

Respiratory Ecology of Macroinvertebrates in a Swamp–River System of East Africa¹

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ABSTRACT

Hypoxia (oxygen scarcity) is widespread in tropical freshwaters, particularly in dense swamps, and may be an important factor structuring benthic macroinvertebrate communities. Macroinvertebrates show a diversity of respiratory modes ranging from atmospheric breathing to tracheal gill breathing, and these adaptations affect their ability to use hypoxic water. The objectives of this study were to (a) describe the benthic macroinvertebrate community from ten swamp and river sites in Kibale National Park, Uganda, (b) determine the degree to which dissolved oxygen explains variation in abundance of respiratory groups (taxa with a similar respiratory mode) among sites, and (c) test for significant seasonal variation in the abundance of the numerically dominant respiratory groups. Macroinvertebrates from monthly collections over a two-year period were identified to the lowest taxonomic level necessary to place them in functional respiratory groups. Across all sites, both the relative and absolute abundance of atmospheric breathers (*e.g.*, pulmonate snails and nepids) and mantle/cenidia breathers (primarily fingernail clams) were negatively correlated with dissolved oxygen, while the abundance of tracheal gill breathers (*e.g.*, anisopterans and zygopterans) was positively correlated with dissolved oxygen. We did not detect significant seasonal trends in catch per unit effort of numerically dominant respiratory groups. Dissolved oxygen concentration was a good predictor of the abundance of some respiratory groups and may be a key factor in maintaining the structure and diversity of these assemblages.

Key words: air breathers; aquatic insects; hypoxia; papyrus swamp; tracheal gills; Uganda.

EFFECTIVE OXYGEN UPTAKE IS CRITICAL TO THE LONG-TERM SURVIVAL of most aquatic invertebrates; however, the physical properties of water make dissolved oxygen acquisition a challenge even under normoxic conditions. A given volume of water contains about 1/30th the oxygen of the same volume of air, and water is about *ca* 800 times denser than air (Dejours 1994, Nikinmaa & Salama 1998). In addition, there are many aquatic systems in which water does not remain saturated with oxygen, in particular, waters characterized by low light, reduced mixing, and high rates of organic decomposition.

Aquatic macroinvertebrates exhibit an impressive diversity of respiratory adaptations. These strategies have associated costs and benefits that vary with ecological context and affect the ability of invertebrates to use hypoxic waters. Numerous studies have considered the influence of dissolved oxygen availability on the behavior, growth, energetics, and/or survival of various aquatic macroinvertebrate taxa including chironomid larvae (Walshe 1948), zygopteran larvae (Eriksen 1986), plecopteran larvae (Madsen 1968, Gaufin *et al.* 1974), ephemeropteran larvae (Gaufin *et al.* 1974, Winter *et al.* 1996), trichopteran larvae (Fox & Sidney 1953, Gaufin *et al.* 1974), dipteran larvae (Gaufin *et al.* 1974), crustaceans (Huddart & Arthur 1971, Gaufin *et al.* 1974, Sprague 1963, Stickle *et al.* 1989), mollusks (Stickle *et al.* 1989), and hirudiniids (Davies *et al.* 1992). As a consequence of dramatic variation among taxa in hypoxia tolerance, there is often a close association between dissolved oxygen availability and the presence or absence of particular aquatic invertebrate groups within a community (Hoback & Stanley 2001). This has facilitated the use of aquatic invertebrates as bio-indicators of water quality (Hellowell 1986, Rosenberg & Resh 1993).

Much of our understanding of the links be-

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tween dissolved oxygen and invertebrate assemblage structure in freshwater and marine systems derives from studies linking general indices of community structure (e.g., richness or diversity) to dissolved oxygen availability (Flemmer *et al.* 1999, Riccer & Montagna 1999). Another useful metric may be the abundance and diversity of taxa grouped by respiratory mode. We use the term respiratory mode to characterize groups of taxa with similar respiratory strategies that exploit oxygen in a similar fashion. This functional categorization facilitates comparison of communities by focusing on specific respiratory modes, and permits an evaluation of the role of dissolved oxygen as a predictor of groups of taxa that share a similar respiratory strategy regardless of taxonomic affiliation. We do not imply that these groups interact among themselves more strongly than with other members of the community.

For aquatic insects, Eriksen *et al.* (1996) recognize eight major respiratory strategies: atmospheric, plant breathers, temporary air store, permanent air store (plastrons), permanent air store (spiracular gills), tracheal gills, cutaneous breathers, and insects with hemoglobin. Other aquatic invertebrates, such as oligochaetes and air-breathing gastropods, can also be placed into these or other respiratory categories.

Insects that use aerial respiration and rely on either stationary air sources (atmospheric breathers) or transportable air stores are characterized by open tracheal systems that exchange respiratory gases with the atmosphere through spiracles (Eriksen *et al.* 1996). Atmospheric breathers are not dependent on the oxygen concentration of the water in which they reside but must periodically connect directly with the atmosphere or remain more or less permanently at the air-water interface (Ward 1992, Williams & Feltmate 1992, Eriksen *et al.* 1996). Plant breathers pierce and tap specialized air chambers in aquatic plants with modified spiracles (Eriksen *et al.* 1996); but they are not reported in this study. Other noninsect aquatic macroinvertebrates that can be classified as atmospheric breathers include the air-breathing gastropods. In this group (pulmonate snails), the mantle cavity has been converted into a pulmonary chamber, and in most species, periodic excursions to the surface are used to obtain a fresh supply of air (Pennak 1989, Healy 2001). Transportable air store breathers are insects that carry their own air supply and can stay submerged longer and be more active than atmospheric breathers. When a transportable air store is exposed to the water, it serves as an air reserve but

can also act as a physical gill extending the time under water (Ward 1992, Williams & Feltmate 1992, Eriksen *et al.* 1996). Three types of transportable air stores are found in insects: temporary air storage, permanent air storage (plastron), and permanent air storage (spiracular gills).

