Limnol. Oceanogr., 50(2), 2005, 566–577

Secondary production of a dominant oligochaete (*Monopylephorus rubroniveus*) in the tidal creeks of South Carolina and its relation to ecosystem characteristics

David J. Gillett[1]
Grice Marine Biological Laboratory, 205 Fort Johnson Road, Charleston, South Carolina 29412

A. Frederick Holland
Hollings Marine Laboratory, 219 Fort Johnson Road, Charleston, South Carolina 29412; and
South Carolina Department of Natural Resources Marine Resources Research Institute, 217 Fort Johnson Road, Charleston, South Carolina 29412

Denise M. Sanger
South Carolina Department of Natural Resources Marine Resources Research Institute, 217 Fort Johnson Road, Charleston, South Carolina 29412

Abstract

Measurements of the annual production of the oligochaete *Monopylephorus rubroniveus*, microphytobenthos, pore-water ammonia, sediment composition, and water quality were made from January through December 2001 in the upper and lower reaches of two tidal creeks in southeastern South Carolina. Secondary production of *M. rubroniveus* was greater in the shallow upper reaches of tidal creeks (1.0–10.5 g ash-free dry weight [AFDW] m^{-2} yr^{-1}) than in the lower reaches (0.05–0.2 g AFDW m^{-2} yr^{-1}), as were benthic chlorophyll *a* levels and pore-water ammonia concentration. Production of *M. rubroniveus* was greater in both reaches of Okatee Creek (0.1–10.5 g AFDW m^{-2} yr^{-1}) than in Malind Creek (0.05–2.0 g AFDW m^{-2} yr^{-1}). The only significant difference in environmental characteristics between the two creeks was a greater incidence of hypoxia (dissolved oxygen $<$ 28% air saturation) in Malind Creek than in Okatee Creek, 5% of all records observed versus 0.3%, respectively. The rates of production estimated for *M. rubroniveus* in these creeks were relatively high compared with similar macrobenthos in other environments. Furthermore, the pattern of production within and between creeks provides a basic understanding of energy and material flows out of these important ecosystems and the processes that influence them.

Secondary production is an integrative ecological measure that provides information about organismal responses to environmental conditions over a defined time period. Production integrates the results of growth, reproduction, mortality, immigration, and emigration processes (Crisp 1984). Most benthic assessments do not measure secondary production because of the time, effort, and expense involved with estimating production for many species at multiple sampling locations. As a result, these studies offer only a snapshot of benthic community condition and provide little insight into the role of benthic organisms in ecosystem processes (Diaz and Schaffner 1990; Tumbiolo and Downing 1994). When studies of secondary production have been conducted, investigators have traditionally either (1) directly measured the production of the community or a few specific taxa (e.g., Hynes and Coleman 1968; Thompson and Schaffner 2001), which provides relatively precise estimates of production for a large investment of time and labor or (2) empirically calculated benthic production using biomass data, typically from one sampling event, with P : B ratios or novel mathematical equations that incorporate taxon-specific growth rates, and/or environmental parameters (e.g., Banse and Mosher 1980; Wilber and Clarke 1998), which provides a much simpler, though less precise approach.

Salt marshes and tidal creeks are a prominent, highly productive feature of temperate coastal zones around the world (Mitsch and Gosselink 2000), and numerous researchers have established the value of tidal creeks as nursery grounds for economically, ecologically, and recreationally important finfish and crustaceans (e.g., Wenner and Beatty 1993; Kneib 1997; Miller et al. 2003). The dominant macrobenthic organisms that support those nekton in Southeastern tidal creeks are polychaetes and oligochaetes (West 1985; Lerberg et al. 2000; Gillett 2003). The numerically dominant macro-

[1] Present address: Virginia Institute of Marine Science, P.O. Box 1346, Gloucester Point, Virginia 23062 (gillett@vims.edu).

Acknowledgments

We thank past and present members of the South Carolina Department of Natural Resources Marine Resources Research Institute's Tidal Creek Project who helped in collecting and processing samples used in this study, especially Chris Gawle and Mandy Ferguson. This research was part of David Gillett's Master's thesis at the University of Charleston, Charleston, South Carolina, and we thank all of the people at the Grice Marine Biological Laboratory who played a part in earning that degree. We also thank Loren Coen, Craig Plant, Linda Schaffner, and two anonymous reviewers for helpful comments on earlier versions of this manuscript. This article was funded as a result of work sponsored by the National Oceanic and Atmospheric Administration Center for Sponsored Coastal Ocean Research/Coastal Ocean Program, through the South Carolina Sea Grant Consortium. This publication does not constitute an endorsement of any commercial product or intend to be an opinion beyond scientific or other results obtained by NOAA. This is publication 265 of the Grice Marine Biological Laboratory.

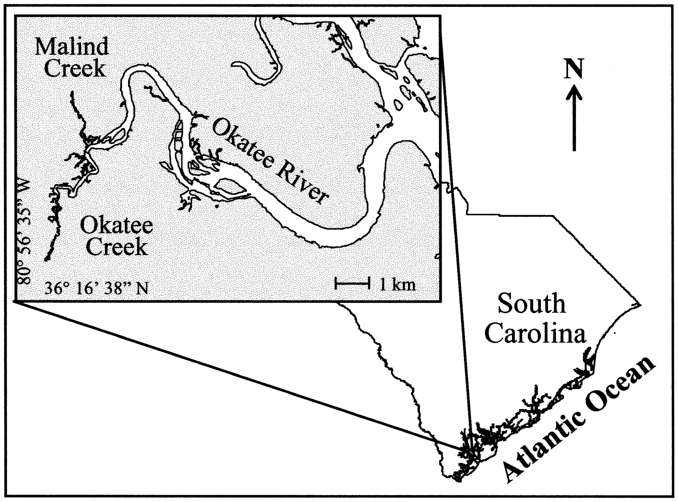

Fig. 1. A map of southeastern South Carolina showing the location of Okatee Creek and Malind Creek near Bluffton, South Carolina.

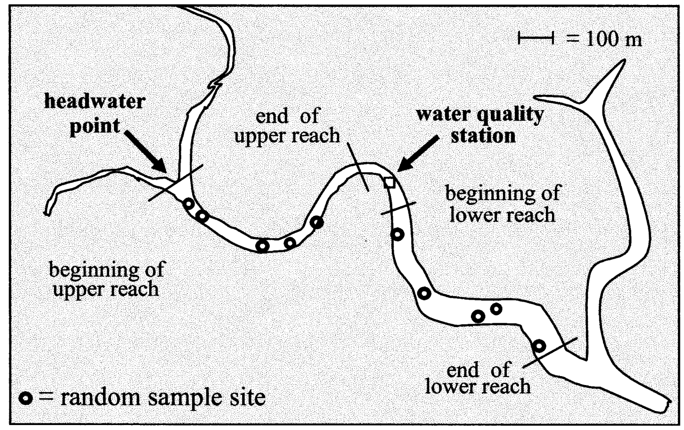

Fig. 2. A schematic showing the sample design within a creek. The creek is divided into two 750-m reaches, with a water-quality station located between the two reaches. Five intertidal sampling stations were selected monthly in each reach at a random distance from the beginning of the reach and on a random side of the creek.

benthic organism found in shallow South Carolina tidal creeks is the oligochaete *Monopylephorus rubroniveus* Levinsen 1884 (Tubificidae), accounting for between 10% and 90% of the total benthic macrofaunal abundance in headwater tidal creeks (Lerberg et al. 2000). Oligochaetes, such as *M. rubroniveus,* are more nutritious (5.5 kcal g^{-1} dry weight) than most other macrobenthic infauna typically found in tidal creeks (Cummins and Wuycheck 1971) and are important consumers of benthic primary and bacterial production (Giere and Pfannkuche 1982). In New England salt marshes, Sardá et al. (1996) found that between 18% and 50% of the total benthic production in tidal creeks was attributable to oligochaetes, even though their standing stock biomass was an order of magnitude less than the other macrobenthos. Sardá et al. (1996) attributed the greater production of oligochaetes to their greater abundance and turnover compared with the other macrobenthos.

Many studies have been conducted characterizing the macrobenthic community of tidal creeks and how they are important to the marsh/creek ecosystem (e.g., Lerberg et al. 2000; Posey et al. 2002; Holland et al. 2004). However, little work has been done to estimate the role of macrobenthos in the energy and material flows of tidal creeks. Given their dominance in the benthic community of tidal creeks, the authors chose to begin production studies with *M. rubroniveus.* The goals of this research were to obtain estimates of the secondary production of the numerically dominant macrobenthic organism, *M. rubroniveus,* for two creeks in South Carolina, using a direct estimation approach and to identify environmental factors that influenced production.

