

Importance of detrital algae, bacteria, and organic matter to littoral microcrustacean growth and reproduction

A. Maria Lemke¹

Aquatic Biology Program, Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama 35487

Michael J. Lemke

Biology Department, University of Illinois at Springfield, Springfield, Illinois 62703

Arthur C. Benke

Aquatic Biology Program, Department of Biological Sciences, University of Alabama, Tuscaloosa, Alabama 35487

Abstract

Cumulative incorporation of radiolabeled algal ($\text{NaH}^{14}\text{CO}_3$) and bacterial (^{14}C -acetate) carbon associated with benthic organic matter (BOM) was measured at timed intervals to determine the relative importance of algal, bacterial, and detrital components of BOM to the growth and reproduction of *Eurycerus vernalis* (Chydoridae). Five times more algal than bacterial carbon was incorporated, which corresponded to relative amounts of algal and bacterial carbon quantified from the BOM. Algal and bacterial carbon provided 38% and 8% of the carbon required for *Eurycerus* growth and reproduction, respectively. Approximately 54% of the carbon required for *Eurycerus* growth was presumably provided by nonlabeled microbes (e.g., fungi, protists) or detritus. Parallel studies were conducted to measure the growth and reproduction for *Eurycerus* fed diets varying in amounts of algae, bacteria, and detritus. Effects of diet were especially noticeable in early instar growth and reproduction. Individuals fed diets with high algal and bacterial biomass relative to detrital content exhibited higher maximum somatic growth rates ($75\text{--}89\% \text{ d}^{-1}$) than those fed aggregate and particulate detritus ($51\text{--}60\%$). Egg production and net reproductive rate were highest for females fed nutrient-supplemented algae and corresponded to increased survivorship, early reproduction, and larger clutches. Survivorship was highest for females fed aggregate detritus; however, the percentage of total growth allocated toward egg production was similar for individuals fed aggregate detritus and cultured algae ($67\text{--}82\%$). Relative trophic importance of algae and bacteria as constituents of BOM likely depends on their relative abundance, but the two in combination can be substantially more important than the detritus alone.

Significant progress has been made in understanding the importance of algal quality and quantity to zooplankton reproduction and survival and zooplankton ingestion and assimilation rates of various algal species in freshwater pelagic and marine coastal systems (e.g., Lampert 1978; Kilham et al. 1997; Vargas et al. 2006). Planktonic bacteria, allochthonous material, and detritus have also been shown to be important components of zooplankton diets as either supplementary or primary sources of carbon (Hessen et al. 1990; Hart et al. 2000; Grey et al. 2001). Most of the primary production in aquatic freshwater systems is not consumed by zooplankton, however, but enters the detrital pool, where it is either microbially metabolized or consumed by metazoan heterotrophs (Wetzel 1995, 2001).

Thus, in many situations, detrital and associated benthic microbial food webs are also important components of energy flow through aquatic ecosystems (e.g., Pomeroy 1980). Integration of benthic food resources into aquatic food webs has shown in several studies that upper trophic levels may actually be supported by benthic rather than planktonic food web pathways in some shallow lakes and wetlands (Sierszen et al. 2004; Rautio and Vincent 2006).

In contrast to the zooplankton communities of more pelagic environments, vegetated wetlands support a high diversity and biomass of benthic microcrustaceans, many of which are considered detritivores. Bowen (1984) classified detrital particulate organic matter into two categories according to the pathway in which it is formed: decomposing plant fragments containing remnant lignin and cellulose and organic aggregates derived from dissolved organic matter, such as from macrophyte leachates and exudates. Subsequent research, however, suggests that both plant fragments and organic aggregates are even more complex. Plant fragments are typically coated with bacterial and microalgal exopolymers as well as attached microbes (bacteria, algae, and fungi) that represent abundant sources of potentially labile carbon for macroconsumers (Decho and Moriarty 1990; Decho 1993). Organic aggregates derived from dissolved organic matter, on the other hand, are difficult to separate from inorganic

¹To whom correspondence should be addressed. Present address: The Nature Conservancy, Illinois Chapter, 301 SW Adams St., Suite 1007, Peoria, Illinois 61602 (mlemke@tnc.org).

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particles and egested fecal material, all of which have been colonized by both heterotrophic and autotrophic microbes and bound within an exopolymer matrix (Lush and Hynes 1973; Alber and Valiela 1994; Wotton 2007). These complex forms of detritus and their associated labile components have separately been reported to be major food resources for crustaceans and macroinvertebrates (Hargrave 1970; Marchant and Hynes 1981; Vos et al. 2002). For the purposes of this study, we will refer to the plant fragments as particulate BOM (benthic organic matter) and to the complex, more finely divided, aggregated material as aggregate BOM.

A broader understanding of how BOM is utilized by benthic microcrustaceans can lead to insights as to how these consumers may contribute to the energy flow within wetland ecosystems. Consumption of microbial and detrital food resources has been documented for several species of benthic copepods (Carmen and Thistle 1985; Decho and Moriarty 1990; Perlmutter and Meyer 1991) and the littoral chydorid *Eurycerus lamellatus* (Smirnov 1962; Fryer 1963). Carmen and Thistle (1985) provided essential information about the energy intake provided by BOM to microcrustaceans in terms of the ingestion and assimilation of BOM components. However, short-term physiological rate measurements do not necessarily reflect resource utilization in terms of realized growth and reproduction (e.g., Lampert 1977; Lynch et al. 1986). Growth and reproduction are important measures of secondary production, an integrative measure of the success of a population (Benke 1993), and a functional measure of energy flow pathways in food webs (Benke 1984).

The purpose of this study was to quantify the relative importance of algae, bacteria, and detritus of wetland-derived BOM as utilizable energy resources to the littoral microcrustacean *Eurycerus vernalis* as related to growth, reproduction, and secondary production. High biomass and secondary production values estimated for *Eurycerus* from a small wetland in the southeastern U.S. indicate that *Eurycerus* is an important component of the microcrustacean community in shallow, vegetated habitats (Lemke 2000; Lemke and Benke 2004). The first objective was to measure the incorporation of ^{14}C -radiolabeled algal and bacterial carbon from aggregate BOM by *Eurycerus* and to determine the relative contribution of each component to the energy required by *Eurycerus* for growth and reproduction. The second objective was to measure the relative contributions of algae, bacteria, and detrital components of BOM to *Eurycerus* size-specific growth and reproduction.

Methods

E. vernalis (Chydoridae) is a southern species first described by Hann (1982) that inhabits shallow areas of vegetated ponds and wetlands. *Eurycerus* and BOM were collected from the Talladega wetland (Benke et al. 1999), a small wetland pond (13,600 m²) within the Talladega Wetland Ecosystem on the upper Coastal Plain in northeastern Hale County (32°52'N, 87°26'W), Alabama. Microcrustacean research was conducted in two distinct

zones defined by Benke et al. (1999) in relation to vegetation type and water depth. The *Nymphaea* zone (7,200 m²) ranged from 0.2 to 1.0 m in depth and was dominated by the floating-leafed water lily, *N. odorata*, during summer and fall, and the open-water zone (1,100 m²) averaged 1.5 m in depth and lacked vegetation. *Eurycerus* inhabited the *Nymphaea* zone almost exclusively (Lemke 2000). Surface waters were relatively nutrient poor (Stanley and Ward 1997), and monthly water temperatures ranged from 7.7°C to 28.1°C (Benke et al. 1999). During the ^{14}C -incorporation experiment (15–17 March 1994), pH of wetland water was 5–6, and mean daily water temperature was 13.1°C. During the growth experiment (01 November–13 December 1993), average monthly water temperatures in the wetland ranged from 9.4°C to 12.4°C.