Insects with closed tracheal systems have no functional spiracles, so gas exchange must occur by diffusion through the cuticle. This group includes two major respiratory categories: cutaneous respiration and tracheal gills (Eriksen *et al.* 1996). Many larger and more active water-breathing insects have developed tracheal gills (e.g., mayfly, dragonfly, and damselfly larvae) that can be important sites for gas exchange, but when external, may also serve other functions including locomotion (Burnside & Robinson 1995) and predator escape (Robinson *et al.* 1991). Virtually all aquatic insects use cutaneous respiration to satisfy some portion of their oxygen uptake (Ward 1992). Some insects, however, rely entirely on this respiratory mode during the aquatic component of their life cycle or during their early life stages (Ward 1992, Eriksen *et al.* 1996). Other noninsect taxa that rely on cutaneous respiration include several of the oligochaetes and hirudineans (Rouse & Anderson 2001). Among cutaneous breathers, there is much variation in tolerance to hypoxia. For example, some oligochaetes have hemoglobin and can tolerate extreme hypoxia (Barnes 1974). Among aquatic insects, hemoglobin is restricted to some species of notonectids and chironomids (Eriksen *et al.* 1996), the latter of which are cutaneous breathers. In this study, taxa relying primarily on cutaneous respiration were rare in our samples and were grouped together regardless of the presence of respiratory pigments; however, we also independently analyzed relationships between dissolved oxygen and abundance for chironomids with respiratory pigments.

Water-breathing mollusks (particularly clams) and freshwater prawns (Decapoda) were common at some sites reported in this study. In water-breathing mollusks, the majority of respiratory exchange is effected by one or more pair(s) of ctenidial gills housed in the mantle cavity, although the mantle and general body surface may also contribute to respiratory exchange (Pennak 1989, Barnes *et al.* 2001). In freshwater prawns, a large carapace that covers the head and thorax encloses the gills, which we refer to as thoracic gills (Barnes *et al.* 2001, Greenaway 2001).

In this study, we considered the importance of dissolved oxygen concentration as a predictor of the abundance of macroinvertebrate respiratory groups

in an East African river–swamp system. Our objectives were to (1) describe the benthic macroinvertebrate community from ten sites in a swamp–river system in Kibale National Park, Uganda with respect to functional respiratory groups; (2) determine the degree to which the dissolved oxygen concentration can explain variation in the relative and absolute abundance of individual respiratory modes among sites; and (3) test for significant seasonal variation in the abundance of the numerically dominant respiratory groups. Our sites included dense papyrus swamps, fast-flowing rivers, and intermittent streams. Mean dissolved oxygen concentration varied among these sites from extreme hypoxia to normoxia (Chapman *et al.* 1999, 2000), providing a high level of natural variation in dissolved oxygen.

METHODS

STUDY SITE.—Macroinvertebrates were sampled from a swamp–river system in Kibale National Park in western Uganda ($0^{\circ}13'–0^{\circ}41'N$, $30^{\circ}19'–30^{\circ}32'E$). The park is an equatorial moist evergreen forest, transitional between lowland rain forest and montane forest (Chapman & Lambert 2000). Approximately 60 percent of the 766 km² park is characterized by tall forest with the canopy generally 25–30 m high, and the remainder is comprised of a mosaic of wetland, grassland, pine plantations, thicket, and colonizing forest (Chapman & Lambert 2000). Rainfall in Kibale National park averages 1749 mm of rainfall annually (1990–2001), with two distinct wet and dry seasons. The drier months include May–August and December–February. The rainy season produces higher dissolved oxygen levels in swamps and intermittent streams than the dry season (Chapman *et al.* 1998, 2000).

The forest is drained by two major perennial rivers, the Dura and Mpanga rivers, both of which are tributaries of Lake George (Fig. 1). These rivers are fed by numerous small forest streams, many of which are intermittent. Extensive valley swamps dominated by papyrus (*Cyperus papyrus*) characterize both river systems. Ten sites were selected for this study to include swamp, intermittent stream, and river habitat within the two river systems. The Rwembaita Swamp is one of the largest in Kibale National Park, 6.5 km in length, and feeds the Njuguta River, a tributary of the Mpanga River. The swamp is dominated by papyrus averaging 5 m in height. In the dense swamp, minimal exposure to incident light, low levels of mixing, and

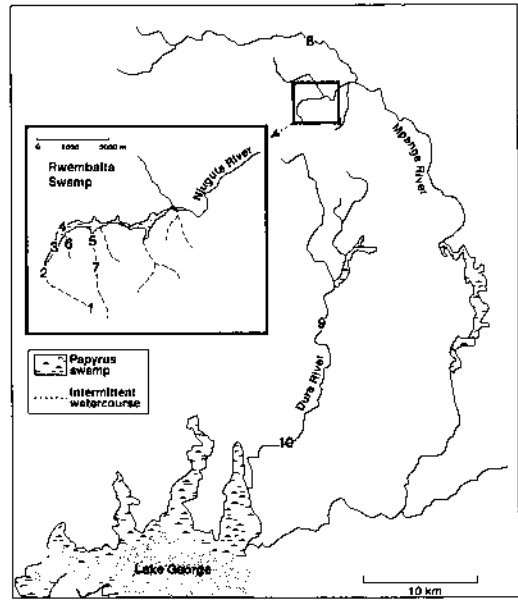


FIGURE 1. Map of Kibale National Park, Uganda, indicating the two major drainage systems (Dura River and Mpanga River), the Rwembaita Swamp system, and the ten sites in which benthic macroinvertebrates were sampled over a two-year period. 1: Mikana-up; 2: Mikana-low; 3: Rwembaita Swamp-up (RSW-up); 4: Rwembaita Swamp-mid (RSW-mid); 5: Rwembaita Swamp-low (RSW-low); 6: Inlet Stream West (Inlet West); 7: Inlet Stream East (Inlet East); 8: Mpanga River (Sebatoli); 9: Dura River-mid (Dura-mid); and 10: Dura River-powerline (Dura-PL).

high rates of organic decomposition produce extremely hypoxic conditions (Chapman & Liem 1995; Chapman *et al.* 1998, 1999, 2000). Three sites in Rwembaita Swamp were sampled (Fig. 1); these sites were characterized by extreme hypoxia, but mean dissolved oxygen levels varied among the sites. All three swamp sites were characterized by low flow and shallow depth (average depth of sampling sites = 33 cm). Three perennial river sites (width *ca* 10–15 m) situated in primary forest were sampled: Mpanga River (Sebatoli), Dura River (mid), and Dura River (Powerline, PL; Fig. 1). These three river sites were characterized by relatively deeper water (average depth of sampling sites = 50 cm), faster flow, and much higher dissolved oxygen concentration than the swamp sites. Samples were also taken from four intermittent stream sites (1–2 m in width) situated in secondary forest: Mikana Stream (up), Mikana Stream (low), Inlet Stream East, and Inlet Stream West (Fig. 1). Flow in these systems was intermittent and depth was relatively shallow (average depth of sampling sites

= 25 cm). Mean dissolved oxygen values varied among the four sites but were generally intermediate between the hypoxic swamp and the perennial river sites.

