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

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Abstract

Benthic suspension feeders are functionally important components of many shallow estuarine and coastal ecosystems. Their relative importance in material and energy cycling depends on physical and biological factors, of which population dynamics of individual species are a key feature. We studied the demographics and secondary production of a population of the tubicolous, suspension feeding polychaete, *Chaetopterus* cf. *variopedatus,* of southern Chesapeake Bay, Virginia, to better understand its functional role in an estuarine ecosystem. Average worm densities in the study region ranged from 30 to >1000 individuals m^{-2} and were greatest after the summer recruitment period. Recruitment success varied threefold between 1994 and 1995. A two-cohort model (juveniles and adults) with seasonality best described the data. High secondary production (18 g C m^{-2} yr^{-1} in 1994, 34 g C m^{-2} yr^{-1} in 1995) was mainly due to rapid growth and maturation of new recruits during summer and tube production. An interannual difference in production was associated with the interannual difference in recruitment success. General temporal trends of primary production and worm production were similar, and the worm population required 35%–100% of the estimated annual net water column community production per m^2 for this region of the estuary. *Chaetopterus* cf. *variopedatus* is an important component of the lower bay ecosystem and should be considered when modeling carbon, nutrient, and energy flow. Our results further demonstrate that temporal variations in population dynamics lead to significant temporal variability in the relative importance of benthic suspension feeder effects for ecosystem function.

In many shallow marine and estuarine ecosystems benthic suspension feeders, especially bivalves, have been shown to provide significant links between the water column and sediments (Dame 1996; Wildish and Kristmanson 1997). As a result, they have important effects on carbon, nutrient, and energy flow. The relative importance of benthic suspension feeders in material and energy cycling within an estuarine ecosystem will depend, in part, on the population dynamics of individual species. Important parameters include density, biomass, reproductive state, life span, maximum sizes of individuals, growth rates, biomass turnover, and secondary production (Cloern 1982; Alpine and Cloern 1992; Heip et al. 1995). Thus, elucidating the population dynamics and secondary production of benthic suspension feeders will lead to a better understanding of their functional role in aquatic ecosystems.

The large, tubicolous, suspension feeding polychaete

Chaetopterus cf. *variopedatus* (sensu Enders 1909; previously reported as *C. pergamentaceus,* Thompson and Schaffner 2000 and *C. variopedatus,* Schaffner 1990) is an important component of the soft sediment benthic community of lower, polyhaline, Chesapeake Bay, where relatively stable populations (densities of ~100 individuals m^{-2}) have been reported since the 1980s (Huggett 1987; Schaffner 1990; Schaffner et al. 2001). *Chaetopterus* cf. *variopedatus* was reported in the Chesapeake Bay as early as 1930 (Cowles 1930) and is found in other marine and estuarine communities along the east coast of the United States between New England and Florida, whereas related species are found worldwide (Eckberg and Hill 1996 and references therein). For this study, we investigated the population dynamics of *C.* cf. *variopedatus,* within the lower Chesapeake Bay, during two consecutive years. Demographic parameters including density, size structure, reproductive activity, and growth rates were determined on the basis of semimonthly to monthly sampling over a 2-yr period. Seasonal, interannual, and stage-based estimates of secondary production provide insights regarding the relationships between *C.* cf. *variopedatus* and the dynamics of carbon, nutrient, and energy flow in the lower Bay ecosystem.

Methods

Study region—The study region, located within lower Chesapeake Bay east of the mouth of the York River subestuary, encompasses ~54 km^2 at water depths of 10–15 m. Station locations are shown in Thompson and Schaffner (2000). General descriptions of the lower Bay environment

are given in Schaffner (1990), Wright et al. (1997), and Schaffner et al. (2001). Bottom water salinity of 18‰–27‰, bottom water temperature of 2°C–27°C, mean tidal range of 60 cm, and maximum tidally induced current speeds of 20–40 cm s⁻¹ at 1 m above the bed are characteristic. Sediments are primarily silts (40%–50%) and fine sands (40%–50%). The study region does not suffer hypoxia or anoxia during the summer, as is observed further north in the Bay. The benthic fauna consists of a diverse assemblage of suspension and deposit feeders with *C.* cf. *variopedatus* often being the biomass dominant.

Field sampling—Ten random and two fixed stations were sampled between January 1994 and December 1995. We used an Ocean Instruments spade box core ($20 \times 30 \times 30$ cm deep) to collect one or two core sample(s) per station during years 1 and 2, respectively. Sampling was monthly during winter/spring and semimonthly during the summer/fall, although some scheduled 1995 sampling dates were missed. Because of the fragile nature of the worms, three methods were used to ensure their complete removal from the sediment: (1) a 5 cm diameter $\times$ 5 cm deep subcore was collected and fixed intact to capture fragile new recruits; (2) surface sediment from the 0–2 cm depth interval was removed and elutriated through a 125-μm screen to collect small worms that are easily damaged; and (3) larger worms were directly dissected from the sediment. All specimens removed from the cores were fixed immediately in 10% formalin.

