The response of phytoplankton and zooplankton to river damming in three cascading reservoirs of the Tana River, Kenya

Eric Ochieng Okuku,[1,2]* Mwakio Tole,[3] Linet Imbayi Kiteresi[2] and Steven Bouillon[1]

[1]Department of Earth & Environmental Sciences, Division of Soil and Water Management, Katholieke Universiteit Leuven, Leuven, Belgium, [2]Kenya Marine and Fisheries Research Institute, Mkomani English Point, Mombasa, Kenya and [3]Department of Environmental Sciences, School of Agriculture and Environmental Sciences, Pwani University, Kilifi, Kenya

Abstract

River damming reduces the ecological heterogeneity of ecosystems, with a resultant shift of communities adapted to lotic conditions to those better adapted to the newly created lentic environment. Whereas the response of phytoplankton and zooplankton community composition and structure to river damming has been extensively studied in individual reservoirs, this study assessed three cascading reservoirs on the Tana River, Kenya. A total of five sampling campaigns were carried out in 2011, 2012 and 2013 for different sampling sites within each of the reservoirs, as well as upstream and downstream of the reservoirs. Plankton communities within each of the three reservoirs, and upstream of the reservoirs, were compared, indicating (i) the disappearance of 13 phytoplankton and 2 zooplankton taxa; (ii) the appearance (invasion) by 26 phytoplankton and 33 zooplankton taxa; and (iii) an opportunistic presence of 7 phytoplankton and 6 zooplankton taxa. Thirty-two genera of potentially harmful algae were also encountered, suggesting a potential future threat of harmful algal blooms. A significant reduction in phytoplankton diversity and taxa evenness was also observed, as well as increases in overall abundance in the reservoirs, compared to the river upstream of the study reservoirs. However, these ecological indices were restored to the original levels observed upstream of the study reservoirs at sites hundreds of kilometres downstream of the reservoirs.

Key words

community structure, damming disturbance, plankton, taxa abundance.

INTRODUCTION

Water is widely regarded as the most essential of our natural resources. The benefits of water in economic development, however, are often accompanied by the degradation of aquatic ecosystems and reduced biodiversity, with potentially serious but unquantified costs (Vörösmarty *et al.* 2005). Rivers maintain unique biotic resources and irreplaceable biodiversity, for example, because of their local environmental heterogeneity and the complexity of riverine processes, allowing for many species with a variety of life traits and population strategies to coexist. However, they have highly been modified and adapted to meet the ever-changing needs of society (Galloway 2000), with impacts on these systems ranging from supracatchment effects to local impacts (Boon 1992). Riverine biodiversity is currently in a state of crisis as a consequence of decades of human interventions through river damming, diversions and pollution (Syvitski *et al.* 2005).

Reservoirs reduce biological diversity by flooding land, fragmenting habitats, isolating species and interrupting the exchange of nutrients between ecosystems (WCD 2000). They also convert extensive reaches of stream habitat into standing water (Graf 2001), thus reducing water and sediment flows to downstream habitats (Olden & Naiman 2010); forming barriers for fish migration; extirpating shallow-water species through fluctuating water levels and by altering fish spawning patterns

(Malmqvist & Rundle 2002) and plankton community structure and composition.

Plankton constitute the base of the food webs in aquatic ecosystem (Kiteresi *et al.* 2012), thereby playing a significant role in the global cycling of carbon, nitrogen, phosphorus and other elements (Hudson *et al.* 1999). Studies of plankton abundance, distribution and community composition fundamentally contribute to our understanding of the structure and functioning of aquatic ecosystems and could be used to provide insights into the responses of aquatic systems to environmental changes (e.g. Paerl *et al.* 2010). Although successional shifts in plankton community structure are naturally expected in rivers because of changes in environmental variables such as nutrients and other physicochemical variables (Madhu *et al.* 2007), such shifts are heightened by river damming.

Reservoirs are considered favourable environments for the development of plankton communities, which may establish diverse assemblages in relatively short periods of time after their impoundment (Rocha *et al.* 1999). Long-term assessments of phytoplankton changes in some of Africa's reservoirs, however, have revealed a progressive change in species composition commencing after impoundment (Viner 1969; Dejenie *et al.* 2008, 2012), which may be superimposed on the predamming annual seasonal changes. These changes are often characterized by progressive colonization by species absent in the inflowing river (Petr 1975). Thus, reservoirs provide new opportunities for colonization and act as stepping stones for the spread of invaders and proliferation of species by replacing spatially heterogeneous stream habitats with homogeneous spatially distributed standing waters (Gao *et al.* 2010). This habitat modification can displace local assemblages adapted to tolerate human perturbations, thereby resulting in the homogenization of freshwater biota (Prenda *et al.* 2006; TSS 2006). Reservoirs provide new habitats for passively dispersing numerous plankton species, aquatic plants and planktonic larvae of benthic invertebrates, for example, that cannot persist in strong unidirectional flows in unmodified rivers.

Whereas most plankton studies have been carried out in a number of individual reservoirs (e.g. Uku & Mavuti 1994; Kotut *et al.* 1998), only a handful of studies have determined the impacts of several cascading reservoirs on the ecological structure and functioning of the dammed rivers (e.g. Barbosa *et al.* 1999; Jorcin & Nogueira 2005; Naliato *et al.* 2009). To this end, the Tana River (Kenya) represents an ideal system to study the effects of multiple dams, because it currently contains five cascading reservoirs, mainly developed for hydroelectric power generation. Furthermore, preconstruction environmental studies in Kenya recommended a regular monitoring of the ecology of the reservoirs because of the country's past experiences with eutrophication-related lake problems. However, very limited limnological attention has been directed to Kenya's reservoirs (e.g. Uku & Mavuti 1994; Kotut *et al.* 1998; Tamooh *et al.* 2012). Accordingly, the present study focused on three of the Tana River's cascading reservoirs to determine their impacts on their phytoplankton and zooplankton community structure and composition.

MATERIALS AND METHODS
Study sites

This study was carried out in the Tana River basin, Kenya (Fig. 1), which has a length of ~1000 km, rising in the Aberdare Range and Mount Kenya of central Kenya and subsequently draining through the arid and semi-arid lands in the eastern part of the country to enter the Indian Ocean through a fan-shaped delta (Tamooh *et al.* 2012). A total of five cascading reservoirs (constructed on the mainstream of Tana River between 1968 and 1981) offer an ideal opportunity to study the effects of reservoirs on the Tana River plankton. Masinga, Kamburu and Gitaru reservoirs were selected for this study because of the differences in their sizes, depth profiles and water residence times (Table 1). These three reservoirs were intended to provide a better understanding of how the reservoirs' plankton community structure and composition are influenced by these features.

To determine the impacts of river damming on plankton community composition and structure, the upper reaches and lower reaches of the three reservoirs were sampled, because these reaches experience different physical, chemical and biological forcings (Ward & Stanford 1995). Sampling sites in the reservoirs were selected based on criteria identified by Thornton (1990) as follows: three sites were selected in Masinga Reservoir (Masinga upper reaches, MUR; Masinga mid-reaches, MMR; Masinga lower reaches, MLR). Considering their smaller sizes, two sampling sites were selected in Kamburu (Kamburu upper reaches, KUR; Kamburu lower reaches, KLR) and Gitaru (Gitaru upper reaches, GUR; Gitaru lower reaches, GLR) reservoirs (Fig. 1). The upper reach sampling sites were located near the reservoir inlets (characterized by high water flow rates), while the lower reach sites were located towards the reservoir exits (close to the hydropower turbines and characterized by lower water flow) and the mid-reach sites were intermediate. Riverine inflow sites were also selected to act as
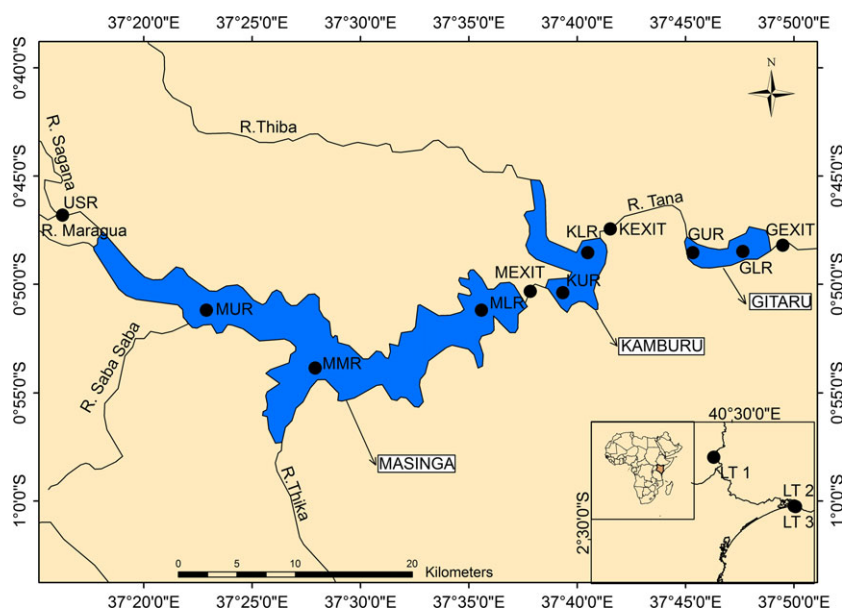
Fig. 1. Map showing sampling sites (upstream of reservoir; within reservoirs; downstream of reservoirs) along the Tana River, Kenya.

Table 1. Main characteristics of the three Tana River study reservoirs (modified from Brown *et al.* 1996; water residence time calculated from 2011 and 2012 data of authors)

Reservoir	Altitude (m)	Year commissioned	Capacity ($\times 10^6$ m^3)	Surface area (km^2)	Original Maximum depth (m)	Installed capacity (MW)	Water residence time (days)
Masinga	1050	1981	1560	120	50	40	149
Kamburu	1010	1974	123	15	56	96	16
Gitaru	924	1978	20	3.1	30	225	3

reference sites before the river water flowed into the reservoirs. The inflow sites were located upstream of the reservoir site USR (on the main Tana River, representing inflows into Masinga Reservoir and also acting as an inflow for the study area), at the Masinga exit, MEXIT (inflow into Kamburu Reservoir), and the Kamburu exit, KEXIT (inflow into Gitaru Reservoir). Outflow sites were also included to provide data for comparison with the inflow data, to facilitate understanding of the role of reservoirs in modifying limnological variables. The outflow sites included MEXIT (outflow from Masinga Reservoir), KEXIT (outflow from Kamburu Reservoir) and Gitaru exit, GEXIT (outflow from Gitaru Reservoir).

Phytoplankton data collected from three sites (hereafter referred to as 'downstream of the reservoirs stations', DRS) in the Lower Tana, just above the Tana estuary within the framework of HABs project, were used to determine whether there was recovery of the ecological characteristics of the river downstream of the reservoirs. Zooplankton was not sampled at the DSR sites,

because it was outside the scope of the HABs project. Other small rivers flowing into the reservoirs (e.g. Rivers Sabasaba, Thika, Chania and Thiba) were not considered in this study because of the limited time of the survey and challenges in obtaining adequate logistical support.

