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Impact of Nile tilapia Cage Culture on Water and Bottom Sediment Quality: The ability of a Eutrophic Lake to Absorb and Dilute Perturbations

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Abstract

Environmentally sustainable aquaculture depends on sound understanding of the impact of aquaculture derived organic matter (AOM) and the ability of aquaculture systems to absorb and dilute perturbations. We assessed the impact of AOM from cage culture of Nile tilapia on the ecology of Lake Victoria, Kenya using cages near Anyanga beach in Siaya County from December 2018 to October 2019. Four locations were surveyed for organic loading from cage culture: 0 m, 50 m, 150 m and 500 m (as a control site) away from the cages. The cage aquaculture caused increased P and N concentration near the cages and a decreased N:P molar ratio. These changes stimulated algal growth which, in turn, affected water quality. Organic material accumulated on the bottom under the cages, increasing benthic BOD (BOD, >10 mg g-1), a sensitive indicator of the ecological footprint of the cage aquaculture. Furthermore, the negative ORP in the benthic layer suggested anoxic bacterial metabolism, possibly causing buildup of sulphides and methane. These changes caused changes in the abundance and composition of both limnetic and benthic communities. At the beginning of the study, there were 22 zoobenthic taxa around the cages and 18 at the reference sites. Only 3 saprophilous taxa, chiefly gastropods (*Physella* spp.), bivalves (*Sphaerium* spp.) and oligochaetes (*Tubifex* spp.) were present at the cage site and 17 at the reference site at the end of the culture period. Shannon diversity index exhibited a declining tendency with the length of culture period at the cage site, signifying a negative impact of aquaculture on biodiversity. Water quality recovery after cage disturbance is rapid (<4 months) as there was no significant difference in the water quality recorded at the cage site and the other sampling sites after a fallow period of four months. However, sediment and meiofaunal recovery were far from complete. Moving the cages slightly (50-100 m) away from the former location may allow the benthic communities to recover and alleviate the problem. In addition, fallowing period, for the Anyanga site in particular, should be extended from 4 to at least 5 months to allow for the environment to recover. With the rapid increase of cage fish farming in the Great Lake's Region and with potential in other lakes, there is a need to develop regulations to guide the industry and continuous monitoring of the environment as to provide information to guide investment and to ensure sustainable cage farming.

KEYWORDS Benthos; fallowing; aquaculture; redox, pollution.

1 INTRODUCTION

Natural fish stocks in African inland waters are declining while the demand for fish protein is increasing because of rapid human population growth and growing awareness of nutritional and health benefits associated with fish consumption (Akintola et al., 2013; FAO, 2016; Anderson et al., 2017). Decreased catches have increased the interest in cage culture as an alternative source of fish (Aura et al., 2018a; Musinguzi et al., 2019; Hamilton et al., 2020; Musa et al., 2021a) and aquaculture will necessarily play a central role in bridging the widening gap between fish demand and supply (Obiero et al., 2019; FAO, 2020).

Large-scale culture of fish in cages is a common practice in different parts of the world (Carrol et al., 2003; Perez et al., 2005; Garcia, de Souza et al., 2015). In African inland waters, cage aquaculture is growing (Kifuko, 2015; Njiru et al., 2018; Aura et al., 2018a; Musinguzi et al., 2019; Hamilton et al., 2020). For example, between 2016 and 2019 the total number of cages in the Kenyan part of Lake Victoria increased from 1663 to more than 4537 and further growth is expected (Hamilton et al., 2020).

Concerns have been raised about the environmental impact of cage aquaculture (Bondad-Reantaso et al., 2005; Boyd et al., 2008; Kashindye et al., 2015). In African inland waters, the primary concern is eutrophication due to discharge of particulate and dissolved nutrients such as uneaten waste feed, metabolites and fecal matter (Garcia de Souza et al., 2015; Dauda et al., 2019). The accumulation of organic material in sediments increases the metabolic activity of bacteria which, in turn, can create anoxic conditions in sediments (Henderson et al., 1997; Karakassis et al., 1998; Porrello et al., 2005). Changes in sediment chemistry due to organic loading alters species abundance and biomass of macroinvertebrates (Braaten, 2007; Ngupula & Kayanda, 2010; Villnas & Bonsdorff, 2011; Kashindye et al., 2015; Egessa et al., 2018). Cage aquaculture can also affect the water quality by reducing dissolved oxygen in the water column (Kashindye et al.,

