenberg (1996) have shown that lateral transport of material to suspension feeders positively affects the growth and production of these organisms. Due to the dynamic nature of the bay, transport of material from shallower areas may be important to sustain high productivity in these suspension feeding worms. Also, the residual circulation eddy may increase production in this area of the bay (see above; Hood et al. 1998; Kiørboe 1993). The possibility that a large portion of the phytoplankton biomass of the lower Chesapeake Bay may be consumed by the benthos has been suggested by Smith and Kemp (1995). Our results clearly indicated that this is likely and that there is strong benthic-pelagic coupling in the lower bay.

It is a generally accepted concept that benthic suspension feeders may be food limited. We expect food-limitation at our study site when water column production is low, i.e. late fall and winter as well as for a short time in late spring. These are the periods in which negative production was noted.

We have shown in this study that Chaetopterus pergamentaceus play an important role in benthic-pelagic coupling. Like better-studied suspension feeding bivalves, C. pergamentaceus transfers large quantities of matter and energy between the pelagic and benthic subsystems and thereby affects food web dynamics and nutrient cycling. Unlike long-lived bivalves which are thought to increase ecosystem stability (Dame...
1990; Herman and Scholten 1990), this polychaete was shown to have high interannual variation in density and biomass with high mortality rates; thus its role in ecosystem stability is undetermined. By virtue of the high biomass of the tubes and tissues, this polychaete represents an important avenue for storage of carbon and nutrients. The same is true for other large suspension feeders like bivalves; however, perhaps not true for smaller more ephemeral suspension feeders such as hydroids or tunicates which are also common in the Chesapeake Bay. Thus, Chaetopterus pergamentaceus has many qualities similar to and seems to function in a similar role as bivalves in the lower Chesapeake Bay ecosystem. This polychaete should be thought of as keystone species (Dame 1996) and should be included in future studies or models of the estuary, e.g. Dame (1999) and Dame and Prins (1998).
Local Demographics of the Polychaete *Chaetopterus pergamentaceus* within the Lower Chesapeake Bay and Relationships to Environmental Gradients

In press in modified form in Bulletin of Marine Science
Special issue for the 6th International Polychaete Conference
with the following authors: M. L. Thompson and L.C. Schaffner.
ABSTRACT

*Chaetopterus pergamentaceus* is an abundant and functionally important species within the soft sediment, subtidal benthic community of lower Chesapeake Bay. The present study elucidates spatial relationships in density, individual ash free dry weight, total station ash free dry weight and growth rates for juveniles and adults from two years of sampling (1994, 1995) at 12 stations in the lower Chesapeake Bay. A strong inverse relationship ($r^2 = 0.69$) was observed between growth rates and total density for juveniles when data from a low (1994) and high (1995) recruitment year were considered. Stations characterized by high density/low growth had the following in common: 1) depth (maximum for region); 2) proximity to the center of a major circulation eddy; 3) proximity to a channel; and 4) higher physical energy in the benthic boundary layer region. The study provides evidence that spatial variation in population processes, concordant with major environmental gradients, may influence population dynamics. However, deconvoluting the effects of these environmental parameters on the population dynamics of this polychaete requires further experimentation.
INTRODUCTION

*Chaetopterus pergamentaceus* (provisional specification Mary Petersen pers. comm., Eckberg and Hill 1996; formally *Chaetopterus variopedatus*, e.g. Enders 1909) is an abundant species within the soft-sediment, subtidal benthic community of lower Chesapeake Bay, where relatively high densities of this polychaete have been observed for at least the last 15 years (Diaz *et al.* 1985; Schaffner 1990, Schaffner 1993). This suspension feeding polychaete inhabits a parchment-like semicircular tube that can penetrate over 15 cm below the sediment surface. Specialized parapodia are used to pump water through the tube. Particles are trapped on a mucus net which is then formed into a food ball and ingested (Enders 1909; MacGinitie 1939; Brown 1975; Flood & Fiala-Medioni 1982; Riisgaard 1989). The tubes are well oxygenated, house commensal organisms and are likely to have significant effects on sediment biogeochemistry. Some aspects of the ecology of *C. pergamentaceus* are known from previous investigations outside of Chesapeake Bay. McNulty and Lopez (1969) reported year-round recruitment of this polychaete in Florida, while in North Carolina recruitment occurred in early summer with rapid growth to adulthood by the end of summer (Enders 1909).

Within the Chesapeake Bay, Schaffner (1990) found that *C. pergamentaceus* positively influenced macrofaunal abundance and altered community diversity and composition. In studies of benthic boundary layer processes within the lower bay, Wright *et al.* (1997) concluded that tubes of *C. pergamentaceus* and associated epifauna increased the hydraulic roughness of the sediment bed thereby modifying the near-bed flow regime, as well as sediment resuspension and transport processes. The
feeding activity of this polychaete also alters particle size distributions via pelletization of suspended material and enhances deposition of organic matter, which may have important implications for ecosystem processes (Wright et al. 1997; Thompson and Schaffner, unpub. data). Thus, this polychaete is a functionally important species and serves as an important link in benthic-pelagic coupling. Despite its importance in the Chesapeake Bay estuary, the ecology of *C. pergamentaceus* in the lower bay remains poorly described.

The lower Chesapeake Bay study region is part of a physically complex estuarine environment. Schaffner et al. (1987) described a general environmental gradient in the lower mainstem bay of higher physical energy, salinity, and fine sand sediments in the southeast compared to the northwest. Wright et al. (1997) reported an increase in physical energy toward the southeast associated with wave agitation in proximity of the bay mouth and relatively strong tidal currents while a moderation of physical energy in the northwest is evident in boundary layer processes and sea bed dynamics (Wright et al. 1997; Dellapenna et al. 1998). A food gradient may be tied to the presence of a residual circulation pattern in the bay - a strong, cyclonic eddy with related regional upwelling and downwelling (Figure 2-1; Hood et al. 1998). High concentrations of pelagic organisms such as phytoplankton and various larvae are retained within this residual water circulation feature. Both physical and biological gradients may play a role in regulating local scale population trends of *C. pergamentaceus*.

Given the significant environmental gradients observed within the study region, it is of interest to determine how factors and mechanisms that affect individual organisms
may interact to regulate overall population structure for this species. The goal of this paper is to identify spatial trends in *C. pergamentaceus* population dynamics and potential links with known environmental gradients. We present evidence for the existence of distinct spatial patterns with respect to juveniles, not adults, in density, individual ash free dry weight (AFDW), and total station AFDW within a high recruitment year, but causal relationships with environmental gradients require further investigation.

**MATERIALS AND METHODS**

**SITE** - The study region is located within lower Chesapeake Bay encompassing approximately 54 km² (Figure 1-1, Chapter 1; Figure 2-1). This region has water depths of 10 - 15 m, bottom water salinities of 20-27 ppt and a annual range in bottom water temperature of 4-25°C. The mean tidal range in this region is 60 cm with maximum tidally-induced current speeds of 20-40 cm s⁻¹ at 1 m above the bed. Sediments are primarily silts (40 - 50%) and fine sands (40 - 50%) (Schaffner *et al.* 2000). Summer hypoxia or anoxia are not observed in this region of the bay. The benthic fauna consists of a diverse assemblage of suspension and deposit feeders with *Chaetopterus pergamentaceus* often being the biomass dominant (Schaffner 1990; Wright *et al.* 1997).

**FIELD SAMPLING** - Each of 12 stations was sampled for a period of two years beginning January 1994 and ending December 1995. Worms were collected using an Ocean Instruments spade box core (20 x 30 x 30 cm deep). One box
Figure 2-la. Study region in the lower Chesapeake Bay with solid circles indicating station locations relative to the overlying residual water circulation eddy, as indicated by the shaded area in which the lighter portion represents the eddy center (adapted from Hood et al. 1998).

Figure 2-1b. Station locations (solid circles) relative to depth contours of 3 m increments with increasing depth toward the right into a channel then shallowing toward shore.
core per station was collected during year 1 (1994) while two box cores per station were collected during year 2 (1995), in order to increase the number of worms collected. Samples were collected monthly from each station during winter and spring and semimonthly during summer and fall, the periods of recruitment and rapid growth. Due to extreme weather and loss of a boat engine, some scheduled 1995 sampling dates were missed. Three methods were utilized to ensure complete removal of *C. pergamentaceus* from each core. First, a 5 cm diameter by 5 cm deep subcore was collected and fixed intact to retain fragile new recruits. Second, the remaining surface sediment, 0 - 2 cm, was removed and elutriated onto a 125 μm screen to collect the very small worms. Last, larger worms were removed directly from the remaining sediment. All *C. pergamentaceus* removed from the cores were fixed in 10% formalin and stored in 2% formalin until laboratory analysis.

**LABORATORY METHODS** - Density, individual AFDW, and total station AFDW were determined for each sample. Briefly, length of body region A multiplied by the width (at setiger 4), collectively termed head area, were measured to the nearest 0.1 mm (Figure 1-2, Chapter 1) using a dissecting scope equipped with ocular micrometer for smaller specimens and Vernier calipers for larger specimens. Head area was found to be a reliable indicator of worm size described by the equation $\text{AFDW} = \left[ (0.0224 \times \text{length}) + (0.0303 \times \text{width}) \right]^3$ ($N = 40; r^2 = 0.93; p < 0.001$; due to heteroscedasticity, observations were weighted by $1/\text{variance}$; Neter *et al.* 1990). Size measurements were then used to calculate AFDW using this regression.

Using distinct modes in the size distribution, the population was separated into
juveniles and adults. The adult category is likely represented by more than one cohort of mature individuals since tagging of individual worms in a population in South Carolina has shown that these polychaetes can live over three years (Michael Grove, pers. comm.); yet, once adult size is reached the cohorts cannot be distinguished. After the data were separated into juveniles and adults, they were then grouped by season. General trends in density, individual AFDW and total station AFDW (sum of individual AFDWs) were graphed as area bubble plots with stations spatially arranged by latitude and longitude. Juvenile growth rate, found by regressing head area (mm$^2$) against time (day), was plotted versus density to detect general trends.

RESULTS AND DISCUSSION

For juveniles, spatial patterns in density, individual and total station AFDW, and growth rate were observed when recruitment was highly successful (1995), but not during a low recruitment year (1994) (Figures 2-2, 2-3, 2-4). In 1995, stations with higher worm densities had lower individual AFDWs but overall higher total station AFDW. Common parameters among these stations were depth (maximum in the study region; Figure 2-1), proximity to central portion of the residual water circulation eddy (Figure 2-1), proximity to a channel edge (Figure 2-1), and in an area of higher physical energy within the benthic boundary layer (Wright et al. 1997). No obvious spatial patterns were observed for adults (data not shown).

The spatial pattern in the juvenile population of C. pergamentaceus in the lower Chesapeake Bay may be influenced by environmental gradients driven by physical processes. Physical processes affect populations directly via alterations in processes
Figure 2-2. Juvenile average density (# of individuals • 0.06 m⁻²). Data are graphed as area bubble plots by stations arranged by latitude and longitude, separated by year, and grouped by season. Solid lines are depth contours in meters.

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Figure 2-3. Juvenile average individual ash free dry weight (g AFDW \(^{-\text{individual}^{-1}}\)) with data graphed as area bubble plots with stations arranged by latitude and longitude, separated by year, and grouped by season. Note Scale changes. Solid lines are depth contours.
Figure 2–4. Total juvenile ash free dry weight (g AFDW \(\cdot\)individual\(^{-1}\)) at each station. Data are graphed as area bubble plots with stations arranged by latitude and longitude, separated by year, and grouped by season. Note scale changes; summer 1994 is an order of magnitude less. Solid lines are depth contours.
such as recruitment and feeding success, and indirectly via effects on biotic interactions (Menge and Olson 1990, Hall 1994, Cosson et al. 1997). Effects may be positive or negative, depending on the intensity, scale and nature of physical factors in the system (Hall 1994). Environmental gradients driven by physical processes are important features of estuarine environments (Boesch et al. 1976; Wright et al. 1987; Day et al. 1989; Schaffner et al. 2000). Unfortunately, effects of major physical gradients and the cyclonic eddy feature of the lower bay on the population dynamics of this polychaete can not be clearly resolved in this study because many of the gradients are confounded. Nonetheless, this study provides evidence that spatial variation in population processes, concordant with major environmental gradients, influences population dynamics of *C. pergamentaceus* in this estuary. We suggest that future investigators should focus on relationships between juvenile recruitment and growth processes relative to the environmental gradients that influence benthic-pelagic coupling, larval retention processes, food availability and seabed dynamics. All of these factors are expected to play a role in the success of this polychaete in lower Chesapeake Bay.

A derived relationship for juveniles shows a strong inverse relationship between growth rates and total densities (Figure 2-5). When recruitment is successful, intraspecific competition must be considered. Both food and space are potentially important density dependent factors that limit benthic suspension feeders (Frechette and Lefaivre 1990; Kamermans et al. 1992; Beukema and Cadee 1997; Josefson and Conley 1997). Crowding reduces growth rates, decreases average organism size, and skews size frequency distributions to smaller size individuals (Branch 1975; Woodin...
Figure 2-5a. Growth rate of juveniles. Data are graphed as area bubble plots with stations arranged by latitude, separated by year, and grouped by season. Solid lines are dept contours in meters.

Figure 2-5b. Derived inverse relationship between juvenile density (# of individuals × 0.06 m²) and growth rate (change in head area, mm², with time, julian day). Solid squares (■) are 1994 shallow water stations (<12 m). Empty squares (□) are 1994 deep water stations (>12 m). Solid circles (●) are 1995 shallow water stations (<12 m). Empty circles (○) are 1995 deep water stations (>12 m).
1976; Begon et al. 1986). This is consistent with the patterns observed for 1995 (Figures 2-3, 2-5; Figure 1-6, Chapter 1). The 1995 cohort of juveniles yielded a higher total AFDW than the 1994 cohort, despite lower growth rates (Figure 2-4). Individual AFDW was lower at higher density stations, particularly in the fall due to the integrated effects of time on juvenile growth and density (Figure 2-3). Yet, total AFDW was highest at high density stations regardless of the lower growth rate (Figure 2-4). Although density dependent factors may affect the population, the carrying capacity of the environment with respect to C. pergamentaceus does not appear to have been reached.

High interannual variability, resulting from variable recruitment success, was apparent for this population. Variable recruitment success led to interannual differences in factors affecting the population dynamics, e.g. an intuitive conclusion for our study is that in some years (i.e. 1994) low recruitment will limit the population while in other years (i.e. 1995) high recruitment allows for the potential of density dependent factors to limit the population. Variable recruitment in time and space due to irregularities in physical transport of larvae, spawning, and larval survivorship within the water column is a generally recognized concept. Based on better studied species such as crabs and fish (Johnson and Hester 1989; Norcross and Wyanski 1994; Ault et al. 1995; and many others) we expect that physical processes affecting recruitment will be important in lower Chesapeake Bay. Although Ólafsson et al. (1994) concluded that recruitment limitation is not the dominant factor describing population patterns in marine soft-sediment communities, population patterns are still likely to correspond to recruitment peaks even if the peaks are dampened by post-recruitment density dependent factors.
(Caley et al. 1996). For example, Zajac and Whitlatch (1988) found that density fluctuations in the polychaete *Nephtys incisa* were primarily related to recruitment variations. Thus, the relative importance of recruitment limitation vs post-recruitment density dependent factors in affecting population structure may change temporally.

**SUMMARY**

There are interannual differences in factors structuring the population of *C. pergamentaceus*. For juveniles, a strong inverse relationship was observed between growth rates and total density when data from a low and high recruitment year were considered. Concordant with environmental gradients, spatial patterns were evident among juveniles within a successful recruitment year. The role of gradients in physical energy, depth, a residual circulation pattern, and larval supply that may influence recruitment require further investigation. Experiments are needed that will help us to better understand the ecological role of *C. pergamentaceus* in this estuarine environment. Our results provide evidence that spatial variation in population processes, concordant with major environmental gradients, strongly influences population dynamics of *C. pergamentaceus* in this estuary. Due to the implications for ecosystem processes, understanding population dynamics of resident species within marine and estuarine soft-sediments warrants additional study.
Chapter 3

Organic matter processing by the polychaete *Chaetopterus pergamentaceus*, a dominant suspension feeder of lower Chesapeake Bay

This paper will be submitted for publication after further revision with the following authors: M. L. Thompson, L. C. Schaffner, E. A. Canuel, and S. Macko.
ABSTRACT

A key feature of estuarine and coastal ecosystems is the diversity of sources and quality of organic matter available to secondary consumers; thus the base of many estuarine food webs may be difficult to identify. The suspension feeding polychaete Chaetopterus pergamentaceus is a dominant benthic species within the lower Chesapeake Bay. We used a combination of techniques including bulk parameters, lipid biomarker, and isotopic analyses to examine the organic matter sources that fuel growth and reproduction of C. pergamentaceus and to examine its role in benthic-pelagic coupling in the lower Chesapeake Bay. Locally produced organic matter, primarily fresh phytoplankton and recycled material from microbial sources is utilized for growth and reproduction. The spring bloom is used for gamete proliferation and some storage of essential fatty acids while a combination of phytoplankton and bacteria support the high growth rate and secondary productivity of this worm. Terrestrial materials are not important source of organic matter to this polychaete. Fecal pellets produced by C. pergamentaceus have a high nutritional content and may represent a food source to other benthos. The sediments have a biomarker signature different than the fecal pellets. This suggests that sediments are either highly reworked by the benthic community or physical transport processes influence the biomarker signatures. Our results indicate that growth and secondary productivity of C. pergamentaceus are tightly linked to the water column production and that this worm is highly dependent on benthic-pelagic coupling with its role being to enhance the quantity of organic matter deposited, but with little change in quality.
INTRODUCTION

A key feature of estuarine and near-shore coastal ecosystems is the diversity of sources and quality of organic matter available to fuel secondary consumers (Tenore 1988). Allochthonous production derives from marine and freshwater phytoplankton, freshwater marshes, and terrestrial sources. Autochthonous sources include production from in situ phytoplankton, benthic algae, seagrasses as well as oligohaline to saltwater marshes. In terms of discrete biochemical components, the quality or essential characteristics of organic matter varies depending on its source(s), environmental factors specific to the sources, and which biochemical components (e.g. polyunsaturated fatty acids, lipids, amino acids, nitrogen, or carbohydrates) are of interest. For example, phytoplankton generally contain high amounts of polyunsaturated fatty acids (PUFAs), while marine vascular plants, which are poor sources of PUFAs, are a good source of nitrogen (Tenore 1988).

Spatial and temporal variations in the availability of various sources and quality of organic matter can make it difficult to identity the base of estuarine food webs (Deegan and Garritt 1997). Variations along and across an estuary are important in space and time. For example, interactions between primary production and physical processes, such as river flow, estuarine circulation, and tidal currents, influence the delivery of organic matter to consumers. Availability of organic matter to the benthos also may be affected by pelagic processes (Graf 1992) as well as benthic boundary layer flow processes (Frechette et al. 1989). Hydrodynamic conditions (e.g. vertical structure of the water column) influence particle concentrations and availability by controlling particle sinking and resuspension, which determines the
flux of material to suspension feeding organisms (Taghon et al. 1980; Muschenheim 1987). Feeding behavior may change in differing hydrodynamic conditions as well as in response to variations in particle concentration and composition (Wildish and Kristmanson 1997). Nevertheless, data from recent studies suggest that consumers tend to utilize organic matter produced in region of the estuary in which they reside (Deegan and Garritt 1997).