Sample collection, preparation and analysis

Samples were collected at all sites during five sampling campaigns in 2011, 2012 and 2013, selected to cover both wet and dry seasons (Fig. 2), apart from the DSR sites sampled only in March 2011, May 2011 and January 2012. Phytoplankton samples were collected by filtering 20 L of surface water through a 20 μm phytoplankton net, and fixed using Lugol's reagent. Zooplankton samples from the reservoir sites were obtained by towing a plankton net (332 μm mesh size) for 10 min against the water current, while the samples from the USR and LT1 sites were obtained by collecting 200 L of surface water (using a bucket) and filtering it through the 332 μm mesh sized net. Zooplankton samples were preserved
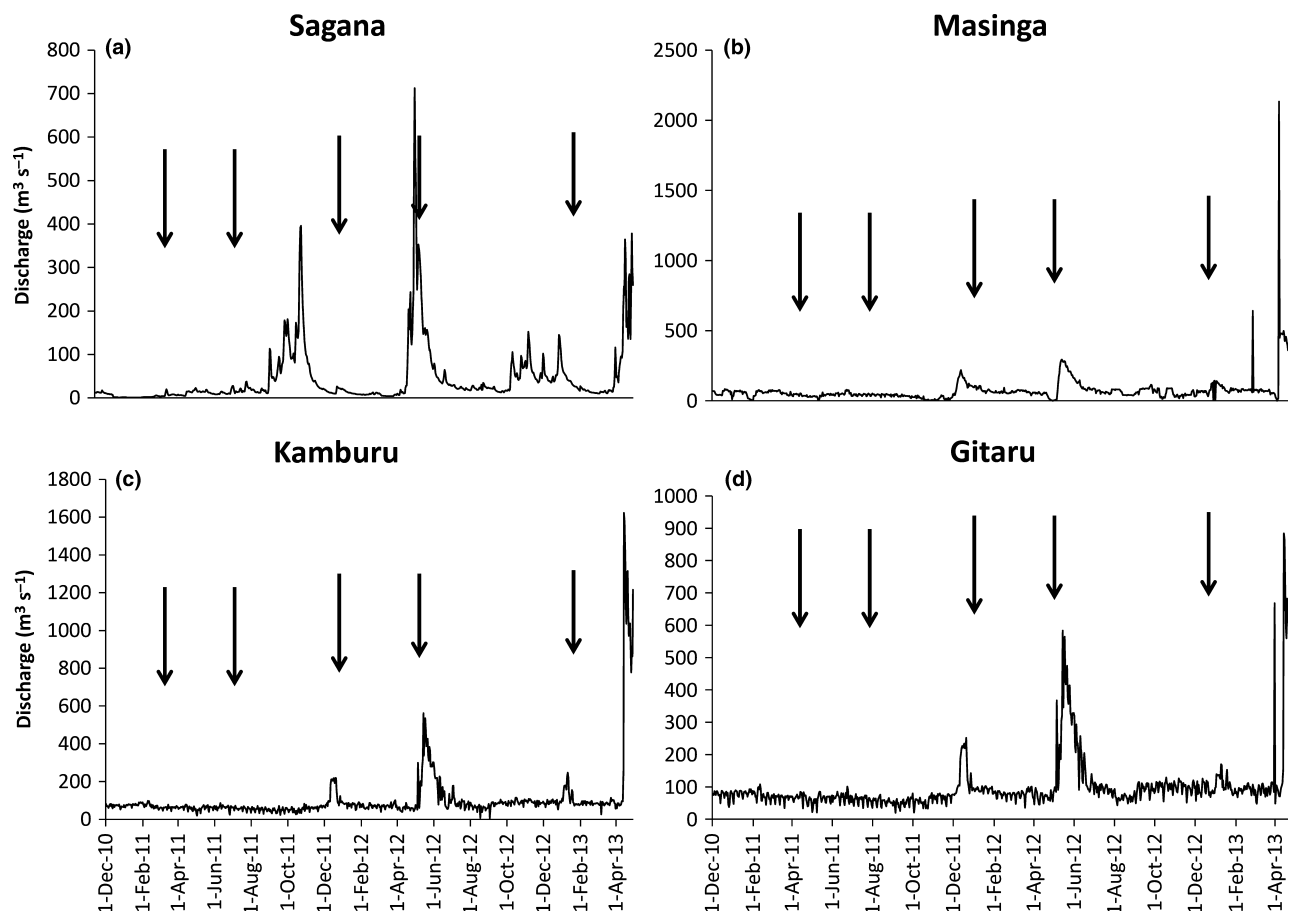
Fig. 2. Time series of discharges at the different sampling sites during the study period (arrows indicate sampling dates).

with 5% buffered formalin and transported to the laboratory for further analysis. It is noted that phytoplankton and zooplankton abundance and richness could have been underestimated in this study because of the use of 20 and 332 μm mesh sizes for phytoplankton and zooplankton sampling, respectively. Comparisons among the systems are still valid, however, assuming that any potential underestimation was uniform across all the sampling sites.

A range of additional environmental parameters including temperature, pH, electrical conductivity and dissolved oxygen (DO) concentration were measured concurrently using a handheld multiparameter probe (YSI Professional Plus, Ohio USA). Surface water samples for the determination of total suspended matter (TSM), chlorophyll-a (Chl-*a*) and nutrient concentrations were collected with a vertical Niskin bottle at the reservoir sites, and with a bucket at the other sites. Samples for the determination of dissolved nutrient concentrations were collected in acid-washed polyethylene bottles following double filtration on precombusted 47-mm GF/F filters and through 0.2 μm syringe filters, and preserved using

HgCl$_2$. The methods described by APHA (1998) and Parsons *et al.* (1984) were used to measure dissolved ammonium (NH$_4^+$-N), nitrate + nitrite {(NO$_3^-$ + NO$_2^-$)-N}, orthophosphate (PO$_4^{3-}$-P) and silicate (SiO$_2$) concentrations in the water samples, while chlorophyll-*a* was measured following the methods outlined by APHA (1975).

Chl-*a* and total suspended matter (TSM) samples were collected through filtration of a known volume of water from each sampling site (on precombusted 47 mm diameter GF/F filters), using a hand-operated vacuum pump. Chl-*a* filters were placed inside cryotubes and frozen in liquid nitrogen until analysis, whereas TSM samples were air-dried for a few minutes in Petri dishes and subsequently oven-dried at 50 °C. The TSM was determined by calculating the difference between the final and initial weights of the precombusted filters (Bouillon *et al.* 2009).

Community respiration samples were collected by overfilling two 500 mL borosilicate respiration bottles, which were stoppered and stored in an insulated box for 24 h. DO measurements were taken before and after incubation, using a DO meter (YSI Professional Plus, Ohio USA). The average community respiration rate was

calculated by dividing the difference in DO after incubation with the incubation time.

Numerical analyses and species identification were carried out using the sedimentation method (Üthermöhl 1958). Plankton were identified to species level whenever possible, although identification was only possible to genus level in most cases.

Data analysis

The phytoplankton and zooplankton community structures were expressed as ecological indices (taxa richness, abundance, Shannon–Wiener's diversity indices and Pielou's evenness). Taxa richness was taken as the total number of taxa found in a sample, while Shannon–Wiener's species diversity index was calculated from the taxa and abundance data for each site for each sampling campaign (Shannon 1948).

Environmental variables and taxa abundance, diversity, evenness and richness have been reported as means, along with the associated standard errors (SE) to show the seasonal variability. Pearson product–moment correlation was used to determine the relationships between environmental parameters and phytoplankton indices, as well as between phytoplankton and zooplankton indices. The existence of significant differences in taxa indices in the reservoirs, and upstream or downstream of the reservoirs, was tested by paired *t*-tests. Data were tested for homogeneity of variances, using Kolmogorov–Smirnov goodness-of-fit test prior to *t*-test analysis to ensure the absence of relationships between variances and means. Multivariate analysis was carried out using canoco software (Lepš & Šmilauer 2003) and triplot representation of the redundancy analysis (RDA) ordination plot given.

Phytoplankton and zooplankton taxa were categorized into four groups to provide an insight into their adaptation to river damming disturbance (e.g. Naiman & Décamps 1997). The groups included extinction (the absence of some taxa in the reservoirs that were present at the USR site), invasion (the presence of some taxa in the reservoirs that were absent at the USR site), proliferation (the rapid increase in taxa abundance in the reservoirs, compared to the USR site) and endurance (taxa existing in similar abundance in the reservoirs and the USR site).

RESULTS
Limnological parameters

The mean surface water temperatures were relatively elevated in the reservoirs (range: 23.8 ± 0.6 26.4 ± 0.4 °C), compared to the water temperatures at USR site (22.2 ± 1.0 °C) (Table 2). The DO concentrations

Table 2. Mean environmental variables measured for sampling sites (mean±SE).

Station	Temperature (°C)	Dissolved oxygen (mg L^{-1})	Electrical conductivity (μS cm^{-1})	pH	TSM (mg L^{-1})	NH$_4^+$ (μM)	NO$_3^-$ (μM)	PO$_4^{3-}$ (μM)	SiO$_2$ (μM)	Chl-*a* (μg L^{-1})
USR	22.2 ± 1.0	7.49 ± 1.00	111 ± 13	7.30 ± 0.09	40.0 ± 15.5	1.31 ± 0.57	3.90 ± 1.94	3.59 ± 1.51	294 ± 21	2.53 ± 0.44
MUR	25.5 ± 1.2	7.28 ± 0.43	125 ± 4	8.03 ± 0.11	15.4 ± 4.1	1.33 ± 0.57	3.4 ± 1.6	1.00 ± 0.23	186 ± 43	5.31 ± 3.18
MMR	26.4 ± 0.4	6.82 ± 0.43	136 ± 10	8.19 ± 0.08	17.6 ± 4.7	1.04 ± 0.48	3.64 ± 2.04	0.94 ± 0.23	206 ± 6	10.92 ± 2.49
MLR	25.2 ± 0.5	7.05 ± 0.63	129 ± 11	7.96 ± 0.07	20.1 ± 10.8	0.80 ± 0.28	4.78 ± 2.55	1.83 ± 0.79	204 ± 10	10.46 ± 2.36
MEXIT	23.2 ± 0.5	3.46 ± 0.91	116 ± 11	7.00 ± 0.27	106.0 ± 67.7	1.95 ± 0.62	4.59 ± 1.77	1.10 ± 0.33	213 ± 15	8.48 ± 0.66
KUR	25.3 ± 1.0	7.48 ± 0.74	122 ± 8	8.15 ± 0.14	47.0 ± 23.9	0.92 ± 0.39	3.81 ± 2.03	1.02 ± 0.36	224 ± 20	1.44 ± 1.44
KLR	25.5 ± 0.6	6.96 ± 0.48	129 ± 10	8.03 ± 0.14	34.8 ± 16.7	1.27 ± 0.45	3.99 ± 1.55	1.25 ± 0.57	220 ± 10	9.64 ± 1.39
KEXIT	24.0 ± 0.4	6.48 ± 0.4	124 ± 16	7.25 ± 0.36	45.3 ± 20.8	1.31 ± 0.57	4.02 ± 2.13	1.10 ± 0.15	222 ± 8	4.38 ± 0.65
GUR	23.8 ± 0.6	6.91 ± 0.24	126 ± 13	7.43 ± 0.16	33.8 ± 16.0	0.97 ± 0.14	5.23 ± 2.38	1.42 ± 0.35	224 ± 7	4.83 ± 0.94
GLR	25.5 ± 0.6	7.44 ± 0.42	126 ± 9	7.79 ± 0.19	33.4 ± 16.8	1.36 ± 0.37	5.33 ± 1.99	1.42 ± 0.43	223 ± 9	5.59 ± 0.90
GEXIT	24.8 ± 0.3	6.57 ± 0.40	127 ± 11	7.64 ± 0.21	36.3 ± 18.2	1.24 ± 0.39	5.09 ± 2.00	1.52 ± 0.65	215 ± 13	5.57 ± 0.66

remained relatively similar for all the sampled sites (range: 6.57 ± 0.40–7.49 ± 1.00 mg L^{-1}), except for the extremely low DO levels in water discharged from Masinga Reservoir (mean: 3.46 ± 0.91 mg L^{-1}). There was a general decline in the mean TSM concentrations in the reservoirs (mean range: 15.4 ± 4.1–47.0 ± 23.9 mg L^{-1}), compared to the concentrations in the inflows into the reservoirs (mean range: 40.0 ± 15.5–106 ± 67.7 mg L^{-1}).

