


Effects of turbidity and introduced tilapia (*Oreochromis* spp) on macrophytes and invertebrates in a shallow tropical lake

Laurence Adel Rasoamihango^{1,2}, Felix Razafindrajao³, Harison Andriambelo², Lily Arison Rene de Roland^{1,4} and Andrew J. Bamford^{5,*} 

¹ Université de Toliara, École Doctorale de la Biodiversité et Environnements Tropicaux, BP304, Toliara 601, Madagascar

² Wildfowl and Wetlands Trust, Antananarivo 101, Madagascar

³ Durrell Wildlife Conservation Trust, BP8511, Antananarivo 101, Madagascar

⁴ The Peregrine Fund, BP4113, Antananarivo 101, Madagascar

⁵ Wildfowl and Wetlands Trust, Slimbridge GL2 7BT, UK

Received: 18 February 2022 / Accepted: 1 December 2022

Abstract – Tropical freshwater wetlands are subject to multiple stressors but there is little information on which stressors cause wetland degradation. Increased turbidity is considered a major cause of degradation, but the effects of introduced fish are often overlooked. Tilapia are frequently introduced in tropical regions, especially species in the genus *Oreochromis*, and the ecological effects of introducing tilapia are poorly studied. We used enclosure experiments in a shallow lake in Madagascar to assess the effects of tilapia and turbidity on macrophytes and benthic invertebrates, and to test management interventions designed to increase both. Tilapia at high and low stocking densities had negative effects on survival of Charophyte algae and water lilies, but no direct effect on benthic invertebrate abundance or diversity. Invertebrate abundance was highest on submerged Charophytes, so herbivory by tilapia indirectly affected invertebrates. Turbidity affected Charophyte survival, and abundance and diversity of non-Dipteran insects. As a complication, tilapia may increase turbidity by re-suspending the lake sediment. Our results suggest that herbivory by tilapia is a plausible cause of the removal of macrophytes from the lake and an impediment to their re-establishment. Tilapia are widely introduced in tropical areas as a food resource. Our results demonstrate serious consequences to these introductions.

Keywords: Aquatic herbivory / submerged macrophyte / floating macrophyte / *Cyperus papyrus*

1 Introduction

In the biodiversity hotspot of Madagascar, freshwater ecosystems receive little attention compared to forest and marine systems (Bamford *et al.*, 2017) despite containing similar proportions of endangered species (Máiz-Tomé *et al.*, 2018) and being more threatened (Kull, 2012, Bamford *et al.*, 2017). Stressors faced by wetlands in Madagascar are typical of tropical countries, including habitat clearance for agriculture, invasive species, deforestation, and pollution (Junk *et al.*, 2013, Bamford *et al.*, 2017, Máiz-Tomé *et al.*, 2018, Williams-Subiza and Epele, 2021). Also in common with other tropical regions, freshwater wetlands are under-represented in protected area networks (Bamford *et al.*, 2017, Reis *et al.*, 2017). The overwhelming majority of lakes in Madagascar have turbid water, few benthic invertebrates and few submerged or floating macrophytes (Bamford *et al.*, 2017). While there is no

data on algae or plankton, the vast majority of lakes appear to be eutrophic. High rates of sedimentation due to deforestation are generally blamed for turbid, eutrophic lakes (*e.g.*, Máiz-Tomé *et al.*, 2018), as increased sedimentation is well known to have severe consequences for lakes (Donohue and Molinos, 2009). However, there is little data on the extent or impacts of wetland stressors, so it is not clear if deforestation is the sole cause of turbidity in Malagasy lakes, or if turbidity is the sole cause of the lack of submerged macrophytes and benthic invertebrates.

Nearly all lakes in the country contain several species of introduced fish (Sparks and Stiassny, 2003, Bamford *et al.*, 2017). Competition from and predation by introduced species is often blamed for declining native fish populations (Sparks and Stiassny, 2003, Canonico *et al.*, 2005), but their role in causing other changes to the lake ecosystems has not been studied in detail (Canonico *et al.*, 2005, Vejříková *et al.*, 2018). For example, common carp *Cyprinus carpio* can have a substantial role in increasing turbidity and reducing populations of benthic invertebrates and submerged macrophytes

*Corresponding author: andrew.bamford@wwt.org.uk

(e.g. Zambrano *et al.*, 2001, Williams *et al.*, 2002, Miller and Crowl, 2006). Carp are widespread in Madagascar and their effect on lake systems is often overlooked. However, the most widespread introduced fish in Madagascar are various tilapia, and the ecological effects of these species are poorly studied anywhere in their introduced range. Two species in the genus *Oreochromis*, Nile and Mozambique tilapia (hereafter referred to as tilapia), are most commonly introduced and they live feral in every country where they have been cultured (Canonico *et al.*, 2005). In Madagascar, they are deliberately introduced to lakes to provide protein and livelihoods in poor communities. Their ability to thrive in a wide range of environmental conditions makes them well suited to this role (Canonico *et al.*, 2005) and consequently tilapia dominate the catch in many lakes in Madagascar (e.g. Lammers *et al.*, 2020). The role of tilapia in outcompeting native fish species is well studied, but there is less information on effects they have on other aspects of the lake ecosystems.

Here, we aim to determine the effects of two wetland stressors, introduced tilapia and turbidity, on macrophytes and benthic invertebrates. An additional aim was to determine if management interventions can quickly increase the abundance of either macrophytes or invertebrates. We utilise *in situ* enclosure experiments to (1) quantify the effects of tilapia and turbidity on macrophyte survival and invertebrate abundance and diversity, (2) determine if tilapia play a role in increasing turbidity, (3) determine if tilapia effects vary with stocking density, and (4) test management interventions including re-introducing macrophytes and adding woody debris to the sediment.

