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LIFE HISTORY AND TROPHIC BASIS OF PRODUCTION OF THE MAYFLY *CALLIBAETIS FLUCTUANS* (WALSH) (EPHEMEROPTERA: BAETIDAE) IN A MITIGATED WETLAND, WEST VIRGINIA, USA

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Abstract: We determined the life history, secondary production, and trophic basis of production for *Callibaetis fluctuans* in a mitigated wetland at the Green Bottom Wildlife Management Area, Cabell County, West Virginia, USA. Quantitative benthic samples were collected from three sites covering a range of water depths and vegetation types from January to December 1994. Length-frequency histograms were constructed for each sample date, and secondary production was calculated using the size-frequency method. Foregut analyses were conducted seasonally to determine diet. *Callibaetis fluctuans* had a multivoltine life cycle with at least three cohorts. Fast larval growth occurred during the spring and fall, whereas an overwintering cohort had slower growth. Total annual production was 208.0 $mg \cdot m^{-2} \cdot yr^{-1}$ (AFDM) with a production-to-biomass ratio of 12.6. Amorphous detritus comprised >80% of the diet in all seasons and accounted for 70% of total production. To account for this production, *C. fluctuans* consumed 3675 $mg \cdot m^{-2} \cdot yr^{-1}$ of detritus. This is one of the first studies to provide production estimates for an aquatic insect in a permanently inundated wetland.

Key Words: wetland, aquatic insect, *Callibaetis*, secondary production, diet, life history, detritus

INTRODUCTION

In the early 1900s, government incentives to create land for agriculture resulted in the draining of many wetlands. In recent years, however, an awareness of the natural value of wetlands has increased greatly. Wetlands are now recognized for their value in water purification and floodwater retention, for their use by migratory waterfowl, as recreational areas, and as a unique habitat for many plants and animals (Mitsch and Gosselink 1993, Sharitz and Batzer 1999). Section 404 of the Clean Water Act requires that the loss of wetlands due to human activities must be mitigated by restoring or creating other wetlands (Kusler and Ketula 1990). As a result, created wetlands are now common in the United States. However, our knowledge of the biological or ecological ‘‘success’’ of these created wetland systems is lacking (Fairchild et al. 1999).

Aquatic insects are abundant in many wetlands and comprise a key component of the trophic structure (Fairchild et al. 1999), yet we know relatively little about insect communities in these systems. Because of the success of using invertebrates as indicators of ecosystem function and community health in other freshwater habitats (Plafkin et al. 1989, Rosenberg and Resh 1993, Merritt and Cummins 1996, Wallace et al. 1996, Karr and Chu 1999), monitoring invertebrate populations in wetlands may be a valuable conservation tool.

Several studies have compared invertebrate communities in created wetlands with those of natural systems (e.g., Streever and Crisman 1993, Scatolini and Zedler 1996, Streever et al. 1996, Fairchild et al. 1999). These studies have focused on colonization rates, taxonomic composition, or trophic structure.

However, the determination of ecological ''success'' has been hindered by not measuring secondary production. Secondary production is the best way to determine the ''success'' of a population because it incorporates abundance, biomass, growth, reproduction, and survival (Benke 1993). Secondary production estimates are therefore a vital link between populations and ecosystems and provide a useful measure of ecosystem function. Our knowledge of invertebrate production in wetlands lags far behind that of lakes and streams (Smock 1999). Information on insect production in permanently inundated wetlands and created wetlands is particularly rare.

The trophic basis of production estimates the amount of resources consumed to account for observed secondary production (Benke and Wallace 1980) and can be calculated with additional data for larval diet. Trophic basis of production is a valuable measure because it is the best estimate of the role of taxa in food web dynamics (Benke and Wallace 1997).

