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Does the decline of gastropods in deep water herald ecosystem change in Lakes Malawi and Tanganyika?

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SUMMARY

1. Ancient, deep lakes have traditionally been considered as stable, ecological islands, well buffered from environmental change because of their great depth. However, they are not immune to anthropogenic and climatic stress. Ecosystems of the permanently stratified warm Lakes Malawi and Tanganyika in the Great East African Rift are particularly delicate. Their stratification regime has historically limited the distribution of benthic biota to a 'bathtub ring of biodiversity', namely substrata in the upper, oxygenated water layer.

2. We use historical data on the endemic deep-water molluscs of these lakes to assess present-day stress on their benthic ecosystems. During the 20th century, these molluscs have probably decreased in abundance and migrated to shallower water.

3. These apparent trends have a significance beyond species-based conservation, foremost because deep-water organisms heavily rely on the position and temporal stability of the oxycline and therefore provide an early warning of large-scale changes in the distribution of dissolved oxygen. Oxygen demands have increased in the East African Great Lakes over the last century whereas ventilation of deep water has remained the same or declined.

4. The combination of these factors is resulting in a narrowing of the ring of biodiversity and a changed nutrient flux through this ring. Reduction in the habitat available inevitably puts biota at risk, whereas changes in nutrient flux may cause shifts in the entire ecosystem or the collapse of parts of it.

5. Considering the socioeconomic value of these lakes and the potentially grave implications for their faunal biodiversity and entire ecosystems, existing evidence of faunal decline, especially in taxa that depend strongly on the stratification regime, is of great concern. Moreover, because the factors responsible are widespread and include surface-water warming, increased run-off and eutrophication, respiration stress may also develop in other tropical and subtropical lakes.

Keywords: anthropogenic stress, benthic invertebrate conservation, climate change, deoxygenation, stratification

Introduction

Ancient lakes are natural laboratories of evolution whose biota have been sheltered from environmental change and had sufficient ecological opportunities and time for endemic species flocks to evolve (Bourguignat, 1889; Brooks, 1950; Fryer & Iles, 1972; Martens, 1997). Although ancient lakes have withstood past environmental change well (Boss, 1978; Michel *et al*., 1992), they cannot escape anthropogenic threats and climatically induced stress (Fryer, 1972a; Cohen, 1994; Ogutu-Ohwayo *et al*., 1999; Moore *et al*., 2009). Faunal change, including a decline in population densities and the loss of endemic species, is evident in many ancient lakes, but it is difficult to assess

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from qualitative data (e.g. Albrecht *et al.*, 2009) and it is rarely addressed in the light of anthropogenic and climatically induced changes (Fryer, 1972a; Lévêque, Balian & Martens, 2005). Forty years after Fryer's (1972a,b) first discussion and warning of ecosystem change in the East African Great Lakes, the fragility of these ecosystems still remains poorly synthesised, except perhaps in the context of fisheries. In this study, we aim to point out that oxygen-demanding pollution and potential changes in the temperature stratification in particular are substantial threats to aquatic life in the East African Rift.

Most of the biodiversity and biomass in Africa's deep meromictic (permanently stratified) lakes is concentrated in the upper, well-mixed and oxygenated waters (mixolimnion) near the shores (Gondwe, Guildford & Hecky, 2008; Bergamino *et al.*, 2010). Hence, there is a so-called 'bathtub ring of life' in the littoral and upper sublittoral zones and in the waters directly above them (Cohen, 1994). We highlight perceived changes in the abundance and distribution of deep-water molluscs in the African ancient Lakes Tanganyika and Malawi. Deep-water molluscs live below the primary thermocline and down to where sufficient dissolved oxygen (DO) remains (*c.* 2.5 mg L^{-1}; Donnelly & Appleton, 1985). These waters are not mixed daily, but do mix at least once a year. Because deep-water molluscs are adapted to live on nutrient-enriched mud, where DO concentration is low, and because of their limited mobility, they are highly vulnerable to shifts in the interface between oxygenated and anoxic waters. The loss of some deep-water endemics is thus not merely of concern for species-based conservation but can provide information on changes in the stratification regime. Using available literature information, we provide a conceptual model of environmental changes in African ancient lake ecosystems that allows explaining the putative trends in deep-water molluscs but simultaneously provides insight into feedback mechanisms that are relevant to other biota and the ecosystems in general.

Methods

The data presented in this opinion paper have primarily been compiled from the literature, but malacological information was also obtained from the study of museum collections and recent field campaigns. We included only malacological records explicitly stating that specimens were alive or when shells, opercula and wet collections unambiguously indicate that material was collected alive.

The collections of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium), the Royal Museum for Central Africa (Tervuren, Belgium), the National History Museum (London, U.K.) and the Museum für Naturkunde (Berlin, Germany) were mainly used to cross-reference published records and to obtain complementing metadata. Holdings of deep-water molluscs that remain unreported in the scientific literature were found at the Centre for Health Research and Development (Copenhagen, Denmark), the Smithsonian National Museum of Natural History (Washington DC, U.S.A.), the Academy of Natural Sciences (Philadelphia, U.S.A.) and the Harvard Museum of Comparative Zoology (Cambridge, U.S.A.). We attempted to obtain additional information from curators, their registers and databases.

