tween 1200 and 1400 h. Based on previous observations of the system, we selected sites which varied in cover, depth, current, and bottom type, and which maintained water throughout the dry season. We limited our observations to areas of the swamp utilized by fish populations. pH was recorded for each site concurrently with oxygen and temperature using a hand held pH meter. Maximum water depth at each station and water current (ranked on a scale of 0 to 3; 0 = no current, 1 = low, 2 = medium, 3 = high) were also recorded at sites during each sampling event.

Results

Dissolved oxygen averaged 1.18 mg L^{-1} during the study period, with a range of 0.28 mg L-1 in March to 3.13 mg L^{-1} in November (Fig. 1).

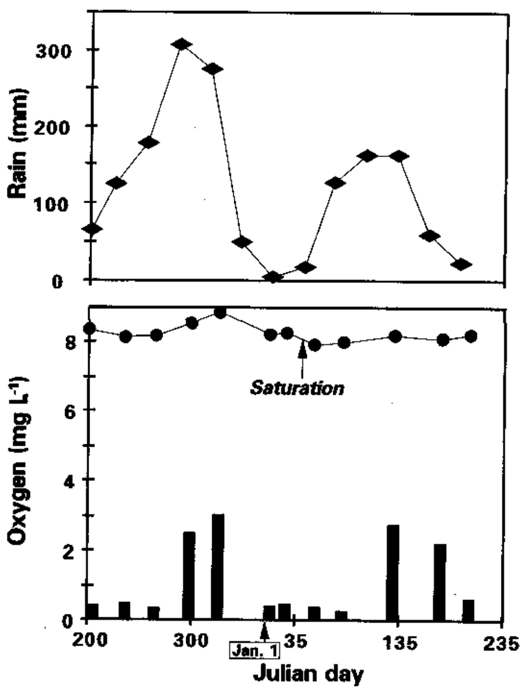

Fig. 1. a – Average monthly rainfall in Kibale Forest, Uganda, based on rain data collected by the Makerere University Biological Field Station, at a site approximately 3 km from the Rwembaita Swamp. b – mean dissolved oxygen concentration (mg L^{-1}); each value represents the average of duplicate samples for 6 stations in the Rwembaita Swamp relative to estimated saturation (mg L^{-1}) based on average water temperature for a given date (July 1991 to July 1992).

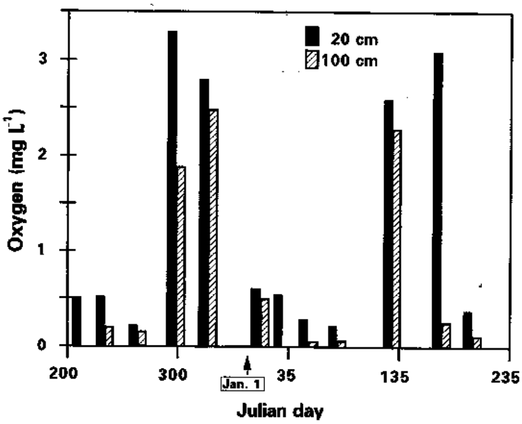

Fig. 2. Differences in dissolved oxygen concentration (mg L^{-1}) between surface waters (< 20 cm) and 1 meter of depth for the deepest station sampled in the Rwembaita Swamp (July 1991 to July 1992).

Seasonal (wet-dry) increases in dissolved oxygen correlated with the biannual rainfall pattern (Pearson's $r = 0.764$, $P = 0.004$, Fig. 1). During the months of heaviest rainfall (October/November, and April/May), dissolved oxygen levels were much higher (mean = 2.64 mg L^{-1}) than the remainder of the year (mean = 0.43 mg L^{-1}). However, dissolved oxygen never exceeded 50 % of saturation, even during peak flood conditions (Fig. 1). Rank estimates of water current showed seasonal increases which were correlated with both high rainfall ($r = 0.816$, $P = 0.001$) and associated high levels of dissolved oxygen ($r = 0.658$, $P = 0.020$).

Microhabitat variation in dissolved oxygen was low relative to the marked seasonal variation. Average values among the six microsites over the period of study ranged between 0.99 and 1.26 mg L^{-1}. During the period of the lowest dissolved oxygen, oxygen values ranged among sampling sites from 0.2 to 0.4 mg L^{-1}. When average oxygen levels were the highest, values ranged from 2.8 to 3.2 mg L^{-1} among sites. The site with the highest oxygen values during the driest months (mean = 0.53 mg L^{-1}, n = 8 months) was a channel with the fastest water flow of the habitats examined. In the deepest site, where it was possible to collect oxygen readings from water over a meter deep, oxygen profiles were clinograde, averaging 1.26 mg L^{-1} over the year in the upper 20 cm of the water column and 0.82 mg L^{-1} at 1 meter (Fig. 2).