The goals of this study were to examine the life history, secondary production, and trophic basis of production of the mayfly *Callibaetis fluctuans* (Walsh) in a mitigated wetland. This study was designed to add to our knowledge of mayfly life histories and to provide much needed information on secondary production in wetland ecosystems. *Callibaetis fluctuans* is widely distributed in North America, ranging from southern Canada to Louisiana (Check 1982). Mayflies in the genus *Callibaetis,* which inhabit lentic environments, are unusual in that they are ovoviviparous (Berner 1941, Edmunds 1945, Gibbs 1979) and are tolerant of low dissolved oxygen (Edmunds et al. 1976, Berner and Pescador 1988). Members of this genus also possess chloride cells in their integument that function in osmoregulation (Wichard et al. 1973), and at least one species, *C. floridanus,* has been collected in brackish water (Berner and Sloan 1954). Previous studies have shown that most *Callibaetis* species are either multivoltine (Trost and Berner 1963, Gibbs 1979, Clifford 1982) or bivoltine (Christman and Voshell 1992). However, the only life-history information for *C. fluctuans* is from Canada (Judd 1949). Determination of life history and production for multivoltine insects is often difficult as a result of rapid growth and asynchronous development (e.g., Benke and Jacobi 1986, Benke 1993). The fact that *Callibaetis* adults are relatively long-lived (Edmunds et al. 1976) adds to this problem. Extended oviposition periods can also lead to the simultaneous presence of many instars (Winterbourn 1974, 1978).

Study Site

The Green Bottom Wildlife Management Area (GBWMA) is adjacent to the Ohio River in Cabell Co., West Virginia, USA (82° 14′00 W, 35°00′30″N). The GBWMA was established as a mitigation area incurred by the building of the Gallipolis Locks and Dam replacement project. The area encompasses ca. 330 ha and contains forests (65 ha), agricultural land (209 ha), and natural riparian wetlands (56 ha). The GBWMA is a refuge for a diversity of wildlife and is used heavily by migratory waterfowl (WVDNR 1991).

In 1990, the U.S. Army Corps of Engineers (Huntington District) increased wetland area in the GBWMA by installing a levee along its western boundary along with a pumping station on the Ohio River. Although the pumping station was never used, rainwater permanently filled the new area, adding about 40 ha of wetland within the GBWMA. The integrity of an existing wetland was maintained by installation of a preservation weir.

After four years of inundation, flora that have colonized the new wetland include common rush (*Juncus effusus* L.), large burreed (*Sparganium eurycarpum* Engelm.), reed canary grass (*Phalaris arundinacea* L.), water smart weed (*Polygonum amphibium* L.), mild water pepper (*Polygonum hydropiperoides* Michx.), cattail (*Typha latifolia* L.), watermeal (*Wolffia punctata* Griseb.), and duckweeds (*Lemna minor* L. and *Spirodela polyrhiza* [L.] Schleid.). The area is relatively open and lacks mature woody vegetation along its margin. The wetland remains inundated throughout the year, although water level fluctuates greatly with season. A maximum water depth of ca. 2 m occurs in early spring after snowmelt. The annual mean water depth is ca. 0.5 m. Water is slightly alkaline, with a pH range of 7.0–7.8. In 1994, near surface dissolved oxygen ranged from 6 mg/L in June to 12 mg/L in December and February. Temperature data were collected for each sample date from April through October using a max/min thermometer. The thermometer was not retrievable in other months due to ice cover and high water. However, the available temperature data cover most of the critical period of growth and emergence for *Callibaetis.* Monthly average water temperatures ranged from 17.3 °C in October to 26.3 °C in June; the mean was 22.1°C.

MATERIALS AND METHODS

Callibaetis fluctuans was collected from three sites within the mitigated wetland from January to December 1994. The three sites were chosen to cover the range of vegetation types and water depths present. Site 1 was a shallow site (mean = 28 cm) dominated by *J. effusus.* Site 2 was a deep site (mean = 66 cm) dominated by *P. arundinacea,* and Site 3 was also a deep site (mean = 55 cm) dominated by *P. coccineum* and *P. hydropiperoides.* Collections were made monthly except from April 24 to October 28, when samples were collected weekly because we suspected that *C. fluctuans* grew rapidly during this time. Three samples were collected at each site on each collection date (n = 252) using a box sampler (48.26 cm × 48.26 cm × 78.74 cm) and a D-shaped dredge (1-mm mesh). Collection of early instar larvae was limited by the relatively large mesh size (Zelt and Clifford 1972). The box sampler was placed in the vegetation and pressed 5 cm into the substrate. The dredge was then inserted into the sampler and scraped across the substrate. Samples were placed in plastic bags, preserved with 70% ethanol, and returned to the lab for sorting.