Incorporation experiment

Aggregate BOM was pipetted from the surface layer of wetland sediments from the *Nymphaea* zone and sieved to create a thick slurry of 38- to 500- μm particles. This slurry was divided in half and used to prepare algal and bacterial ^{14}C -radiolabeled working solutions.

Three algal working solutions were prepared by mixing one part original slurry with four parts 0.22- μm filtered wetland water (FWW). Solution A1 was used to characterize the BOM (see “Methods,” “Characterization of aggregate BOM”). Solution A2 was radiolabeled by adding 60 mL of $\text{NaH}^{14}\text{CO}_3$ (1.11×10^7 Bq, Amersham) to 30 g of the original, undiluted slurry to obtain a final concentration of 1.85×10^5 Bq $\text{NaH}^{14}\text{CO}_3$ mL⁻¹ slurry (2:1 dilution). This radiolabeled working solution is termed the aggregate algal solution (Ag_A) and was eventually fed to *Eurycerus*. Solution A3 was used in the feeding study as a killed-control (K_A) to account for adsorption of the label onto the exoskeleton of *Eurycerus*. K_As were prepared with formaldehyde (final concentration = 5%) before incubation. Algal working solutions were incubated for 13 h at 21.7°C on a slow shaker (100 rpm) with constant light. Excess $^{14}\text{CO}_2$ was captured by methods modified from Wetzel and Likens (2000). After the incubation, FWW was added to Ag_A and K_A to obtain a final dilution each of 4:1. Three subsamples each from Ag_A and K_A were prepared for radioassay and used to calculate specific activity. Subsamples were preserved with formaldehyde (final concentration = 5%), filtered through cellulose acetate (0.22- μm pore size, Millipore), and rinsed with filtered dH₂O. Filters were dried overnight and exposed to 1 mL of ethyl acetate for 1 h and 1 mL of Soluene-350 tissue solubilizer (i.e., STS; Packard) overnight. Hydrogen peroxide was added to remove any color, and samples were neutralized with glacial acetic acid; 10 mL of scintillation cocktail (Pico-Flour 40, Packard) was added before the radioassay.

Three bacterial working solutions were prepared at a 4:1 dilution of FWW:original slurry. Solution B1 was used to characterize the BOM (see “Methods,” “Characterization of aggregate BOM”). Solution B2 was radiolabeled with [^{14}C]-acetic acid (7.4×10^6 Bq mL⁻¹, specific activity of

2.072×10^9 Bq mmol⁻¹, Amersham) at a final concentration of 5.55×10^4 Bq mL⁻¹ working solution (Ag_B). Working solution B3 was prepared as the killed-control (K_B). Ag_B and K_B samples were incubated on a shaker (100 rpm) at 20°C for 130 min, and excess ¹⁴CO₂ was captured. After the incubation, three subsamples were removed each from Ag_B and the K_B, preserved with formalin (final concentration = 5%), filtered, and radioassayed to determine specific activity.

Feeding procedures—Feeding procedures were identical for Ag_A, Ag_B, K_A, and K_B treatments. Unincorporated radiotracer was rinsed from the aggregate BOM, and 3 mL of each treatment was added with 25 mL of FWW to one of eight feeding chambers (3 Ag_A, 3 Ag_B, 1 K_A, and 1 K_B). One hundred seventy-five *Eurycerus* were added to each Ag-chamber, and 30 were added to each K-chamber. Fifteen animals were removed from each Ag-chamber at eight intervals (30, 75, 120, 165, 225, 285, 345, and 435 min) and rinsed. Five individuals were transferred to STS and used to measure the ingestion of ¹⁴C at each interval. Ten animals were used to measure the respiration and egestion of ¹⁴C at each interval and the cumulative incorporation of ¹⁴C over the 435-min feeding period. The 10 animals were placed together into a respiration chamber with unlabeled FWW and no food for 30 min (Decho 1993; Lemke 2000; Wetzel and Likens 2000). Control chambers contained no animals but were otherwise identical. After 30 min, animals were transferred into STS to measure incorporation, and feces were collected on 22- μ m-pore-size cellulose acetate filters. Filters were rinsed, dried, and prepared for radioassay as previously described. Five animals were removed from the K-chamber at three intervals (30, 225, and 435 min), rinsed, and transferred to STS. Vials containing STS were covered overnight to allow complete digestion of the tissue and were prepared for a radioassay on a Beckman LS 3801 liquid scintillation counter.

Characterization of aggregate BOM—Subsamples were removed from A2 and B2 solutions and prepared for algal and bacterial enumeration, algal biovolume and bacterial biomass estimation, ash-free dry mass (AFDM), carbon, hydrogen, and nitrogen (CHN) analysis, and chlorophyll *a* (Chl *a*) extraction (Porter and Feig 1980; Wetzel and Likens 2000). Specific activity of bacteria and algae was calculated (cell biovolume DPM⁻¹). Relative amounts of algal and bacterial carbon available in the working solutions were calculated by CHN analyses (Carlo Erba CHNS analyzer, EA1108) and the conversions of cell biovolume to pg C μ m⁻³ for bacteria (0.22 pg of C μ m⁻³, Bratbak and Dundas 1984) and algae (0.2 pg of C μ m⁻³, Strathmann 1967; Wetzel and Likens 2000).

Energetic calculations—Calculations for algal and bacterial carbon incorporated, ingested, egested, and respired (pg C per μ g C *Eurycerus*) were modified from equations published by Edwards and Meyer (1987). Radioactivity measurements for *Eurycerus* (disintegrations per minute [DPM] ind⁻¹) were converted to DPM μ g *Eurycerus* (dry mass) by a length-mass regression (Lemke and Benke 2004)

and used with CHN analyses to calculate μ g C μ g⁻¹ *Eurycerus*. Incorporation and ingestion were calculated as cumulative measures over the 435-min feeding period, whereas egestion and respiration calculations represent measurements acquired during timed intervals. Incorporation rates of algal and bacterial carbon by *Eurycerus* were calculated as μ g C_{algal, bacterial} incorporated μ g⁻¹ C *Eurycerus* h⁻¹ for each interval (Findlay et al. 1984). Daily incorporation rates of algal and bacterial carbon (μ g C_{algal, bacterial} μ g⁻¹ C_{Eury} day⁻¹) were estimated and divided by daily total growth rates of fifth-instar *Eurycerus* (μ g C_{Eury} day⁻¹) reared at 20°C (Lemke and Benke 2004) to get the fraction of the carbon required by *Eurycerus* for growth and reproduction that could theoretically be supplied by algal and bacterial carbon.

Growth experiment

Experimental design—Laboratory growth experiments were conducted in 50-mL beakers at 20°C (model 818, Precision Scientific) with a 12:12 light:dark cycle. Seventy gravid females were collected from the wetland and randomly assigned to one of six experimental treatments or to a control. Juveniles released from brood chambers within 12–24 h were transferred to assigned treatments (*n* = 10 individuals treatment⁻¹) with 40 mL of 0.7- μ m FWW (Whatman GF/F). Fresh food and FWW were supplied every 24–72 h. Early instars were measured to the nearest 20 μ m every 24 h; the length and number of eggs produced were recorded every 48–72 h for reproductive instars.

Treatments—Control beakers contained FWW with no additional food source. Treatments were grouped into two categories: wetland BOM (BOM) and cultured treatments (CT). BOM treatments were further defined as either aggregate BOM or particulate BOM and included (1) aggregate BOM with microbiota, (2) particulate BOM with microbiota, and (3) particulate BOM without microbiota (i.e., autoclaved BOM). Known volumes of aggregate BOM pipetted from the surface of wetland sediments were fed directly to *Eurycerus*. Particulate BOM was collected by gently scraping a 500- μ m dip net along the wetlands sediments and rinsing the BOM with autoclaved distilled H₂O onto a 53- μ m sieve to remove loosely associated aggregate BOM. BOM that was retained on the sieve was considered particulate BOM, and preweighed portions were fed to a second group of *Eurycerus*. A third group was fed particulate BOM that had been autoclaved and rinsed. Cultured treatments were grown on coverslips in wetland mesocosms under greenhouse conditions. Light and nutrient levels were varied to produce coverslip treatments defined as low (CT_{low}), medium (CT_{med}), or high (CT_{high}) algal and bacterial biomass (Lemke 2000). Coverslips were placed directly into the 40-mL beakers during feeding and were exchanged every 24–48 h.