There was a slight decline in the mean dissolved NH$_4^+$-N concentrations through Kamburu (from 1.95 ± 0.62 to 1.31 ± 0.57 μM) and Gitaru (from 1.31 ± 0.57 to 1.24 ± 0.39 μM) reservoirs (Table 2). The decline in the mean dissolved NH$_4^+$-N concentrations was accompanied by a slight increase in the mean dissolved $\{(NO_3^- + NO_2^-)$-N$\}$ concentrations in Masinga (from 3.4 ± 1.6 to 4.78 ± 2.55 μM), Kamburu (from 3.81 ± 2.03 to 3.99 ± 1.55 μM) and Gitaru (from 5.23 ± 2.38 to 5.33 ± 1.99 μM) reservoirs. The mean dissolved PO$_4^{3-}$-P concentrations were lower in the reservoirs (0.94 ± 0.23–1.42 ± 0.43 μM), compared to the concentration at USR site (3.59 ± 1.51 μM). The dissolved SiO$_2$ concentrations decreased from USR site (mean: 294 ± 21 μM) to Masinga Reservoir (mean range: 186 ± 43–224 ± 20 μM). A relatively constant concentration, however, was observed down cascade.

Phytoplankton abundance and diversity

A total of 77 phytoplankton taxa belonging to 65 families were observed in this study (Table 3). The reservoirs contained a higher phytoplankton abundance (mean range: $38\,250 \pm 22\,908$–$467\,917 \pm 237\,803$ cells L^{-1}), compared to the abundance at USR site (mean: $10\,833 \pm 5116$ cells L^{-1}; Figs 3b, 4). The Gitaru Reservoir phytoplankton abundance differed significantly from the abundance observed at USR site (paired t-test, $P < 0.05$) and DSR (paired t-test, $P < 0.05$), while the abundance in Kamburu Reservoir differed significantly from the levels at the DSR site (paired t-test, $P < 0.05$).

Table 3. Plankton taxa encountered in study reservoirs (brackets indicate harmful algae, according to LIFEHAB 2001).

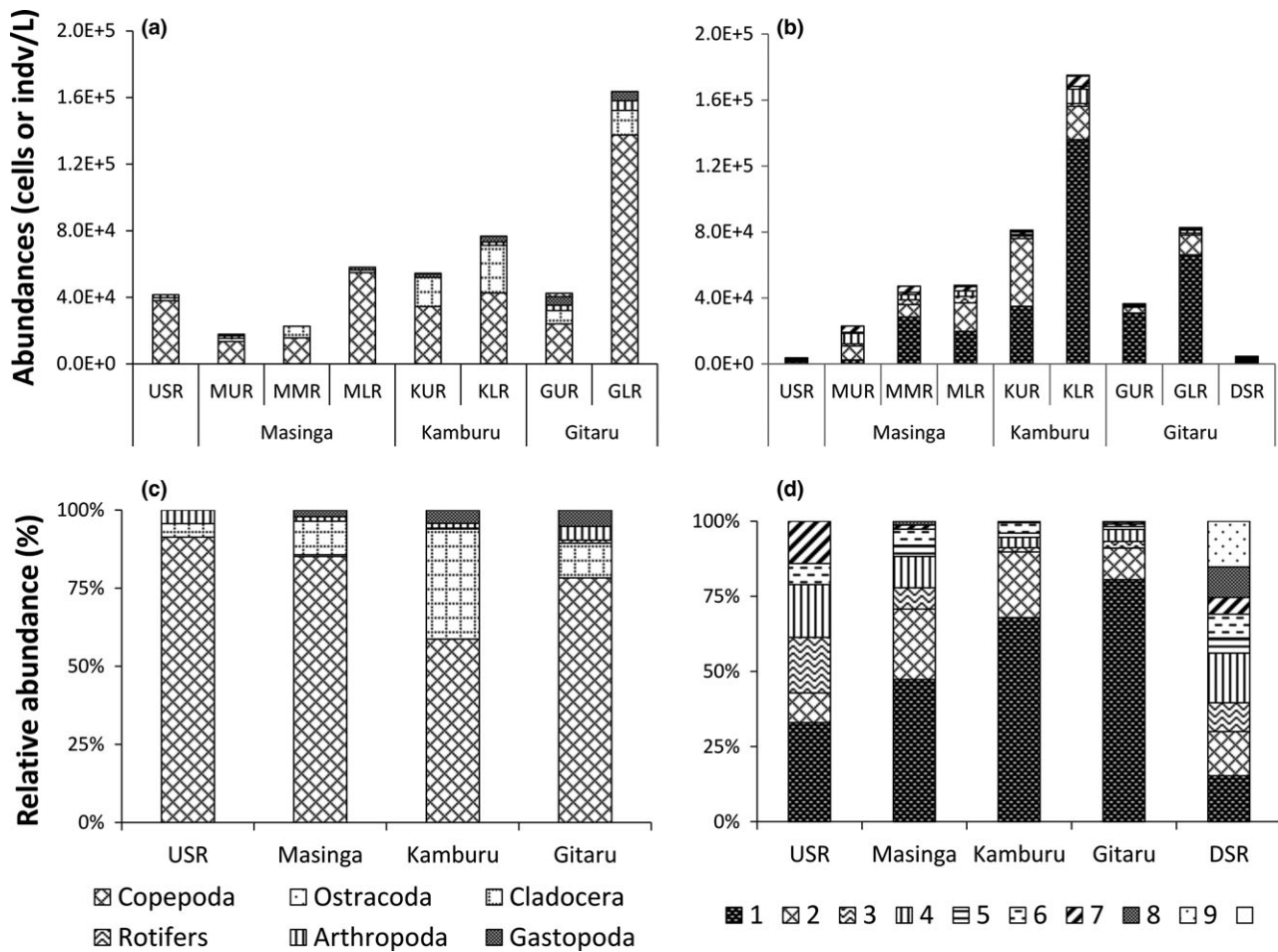| Phytoplankton taxa			Zooplankton taxa	
Actinoptychus	(Eutreptiella)	Phacus	Abedus spp.	Epischura spp.
(Amphora)	(Fischerella)	Platymonas	Acanthocyclops robustus	Eucalanus spp.
(Anabaena)	Fragilaria	Pleurosigma	Aglaodiaptomus leptopus	Eucyclops elegans
Asterionella	(Gambierdiscus)	(Prorocentrum)	Alona guttata	Gastropoda taxa larvae
Biddulphia	(Gonyaulax)	(ProtoPeridinium)	Anopheles spp.	Hesperocorixa spp.
Bleakleleya	(Guinardia)	(Prymnesium)	Branchionus calyciflorus	Hydracarina spp.
Botryococcus	(Gymnodinium)	Pseudo-Anabaena	Ceriodaphnia spp.	Leptodiaptomus nudus
Cerataulina	(Gyrodinium)	(Pseudo-Nitzschia)	Ceriodaphnia lacutris	Leptodiaptomus sicilis
(Ceratium)	Gyrosigma	Pteromonas	Chaoborus americanus	Leptodiaptomus minutus
(Chaetoceros)	Haslea	Pyramimonas	Chaoborus punctipennis	Leptodiaptomus spp.
Chlamydomonas	Hydrodictyon	(Rhizosolenia)	Chaoborus spp.	Macrothrix spp.
Choanoflagellidea	(Leptocylindricus)	Scenedesmus	Chironomus spp.	Mesocyclops edax
Closterium	(Lyngbya)	(Scrippsiella)	Conochilus unicornis	Mesoveliinae
Coccolith	Melosira	(Skeletonema)	Daphnia middendorffiana	Microcyclops rubellus
Coccomonas	Merismopedia	Spirulina	Daphnia spp.	Microcyclops varicans
Coelastrum	Microcoleus	Staurodesmus	Diacyclops spp.	Onychodiaptomus birgei
(Coscinodiscus)	(Microcystis)	Stephanodiscus	Diacyclops thomasi	Orthocyclops modestus
Cosmarium	Navicula	Striatella	Diacylops bicuspidatus	Ostracoda
Cyclotella	(Nitzschia)	(Synedra)	Diaphanosoma birgei	Simocephalus exspinosus
Cymbella	(Noctiluca)	Synura	Diaptomus clavipes	Skistodiaptomus oregonensis
(Dictyocha)	Odontella	(Tabellaria)	Diaptomus siciloides	Skistodiaptomus pallidus
Dinobryon	(Oscillatoria)	Thalassionema	Diaptomus spp.	Skistodiaptomus reighardi
(Dinophysis)	(Ostreopsis)	(Thalassiosira)	Dixa spp.	Skistodiaptomus spp.
Diploneis	Pandorina	Uroglena	Donacia spp.	Tipulidae
Ditylum	Pediastrum	Volvox	Epischura lacustris	
Euglena	(Peridinium)			

Fig. 3. Spatial distribution of zooplankton (a), phytoplankton (b) and relative contribution of major zooplankton (c) and phytoplankton (d) groups upstream of study reservoirs (USR), within the reservoirs (MUR, MMR, MLR, KUR, KLR, GUR and GLR), and downstream of the reservoirs (DRS) (1 = Bacillariophyceae; 2 = Cyanophyceae; 3 = Chlorophyceae; 4 = Syndiniophyceae; 5 = Chrysophyceae; 6 = Prasinophyceae; 7 = Euglenaceae; 8 = Hexamitidae; the Arthropoda phylum includes members of the Belostomatidae, Chaoboridae, Chironomidae, Chrysomelidae, Eucalanidae, Corixidae, Hydrachnellae, Mesoveliidae, Aeshnidae and Tipulidae).

The lotic zones of the reservoirs exhibited a lower phytoplankton abundance (mean range: 38 250 ± 22 908–158 583 ± 97 586 cells L^{-1}), compared to the lentic zones (mean range: 123 000 ± 17 000–467 917 ± 237 803 cells L^{-1}), as shown in Table 4.

The phytoplankton taxa diversity was significantly higher at USR site (mean: 2.05 ± 0.21) and DSR (mean: 2.07 ± 0.17), whereas it remained markedly low in the reservoirs, exhibiting a decline from MUR (mean: 1.55 ± 0.09) to GEXIT (mean: 0.76 ± 0.42) as shown in Table 4 and Figure 4(P1). This observation was further confirmed by a significant difference in the phytoplankton diversity at USR site, compared to the diversities in Masinga (paired *t*-test, $P < 0.05$), Kamburu (paired *t*-test, $P < 0.01$) and Gitaru (paired *t*-test, $P < 0.01$) reservoirs. Similarly, the phytoplankton diversity at DSR was

significantly different from the diversity in Masinga (paired *t*-test, $P < 0.01$), Kamburu (paired *t*-test, $P < 0.01$) and Gitaru (paired *t*-test, $P < 0.01$) reservoirs.

