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Two hundred years of a diverse *Daphnia* community in Lake Naivasha (Kenya): effects of natural and human-induced environmental changes

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SUMMARY

1. We used fossil diapausing eggs extracted from ^{210}Pb-dated sediment cores to reconstruct historical changes in the *Daphnia* community of Lake Naivasha, a climate-sensitive lake in Kenya which over the past 200 years has experienced a series of well-documented natural and anthropogenic environmental changes.
2. Contiguous sampling and analysis of four cores yielded ephippial capsules of eight *Daphnia* species. Only two of these had been recorded previously in live collections from Lake Naivasha, and one species is new to science. The four more common species (*Daphnia barbata*, *D. laevis*, *D. magna*, and *D. pulex*) show striking differences in abundance patterns and population dynamics through time. Four other species (*D. lumholtzi*, *D. curvirostris*, *D. longispina* s.l., and *Daphnia* sp. nov. type Limuru.) appear to have been present only occasionally. Nevertheless, between 1895 and 1915 seven species of *Daphnia* inhabited Lake Naivasha simultaneously.
3. Despite considerable natural environmental change associated with climate-driven lake-level fluctuations, the *Daphnia* community of Lake Naivasha has been severely affected by human activities over the past century, especially the introduction of exotic fishes and water-quality changes because of agricultural soil erosion. The recent reappearance of large-bodied *Daphnia* species (*D. magna*, *D. barbata*, *D. lumholtzi*, *Daphnia* sp. nov. type Limuru) after 20–110 years of absence can be explained by their release from fish predation, following a dramatic increase in turbidity caused by excess clastic sediment input from eroded catchment soils. The small-bodied species *D. laevis* has fared less well recently, presumably because the benefit of lowered predation pressure is counteracted by more pronounced negative effects of increased turbidity on this species and loss of submerged macrophyte beds which formerly served as predation refuge.
4. Our results suggest that, despite considerable environmental instability and the absence of specialised zooplanktivores, top-down control of fish on large zooplankton is important in Lake Naivasha. Predation pressure from fish has led to clear-cut shifts in local *Daphnia* species composition, but failed to drive the larger taxa to extinction.

Keywords: diapausing eggs, ephippia, paleolimnology, population dynamics, tropical limnology

Introduction

Subfossil remains of zooplankton preserved in lake sediments have commonly been used to reconstruct population and community changes in response to anthropogenic impact on aquatic ecosystems (e.g.

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Birks *et al.*, 1976; Brugam, 1978; Brugam & Speziale, 1983), and to monitor the long-term effects of whole-lake experiments (Kitchell & Kitchell, 1980; Leavitt, Carpenter & Kitchell, 1989). Increasingly, aquatic ecologists also use diapausing eggs to study long-term population dynamics and genetics of zooplankton (e.g. Hairston *et al.*, 1999; Cousyn *et al.*, 2001; Jeppesen *et al.*, 2001). Much of this attention is directed at *Daphnia*, which occupy a central place in many aquatic food webs, grazing strongly on phytoplankton while being important prey items themselves for vertebrate and invertebrate predators (Lampert, 1987). Because sexually produced diapausing eggs are very well preserved in lake sediments, they are often found in great abundance and are easy to work with. Moreover, the long-lasting viability of these eggs and excellent preservation of weak tissues inside the ephippial capsule allow resurrection of former populations and the use of genetic markers to reconstruct changes in the genetic structure of *Daphnia* populations over time (Weider *et al.*, 1997; Cousyn *et al.*, 2001).

To date, no paleolimnological study has dealt specifically with *Daphnia* in tropical lakes. This can partly be attributed to the general appreciation that *Daphnia* is uncommon in the wet tropics (Fernando, Paggi & Rajpaksa, 1987; Dumont, 1994). Yet in equatorial East Africa, *Daphnia* occur in a fairly large number of permanent lakes, with nine species reported so far (Green, 1993, 1995). The environmental control of *Daphnia* population dynamics in these lakes is likely to be complex, for several reasons. First, most East African lakes are river-fed amplifier systems located in hydrologically closed drainage basins (Livingstone & Melack, 1984), so natural rainfall variability is often translated into radical long-term (inter-annual to decade-scale) fluctuations in lake level and water chemistry. Consequently, their zooplankton communities continually change in response to altered habitat conditions involving fluctuations in osmotic stress, turbidity, food availability, and vulnerability to predation (Kalk, 1979). Secondly, as in north-temperate lakes, fish communities of many African lakes have been extensively manipulated through the introduction of exotic species and other kinds of fisheries development and regulation (Ogutuohwayo & Hecky, 1991). In fact, fish introductions have been implicated in the present scarcity of *Daphnia* in crater lakes of tropical West Africa (Green, Corbet & Betney, 1974), where natural habitat stability is fairly high. In the fluctuating lakes of East Africa, fish and zooplankton communities alike are also affected by continuous habitat instability (Hickley *et al.*, 2002). Changes in *Daphnia* species composition and population abundance through time are therefore likely to reflect a complex interplay between bottom-up and top-down mechanisms of environmental regulation.

In this study we document 200 years of change in the *Daphnia* community of Lake Naivasha (Kenya), one of two large freshwater lakes in the Eastern Rift Valley of Kenya, to determine the relative importance of natural environmental changes and human impact on long-term *Daphnia* population dynamics. We reconstruct the history of the *Daphnia* community using subfossil diapausing eggs recovered from sediment cores collected in Crescent Island Crater, a submerged basin along the eastern shore of Lake Naivasha. On account of its relatively great depth and high sedimentation rates, Crescent Island Crater has accumulated an undisturbed, high-resolution sediment record of Lake Naivasha's environmental history. Background information on natural and anthropogenic environmental change over the past 200 years is drawn from earlier paleolimnological studies (Verschuren, 1999; Verschuren *et al.*, 1999; Verschuren, Laird & Cumming, 2000), supplemented with historical data on fish introductions and other human activities that have affected Lake Naivasha since the early colonial period (e.g. Harper, Mavuti & Muchiri, 1990).