Availability and quality of organic matter have important implications for consumer utilization in terms of both extrinsic and intrinsic factors. Factors affecting utilization extrinsic to the consumer include environmental parameters such as seasonal variations in temperature, oxygen availability, and primary production cycles associated with light and nutrient regimes. Factors affecting utilization intrinsic to the consumer include functional abilities, such as activity level, growth and reproductive cycles, that take place within the metabolic confines set by the extrinsic factors. The temporal variability of the extrinsic factors influences the intrinsic factors creating a hierarchy regulating population dynamics (Zajac and Whitlatch 1985; Marsh and Tenore 1990). Thus the availability and quality of organic matter determines utilization and interacts with natural growth cycles, reproduction, and demographics. The structure of consumer populations is altered via changes in growth rates, metamorphosis and settlement, and egg production or viability of consumer populations (Enright et al. 1986a,b for oysters; Gremare et al. 1989 for polychaetes; Munk 1993 for sprat; Sterner et al. 1993 for herbivorous zooplankton; Müller-Navarra 1995b for Daphnia; Thompson et al. 1996 for oysters; Ban et al. 1997 for copepods; Soudant et al. 1998 for larval scallops).
Our understanding of food quality effects on consumer populations is limited by our ability to identify the component(s) of the food that are limiting (Smith 1991; Brett 1993). The essential dietary component(s) necessary for a particular consumer may change throughout its life (i.e. the component necessary for growth may differ from the component necessary for metamorphosis or reproduction; Soudant et al. 1998). Often the limiting component(s) for a particular consumer have not yet been identified.

Various approaches have been used to evaluate food quality. Traditionally, energetic content was used (Lindeman 1942). More recently, an elemental stoichiometric approach based on elemental ratios has been applied (Elser and Hassett 1994; Elser et al. 1996). Others have argued that commonly measured parameters such as carbon, nitrogen, phosphorus, and chlorophyll that often serve as proxies for food do not adequately characterize the food in terms of limiting components (Müller-Navarra 1995b; Tang and Dam 1999). Biochemical analyses have shown that essential dietary components such as protein (Giani 1991), fatty acids (Ahlgren et al. 1990; Müller-Navarra 1995a,b; Demott and Müller-Navarra 1997), amino acids (D'Avanzo and Valiela 1990), and vitamins (Hapette and Poulette 1990) may be a better determinant of food quality. For example, many lipid components, e.g. polyunsaturated fatty acids (PUFAs) and some sterols, are known to be essential nutrients to invertebrates (Müller-Navarra 1995b; Gremare et al. 1989; Soudant et al. 1998).

Utilization of organic matter by consumers can be evaluated using a number of approaches including food web analysis using lipid biomarkers and stable isotopes.
By comparing the lipid distribution and isotopic composition of consumers and resources, it may be possible to gain insights into how food availability and quality (as determined by lipid distribution) affect the consumer population.

Lipid biomarkers have been successfully employed to trace the flow of organic matter in a variety of aquatic ecosystems (Currie and Johns 1988; Fraser et al. 1989; Mudge and Norris 1997). Trophic relationships can be delineated by comparing the fatty acid (FA) composition of phytoplankton to zooplankton (Graeve et al. 1994; and references therein) and to organisms at higher trophic levels such as fish (Fraser et al. 1989; St. John and Lund 1996). Although, the FA composition of phytoplankton can be variable and cannot be considered an unequivocal indicator of the presence of a particular phytoplankton class (Fraser et al. 1989). The use of sterols and stable isotopes in combination with FAs provides a more comprehensive and valid analysis.

Naturally occurring stable isotopes of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$), have been utilized to trace the flow of organic matter in a variety of ecosystems (Petersen et al. 1985; Deegan and Garritt 1997). The structure of a food web can be determined by comparing the isotopic composition of consumers, predators, and resources, assuming that there is variability in isotopic composition of various resources and that the isotopic value of the consumer accurately reflects the assimilated source.

An organism's isotopic composition depends on the biological fractionation associated with the assimilation of the organic matter and the isotopic composition of assimilated organic matter. Biological fractionation is the change in isotopic
signature between the consumer and the source which is generally between a 0 to 1 
\% increase in $\delta^{13}$C, 2 to 4 \% for $\delta^{15}$N, and insignificant in $\delta^{34}$S. Therefore, $\delta^{13}$C 
and $\delta^{34}$S are often used to identify the source(s) of organic matter supporting 
consumers while $\delta^{15}$N is more useful in determining trophic level. The use of a 
combination of multiple stable isotopes is a more powerful approach than use of a 
single isotope (Petersen et al. 1985).

Within the lower Chesapeake Bay, the large, tubiculous, suspension feeding 
polychaete Chaetopterus pergamentaceus (provisional specification Mary Petersen, 
pers. comm.; Eckberg and Hill, 1996; formally Chaetopterus variopedatus e.g. 
Enders 1909) is an important component of the soft sediment benthic community 
where it has maintained relatively stable populations for at least the last 15 years 
(Schaffner 1987, 1990). This polychaete has been reported in other marine and 
estuarine communities along the east coast of the United States (reported as C. 
variopedatus - Enders 1909; Eckberg and Hill 1996). Chaetopterus pergamentaceus 
exhibits rapid growth and high secondary productivity during summer, coincident 
with a maximum peak in gross primary production rather than the spring diatom 
bloom (Chapter 1). Maximum individual growth coincides with times when small 
phytoplankton and microbes are thought to dominate production in the overlying 
water column (Chapter 1).

Chaetopterus pergamentaceus uses a mucus net, which should effectively retain 
particles as small as $\sim 0.5 \mu m$, to filter water which is pumped through its tube with 
specialized parapodia. The net is then formed into a food ball and transported to the 
mouth for ingestion (Enders 1909; MacGinitie 1939; Brown 1975; Flood and Fiala-
Medioni 1982; Riisgaard 1989). An early study by Enders (1909) identified diatoms, molluscan embryos, copepods, and other young crustaceans in worm guts collected during the summer from a tidal flat in North Carolina. The green color of the gut was recognized by the earliest researchers to be chlorophyll-type pigments (Lankester et al. 1898) including phaeophorbides $a$, $b$, and others as well as other pigments including $\beta$-carotene and xanthophyll derived from food intake (Kennedy and Nicol 1959). Thus, the potential source(s) of organic matter that fuel the high secondary productivity of this polychaete within the lower Chesapeake Bay may be numerous and include microbes, pico- and nano plankton, larger phytoplankton, zooplankton, and detritus.

For most shallow water environments, ecosystem function depends on the cycling and flow of materials and energy between benthic and pelagic subsystems. Numerous studies have now demonstrated that benthic suspension feeders are important links between the water column and sediment in coastal ecosystems where they can exhibit high densities and biomass (Cloern 1982; Cohen et al. 1984; Loo and Rosenberg 1989; Alpine and Cloern 1992; Graf 1992; Heip et al. 1995). These organisms increase nutrient regeneration (Doering 1989) partially due to bioturbation and bioirrigation and the resulting indirect effects such as stimulation of microbial processes (Kristensen et al 1991; Barbanti et al. 1992) and partially as a result of excretion (Kemp et al. 1990), which may increase phytoplankton production (Doering et al. 1986; Prins and Smaal 1990). However, suspension feeders can consume more than 50% of the water column production, which may result in a reduction of planktonic biomass (Cohen et al. 1984; Loo and Rosenberg 1989;

The primary goal of this study was to determine the source(s) of organic matter that fuel benthic secondary production in the lower Chesapeake Bay by examining trophic dynamics of a dominant suspension feeder, the polychaete *C. pergamentaceus*. Differences between adults (cohort 1) and juveniles (cohort 2) were used to determine which sources of organic matter fueled reproduction versus growth. Another goal was to resolve temporal and spatial variation in the source(s) of organic matter for the region studied. Lastly, we elucidated the role of this worm in benthic-pelagic coupling by examining suspended particulate matter, gut contents, fecal pellets and surface sediments.

We used a combination of techniques including visual examination (dissecting and epifluorescence microscopy); chlorophyll $a$; elemental carbon and nitrogen; lipid biomarker; and isotopic analyses of carbon, nitrogen, and sulfur on several types of worm samples (Table 3-1). Samples were selected as follows: 1) gut contents provide an instantaneous view of the material currently being removed from the water column; 2) tissue from the anterior body region (Region A; Chapter 1) to yield an integrated view of assimilated organic matter; 3) eggs (mostly eggs but also
Table 3-I. Sampling information on dates for which lipids biomarker analysis occurred in addition to other methods. Samples for visual, chlorophyll $a$, carbon and nitrogen, and isotopic analyses were evaluated on additional dates to provide ancillary temporal data. Methods are as follows: visual analysis (V); chlorophyll $a$ (chl-$a$); carbon and nitrogen (C&N); lipid biomarkers (L); and stable isotopes (I).

<table>
<thead>
<tr>
<th>Sample Type</th>
<th>Sampling Date WT</th>
<th>Sampling Date CS</th>
<th>Cohort</th>
<th>Methods Applied</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suspended</td>
<td>05/09/95</td>
<td>-</td>
<td>C&amp;N, L</td>
<td></td>
</tr>
<tr>
<td>Particulate</td>
<td>07/24/95</td>
<td>-</td>
<td>C&amp;N, L</td>
<td></td>
</tr>
<tr>
<td>Matter</td>
<td>09/19/95</td>
<td>-</td>
<td>C&amp;N, L</td>
<td></td>
</tr>
<tr>
<td>Gut Contents</td>
<td>04/05/95 05/22/95</td>
<td>04/05/95 08/10/95</td>
<td>1 1,2</td>
<td>V, chl-$a$, C&amp;N, L, I</td>
</tr>
<tr>
<td>Fecal Pellets</td>
<td>04/05/95 08/10/95</td>
<td>04/05/95 12/08/95</td>
<td>1 2</td>
<td>V, chl-$a$, C&amp;N, L, I</td>
</tr>
<tr>
<td>Sediment</td>
<td>08/16/94 04/05/95</td>
<td>-</td>
<td>chl-$a$, C&amp;N, L, I</td>
<td></td>
</tr>
<tr>
<td>Tissue</td>
<td>04/05/95 05/22/95</td>
<td>04/05/95 08/10/95</td>
<td>1 1,2</td>
<td>C&amp;N, L, I</td>
</tr>
<tr>
<td>Eggs/Tails</td>
<td>04/05/95 07/11/95</td>
<td>04/05/95 07/27/95</td>
<td>1 1</td>
<td>C&amp;N, L, I</td>
</tr>
<tr>
<td></td>
<td>08/10/95</td>
<td>08/10/95</td>
<td>1 2</td>
<td>C&amp;N, L, I</td>
</tr>
<tr>
<td></td>
<td>12/08/95</td>
<td>12/08/95</td>
<td>2 2</td>
<td>C&amp;N, L, I</td>
</tr>
</tbody>
</table>
contained other reproductive material and some worm tissue from the tail) to allow
determination of organic matter sources important in reproduction; and 4) fecal
pellets to provide an instantaneous view of the material being deposited on the
sediment surface. In addition to the worm samples, suspended particulate matter
(SPM) was used to assess the availability of organic matter to the suspension feeding
community and surface sediment was analyzed to provide an integrated view of the
organic matter composition deposited at the sediment-water interface and potentially
available for benthic assemblages in the region. Comparisons of sample types on
various sampling dates, employing a variety of methods, were used to meet the
aforementioned objectives (Table 3-II).

MATERIALS AND METHODS

SITE - The study region within the lower polyhaline portion of Chesapeake Bay
(Figure 1-1, Chapter 1), has previously been described in Chapters 1 and 2.

Organic matter in the region includes bacteria, diatoms, dinoflagellates, and
detritus which may come from a variety of sources including local in situ production,
entainment from the ocean, resuspension from nearby shoals, detritus from marshes
(Spartina alterniflora and others), seagrasses (Zostera marina), and terrestrial inputs
from river runoff. The dominant source(s) of organic matter in lower Chesapeake
Bay appears to be autochthonous and include a mixture of fresh and detrital
phytoplankton, zooplankton, and bacteria (Canuel and Zimmerman 1999).
Table 3-II. Sampling scheme applied to objectives.

<table>
<thead>
<tr>
<th>Objective</th>
<th>Scheme</th>
</tr>
</thead>
<tbody>
<tr>
<td>I Determine Source of Organic Matter</td>
<td>SPM and gut contents used as an indication of availability of organic matter. Differences between gut contents and fecal pellets represents utilization. Differences between gut contents and tissue and eggs represents assimilation.</td>
</tr>
<tr>
<td>II Evaluate Organic Matter Sources for Reproduction versus Growth.</td>
<td>Use organic matter source differences between two cohorts - cohort 1, which consisted of adults, and cohort 2, which consisted of new recruits and juveniles that grew into adults during the period of investigation. Direct comparison between cohorts for gut contents, fecal pellets and worm tissue on 08/10/95.</td>
</tr>
<tr>
<td>III Examine Temporal Variation</td>
<td>Analyzed objectives I and II at various time periods over an annual time period.</td>
</tr>
<tr>
<td>IV Examine Spatial Variation</td>
<td>Analyzed differences between WT and CS for gut contents, fecal pellets, and tissue on 04/95.</td>
</tr>
<tr>
<td>V Evaluate Benthic-Pelagic Coupling</td>
<td>Analyzed differences among gut contents, fecal pellets, and sediments at various time periods over an annual time period.</td>
</tr>
</tbody>
</table>
SAMPLE COLLECTION - During 1995, samples of surface sediment and *C. pergamentaceus* were collected with an Ocean Instruments spade box core (20 cm x 30 cm x 30 cm deep) at two sites with the lower Chesapeake Bay, designated WT and CS (Figure 1-1, Chapter 1). The sites were chosen to address spatial variability across the region where *C. pergamentaceus* is known to be abundant (Schaffner 1990; Chapter 1). Temporal variability was addressed by seasonal collections of samples, but some scheduled 1995 sampling dates were missed due to extreme weather and loss of a boat engine.

*Chaetopterus pergamentaceus* were removed from the sediment. Some worms were fixed in 10% formalin immediately. Other worms were taken out of their tubes and either placed in solvent rinsed, ashed foil and frozen while aboard ship and subsequently stored in an ultracold freezer at -80°C until analysis, or dissected immediately placed in light-free foil-wrapped vials, and kept frozen until analysis. Surface sediment (uppermost 0.5 cm) was removed from the box core with solvent rinsed spatulas and transferred to pre-combusted (450°C for 4 hours) glass jars and placed in a freezer aboard ship and stored in an ultracold freezer at -80°C until analysis.

Due to logistical constraints, collection of SPM samples occurred as much as two weeks from the worm and sediment sampling (Table 3-1). Forty liter water samples were taken 1 m above the bed see Canuel and Zimmerman (1999) for details.

VISUAL DETERMINATION OF DIETARY COMPONENTS - Samples initially fixed in 10% formalin were subsequently diluted to 2% for sample storage. Gut contents
from a minimum of three worms were viewed under a dissecting microscope at magnification 30 x or less. In addition to the dates listed in Table 3-I, samples collected on Jan. 25, July 27, Aug. 24, and Dec. 8 1995 were also examined.

Samples of gut contents and pellets for epifluorescence microscopy were obtained from samples of C. pergamentaceus that were frozen at -80°C. Just prior to analysis, these samples were dissected from the worm, sonicated (to break up the organic matrix), fixed in gluteraldehyde, and then stained with DAPI, Acridine Orange, and Proflavin (Quinby, pers. comm.).

CHLOROPHYLL a - Worm guts and fecal pellets were obtained by dissection immediately after sample collection, placed in light-free foil-wrapped vials, and kept frozen until analysis, always within 30 days. An aliquot of surface sediment was treated in the same manner. Chlorophyll a was extracted using a solution of 40% methanol, 40% acetone, and 10% water with subsequent quantification by spectrophotometric analysis (Lorenzen 1967; as modified by Pinckney et al. 1994).

ORGANIC CARBON AND TOTAL NITROGEN - Aliquots of samples taken for lipid analysis were used when available; when unavailable and to increase sample size or provide ancillary temporal data, additional worm dissections from frozen samples rendering tissue, gut, fecal pellets, and eggs were utilized. Thus, some samples have replicates while others do not. All samples were dried at 50°C and ground to a powder. Sediment samples were acidified to remove carbonates. Samples were weighed into silver boats and analyzed on a Fison Model EA 1108 elemental analyzer.
to determine organic carbon and total nitrogen content.

**LIPID ANALYSIS** - SPM samples were filtered (Gelman A/E) and then stored in a 2:1 (v:v) of methylene chloride:methanol or chloroform:methanol until analysis. For methodological details on lipid extraction for these samples see Canuel and Zimmerman (1999).

Just prior to worm tissue analyses, worms from each collection date were dissected yielding worm tissue from Region A (Figure 2; Chapter 1), gut contents, fecal pellets and eggs when available. Similar tissue types from a minimum of three worms were pooled to form one sample per date per tissue type. Preliminary analysis of pooled vs individual samples revealed that the distribution of major lipids were comparable between samples, yet the use of pooled lipids allowed for analysis of trace compounds present at or below detection limits in individual samples. During late summer when adults were discernable from juveniles, samples were analyzed by cohort. Each sample was then subsampled, if enough material was available, for carbon and nitrogen content, and stable isotope analyses.

Worm samples (~300 mg) were ground by mortar and pestle and total lipids extracted using a modification of the Bligh and Dyer (1959) method, aided by sonication. An overnight extraction in 1:2 (v:v) chloroform:methanol was followed by several 2:1 (v:v; 2 x 1 hour) chloroform:methanol extractions. After each extraction the samples were centrifuged (10 minutes, 4°C; = 500G) and the extract decanted to a 60 ml separatory funnel. After the first three extractions, chloroform:methanol:20% NaCl in water were added to the separatory funnels to

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obtain a final ratio of 2:2:1 (v:v:v). The extracts were shaken and allowed to separate into two phases; the lower organic phase collected to a pear shaped flask and refrigerated overnight. The worm tissue was further extracted overnight in chloroform which was then added to the aqueous phase (see above), shaken and allowed to separate into two phases. The aqueous phase was re-extracted two additional times by the addition of chloroform and water in equal proportions.

Sediment samples were extracted similarly to Canuel and Martens (1993). Samples were thawed, homogenized, and aliquots (~10g wet weight) were extracted, with the aid of sonication, with 2:1 (v:v; 1 x overnight; 2 x 1 hour) methylene chloride:methanol. After each extraction the samples were centrifuged (20 minutes, 20°C; ~600G) and the extract decanted to a 250 ml separatory funnel. Methylene chloride:methanol:20% NaCl in water were added to the extract to obtain a final ratio of 2:2:1.8 (v:v:v). The extracts were shaken and allowed to separate into two phases, the lower organic phase collected to a round bottom flask and refrigerated overnight. The sediment was further extracted overnight in hexane which was then added to the aqueous phase (see above), shaken, and allowed to separate into two phases. The aqueous phase was re-extracted two additional times by the addition of hexane and water in equal proportions.

For worm and sediment samples, the organic phase extracts were combined and left over anhydrous Na₂SO₄ crystals overnight to remove trace levels of H₂O. The total lipid extract (TLE) was concentrated using turbo evaporation (Zymark) and quantified gravimetrically.

The remainder of the lipid protocol for both sediment and tissue is a modification
Canuel and Martens (1993) method. A portion of the extract (~1 mg dry weight of lipid or no more than half of TLE) was evaporated to dryness (under N₂) and saponified using 1N KOH in methanol:water (80:20; 3 ml; pH = 12) for 2 hours at 110 °C. When cooled, neutral lipids were extracted with hexane (3 x 5 ml; 1 hour separation time). After addition of 3N HCl to reduce the pH to ~ 2, acidic lipids were extracted with hexane (3 x 5 ml; 1 hour separation time). Neutral and acidic lipids were dried over anhydrous Na₂SO₄ crystals overnight. Fatty acids were converted to methyl esters using 3% BF₃·CH₃OH under N₂ at 85 °C for 1 hour. When cooled the methyl esters were extracted with hexane (3 x 5 ml; 1 hour separation time) and dried over anhydrous Na₂SO₄ crystals overnight.