Adults were collected using two "DAY" emergence traps (61 cm × 61 cm) (LeSage and Harrison 1979) that were placed in the wetland from April 24 to October 28, 1994. Traps were placed over emergent vegetation at two sites where benthic samples were collected. Traps were checked weekly for adults.

In the laboratory, *C. fluctuans* larvae were removed from the benthic samples using a dissecting microscope. Total body length was measured for all larvae using a digitizer. The length measurements were categorized into 0.5-mm size classes, and size-frequency histograms were constructed for each sample date. Weekly sampling dates were combined (n = 14) when there was no apparent change in the size-frequency distributions.

To estimate secondary production, biomass was first determined using a length-mass regression for *Callibaetis* sp.: dry mass = 0.00081 × length $^{3.547}$ (Benke et al. 1999). Dry mass was then multiplied by 0.928 to convert to ash-free dry mass (AFDM) (Benke et al. 1999). Annual production was calculated by the size-frequency method (Hynes and Coleman 1968, Hamilton 1969). The annual production/biomass (P/B) turnover ratio was calculated using a weighted mean of monthly biomass because the sampling intervals were unequal over the year. The cohort production interval (CPI) (Benke 1979) was estimated from size-frequency distributions.

Foregut analyses were conducted seasonally (April, July, October, and December 1994) using three larvae, one from each of three size classes, for each season. Foreguts were removed with microdissecting scissors, placed into 3 ml of water with three drops of iodine, and homogenized. One ml of the homogenate was placed in a Sedgwick-Rafter cell. A compound microscope equipped with a Whipple ocular grid was then used to randomly survey 30 grids for each individual in each season. The relative abundance of food items was determined by calculating percentages of Whipple grid squares within each field. Gut contents were categorized into amorphous detritus, filamentous algae, diatoms, and minerals.

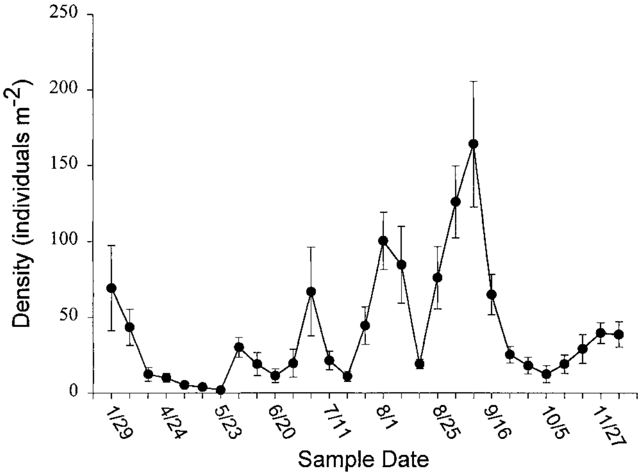

Figure 1. Densities of larval *Callibaetis fluctuans* by sample date in 1994 from the Green Bottom Wildlife Management Area (GBWMA), WV. Bars represent one standard error.