Our efforts to sample deep-water molluscs consist of dredging campaigns using hand-operated dredges from motorboats. We inquired with earlier collectors (e.g. David H. Eccles, Pieter Kat, Andrew Cohen, Henry Madsen, Thomas Kristensen) about sampling methodologies and about the possible existence of additional unpublished records of deep-water gastropod or information on the unpublished museum holdings they had collected. A qualitative, historical comparison (see Supporting information) indicates that efforts by various parties to sample deep-water organisms were all made with very similar equipment. This suggests that sampling techniques and logistics or bias in sampling efforts do not explain the observed trends.

Material was evaluated with reference to the modern taxonomy (Mandahl-Barth, 1972; Brown, 1994; West *et al.*, 2003; Strong & Glaubrecht, 2007, 2010; Schultheiß *et al.*, 2009, 2011), which admittedly is not fully resolved and stabilised, certainly not for Lake Tanganyika (Michel, 2004; Glaubrecht, 2008). This implies that the Tanganyikan deep-water gastropod assemblage conservatively accepted here may be subject to change when other taxa, which appear to have a wide depth distribution, are subjected to further systematic research.

Trends in deep-water gastropods

In studying the assemblage of freshwater gastropods in deep water in Lakes Malawi and Tanganyika (Fig. 1), two observations have been made. First, there has been a decline over the last few decades in the number of specimens of deep-water molluscs taken per unit effort (P. Kat, T. Geertz, R. Schultheiß & B. Van Bocxlaer, unpubl. data 2011; A. S. Cohen, unpubl. data 2010). Even though the population densities and the distribution of benthic animals are remarkably variable, both spatially and over time (Hewitt, Thrush & Cummings, 2001), decreasing sampling success suggests a decline in abundance. Second, the depth distribution of deep-water species