Both acidic and neutral lipids were isolated into constituent classes by adsorptive chromatography on silica gel columns (Sigma silica gel; 63-200 μm) using solvents of increasing polarity -10 ml hexane, 5 ml 25% toluene in hexane, 5 ml 5% ethyl acetane in hexane, 5 ml 10% ethyl acetane in hexane, 5 ml 15% ethyl acetane in hexane, and 5 ml 20% ethyl acetane in hexane successively (Wakeham and Canuel 1989). The columns (6 mm diameter x 150 mm long) contained 1 g of 5% deactivated silica. Samples were concentrated to 0.5 ml by evaporation with N₂ before addition to the column. For the neutral lipids, fractions 5 and 6 contained the sterols; for acidic lipids, fractions 3 and 4 contained the fatty acid methyl esters (FAMEs). The collected fractions were concentrated by evaporation under N₂ and stored at -20°C until analysis by gas chromatography (GC).

The sterols were derivatized to their trimethylsilyl-ethers (TMS) with bis-(trimethylsilyl)-trifluoroacetamide (BSTFA) and acetonitrile at 70°C for 15 minutes.
Sterols (as TMS ethers) and fatty acid methyl esters were analyzed on a 30 m x 0.32 mm internal diameter DB-5 (dimethylphenylsilicone) fused silica capillary column (J&W Scientific; 0.25 μm film thickness). The analyses were performed on a Hewlett Packard 5890 Series II gas chromatograph using helium as the carrier gas and a flame ionization detector. FAME analysis temperatures were as follows: 60° to 110° at 30°C per min, 110° to 280° at 3°C per min with a 5 min. hold at 280°C. Sterols were analyzed using the following temperature program: 60° to 170° at 30°C per min, 170° to 225° at 3°C per min, 225° to 310° at 2°C per min, and held at 310°C for 5 min. Data were collected and processed using ChemStation (Hewlett Packard). All GC peaks were quantified relative to internal standards added prior to GC analysis - methyl heneicosanoate for fatty acids and 5α (H)-cholestane for sterols. Initial identifications were made by comparison with retention times of known standards; peak identifications were verified by GC-MS analysis of selected samples (Hewlett Packard 6890 Series Gas Chromatograph - Mass Selective Detector; DB-5MS column).

Fatty acids are designated as A:BωC where A is the total number of carbons, B is the number of double bonds, and C is position of the first double bond from the aliphatic (ω) end of the molecule. Sterols are designated by carbon number and the "Δ" notation is used to indicate the position of the double bonds (Killops and Killops 1993).

Except for SPM data, all results were corrected for percent recovery using the average percent recovery for FA and sterols separately (i.e. all FA were corrected to the average percent recovery of 60% while all sterols were corrected to 65%.
STABLE ISOTOPE DETERMINATION - When available, aliquots of samples taken for lipid analysis were used; additional worm dissections yielding body tissue, gut contents, fecal pellets, and eggs were also utilized. Due to logistical constraints, SPM samples were not isotopically analyzed. All samples were dried at 50°C and ground to a powder. Sediment samples were treated with HCl until no release of CO$_2$ was visible, and dried again. A Fisons NA1500 NCS elemental analyzer was used to determine carbon and nitrogen content. The resulting CO$_2$ and N$_2$ from combustion were analyzed on a VG Optima isotope ratio mass spectrometer. Stable isotopic ratios are expressed as:

$$ R = \frac{X_h}{X_l} $$

where $X_h$ and $X_l$ refer to the heavier and lighter isotope respectively. Isotopic values are reported using the delta ($\delta$) notation where

$$ \delta X [\%] = \left[ \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right] \times 10^3 $$

in parts per mil deviations relative to the standards, PeeDee Belemnite for $\delta^{13}$C, air for $\delta^{15}$N and Canyon Diablo triolites for $\delta^{34}$S.

RESULTS

VISUAL DETERMINATION OF DIETARY COMPONENTS - Observations of gut samples of $\leq 30x$ magnification revealed the presence of diatom tests and small
animals or parts of animals, i.e. a copepod, hydroid, amphipod. However, at this magnification the vast majority of gut contents appeared to be an amorphous matrix of deep green color, which together with the diatom tests suggested phytoplankton as a potential food source. In late summer a protozoan was abundant in the gut contents, yet it was not in the food ball formed from the mucus net. Thus, its presence may indicate an infection rather than a food source. More work on this is currently underway, but will not be addressed in this paper.

Epifluorescence microscopic analysis of gut contents and fecal pellets showed both living and dead diatoms (centric and pennate) as well as flagellates, heterotrophic bacteria, and cyanobacteria (Figure 3-1).

**CHLOROPHYLL a** - Chlorophyll a concentrations were high in both the gut (300 - 2100 µg g wet wt⁻¹) and fecal pellets (15 - 550 µg g wet wt⁻¹) indicating the likely importance of phytoplankton in the diet of *C. pergamentaceus* (Figure 3-2). Within the gut and fecal pellets samples, the highest chl-a concentrations were observed in the summer/fall. However, samples for the spring bloom period, as determined by peaks in phytoplankton from the Chesapeake Bay Monitoring Program (see appendix) are mostly lacking; sampling of worm tissues began after the spring bloom in 1994 and due to inclement weather and loss of a boat engine only the end of the bloom (early April) was sampled in 1995. Sediment samples (0.5 to 5.1 µg g wet wt⁻¹) show no obvious seasonal trends.
Figure 3-1. Photographs of epifluorescence microscopy from gut contents and fecal pellets of *Chaetopterus pergamentaceus*. A. Gut contents from 08/10/95 showing remnants of a possible diatom and bacteria; blue light; scale slot is 65.1 μm. B. Gut contents from 08/10/95 showing phytoplankton remnants and bacteria; blue light; 65.1 μm. C. Fecal pellets from 5/22/95 showing a diatom and bacteria; green light; scale slot 32 μm. D. Fecal pellets from 5/22/95 showing a pinnate diatom; blue light; scale slot is 65.1 μm. E. Fecal pellets from 5/22/95 showing a chain of diatoms (*Skeletonema*); blue light; scale slot is 65.1 μm.
Figure 3-2: Chlorophyll a in gut contents, fecal pellets, and surface sediment (0 to 5 mm). Error bars are ± 1 standard error (n = 3, or n = 1 when noted by *). All samples from Wolf Trap site only.
CARBON & NITROGEN - The average carbon to nitrogen ratio (C:N; on a molar basis) of SPM varied little during the period of investigation and averaged (± s.e.) 7.6 ± 0.8 (Figure 3-3). The C:N ratio of fecal pellets (5.7 ± 0.39) also varied little, yet, were within the range observed for SPM. Sediments (9.4 ± 0.05) changed little during the period of investigation, but had higher C:N ratios then SPM and fecal pellets. Gut contents had a maximum C:N of 12.3 in April, declined to a minimum of 5.2 in August and then increased to 7.2 in December (Figure 3-3). The carbon and nitrogen contents of the gut samples were, in general, higher by a factor of 2 compared with values for SPM, suggesting the possibility that *C. pergamentaceus* has the ability to feed selectively. Worm tissue and eggs had low C:N ratios (3.9 ± 0.31 and 4.6 ± 0.15, respectively) that varied little during the period of investigation.

Worm tissues had high carbon and nitrogen contents, with body tissues less variable than eggs.

LIPID ANALYSIS - Total lipid concentration or extract (TLE) was lower in SPM and sediment samples compared to all other sample types. The total lipid content of SPM samples averaged 5.61 ± 0.88 (mean ± s.e.; mg TLE g⁻¹ dry weight), with the lowest values occurring in July (Figure 3-4). Lipid concentrations in fecal pellets (32.63 ± 5.53) were lower than gut contents reflecting assimilation of gut materials and showed no detectable seasonal trends. Concentrations of lipids in sediment samples (0.43 ± 0.06) were lowest of all sample types with a trend of highest concentration in the spring and subsequent decreases throughout the year. Lipid contents in gut samples...
Figure 3-3: Carbon:nitrogen ratios (mol C/mol N; left panels) and percent and carbon and nitrogen on a dry weight basis (right panels). When two samples from the same date were analyzed, mean values (± one standard deviation) are presented.
Figure 3-4: Total lipid extract (TLE) normalized to gram dry weight (left panels) and milligrams organic carbon (right panels). In the upper graphs, note that fecal pellets are scaled to the left axis while suspended particulate matter (SPM) and sediments are scaled to the right axis.
averaged 174.66 ± 29.83 with enrichment for cohort 1 during the spring and depletion during the summer; cohort 2 gut contents were highly variable. Nonetheless, lipid content of the gut samples was much higher than SPM indicating possible selective feeding or a temporal build up of lipids in the gut due to the digestive processes associated with translocating the lipids from the gut to other parts of the worm (Kennedy and Nicol 1959). Lipid concentrations in tissue averaged 70.79 ± 5.46 and 82.88 ± 20.15 for cohort 1 and 2 respectively, showing a slight trend of increasing TLE in the summer with relative depletion in the spring and fall. Eggs had the highest lipid content during spawning periods (May and August) with an overall mean of 101.64 ± 18.63.

Comparing total lipid extract (TLE) normalized to dry weight among sample types allows inferences based on the overall quantity of lipid; however, TLE will vary with organic carbon content. To allow for more meaningful TLE comparisons between sample types which vary in organic carbon content, lipid concentrations were normalized to organic carbon (OC). The organic carbon normalized lipid concentration in SPM averaged 0.18 ± 0.05 (mean ± s.e.; mg TLE mg⁻¹ OC) with a peak in July. The mean lipid concentration for fecal pellets was 0.39 ± 0.11 with high variability and too few data points to detect a trend. Sediment samples had considerably lower lipid concentrations (0.06 ± 0.004) and less variability with highest concentrations in the spring which decreased throughout the remainder of the study. Gut contents averaged 0.45 ± 0.07 (0.55 ± 0.04 and 0.35 ± 0.12 for cohorts 1 and 2 respectively) showing enrichment in the spring through early August with a depletion in late August and subsequent increase throughout the fall. The depletion
occurred coincident with a decline in phytoplankton abundance (CB Monitoring program) and the addition of a secondary juvenile cohort into cohort 2 (Chapter 1). SPM and gut contents were within the same range indicating that if the worms are selectively feeding, they are selecting the organic matter component of the SPM and disregarding other suspended materials. Tissue showed a slight increase from the spring to summer among cohort 1; cohort 2 had the highest lipid content in early August for a mean of all tissue data of 0.20 ± 0.03. During times of suspected spawning (May and August) the eggs had the highest lipid content with a mean for all samples of 0.34 ± 0.08.

**FAMES** - When normalized to organic carbon content, total fatty acid concentrations (ΣFAs) show enrichment in the spring for SPM, sediments, gut contents of cohort 1, tissue of cohort 1, and eggs consistent with the timing of the spring bloom (Figure 3-5). The mean (± s.e.; μg FA mg⁻¹ OC) FA concentration across time periods was higher for SPM (29.73 ± 5.72) and fecal pellets (14.7 ± 3.75) than sediments (6.46 ± 1.00). The FA concentration in gut contents for cohort 1 (34.57 ± 20.10) were in the same range as the SPM and fecal pellets which may suggest effective selection of organic matter from SPM but no differential digestion/absorption with respect to total FAs. The FA concentration in gut contents for cohort 2 (11.24 ± 3.24) was lower than the SPM which may suggest that cohort 2 may be meeting some of its nutritional needs from lipid stores and not from filtration. The average FA concentration in tissue (8.01 ± 3.69) was lower than the SPM while the average for eggs (24.15 ± 18.74) was equal to SPM but with higher
variability. Both tissue and eggs showed enrichment during the spring bloom.

Approximately 30 - 40 fatty acids were identified in most samples, yet often fewer than ten compounds represented the bulk ($\geq 70\%$) of the distribution (Table 3-III). Even-numbered C14-18 saturated FAs (SFAs) and monounsaturated FA (MUFAs) as well as C18-22 polyunsaturated FAs (PUFAs) were characteristic of the samples although the abundance of individual FAs exhibited temporal fluctuations (Table 3-III; Figure 3-6).

SPM was characterized by a dominance of 16:0 and 18:1, which although dominant in marine organisms are not indicative of particular organic matter source(s) (Table 3-IV; Figure 3-6). The diatom marker 16:1ω7 was proportionally more abundant in the late summer compared to the late spring and early summer while the general phytoplankton markers C18 PUFAs were proportionally more abundant in the spring. However, May sampling may have missed the influx of material associated with the spring bloom, which occurs in March/April in southern Chesapeake Bay (Gilbert et al. 1995).

Fecal pellets had a more even distribution of components, although the diatom markers 16:1ω7 and 20:5ω3 were proportionally more abundant in the spring and fall.

Sediment samples were dominated by the 16:1ω7 (dominant in diatoms and other phytoplankton) and the more ubiquitous compounds 16:0 and 18:1. The PUFAs, 20:5ω3 (diatom and other phytoplankton), 18:n (general phytoplankton), and C22 PUFAs (exclusive of ω6 FAs; small phytoplankton) were depleted in the sediments relative to the SPM and worm samples.
Table 3-III. Relative abundance of dominant fatty acids (%Σ FAs). C₂₂ PUFAs exclusive of ω6 FAs.

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Figure 3-5: Total Fatty acid (left panels) and total sterol (right panels) concentrations normalized to milligrams organic carbon. Totals represent the sum of individual compounds within each compound class.
Figure 3-6a: Percent abundance of selected fatty acids expressed relative to the ΣFA concentrations associated with each sample type. See Figure 3-6b for legend details.
Figure 3-6b: Percent abundance of selected fatty acids expressed relative to the ΣFA concentrations associated with each sample type. Total fatty acid recovered (μg ΣFA / mg OC) is provided above each column. See Table III for sampling dates. All samples collected from WT except where noted as CS. C₂₂ PUFAs exclusive of omega 6 FAs. Fatty acid notations refer to A:BωC where A is the number of carbon atoms, B is the number of double bonds, and C is the position of the first double bond from the aliphatic (ω) end of the molecule.

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The ubiquitous marker 16:0 constituted a large fraction of the FAs in the gut contents throughout the year. The phytoplankton biomarkers C18 PUFAs, 16:1ω7 and 20:ω5 were proportionally more abundant in the spring and fall while biomarker compounds for small-celled phytoplankton (22:5ω3 and 22:6ω3) were proportionally more abundant in mid-to late summer. The proportions of the remaining components changed little in the gut contents throughout the year.

The eggs had a seasonally variable distribution of FA components without consistent dominance of one or a few biomarkers. In general PUFAs, indicative of "fresh" phytoplankton, were a large fraction of the eggs (Figure 3-6b).

Spatial variability in worm tissue, gut content, and fecal pellet composition was addressed with samples collected from WT and CS in April 1995. FA composition was similar in tissue collected from both sites and dominated by C22 PUFAs and 16:0. Gut contents were also similar from both sites and dominated by C18 PUFAs, 16:0 and 16:1ω7. However, the fecal pellets were unexpectedly different between sampling sites with CS having proportionally more 16:1ω7, 20:5ω3 and C18 PUFAs. In comparison, fecal pellets from WT had more 18:1 and C22 PUFAs. CS also had a two-fold higher concentration of FAs; however, it is difficult to assess whether these differences are real or due to variation in organism feeding and assimilation and/or changes in particle composition arising from tidal resuspension (Canuel unpub. data).

Cohort specific variability was directly addressed by comparing samples from August 10th 1995; cohort 1 had proportionally more 16:0, 16:1ω7, and C20,22 MUFAs while cohort 2 was enriched in C22 PUFAs.
Table 3-IV. Summary of lipid source indicators from literature

<table>
<thead>
<tr>
<th>Component</th>
<th>Source $^3$</th>
<th>Source Specific Assignment</th>
</tr>
</thead>
<tbody>
<tr>
<td>FAMES</td>
<td></td>
<td></td>
</tr>
<tr>
<td>14:0</td>
<td>marine</td>
<td>marine</td>
</tr>
<tr>
<td>16:0</td>
<td>ubiquitous</td>
<td>non-source</td>
</tr>
<tr>
<td>18:0</td>
<td>phytoplankton, zooplankton, bacteria</td>
<td>specific</td>
</tr>
<tr>
<td>$\Sigma$18:1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>iso- and anteiso $\mathrm{C}<em>{13}$, $\mathrm{C}</em>{15}$, $\mathrm{C}_{17}$</td>
<td>sulfate reducing bacteria</td>
<td>Bacterial</td>
</tr>
<tr>
<td>16:1$\omega$7</td>
<td>diatoms and other phytoplankton</td>
<td>Not included in source specific analysis of FA (Figure 3-7)</td>
</tr>
<tr>
<td>$\Sigma$18:$\omega$n</td>
<td>diatoms, Chrysophyceae, Haptophyceae</td>
<td>“Fresh” Algal</td>
</tr>
<tr>
<td>20:5$\omega$3</td>
<td>diatoms other phytoplankton</td>
<td>“Fresh” Algal</td>
</tr>
<tr>
<td>$\mathrm{C}_{22}$ PUFAs</td>
<td>small phytoplankton, e.g. flagellates, cryptophytes</td>
<td>Faunal</td>
</tr>
<tr>
<td>Exclusive of $\omega$6 FA</td>
<td></td>
<td></td>
</tr>
<tr>
<td>20:1$\omega$11, 22:1$\omega$11</td>
<td>faunal, internal synthesis</td>
<td>Faunal</td>
</tr>
<tr>
<td>$&gt;\mathrm{nC}_{22}$</td>
<td>vascular plants, microalgae (trace)</td>
<td>Terrestrial</td>
</tr>
</tbody>
</table>

$^2$References given in text.

$^3$ Sources are assigned based on predominance of specific compounds in a particular organism(s) but are not always exclusive to that particular source nor do the compounds occur in all species of a particular group.
<table>
<thead>
<tr>
<th>Sterols</th>
<th>26</th>
<th>Faunal, internal synthesis</th>
<th>Faunal</th>
</tr>
</thead>
<tbody>
<tr>
<td>$27\Delta^5$</td>
<td></td>
<td>zooplankton (crustaceans), phytoplankton (trace), internal synthesis</td>
<td>Ubiquitous, Non-source specific</td>
</tr>
<tr>
<td>$28\Delta^5$</td>
<td></td>
<td>ubiquitous plants, phytoplankton</td>
<td></td>
</tr>
<tr>
<td>$27\Delta^5.22$</td>
<td></td>
<td>unicellular algae, dinoflagellates, diatoms, zooplankton molts</td>
<td></td>
</tr>
<tr>
<td>$28\Delta^5.22$</td>
<td></td>
<td>diatoms, dinoflagellates, numerous phytoplankton</td>
<td>Phytoplankton</td>
</tr>
<tr>
<td>$28\Delta^5.24(28)$</td>
<td></td>
<td>diatoms, seagrasses</td>
<td></td>
</tr>
<tr>
<td>$29\Delta^5.24(28)$</td>
<td></td>
<td>algae, seagrasses</td>
<td></td>
</tr>
<tr>
<td>$29\Delta^5$</td>
<td></td>
<td>vascular plants, seagrasses, green algae, cyanobacteria</td>
<td></td>
</tr>
</tbody>
</table>
Separating the Σtotal FA into source specific FA shows that autochthonous FAs, primarily of algal sources, are the most abundant for every sample type on every date with the exception of sediment samples (Table 3-V; Figure 3-7). Concentrations of algal FA were highest in spring for all sample types. Concentrations of terrestrial FA were low, less than 6%, and many samples contained no terrestrial FAs. Concentrations of bacterial FAs peaked in the spring for most sample types, except SPM, although the percent abundance of bacterial FAs was often highest in the summer (Table 3-V; Figure 3-7).

