Verh. Internat. Verein. Limnol. | 27 | 3599–3603 | Stuttgart, September 2001

Invertebrate community structure and oxygen availability in an intermittent stream/wetland/river system of the Ugandan highlands

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Introduction

Although there is much information on the community structure and function of stream macroinvertebrates in temperate regions (HYNES 1970, WHITTON 1975, ALLAN 1996), factors influencing macroinvertebrate community structure in tropical waters are largely unknown (BISHOP 1973, HYNES 1975, BEADLE 1981). However, one character that may strongly influence macroinvertebrate faunal structure and diversity in the tropics is dissolved oxygen.

Hypoxia is widespread in tropical fresh waters, particularly in floodplain pools, inundated forests, and permanent swamps (CARTER & BEADLE 1930, CARTER 1955, KRAMER et al. 1978, CHAPMAN et al. 1998). In East Africa, hypoxia is prevalent in extensive dense wetlands dominated by papyrus (*Cyperus papyrus*) (CARTER 1955, BEADLE 1981, CHAPMAN et al. 1998). Vegetation height averages 3–4 m and associated low light and mixing along with high rates of decomposition result in low redox potential and oxygen availability (CARTER 1955, BEADLE 1981).

The macroinvertebrate faunas of papyrus swamps are not well studied; however, BEADLE (1981) found several species of macroinvertebrates in the vegetative mat and anoxic pools of papyrus swamps in Uganda including several air breathers (adult Hemiptera, Coleoptera). Although air-breathing may be a widespread strategy among macroinvertebrates in the dense interior of papyrus swamps, there are few data for a comparison of the faunal composition of papyrus swamps to associated flowing waters. In addition, the increase of dissolved oxygen associated with seasonal variation in rainfall may increase the richness of water breathers in the dense swamp interior.

In this study, we compare the macroinvertebrate community of a dense papyrus swamp site in western Uganda to a nearby river and stream site in the same drainage where oxygen levels are much higher. First, we compare overall richness and relative abundance of major macroinvertebrate taxa among the three sites. Then, we examine trends in diversity, richness, and respiratory strategies of the macroinvertebrate communities relative to seasonal variation in oxygen conditions.

Materials and methods

This study was conducted in Kibale National Park located near the foothills of the Rwenzori Mountains in western Uganda. A detailed description of the site is given in CHAPMAN & LIEM (1995). Approximately 60% of the 766-km² park is characterized by tall forest with canopy generally 25–30 m high, and the remainder is a mosaic of wetland, grassland, pine plantations, thicket, and successional forest (BUTYNSKI 1990). Kibale Forest is drained by two major everflowing rivers, Dura and Mpanga, which discharge into Lake George in the Queen Elizabeth National Park south of Kibale. Both rivers are fed by numerous small forest streams, many of which are intermittent. Extensive valley swamps dominated by papyrus characterize both drainage systems.

Mean annual rainfall in Kibale Forest (1977–1996) averages 1678 mm (range, 1205–2139 mm). Rainfall tends to be well dispersed; however, there are distinct bimodal wet and dry seasons. May through August and December through February constitute the dry seasons, with May–August being the driest months.

The primary study site, Rwembaita Swamp, is one of the larger papyrus (*Cyperus papyrus*) swamps in the park (approximately 6.5 km in length) and feeds the Njuguta River, a tributary of the everflowing Mpanga River. The swamp begins in the forest as a small intermittent stream (Mikana Stream) and is also fed by other small intermittent streams. During drier periods, open water in the swamp is restricted to small pools and deeper stream channels. Increased water levels in the papyrus swamp, during the rainy periods, create a maze work of interconnected channels, large pools, and inundated grassland areas.

Three sites were studied in the Rwembaita/

0368-0770/01/0027-03599 $ 1.25

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Mpanga drainage. The first was in the dense interior of the Rwembaita Swamp; the second in the upper reaches of Mikana Stream; and the third was an ever-flowing site (Sebatoli) on the Mpanga River into which the swamp eventually feeds. Invertebrates were sampled by a modified sweep net technique that included dredging approximately 2–3 cm of the substrate on a 0.5-m sweep. This method was adapted because of problems associated with comparing samples obtained by traditional dredge sampling among the three habitats (swamp, intermittent stream, river). Use of a dredge required that the samples be taken in soft substrates which were uncommon in the Mpanga River (Sebatoli). In addition, the possibility of losing swimming organisms due to evasion of the dredge made the semi-quantitative sweep net a better choice in this particular situation. Sites were sampled monthly from August 1996 to July 1997. At the Rwembaita Swamp site, an average of 12 sweep samples was taken among six stations across the width of the swamp, while at Mikana Stream, two sweep samples were taken at each of 13 stations. We selected more sites at Mikana Stream to ensure that some stations would maintain water during the drier periods. At the Mpanga River, 12 sweep samples were taken among four sites separated by 60 m of flowing river. Samples were picked on site and preserved in 5% formalin. Dissolved oxygen was recorded for each site using a YSI Model 51B dissolved oxygen meter. Preserved samples were transported to the University of Florida, transferred to 50% isopropynol and identified to order according to MERRIT & CUMMINS (1984).