2 Methods

2.1 Study site

Lake Sofia, in the northern highlands of Madagascar (Bealanana District, Sofia Region), is in relatively good condition. The lake retains a large, healthy marsh, dominated by *Cyperus papyrus*, and is a dry season refuge to large numbers of ducks, including the Endangered Meller's duck *Anas melleri*. Lake Sofia is representative of stressors faced by wetlands in Madagascar, but most are present at low levels (Bamford *et al.*, 2017). For example, there is marsh clearance for agriculture, but natural vegetation surrounds the lake. Sedimentation is lower than at similar sized lakes. Crucially for our aims, tilapia are the only introduced non-native species of fish, and fishing pressure is low. Despite all this, Lake Sofia is a eutrophic lake with few benthic invertebrates, limited floating macrophytes and no submerged macrophytes. This state may represent a recent change, as photographs show abundant floating vegetation covering the lake as recently as 1960. Residents report that this vegetation consisted of water lilies, and that fish used to be more abundant in the lake. No information is available on the native fish community, with most residents stating there were no fish in the lake before the introduction of tilapia. Small lakes in the catchment have abundant submerged vegetation, mostly Charophyte algae. It is reasonable to suppose that Lake Sofia contained similar algae, as is typical for a papyrus-dominated lake (Pacini *et al.*, 2018).

Lake Sofia is 1100 metres above sea level and covers 2 km², reaching a maximum depth of 4 m in the rainy season or 3 m in the

dry season. There is 3.5 km² of papyrus-dominated marsh, with a fringe of floating mats of grasses and ferns and few water lilies (*Nymphaeaceae* species). Beyond the marsh are 17 km² of rain-fed rice fields. The lake catchment is almost entirely deforested, but historically would have been part of Madagascar's eastern rainforest belt. The lake has simple hydrology, being river fed with two main inflows plus numerous small seasonal channels. There is a single outflow. Rainfall averages 1500 mm annually, mostly from January to March. There is little flow modification. Catchment soils are mainly ferrosols, red clay based soils with little organic content (Ramifehriarivo *et al.*, 2016). Water quality measurements suggest the lake is eutrophic, with high phosphate levels (30 µg/l), low nitrate levels (160 µg/l), and high turbidity (16 NTU, or secchi depth of 0.6 m). The water is well oxygenated, with no difference between the surface (7.5 mg/l) and 2 metres depth (7.0 mg/l), although there is a drop in DO levels below 2 m. Benthic Chironomidae abundance is low (mean ± S.E. = 100 ± 11 individuals m⁻²). See Pruvot *et al.* (2020) for additional detail.

2.2 Enclosure experiments

We used a split-plot experimental design to manipulate the presence of tilapia and the substrate type. It was not possible to manipulate the turbidity level in this *in situ* experiment. As a proxy, we instead varied depth, with treatments placed close to the surface and at 1.5 m depth. Water quality analysis (see Study Site above) show no difference in nutrient levels between the surface and 1.5 m depth, so only light levels and pressure differ. Substrates tested were introduced water lilies and Charophyte algae, plus coarse woody debris and lake sediment transplanted as a control. The experiment was run twice with different fish stocking densities. Six cages were constructed as fish enclosures (Fig. 1). Each cage measured 1.5 m (W) × 1.5 m (D) × 2.0 m (H), made from a wooden frame with 1.5 mm wire mesh sides and bottoms. The mesh allows small invertebrates to pass. It may also allow small fry fish through, but this is not likely to cause a problem over the length of these experiments. Four treatments were made, in plastic trays (measuring 35 cm × 35 cm × 20 cm deep):

- Lake sediment as a control (2 litres of wet sediment).
- Coarse woody detritus (1.5 kg dry weight).
- Charophytes (*Charophyceae* species, 500 g wet weight) growing in sediment (1 litre wet sediment).
- Water lilies (*Nymphaeaceae* species, whole plants) growing in sediment.

Lake sediment was transplanted directly from the area of the experiments. Detritus was taken from native forests near the lakeshore. Charophytes were transplanted from another lake (3 m deep) within the Lake Sofia catchment and rinsed clean. Few Charophytes remain in the study area so we were limited to the single species that could be sourced locally. Water lilies were transplanted from the marsh surrounding the lake. Detritus for the treatments was measured by dry weight, but Charophytes and sediments had to be measured by wet weight or volume. Water lilies were transplanted as whole plants, so no standardisation in size was possible. Two trays of each treatment were placed into each enclosure, one suspended close to the surface and suspended at 1.5 m depth (deep vs.

shallow, as a proxy for turbid and non-turbid conditions). This does not apply to the water lilies, which were placed near the surface only.

Finally, tilapia from the lake were then introduced into three of the cages. The experiment was run twice, with different fish stocking densities. In Experiment I we used four tilapia per cage, and in Experiment II we used two tilapia per cage. Tilapia were caught from the lake and fish of roughly equal size (11–13 cm total length) were selected for the experiment. Experiment I ran from March 2020 until May (7 weeks) and Experiment II ran from September 2020 until November (6 weeks). The experiments were stopped when the wire mesh used to construct the cages started to degrade before any fish could escape or enter. The cages were located in the lake within 10 metres of the emergent fringing vegetation.

The cages were checked daily during the experiments, but to avoid disturbance the individual treatments were not checked. Turbidity and dissolved oxygen were measured weekly at the surface and bottom of cages using a Micro 600 DO meter and Photometer 7100, both made by Palintest (Gateshead, UK). At the end of the experiment, we retrieved the treatments by gently pulling them up to the surface and immediately searching for invertebrates. Specimens were stored in ethanol for later identification. The remaining sediment and plant material was dried and dry weight recorded. Water lilies were photographed at the start and end of the experiments, and their relative size at the end (compared to the start) was scored based on the number of leaves and the size of each leaf.