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Limnological observations of a papyrus swamp in Uganda: implications for fish faunal structure and diversity

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Introduction

Papyrus (*Cyperus papyrus*) is extensively distributed in East and Central Africa, dominating much of the 85,000 km^2 of permanent swamp on the African continent (Beadle & Lind 1960, Beadle 1981, Thompson & Hamilton 1983). In Uganda alone, there are 6,475 km^2 of permanent swamp, covering approximately 2.7% of the country (Beadle & Lind 1960). Papyrus is the largest sedge in the world, normally attaining heights of 3–4 meters, and typically comprising over 95 % of the plant biomass of the swamp (Thompson 1976, Thompson et al. 1979). The dense canopy of papyrus limits both mixing of the water column and light, intercepting over 90 % of the incoming radiation (Jones & Mithuri 1985, Thompson et. al. 1979). In combination with high rates of organic decomposition, these conditions result in extremely low oxygen levels in the water beneath the swamp canopy (Carter 1955, Beadle & Lind 1960, Chapman & Liem 1995). Such depleted oxygen conditions should limit the use of these wetlands to organisms that can withstand the near anoxic conditions that can prevail in their dense interior.

The few accounts of fish communities in papyrus swamps include primarily air breathers (Carter 1955, Beadle 1981). However, some water-breathing fishes are also found (Beadle 1932, Carter 1955, Chapman & Liem 1995). Such species tend to have extremely efficient oxygen uptake mechanisms and often inhabit the ecotonal area between the swamp and open waters or open pools within the swamps where oxygen is higher (Carter 1955, Chapman & Liem 1995). Despite the depauperate fish fauna that is characteristic of the dense interior of papyrus swamps, these habitats may contribute to the maintenance of fish faunal diversity on a regional scale. For air-breathing fishes, papyrus swamps and other oxygen depleted wetlands are not likely to be a barrier to dispersal (Roberts 1975). However, for water-breathing fishes that are intolerant of low oxygen conditions, swamps may inhibit dispersal and serve as an isolating mechanism.

In order to understand or predict the function of papyrus swamps in the maintenance of fish faunal structure and diversity, we must define seasonal and spatial variation in oxygen regimes. Accessibility to the dense interior of swamps may be facilitated by seasonal enhancement in dissolved oxygen or selection of microhabitats with higher oxygen levels. The current study examines seasonal and spatial variation in dissolved oxygen in a valley papyrus swamp in western Uganda. Observations on water temperature, pH, rainfall, and current are also reported, and we discuss the implications of our limnological observations for fish faunal structure and diversity on the African continent.

Methods

Study site and species

This study was conducted in the Kibale National Park in western Uganda (0°13′–0°41′ N and 30°19′–30°32′ E). About 60 % of the park is tall forest, and the remainder of the area is comprised of grassland, swamp, and colonizing forest. Kibale Forest is drained by two major rivers, the Dura and Mpanga; both are tributaries of Lake George and are fed by numerous small rivers and intermittent tributaries. The study site, Rwembaita Swamp, is one of the larger papyrus swamps in the park (approximately 6.5 km in length) and feeds the Njuguta River, a tributary of the Mpanga River. Mean annual rainfall in the Kibale Forest (1987–1991) averages 1740 mm (range 1607–1864 mm). Rainfall is dispersed over the year; however, there are distinct bimodal wet and dry seasons. May through August and December through February tend to be the driest months, with the May-August dry period of longer duration.

Limnological parameters

Duplicate readings of dissolved oxygen and water temperature using a YSI meter (Model 51B) were taken at six stations in the Rwembaita Swamp monthly between July 1991 and July 1992. In the closed cover of the forest and papyrus swamp, diel variation in dissolved oxygen and water temperature tends to be low (Chapman & Liem 1995). Therefore, measurements were taken once per sampling date be-

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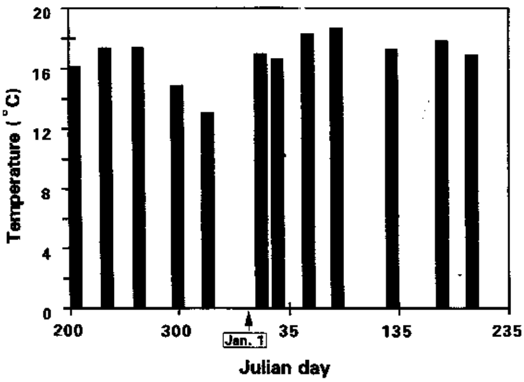

Fig. 3. Monthly variation in mean water temperature (°C); each value represents the average of duplicate samples for 6 stations in the Rwembaita Swamp (July 1991 to July 1992).