Bottom-water samples (1 m above sediment) for salinity (refractometer) and dissolved oxygen content (Winkler titration) were collected by Niskin bottle. Sediment temperature was recorded in the upper 0.5 cm of each box core. To estimate labile organic matter input as an indication of relative food availability for benthic animals (Josefson and Conely 1997), a subcore (2.7 cm diameter $\times$ 0.5 cm deep) was collected for chlorophyll and phaeopigment analysis from each of three box cores collected at the fixed stations on each sampling date. These samples were stored frozen in the dark until analysis within 30 d.

Laboratory analyses—Spectrophotometric chlorophyll *a* and phaeopigments were analyzed after the procedure of Pinckney et al. (1994). To determine worm ash-free dry weight (AFDW) to size relationships, measured specimens were ashed for 4 h at 450°C. No corrections were made for weight loss due to fixation in 10% formalin and subsequent storage in 2% formalin. Measured specimens included male and female worms ranging from juveniles to fully gravid to partially or totally spent individuals. To obtain tube AFDW, tubes were rinsed with a high-pressure hose to remove adherent sediment and then ashed at 450°C for 4 h.

Population structure—Density, population size structure, and reproductive condition of *C.* cf. *variopedatus* were determined for each sample. Length of the ventral side of the anterior region prior to the aliform notopodia (referred to as head length), width at setiger 4, and overall length (when possible) were measured to the nearest 0.1 mm. Head area was calculated as head length multiplied by width at setiger

4. Comparisons of coefficients of determination from regressions of each measurement versus AFDW were used to determine the most reliable indicator of size (largest r^2 value).

Size frequency histograms relating head area (most reliable indicator of size; see ''Results'') to number of individuals were constructed. Cohorts were delineated on the basis of distinct modes in the size distribution; but, once adult size was 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 von Bertalanffy growth function from head area-frequency data by use of all sampling dates (Fournier et al. 1990).

Fecundity estimates—Female fecundity was determined by extracting all oocytes from the first tail segment. After dilution and mixing of oocytes with distilled water, aliquots (generally several hundred eggs but occasionally fewer) were viewed by use of image analysis and measured to the nearest 0.1 μm. Regressions were used to investigate relationships between worm size, egg size, number of eggs per segment, egg diameter, and time.

Production estimates—Worm production (g AFDW m⁻² yr⁻¹) was estimated by use of the increment summation method (Downing and Rigler 1984) on the basis of AFDWs calculated from a weighted least-squares regression relating organism size (head area) to AFDW.

Egg production due to egg release to the water column was estimated for each sampling interval. Egg volume, calculated from egg diameter, was converted to wet weight by use of the density of protoplasm (1.2 g cm⁻³) and then AFDW (0.9 g AFDW = 6.0 g wet weight; Waters 1977; Seitz and Schaffner 1995). The number of eggs per segment was estimated, then multiplied by the number of ovigerous segments per adult (number of segments = 7.469 $\times$ head area $^{0.25}$ − 5.55; $P < 0.01$, $r^2 = 0.83$; Thompson unpubl. data), then divided by 2 because the number of eggs per segment decreases toward the tail. This conservative estimate of eggs per female was multiplied by number of females per unit area (0.5 $\times$ the number of adults), yielding 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. Tube production was estimated by use of two separate best-fit regressions that related tube AFDW to worm AFDW.

Statistical methods—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—Although total freshwater flow from the major tributaries into Chesapeake Bay was almost 1.7 times greater in 1994 than in 1995, trends in sediment tem-
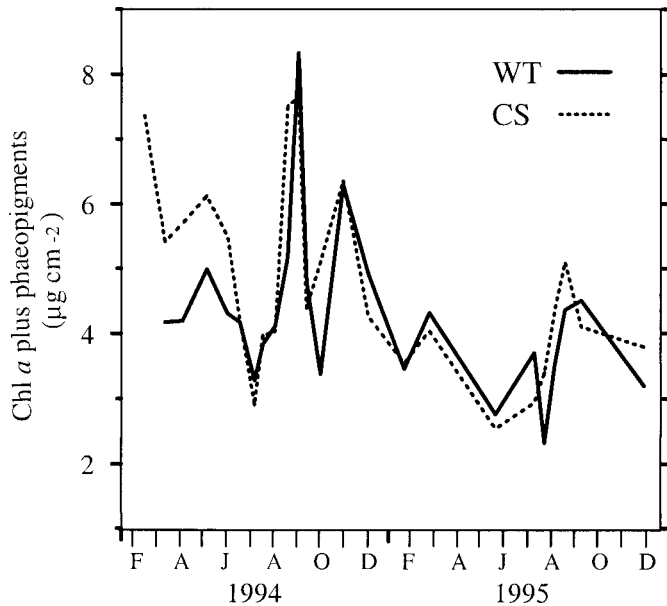
Fig. 1. Sediment Chl *a* and phaeopigments for samples collected at two fixed stations (CS and WT) within the lower Chesapeake Bay study region.

perature, bottom water dissolved oxygen, and salinity were similar between years in our study region (U.S. Geological Survey 2000; Wilks' Lambda in a MANOVA analysis; $F = 0.363$; df = 3, 4; $P = 0.78$). Pigment concentrations (Chl *a* plus degradation products, primarily phaeopigments), used as an indicator of food availability to the benthos, were significantly greater in 1994 compared with 1995 (Fig. 1; ANOVA, $F = 56.21$; $P < 0.01$; data were homoscedastic; Cochran's $C = 0.24$; $k = 8$; $P > 0.05$).

