Strong effects of occasional drying on subsequent water clarity and cyanobacterial blooms in cool tropical reservoirs

MEKONEN TEFERI*,†, STEVEN A. J. DECLERCK†, TOM DE BIE*, PIETER LEMMENS*, ABRAHA GEBREKIDAN§,¶, TSEHAYE ASMELASH**, TADESSE DEJENIE†, KINDEYA GEBREHIWOT††, HANS BAUER‡‡, JOZEF A. DECKERS§§, JOS SNOEKS¶¶, JOS SNOEKS*** AND LUC DE MEESTER*

*Laboratory of Aquatic Ecology, Evolution and Conservation, KU Leuven, Leuven, Belgium
†Department of Biology, Mekelle University, Mekelle, Ethiopia
‡Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, the Netherlands
§Department of Chemistry, Mekelle University, Mekelle, Ethiopia
¶Department of Chemical Engineering, Process Engineering for Sustainable Systems, KU Leuven, Heverlee, Belgium
**Department of Microbiology, Mekelle University, Mekelle, Ethiopia
††Department of Land Resource Management and Environmental Protection, Mekelle University, Mekelle, Ethiopia
‡‡WildCRU, University of Oxford, Tubney House, U.K.
§§Division of Soil and Water Management, KU Leuven, Leuven, Belgium
***Laboratory of Biodiversity and Evolutionary Genomics, KU Leuven, Leuven, Belgium

SUMMARY

1. In semi-arid regions, the construction of small reservoirs is important in alleviating water shortage, although many have poor water quality with high turbidity and dense blooms of algae and cyanobacteria, and there are large differences in the ecology of such reservoirs.
2. We took advantage of two exceptionally dry years in northern Ethiopia to study the effect of a dry period and the associated fish kills on reservoir ecology and water quality. We studied 13 reservoirs, seven of which dried up in 2009. Four of the latter dried up again in 2010. We monitored the ecology of these reservoirs from 2009 to 2011, hypothesising that the pattern of reservoir drying would explain ecological differences among them.
3. Reservoirs that refilled after drying had a significantly lower fish biomass, lower biomass of phytoplankton (expressed as chlorophyll-a) and cyanobacteria (Microcystis), clearer water, greater macrophyte cover and lower nutrient concentrations than reservoirs that did not dry. Although the differences in water quality were most striking in the wet season after a drying event, there were persistent effects on reservoir ecology. The three categories of reservoirs we distinguished, based on their behaviour in 2009 and 2010, also showed differences in 2004, a year during which none of the reservoirs dried out. While drying evidently results in better water quality, we could not disentangle the effects of drying per se from that of reductions in fish biomass. The total combined effect was highly significant in all 3 years, whereas the separate effects of drying and loss of fish were only significant in 2004.
4. Our results suggest that differences in water quality and ecology among reservoirs depend on their propensity to dry out. Drying might be used as a restoration measure to reduce potentially harmful cyanobacterial blooms in reservoirs.

Keywords: Ethiopia, fish biomass, Microcystis, reservoir ecology, water clarity
Introduction

Reservoirs are large, man-made impoundments of water, usually constructed where natural freshwater bodies are rare or where the water available is unsuitable for human use (Lowe-McConnell, 1966; Wetzel, 2001). These water-bodies are constructed worldwide for a variety of purposes, mostly for irrigation, flood control, household use, watering of livestock or hydropower. Most reservoirs in semi-arid regions are shallow and show wide fluctuations in water level (Gasse, 2000; Vallet-Coulomb et al., 2001; Coops, Beklioglu & Crisman, 2003; Naselli-Flores & Barone, 2005; Beklioglu, Altinayar & Tan, 2006; Özen et al., 2010; Bucak et al., 2012). Seasonal fluctuations in water level are generally larger in reservoirs than in natural lakes. Despite their importance, many reservoirs are poorly managed and suffer from a wide range of problems, such as excessive algal blooms, toxic cyanobacteria, turbidity, exotic species and increased salinity (Holden, Jones & Taggart, 2001). Toxic cyanobacterial blooms in eutrophic waters (Codd, Ward & Bell, 1997; Chorus & Bertram, 1999; Graham, 2007) can cause health hazards to animals and humans (Bell & Codd, 1994; Codd et al., 1997; Codd, Metcalf & Beattie, 1999). Understanding the mechanisms that determine water quality and the occurrence of cyanobacterial blooms in reservoirs is, therefore, of crucial importance for management.