Methods

Study site

Hydrological setting. Lake Naivasha is a large (approximately 135 km^2) shallow ($z_{\max}$ approximately 5 m) freshwater lake located at 1885 m a.s.l. just south of the Equator in Kenya's Eastern Rift Valley. In the prevailing semi-arid climate, the lake's water balance is maintained by a significant contribution of surface inflows from the Malewa River, which drains wet highlands in the Nyandarua (Aberdare) mountains to the east. Nevertheless, natural long-term rainfall variability has caused Naivasha's surface level to fluctuate between about 1882 and 1897.5 m a.s.l. in just the last 120 years (Fig. 1). This led to major

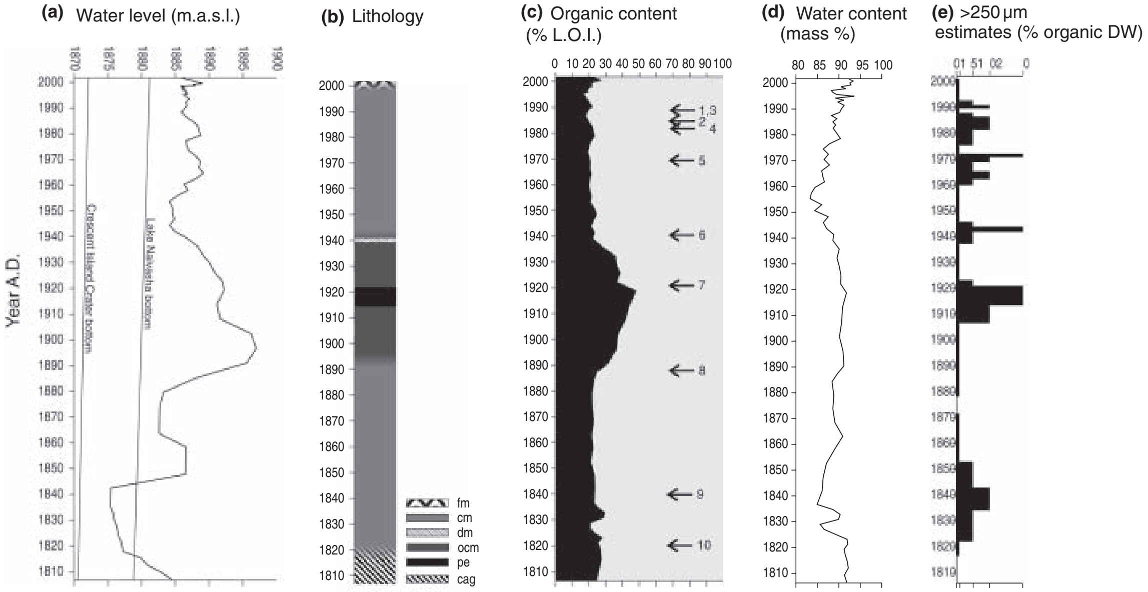


Fig. 1 Lithostratigraphy and composition of core NC01–1S in relation to historical lake-level changes and time markers. (a) Water-level changes over the past 200 years relative to the bottom elevations of Crescent Island Crater and the main basin of Lake Naivasha; from Verschuren (2001). (b) Stratigraphic distribution of sediment types; fm: flocculent mud; cm: clayey mud; dm: diatom mat; ocm: organic clayey mud; pe: peat; cag: clayey algal gyttia. (c) Organic matter content expressed as Loss On Ignition (% L.O.I.). Arrows indicate historical time markers used for relative dating of the four studied cores (see text). (d) Water content of core NC01–1S. (e) Relative abundance of coarse plant remains (>250 μm) as percentage of total organic matter, reflecting historical variation in submerged macrophyte beds.

changes in lake depth ($z_{\max}$ 4–19 m) and surface area (from <100 to >200 km^2), which in turn will profoundly have affected ecosystem functioning and resident plant and animal communities. When the first European settlers arrived in 1883, Lake Naivasha was recovering from a pronounced lowstand (Sikes, 1935; Fig. 1), rising to the historical peak elevation of 1897.5 m in 1894 (Åse, 1987). In 1908–10 the lake level dropped to about 1890 m and remained at that level until the mid-1920s. Progressive decline throughout the late 1920s and 1930s then culminated in a historical lowstand in 1946, which persisted until 1957. Following a renewed rise to 1887 m in the late 1950s and early 1960s, the lake fluctuated around 1885 m a.s.l., with short-lived transgressions during El Niño years, and relative lowstands in the mid-1970s, late 1980s and mid-1990s. Despite these considerable fluctuations in lake depth and volume, Lake Naivasha has remained fresh throughout the historical period (range 233–499 μS cm^{-1}; Verschuren, 1999) because continuous seepage to the groundwater prevents accumulation of dissolved salts (Gaudet & Melack, 1981). The lake is surrounded by a swampy fringe of *Cyperus papyrus* L. (papyrus), and shallow areas with submerged weedbeds, dominated by *Najas horrida* A. Br. ex Magnus and *Potamogeton* spp. (Gouder de Beauregard *et al.*, 1998). In 1995 Lake Naivasha was designated a Ramsar wetland site of international importance for waterfowl and migrating birds. Water extraction, destruction of papyrus swamps, and fertiliser use by a sprawling floriculture industry on the shores of Lake Naivasha are presently the most serious ecosystem-level threats (Harper & Mavuti, in press).

Fisheries. At the beginning of the 20th century, Lake Naivasha contained no fish apart from the small endemic topminnow *Aplocheilichthys antinorii* (Vinc.) (Worthington, 1932). This paucity of species in the natural community of Lake Naivasha is probably because of repeated drying out of the lake in the relatively recent past (e.g. 1800–40; Harper *et al.*, 1990; Verschuren *et al.*, 2000). The first official record of fish stocking dates from 1925–26, when the cichlid *Oreochromis spilurus niger* (Gunther) was introduced (Siddiqui, 1977; Hemsing, 1987), followed in 1927–29 by the introduction of the American largemouth bass, *Micropterus salmoides* Lacepede. Both species proliferated in the 1930s but suffered strong population declines during low water levels of the late 1940s and early 1950s, when the lake shrank to less than 80 km^2 and a maximum depth of 3–4 m. Largemouth bass, apparently extinct, were reintroduced on several occasions between 1951 and 1956. The stocking in 1956 also included *Tilapia zillii* (Gervais) and, accidentally, *Oreochromis leucostictus* (Trewavas). The latter species unexpectedly flourished, and has dominated commercial catches from the late 1960s onwards (Siddiqui, 1977; Harper *et al.*, 1990). *Oreochromis spilurus niger* survived the 1940s lowstand but eventually disappeared around 1970. The indigenous *A. antinorii* was also last reported around that time (Siddiqui, 1979). *Oreochromis niloticus* L. was introduced in 1965 and apparently persisted for only a few years, although it may still be present (Harper *et al.*, 1990). Three small cyprinodont fish, *Gambusia* sp., *Poecilia* sp., and *Lebistes reticulata* Peters were introduced at various times for mosquito control, but only the latter is still present today (Hickley *et al.*, 2002). Finally, in 2001, common carp (*Cyprinus carpio* L.) was introduced to Lake Naivasha (Hickley *et al.*, in press).