2015), elevating the levels of ammonia and CO_2 (Aura et al., 2018a) and increase the risk of algal blooms (Aura et al., 2018b; Mwamburi et al., 2020). These ecological changes can affect the production of wild populations in the area and may also create conflicts between cage culture and fisheries (Njiru & Aura, 2019).

The ecological effects of cage aquaculture depend primarily on the biomass produced, area, depth of the lake and water exchange rate (Phillips et al*.,* 1985; Huang, 1997). The environmental effects of nutrient enrichment are also site-specific and depend on local chemical features (Wu, 1995). Freshwater systems are often more vulnerable than marine systems to nutrient loads due to smaller size and in essence low ecological carrying capacity. For many decades, Lake Victoria, just as many other African inland waters, has suffered from severe eutrophication (Verschuren et al., 2002; Mwamburi et al., 2020), with regular and massive algal blooms occurring for at least the last 30 years (Ochumba & Kibaara, 1989; Mwamburi et al., 2020). The lake has seen a five-fold increase in turbidity since the early 1930s (Mwamburi et al., 2020) with Secchi disc measurements below 1 m, specifically in shallow waters < 25 km from shoreline, bays and gulfs as well as the other semi-enclosed inshore areas of Lake Victoria (Lung'ayia et al., 2001; Mwamburi et al., 2020). In addition, the long retention time of Lake Victoria (residence time: 23 years; flushing time 123 years), means that pollutants entering the lake can accumulate. A regulatory framework for cage aquaculture in Lake Victoria is inadequate and, therefore, uncontrolled growth of the sector may degrade the environment and threaten the future of capture fisheries even more. Almost all cages in African inland lakes are located in shallow waters (4-8 m) (Musinguzi et al., 2019) despite recommendations that cages should be placed in deeper waters (> 10 m) (Kamadi, 2018). Furthermore, cage aquaculture installations in African inland lakes are commonly located -

inappropriately - near protected areas, in eutrophic and hypertrophic waters and close to the shoreline, where important nursery grounds for wild fish are to be found (Musinguzi et al., 2019).

There is a paucity of information on the impact of cage aquaculture on enrichment in tropical/subtropical waters. Several published studies on aquaculture in African inland waters (Mwebaza-Ndawula et al., 2013; Kashindye et al., 2015; Nabirye et al., 2016; Egessa et al., 2018) have only evaluated the impacts during the culture periods while none of these studies addressed recovery during fallowing periods and long-term effects. The primary objective of the current study was to assess environmental consequences of cage culture in Lake Victoria and the ability of the ecosystem to absorb and dilute perturbations to guide the development of cage culture in the Great Lakes region.

2 MATERIALS AND METHODS

2.1. Study Area

The study was conducted at Anyanga beach, Kadimo Bay, Lake Victoria, Kenya (Figure 1) from December 2018 to October 2019. Kadimo Bay was chosen for study as it is the main center of aquaculture in Lake Victoria, Kenya (Aura et al., 2018a; Hamilton et al., 2020). The farm had fish in 600 cages (2 m × 2 m × 2 m), stocked with 2000 tilapia (average initial body mass 15 g), with 6 months production cycle. Prior to the study, the farm had been in operation for three years with a fallow period of 4 months between production cycles. The sampling stations were located at the edge of the cages (0 m) and then 50 m and 150 m away from the cages towards the center of the bay (Figure 1). A reference station was located 500 m away from the cages. The sampling stations were geo-referenced for future comparisons using Garmin, 78S, IC; 1792A-01664, FCC ID: IPH-01664 Global Positioning System (GPS). Mean depth at cages was 3.0 m; 50 m = 3.2; 150= 3.5 and reference site had a depth of 4.6 m