2.3 Statistical analysis

Analyses were carried out in R v4.0.5 (R Core Team, 2021). Invertebrate abundance was measured as counts of individuals, diversity as Gini-Simpson index calculated on insect genera. We related response variates to explanatory variables in GLMs, assuming a Gaussian distribution for weight and size variates (plants and substrate), a quasi-binomial distribution for diversity indices, and a quasi-poisson distribution for invertebrate counts. Quasi-poisson distributions were used to account for model dispersion being divergent from 1. Experiments I and II were analysed separately, and then pooled data from the two experiments was analysed with experiment number included as a two-level random effect. Significance levels were checked using an ANOVA on the full model. Model performance and assumptions were checked using the package *performance*.

3 Results

3.1 Effects on macrophyte survival and substrate suspension

Charophyte survival was affected by both depth and fish presence in both experiments and in the overall data (Tab. 1). The mass of Charophytes was zero in all samples when fish were present, and greater mass of Charophytes remained in the shallow treatments (Fig. 2). Results were the same in Experiments I and II, so there was no seasonal effect and no effect of stocking densities.

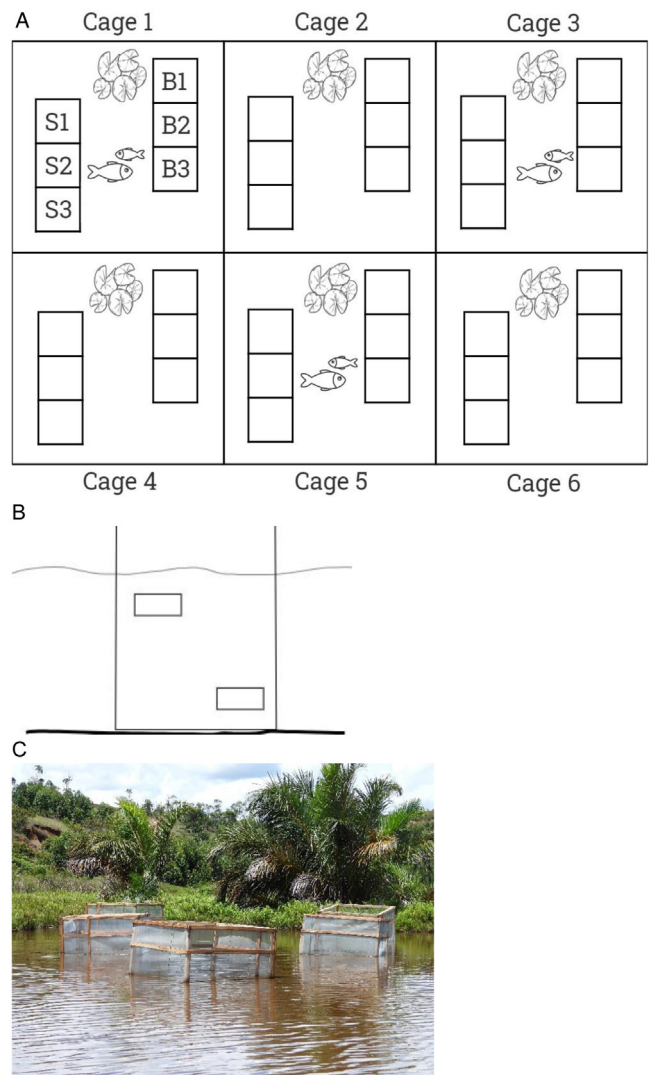


Fig. 1. (A) The experimental set up, a split-plot design with fish introduced into 3 of the 6 cages, and three treatments in each cage near the surface (S) and the same three treatments at 1.5 m depth (B), plus a Nymphaeaceae plant transplanted into each cage. Treatments were assigned positions at random for each cage. The three treatments were: lake sediment, woody detritus, and transplanted Charophyte plants. The experiment was run twice with different fish stocking densities. (B) A side on view of one cage to show the differing depths. (C) A photograph of the cages *in situ*, February 2020.

Water lily survival was also affected by fish presence ($F_{1,34} = 6.3$, $P = 0.01$). Fish presence was associated with a decrease in plant size or slower growth (Fig. 2). This effect was not significant in each experiment analysed individually, but was significant when data from both experiments were pooled.

Substrate weight was affected by fish presence (Linear regression on log weights, $F_{1,79} = 4.7$, $P = 0.03$). Dry weight of sediment remaining in the tray at the end of the experiment was less when fish were present (Fig. 3). Dry weight of detritus at the end of the experiment was also less with fish presence.

Table 1. Results of GLMs exploring the effects of fish presence, turbidity and substrate type on invertebrates and macrophytes. GLMs on abundance were fitted assuming a quasi-Poisson distribution, GLMs on diversity assumed quasi-binomial distribution and all other GLMs assumed Gaussian distribution.