Materials and methods

Study area and sampling—Okatee Creek and Malind Creek are located in the Okatee River Basin near Bluffton, South Carolina (Fig. 1). These two creeks were selected as our study sites to correspond to the South Carolina Sea Grant's Land Use-Coastal Ecosystems Study. The watershed of Malind Creek (1,030 ha) was relatively undeveloped and predominantly forested (83% of land cover), with 5.6% impervious cover. The Okatee Creek watershed (2,576 ha) was recently developed for suburban use (27% of land cover) and had 8.0% impervious cover (Gillett 2003). Each creek was stratified into two 750-m reaches (Fig. 2) and sampled monthly from January 2001 through January 2002. For most of 2001, the southern portion of South Carolina experienced mild drought conditions, with moderately reduced precipitation and lower mean temperatures compared with 30-yr mean values (Southeast Regional Climate Center 2004). Approximately every 4 weeks, five sampling sites were randomly selected within each reach of the two creeks to evaluate the secondary production of *M. rubroniveus,* microphytobenthic standing stock, pore-water ammonia concentration, sediment composition, and sediment total organic carbon (TOC). Sample sites were located intertidally, approximately 1.5 m below mean high tide on a randomly selected side of the creek in order to minimize depth/duration of submersion bias within and among reaches.

Benthic chlorophyll *a* (Chl *a*) samples were taken to a depth of 1 cm with a 38.5-mm^2 plastic core and placed on ice. Within 6 h, the cores were placed in 10 ml of 100% acetone in the dark, at 4°C for 24 h, and agitated every 8 h. Samples were brought to room temperature, centrifuged for 2 min at 3,000 rpm, and the Chl *a* in the supernatant was measured with an ultraviolet-Vis spectrophotometer (Method 3.1 in Strickland and Parsons 1972).

Samples of surface sediment (upper 2–3 cm) were collected at each site and analyzed to determine percentage water, percentage silts and clays (<63 μm), and percentage sand (≥ 63 μm) using a modification of the pipette method (Plumb 1981). Instead of measuring silts and clays as separate values, they were measured as a combined silt/clay fraction (Lerberg et al. 2000). TOC content was measured for each sample by combustion of acidified and dried sediments in a CHN-S analyzer.

Two 11.9-cm^2 cores of sediment were collected from each site to a depth of 3 cm to determine pore-water ammonia levels. Samples were kept on ice and processed within 6 h of collection. Each sample was homogenized and centrifuged at 4,700 rpm. Ammonia concentrations were measured in the supernatant using the salicylate-cyanurate colorimetric method (Hach Company 1994).

Oligochaetes were collected to a depth of 16 cm with a 45.6-cm^2 core. Each sample was sieved through a 500-μm sieve and preserved in 10% seawater-buffered formalin containing rose bengal. All organisms were separated from the detrital matter under magnification ($\times$3) and the oligochaetes were counted and identified to the lowest possible taxonomic level. One of every 10 samples was randomly selected and reinspected by a South Carolina Department of Natural Resources benthic taxonomist. If greater than 10% of a taxon in a sample was either miscounted or misidentified, all 10 samples were reidentified and enumerated again for the disputed taxa.

Water quality was measured every 30 min at a site between the upper and lower reaches of Malind and Okatee creeks from January 2001 to January 2002 (Fig. 2). Measurements were made 10 cm above the bottom of the creek channel. Monitoring units were calibrated before deployment and measured temperature, salinity, pH, dissolved oxygen (mg L^{-1} and percentage air saturation), and depth. Postdeployment quality-assurance criteria used to assess the reliability of the water-quality data were dissolved oxygen within $\pm$10% of air saturation, pH within $\pm$0.2% of 7.0 and 10.0 standards, and salinity within $\pm$0.5 of a 19.6 KCl standard. Units were deployed for approximately 1 week during warm periods and approximately 2 weeks during cool periods. Water-quality measurements from a midway point in the creeks has been shown to be representative of the water quality at many points along the length of the creek due to the relatively small water volume and ebb- and flood-tide flushing patterns (Holland unpubl.)

Biomass estimation—One hundred and six cultured *M. rubroniveus* were preserved in 10% seawater-buffered formalin and stored in 70% isopropyl alcohol. Total length; length to the 9th, 10th, and 11th segments; and width of the 9th, 10th, and 11th segments were measured from digital images using a dissecting microscope and Opitmas imaging software. The reproductive organs of *M. rubroniveus* are located in segments 10 and 11, and along with segment 9, are frequently the widest segments of the oligochaete (Baker and Brinkhurst 1981, pers. comm.). Variation in the length and width of segments 9–11 should account for differences in biomass between reproductive and immature specimens that would not be addressed by length measurements alone. Additionally, undamaged specimens were rarely collected from the field and it was useful to have an estimation process that would work with incomplete specimens.

After the length and width measurements were taken, the worms were patted dry and weighed (preserved WW). Specimens were then dried at 60°C for 24 h, stored in a desiccator, and weighed (dry weight). Because of their small size (<0.1 mg dry weight per individual), worms were pooled into groups of 2–12 worms and combusted at 450°C for 4 h to estimate ash-free dry weight (AFDW). Weights were determined with a Cahn C-33 microbalance ($\pm 1 \times 10^{-2}$ mg). Stepwise linear regression (SAS for Windows® v 8.1) was used to identify the morphometric measurement(s) that provided the best estimate of preserved wet weight (WW) and dry weight (DW; Freund and Littell 1991). In separate calculations, the relationships between WW, DW, and AFDW were evaluated using a simple linear regression (Littell et al. 1991).

Calculation of production—Production estimates were made using a biomass frequency method for continually recruiting benthic organisms that makes the following assumptions: (1) only one taxon is evaluated; (2) regardless of the timing of recruitment, all individuals of similar size grow at approximately the same rate; (3) all individuals have the potential to grow to the maximum size observed; (4) the rate of mortality is the same for all individuals; and (5) sampling frequency is shorter than one generation time. The greater the departure from these assumptions, the greater the uncertainty introduced into the estimates. At high levels of uncertainty, the ability to distinguish fine-scale production differences in space and time will be reduced (Morin et al. 1987).

The detailed calculation of production is as follows. The organisms were collected from the time periods of interest (at least two sampling events) and sorted into predetermined biomass classes. The difference in mean biomass between two successive size classes was multiplied by the abundance of the smaller size class of the two. This calculation was repeated for all size classes and the products were summed. To this sum, the product of the mean biomass of the last size class and the abundance of the last size class were added. This process can be expressed as in Eq. 1:

$$P = \left[\sum_{x=1}^{i} (\bar{B}_{x+1} - \bar{B}_x)(A_x) + (\bar{B}_{x+2} - \bar{B}_{x+1})(A_{x+1}) + \cdots + (\bar{B}_{x_i} - \bar{B}_{x_i-1})(A_{x_i-1})\right] + (\bar{B}_{x_i})(A_{x_i}) \qquad (1)$$

where P is production in units of biomass area^{-1} time^{-1}, B is mean biomass of size class x, A is abundance of worms in size class x, and i is the number of size classes.

Field-collected *M. rubroniveus* from January through December 2001 were sorted into groups by creek and reach (i.e., Malind upper, Malind lower, Okatee upper, and Okatee lower) for each month. Digital images were taken of up to 100 randomly selected worms that were intact to at least segment 10 from each group and the biomass was estimated using the defined allometric relationships. The biomass data for each creek and reach were then classified into 10 biomass classes. The abundance of each creek–reach group was adjusted to account for the total number of *M. rubroniveus* collected in relation to the number that were measured. This adjusted value was then multiplied by an area constant to estimate the total number per square meter. The abundance and biomass values were used to estimate secondary production from January to December 2001 with Eq. 1.

Statistical analyses—A three-way analysis of variance (ANOVA) was used to evaluate differences among season, creek, and reach using SAS for Windows® v.8.1 (Littell et

Table 1. Summary of the three-way ANOVAs of the benthic environmental characteristics and *M. rubroniveus* abundance and biomass, with the parameter evaluated, the number of samples, the model r^2, and probability of significance, the F-statistic, and degrees of freedom (model, error), the probability of significance of each treatment variable, significant interaction terms, and least square means contrasts. The least square means variables are in order from largest to smallest and an underline implies the treatments were not significantly different at $\alpha = 0.05$. S, season; C, creek; R, reach; Sp, spring; Su, summer; Au, autumn; Wi, winter; Up, upper; Low, lower; ML, Malind Creek; OC, Okatee Creek.