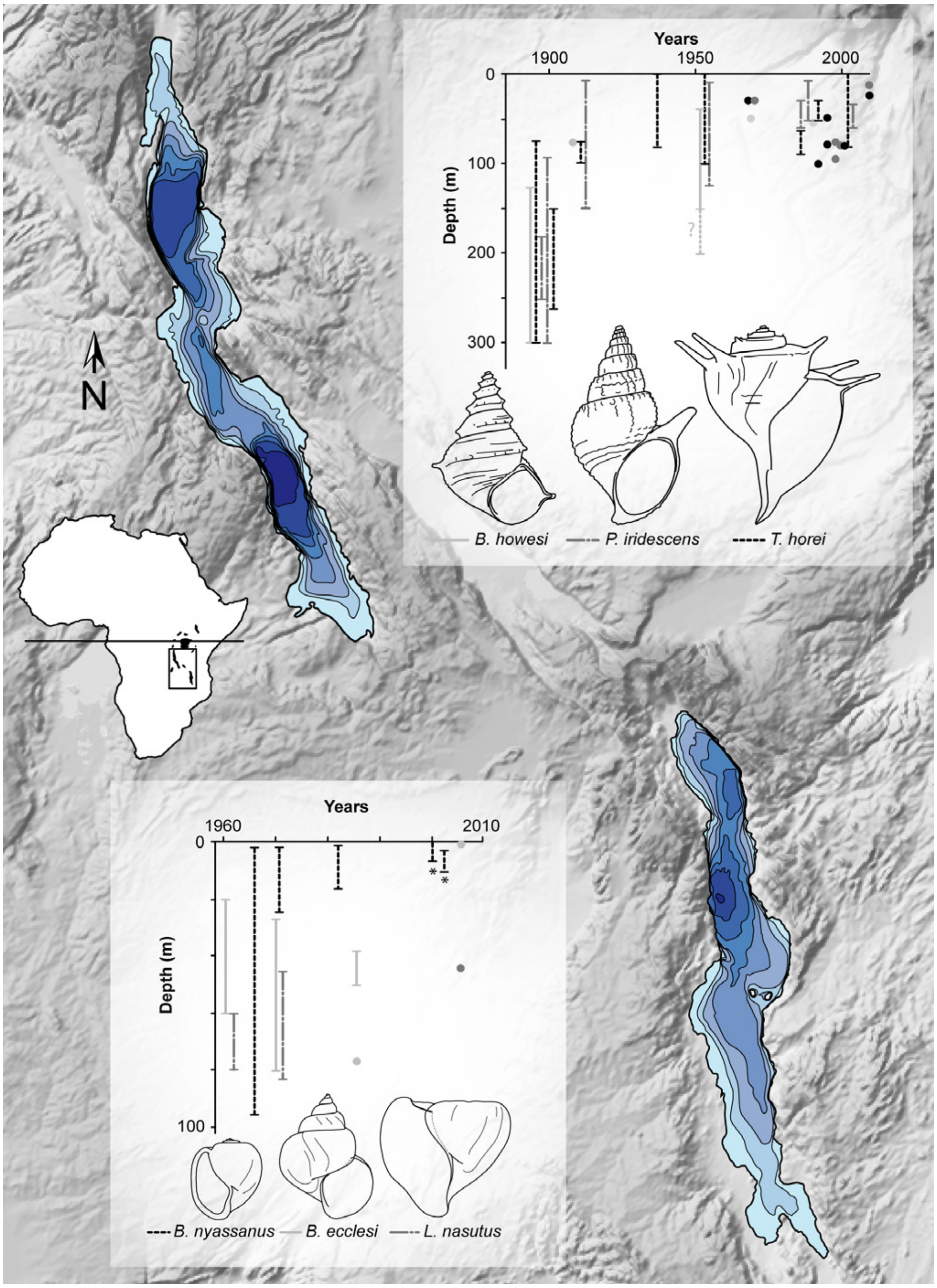

Fig. 1 Map of ancient Lakes Tanganyika (top) and Malawi (bottom) and data on their deep-water gastropod fauna. Insets show the depths from which material of these species was recovered. For Lake Tanganyika, data are from Moore (1898a,c, 1899), Stappers (in 1910; Brooks, 1950 and Leloup, 1953), Beauchamp (in 1937; Brooks, 1950), Leloup (1953), Kat (in 1986; Strong & Glaubrecht, 2007), West in 1989 (West, 1997), Verschuren in 1998 (D. Verschuren, unpubl. data 2011), Wilson and Lorenz (in 2000 and 2002, respectively; Strong & Glaubrecht, 2010), Kinyanjui *et al.* (2002) and Buescher in 2009 (J. A. Todd, unpubl. data 2012). For Lake Malawi, data are from Eccles (D. H. Eccles, unpubl. data 2010; data for 1961 and subsequent years mapped together at 1961), Wright *et al.* (1967), Mandahl-Barth (1972), Louda *et al.* (1983), Kat in 1986 (P. Kat, unpubl. data 2010), Kristensen *et al.* (T. Kristensen, unpubl. data 2011, data from multiple years mapped together at 2000), Genner & Michel (2003) and the present authors in 2006–10. Asterisks (*) indicate records where no collecting attempts were made beyond littoral and shallow sublittoral waters.

appears to have moved upwards over the past few decades (Brooks, 1950; Verburg, Hecky & Kling, 2003) (see Supporting information). Both trends may be evident in both lakes, but the decline in abundance is most apparent in Lake Malawi, whereas changes in the depth distribution are better documented for Lake Tanganyika.

In Lake Malawi, three nominal deep-water species occur: *Lanistes nasutus* Mandahl-Barth, 1972 (*c.* 46–82 m), *Bellamya ecclesi* (Crowley & Pain, 1964) (*c.* 28–80 m) and *Bulinus nyassanus* (Smith, 1877) (*c.* 1–95 m) (Wright, Klein & Eccles, 1967; Mandahl-Barth, 1972) (Fig. 1). Surveys indicate that deep-water molluscs are confined to the nutrient-rich southern part of the lake (Crowley, Pain & Woodward, 1964). The first finds of *B. ecclesi* were made by Eccles in 1961, who also recovered *B. nyassanus* with depth information (Crowley *et al.*, 1964; Wright, Klein & Eccles, 1967). Cridland recollected *B. ecclesi* and added *L. nasutus* to the species list in 1969 (Mandahl-Barth, 1972). In 1981, Louda *et al.* (1983) recorded *B. nyassanus* at depths of 1.5–16.5 m when studying vertical depth gradients in mollusc distribution, as did Genner in 2002 (Genner & Michel, 2003). Kat dredged many specimens of *B. ecclesi* during a 1-h attempt in 1986, but did not find other deep-water taxa (P. Kat, unpubl. data 2010). Our own efforts in 2006–10 consisted of several months of mollusc sampling, including a total of almost 8 weeks of intensive dredging for deep-water species, but only a single juvenile, probably belonging to *L. nasutus*, was found (Schultheiß *et al.*, 2009). We secured our single individual of *B. ecclesi* while searching for shallow-water molluscs (unrelated to our efforts to sample deep-water species) on sands at 0.3 m depth. This finding is surprising because previous parties predominantly explored shallow-water habitats, but never recorded it there. Other malacologists that have collected in the Malawi Basin for decades (H. Madsen, unpubl. data 2010; T. Kristensen, unpubl. data 2011) did not obtain deep-water molluscs either, apart from *B. nyassanus* in shallow waters (0–6 m), but they did not make sampling deep waters a research priority.