Characterization of food treatments—Three replicate subsamples were collected from each treatment on three dates during the study for characterization. Aggregate and particulate BOM subsamples were analyzed for algal

biomass, bacterial enumeration and biovolume, AFDM, and CHN analyses. CT samples were analyzed for algal biomass and bacterial enumeration and biovolume. Algal biomass was estimated as $\mu\text{g Chl } a$ available day^{-1} , and bacterial biovolume was estimated as μm^3 available day^{-1} .

Response variables—Individual DM (W) in μg was estimated from total length by regression analysis (Lemke and Benke 2004). Mean daily somatic growth rate (g) was calculated as $g = \ln(W_F/W_I)/\Delta t$, where W_F and W_I are the final and initial DM of an individual during an instar of duration Δt (in days). Total growth rate (g_T , % day^{-1}) was calculated for each instar as $g_T = (\ln((W_F + W_E)/W_I)/\Delta t) \times 100$, where W_E = egg mass (2.23 μg of dry mass [DM] egg^{-1} , Lemke and Benke 2004) produced during a particular instar. The relationship between growth rate and individual DM of each instar was described as $\log g = Y - a(\log W_i)$, where g is predicted growth rate, and W_i is individual DM. The percentage of total growth allocated toward egg production during each instar was calculated as $W_E/((W_E + W_F) - W_I) \times 100$ and was used to estimate the average percentage of total growth that was allocated toward egg production over an individual's lifetime ($G_{E(L)}$).

Innate capacity of population increase (r) was estimated by treating all individuals reared at a particular temperature as one cohort. Net reproductive rate was calculated as $R_0 = \sum l_x b_x$, where x = age (days), l_x = proportion of individuals surviving at the beginning of each interval (x), and b_x = number of juveniles produced female^{-1} during that interval (x). Euler's equation, $1 = \sum (l_x b_x e^{-rx})$, was solved iteratively to obtain a precise solution for r , and generation time was calculated as $G = \ln R_0/r$. In our study, r and G were used only for comparison among treatments and with other laboratory studies.

Effects of treatments on life-history parameters (initial and final lengths and mass; mean and maximum life span; age, length, and mass at first reproduction; number of clutches and eggs produced over a lifetime; and egg development time) were tested with Kruskal–Wallis one-way analysis of variance on ranks, followed by either Student–Newman–Keuls (SNK) method (equal ns) or Dunn's method (unequal ns) if the analysis of variance signified statistical differences among means. Slopes and y -intercepts were compared by analysis of covariance, followed by Tukey's multiple comparison, if statistical differences existed ($p < 0.05$).

Results

Incorporation experiment—Specific activity was calculated as $281.0 \pm 64.8 \mu\text{m}^3$ of DPM^{-1} for algae and as $16.9 \pm 4.7 \mu\text{m}^3$ of DPM^{-1} for bacteria by the estimations for algal and bacterial abundances, biovolume, and radioactivity (Table 1). Aggregate BOM was composed of an estimated $13.0 \pm 3.1 \text{ mg}$ of algal carbon and $2.3 \pm 0.7 \text{ mg}$ of bacterial carbon g^{-1} of AFDM working solution, based on the conversion factor of 0.013 g of AFDM mL^{-1} of working solution. Aggregate BOM contained 56% ash by DM and contained 10.7% total carbon (0.107 g of C g^{-1} of dry weight [DW] working solution). These values converted to

192 mg of C g^{-1} of AFDM working solution (0.107 g of C g^{-1} of DW \div 0.558 g of AFDM g^{-1} of DW). Thus, algal and bacterial carbon combined made up 8% of the total carbon in the working solution ($(15.3 \text{ mg of C} \div 192 \text{ mg of C}) \times 100$). *Eurycerus* was composed of 46% carbon and was estimated at 36.7 μg of DW ind^{-1} for fifth-instar females. These estimates were used to convert individual *Eurycerus* to units of carbon (16.9 μg of C ind^{-1}).

Five times more algal than bacterial carbon was incorporated (i.e., accrued as biomass) by *Eurycerus* (Fig. 1). Incorporation of algal and bacterial ^{14}C by *Eurycerus* was observed within 30 min of exposure and continued to increase steadily up to about 4 h (Fig. 1A,B). Ingestion of algal carbon was significantly higher than incorporation at the first 30-min interval (t -test, $t = 4.157$, $df = 4$, $p = 0.014$), and ingestion of bacterial carbon was significantly higher than incorporation at 30-min (t -test, $t = 6.137$, $df = 4$, $p = 0.004$), 75-min (t -test, $t = 5.474$, $df = 4$, $p = 0.005$), and 165-min (t -test, $t = 3.143$, $df = 4$, $p = 0.035$) intervals. *Eurycerus* continued to incorporate algal and bacterial carbon during the feeding period (Fig. 1A,B), although incorporation rates continually decreased over time (Fig. 1C,D). Mean incorporation rates for algal and bacterial carbon were 0.11 ± 0.01 and $0.02 \pm 0.003 \mu\text{g}$ of C μg^{-1} of *Eurycerus* C day^{-1} , respectively. Incorporation rates relative to carbon requirements for growth and reproduction of fifth-instar *Eurycerus* indicate that algae represented $38\% \pm 5\%$ of the necessary carbon compared with the available bacterial carbon of $8\% \pm 1\%$. Respired algal and bacterial ^{14}C averaged $<1\%$ ingested ^{14}C , and egested ^{14}C consisted of 12–18% of the total ^{14}C ingested.

Growth study

The various food treatments exhibited a substantial range of algal and bacterial biomass (Table 2). Algal biomass was lowest on coverslips incubated at reduced light conditions (CT_{low}), followed by particulate autoclaved and nonautoclaved BOM. Although algal biomass was highest on aggregate BOM and coverslips that were incubated with light (CT_{high} and CT_{med}), they were not significantly different from the particulate BOM (autoclaved or nonautoclaved). Bacterial biovolume was lowest on particulate BOM (autoclaved or nonautoclaved) but differed significantly only from the aggregate BOM. Aggregate BOM showed substantially higher bacterial biovolume than the other treatments but did not differ significantly from CT_{high} and CT_{med} .

Mean initial length ($0.68 \pm 0.005 \text{ mm}$) and mass ($5.13 \pm 0.10 \mu\text{g}$ of DM) were not significantly different among *Eurycerus* individuals assigned to each food treatment (Kruskal–Wallis ANOVA, $H = 11.877$, $df = 6$, $p = 0.065$; $H = 10.616$, $df = 6$, $p = 0.101$). Final length ($0.70 \pm 0.01 \text{ mm}$ of DM) and mass ($5.74 \pm 0.35 \mu\text{g}$ of DM) of the control group (FWW) and *Eurycerus* fed autoclaved particulate BOM were significantly lower than all the other experimental treatments (Kruskal–Wallis ANOVA, $H = 51.944$, $df = 6$, $p < 0.001$; Dunn's $p < 0.05$), except for individuals reared on nonautoclaved particulate BOM ($1.17 \pm 0.08 \text{ mm}$, $20.67 \pm 3.63 \mu\text{g}$ of DM; Dunn's $p >$

Table 1. Estimated abundance, biovolume, and radioactivity of the algal and bacterial components of the radiolabeled aggregate BOM (i.e., working solution [WS]) used to determine the incorporation of algae and bacteria by *Eurycerus vernalis*. Standard errors are shown in parentheses.