Parameter	n	r^2/p	F/df	Season	Creek	Reach	Interactions	Season effect	Creek effect	Reach effect
Benthic Chl *a* (mg m^{-2})	258	0.449 <0.0001	13.19 15, 242	<0.0001	0.0950	0.0022	S×C R×C R×C×S	Wi Sp Au Su	ML OC	Up low
Percent silts and clays	259	0.049 0.0229	2.66 5, 253	0.7514	0.0805	0.0029		Su Au Wi Sp	OC ML	Low up
Percent total organic carbon	255	0.008 0.8457	0.40 5, 249	0.5811	0.8412	0.8869		Su Wi Au Sp	ML OC	Low up
Log$_{10}$ porewater ammonia (mg L^{-1})	258	0.618 <0.0001	32.85 12, 245	<0.0001	0.0826	<0.0001	S×C R×S R×C	Su Au Sp Wi	OC ML	Up low
Log$_{10}$ *M. rubroniveus* (No. m^{-2})	260	0.416 <0.0001	36.19 5, 254	0.0053	<0.0001	<0.0001		Wi Au Su Sp	OC ML	Up Low
Individual *M. rubroniveus* biomass (AFDW)	2,199	0.269 <0.0001	73.31 11, 2187	<0.0001	<0.0001	<0.0001	S×C R×S	Wi Au Sp Su	OC ML	Up low

al. 1991). Parameters evaluated included benthic Chl *a,* pore-water ammonia concentration, sediment composition (as percentage silts and clays), percentage total organic carbon in sediments, *M. rubroniveus* abundance, and mean *M. rubroniveus* biomass per individual. In addition, a two-way ANOVA with creek and season as treatments was performed on the occurrence of low dissolved oxygen levels (percentage of time below 28% air saturation) and low salinity (percentage of time below 5). Seasons were defined as spring, 21 March–20 June; summer, 21 June–20 September; autumn, 21 September–20 December; and winter, 21 December–20 March.

Data were transformed as noted to obtain normality and homogeneity of the variance of model residuals. The residuals of the biomass ANOVA could not be corrected for deviation from normality and skewed variance despite using a variety of different transformations (log 10, square root, etc.). Therefore, the three-way ANOVA was performed on nontransformed data as ANOVA is robust for departures from normality (Zar 1998), all treatments were highly significant ($p < 0.0001$), and the authors desired to maintain a three-way comparison. All significant ($\alpha = 0.05$) treatments and interaction terms were evaluated using a contrast of least square means. Least square means were considered significantly different at $\alpha = 0.05$.

Correlation analysis (using Pearson's coefficients) was used to evaluate associations between *M. rubroniveus* abundance and the environmental parameters (i.e., Chl *a,* pore-water ammonia, and percentage silts and clays) measured at each site. The goal of these analyses was to determine if the abundance of *M. rubroniveus,* as a surrogate for production, was associated with environmental conditions. Similar analyses could not be accomplished using production estimates because they were calculated at the scale of a reach.

Results

Environmental characteristics—No significant differences in the Chl *a* concentration, percentage TOC in sediments, percentage silts and clays, and pore-water ammonia concentration were found between Okatee and Malind creeks (Table 1). Benthic Chl *a* concentrations were higher ($p < 0.0001$) in the winter than in the spring and autumn. The autumn and summer benthic Chl *a* concentrations were not significantly different from each other (Fig. 3A). The upper reaches of both creeks had significantly higher Chl *a* concentrations than the lower reaches ($p < 0.0001$). The reach–creek interaction term was significant ($p = 0.0028$). Chl *a* concentrations in the upper reach of Malind Creek were similar to the upper reach of Okatee Creek and lower reach of Malind Creek, all of which were higher than the benthic Chl *a* in the lower reach of Okatee Creek.

There were no significant differences in percentage TOC between creek, reach, or season (Fig. 3B). There was, however, a significant difference in percentage silts and clays between reaches ($p = 0.0029$). Sediments from the lower reaches of both creeks contained more silts and clays than those from the upper reaches (Fig. 3C). There were no differences in sediment composition between creeks or among seasons. Pore-water ammonia concentrations were significantly higher ($p < 0.0001$) in the summer than in the autumn and the spring (Fig. 3D). The lowest pore-water ammonia concentrations occurred in the winter. The upper reaches of both creeks had significantly higher ($p < 0.0001$) pore-water ammonia concentrations than the lower reaches. The creek–reach interaction term was significant for pore-water ammonia concentration ($p = 0.0011$). This occurred because the upper reaches of Okatee and Malind creeks had similar ammonia concentrations, but the lower reach of Okatee Creek had higher levels than those of Malind Creek.

Salinity, dissolved oxygen, pH, and temperature records were very dynamic (Fig. 4). In Malind Creek, ranges were 0–38 for salinity, 0–192% saturation for DO, 4.6–8.6 for pH, and 0–35°C for water temperature. The ranges in Okatee Creek were 0–38 for salinity, 0–173% saturation for DO, 5.6–8.6 for pH, and −3–35°C for water temperature. A two-

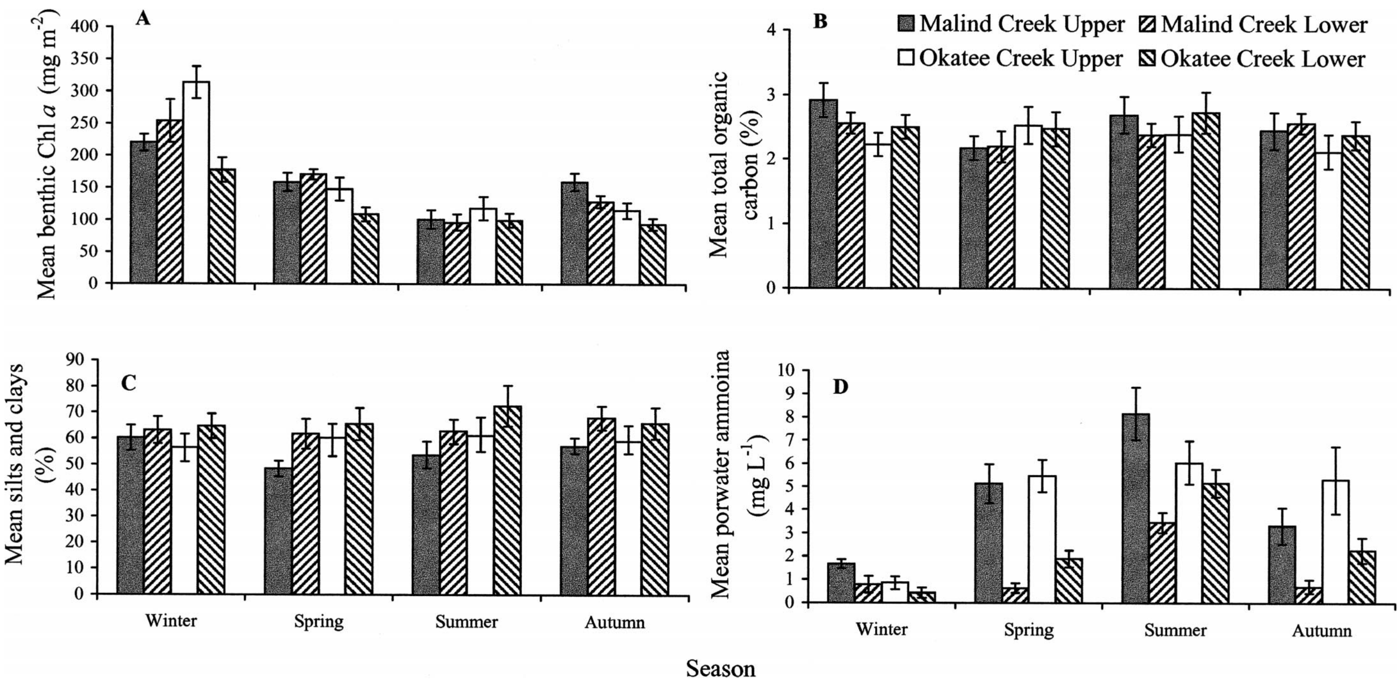

Fig. 3. Mean seasonal sediment characteristics measured from January to December 2001. (A) benthic Chl *a,* (B) percentage total organic carbon, (C) percentage silts and clays, and (D) pore-water ammonia concentration. The error bars represent ±1 SE.

way ANOVA showed that Malind Creek experienced hypoxic conditions (<28% saturation) more often than Okatee Creek ($p < 0.0089$). Five percent of the dissolved oxygen records from 1 January 2001 to 31 January 2002 in Malind Creek were below 28% air saturation. Hypoxic conditions occurred only 0.3% of the time in Okatee Creek. There was no difference ($p = 0.238$) in the amount of time low salinity occurred in Okatee Creek (30% of the year) and Malind Creek (21% of the year) (Table 2).