Much research has been carried out on the restoration of eutrophic lakes (Scheffer, 1998; Moss, 2010). Reduction in external nutrient inputs is often not sufficient to restore water clarity in shallow lakes and reservoirs. Additional measures are needed, such as biomanipulation of the fish assemblage, removal of sediments or lake drawdown (Jeppesen et al., 2005, 2012; Van Wichelen et al., 2007). Several studies in temperate regions have shown that complete drying of waterbodies may be a powerful management tool in shallow lakes (Van Geest et al., 2005). A complete drawdown results in a consolidation of the lake sediment and nutrient loss due to permanent sedimentation (James et al., 2001; Sondergaard, Jensen & Jeppesen, 2003). A complete drawdown also facilitates control of fish biomass and removal of accumulated sediments (Scheffer, 1998; Jeppesen et al., 2012). Benthivorous fish are a key cause of turbidity in shallow lakes as they stir up the sediment during feeding (Havens, 1993; Horppila et al., 1998; Scheffer, Portielje & Zambrano, 2003). In contrast to the large body of literature on lake management in temperate regions, very little is known about how reservoir drying affects the ecology of reservoirs in the tropics and subtropics (Jeppesen et al., 2012).

In the semi-arid highland region of Tigray, North Ethiopia, more than 70 small reservoirs with a surface area between two and 50 hectares have been constructed over the last three decades (Haregeweyn et al., 2006; Dejenie et al., 2008). Due to severe soil erosion caused by land degradation (Nyssen et al., 2005), excessive nutrient loads are associated with sediment influx to these reservoirs (De Wit, 2003; Haregeweyn et al., 2006). Thus, Dejenie et al. (2008) surveyed 32 reservoirs in Tigray and found that many had high nutrient concentrations, high phytoplanктон biomass, low water transparency and no or only a poorly developed vegetation of submerged macrophytes. Cyanobacteria blooms (mainly Microcystis) are frequent (Dejenie et al., 2008; Van Grembergh et al., 2011) in these reservoirs. Daphnia are generally rare in the tropics (Chiambeng & Dumont, 2005), but they do occur in fishless lakes (Iglesias et al., 2011), at higher altitudes (Mergeay et al., 2006), and they also occur in the reservoirs of the Ethiopian highlands (Dejenie et al., 2008, 2012). With the exception of introduced Tilapia (Oreochromis niloticus or Tilapia zillii) in a few locations, fish assemblages in the northern Ethiopian reservoirs are composed exclusively of species of the riverine Cyprinid Garra. This genus is widespread in rivers and lakes of Asia and Africa (Getahun & Stiasny, 1998; Tudorancea & Taylor, 2002; Zhou, Pan & Kottelat, 2005). Large populations of Garra are found in many reservoirs in Tigray, probably as the result of high nutrient loading and the absence of piscivorous fish (Dejenie et al., 2008; Teferi et al., 2013). Many tropical and warm subtropical lake systems are indeed characterised by a very high abundance of small fish (Meerhoff et al., 2007; Teixeira-de Mello et al., 2009).

High densities of benthivorous fish can increase nutrient availability and lead to phytoplankton blooms through excretion and resuspension of sediments (Scheffer, 1998; Teixeira-de Mello et al., 2009; Jeppesen et al., 2012). Indeed, Dejenie et al. (2008) found that the biomass of Garra was associated with high concentration of phosphorus in Ethiopian reservoirs. In enclosures with Garra, they also found more nutrients and higher biomass of phytoplankton and zooplankton in the water column, and higher amounts of suspended matter than in fishless enclosures (Dejenie et al., 2009), suggesting that Garra may increase primary production indirectly through bottom-up effects. Garra could also increase phytoplankton biomass by exerting a top-down effect on Daphnia (Dejenie et al., 2009).

In this study, we took advantage of a natural whole-reservoir experiment caused by two consecutive exceptionally dry years in Tigray. A poor rainy season in
2008, followed by an extended dry period, resulted in a substantial number of reservoirs in the highlands of Tigray drying completely in April–June 2009, and some went dry again in April–June 2010. We took this opportunity to test for the effects of a reservoir drying out for a limited period, and the associated fish kills, by comparing temporal ecological changes between reservoirs that dried out and those that remained wet in April–June 2009 and 2010. We hypothesised that reservoir drying would improve water quality and reduce cyanobacterial blooms in tropical reservoirs.

Methods

Study area and design

Tigray is in the northern Ethiopian highlands between 12° and 15°N and between 37°10’E and 40°10’E (see Figure S1 in Supporting Information). It belongs to the African dry lands, often referred to as Sudano-Saharan region (Warren & Khogali, 1992). The climate is cool tropical continental, with an extended dry season of nine to 10 months and a maximum effective rainy season of 50–60 days in July–August (HTS, 1976). Average annual rainfall in Tigray is between 450 and 980 mm (data from National Meteorology office, Mekelle branch; Lemma, 1996).

We selected 13 reservoirs that were a subset of the 32 previously studied by Dejenie et al. (2008) and represent both reservoirs that did and did not dry up in 2009 and 2010, two exceptionally dry years. We distinguished three categories: reservoirs that dried up in both 2009 and 2010, reservoirs that dried up only in 2009 and reservoirs that did not dry up during the study period (Fig. 1; Table 1). All reservoirs studied were visited regularly in the period 2003–2011, and none dried in the period from 2003 till 2008. All reservoirs lose water due to evaporation; the fact that some dried up completely and others did not was in part due to differences in water withdrawal for irrigation purposes.