	Algae	Bacteria
Abundance (No. cells mL ⁻¹ WS)	2.55 × 10 ³ (±320)	1.05 × 10 ⁹ (±1.37 × 10 ⁸)
Biovolume (μm ³ cell ⁻¹)	3.3 × 10 ⁵ (±8.9 × 10 ⁴)	0.13 (±0.03)
Radioactivity (DPM mL ⁻¹ WS)	2.97 × 10 ⁶ (±5.12 × 10 ⁴)	7.94 × 10 ⁶ (±1.93 × 10 ⁵)

0.05). Final length (range = 1.04–1.71 mm) and mass (range = 15.4–54.5 μg of DM) were not significantly different among individuals reared with cultured, aggregate BOM and nonautoclaved particulate treatments (Dunn's *p* > 0.05). Mean life span was significantly shorter for individuals fed autoclaved particulate BOM and FWW (2.7 ± 0.4 d; Kruskal–Wallis ANOVA, *H* = 38.666, *df* = 6, *p* < 0.001; SNK, *p* < 0.05) but did not differ significantly among the other treatments (range = 11.1–26.7 d; SNK, *p* > 0.05).

Similar growth patterns were observed for individuals among cultured, aggregate, and particulate BOM treatments, in that individuals grew rapidly during early stages and gradually slowed as they became reproductive between the ages of 10 and 15 d (Fig. 2A). Rate of increase for total length (i.e., growth plus egg production) was slower for

Eurycerus fed BOM (aggregate and particulate) and CT_{low} than for *Eurycerus* fed CT_{high} and CT_{med}. Survivorship initially decreased precipitously for individuals fed food from CT_{low} and CT_{med} treatments (Fig. 2B), and although this decline continued for individuals fed food from the CT_{low} treatment, the survivorship curve declined less steeply for animals reared on CT_{med}. Survivorship decreased steadily for individuals fed particulate BOM over time. Survivorship remained high for individuals reared on aggregate BOM and CT_{high} treatments; however, it declined sharply for CT_{high} individuals after 35 d.

Females reared on CT_{high} and CT_{med} were larger at reproduction than those fed either form of BOM (ANOVA, *F* = 11.479, *df* = 3, *p* < 0.001; Tukey, *p* < 0.05; Table 3). Individuals fed CT_{high} reproduced earlier than those reared on either form of BOM (Kruskal–Wallis ANOVA, *H* =

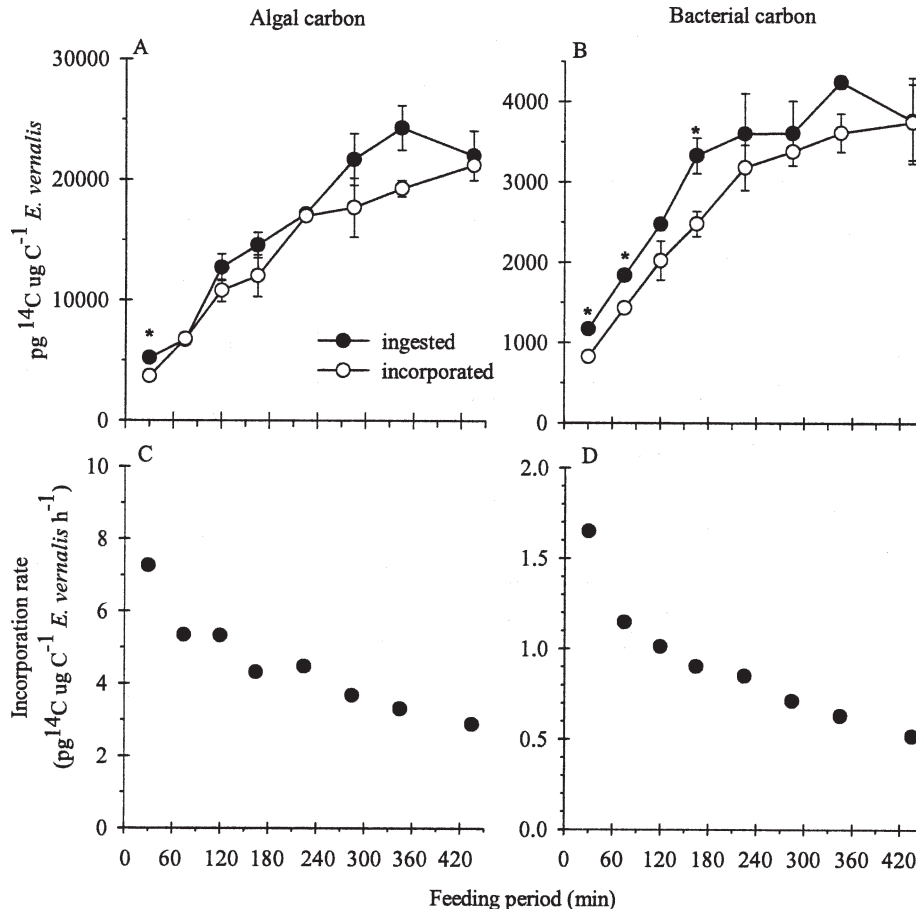


Fig. 1. Cumulative (A, B) uptake and (C, D) incorporation rates of ¹⁴C-labeled algal and bacterial carbon by *Eurycerus vernalis*.

Table 2. Treatments fed to *Eurycerus vernalis* during the laboratory growth study. Treatments are quantified in terms of mean algal biomass (μg) and bacterial biovolume (μm^3) that were available to *Eurycerus* individuals at the beginning of each feeding period. Algal biomass and bacterial biovolume were statistically compared among treatments by the Kruskal–Wallis one-way analysis of variance on ranks, followed by Dunn’s all-pairwise comparison. Letters indicate statistical differences; means with same letters are not significantly different, $\alpha = 0.05$.

Treatment	Algal biomass (μg Chl <i>a</i>)	Bacterial biovolume ($\times 10^6 \mu\text{m}^3$)
Aggregate BOM	2.23 (0.32) a	210.7 (15.8) a
Light + nutrients (CT _{high})	2.11 (0.23) a	9.8 (1.8) ab
Light (CT _{med})	1.74 (0.27) a	6.8 (0.2) ab
Particulate BOM	1.20 (0.21) ab	0.6 (0.1) b
Particulate autoclaved BOM	0.83 (0.09) ab	0.008 (0.005) b
Dark (CT _{low})	0.29 (0.03) b	3.8 (0.5) b

16.204, $df = 3$, $p = 0.001$; Dunn’s $p < 0.05$), and females fed CT_{med} were intermediate (Table 3). CT_{high} females produced significantly more eggs clutch⁻¹ (Kruskal–Wallis ANOVA, $H = 42.601$, $df = 3$, $p < 0.001$; Dunn’s $p < 0.05$; Table 3) and cumulatively more eggs over their lifetime (Fig. 2C) than those reared on CT_{med} or either form of BOM. The average number of clutches female⁻¹ did not differ statistically among the treatments (Kruskal–Wallis ANOVA, $H = 5.255$, $df = 3$, $p = 0.154$; Table 3); CT_{low} females did not produce eggs and were not included in the statistical comparisons. Egg production declined after ≈ 30 d for females fed CT_{high} in conjunction with decreased survivorship but continued to increase for individuals fed aggregate BOM (Fig. 2C).

The innate capacity of increase (r) was highest for individuals reared on CT_{high}, lowest for individuals fed particulate BOM, and ranged in the middle for individuals fed aggregate BOM and CT_{med} (Table 3). Generation times (G) were longest for individuals fed aggregate BOM and similar for all other treatments. Net reproductive rate (R_0) was 2.5–5.5 times higher for individuals reared on CT_{high} than for those fed the other treatments and was lowest for animals fed particulate BOM.