SAMPLING METHODS.—Duplicate readings of dissolved oxygen and water temperature were collected monthly over the two year study (April 1996–May 1998) at an average of six representative habitats (microsites) within each of the ten sites using a YSI meter (model 51B or model 95). Microsites were selected to cover the range of major habitats in each site. In the closed cover of the forest and papyrus swamp, diel variation in dissolved oxygen and water temperature tends to be very low (Chapman & Liem 1995, Chapman *et al.* 1998). Therefore, measurements were taken once per sampling day between 1100 and 1500 h. Rainfall data were collected at the Makerere University Biological Field Station, located *ca* 3 km from the Rwembaita Swamp.

Benthic macroinvertebrate samples were collected monthly at each microsite for which dissolved oxygen was measured. Due to elephant and rebel activities that precluded sampling of some sites in some months and loss of some samples to desiccation in transit, sample size (number of collections) averaged 20 per site. At each swamp and stream location, duplicate scoop nets (frame size 12 x 16 inches, depth of 7 inches, mesh size 1/8 inch) were taken by disturbing and scooping the bottom substrate. At the three larger rivers, triplicate samples were taken (side, middle, and opposite side of the river) at each of six sites. At the swamp sites, samples were taken in pools on the mat and within deeper channels. Samples from all microsites within a location were combined to produce a monthly sample. We chose to sample with scoop nets because our protocol included a broad range of sites from dense swamp to gravel streambed. Therefore, other conventional sampling gears (*e.g.*, dredges/cores) would have been difficult to standardize across sites. Scoop net samples were sorted directly in the field. We therefore primarily collected large macroinvertebrates visible to the naked eye. Most organisms were benthic, but occasional mid-water and surface-dwelling invertebrates were captured by the net. Although this sampling method was selective, it did permit standardization across a broad range of habitat types.

Samples were preserved in formalin and later transferred into 70 percent ethanol. The macroinvertebrates were identified to the taxonomic level necessary to place them in functional respiratory

categories based on the major mode of oxygen uptake (atmospheric breathers, temporary air store, permanent air store breather (plastron), permanent air store (spiracular gills), cutaneous respiration, tracheal gills, and mantle/ctenidia, and thoracic gills). Plant breathers were not found in our study.

ANALYSES.—We describe mean values (\pm SE) of dissolved oxygen concentration for each site, where means represent the average of monthly samples. To evaluate the relative degree of seasonal variation in oxygen among sites, we used the coefficient of variation (*CV*; Sokal & Rohlf 1981). The *CV* was calculated as the standard deviation of the monthly mean dissolved oxygen concentration divided by the mean.

The relative abundance and catch per unit effort of taxa comprising respiratory groups were determined for each site. This was done for the cumulative sample for each individual site (combined across the 2 yr sampling period). Relative abundance was calculated as the number of organisms of a particular respiratory mode at a site expressed as a percentage of the total number of benthic macroinvertebrates collected, and catch per unit effort was calculated as the number of a particular taxa per scoop sample (multiplied by 10 for presentation). Linear regression analyses were used to detect significant relationships between the abundance of macroinvertebrates of different respiratory modes and dissolved oxygen concentration. To examine seasonal changes in abundance, we selected the eight wettest and the eight driest months for each site over the study period, and the catch per unit effort of the three numerically dominant respiratory categories was calculated for these two periods. Two-way ANOVA was used to detect effects of season (wet vs. dry) and site (swamp, intermittent stream, and river).

RESULTS

DISSOLVED OXYGEN CONCENTRATION.—Mean monthly dissolved oxygen concentration (DO) was highly variable among sites. The lowest mean values were recorded at the three swamp sites, and ranged from 1.08 ± 0.14 mg/liter (SE) at RSW-mid to 2.55 ± 0.19 mg/liter at RSW-low (Fig. 2). At the intermittent sites, dissolved oxygen ranged from 3.79 ± 0.18 mg/liter at Inlet East to 7.12 ± 0.19 mg/liter at Mikana-low (Fig. 2). The three river sites were very similar in mean DO values, ranging from 6.31 ± 0.20 mg/liter at Dura-PL to 7.46 ± 0.16 mg/liter at the Mpanga River (Sebatoli; Fig. 2).

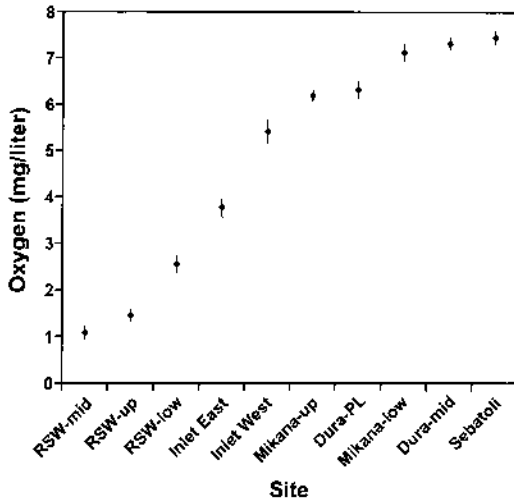


FIGURE 2. Mean monthly dissolved oxygen concentration (mg/liter \pm SE) at ten sites in Kibale National Park, Uganda. Sites included three swamp sites (RSW-mid, RSW-up, and RSW-low), four intermittent stream sites (Inlet East, Inlet West, Mikana-up, and Mikana-low), and three river sites (Dura-PL, Dura-mid, and Mpanga-Sebatoli); site locations are indicated in Figure 1. Means represent the average of monthly samples taken at several microsites within each location.