Response variate	Explanatory variable		
	Tilapia	Turbidity	Substrate
Chironomidae: abundance (count)	No effect Exp I ($F_{1,46} = 11.3, P = 0.002$) Exp II ($F_{1,46} = 0.6, P = 0.4$) Overall ($F_{2,93} = 0.6, P = 0.5$)	No effect Exp1 ($F_{1,46} = 2.2, P = 0.1$) Exp2 ($F_{1,46} = 0.3, P = 0.6$) Overall ($F_{1,94} = 0.9, P = 0.4$)	Negative effect of sediment Exp1 ($F_{3,44} = 3.9, P = 0.01$) Exp2 ($F_{3,44} = 6.8, P < 0.001$) Overall ($F_{3,93} = 8.2, P < 0.001$)
Chironomidae: diversity (Gini-Simpson)	No effect. Exp I ($F_{1,46} = 0.0, P = 0.9$) Exp II ($F_{1,46} = 0.9, P = 0.3$) Overall ($F_{2,93} = 0.4, P = 0.5$)	Negative effect. Exp I ($F_{1,46} = 5.3, P = 0.03$) Exp II ($F_{1,46} = 5.6, P = 0.02$) Overall ($F_{1,94} = 10.8, P = 0.001$)	No effect. Exp I ($F_{3,44} = 1.1, P = 0.4$) Exp II ($F_{3,44} = 0.4, P = 0.8$) Overall ($F_{3,92} = 0.4, P = 0.8$)
Non-diptera: abundance (count)	No effect. Exp I ($F_{1,46} = 0.0, P = 1.0$) Exp II ($F_{1,46} = 0.3, P = 0.6$) Overall ($F_{2,93} = 0.08, P = 0.8$)	Negative effect. Exp I ($F_{1,46} = 4.9, P = 0.03$) Exp II ($F_{1,46} = 47.5, P < 0.001$) Overall ($F_{1,94} = 43.0, P < 0.001$)	Positive effect of charophytes. Exp I ($F_{3,44} = 1.0, P = 0.4$) Exp II ($F_{3,44} = 7.9, P < 0.001$) Overall ($F_{3,93} = 5.4, P = 0.001$)
Non-diptera: diversity (Gini-Simpson)	No effect. Exp I ($F_{1,46} = 2.1, P = 0.1$) Exp II ($F_{1,46} = 0.4, P = 0.5$) Overall ($F_{2,93} = 0.0, P = 1.0$)	Negative effect. Exp I ($F_{1,46} = 2.1, P = 0.1$) Exp II ($F_{1,46} = 20.2, P < 0.001$) Overall ($F_{1,94} = 31.3, P < 0.001$)	No effect. Exp I ($F_{3,44} = 1.1, P = 0.3$) Exp II ($F_{3,44} = 0.9, P = 0.4$) Overall ($F_{3,93} = 0.4, P = 0.5$)
Charophyte (dry weight)	Negative effect Exp I ($F_{1,10} = 9.0, P = 0.01$) Exp II ($F_{1,10} = 12.1, P = 0.007$) Overall ($F_{1,33} = 20.38, P < 0.001$)	Negative effect Exp I ($F_{1,10} = 9.0, P = 0.01$) Exp II ($F_{1,10} = 12.9, P = 0.006$) Overall ($F_{1,33} = 12.3, P = 0.001$)	N/A
Water lily (relative size)	Negative effect. Exp I ($F_{1,10} = 0.08, P = 0.7$) Exp II ($F_{1,10} = 0.8, P = 0.4$) Overall ($F_{1,34} = 8.0, P = 0.008$)	N/A	N/A

3.2 Invertebrates

Chironomidae were by far the most abundant invertebrates recorded (Tab. S1), and most individuals belonged to species in the genus *Chironomus*. Other insect taxa were recorded too infrequently for analysis on their own, but we could analyse abundance and diversity of all non-Dipteran insects pooled (a mixture of Ephemeroptera, Trichoptera, Odonata and Hemiptera). Odonata accounted for 61% of this abundance, Hemiptera 20%, Ephemeroptera 16% and Trichoptera 3%. Abundance of non-Dipteran insects was greater in experiment two, while Chironomid abundance was roughly equal between the two experiments.

Chironomidae abundance was unaffected by either tilapia or depth (Tab. 1, Fig. 4a), while diversity was negatively affected by depth but not tilapia. This reduction in diversity was caused by an increased dominance of the genus *Chironomus*, which accounted for 95% of specimens in the turbid treatments, versus 77% in the surface treatments. Both abundance and diversity of non-Dipteran insects were affected by depth but neither were affected by tilapia (Tab. 1, Fig. 4b). All groups were less common in the deep treatments so that often only one specimen was found in each treatment, hence the lower diversity score. Substrate type had an effect on abundance of both groups: Chironomidae were more abundant on detritus and Charophytes than on control sediment (Tab. 1, Fig. 4a), and non-Dipteran insects were more abundant on Charophytes than on detritus and control sediment (Tab. 1,

Fig. 4b). The effects of fish presence, depth and substrate type and significance levels were similar in experiments one and two, suggesting that fish stocking density does not influence their effect on invertebrates.

4 Discussion

Quantitative assessments of the effects of local stressors on ecological responses are rare in tropical systems (Jackson *et al.*, 2016, Williams-Subiza and Epele, 2021). While the experiments reported here were short term and small scale, the results of this type of experiment can help us understand the factors causing changes to the ecosystem and limiting factors on restoration (Ratajczak *et al.*, 2018). Our results identified strong effects of turbidity and introduced tilapia on a lake system in Madagascar.

As water chemistry is broadly similar between the shallow and deep treatments, and the transplanted Charophytes were taken from deeper water than the deep treatments so depth is not directly having an adverse effect, we conclude that the depth effect in our experiments is due to reduced light levels due to the turbidity level in the lake. Both turbidity and tilapia had an impact on macrophytes in the lake. Turbidity affected invertebrates, lowering abundance and diversity of non-Dipteran insects and reducing diversity of Chironomidae, but we recorded no effect of tilapia on invertebrates. The strongest effect on invertebrate abundance was from substrate type, with