Somatic growth rates were as high as 89% d⁻¹ and 75% d⁻¹ for individuals reared with CT_{high} and CT_{med}, respectively (Fig. 3A,C). Maximum somatic growth rates were 73% d⁻¹ for *Eurycerus* reared on CT_{low} (Fig. 3E), 60% d⁻¹ for individuals reared on particulate BOM (Fig. 3G), and 51% d⁻¹ for *Eurycerus* fed aggregate BOM (Fig. 3I). Differences between somatic and total growth rates were observed for reproductive females reared on CT_{high}, CT_{med}, and both forms of BOM (Fig. 3). When *Eurycerus* became reproductive, ≈ 60 –90% of the biomass produced between molts was represented by eggs for individuals fed CT_{high}, CT_{med}, and aggregate BOM (Fig. 4A–C). Females fed particulate BOM allocated less energy into egg production (Fig. 4D), and females fed CT_{low}, autoclaved BOM, and FWW did not successfully produce eggs. Of those individuals that did reproduce, the mean contribution of eggs to total growth over an individual’s lifetime ($G_{E(L)}$) ranged from 10% to 38% (Table 3). The percentage of growth allocated toward reproduction was similar for *Eurycerus* reared on aggregate BOM and the CT_{high} treatment, which was 2–4 times higher than the $G_{E(L)}$ of individuals reared on particulate BOM or CT_{med}.

The relationship between somatic growth ($\log g_s$) and mass ($\log W$) was significant for individuals reared on CT, aggregate, and particulate BOM treatments and explained 48–72% of the variance (Table 4). Slopes ranged from -1.07 to -1.28 and were not significantly different among the treatments (ANCOVA, $F_{4,200} = 1.02$, $p > 0.05$). The y -intercepts for somatic growth equations were significantly higher for CT_{high} and CT_{med} than the other three treatments (ANCOVA, $F_{4,200} = 18.39$, $p < 0.05$; Tukey, $q > 3.858$) but were not significantly different for individuals reared on CT_{high} and CT_{med} (Tukey, $q = 1.18$, $p > 0.05$). Although regression coefficients for total growth were significant, they explained only 0.07–32% of the variance, and the slopes were not significantly different (ANCOVA, $F_{4,200} = 1.28$, $p > 0.05$). The y -intercepts for total growth equations were significantly higher for individuals reared on CT_{high} and CT_{med} than those fed aggregate and particulate BOM (ANCOVA, $F_{4,200} = 12.5$, $p < 0.05$; Tukey, $q > 3.858$) but were not significantly different among individuals reared on CT_{high} and CT_{med} (Tukey, $q = 1.89$).

Discussion

There are several assumptions inherent to the approach taken in this study with regard to radiolabeling bacteria and algae and the subsequent incorporation of ¹⁴C by *Eurycerus*. First, it is assumed that the radiolabels were incorporated specifically by the targeted organisms (i.e., algae or bacteria). Several investigations have shown that, over a wide range of concentrations, the uptake of acetate is due almost exclusively to bacteria and is negligible by sediment algae (Wright and Hobbie 1966; Munro and Brock 1968); similarly, Carmen (1990) showed that ¹⁴C-bicarbonate is taken up only by algae. Second, it is important that the specific activity did not change markedly during the feeding period. Pilot studies were used to determine the time frame during which the uptake of radiolabel by algae and bacteria reached an asymptote; thus, the major concern is with the decrease of radioactivity over time. Although the BOM was not measured directly during the 7.25-h study, the continual increase of incorporated radiolabeled food by *Eurycerus* during this study suggests that the specific activity was not substantially decreased. Decreased ingestion of ¹⁴C-labeled algae and bacteria between 6 and 7 h may be an indication

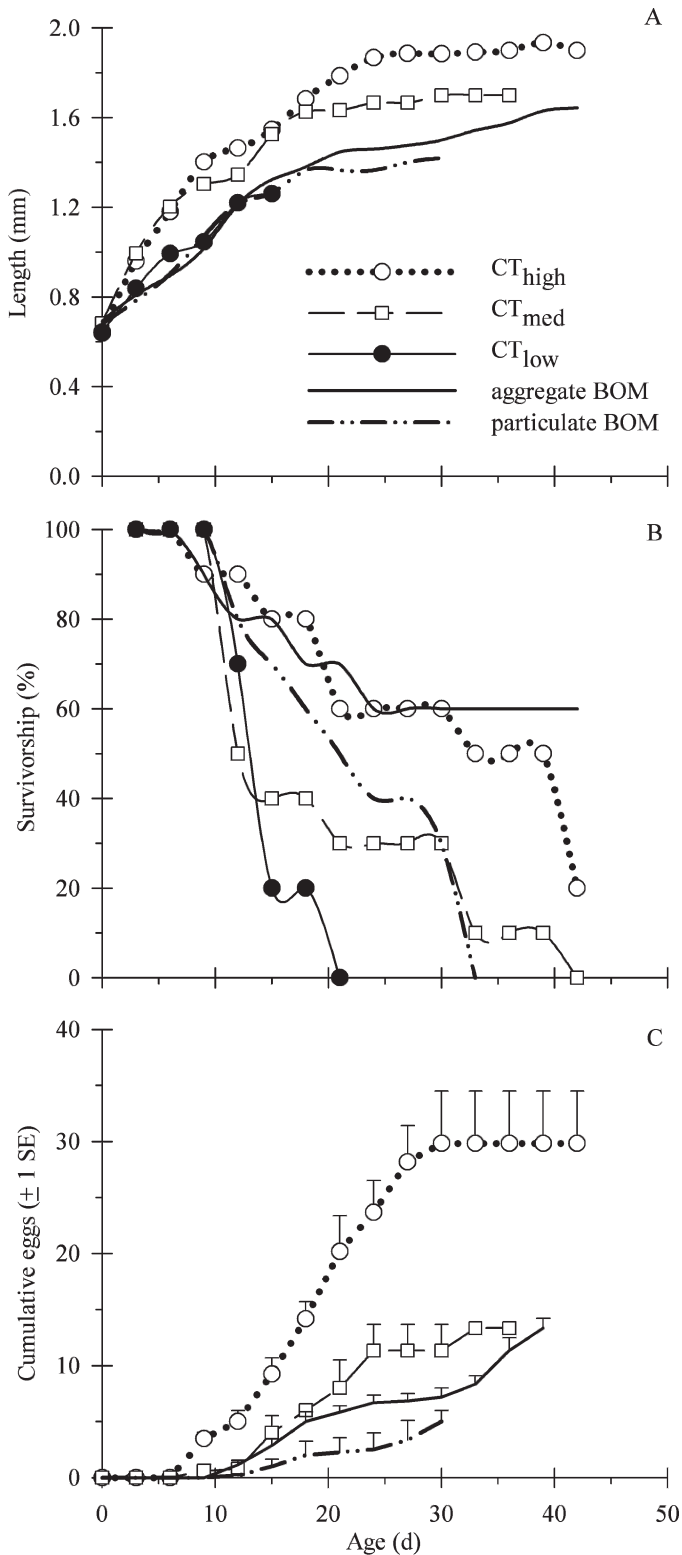


Fig. 2. Mean (A) length (± 1 SE), (B) survivorship, and (C) cumulative egg production (± 1 SE) versus age for *Eurycerus vernalis* fed cultured food (natural light with added nutrients (CT_{high}), natural light (CT_{med}), or low light (CT_{low}), or wetland benthic organic matter (aggregate BOM or particulate BOM). Individuals fed particulate autoclaved BOM did not grow or reproduce; thus, values for this treatment are not included.

of decreasing radioactivity of the food material, but this cannot be substantiated by data from this study. Third, we have assumed that purging $^{14}CO_2$ from the labeled solutions and rinsing any unincorporated radiolabel from the samples substantially reduced any excess transfer of $^{14}CO_2$ from the bacteria to the algae during the feeding period.