The phytoplankton taxa evenness was higher at the USR site (mean: 0.83 ± 0.06) and DRS site (mean: 0.87 ± 0.04), whereas it remained markedly low in the reservoirs, exhibiting a pronounced decline from MUR (mean: 0.68 ± 0.04) to GEXIT (mean: 0.3 ± 0.14), as shown in Table 4 and Figure 4(P3). This observation was further confirmed by significant differences in the phytoplankton taxa evenness observed at USR site, compared to Masinga (paired *t*-test, $P < 0.05$), Kamburu (paired *t*-test, $P < 0.01$) and Gitaru (paired *t*-test, $P < 0.01$) reservoirs. Similarly, the phytoplankton taxa evenness at DSR site differed significantly from the taxa evenness observed in Masinga (paired *t*-test, $P < 0.01$), Kamburu
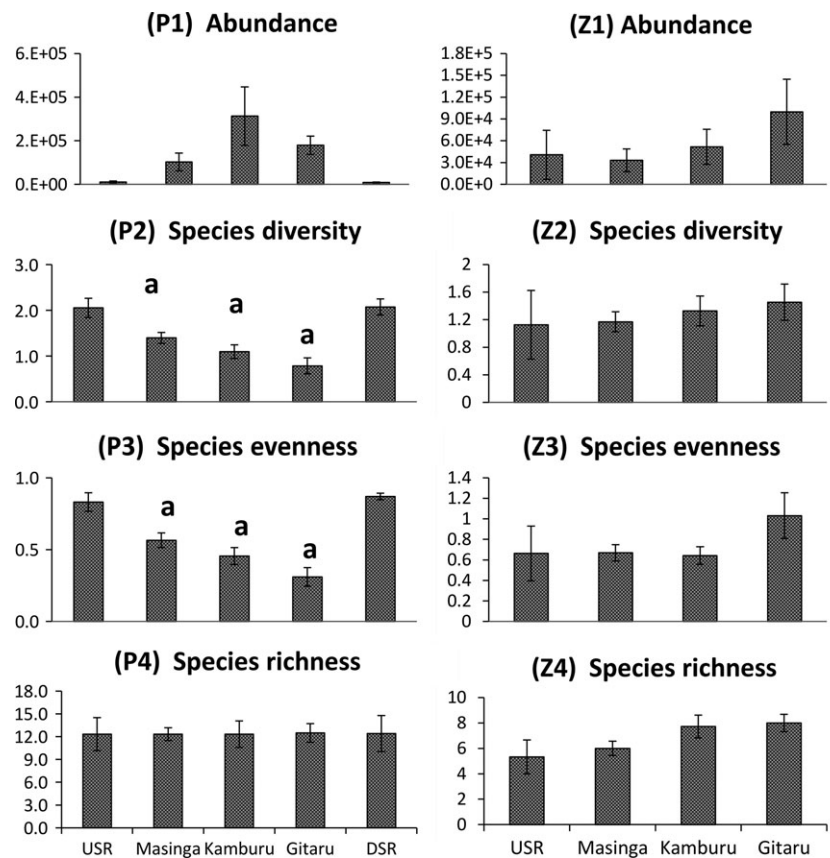
Fig. 4. Spatial distribution of phytoplankton (P1-4) and zooplankton (Z1-4) ecological indices upstream of study reservoirs (USR), within the reservoirs (Masinga, Kamburu and Gitaru) and downstream of the reservoirs (DRS).

(paired *t*-test, $P < 0.01$) and Gitaru (paired *t*-test, $P < 0.01$) reservoirs. These findings confirm that the river damming has profound impacts on river ecology.

The phytoplankton taxa number was higher upstream and downstream of the reservoirs (mean range: 12.3 ± 2.2–20.5 ± 1.5) compared to the taxa numbers observed within the reservoirs (mean range: 10.0 ± 1.0–14.3 ± 1.0), as shown in Table 4 and Figure 4P1. Higher phytoplankton taxa numbers within the reservoirs were observed in MMR (mean: 14.3 ± 1.0) and GLR (mean: 14.0 ± 1.7), while the rest of the reservoir sites had lower mean taxa numbers, ranging from 10.0 ± 1.0 in MUR to 13.3 ± 1.5 in KLR (Table 4; Fig. 4). The sites between the reservoirs generally had the lowest mean taxa numbers ranging from 8.0 ± 2.9 in MEXIT to 10.7 ± 2.2 in GEXIT.

Zooplankton abundance and diversity

A diverse zooplankton assemblage (consisting of 48 zooplankton taxa and 1 gastropoda taxa larvae) was noted in this study (Table 3). A high abundance of zooplankton was observed in the lentic zones (mean range: $56\ 299 \pm 42\ 415$–$157\ 900 \pm 79\ 142$ individuals m^{-3}), compared to the lotic zones of the reservoir (mean range: $17\ 644 \pm 10\ 351$–$37\ 151 \pm 20\ 905$ individuals m^{-3}), as shown in Table 4.

The zooplankton abundance, diversity, richness and evenness were relatively higher in the reservoirs, compared to the levels at USR site (Table 4; Fig. 4Z1-4). The zooplankton abundance generally exhibited similar trends as phytoplankton, being equally more abundant in the reservoirs (Fig. 4P1 and Z1), compared to sites outside the reservoir.

Copepods were the most abundant taxa (91.3%) at the reservoir upstream sites, followed by cladocerans (4.3%) and arthropod larvae (4.3%) (Fig. 3a,c). Copepods were also the most abundant taxa in the reservoirs, with a relative abundance of 86.6%, 61.3% and 82.6%, for Masinga, Kamburu and Gitaru reservoirs, respectively (Fig. 3a,c).

Plankton community adaptation to damming disturbance

Thirteen phytoplankton taxa and two zooplankton taxa present at the USR site were not encountered in the reservoirs and could be considered extinct (Table 5), while six zooplankton and seven phytoplankton taxa were present in high abundance in the reservoirs, compared to the USR site, and could be classified as opportunistic. Extinction rates were relatively higher in Kamburu and Gitaru reservoirs, compared to Masinga Reservoir (Fig. 5). The number of opportunistic taxa progressively

Table 4. Spatial variation in phytoplankton and zooplankton ecological indices in study area (phytoplankton abundance in cells L^{-1}; zooplankton abundance in individuals m^{-3})

Plankton group	Sampling site	Abundance	Taxa Diversity	Taxa Evenness	Taxa Richness
Phytoplankton	USR	10 833 ± 5116	2.05 ± 0.21	0.83 ± 0.06	12.3 ± 2.2
	MUR	38 250 ± 22 908	1.55 ± 0.09	0.68 ± 0.04	10.0 ± 1.0
	MMR	141 450 ± 89 722	1.31 ± 0.25	0.49 ± 0.09	14.3 ± 1.0
	MLR	123 000 ± 17 000	1.34 ± 0.25	0.54 ± 0.08	12.0 ± 1.0
	MEXIT	25 000 ± 3031	1.35 ± 0.20	0.65 ± 0.12	8.0 ± 2.9
	KUR	158 583 ± 97 586	1.23 ± 0.24	0.54 ± 0.08	11.3 ± 3.5
	KLR	467 917 ± 23 7803	0.96 ± 0.18	0.37 ± 0.05	13.3 ± 1.5
	KEXIT	134 917 ± 38 894	0.75 ± 0.16	0.33 ± 0.02	10.7 ± 3.5
	GUR	112 500 ± 43 765	0.77 ± 0.35	0.31 ± 0.13	11.0 ± 1.5
	GLR	246 833 ± 47 587	0.8 ± 0.18	0.31 ± 0.07	14.0 ± 1.7
	GEXIT	188 833 ± 23 137	0.76 ± 0.42	0.30 ± 0.14	10.7 ± 2.2
	LT1	3000 ± 1750	1.92 ± 0.31	0.96 ± 0.04	8.0 ± 3.0
	LT2	11 125 ± 1875	2.72 ± 0.03	0.90 ± 0.03	20.5 ± 1.5
	LT3	9722 ± 2776	2.13 ± 0.17	0.88 ± 0.02	13.1 ± 2.5
Zooplankton	USR	41 375 ± 33 711	1.13 ± 0.50	0.66 ± 0.27	5.3 ± 1.3
	MUR	17 644 ± 10 351	1.12 ± 0.31	0.60 ± 0.18	7.0 ± 1.3
	MMR	22 458 ± 11 951	1.25 ± 0.15	0.76 ± 0.09	5.3 ± 0.7
	MLR	56 299 ± 42 415	1.18 ± 0.30	0.67 ± 0.13	5.5 ± 0.7
	MEXIT	30 828 ± 21 110	1.49 ± 0.28	0.70 ± 0.12	9.3 ± 2.3
	KUR	52 233 ± 48 410	1.16 ± 0.43	0.55 ± 0.18	7.7 ± 1.5
	KLR	73 592 ± 50 207	1.69 ± 0.30	0.85 ± 0.04	8.8 ± 2.8
	KEXIT	51 285 ± 29 511	1.46 ± 0.25	0.71 ± 0.07	7.8 ± 1.3
	GUR	37 151 ± 20 905	1.57 ± 0.46	0.72 ± 0.18	8.3 ± 1.2
	GLR	157 900 ± 79 142	1.34 ± 0.35	0.65 ± 0.14	7.7 ± 0.9
	GEXIT	24 436 ± 15 075	1.45 ± 0.28	0.67 ± 0.11	8.4 ± 1.1

reduced from Masinga to Gitaru reservoirs, whereas the number of enduring species remained similar in the three reservoirs (Fig. 5).

DISCUSSION
Limnological parameters

River damming altered virtually all environmental variables in the study reservoirs (Table 2). The observed gradual reduction in TSM down the reservoirs may have resulted from reduced water flow speed, favouring the settling of particles in the water. The elevated temperature in the reservoir water, compared to that in the river water upstream of the reservoirs, is likely attributable to the long water residence time, while the sudden decrease in water temperature below Masinga Reservoir reflects cold bottom water released from the reservoir (Pacini *et al.* 1999). The extremely low DO levels in the Masinga Reservoir outflow water is likely attributable to low

oxygen conditions caused by a high oxygen demand in the bottom waters and sediments because of remineralization of sedimenting organic matter, and a limitation of oxygen exchange with the atmosphere by seasonal water stratification (Pacini *et al.* 1999).

The relatively elevated observed temperature in the reservoirs, and reduced water flow (reduced turbidity), may be among the factors contributing to the increased Chl-*a* concentrations and the observed plankton community structuring in the reservoirs (Table 6A), as evidenced from the observed relationship between TSM and Chl-*a* (*Pearson's product-moment correlation*, $r = 0.56$, $P < 0.05$). Significant relationships also existed between temperature and phytoplankton diversity (*Pearson's product-moment correlation*, $r = 0.54$, $P < 0.05$) and between temperature and zooplankton diversity (*Pearson's product-moment correlation*, $r = -0.47$, $P < 0.05$) and evenness (*Pearson's product-moment correlation*, $r = -0.57$, $P < 0.05$). The results of the present study, for example,