The variation among months, reflecting seasonal change, was highest at the three swamp sites ($CV = 0.66, 0.44,$ and 0.37 for RSW-mid, RSW-up, and RSW-low, respectively). Mean levels were generally higher in the wet season. At the river sites, variation was much lower over the year ($CV = 0.14, 0.08,$ and 0.10 for Dura-PL, Dura-mid, and Sebatoli, respectively). Intermittent stream sites were intermediate in their levels of seasonal variation ($CV = 0.23, 0.23, 0.10,$ and 0.13 for Inlet East, Inlet West, Mikana-up, and Mikana-low, respectively), but generally showed seasonal increase in DO associated with seasonal increase in precipitation. Water temperature varied little across sites, ranging from an average of 17.2°C at Mikana-low to 19.2°C at the Mpanga River (Sebatoli).

INTERSITE VARIATION IN THE ABUNDANCE OF RESPIRATORY MODES.—Assemblage structure based on the abundance of groups characterized by respiratory mode varied dramatically among sites (Table 1). The three swamp sites were dominated by two respiratory modes. Water-breathing mollusks (mandel/ctenidia breathers) were the most numerically abundant benthic macroinvertebrates at the swamp sites, comprising 44, 55, and 66 percent of the collected invertebrates at RSW-mid, RSW-up,

and RSW-low, respectively (Table 1 and Fig. 3). At the swamp sites, this respiratory group consisted entirely of the clam *Sphaerium* sp. Atmospheric breathers were also extremely common at the swamp sites, comprising 38, 32, and 27 percent of collected invertebrates at the same three sites, respectively. Atmospheric breathers consisted primarily of the pulmonate snail (*Biomphalaria* sp.) and water scorpions (Nepidae; Table 1 and Fig. 3). Surprisingly, tracheal gill breathers (primarily odonates) also occurred at the swamp sites (5, 9, and 5% for RSW-mid, up, and low, respectively). Other groups, including invertebrates with temporary air stores (e.g., gyrenid, dytiscid, and hydrophilid adults) and cutaneous breathers (e.g., chironomids, hirudinids, and oligochaetes) also occurred at the swamp sites but in low abundance (Table 1 and Fig. 3). We did not record invertebrates with permanent air stores (e.g., plastrons or spiracular gills) or any non-air-breathing gastropods in the swamp waters (Table 1). Catch per unit effort data revealed very similar patterns to relative abundance trends.

Assemblage structure at the three river sites was in sharp contrast to the three swamp sites. Most notable was the very high percentage of tracheal gill breathers (81, 56, and 86% for Dura-mid, Dura-PL, and Sebatoli, respectively; Table 1 and Fig. 3). The tracheal gill breathers consisted primarily of odonates, but also included ephemeropterans, plecopterans, and trichopterans (Table 1). Atmospheric breathers were rare at the three river sites and consisted primarily of tipulid larvae (Table 1). Water-breathing mollusks occurred at all the river sites. Unlike the swamp site, the clam *Sphaerium* sp. was extremely rare, but prosobranch snails were found at two of the three river sites. Members of other respiratory groups were recorded in low abundance, including one respiratory mode not recorded from our swamp sites (permanent air store breathers with plastrons).

Assemblage structure varied substantially across the four intermittent streams, which may have reflected the range of variation in their physicochemical characteristics and position relative to the swamp in which they feed. In general, the four streams were characterized by a higher relative abundance of tracheal gill breathers than the swamp, but a lower abundance than the three river sites (40, 20, 71, and 47% for Inlet East, Inlet West, Mikana-up, and Mikana-low, respectively; Table 1 and Fig. 3). It is notable that the highest relative abundance of tracheal gill breathers was recorded at Mikana-up, the site farthest from the Rwembaita Swamp (ca 1200 m upstream). Atmo-

spheric breathers occurred in relatively high abundance at the three stream sites near the swamp (33, 25, and 30% for Inlet East, Inlet West, and Mikana-low, respectively), but were rare at Mikana-up (9%; Table 1 and Fig. 3). Water-breathing mollusks (consisting primarily of *Sphaerium* sp.) occurred in high abundance at Inlet West (48%) and Inlet East (21%), but were extremely rare at Mikana-low (0.8%) and absent from Mikana-up. All other respiratory groups, with the exception of decapods (thoracic gills), were captured in low abundance at one or more of the intermittent stream sites (Table 1 and Fig. 3).

DISSOLVED OXYGEN AS A PREDICTOR OF THE ABUNDANCE OF RESPIRATORY MODES.—Across the ten sites, the relative abundance of air breathers and water-breathing mollusks (mantle/ctenidia) was negatively related to mean dissolved oxygen concentration (atmospheric breathers: $r = -0.753$, $P = 0.012$; mantle/ctenidia: $r = -0.837$, $P = 0.003$, Figs. 4 and 5). The relationship between dissolved oxygen concentration and the relative abundance of water-breathing mollusks was driven by one taxon (the clam *Sphaerium* sp.); the relationship was not significant when the clams were removed from the group ($r = 0.294$, $P = 0.409$). The relative abundance of tracheal gill breathers was positively correlated with dissolved oxygen ($r = 0.875$, $P = 0.001$), and the abundance of invertebrates with permanent air stores (plastrons) showed a similar trend ($r = 0.561$, $P = 0.091$; Figs. 4 and 5). For all cutaneous breathers and for just chironomids, we analyzed the relationship with dissolved oxygen concentration and detected no significant relationships (Fig. 4). Dissolved oxygen was not a significant predictor of the relative abundance of the other respiratory modes (Fig. 4). Relationships between catch per unit effort of respiratory groups and mean DO showed very similar trends (Fig. 4).

SEASONAL TRENDS.—To examine seasonal trends, we focused on the three dominant respiratory categories (atmospheric breathers, tracheal gill breathers, and water-breathing mollusks [primarily *Sphaerium* sp.]). Across the ten sites, the catch per unit effort of the three respiratory groups was similar between the dry season (eight driest months combined) and the wet season (eight wettest months combined; Fig. 6). Two-way ANOVA was used to detect effects of season (wet vs. dry) and habitat (swamp, intermittent stream, and river). For all three respiratory modes, habitat effects were significant; however, there was no significant season ef-

fect or interaction of habitat and season for any of the three groups (Table 2).