Sample collection and processing

All reservoirs were sampled in September 2009, 2010 and 2011, when the reservoirs were at full capacity. Sampling took place between 10 and 25 September, that is, just after the rainy season, and between 9:00 a.m. and 12:00 a.m. On each sampling occasion and for each reservoir, we measured a range of morphometrical, regional and local ecological characteristics. The morphometric and regional characteristics measured were surface area, depth, altitude and reservoir age. Abiotic environmental variables measured were Secchi depth, pH, oxygen, nutrient concentrations (total phosphorus and total nitrogen), suspended matter, conductivity and temperature. In addition, we quantified a number of biotic variables related to regime shifts between the turbid and the clear-water state in shallow lakes (Scheffer et al., 2003): vegetation cover, fish biomass, phytoplankton biomass (as chlorophyll-a concen-
Table 1  Drying history and classification of the studied reservoirs. N represents reservoirs that did not dry up at the end of the dry season (April–June) of a given year; D represents reservoirs that dried up completely in the given year. Reservoirs are allocated to one of three categories based on whether they dried up in 2009 and 2010.

<table>
<thead>
<tr>
<th>Reservoir name</th>
<th>Coordinates</th>
<th>Drying history April–June 2009</th>
<th>Drying history April–June 2010</th>
<th>Categories</th>
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</thead>
<tbody>
<tr>
<td>Adi Asmee</td>
<td>38.96</td>
<td>N</td>
<td>N</td>
<td>‘Permanent in study period’ (n = 6)</td>
</tr>
<tr>
<td>Bokoro</td>
<td>39.57</td>
<td>N</td>
<td>N</td>
<td></td>
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<tr>
<td>Era Quihila</td>
<td>39.60</td>
<td>N</td>
<td>N</td>
<td></td>
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<tr>
<td>Gereb Awso</td>
<td>39.56</td>
<td>N</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>Ruba Feleg</td>
<td>39.73</td>
<td>N</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>Tsinkanet</td>
<td>39.54</td>
<td>N</td>
<td>N</td>
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</tr>
<tr>
<td>Dur Ambesa</td>
<td>39.44</td>
<td>D</td>
<td>N</td>
<td>‘Only dry in 2009’ (n = 3)</td>
</tr>
<tr>
<td>Gereb Beati</td>
<td>39.48</td>
<td>D</td>
<td>N</td>
<td></td>
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<tr>
<td>Shilanat IV</td>
<td>39.54</td>
<td>D</td>
<td>D</td>
<td>‘Dry in 2009 and 2010’ (n = 4)</td>
</tr>
<tr>
<td>Gereb Mihiz</td>
<td>39.47</td>
<td>D</td>
<td>D</td>
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<tr>
<td>Gum Selasa</td>
<td>39.54</td>
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<td>D</td>
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<tr>
<td>Mai Gassa I</td>
<td>39.49</td>
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<tr>
<td>Mai Gassa II</td>
<td>39.49</td>
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Drying had a profound impact on the ecology of the reservoirs. RDA performed on the entire set of local environmental conditions showed a strong effect in each of the years studied. The proportion of total variation in these variables explained by drying was 33.8\% ($F$-ratio = 2.558, $P$ = 0.009) in 2009, 40.5\% ($F$-ratio = 3.409, $P$ = 0.006) in 2010; dry only in 2009; no drying) did not differ in any of the morphometric and regional variables measured, except for surface area (see Table S1; Figure S2). The reservoirs that were more likely to dry were generally large, because large reservoirs are used more intensively for irrigation.

The three categories of reservoirs (dry in both 2009 and 2010; dry only in 2009; no drying) did not differ in any of the morphometric and regional variables measured, except for surface area (see Table S1; Figure S2). The reservoirs that were more likely to dry were generally large, because large reservoirs are used more intensively for irrigation.

Recolonisation of reservoirs by fish following drying

Reservoirs that dried out naturally became fishless. The reservoirs refilled during July and August, mainly by surface run-off. Of the seven reservoirs that dried during the dry period in 2009, three were recolonised by fish immediately upon refilling in August 2009 (Fig. 1). Of the remaining four reservoirs, two had been recolonised by December 2009 and one by March 2010. One reservoir (Gum Selasa) remained fishless for an entire year (Fig. 1; see also Table 1). During the dry period of 2010, four reservoirs dried up again for a second time, fish recolonising them within 1–2 months of their refilling, except again for Gum Selasa, where we caught no fish until December 2010.

Impact of drying on reservoir characteristics: 2009–2011

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To test whether drying influenced limnological and ecological characteristics of the reservoirs, we took both a multivariate and a univariate approach. First, we applied standardised redundancy analysis (RDA) to the entire set of measured variables to test for any systematic differentiation between the three categories of reservoirs (Leps & Smilauer, 2003; Legendre & Legendre, 2012). We used standardised principal component analysis (PCA) to explore visually patterns of associations among variables and between variables and the drying categories. All these analyses were carried out for each sampling year separately to evaluate the consistency of patterns across years. In addition to the multivariate analysis, we studied the detailed response of each variable to the drying regimes with one-way ANOVAs testing for an effect of drying regime (never dry, sometimes dry and regularly dry) on each of the variables separately.