Although fish stocking started in the 1920s, commercial gill-net fishing began only in 1959. Overfishing and a steady decline in net mesh sizes led to a sharp decline in the annual catch by 1970–72, and a near collapse of the Lake Naivasha fishery by 1975–76 (Siddiqui, 1977; Aloo, 1996). Strict enforcement of minimum mesh sizes allowed the fishery to recover in the late 1970s and 1980s to about one quarter of the 1960s peak catches. Since the mid-1990s the Lake Naivasha fishery has again been performing very poorly, presumably because of significant unlicensed fishing, exacerbated by poor recruitment because of the destruction of submerged weedbeds following the introduction of the Lousiana red swamp crayfish *Procambarus clarkii* (Girard) in 1970 (Harper, 1991; Smart *et al.*, 2002). A new temporary ban on fishing with nets is intended to remedy this situation (Muchiri, 2001).

The Daphnia *community.* Prior to this study, two species of *Daphnia* were known to occur in Lake Naivasha: *D. (Hyalodaphnia) laevis* Birge and *D. (Daphnia) pulex* Leydig. *Daphnia (Hyalodaphnia) laevis* was reported in most historical zooplankton collections, from 1930–31 (Lowndes, 1936; as *D. longispina*, see Fernando *et al.*, 1987), 1978–80 (Mavuti & Litterick, 1981), 1982–86 (Harper, 1987), and 1990–91 (Uku & Mavuti, 1994). *Daphnia pulex* was first found in 1980, prompting the suggestion that it may not be indigenous to the lake but that it was inadvertently introduced in the late 1970s (Mavuti, 1983; Uku & Mavuti, 1994). The only other *Daphnia* species previously reported from Lake Naivasha is *D. galeata* Sars (Lowndes, 1936), but the taxonomic status of these specimens is unclear; it probably refers to the helmeted form of *D. laevis.*

Sediment core analysis

Four sediment cores (NC91–1S: 90 cm, *c.*1870–1991 AD; NC91–2S: 83 cm, *c.*1860–1991 AD; NC93–1S: 122 cm, *c.*1880–1993 AD; NC01–1S: 158 cm, *c.*1810–2001 AD) with undisturbed sediment-water interfaces were collected in Crescent Island Crater using a rod-operated single-drive piston corer (Wright, 1980) and extruded upright in the field in 1- or 2-cm increments with a fixed-interval sectioning device. Cores NC91–1S and NC91–2S were retrieved in 15 and 11 m water depth in the south-eastern portion of the crater basin. Cores NC93–1S and NC01–1S were retrieved near the deepest point of the crater, which at the time of coring (August 1993 and 2001) was in 15.35 m and 14.50 m water depth, respectively (because of lake-level decline, 2001 water depths at core sites NC91–1S and NC91–2S were about 13 and 9 m). Additionally, surface-mud samples representing approximately the last 10 years of sedimentation were taken in July 2001 using a 225 cm^2 Ekman grab, from near the centre of Crescent Island Crater and the shallow north-east sector of Lake Naivasha adjacent to the crater. Live zooplankton samples were taken at the same locations with a 150-μm mesh towing net and preserved in 100% ethanol.

In the laboratory, water content, dry weight (DW), and organic-matter (OM) content of all core and grab samples were determined by loss-on-ignition methods (Bengtsson & Enell, 1986). Sediment chronology is based on a series of stratigraphic marker horizons corresponding to known historical events; lithostratigraphic correlation between NC01–1S and the ^{14}C-dated top section of core NC93–2L (Verschuren, 2001); and correlation of OM profiles to core NM93–1S from the main basin of Lake Naivasha, which was dated by ^{210}Pb analysis (Verschuren, 1999). Age at depth for each individual core increment was estimated by linear interpolation between identified time-marker horizons. The record of aquatic macrophyte abundance in NC01–1S is reconstructed semiquantitatively using five abundance classes of plant macrofossils (>250 μm) in, estimated using five classes [0 (negligible), 1 (0.1–1% of total dry organic matter), 5 (1.1–5%), 10 (6–15%) and 20 (16–25%)], with reference to a quantitative analysis of plant macrofossils in NC93–1S (Verschuren, 1999).

Subfossil *Daphnia* ephippia were extracted from contiguous 1- or 2-cm core increments by washing 15–70 mL of untreated sediment through a 150 μm mesh sieve, and scanning the retained residue at 10–90× magnification under a stereo-dissecting microscope. Recently deposited ephippia recovered in Ekman grab samples were processed in similar fashion. Ephippia were identified to species level by comparison with intact ephippial females from the active population of Lake Naivasha and nearby lakes and ponds, and with diagnoses and images in Brooks (1957), Hebert (1995) and Korinek (2000). Mergeay, Verschuren & De Meester (in press) present an illustrated identification key to all *Daphnia* species encountered in this study.

Ephippia were measured according to Jeppesen *et al.* (2002), to infer changes in the body size of adult *Daphnia*. Ephippium abundance is expressed as number of ephippia per gram dry sediment, to account for sediment compaction in older core increments. We did not correct for changes in dry sediment accumulation rate between successive time-marker horizons, because the temporal resolution of this information is much lower than that of the ephippial data. Moreover, observed order-of-magnitude changes in ephippial abundance would be relatively unaffected by such corrections. Interpretation of ephippium abundance patterns through time is based on the combined ephippial data from all four cores, which by taking into account spatial variability in ephippium burial rates across the lake floor (Carvalho & Wolf, 1989) strengthens inferences drawn from those abundance patterns. Combination of ephippial data from all four cores can also establish continuity of species presence through time when fossil yields are low. This approach is, however, highly demanding on core depth-age models. Unavoidable variability in the sedimentary evidence for the historical events used as time markers result in minor mismatches between cores in the exact timing of reconstructed changes in ephippium abundances. We here present those ephippium abundance data in a single plot for each species, using the mean value of all four cores for each time interval. Changes in ephippium abundance trough time are assumed to reflect order-of-magnitude changes in the active populations (Verschuren & Marnell, 1997), rather than a perfect representation of active population density, and should be interpreted as such.

Results

Lithology and relative dating

Sediments deposited in Crescent Island Crater over the past 200 years have been described in detail by Verschuren (1999, 2001, to whom we refer for information on the lithology and chronology of cores NC91–1S, NC91–2S and NC93–1S. The sediment composition of NC01–1S (Fig. 1b,c) is very similar to these other cores. It consists mainly of soft clayey mud with OM content between 15 and 25%, increasing to more than 35% in a section of organic clayey mud at 80–104 cm depth and to more than 45% in a horizon of black peat at 92–96 cm depth. The lowermost 10 cm consists of (clayey) algal gyttja. Besides the black peat horizon, coarse (>250 μm) plant fragments are also abundant around 124 cm and 132 cm depth.