DISCUSSION

Aquatic macroinvertebrates exhibit a wide diversity of respiratory adaptations from atmospheric breathers to those dependent on uptake of dissolved oxygen. In the rivers, streams, and swamps of Kibale National Park, Uganda, assemblage structure of the macroinvertebrate communities based on respiratory mode was highly variable among sites, and dissolved oxygen concentration was a significant predictor of the relative and absolute abundance of the numerically dominant respiratory modes.

PATTERNS OF DISSOLVED OXYGEN CONCENTRATION.—Hypoxic waters are prevalent in extensive areas of papyrus swamps (*C. papyrus*) that dominate much of the 85,000 km² of permanent wetland on the African continent (Beadle 1981, Thompson & Hamilton 1983). In the papyrus-dominated Rwembaica Swamp, we found that dissolved oxygen concentration averaged 1.7 mg/liter across our three swamp sites. These values were not unusually low for papyrus swamps and some other heavily vegetated tropical swamps. Carter (1955) reported oxygen values averaging less than 0.1 mg/liter for the nearshore areas of littoral papyrus swamps in Lake Victoria, and average values of 2.5 mg/liter for the interface between papyrus and pelagic waters. Elsewhere in the tropics, Carter and Beadle (1930) found widespread extreme hypoxia in the swamps of the Paraguayan Chaco, where oxygen levels within 1 cm of the surface fell to less than 0.1 mg/liter for many days at a time.

Our four intermittent stream sites varied in mean oxygen levels from 3.8 mg/liter at Inlet East to 7.8 mg/liter at Mikana-low. It is likely that the intersite variation reflected a number of factors, including gradient, wetland input, groundwater, and terrestrial contributions. Upstream of Inlet East is a large wetland, which feeds hypoxic waters into this low-gradient stream. In contrast, Mikana-low originates from a small forest wetland 1200 m upstream and sits below a small waterfall. The three river sites were characterized by high DO with the lowest mean value at Dura-PL, which may have reflected the input of a large papyrus swamp ca 3 km upstream of the site.

Seasonal variation characterized by the coefficient of variation in monthly values was highest at the swamp sites and lowest at the river sites. In our

TABLE 1. The relative abundance of benthic macroinvertebrates in respiratory mode categories from scoop net samples collected at ten sites (three swamp, four intermittent stream, and three river) in Kibale National Park, Uganda. Samples were collected over a two-year period and identified to the lowest taxonomic level that allowed assignment to a respiratory category. The total number of specimens is indicated for each site in the final row, and sites refer to locations indicated in Figure 1. L: larval; A: adult; and All: all life history stages.

Respiratory Mode	Taxa and Life Stage		RSW-mid	RSW-up	RSW-low	Inlet East
Atmospheric breathers	Diptera:	Tipulidae (L)	0.00	1.27	0.44	2.07
		Tabanidae (L)	0.00	0.00	0.00	0.00
	Hemiptera:	Geridae (L, A)	0.00	0.21	0.00	0.00
		Nepidae (L, A)	4.50	12.10	3.09	4.14
	Gastropoda:	Velidae (L, A)	0.00	0.00	0.00	0.69
Physidae (All)		0.20	0.00	9.56	10.34	
Temporary air store	Coleoptera:	<i>Biomphalaria</i> (All)	33.54	18.47	13.53	15.86
		Dytiscidae (A)	1.23	0.85	0.29	0.00
		Gyrinidae (A)	2.04	0.85	1.18	3.45
	Hemiptera:	Hydrophilidae (A)	1.23	0.42	0.15	0.69
		Belostomatidae (L, A)	0.20	0.00	0.00	0.00
		Corixidae (L, A)	0.20	0.00	0.00	0.00
		Naucoridae (L, A)	0.00	0.21	0.00	0.00
Permanent air store (plastrons)	Coleoptera:	Notonectidae (L, A)	0.20	0.00	0.00	0.00
		Pleidae (L, A)	0.00	0.00	0.00	0.00
Permanent air store (spiracular gills)	Coleoptera:	Elmidae (A)	0.00	0.00	0.00	0.00
		Simuliidae (P)	0.00	0.00	0.00	0.00
Tracheal gills	Ephemeroptera (L)		0.41	0.21	0.59	5.52
	Coleoptera:	Gyrinidae (L)	0.00	0.00	0.00	4.83
		Elmidae (L)	0.00	0.00	0.00	0.00
Cutaneous	Odonata (L)		7.98	5.10	4.41	24.83
	Plecoptera (L)		0.00	0.00	0.00	0.00
	Trichoptera (L)		0.61	0.00	0.44	4.83
	Hydracarina (All)		0.00	0.00	0.00	0.00
	Diptera:	Ceratopogonidae (L)	0.00	0.00	0.15	0.00
		Chironomidae (L)	2.45	4.46	0.00	0.69
	Turbellaria		0.00	0.00	0.00	0.00
	Annelida:	Hirudinea (All)	0.00	0.42	0.00	0.00
		Oligochaeta (All)	0.61	0.64	0.00	0.69
	Nematoda		0.00	0.00	0.00	0.00
Mantle/ctenidia	Gastropoda:	Prosobranchia	0.00	0.00	0.00	0.00
		Bivalvia:	<i>Sphaerium</i> sp.	44.17	54.78	66.18
Thoracic gills	Decapoda (All)		0.41	0.00	0.00	0.00
Unknown			0.00	0.00	0.00	0.69
Total no. of specimens			489	471	680	145

earlier studies of these systems, we found that dissolved oxygen in the swamp increases with seasonal precipitation, but there is a potential lag effect because of the extensive lateral expansion of the swamp in the early stages of seasonal flooding that retards the anticipated increase in water flow (Chapman & Liem 1995) and the resuspension of oxygen-demanding materials (Chapman *et al.* 2000). Intermittent stream sites in Kibale also show seasonal increases in DO associated with rainfall; however, their response time is faster (Chapman *et al.* 2000).