In addition to the sampling campaigns of 2009, 2010 and 2011, we also analysed the data obtained for the same 13 reservoirs in September 2004. The 2004 data are a subset of the data analysed by Dejenie et al. (2008). The sampling protocols in this study were identical to those applied in this study. Given that none of the reservoirs dried out in the 2 years preceding September 2004, this analysis provided us with a longer-term perspective on the influence of previous drying on the ecology of the reservoirs in periods when no such drying occurred. In addition, given that there was a 5- to 7-year time period between this first and the current sampling campaigns, the combined data also provided some insight into the stability of the ecological characteristics of the reservoirs as characterised by their propensity to dry out.

The effects of drying may result from the associated fish kills that can potentially have strong effects on the ecology of reservoirs, because of their role in the aquatic food web and their impact on sediment resuspension and internal eutrophication. Drying could, however, also have effects independent of those of fish. We carried out a variation partitioning analysis using partial RDA (Peres-Neto et al., 2006) to decompose total variation in environmental variables into a purely fish-related component, a purely drying-related component, a component representing the combined effects of both, and the remaining unexplained variation.

Prior to analyses, we log-transformed all environmental variables except pH. RDAs were carried out with CANOCO v4.5, and the significance of the models was tested with 999 Monte Carlo permutations (reduced model). Partial RDA for variation partitioning was performed in R v2.8.1; R Development Core Team 2008, using the RDA and VARPART functions of the vegan library (Oksanen, 2005; Peres-Neto et al., 2006). ANOVA and Tukey’s post hoc comparisons were performed using the statistical software package STATISTICA 11 (StatSoft, Inc., Tulsa, OK, U.S.A.).

Results

Recolonisation of reservoirs by fish following drying

Reservoirs that dried out naturally became fishless. The reservoirs refilled during July and August, mainly by surface run-off. Of the seven reservoirs that dried during the dry period in 2009, three were recolonised by fish immediately upon refilling in August 2009 (Fig. 1). Of the remaining four reservoirs, two had been recolonised by December 2009 and one by March 2010. One reservoir (Gum Selasa) remained fishless for an entire year (Fig. 1; see also Table 1). During the dry period of 2010, four reservoirs dried up again for a second time, fish recolonising them within 1–2 months of their refilling, except again for Gum Selasa, where we caught no fish until December 2010.
\( P = 0.002 \) in 2010 and 37.9\% \( (F \text{-ratio} = 3.048, \, P = 0.006) \) in 2011 (Table S2). PCA also showed consistent differences among the three reservoir categories across years. PCA1 always showed high eigenvalues \( (39.5\%, \, 40.7\% \text{ and } 42.4\% \text{ in } 2009, \, 2010 \text{ and } 2011, \text{ respectively}) \) and in all 3 years reflected a gradient from drying reservoirs with few or no fish, relatively high macrophyte cover and high transparency to permanent reservoirs with abundant fish, phytoplankton and Microcystis biomass and high TP and suspended material (Fig. 2). Zooplankton and Daphnia biomass rather tended to show no or only a weak association with this gradient. From the PCA, it is also clear that reservoirs that fell dry only in 2009 showed intermediate characteristics to the reservoirs that did not dry out and the reservoirs that dried in both years (Fig. 2).

Detailed ANOVAs followed by Tukey post hoc comparisons performed on individual key variables revealed that, in each of the three consecutive years, permanent reservoirs had a significantly higher fish biomass, total phytoplankton biomass (chlorophyll-a), Microcystis biomass, total phosphorus and suspended matter concentration than reservoirs that dried out once (2009) or twice (2009 and 2010) (Fig. 3; Table 2). Although also pronounced, patterns tended to be somewhat more complex and variable through time for macrophyte cover and Secchi depth (Fig. 3). Just after the first drying in 2009, macrophyte cover and water transparency were substantially higher

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**Fig. 2** Triplot of standardised PCA on the data for environmental variables of reservoirs that did not dry out in 2009–2010 (filled circles), dried only in 2009 (filled squares) or dried in both 2009 and 2010 (filled diamonds), separately for the sampling campaigns of September 2009, 2010 and 2011, and for the data of 2004 (Dejenie et al., 2008). Reservoir names are given in abbreviations: for example, Adi Asme’e: AAs; Bokoro: BOK (for full names of reservoirs, see Table 1). Filled down-pointing triangles represent centroids and show the average position of each category of reservoirs.