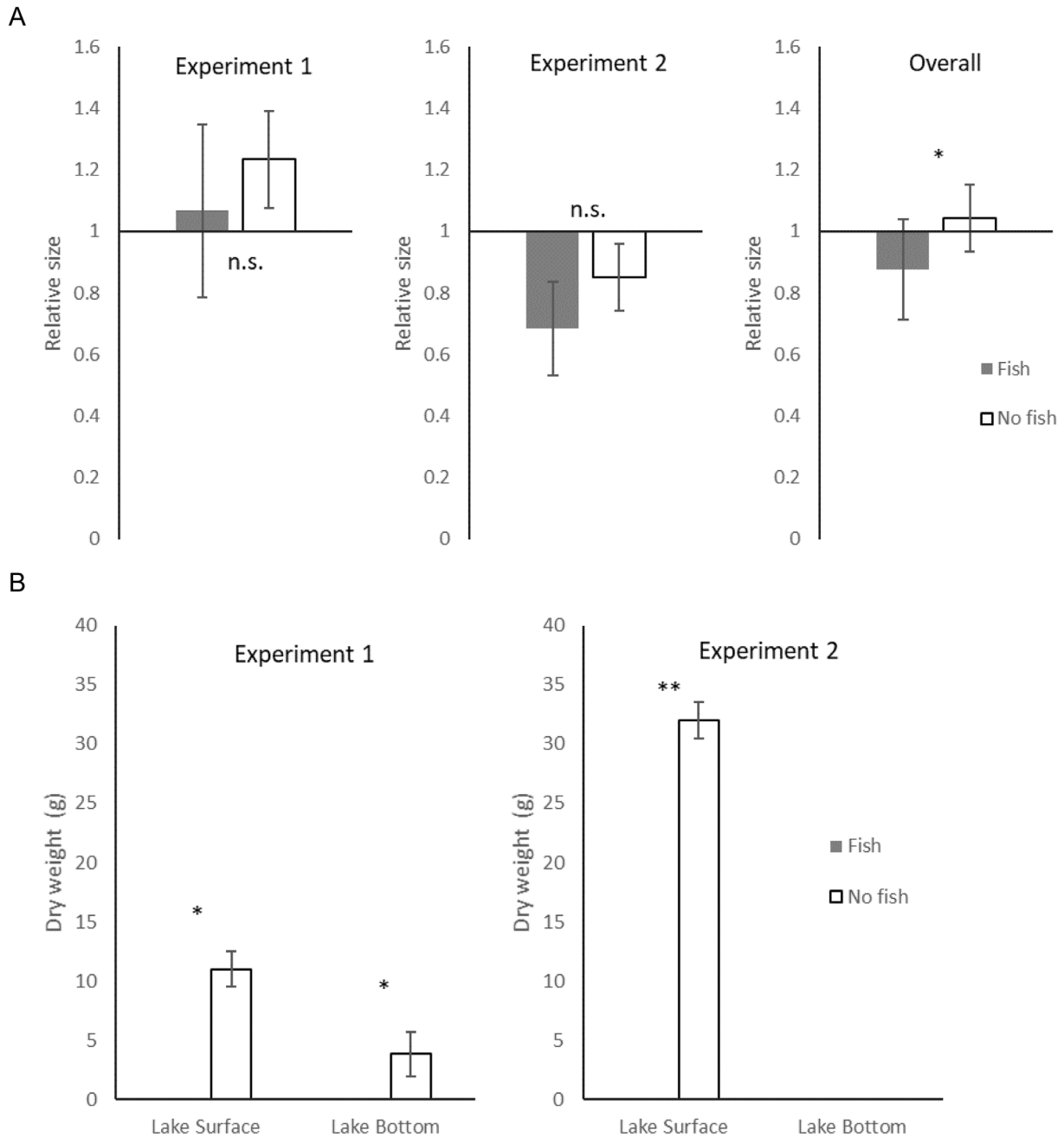


Fig. 2. Effects of treatments on macrophytes in the two experiments. (A) Changes in size of water lilies over the course of the experiments. (B) Charophytes remaining at the end of the experiments. Results from the two experiments are pooled, as the outcome was the same in both cases. (Note that in the presence of fish, remaining Charophyte dry weight was always 0). n.s. = Not Significant, * = $P < 0.05$, ** = $P < 0.01$.

the lowest abundance on the control sediment, so our results suggest that this sediment is poor invertebrate habitat. The mechanism by which tilapia affect macrophytes appears to be direct, herbivory, and leads to an indirect effect of fish on invertebrates, by consuming macrophytes that are beneficial habitat. This may be an oversimplification, as tilapia diet may vary with age and resource availability (Rao *et al.*, 2015), so direct effects on invertebrates may occur with different age tilapia.

Our results suggest that tilapia are suspending sediment and so potentially increasing turbidity in the lake, and thus

indirectly affecting invertebrates (and Charophytes) in another way. This is surprising for a species not noted as being benthivorous, but this effect of tilapia on sediment has also been reported by Attayde *et al.* (2007) and Zhang *et al.* (2017). Overall, our results indicate complex effects of a single introduced fish species on a lake ecosystem. Many lakes in Madagascar have both tilapia and common carp, plus several other species too (Sparks and Stiasny, 2003, Bamford *et al.*, 2017, Lammers *et al.*, 2020), and the effects resulting from these interactions may be difficult to predict.

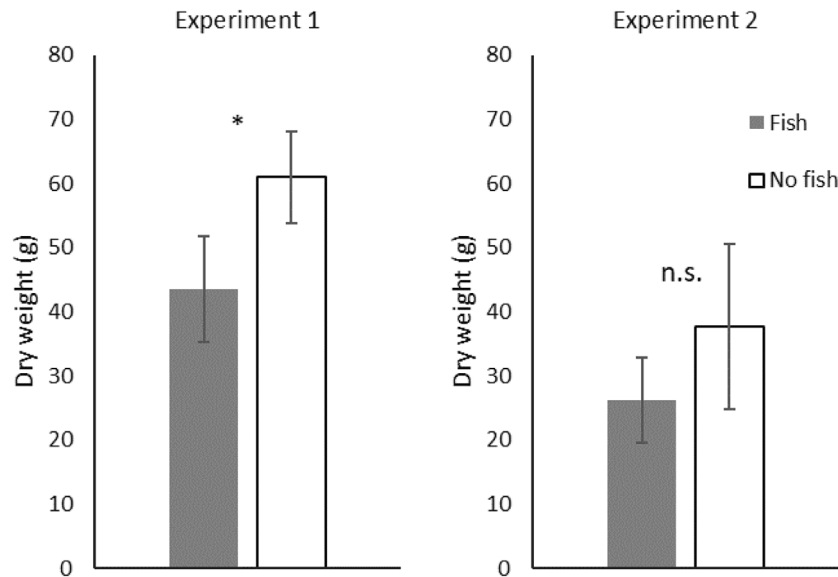


Fig. 3. Sediment remaining at the end of the experiments. n.s. = Not Significant, * = $P < 0.05$, ** = $P < 0.01$.