Records of deep-water molluscs in Lake Tanganyika pre-date those for Lake Malawi, and because sampling has been more successful, more indications exist for a putative dispersal of deep-water gastropods to shallower waters in Tanganyika. Three nominal deep-water gastropods occur in Lake Tanganyika, namely *Paramelania iridescens* (Moore, 1898), *Bathanalia howesi* Moore, 1898 and *Tiphobia horei* Smith, 1880 (Leloup, 1953; Brown, 1994). The first may require taxonomic revision (J. A. Todd, unpubl. data 2012). Moore (1898a) recorded these three species down to depths of *c.* 300 m in the southern part of the lake and elsewhere stated explicitly that *P. iridescens* was sampled alive from substrata at depths of 91–305 m (Moore, 1899), *T. horei* from 152 to 260 m (Moore, 1898c), and *B. howesi* from depths of 289 m (Moore, 1898b) and 243 m (Moore, 1898c). Leloup (1953) altered the maximum depth ranges for Tanganyikan deep-water molluscs to 150–200 m, because of the lesser maximum depths at which he and others (e.g. Stappers, 1914) obtained material and because he doubted that deep-water molluscs could live deeper in the absence of oxygen. Changes in this lower boundary of the distribution of molluscs may partly relate to uncertain depth estimates (see Supporting information), although similar changes are also reported in the upper boundary of the depth distribution for all three species. For example (Fig. 1), *T. horei* was found (alive) down to 300 m but not above 76 m depth in 1895 (Moore, 1898a), between 76 and 100 m depth by Stappers in 1910–12 (Brooks, 1950; Leloup, 1953) and more shallow still by Beauchamp in 1937 (0–80 m; Brooks, 1950), while it occurred from the surface down to 100 m (perhaps 125 m) depth in 1946 (Leloup, 1953). Later, it was found at 30 m in 1969 by Wetterberg (collections of the Centre for Health Research and Development), at 70–90 m in 1986 by Kat (Strong & Glaubrecht, 2007), at 30–53 m, with one record at 100 m in 1989–95 (West, 1997), and at 80 m in 2000 by Wilson (Strong & Glaubrecht, 2010). In 2002, it was found regularly in waters shallower than 60 m, in very small numbers up to 80 m and not below 80 m (Kinyanjui, Cohen & Michel, 2002), while Buescher sampled it at 25 m in 2009 (J. A. Todd & E. Michel, unpubl. data 2012). Because efforts to sample molluscs have always been more intensive in shallow than in deep water, at least the shoaling of the upper boundary is well substantiated (Fig. 1).

Model of the decline and range-shift of deep-water molluscs

In Lakes Malawi and Tanganyika, a large mass of anoxic water, the monimolimnion, extends below the upper mixolimnion (Beauchamp, 1940). Although perhaps less pronounced than the boundary of hypoxic/anoxic conditions, the shallow euphotic zone (upper 20–50 m) is also unfavourable for deep-water molluscs because they are adapted to life in the dark, away from visual predators such as molluscivorous fish (Evers *et al.*, 2006). Some of their adaptations to avoid sinking into soft substrata, for example inflated, often light and thin shells with large apertures or apertural projections (Fig. 1), contrast with the antipredator defences of species living in the euphotic zone, such as heavy calcification and nodular ornamentation (Berthold, 1990a,b; Brown, 1994). Anthropogenic disturbance and climatic change appear to have restricted the occurrence of suitable habitat for deep-water organisms by affecting both ends of their original range. The lower boundary associated with anoxic waters is shifting upwards (Fig. 2), while the euphotic zone is expanding downwards (Fig. 3).