Population structure—Average densities of *C*. cf. *variopedatus* ranged from 30 to a maximum of 1,000 individuals m^{-2} in late summer (Fig. 2), after the period of recruitment during late July/early August of 1994 and late June/July of 1995 (Fig. 3). Rapid growth occurred throughout the summer and fall, with juveniles reaching adult size by the fall. In 1995, recruitment was nearly three times that of 1994.

The male:female ratio varied but was 50:50 when averaged over the study (Cochran-Mantel-Haenszel statistic, $\chi^2 = 5.626$; df = 1; $P = 0.02$). The size data were not normally distributed (Shapiro-Wilks test, $P < 0.01$) because of bimodality arising from the convergence of two cohorts but were homoscedastic (Cochran's $C = 0.51$; $k = 2$, df = 286; $P > 0.05$). The Kruskal-Wallis test of analysis of variance by ranks showed that the mean size of males and females did not differ ($\chi^2 = 0.20$; 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 ($\pm$SD) for the theoretical mean asymptotic size (head area) if the worms were to grow indefinitely are $S_\infty = 168$ mm$^2 \pm 17$, and the von Bertalanffy $K = 0.81$ yr$^{-1} \pm 0.01$, higher values of which result in a more rapid approach to asymptotic size. Although S_∞ is the average asymptotic size estimated for the population, the asymptote might be greater or smaller for the
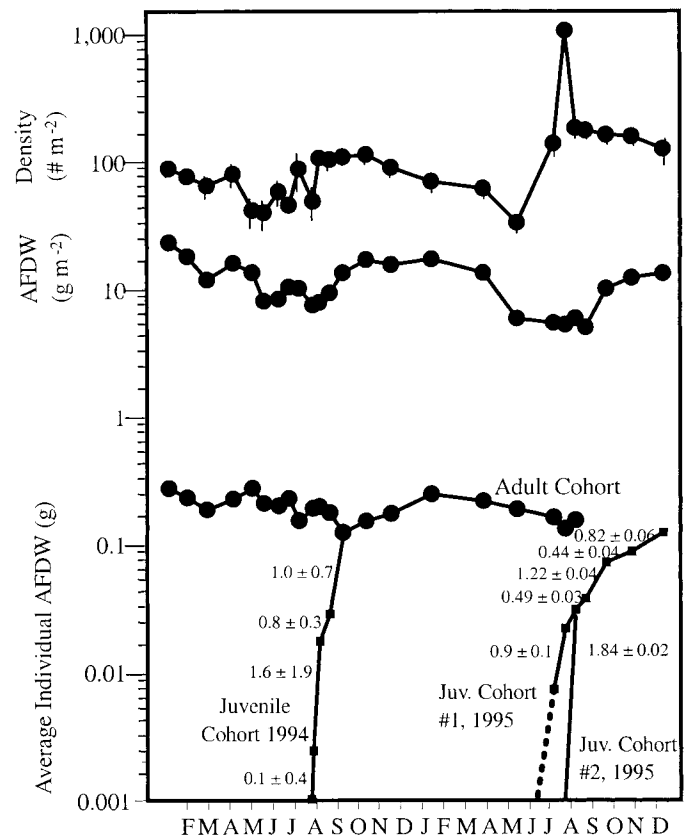

Fig. 2. *Chaetopterus* cf. *variopedatus* population parameters for 1994 and 1995. For density data, bars indicate SE. Average growth rates ($\pm$SD) in mg AFDW d^{-1} are denoted adjacent to juvenile cohorts. Dotted line represents an estimate based on previous year's data.

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.

In a study of *C. variopedatus* in shallow waters of coastal South Carolina, annual mortality of tagged worms was ~75%, with slightly higher survival in the subtidal versus intertidal, but some tagged individuals lived >3 yr (Michael Grove, pers. comm.). Thus, the proportion of older individuals (age class 2 or greater) for the present study is likely to be small. MULTIFAN yielded a mortality rate of 2.7 yr^{-1} for our data, which indicates that the annual survival rate was ~7%. This modeled rate appears to be highly influenced by the 1995 recruitment data, and the actual survival rate between years for adults would seem to be somewhat higher (Figs. 3 and 4). An assumption of two cohorts, juveniles and adults, seems a reasonable approximation.