Table 5. Phytoplankton and zooplankton response to river damming

Functional adaption	Phytoplankton Taxa	Zooplankton taxa
Extinction	*Tabellaria* spp, *Chaetoceros* spp, *Odontella* spp, *Pleurosigma* spp, *Odontella* spp, *Eutreptiella* spp, *Melosira* spp, *Chlamydomonas* spp, *Dinophysis* spp, *Biddulphia* spp, *Diploneis* spp, *Cymbella* spp and *Amphora* spp	*Donacia* spp. and *Leptodiaptomus nudus*
Invasion	*Microcystis* spp, *Dictyocha* spp, *Volvox* spp, *Pandorina* spp, *Ceratium* spp, *Cosmarium* spp, *Synura* spp, *Synedra* spp, *Anabaena* spp, *Uroglena* spp, *Euglena* spp, *Coccomonas* spp, *Peridinium* spp, *Choanoflagellidea* spp, *Hydrodictyon* spp, *Pteromonas* spp, *Coelastrum* spp, *Coccolith* spp, *Asterionella* spp, *Gyrosigma* spp, *Dinobryon* spp, *Lyngbya* spp, *Cyclotella* spp, *Pseudo-Anabaena* spp, *Fischerella* spp and *Platymonas* spp	*Abedus* spp., *Alona guttata*, *Anopheles* spp., *Branchionus calyciflorus*, *Ceriodaphnia* spp., *Ceriodaphnia lacutris*, *Chaoborus americanus*, *Chaoborus punctipennis*, *Daphnia middendorffiana*, *Daphnia* spp., *Diacyclops* spp., *Diacyclops thomasi*, *Diacylops bicuspidatus*, *Diaptomus clavipes*, *Diaptomus* spp., *Dixa* spp., *Epischura* spp., *Eucalanus* spp., *Eucyclops elegans*, *Gastropoda larvae.*, *Hesperocorixa* spp., *Hydracarina* spp., *Leptodiaptomus sicilis*, *Macrothrix* spp., *Microcyclops rubellus*, *Microcyclops varicans*, *Onychodiaptomus birgei*, *Orthocyclops modestus*, *Ostracoda*, *Simocephalus exspinosus*, *Skistodiaptomus oregonensis*, *Skistodiaptomus reighardi* and *Skistodiaptomus* spp.
Opportunistic	*Oscillatoria* spp, *Staurodesmus* spp, *Pediastrum* spp, *Guinardia* spp, *Pyramimonas* spp, *Nitzschia* spp, and *Microcoleus* spp	*Aglaodiaptomus leptopus*; *Mesocyclops edax*; *Diaphanosoma birgei*; *Diaphanosoma birgei*; *Epischura lacustris*; *Acanthocyclops robustus*
Endurers	*Navicula* spp, spirulina spp and *Closterium* spp	
Avoiders	*Coscinodiscus* spp	*Diaptomus siciloides*, *Choronomus* spp, *Leptodiaptomus minutus*

demonstrate that zooplankton evenness was negatively related to temperature (*Pearson's product-moment correlation*, $r = -0.57$, $P < 0.05$) and TSM (*Pearson's product-moment correlation*, $r = -0.57$, $P < 0.05$), while phytoplankton evenness exhibited a positive relationship with NH_4^+ (*Pearson's product-moment correlation*, $r = 0.57$, $P < 0.05$, Table 6A). A significant negative relationship was observed between zooplankton taxa richness and TSM, which is a function of water turbidity (*Pearson's product-moment correlation*, $r = -0.61$, $P < 0.05$). The observed slight decline in the dissolved NH_4^+-N concentrations, when comparing the inflowing and outflowing waters from Kamburu and Gitaru reservoirs (Table 2), may be attributable to phytoplankton preference for dissolved NH_4^+-N to $\{(NO_3^- + NO_2^-)$-N$\}$. Dissolved NH_4^+-N preference by phytoplankton has been attributed to high energy requirements associated with the assimilation of $\{(NO_3^- + NO_2^-)$-N$\}$ as a nitrogen (N) source (Eppley

et al. 1969; Yajnik & Sharada 2003). Thus, a significant reduction in the dissolved NH_4^+-N concentration down the cascade, due to high plankton abundance in the reservoirs, was expected. A non-significant reduction in NH_4^+-N was observed in the reservoirs, however, which may be attributable to the high regeneration/respiration rate in the reservoirs (range: 0.35 ± 0.087–1.33 ± 0.16 μmol L^{-1} h^{-1}), compared to the stations outside the reservoirs (range: 0.03 ± 0.08–0.26 ± 0.21 μmol L^{-1} h^{-1}) that may have produced remineralized dissolved ammonium that readily offset the phytoplankton NH_4^+-N demand and, therefore, the observed non-significant reduction of NH_4^+-N concentrations down the cascade.

The lower dissolved PO_4^{3-}-P concentrations in the reservoirs, compared to the concentration at the USR site, may have been caused by an elevated uptake by phytoplankton and by the subsequent sedimentation of
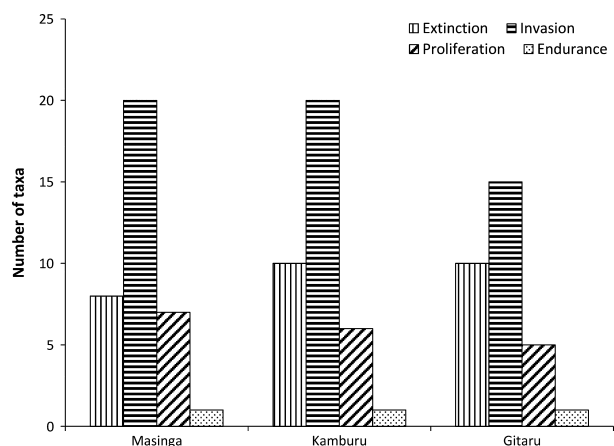
Fig. 5. Functional adaptations of plankton in Masinga, Kamburu and Gitaru reservoirs in response to river damming.

dead phytoplankton cells. Furthermore, PO_4^{3-}-P is known to attach to sediments. Thus, the reduced levels in the water column probably also resulted from particle sinking. The observed reduction in the dissolved SiO_2 concentration in Masinga Reservoir, compared to USR site, is a common phenomenon in the reservoirs, typically linked to its utilization by diatoms (which were abundantly present in the reservoirs), which deplete the dissolved SiO_2 in the water column by incorporating silica in their cell structure, as well as the associated losses of the dead cells to the sediments (Uku & Mavuti 1994; Dürr *et al.* 2011). The more or less constant SiO_2 concentration observed at the reservoir sites (after the initial reduction of dissolved silicates in Masinga, compared to the Masinga Reservoir inflow), however, may be a result of regeneration (e.g. dissolution of sedimented diatom frustules that replenish the assimilated dissolved SiO_2 of the water column).

Spatial distribution of phytoplankton and zooplankton

Phytoplankton spatial distribution

The observed high phytoplankton abundance in the study reservoirs, compared to the USR and DSR sites (Fig. 4), is likely linked to the reduced water turbidity (e.g. low TSM levels) resulting from reduced water velocities and the associated settling down of particles in the reservoirs (Table 2). The high phytoplankton biomass and abundance have similarly been reported in systems with longer water residence times, and more static flow conditions, compared to systems with short water residence times and/or highly variable flow velocities (Søballe & Kimmel 1987; Sullivan *et al.* 2001).

The observed lower phytoplankton abundance in the reservoir lotic zones, compared to the lentic zones

(Table 4), was similarly reported for other water systems by Wetzel (2001), who indicated that the lotic zones of reservoirs operate like an extension of the river, in which turbulence, sediment instability, high turbidity, reduced light availability and other riverine characteristics limit the algal production.

Reservoirs have been described as a hybrid between rivers and natural lakes (Kimmel & Groeger 1984; Søballe & Kimmel 1987), with intermediate properties (e.g. flow velocity and water residence time that influence plankton dynamics (Kimmel & Groeger 1984) and longitudinal zonation, ecological structure and function of different aquatic ecosystems (Søballe & Kimmel 1987). The results of the present study, however, indicate that positive relationships between water retention time and phytoplankton abundance was only true when considering a single reservoir not serially placed along a river. A phytoplankton carry-over effect (release from the preceding reservoir) was witnessed in the case of cascading reservoirs, with the smaller reservoirs (Kamburu and Gitaru) having higher abundance than Masinga Reservoir, despite their much shorter retention time (Table 1).

Spatial distribution of zooplankton

The high abundance of zooplankton observed in the lentic zones of the study reservoirs, compared to the lotic zones (Table 4), may be attributable to the reduced water speed (longer retention times) in the reservoirs, with the associated reduction in advective downstream losses. This zonation pattern is consistent with the findings of Basu and Pick (1997) and Reckendorfer *et al.* (1999). Similarly, Basu and Pick (1996) and Thorp *et al.* (1994) attributed lower zooplankton biomass and abundance in the lotic systems, compared to lakes (with similar nutrient and Chl-*a* concentrations), to shorter water retention times.

Plankton communities dominance

The varied representation of the main taxa observed at different sampling sites/reservoirs (Figs 3b,d and 6) suggests varied community resilience to damming disturbances. The inverse relationship between zooplankton evenness and temperature ($r = -0.57$, $P < 0.05$) and TSM ($r = -0.57$, $P < 0.05$) in the present study indicates that different planktonic species can tolerate varying ranges of physicochemical parameters. These differences in tolerance levels determine the dominance of species in different places and at different times (Sommer *et al.* 1993). Bacillariophyta, Cyanophyta and Dinoflagellates, for example, exhibited high abundance in the reservoirs, compared to the USR and DSR sites (Fig. 3b,d). The relatively high abundance of copepods and cladocerans in the mid-

Table 6. Correlation matrix of (A) plankton indices and environmental parameters, (B) phytoplankton and zooplankton indices

	Phytoplankton Abundance	Phytoplankton Diversity	Phytoplankton Evenness	Phytoplankton Richness	Zooplankton Abundance	Zooplankton Diversity	Zooplankton Evenness	Zooplankton Richness
(A)								
Temperature	−0.07	**(0.54)**	0.46	0.23	−0.42	**(−0.47)**	**(−0.57)**	−0.21
DO, mg L^{-1}	0.31	0.06	0.08	−0.05	0.16	0.04	−0.10	0.34
Conductivity	−0.05	−0.04	−0.02	−0.06	0.39	−0.05	0.10	−0.31
TDS	−0.04	−0.13	−0.09	−0.08	0.44	0.01	0.19	−0.29
pH	0.32	0.27	0.27	0.11	0.25	−0.44	−0.38	−0.38
TSM	−0.16	0.25	0.01	**(−0.61)**	−0.26	**(−0.61)**	**(−0.57)**	**(−0.49)**
NH$_4$	−0.31	0.36	**(0.55)**	**(−0.48)**	−0.29	0.25	0.11	0.36
NO$_3$	0.29	−0.19	−0.42	**(0.56)**	0.10	−0.35	−0.46	−0.06
PO$_4$	−0.17	0.22	0.17	0.08	−0.12	−0.06	−0.07	−0.12
SiO$_2$	−0.00	−0.08	−0.11	0.03	−0.42	0.22	0.26	0.17
Chl-*a*	**(0.56)**	0.12	−0.07	**(0.54)**	−0.28	−0.41	−0.34	−0.28
(B)								
Phytoplankton abundance	1.00	–	–	–	–	–	–	–
Phytoplankton diversity	−0.40	1.00	–	–	–	–	–	–
Phytoplankton evenness	**(−0.51)**	**(0.90)**	1.00	–	–	–	–	–
Phytoplankton richness	0.37	0.22	−0.20	1.00	–	–	–	–
Zooplankton abundance	0.16	−0.43	−0.37	−0.22	1.00	–	–	–
Zooplankton diversity	−0.32	−0.42	−0.11	**(−0.81)**	0.17	1.00	–	–
Zooplankton evenness	−0.43	−0.29	−0.03	**(−0.71)**	0.15	**(0.93)**	1.00	–
Zooplankton richness	0.09	**(−0.55)**	−0.28	**(−0.65)**	0.16	**(0.76)**	**(0.48)**	1.00

Bold and bracketed *r* values are statistically significant, $P < 0.05$.

and lower reaches of the reservoirs is probably attributable to longer water residence times, enabling these taxa to complete their reproductive cycles before any advective losses, as well as reduced water turbidity as reported for other water systems by Basu and Pick (1996). High turbidity is known to cause high mortality of juvenile zooplankton and suppression of their growth, through reduced food availability and visibility (Wetzel 2001).