2.4. Water quality

Temperature, dissolved oxygen (DO), pH and alkalinity were monitored using a multi-parameter meter (Hanna Instruments, Model 8519N, Singapore). Secchi depth was measured using a standard Secchi disk. Diurnal fluctuations of DO and pH were monitored at the cage and reference stations using a multi-parameter meter (Hanna Instruments, Model 8519N, Singapore) from 0600 hours till 0600 hours of the following day at an interval of 4h. Water samples for chemical analysis were collected in triplicate at a depth of 1 m from the surface using a Van Dorn water sampler. Pre-cleaned 1-litre sample bottles were used and the samples preserved on ice and transported the same day to Kenya Marine and Fisheries Research Institute (KMFRI) Kisumu laboratory for analyses. Total phosphorus (TP), total nitrogen (TN) and total ammonia-N and BOD were determined using photometric methods adopted from APHA (2005). Concentration of CO_2 was measured using CO2sys and adjusted for temperature, pH and alkalinity (https://cdiac.ess-dive.lbl.gov/ftp/co2sys/). Water quality was measured at the beginning of the culture period (day 0), at days 90 and 180 of the culture period and twice during the fallowing period, at day 240 and day 300. The diurnal fluctuations were monitored at day 0 and day 180

2.5. Plankton

Water samples for zooplankton and chlorophyll *a* (as an indicator of phytoplankton) were collected in triplicates and analyzed using the methods described by Greenberg et al. (1992). Zooplankton samples were collected with a conical plankton net (Nansen type; mesh size 60 µm; mouth diameter 0.25 m), towed vertically through the water column, as described by Mwebaza-Ndawula (2013). The samples were preserved in a 5% formalin solution. In the laboratory, each sample was made to a known volume, thoroughly shaken for uniform distribution and a sub-sample taken, placed in a counting chamber and examined under inverted microscope at 100X magnification for

taxonomic determination, and at 40X for counting. Zooplankton were identified to genus and where possible to the species level. Rotifers were sorted out using a fine glass capillary tube onto slides with glycerin mixed with distilled water and examined under a compound microscope at 100X. For copepods, identification keys by Dussart & Defaye (1995) were used. The keys by Korovchinsky (1992) and Smirnov (1996) were used for Cladocera identification while Koste & Shiel (1987) and Segers (1995) were used for the identification of rotifers.

Water samples (2 L) for the quantification of total chlorophyll-*a* were collected at the surface (photic zone) in triplicate at each station using sampling bottles, filtered on site, using Whatman GF/C filters. The filter together with the seston was folded and then covered by aluminum foil and stored in a freezer overnight to aid in the bursting of the cells. Chlorophyll-*a* was extracted using reagent-grade acetone under subdued light. The seston and the filter were homogenized in a tissue grinder at around 5000-rpm for about 1 minute, covered with 5 ml of 90% aqueous acetone. The samples were transferred into screw-cap vial/centrifuge tube, the grinder rinsed with 90% acetone and the rinse added to the extraction slurry. The volume was adjusted to 10 ml with 90% acetone and the sample left for at least 8 hours in the dark at 4°C for chlorophyll-*a* extraction. After incubation, the sample was centrifuged for 10 minutes and the clarified extract was decanted into a clean test tube. Light absorbance of the Chlorophyll-*a* extract was measured with a UV-visible Beckman DU64OB spectrophotometer with the sample placed in 1-cm cell cuvettes, at 750 nm and 663 nm. Subsequently, concentrations were estimated, using the equations of Jeffrey & Humphrey (1975) after subtracting absorbance at 750 nm from all absorbance values to account for turbidity:

$$Chlorophyll\ a\ (mg \cdot l^{-1}) = \frac{11.85 \times E664 - 1.54 \times E647 - 0.08 \times E630}{L} \times V$$

In which:

V = Volume of acetone 90%

L= Volume of water sample

E664 = Value of absorbance at wavelength 664 nm

E647 = Value of absorbance at wavelength 647 nm

E630 = Value of absorbance at wavelength 630 nm

2.6. Surface sediment (0-2 cm) granulometry and nutrient parameters

Sediment samples for analysis of total nitrogen (TN), total phosphorus (TP), total organic carbon (TOC), and biological oxygen demand (BOD) were collected using a Ponar grab (238-cm^2 open jaw area) by taking three vertical hauls of sediment at each sampling point. Sediment samples were collected at the beginning and the end of the culture period and then during fallowing two and four months following the culture period. The samples were placed in clean labelled sample bags and transported to KMFRI laboratory for analyses. Total nitrogen and TP in sediments were analyzed based on methods by Huang (1999). Oxidation Reduction potential (ORP) was measured using a multi-parameter meter (Hanna Instruments, Model 8519N, Singapore).

