Freshwater Biology (2006) **51,** 399–411 doi:10.1111/j.1365-2427.2005.01494.x

Daphnia community analysis in shallow Kenyan lakes and ponds using dormant eggs in surface sediments

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SUMMARY

1. Water fleas of the genus *Daphnia* are considered rare in tropical regions, and information on species distribution and community ecology is scarce and anecdotal. This study presents the results of a survey of *Daphnia* species distribution and community composition in 40 standing waterbodies in southern Kenya. The study sites cover a wide range of tropical standing aquatic habitats, from small ephemeral pools to large permanent lakes between approximately 700 and 2800 m a.s.l. Our analysis combines data on *Daphnia* distribution and abundance from zooplankton samples and dormant eggs in surface sediments.

2. Nearly 70% (27 of 40) of the sampled waterbodies were inhabited by *Daphnia*. Although their abundance in the active community was often very low, this high incidence shows that *Daphnia* can be equally widespread in tropical regions as in temperate regions.

3. Analysis of local species assemblages from dormant eggs in surface sediments was more productive than snapshot sampling of zooplankton communities. Surface-sediment samples yielded eight *Daphnia* species in total, and allowed the detection of *Daphnia* in 25 waterbodies; zooplankton samples revealed the presence of only four *Daphnia* species in 16 waterbodies.

4. *Daphnia barbata*, *D. laevis*, and *D. pulex* were the most frequently recorded and most abundant *Daphnia* species. Canonical correspondence analysis of species–environment relationships indicates that variation in the *Daphnia* community composition of Kenyan waters was best explained by fish presence, temperature, macrophyte cover and altitude. *Daphnia barbata* and *D. pulex* tended to co-occur with each other and with fish. Both species tended to occur in relatively large (>10 ha) and deeper (>2 m) alkaline waters (pH 8.5). *Daphnia laevis* mainly occurred in cool and clear, macrophyte-dominated lakes at high altitudes.

Keywords: Africa, *Daphnia pulex*, ephippia, Lake Naivasha, tropical limnology, zooplankton

Introduction

In temperate regions, water fleas of the genus *Daphnia* occupy a central place in freshwater food webs, being both important consumers of phytoplankton and important prey items for fish and invertebrate predators (Lampert, 1987; Lampert & Sommer, 1997). The presence or absence of this large-bodied zooplankton thus often has important ecosystem-level consequences (Scheffer, 1999). In tropical regions, however, *Daphnia* are usually found to be much less common, especially in the warmer lowland regions (reviewed in Fernando, Paggi & Rajpaksa, 1987). The apparent scarcity of *Daphnia* in the tropics (22°N to 22°S) has been attributed to various factors. Presence of highly specialised zooplanktivorous fishes combined with the lack of a seasonal or deep-water refuge from predation

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has often been considered decisive (Hebert, 1978; Dumont, 1994). Dumont (1994) also pointed out that tropical cladoceran species, both those with planktonic and epibenthic lifestyles, tend to occur mostly at very low densities, so that their apparent lower incidence and local diversity in tropical waters may partly be due to inadequate sampling. Intensive faunal surveys in Thailand and Cameroon have confirmed this idea, and revealed that regional species diversity is comparable to or exceeds that in temperate regions for most cladoceran genera, but not for *Daphnia* (Chiambeng & Dumont, 2005; Maiphae, Pholpunthin & Dumont, 2005). In his survey of tropical planktonic Cladocera, Green (1995) reported 10 species of *Daphnia* in Africa, their patterns of distribution markedly influenced by altitude. However, only four species are believed to occur in the African tropical lowlands (<500 m a.s.l.; Fernando *et al.*, 1987; Green, 1995).

Existing reviews of *Daphnia* species distribution in tropical regions (Fernando *et al.*, 1987; Dumont, 1994; Green, 1995) have mostly focused on lakes, were mainly based on literature data stemming from qualitative or partial surveys, and provide little ecological information. Comprehensive standardised datasets on the distribution, abundance and local diversity of tropical *Daphnia* species and their relation to important environmental gradients are scarce or non-existent. Also, small and semi-permanent or ephemeral waterbodies, which have been rarely included in previous surveys, can be expected to have a different cladoceran fauna than lakes because they have different predator communities (absence of fish, more macroinvertebrate predators) and are subject to the effects of seasonal drying and large circadian temperature variation (Brendonck & Williams, 2000). There is clearly a need for a more thorough analysis of both the auto-ecological and community ecological characteristics of tropical *Daphnia*. Such data may contribute to a better general understanding of the functioning of tropical aquatic ecosystems, and can also help to clarify the underlying mechanisms behind species shifts that result from increased anthropogenic impact.

This paper presents an analysis of the *Daphnia* communities of 40 tropical waterbodies situated along important ecological gradients in the southern and south-western part of Kenya. The survey covers a sizable fraction of all standing freshwater habitats in the region, ranging from small ephemeral pools to large permanent lakes, in the highlands and at lower altitudes. The data are analysed both from an auto-ecological and from a community ecological perspective. Our data were collected from samples of the active community in the zooplankton and of ephippia extracted from surface sediments. The latter represent the species diversity of diapausing (dormant) eggs in the local egg bank, deposited by local *Daphnia* populations in past growing seasons (reviewed in Brendonck & De Meester, 2003) and thus integrate both spatial and temporal variation in the local communities (Vandekerkhove *et al.*, 2005). Analysis of dormant communities (egg banks), or of other remains of the cladoceran exoskeleton preserved in lake sediments, yields a more complete assessment of local cladoceran species diversity and average community composition than snap-shot sampling of the active community (Frey, 1960; May, 1986; Havel, Eisenbacher & Black, 2000; Vandekerkhove *et al.*, 2005).

Methods

Study area

Field surveys in southern Kenya during August 2001 and January 2003 yielded samples of zooplankton and of recently deposited surface sediments from 40 standing waterbodies (Table 1; Fig. 1), with surface elevations ranging from 700 to 1200 m a.s.l. in the south-eastern lowlands (12 sites) to between 900 m and 2800 m a.s.l. in the central Rift Valley and adjacent highlands (29 sites). Seasonal temperature variation in this equatorial region is limited, and patterns of local mean annual temperature are closely linked with altitude (Kiai, Mwangi & Bosire, 2002). Rainfall seasonality is strong throughout the study region, being predominantly bimodal east of the Rift Valley but trimodal in western Kenya. Annual rainfall totals range from 350 mm in the arid south to 1100–1500 mm over the highlands flanking the Rift Valley. Natural vegetation near the study sites ranges from dry *Acacia* bushland and wooded savannah to mountain forest at higher elevations, but much of the latter has been replaced by a cultural landscape.