Modeling that used MULTIFAN revealed intense seasonal oscillations in growth (amplitude = 0.950 $\pm$ 0.008, where 0 = no seasonal oscillation in growth and 1 = no growth during some seasons). This seasonal growth can be seen in the similar trends within cohorts between years, an indication that age was an important factor in growth (Fig. 2). High growth rates occurred during late summer among new recruits and juveniles, whereas the mean size of adult worms decreased throughout winter. There were no significant dif-
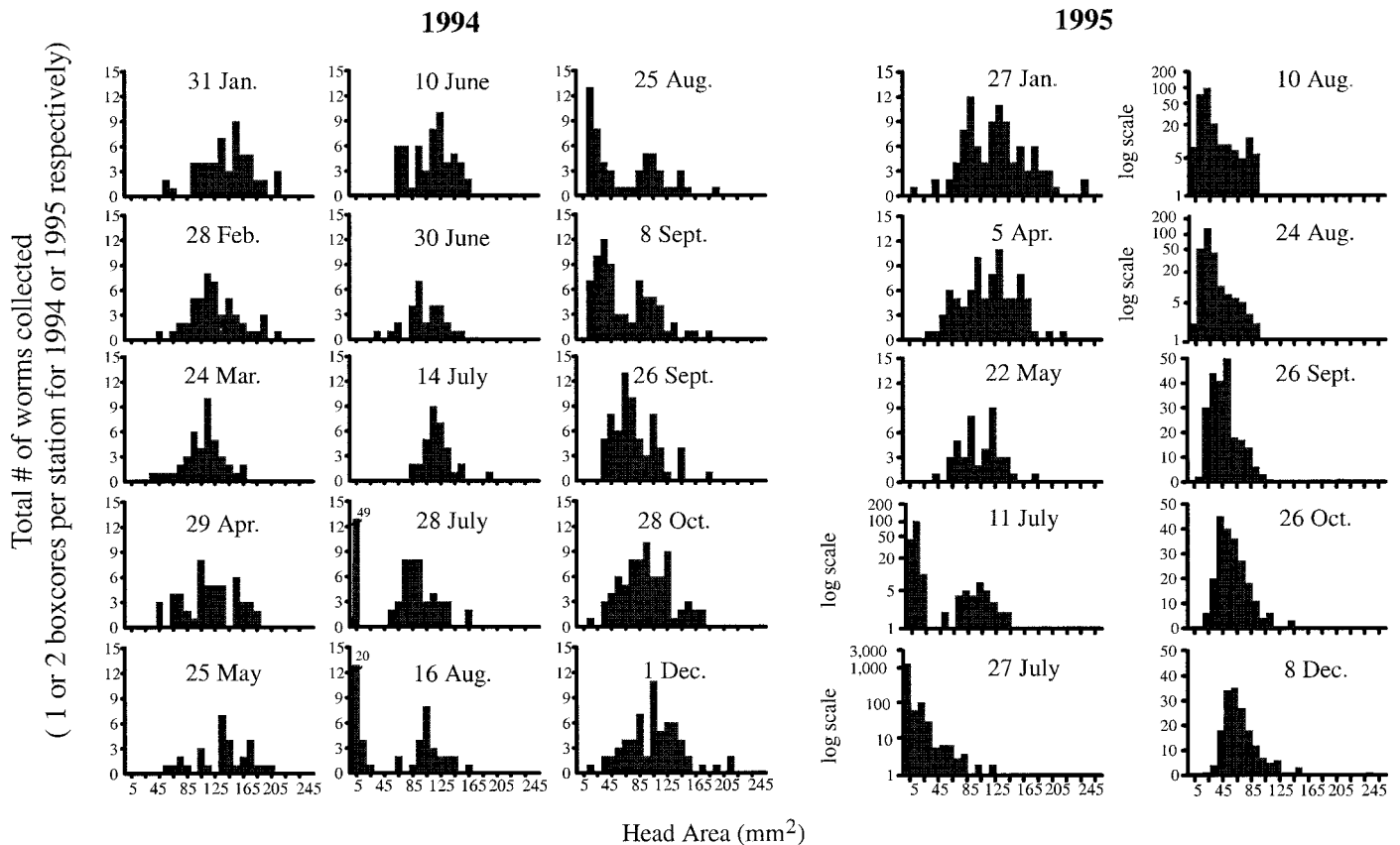
Fig. 3.   Size (head area) frequency histograms for each sampling date. In 1994, one box core was taken at each of 12 stations on every sampling date. In 1995, two box cores were taken at each of 12 stations on each sampling date. Note changes in *y* axis scaling.

ferences between the slopes of the regression lines within the adult cohort, which indicates that head area decreased at the same rate in both years (ANCOVA; $F = 3.89$; df = 1, 14; $P > 0.05$), even though head area was significantly larger in 1994 compared with 1995 (ANCOVA; $F = 4.54$; df = 1, 15; $P < 0.001$). This suggests that the rate of decline in the adult population was 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; $n = 77$; $r^2 = 0.73$; $P < 0.01$) compared with 1995 (head area = 0.50 × day + −85.5; $n = 82$; $r^2 = 0.74$; $P < 0.01$).

Fecundity—Gravid females were found from May 1994 throughout most of the remainder of the study. We could not determine the percentage of gravid females because 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, and 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 >1 million eggs per female, and was comparable to other large

infaunal polychaetes (Seitz and Schaffner 1995 and references therein) and to what has been observed in laboratory experiments with *C. pergamentaceus* (Eckberg and Hill 1996). No statistical relationships were noted among egg diameter versus time, number of eggs or female size, or number of eggs versus female size or time. By virtue of their larger size, which equates to more ovigerous segments, larger females produce more eggs; but there were not more eggs per segment, nor were the eggs larger. We could not determine larval development time because spawning was not epidemic, and larvae may have been imported from other areas. If we assume that all new recruits were spawned within the Chesapeake Bay, larval development time could be ≤2 months.

Secondary production—Head area was significantly related to AFDW and can be described by the equation AFDW = [(0.0224 × length) + (0.0303 × width)]³ ($N = 40$, $r^2 = 0.93$, $P < 0.001$; because of heteroscedasticity, observations were weighted by variance⁻¹). Estimates of secondary production were based on this regression. Because of high growth rates, production for juveniles was generally positive. Adult production was usually negative because of declines in size and density, except during late 1994, when the merging of juveniles into the adult cohort resulted in positive production for adults.