Plankton community structure
Phytoplankton community structure

Although a number of plankton studies on reservoirs have reported strong relationships between phytoplankton abundance and nutrient availability, with some citing nutrients as the principal factor controlling phytoplankton abundance in fresh water (Quiblier *et al.* 2008; McCarthy *et al.* 2009), the lack of a significant relationship between nutrient levels and phytoplankton abundance in the present study confirms that other factors may have contributed in controlling phytoplankton abundance in the study reservoirs (Table 6A). Non-dependency of phytoplankton composition and diversity indices on nutrients was also reported by Danilov and Ekelund (1999) and Karydis and Tsirtsis (1996), whereas Wehr and Descy (1998) concluded that even though the variations in water chemistry may alter the relative proportions of a few dominant taxa, it often has little effect on the overall phytoplankton assemblages.

The dominance of Bacillariophyceae (diatoms) observed in the reservoirs (Fig. 3d) may be the result of

their boom and bust nature. When light and nutrient conditions in the upper mixed water layer become favourable (as evident in the reservoirs), the diatoms, which are opportunistic r-strategists (organisms with high growth rate), quickly out-compete other organisms, thereby dominating the water column phytoplankton communities (Furnas 1990). Dominance of diatoms in tropical reservoirs is a common phenomenon (Wood & Talling 1988), which is related to the availability of silicic acid (Egge & Aksnes 1992), as well as the production of silica frustules that require 80% less energy to synthesize, compared to organic cell walls in other phytoplankton, thereby facilitating greater investment in growth (Raven 1983).

The observed significant negative correlation between phytoplankton species richness and TSM (Table 6A) indicates that water clarity (a function of water retention time) could play an important role in structuring phytoplankton community. This is consistent with the findings of Reynolds *et al.* (2002), who studied the role of physical interactions in controlling phytoplankton dynamics in lentic habitats with minimal contribution from biotic interactions.

The lower phytoplankton diversity observed in the reservoirs, compared to the USR and DSR sites, may be attributable to reduced ecological heterogeneity in the reservoirs resulting from altered flow regimes. The reservoirs generally convert the formerly ecologically heterogeneous environment (with associated ripples, pools and interaction with riparian land) into a homogeneous one, thereby interfering with successional trajectories, habitat diversification, migratory pathways and other processes that can reduce the biodiversity (Naveh & Liebermann 1994; Herault & Honnay 2005). The higher taxa diversity at the USR and DSR sites could also be attributed to a 'portfolio effect' that recognizes that, although different taxa abundance can respond differently to a given environmental perturbation, the diverse responses average when considered together, thereby creating a stabilizing function that preserves the integrity of the overall assemblage despite existing disturbances (Doak *et al.* 1998).

The interaction between the River Tana and the riparian landscape is greatly reduced in the dammed areas of the river, compared to undammed areas, thereby resulting in lower taxa richness observed in the reservoirs. This is consistent with the findings of Shurin and Havel (2002) and Ward *et al.* (1999), which supported the important role of riverine riparian landscape in structuring species composition and richness patterns. Nogueira *et al.* (2010) similarly reported reservoir morphological complexity as an important factor controlling phytoplankton richness and diversity. This was confirmed in

Masinga Reservoir, which exhibited higher taxa diversity, compared to Kamburu and Gitaru reservoirs, because of its higher morphological complexity resulting from its dendritic shape (Pacini *et al.* 1999).

Zooplankton community structure

Zooplankton taxa abundance, diversity, richness and evenness remained relatively higher in the reservoirs, compared to USR site (Table 4; Fig. 4Z1-4). Generally, zooplankton abundance generally exhibited a trend similar to that of their main food source (phytoplankton), which was equally more abundant in the reservoirs (Fig. 4P1 and Z1). Food availability has been shown to have a strong bottom-up control on zooplankton biomass, abundance and species composition in many aquatic systems (Morales-Baquero *et al.* 1994; Burns & Dodds 1999). Furthermore, zooplankton dynamics has been reported to exhibit a gradient similar to that of their food sources (Neary *et al.* 1994).

The lack of a significant negative relationship between phytoplankton and zooplankton abundance indicates an absence of a strong top-down control on the phytoplankton community. This finding confirms the reported inability of zooplankton to shape or control phytoplankton in tropical reservoirs (Melo & Huszar 2000; Ruckert & Giani 2008). This finding is different from that of Mineeva *et al.* (2008), however, who reported that phytoplankton was controlled by physical processes in the lower retention time systems, while biotic interactions are more important in higher water retention time systems.

The observed dominance by copepods in the reservoirs was not surprising. However, this study only reported high abundance and dominance of copepods and cladocerans, a finding different from documented works on other African water bodies, including Lake Cubhu (Martin & Cyrus 1994), Ogun and Ona rivers (Akin-Oriola 2003) and Niger-Sokoto River (Jeje & Fernando 1992), which also reported a high abundance of rotifers, in addition to copepods and cladocerans.

The relatively high abundance of copepods and cladocerans in the reservoirs may have been caused by a mixture of factors, including reduced water flow speed (reduced advective losses), high growth rates and the abundant diatoms on which they graze. An increase in zooplankton number and biomass, following an increase in phytoplankton biomass and production, was similarly reported by Rocha *et al.* (1999). *Daphnia* are known to have large body size, enabling them to graze on large quantities and diverse forms of the abundant phytoplankton. This morphological feature probably facilitated the

predominance of *Daphnia* among the cladocerans. The low abundance of rotifers observed in the reservoirs (although not ascertained in this study) may be attributable to extensive grazing by the abundant *Daphnia* in the reservoirs. Similarly, the lower abundance of rotifers in the reservoirs could have resulted from increased water residence time in the reservoirs. Lower abundance of rotifers in reservoirs was also reported by Baranyi *et al.* (2002), who attributed rotifers dominance to low or medium water residence times, and crustaceans dominance to longer residence times.

The higher zooplankton taxa number encountered in the reservoirs (Fig. 4Z4) agrees with the findings of Rocha *et al.* (1999), who reported higher species richness in reservoirs. Reservoirs have several biotic (reproduction, completion, predator and food availability) and abiotic factors (temperature, transparency, nutrients, water retention time and age) that closely interact with, and modify, each other to cause the high species numbers observed in reservoirs (Søballe & Kimmel 1987; Basu & Pick 1996), similar to the present study, with the significant negative relationship between zooplankton taxa richness and TSM (*Pearson's product-moment correlation*, $r = -0.49$, $P < 0.05$), which is a function of water turbidity.

The observed positive correlation between phytoplankton diversity and evenness (*Pearson's product-moment correlation*, $r = 0.90$, $P < 0.05$) and the negative correlation between taxa evenness and abundance (*Pearson's product-moment correlation*, $r = -0.51$, $P < 0.05$, Table 6B) confirm that phytoplankton species diversity was mostly affected by population evenness, compared to species number. A strong positive correlation between phytoplankton taxa evenness and species diversity, which has been reported in other studies (e.g. Stirling & Wilsey 2001; Ricotta & Avena 2003), was also confirmed in the present study. Positive correlations between zooplankton diversity and richness (*Pearson's product-moment correlation*, $r = 0.76$, $P < 0.05$) and evenness (*Pearson's product-moment correlation*, $r = 0.48$, $P < 0.05$), however, indicate that both species number and densities can influence zooplankton species diversity.

Community resistance and resilience to river damming disturbance

Riverine system is known to function as an ecological network, with longitudinal and transversal transfer of water, sediments and nutrients (Petts & Bradley 1997). Obstructing a river, however, dissipates its energy to create a lentic habitat (disturbance), which typically results in changes in the community composition and structure

by an influx (colonization/invasion) of species from the drainage network, and a loss (extinction) of species less adapted to the changed environmental conditions. To this end, colonization and extinction of local populations are important aspects of community composition and diversity for defining long-term conservation objectives (Hanski 1999). Plankton in the present study were classified into four broad functional adaptations categories of population strategies (Fig. 5 and Table 5).

Community invasion

Altered conditions created by reservoir development, including altered flow regimes, reduced ecological heterogeneity, increased resource availability and low species biodiversity in the reservoirs, may comprise the main reasons for the observed species invasion in the cascade, namely 26 phytoplankton and 33 three zooplankton taxa not encountered upstream of the reservoirs, but successfully colonizing the reservoirs. Spatiotemporal heterogeneity in physiochemical environment and food resources in the reservoirs, for example, may have provided multiple niches for invasive species. The high phytoplankton abundance observed in the present study may have created a favourable environment for zooplankton invasion in the reservoirs by reducing the abundance of native species and the intensity of biotic interactions, thereby creating a 'resource gap' which may have been filled by potential invaders. An increased susceptibility of communities to invasion resulting from anthropogenic disturbances elsewhere has also been documented by Orians (1986). Furthermore, Davis *et al.* (2000) and Havel *et al.* (1995) predicted that communities become more susceptible to invasions whenever and wherever there is an increase in the availability and quantity of unused resources.

The observed invasive species in Masinga, Kamburu and Gitaru reservoirs (Fig. 5) indicate that the three reservoirs are highly connected river–reservoir systems, thereby exhibiting a great potential for enhancing colonization rates of invasive species from downstream transport. This is supported by propagule pressure theory, which identifies the degree of immigration by new individuals as a major factor predicting the success of invaders in colonizing new ecosystems (Kolar & Lodge 2000). Masinga Reservoir behaved in the present study as a source of colonizing organisms. Once an invasive population was established in Masinga Reservoir, it served as a stepping stone for further invasions in the downstream reservoirs, thereby greatly enhancing their invasion rates (e.g. Shigesada & Kawasaki 1997). Masinga Reservoir similarly modified the hydrological

and ecological interactions of Kamburu and Gitaru reservoirs, thereby increasing the chances of invasion of these reservoirs.

The observed high taxa diversity upstream and downstream of the reservoirs may have contributed to the resistance of these systems to species invasion, consistent with the findings of Kennedy *et al.* (2002) that high species diversity and ecological interactions increased the resistance to invasion. The findings of the present study also support the insurance hypothesis (Tillman 1999), which postulates that more diverse assemblages are more likely to display a range of functional traits, thereby increasing the probability of one species compensating for the negative responses of other species to disturbances. Furthermore, Elton (1958) reported that intense interspecific interactions (predation, competition and parasitism) in the natural systems provided a barrier to potential colonization.

Daphnia species were reported in the present study as being invaders. *Daphnia* are known to have large bodies, and possess morphological structures such as spines, helmets and neck teeth that create a handling difficulty for most of their predators (Kolar & Wahl 1998; Tollrian & Dodson 1999). These mechanisms create a selective predation which may have discriminated *Daphnia*, making them successful invaders in the reservoirs.

Community extinction and proliferation

Damming rivers alters habitats from being heterogeneous lotic to homogenous lentic habitats, thereby eliminating organisms that are better adapted to the substituted habitat, while creating vacant niches (Elton 1958; Kolar & Wahl 1998) with lowered competition and predation rates (Lodge 1993), which opportunistic organisms can take advantage of and proliferate (Table 5). Opportunistic (K-selected) taxa generally demonstrate more competitive traits with a significant investment on growth, which may have contributed to their dominance in the study reservoirs.