Field and laboratory techniques

Surface-water temperature, conductivity and pH were measured using a Hydrolab Quanta® multiprobe (Hach Environmentals, Loveland, CO, U.S.A.).

Table 1 Studied waterbodies in Kenya and some of their characteristics

No.	Name	Code	Geographical position	Alt (m a.s.l.)	Max. depth (m)	pH	Secchi depth (m)	Temp (°C)	Cond. (μS cm^{-1})	Fish PA	Litt. 0–4	Macr. 0–4	Chl *a* (μg L^{-1})	Area (ha)
1	Lake Jipe	Jipe	03°34.60′S, 37°46.05′E	735	1.8	8.5	0.30	28.5	1140	1	4	0	45.4	2500
2	Temp. pond Taveta-Taita 1	TaiTa1	03°24.52′S, 38°03.54′E	1115	0.5	8.8	0.10	32.3	100	0	0	0	15.6	0.015
3	Temp. pond Taveta-Taita 2	TaiTa2	03°24.64′S, 38°02.25′E	1103	0.3	8.2	0.10	28.0	150	0	0	0	32.3	0.02
4	Temp. pond Taveta-Taita 3	TaiTa3	03°24.68′S, 37°49.74′E	1102	0.5	7.7	0.10	28.2	235	0	0	0		0.02
5	Perm. pond Voi-Nairobi 1	VoNb1	02°45.41′S, 38°15.27′E	695	0.5	7.6	0.10	32.6	53	0	0	0		0.04
6	Perm. pond Voi-Nairobi 2	VoNb2	02°21.05′S, 37°53.33′E	1031	0.6	7.7	0.10	31.5	236	0	0	0		0.04
7	Amboseli Olokenya swamp	Amb1	02°42.11′S, 37°18.68′E	1155	1.0	7.1	0.80	19.8	179	1	3	3	56.9	1.2
8	Amboseli Serena Lodge	Amb2	02°42.00′S, 37°15.42′E	1159	1.0	7.2	0.80	21.4	172	1	3	3	32.6	15
9	Amboseli Enamishera	Amb3	02°40.21′S, 37°14.63′E	1150	1.5	7.8	0.80	24.7	255	1	4	3	128.9	30
10	Amboseli Lake Kioko	Amb4	02°38.50′S, 37°13.55′E	1153	1.2	7.8	0.50	25.0	539	1	4	4		50
11	Amboseli Lake Amboseli	Amb5	02°36.07′S, 37°12.52′E	1150	0.1	9.5	0.01	29.1	4690	0	0	0	397.6	10000
12	Temp. pond Kajiado	Kaji	01°50.20′S, 36°47.88′E	1757	0.8	6.6	0.25	24.0	150	0	2	0		0.01
13	Nairobi Nat. Park Narogomon dam	NbNP1	01°21.00′S, 36°47.92′E	1707	3.8	7.0	0.40	21.3	188	1	4	0	80.7	1.5
14	Nairobi Nat. Park Hyena Dam	NbNP2	01°20.30′S, 36°48.64′E	1709	1.5	7.1	0.30	21.7	260	1	3	0	128.9	1
15	Nairobi Nat. Park 3	NbNP3	01°21.86′S, 36°50.58′E	1709	1.0	6.8	0.60	23.0	141	1	2	0	72.6	0.015
16	Nairobi Nat. Park 4 (river)	NbNP4	01°21.57′S, 36°51.24′E	1664	1.5	7.1	0.40	21.0	150	0	2	0		0.02
17	Nairobi Nat. Park Hyrax valley	NbNP5	01°22.86′S, 36°46.98′E	1716	1.0	7.6	0.40	23.5	250	1	3	1		1
18	Semiperm. pond Limuru 1a	Lim1a	01°6.99′S, 36°37.89′E	2306	1.2	7.3	0.15	21.5	201	0	1	0		0.15
19	Semiperm. pond Limuru 1b	Lim1b	01°6.99′S, 36°37.89′E	2306	0.8	7.3	0.15	21.5	201	0	0	0		0.15
20	Lake Limuru 2	Lim2	01°6.34′S, 36°37.82′E	2294	2.5	7.5	0.70	23.1	155	1	2	4	22.3	25
21	Lake Limuru 3	Lim3	01°8.35′S, 36°40.73′E	2135	4.5	7.8	0.50	24.6	414	1	0	0	72.2	1.5
22	Lake Naivasha main	LN	00°46.34′S, 36°21.66′E	1897	4.5	9.2	0.20	22.9	292	1	4	1		15000
23	Lake Naivasha Crater	ClC	00°45.80′S, 36°24.55′E	1897	14.0	8.7	1.20	22.5	375	1	0	0	87.4	195
24	Lake Oloidien	Oloid	00°48.89′S, 36°15.85′E	1897	3.0	10.0	0.30	23.3	2590	1	0	0	374.5	600
25	Eldoret Sigawet Dam	Sigaw	00°35.08′N, 35°13.06′E	2014	1.5	8.5	0.20	22.5	214	1	2	0	121.7	5
26	Lake Katalin	Katal	00°38.42′N, 35°28.90′E	2337	4.5	6.6	0.37	19.5	78	0	2	2	28.9	15
27	Perm. pond Eldoret Nakuru 1a	ElNa1a	00°26.41′N, 35°18.32′E	2185	0.5	6.9	0.50	14.1	196	0	1	4	26.5	0.1
28	Perm. pond Eldoret Nakuru 1b	ElNa1b	00°26.41′N, 35°18.32′E	2185	0.4	7.6	0.30	16.2	381	0	0	1		0.03
29	Perm. pond Eldoret Nakuru 2	ElNa2	00°21.65′N, 35°21.08′E	2217	1.5	6.9	0.50	14.5	171	1	1	3		0.05
30	Perm. pond Eldoret Nakuru 3	ElNa3	00°19.99′N, 35°21.92′E	2214	0.8	7.0	0.40	16.3	221	0	4	1		0.03
31	Lake Narasha	ElNa4	00°2.65′N, 35°32.47′E	2764	7.2	5.6	2.20	16.0	34	0	3	3	13.8	200
32	Perm. pond Eldoret Nakuru 5	ElNa5	00°3.60′S, 35°38.38′E	2471	0.8	6.6	0.25	20.8	204	0	4	2		0.01
33	Perm. pond Eldoret Nakuru 6	ElNa6	00°4.92′S, 35°39.49′E	2536	0.5	6.6	0.10	24.9	117	0	4	0	33.1	0.2
34	Perm. pond Nakuru Naivasha 1	NaNa1	00°19.42′S, 36°9.12′E	1917	1.0	7.2	0.10	24.0	201	0	0	0		0.05
35	Perm. pond Nakuru Naivasha 2	NaNa2	00°20.50′S, 36°10.14′E	1920	1.0	7.8	0.20	20.4	178	0	2	0		0.05
36	Lake Ol Bolossat	OlBol	00°9.91′S, 36°25.98′E	2358	2.0	9.0	0.20	20.6	1960	1	1	0	86.6	2000
37	Ol Bolossat pond 1	OB1	00°10.10′S, 36°26.02′E	2350	1.5	8.5	0.20	19.5	250	1	1	1		0.015
38	Ol Bolossat pond 2	OB2	00°10.10′S, 36°26.02′E	2350	1.5	8.4	0.20	19.4	250	1	1	1		0.02
39	Lake Baringo	Barin	00°39.12′N, 36°03.64′E	967	4.0	8.5	0.05	26.0	1600	1	3	0	311.9	10800
40	Mogotio Kapchelukung Dam	Mogot	00°05.00′N, 36°05.00′E	1200	1.5	7.1	0.20	22.2	90	1	1	2	33.2	0.9