Temporal variations in the lability and source of organic matter were examined using the ratio of PUFAs:SFAs. FA reactivity generally increases with increasing level of unsaturation (double bonds); thus higher PUFA:SFA ratios indicate increased lability. The ratio of 16:1ω7 to 16:0 is also useful as it provides an index for diatom vs. flagellate based food webs (Figure 3-8; Fraser et al. 1989; St. John and Lund 1996). Gut content and tissue samples show a seasonal pattern of increased lability in the spring and fall/winter consistent with increases in diatom production during winter/spring months while the summer is a time of intense pelagic recycling when nano- and picoplankton are dominating the phytoplankton (Figure 3-8; Marshall and Lacouture 1986; Malone et al. 1991; Chesapeake Bay Program data). The increased importance of diatoms in spring is supported by the 16:1ω7 to 16:0 (Figure 3-8).
Percent of fatty acids attributed to various sources. Algal components are $C_{18}, C_{20},$ and $C_{22}$ PUFAs exclusive of $\omega 6$ FAs. Terrestrial components are long-chained saturated FAs (i.e. $\geq C_{22}$). Bacterial components are normal, iso- and anteiso-branched $C_{13}, C_{15},$ and $C_{17}$ FAs. Mixed marine components are non-source specific marine and estuarine FAs, i.e. $14:0, 16:0, 16:1\omega 7, 18:0,$ and $\Sigma 18:1$.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Date</th>
<th>Station</th>
<th>Cohort</th>
<th>$\Sigma FA_{\mu g FA \cdot mg^{-1} OC}$</th>
<th>Algal</th>
<th>Terrestrial</th>
<th>Bacterial</th>
<th>Mixed Marine</th>
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<tr>
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<td>WT</td>
<td>-</td>
<td>32.6</td>
<td>10.2</td>
<td>0.0</td>
<td>9.0</td>
<td>72.7</td>
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<tr>
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<td>11.5</td>
<td>0.0</td>
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<td>75.8</td>
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<td>5.8</td>
<td>41.4</td>
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<td>0.9</td>
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<td>5.1</td>
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</tr>
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<td>20.6</td>
</tr>
</tbody>
</table>

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Figure 3-7. Source specific fatty acids. Black symbols indicate cohort 1, gray symbols indicate cohort 2. Algal components are C\textsubscript{18}, C\textsubscript{20} and C\textsubscript{22} PUFAs exclusive of omega 6 FAs; Terrestrial components are long-chain saturated FA (i.e. > C\textsubscript{22}); Bacterial FAs components are normal, iso-, and anteiso-branched C\textsubscript{13}, C\textsubscript{15}, and C\textsubscript{17} FAs. Note scale differences.
FAMES, BENTHIC-PELAGIC COUPLING - Gut contents and SPM samples were generally similar in terms of the dominant compounds given that the samples were taken as much as two weeks apart (Figure 3-6). For this study, gut contents, which were sampled more frequently, were used as a proxy for the organic material nominally available to the polychaete. The components with multiple sources (i.e. 16:0, 18:0 and 18:1) peaked in availability as defined by gut contents during mid-summer when primary production peaked (Kemp et al. 1997). The C_{22} PUFAs, typical of small phytoplankton such as flagellates and cryptophytes were not the primary available component except during the late summer.

The dominant FA in the worm tissues changed seasonally with 16:0 and C_{22} PUFAs being the dominant storage components. However, the relative abundance of C_{22} PUFAs declined during summer, a time of rapid growth and development (Figure 3-6). In the summer the C_{22} PUFAs, were stored in tissue in a lower proportion than their availability based on the gut contents, which indicates rapid utilization by cohort 2 of these PUFAs in the late summer compared to storage of these components during the rest of the year. The fact that C_{22} PUFAs were enriched in tissue relative gut contents in the spring but not in August and were depleted in September suggests that cohort 2 may be using lipid stores for a component of its growth. Using the same tissue to gut content comparisons, the C_{18} PUFAs as well as 18:0 and 18:1 do not appeared to be preferentially stored in either tissue or the eggs at any time of the year. Eicosopentenoic acid (20:5\omega3) showed evidence of storage in the spring but storage was generally in direct proportion to its availability (Figure 3-6). Thus, there is potential for this component to be limiting.
Figure 3-8: Ratios of PUFA to SFA and 16:1ω7 to 16:0. A higher PUFA : SFA ratio indicates greater organic matter lability, while a higher 16:1 : 16:0 ratio indicates a greater diatom versus flagellate dominance.

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except during the spring. While it is possible that assimilation of the various PUFAs may change temporally, this reasoning is not intuitive and not considered likely. The general pattern that emerges is storage of essential PUFAs by adults and utilization of these components by fast growing juveniles.

The relative proportion of particular FAs in the fecal pellets varied temporally and generally tracked the gut contents indicating no selective digestion. However, the FAs for the April WT samples showed differences between the gut contents and fecal pellets (see above; Figure 3-6). We can only make direct comparisons between fecal pellets and sediments in April, when samples were collected on the same day, and in August, when samples were collected about 2 weeks apart. For these samplings, 16:1ω7 was proportionally higher while 20:5ω3 and Cω2 PUFAs were lower in sediments versus pellets. Generally, the gut contents and fecal pellets were similar in terms of relative proportions of components while the sediments were different (Figure 3-6).

STEROIDS - When total sterol concentrations were normalized to organic carbon, SPM averaged 4.16 ± 1.77 (mean ± s.e.; mg Σsterol mg⁻¹ OC) and peak in July (Figure 3-5). Fecal pellet samples (17.91 ± 4.47) and sediments (1.70 ± 0.24) were enriched in sterols during spring and decreased throughout the remaining sampling period. Gut contents (12.19 ± 1.80) were enriched in sterols relative to SPM with the highest concentration found during spring. Tissue samples (20.13 ± 3.84) showed enrichment in spring for cohort 1 and mid-summer for cohort 2. Eggs samples (27.78 ± 12.44) showed high variability and were enriched during periods
of suspected spawning, May and August.

Approximately 20 - 30 sterols were identified in most samples, but five to seven compounds generally dominated the distributions (Table 3-VI; Figure 3-9). As expected cholesterol (C27Δ5), which is abundant in animals and present at low levels in some phytoplankton as well as potentially synthesized by the worm, was the dominant component in all sample types on all sampling dates (Table 3-VI). In general, the non-specific phytoplankton markers cholest-5,22-dien-3β-ol (27Δ5,22) and 24-methylcholest-5-en-3β-ol (C28Δ5) increase during the summer. For all sample types, the diatom biomarker 24-methylenecholesterol (28Δ5,24(28)) and the algal biomarker 24-ethylcholest-5,24(28)dien-3β-ol (29Δ5,24(28)) were elevated during spring and often in September and December samplings. Dinosterol (4α,23,24-trimethylcholest-22-en-3β-ol; 30Δ22), a biomarker for dinoflagellates, could not be positively identified in the samples.

The ratio of campesterol:stigmasterol:sitosterol (24-methylcholest-5-en-3β-ol : 24-ethylcholesta-5,22-dien-3β-ol : 24-ethylcholest-5-en-3β-ol; C28Δ5 : C29Δ5,22 : C29Δ5) can be used to assess whether C29Δ5 is primarily derived from phytoplankton or terrestrial sources (Volkman 1986). The gut content samples ranged from 1:0.44:0.16 to 1:2.22:1.16; values are closer to phytoplankton sources rather than terrestrial vascular plants (1:1.6:6.6). This suggests that this compound is derived from autochthonous rather than allochthonous sources in southern Chesapeake Bay.
Table 3-VI. Percent relative abundance (% Σ sterols) for samples collected from the lower Chesapeake Bay.

<table>
<thead>
<tr>
<th>Sample</th>
<th>Date</th>
<th>Station</th>
<th>Cohort</th>
<th>Σ sterols (µg/mgC)</th>
<th>26</th>
<th>27Δ5,22</th>
<th>27Δ5</th>
<th>28Δ5</th>
<th>28Δ5,24(28)</th>
<th>28Δ5</th>
<th>29Δ5</th>
<th>29Δ5,24(28)</th>
<th>Sum</th>
</tr>
</thead>
<tbody>
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<td>03/09/95</td>
<td>WT</td>
<td>-</td>
<td>2.7</td>
<td>9.1</td>
<td>8.1</td>
<td>16.3</td>
<td>23.2</td>
<td>13.6</td>
<td>0.0</td>
<td>7.7</td>
<td>9.5</td>
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<tr>
<td></td>
<td>07/24/95</td>
<td>WT</td>
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<td>7.7</td>
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<td>47.5</td>
<td>8.6</td>
<td>3.9</td>
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<td>6.2</td>
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As with FAMES, gut contents were taken as a proxy for the material potentially available to the polychaete. Aside from cholesterol, all of the percent sterol distributions in the worm tissue paralleled the distributions of the gut contents. Total sterol concentrations in tissue were elevated in late August (45.1 μg mg\(^{-1}\) OC) compared to all other sampling times (16.6 ± 4.4 μg mg\(^{-1}\) OC) while the availability of sterols (as indicated from concentrations of sterols in gut contents) was not elevated during this time period (Figure 3-9). One explanation for this observation is that August is a time of intense storage of sterols. Alternatively, juvenile worms recruited during this time period and the high content of sterol components could be the remnants of storage components from the eggs. Eggs were found to be enriched in all sterols during spawning periods.

Spatial variability between WT and CS was addressed with samples collected during April 1995. As with the FAs, in terms of relative proportion of components, our data show spatial homogeneity in sterol composition of gut contents and tissue samples (Figure 3-9). While lipid concentrations were similar in tissue samples, gut contents at CS had over a two fold higher concentration of sterols than at WT. As was the case for FAs, given variations in animal metabolism and feeding and SPM composition, we are unable to establish the significance of this observation (Canuel unpub. data). Similar to the FAs, fecal pellets were different between the sites with CS having proportionally more C28Δ5,24(28) and less C27Δ5,22 and C28Δ5.
Figure 3-9a: Percent abundance of selected sterols expressed relative to the sterol concentrations associated with each sample type. Total sterol concentration (μg sterol / mg OC) are provided above each column. See Table III for sampling dates. See Figure 2-9b for sterol nomenclature.
Figure 3-9b: Percent abundance of selected sterols expressed relative to the sterol concentrations associated with each sample type. Total sterol recovered (µg sterol / mg OC) is provided above each column. See Table III for sampling dates. Compound names are provided in the text. Sterols are designated as AΔX,Y where A refers to the total number of carbon atoms, and ΔX,Y to the position(s) of the double bonds following the ring numbering conventions for sterols (Killops and Killops 1993).
Cohort specific variability was addressed with samples from August 10th 1995. No compositional differences were noted for tissues collected from cohorts 1 and 2. Cohort 1 gut contents had proportionally more 28Δ5,24(28) and less 28Δ5 than cohort 2.

For a given sampling, the suspended particulate matter, gut contents, and fecal pellets were generally similar in terms of relative proportions of individual sterols while the sediments were different from all other sample types (Figure 3-9), most noticeably in the abundance of the algal biomarker 29Δ5,24(28). Cholesterol was dominant in all time periods for fecal pellets and sediments with a lower concentration and slightly lower proportion in sediments. This suggests storage/utilization of cholesterol by this polychaete, similar to what has been shown for copepods (Harvey et al. 1989). Also, the relative quantities of the remaining sterols in the sediments varied temporally and not in unison with the fecal pellets.

**Stable Isotopes** - For this study, no isotope data are available for SPM. Fecal pellets showed high temporal variability of the δ¹³C and δ¹⁵N signals, both of which were depleted and enriched during summer, only one month apart (Figure 3-10, 3-11). The temporal pattern for δ¹³C composition of the fecal pellets in the summer tracked the composition of the gut contents with a correlation (r) of 0.97 whereas δ¹⁵N showed no correlation (0.13). There was no consistency between fecal pellets and gut contents during the spring yielding an annual correlation of 0.50 and 0.14 for δ¹³C and δ¹⁵N respectively. Sediment samples show no temporal trend for δ¹³C, yet sediment δ¹⁵N was enriched during the spring.
Figure 3-10: Natural abundance $^{13}$C and $^{15}$N values. Where multiple samples from the same date were analyzed, mean values ($\pm$ one standard deviation; $n = 2$ to 3) are presented. Unless otherwise noted, all samples were collected in 1995.
Boxes indicate ranges for organic matter:
1 = estuarine POM;
2 = oligohaline phytoplankton;
3 = terrestrial plants;
4 = freshwater marshes;
5 = marine and estuarine phytoplankton;
6 = macroalgae;
7 = salt marshes;
8 = benthic microalgae.

Data from W. Boynton, University of Maryland, pers. comm.

Figure 3-11: Natural abundance $^{13}$C vs $^{15}$N plots and $^{13}$C vs $^{34}$S plots.
The isotopic composition of worm gut contents showed temporal variation in δ¹³C on a short-term (weeks, months) and a seasonal basis. Seasonal variation was observed in relatively depleted values in the spring (-22.0 ± 0.8) and more enrichment in the summer/fall (-19.3 ± 0.7; Figure 3-10). Isotopic composition generally falls well within the range for estuarine particulate organic matter with a significant phytoplankton component (Figure 3-11). The nitrogen isotope signal also showed short-term (weeks, months) temporal variability preventing detection of any seasonal trends. The nitrogen isotopic composition of gut contents was the most depleted and the most enriched during summer, only two weeks apart. The variability in the carbon and nitrogen isotope signals may reflect a change in diet, in the recycling of nutrients, or in availability of material from the upper water column due to physical mixing. The isotopic signal for carbon and nitrogen showed no differences between cohorts when direct comparisons were made with the 08/10/93 data (Figure 3-10). Gut content data for δ³⁴S are limited, but were typical of estuarine particulate organic matter and phytoplankton (Figure 3-11).

Worm tissue generally fell within the range of -16 to -21 for δ¹³C. Cohort 1 tissue was most depleted in δ¹³C and δ¹⁵N during the winter. Although one tissue data point in August suggests depletion, this point may be an outlier due to senescence in cohort 1 (see discussion for details). Cohort 2 showed peak enrichment for both δ¹³C and δ¹⁵N in summer, but no obvious temporal trends were noted. Including the outlier (see discussion for details), the correlation (r) between gut and tissue was 0.47 for δ¹³C with no correlation (-0.07) for δ¹⁵N; without this point, the correlation was 0.70 for δ¹³C with no correlation (-0.02) for δ¹⁵N. The
isotopic signal for carbon and nitrogen showed large differences between cohorts when direct comparisons were made with the 08/29/95 data possible due to senescence in cohort 1 (see discussion details on the outlier; Figure 3-10).

Eggs showed high variability for both $\delta^{13}C$ and $\delta^{15}N$; yet were enriched for both isotopic signals during times of suspected spawning, spring and mid-summer.

In general due to excretion of the lighter $\delta^{15}N$ by consumers, a $\delta^{15}N$ shift of 2 to 4 $\%_0$ is expected between food sources and body tissues (Lajtha and Michner 1994). In the spring, we did not observe the characteristic $\delta^{15}N$ shift of 2 to 4 $\%_0$ between the guts contents and tissue, however, a $\delta^{15}N$ shift was noted between the gut contents and the eggs indicating that this worm was shunting material directly to the eggs and not into body tissue. During the summer, the fecal pellets had a lighter isotopic signature than the gut contents as expected; yet, the $\delta^{15}N$ shift was not observed in tissue or eggs potentially indicating a time lag for body tissue to turn over to current isotopic composition of the gut contents.

**DISCUSSION**

**SOURCES OF ORGANIC MATTER** - All of the data collected in this study point to autochthonous phytoplankton as the primary food source for *C. pergamentaceus*. High concentrations of C_{18}, C_{20} and C_{22} PUFAs (exclusive of $\omega 6$ FAs) found in the gut contents throughout 1995 indicate the presence of “fresh” or recently viable algal cells (Shaw and Johns 1985) and are definitively of plankton (Saliot et al. 1988). The high percentage of 20:5$\omega 3$ and 16:1$\omega 7$ suggests a food source including diatoms (Viso and Marty 1993). However, the presence of C_{18} PUFAs derived from
Chrysophyceae, Haptophyceae, and/or dinoflagellates suggests that other groups of phytoplankton also are important (Fraser et al. 1989; Viso and Marty 1993; Graeve et al. 1994).

Branched FA such as iso- and anteiso C_{13}, C_{15}, and C_{17}, which are generally indicative of sulfate-reducing bacteria (Kaneda 1991), constituted a very small fraction of the total FAs, less than 7% of gut contents and less than 3% of SPM. The BrFAs in the guts may derive, at least in part, from gut flora and do not necessarily represent intake of bacterially derived organic matter. However, while the branched FAs are exclusive of certain groups of bacteria, other bacterial FAs may not be distinguishable from algal FAs (Wakeham 1995). Several FA components (e.g. 14:0, 16:0, and 18:1) abundant in this study are not source specific and are known to be prevalent in bacterial and plankton organic matter (Canuel and Zimmerman 1999 and references therein).

Faunal dietary input may be reflected in the 20:1ω11 and 22:1ω11 compounds present in gut contents (Falk Petersen et al. 1986). However, these compounds may also be synthesized by the worm, so while their presence should be noted, no conclusions regarding the sources of these components can be drawn.

Long chain saturated FAs >nC_{22}, typically considered terrestrial biomarkers, were present at very low levels. Small amounts of long chain FAs in marine environments may also come from microalgae (Volkman et al. 1989). In either case, low concentrations of these components suggest that allochthonous sources of organic matter are significantly less important than autochthonous sources. Moreover, the overall dominance of short-chained FAs (<C_{20}) even in some of the ubiquitous non-
specific FAs suggests the importance of autochthonous sources. Canuel and Zimmerman (1999) had similar findings regarding the importance of terrestrial organic matter for this region of the Chesapeake Bay.

Thus, the presence of the more universal FAs in combination with the biomarkers specific to phytoplankton indicates that the organic matter ingested by this polychaete is primarily from phytoplankton with inputs of recycled material from microbial sources and some potential faunal input. This finding is also supported by the stable isotope results.

Although some sterols are not source-specific, reasonable inferences about organic matter sources can be made using the relative proportion of various sterols (Volkman et al. 1981; Volkman 1986). Cholesterol may be derived from phytoplankton or zooplankton sources (Volkman et al. 1986), or possibly internally synthesized by this polychaete; thus it does not indicate an organic matter source. Ignoring cholesterol, the dominant sterols in the gut contents are known to come from a variety of sources, mostly of phytoplankton origin. Cholest-5,22-dien-3β-ol (27Δ5,22) may be derived from unicellular algae, dinoflagellates, diatoms, and zooplankton molts (Volkman 1986). Brassicasterol (28Δ5,22) was previously thought to generally be the dominant sterol in diatoms (Volkman 1986) but recent evidence indicates that other algal groups often have this component while few diatom species do (Barrett et al. 1995). The diatom marker 28Δ5,24(28) may also be derived in small amounts from seagrasses (Volkman et al. 1981). While 29Δ5 was previous thought to be derived mainly from vascular plants, it can also be derived from seagrasses and algal sources including, but not limited to green algae.
and cyanobacteria (Volkman et al. 1981; Volkman 1986). Lastly, 29Δ5,24(28) can be found in algae and is a minor component in seagrasses (Volkman et al. 1981; Volkman 1986). Thus while the source of any one of the major sterols may vary, by looking at the array of sterols the conclusion is that the organic matter source is mainly of mixed planktonic origin. C36 sterols may be synthesized by the worm or obtained from faunal sources in the diet (Volkman et al. 1981). Examination of the sterol biomarker data supports the conclusions drawn from the FA data; the polychaete C. pergamentaceus utilizes organic matter that is primarily of phytoplanktonic origin.