Water temperatures in the dense interior of the valley swamp were cool, averaging 16.8 °C over the year. Average values varied from 13.0 °C in November to 18.7 °C in March (Fig. 3). Highest temperatures occurred during the driest months and coincided with the lowest oxygen conditions in the swamp. pH averaged 7.0 over the year and displayed little annual variation, ranging from 6.6 in September to 7.5 in March.

Discussion

Papyrus swamps and patterns of dissolved oxygen

Oxygen levels in the Rwembaita Swamp, which averaged only 1.2 mg L-1 and were less than 0.7 mg L^{-1} for most of the year, are not unusually low for papyrus swamps and some other heavily vegetated tropical swamps. CARTER (1955) reported oxygen values averaging less than 0.1 mg L^{-1} for the nearshore areas of littoral papyrus swamps in Lake Victoria, and average values of 2.5 mg L^{-1} for the interface between papyrus and pelagic waters. He also noted that the water of the grass swamp on the shore side of the papyrus was not noticeably different from conditions in the papyrus zone. In the papyrus valley swamps of the Lake Victoria Basin near Jinja, Uganda, CARTER (1955) also reported extremely low oxygen levels, averaging 0.7 mg L^{-1} (8 % saturation). Similarly, in the dense papyrus at the mouth of the Chambura River in Uganda, BEADLE (1932) found no detectable oxygen within a few cm of the mat surface. Elsewhere in the tropics, CARTER & BEADLE (1930) found widespread oxygen deficiency in the swamps of the Paraguayan Chaco where oxygen levels within 1 cm of the surface, fell to less than 0.1 mg L^{-1} (2 % saturation) for many days at a time. CARTER (1934) found similar, although less severe, oxygen deficiency in rain forest swamps of Guyana associated with the stagnant waters containing large amounts of decaying vegetation.

The current study characterized seasonal peaks of oxygen associated with biannual flooding, which may provide opportunities for fishes to use or move through papyrus. However, even peak flood values never reached 50 % saturation, and thus may pose a barrier for some hypoxia intolerant species. Other studies have also reported a modest seasonal increase in oxygen during the rains. CARTER (1955) found that the distance from the edge of the papyrus in Lake Victoria and the anoxic-oxic boundary increased during seasonal rains; however, in the dense interior of the papyrus nearshore, oxygen was present in surface waters only where current was rapid. In his study of the Ugandan valley swamps, CARTER (1955) reported an increase in oxygen values in surface waters from <0.5 mg L^{-1} in the dry season to 1.4 mg L^{-1} during the rainy period.

Microhabitat variation in surficial oxygen was low among the sampling sites. However, even small differences may be important to fishes during the dry season, when dissolved oxygen is particularly limiting. In addition, we measured dissolved oxygen only in areas which retained water throughout year. Other areas of the swamp that are more ephemeral and those beneath the often floating swamp mat are often lower in dissolved oxygen concentration (CRISMAN & OTTO unpublished data). In Lake Victoria, CARTER (1955) found that water below the mat in the outer part of the papyrus zone was much more severely deoxygenated than surface waters.

Papyrus swamps and fish diversity

Despite the limited diversity of fishes in papyrus swamps, these habitats may contribute to the maintenance of faunal diversity in the Lake Victoria Basin. Continued swamp degradation by humans may precipitate a decline in the diversity of indigenous fishes through loss of habitat, faunal mixing, and destruction of refugia.

For some air-breathing fishes, papyrus swamps are important habitats that are used throughout the year or seasonally as breeding grounds. Within the Lake Victoria Basin, for example, some fish species including *Ctenopoma muriei, Clarias liocephalus*, and *Nothobranchius* sp. are found principally in papyrus swamps and other wetlands. Thus, loss of wetlands will result in loss of habitat for some indigenous fishes.