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in the reservoirs that had fallen dry than in the permanent systems. During the year of the second drought (2010) and in the subsequent year (2011), however, a clear differentiation occurred between reservoirs that had only fallen dry once and reservoirs that fell dry twice consecutively, the latter being characterised by much higher macrophyte cover and water transparency, whereas the former shifted back to a situation similar to permanent reservoirs (Fig. 3; Table 2). The reservoirs that dried out only in 2009 generally showed intermediate characteristics to those that fell...
Table 2 ANOVA results for the effect of reservoir categories (reservoirs that did not dry out in 2009 nor in 2010; reservoirs that dried out only in 2009; reservoirs that dried out in both 2009 and 2010) on the abiotic and biotic ecological characteristics of the studied reservoirs. The effect of drying was tested for the biomass of fish, *Microcystis*, total zooplankton and *Daphnia*, percentage macrophyte cover, chlorophyll-a (Chl-a) concentration, total phosphorus (TP), total nitrogen (TN), suspended matter (SM), Secchi depth, dissolved oxygen, temperature, pH and conductivity. All environmental variables were measured during the sampling campaigns of September 2009, 2010 and 2011. In addition, we also analysed the data collected in September 2004 by Dejenie *et al.* (2008). All variables except pH were log-transformed.

|-------------------------------------|------------|------------|------------|------------|      |           |           |           |           |      |           |           |           |           |      |           |           |           |           |      |
| Fish biomass (g; LOG)               | 2          | 37.16      | 18.58      | 19.32      | 0.0003 | 2          | 20.28      | 10.14      | 11.08      | 0.002 | 2          | 4.55       | 2.27       | 9.93       | 0.004 | 2          | 3.12       | 1.56       | 4.60       | 0.038 |
| *Microcystis* biomass (µg C L⁻¹; LOG) | 2          | 69.79      | 34.89      | 8.51       | 0.006  | 2          | 37.63      | 18.81      | 6.26       | 0.017 | 2          | 46.14      | 23.07      | 7.03       | 0.012 | 2          | 0.23       | 0.11       | 1.48       | 0.270 |
| Chlorophyll-a biomass (µg L⁻¹; LOG) | 2          | 1.90       | 0.95       | 9.079      | 0.005  | 2          | 1.00       | 0.50       | 10.72      | 0.003 | 2          | 0.92       | 0.46       | 5.74       | 0.021 | 2          | 0.38       | 0.19       | 4.79       | 0.058 |
| Total zooplankton biomass (µg L⁻¹; LOG) | 2          | 0.28       | 0.14       | 0.50       | 0.621  | 2          | 0.82       | 0.41       | 0.47       | 0.634 | 2          | 0.024      | 0.012      | 0.051      | 0.949 | 2          | 0.87       | 0.43       | 3.89       | 0.056 |
| Daphnia biomass (µg L⁻¹; LOG)       | 2          | 0.11       | 0.05       | 0.25       | 0.789  | 2          | 1.00       | 0.50       | 1.82       | 0.211 | 2          | 0.11       | 0.06       | 0.28       | 0.759 | 2          | 1.40       | 0.70       | 2.29       | 0.151 |
| Macrophyte cover (%) ; LOG          | 2          | 0.24       | 0.12       | 3.23       | 0.044  | 2          | 4.38       | 2.19       | 6.10       | 0.018 | 2          | 4.87       | 2.43       | 8.96       | 0.005 | 2          | 0.24       | 0.12       | 3.23       | 0.082 |
| Secchi disc (m; LOG)                | 2          | 0.10       | 0.05       | 4.39       | 0.040  | 2          | 0.041      | 0.020      | 4.66       | 0.036 | 2          | 0.26       | 0.13       | 5.95       | 0.019 | 2          | 0.007      | 0.003      | 0.60       | 0.564 |
| TP concentration (µg L⁻¹; LOG)       | 2          | 0.99       | 0.50       | 5.50       | 0.024  | 2          | 0.66       | 0.33       | 5.95       | 0.019 | 2          | 0.87       | 0.43       | 6.25       | 0.017 | 2          | 0.44       | 0.22       | 3.55       | 0.068 |
| TN concentration (µg L⁻¹; LOG)       | 2          | 1.83       | 0.91       | 1.09       | 0.372  | 2          | 2.51       | 1.25       | 1.51       | 0.267 | 2          | 0.15       | 0.07       | 0.93       | 0.425 | 2          | 0.07       | 0.03       | 1.51       | 0.265 |
| Suspended matter (µg L⁻¹; LOG)       | 2          | 1.58       | 0.79       | 4.98       | 0.031  | 2          | 0.89       | 0.44       | 5.59       | 0.023 | 2          | 0.86       | 0.43       | 10.81      | 0.003 | 2          | 0.29       | 0.14       | 3.82       | 0.058 |
| Dissolved oxygen (mg L⁻¹; LOG)       | 2          | 0.012      | 0.006      | 2.447      | 0.136  | 2          | 0.04       | 0.02       | 12.12      | 0.002 | 2          | 0.017      | 0.008      | 4.96       | 0.031 | 2          | 0.01       | 0.008      | 1.05       | 0.283 |
| Temperature (°C; LOG)               | 2          | 0.005      | 0.002      | 2.22       | 0.159  | 2          | 0.006      | 0.003      | 1.736      | 0.225 | 2          | 0.001      | 0.0009     | 1.011      | 0.398 | 2          | 0.003      | 0.001      | 1.103      | 0.369 |
| pH                                  | 2          | 0.302      | 0.151      | 0.362      | 0.704  | 2          | 0.248      | 0.124      | 0.506      | 0.617 | 2          | 0.138      | 0.069      | 0.298      | 0.748 | 2          | 2.344      | 1.72       | 6.441      | 0.015 |
| Conductivity (µS L⁻¹; LOG)          | 2          | 0.044      | 0.022      | 0.889      | 0.441  | 2          | 0.037      | 0.018      | 0.535      | 0.601 | 2          | 0.017      | 0.008      | 1.124      | 0.362 | 2          | 0.137      | 0.068      | 2.547      | 0.127 |
dry in both 2009 and 2010 and the reservoirs that did not dry at all (Fig. 3). Overall, zooplankton and *Daphnia* biomass did not differ strongly between reservoir categories.