There are reasons to be cautious interpreting our results on invertebrates. First, it is not ideal grouping all non-Dipteran insects, as different groups may respond differently – for example in small lakes in Europe, fish presence is negatively associated with Coleoptera, and positively associated with Odonata, Hemiptera and Trichoptera (Hinden *et al.*, 2005, Hassall *et al.*, 2011). In contrast, our results suggest no effect on Odonata and a negative effect on Hemiptera. Second, the lake may lack invertebrates that are sensitive to the stressors present in the lake (including tilapia presence), so they could not colonise our experiments. Third, swimming insects may transiently visit our experimental set up, unlike more sedentary Chironomidae, so our experimental design may underestimate numbers of these groups. These factors mean that tilapia effects on insects may be underestimated in our results.

Turbidity in Malagasy lakes is assumed to be increasing due to increased sediment run-off caused by deforestation (*e.g.* Máiz-Tomé *et al.*, 2018). This may be an oversimplification, as we have already noted a role for introduced fish and burning of grasslands may contribute to turbidity (Brosens *et al.*, 2022). The extent to which increased sediment loading and eutrophication are related is unclear at Lake Sofia. Catchment soil contains low levels of organic material, so sediment run-off may not contribute to nutrient levels in the lake. However, increased sediment loading alone can affect lakes, including declines in submerged macrophytes and benthic invertebrates, a reduction in plankton abundance and reduced primary productivity (Donohue and Mollinos, 2009). In theory, the surrounding papyrus marsh should filter inflowing water and remove suspended solids. Turbidity is lower inside the papyrus than outside at Lake Sofia, indicating that the marsh is preventing some allochthonous inputs. The width of the marsh is critical to filtration, however (Boar, 2006), and the marsh at Lake Sofia is thin on numerous small inflows. A critical need for lake management, therefore, is to understand where suspended solids are coming from, and to determine if there is a link between sediment input and eutrophication.

The major role of herbivory in shaping aquatic ecosystems has only recently become apparent and it remains understudied in tropical regions (Bakker *et al.*, 2016, Wood *et al.*, 2017, Vejříková *et al.*, 2018). Our results suggest that *Oreochromis* fish are capable of suppressing both Charophytes and water lilies. Anecdotal evidence from a nearby lake to which tilapia were introduced in 2018 and which rapidly lost all submerged Charophytes (but not yet all water lilies) suggests that tilapia are easily capable of clearing a lake of macrophytes. Water lilies were abundant at Lake Sofia in historical photographs, and herbivory by tilapia is a plausible cause of their removal and an impediment to their re-establishment. This hypothesis tallies with local reports, which say that fish were introduced around 30 years ago and consumed the lilies. Fish in particular can exert a strong effect on macrophytes (Wood *et al.*, 2017), due to their inability to move to new sites as resources are depleted. These results have implications for lake management. A coalition of conservation NGOs and local associations aims to make Lake Sofia more suitable for the critically endangered Madagascar pochard *Aythya innotata*, which would involve re-establishing macrophyte populations and increasing invertebrate abundance. However, even with reduced turbidity, reintroduction of submerged and floating macrophytes will be impeded by tilapia in the lake (see Liu *et al.*, 2018). Our results confirm results from temperate systems that invertebrates can be boosted by addition of coarse debris, but this is often only viable in the short term (Thompson *et al.*, 2018).

Oreochromis species are widely introduced in the tropics (Canonico *et al.*, 2005). These fish are valued for their ability to thrive in poor quality water and thus provide protein in impoverished regions. However, little consideration is given to the ecological effects of these introductions (Cucherousset and Olden, 2011) even though there are well-known negative effects (Canonico *et al.*, 2005), in particular their role in outcompeting native species. However, other negative effects of introducing tilapia have not been studied in-depth. This includes their role in increasing turbidity and their role as herbivores (but see McCrary *et al.*, 2001; Doupé *et al.*, 2010), both demonstrated here.