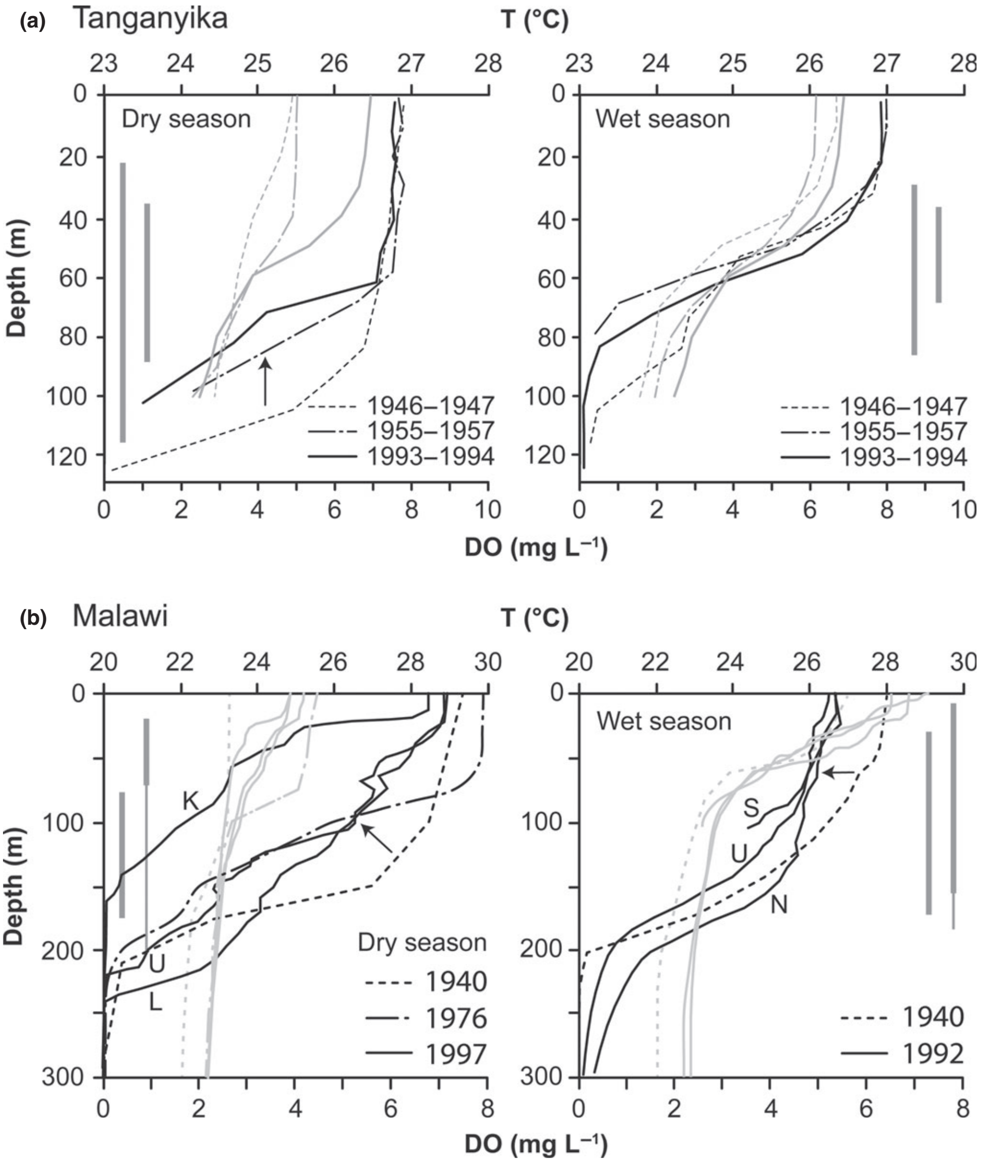

Fig. 2 Temperature–depth (grey) and DO–depth (black) profiles for Lake Tanganyika (a) and Lake Malawi (b) in the dry (May–September) and wet season (October–April). Lake Tanganyika data are from Dubois (1958), Van Meel (1987) and Plisnier (1997) (1946–47, 1955–57 and 1993–94 series, respectively). The depth of the oxycline was shallower in 1993–94 than in 1955–57, and even more so than in 1946–47 (all profiles from the very north of the lake). Partly because of a substantial increase in the wet season surface-water temperature, seasonal differences in the position of the oxycline have become less pronounced. Lake Malawi data are from Beauchamp (1940; from the northern part of the lake), Gonfiantini *et al.* (1979; from nearby Usisya), Halfman [1993; from nearby Usisya (U), Nkhotakota (N), just south of Senga Bay (S)) and Vollmer *et al.* (2002; from nearby Usisya (U), Likoma Island (L) and from halfway between Karonga and Chilumba (K)] (1940, 1976, 1992 and 1997 series, respectively). No unambiguous changes in the oxycline position have occurred in Lake Malawi, which results partly from more significant deep-water warming (compared to Lake Tanganyika) that coincides with surface-water warming. However, DO concentrations at and directly below the thermocline up to *c.* 150 m of depth have been substantially reduced since 1940. Grey bars in each graph represent suitable depth ranges for deep-water gastropods in the 1940s (left) and 1990s (right).

Upward displacement of the oxycline

The oxycline in Lake Tanganyika has become progressively shallower in the period from 1946 to 1994, and simultaneously, the seasonal displacement of the oxycline has decreased (Fig. 2a) (Plisnier, 1997; O'Reilly *et al.*, 2003; Verburg *et al.*, 2003). This results from a strengthening of the temperature-based density stratification caused by a warming trend in the surface waters that outpaces deep-water warming (Plisnier, 1997, 2000; O'Reilly *et al.*, 2003; Verburg *et al.*, 2003; Tierney *et al.*, 2010). Because of the more pronounced temperature stratification, the oxygen

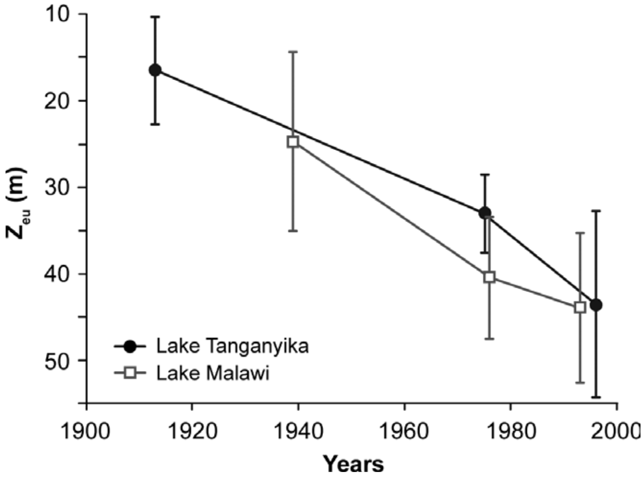

Fig. 3 Change in the mean depth of the euphotic zone (Z_{eu}) in pelagic waters is similar in Lake Malawi and Lake Tanganyika. Euphotic zone depth was calculated from attenuation K, which was either determined from the vertical absorption with depth of underwater light or from Secchi disc data using the equation in Verburg *et al.* (2003). Bars indicate standard deviations; modified from Verburg & Hecky (2009).

consumed by metabolic respiration in deeper oxygenated waters is not compensated for by mixing, resulting in oxygen depletion. Moreover, eutrophication and therefore increasing oxygen consumption may regionally superimpose on more widespread changes in mixing (Alin *et al.*, 1999).