DISSOLVED OXYGEN AS A PREDICTOR OF THE ABUNDANCE OF RESPIRATORY MODES.—Across the ten sites, mean dissolved oxygen concentration was a significant predictor of both the absolute and relative abundance of the most numerically dominant respiratory groups. The CPUE of atmospheric breathers was negatively correlated with dissolved oxygen concentration. In Kibale National Park, this respiratory mode was dominated by pulmonate snails (*Biomphalaria* sp.) and nepids (*Laccotrephes brachialis* and *Ranatra fuscoannulata*). This group is well adapted to low dissolved oxygen availability

TABLE 1. *Extended.*

Inlet West	Mik-up	Dura-PL	Mik-low	Dura-mid	Sebatoli
1.00	2.72	0.77	2.73	0.76	0.28
0.00	0.34	0.00	0.27	0.00	0.00
0.00	0.17	0.00	0.27	0.25	0.00
4.98	2.55	0.00	9.84	0.00	0.28
0.00	0.17	0.00	0.00	0.00	0.00
0.00	0.00	0.00	0.27	0.00	0.00
19.40	3.23	0.52	17.21	0.25	0.56
0.00	0.68	0.00	2.19	0.00	0.00
3.98	3.40	0.00	4.10	0.00	0.28
0.00	0.51	0.00	1.37	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.00
0.50	0.00	0.00	0.00	0.25	0.00
0.00	0.17	2.58	0.00	2.03	7.50
0.00	0.51	0.00	0.00	0.00	0.00
0.00	0.00	0.26	0.00	0.00	0.00
0.00	0.00	0.26	0.27	0.51	0.00
0.50	0.17	0.00	0.00	0.00	0.00
1.99	10.88	6.19	10.66	15.99	43.61
0.50	0.17	0.00	3.55	0.00	0.00
0.00	0.00	0.00	0.00	0.00	0.28
12.94	49.66	47.16	6.28	52.54	39.44
0.50	0.17	0.00	2.19	4.57	0.28
4.48	9.86	2.58	24.32	8.12	3.06
0.00	0.00	0.00	0.00	0.25	0.00
0.50	0.17	0.00	0.00	0.00	0.00
0.00	1.70	0.77	6.28	0.25	0.00
0.00	10.71	0.26	0.27	0.25	0.00
0.00	0.34	0.00	5.19	0.00	0.00
0.50	1.70	6.19	1.37	1.27	1.94
0.00	0.00	0.00	0.27	0.25	0.00
0.50	0.00	5.15	0.55	0.00	0.56
47.76	0.00	0.00	0.27	0.25	1.67
0.00	0.00	27.06	0.00	12.18	0.00
0.00	0.00	0.26	0.27	0.00	0.28
201	588	388	366	394	360

because their oxygen uptake is independent of dissolved oxygen. Nepids (Nepidae) comprised a large component of atmospheric breathers in the swamp. They often rest on vegetation but must return repeatedly to the surface to breathe. Their abundance in the swamp sites was very high and may have been underestimated by our benthic-oriented sampling. Interestingly, Mikana Stream (low), an intermittent stream site, also had a high abundance of atmospheric breathers even though it was characterized by relatively high dissolved oxygen content. This site, however, is at the outflow of the stream into the swamp where snails (atmospheric breathers) are very common. It may represent an

ecotone area in which the composition of the fauna is affected by the adjacent swamp site. In the fast-flowing river sites, air breathers may also be limited by the rapid flow that may constrain stable connection with the atmosphere (Eriksen *et al.* 1996).

The absolute and relative abundance of the fingernail clam *Sphaerium* sp. was negatively related to dissolved oxygen concentration. The fingernail clams are euryoxic, withstanding a wide range of dissolved oxygen conditions (McKee & Mackie 1983, Holopainen & Penttinen 1993). This allows them to reside in the hypoxic swamps and intermittent streams. Hypoxic conditions, however, may come at a cost by greatly reducing their metabolic

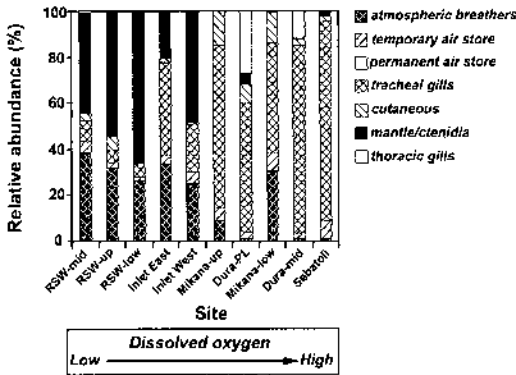


FIGURE 3. The relative abundance of benthic invertebrates grouped by respiratory mode at ten sites in Kibale National Park, Uganda. Values represent the average of monthly samples collected over two-years. Sites included three swamp sites (RSW-mid, RSW-up, and RSW-low), four intermittent stream sites (Inlet East, Inlet West, Mikana-up, and Mikana-low), and three river sites (Dura PL, Dura-mid, and Mpanga-Sebatoli); site locations are indicated in Figure 1.

rate. In their study of two sphaerid species (*Pisidium amnicum* and *Sphaerium corneum*), Holopainen and Penttinen (1993) found that the clams suppressed their metabolic rate to 7.5 percent of their active level in anoxic water. This cost may be offset by a reduced competitive environment in the hypoxic swamp waters.