Alt, altitude; Max., maximum; Temp, temperature; Cond., conductivity; Fish PA, fish presence (1) or absence (0); Litt., littoral vegetation cover (see Methods for definition of the four classes); Macr., macrophyte cover (see text for classes); Chl *a*: chlorophyll *a* concentration.

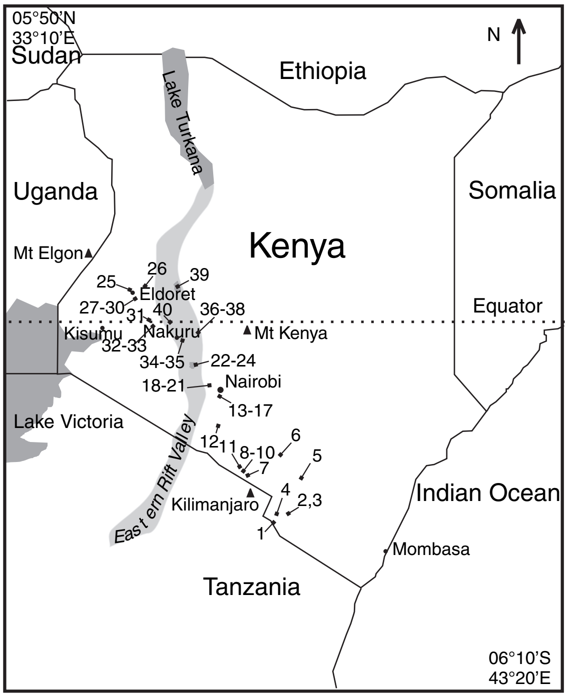

Fig. 1 Schematic map of Kenya with location of the 40 study sites. Site numbers refer to Table 1.

Water transparency was measured with a standard 20-cm diameter Secchi disc. Geographical positions and approximate surface elevations were determined using a hand-held GPS unit (Garmin International Inc., Olathe, KS, U.S.A.). Abundance of aquatic macrophytes (vertical projection of floating and submerged aquatic plants) and emergent littoral vegetation was estimated on a scale from 0 to 4 (0: no aquatic or littoral vegetation; 1: 1–5% cover of water surface or shoreline contour; 2: 5–10%; 3: 10–25%; 4: >25%). Free-floating water plants (e.g. *Pistia stratioides*) were also included in this estimate. Fish presence was primarily assessed from fish scales and bones in surface sediments, validated by field observations of fish and/or piscivorous birds or fishery information from local people. Open-water surface area was taken from the literature or (for most small ponds) estimated in the field from GPS data. Phytoplankton standing stock (an estimate of lake trophic status) was estimated by measuring the chlorophyll *a* content of surface water, determined from methanol extracts using the spectrophotometric method proposed by Talling & Driver (1963). Chlorophyll *a* data were available for only 21 of the 40 study sites.

The zooplankton community was sampled qualitatively using a conical tow-net (25 cm diameter) of 150 μm mesh, combining vertical and horizontal hauls, and taking care to include zones with submerged macrophytes and littoral vegetation. Samples were washed in the net and preserved in 100% ethanol. Offshore surface sediments were sampled from a boat using a weighted Wildco Fieldmaster® (Buffalo, NY, U.S.A.) horizontal water sampler, ensuring that only the topmost layer of unconsolidated surface mud was taken. In small ponds and other very shallow waterbodies, surface sediment was collected manually. The sampled sediment volume varied between 200 and 500 mL, with variable water content.

Daphnia in the zooplankton samples were identified to species with reference to Kořinek (1999), and counted at 50× magnification under transmitted light until 300 specimens had been encountered or the whole sample was processed. Surface-sediment subsamples (approximately 100 mL) were washed through a 250 μm mesh sieve, and the retained residue was scanned for *Daphnia* ephippia at 20–50× magnification, until exhaustion of the sample. Ephippia were identified to species with reference to Mergeay, Verschuren & De Meester (2005). Recent genetic information on inter- and intraspecific relationships in African *Daphnia* (J. Mergeay, unpublished data) suggests that their taxonomy will need significant revision. The morphological identification criteria used here are based solely on Kenyan populations of the discussed taxa. We stress that the relationship of African material with the type population is often uncertain, and that Kenyan populations may also be genetically and morphologically distinct from other African populations.

Uni- and multivariate statistical analyses

We first explored patterns of covariation between the environmental variables (altitude; lake area; surface-water temperature, pH, conductivity, chlorophyll *a* content; Secchi transparency; fish presence/absence; aquatic and littoral vegetation cover) using correlation and standardised principal component analyses (PCA). Variables whose distribution among study sites was positively skewed around the mean (lake area and surface-water conductivity) were log-transformed.

Multivariate statistical analyses were restricted to ephippium abundance data from sediment samples, as these provided a more complete representation of local species diversity than the zooplankton samples. Species with a total inventory of 10 or less specimens over all study sites (Table 2) were excluded from the numerical analyses. Relationships between *Daphnia* community composition (partim the four most frequently found species: *Daphnia barbata* Weltner, *Daphnia laevis* Birge, *Daphnia pulex* Leydig and *Daphnia* sp. nov. type Limuru) and local environmental variables were evaluated by (partial) canonical correspondence analysis (CCA) using the software program Canoco 4.5 (ter Braak & Šmilauer, 1998). The long principal gradient in detrended correspondence analysis (DCA axis 1 length = 5.78 SD) favoured application of an ordination technique based on unimodal species responses (Lepš & Šmilauer, 2003). A manual forward-selection procedure was used to identify the most parsimonious set of environmental variables explaining the greatest fraction of variation in *Daphnia* community composition. Only variables that explained a significant amount of variation ($P < 0.05$) in the species data were retained, significance levels being assessed using unrestricted Monte Carlo permutation tests (999 permutations).