Our results are consistent with those of Canuel and Zimmerman (1999) who showed that most organic matter in lower Chesapeake Bay is autochthonous material derived primarily of planktonic and microbial sources. Recent evidence indicates that terrestrial derived organic matter is of minimal direct importance at higher trophic levels in estuarine ecosystems and that consumers utilize locally produced organic matter (e.g. Simenstad and Wissmar 1985; Bunn et al. 1989; Deegan and Garritt 1997). Peterson et al. (1985) found that ribbed mussels living in the salt marsh tended to use marsh derived organic matter while mussels living near the creek mouth used marine phytoplankton. Blue mussel growth has been correlated to local seston composition and locally produced stable carbon isotopes signatures (Ruckelshaus et al. 1993).

Deegan and Garritt (1997) also showed that consumers tended to utilize organic matter produced in the region of the estuary in which they reside. Their study was conducted in a much smaller and shallower system than Chesapeake Bay with
stronger tides and shorter water residence time. Thus, their system should have been ideal for uniform delivery of organic matter throughout the system. Nonetheless, consumers in that study utilized local sources. Thus, we might expect that consumers in larger estuaries, such as Chesapeake Bay, might also utilize local sources.

**Sources of Organic Matter that Fuel the High Secondary Productivity and Reproduction of this Polychaete** - Most PUFAs are considered essential or semi-essential for consumers (Demott and Müller-Navarra 1997; Enright et al. 1986a,b), because they cannot be synthesized by consumers or are synthesized too slowly for optimal growth. However, the lipid requirements of organisms can be variable even among related taxa (Demott and Müller-Navarra 1997).

The qualitative and quantitative lipid requirements of the polychaete *C. pergamentaceus* are unknown. For the polychaete *Capitella* sp. I, reduced growth was found when organic matter lacked PUFAs and amino acids (Marsh et al. 1989). If the assumption is made that *C. pergamentaceus* are like other suspension feeders, such as juvenile bivalves, then a key component in their diet is the availability and balance of fatty acids (Enright et al. 1986a,b). PUFAs are known to be an essential component of a nutritious diet for oysters (*Crassostrea virginica*; Chu and Dupuy 1980). High levels of 22:6w3, 20:5w3, and carbohydrates from mixed algal diets were found to be the best diet for the oyster, *Ostrea edulis* (Enright et al. 1986a). Thompson et al. (1993) found that short chained saturated FAs (14:0 and 16:0)
produced the highest growth rates in the Pacific oyster (*Crassostrea gigas*) due to a higher efficiency of energy release; however, these compounds are readily available from many sources and are most likely never limiting. Müller-Navarra *et al.* (2000) showed a relationship between growth rate and 20:5ω3 due to a higher transfer efficiency between producers and consumers associated with that compound. Soudant *et al.* (1998) indicated 22:6 to be essential for settlement and metamorphosis for the scallop *Pecten maximus*. Some animals may not have a dietary requirement for 20:5 or 22:6 since some marine fauna have a limited ability to synthesize these components from 18:2 (Kanazawa *et al.* 1979), yet growth rates and larval survival usually increase when these PUFAs are in the diet (Volkman *et al.* 1989). Generally, young and developing marine animals are thought to require 22:6 (Enright 1986b).

The data suggest that the C$_{20}$ and C$_{22}$ PUFAs, typically considered essential to most marine animals and often required for growth and development of juveniles, are also essential or semi-essential to the polychaete *C. pergamentaceus* during its high growth phase and may be limiting. Decreases in the essential PUFAs in tissue tissues during the summer suggest rapid utilization of 20:5ω3 and C$_{22}$ PUFAs compared to storage of these components during the spring. There is also evidence suggesting additional storage of these compounds in the fall. The pattern of PUFA usage/storage is consistent with the high growth rate and high secondary production of new recruited and juvenile *C. pergamentaceus* during the summer (Chapter 1).

Our data are consistent with data from Chesapeake Bay Monitoring Program which shows that diatoms and cryptophytes were the dominant phytoplankton in the
lower Chesapeake Bay during the course of this study (1995; Chesapeake Bay Monitoring data; see appendix). Diatoms and other phytoplankton such as flagellates, in particular cryptomonads, are generally considered to be the main sources of C₃₀ and C₂₂ PUFAs in marine environments (Viso and Marty 1993). Thus the sources(s) of organic matter that fuel the high growth and secondary productivity of *C. pergamentaceus* appear to be predominantly diatoms and small flagellates, such as cryptophytes. No clear pattern of preferential storage or usage was noted for any sterol (Figure 3-9) although sterol biomarkers supported the general importance of phytoplankton to this organism.

Eggs of *C. pergamentaceus* contained about 4 to 17 % lipids on a dry weight basis or 12 to 70 % lipids on an organic carbon basis which is comparable to a variety of marine eggs including many fish species, copepods, and bivalves (Falk-Petersen *et al.* 1986; Klungsøy *et al.* 1989; Honkoop *et al.* 1999). Lipids are important components of eggs, serving as energy reserves and membrane constituents. For a wide variety of marine invertebrates and fish, lipid acquisition during oogenesis may come directly from transfer from other body constituents and/or dietary intake, which is known to strongly influence the lipid composition of oocytes (Soudant *et al.* 1996; references therein).

A high PUFA content in eggs has been used to underscore the essential role of these compounds in the development of larvae (Falk-Petersen *et al.* 1986; Klungsøy *et al.* 1989; Soudant *et al.* 1996). The eggs of *C. pergamentaceus* contained high levels of PUFAs, comprising 20 to 51 % of the total FAs. Eggs collected during spawning (May and August) also contained the highest quantities of sterols and FAs,
of all sample types. In particular, the major components in the eggs were C\textsubscript{22} PUFAs, components which have previously been shown to be essential for a variety of marine animals and possibly for this polychaete (see above). It is likely that PUFAs play an essential role in worm development from egg through juvenile settlement as has been found for other invertebrates and fish. Altered fecundity, hatching rate, and other abnormalities have been noted when essential FAs are deficient in the eggs (Watanabe \textit{et al.} 1984; Soudant \textit{et al.} 1998).

The proportion of C\textsubscript{20:1} and C\textsubscript{22:1} in the eggs is considerably higher in the spring and fall compared to the gut contents. \textit{Chaetopterus pergamentaceus} may have the capacity for elongation of C\textsubscript{18} precursors (e.g. Fullarton \textit{et al.} 1995; Kattner and Hagen 1995). Alternatively, temporal variability in preferential storage may play a role.

Cholesterol (27\Delta 5) appears to have been preferentially incorporated in the eggs since the proportion of cholesterol is higher in the eggs than the gut contents. Soudant \textit{et al.} (1998) had similar finding for scallops and suggested that cholesterol played an important role in early larval development or larval growth. They also found preferential incorporation of stigmasterol (29\Delta 5,22) and 29\Delta 5 similar to that for cholesterol. However, our study did not show preferential incorporation of neither 29\Delta 5,22 nor 29\Delta 5 in the eggs; aside from cholesterol, all the sterols had distributions similar to the gut content samples suggesting no selectivity.

Direct comparisons between cohort 1 (adults) and cohort 2 (juveniles) were restricted to samples from August 10\textsuperscript{th} 1995, a spawning period. The overriding difference between cohorts was a depletion of essential PUFAs in cohort 1 in both
guts and tissues as well as different isotope signals in the tissue samples. Juveniles, by virtue of their smaller size, may have a shorter gut residence time (Forbes and Lopez 1990; Hawkins *et al.* 1990). Thus, the difference in gut contents may represent a temporal difference in the organic matter available. Although, temporal variation driven by tidal cycles, on the order of hours, may change the quantity of material, the quality of material is thought to be consistent (Canuel, pers. comm.).

High mortality was noted for Cohort 1 in August, perhaps due to post spawning mortality (Chapter 1), an inability to intake organic matter faster than metabolic demand, or both. Organic matter composition showed short-term variability, on the order of weeks (see below), which could conceivably affect larger worms that have higher energetic requirements. The data suggest that cohort 1 used stored PUFAs for gamete production; the use of stored components for reproductive purposes has been noted in other invertebrates such as bivalves (Graf 1992; Soudant *et al.* 1998). Thus perhaps the differences noted between cohorts reflects senescence in the adult population due to diversion of essential components into reproduction.

In summary, our data indicate that cohort 1 used the spring bloom (mainly diatoms) for egg production and some storage of essential FA in body tissues. During the summer, utilization of the combination of diatoms and smaller phytoplankton (e.g. cryptophytes, cyanophytes, nano- and pico plankton) was for metabolic maintenance or reproduction by cohort 1 and to support the high growth and high secondary productivity for cohort 2. Similarly, Christensen and Kanneworff (1985) found that for several bivalves in the Oresund sedimenting phytoplankton from the spring bloom was used for gonadal proliferation whereas food intake during...
the summer was used for somatic growth. This general pattern may hold for other marine macrofauna that tend more toward the ‘equilibrium’ type rather than the ‘opportunist’ type.

A general paradigm for estuarine benthic ecology is that food resources are abundant immediately following sedimentation of the spring bloom, while food resources are limited in the summer when the organic matter is dominated by older more refractory materials (Marsh and Tenore 1990). Thus, the spring bloom is thought to support most estuarine benthic production (Marsh and Tenore 1990). In contrast, Thompson and Schaffner (Chapter 1) found that the timing of maximum individual worm growth for *C. pergamentaceus* was during the summer, coincident with a seasonally maximal peak in gross primary production (Kemp et al. 1997) and in net plankton community production (Smith and Kemp 1995), not the spring bloom. Recent evidence indicates that patches of high particle concentrations exist within the Chesapeake Bay which may provide a constant and high food concentration (Hood et al. 1998). One such patch, the result of a residual circulation eddy, is located in the vicinity of our study region (Figure 8a, Chapter 2). This eddy has associated upwelling and downwelling zones, strongly influences plankton distributions, and may induce phytoplankton growth (Hood et al. 1998). This circulation pattern may result in high phytoplankton production resembling a mini-spring bloom condition in which the production of large phytoplankton such as diatoms may be enhanced (as per Kiørboe 1993). Thus, physical processes enhance benthic-pelagic coupling and may favor enhanced secondary production in the benthos (Nixon 1988; Schaffner et al. 2000).
TEMPORAL VARIATIONS IN ORGANIC MATTER - We found evidence for seasonal temporal variability in organic matter sources. Seasonally lower C:N ratios (Figure 3-3) for gut contents in mid summer may be indicative of a higher quality of material being ingested during that time period (Valiela 1995), ingestion of relatively more bacteria (Goldman et al. 1987; Lee and Fuhrman 1987), or less resuspension of refractory organics (Wright et al. 1997; Schaffner et al. 2000). Our FA data show a seasonal pattern of increased lability (higher PUFA:SFA) and dominance of diatoms versus other phytoplankton (higher 16:1ω7:16:0; Figure 3-8). The diatom biomarker 28Δ5,24(28) and the algal biomarker 29Δ5,24(28) showed a decrease in the summer compared to the spring and fall (Figure 3-9). However, most of the sterols are derived from numerous algal sources and therefore lack a seasonal trend. The seasonal changes in the carbon isotope signal for gut contents may reflect a change in diet (Gearing et al. 1984) or a change in the recycling of nutrients (Cifuentes et al. 1988; Rau et al. 1990).

Our data also potentially indicate short-term variability in the mid-summer of 1995. Chlorophyll a values (Figure 3-2), the FA data (Figures 3-6 and 3-7), and the carbon and nitrogen isotope signals (Figure 3-10) are variable on a short-term basis in the summer concomitant with changes in the quantity and composition of phytoplankton (Chesapeake Bay Monitoring Data; see appendix).

Our results are consistent with those of Canuel and Zimmerman (1999) who found temporal variability in the composition of SPM was driven by seasonal phytoplankton production. The phytoplankton data from the Chesapeake Bay Program show a seasonal pattern in diatom abundance opposite to the seasonal
abundance patterns of small plankton such as flagellates, cryptomonands, and picoplankton (Chesapeake Bay Monitoring data; see appendix). These data are consistent with the general trends we observed. Further, the phytoplankton data from the Chesapeake Bay Program show short-term variability, on the order of a few weeks, in the quantity and composition of phytoplankton which is consistent with our data. Thus, these results suggest tight benthic-pelagic coupling with the worm reflecting changes in the water column productivity.

**Spatial Variability in Organic Matter** - A spatial pattern in juvenile density and growth rates of the population of *C. pergamentaceus* was observed in the lower Chesapeake Bay for a high recruitment year (1995) but not a low recruitment year (1994; Chapter 2). Are these spatial demographics influenced by environmental gradients driven by physical processes such as the quality of food? Our compositional data for fecal pellets, gut contents, and worm tissue of cohort 1 (adults) collected in April may yield insights regarding August cohort 2 (juvenile) growth rates.

Our lipid data show spatial homogeneity for the long term integrated view of assimilated matter (tissue) and gut contents leading to the conclusion that there is no spatial difference in the availability or quality of organic matter. These results are similar to the findings of Canuel and Zimmerman (1999) who found spatial homogeneity in organic matter sources within the lower bay. Physical processes enhance mixing in the lower bay which should lead to efficient delivery of organic matter to the benthos (Schaffner *et al.* 2000). The lipid data for the fecal pellets...
showed spatial heterogeneity; the implications of which are unresolved. Variations in fecal pellets may reflect variability in fecal pellet composition not tied to the sites. For example, there may be metabolic differences in worms between the sites, due to environmental parameters (Chapter 2), which affects assimilation/utilization of organic matter. Difference between sites cannot be resolved with our limited data set; however, due to the potential implications additional study on this topic warranted.

BENTHIC-PELAGIC COUPLING - *Chaetopterus pergamentaceus*’s role in benthic-pelagic coupling is to enhance the quantity of organic matter deposited, but it appears to have little effect on quality. Gut contents had a much higher TLE on a dry weight basis, but, not on an organic carbon basis than SPM which may suggest that *C. pergamentaceus* exhibits selective feeding on organic material. Preferential ingestion of organic matter from SPM has been found for some bivalves (e.g. Newell and Jordan 1983). However, these results also may derive from digestive processes. Kennedy and Nicol (1959) discuss ‘pigment spherules’ found in the gut epithelial cells of this polychaete which may suggest possible buildup of some pigments and other lipids in the gut wall for reason unknown, but perhaps for preliminary storage or additional digestion. The fecal pellets also have more lipid than SPM on a dry weight but not on an organic carbon basis, which supports the idea of selective feeding. If this polychaete exhibits selective feeding, this could have important ramifications for benthic-pelagic coupling and we recommend this as an area for future study.
In general there are no differences in FA component distributions between the gut contents and the fecal pellets, which indicates that digestion is not selective. Thus, deposition of fecal pellets represents an increase in the quantity of organic material reaching the benthic community but not a change in the quality of organic material.

However, this biodeposition may be an important process by which suspended matter is incorporated into sediments. Given the amount of chlorophyll present in fecal pellets, the higher amount of TLE on a dry weight compared to SPM, and the worm densities (Chapter 1), deposition of fecal pellets on the sediment can easily be hypothesized as an important mechanism for enhancing flux to the sediment-water interface (Figure 3-2). Epifluorescence microscopy showed that fecal pellets contained partially digested as well as potentially viable plankton cells which would be deposited on the sediment surface. Carbon and nitrogen percentages in the fecal pellets fall within the range found for other suspension feeders in coastal systems (Navarro and Thompson 1997; Jaramillo et al. 1992; Haven and Morales-Alamo 1966). Thus, the feces are of high nutritional value for detritivores as well as other grazers and may act as a food source to the benthos (e.g. Navarro and Thompson 1997; Johannes and Satomi 1966).

During our study, sediment total lipid extract on a dry weight and on a carbon basis was maximized in spring, yet on an organic carbon basis it was fairly constant as was the C:N ratio. Sediments showed a distinct seasonal trend in the PUFA:SFA and $C_{16:1}$:$C_{16:0}$ ratios (Figure 3-7) indicating a seasonal input of relatively more labile diatom material in the spring and fall, a pattern also observed in the gut contents and
consistent with fecal pellets. Navarro and Thompson (1997) found extreme seasonal variability with maximum biodeposition and maximum organic carbon content during the spring bloom for the mussel *Modiolus modiolus*. Short-term variability in organic matter deposition was not addressed in this study and may be important since lipid and isotope data suggested short-term variability in organic matter sources. Daily variation in biodeposition can exceed weekly and monthly changes for the oyster *Crassostrea virginica* (Haven and Morales-Alamo 1966).

A direct comparison between fecal pellets and sediments in only possible in April, when both sample types were collected on the same day, and August when samples were collected about 2 weeks apart. Generally, the dominant compounds are similar between the sample types. Yet FAs in the sediments are enriched in 16:1ω7 and depleted in PUFAs compared to the fecal pellets. Most PUFAs are considered essential or semi-essential for consumers (Demott and Müller-Navarra 1997; Enright *et al.* 1986a,b;) and are labile compounds. It would not be surprising if these reactive compounds did not persist in the sediments due to utilization by microorganisms and other benthos. The lower bay region is known to have a diverse assemblage of benthos and is highly bioturbated (Schaffner 1990; Schaffner *et al.* 2000). Further, carbon in the fecal pellets is highly enriched in lipids compared to the sediments suggesting rapid loss of lipid components following deposition, or potentially the fecal pellets do not become part of the sediment compartment. Physical processes in this region are known to modify and rework the bed sediments. However, while sediment resuspension is generally rare within this region of the lower bay (Wright *et al.* 1997; Schaffner *et al.* 2000), a flocculent layer above the
sediment is resuspended more frequently. Perhaps the fecal pellets are resuspended with the flocculent layer and redeposited in a more quiescent area of the bay.

For sterols, the relative abundance of cholesterol differed between the fecal pellets and the sediment; but given the varied sources for this component, we can draw no conclusions. The other major difference was the inconsistency in relative abundance of the general algal biomarker $29\Delta5.24(28)$ for each of the sampling periods. This compound was present in fecal pellets but not sediments in April which suggests that physical processes play a role in sediment signature (see above) or the source for this biomarker was part of the spring bloom and that this suspension feeding worm can exploit a sedimenting food source before it appears on the sediment surface. Similar results have been found for other suspension feeders (e.g. Christensen and Kanneworff 1985). In August, $29\Delta5.24(28)$ was present in sediments but not in fecal pellets, nor was it present in the gut contents which suggest that the biomarker may have been deposited earlier in the year and has yet to be utilized by the benthos. Some sterols have been shown to degrade at slower rates compared to other lipid components and are fairly resistant to faunal degradation (Harvey et al. 1989; Harvey and Macko 1997). Alternatively, lipid and isotope samples were not frequent enough to investigate short-term temporal variability for input to the sediment bed, which may be important since our gut content and tissue data indicate that short-term variability in organic matter sources existed during the summer of 1995 (see above). Additionally, the possibility also exists that organic matter is being transported into the region and deposited on the bed by lateral advection (Wright et al. 1997; Schaffner et al. 2000) and therefore
affecting the sediment biomarker signatures independent of SPM.

Our results clearly indicate that fecal pellets represent a potentially important avenue of organic matter flux to the benthic community. Since the signature of the fecal pellets was not paralleled in the adjacent sediments, we cannot determine whether short-term variability in organic matter deposition had a significant influence, if the fate of the pellets was rapid utilization by the benthos, or if resuspension and transportation of the pellets to other areas of the lower bay occurred.