Production estimates for the 1994 adult cohort varied be-

Table 1. Secondary production estimates of *Chaetopterus* cf. *variopedatus* from lower Chesapeake Bay. Data are g AFDW m^{-2} d^{-1} except totals, which are g AFDW m^{-2} interval^{-1}. Data in parentheses are g C m^{-2}.

Interval ending	No. of days	Adults	Cohort 1	Cohort 2	Oocytes	Worm total	Tube	Tube total	Interval total
28 Feb 94*	59	−0.06	0.0	0.0	0.0	−3.55	0.0	0.0	−3.55
24 Mar 94	24	−0.15	0.0	0.0	0.0	−3.54	0.0	0.0	−3.54
29 Apr 94	35	0.09	0.0	0.0	0.0	3.14	0.09	3.12	6.26
25 May 94	24	0.13	0.0	0.0	0.018	3.64	Trace	0.11	3.75
10 Jun 94	19	−0.22	0.0	0.0	0.073	−2.77	0.0	0.0	−2.77
30 Jun 94	20	−0.22	0.0	0.0	0.053	−3.43	0.0	0.0	−3.43
14 Jul 94	14	0.40	0.0	0.0	0.077	6.66	0.0	0.0	6.66
28 Jul 94	14	−0.37	Trace	0.0	0.104	−3.69	0.04	0.61	−3.08
16 Aug 94	19	0.12	0.01	0.0	0.055	3.57	0.02	0.47	4.04
25 Aug 94	9	0.03	0.12	0.0	0.069	1.98	0.20	1.77	3.75
8 Sep 94	14	−0.07	0.06	0.0	0.021	0.11	0.01	0.14	0.25
26 Sep 94	18	0.21	0.0	0.0	0.000	3.73	0.24	4.23	7.96
28 Oct 94	32	0.10	0.0	0.0	0.026	3.92	0.03	1.11	5.03
31 Dec 94*	64	0.04	0.0	0.0	Trace	2.27	0.14	8.94	11.21
27 Jan 95*	27	−0.07	0.0	0.0	0.007	−1.74	0.29	7.83	6.09
5 Apr 95	68	−0.02	0.0	0.0	Trace	−1.40	0.0	0.0	−1.40
22 May 95	47	−0.02	0.0	0.0	0.021	0.21	Trace	0.0	0.21
11 Jul 95	55	−0.01	0.03**	0.0	0.012	1.92	0.01	0.72	2.64
27 Jul 95	11	0.03	0.18	Trace	0.013	2.44	0.26	2.82	5.26
10 Aug 95	14	−0.08	1.12	0.0	0.041	15.08	0.18	2.57	17.65
24 Aug 95	14	0.0	0.08	0.0	0.052	1.90	0.12	1.67	3.57
26 Sep 95	33	0.0	0.18	0.0	0.024	6.56	0.18	6.04	12.60
26 Oct 95	30	0.0	0.08	0.0	0.001	2.52	0.08	2.53	5.05
31 Dec 95*	66	0.0	0.08	0.0	Trace	5.01	0.07	4.43	9.44
1994 total	AFDW	1.77	2.08	0.0	8.20	12.05		20.49	32.54
	Carbon	(0.98)	(1.15)	0.0	(4.55)	(6.69)		(11.38)	(18.08)
1995 total	AFDW	−5.57	33.94	Trace	4.12	32.50		28.60	61.10
	Carbon	(−3.09)	(18.84)		(2.28)	(18.06)		(15.89)	(33.94)
total	AFDW	−3.80	36.00	Trace	12.32	44.54		49.09	93.63
	Carbon	(−2.11)	(19.99)		(6.83)	(24.74)		(27.27)	(52.02)

* To calculate total annual production for 1994, daily production for the interval 1 January–30 January 1994 was estimated using daily production for the interval 31 January–28 February 1994, and daily production for 2 December–31 December 1994 was determined based on daily production for the interval 1 December 1994–27 January 1995. To calculate total annual production for 1995, daily production for the interval 1 January–27 January 1995 was determined based on daily production for the interval 1 December 1994–27 January 1995, and daily production for 9 December–31 December 1995 was estimated using daily production for the interval 26 October–8 December 1995. Refer to Figure 3 for the actual dates on which samples were collected for production estimates.

** Back calculated from 1994 data because of missing 1995 data.

tween sampling dates, likely because of the combined effects of spawning, growth and patchiness (Table 1). Worm size and density declined throughout the winter, which resulted in negative production in February and March. In April, worm size and density increased, which resulted in a positive production estimate. Despite a decrease in density, production remained positive in May, which suggests that worm growth was important. Negative production was calculated for June because of declines in worm density and size, but oocyte production was high. Thus, it is likely that energy was diverted into reproduction rather than growth and that some postspawning mortality occurred. In mid-July, a few large polychaetes were collected (because of patchiness or rapid growth of individuals), resulting in a large positive production. Two weeks later, these worms were not collected (because of patchiness or postspawning 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 was due to worm growth, decreased energy toward reproduction, and a loss of larger worms, which is likely due to postspawning 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 were generally similar to 1994. Because 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. Density and worm size declined throughout the winter and spring, which resulted in negative production. The juvenile cohort production in 1995 was of greater 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, which became indistinguishable from the first juvenile cohort in that sampling period.