The independent contribution of each environmental variable to explained variance in the species data was evaluated using variation partitioning. Possible spatial structure in the dataset was accounted for by specifying spatial variables of the sampling locations as covariables (Borcard, Legendre & Drapeau, 1992). Spatial variables were derived from the geographical coordinates of the sampled sites. The most appropriate geographical measures were subjected to a forward selection procedure in a CCA on the *Daphnia* community data. The variables subjected to this selection were x, y, xy, x^2, y^2, x^2y, xy^2, x^3, y^3, with x and y being the distances of the sampled waterbodies from a reference location at 35°00′E and 04°00′S. The whole variation of the species abundance data was thus partitioned into independent components: (i) non-spatial environmental variation, (ii) spatially structured environmental variation, (iii) purely spatial species variation and (iv) unexplained (residual) variation and stochastic fluctuations (Borcard *et al.*, 1992).

Multivariate statistical analysis of the ephippium abundance data reveals the association of major environmental gradients with local *Daphnia* communities as a whole, but has comparatively little power to

Table 2 Studied waterbodies containing *Daphnia* in the zooplankton samples (A) and/or as dormant eggs in surface-sediment samples (D); numbers are counts of the total *Daphnia* community (see Methods). Atot and Dtot: total number of species found in a particular waterbody in the zooplankton (active community) and surface-sediment (dormant community), respectively.

Species	Community	TaiTa1	TaiTa3	Amb2	Amb5	Kaji	NbNP1	NbNP2	NbNP3	Lim1a	Lim1b	Lim2	LN	CIC	Oloid	Sigaw	ElNa1a	ElNa1b	ElNa2	ElNa3	ElNa4	ElNa5	ElNa6	OlBol	OB1	OB2	Barin	Mogot
barbata	A				3	2							221	300										297	31	24	300	300
laevis	A						300														300	4	15					
pulex	A												79															
sp. nov. Limuru	A									300	300	2												3				
barbata	D	1			5			66	8				161	263		1								85	15	18	148	2
laevis	D		1				15					4				24	160	61	5	11	13		1	2			1	2
longispina	D			10																								
lumholtzi	D												2															
magna	D												2		1									2				
obtusa	D											1																
pulex	D						5					115	137	14		1								6			9	
sp. nov. Limuru	D									98	116	7												4				
	Atot	0	0	0	1	1	1	0	0	1	1	1	2	1	0	0	0	0	0	0	1	1	1	2	1	1	1	1
	Dtot	1	1	1	1	0	2	1	1	1	1	4	4	2	1	3	1	1	1	1	1	0	1	5	1	1	3	2

See Table 1 for site codes.

detect species-specific responses to these gradients. We therefore complemented multivariate analysis of the species-environment data with univariate analyses of the distribution patterns of the four most frequent *Daphnia* species and *Daphnia* as a genus. The associations between species occurrences and environmental variables were evaluated by applying Mann–Whitney *U*-tests on the difference between the mean values of environmental variables in the group of lakes that contained the species and the group of lakes lacking the species; two-tailed Fisher exact tests were used to test for associations between *Daphnia* and fish and associations among *Daphnia* species. In exploratory studies like this one, strict application of sequential Bonferroni correction for multiple statistical testing may lead to awkward situations, because the more variables one studies and the more effort one makes to detect meaningful patterns, the less statistical power one has to detect the patterns. We therefore decided not to use any correction of significance value [see Moran (2003) for a more exhaustive argument].

Results

Limnological characterisation of the studied waters

The 40 studied waters vary strongly in environmental and habitat characteristics (Table 1), ranging from small watering holes and ponds to large lakes and reservoirs, and from warm turbid temporary waters without vegetation to cooler, macrophyte-rich permanent lakes. When present, fish communities mostly appear dominated by perciform species (e.g. cichlids), as indicated by a dominance of ctenoid fish scales found in surface sediments.

Surface-water conductivity (range 34–4690 $\mu S\ cm^{-1}$) of the sampled waters showed positive correlation with pH (range 5.6–10.0; $P = 0.0001$, $R = 0.69$), chlorophyll *a* (range 13.8–398 $\mu g\ L^{-1}$; $P = 0.0001$, $R = 0.68$), and with lake surface area (range 0.01–15000 ha; $P = 0.0001$, $R = 0.75$). Submerged and floating vegetation cover was positively correlated with transparency (Secchi depth range 0.01–2.20 m; $P = 0.03$, $R = 0.47$) and negatively with surface-water temperature (range 14.1–32.6 °C; $P = 0.03$, $R = -0.48$). Transparency was also positively correlated with lake depth (range 0.1–14 m; $P = 0.002$, $R = 0.63$). As expected, temperature was negatively correlated with altitude (range 695–2764 m; $P = 0.002$, $R = 0.63$). As lakes inhabited by fish tended to be larger and deeper than lakes without fish, they were characterised by higher conductivity and higher pH as well (Mann–Whitney *U*-tests: *P*-values 0.005, 0.009 and 0.02, respectively).

A PCA ordination was made of all 40 sampled waters and measured environmental variables (Fig. 2a). Because chlorophyll *a* data are lacking for some waterbodies, chlorophyll *a* was included as a supplementary neutral (passive) variable and as such does not influence the ordination (Lepš & Šmilauer, 2003). Eigenvalues for PCA axes 1–4 are 0.309, 0.245, 0.130 and 0.111, respectively, with axes 1 and 2 capturing over 55% of the variation in the environmental data. PCA axis 1 is positively related to pH, conductivity, chlorophyll *a*, surface area and temperature, and negatively related to altitude, transparency and submerged/floating vegetation cover. PCA axis 2 is positively related to surface area, depth, fish presence, transparency, and submerged/floating and littoral vegetation cover, and negatively related to temperature. Sampling sites located in the upper left quadrant of the ordination are typically large, alkaline lakes with relatively high conductivity, high phytoplankton standing stock, and presence of fish. Sampling sites in the opposite quadrant are mainly small ponds devoid of fish, with low conductivity and pH often below 7. Waters in the central lower part of the ordination are mainly small and shallow ponds at low altitudes with high temperature and turbidity, devoid of aquatic macrophytes. In the right upper corner of the ordination are a low number of relatively cold and transparent lakes at high altitudes with well-developed submerged and littoral vegetation. Some geographic structuring is obvious because waters within each main region tend to be similar with respect to morphometric and physico-chemical characteristics (e.g. aggregation of the southern road-side pools Taveta-Taita 1–3 and Voi-Nairobi 1–2).