The dating of core NC01–1S is based on ten markers it has in common with the other cores (Fig. 1c). Marker 1, indicated by the presence of characteristic chitinous remains, represents a recent population of the conchostracan *Cyclestheria hislopi* (Baird), known to have been present in Lake Naivasha during the period 1989–91 (D. M. Harper, Leicester University, pers. comm.). Marker 2 represents a similar appearance of *Cyclestheria* dated to around 1984. Markers 3–5 represent documented outbreaks of the exotic water fern *Salvinia molesta* in 1969, 1982 and 1989 (Gaudet, 1976; Harper *et al.*, 1990; Verschuren, 1999). Markers 6 and 8 are the top and bottom of the above-mentioned section of dark organic clayey mud, deposited during the early 20th-century lake highstand, dated by ^{210}Pb analysis to about 1940 and 1890, respectively (Verschuren, 1999). Markers 7 and 9 are thin layers of abundant plant remains, mostly of *C. papyrus* and *Ceratophyllum demersum* L., deposited around 1920 and 1840. Finally, marker 10 is the top of a long section of gelatinous algal gyttja, dated to around 1820 and represents the end of a long period of high lake level spanning the 17th and 18th century (Verschuren, 2001). Markers 3–5, 7, 9, and two further horizons dated to around 1943 and 1963 are all manifested by abundant coarse plant remains (Fig. 1e: values exceeding 5% of total dry OM), inferred to represent episodes when habitat of submerged and/or floating aquatic vegetation occurred in the vicinity of the core site.

Fossil abundance patterns of Daphnia *ephippia*

Depending on the core considered, the four studied sediment profiles represent the last 120–200 years of Lake Naivasha history. They yielded fossil ephippia of eight *Daphnia* species: four of the subgenus *Ctenodaphnia* (*D. barbata* Weltner, *D. lumholtzii* Sars, *D. magna* Straus and *Daphnia* sp. nov. type Limuru); three *Hyalodaphnia* (*D. curvirostris* Eylman, *D. laevis* Birge and *D. longispina* s.l. Müller), and one belonging to *Daphnia* s. s. (*D. pulex* Leydig). *Daphnia* ephippia were recovered from most of the core intervals analysed, in densities of up to 150 ephippia g^{-1} DW. Four species were sufficiently common to be considered indigenous to Lake Naivasha: *D. barbata*, *D. laevis*, *D. magna*, and *D. pulex*. The four other species were found in just a few core intervals, mostly as isolated specimens.

Fossil abundance patterns of the five common *Daphnia* species show striking differences in population dynamics through time (Fig. 2). Abundance patterns of the different species are very similar in all the cores. *D. magna*, the largest species, dominated the community during the lowstand of 1820–40 (Fig. 2a). Its abundance dropped following modest lake-level rise in the mid-19th century, and stayed low until the 1870s. *Daphnia magna* recovered during a second, less pronounced lowstand in the 1870–80s. It remained common throughout the major transgression of the late 19th century and the ensuing early 20th-century highstand, until around 1930 when it was suddenly reduced to very low levels. From the 1930s to the late 1960s, *D. magna* appears to have been present only sporadically (a total of eight ephippia were found). Around 1970 *D. magna* reappeared for a short period with significant numbers of ephippia in all of the cores, but by 1980 this population had again disappeared. The most recent evidence of *D. magna* in Lake Naivasha is a single ephippium deposited around 1990. Another recent ephippium was found, however, in an Ekman grab taken in the main basin of Lake Naivasha. The average size of *D. magna* ephippia deposited in Crescent Island Crater has declined over the past 200 years, especially after 1925 (Fig. 2a). Specifically, *D. magna* inhabiting the lake before 1925 were significantly larger than those present after that date (1820–1925: 1.391 ± 0.142 mm, $n = 71$; 1925–1980: 1.253 ± 0.105 mm, $n = 27$).

Daphnia barbata appeared in low numbers around 1830, during the early 19th-century lowstand (Fig. 2b). Its population rapidly expanded during the modest mid-19th-century highstand, quickly replacing *D. magna* as the dominant large cladoceran in Lake Naivasha. *D. barbata* somewhat declined in abundance during the late 19th-century transgression, but remained common until around 1930, when, like *D. magna*, it rather suddenly disappeared. *Daphnia barbata* showed up again briefly in the late 1930s, disappearing once more during the 1940s period of low lake level. Apart from a single ephippium deposited in the mid-1960s, *D. barbata* is absent from the sediment record during most of the past 60 years, until it suddenly reappeared around 1994. Ephippium abundances of this species remain high up to the sediment surface (2001 in NC01–1S). Presently *D. barbata* is the commonest large cladoceran in Lake Naivasha together with *D. pulex*. Ephippia of *D. barbata* remained approximately the same size throughout the historical period until their disappearance in the 1940s, but were always quite small (1830–1950: 0.753 ± 0.048 mm, $n = 144$) compared with those of the local *D. magna* and *D. pulex* (Fig. 2). In contrast, ephippia of the recent *D. barbata* population in Lake Naivasha are significantly larger (1995–2001: 0.932 ± 0.058 mm, $n = 27$).

Daphnia pulex first appears in the cores around 1850, but apart from two short-lived upsurges during the late 19th-century transgression it persisted at rather low densities (<3 ephippia g^{-1} DW) until around 1930 (Fig. 2c). A first episode of rapid expansion in the 1930s was cut short by 1940, but at the beginning of the 1950s *D. pulex* experienced an explosive population increase, as evidenced by peak densities of 100–150 ephippia g^{-1} DW around 1956–58. This period of very high abundances lasted only a few years (possibly just one), and it was followed by a strong decrease