Papyrus swamps may also be important in minimizing faunal mixing by creating barriers to the dispersal of fish species that are intolerant of low oxygen. For air-breathing fishes, papyrus swamps and other large swampy divides are not likely to be barriers to dispersal. However, for hypoxia intolerant water breathers, these swamps may limit movement and serve as an isolating mechanism. For water breathers that can survive in the dense interior of papyrus, swamp exploitation is likely to be limited by oxygen availability and the efficiency of oxygen uptake for individual species. This has two implications. First, for indigenous fishes that are intolerant of hypoxic waters, papyrus swamps may be important in promoting faunal diversification by reducing rates of dispersal between populations. This may result in geographical variation between swamp populations and those from open water sections of the drainage or among populations separated by extensive swampy divides. Second, papyrus swamps may function to limit the range extension of introduced fishes. This may be extremely important in the Lake Victoria Basin, where the spread of introduced species threatens the integrity of many indigenous faunas in lakes and rivers.

The small cyprinid *Barbus neumayeri* inhabits the dense interior of papyrus swamps (Chapman & Liem 1995). Large gills, the use of aquatic respiration at the air-water interface (aquatic surface respiration, ASR, Kramer & McClure 1982) where diffusion produces an oxygen rich micro-layer of surface water, and selection of microhabitats with higher levels of dissolved oxygen permit this species to survive in hypoxic swamps (Chapman & Liem 1995). Chapman & Liem (1995) found that the swamp population had gills that were approximately 35 % larger in total gill filament length than a population from a constant flowing section of the drainage. In addition, Olowo & Chapman (1996) compared the respiratory behavior of *B. neumayeri* from the dense interior of a papyrus swamp to populations from eight stream and river sites with higher oxygen levels and found evidence of small scale geographical variation in behavior between swamp and fluvial populations. These studies suggest that for water breathers like *Barbus neumayeri*, strong selection for hypoxia tolerance appears to produce variation among populations, particularly in traits related to oxygen uptake. The patchy distribution of swamps choking many river valleys in Africa may impose a heterogeneity in environmental pressures resulting in geographical variation between swamp populations and those from open water sections of the drainage. Whether this variation in the behavior and morphology of *B. neumayeri* is phenotypic or genotypic is not known; however, Chapman & Liem (1995) found both a restricted distribution and limited movement in the *B. neumayeri* population of the Rwembaita Swamp, which may contribute to genetic diversification.

The potential role of wetlands in the maintenance of fish faunal structure and diversity is best exemplified by the recent history of the Lakes Victoria, Kyoga, and Nabugab. The species flock of haplochromine cichlid fishes in Lake Victoria is one of the most extensive and recent radiations of vertebrates known. However, an estimated 200 of the 300+ species of fish (90 % haplochromines) native to the lake are thought to have declined or disappeared since the early 1980's (Witte et al. 1992). Predation by the introduced Nile perch is thought to be one of the most significant factors underlying this mass extinction (Kaufman 1992, Witte et al. 1992).

The severity of the loss in species richness and diversity has led to a series of studies directed at identifying potential faunal refugia. Several lines of evidence now suggest that wetlands may protect some fishes from Nile perch predation by providing both structural and low oxygen refugia for prey species and serving as barriers to the dispersal of the Nile perch. First, Fish (1956) found that Nile perch require water with high dissolved oxygen, since their blood has a low affinity for oxygen. Further physiological work has shown that Nile perch have a relatively high critical oxygen tension which supports a low tolerance to extreme hypoxia

(Schofield & Chapman unpublished data). Thus, the expansion of Nile perch from lakes into river systems may be limited by river mouths and valleys choked with papyrus. Second, Chapman et al. (1995) found that some of the cichlids from Lake Victoria can tolerate extremely low levels of oxygen and that lacustrine cichlids endemic to Lake Victoria are more tolerant of hypoxia than ecologically similar species from Lake Tanganyika. This suggests that environments with low oxygen, such as papyrus swamps, are, or have been historically, an important habitat for fishes in Lake Victoria. Third, survey data in Lake Nabugabo, Uganda, where native populations have declined or disappeared since the introduction of the Nile perch in 1960, indicate that many of the species thought to be rare or extinct in Nabugabo can still be found in wetland areas (lagoons, peripheral swamps, and papyrus choked rivers), where Nile perch are rare (Chapman et al. 1996). Many species found in the wetland lagoons and papyrus choked tributary areas of Lake Nabugabo are extremely tolerant of hypoxia. In a detailed study of the ecotonal areas of Lake Nabugabo, Chapman et al. (1996) found several lines of evidence to suggest that wetlands protect some fishes from Nile perch predation including: a low abundance of Nile perch in wetland ecotones relative to open nearshore areas; a negative relationship between species richness among ecotones and dissolved oxygen; and a positive relationship between species richness among ecotones and structural complexity. It is possible that wetlands in the Lake Victoria Basin may serve as refugia from Nile perch predation, and that fishes tolerant of hypoxia may use the denser wetlands without adverse effects from the low oxygen conditions that occur there.