**Longer-term impact of the propensity to dry: data from 2004**

The propensity to dry was also found to be associated with reservoir characteristics even in the absence of recent drying. According to an RDA, the difference in ecological variables measured in 2004 (Table S2) from 13 reservoirs that had not dried out for at least 2 years can be explained by categories defined in 2009/2010 (Table 1). Ecological gradients between the drying and permanent categories also show similarity with the patterns observed for 2009–2011 (Fig. 2), although there are some minor differences. For the period 2009–2011, the pattern is very consistent, with reservoirs experiencing drying having clear water, high oxygen concentration and abundant macrophytes, whereas permanent reservoirs had a high biomass of fish, *Microcystis* and chlorophyll-a as well as high total phosphorus and suspended matter. In 2004, the pattern was similar for most variables, except for *Microcystis* biomass and oxygen, which did not seem to be associated with probability of drying. Furthermore, during 2004, total zooplankton biomass was relatively high in permanent reservoirs.

**The role of fish versus general effects of drying**

We quantified the unique contribution of drying and fish biomass on variation in environmental characteristics using a variation partitioning following RDA (Table 3; Fig. 4). The total combined variation explained by both fish and drying was highly significant in all study years, whereas the unique effects of drying and fish were not significant in any of the three study years, except 2004.

**Discussion**

Our results strongly suggest that the propensity to dry out has important consequences for water quality of reservoirs in the semi-arid regions of the cool tropics. This has implications for both our understanding of reservoir ecology in semi-arid regions as well as for reservoir management.

**Impact of drying on reservoir ecology**

Complete drying affected key ecological characteristics of the study reservoirs, resulting in lower nutrient availability and phytoplankton, *Microcystis* and fish biomass, and increased vegetation cover and water transparency. Reservoir drying thus leads to an overall increase in water quality. These observations are generally similar to those observed in temperate regions (Scheffer, 1998; Van Geest *et al.*, 2005; Jeppesen *et al.*, 2012). The observed differences in ecological characteristics of the reservoirs were generally associated with drying and not with any other particular morphometric or local characteristic of the reservoirs (such as altitude, average depth or age). The reservoir categories differed in surface area, with larger areas being more likely to dry out (because they are more often used for irrigation). The characteristics of the reservoirs that dried out (low fish and phytoplankton biomass, higher transparency) are not typical for large compared with small reservoirs, so it is safe to conclude that it is drying, not surface area, which is the underlying cause of the observed differences. Interestingly, two consecutive dry years created a longer-lasting effect on macrophytes and transparency than a single event. Whereas macrophyte cover and water clarity resembled that in permanent reservoirs within 1 year of the first drying event in those reservoirs that dried only in 2009, the reservoirs that fell dry twice still showed a greater coverage of macro-

**Table 3** Result of variation partitioning following redundancy analysis testing for the relative importance of reservoir drying and fish biomass on ecological characteristics of the 13 reservoirs studied in 2009, 2010 and 2011. Data from 2004 from Dejenie *et al.* (2008) are also shown.

<table>
<thead>
<tr>
<th>Explanatory variable</th>
<th>2009</th>
<th>2010</th>
<th>2011</th>
<th>2004</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish effect</td>
<td>1</td>
<td>0.489</td>
<td>0.001**</td>
<td>1</td>
</tr>
<tr>
<td>Drying effect</td>
<td>2</td>
<td>0.451</td>
<td>0.007**</td>
<td>2</td>
</tr>
<tr>
<td>Fish + drying effect</td>
<td>3</td>
<td>0.468</td>
<td>0.010*</td>
<td>3</td>
</tr>
<tr>
<td>Pure fish effect</td>
<td>1</td>
<td>0.017</td>
<td>0.238NS</td>
<td>1</td>
</tr>
<tr>
<td>Common effect</td>
<td>0</td>
<td>0.471</td>
<td>NT</td>
<td>0</td>
</tr>
<tr>
<td>Pure drying effect</td>
<td>2</td>
<td>0.020</td>
<td>0.543NS</td>
<td>2</td>
</tr>
</tbody>
</table>

NT, non-testable; NS, non-significant, *significant at $P < 0.05$, **highly significant at $P < 0.01$. 