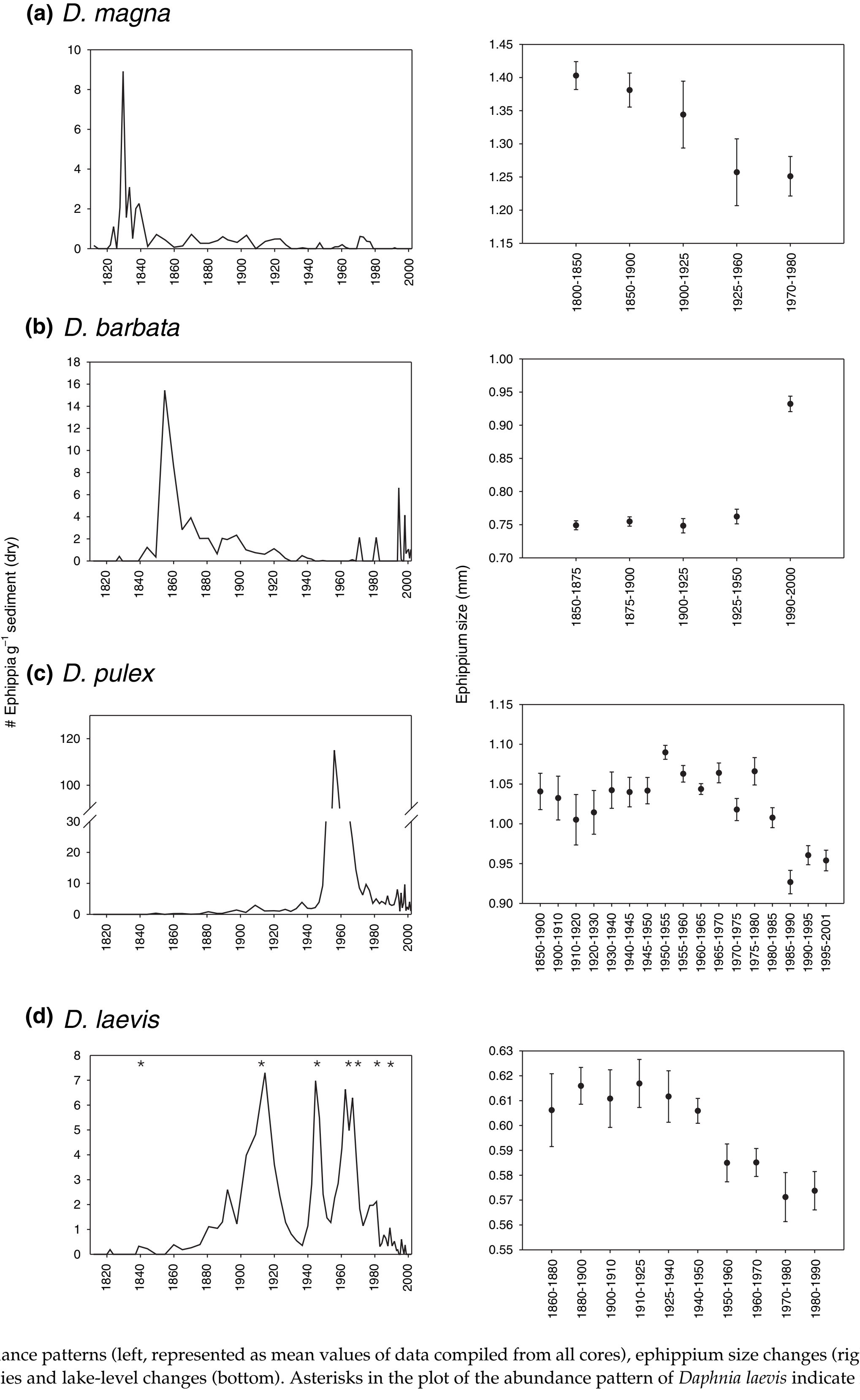
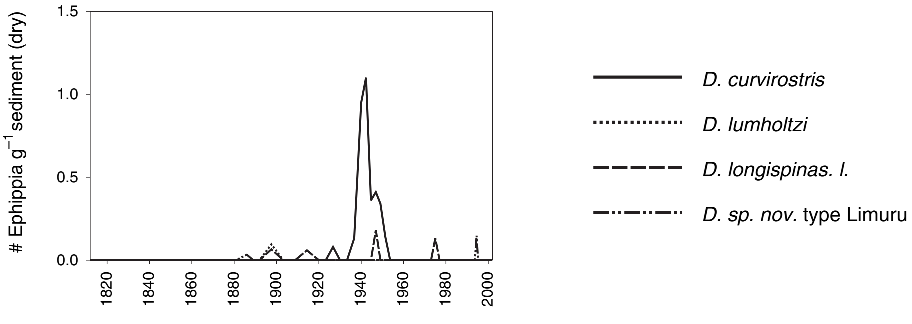


Fig. 2 Abundance patterns (left, represented as mean values of data compiled from all cores), ephippium size changes (right) of all the common species and lake-level changes (bottom). Asterisks in the plot of the abundance pattern of *Daphnia laevis* indicate macrophyte peaks.

(e) Other species



(f) Lake level changes

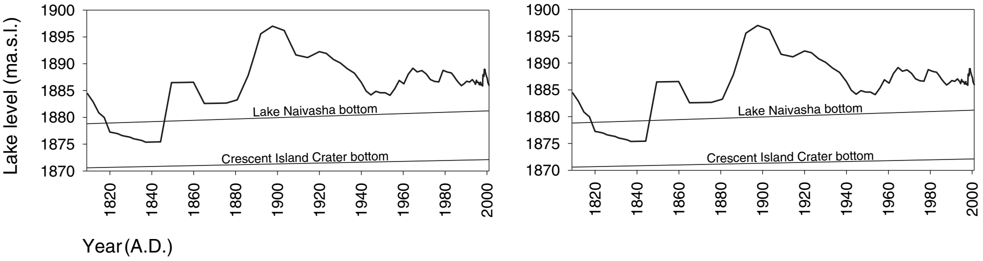


Fig. 2 (*Continued*).

starting in the late 1950s, which brought the population back to intermediate levels by 1980. Since then, ephippium abundances have fluctuated, with a slight tendency to increase. *D. pulex* ephippia were fairly large but variable in size between 1850 and 1985 (1.050 ± 0.127 mm, $n = 1197$), without a clear trend. Ephippia deposited after 1985, however, are significantly smaller than the earlier ones (0.949 ± 0.107 mm, $n = 265$) (Fig. 2c). Ephippia from the early 1950s population explosion are also significantly larger (1.093 ± 0.138 mm, $n = 205$) than those deposited shortly before (1.042 ± 0.101 mm, $n = 55$).

The presence of *D. laevis* in Lake Naivasha is characterised by a series of peak abundances in the periods 1890–1900, 1915–25, 1945–50, and 1960–70; and a less obvious maximum in the early 1980s (Fig. 2d). In our record, *D. laevis* first appeared around 1820 but remained uncommon until about 1870. It benefited from the 1870–80s lowstand, after which the population quickly increased to reach its first peak development around 1900. Combining the data of all cores we can surmise a near-continuous presence of this species in Lake Naivasha since 1860. In all cores *D. laevis* is, however, absent from the most recent sediments, indicating extinction from the active population in the late 1990s. This is confirmed by its absence in zooplankton samples and surficial Ekman grabs from both the main basin and Crescent Island Crater taken in 2001 and 2003. The average size of *D. laevis* ephippia experienced a decreasing trend during the 20th century, with an abrupt decrease after 1950 (Fig. 2d; before 1950: 0.610 ± 0.048 mm, $n = 160$; 1950–98: 0.580 ± 0.042 mm, $n = 131$).