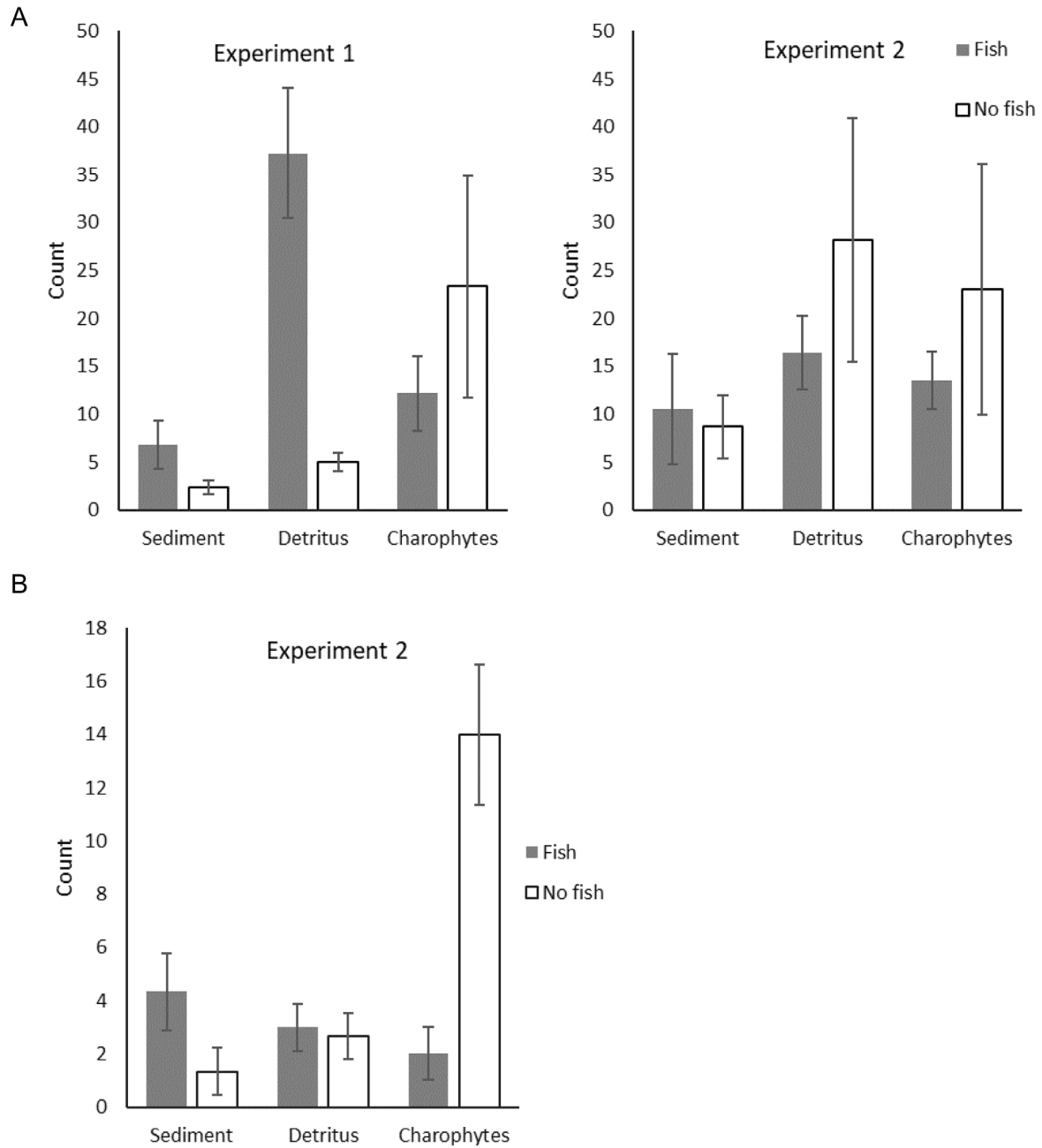


Fig. 4. Insect abundance at the end of the experiments. (A) Chironomidae abundance (all genera) with shallow and deep samples combined, showing results from experiment 1 (high fish stocking density) and experiment 2 (low fish stocking density). (B) Non-Dipteran insect abundance (all genera), showing only the surface treatments in experiment 2.

Acknowledgements. Fieldwork in such a difficult to reach location takes the help of a large number of people. Particular thanks must go to Jocelyn Rafaly, Randrianarimangason Floriot and all the other WWT and Durrell staff at Lake Sofia. Kevin Wood helped with information on aquatic herbivory and Lucy Smith helped tracked down literature on tilapia. Geoff Hilton and Viv Jones have been supportive of this work. We thank an anonymous reviewer whose comments substantially improved the manuscript. This research was funded by a British Ecological Society research grant awarded to AJB (ref: SR21\100726) and

we thank the BES for their flexible approach to conducting research during the Covid-19 pandemic.

Supplementary Material

Table S1. Supplementary Table 1. Counts of all macro-invertebrate taxa recorded during the experiments.

The Supplementary Material is available at <https://www.kmae.org/10.1051/kmae/2022025/olm>.