Summary

Papyrus swamps are a habitat of great ecological importance in the Lake Victoria Basin of East Africa. Our study of seasonal and spatial variation in the oxygen regime of a valley swamp in western Uganda demonstrates that dissolved oxygen is both limiting for much of the year and varies little among microhabitats within the dense interior of the swamps. Higher levels of dissolved oxygen are associated with seasonal flooding and may provide seasonal access to areas of swamps for species tolerant of moderate hypoxia. Given the extreme conditions that prevail in the dense interior of papyrus swamps, extensive wetlands may serve as barriers to the movement of hypoxia intolerant species, and provide both important habitats for air breathers and potential refugia for hypoxia tolerant species from intolerant predators.

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References

Beadle, L. C., 1932: Scientific results of the Cambridge Expedition to the East African Lakes, 1930–1. 3. Observations on the bionomics of some East African swamps. – *J. Linn. Soc. (Zool.)* **38**: 135–155.

Beadle, L. C., 1981: *The Inland Waters of Tropical Africa. An Introduction to Tropical Limnology.* – Longman, London, 475 pp.

Beadle, L. C. & Lind, E. M., 1960: Research on the swamps of Uganda. – *Uganda J.* **24**: 84–97.

Carter, G. S., 1955: *The Papyrus Swamps of Uganda.* – Heffer, Cambridge, 25 pp.

Carter, G. S. & Beadle, L. C., 1930: The fauna of the swamps of the Paraguayan Chaco in relation to its environment. I. Physico-chemical nature of the environment. – *J. Linn. Soc. (Zool.)* **37**: 205–258.

Chapman, L. J., Chapman, C. A. & Chandler, M., 1996: Wetland ecotones as refugia for endangered fishes. – *Biol. Cons.* **78**: 263–270.

Chapman, L. J., Chapman, C. A., Ogutu-Ohwayo, R., Chandler, M., Kaufman, L. & Keiter, A. E., 1996: Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. – *Cons. Biol.* **10**: 554–561.

Chapman, L. J., Kaufman, L. S., Chapman, C. A. & McKenzie, F. E., 1995: Hypoxia tolerance in twelve species of East African cichlids: Potential for low oxygen refugia in Lake Victoria. – *Cons. Biol.* **9**: 1–15.

Chapman, L. J. & Liem, K. F., 1995: Papyrus swamps and the respiratory ecology of *Barbus neumayeri*. – *Envir. Biol. Fish.* **44**: 183–197.

FISH, G. R., 1956: Some aspects of the respiration of six species of fish from Uganda. – *J. Exp. Biol.* 33: 186–195.

JONES, M. B. & MUTHURI, F. M., 1985: The canopy structure and microclimate of papyrus (*Cyperus papyrus*) swamps. – *J. Ecol.* 73: 481–491.

KAUFMAN, L. S., 1992: Catastrophic change in species-rich freshwater ecosystems: the lessons of Lake Victoria. – *Bioscience* 42: 846–858.

MUTHURI, F. M., JONES, M. B. & IMBAMBA, S. K., 1989: Primary productivity of papyrus (*Cyperus papyrus*) in a tropical swamp; Lake Naivasha, Kenya. – *Biomass* 18: 1–14.

OLOWO, J. P. & CHAPMAN, L. J., 1996: Papyrus swamps and variation in the respiratory behaviour of the African fish *Barbus neumayeri.* – *Afr. J. Ecol.* 34: 211–222.

THOMPSON, K., 1976: Swamp development in the headwaters of the White Nile. – In: RZOSKA, J. (ed.): *The Nile, Biology of an Ancient River*: 177–196. – Junk, The Hague, Netherlands, 415 pp.

THOMPSON, K. & HAMILTON, A. C., 1984: Peatlands and swamps of the African continent. – In: GORE, A. J. P. (ed.): *Ecosystems of the World 4B Mires: Swamp, bog, fen and moor.* 331–373. – Elsevier, Amsterdam, Netherlands, 479 pp.

THOMPSON, K., SHEWRY, P. R. & WOOLHOUSE, H. W., 1979: Papyrus swamp development in the Upemba Basin, Zaire: studies of population structure in *Cyperus papyrus* stands. – *Bot. J. Linn. Soc.* 78: 299–316.

WITTE, F., GOLDSCHMIDT, T., WANINK, J., VAN OIJEN, M., GOUDSWAARD, K., WITTE-MAAS, E. & BOUTON, N., 1992: The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. – *Env. Biol. Fishes* 34: 1–28.

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