Daphnia *occurrence in zooplankton and surface-sediment samples*

Zooplankton communities at the time of sampling, during the long (August 2001) or short (January 2003) dry seasons, were often dominated by small copepods and/or small cladocerans like *Ceriodaphnia*, *Moina* and *Diaphanosoma*. *Moina* typically dominated in small and

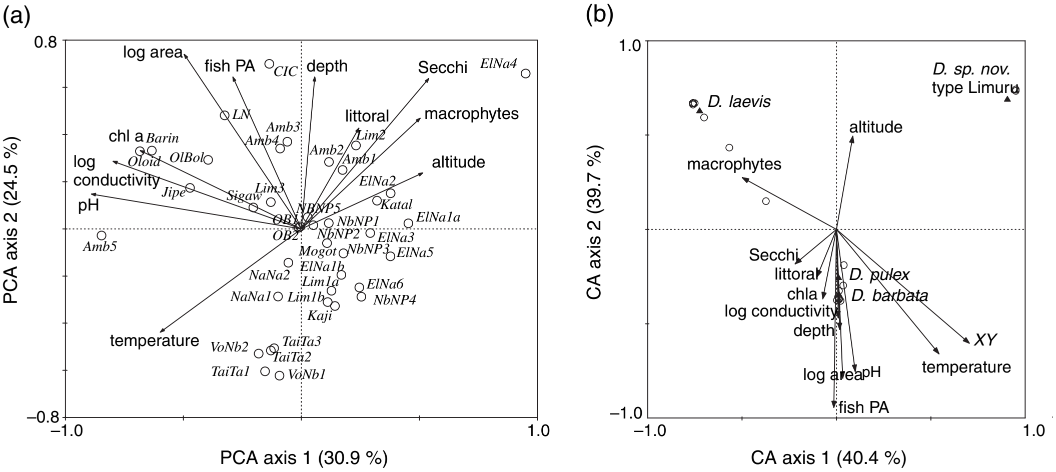

Fig. 2 (a) Principal component analyses ordination of the 40 study sites (circles) and 11 selected environmental variables (vectors); Chlorophyll *a* is included as a neutral variable. Site abbreviations as in Table 1. (b) CA ordination showing sample locations with *Daphnia* (circles), the four most common *Daphnia* species (triangles), and the environmental variables (vectors; represented as neutral variables). The spatial variable *xy* represents the geographical site location (see Methods).

temporary waters, whereas *Diaphanosoma* was most common in lakes and large reservoirs, and *Ceriodaphnia* was abundant in both environments. *Daphnia* were found at 16 sites (Table 2), representing four species: *D. barbata*, *D. laevis*, *D. pulex* and an undescribed species of the of the *D. dolichocephala* complex in subgenus *Ctenodaphnia* (J. Mergeay, unpublished data) which we here designate as *Daphnia* sp. nov. type Limuru. *Daphnia* rarely dominated zooplankton communities numerically, and were often only present in low numbers. They were, however, abundant in Lake Naivasha, Narogomon Dam in Nairobi National Park, Lake Ol Bolossat, Lake Baringo, Mogotio Dam, Lake Narasha and in the semi-permanent Limuru ponds 1a and 1b. Zooplankton communities typically contained only a single *Daphnia* species at the time of sampling, with the exception of Lake Limuru 2, the main basin of Lake Naivasha, and Lake Ol Bolossat.

For many waterbodies, only a few individuals or ephippia were found per sample (Table 2). Analysis of ephippia in surface sediments yielded more *Daphnia* species and in a higher proportion of lakes than the zooplankton samples. *Daphnia* ephippia were found in 25 of the 40 sampled waterbodies (Table 2). In addition to the four species found in the zooplankton, surface-sediment samples yielded four more species: *D. longispina* O.F. Müller, *D. lumholtzi* Sars, *D. magna* Straus, and *D.* cf. *obtusa* Kurz. Surface sediments also showed nine waters to be inhabited by two or more species, and five waters by three or more species.

In two ponds (Kajiado and Eldoret-Nakuru 5), occurrence of *Daphnia* in the zooplankton (*D. barbata* and *D. laevis*, respectively) was not complemented by recovery of their ephippia from surface sediments. Consequently, the combination of both datasets reveals the presence of *Daphnia* in 27 of the 40 Kenyan waters sampled in this study.

Multivariate community analysis

Fig. 2b shows a CA ordination of the sampled lakes containing *Daphnia* and the four most commonly recorded *Daphnia* species. The triple ordination plot also presents the environmental variables and the geographical variable *xy* as neutral variables. Manual forward selection combined with Monte Carlo permutation testing in CCA reduced the number of significant environmental variables to four: fish presence, temperature, macrophyte cover and altitude, which together explained 80.8% of the total variation in the *Daphnia* communities (*F*-value: 19.01; $P = 0.001$). Of the spatial variables only *xy* (SE–NW gradient) explained a significant part of the variation in the species data. Variation partitioning between the environmental and spatial variables in CCA attributed 51.3% of total *Daphnia* community variation to environmental variation alone (*F*-value: 16.46; $P =$

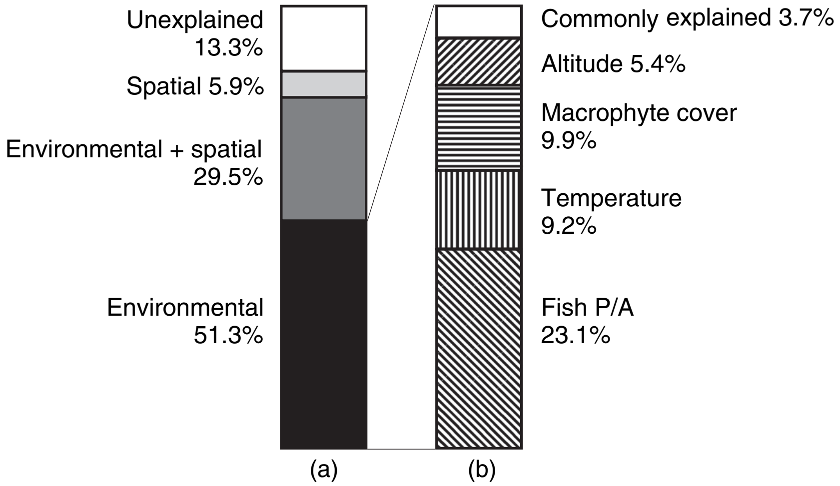

Fig. 3 Results of variation partitioning. (a) Proportion of the variation explained by environmental and spatial variables, after variation partitioning. (b) Proportion of unique environmental variation explained by each of the four selected environmental variables.