A warming trend of the Lake Malawi surface waters comparable to that in Lake Tanganyika has been reported and results mainly from increased temperature in the dry season (May–September; Fig. 2b) (Vollmer *et al.*, 2005). However, in Lake Malawi the increase in surface-water temperature coincides with significant deep-water warming (Beauchamp, 1953; Patterson & Kachinjika, 1995; Vollmer *et al.*, 2005), which probably reduces density stratification (Fig. 2b). Over the last six decades, the temperature stratification during the wet season (the period of strongest stratification; October–April) over the full depth range has significantly weakened, whereas below 100 m it has remained roughly constant (Vollmer *et al.*, 2005). This reduced stratification during the wet season has allowed faster erosion of the thermocline in the dry season, followed by enhanced convective mixing. Verburg *et al.* (2003) have suggested that stratification has strengthened and mixing reduced in Lake Malawi over the last few decades, but this probably applies mainly to very deep waters (>100 m), where reduced mixing can be attributed to lesser intrusions of cool water (Vollmer *et al.*, 2005), or to the northern part of the basin (Branchu *et al.*, 2010) where biodiversity is lower and deep-water molluscs do not occur (Eccles, 1962). Given that the oxycline for Lake Malawi (Fig. 2b) is considerably deeper than the thermoclines, mixing across the thermocline is substantial and in any case more so than for Lake Tanganyika (Fig. 2a). A slight decrease in wind stress has been observed in the Malawi Basin (Patterson & Kachinjika, 1995), whereas no trend was obtained from a reanalysis of wind speed data by the National Centers for Environmental Prediction (Vollmer *et al.*, 2005), but the applicability of these reanalyses may be limited (Bengtsson, Hagemann & Hodges, 2004; Simmons *et al.*, 2004). Compilation of oxygen profiles for Lake Malawi (Fig. 2b) provides little information on the strength and changes in stratification over time, but indicates that DO concentrations at the thermocline and up to *c.* 150 m of depth have been substantially reduced since 1940. A partial explanation is that the reduced stratification would allow occasional mixing of water that previously belonged to the upper monimolimnion. However, at least in the south of Lake Malawi, a dramatic increase has occurred in sedimentation and eutrophication at depths where deep-water gastropods live (or formerly lived), and the attendant increased nutrient load provokes increased oxygen consumption (Otu *et al.*, 2011), so that hypoxic conditions could expand there to shallower waters even without a change in the mixing regime.

Given the very limited mobility of deep-water molluscs, that is, slow and without the ability to migrate vertically through the water column, they are very vulnerable to oxygen-demanding pollution and any type of perturbation in the position of the oxycline. Their current distribution and the potential retreat to shallow water may result mainly from extreme, singular changes in the position of the oxycline, such as progressing internal waves or changes in the amplitudes of standing internal waves of hypoxic waters, rather than from mean trends in the stratification regime. Unfortunately, few or no data exist on possible changes in the frequency and magnitude of such singular events. Nevertheless, their occurrence is documented for Lake Malawi. In 1937, for example, mass fish mortality took place around Nkhata Bay owing to local upwelling of anoxic water in the wake of mixing across the oxycline (Eccles, 1974).

Downward expansion of the euphotic zone

Increased transparency and a downward expansion of the euphotic zone have been documented for both lakes (Fig. 3; Verburg *et al.*, 2003; Verburg & Hecky, 2009). The increased transparency mainly results from reduced nutrient availability in the upper waters and a subsequent decrease in algal primary production (Wetzel, 1983; O'Reilly *et al.*, 2003; Verburg *et al.*, 2003; Stenuite *et al.*, 2007; Verburg & Hecky, 2009; Tierney *et al.*, 2010). Primary production is concentrated in the littoral zones, certainly in the wet season, and decreases offshore (Gondwe *et al.*, 2008; Bergamino *et al.*, 2010). Changes in light penetration to deeper substrata directly affect the benthic community, for example by altering the distribution ranges of biota. Limited nutrient availability offshore and deeper light penetration potentially increase benthic primary production in comparison with pelagic phytoplankton production and may even adjust the ratio between nearshore/offshore productivity in general. Deeper light penetration and/or migration of deep-water molluscs to shallower substrata (to escape ascending hypoxic and anoxic conditions) would probably result in an increased vulnerability to predators on them. Moreover, it may provoke increased competition with the better adapted shallow-water species that already occupy this niche, and that may simultaneously expand their ranges downwards because of increased transparency. The ramifications of such changes are poorly understood. However, McIntyre *et al.* (2005) demonstrated several direct and indirect effects of increased sedimentation on nutrition, predation, parasitism and other life history traits in shallow-water gastropods of Lake Tanganyika, and effects of environmental change on deep-water taxa are likely to be of similar complexity. The migration of deep-water taxa to shallow water would probably not be successful for thin-shelled, unarmoured, deep-water species or where the habitat is already crowded, but it may work for armoured species and those that are successful in avoiding competition. This may be the case for *P. iridescens* and *T. horei*, species that appear to have successfully colonised the upper 75 m in Lake Tanganyika (Fig. 1). Increased run-off may locally and seasonally (during the wet season) create habitats that are not affected by increased light penetration and high predation incidence (McIntyre *et al.*, 2005), but such habitats are regularly unfavourable for benthic invertebrates because increased run-off and high deposition rates of coarse-grained, largely inorganic, terrigenous substrata in medium to deep water (up to *c.* 120 m) reduces habitat heterogeneity, foraging opportunities and food quality for deep-water molluscs. Such effects are taking place on the north-eastern shores of Lake Tanganyika (Eggermont & Verschuren, 2003; Cohen *et al.*, 2005; McIntyre *et al.*, 2005) and in the southern regions of Lake Malawi (Otu *et al.*, 2011).