If pronounced abundance peaks over the past century are defined as each instance when ephippial abundances exceeded 10% of the sum of the three highest abundances ever, the record of *D. laevis* in NC01–1S displays four episodes of peak population density: 1915–20, 1940–45, 1960–65, and 1990. The timing of these abundance maxima tends to coincide with peaks in aquatic plant macrofossils (Figs 1e & 2d). If we consider the NC01–1S record of about 190 years to have a time resolution of five years centred on the seven episodes of inferred high aquatic macrophyte abundance, the frequency of these episodes is 0.183. Substituting 0.183 in a binomial distribution, the maximum probability ($P_{\max}$) that all four *D. laevis* peaks would, by chance alone, correspond to an equal number of peaks in plant macrophyte remains equals 0.0006. Values of $P_{\max}$ calculated for the other cores (NC93–1S, NC91–1S and NC91–1S) are also all significantly low (<0.007). Since there is no reason to suggest that the taphonomy of *D. laevis* ephippia is more similar to the taphonomy of aquatic plant remains than to the taphonomy of ephippia of any of the other *Daphnia* species, we conclude that historical population abundance of *D. laevis* in Lake Naivasha was positively related to the occurrence of submerged or floating vegetation in their aquatic habitat.

Daphnia curvirostris was found in only a few consecutive core increments representing the period 1930–50, with a total of 62 ephippia in the four cores combined (Fig. 2e). This species appears to have peaked between 1940 and 1945 at the start of the mid-20th-century lowstand, but disappeared a few years later.

Fossil yields of the three remaining *Daphnia* species are several orders of magnitude lower than those of the species discussed above (Fig. 2e). Only two fossil ephippia of *D. lumholtzi* were found, together in one core interval deposited around 1904. However, two recently deposited *D. lumholtzi* ephippia were found in surficial sediment samples from the main basin of Lake Naivasha. *Daphnia* sp. nov. type Limuru was found in two intervals, one from around 1885 and one from around 1995. *Daphnia longispina* s.l. was found in four intervals, totalling five ephippia deposited between 1900 and 1975.

Discussion

Biodiversity and biogeography

Few other tropical lakes have such a well documented environmental history as Lake Naivasha, yet repeated live zooplankton surveys (Lowndes, 1936; Mavuti & Litterick, 1981) and monthly monitoring over periods of several years in the late 1970s, 1980s and early 1990s (Mavuti, 1983; Harper, 1987; Uku & Mavuti, 1994) never came close to revealing the true local species diversity in the genus *Daphnia*, as documented by this study. Our analysis adds six species to the *Daphnia* fauna of Lake Naivasha, of which three have been present in considerable numbers during major portions of the lake's 20th-century history. Failure to detect *D. magna*, *D. barbata*, and *D. curvirostris* in live collections can be explained, at least partly, by the fact that all live surveys were conducted during periods when, according to the sediment record, these species were absent or very rare.

Considering the overall paucity of *Daphnia* in tropical regions (Fernando *et al.*, 1987; Dumont, 1994), the *Daphnia* species richness of Lake Naivasha is remarkable. The number of species that occurred at Lake Naivasha over the past century is almost as high as the total *Daphnia* species diversity recorded in a live zooplankton survey of 98 lakes across the whole of tropical Africa (Green, 1995). In Lake Naivasha, different *Daphnia* species did not simply replace each other through time: the four most common species (*D. magna*, *D. barbata*, *D. laevis*, and *D. pulex*) actually coexisted for much of the period between 1860 and 1930. Moreover, sediments deposited in the two decades comprising the major late 19th-century lake-level rise contain ephippia of seven species. There are several plausible and possibly complementary explanations for this unique species richness. First, the general instability of the Lake Naivasha ecosystem

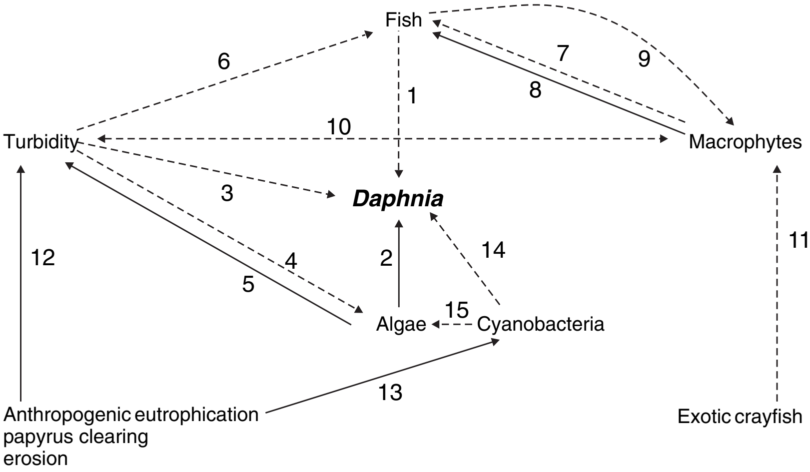


Fig. 3 The assumed interplay between different factors, directly and indirectly influencing *Daphnia* in Lake Naivasha. Dotted lines stand for negative correlations, straight lines for positive correlations. Two negative interactions result in an indirect positive interaction. See text for explanation of numbers.

because of continuous lake-level changes creates constantly fluctuating habitat conditions and selection pressures, which in turn may cause ever-changing competitive relationships. Secondly, Lake Naivasha is a large lake with a multitude of microhabitats, and can therefore be expected to harbour species with different niches simultaneously. Thirdly, the storage function of Lake Naivasha's evidently extensive diapausing egg bank allows local persistence of species (Chesson, 1983, 1994; Cáceres, 1997). This certainly occurs on a seasonal time scale, with almost complete separation in time of *D. laevis* and *D. pulex* observed during monthly monitoring from 1982 to 1986 (Harper, 1987).

Among the eight species found, only three are typical of the lowland tropics: *D. laevis*, *D. barbata* and *D. lumholtzi* (Fernando *et al*., 1987). *Daphnia curvirostris* is mainly distributed the Palearctic region (but see Hebert, 1995 and Duffy *et al*., 2000) but it also occurs at high elevations in the Afrotropical region (Green, 1995). Similarly, *D. pulex* has a near-cosmopolitan distribution but is mostly restricted to high elevations in the tropics (Green, 1995). Of the remaining three species, *Daphnia* sp. nov. type Limuru is new to science (V. Korinek, pers. comm. 2003), while the known distribution range of *D. magna* and *D. longispina* s.l. is mostly restricted to higher northern and southern latitudes. *Daphnia magna* was not considered indigenous to tropical Africa (Fernando *et al*., 1987), and was only recently discovered in Lake Victoria (Jonna & Lehman, 2002). Our data show it has occurred in Lake Naivasha since at least 1820, essentially excluding the possibility of inadvertent anthropogenic introduction to tropical Africa. Our data further indicate that also *D. pulex* is indigenous to Lake Naivasha, contradicting the suggestion made by Mavuti & Litterick (1981) that *D. pulex* must have been introduced in the late 1970s.