Production estimates—Monopylephorus rubroniveus accounted for 74% of the oligochaete abundance in Malind and Okatee creeks. The highest abundance occurred in the upper reach of Okatee Creek in February (47,633 individuals m^{-2}) and the lowest occurred in the lower reach of Malind Creek in May, when no specimens were collected (Fig. 5A,B). *Monopylephorus rubroniveus* collected from Okatee Creek had more biomass than those collected from Malind Creek ($p < 0.0001$). The mean biomass per worm and abundance of *M. rubroniveus* were greatest in winter, followed by autumn, spring, and summer ($p < 0.0001$), indicating that substantial recruitment and population growth occurred during the winter months (Table 1). Worms collected from the upper reaches of both creeks were larger than those collected from the lower reaches ($p < 0.0001$). However, the season with creek and season with reach interactions of the three-way ANOVA for biomass were both significant (Table 1). The biomass of an individual worm was greater in Okatee Creek during the winter and spring but was similar in both creeks during the summer and autumn. Furthermore, there was no difference in biomass between the upper and lower reaches of the creeks during the summer, whereas during the remainder of the year, biomass of worms from the upper reaches was higher (Fig. 6). Abundance of *M. rubroniveus* in Malind and Okatee creeks was positively correlated with Chl *a* concentration ($p < 0.0001$), though the correlation was not very strong ($r = 0.297$). There was no correlation between abundance of *M. rubroniveus* and pore-water ammonia concentrations ($r = -0.001$, $p = 0.985$) or percentage silts and clays in the sediment ($r = -0.03$, $p = 0.607$).

Equation 2 describes the relationship between preserved mg WW of *M. rubroniveus* and mg (DW). Equation 3 describes the relationship between mg AFDW and mg DW.

$$\mathrm{WW} = (\mathrm{DW} \times 4.1592) - 0.0153 \quad (n = 105;\ r^2 = 0.86;\ p < 0.0001) \tag{2}$$

$$\mathrm{AFDW} = (\mathrm{DW} \times 0.9776) - 0.0052 \quad (n = 27;\ r^2 = 0.99;\ p < 0.0001) \tag{3}$$

Based on stepwise linear regression of morphometric measurements and biomass, ln length to the 10th segment and ln width of the 10th segment had the smallest error mean square (Mallow's C(P)) and, therefore, were the best predictors of ln DW. To determine if the growth rate and size of the cultured *M. rubroniveus* were different from field-collected worms, the regression created from cultured worms was compared with a similar regression developed from 100 randomly selected field-collected worms. The slopes of the lines for the two data sets were different ($F_{3,177} = 3.88$; $p < 0.025$). Size-frequency histograms (Fig. 7A,B) indicated that the cultured worms contained a higher proportion of small worms than the field-collected specimens. In order to incorporate the complete size range of *M. rubroniveus* widths and lengths into the production calculations, the culture and

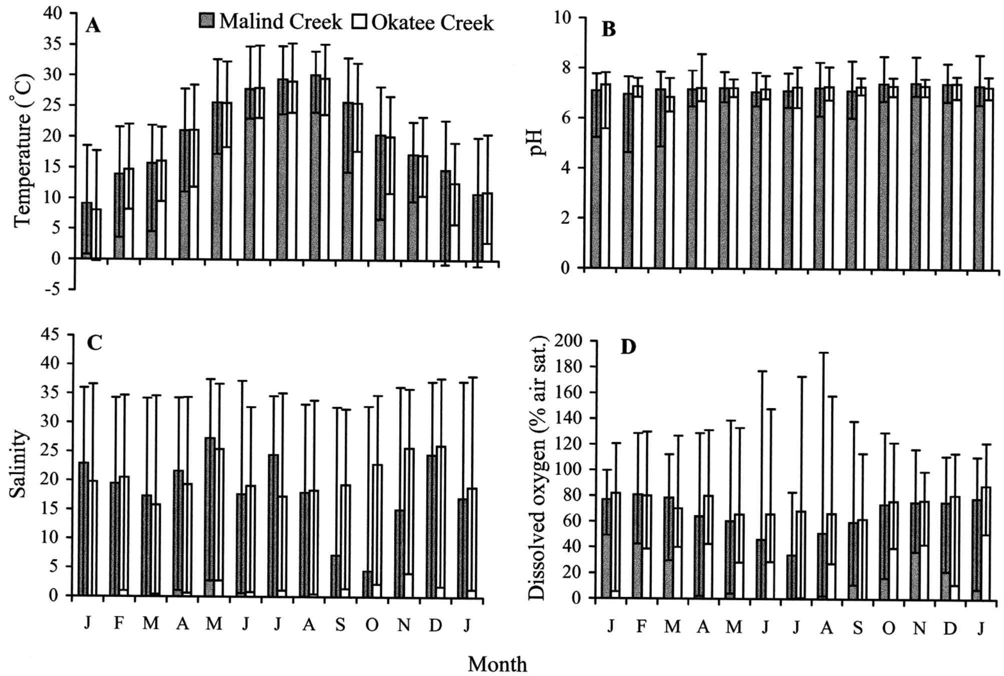

Fig. 4. Mean monthly water quality characteristics measured from January 2001 to January 2002 with the bars representing maximum and minimum values of each month. (A) temperature, (B) pH, (C) salinity, and (D) dissolved oxygen.

field-collected data were pooled and used to define a final biomass regression (Eq. 4).

$$\ln \mathrm{DW} = (\ln W_{10} \times 1.62303) + (\ln L_{10} \times 1.06101) - 1.90887 \qquad (n = 182;\ r^2 = 0.66;\ p < 0.0001) \tag{4}$$

where W_{10} = width at the 10th segment and L_{10} = length to the 10th segment.

Figure 8A depicts a cumulative size-frequency histogram of *M. rubroniveus* collected January–December 2001 in the upper reach of Okatee Creek. In cumulative frequency distributions representing multiple cohorts and age classes, the frequency of smaller (younger) specimens would be expected to exceed the frequency of larger (older) organisms. Underrepresentation of smaller size/age classes, such as depicted in Fig. 8A and in the histograms of the other reaches, generally occurs because the smaller organisms were undersampled.

Two corrections were made to the size-frequency data to address the apparent sampling bias that resulted in underrepresentation of the smallest size classes. In the first correction, the number of *M. rubroniveus* from the undersampled size classes was set equal to the number of worms found in the smallest size class the authors believed to be accurately sampled (Fig. 8B). This approach included only the minimum number of smaller worms in the estimations and probably still underestimated the actual abundance of worms in the creeks. For the second correction, a curve that best described the changes in abundance across the accurately sampled size classes was defined and used to extrapolate the abundance of the underrepresented size classes (Fig. 8C,D).

Abundance data from similar benthic samples processed with a nested series of sieves (500, 250, and 180 μm) indicated that using only a 500-μm sieve likely underrepresented the abundance of *M. rubroniveus,* missing between 24% and 78% of the individuals present in a sample (Gillett

Table 2. Summary of the two-way ANOVAs of low salinity and low dissolved oxygen, with the parameter evaluated, the number of samples, the model r^2, probability of significance, the F-statistic, and degrees of freedom (model, error), the probability of significance of each treatment variable, significant interaction terms, and least square means contrasts. The least square means variables are in order from largest to smallest and an underline implies the treatments were not significantly different at $\alpha = 0.05$. S, season; C, creek; R, reach; Sp, spring; Su, summer; Au, autumn; Wi, winter; ML, Malind Creek; OC, Okatee Creek.