Potential harmful algae and associated ecosystem/human health implications

Phytoplankton are important primary producers that form the base of the aquatic food chain. Nevertheless, some plankton species may be harmful to human and other vertebrates (Crawley 1986). Thirty-two taxa of potentially harmful algae were encountered in the present study (Table 3). Whereas there was a higher taxa number of potentially harmful algae downstream of the reservoirs, their cell densities were low, compared to the in-reservoir levels. A total of 7 potentially harmful algal taxa (but in

low densities) were observed upstream of the reservoir, whereas the reservoirs themselves contained a total of 10 taxa in relatively high densities. Harmful algae species are of special concern because they are a potential cause of mortality to organisms when present in high numbers because of the development of anoxic conditions or production of biotoxins. Biotoxins are also responsible for extensive fish and shellfish die-offs, as well as mortality to birds, mammals and other animals in the same food webs (LIFEHAB 2001). The wide distribution of potentially harmful algal taxa from the upstream to the downstream end of the reservoirs agrees with the findings of Hallegraeff (1993), LIFEHAB (2001) and Van Dolah (2000), who reported that harmful algae taxa have increased worldwide, ranging in water from fresh to estuarine and marine and exhibiting enormous impacts on aquatic ecosystems (Smayda 1990). The study reservoirs, however, promoted the development of potentially harmful algal taxa present in very high densities, compared to the riverine stations.

Dinophysis sp., *Pseudo-Nitzschia* sp., *Gamberidiscus*, *Anabaena* sp. and *Nodularia spumigena* were encountered in the reservoirs, being known to cause discoloration, anoxic conditions and produce toxins that can accumulate in the food chain, causing toxicity to humans and other higher animals. *Dinophysis* sp. produces okadaic acid, for example, which causes diarrhoetic shellfish poisoning (DSP), a condition characterized by gastrointestinal tract symptoms (nausea, diarrhoea, vomiting, abdominal pain) that follow chronic exposure and that may evolve into digestive system tumours. *Pseudo-Nitzschia* sp. produces domoic acid, which causes amnesic shellfish poisoning (ASP), with signs of short-term memory loss accompanied by gastrointestinal tract and neurological symptoms. *Anabaena* sp. produces microcystin (Granéli & Hansen 2006), while cyanobacteria *Oscillatoria* sp. are known to produce debromoaplysia toxin (Pattanaik *et al.* 2010), which are highly inflammatory and potent skin tumour-promoting compounds.

CONCLUSIONS AND RECOMMENDATIONS

Tana River damming generally altered the river hydrology and the associated transport of materials, thereby resulting in habitat fragmentation, species isolation and reduced ecological heterogeneity. This situation has resulted in increased rates of extinction, proliferation and invasion in Masinga, Kamburu and Gitaru reservoirs.

The cascading reservoirs resulted in reduced phytoplankton diversity, evenness and richness. Whereas ecological recovery was observed downstream of the study reservoirs, it is noted that the exact point of recovery

was not ascertained in the present study. Thus, downstream ecological effects may have been experienced in the immediate downstream stretch affected by the reservoirs.

Even though no major impacts of harmful algae have been reported in the Tana River reservoirs, the presence of the various potentially harmful algal taxa in the study reservoirs is an indication of potential threat of future bloom occurrences, with the risks of biotoxin contamination in the expected scenarios of future increased reservoir construction, eutrophication and climate change.

There is an urgent need to devise ways through which the reported ecological impacts of reservoirs can be addressed. This observation is consistent with the growing need to preserve and restore aquatic and riparian biological diversity before extinction eliminates the opportunity (Kauffman *et al.* 1997). Such efforts are particularly important to seriously consider, even as the Government of Kenya plans to construct additional reservoirs in River Tana, including the proposed 1.5 billion euros High Grand Falls Reservoir.

ACKNOWLEDGEMENTS

REFERENCES

Akin-Oriola G. A. (2003) Zooplankton association and environmental factors in Ogunpa and Ona rivers, Nigeria. *Rev Biol Trop.* **51**, 391–8.

APHA (1975) Standard Methods for the Examination of Water and Wastewater, 12th edition. American Public health Association Inc. Washington DC New York.

APHA (1998) Standard Method for The Examination of Water and Waste-Water, 20th edn. American Public health Association Inc. Washington DC, New York.

Baranyi C., Hein T., Holarek C., Keckeis S. & Schiemer F. (2002) Zooplankton biomass and community structure in a Danube River floodplain system: effects of hydrology. *Freshwater Biol.* **47**, 473–82.

Barbosa F. A. R., Padisak J., Espindola E. L. G., Borics G. & Rocha O. (1999) The cascading reservoir continuum concept (CRCC) and its application to the river Tietê-Basin, São Paulo State, Brazil. In: Theoretical Reservoir Ecology and its Applications (eds J. G. Tundisi & M. Straskraba) pp. 425–37. Brazilian Academy of Sciences, International Institute of Ecology and Backhuys Publishers, Leiden, the Netherlands.

Basu B. K. & Pick F. R. (1996) Factors regulating phytoplankton and zooplankton biomass in temperate rivers. *Limnol. Oceanogr.* **41**, 1572–7.

Basu B. K. & Pick F. R. (1997) Phytoplankton and zooplankton development in a lowland river. *J. Plankton Res.* **19**, 237–53.

Boon P. J. (1992) Essential elements in the case for river conservation. In: River Conservation and Management (eds P. J. Boon, P. Calow & G. E. Petts) pp. 11–33. John Wiley & Sons Ltd, Wiley Chichester.

Bouillon S., Abril G., Borges A., Dehairs F., Govers G., Hughes H., Merckx R., Meysman F. J. R., Nyunja J., Osburn C. & Middelburg J. J. (2009) Distribution, origin and cycling of carbon in the Tana River (Kenya): a dry season basin-scale survey from headwaters to the delta. *Biogeosciences* **6**, 2475–2493.

Brown T., Schneider H. & Harper D. (1996) Multi-scale estimates of erosion and sediment yields in the upper Tana basin, Kenya. In: Erosion and Sediment yield: Global and Regional perspectives. Proceedings of the Exeter Symposium, July 1996 (eds D. E. Walling & B. W. Webb) pp. 49–54. IAHS Press, Wallingford, UK, IAHS Publ. 236.

Burns C. W. & Dodds A. (1999) Food limitation, predation, and allelopathy in a population of Daphnia carinata. *Hydrobiologia* **400**, 41–53.

Crawley M. J. (1986) The population biology of invaders. *Phil. Trans. R. Soc. B.* **314**, 711–29.

Danilov R. A. & Ekelund N. G. A. (1999) The efficiency of seven diversity and one similarity indices based on phytoplankton data for assessing the level of eutrophication in lakes of central Sweden. *Sci. Total Environ.* **234**, 15–23.

Davis M. A., Grime J. P. & Thompson K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* **88**, 528–34.

Dejenie T., Asmelash T., Meester L. *et al.* (2008) Limnological and ecological characteristics of tropical highland reservoirs in Tigray, Northern Ethiopia. *Hydrobiologia* **610**, 193–209.

Dejenie T., Declerck S. A. J., Asmelash T. *et al.* (2012) Cladoceran community composition in tropical semi-arid highland reservoirs in Tigray: a metacommunity perspective applied to young reservoirs. *Limnologica* **42**, 137–43.

Doak D. F., Bigger D., Harding E. K., Marvier M. A., O'Malley R. E. & Thomson D. (1998) The statistical averaging. *Am Nat.* **151**, 264–76.

Dürr H. H., Meybeck M., Hartmann J., Laruelle G. G. & Roubeix V. (2011) Global spatial distribution of natural riverine silica inputs to the coastal zone. *Biogeosci.* **8**, 597–620.

Egge J. K. & Aksnes D. L. (1992) Silicate as regulating nutrient in phytoplankton competition. *Mar. Ecol. Prog. Ser.* **83**, 281–9.

Elton C. S. (1958) The Ecology of Invasions by Animals and Plants. University of Chicago Press, Chicago, IL, USA.

Eppley R. W., Rogers J. N. & McCarthy J. J. (1969) Half-saturation constants for uptake of nitrate and ammonium by marine phytoplankton. *Limnol. Oceanogr.* **14**, 912–20.

Galloway G. E. (2000) Three centuries of river management along the Mississippi river: engineering and hydrological aspects. In: New Approaches to River Management (eds A. J. M. Smits, P. H. Nienhuis & R. S. E. W. Leuven) pp. 51–64. Backhuys Publishers, Leiden, the Netherlands.

Gao X., Zeng Y., Wang J. & Liu H. (2010) Immediate impacts of the second impoundment on fish communities in the Three Gorges Reservoir. *Environ. Biol. Fishes* **87**, 163–73.

Graf W. L. (2001) Damage control: restoring the physical integrity of America's rivers. *Ann. Assoc. Am. Geogr.* **91**, 1–27.

Granéli E. & Hansen P. (2006) Allelopathy in harmful algae: a mechanism to compete for resources? In: Ecology of Harmful Algae. Ecological Studies Series 189 (eds E. Granéli & J. T. Turner) pp. 189–201. Springer-Verlag, Berlin and Heidelberg, Germany.

Hallegraeff G. M. (1993) A review of harmful algal blooms and their apparent global increase. *Phycologia* **32**, 79–99.

Hanski I. (1999) Metapopulation Ecology. Oxford University Press, New York, NY, USA.

Havel J. E., Mabee W. R. & Jones J. R. (1995) Invasion of the exotic cladocerans Daphnia lumholtzi into North American reservoirs. *Can. J. Fish Aquat. Sci.* **52**, 151–60.

Herault B. & Honnay O. (2005) The relative importance of local, regional and historical factors determining the distribution of plants in fragmented riverine forests: an emergent group approach. *J. Biogeogr.* **32**, 2069–81.

Hudson J. J., Taylor W. D. & Schindler D. W. (1999) Planktonic nutrient regeneration and cycling efficiency in temperate lakes. *Nature* **400**, 659–61.

Jeje C. Y. & Fernando C. H. (1992) Zooplankton association in the middle Niger-Sokoto Basin (Nigeria- West Africa). *Int Revue ges. Hydrobiol.* **77**, 37–253.

Jorcin A. & Nogueira M. G. (2005) Phosphate distribution along a cascade of reservoirs (Paranapanema River, SE, Brazil). In: Phosphates in Sediments: Proceedings of the 4th International Symposium (eds L. Serrano & H. L. Golterman) pp. 77–86. Backhuys Publishers, Leiden, the Netherlands.

Karydis M. & Tsirtsis G. (1996) Ecological indices: a biometric approach for assessing eutrophication levels in the marine environment. *Sci. Total Environ.* **186**, 209–19.

Kauffman J. B., Beschta R. L., Otting N. & Lytjen D. (1997) An Ecological Perspective of Riparian and Stream Restoration in the Western United States. *Fisheries* **22**, 12–24.

Kennedy T. A., Naeem S., Howe K. M., Knops J. M. H., Tilman D. & Reich P. (2002) Biodiversity as a barrier to ecological invasion. *Nature* **417**, 636–8.

Kimmel B. L. & Groeger A. W. (1984) Factors controlling primary production in lakes and reservoirs: a perspective. Lake and Reservoir Management Report No. EPA440/584001, U.S. Environmental Protection Agency, Washington D.C. pp. 277–81.

Kiteresi L. I., Okuku E. O., Mwangi S. N. *et al.* (2012) The influence of land based activities on the phytoplankton communities of Shimoni-Vanga system. *Int. J. Environ. Res.* **6**, 151–62.

Kolar C. S. & Lodge D. M. (2000) Freshwater nonindigenous species: interactions with other global change. In: Invasion Species in a Changing World (eds H. A. Mooney & R. J. Hobbs) pp. 3–30. Island Press, Washington, DC, USA.

Kolar C. S. & Wahl D. H. (1998) Daphnid morphology deters fish predators. *Oecologia* **116**, 556–64.

Kotut K., Krienitz L. & Muthari M. (1998) Temporal changes in phytoplankton structure and composition at the Turkwel Gorge Reservoir, Kenya. *Hydrobiologia* **368**, 41–59.

Lepš J. & Šmilauer P. (2003) Multivariate Analysis of Ecological Data Using CANOCO. Cambridge University Press, Cambridge, UK.