0.001). Spatially structured environmental variation embodied approximately 29.5% of the explained variation, while the purely spatial species variation (not shared by environmental variation) was only 5.9% of the total explained variation (*F*-value: 7.55; $P = 0.001$) (Fig. 3a). Fish presence, temperature, macrophyte cover and altitude all remained significant in a partial CCA after correction for spatial species variation, uniquely explaining 23.1%, 9.2%, 9.9% and 5.4% of the total variation in the species data, respectively ($P < 0.005$; Fig. 3b). The residual variation not linked to environmental or spatial variables amounted to 13.3% of the total.

Species-specific analysis of Daphnia *occurrence*

The genus *Daphnia* was recorded in 27 of the 40 sampled waterbodies. The only associations between *Daphnia* occurrence (as a genus) and environmental variables significant in univariate analysis were those with altitude and temperature. Kenyan lakes containing *Daphnia* tended to be located at higher altitudes and have lower water temperatures than lakes without *Daphnia* (Mann–Whitney *U*-tests: *P*-values <0.07).

D. barbata was recorded from 13 waters (approximately 32%). Lakes containing *D. barbata* had significantly lower scores on PCA axis 1 than lakes lacking it (Mann–Whitney *U*-test: $P = 0.004$). This species thus tended to occur in the larger, turbid lakes characterised by high pH and conductivity and by the presence of fish. Lakes with *D. barbata* had on average a higher pH than lakes lacking it (Fig. 4; Mann–Whitney *U*-test: $P = 0.018$). Lakes with *D. barbata* also tended to contain fish (two-tailed Fisher exact test: $P = 0.045$). More specifically, 10 of the 13 lakes with *D. barbata* contained fish, whereas of the 27 lakes without *D. barbata*, only 11 contained fish.

Daphnia laevis occurred in 14 of 40 lakes and ponds, and was found mostly in the colder, macrophyte-rich waters at higher altitudes (Fig. 4; Mann–Whitney *U*-tests: $P = 0.0029$, $P = 0.049$ and $P = 0.028$, respectively). No association of *D. laevis* with fish was apparent from this dataset (two-tailed Fisher exact test: $P = 0.51$).

Daphnia pulex was found in seven lakes, of which five also contained *D. barbata*; hence *D. pulex* showed a strong tendency to co-occur with this species (two-tailed Fisher exact test: $P = 0.027$). *Daphnia pulex* was found almost exclusively in lakes with surface area greater than 10 ha and depth >2 m (Fig. 4; Mann–Whitney *U*-test: $P = 0.0017$ and $P = 0.0011$, respectively). These lakes were also characterised by a relatively high pH (mostly >7.5; Mann–Whitney *U*-test: $P = 0.036$) and fish presence (all lakes with *D. pulex* contained fish; two-tailed Fisher exact test: $P = 0.009$).

Daphnia sp. nov. type Limuru was found in only four waters, all above 2200 m altitude (Fig. 4). These include both temporary and permanent aquatic systems: three (Lake Ol Bolossat and the semipermanent Limuru ponds 1a and 1b) are turbid and the fourth (Lake Limuru 2) is relatively clear and macrophyte-rich.

Discussion

The fraction of waterbodies containing *Daphnia* in this study (67%) is comparable with that reported from surveys from temperate regions (Anderson, 1974;

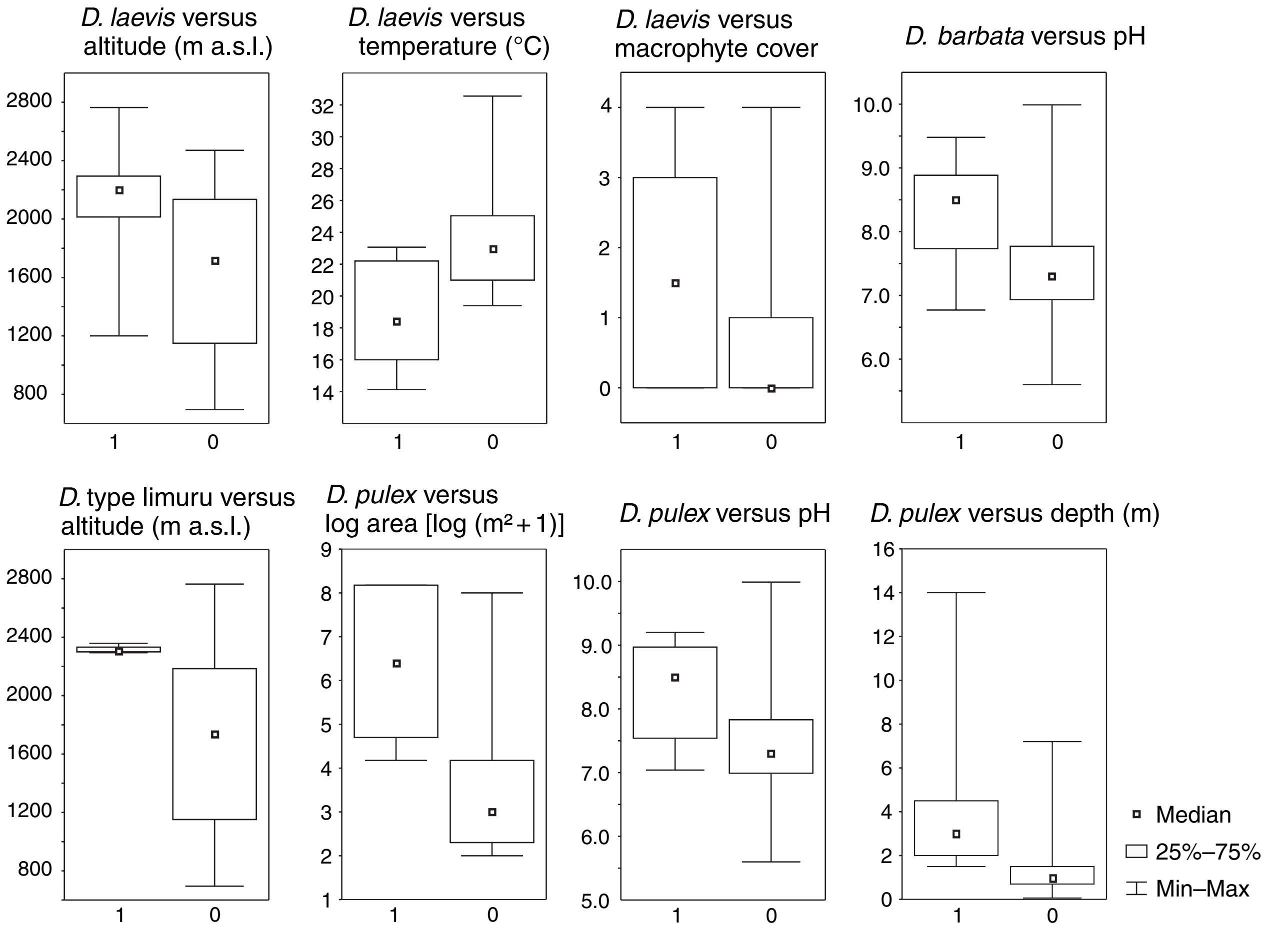

Fig. 4 Mann–Whitney *U*-tests on associations of Kenyan *Daphnia* species with selected environmental variables, using presence/absence data of dormant eggs in surface sediments.