Incorporation of microbial carbon associated with BOM

Similar incorporation patterns of radiolabeled algal and bacterial carbon by *Eurycerus* indicate that these microcrustaceans are not selective feeders but that they indiscriminately ingest algae and bacteria associated with the BOM as part of their diet. These results were supported by the concurrent fivefold difference between the measured radioactivity of *Eurycerus* fed aggregate BOM labeled with ^{14}C -bicarbonate and ^{14}C -acetate and the concentrations of algal and bacterial carbon associated with the aggregate BOM food source itself. Nonselective feeding habits were also observed for the European species *E. lamellatus* by Fryer (1963), who reported that the relative amounts of diatoms, plant fragments, and inorganic particles found in the gut contents of *E. lamellatus* reflected food resource availability. Although Fryer (1963) reported that *E. lamellatus* exhibited little selectivity, he did observe them to reject large filamentous fragments of *Oscillatoria* and *Spirogyra*.

Because *Eurycerus* do not feed selectively, their growth and reproduction rates will undoubtedly reflect the biomass and quality of organic matter available in BOM. However, incorporated algae met only 38% of fifth-instar *Eurycerus* carbon requirements for growth and reproduction, with an additional 8% provided by bacterial carbon. Thus, approximately 54% of the carbon required for growth of fifth-instar *Eurycerus* was not provided by the algae or bacteria but presumably by nonlabeled microbes (e.g., fungi, protists), microbial exudates, or detrital components of the BOM. Reduced survival of *Eurycerus* fed autoclaved detritus suggests that detritus alone contributes little to *Eurycerus* nutrition and that the nonlabeled microbes and microbial exudates, in addition to algae and bacteria, support *Eurycerus* growth and reproduction. In planktonic systems, detritus as a food resource has generally been found to support lower zooplankton growth and reproductive rates than edible algae. Results from such studies are equivocal, however, and appear to vary according to zooplankton species and trophic state of the system. Hessen et al. (1990) reported that the incorporation of epilimnetic algal, bacterial, and detrital carbon was strongly species-dependent and that detrital particles supported 46–82% of body carbon for five planktonic species. Hessen et al. (1990) suggest that fluxes of carbon from detritus to zooplankton are significant pathways of energy transfer that characterize acidic, humic lakes in which the detritus rather than phytoplankton dominates the particulate organic carbon pool. In contrast, Ojala et al. (1995) found detrital material to be of limited nutritive value to *Daphnia longispina* population growth in a polyhumic lake,

Table 3. Mean (± 1 SE) age (A_R), length (L_R), and mass (W_R) at first reproduction, lifetime number of clutches female⁻¹, number of eggs produced clutch⁻¹, % biomass allocated toward egg production over an individual's lifetime ($G_{E(L)}$), innate capacity of population increase day⁻¹ (r), generation time (G) in days, and net reproductive rate (R_0) for *Eurycerus vernalis* reared with laboratory-cultured treatments (CT) or wetland benthic organic matter (BOM). Means designated by different letters are significantly different ($\alpha = 0.05$; Kruskal–Wallis one-way analysis of variance, followed by Dunn's all-wise comparison if significant or analysis of variance followed by Tukey's honest significant difference method). Individuals fed particulate autoclaved BOM and cultured food under low light conditions (CT_{low}) did not reproduce; thus, these values are not included.

Treatment	A_R (days)	L_R (mm)	W_R (μg)	Eggs clutch ⁻¹	Clutches female ⁻¹	Clutches lifetime ⁻¹	$G_{E(L)}$ (%)	R	G	R_0
CT _{high}	9.4 a (0.6)	1.4 a (<0.1)	33.0 a (0.8)	5.9 a (0.4)	4.5 (0.6)	35	36	0.14	20.8	19.8
CT _{med}	11.6 ab (0.7)	1.5 a (<0.1)	35.5 a (2.0)	3.3 b (0.4)	3.7 (0.7)	11	17	0.06	20.2	3.6
Particulate BOM	14.1 b (0.9)	1.3 b (<0.1)	25.7 b (1.5)	1.7 b (0.3)	3.0 (0.1)	6	10	0.00	18.6	1.0
Aggregate BOM	13.4 b (0.4)	1.3 b (<0.1)	26.6 b (1.2)	2.5 b (0.2)	4.3 (0.3)	25	38	0.07	29.6	7.7

even though 75% of carbon was bound in particulate detritus.

Seasonal changes in food resource availability and quality can influence the relative importance of microbial and detrital carbon to microcrustacean consumers. Grey et al. (2001) reported a seasonal pattern of food resource utilization in an oligotrophic, temperate lake in which zooplankton relied on allochthonous particulate organic matter during winter months and switched to algal-derived autochthonous carbon during the summer. Similarly, microbial food web studies conducted by Hart et al. (2000) showed that the relative importance of bacteria and protists in planktonic cladoceran diets varied according to season and availability of edible phytoplankton. Benthic microbial production in the Talladega wetland exhibited distinct seasonal variation over the time period (1993–1994) that we conducted our incorporation and growth experiments (Stanley et al. 2003). Aggregate BOM that was radiolabeled for the incorporation experiment was collected from the Talladega wetland during March 1994, a time period that coincided with low and intermediate production of benthic bacteria and algae, respectively (Stanley et al. 2003). Thus, our conclusion that aggregate BOM contained insufficient algal and bacterial biomass to support *Eurycerus* growth during this time period suggests that other food resources are utilized by *Eurycerus* during those periods of reduced algal and bacterial availability. Comparatively higher benthic microbial production during previous and successive months suggests that there were time periods in which adequate algal and bacterial resources could sustain *Eurycerus* populations. Bacterial production did exceed algal production on occasion; however, estimates of daily algal production on sediments were generally 2- to 25-fold higher than that of bacteria for any given month (Stanley et al. 2003). Although the relative importance of algal, bacterial, and other microbial resources varied temporally, high benthic algal production suggests that algae were a primary food resource for *Eurycerus* populations in the Talladega wetland.

There are several possible explanations for the low respiration and egestion measured during this study. *Eurycerus* may require longer than the 8 h allowed in this study to respire ¹⁴C-labeled food. In a similar study, Schindler (1968) reported that the large planktonic cladoceran, *Daphnia magna*, did not respire ¹⁴CO₂ until

more than 16 h after the initial ingestion of the unlabeled food even though they egested radioactive food within 30–60 min of being transferred to nonradioactive food. In addition, because *Eurycerus* populations were not fed while they were in the respiration chambers, they may not have completely cleared their guts of radiolabeled food.

Microbial contribution to detritivore growth and reproduction

High quantities of algae and bacteria did not necessarily predict the ability of *Eurycerus* to utilize a particular food treatment for growth and reproduction. *Eurycerus* juveniles initially grew faster when fed cultured treatments, despite the lower algal biomass (i.e., CT_{low}) and bacterial biovolume (i.e., CT_{low}, CT_{med}, and CT_{high}) associated with these treatments versus the aggregate BOM treatment. Lower growth rates of *Eurycerus* reared on aggregate BOM suggest that the added detrital component decreased overall food quality relative to cultured treatments. Consumers fed detritus typically reflect the assumed lower quality of this resource by exhibiting reduced assimilation efficiencies, ranging between 20% and 35% for *E. lamellatus* and generally <20% for benthic and planktonic microcrustaceans (Smirnov 1962; review in Berrie 1976; Hessen et al. 1990). Similarly, growth and reproduction patterns of *E. vernalis* reflected increased utilization of algae and bacteria with decreased quantities of associated detritus.