CONCLUSIONS - Our results indicate that a key benthic suspension feeder of lower Chesapeake bay, *C. pergamentaceus*, utilizes locally produced organic matter, primarily fresh phytoplankton and recycled material from microbial sources with minimal to no terrestrial input. Secondary production *Chaetopterus pergamentaceus* closely tracks gross primary production suggesting a benthic system tightly coupled to the water column. We found that autochthonous algal sources are the dominant organic matter source in this region of the estuary. The spring bloom is used by *C. pergamentaceus* for egg production and some storage of essential FA in body tissues, while a combination of diatoms, smaller phytoplankton (e.g. cyanobacteria, cryptophytes), and possibly bacteria supported the high growth rate and high secondary productivity of the polychaete during the summer months. Fecal pellets from this polychaete have a high nutritional content and may represent a food source to other benthos. The sediments had a distinctly different biomarker signature than the fecal pellets suggesting that sediments are highly reworked by the benthos or that
fecal pellets are not permanently deposited in the sediment bed of this region of the estuary. The results of this study indicate that growth and secondary productivity of *C. pergamentaceus* are linked to the water column production and that this worm is highly dependent on benthic-pelagic coupling with its role being to enhance the quantity of organic matter deposited but with little change in quality.
Chapter 4

The *in situ* filtration rate of the suspension feeding polychaete *Chaetopterus pergamentaceus*: comparison to laboratory obtained values and implications for benthic-pelagic coupling.

This may be submitted as a note for publication after further revision with the following authors:

M. L. Thompson, L. C. Schaffner, and M. R. Patterson.
ABSTRACT

The suspension feeding polychaete *Chaetopterus pergamentaceus* is widely distributed at subtidal depths in the lower, polyhaline Chesapeake Bay. Benthic-pelagic coupling by this polychaete is thought to be an important factor in the function of the lower bay ecosystem. This study established the following about the *Chaetopterus* population in the lower bay: 1) approximately 25% of worms pump at any given time; 2) filtration rate varies among individuals and through time for the same individual; 3) there is a relationship between worm size, in terms of AFDW, and average filtration rate; 4) filtration rate is not correlated with ambient current velocity; 5) there is evidence for induced flow through the worm tubes, however, worms can control the flow of water through their tube. *Chaetopterus pergamentaceus*, with a filtration rate comparable to that of oysters has the potential to transfer large quantities of inorganic as well as organic matter and energy between the pelagic and benthic subsystems with important implications for food web dynamics and nutrient cycling. This polychaete may be thought of as a keystone species, or habitat bioengineer, in the lower Chesapeake Bay and should be included in future studies or models of the estuary.
**INTRODUCTION**

Numerous studies have demonstrated that benthic suspension feeders are important links between the water column and sediment in coastal ecosystems (Graf 1992; Heip *et al.* 1995) where they can exhibit high densities and biomass (Cloern 1982; Alpine and Cloern 1992). Benthic suspension feeders increase nutrient regeneration (Doering 1989) partially due to bioturbation and bioirrigation and the resulting indirect effects such as stimulation of microbial processes (Kristensen *et al.* 1991; Barbanti *et al.* 1992) and partially as a result of excretion (Kemp *et al.* 1990), which may increase phytoplankton production (Doering *et al.* 1986; Prins and Smaal 1990). Yet, they also have the potential to reduce planktonic biomass (Cohen *et al.* 1984; Loo and Rosenberg 1989; Alpine and Cloern 1992; Gerritesen *et al.* 1994).

Benthic suspension feeders have been found to enhance deposition of suspended particulate materials, influence particle transport potential via pelletization, and act as sinks for organic matter (Haven & Morales-Alamo 1970; Taghon *et al.* 1984; Loo and Rosenberg 1989; Heip *et al.* 1995; Pile *et al.* 1997a & b).

The strength of biologically mediated benthic-pelagic coupling depends on factors such as local hydrodynamic conditions, the quality and quantity of suspended material, and the filtration capacity of a suspension feeding population. Benthic boundary layer flow processes can affect feeding ecology (Frechette *et al.* 1989). Hydrodynamic conditions, e.g. vertical structure of the water column in terms of velocities and particle concentrations, influence particle availability which determines the flux of material to a suspension feeder (Taghon *et al.* 1980; Muschenheim 1987).
Further, feeding behavior may change in differing hydrodynamic conditions as well as with different particle concentrations and compositions (Wildish and Kristmanson 1997 and references therein).

Within the lower Chesapeake Bay, the large, tubiculous, suspension feeding polychaete *Chaetopterus pergamentaceus* (provisional specification Mary Petersen, pers. comm.; Eckberg and Hill 1996; formally *Chaetopterus variopedatus*, e.g. Enders 1909) is an important component of the soft sediment benthic community where it has been observed to maintain relatively stable populations for at least the last 15 years (Huggett 1987; Schaffner 1987, 1990). This polychaete has also been reported in other marine and estuarine communities along much of the east coast of the United States (reported as *C. variopedatus* - Enders 1909; Eckberg and Hill 1996). *Chaetopterus pergamentaceus* inhabits a parchment-like semicircular tube that can penetrate over 15 cm below the sediment surface. The ends of the tube taper to constricted openings. Specialized parapodia are used to pump water through the tube. Particles are trapped on a mucus net which is then formed into a foodball and ingested (Enders 1909; MacGinitie 1939; Brown 1975; Flood & Fiala-Medioni 1982; Riisgård 1989).

Benthic-pelagic coupling by *C. pergamentaceus* is thought to be an important factor in the ecosystem function of the lower Chesapeake Bay (Chapters 1 and 3). The bay population exhibits fast growth and high secondary productivity during summer, coincident with a seasonal maximum peak in gross primary production (Chapter 1). Maximum individual growth coincides with times when small phytoplankton and microbes dominate production in the overlying water column.
(Marshall and Lacouture 1986; Malone et al. 1991), and phytoplankton are a dominant component of its diet (Chapter 3). Determining the in situ filtration capacity of this polychaete population will lead to a better understanding of benthic-pelagic coupling in Chesapeake Bay and coastal systems in general by allowing an estimate of population level effects such as carbon flux.

The aim of the present work was to study the in situ filtration rate of the suspension feeding polychaete Chaetopterus pergamentaceus with particular interest in comparing our in situ rates versus published laboratory obtained filtration rates. Our data were collected through field studies in the years 1994, 1995, and 1996.

**Material and Methods**

**SITE** - The study region within the lower polyhaline portion of Chesapeake Bay (Figure 1-1, Chapter 1), has been described in Chapters 1 and 2. All data were collected in situ by divers at the WT and CS sites.

**DATA COLLECTION** - Divers observed the number of worms actively pumping, the frequency of biodeposition of fecal pellets, and other behaviors in a given area using quadrant sizes ranging from 1 m² to 10 cm².

Actively pumping worms were located using visual identification of a tube outflow plume after fluorescein dye was ejected near the worm tube. Worm pumping (outflow current velocity) was measured with heated thermistor flowmeters (LaBarbera and Vogel 1976; 2-mm-diameter heads) on four separate dates. On 6 Sept. 1994, 29 March 1995, and 20 June 1995 a hand held thermistor flowmeter was held at the same height as the worm tubes and over worm outflow current plumes.
for between 30 to 60 seconds to obtain ambient current and worm outflow current velocity measurements. On 27 August 1996 a six-channel thermistor flowmeter was deployed for 18 hours with one probe placed at worm tube height away from the tubes with the remaining five probes placed approximately 1 mm above worm tube opening; divers regularly monitored the thermistors and repositioned them as needed. One thermistor had to be removed from any analysis due to the repeated burial and almost constant disturbance of that thermistor by crabs and fish. The concurrent measurements of ambient flow as well as worm pumping flow rates on this deployment allowed for the determination of ambient flow speeds that may have affected worm pumping.

Mean flow speed (average flow speed per minute with a measurement collected every 5 seconds on each channel) was recorded on a LICOR LI-1000 datalogger. Flow time series records were analyzed with a Hanning-windowed Fast Fourier transform to determine the existence of flow periodicities (Barber 1961). A signal processing program (written in Mathematica) used to analyze all data yielded maximum and mean flow speed and spectral characteristics. Correlations between the worm outflow current speed and the ambient current speed were used to investigate possible links between ambient flow and worm pumping behavior.

Volume flow rate (= filtration rate) was calculated as approximating "plug flow", i.e. the product of the outflow current speed and the cross-sectional area of the end of the worm tube. The diameter of the end of the worm tube was measured in situ with calipers and then converted to area assuming the opening to be a circle. Riisgård (1989) calculated that flow is likely represented by laminar pipe flow within
the tube indicating that the measured flow speed near the center of the worm tube is the maximum, whereas volume flow rate should be calculated from the mean flow speed (Vogel 1994). Yet, an outflow current plume may not approximate laminar flow; rather the shape of the exit plume may be more rectangular, as has been observed for ascidians (Fiala-Medioni 1978). Further, the area of the thermistor probe in comparison to the tube cross-sectional area is likely not small enough to accurately measure only the most interior maximum flow of the exit plume. Thus estimating volume flow rate as "plug flow" is appropriate.

Water flow behavior in organism burrows can be approximated as water flow through a pipe. In theory, volume flow rate through a pipe is proportional to the fourth power of the radius, assuming laminar flow. To test this relationship in *C. pergamentaceus* tubes, filtration rate was regressed against the fourth power of tube radius.

Multiple regression was used to investigate the relationship between filtration rate, worm size (ash free dry weight; AFDW), and temperature. The worm AFDW was calculated from tube diameter using the following equation (Thompson unpub. data):

\[
AFDW = 0.00487 \times \exp (0.871 \times \text{tube diameter}) \quad (n = 771; r^2 = 0.43) \quad \text{Eq. 1}
\]

### RESULTS

Diver observations indicated that about 25% of worms were pumping at any given time. Forceful ejection of feces occurred every 5 to 10 minutes consisting of between 1 to 10 fecal pellets. During the 27 August 1996 deployment pseudofecal...
production was observed every 15 to 30 minutes and consisted of the mucus net plus filtrate.

Filtration rate (L hr⁻¹) varied between 17.7 for the largest worm to 0.3 for the smallest worm (Table 4-1) with values varying among individuals and through time for a given individual (Figure 4-1). Highest filtration rates occurred during the warmest time of the year, i.e. late summer, and among the largest worms. A multiple regression of filtration rate to worm AFDW (size) and temperature indicated that only AFDW was significant (p < 0.001) and not temperature (p > 0.6). However, due to the paucity of filtration data at varying temperature regimes no conclusions about the affect of temperature should be drawn. Removing temperature from the regression yields the following result:

\[ \text{Filtration Rate} = 22.17 \times \text{worm AFDW} + 0.048 \]  
\[ \text{Eq. 2} \]

\( (n = 9; \text{DF} = 1; p = 0.0004; r^2 = 0.83) \). The intercept was not significantly different than zero (p = 0.9). The majority of data points within this regression correspond to summer temperatures of 22.5° to 25°C. In general, filtration rate is thought to be influenced by temperature (Newell 1979); thus the relationship of filtration rate to AFDW in this study is valid only within the 22.5° to 25°C temperature range.

Filtration rate (L hr⁻¹) was significantly related to the fourth power of tube radius (cm)

\[ \text{Filtration Rate} = 845.18 \times \text{tube radius}^4 + 1.44 \]  
\[ \text{Eq. 3} \]

\( (n = 10; \text{DF} = 1; p < 0.001; r^2 = 0.93) \). Thus, a small increase in burrow size leads
Table 4-1. Field measurements of flow data of *Chaetopterus pergamentaceus* in the lower Chesapeake Bay. Standard deviations given for flow speed except for 06 September 94 ambient flow and for all data on 20 June 95 when that information is unavailable.

<table>
<thead>
<tr>
<th>Date</th>
<th>Ambient Flow (cm s(^{-1}))</th>
<th>Duration of Data Collection</th>
<th>Worm Tube Diameter (mm)</th>
<th>Maximum Flow Speed (cm s(^{-1}))</th>
<th>Mean Flow Speed (cm s(^{-1}))</th>
<th>Mean Flow Volume (L hr(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>09/06/94</td>
<td>36.1</td>
<td>&lt; 1 minute</td>
<td>7.5</td>
<td>-</td>
<td>11.1 ± 13.8</td>
<td>17.65</td>
</tr>
<tr>
<td>03/29/95</td>
<td>12.3 ± 11.7</td>
<td>&lt; 1 minute</td>
<td>1.5</td>
<td>-</td>
<td>6.3 ± 3.7</td>
<td>0.40</td>
</tr>
<tr>
<td>11.7 ± 5.8</td>
<td>&lt; 1 minute</td>
<td>3.5</td>
<td>-</td>
<td>9.0 ± 3.9</td>
<td>3.13</td>
<td></td>
</tr>
<tr>
<td>9.9 ± 3.2</td>
<td>&lt; 1 minute</td>
<td>1.0</td>
<td>-</td>
<td>10.9 ± 8.6</td>
<td>0.32</td>
<td></td>
</tr>
<tr>
<td>06/20/95</td>
<td>12.1</td>
<td>&lt; 1 minute</td>
<td>3.1</td>
<td>-</td>
<td>3.6</td>
<td>0.97</td>
</tr>
<tr>
<td>12.1</td>
<td>&lt; 1 minute</td>
<td>3.0</td>
<td>-</td>
<td>4.0</td>
<td>1.01</td>
<td></td>
</tr>
<tr>
<td>08/27/96</td>
<td>9.8 max</td>
<td>~18 hours</td>
<td>4.4</td>
<td>14.2</td>
<td>9.2 ± 1.0</td>
<td>5.04</td>
</tr>
<tr>
<td>7.5 ± 1.2</td>
<td>~18 hours</td>
<td>1.8</td>
<td>16.3</td>
<td>9.6 ± 2.6</td>
<td>0.88</td>
<td></td>
</tr>
<tr>
<td>mean</td>
<td>~18 hours</td>
<td>3.7</td>
<td>18.4</td>
<td>10.8 ± 2.3</td>
<td>4.18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>~18 hours</td>
<td>4.6</td>
<td>14.7</td>
<td>9.3 ± 1.3</td>
<td>5.56</td>
<td></td>
</tr>
</tbody>
</table>
Figure 4-1. Time series of outflow current from worm tubes and ambient current from August 1996.
to a dramatic increase in filtration rate. Flow through the tubes of *C. pergamentaceus* can be modeled assuming an analogy to pipe flow.

The 27 August 1996 data of tube outflow velocity and ambient current velocity showed correlations of -0.48, -0.36, -0.35, and 0.35 indicating that tube outflow velocities were largely decoupled from the flow field. Yet, the periodicity in worm filtration rate showed some of the harmonics for the tidal signal (Figure 4-2). Analysis of the ambient water flow data at 54 cm above the bottom (data courtesy of C. Friedrichs), collected simultaneous to worm pumping data on 27 August 1996, showed the periodicity of the tidal signal at 12.3 and 6 hours as well as harmonics of the tidal signal due to the tidal asymmetry in the bay. The data record using the thermistors for ambient flow was only 18 hours long so we could not resolve the 12.3 or 6 hour tidal signal, but the subsequent tidal harmonics were evident. Data records for individual worms showed some of the harmonics for the tidal signal (Figure 4-2). Thus, there was the potential for induced flow through the worm tubes. However, not all of the harmonics are evident; thus, we conclude that worm behavior affected water flow through tubes.

**DISCUSSION**

The *in situ* estimates of individual filtration rates for this study are comparable to rates previously measured for *Chaetopterus* and other invertebrates in laboratory studies (Table 4-II). In particular, it should be noted that the highest value observed (17.65 L hr⁻¹) in this study is comparable to the result of 18 L hr⁻¹ for a very large *Chaetopterus* at 24°C (Aksuk and Sveshnikov 1971, as cited in Brown 1977).
Table 4-II. Comparison of filtration / irrigation rates found in this study for *Chaetopterus pergamentaceus* to rates found for this polychaete, or a closely related polychaete *Chaetopterus variopedatus*, in other studies and to filtration rates of other invertebrates.

<table>
<thead>
<tr>
<th>Species</th>
<th>Volume Filtered (L hr(^{-1}) individual(^{-1}))</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Chaetopterus pergamentaceus</em></td>
<td>0.32 - 17.65</td>
<td>This study; dependent on size.</td>
</tr>
<tr>
<td><em>Chaetopterus variopedatus</em> or C. <em>pergamentaceus</em></td>
<td>0.5 - 18(^2)</td>
<td>Wells and Dales 1951; Aksuk and Sveshnikov 1971 (as cited in Brown 1977)(^2); Brown 1977; Riisgård 1989</td>
</tr>
<tr>
<td><em>Diopatra cuprea</em> (Polychaete)</td>
<td>0.07(^3)</td>
<td>Magnum <em>et al.</em> 1968</td>
</tr>
<tr>
<td><em>Nereis virens</em> (Polychaete)</td>
<td>0.18(^3)</td>
<td>Kristensen <em>et al.</em> 1991</td>
</tr>
<tr>
<td><em>Mya arenaria</em> (Bivalve)</td>
<td>0.34(^4)</td>
<td>Mangum and Burnett 1975</td>
</tr>
<tr>
<td><em>Mytilus edulis</em> (Bivalve)</td>
<td>1-5(^4)</td>
<td>Møhlenburg and Riisgård 1979; Newell <em>et al.</em> 1998</td>
</tr>
<tr>
<td><em>Crassostrea virginica</em> (Bivalve)</td>
<td>2-10(^4)</td>
<td>Riisgård 1988</td>
</tr>
</tbody>
</table>

\(^2\) The high value of 18 L hr\(^{-1}\) was reported by these authors; all other reported values ranged between ~0.4 and ~2 L hr\(^{-1}\).

\(^3\) Irrigation rate.

\(^4\) Based on clearance rate.
Figure 4-2. Periodicity in pumping rates of *Chaetopterus pergamentaceus* (n=4) in the lower Chesapeake Bay compared to the tidal periodicity of 12.3 and subsequent tidal harmonics.
majority of literature values for *Chaetopterus* are between 0.4 and \(\sim 2\) L hr\(^{-1}\).

In general, caution should be used when extrapolating filtration rates taken over a period of less than a minute to longer time scales as was done for some data in this study. In a study of worms in a South Carolina intertidal flat, Grove (1998) found pumping by individual worms only about 60% of the time. In addition, the filtration rate from a burst of activity may be different than a long duration filtration rate (Enders 1909; Wells and Dales 1951). However, since our measurements were made *in situ* on undisturbed worms and because data fall within the known range of filtration rates and within the range for the 18 hour deployment, we are confident that our results are representative of *in situ* filtration rates.

The filtration rate of *Chaetopterus* might be affected by the presence of commensal organisms as has been shown for some bivalves (Bierbaum and Shumway 1988). Pea crabs (Family Pinnotheridae) *Pinnixa chaetopterana* and *Polyonyx gibbesi* are known to be commensal with *Chaetopterus* (Schaffner unpub data; Grove 1998). We did not examine the tubes of the worms used in this study and therefore we do not know which, if any, housed commensal organisms and what affect, if any, that had on our filtration rates. Grove (1998) found slightly, but not significantly, elevated filtration rates for worms that house the commensal pea crab *Polyonyx*, although the presence of the commensal crabs had no long term effect on the host worms.

As expected, tube size was found to significantly affect the filtration rate; a small increase in tube diameter leads to a dramatic increase in filtration rate. This relationship does not necessarily indicate that a small change in worm size leads to
a large increase in filtration rate. In general worm AFDW was not highly correlated with tube size ($r^2 = 0.42$). This polychaete grows continuously yet the tube size is increased incrementally.

Hydrodynamic conditions may affect filtration rates of suspension feeders either directly or indirectly by affecting the apparent flux of material (Wildish and Kristmanson 1997). Worm pumping and ambient current were not correlated in this study, however, the range of ambient flow velocities was fairly low $< 5 \text{ cm s}^{-1}$ (Figure 4-1); this narrow range may have been insufficient to reveal a significant relationship. Also, other factors such as suspended load and organic flux may influence the filtration rate thereby potentially nullifying or altering any affect of ambient flow velocity (Wildish and Kristmanson 1997). Thus, no conclusions about the affect of ambient flow velocity on the filtration rate of this polychaete should be drawn at this time.