Excluding tube production, adults accounted for 15% of

Table 2. Production to biomass estimates for *Chaetopterus* cf. *variopedatus* from lower Chesapeake Bay.

	Biomass (g C m^{-2})	Production (g C m^{-2} yr^{-1})	P/B
Excluding tubes			
1994	6.7	6.7	1
1995	5.2	18.1	3.5
Average	6	12	2
Including tubes			
1994	10.7	18.1	1.7
1995	11.3	33.9	3
Average	11	26	2.4

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, adult somatic growth resulted in negative production (−10%), and 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. This is due to the exceedingly high production of the second 1995 juvenile cohort, which grew rapidly but over a short time period, relative to the overall faster growing juveniles of 1994.

Tube production was calculated by use of two regressions relating tube AFDW to worm AFDW, one regression for actively growing worms [tube AFDW = exp(−0.156) × (worm AFDW$^{0.87}$)] ($N = 6$) and another regression that included overwintering worms [tube AFDW = exp(1.817) × (worm AFDW$^{1.337}$)] ($N = 9$). Estimates of tube production were based on these regressions; conversions to carbon (C) were made by use of 0.9 g AFDW = 0.5 g C (Table 1; Waters 1977). Total tube production for the population was estimated to be 20 g AFDW m^{-2} in 1994 and 29 g AFDW m^{-2} in 1995.

On an areal basis, and excluding tube production, the estimate of worm secondary production for adults in 1994 was ~1 g C m^{-2} compared with approximately −3 g C m^{-2} for 1995 (Table 1). The rapidly growing juveniles produced ~1 g C m^{-2} in 1994, whereas 1995 juvenile production was ~19 g C m^{-2}. Egg production was ~5 and ~2 g C m^{-2} in 1994 and 1995, respectively. Tube production was ~11 and ~16 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 and ~34 g C m^{-2} in 1994 and 1995, respectively, with an average annual production of 26 g C m^{-2} for the study.

The ratio of annual production to mean biomass (P/B ratio) was calculated as 2.0 and 2.4, excluding and including tubes, respectively (Table 2). On a yearly basis, the P/B ratio ranged from 1.0 to 3.5 for 1994 and from 1.7 to 3.0 for 1995, excluding and including tubes, respectively.

Discussion

We have shown that *C.* cf. *variopedatus* is an abundant and productive benthic suspension feeder of lower Chesa-peake Bay. The population exhibits seasonal and interannual variations in growth, reproduction, and secondary production. We found that recruitment varied threefold between 1994 and 1995, with a seasonal peak in the summer and limited recruitment in fall. A two-cohort model of juveniles and adults, with seasonality, best described the data, even though more than two age classes were likely present. The high secondary production we observed was mainly due to rapid growth and maturation of new recruits and tube production. Interannual variability in production was due to inconsistency in recruitment success. The general scheme for this population is that the overwintering population consists of adults and maturing juveniles that spawn the following summer. Spawning is not epidemic among females or complete within a female. Some, but not all, summer recruits spawn during the same summer. Densities are lowest prior to recruitment of juveniles. The life span of *C.* cf. *variopedatus* in lower Chesapeake Bay can exceed 1 yr, but few individuals lived >1 yr during the period of our study.

Populations are influenced by a multitude of factors, some of which are destabilizing, such as larval transport processes or unpredictable food supply, and some of which can be stabilizing, such as density-dependent growth and reproduction. Many estuarine invertebrates exhibit high interannual variability in abundance as a result of variations in reproductive output or recruitment success (Zajac and Whitlatch 1988; Seitz and Schaffner 1995). Thus, it is not surprising to find high interannual variability in abundance because of recruitment variation in this study. An end result of interannual recruitment variability is that macrofauna production can be variable between years (Möller and Rosenberg 1983).

Differences in production for juvenile worms between 1994 and 1995 may reflect a number of factors. We (Thompson and Schaffner 2000) found that the Chesapeake Bay population of *C.* cf. *variopedatus* exhibited spatial variations in juvenile abundance, biomass, and growth over the 2-yr study period. Lower growth rates in 1995 compared with 1994 paralleled higher juvenile densities and lower food availability (as indexed by pigment concentrations), which suggests that juvenile growth rates were density-dependent. In 1995 juveniles also invested energy into reproduction, a phenomenon not seen in 1994. Thus, the slower growth of the 1995 juvenile cohort might also be related to worm spawning behavior, which may or may not be tied to food availability to the juveniles.