Higher growth rates for *Eurycerus* fed CT_{high} versus those fed wetland BOM may also be related to the higher food quality of benthic algae cultured under high-nutrient laboratory conditions. Higher growth and reproduction for planktonic zooplankton fed algal diets grown on high-nutrient media have been well documented (e.g., Groeger et al. 1991; Kilham et al. 1997). In addition, high nutrient conditions may have altered the algal species composition in such a way as to increase the availability of edible species. *E. lamellatus* has been reported to be unable to utilize some small green algae and to reject some large, filamentous algae that may be present in BOM (Smirnov 1962; Fryer 1963). The comparably lower growth rates for *Eurycerus* fed wetland BOM (particulate and aggregate) suggest that the overall quality of the natural wetland food was less optimal than CT_{high} for growth and reproduction.

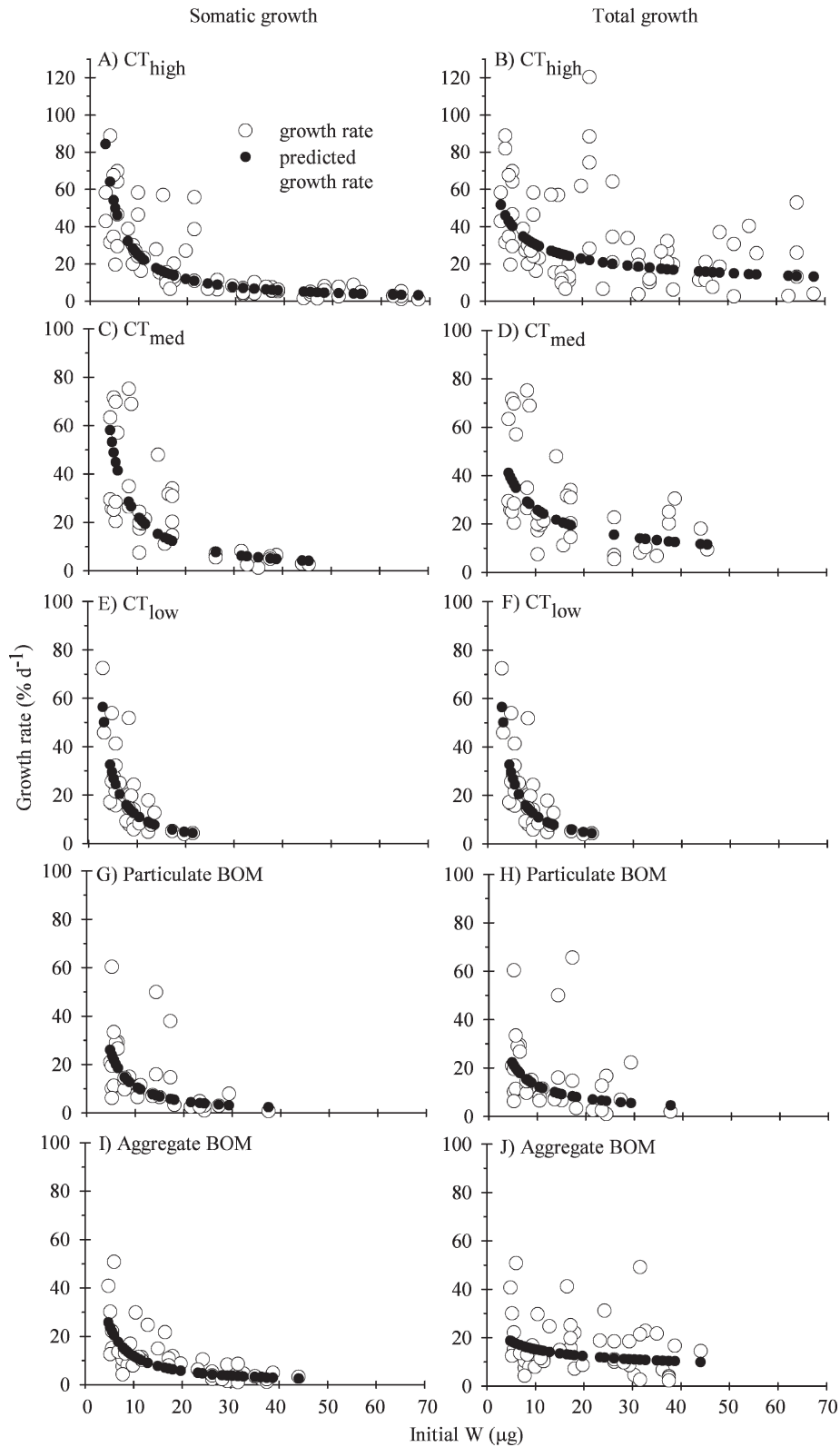


Fig. 3. Somatic and total growth rates versus individual dry mass of *Eurycerus vernalis* fed cultured food ((A, B) natural light with added nutrients (CT_{high}), (C, D) natural light (CT_{med}), or (E, F) low light (CT_{low})), or wetland benthic organic matter ((G, H) particulate BOM or (I, J) or aggregate BOM). The filled circles represent predicted total and somatic growth rates based on mass-specific linear regression equations developed for *E. vernalis*. Individuals fed particulate autoclaved BOM did not grow; thus, values for this treatment are not included.