To determine the trophic basis of production, we used assimilation efficiencies of 30% for filamentous algae and diatoms and 10% for amorphous detritus, as reported by Benke and Wallace (1980). A net production efficiency of 40% was used for all food categories (Webster 1983, Smock and Roeding 1986). Although production and assimilation efficiencies differ among species and are influenced by external factors such as food quality and temperature (Sweeney and Vannote 1981), the values used here are consistent with previous studies and should provide reasonable estimates for *C. fluctuans.*

RESULTS

Larval densities were generally low throughout the year, with highest densities occurring in September. There were four successively increasing peaks in abundance during the year (Figure 1), which indicates that there may have been four cohorts. However, analysis of the size-frequency histograms (Figure 2) showed only three cohorts clearly. Unfortunately, attempts to collect quantitative emergence samples were unsuccessful. However, it was evident from larval size distributions that three emergence periods occurred: Cohort 1—March through May, Cohort 2—late June, and Cohort 3—late September-early October. During July and August, larval growth slowed compared to spring and fall. Larvae of the largest size class (10.5–10.9 mm) were found only in Cohort 1 during April and May.

Because the second and third cohorts reached a smaller terminal size, we calculated production separately for each cohort to be conservative. As a result,

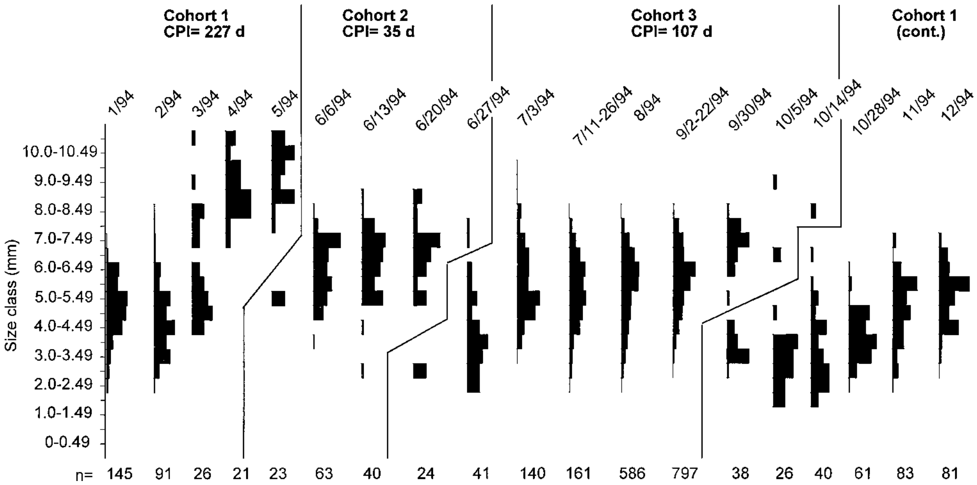

Figure 2. Length-frequency histograms for larval *Callibaetis fluctuans* from the Green Bottom Wildlife Management Area (GBWMA), WV. Figure divided into cohorts with their respective cohort production interval (CPI). Bars represent the percentage of total larvae in each size class on each sample date. n = number of larvae collected on each sample date.

correcting for the CPI was unnecessary. In addition, the first size classes were omitted from the analyses when production was negative because these early instars are difficult to accurately sample and stadia are short. Omission of early size classes had a 7–14% effect on the overall annual production estimate. Treating each cohort individually, we estimated a CPI of 227 d for Cohort 1, 35 d for Cohort 2, and 104 d for Cohort 3 (Figure 2). Secondary production was estimated as 44.50, 37.12, and 126.39 mg·gm^{-2}·yr^{-1} (AFDM) for cohorts 1, 2, and 3, respectively (Table 1). Total annual production for *C. fluctuans* was 208.0 mg·m^{-2}·yr^{-1} (AFDM), with an annual P/B ratio of 12.6.

Results from the dietary analysis showed that *C. fluctuans* was a detritivore (Figure 3) and would therefore be considered a collector-gatherer. Amorphous detritus comprised >80% of fore-gut contents in all seasons. Filamentous green algae comprised 4–18% of the diet. Diatoms and minerals were seldom encountered. Only minor seasonal changes in diet were apparent; the proportion of detritus increased slightly from spring to winter, whereas filamentous green algae decreased over the same period. There were no apparent differences in food types between early and late instars.