For *C.* cf. *variopedatus,* age was an important factor in growth and production, with the highest rates occurring in the late summer among new recruits and juveniles, whereas the overwintering adult population declined in size and density. The scenario of early summer recruitment followed by rapid growth and development to maturity during the late summer to fall may be common for many annual and longer-lived invertebrates in temperate estuaries (Seitz and Schaffner 1995). This strategy contrasts with the one exhibited by relatively short-lived (weeks to months) estuarine opportunists, which tend to settle, grow, and reproduce in spring through early summer. Most of the macrobenthic species that populate the mesohaline reaches of Chesapeake Bay exhibit the opportunistic life history strategy (Marsh and Tenore 1990), whereas faunal assemblages of the lower bay include
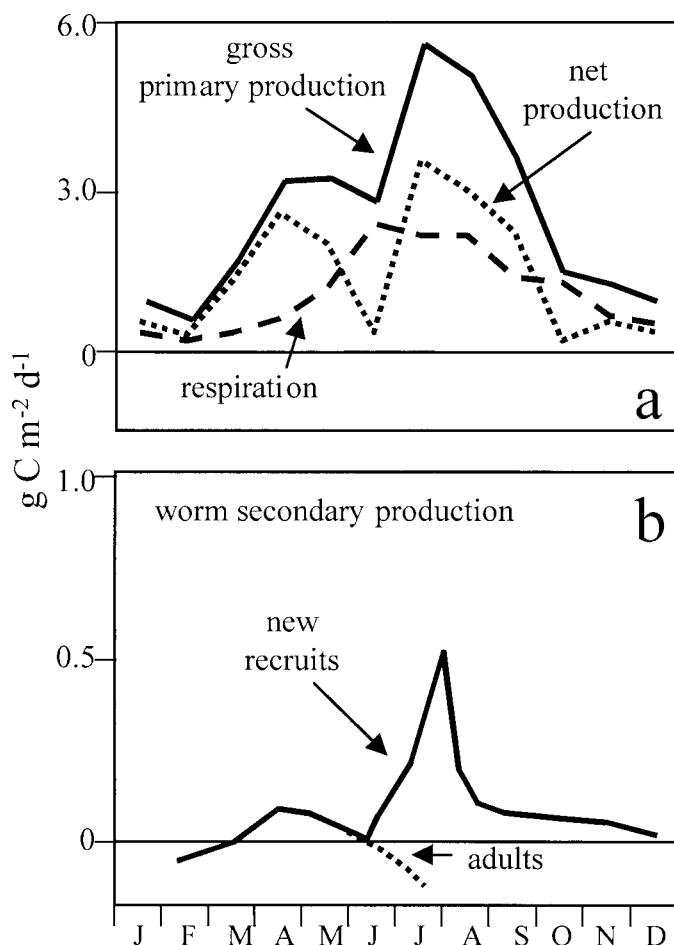
Fig. 4. (a) Trends in gross primary production, water column respiration, and net water column community production, adapted from Kemp et al. 1997 by use of a photosynthetic quotient (CO_2: O_2) of 1.2 and a respiratory quotient (CO_2:O_2) of 1. Net water column production was taken as the difference between gross primary production and water column respiration. (b) Trends in secondary production of *Chaetopterus* cf. *variopedatus,* with adults shown separately when two cohorts are present.

both opportunists and species that have longer life spans (Schaffner 1990, Schaffner et al. 2001). As a result, we expect macrofauna to differentially affect the cycling of organic matter and nutrients in these different regions of the estuary.

Worm secondary production closely mirrored the general pattern observed for gross primary production in the lower bay region (Fig. 4; Kemp et al. 1997). The overwintering population of *C.* cf. *variopedatus* began to grow, produce eggs and sperm, and exhibit positive production in early spring, concurrent with the spring bloom of phytoplankton. Also during this time, labile organic matter in surface sediments, as estimated from sediment pigments, reached a peak (Fig. 1). We found negative worm production during early summer, a time when planktonic respiration is at its maximum, whereas net plankton community production dips between two peaks. Worm recruitment and the subsequent period of rapid juvenile growth coincide with the annual peak in gross primary production and in net plankton community

production (Smith and Kemp 1995; Kemp et al. 1997). Interestingly, this is also the time period when small phytoplankton and microbes are thought to dominate production in the overlying water column (Marshall and Lacouture 1986). As discussed further below, availability of pelagic production to the benthos may be enhanced by physical mixing processes (Hood et al. 1999).

The average secondary production estimate of 12 g C m^{-2} yr^{-1} (ranging from 6.7 to 18.0, excluding tube production) for *C.* cf. *variopedatus* lies within the upper range of production values previously reported for estuarine and marine species by Robertson (1979) and Warwick (1980). It is particularly high when compared with infaunal deposit feeding polychaetes (conversion to g C m^{-2} yr^{-1} by use of the method of Waters 1977) such as *Nephtys incisa* (4.7 g C m^{-2} yr^{-1}; Warwick 1980) and *Loimia medusa* (1.7 g C m^{-2} yr^{-1}; Seitz and Schaffner 1985) but is comparable to values reported for infaunal suspension feeding bivalves, such as *Tagelus divisus* (10.5 g C m^{-2} yr^{-1}; Warwick 1980) and *Mercenaria mercenaria* (7 g C m^{-2} yr^{-1}; Warwick 1980).

Our secondary production estimates for *C.* cf. *variopedatus* are comparable to previous estimates obtained by Huggett (1987) for a nearby region of lower Chesapeake Bay. For a study based on quarterly sampling conducted over a 1-yr period, he reported annual secondary production estimates of 12–23 g AFDW m^{-2} yr^{-1} for *C.* cf. *variopedatus* at two regions located to the northwest of our study region, with P/B ratios of 2.7–3.1. Average densities at his sampling sites ranged from a high of 455 individuals m^{-2} in February 1984 to a low of 0 individuals m^{-2} during August and November of 1984, with average densities for his study of ~100 individuals m^{-2}. Huggett did not include fragile juveniles or tube production in his estimates. Thus, production of *C.* cf. *variopedatus* in the lower Chesapeake Bay may at times exceed our estimates.