Discussion

As multicellular life in ancient meromictic African lakes is restricted to the mixolimnion, it is alarming that the oxycline may be ascending to shallower waters, at least in Lake Tanganyika, and that in Lakes Malawi, Tanganyika and Victoria oxygen consumption at the sediment–water interface and in the lower part of the oxygenated water column is increasing owing to increased sediment influx, associated eutrophication and a consequent increase in microbial activity (Alin *et al.*, 1999; Verschuren *et al.*, 2002; Hecky *et al.*, 2010; Otu *et al.*, 2011). The warm nature of these lakes moreover increases the susceptibility to oxygen depletion: at an atmospheric pressure of 760 mmHg fully oxygen-saturated freshwater at 25 °C contains 8.2 mg L^{-1} DO, whereas at 15 °C this is 10.1 mg L^{-1} DO and at 5 °C this is 12.7 mg L^{-1} DO (*c.* 1.55 × the concentration at 25 °C). On the other hand, biochemical reaction rates, and thus oxygen consumption, are at least doubled when temperatures increase with 10 °C ($Q_{10} \geq 2$; Fryer, 1972a). Moreover, depletion of the oxygen available to deep-water biota is accelerated because the ventilation of deeper waters has remained the same or declined (Plisnier, 1997, 2000; Vollmer, Weiss & Bootsma, 2002; O'Reilly *et al.*, 2003; Verburg *et al.*, 2003; Verburg & Hecky, 2009, Branchu *et al.*, 2010; Tierney *et al.*, 2010). Deep-water deoxygenation has also been demonstrated for Lake Victoria (Hecky *et al.*, 1994). Two series of monthly oxygen profiles taken 30 years apart (1961–62 and 1992, respectively) at one locality in the lake suggested a significant decline in oxygen availability at 40 m of depth and deeper. High-resolution palaeolimnological data later corroborated these results and indicate that the modern conditions of persistent deep-water anoxia had become widespread by 1970 (Verschuren *et al.*, 2002). Discussion of the potential biological effects of this deoxygenation in Lake Victoria was restricted to primary productivity and the economically important fish community (Wanink *et al.*, 2001 and references therein), but other biota must also have been affected. In fact, eradication of certain haplochromine fishes by the Nile perch, via elimination of deep-water refugia that had previously protected these fishes from excessive predation (Verschuren *et al.*, 2002), is much in line with the scenario we presented for molluscs. Some Lake Victoria molluscs that are restricted to the deeper waters [e.g. *Bellamya phthinotropis* (von Martens, 1892), *Coelatura cridlandi* Mandahl-Barth, 1954] have become difficult to collect (e.g. Mandahl-Barth, 1988). Some important components of our model may hence be valid for other tropical African lakes, including Lake Victoria.

The East African Great Lakes, except perhaps Lake Victoria, are traditionally perceived as pristine ecosystems that have not responded dramatically to changes in climate, run-off, anthropogenic sedimentation, nutrient loading and various other sources of pollution, biotic exploitation and the introduction of alien species yet. However, continued strengthening or weakening of the temperature stratification in meromictic lakes and generally increased anthropogenic demands may ultimately have far-reaching ecological effects. One could wonder to what extent pristine conditions still apply to the ecosystems of Lake Malawi and Lake Tanganyika with their complex biotic and abiotic feedback systems. In the pelagic ecosystem of Lake Tanganyika, for example, primary production largely depends on nutrient recycling from deep water to the nutrient-depleted oxygenated waters. Changes in the temperature stratification explain observed shifts in primary productivity and their far-reaching biological effects, for example on fisheries (O'Reilly *et al.*, 2003; Verburg *et al.*, 2003). Climatically and anthropogenically induced changes that affect the pelagic ecosystem appear also to be taking place in the benthic ecosystem (e.g. Cohen *et al.*, 2005). This could be caused, for example, by changes in the nutrient flux to the benthos, oxygen depletion owing to microbial decomposition and frequent, large-scale upwelling of anoxic waters. Ecosystem stress is perhaps detectable earlier in individual groups of benthic taxa, but monitoring them also faces more practical difficulties and is more time consuming (McIntyre *et al.*, 2005).