Approximately 70% of *C. fluctuans* production was attributed to amorphous detritus, while the remainder was due to filamentous green algae (Table 2). To account for this production, larvae would have consumed approximately 3,675 and 500 mg·m^{-2}·yr^{-1} of detritus and green algae, respectively. The total amount of egestion was 3,663 mg·m^{-2}·yr^{-1}.

DISCUSSION

The size-frequency histograms indicated there were probably three cohorts during the year. The only other study on the life history of *C. fluctuans* reported a univoltine population in an Ontario marsh (Judd 1949). However, colder temperatures at higher latitudes often result in slower growth and fewer generations per year (Sweeney 1984, Newbold et al. 1994). Warm summer temperatures in the GBWMA wetland undoubtedly increased growth and development (Sweeney 1984, Newbold et al. 1994) compared to the Ontario population. Multivoltinism is common among members of the family Baetidae (see Wallace and Anderson [1996] for review) and has been documented for numerous mayfly species in a subtropical river (Jacobi and Benke 1991, Benke and Jacobi 1994).

The effect of temperature on life cycles is apparent when comparing the three cohorts of *C. fluctuans*. Larvae in Cohort 1 overwintered, had the longest development time (227 d), and had the lowest production as a result of reduced growth. However, the larvae of this cohort reached a larger terminal size than subsequent cohorts, which is common in multivoltine populations (e.g., Rhame and Stewart 1976, Illies 1979, Kondratieff and Voshell 1980, Wise 1980, Allan 1985). Larvae of Cohort 2 had the shortest generation time (35 d) as water temperatures rose 5°C from May to June. Several authors have reported faster larval development as a result of increasing temperature (Vannote and Sweeney 1980, Sweeney 1984, Jacobi and Benke 1991, Benke et al. 1992, Newbold et al. 1994). Cohort 3, however, is more difficult to interpret. The cohort development time of 107 d is longer than would

Table 1. Secondary production calculations for the 3 cohorts of *Callibaetis fluctuans* from the Green Bottom Wildlife Management Area, Cabell, Co., WV. (* = not included in final production estimates, AFDM = Ash-free dry mass).

Size Class	No./m^2	W (mg)	B (mg/m^2)	No. Lost	Weight at Loss (mg/m^2)	Biomass Loss (mg/m^2)	×10
Cohort 1							
1	0.2	0.001	0.0002	−1.7	0.01	−0.02	−0.2*
2	1.9	0.02	0.04	−2.5	0.05	−0.11	−1.1*
3	4.4	0.07	0.31	−1.7	0.12	−0.20	−2.0*
4	6.1	0.17	1.04	0.9	0.26	0.23	2.3
5	5.2	0.34	1.77	3.1	0.48	1.49	14.9
6	2.1	0.62	1.30	1.5	0.83	1.24	12.4
7	0.6	1.03	0.62	−0.1	1.32	−0.13	−1.3
8	0.7	1.60	1.12	0.3	1.99	0.60	6.0
9	0.4	2.38	0.95	0.0	2.89	0.00	0.0
10	0.4	3.39	1.36	0.4	3.39	1.36	13.6
	Total B (mg) =		8.50		Total mg (dry mass) =		47.90
	Total B (mg AFDM) =		7.89		Total mg (AFDM) =		44.45
					Cohort P/B =		5.64
Cohort 2							
1	0.0	0.001	0.00	−0.1	0.01	−0.001	−0.01*
2	0.1	0.02	0.002	0.0	0.05	0.00	0.0*
3	0.1	0.07	0.01	−0.6	0.12	−0.07	−0.6*
4	0.7	0.17	0.12	−2.4	0.26	−0.61	−4.9*
5	3.1	0.34	1.05	−0.8	0.48	−0.38	−3.0
6	3.9	0.62	2.42	−0.1	0.83	−0.08	−0.6
7	4.0	1.03	4.12	3.4	1.32	4.49	35.9
8	0.6	1.60	0.91	0.6	1.60	0.96	7.7
	Total B (mg) =		8.66		Total mg (dry mass) =		40.0
	Total B (mg AFDM) =		8.04		Total mg (AFDM) =		37.12
					Cohort P/B =		4.62
Cohort 3							
1	0.0	0.001	0.00	−1.5	0.01	−0.02	−0.2*
2	1.5	0.02	0.03	−2.5	0.05	−0.11	−1.0*
3	4.0	0.07	0.28	−4.2	0.12	−0.50	−4.5*
4	8.2	0.17	1.39	−4.5	0.26	−1.15	−10.4*
5	12.7	0.34	4.32	−3.0	0.48	−1.44	−13.0
6	15.7	0.62	9.73	9.5	0.83	7.84	70.6
7	6.2	1.03	6.39	5.4	1.32	7.10	63.9
8	0.8	1.60	1.28	0.7	1.99	1.39	12.5
9	0.1	2.38	0.24	0.1	2.38	0.24	2.2
	Total B (mg) =		23.66		Total mg (dry mass) =		136.20
	Total B (mg AFDM) =		21.96		Total mg (AFDM) =		126.39
					Cohort P/B =		5.76