Parameter	n	r^2/p	F/df	Season	Creek	Interactions	Season effect	Creek effect
Percent of time salinity below 5	24	0.120 0.6324	0.65 4, 19	0.7133	0.2816		Wi Su Sp Au	ML OC
Percent of time below 28% air saturation	24	0.650 0.0078	4.25 7, 16	0.0385	0.0089	S×C	Su Sp Au Wi	ML OC

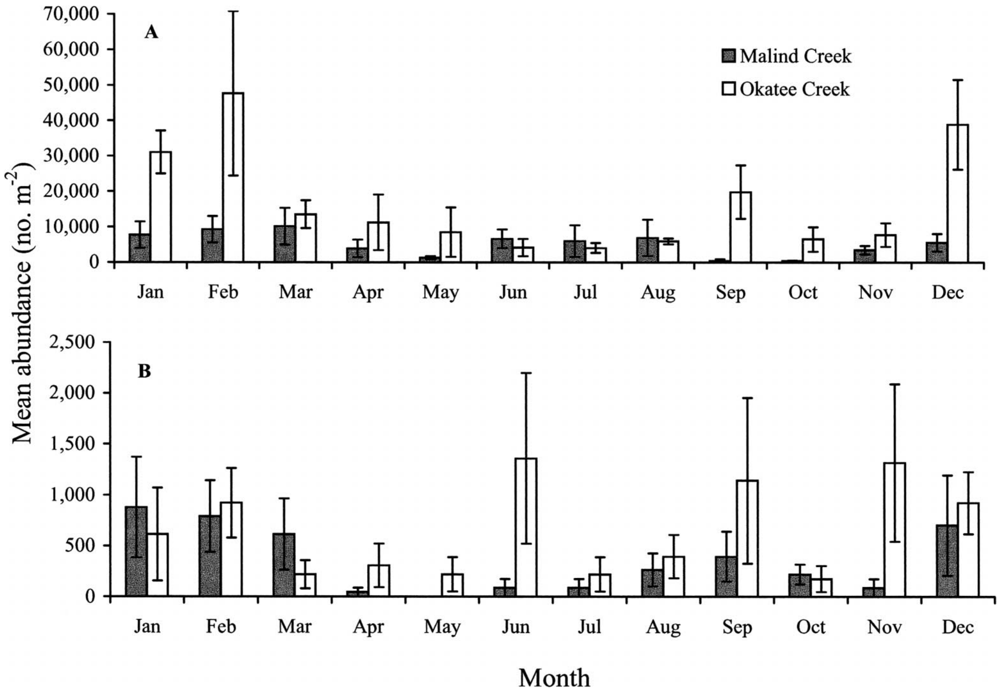

Fig. 5. Mean abundance of *M. rubroniveus* collected from (A) the upper reaches and (B) lower reaches of Malind and Okatee creeks from January through December 2001. The error bars represent ±1 SE.

2003). The authors feel that these data indicate that the second correction method was closer to matching the natural pattern. However, both adjustments were used to estimate secondary production and provide a range of production estimates that likely bracketed the true value (Table 3).

Production was also calculated with the second abundance correction data and the Hynes method in order to compare our method to a similar commonly used and accepted method (Menzie 1980). The Hynes method production estimates were similar to the data in Table 3: 10.01 g AFDW m^{-2} yr^{-1}

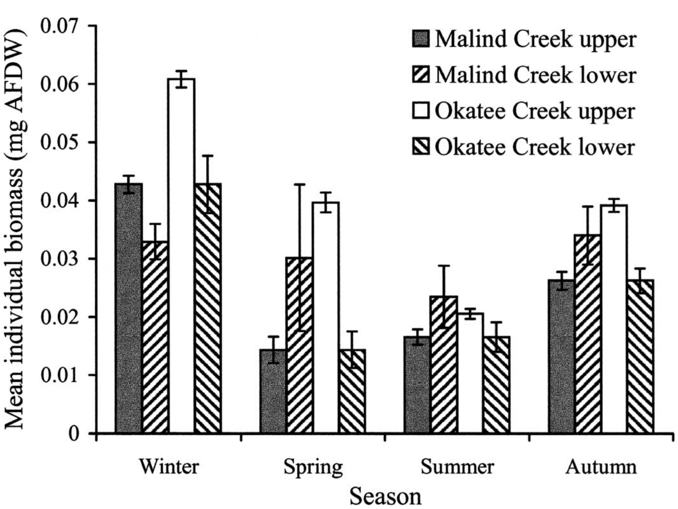

Fig. 6. Mean biomass of individual *M. rubroniveus* in mg AFDW from winter, spring, summer, and autumn. The error bars represent ±1 SE.

and 0.13 g AFDW m^{-2} yr^{-1} in the upper and lower reaches of Okatee Creek, respectively; and 2.01 g AFDW m^{-2} yr^{-1} and 0.10 g AFDW m^{-2} yr^{-1} in the upper and lower reaches of Malind Creek, respectively.

Production to biomass ratios (P : B or turnover ratios) were calculated using the production estimates and the mean monthly biomass (the sum of 12 months of biomass data, divided by 12), the maximum monthly biomass (the month with the highest biomass in the year), the January biomass, and the June biomass (typical sampling periods for benthic programs); $P:B_{mean}$, $P:B_{max}$, $P:B_{Jan}$, and $P:B_{Jun}$, respectively (Table 3). The upper reaches of Okatee Creek had the highest and lowest $P:B_{mean}$ ratios (3.8–10.9), depending on the calculation method that was used. P : B ratios calculated using the maximum monthly biomass are the least likely to overestimate the actual turnover rate (Banse and Mosher 1980) and were similar for all creeks and reaches. $P:B_{Jan}$ ratios were similar to, but slightly lower than, the $P:B_{mean}$ values. The $P:B_{Jun}$ values were high and likely overestimated the turnover rate because of the extremely low standing stock values (both biomass and abundance) found in the summer.

Discussion

*Why measure production?*The study of macrobenthic communities has progressed over the last half century from an initial focus on defining the species that were present in different habitats, characterizing their feeding and reproductive behavior, and estimating their growth rates to an evaluation of the role of macrobenthic populations and communities in ecosystem processes (e.g., Sanders 1958;

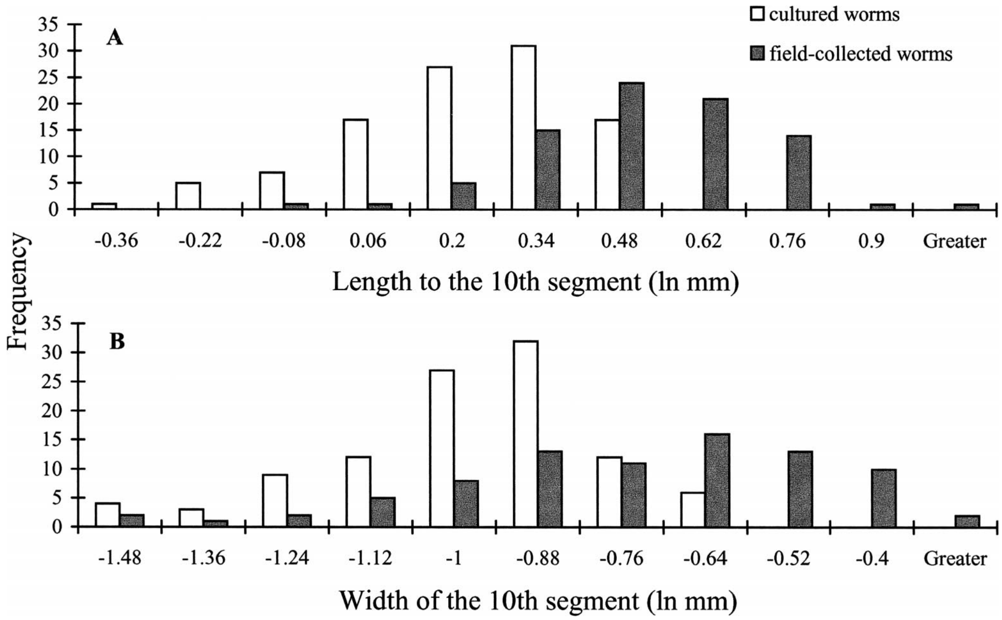

Fig. 7. A comparison of (A) length to the 10th segment and (B) width of the 10th segment of cultured and field-collected *M. rubroniveus.*