Environmental regulation of Daphnia *in Lake Naivasha*

Few previous studies on tropical systems have emphasised the important interplay between fish predation, macrophyte cover, turbidity, and food in the population dynamics of large cladocerans. Fig. 3 is an attempt to visualise this interplay based on an understanding of literature data, using processes that, in our opinion, influence the *Daphnia* community: predation by fish (1) directly affects densities of *Daphnia* negatively, whereas *Daphnia* densities are positively related to the availability of algae (2). Both turbidity and macrophytes provide a refuge for *Daphnia* against fish predation, because of decreased visibility (6, 7). Turbidity can also impact *Daphnia* negatively because of obstruction of the filter apparatus and the resulting decrease in feeding efficiency (3). Moreover, turbidity can decrease algal growth by shading (4), whereas algae themselves increase turbidity (5). Macrophytes provide essential spawning places for cichlids (8). Herbivory (9, 11) is detrimental to macrophytes, which eventually results in destabilisation of the lake floor, and hence, increased resuspension of sediments and higher turbidity (10). Anthropogenic eutrophication, papyrus clearing and increased erosion directly increase turbidity (12) and trophic state. Eutrophication also leads to a dominance of cyanobacteria (13, 15), which have a lower nutritional value and can be toxic for *Daphnia*. In this scheme the impact on *Daphnia* is generalised. The different factors have, however, a differential impact on different *Daphnia* species, resulting in species shifts. For example, our results suggest that the balance of negative direct effects of turbidity and the positive indirect effects of turbidity through fish is positive for *D. barbata* and negative for *D. laevis*, at least in relative terms (increased competitive strength of *D. barbata*), resulting in a species shift. Considering species shifts within the *Daphnia* community, one also has to take into account the impact of competition from the other *Daphnia* species on the focal species, as species shifts are determined by relative fitness.

Visual predation by fish on large zooplankton is considered a major factor structuring the zooplankton community of lakes through top-down control (Kerfoot & Sih, 1987; Carpenter & Kitchell, 1993). Lake Naivasha is devoid of specialised zooplanktivorous fish, and is therefore considered to have an incomplete aquatic food web (Mavuti, 1990; Hickley *et al*., 2002). This view on the food web of Lake Naivasha contrasts with the long-term perspective offered by the present study, which suggests a significant influence of fish predation on *Daphnia* community history in Lake Naivasha, notwithstanding the marked physical changes in lake level, macrophyte cover, water transparency, and trophic status the lake has experienced over the past century and longer. The fish species introduced to Lake Naivasha are thought to have little impact on the large zooplankton (Mavuti, 1990) because of their mainly herbivorous, omnivorous or piscivorous diets. Their juveniles, however, are likely to be all zooplanktivorous (e.g. Elhigzi, Haider & Larsson, 1995). There are many indications in our study for the impact of fish on *Daphnia* species composition. For example, *D. magna* was common in Lake Naivasha throughout the 19th and early 20th centuries, but disappeared (or was decimated beyond detection) within a few years after introduction of largemouth bass and cichlid fishes in the late 1920s. Because of its large size (2–5 mm), *D. magna* is especially prone to visual predation by fish. Whether fish stocking was the principal reason for the population collapse of *D. magna* in Lake Naivasha is uncertain, but it probably accelerated the process. Certainly, the temporary reappearance of this species around 1970, recorded in all four cores (Fig. 2a), is consistent with reduced predation pressure during the early 1970s fisheries crash that had resulted from two decades of unregulated overfishing (Siddiqui, 1977; Aloo, 1996). Further, ephippia deposited at that time, as well as all isolated specimens recovered from post-1930s sediments, are significantly smaller than the ephippia deposited before 1925 (Fig. 2a), pointing to size-selective predation after the fish introductions. Like *D. magna*, also *D. barbata* was reduced to below detection shortly after the first fish introductions. Following a short-lived recovery around 1940, possibly allowed by predation release because of increased turbidity in the final phase of the 1920–30s drawdown, it disappeared from the lake for more than half a century.

Significant impact of fish predation on *D. pulex* in Lake Naivasha is suggested by the inverse relationship between *D. pulex* abundance in monthly live collections between 1982 and 1986 (Harper, 1987) and the annual fish catches during that period (Hickley *et al.*, 2002). As far as core chronology allows, these short-lived fluctuations are also evident in abundance patterns of *D. pulex* ephippia in the 1980s sections of three of the four cores we analysed (Fig. 2c). Judging from the fossil evidence, however, *D. pulex* seems to have suffered less from the early 20th-century fish introductions than *D. magna* and *D. barbata*. The mean body size of this species did not change significantly during that period (Fig. 2c), and its abundance even increased temporarily in the 1930s before returning to pre-1925 levels. Fish populations declined strongly during the historical lowstand of the late 1940s and early 1950s and largemouth bass may have become extinct (Siddiqui, 1977). Restocking of both bass and cichlids began in 1951 but did not seem to have much effect until around 1960, when the lowstand had already ended with a strong lake-level rise (Fig. 1a). The extremely high *D. pulex* ephippium abundances dated to 1956–58 (Fig. 2c) are probably related to the near-absence of fish in the later phase of that mid-20th-century lowstand, and the first few years of the ensuing lake-level rise before extensive restocking with fish. Consistent with this scenario, the mean size of *D. pulex* during the 1950s population explosion was larger than at any other time in the past 150 years. High fish densities in the 1960s (inferred from catch data; Hickley *et al.*, 2002) may have brought *D. pulex* back to intermediate abundances, but not as low as its average pre-1925 levels. Also, body size was apparently not affected in the 1960s. *D. pulex* experienced a drastic size reduction only from the 1980s onwards (Fig. 2c). During most of this period, however, fish densities were no more than 1/4–1/3 of their 1960s peak values; ineffective regulation actually led to repeated collapse of the Lake Naivasha fishery in recent decades (Siddiqui, 1979; Muchiri, 2001). Therefore, the concomitant size reduction in *D. pulex* cannot be attributed simply to increased predation pressure. We presume that size reduction in Lake Naivasha *D. pulex* since the 1980s may be an indirect effect of the disappearance of submerged macrophytes over the same period (see below), which may have rendered *D. pulex* more sensitive to visual predation by fish (Timms & Moss, 1984; Burks, Jeppesen & Lodge, 2001) despite relatively low fish densities.