Anthropogenic and climatic stressors affect several interactions in the ecosystems on a variety of spatial (localised within bays up to the entire lake basin) and temporal scales (seasonal up to hundreds or even thousands of years). Moreover, they affect a diversity of processes, ranging from the individual level (e.g. metabolic requirements, foraging opportunities, predation, parasitism) to larger scale ecosystem effects (e.g. onshore versus offshore primary productivity, systematic respiration stress, nutrient recycling efficiency). The relevance of individual factors and the interactions between them may differ from lake to lake (Bootsma & Hecky, 1993). Whereas our understanding of the complex feedbacks operating in the meromictic African lakes is still incomplete, studies increasingly indicate that the stress caused affects many interactions between the taxa that make up their diverse and speciose communities. The fact that multiple stressors interact with one another creates a general burden that may reduce ecosystem resilience and increase susceptibility to sudden state transitions (Scheffer *et al.*, 2001). A seemingly isolated perturbation unrelated to the conditions that caused the decrease in resilience can become a trigger for wholesale change.

More generally, rare events associated with rapid environmental change appear to be the primary causes of extinction over geological time scales (Raup, 1991a,b; Payne *et al.*, 2011). Sudden nonlinear effects in response to minor gradual changes have been observed in many types of terrestrial, freshwater and marine ecosystems, including Lake Victoria (Scheffer *et al.*, 2001; Dodds *et al.*, 2010; Hecky *et al.*, 2010). Whereas the direct magnitude of climatically and antropogenic-induced changes can have important effects, the velocity at which change occurs probably has more biological relevance (Sandel *et al.*, 2011). It is particularly alarming that the velocity of climate change on the African continent has been relatively modest in the past compared with estimates for the future (Hulme *et al.*, 2001; Sandel *et al.*, 2011). On a global scale, regions presently with rapid climate change have few geographically restricted (endemic) taxa that disperse poorly (Jansson, 2003; Sandel *et al.*, 2011). Many taxa inhabiting the East African Great Lakes fall within this category and, therefore, pose a legitimate conservation concern. Although the data above suggest that sudden state transitions are plausible for Lakes Malawi and Tanganyika, we do not argue that they are imminent and/or inevitable. Nevertheless, we want to emphasise that it would be too optimistic to assume that complex biotic and abiotic interactions will compensate ecosystem change sufficiently to sustain the demands we make on these lakes.

Previous warnings that some species flocks, primarily of fish, in the East African Great Lakes are endangered (Fryer, 1972a,b) were based on data of a similar nature to ours. Although these warnings were considered, by several fishery management parties, to be unwarranted, premature and beyond the available data on fish stocks (Jackson, 1973; Stoneman, Meecham & Mathotho, 1973; rebuttal by Fryer, 1973), they proved to be justified in retrospect (Cohen, 1994). Evidence of increased human impact on the ecosystems of these lakes has become undeniable (e.g. Genner *et al.*, 2004; Cohen *et al.*, 2005; McIntyre *et al.*, 2005; Hecky *et al.*, 2010; Otu *et al.*, 2011), even though it is notoriously difficult to demonstrate quantitatively ecosystem change or not, because the required long-term and large-scale monitoring is mostly lacking (Bootsma & Hecky, 1993; Johnson *et al.*, 2011). The scattered nature and poor comparability of the data available often compromise statistical efforts and/or result in restricted analytical power. Null hypotheses of a *status quo* are often difficult to reject with historical data, let alone the fact that such data would not allow the separation of a genuine lack of change from compensatory adaptations at different levels in the ecosystem (Doak & Morris, 2010). Finally, in systems such as Lake Malawi and Lake Tanganyika, the rate of change potentially outpaces the time required to collect sufficient data for monitoring such vast, deep-water ecosystems (Cohen, 1994, 1995; Coulter *et al*., 2006). Moreover, the buffering effect of the monimolimnion (e.g. by accumulating pollutants) and the long water flushing times of African lakes in general (750, 7000, 140 years for Lakes Malawi, Tanganyika and Victoria, respectively; Bootsma & Hecky, 1993) will cause considerable ecosystem hysteresis. This drastically increases the possibility of irreversible change having taken place by the time sufficient data are collected to demonstrate trends unambiguously. Fishing currently supplies 25–40% of the animal protein in the diet of humans in countries bordering Lake Malawi and Lake Tanganyika (Mölsä *et al*., 1999), and further decreases in fish yields will potentially have grave socioeconomic consequences. Scientific evidence must be offered at the appropriate times in political decision-making processes, as it often has limited use after critical decisions have been made (Sutherland *et al*., 2010). Acknowledging this, and that anticipation is a prerequisite for biodiversity management, we think it important to report potential early warning signals of ecosystem change in the East African Great Lakes. They are too valuable to be treated merely as anecdotes or to be reviewed only when drastic and potentially irreversible ecosystem changes already have taken place.

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Data S1. Methodological information on comparability of historic sampling.

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