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phytes and had clearer water than permanent reservoirs in 2011. Importantly, our data not only suggest that drying affects water quality in reservoirs, but show that the propensity to drying has longer-term consequences for the ecology of the reservoirs. This is most clearly seen in the principal component analysis where, in all four sampling campaigns, reservoirs belonging to the same categories cluster together (Fig. 2). This is intriguing because the reservoir categories are identified based on the behaviour of the reservoirs in both 2009 and 2010. While it might be intuitive that the three categories of reservoirs show different ecological characteristics in 2010 and, if the effect of drying persists for more than 1 year, in 2011, the fact that the same pattern was observed in 2009 and 2004 is more striking. Because all reservoirs have been regularly visited since 2002, we know that none of them fell dry in the 2 years preceding the sampling campaign of 2004. Similarly, none of the reservoirs fell dry in the period 2004–2008. The droughts of 2009 and 2010 were indeed exceptional for this region. In 2009, the reservoirs that fell dry only in 2009 differed from those that also dried in 2010 in both fish and Microcystis biomass (Fig. 3). This pattern is similar to that observed in 2010. While the pattern is easy to explain in 2010, the observations of 2009 pre-date the second dry period (2010), suggesting that the reservoirs differ also in the long term. For 2004, the ANOVAs indicate that the major differences are among the permanent reservoirs and the reservoirs that showed one or two dry periods in 2009–2010. This is the case for fish and zooplankton biomass, and also to some degree for the amount of suspended matter. While statistically insignificant, Fig. 3 also shows gradual changes in some environmental variables (e.g. Microcystis biomass, TN, TP, chlorophyll-a) between permanent reservoirs and those that dried out once or twice. This also explains why the multivariate analysis (Fig. 3) showed a clear gradient in ecological characteristics with increasing propensity for drying. The propensity to dry thus seems to affect the ecology of the reservoirs over the longer term.

While, in general, the differences between reservoir categories in 2004 were similar, even if reduced, to those observed in 2009–2011, the patterns of Microcystis and zooplankton/Daphnia biomass are noteworthy excep-

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**Fig. 4** Result of variation partitioning following redundancy analysis testing for the relative importance of reservoir dry-stand and fish biomass on ecological characteristics of the 13 study reservoirs in 2009–2011 and data of 2004. NT, non-testable; NS, non-significant, * significant at $P < 0.05$, ** highly significant at $P < 0.01$. 
tions. In 2009–2011, we observed that greater fish biomass in the permanent reservoirs was associated with higher chlorophyll-a and *Microcystis* but not with zooplankton biomass. This suggests a bottom-up effect of fish on phytoplankton (via nutrients) rather than top-down control of zooplankton by fish. In 2004, a high fish biomass in the permanent reservoirs was associated with a high zooplankton biomass (Fig. 3) and was not related to a higher chlorophyll-a and *Microcystis* biomass. This pattern suggests that the zooplankton, that included *Daphnia*, might have contributed to the control of phytoplankton and, particularly, *Microcystis*.

The effect of drying on reservoir characteristics may be related to a drastic reduction in fish density (Scheffer, 1998; Beklioglu et al., 2007; Jeppesen et al., 2012). Alternatively, it may be related to processes that are independent of the presence of fish, such as a reduction in the carbon pool by increased aerobic microbial activity (Corstanje, 2003), increased phosphorus uptake along with the oxidation of iron (Scheffer, 1998; Moss, 2010), sediment compaction leading to reduced sediment resuspension (James et al., 2001) and increased germination rates of macrophytes (Scheffer, 1998). The relation between drying and fish biomass is unidirectional: drying is a key driver of fish biomass, whereas fish biomass does not affect drying. The global models in our variation partitioning analysis explain a large proportion of the variation and are highly significant (see Table 3; Fig. 4). The effects of fish and drying alone (corrected for the effect of fish) nor the effect of drying alone (corrected for the effect of fish) explain a significant part of the variation in environmental conditions. Thus, we cannot say that drying affects reservoirs independently of fish or that fish affect reservoirs independently of drying. In the 2004 data set, both the pure effects of fish and drying were significantly associated with the ecological characteristics of the reservoirs. The 2004 data set thus provides evidence for separate effects of fish and drying. These 2004 data suggest that there is both an effect of fish independent of drying out as well as a long-term effect of propensity to dry out that is independent from changes in fish biomass.

Our results indicate that the propensity to dry out is an important predictor of the ecological characteristics of reservoirs in semi-arid regions. The impact of drying is probably mediated by a major disturbance to the fish assemblage as well as through an effect on nutrient dynamics and sediment characteristics. Following drying, fish must recolonise the reservoirs and need time the populations to increase. In our 2004 data set, there were also pronounced differences in fish density between permanent reservoirs and those that dry out. The lower fish densities are probably a legacy of the disturbance caused by occasional drying events.