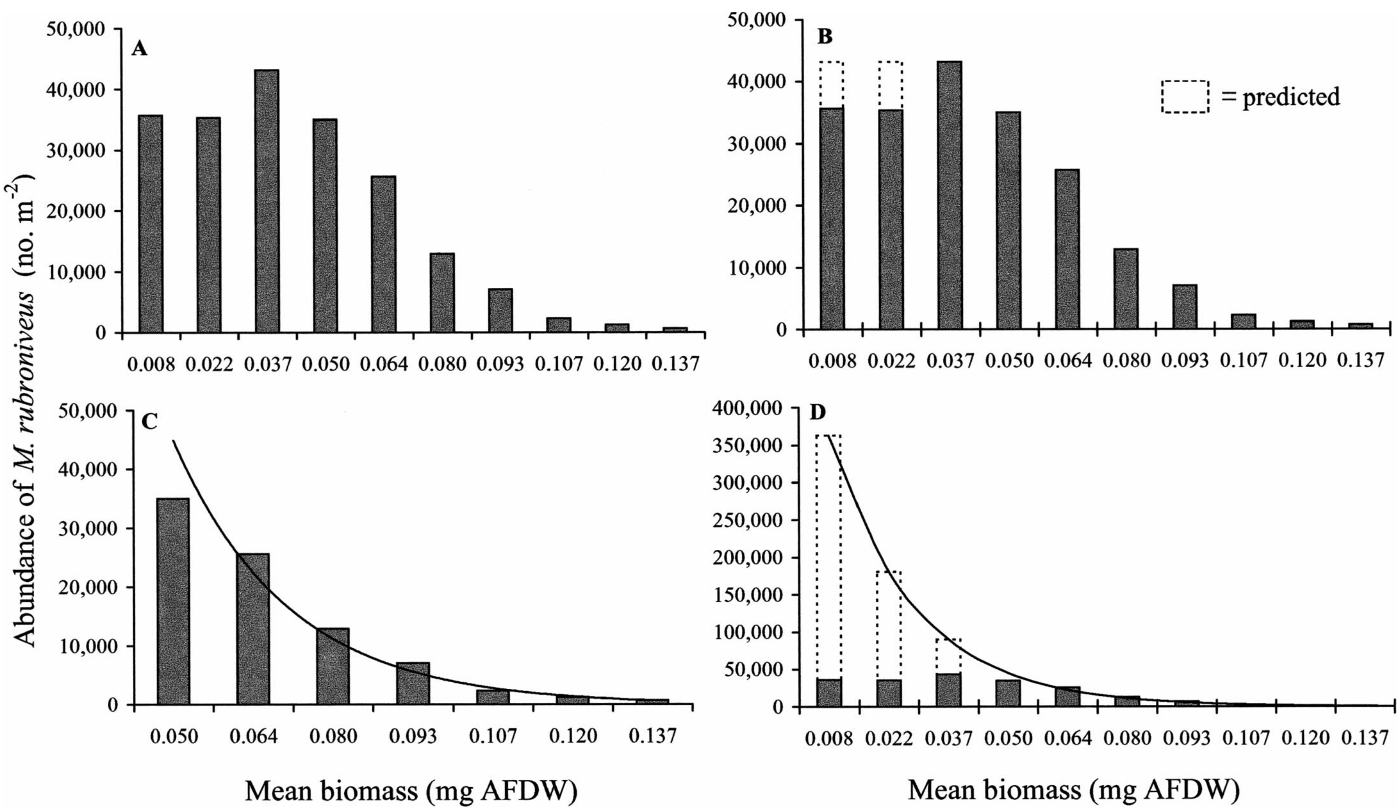

Fig. 8. Cumulative biomass (mg AFDW) frequency histograms for *M. rubroniveus* collected from the upper reach of Okatee Creek from January to December 2001 (A) without any correction, (B) with the minimum abundance correction in dashed lines, (C) with only the size classes that were sampled correctly and a best fit line for that abundance distribution, and (D) with extrapolated abundance values predicted from the best-fit line in dashed lines.

Table 3. Production (g AFDW m^{-2} yr^{-1}) and production to biomass ratios for *M. rubroniveus*. The hyphenated values are the minimum and maximum production estimates that were made using the minimum and maximum abundance corrections, respectively. $P:B_{Jun}$ was calculated with the biomass from Jun 2001.

		Production : Biomass ratios			
Creak–reach	Production	$P:B_{mean}$	$P:B_{max}$	$P:B_{Jan}$	$P:B_{Jun}$
Malind upper	1.02–2.19	5.17–9.3	1.6–2.9	3.2–6.8	13.1–28.0
Malind lower	0.05–0.11	4.3–7.6	1.5–2.6	2.3–5.0	13.6–29.8
Okatee upper	3.15–10.45	3.8–10.9	0.9–2.6	2.2–7.2	50.3–166.9
Okatee lower	0.11–0.15	6.4–7.7	2.7–3.3	5.1–7.1	7.89–10.9

Gerritsen et al. 1994). The development of species lists and life-history information was generally followed by surveys that estimated spatial and temporal distribution, abundance, and biomass in relation to environmental conditions. While this information evaluated relationships between macrobenthic communities and environmental conditions, it was descriptive and only partially addressed how the responses of macrobenthic organisms to changes in environmental conditions affected ecosystem processes. Production represents the cumulative response of a population to food availability, emigration and immigration, predation, reproductive success, physiological stress, and a variety of other natural and anthropogenic factors through time into one number (Crisp 1984). Production studies provide important information about the rate and magnitude of energy and material fluxes into and out of the benthic community in response to environmental changes, such as organic enrichment or chemical contamination that cannot be determined by point-in-time abundance and biomass measurements (e.g., Martinet et al. 1993; Sardá et al. 1996; Shieh et al. 2002). These types of data are essential in understanding and modeling ecosystem-level issues, such as determining energy supply and demand for higher trophic levels (e.g., Gerritsen et al. 1994; Wilbur and Clarke 1998) or how disturbance alters trophic structure and transfer efficiency (e.g., Shieh et al. 2002). When possible, secondary production estimates should be incorporated into benthic monitoring and assessment studies because of the integrative insight they provide into the role of benthic organisms in ecosystem processes beyond comparatively less useful static, standing stock assessments. Directly measuring only the dominant fauna or empirically estimating production of the entire benthic community are possible approaches to mitigating the increased costs associated with production measurements.

Validity and application of the method—The estimation of *M. rubroniveus* production from changes in mean biomass throughout the year using methods developed in this article produced results similar to the Hynes method (difference only 4% to 15%). The Hynes method (Hynes and Coleman 1968; Menzie 1980) has been a frequently used approach to directly estimate secondary production of benthic fauna (e.g., Lafont 1987; Sardá et al. 1996). Computer simulations of how size-frequency methods (e.g., the Hynes method and the one used in this article) estimate production over a range of life histories, and sampling programs indicate that these methods typically underestimate production between 10% and 50%, but are most accurate, and are superior to other methodologies when studying asynchronously reproducing organisms, like *M. rubroniveus* (Morin et al. 1987).

The data used to estimate the production of *M. rubroniveus* satisfied all of the assumptions of the method presented above, with the exception of constant growth rate throughout the sampling period (assumption 2). Through the year, mean water temperatures varied by ~20°C. Given the temperature variation, some variation in *M. rubroniveus* growth rates would be expected. Unfortunately, virtually nothing is known about the physiology of *M. rubroniveus* and no correction could be made to the production estimates. Despite this, the temperature patterns were similar between the creeks (Fig. 4A) and to those typically seen in temperate latitudes. Therefore, the authors believe that the temperature variation may have affected the accuracy of the production estimates but not their precision in comparison with other estimates made with similar methodologies.

The estimation method described here is mathematically simple and the only data required are changes in biomass and abundance over time. This method is most effective when organisms can be separated and measured by species. However, different species with similar body dimensions could be measured together, though an unknown bias would be introduced. Caution should be taken, though, not to lump different species of similar size but different life history characteristics (e.g., treating all oligochaetes as one taxon). Sampling should occur at least once per generation time and over multiple generations to incorporate variability that occurs from generation-to-generation. Also, the duration of a sampling program should be at least 1 yr in temperate zones to incorporate seasonal variations.

Spatial differences in production—Spatial differences in secondary production should provide insight into processes that affect macrobenthic organisms. In this study, the spatial patterns of *M. rubroniveus* production provided an indication of differing processes within and possibly between tidal creeks. As only two creeks were sampled, we were unable to definitively link watershed differences to secondary production. However, previous studies of tidal creeks similar to Okatee and Malind creeks throughout South Carolina have demonstrated that there are significant differences in the chemical and physical gradients along the length of a creek and between creeks with different watershed types. These differences, including water quality, nutrient inputs, chemical contamination, microphytobenthic abundance, and sediment composition, have been shown to affect the abundance of *M. rubroniveus* (Lerberg et al. 2000; Van Dolah et al.

Table 4. A comparison of directly measured production values and P : B ratios (where available) for a variety of benthic organisms. Secondary production is in g m^{-2} yr^{-1} of AFDW, ash free dry weight; DW, dry weight; and WW, wet weight. o, oligochaete; p, polychaete; b, bivalve, and c, copepod.