J. Vandekerkhove, unpublished data). Poor knowledge of *Daphnia* distribution and ecology in tropical regions has led to the presumption that *Daphnia* species diversity in tropical regions is low, and its occurrence in available aquatic habitats sporadic. However, as reviews (Fernando *et al*., 1987; Dumont, 1994) focused on the lowland tropics only, almost two-thirds of and sub-Saharan Africa was ignored. Recent more detailed studies seem to confirm that lowland African rainforests are largely devoid of *Daphnia* (Chiambeng & Dumont, 2005), but that tropical *Daphnia* species diversity increases substantially when highland regions are included (Green, 1995). As the large majority (37 of 40) of waters sampled in this study were located above 1000 m elevation, this may have contributed to both the high species diversity and occurrence of *Daphnia* reported here. Indeed, we detected a direct positive association between *Daphnia* occurrence and altitude in Kenya, with most *Daphnia* populations occurring between 1700 and 2300 m elevation.

Another reason for the relatively high incidence of *Daphnia* in our study lakes may be the sampling methodology. Most previous surveys in tropical regions only considered active *Daphnia* communities present in the zooplankton, and typically collected at a single sampling occasion. In contrast, we also considered species diversity and occurrence derived from the analysis of *Daphnia* dormant egg banks contained in surface sediments. These produced twice as many *Daphnia* species as the zooplankton samples, and recorded *Daphnia* at a considerably higher fraction of sites. This is because egg banks integrate temporal variability in community species composition, whereas samples of the active zooplankton merely produce a snap-shot picture (Frey, 1960; May, 1986; Havel *et al*., 2000; Vandekerkhove *et al*., 2005). The low density of *Daphnia* in both our zooplankton and sediment samples indicates that in these tropical aquatic systems in particular, *Daphnia* may be easily overlooked when one only uses snapshot zooplankton sampling.

Daphnia barbata and *D. pulex* tended to coexist and showed a remarkably high similarity in habitat choice: both species occurred most in relatively large, fish-containing lakes characterised by high pH and conductivity. There was a distinct ecological differentiation between these two species and *D. laevis*. The latter species tended to occur in vegetated cold-water lakes at higher altitudes. *Daphnia* sp. nov. type Limuru was also exclusively found above 2200 m elevation, but the low number of available observations precludes a detailed ecological characterisation of this species. Presence of *D. barbata* in the zooplankton samples of Lake Amboseli indicates that active populations of this species tolerate high temperature (approximately 30°C), conductivity (approximately 5000 μS cm^{-1}) and pH (9.5).

As revealed by CCA of ephippium abundance data, *Daphnia* community composition in our Kenyan study lakes showed significant associations with four environmental variables: the presence of fish, temperature, macrophyte cover and altitude. It is possible that the importance of lake trophic status was underestimated in this study, because incomplete data on phytoplankton standing stock (chlorophyll *a*) prevented adequate analysis. There was also some spatially determined structure in the dataset, but this could not account for the observed associations between *Daphnia* community structure and the selected environmental variables. The complex interplay between trophic state, turbidity, macrophyte cover and fish species composition and density in most lakes is generally acknowledged (Scheffer *et al.*, 1993). The interplay between these variables influences species composition of the zooplankton community, including the relative success of *Daphnia* species. The typically high degree of covariance between these variables makes a straightforward interpretation of associations between *Daphnia* species and individual environmental variables difficult. Nevertheless, variation partitioning indicated an independent contribution of each of the four selected variables to community variation in the present study. Furthermore, at least three of the four selected variables (fish predation, vegetation and temperature) are known potentially to affect populations of *Daphnia* species directly or indirectly (Scheffer *et al.*, 1993; Moore, Folt & Stemberger, 1996).

Fish presence explained most of the variation in *Daphnia* community composition. The occurrence and abundance of *D. barbata* and *D. pulex* ephippia showed significant positive associations with fish. These patterns are remarkable because fish (especially juveniles) are in general very efficient zooplanktivores that selectively feed on large zooplankton, in temperate as well as in tropical regions. Moreover, the apparent scarcity of *Daphnia* in tropical regions has mostly been attributed to intensive fish predation (Fernando *et al.*, 1987; Dumont, 1994). Most of the fish-containing waterbodies in the region host populations of perciform (cichlid) species. Many were historically stocked with tilapine species, whose juveniles are known to feed heavily on zooplankton (e.g. Elhigzi, Haider & Larsson, 1995). Fish may positively affect zooplankton production through nutrient regeneration (Attayde & Hansson, 2001; Rejas *et al.*, 2005), but it is improbable that such an indirect mechanism would determine the presence of *Daphnia*. Most probably, the positive association between fish and both *Daphnia* species is indirect instead, and arises because both fish and *Daphnia* tend to occur in a similar type of habitat. Indeed, fish were mainly found in the larger lakes with high pH and conductivity. A more detailed analysis on the subset of lakes with fish revealed that lakes with *D. barbata* were, on average, significantly more turbid than lakes without it (Mann–Whitney *U*-test; $P = 0.013$). A similar but non-significant trend was observed for *D. pulex*. In summary, these results suggest that, in our study region, (i) *D. barbata* and *D. pulex* share the habitat preferences of fish, (ii) these two relatively large-bodied *Daphnia* species manage to coexist with zooplanktivorous fish, and (iii) turbidity may be an important factor that reduces the efficiency of fish predation in these systems. In turbid tropical lakes fish predation may thus potentially suppress *Daphnia* populations but is not strong enough to result in their complete eradication.