**Implications for reservoir management**

Our results suggest that occasional drying should lead to increased water quality, with fewer or less intensive blooms, lower *Microcystis* biomass, lower biomass of fish, higher transparency and more abundant aquatic vegetation. Allowing reservoirs to dry out should therefore be considered as a management option for increasing water quality and to prevent noxious cyanobacterial blooms in eutrophic reservoirs such as these. This is badly needed, as many reservoirs suffer from severe (Dejenie et al., 2012) and toxic (Van Gremberghe et al., 2011) *Microcystis* blooms, which may profoundly affect the rural community, as the reservoirs are routinely used for watering livestock. *Microcystis* can cause liver diseases (Jochimsen et al., 1998; Codd et al., 1999). Although not intended as a drinking water supply, the reservoirs are occasionally also used by people for drinking (Teferi et al., pers. obs.). Microcystine toxins have also been observed to accumulate in fish meat (Magalhães et al., 2003) and other components of the human diet (Ibelings & Chorus, 2007) so that *Microcystis* blooms may hamper exploitation of reservoirs for culturing fish. Finally, microcystine toxins have even been observed to produce toxic residues in crops irrigated with water containing *Microcystis* blooms (Codd et al., 1999; McElhiney, Lawton & Leifert, 2001; Chen et al., 2004; Peuthert, Chakrabarti & Pflugmacher, 2007; Crush et al., 2008), so even the use of reservoir water for irrigation poses a risk unless water quality is improved. Our observation that drawdown may help improve water quality is in line with many observations, particularly in temperate systems (Jeppesen et al., 2012).

We could not distinguish between the separate effects of fish removal and drying, so it is difficult to assess whether fish removal *per se* would already reduce the likelihood of *Microcystis* blooms. There is some circumstantial evidence that fish removal improves water quality. First, an enclosure experiment in two reservoirs suggested that the presence of fish does promote *Microcystis* blooms (Dejenie et al., 2009). Second, in the present study we did observe a pure effect of fish presence on water quality for the 2004 data set. However, it is likely that the effect will be enhanced by drying, which is also evident from the
2004 data set. In addition, drawdown is the most efficient way to remove fish from the reservoirs.

Our results provide some information on the frequency with which drawdown should be implemented to result in an improved water quality. First, we observed long-term effects of drying in systems in which we observed only one or two drying events in a period of 8 years (2003–2011) and effects that persisted through two wet years. This suggests that regular drying, as observed here, in the order of perhaps one event every 5 years, might be sufficient to produce improvements in water quality. On the other hand, we also found indications that two consecutive dry periods might result in stronger and longer-lasting responses in terms of transparency and macrophyte development.

With particular reference to the control of *Microcystis* blooms, the data from 2004 do warn against too much optimism. Although not significant, there was some indication of higher *Microcystis* biomass in reservoirs with a greater propensity to dry out. This could be related to the greater densities of *Daphnia* in the more permanent reservoirs, but how this is related to probability of drying, particularly given the higher fish biomass in permanent reservoirs, is unclear. One possibility is that phosphorus concentrations in the permanent reservoirs are higher, thus supporting stronger development of *Daphnia*, although this remains speculative.

Implementing drying as a strategy for improving water quality may be an effective and relatively easy management strategy for reservoirs in semi-arid regions. However, there are several practical problems in a socio-economic context. First, a forced drawdown may be risky if the dry season is unexpectedly extended and water is needed. However, a large quantity of water in the reservoirs is currently lost because irrigation in Tigray often starts only 4 months after the end of the rainy season, from January till May/June (Eyasu, 2005). Eyasu (2005) has calculated that this is not an efficient use of the limited water stored in reservoirs. He suggests starting irrigation soon after the end of the rainy season, although the implications of such changes in irrigation schemes for agricultural production still need to be evaluated more carefully. We suggest that such a change in irrigation might result in a win-win situation for both the quality and quantity of water, with water being used more effectively for irrigation and with higher water quality in the subsequent season. However, the reservoirs are also used for watering cattle and a forced drawdown, combined with an extended dry season or a poor subsequent rainy season, may lead to problems for livestock herders. Even though the reservoir water contains toxic cyanobacteria that may be a health hazard to cattle, farmers may still prefer this to having no access to water at all. Therefore, the implementation of regular forced drawdowns of reservoirs as a management strategy could probably be implemented only if alternative sources of water for cattle are available.

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References


Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** ANOVA results for the effect of reservoir categories (reservoirs that did not dry out in 2009 nor in 2010; reservoirs that dried out only in 2009; reservoirs that dried out in both 2009 and 2010) on the morphometric and regional characteristics of the studied reservoirs.

**Table S2.** Results of the redundancy analysis: amount of variation in ecological variables explained by reservoir drying for the sampling campaigns of 2009, 2010 and 2011, and for the data collected in 2004 by Dejenie et al. (2008).

**Figure S1.** Map of Ethiopia and the location of the 13 reservoirs in Tigray region, northern Ethiopia.

**Figure S2.** Morphometric and regional characteristics of the 13 reservoirs in relation to drying (black: no drying in 2009 nor 2010; light grey: drying only in 2009; dark grey: drying in both 2009 and 2010).

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