Analyses of grain size in sediments were performed as described by Egessa et al. (2018). A sample of wet sediment (15 ml) from each station was digested overnight in 30 ml of 30% H_2O_2 to remove organic matter. The excess H_2O_2 was then removed by boiling the sample. The soil particles were then dispersed using 5 ml of 10% sodium hexametaphosphate, agitated, and allowed to settle overnight, followed by wet sieving using 2, 1, and 0.5-mm diameter test sieves. The grain size fractions for each sample were put into weighed crucibles and oven-dried at 105°C to a constant dry weight followed by heating at 550 °C in a furnace for 4 h to obtain ash weight. The

amount of organic matter in a sample was then estimated as the difference between dry and ash weight.

2.7. Community composition and abundance of macro-benthic fauna

Macro invertebrate samples were collected using a Ponar grab by taking three vertical hauls of sediment at each sampling point, followed by sieving through a 400-µm mesh, to concentrate the sample. The concentrated samples were placed in clean, labeled sample bottles and preserved in 70% alcohol for taxonomic identification and enumeration in the laboratory. Macroinvertebrates were identified with the aid of different keys: Merrit & Cummins (1978); Quigley (1977); IFM (2006). Composition and density of macro-benthic fauna was monitored at the beginning of the study, on day 90 and day 180 of the culture period. They were also monitored on day 240 and 300 during the fallowing period.

The macroinvertebrate assemblage composition was determined using number of taxa (*S*), total number of individuals, and relative abundance of each taxon. The Shannon-Wiener diversity index (*H′*) was used to assess diversity as follows:

$$H' = \sum_{i=1}^{R} p_i \ln p_i$$

where p_i is the proportion of individuals belonging to the *i*th species. An associated evenness H'/H' max (Pielou, 1975) was also calculated.

2.9. Data analyses

Microsoft Excel 2016 was used for data entry and cleaning while STATISTICA version 6.0 was used for statistical analyses. Descriptive analysis of mean and Standard Error of the mean for water quality, order and genera abundance in stations and for sampling dates were carried out. One-way analysis of variance (ANOVA) was used to test for statistical significance in the mean variation of

water and sediment quality parameters between stations and time. Diversity of macro-benthic invertebrates was calculated by means of Shannon-Wiener index (Shannon and Weaver 1949) but due to small sample size, the data did not conform to assumptions of ANOVA, hence significant differences in Shannon diversity index (H') between station and time were determined using Kruskal-Wallis tests. The percentages of gravel (> 2 mm), very-coarse sand (1–2 mm), coarse sand (0.5–1 mm), and fine sand/silt/clay (< 0.5 mm) were computed for the stations to support interpretation of bottom faunal data. Anderson-Darling test and histogram plots were used to evaluate the data for normal distribution, and for homogeneity of variance, by assessing residual plots and employing Bartlett's and Levene's tests. The level of significance was estimated at $p < 0.01$.

3 RESULTS

3.1. Effects of cage aquaculture on nutrients and chlorophyll *a*

At the beginning of the production cycle, there were no significant differences in chlorophyll *a* ($F(3) = 0.056$, $P = 0.826$), TP ($F(3) = 0.345$, $P = 0.782$), TN ($F(3) = 0.039$, $P = 0.883$) and N:P molar ratio ($F(3) = 0.432$, $P = 0.746$) among different sampling stations (Figure 2). However, at the time of harvest, chlorophyll *a* ($F(3) = 5434.75$, $P < 0.0001$) , TP ($F(3) = 3468.93$, $P < 0.0001$) and TN ($F(3) = 39572.24$, $P < 0.0001$) had all increased significantly by 108%, 93% and 100% respectively by the cages (Figures 2a, b, c). The N:P molar ratio decreased by more than 40% by the cages and was significantly lower than at the other sampling stations at the time of harvest (Figure 2d). In contrast, there was no significant change in nutrient concentrations at any other sampling location during the production and fallowing periods (Figure 2). During the four-month

fallowing period, chlorophyll *a,* TP, TN, and N:P molar ratio by the cages recovered, with concentrations comparable to those observed at the other sampling stations.