Periodicities in worm pumping of about 15 - 20 minutes due to feeding activities (MacGinitie 1949; Wells and Dales 1951) or due to periodic reversals in the tube (Grove 1998) were expected. Additionally, a four to five minute periodicity (Enders 1909; Wells & Dales 1951) or a 5 to 10 minute periodicity (this study) may be expected to predominate due to the semi-regular forceful ejection of feces. However, the only periodicities evident in this study were coincident with the periodicities of the tidal harmonics. Wells and Dales (1951) state that several irrigation patterns may be exhibited by this polychaete depending upon environmental conditions. The regular patterns observed in the laboratory may not be observed in situ due to the predominantly varying effects of environmental conditions.
Bivalves, such as oysters and mussels, are often thought of as keystone species, or habitat bioengineers, because they play a significant role in converting critical resources or providing habitat utilized by other species (Jones et al. 1994). My results indicate that the range of filtration rates recorded for *C. pergamentaceus* are comparable to those reported for better studied suspension feeders. Given the relatively high population densities (Chapter 1) and the filtration capacity of individual worms, *C. pergamentaceus* can be expected to act as a keystone species or habitat bioengineer for the lower Chesapeake Bay, and it should be included in future studies and models of the lower bay estuary.
Chapter 5

An energy budget for the suspension feeding polychaete *Chaetopterus pergamentaceus* within the lower Chesapeake Bay.

This paper will be submitted for publication after further revisions with the following authors: M. L. Thompson and L. C. Schaffner
ABSTRACT

For most shallow water environments, ecosystem function depends on the cycling and flow of materials and energy between benthic and pelagic subsystems. Numerous studies have now demonstrated that benthic suspension feeders are important links between the water column and sediment in coastal ecosystems. Developing an energy budget for dominant benthic suspension feeders can aid in our understanding of estuarine and coastal systems. The suspension feeding polychaete Chaetopterus pergamentaceus is a key benthic species within the lower Chesapeake Bay. The objective of this study was to construct an energy budget for C. pergamentaceus within the lower Chesapeake Bay using the population dynamics (Chapter 1), food composition (Chapter 3), filtration rates (Chapter 4), and biodeposition information (Schaffner unpub data). Our energy budget accounts for ~76% of the material consumed. Our results indicate this polychaete may filter a large portion of or an amount equivalent to the net water column community production. When considered on a daily basis, the potential carbon flux via the filtration rate may be greater than the net water column production. Chaetopterus pergamentaceus accounts for a minimum of 28% to 41% of benthic respiration in the lower Chesapeake Bay. This study lends additional and independent support to the conclusions of Chapters 1 and 3 that Chaetopterus pergamentaceus plays a strong role in benthic-pelagic coupling.
INTRODUCTION

For most shallow water environments, ecosystem function depends on the cycling and flow of materials and energy between benthic and pelagic subsystems. Numerous studies have now demonstrated that benthic suspension feeders are important links between the water column and sediment in coastal ecosystems where they can exhibit high densities and biomass (Cloern 1982; Cohen et al. 1984; Loo and Rosenberg 1989; Alpine and Cloern 1992; Graf 1992; Heip et al. 1995). Benthic suspension feeders increase nutrient regeneration (Doering 1989), partially from bioirrigation and bioturbation and partially as a result of excretion (Kemp et al. 1990), which may increase phytoplankton production (Doering et al. 1986; Prins and Smaal 1990). Yet, suspension feeders can consume a significant percentage of water column production causing a reduction of planktonic biomass (Cohen et al. 1984; Loo and Rosenberg 1989; Alpine and Cloern 1992; Gerritesen et al. 1994). Benthic suspension feeders enhance deposition of material from the water column, influence particle transport potential by pelletization of suspended material, and act as sinks for organic matter (Haven & Morales-Alamo 1970; Tagon et al. 1984; Loo and Rosenberg 1989; Heip et al. 1995; Pile et al. 1997a & b).

Developing an energy budget for dominant benthic suspension feeders can aid in our understanding of estuarine and coastal systems. The general equation for an energy budget of an organism is the following:

\[ \text{consumption (C)} = \text{production (P)} + \text{respiration (R)} + \text{waste products (D)} \quad \text{Eq. 1} \]
where production can be subdivided into somatic growth plus reproduction, respiration is the energy loss through metabolism, and waste products can be subdivided into fecal losses (biodeposition) and excretion. The portion of the consumed material that is utilized by the consumer is termed assimilation (A) and is technically production plus respiration and excretion. In practice assimilation is generally thought of as production plus respiration and has been termed absorption (e.g. Huebner and Edwards 1981; Loo and Rosenberg 1989).

Availability and quality of organic matter have important implications for consumer utilization in terms of the relationship between net energy gained from the environment and the temporal strategies organisms have for growth and reproduction. Factors affecting utilization extrinsic to the consumer include environmental parameters such as seasonal variations in temperature, oxygen availability and primary production cycles. Generally, organisms are thought to have a higher demand for food resources when stressed by environmental factors due to an increase in metabolic rate. However, some organisms have the ability to compensate, through physiological processes, for changes in environmental variables to minimize metabolic expenditures while others do not (Newell 1979; Valiela 1995). This phenotypic plasticity is an important trait upon which evolution acts to determine range distribution of taxa. Food resources will determine the need to regulate metabolic losses so that energetic turnover is compensated for by food supply (Newell 1979; Valiela 1995). Factors affecting utilization intrinsic to the consumer include nutritional state and functional abilities, such as activity level, growth and reproductive cycles, that take place within the metabolic confines set by
the extrinsic factors. For a given species, metabolism decreases during starvation due to the physiological cost of digestion, increases with increasing activity, increases during reproductive output, and is thought to be a constant power of the body weight (Newell 1979). The temporal variability of the extrinsic factors influences the intrinsic factors creating a hierarchy regulating population dynamics (Zajac and Whitlatch 1985; Marsh and Tenore 1990). The compensatory mechanisms for extrinsic factors and intrinsic factors are interwoven to maintain the energy balance of the organism (Newell 1979) thus providing the maximum energy gain from food resources.

Within the lower Chesapeake Bay, the large, tubiculous, suspension feeding polychaete *Chaetopterus pergamentaceus* (provisional specification Mary Petersen, pers. comm.; Eckberg and Hill, 1996; formally *Chaetopterus variopedatus* e.g. Enders 1909) is an important component of the soft sediment benthic community where it has maintained relatively stable populations for at least the last 15 years (Schaffner 1987, 1990). *Chaetopterus pergamentaceus* exhibits fast growth and high secondary production during summer, coincident with the seasonal maximum in primary production rather than the spring diatom bloom (Chapter 1). *Chaetopterus pergamentaceus* uses a mucus net, which effectively retains particles as small as ~0.5μm, to filter water which is pumped through its tube with specialized parapodia; the net is then formed into a food ball and transported to the mouth for ingested (Enders 1909; MacGinitie 1939; Brown 1975; Flood & Fiala-Medioni 1982; Riisgård 1989). Locally produced organic matter, primarily fresh phytoplankton and recycled material from microbial sources with minimal to no terrestrial input, is
utilized for growth and reproduction (Chapter 3). Although the filtration rate varies among individuals and through time for the same individual, there is a relationship between worm size, in terms of AFDW, and average filtration rate (Chapter 4).

The objective of this study was to construct an annual energy budget for *C. pergamentaceus* within the lower Chesapeake Bay using the population dynamics (Chapter 1), food composition (Chapter 3), filtration rates (Chapter 4), biodeposition information (Schaffner unpub data), and respiration (literature derived).

**METHODS AND RESULTS**

**SITE** - The study region within the lower polyhaline portion of the Chesapeake Bay (Figure 1-1, Chapter 1) has been described in Chapter 1.

**POPULATION FILTRATION RATE** - In order to estimate a carbon and energy budget for *C. pergamentaceus* several aspects of physiological processes had to be estimated. The relationships, if any, between filtration rate and environmental variables such as temperature for *C. pergamentaceus* have yet to be explored. Taking a conservative approach, we employed a $Q_{10}$ value of 2 to this relationship, which is consistent with known $Q_{10}$ values for other polychaetes (Coyer and Mangum 1973). To account for thermal cessation of activity, we assumed no filtering at temperatures lower than ~3°C (e.g. Loo and Rosenberg 1989).

We calculated the preliminary filtration rate using the AFDW of worms collected from throughout the year (data from chapter 1) and the regression equation relating
filtration rate to AFDW (Chapter 4). The preliminary filtration rate was adjusted for temperature with the following equation:

\[
\text{Filtration Rate}_{\text{temperature corrected}} = \text{Filtration Rate}_{\text{preliminary}} \cdot Q_{10}^{(T_e - T_p)/(T_e - T_{10})} \quad \text{Eq. 2}
\]

assuming the filtration rate \(_{\text{preliminary}}\) represented a temperature of ~23.5°C, \(Q_{10}\) was 2, \(T_e\) was environmental temperature, and \(T_p\) was 23.5°C. The temperature corrected filtration rate was multiplied by the number of worms filtering on a sampling date (25% of density; Chapters 1,4) to obtain an estimate of filtering capacity of the population on a specific date (Figure 5-1; Table 5-1).

**CONSUMPTION ESTIMATES** - To determine the net effect of the *C. pergamentaceus* population on the flux of materials, an estimate of ingested material, or consumption, was calculated in two ways: 1) on the basis of our filtration rate data; and 2) on the basis of worm secondary production.

Using the filtration rate data, we estimated the filtering capacity by multiplying the filtration rate by a total organic carbon value for suspended particulate matter (1.0 or 0.5 mg L\(^{-1}\), for summer and winter respectively; Wetzel and Neilson 1988). We assumed a retention efficiency of 80 to 100% for the summer (mid-June through Sept.) and winter (Oct. through mid-June) respectively based on Jørgensen et al.'s (1984) laboratory obtained retention efficiencies in association with a predominance of smaller particles in the summer and larger particles in the winter (Mashall and Lacounter 1986; Malone et al. 1991). The estimate yields total carbon flux in g Carbon m\(^{-2}\) yr\(^{-1}\) for the population of *C. pergamentaceus* (Figure 5-2; Table 5-1, 5-
Table 5-I. Estimate of carbon (C) flux from the water column to *Chaetopterus pergamentaceus*. An estimate of the carbon value of 1.0 and 0.5 mg L\(^{-1}\) was used for the summer (mid-June through Sept.) and winter (Oct. through mid-June) respectively (Wetzel and Neilson 1988). A retention efficiency of 80% in the summer and 100% in the winter was estimated using Jørgensen *et al.'s* (1984) laboratory obtained retention efficiencies in association with a predominance of smaller particles in the summer and larger particles in the winter. Population filtration rate assumes 25% of the worm population was filtering (see text). Sampling interval is defined as the time between samplings.

<table>
<thead>
<tr>
<th>Date</th>
<th>Temp (°C)</th>
<th>Population Filtration Rate (L hour(^{-1}) m(^{-2}))</th>
<th>Carbon Flux (g C m(^{-2}) day(^{-1}))</th>
<th>Total Carbon Flux (g C m(^{-2}) sampling interval(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>01/31/94</td>
<td>1.5</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>02/25/94</td>
<td>4.8</td>
<td>28.3</td>
<td>0.34</td>
<td>9.5</td>
</tr>
<tr>
<td>03/24/94</td>
<td>7.8</td>
<td>26.6</td>
<td>0.32</td>
<td>7.7</td>
</tr>
<tr>
<td>04/29/94</td>
<td>16.1</td>
<td>29.1</td>
<td>0.35</td>
<td>11.5</td>
</tr>
<tr>
<td>05/26/94</td>
<td>15.5</td>
<td>47.9</td>
<td>0.57</td>
<td>16.1</td>
</tr>
<tr>
<td>06/10/94</td>
<td>19.6</td>
<td>61.9</td>
<td>0.74</td>
<td>12.6</td>
</tr>
<tr>
<td>06/30/94</td>
<td>24.3</td>
<td>37.2</td>
<td>0.71</td>
<td>14.3</td>
</tr>
<tr>
<td>07/11/94</td>
<td>21.8</td>
<td>77.5</td>
<td>1.48</td>
<td>16.4</td>
</tr>
<tr>
<td>07/27/94</td>
<td>23.3</td>
<td>57.4</td>
<td>1.10</td>
<td>18.7</td>
</tr>
<tr>
<td>08/10/94</td>
<td>22.8</td>
<td>53.6</td>
<td>1.03</td>
<td>17.5</td>
</tr>
<tr>
<td>08/25/94</td>
<td>22.3</td>
<td>52.7</td>
<td>1.01</td>
<td>14.2</td>
</tr>
<tr>
<td>09/15/94</td>
<td>21.8</td>
<td>49.4</td>
<td>0.95</td>
<td>10.4</td>
</tr>
<tr>
<td>09/27/94</td>
<td>22.8</td>
<td>71.4</td>
<td>1.37</td>
<td>26.1</td>
</tr>
<tr>
<td>10/26/94</td>
<td>15.8</td>
<td>56.2</td>
<td>0.53</td>
<td>16.7</td>
</tr>
<tr>
<td>12/01/94</td>
<td>11.0</td>
<td>36.7</td>
<td>0.61</td>
<td>38.8</td>
</tr>
<tr>
<td>01/27/95</td>
<td>3.0</td>
<td>23.9</td>
<td>0.29</td>
<td>7.5</td>
</tr>
<tr>
<td>04/06/95</td>
<td>9.3</td>
<td>28.0</td>
<td>0.34</td>
<td>23.1</td>
</tr>
<tr>
<td>05/22/95</td>
<td>18.3</td>
<td>24.3</td>
<td>0.29</td>
<td>13.4</td>
</tr>
<tr>
<td>07/14/95</td>
<td>26.0</td>
<td>33.2</td>
<td>0.64</td>
<td>33.8</td>
</tr>
<tr>
<td>07/28/95</td>
<td>26.8</td>
<td>41.7</td>
<td>0.80</td>
<td>11.2</td>
</tr>
<tr>
<td>08/10/95</td>
<td>24.0</td>
<td>43.1</td>
<td>0.83</td>
<td>10.7</td>
</tr>
<tr>
<td>08/25/95</td>
<td>26.0</td>
<td>44.0</td>
<td>0.85</td>
<td>12.7</td>
</tr>
<tr>
<td>09/26/95</td>
<td>21.5</td>
<td>56.6</td>
<td>0.85</td>
<td>34.7</td>
</tr>
<tr>
<td>10/26/95</td>
<td>18.5</td>
<td>54.4</td>
<td>1.09</td>
<td>19.6</td>
</tr>
<tr>
<td>12/08/95</td>
<td>8.0</td>
<td>29.3</td>
<td>0.65</td>
<td>39.8</td>
</tr>
</tbody>
</table>

1994 Total 1995 Total
0.63 0.56
230 206

Average 0.6
218

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Table 5-II. Carbon and energy parameters for the population of *Chaetopterus pergamentaceus* in lower Chesapeake Bay. Conversions from carbon to energy using 1 g organic carbon to 42 kJ (Lalli and Parsons 1993). Consumption was estimated using three methods: 1) based on filtration rate; 2) based on secondary production using the method of Loo and Rosenberg (1989) in which production was added to respiration with the sum being divided by an assimilation efficiency (see text for details); 3) based on secondary production assuming ecological efficiencies of 10% and 20% and back calculating to obtain an estimate of ingestion. Absorbed or assimilated food is production plus respiration. Respiration was calculated using parameters from the literature (see text; Riisgård 1989). Production values are from Chapter 1.

<table>
<thead>
<tr>
<th></th>
<th>Carbon (g C m$^{-2}$ yr$^{-1}$)</th>
<th>Energy (kJ m$^{-2}$ yr$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range</td>
<td>Average</td>
</tr>
<tr>
<td><strong>Consumption (C)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Filtration Rate</td>
<td>230 - 206</td>
<td>218</td>
</tr>
<tr>
<td>2nd Production</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Loo &amp; Rosenberg</td>
<td>85 - 108</td>
<td>97</td>
</tr>
<tr>
<td>Ecological Efficiency</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10%</td>
<td>180 - 340</td>
<td>260</td>
</tr>
<tr>
<td>20%</td>
<td>90 - 170</td>
<td>130</td>
</tr>
<tr>
<td><strong>Biodeposition (D)</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fecal Pellets</td>
<td>20 - 45$^{1}$</td>
<td>32.5</td>
</tr>
<tr>
<td>Pseudofeces</td>
<td>unknown</td>
<td>unknown</td>
</tr>
<tr>
<td><strong>Absorbed Food (A)</strong></td>
<td>64 - 81</td>
<td>72.5</td>
</tr>
<tr>
<td><strong>Respiration (R)</strong></td>
<td>35 - 43</td>
<td>39</td>
</tr>
<tr>
<td><strong>Production (P)</strong></td>
<td>18 - 33</td>
<td>26</td>
</tr>
</tbody>
</table>

$^{1}$ Range of the minimum values between 1994 and 1995. Thus representing a minimum value.
Figure 5-1. Estimated filtration rates for the population of *Chaetopterus pergamentaceus* in lower Chesapeake Bay.
Figure 5-2. Trends in gross plankton community production (adapted from Kemp et al 1997), Chaetopterus pergamentaceus (Chapter 1), and the potential flux of carbon via this polychaete's filtration rate through time.
Using the worm secondary production, we estimated the ingested material via two methods. First, we used the method of Loo and Rosenberg (1989) in which ingested food equals the sum of production (Chapter 1) and respiration (see below) divided by the assimilation efficiency. Respiration rate was calculated using Riisgård's (1989) relationship of $R = 1.9W^{0.59}$ ($r^2 = 0.69$; for a temperature of 16°C) where $R$ is respiration rate ($\mu l O_2 h^{-1}$) and $W$ is dry body weight (mg). This respiration rate was assumed to be a standard metabolic rate for this polychaete and was applied to all worms. An increase from the standard metabolic rate to an active metabolic rate for invertebrates varies among species, from 1.5 in a sabellid polychaete (Shumway et al. 1988), to 4.6 for blue crabs (Booth and McMahon 1992), to 4 - 10 for a variety of polychaetes (Coyer and Mangum 1973; Kristensen 1989 and references therein). Taking a conservative approach, we assumed a metabolic increase for an actively pumping worm of 4 times the standard metabolic rate and applied that to a quarter of the density since ~25% of *C. pergamentaceus* were actively pumping (Chapter 4). Respiration rate was temperature corrected using a $Q_{10}$ value of 2 in a similar manner to filtration rate (see above). Oxygen concentration was converted to grams carbon (molar conversion of 1.0; Smith and Kemp 1995) then to energy (Lallie and Parsons 1993). To estimate assimilation efficiency we used a ratio of organic content in the worm feces to the organic content of the gut (data from Chapter 3) which was ~0.75.

The second method of determining consumption used the worm production values of 18.1 and 33.9 g C m$^{-2}$ for 1994 and 1995 respectively (Chapter 1).
Assuming ecological efficiencies of 10% to 20%, we found that the worms ingested 90 to 180 g C m$^{-2}$ in 1994 and 170 to 340 g C m$^{-2}$ in 1995 which were converted into energetic equivalents (Table 5-II; Lalli and Parsons 1993).

**BIODEPOSITION AND EXCRETION** - Biodeposition in the form of fecal pellets was estimated using diver observations of the frequency and amount of fecal pellet production, 25% of worms filtering, percent organic carbon of the pellets (Chapter 4), density data (Chapter 1), and an estimate of the dry weight per pellets (unpub data; Table 5-III). Biodeposition via pseudofeces has been observed for this polychaete but not quantified (Schaffner unpub. data; Table 5-III).