Daphnia community composition was also significantly associated with temperature. Whereas no association with temperature was found for *D. barbata* and *D. pulex*, both the probability of occurrence and abundance of *D. laevis* decreased with increasing temperatures. In our study region, temperature within an area varied substantially with altitude (e.g. Lake

Baringo: 25°C, 967 m a.s.l.; Lake Katalin: 19°C, 2337 m a.s.l.) but depended also on the origin of the surface water. The Olokenya Swamp in Amboseli National Park (altitude: 1155 m a.s.l.), for example, receives significant subsurface inflow of shallow groundwater originating on Mt Kilimanjaro and had a water temperature of 19°C, whereas the nearby rain-fed Lake Amboseli at a similar altitude had a temperature of 29°C (Table 1). The result of such large among-lake temperature differences is that species with different temperature optima can be found in the same regional species pool although they are unlikely to co-occur locally (e.g. *D. barbata* and *D. dolichocephala*; Mergeay *et al.*, 2005). *Daphnia laevis* has previously been reported from tropical lowlands (Fernando *et al.*, 1987), however in Kenya we mostly found it in the highlands where relatively low surface-water temperatures (<20°C) prevail. Some of the generalisations made by Fernando *et al.* (1987) were based on the assumption that South American and African *D. laevis* are the same species. Recent genetic analyses, however, indicate that they are different species, and that even within Africa, *D. laevis* is composed of several regional cryptic species (J. Mergeay & A. Petrusek, unpublished data). Ecological differences between these cryptic species may account for the discrepancy between our findings and those of Fernando *et al.* (1987).

The third environmental variable contributing significantly to the explained variation in our dataset on Kenyan *Daphnia* is macrophyte cover. This was mainly because of the positive association of *D. laevis* with water plants; no significant relations were found between macrophyte cover and *D. barbata* or *D. pulex*. In temperate regions, water plants are important stabilisers of the clear-water state of shallow lakes (Scheffer *et al.*, 1993; Scheffer, 1999; Burks, Jeppesen & Lodge, 2001; Williams, Moss & Eaton, 2002). Water plants also mediate trophic interactions between organisms (Jeppesen *et al.*, 1997) and may indirectly affect populations of *Daphnia* species by providing refuges against fish predation or by reducing phytoplankton productivity (through competition for light and nutrients or allelopathy and by promoting sedimentation of algal cells). *Daphnia laevis* tended to occur in the more transparant lakes and hence showed a stronger association with macrophytes than *D. barbata* and *D. pulex*. It follows that *D. laevis* is generally less protected by turbidity against visual predation. One modestly transparent lake in our data set without submerged or floating macrophytes (Narogomon Dam in Nairobi National Park) contained both fish and abundant *D. laevis*. Presumably its coexistence with fish in this location is also aided by an extensive belt of littoral vegetation, which may serve as additional predation refuge.

The fourth variable that explained a significant part of the observed variation in the *Daphnia* community composition was altitude. Associations between altitude and community composition are often difficult to interpret because of the high degree of covariance between altitude and many other potentially important environmental factors (the problem of multicollinearity; Graham, 2003). Altitude can be expected to be strongly correlated with temperature, intensity of UV-radiation, lake morphometry and lake productivity. In our analyses, temperature was incorporated separately in the CCA-model and thus cannot account for the altitude effect. Neither can lake morphometric variables, as the forward selection procedure failed to single out lake size or depth as significant, and because replacement of the variable altitude by these two variables considerably reduced the explanatory power of the model. Instead, we believe that the influence of altitude on *Daphnia* community composition in Kenyan lakes may reflect a productivity gradient. Productivity is expected to be higher in waterbodies situated at low elevation, because of differences in soil characteristics amplified by different land-use practices along the altitudinal gradient. Specifically, pastoralism and cattle breeding in Kenya is more widespread in the drier lowlands than in the moist highlands. Trampling and defecation by cattle near and in ponds and lakes may promote the dominance of phytoplankton over aquatic macrophytes (S. Declerck, unpublished data). Information on the nutrient budget and primary productivity is missing for most of our study lakes, but our own available data on surface-water chlorophyll *a* content give some support to the idea of a regional productivity gradient linked to elevation. In univariate analysis, chlorophyll *a* showed a negative but non-significant association with altitude. In multivariate statistical analysis, replacement of the altitude variable by chlorophyll *a* only resulted in a minor decrease in CCA model performance (1.5% decrease in total explained variation), while addition chlorophyll *a* as explanatory variable caused the contribution of altitude to become insignificant. Chlorophyll *a* is not a direct measure of primary phytoplankton productivity, but over the wide gradient of algal standing crop sampled in this study it can be assumed to reflect differences in lake trophic status.

Occurrences of both *D. laevis* and *D.* sp. nov. type Limuru were positively related to altitude in this study. Assuming that altitude is a proxy for lake trophic status, these two species appear to frequent oligotrophic conditions, whereas *D. barbata* tends to be mainly found in more eutrophic situations. This is consistent with data on the recent history of Lake Naivasha, which in recent decades has suffered rapid eutrophication and increased turbidity. Whereas *D. laevis* has now disappeared from the lake, *D. barbata* recolonised it and became the dominant species (Mergeay *et al*., 2004). In South Africa, *D. laevis* is also typically found in relatively clear waterbodies (Hart, 1992, 2001). The fact that these are rare in the Kenyan lowlands or midlands (<1500 m) may explain why *D. laevis* was mostly found at high elevations in our study. Alternatively, Kenyan *D. laevis* may be a true highland species, restricted to higher elevations because of temperature-related ecological preferences.

In conclusion, our results show that *Daphnia* are not necessarily rare in tropical aquatic environments and that different species have specific associations with environmental variables. The analysis of dormant egg banks in addition to zooplankton sampling greatly improves the quality of presence/absence species distribution data for regional surveys of biodiversity and community composition.

Acknowledgments

This study was carried out with permission of the Permanent Secretary of the Ministry of Education, Science & Technology of Kenya under research permit 13/001/11C to D.V., and funded by the KULeuven Research Fund (project OT/00/14) and the Fund for Scientific Research – Flanders, Belgium (project G0086.00). The authors thank K. Mavuti (University of Nairobi, Kenya), W. Shivoga (Egerton University, Kenya), S. Higgins (Kijabe Ltd., Naivasha), the Lake Naivasha Yacht Club, the Lake Naivasha Riparian Association and the people at Kampi Ya Samaki for logistic support, and H. Eggermont and K. De Maeyer for field assistance. We are indebted to the Kenya Wildlife Service for permission to collect samples in the national parks. J.M. was supported by a PhD fellowship from the Institute for the Promotion and Innovation of Science and Technology in Flanders (IWT, Belgium); S.D. is a post-doctoral fellow with the Fund for Scientific Research, Flanders (FWO-Vlaanderen).

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(Manuscript accepted 1 November 2005)