Location	Taxa	Production (g m^{-2} yr^{-1})	P : B	Source
Malind Creek, South Carolina	*Monopylephorus rubroniveus* (o)	0.05–2.19 AFDW	4.34–9.27	This study
Okatee Creek, South Carolina	*M. rubroniveus* (o)	0.11–10.45 AFDW	3.82–10.93	This study
Great Sippewissett Salt Marsh	*M. evertus* (o)	0.63–4.35 DW	2.4–2.7	Sardá et al. (1996)
Great Sippewissett Salt Marsh	*Paarania litoralis* (o)	0.16–0.59 DW	2.4–2.6	Sardá et al. (1996)
Lake Leman, France	Freahwater tubificidae (o)	14.8–16.7 WW	4.9–5.4	Lafont (1987)
Rhone River, France	Freshwater Tubificidae (w/o hair) (o)	53.33–144.3 WW	5.25–8.21	Martinet et al. (1993)
Great Sippewissett Salt Marsh	*Streblospio benedicti* (p)	1.38–2.03 DW	2.6–3.0	Sardá et al. (1996)
Upper Chesapeake Bay	*S. benedicti* (p)	0.001–0.2 AFDW		Holland et al. (1988)
Upper Chesapeake Bay	*Heteromastus filiformis* (p)	0.002–8.9 AFDW		Holland et al. (1988)
Po River Delta, Italy	*Canuella perplexa* (c)	6.78 AFDW	10.4	Ceccherelli and Mistri (1991)
Lower Chesapeake Bay	*Chaetopterus* cf. *variopedatus* (p)	18.0–34.0 AFDW	1.7–3.0	Thompson and Schaffner (2001)
Wassaw Sound, Georgia	*Mercenaria mercenaria* (b)	2.7–7.7 AFDW	0.05–0.23	Walker and Tenore (1984)

2000; Holland et al. 2004) and therefore the authors speculate that they should also affect production.

Though not statistically testable, the authors believe that the magnitude of the difference in *M. rubroniveus* production between creeks (~5–10 times greater in Okatee Creek than in Malind Creek) in addition to the significant differences in abundance and biomass data between the creeks demonstrated that the production rates measured were indeed reflective of environmental differences between the two creeks. Of all the environmental parameters measured, only the frequency of hypoxia displayed a statistically significant difference between Malind and Okatee creeks in a similar pattern to that of *M. rubroniveus* production. Despite having a predominantly forested watershed, Malind Creek experienced hypoxia more frequently than did Okatee Creek, including some hypoxic events even in the winter (Gillett 2003). The hypoxia in Malind Creek was likely related to the flushing rate of the creek, which was half of that in Okatee Creek (Chen unpubl. data). Repeated exposure to hypoxic conditions could be partially responsible for the lower productivity in Malind Creek despite the fact that *M. rubroniveus* is tolerant to hypoxic stress (Sanger unpubl. data). Short-term hypoxic events may cause nonlethal, physiological damage to *M. rubroniveus*, resulting in energy being spent on repair instead of somatic and reproductive growth.

There was an order of magnitude difference in the production of *M. rubroniveus* between the upper and lower reaches of both Malind and Okatee creeks. Benthic Chl *a* and pore-water ammonia in the sediments of the creeks followed a similar pattern, with greater concentrations in the upper reaches and lesser in the lower reaches. These parameters represent a rough approximation of the potential food sources to *M. rubroniveus* and other deposit feeders (i.e., microphytobenthos and sediment microbes, respectively). The large amounts of microphytobenthic and microbial activity in the upper reaches were probably the product of nutrient-rich groundwater and surface-water runoff in the upper reaches compared with the lower reaches (Joye pers. comm.; McKellar pers. comm.). Personal observations that *M. rubroniveus* has been found to aggregate under benthic diatom mats and the positive correlation between Chl *a* concentration and the abundance of *M. rubroniveus* indicates that the production of *M. rubroniveus* was, in part, related to the greater abundance of microphytobenthos. Additionally, previous studies have found that the abundance and production of deposit-feeding macrobenthos are frequently related to abundance of microphytobenthos (Miller et al. 1996; Sandulli and Pinckney 1999).

The microbes in the sediments of the upper reaches should have also supported *M. rubroniveus*; however, no relationship was observed between *M. rubroniveus* abundance and pore-water ammonia concentrations. The lack of a detectable relationship was the product of the times of highest porewater ammonia concentrations (i.e., summer and autumn) corresponding with the times of lowest *M. rubroniveus* abundance, probably due to intense predation by shrimp and juvenile fish. Therefore, the authors suggest that production differences between reaches were partially a product of increased food availability (especially microphytobenthos) but were likely also influenced by predation and other environmental factors that were not measured.

Monopylephorus rubroniveus *production compared with other benthos*—The production estimates of *M. rubroniveus* ranged from 0.05 to 10.45 g AFDW m^{-2} yr^{-1}. Values from the lower reaches were smaller than reported values for freshwater and estuarine oligochaetes, but production in the upper reaches was equal to or greater than most published values for oligochaetes (Table 4). Production estimates for two estuarine oligochaetes, *M. evertus* (0.63–4.35 g DW m^{-2} yr^{-1}) and *Paranais litoralis* (0.59–1.16 g DW m^{-2} yr^{-1}), from tidal creeks in the Great Sippewissett Salt Marsh, Massachusetts (Sardá et al. 1996) were similar to the middle and lower levels of production we observed. Production estimated for freshwater tubificid oligochaetes in a temperate lake in France (14.8–16.7 g WW m^{-2} yr^{-1} or ~ 3.7–4.2 g AFDW m^{-2} yr^{-1}) was also similar (Lafont 1987). Production of freshwater tubificid oligochaetes in a highly enriched, back channel of the upper Rhone River, France (53.3–144.4 g WW m^{-2} yr^{-1} or ~13.3–36.1 g AFDW m^{-2} yr^{-1}) was much higher (Martinet et al. 1993). The P : B ratios for many of the tubificid oligochaetes in Table 4 are similar and this indicates that most of the oligochaetes are capable of similar rates of production. However, the differences in annual production between the different ecosystems illustrates how relatively similar organisms can have very different annual rates of production as a result of the varying environmental characteristics inherent to each system.

Annual production of *M. rubroniveus* was generally less than or equal to that of larger, longer-lived macrobenthic organisms. In the lower Chesapeake Bay, the polychaete *Chaetopterus* cf. *variopedatus* was estimated to produce 18.0–34.0 g AFDW m^{-2} yr^{-1} (Thompson and Schaffner 2001). Production of the hard clam *Mercenaria mercenaria* was estimated to range from 2.7 to 7.7 g AFDW m^{-2} yr^{-1} in Wassaw Sound, Georgia (Walker and Tenore 1984). The P : B of these organisms are lower than those of *M. rubroniveus* (Table 4) because of the size and life history differences (Tumbiolo and Downing 1994). In contrast, the production of *M. rubroniveus* is greater than or equal to that of the harpacticoid copepod *Canuella perplexa* (6.78 g DW m^{-2} yr^{-1}) from the Po River Delta, Italy (Ceccherelli and Mistri 1991). The copepod's P : B ratio is, however, larger than the ratios calculated for *M. rubroniveus.* The differences in production and P : B of copepods in relation to *M. rubroniveus* are a function of the size and biology of meiobenthos compared with macrobenthos.

The results of this study indicate that the estuarine oligochaete *M. rubroniveus*, compared with similar macrobenthos, is capable of relatively large production rates in the tidal creeks of South Carolina. This observation is in accordance with the theory that salt marshes and tidal creeks are some of the most productive ecosystems around the world, which provide an abundant food source for a variety of estuarine nekton. The authors believe that *M. rubroniveus* is an important conduit for the transfer of energy from primary production in tidal creeks to nektonic predators and ultimately to the coastal ocean because of its numerical dominance, relatively high production rate, and ability to maintain that production despite intense predation pressure.

In a larger context, these data reinforce the ideas of Crisp (1984), Diaz and Schaffner (1990), Martinet et al. (1993), etc., that production estimates, by quantifying energy and material flows into and out of a system, provide a basis for understanding how changing environmental conditions affect the function of an ecosystem. The spatial differences in the production of *M. rubroniveus* are indicative of the differences in the environments of the two sample creeks and can provide insight into watershed-scale differences between the two systems. The patterns observed in Malind and Okatee creeks indicate that production of *M. rubroniveus* may be altered by environmental changes between reaches (e.g., microphytobenthic abundance) or watersheds (e.g., occurrence of hypoxia). Further studies measuring these types of parameters, e.g., nutrient input, chemical contamination, etc., as well as emigration/immigration and predation pressure on macrobenthos will create an even better understanding of what the patterns of secondary production in an ecosystem mean. The authors believe that the patterns observed between and within the creeks in this study can be further validated by using the $P : B_{mean}$ values from this study to estimate secondary production of *M. rubroniveus* in tidal creeks with different watershed characteristics throughout the southeast United States. Doing so will provide a more complete understanding of energy and material flows, the processes that influence them, and how alteration of tidal creek environments are affecting the function of these important ecosystems.

References

BAKER, H. R., AND R. O. BRINKHURST. 1981. A revision of the genus *Monopylephorus* and redefinition of the subfamilies Rhyacodrilinae and Branchiurinae (Tubificidae: Oligochaeta). Can. J. Zoo. **59:** 939–965.