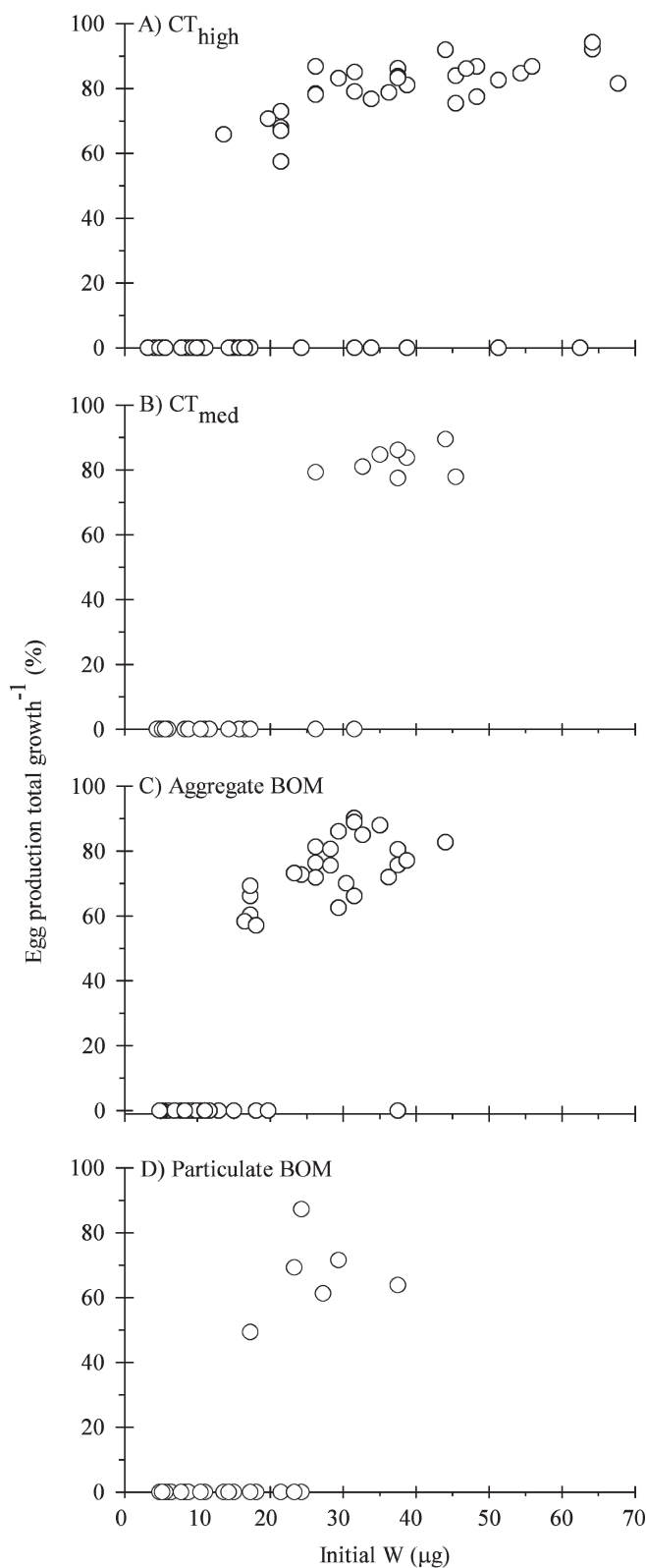


Fig. 4. The percentage of biomass allocated toward egg production by *Eurycerus vernalis* fed cultured food ((A) natural light with added nutrients (CT_{high}) or (B) natural light (CT_{med})) or wetland benthic organic matter ((C) aggregate BOM or (D) particulate BOM). Individuals fed particulate autoclaved BOM and food cultured under low light conditions (CT_{low}) did not reproduce; thus, these values are not included.

Growth rates for *Eurycerus* fed aggregate and particulate BOM in this study fell within the lower range of previously recorded growth rates in which individuals were grown at 20°C on wetland BOM (Lemke and Benke 2004). Because experimental growth rates represent those that occur in the field, results from these studies support the previous assumption that food quality and quantity vary seasonally for wetland populations of *Eurycerus*. Sustained growth and reproduction by individuals reared on aggregate BOM suggest that similar supplementary sources of carbon available in the sediments (e.g., exudates, fungi, protists) are utilized by *Eurycerus* during periods of low algal productivity, as has been reported from planktonic habitats (Hart et al. 2000).

The effect of food type was especially noticeable in the growth of early instars and reproductive ability of adults. Significantly higher cumulative egg production and R_0 of individuals fed CT_{high} were the combined results of the high percentage of females that lived to reproduce, early reproduction, and the production of larger clutch sizes. Increased egg production by individuals fed CT_{high} may have resulted from the ingestion of different algal species (e.g., Vargas et al. 2006) associated with high-nutrient conditions; however, it was more likely related to the allocation of less energy toward processing detritus relative to egg production. Although growth rates and reproductive output were lower for individuals fed aggregate BOM, the overall production of eggs represented a similar fraction of these individuals' lifetime production (38%) as individuals reared on CT_{high} (36%), which were both higher than individuals reared on CT_{med} treatments (17%) and particulate BOM (10%). The amount of overall growth allocated toward egg production was lower for individuals in all treatments compared with previous studies (60%, Lemke and Benke 2004); however, upon maturation, egg production constituted 67–82% of total production, which falls within the range from previous studies (81%, Lemke and Benke 2004).

Individuals reared on CT_{high} and CT_{med} exhibited lower survivorship than those fed aggregate BOM. Reduced life spans have also been observed for several planktonic cladocerans and copepods fed treatments enriched with algae (Pace et al. 1983; Martínez-Jerónimo et al. 1994; Hopp et al. 1997) and have been attributed to higher energetic costs of reproduction and increased metabolic requirements involved with feeding on nutrient-rich food. Survivorship was high at the termination of the study for females fed aggregate BOM, and cumulative egg production was increasing as females continued to produce new eggs. High survivorship and the percentage of growth allocated toward egg production by females fed aggregate BOM suggest that cumulative egg production would have been higher for these individuals had the study been extended.

Energy flow through benthic assemblages

Combined studies of the Talladega wetland suggest that benthic microbial production supports high secondary production of benthic microcrustaceans, especially during

Table 4. Linear regression coefficients for $\log g_{(s \text{ or } t)} = Y - a(\log W)$, where g_s = somatic growth, g_t = total growth, and W = dry mass for *Eurycercus vernalis* juveniles reared on food that was cultured in the laboratory under varied light and nutrient levels (CT) or wetland benthic organic matter (BOM). Statistical differences were tested by analysis of covariance followed by modified Tukey's multiple comparison, if statistical differences existed ($p < 0.05$). Coefficients with different letters indicate significant differences. Individuals fed particulate autoclaved BOM did not grow; thus, values for this treatment are not included ($*p < 0.05$; $**p < 0.001$).

Treatment	y-intercept		Slope		R ²		n
	Somatic	Total	Somatic	Total	Somatic	Total	
CT _{high}	2.47 a	1.94 a	-1.08	-0.45	0.72**	0.20**	69
CT _{med}	2.51 a	1.97 a	-1.15	-0.55	0.64**	0.32**	39
CT _{low}	2.35 b	—	-1.28	—	0.63**	—	32
Particulate BOM	2.22 b	1.88 b	-1.18	-0.78	0.48**	0.23**	38
Aggregate BOM	2.14 b	1.47 b	-1.07	-0.29	0.61**	0.07*	52

winter, when planktonic microbial and zooplankton production is low (Lemke 2000; Stanley et al. 2003; Lemke and Benke 2004; this study). *Eurycercus* populations emerge from ephippia in early fall, reproduce parthenogenetically throughout winter, and begin producing ephippia in early-late spring (Lemke and Benke 2004), contributing 11–18% of total annual microcrustacean production in vegetated *Nymphaea* habitats (Lemke 2000). High densities of late-instar detritivorous harpacticoids also emerged from diapausal cysts during fall and reproduced throughout the winter, contributing 28–54% of total annual microcrustacean production in open-water habitats of the Talladega wetland (Lemke 2000). Benthic algal production during the winter remained relatively high compared with bacterial production (Stanley et al. 2003) and supports our previous conclusions from this study that benthic algal carbon represents an important contribution to *Eurycercus* secondary production. Feeding and growth studies suggest that bacteria were likely utilized primarily as a supplementary source of carbon (e.g., Pace et al. 1983; Lair 1991); however, temporal variation in benthic bacterial production (Stanley et al. 2003) may have altered the relative importance of bacterial carbon to *Eurycercus* growth and reproduction during the spring and winter months. The growth and survival of benthic detritivores have also been shown to be positively correlated with labile organic matter content associated with detritus collected from lake and stream sediments (Vos et al. 2002). Our study was limited to characterizing the algal and bacterial carbon associated with BOM and did not attempt to separate out other components (e.g., exopolymers, feces) that may have directly or indirectly provided supplementary energy resources to *Eurycercus* (e.g., Wotton 2007). Given the dynamics of benthic microbial productivity and nutritional quality, the ability to utilize multiple carbon sources associated with detritus should be beneficial to benthic detritivores.

In conclusion, we have demonstrated the functional importance of benthic algal and bacterial carbon to microcrustacean growth and reproduction and explored the implications of detrital food web pathways for secondary production of benthic detritivores in wetland ecosystems. *E. vernalis* does not appear to feed selectively but appears to be capable of utilizing the algal and bacterial

resources that are available. Both algae and bacteria were incorporated by *Eurycercus* and were important constituents of the BOM for *Eurycercus* growth and reproduction. Algal and bacterial carbon accrued as biomass by *Eurycercus* represented only 46% of the carbon required for growth, suggesting carbon from detrital or other microbial components of the BOM is important. Higher availability of algal carbon in the BOM suggests that benthic algae support growth and reproduction of *Eurycercus*; however, temporal changes in the ratio of algal:bacterial carbon likely alter the relative importance of these food resources to *Eurycercus* population growth. Indiscriminate ingestion and incorporation of benthic microbial carbon into consumer secondary production by *Eurycercus* and other detritivores in the Talladega wetland may provide an important pathway for energy flow from sedimentary carbon sources to other benthic or planktonic predatory consumers.

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