3.2. Effects of cage aquaculture on zooplankton

The production cycle had significant effects on the composition of the zooplankton community at the cage station, but not at other locations (Figure 3). The zooplankton community consisted mainly of three taxonomic groups: Rotifera, Cladocera and Copepoda (Figure 3). A total of 14 species of zooplankton were identified in the samples collected. Eight species of Rotifera (*Brachionus falcatus, Brachionus angularis, Brachionus calyciflorus, Filinia* spp*., Asplanchna* spp*., Lecane* spp*., Euchlanis* spp*., Keratella tropica*), four species of Cladocera (*Moina micrura, Bosmina longirostris, Daphnia lumholtzi, Chydorus* spp.) and two species of Copepoda and nauplii (Copepod nauplii*, Cyclopoida* spp*., Calanoida* spp.) were identified (Appendix 1).

At the beginning of the production cycle, there was no significant difference ($P > 0.05$) in the abundance of the different taxonomic groups among the sampling sites (Figure 3). However, during the production cycle, the abundance of rotifers at the cage site increased significantly ($P < 0.001$) over six-fold while the abundance of Cladocera and Copepoda decreased ($P < 0.001$) by 47% and 58%, respectively. No significant changes in abundance during the production cycle were found at other sampling locations (Figure 3, Appendix I).

In addition to changes in total abundance, the abundance of species within each taxonomic group changed. At the beginning of the production cycle all the eight Rotifera species were present at the cage station, though not in similar proportions (8.5-15.9%). However, at the end of the culture period, when the total abundance of Rotifera was at a maximum (Figure 3), a total of six species (*B. falcatus, Filinia* spp*, Asplanchna* spp, *Lecane* spp*., Euchlanis* spp*., K. tropica*) out of the eight initially present at the cage station had disappeared from the samples. Dominating at the

cage site was *B. angularis* and *B. calyciflorus* that had increased in numbers at the cage station on day 180 (Appendix I). After fallowing period of 4 months the Rotifera returned to similar composition as before the production cycle began, with all the eight species present, though still not in similar proportions.

The composition of Cladocera at the cage site changed during the production cycle, while at other locations the composition did not change (Appendix I). On day 0, all four species were present in similar proportions (23.8-26.3%) at all sampling locations. At the end of the production cycle, only *Moina micrura* (100%) was present in the samples at the cage station and had nearly trebled in numbers. After fallowing, the composition of Cladocera returned to pre-production conditions, with all four species present.

The composition of Copepoda changed at the cage site during the production cycle but not at other locations (Appendix I). The initial composition of Copepoda was about equal numbers of Copepod nauplii, Calanoids and Cyclopoida. However, both Calanoids and Cyclopoida had disappeared from the cage site samples by day 180, with only Copepod nauplii dominating the cage site (100%). However, the species composition of Copepoda was restored to pre-production levels after 90 days of fallowing.

3.3. Effects of cage aquaculture on water quality

There was no significant difference in DO ($F(3) = 0.5454$ $P = 0.688$) (measured at 10 am), BOD ($F(3) = 0.036$, $P = 0.889$), Secchi depth ($F(3) = 0.356$, $P = 0.779$), and NH_3 ($F(3) = 0.045$, $P = 0.965$) (Figure 4) among sampling locations at the beginning of the production cycle. However, both DO ($F(3) = 424.6$, $P < 0.001$) and Secchi disk readings ($F(3) = 89.5$, $P < 0.0001$) decreased over time while BOD ($F(3) = 330.3$, $P < 0.0001$) and NH_3 ($F(3) = 386.0$, $P < 0.001$) increased progressively at the cage site (Figure 4). On day 180, the DO was reduced by 48.3%, Secchi depth