BANSE, K., AND S. MOSHER. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. **50:** 355–379.

CECCHERELLI, V. U., AND M. MISTRI. 1991. Production of the meiobenthic harpacticoid copepod *Canuella perplexa.* Mar. Ecol. Prog. Ser. **68:** 225–234.

CRISP, D. J. 1984. Energy flow measurements, p. 284–372. *In* N. A. Holme and A. D. McIntyre [eds.], Methods for the study of marine benthos. Blackwell Scientific Publications.

CUMMINS, K. W., AND J. C. WUYCHECK. 1971. Caloric equivalents for investigation in ecological energetics. Mitt. Int. Verein. Limnol. **18:** 1–158.

DIAZ, R. J., AND L. C. SCHAFFNER. 1990. The functional role of estuarine benthos, p. 25–56. *In* M. Haire and E. C. Krome [eds.], Perspectives on the Chesapeake Bay, 1990. Advances in Estuarine Sciences. United States Environmental Protection Agency.

FREUND, R. J., AND R. C. LITTELL. 1991. SAS system for regression, 2nd ed. SAS Institute.

GERRITSEN, J., A. F. HOLLAND, AND D. E. IRVINE. 1994. Suspension-feeding bivalves and the fate of primary production: An estuarine model applied to Chesapeake Bay. Estuaries. **17:** 403–416.

GIERE, O., AND O. PFANNKUCHE. 1982. Biology and ecology of marine Oligochaeta, a review. Oceanogr. Mar. Biol. Annu. Rev. **20:** 173–308.

GILLETT, D. J. 2003. The ecology of tidal creek oligochaetes: Changes in abundance and secondary production of the numerically dominant species *Monopylephorus rubroniveus* (Levinsen, 1884). Master's thesis, Univ. of Charleston.

HACH COMPANY. 1994. Method 8155, p. 61-43–61-49. DR/700 colorimeter manual. Hach Chemical Company.

HOLLAND, A. F., D. M. SANGER, C. P. GAWLE, S. B. LERBERG, M. S. SANTIAGO, G. H. M. RIEKERK, L. E. ZIMMERMAN, AND G. I. SCOTT. 2004. Linkages between tidal creek ecosystems and the landscape and demographic attributes of their watersheds. J. Exp. Mar. Biol. Ecol. **298**: 151–178.

———, A. T. Shaughnessy, L. C. Scott, V. A. Dickens, J. A. Ranasinghe, and J. K. Summers. 1988. Progress report: Long-term benthic monitoring and assessment program for the Maryland portion of Chesapeake Bay (July 1986–October 1987), V I. Maryland Power Plant Research Program.

HYNES, H. B. N., AND M. J. COLEMAN. 1968. A simple method of assessing the annual production of stream benthos. Limnol. Oceanogr. **13:** 569–573.

KNEIB, R. T. 1997. The role of tidal marshes in the ecology of estuarine nekton. Oceanogr. Mar. Biol. Annu. Rev. **35:** 163–200.

LAFONT, M. 1987. Production of Tubificidae in the littoral zone of Lake Léman near Thonon-les-Bains: A methodological approach, p. 179–187. *In* R. O. Brinkhurst and R J. Diaz [eds.], Developments in hydrobiology, aquatic Oligochaeta. DR W. Junk Publishers.

LERBERG, S. B., A. F. HOLLAND, AND D. M. SANGER. 2000. Responses of tidal creek macrobenthic communities to the effects of watershed development. Estuaries. **23:** 838–853.

LITTELL, R. C., R. J. FREUND, AND P. C. SPECTOR. 1991. SAS system for linear models, 3rd ed. SAS Institute.

MARTINET, F., J. JUGET, AND P. RIERA. 1993. Carbon fluxes across water, sediment, and benthos along a gradient of disturbance intensity: Adaptive responses of the sediment feeders. Arch. Hydrobiol. **127:** 39–56.

MENZIE, C. A. 1980. A note on the Hynes method of estimating secondary production. Limnol. Oceanogr. **25:** 770–773.

MILLER, D. C., R. J. GEIDER, AND H. L. MACINTYRE. 1996. Microphytobenthos: The ecological role of the ''Secret Garden'' of unvegetated, shallow-water marine habitat. II. Role in sediment stability and shallow-water food webs. Estuaries. **19:** 202–212.

MILLER, M. J., D. M. NEMERSON, AND D. W. ABLE. 2003. Seasonal distribution, abundance, and growth, of young-of-the-year Atlantic croaker (*Micropoganias undulates*) in Delaware Bay and adjacent marshes. Fish. Bull. **101:** 100–115.

MITSCH, W. J., AND J. G. GOSSELINK. 2000. Wetlands, 3rd ed. John Wiley.

MORIN, A., T. A. MOUSSEAU, AND D. A. ROFF. 1987. Accuracy and precision of secondary production estimates. Limnol. Oceanogr. **32:** 1342–1352.

PLUMB, R. H., JR. 1981. Procedures for handling and chemical analysis of sediment and water samples. Technical report EPA/CE-81-1. U.S. Environmental Protection Agency, Corps of Engineers Technical Committee on Criteria for Dredged and Filled Materials.

POSEY, M. H., T. D. ALPHIN, L. B. CAHOON, D. G. LINDQUIST, M. A. MALLIN, AND M. B. NEVERS. 2002. Top-down versus bottom-up limitation in benthic infaunal communities: Direct and indirect effects. Estuaries. **25**: 999–1014.

SANDERS, H. L. 1958. Benthic studies in Buzzards Bay. I. Animal–sediment relationships. Limnol. Oceanogr. **3**:245–258.

SANDULLI, R., AND J. PINCKNEY. 1999. Patch sizes and spatial patterns of meiobenthic copepods and benthic microalgae in sandy sediments: A microscale approach. J. Sea Res. **41:** 179–187.

SARDÁ, R., I. VALIELA, AND K. FOREMAN. 1996. Decadal shifts in a salt marsh macroinfaunal community in response to sustained long-term experimental nutrient enrichment. J. Exp. Mar. Biol Ecol. **205:** 63–81.

SHIEH, S., J. V. WARD, AND B. C. KONDRATIEFF. 2002. Energy flow through macroinvertebrates in a polluted plains stream. J. N. Benthol. Soc. **21:** 660–675.

SOUTHEAST REGIONAL CLIMATE CENTER (SERCC). 2004 August 13. SERCC climate interactive rapid retrieval users system (CIRRUS) [accessed 2004 August 24]. Available from http://water.dnr.state.sc.us/water/climate/sercc/services.html

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. p. 310. *In* Stevenson, J. C. [ed.], A practical handbook of seawater analysis. Fisheries Research Board of Canada.

THOMPSON, M. L., AND L. C. SCHAFFNER. 2001. Population biology and secondary production of the suspension feeding polychaete *Chaetopterus* cf. *variopedatus*: Implications for benthic-pelagic coupling in lower Chesapeake Bay. Limnol. Oceanogr. **46:** 1899–1907.

TUMBIOLO, M. L., AND J. A. DOWNING. 1994. An empirical model for the prediction of secondary production in marine benthic invertebrate populations. Mar. Ecol. Prog. Ser. **114:** 165–174.

VAN DOLAH, R. F., D. E. CHESTNUT, AND G. I. SCOTT. 2000. A baseline assessment of environmental and biological conditions in Broad Creek and the Okatee River, Beaufort County, South Carolina. Final report. South Carolina Department of Health and Environmental Control.

WALKER, R. L., AND K. R. TENORE. 1984. The distribution and production of the hard clam, *Mercenaria mercenaria,* Wassaw Sound, Georgia. Estuaries **7:** 19–27.

WENNER, E. L., AND H. R. BEATTY. 1993. Utilization of shallow estuarine habitats in South Carolina, U.S.A., by postlarval and juvenile stages of *Penaeus* spp. (Decepoda: Penaeidae). J. Crust. Biol. **13:** 280–295.

WEST, T. L. 1985. Abundance and diversity of benthic macrofauna in subtributaries of the Pamlico River estuary. J. Elisha Mitchell Sci. Soc. **10:** 142–159.

WILBER, D. H., AND D. G. CLARKE. 1998. Estimating secondary production and benthic consumption in monitoring studies: A case study of the impacts of dredged material in Galveston Bay, Texas. Estuaries. **21:** 230–245.

ZAR, J. H. 1998. Biostatistical analysis, 4th ed. Prentice-Hall.

Received: 20 January 2004
Accepted: 2 November 2004
Amended: 25 November 2004