References

- Attayde JL, Okun N, Brasil J, Menezes R, Mesquita P. 2007. Os impactos da introdução da tilápia do nilo, *Oreochromis niloticus*, sobre a estrutura trófica dos ecossistemas aquáticos do bioma caatinga. *Oecolog Brasiliensis* 11: 450–461.
- Bakker ES, Wood KA, Pagès JF, Veen GF, Christianen MJA, Santamaría L, Nolet BA, Hilt S. 2016. Herbivory on freshwater and marine macrophytes: a review and perspective. *Aquat Bot* 135: 18–36.
- Bamford AJ, Razafindrajao F, Young RP, Hilton GM. 2017. Profound and pervasive degradation of Madagascar's freshwater wetlands and links with biodiversity. *PLoS ONE* 12: 182673
- Boar RR. 2006. Responses of a fringing Cyperus papyrus swamp to changes in water level. *Aquat Bot* 84: 85–92.
- Brosens L, Broothaerts N, Campforts B, Jacobs L, Razanamahandry VF, Van Moerbeke Q, Bouillon S, Razafimbelo T, Rafolisy T, Govers G. 2022. Under pressure: rapid lavaka erosion and floodplain sedimentation in central Madagascar. *Sci Total Environ* 806: 150483.
- Canonico GC, Arthington A, McCrary JK, Thieme ML. 2005. The effects of introduced tilapias on native biodiversity. *Aquat Conserv* 15: 463–483.
- Cucherousset J, Olden JD. 2011. Ecological impacts of non-native freshwater fishes. *Fisheries* 36: 215–230.
- Donohue I, Garcia Molinos J. 2009. Impacts of increased sediment loads on the ecology of lakes. *Biol Rev* 84: 517–531.
- Doupé RG, Knott MJ, Schaffer J, Burrows DW, Lymbery AJ. 2010. Experimental herbivory of native Australian macrophytes by the introduced Mozambique tilapia *Oreochromis mossambicus*. *Aust Ecol* 35: 24–30.
- Hassall C, Hollinshead J, Hull A. 2011. Environmental correlates of plant and invertebrate species richness in ponds. *Biodiv Conserv* 20: 3189–3222
- Hinden H, Oerteli B, Menetrey N, Sager L, Lachavanne JB. 2005. Alpine pond biodiversity: what are the related environmental variables? *Aquat Conserv: Mar Freshw Ecosyst* 15: 613–624.
- Junk WJ, An S, Finlayson CM, Gopal B, Květ J, Mitchell SA, Mitsch WJ, Robarts RD. 2013. Current state of knowledge regarding the world's wetlands and their future under global climate change: a synthesis. *Aquat Sci* 75: 151–167.
- Jackson MC, Loewen CJG, Vinebrooke RD, Chimimba CT. 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. *Glob Change Biol* 22: 180–189.
- Kull CA. 2012. Air photo evidence of land cover change in the highlands: wetlands and grasslands give way to crops and woodlots. *Madag Conserv Dev* 7: 144–152.
- Lammers PL, Richter T, Mantilla-Contreras J. 2020. From safety net to point of no return – are small-scale inland fisheries reaching their limits? *Sustainability* 12: 7299.
- Liu Z, Hu J, Zhong P, Zhang X, Ning J, Larsen SE, Chen D, Gao Y, He H, Jeppesen E. 2018. Successful restoration of a tropical shallow eutrophic lake: strong bottom-up but weak top-down effects recorded. *Water Res* 146: 88–97.
- Máiz-Tomé L, Sayer C, Darwall W, eds. 2018. The status and distribution of freshwater biodiversity in Madagascar and the Indian Ocean islands hotspot. Gland, Switzerland: IUCN. 128p.
- McCrary JK, van den Berghe EP, McKaye KR, Lopez Perez LJ. 2001. Tilapia cultivation: a threat to native fish species in Nicaragua. *Encuentro* 58: 3–19.
- Miller SA, Crowl TA. 2006. Effects of common carp (*Cyprinus carpio*) on macrophytes and invertebrate communities in a shallow lake. *Freshw Biol* 51: 85–94.
- Pacini N, Hesslerová P, Pokorný J, Mwinami T, Morrison EHJ, Cook AA, Zhang S, Harper DM. 2018. Papyrus as an ecohydrological tool for restoring ecosystem services in Afrotropical wetlands. *Ecohydrol Hydrobiol* 18: 142–154.
- Pruvot YZM, de Roland LAR, Rakotondratsima M, Razafindrakoto Y, Razafindrajao F, Rabarisoa R, Thorstrom R. 2020. Breeding ecology and nestling growth of the Madagascar Pond Heron *Ardeola idae* in a monospecific colony at Sofia Lake, northern Madagascar. *Ostrich* 91: 313–325.
- R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Ramifehiarivo N, Brossard M, Grinand C, Razafimahatratra H, Seyler F, Rabenarivo M, Albrecht A. 2016. Mapping soil organic carbon on a national scale: towards an improved and updated map of Madagascar. *Geoderma Regional* 9: 29–38.
- Rao W, Ning J, Zhong P, Jeppesen E, Liu Z. 2015. Size-dependent feeding of omnivorous Nile tilapia in a macrophyte-dominated lake: implications for lake management. *Hydrobiologia* 749: 125–134.
- Ratajczak Z, Carpenter SR, Ives AR, Kucharik CJ, Ramiadantsoa T, Stegner MA, Williams JW, Zhang J, Turner MG. 2018. Abrupt change in ecological systems: inference and diagnosis. *Trends Ecol Evol* 33: 513–526.
- Reis V, Hermoso V, Hamilton SK, Ward D, Fluet-Chouinard E, Lehner B, Linke S. 2017. A global assessment of inland wetland conservation status. *BioScience* 67: 523–533.
- Sparks JS, Stiassny MLJ. 2003. Introduction to the freshwater fishes. In Goodman SM, Benstead JP eds. *The Natural History of Madagascar*. Chicago: University of Chicago Press, pp. 849–882.
- Thompson MSA, Brooks SJ, Sayer CD, Woodward G, Axmacher JC, Perkins DM, Gray C. 2018. Large woody debris “rewilding” rapidly restores biodiversity in riverine food webs. *J Appl Ecol* 55: 895–904.
- Vejířková I, Vejíř L, Lepš J, Kočvara L, Sajdllová Z, Čtvrtlíková M, Peterka J. 2018. Impact of herbivory and competition on lake ecosystem structure: underwater experimental manipulation. *Sci Rep* 8: 12130.
- Williams AE, Moss B, Eaton J. 2002. Fish induced macrophyte loss in shallow lakes: top-down and bottom-up processes in mesocosm experiments. *Freshw Biol* 47: 2216–2232.
- Williams-subiza EA, Epele LB. 2021. Drivers of biodiversity loss in freshwater environments: a bibliometric analysis of the recent literature. *Aquat Conserv* 31: 2469–2480.
- Wood KA, O'Hare MT, McDonald C, Searle KR, Daunt F, Stillman RA. 2017. Herbivore regulation of plant abundance in aquatic ecosystems. *Biol Rev* 92: 1128–1141.
- Zambrano L, Martinez-Ramos, Scheffer M. 2001. Catastrophic response of lakes to benthivorous fish introduction. *Oikos* 94: 344–350.
- Zhang X, Mei X, Gulati RD. 2017. Effects of omnivorous tilapia on water turbidity and primary production dynamics in shallow lakes: implications for ecosystem management. *Rev Fish Biol Fish* 27: 245–254.

Cite this article as: Rasoamihaingo LA, Razafindrajao F, Andriambelo H, Rene de Roland LA, Bamford AJ. 2023. Effects of turbidity and introduced tilapia (*Oreochromis* spp) on macrophytes and invertebrates in a shallow tropical lake. *Knowl. Manag. Aquat. Ecosyst.*, 424, 2.