LIFEHAB (2001) Life histories of microalgal species causing harmful blooms.Report of a European workshop organized jointly by the Fifth Framework Programme Energy, Environment and Sustainable Development of the European Commission, the Institut de Ciències del Mar, CMIMA-CSIC (Barcelona) and the Calvià Town Council (Majorca, Balearic Islands). Calvià, Majorca, Spain, October, p. 214.

Lodge D. M. (1993) Biological invasions: lessons for ecology. *Trends Ecol. Evol.* **8**, 133–7.

Madhu N. V., Jyothibabu R., Balachandran K. K. *et al.* (2007) Monsoonal impact on planktonic standing stock and abundance in a tropical estuary (Cochin backwaters- India). *Estuar. Coast. Shelf Sci.* **73**, 54–64.

Malmqvist B. & Rundle S. (2002) Threats to the running water ecosystems of the world. *Environ. Conserv.* **29**, 134–53.

Martin T. J. & Cyrus D. P. (1994) Zooplankton in the open water of Lake Cubhu, a freshwater coastal lake in Zululand, South Africa. *Water SA* **20**, 107–12.

McCarthy M. J., James R. T. & Chen Y. (2009) Nutrient ratios and phytoplankton community structure in the large, shallow, eutrophic, subtropical Lakes Okeechobee (Florida, USA) and Taihu (China). *Limnology* **10**, 215–27.

Melo S. & Huszar V. L. M. (2000) Phytoplankton in an Amazonian flood-plain lake (Lago Batata, Brasil): diel variation and species strategies. *J. Plankton Res.* **22**, 63–76.

Mineeva N. M., Litvinov A. S., Stepanova I. E. & Kochetkova M. Y. U. (2008) Chlorophyll content and factors affecting its spatial distribution in the Middle Volga reservoirs. *Inland Water Biol.* **1**, 64–72.

Morales-Baquero R., Conde-Porcuna J. M. & Cruz-Pizarro L. (1994) The zooplankton biomass and food availability in four reservoirs of contrasting trophic status. *Archiv Hydrobiol.* **40**, 161–73.

Naiman R. J. & Décamps H. (1997) The ecology of interfaces: riparian zones. *Ann. Rev. Ecol. Syst.* **28**, 621–58.

Naliato D. A. O., Nogueira M. G. & Perbiche-Neves G. (2009) Discharge pulses of hydroelectric dams and their effects in the downstream limnological conditions: a case study in a large tropical river (SE, Brazil). *Lakes Reserv. Res. Manage.* **14**, 301–14.

Naveh Z. & Liebermann J. (1994) From Biodiversity to ecodiversity. *Restoration Ecol.* **2**, 179–89.

Neary J., Cash K. & McCauley E. (1994) Behavioural aggregation of Daphnia pulex in response to food gradients. *Funct. Ecol.* **8**, 377–83.

Nogueira I. S., Nabout J. C., Ibañez M. S. R. & Bourgoin L. M. (2010) Determinants of beta diversity: the relative importance of environmental and spatial processes in structuring phytoplankton communities in an Amazonian floodplain. *Acta Limnologica Brasiliensia* **22**, 247–256.

Olden J. D. & Naiman R. J. (2010) Incorporating thermal regimes into environmental flows assessments: modifying dam operations to restore freshwater ecosystem integrity. *Freshwater Biol.* **55**, 86–107.

Orians G. H. (1986) Site characteristics favouring invasions. In: Ecology of Biological Invasions of North America and Hawaii (eds H. A. Mooney & J. A. Drake) pp. 133–48. Springer-Verlag, New York, NY, USA.

Pacini N., Harper D. & Mavuti K. (1999) Hydrological and ecological considerations in the management of a catchment controlled by a reservoir cascade: the Tana River, Kenya. In: The Sustainable Management of Tropical Catchments (eds D. M. Harper & T. Brown) pp. 239–58. John Wiley & Sons Ltd, New York.

Paerl H. W., Rossignol K. L., Hall S. N., Peierls B. L. & Wetz M. S. (2010) Phytoplankton community indicators of short- and long-term ecological change in the anthropogenically and climatically impacted Neuse River Estuary, NC, USA. *Estuaries Coasts* **33**, 485–97.

Parsons T., Maita Y. & Lally C. (1984) A Manual of Chemical and Biological Methods of Seawater Analysis. Pergamon Press, Oxford, UK, p. 173.

Pattanaik B., Wulff A., Roleda M. Y., Garde K. & Mohlin M. (2010) Production of the cyanotoxin nodularin- A multifactorial approach. *Harmful Algae.* **10**, 30–8.

Petr T. (1975) On some factors associated with the initial high fish catches in new African man-made lakes. *Arch. Hydrobiol.* **75**, 32–49.

Petts G. E. & Bradley C. (1997) Hydrological and ecological interactions within river corridors. In: Contemporary Hydrology: Towards Holistic Environmental Science (ed R. L. Wilby) pp. 241–71. Wiley, Chichester, UK.

Prenda J., Clavero M., Blanco-Garrido F., Menor A. & Hermosa V. (2006) Threats to the conservation of biotic integrity in Iberian fluvial ecosystems. *Limnética* **25**, 377–88.

Quiblier C., Leboulanger C. & Sane S. (2008) Phytoplankton growth control and risk of cyanobacterial blooms in the lower Senegal River delta region. *Water Res.* **42**, 1023–34.

Raven J. A. (1983) The transport and function of silicon in plants. *Biol. Rev.* **58**, 179–207.

Reckendorfer W., Keckeis H., Winkler G. & Schiemer F. (1999) Zooplankton abundance in the River Danube, Austria: the significance of inshore retention. *Freshwater Biol.* **41**, 583–91.

Reynolds C. S., Huszar V. L. M., Kruk C., Naselliflores L. & Melo S. (2002) Towards a functional classification of the freshwater phytoplankton. *J. Plankton Res.* **24**, 417–28.

Ricotta C. & Avena G. (2003) On the relationship between Pielou's evenness and landscape dominance within the context of Hill's diversity profiles. *Ecol. Ind.* **2**, 361–5.

Rocha O., Matsumura-Tundisi T., Espindola E. L. G., Roche K. F. & Rietzler A. C. (1999) Ecological theory

applied to reservoir zooplankton. In: Theoretical Reservoir Ecology and its Applications. International Institute of Ecology, Brazilian Academy of Sciences (eds J. G. Tundisi & M. Straskraba) pp. 29–51. Backhuys Publishers, Leiden, the Netherlands.

Ruckert G. V. & Giani A. (2008) Biological interactions in the plankton community of a tropical eutrophic reservoir: is the phytoplankton controlled by zooplankton? *J. Plankton Res.* **30**, 1157–68.

Shannon C. (1948) A mathematical theory of communication. *Bell Syst. Tech. J.* **27**, 379–423, 623–656.

Shigesada N. & Kawasaki K. (1997) Biological Invasions: Theory and Practice. Oxford University Press, New York, NY, USA.

Shurin J. B. & Havel J. E. (2002) Hydrologic connections and overland dispersal in an exotic freshwater crustacean. *Biol. Invasions* **4**, 431–9.

Smayda T. J. (1990) Novel and nuisance phytoplankton blooms in the sea: evidence for a global epidemic. In: Toxic Marine Phytoplankton (eds E. Granéli, B. Sundström, L. Edler & D. M. Anderson) pp. 29–40. Elsevier, New York, NY, USA.

Søballe D. M. & Kimmel B. L. (1987) A large-scale comparison of factors affecting phytoplankton abundance in rivers, lakes, and impoundments. *Ecology* **68**, 1943–54.

Sommer U., Padisak J., Reynolds C. S. & Juhasz Nagy. P. (1993) Hutchinson's heritage: the diversity disturbance relationships in phytoplankton. *Hydrobiologia* **249**, 1–7.

Stirling G. & Wilsey B. (2001) Empirical Relationships between Species Richness, Evenness, and Proportional Diversity. *Am. Nat.* **158**, 286–99.

Sullivan B. E., Prahl F. G., Small L. F. & Covert P. A. (2001) Seasonality of phytoplankton production in the Columbia River: a natural or anthropogenic pattern? *Geochim. Cosmochim. Acta* **65**, 1125–39.

Syvitski J. P. M., Vörösmarty C. J., Kettner A. J. & Green P. (2005) Impact of humans on the flux of terrestrial sediment to the global coastal ocean. *Science* **308**, 376–80.

Tamooh F., Van den Meersche K., Meysman F. *et al.* (2012) Distribution and origin of suspended matter and organic carbon pools in the Tana River Basin, Kenya. *Biogeosciences* **9**, 2905–20.

Thornton K. W. (1990) Perspectives in reservoir limnology. In: Reservoir Limnology: Ecological Perspectives (eds K. W. Thornton, B. L. Kimmel & F. E. Payne) pp. 1–13. Wiley, New York, NY, USA.

Thorp J. P., Black A. R. & Haag K. H. (1994) Zooplankton assemblages in the Ohio River. Seasonal, tributary,

and navigation dam effects. *Can. J. Fish. Aquat. Sci.* **51**, 1634–43.

Tillman D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* **80**, 1455–9.

Tollrian R. & Dodson S. I. (1999) Inducible defences in Cladocera. In: The Ecology and Evolution of Inducible Defences (eds R. Tollrian & C. D. Harvell) pp. 177–202. Princeton University Press, Princeton, NJ, USA.

TSS (Threatened Species Section) (2006) Recovery Plan: Tasmanian Galaxiidae 2006–2010. Threatened Species Section, Department of Primary TSS.

Uku J. N. & Mavuti K. M. (1994) Comparative limnology, species diversity and biomass relationships of zooplankton and phytoplankton in five freshwater lakes in Kenya. *Hydrobiologia* **272**, 251–8.

Üthermöhl H. (1958) Zur Vervollkommnung der quantitativen Phytoplankton Methodiek. Mitteilung Internationale Vereinigung fuer Theoretische unde Amgewandte Limnologie. Washington D.C. 9, (1–38). pp. 1213.

Van Dolah F. M. (2000) Diversity of marine and freshwater algal toxins. In: Seafood and Freshwater Toxins: Pharmacology, Physiology, and Detection (ed L. M. Botana) pp. 19–43. Dekker, New York, NY, USA.

Viner A. B. (1969) Observation of the hydrobiology of the Volta Lake April 1965-April 1966. In: Manmade Lakes (ed L. Obeng) pp. 195–203. The Accra Symposium 1966, Ghana University Press, Accra.

Vörösmarty C. J., Douglas E. M., Green P. A. & Revenga C. (2005) Geospatial indicators of emerging water stress: an application to Africa. *Ambio* **34**, 230–6.

Ward J. V. & Stanford J. A. (1995) Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation. *Regul. Rivers* **11**, 105–19.

Ward J. V., Tockner K., Edwards P. J. *et al.* (1999) A reference river system for the Alps: the 'Fiume Tagliamento'. *Regul. Rivers. Res. Manage.* **15**, 63–75.

WCD, World Commission on Dams (2000) Dams and Development, A New Framework for Decision Making. Earthscan, London, UK.

Wehr J. D. & Descy J. P. (1998) Use of phytoplankton in large river management. *J. Phycol.* **34**, 741–9.

Wetzel R. G. (2001) Limnology, 3rd edn. Academic Press, CA, USA.

Wood R. B. & Talling J. F. (1988) Chemical and algal relationships in a salinity series of Ethiopian inland waters. *Hydrobiologia* **158**, 29–67.

Yajnik K. S. & Sharada M. K. (2003) Ammonium inhibition of nitrate uptake by phytoplankton: a new relation based on similarity and hyperbolicity. *Curr. Sci.* **85**, 1180–9.