Results

The three sites differed markedly in faunal structure and composition. The macroinvertebrate community in sweep samples from the Rwembaita Swamp was dominated by gastropods (primarily *Biomphalaria* sp., an air breather) and a species of small clam (Fig. 1). The dominant taxa found in Mikana Stream were ephemeropterans, followed by trichopterans and anisopterans, with coleopterans and dipterans of lesser presence (Fig. 1). The ever-flowing Mpanga River site (Sebatoli) was dominated by coleopterans and anisopterans followed by ephemeropterans, hemipterans, and trichopterans (Fig. 1).

Dissolved oxygen differed among the three sites (Fig. 2) averaging only 2.0 mg (range, 0.26 to 4.16) at the Rwembaita Swamp with higher values in both Mikana Stream (mean, 5.1 mg

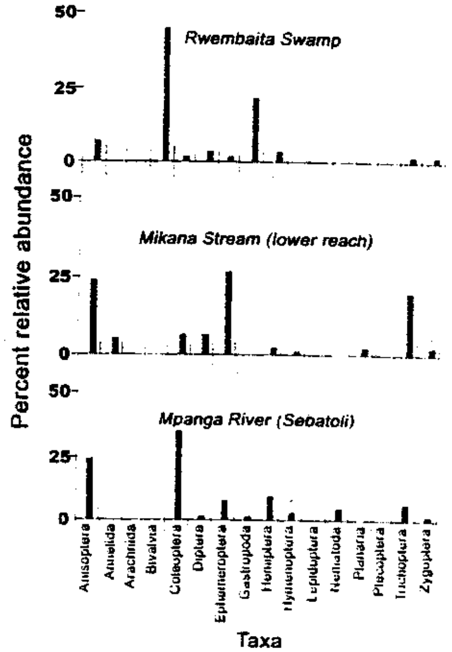

Fig. 1. Percent Composition of invertebrates for Rwembaita Swamp, Mikana Stream, and Mpanga River, from Aug. 1996 to July 1997.

L^{-1}, range, 0.33 to 7.7 mg L^{-1}) and the Mpanga River (mean, 7.2 mg L^{-1}, range 5.0 to 8.1 mg L^{-1}). Given the lower values in the Rwembaita Swamp, reliance on atmospheric oxygen may be a common strategy among successful aquatic macroinvertebrate taxa. To examine this, we compared the percent composition of air-breathing versus water-breathing invertebrates among the three sites.

Air-breathing macroinvertebrates were common in the swamp and primarily included gastropods and nepids (Hemiptera); however, water breathers were dominant in most months (Fig. 3). This pattern was due primarily to the high abundance of clams in all months but August 1997. When clams were excluded from the analysis, air breathers were more common than water breathers in all months except August 1997.

To investigate the relationship between oxygen content and community composition in more detail, the three months with the highest

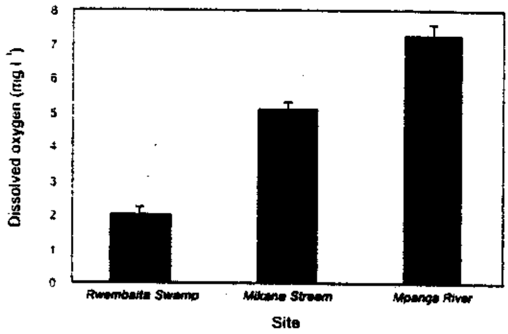

Fig. 2. Average dissolved oxygen values for Rwembaita Swamp, Mikana Stream, and Mpanga River, from August 1996 to July 1997.

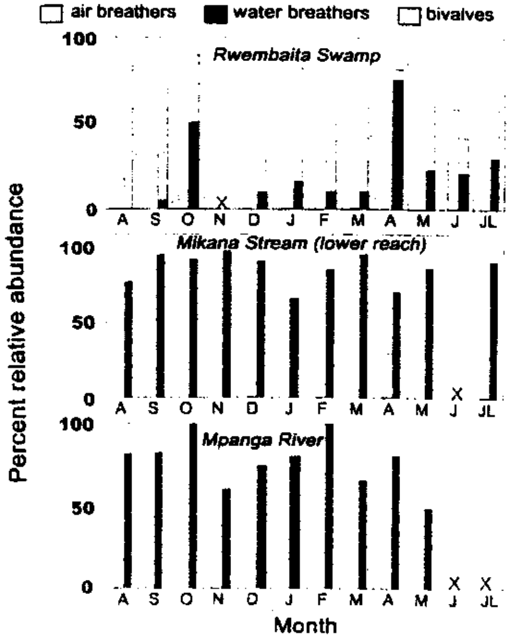

Fig. 3. Percent air and water breathers each month from August 1996 to July 1997. The lightly shaded region represents the percent of invertebrates that are bivalves.

and the lowest oxygen values, respectively, were compared relative to taxa richness, diversity, and respiratory partitioning (air vs. water breathers). Seven taxa were captured during the 3 months of highest DO (Sept., Dec., Mar.), and eight taxa characterized the 3 months of lowest measured DO (Jun., Aug., Oct.). Diversity (Shannon diversity index) was also higher during the low DO months (H' = 0.624) than during the high DO months (H' = 0.555). Surprisingly, the average percent abundance of air breathers present in high DO months was greater (44.7%) than that of low DO months (28.3%).