Total annual *C. fluctuans* production = 208.0 $mg \cdot m^{-2} \cdot yr$.
Total standing stock biomass = 37.89 mg.
Annual P/B = 12.6

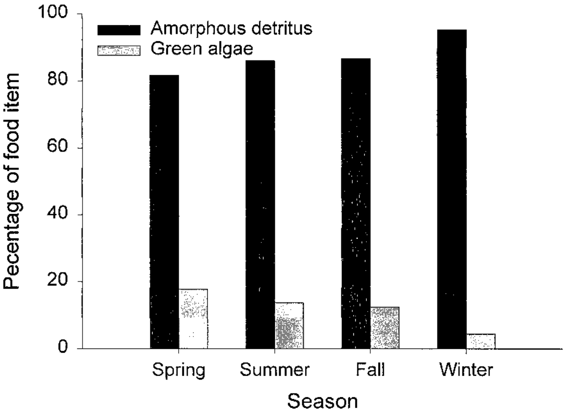

Figure 3. Foregut content of larval *Callibaetis fluctuans* by season from the Greenbottom Wildlife Management Area (GBWMA), WV.

be expected in the warm summer months. The histograms indicate that growth slowed dramatically from mid-July through late September even though temperatures were slightly lower than in June when growth and emergence occurred rapidly. It was possible that growth was reduced after reaching a threshold during the extended warm temperatures (Newbold et al. 1994). Cohort 3 also had the greatest production (126.39 mg·m^{-2}·yr^{-1}) which resulted from increased larval density. The larval abundance data and extended development time indicates that a fourth cohort may have been present during this period. If a fourth cohort were assumed, total annual production would increase to 334.4 mg·m^{-2}·yr^{-1} (126.39 multiplied by a CPI correction factor of 2). Our production estimate of 208.0 mg·m^{-2}·yr^{-1} based on three cohorts may therefore be conservative.

Interpreting the life history and production dynamics of *C. fluctuans* was problematic because of the simultaneous presence of multiple cohorts. As a result, it was difficult to clearly separate individual cohorts since their size did not vary greatly. In such cases, using individual growth rates to calculate production is often required (e.g., Benke and Jacobi 1986, Huryn and Wallace 1986, Huryn 1996). Adding to this difficulty was the fact that no adults were captured during this study. This was likely due to the relatively low densities of *C. fluctuans* in the wetland and the presence of only two emergence traps. Some species of *Callibaetis* are known to avoid emergence traps due to shading and their effects on surface tension (B. Kondratieff, Colorado State University, pers. comm.).