Since the discovery of Lake Naivasha by European colonists, human activities have severely changed the ecosystem of Lake Naivasha through numerous introductions of exotic species and by direct alteration of the environment. Particularly over the past 20–30 years, rapidly increasing catchment deforestation, agricultural soil erosion, and wholesale clearing of papyrus swamps along the lakeshore and inflowing rivers, have resulted in a huge increase of clastic mineral input to the lake (Everard & Harper, 2002). At the same time sedimentation of these clays and silts from the water column is hampered, because greatly increased water withdrawals by nearby flower farms and a geothermal power station are causing a generally downward trend in lake depth (Becht & Harper, 2002). Additionally, submerged macrophyte beds, which used to stabilise the lake bottom, were eradicated over large areas in recent decades because of unchecked browsing by the Louisiana red swamp crayfish (Harper, 1991; Smart *et al.*, 2002). These processes have combined to dramatically increase the amount of suspended mineral matter in the water column. The progressive eutrophication of Lake Naivasha (Harper *et al.*, 1993), the result of excess phosphorus input as a result of fertilizer run-off from the riparian flower farms and other industrial agriculture within the lake catchment (Kitaka, Harper & Mavuti, 2002), also contributes to increasing turbidity. The combination of increased suspended mineral matter and runaway algal growth has caused a dramatic reduction in the transparency of the water column: Secchi disc readings in the main basin show a decrease from 250 cm in 1979 (Mavuti & Litterick, 1981) to 50–75 cm in 1997–98 (Kitaka *et al.*, 2002) and to no more than about 20 cm at the time of this study in August 2001 and January 2003. These water quality changes now appear to start affecting the *Daphnia* community of Lake Naivasha. As mentioned above, the eradication of submerged macrophytes may explain the apparently higher predation pressure on *D. pulex* (reflected in smaller mean body size) despite modest fish densities. *Daphnia laevis*, which typically occurs in more transparent waters (Hart, 2001) and is known to be adversely affected by high turbidity (Hart, 1992), seems to have disappeared since 1998 (Fig. 2d). It was replaced by *D. barbata*, a typical turbid water species (Hart, 1992), which successfully recolonised Lake Naivasha in the mid-1990s after some 50 years of absence (Fig. 2b). The current low water transparency probably releases large *D. barbata* from visual predation by fish, thereby providing opportunities for successful recolonisation. These inferences seem to be confirmed by our analysis of grab samples representing the modern resting egg bank in Crescent Island Crater and the main lake, which besides *D. pulex* contain abundant *D. barbata* but lack *D. laevis*. Interestingly, a grab sample from the northeast sector of Lake Naivasha also contained a few ephippia of *D. magna* and *D. lumholtzi*, two other large *Ctenodaphnia* species that are likely to benefit from turbid water as protection against fish predation. This is also the case for *Daphnia* sp. nov. type Limuru: one of only two ephippia recovered from the cores was deposited in sediments dated to approximately 1995 (Fig. 2f). *Daphnia lumholtzi* is known to cope well with high turbidity (Work & Gophen, 1999). The ecology of *Daphnia* sp. nov. type Limuru is as yet unknown, but three other Kenyan waters where it has now been found (Mergeay *et al.*, in press) are similarly turbid. If high turbidity persists, the general shift to dominance by large *Ctenodaphnia* can be expected to continue. Such conditions presently prevail in the turbid Lake Baringo further north in the Kenyan Rift Valley (Aloo, 2002) and Lake Chilwa in Malawi (Kalk, 1979), where *D. barbata* dominates the zooplankton despite relatively high densities of cichlid fishes.

The current success of relatively large *D. barbata* and recent recolonisation of Lake Naivasha by other large *Ctenodaphnia* species contrast with historical trends in *D. laevis* and *D. pulex*, which show reductions in both population abundance and body size. These changes are not likely to be a direct fish effect, since turbidity has been increasing for the past 20 years and fish densities have been rather low since the 1970s, especially after the most recent fishery collapse in the mid-1990s (Hickley *et al.*, 2002). *Daphnia laevis* was able to coexist with fish in Lake Naivasha until very recently, but experienced a gradual size reduction starting immediately after the first fish introductions in 1925–26 (Fig. 2d). Although variability in ephippium size within each time period is rather large, the negative trend seems to have been halted temporarily in the 1940s, when fish populations were low as they suffered from historically low water levels (Fig. 1a). Taking the entire recorded history in consideration, *D. laevis* was more common during periods when aquatic macrophytes were abundant. This suggests that its coexistence with fish may depend on the presence of submerged or floating vegetation as refuge against fish predation (Burks *et al.*, 2001). Macrophyte abundance is often positively related to water transparency (Scheffer *et al.*, 1993). It seems that, under the conditions prevailing in Lake Naivasha, smaller species perform better in the presence of fish when macrophyte cover is adequate, whereas large *Daphnia* species perform better in the presence of fish when macrophytes are lacking and transparency is low. This is consistent with enclosure experiments in a shallow temperate lake by Cottenie & De Meester (2004), in which exposure to fish in the presence of macrophytes favoured small *Daphnia* species, while exposure to fish in the absence of macrophytes favoured larger *Daphnia*.

The unique species diversity of *Daphnia* in Lake Naivasha, coupled with the long-term historical perspective offered by paleolimnology allowed an evaluation of the distinct response of several members of the genus *Daphnia* to fish in a fluctuating tropical lake ecosystem. These responses are evidently complex, but overall our results point to important interactions between fish predation, macrophyte cover and turbidity in driving *Daphnia* population dynamics and community structure in this system. Our data suggest that, although both zooplankton and fish are affected by large changes in their physical environment, fish execute significant top-down control when not hampered by high turbidity. Eradication of local *Daphnia* populations by fish was often preceded by body size reduction, and this may allow coexistence when predation intensity is weakened by recurrent environmental change or availability of suitable refuges. The very small size of *D. barbata* in the 19th century may have resulted from adaptation to predation by the endemic topminnow *A. antinorii*, which is now extinct, apparently because of predation by the introduced bass (Siddiqui, 1979). Much larger *D. barbata* can now coexist with fish in Lake Naivasha by virtue of the low water transparency resulting from eutrophication and enhanced mineral sediment input. Our results thus point to the interesting interplay between dominance shifts between species on the one hand and shifts in size structure within species in response to different intensity of fish predation and species-specific vulnerability to predation exposure on the other hand. However, at this time, we cannot determine whether and to what extent the historical size shifts observed in several *Daphnia* species involve genetic adaptations.

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