There was a strong positive relationship between the absolute and relative abundances of tracheal gill breathers and dissolved oxygen concentration. The well-oxygenated waters of the river sites were dominated by invertebrates of this respiratory mode, as were the two Mikana stream sites. Inlet Streams East and West had a much lower proportion of tracheal gill breathers. These sites, however, were characterized by lower dissolved oxygen content than the other intermittent stream sites and may represent a threshold for some invertebrates in this respiratory category. Tracheal gill breathers tend to be more sensitive to hypoxia than other aquatic insect larvae such as atmospheric breathers, because they are benthic and extract dissolved oxygen from the aqueous environment by simple diffusion (Wigglesworth 1972). But surprisingly, some tracheal gill breathers were found in our papyrus swamp sites, albeit at a low abundance. These included primarily odonates (both damselfly larvae and dragonfly larvae). In her study of zygopteran assemblages in Kibale, Apodaca (2003) reported the occurrence of adults of six damselfly species in the interior of the Rwembaita

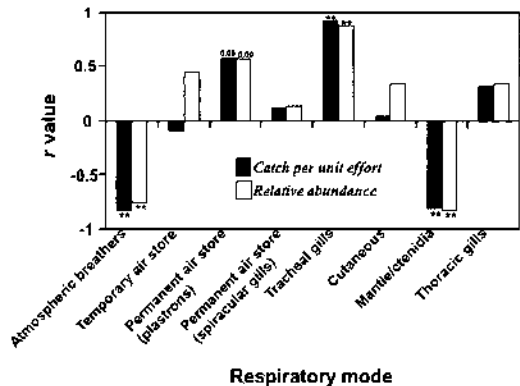


FIGURE 4. Correlation coefficients for the relationship between the abundance of macroinvertebrates grouped by respiratory mode and mean dissolved oxygen concentration across ten sites in Kibale National Park, Uganda (dark bars) and the relationship between catch per unit effort and mean dissolved oxygen concentration (gray bars). * $P < 0.05$, ** $P < 0.01$ (two-tailed test). P -values for marginally significant relationships are presented.

Swamp, some of which occurred throughout the year. These included two swamp specialists within Kibale National Park for which distribution was restricted to the papyrus swamp habitat (*Proischnura subfurcatum* and *Ceriatrigon glabrum* and four more widespread species (Apodaca 2003, Apodaca & Chapman 2004). The low dissolved oxygen levels of the Rwembaita Swamp would represent stressful conditions for many temperate zygopteran species based on contemporary patterns of distribution (Lawton 1971, Eriksen 1986); however, given the widespread occurrence of hypoxia in tropical freshwaters, it is possible that some aquatic insect groups have evolved to exploit such habitats.

Permanent air store breathers (plastrons) were rare in our samples; this relates in part to the fact that many are mid-water or surface-dwelling invertebrates. In our collections, however, their relative and absolute abundances showed a marginal positive relationship with dissolved oxygen. This is consistent with constraints imposed by their gas exchange systems, as oxygen consumption is determined by the rate of oxygen diffusion through the both fixed and limited surface area of the plastron (Eriksen *et al.* 1996). If the oxygen partial pressure is lower in the water than in the plastron, it will diffuse away from the insect. We found no plastron-bearing insects at our papyrus swamp sites, and among intermittent streams, they occurred at the stream with the highest dissolved oxygen level.

Macroinvertebrates with temporary air stores and those with spiracular gills were also quite rare

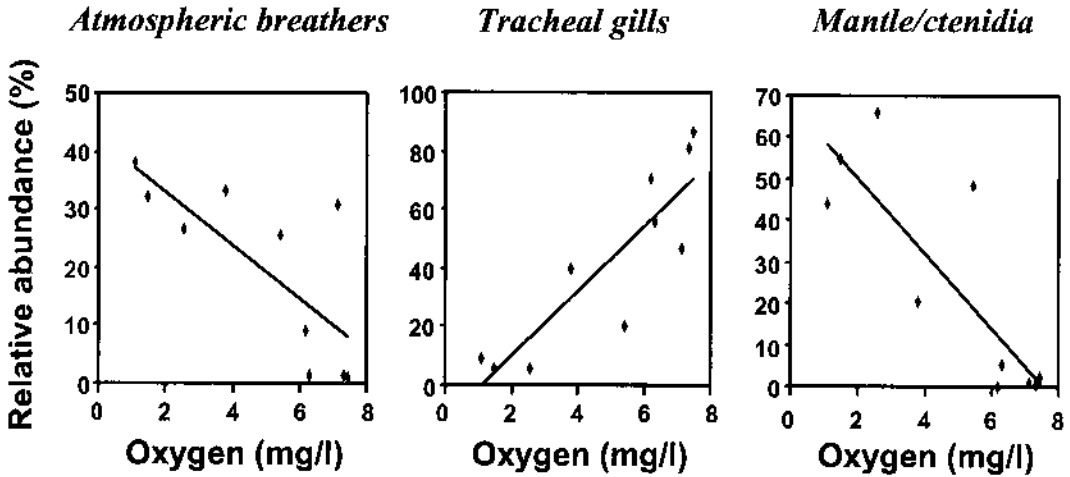


FIGURE 5. Relationship between the relative abundance of (a) atmospheric breathers, (b) tracheal gill breathers, and (c) water-breathing mollusks (mantle/ctenidia), and mean dissolved oxygen concentration across ten sites in Kibale National Park, Uganda.

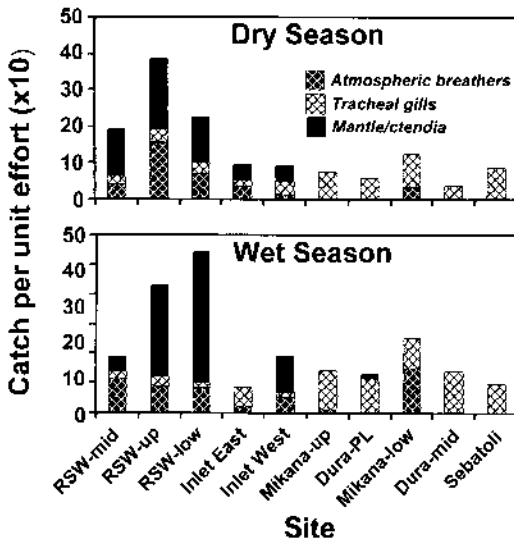


FIGURE 6. The catch per unit effort for three groups of benthic macroinvertebrates categorized by respiratory mode (atmospheric breathers, tracheal gill breathers, and water-breathing mollusks (mantle/ctenidia) in the wet season (8 wettest months combined of the 25 sampled) and dry season (8 driest months) for ten sites in Kibale National Park, Uganda. Sites included three swamp sites (RSW-mid, RSW-up, and RSW-low), four intermittent stream sites (Inlet East, Inlet West, Mikana-up, and Mikana-low), and three river sites (Dura PL, Dura-mid, and Mpanga-Sebatoli).