Tube production by benthic organisms is common and may represent an important, but largely unquantified, 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 in central Long Island Sound. The tubes of *Chaetopterus variopedatus* consist of a secretion from the anterior region of the worm, the nature of which is poorly characterized, but may be mucoproteins, mucopolysaccharides, collagen, and other compounds (Barnes 1965; Brown and McGee-Russell 1971), with adhering sediments. In our study, tube production accounted for approximately half of the total production. Thus, tube production is clearly important for *C.* cf. *variopedatus,* and it should be considered in future estimates of secondary production by benthic organisms.

Production to biomass ratios can be thought of as the turnover rate (resulting from growth and mortality) of populations. Organism P/B ratios are sensitive to population age and size structure, predation regimes, environmental variables such as temperature, which can affect growth rates, and sampling technique, which may be size selective (Robertson 1979). As a generality, organisms with shorter life spans as well as younger age classes within a population have higher P/B ratios (Robertson 1979), which makes them

proportionately more important producers within a system. Given the interannual, demographic differences in the population of *C*. cf. *variopedatus* of the lower Bay, it was not surprising that the annual P/B ratio for 1995 was double that of 1994. Our calculated annual P/B ratios for this worm population were comparable to a variety of macrobenthos with lifespans >1 yr, including other large suspension feeders such as the oyster *Crassostrea virginica* (Dame 1976; Robertson 1979).

Translocation of pelagic production into benthic production via suspension feeding has been widely documented for a variety of ecosystems. Smith and Kemp (1995) suggested that the lower Chesapeake Bay is net autotrophic, with the possibility that a large portion of the phytoplankton biomass produced may be available for export or consumed by macrobenthic organisms. Our results clearly demonstrate that considerable primary production is being transferred to *C*. cf. *variopedatus* in lower Chesapeake Bay. Comparing our worm tissue production values of 6.6–18.0 g C m^{-2} yr^{-1} to water column production of 237 g C m^{-2} yr^{-1} (Smith and Kemp 1995; Kemp et al. 1997), and under the assumption of an ecological trophic transfer efficiency of 10%, we calculate that 25%–75% of net plankton community production is needed to support *C*. cf. *variopedatus* in our study region. If we assume an ecological efficiency of 20%, then the percentages range between 15% and 38%. If we incorporate our estimates of tube production, then between 35% and >100% of the net plankton community production is required to support this species. Similar relationships between benthic suspension feeder production and primary production have been found in northern European waters that are characterized by high primary productivity and efficient delivery of organic matter to the benthos due to physical mixing processes or shallow water depths (Heip et al. 1995; Josefson and Conley 1997). To support and constrain our estimate of 35%–100% of the net water column production supporting *C*. cf. *variopedatus,* we ideally need an estimate of the quantity of the water column production being consumed by other species. However, this information is currently lacking for lower Chesapeake Bay.

In a review of particle processes and dynamics in coastal ecosystems, Heip et al. (1995) suggest that local suspension feeder–mediated fluxes of organic matter to the benthos often exceed regional water column production. They postulate that this is possible because most populations of suspension feeders are patchily distributed in both space and time. On a systemwide basis, suspension feeder production is limited by water column productivity (Heip et al. 1995; Herman et al. 1999). It is interesting to note that, although *C*. cf. *variopedatus* is widely distributed in the lower Chesapeake Bay, our previous experience in the bay led us to select a study region in which we expected that populations densities *C*. cf. *variopedatus* would remain high and relatively stable. Subsequent research indicates that patches of high particle concentrations, which may provide relatively stable, high food concentrations, exist within Chesapeake Bay, and that one such patch, the result of a residual circulation eddy, is located in the vicinity of our study site (Hood et al. 1999). The eddy has associated upwelling and downwelling zones, strongly influences plankton distributions, and may induce enhanced phytoplankton growth. Such a system might also enhance retention of worm larvae. Lateral transport and focusing of organic matter to depositional areas within a system may also enhance the growth and production of benthic suspension feeders (Loo and Rosenberg 1996; Schaffner et al. 2001). Because of the dynamic physical nature of the bay system, lateral or vertical physical transport of material from shoals or the upper water column may play a role in sustaining the high secondary productivity observed for the *C*. cf. *variopedatus* population of lower Chesapeake Bay.

Chaetopterus cf. *variopedatus* plays a significant role in organic matter transformation, storage, and cycling processes in lower Chesapeake Bay, which has important implications for food web dynamics and nutrient cycling. We suggest that, like the better-studied bivalves, *C*. cf. *variopedatus* can be thought of as a keystone species (sensu Dame 1996) and should be included in future studies or models of the estuary. Previous workers have suggested that bivalves, particularly those that live multiple years and maintain high standing stocks, serve to enhance ecosystem stability (Dame 1996). In contrast, the Chesapeake Bay population of *C*. cf. *variopedatus* exhibits significant interannual variations in density, biomass, and secondary production; thus, we predict that its effects on ecosystem stability will be more variable.

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