At Mikana Stream, water breathers were more common than air breathers in all months and consisted primarily of anisopterans, empheropterans, and trichopterans (Fig. 3). Taxa richness values for the 3 months of highest DO (May, Jan., Jul.) and the 3 months of lowest DO (Sep. Oct., Nov.) were both 10. However, diversity was higher during the low DO months (H' = 0.835) than in the months of high DO (H' = 0.714). As was observed in the papyrus swamp, the average percent abundance of air breathers in the stream was greater in high DO months (17.0%) than in the low DO months (5.3%).

At the Mpanga River site, both water and air breathers were common throughout the year. The latter were dominated by hemipterans and adult coleopterans, and water breathers were dominated by anisopterans, ephemeropterans, and trichopterans. Taxa richness was higher in the low DO months (eight taxa, Oct., Nov.r and Dec.) than in high DO months (seven taxa, Mar., Apr. and May). Diversity values followed the same trend as the swamp and stream with higher diversity in the low DO months (H' = 0.717) than in high DO months (H' = 0.666). The average percent abundance of air breathers present also followed the trends found in both the stream and swamp with a higher abundance of air breathers in the months of high oxygen (34.0%) than during the months of lowest oxygen conditions (20.0%).

Discussion

Rzoska (1974) reports faunal differences between rivers and papyrus swamps with the exclusion of macroinvertebrates. In this study, we found there to be a marked difference between the macroinvertebrate communities of the swamp and the stream/river sites. The extremely low DO of the Rwembaita Swamp poses respiratory challenges for aquatic invertebrates inhabiting the dense interior of the papyrus. One would predict a fauna dominated by air-breathing organisms. Although there is a greater percentage of air breathers in the swamp versus the stream/river sites, the abundance of water breathing bivalves shifted the expected dominance of the system to water breathers. The high abundance of bivalves throughout the year in the swamp is particularly intriguing because these taxa are known to be tolerant of short term hypoxic conditions, but not the long term hypoxia associated with the papyrus swamps (PENNAK 1978) This phenomenon clearly warrants further investigation. Exclusion of the bivalves from the analysis shows dominance of the community by air breathing organisms. BEADLE (1981) briefly mentions that a few types of crustaceans also survive in the hypoxic conditions of the papyrus mat, yet the mechanisms employed are not understood.

The DO levels in the Mikana stream and Mpanga River are, on average, moderately high, reaching low levels only during periods of severe drought (CHAPMAN unpublished data). The dominance of water breathing invertebrates in our samples of the stream and river sites may reflect the availability of dissolved oxygen levels in the system, as was the case in a previous stream study in Uganda (MATAGI 1996).

We found that taxa diversity increased at all sites during the months of lowest oxygen availability despite little or no change in taxa richness. An increase in diversity may reflect an increase in the relative abundance of rare organisms or an increase in taxa richness without great change in the relative abundance of dominant groups. In either case, the effect may be due to concentration of organisms due to decreasing flow regimes (BROWN & BUSSOCK 1991) and oxygen availability in the substrate and cover areas (MARIDET et al. 1996). Diversity measurements using a finer taxa resolution may be necessary to clarify diversity and richness trends (VINSON & HAWKINS 1996).

Surprisingly, the average percent abundance of air breathers increased at all sites in months of highest available DO. One explanation of this phenomenon might be that some water breathing organisms may be able to associate with deeper substrata or denser organic deposits due to increased DO and thus the percentage of air breathers captured would naturally be higher. MARIDET et al. (1996) found 70–90% of invertebrates associated with the top 15 cm and our sampling regime included only the top 2–3 cm of substrate. One other important consideration is that of the dipterans. In our samples, the number of dipterans was quite low compared to other stream studies in East Africa by HYNES (1975), VICTOR & OGBEIBU (1985) and MATHOOKO & MAVUTI (1992). This disparity is most likely due to the mesh size of the dip nets employed in our study. Because the dipterans can make up a large percentage of invertebrates sampled, and this taxa includes both air and water breathers (MERRITT & CUMMINS 1984), it seems they may be of considerable importance in clarifying these questions. We have taken dredge samples to identify the dipterans and are further investigating their role in the community structure of these systems.

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