**ENERGETIC RATIOS** - Energetic ratios were calculated (Table 5-IV). The gross growth efficiency (P/C) varied depending on which measure of consumption was used but averaged 22%. The ratio of fecal pellet deposition to consumption (D/C) indicates that a minimum of ~27% of what is consumed is deposited as fecal pellets. The proportion of energy used for respiration (R/C) was 27%. We can account for 76% of the material consumed using the average percent energetic efficiencies.

**DISCUSSION**

The estimated mean annual net water column community production in the lower Chesapeake Bay during 1986 - 1993 was ~240 g C m$^{-2}$ yr$^{-1}$ (Smith and Kemp 1995;
Table 5-III. Biodeposition from *Chaetopterus pergamentaceus* in the lower Chesapeake Bay. Plus/minus values are standard errors.

<table>
<thead>
<tr>
<th>Rate (minutes)</th>
<th>Pseudofeces</th>
<th>Fecal Pellets</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-15 - 30</td>
<td>Every 5 - 10</td>
</tr>
<tr>
<td>Material</td>
<td>Mucus Net with Filtrate</td>
<td>1-10 Pellets</td>
</tr>
<tr>
<td>Dry Weight (mg pellet(^{-1}))</td>
<td></td>
<td>0.3(^2)</td>
</tr>
<tr>
<td>Carbon (%)</td>
<td>n/a</td>
<td>10.3 ± 1.2</td>
</tr>
<tr>
<td>Nitrogen (%)</td>
<td>n/a</td>
<td>2.2 ± 0.3</td>
</tr>
<tr>
<td>Chlorophyll a (mg g(^{-1}) dry wt)</td>
<td>n/a</td>
<td>0.6 ± 0.1</td>
</tr>
<tr>
<td>Total Seston Flux (g m(^{-2}) yr(^{-1}))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1994</td>
<td>n/a</td>
<td>197 - 3940</td>
</tr>
<tr>
<td>1995</td>
<td>n/a</td>
<td>440 - 8830</td>
</tr>
<tr>
<td>Total Carbon Flux (g m(^{-2}) yr(^{-1}))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1994</td>
<td>n/a</td>
<td>20 - 400</td>
</tr>
<tr>
<td>1995</td>
<td>n/a</td>
<td>45 - 900(^3)</td>
</tr>
<tr>
<td>Total Nitrogen Flux (g m(^{-2}) yr(^{-1}))</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1994</td>
<td>n/a</td>
<td>4 - 87</td>
</tr>
<tr>
<td>1995</td>
<td>n/a</td>
<td>10 - 194</td>
</tr>
</tbody>
</table>

\(^2\)Data from 1994, no replicates

\(^3\)Likely an overestimate since dry weight per pellet data was from 1994, a year in which the worms were larger (Chapter 1) which might translate into larger fecal pellets.
Table 5-IV. Energetic ratios for *Chaetopterus pergamentaceus* in lower Chesapeake Bay. The average value for each parameter [absorbed or assimilated (A), production (P), respiration (R), or waste products (D)] is shown except for consumption (C), in which the range in values is shown.

<table>
<thead>
<tr>
<th>Energetic Ratios</th>
<th>Range</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>A/C</td>
<td>22 - 75</td>
<td>49</td>
</tr>
<tr>
<td>P/A</td>
<td></td>
<td>46</td>
</tr>
<tr>
<td>P/C</td>
<td>10 - 34</td>
<td>22</td>
</tr>
<tr>
<td>R/A</td>
<td></td>
<td>56</td>
</tr>
<tr>
<td>R/C</td>
<td>12 - 42</td>
<td>27</td>
</tr>
<tr>
<td>D/C</td>
<td>13 - 43</td>
<td>27</td>
</tr>
<tr>
<td>D/A</td>
<td></td>
<td>57</td>
</tr>
</tbody>
</table>
Kemp et al. 1997) or ~10,080 kJ (conversion 1 g organic carbon = 42 kJ; Lalli and Parsons 1993). This carbon value can be compared to values (primary production, as particulate g C m⁻² yr⁻¹) for other estuarine systems such as 146 for Delaware Bay, 146 for southern San Francisco Bay, 191 for the entire Chesapeake Bay, 208 for the Oosterschelde, 262 for the western Wadden Sea, and 270 for Narragansett Bay (compiled by Dame and Prins 1998).

**Energy Budget** - Our energy budget accounts for ~76% of the material consumed using the average term for consumption, 27% and 49% for biodeposited and assimilated respectively (Figure 5-3). We have the most confidence in the production values since these values were derived from an intensive two year population dynamics study. Thus, the remaining 24% of consumption may be accounted for by considering the range of consumption and biodeposition values, as well as the calculations of respiration.

Consumption values were calculated using a variety of information yielding a wide range of potential values. The calculated values for consumption using the secondary production method of Loo and Rosenberg (1989) were considerably lower than values obtained using the filtration rate. Ingested food as calculated by filtration rate represents the potential food intake whereas the secondary production method of estimating ingestion represents the actual intake (Loo and Rosenberg 1989). Either the filtration rates were overestimated or biodeposition represents a larger fraction of filtered material.

The filtration capacity of the population of the suspension feeding polychaete C.
Figure 5-3. Simplified carbon and energy flow diagram for the suspension feeding polychaete *Chaetopterus pergamentaceus* in the lower Chesapeake Bay. Grey area represents matter and energy within the polychaete. Based on data from Table 5-II. Average values for each parameter shown except for consumption in which the range is shown. Energy uptake as dissolved compounds not included.
*pergamentaceus* varied throughout the year as a result of changing density and size structure of the population (Figure 5-1). The population filtration capacity was highest in the mid- to late summer when the temperatures and worm density were highest, although the average individual was of a small size. The interannual difference is due to 1994 generally having larger worms than 1995 and the higher mortality of adults in 1995 (Chapter 1). The estimate of carbon flux attributable to this suspension feeding polychaete via filtration was quite variable through time; it may have been as great as than 1.5 g C m⁻² day⁻¹ but averaged ~0.6 g C m⁻² day⁻¹ or 218 g Carbon m⁻² yr⁻¹ (Table 5-I; Figure 5-II).

The filtration rate estimates for carbon flux by *Chaetopterus* may be overestimated. Aside from taking issue with any one of the simplifying assumptions of carbon value, retention efficiency, etc, an understanding of the physiological interactions between environmental parameters such as temperature or salinity and filtration rate are unknown for this polychaete. Thus, compensatory mechanisms that adjust filtration rate according to environmental condition (see respiration discussion below for details), if any, present in *C. pergamentaceus* may affect our estimate of filtration rate. Further, the simple calculations used assume that *Chaetopterus* is not limited by local particle depletion, i.e. the hydrodynamics of particle transport are unimportant. A number of researchers have shown that benthic suspension feeders can create a particle depleted layer near the bed (Wildish and Kristmanson 1984; Mushenheim 1987; Frechette *et al.* 1989; Thomsen *et al.* 1995), although, this depleted layer does not necessarily form (Smaal *et al.* 1986). Whether or not a depleted layer forms at the sampling site in the lower Chesapeake Bay has not been
determined; limited evidence to date would suggest it does not (Kline et al. unpub. data). As a rough check on the potential for seston depletion, calculation of the seston depletion index (as per Wildish and Kristmanson 1977) indicated that the seston may become depleted at water velocities of \( \leq 6.7 \text{ cm s}^{-1} \) above the benthic boundary layer. However, typically water velocities are greater than \( 6.7 \text{ cm s}^{-1} \) above the benthic boundary layer (Wright et al. 1992). Thus seston depletion is unlikely.

The potential for refiltration of outflow from worm tubes in the lower Chesapeake Bay is variable. Refiltration is a function of the velocity ratio of outflow jet to the ambient current (Monismith et al. 1990; O’Riordan et al. 1993) and siphon height (O’Riordan et al. 1993). Both the velocity ratio and the height of tube above the bed are variable through time for Chaetopterus in the lower bay (personal observation). Monismith et al. (1990) found that refiltration rates could be as high as 35% for an isolated bivalve while O’Riordan et al. (1993) indicate that as much as 20% refiltration may be possible over a dense bed of suspension feeding bivalves. A refiltration rate of \(~50\%\) would be necessary to put the flux of materials as calculated by filtration rate on par with the flux as calculated by secondary production.

A wide range in biodeposition values for fecal pellets and pseudofeces lends uncertainty to our ability to accurately quantify this portion of the energetic budget. Using minimum values we found that fecal pellets represent \(~27\%\) of consumption. Although pseudofecal production has been observed in the Chaetopterus population

\[1\text{ Using the maximum population filtration of } \sim 80 \text{ L hr}^{-1} \text{ from Table 5-I.}\]
of the lower bay during periods of high near-bed particle transport (Schaffner unpub. data), the quantity and quality of this material has yet to be determined. Production of pseudofeces may partially account for some differences noted in consumption as calculated by filtration rate versus secondary production.

A limitation of our energy budget is a lack of direct measurements of respiration. Some organisms have the ability to compensate, through physiological processes, for changes in environmental variables such as temperature and oxygen availability to minimize metabolic expenditures while others do not. Metabolic expenditures are also a function of intrinsic factors such as activity level, body size, and reproductive cycle. For reviews see Newell (1979) and Valiela (1995). In general, short-term changes in environmental parameters such as temperature nearly always evoke a change in O₂ consumption of at least a Q₁₀ value of ~2. In contrast, there is no pattern of response to long-term, seasonal, temperature changes except that extremes in temperature tend to evoke a cessation of all activity. For example, subtidal invertebrates that do not normally experience a marked short term changes in temperature may show no real change in O₂ consumption or may show an increase in O₂ consumption with an increase in temperature (Newell 1979). Several studies have shown that bivalves acclimate to low winter temperatures and show a constant filtration rate (as reviewed by Grant 1996) which may translate into a level respiration rate. The compensatory mechanisms, if any, present in the polychaete C. pergamentaceus have yet to be explored. Thus estimates for respiration could be improved by in situ measurements and knowledge of C. pergamentaceus's physiological response to the environment. Our estimates have value as a first
ENERGETIC RATIOS - The gross growth efficiency, or ecological efficiency (P/C), was \(-22\%\) for *C. pergamentaceus* and is comparable to a variety of marine invertebrates (Table 5-IV; as compiled by Huebner and Edwards 1981; and Valiela 1995). In general, ecological efficiencies are thought to range between 10\% and 25\% and represents that portion of the consumed food that is available to the next trophic link. In the case of *C. pergamentaceus* predation is considered negligible so the next trophic link is nonexistent.

Our estimate of \(-46\%\) for the growth efficiency in terms of absorbed food (P/A) is high compared to most marine invertebrates, although within a range of known values (Valiela 1995). Using production values for Chapter 1 we find that 52.5\%, 34.5\%, and 13.1\% of production are used for tubes, tissue, and oocytes respectively. These percentages translate into approximately 562kJ, 369kJ, and 140kJ per year for the tubes, tissue and oocytes respectively (Figure 5-3).

The respiration ratios R/C and R/A of \(-27\%\) and 56\% respectively are also within the norm of known invertebrate values (Huebner and Edwards 1981; Valiela 1995).

BENTHIC-PELAGIC COUPLING - The estimate for carbon flux by *C. pergamentaceus* is variable depending upon the methodology. We calculated yearly estimates ranging from \(-40\%\) to 100\% of the average available water column production. Our calculated average ecological efficiency (P/C) of 22\% would
indicate a value closer to -50%; yet this percentage negates carbon flux in the form of pseudofecal production. When considered on a daily basis, the potential carbon flux via the filtration rate may be greater than the net community production. This underscores the strength of benthic-pelagic coupling within the lower bay.

To support and constrain our estimate of 40 - 100 % of the net water column community production supporting C. pergamentaceus, we need an estimate of the quantity of the net water column community production that is consumed by other species. However, information of this type is lacking for the lower Chesapeake Bay. Work on the bay anchovy from the mid-bay suggests that consumption of plankton by the bay anchovy and filter feeding fishes such as menhaden is potentially significant (Cowan and Houde 1993; Wang and Houde 1995). Further, complex interactions among ctenophores, jellyfish, and plankton in the lower bay hamper prediction of plankton consumption and plankton dynamics in the lower bay (Feigenbaum and Kelly 1984). Knowledge of the proportion of phytoplankton grazed by C. pergamentaceus versus by zooplankton would increase our understanding of ecosystem process in the lower bay. However, a direct grazing comparison is unavailable since there are no estimates of zooplankton grazing in the polyhaline region of the main stem of Chesapeake Bay.

Heip et al. (1995) state that suspension feeders can be responsible for large fluxes of organic matter to the benthos that meet or exceed water column production. Their reasoning is that suspension feeders are patchily distributed and on a system wide basis the water column productivity limits the suspension feeders; yet the needs of local patches of suspension feeders may exceed local water column
production. Grizzle & Morin (1989), Graf (1992) and Loo & Rosenberg (1996) have shown that lateral transport of material to suspension feeders positively affects the growth and production of organisms. Due to the dynamic nature of the bay, transport of material from shallower areas may be important to sustain high productivity in these suspension feeding worms. Also, a residual circulation eddy may increase production near our study region of the bay (see Chapter 1; Hood et al. 1998; Kiørboe 1993).

Remineralization of biodeposits from *C. pergamentaceus* can account for a minimum of 46 to 103 g O₂ m⁻² yr⁻¹ of benthic respiration, assuming a respiratory quotient of 1.0 (Kemp et al. 1997). Including this polychaete’s respiration of 32 g C m⁻² yr⁻¹ which equates to 85 g O₂ m⁻² yr⁻¹, the minimum benthic respiration of 131 to 188 g O₂ m⁻² yr⁻¹ can be attributed to this one benthic species. These estimates do not include the potential for indirect effects of worms due to microbial activity stimulation via bioirrigation (e.g. Mayer et al. 1995). Kemp et al. (1997) indicated that benthic respiration was 463 g O₂ m⁻² yr⁻¹ with the dominant consumption term being associated with sulfate reduction. Thus, *C. pergamentaceus* accounts for a minimum of 28% to 41% of all benthic respiration. Clearly, biodeposition by *C. pergamentaceus* represents an important avenue of energy cycling in the lower bay. Future work in this field should focus on the quantity and quality of biodeposition on a seasonal basis.

**CONCLUSION** - Our energy budget accounts for ~76% of the material consumed using the average term for consumption. The possibility that a large portion of the
phytoplankton biomass of the lower Chesapeake Bay may be consumed by the benthos has been suggested by Smith & Kemp (1995). The results from this study clearly indicated that this is likely and that *C. pergamentaceus* may filter a large portion of or an amount equivalent to the net water column community production. When considered on a daily basis, the potential carbon flux via the filtration rate may be greater than the net water column production. *Chaetopterus pergamentaceus* accounts for a minimum of 28% to 41% of all benthic respiration in the lower Chesapeake Bay. This study lends additional and independent support to the conclusions of Chapters 1 and 3, that *Chaetopterus pergamentaceus* plays a strong role in and is highly dependent on benthic-pelagic coupling in the lower bay.
In summary, this dissertation enhances our understanding of the structure and function of aquatic food webs through knowledge of the processes and mechanisms linking pelagic and benthic subsystems. This study focuses on the role played by a dominant, benthic, suspension feeder, the polychaete *Chaetopterus pergamentaceus*, in the transfer of organic matter between the pelagic and benthic subsystems of Chesapeake Bay.

Chapter 1 establishes the life cycle, growth rates, and secondary productivity of *C. pergamentaceus*. Most production is associated with the rapid growth of small individuals that recruit to the population during the summer months. This is a significant finding since it refutes the current dogma that the bay ecosystem is dominated by a pelagic food web during the summer months; a time in which water column utilization of organic matter is thought to prevail. Many bay scientists have argued that the spring bloom fuels benthic production, with little food reaching the bottom for the benthic community during summer. However, the data presented in this dissertation clearly refute this idea. Growth and production of *C. pergamentaceus* tracks gross primary production cycles of the water column with maximum water column production concurrent with maximum worm growth/production during the summer. In contrast, the phytoplankton produced during the spring bloom are used by the worms for gamete production and possibly for some storage of essential nutrients, rather than new growth. Overall, the data suggest that the worms must be tightly linked to water column processes which can
only happen if physical mixing of the water column or circulation processes are sufficient to deliver food to the bottom, an idea expounded upon in Chapter 2.

Chapter 2 examines spatial relationships of growth and productivity for *C. pergamentaceus* at several stations in the lower bay. Two significant relationships were noted. First, growth of individuals is not uniform across the study region, but, is concordant with complex environmental gradients. Observed high growth rates were coincident with the center of a circulation gyre, which was not described until after the field portion of the study was completed, supporting the notion the "physics feeds the benthos". Second, a negative relationship between density and growth rates was noted for juveniles, which may suggest possible food limitation at local levels. However, the effect of density is confounded by other environmental gradients. Future work discerning the effects of various environmental gradients on macrofauna, such as *C. pergamentaceus*, is needed.

In Chapter 3, an array of approaches and techniques were used to delineate the sources of organic matter supporting the growth and productivity of *C. pergamentaceus* and to elucidate the role of this polychaete in the food web dynamics of the lower bay ecosystem. The data indicate that this population of worms is supported by high quality organic matter, derived primarily from fresh phytoplankton. Seasonal changes in the relative importance of major groups of phytoplankton in the water column were tracked by worm gut contents and worm tissues with diatoms being more prevalent in the spring, fall, and winter and smaller phytoplankton dominating in the summer. Thus organic matter utilization by the worm population reflects the major changes observed in the water column.
community with no significant time lags. This further substantiates the close coupling of the worm population with the water column community.

The focus of Chapter 4 was the measurement of *in situ* filtration rates of *C. pergamentaceus*. Previously published experiments conducted in laboratory settings revealed high filtration rates, comparable to large bivalves such as oysters. My data reveal a significant relationship between worm size and filtration rate with similarity between field derived data and previously reported laboratory rates.

Chapter 5 serves as a synthesis of the dissertation. Data and ideas developed in Chapters 1 through 4 were used to develop an energy budget for the population of *C. pergamentaceus* within the context of the lower bay ecosystem. This approach indicated that this polychaete requires a significant fraction for the net community water column production to support its growth and reproduction. Further, this polychaete enhances energy flow from the water column to the benthos via the processes of biodeposition of organic rich fecal pellets and tube construction. Thus, *Chaetopterus pergamentaceus* can be considered an “ecosystem engineer” (as per Jones *et al.* 1994).
Appendix

Figures from the Chesapeake Bay Monitoring Program
Figure Appendix-1: Phytoplankton abundance (# liter\(^{-1}\)) above the pycnocline in lower Chesapeake Bay (Station CB6.4). Data from the Chesapeake Bay Program (http://cobia.chesapeakebay.net).
Below Pycnocline

Diatoms Cryptophyceae
□  Dinoflagellates □  Others

1.6x10
1.4x10
1.2x10
1.0x10
8.0x10
6.0x10
4.0x10
2.0x10

Figure Appendix-2: Phytoplankton abundance (# liter\(^{-1}\)) below the pycnocline in lower Chesapeake Bay (Station CB6.4). Note change in scale from Figure 75. Data from the Chesapeake Bay Program (http://cobia.chesapeakebay.net).
Figure Appendix-3: Primary productivity ($\mu$g C l$^{-1}$ hr$^{-1}$, measured as carbon fixation), chlorophyll $a$ ($\mu$g l$^{-1}$), and assimilation ratio ($\mu$g C $\mu$g chl-$a^{-1}$) through time in the lower Chesapeake Bay (Station CB6.4, above pycnocline). Data from the Chesapeake Bay Program (http://cobia.chesapeakebay.net).
Figure Appendix-4: Picoplankton (cells $1^{-1} * 10^6$) through time in lower Chesapeake Bay (Station CB6.4, above pycnocline). Data from the Chesapeake Bay Program (http://cobia.chesapeakebay.net).
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