Our overall production estimate of 208.0 mg·m^{-2}·yr^{-1} was at the low end of the range of production reported for collector-gatherer taxa in streams (100–1000 mg·m^{-2}·yr^{-1}; Benke 1993). Comparison of *C. fluctuans* production with other insects in permanent wetlands is limited. Most studies have focused on seasonal wetlands (Gladden and Smock 1990, Duffy and LaBar 1994, Leeper and Taylor 1998, Huryn and Gibbs 1999) or non-insect taxa (White 1985, Taylor et al. 1989, Pickard and Benke 1996). Production of *Leptophlebia* sp. was a relatively low 284 mg AFDM·m^{-2}·yr^{-1} with a P/B of 14.2 in a seasonally inundated floodplain in Virginia (Gladden and Smock 1990). The only known production estimate for *Callibaetis* is from a bivoltine population in experimental ponds in Virginia (Christman and Voshell 1992). In that system, *C. floridanus* production was 814 mg AFDM·m^{-2}·yr^{-1}, with a P/B ratio of 16.4. Further studies are needed to determine whether these production estimates are indicative of those from natural, permanent wetlands. It has been shown that invertebrate production increases with inundation time in some temporary wetlands (Gladden and Smock 1990, Leeper and Taylor 1998, Smock 1999), but in permanent wetlands, occasional periods of anoxia and extreme temperatures may limit secondary production. Also, predation pressure may be greater in standing waters compared to running water because of a limited opportunity for immigration and emigration among adjacent habitats (Cooper et al. 1990, Sih and Wooster 1994).

Amorphous detritus was the principal dietary component throughout the year. The percentage of detritus in foreguts increased slightly during the year because

Table 2. Trophic basis of production for *Callibaetis fluctuans* (P = 208.0 mg AFDM·m^{2}·yr) from the Green Bottom Wildlife Management Area, WV.

	Food Type in Foregut (%)	Assimilation Efficiency (AE)	Net Production Efficiency (NPE)	Relative Amount to Production	Proportion of Production Attributed to Food Type (%)	Proportion of Production Attributed to Food Type (mg·m^{-2}·yr)	Gross Production Efficiency (AE × NPE)	Amount Food Type Consumed (mg·m^{-2}·yr)	Amount Egested as Detritus (mg·m^{-2}·yr)
Amorphous detritus	87.4	0.1	0.4	3.5	70.6	147	0.04	3675	3307.5
Filamentous algae	12.0	0.3	0.4	1.44	29	60	0.12	500	350
Diatoms	0.2	0.3	0.4	0.02	0.4	1	0.12	8	5.6

of a reduction in filamentous green algae in December. These results agree with others who have classified *C. fluctuans* as a collector-gatherer (Edmunds et al. 1976, Cushing and Rader 1981, Merritt and Cummins 1996).

Measuring the trophic basis of production is valuable because gut content analyses alone can be misleading since assimilation efficiencies vary by food type (Benke and Wallace 1980, 1997). Our results indicate that about 70% of *C. fluctuans* production was attributable to detritus, even though this food source has the lowest assimilation efficiency of the three food categories present in larval guts. Due to a higher assimilation efficiency, filamentous green algae accounted for about 29% of production despite comprising only 11% of larval diet. As a result of the low quality diet, nearly 88% of the total amount of food consumed was egested as detritus. Generation of frass is an important component of many stream food webs because the organic matter produced subsidizes other taxa (e.g., Benke and Wallace 1980, Vannote et al. 1980, Fisher and Gray 1983, Wallace and Webster 1996). However, it has yet to be demonstrated that similar relationships exist in wetland systems.

To the best of our knowledge, this is the first study to report production of an insect in a permanent wetland. The lack of information regarding insect production in wetlands is surprising. Several factors may be responsible for this fact, including the difficulty in quantitative sampling, the additional time and effort required for production estimates, and fewer researchers working in wetlands. However, wetlands are among the most productive ecosystems (Whittaker and Likens 1975), and further research is needed to gain a better understanding of wetland ecosystem function. This is especially true given the recent concerns regarding wetland loss. Mitigation projects such as the one at the GBWMA have become common, yet we know very little about whether these created wetlands are functioning like natural systems (Kusler and Kentula 1990). Given that production estimates for insects inhabiting lakes and streams now number in the thousands (Benke 1993), it is clear that researchers should next turn to wetland ecosystems. Insect production estimates provide vital information for wetland creation and preservation and will add to our understanding of wetland processes.

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