in our collections. Insects with spiracular gills are often small (*e.g.*, simuliid larvae) and were therefore underrepresented by our sampling method. Simuliid pupae tend to be in fast flowing well-oxygenated waters (Peterson 1996), and our results were consistent with this general habitat association of the family. Temporary air store breathers showed no relationship with dissolved oxygen concentration. Dytiscid, gyrenid, and hydrophilid adults were found across a broad range of sites. Our benthic sampling no doubt underrepresented their abundance because they are often surface-dwelling (*e.g.*, gyrenid adults) or mid-water organisms; however, their occurrence at all three swamp sites was interesting since the length of time that the bubble is effective in oxygen uptake depends on the ratio of the rate of oxygen consumption to the bubble surface area and on the oxygen partial pressure in the surrounding water (Rahn & Paganelli 1968, Mill 1973, Williams & Feltmate 1992, Eriksen *et al.* 1996). Low oxygen in the water decreases the diffusion gradient and the inward diffusion of oxygen into the temporary air store. Thus, swamp-dwelling invertebrates exhibiting this respiratory mode may be very limited in their dive depth or time, or possess very low rates of oxygen consumption.

The CPUE of cutaneous breathers was not related to dissolved oxygen content. Across our sites, this respiratory group was comprised of taxa that are very tolerant of hypoxia and some taxa that are very sensitive to hypoxia. Many species of chironomid larvae are extremely tolerant; oxygen dissolves through the cuticle, is stored in the hemoglobin,

TABLE 2. Two-way analysis of variance showing the effects of habitat (swamp, intermittent stream, and river), season (wet vs. dry), and their interaction on catch per unit effort of benthic macroinvertebrates (\log_{10} transformed) in Kibale National Park, Uganda.

Source of variation	df	MS	F	P
(a) Atmospheric breathers				
Habitat type	2	7.374	29.915	<0.001
Season	1	0.012	0.048	0.829
Habitat \times season	2	0.064	0.259	0.776
Error	14	0.245		
(b) Tracheal gills				
Habitat type	2	0.359	4.390	0.033
Season	1	0.158	1.933	0.186
Habitat \times season	2	0.045	0.548	0.590
Error	14	0.082		
(c) Mantle/ctenidia				
Habitat type	2	8.685	7.782	0.005
Season	1	0.004	0.004	0.954
Habitat \times season	2	0.257	0.230	0.797
Error	14	1.043		

and then released during oxygen-stressed conditions (Eriksen *et al.* 1996, Hoback & Stanley 2001). Other taxa, such as the simuliid larvae, seem to be very sensitive to low oxygen conditions and are found primarily in fast-flowing rivers. Most insects that are strictly cutaneous breathers are very small because they must have a high surface to volume ratio to rely solely on this method of gas exchange (Eriksen *et al.* 1996), and this group was undoubtedly underrepresented in the scoop net samples.

SEASONALITY.—We detected no significant seasonal variation in the catch per unit effort of the dominant respiratory groups. In Kibale, seasonal variation in rainfall is reflected in seasonal increase in flow, dissolved oxygen concentration, and aquatic habitat available in the stream and swamp sites (Chapman & Liem 1995; Chapman *et al.* 1998, 2000); however, the bimodality of the rains associated with the equatorial location of the site buffers the strong seasonal changes that are evident at higher latitudes.

Apodaca and Chapman (2004) found that season was not a significant predictor of the occurrence of adult damselflies at swamp and stream sites in Kibale and suggested unregulated (not limited by season or habitat availability, essentially year-round) development in some species of larval damselflies. Other studies of relatively aseasonal tropical streams have reported no patterns of seasonal change in faunal abundance, species composition, or life cycles. For example, Yule and Pearson (1996)

observed no pattern of seasonal change in faunal abundance or species composition in the benthic invertebrates in mountain rain forest streams on Bouganville Island, Papua New Guinea, which they attributed to the lack of environmental cues permitting synchronization of life cycles. Similarly, Turcotte and Harper (1982) reported evidence of non-seasonality in the life cycles of several ephemeropteran, plecopteran, and trichopteran species in a small Andean stream. In some other relatively aseasonal systems, however, stronger seasonal trends were evident (Bright 1982, Wolda & Flowers 1985). In our study, we focused on the seasonality in the abundance of the dominant respiratory groups. It is quite possible that seasonal variation would have been stronger if we had focused on individual species rather than functional respiratory categories.

CONSERVATION IMPLICATIONS.—In tropical forests, regeneration and restoration programs have focused primarily on terrestrial communities; however, aquatic systems are also subject to major use and conversion. In addition, aquatic systems absorb impacts of land use and thereby accumulate information on terrestrial change over broad spatial scales in flowing river systems and broad temporal scales in static lake environments (Crisman 1988). Aquatic invertebrates are often used as indicators of habitat quality in aquatic systems (Rosenberg & Resh 1993); the sensitivity of particular taxa to environmental stressors offers a tool for evaluating ecosystem health and detecting water quality

change. The value of aquatic faunas and water quality as indicators of terrestrial change has long been recognized, with the vast majority of the work on aquatic bio-indicators focusing on temperate systems; however, there is growing interest in Africa in the use of aquatic invertebrates as indicators of water quality and ecosystem change (Maragi 1996, Dallas 1997, Thorne *et al.* 2000). Tracheal gill breathers seem to be particularly sensitive to environmental toxicants because the gills are very permeable relative to the sclerotized cuticle (Eriksen *et al.* 1996) and may be compromised by some environmental toxicants (Simpson 1980). The results of our study suggest that tracheal gill breathers may be a very useful predictor of the oxygen environment in tropical waters. The combination of low oxygen conditions and environmental toxicants that characterize some polluted waters may lead to severe respiratory stress for this group. There was, however, a notable occurrence of some tracheal gill

breathers in extremely hypoxic waters of our papyrus swamp sites, suggesting that a subset of species in this respiratory category are extremely tolerant of hypoxia. This observation highlights the importance of understanding variation within taxa (*e.g.*, Zygoptera) in response to environmental stressors, particularly if these taxa are used as bio-indicators.

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