by 66.7% and the BOD and NH_3 increased by 181% and 35% respectively. During the fallowing period, the DO, BOD, Secchi depth, and NH_3 at the cage site recovered. Four months after harvesting there was no significant difference in DO ($F(3) = 0.048$, $P = 0.898$), BOD ($F(3) = 0.045$, $P = 0.899$), Secchi depth ($F(3) = 0.354$, $P = 0.789$), and NH_3 ($F(3) = 0.038$, $P = 0.969$) at different sampling sites (Figure 4). The DO ($F(3) = 0.046$, $P = 0.888$), BOD ($F(3) = 0.039$, $P = 0.989$), Secchi depth ($F(3) = 0.044$, $P = 0.889$) and NH_3 ($F(3) = 0.043$, $P = 0.899$) did not change significantly during the production cycle and fallowing period at any other sampling location. There were no significant differences in mean temperature (26.46 ± 1.22; $F(3) = 0.034$, $P = 0.973$), pH (7.96 ± 0.24; $F(3) = 0.041$, $P = 0.983$) and alkalinity (51.03 ± 1.45; $F(3) = 0.456$, $P = 0.749$) among the sampling sites at the beginning and at the end of the culture period. The estimated concentration of CO_2 never exceeded 5 $mg \cdot l^{-1}$.

Both DO and pH showed diurnal fluctuations, increasing during the day and decreasing at night (Figure 5). At the beginning of the production cycle, DO was consistently about 1 $mg \cdot L^{-1}$ lower and the pH about 0.1-0.2 units higher at the cage site than 500 m from the cages, otherwise the amplitude was similar. By the end of the culture period, the amplitudes of the diurnal fluctuations of DO and pH at the cage site were much larger than at the reference site. The lowest level of oxygen (1.5 mg L^{-1}) was recorded at 2 am in the morning at the cage site and corresponds to 21% oxygen saturation.

3.4. Surface sediment (0-2 cm) granulometry.

The surface sediment was mainly (> 85%) composed of gravel at all the sampling sites (Figure 6) and silt/clay was only 2-3%. This changed during the production cycle and, by the time of harvest, the bottom by the cages consisted mainly of silt/clay (85%) while gravel accounted for only 1% (Figure 6) which is consistent with the accumulation of organic matter on the bottom. No

significant changes in the composition of the surface layer were observed at other sampling sites during the production cycle. Following the 4-month fallowing period, the proportion of silt/clay decreased to 61% at the cage site, though still significantly lower ($P < 0.01$) than at other sampling sites.

At the beginning of the production cycle, there were no significant differences (P =0.7-0.9) in the mean concentrations of TOC, TP, and TN, or the levels of BOD and ORP in the bottom layer among the sampling sites (Figure 7). At the end of the production cycle, TOC ($F(3) = 5519.95$, $P < 0.0001$), TP ($F(3) = 14197.14$, $P < 0.0001$), TN ($F(3) = 254.46$, $P < 0.0001$) and BOD ($F(3) = 232.48$, $P < 0.0001$) had all increased at the cage station by 386.5%, 745.8%, 176.1% and 252.7%, respectively (Figure 7). The ORP at the cage site decreased from 122 mV to -110.4 mV during the production cycle, while remaining unchanged at other sampling locations. During the fallowing period, the chemical composition and ORP recovered partly but did not reach pre-production levels ($F(3) = 2542.35$, $P < 0.001$) (Figure 7).

3.5. Community composition and abundance of macro-benthic fauna

The macro-benthic fauna was composed of members from three phyla: Arthropoda, Annelida and Mollusca. Arthropoda was the richest phylum consisting of the class Insecta that had six orders (Ephemeroptera, Diptera, Trichoptera, Plecoptera, Odonata and Hemiptera). At the beginning of the production cycle, the most abundant group in all benthic samples was Diptera (300-305 individuals L^{-1}), followed by Odonata (100-102 individuals L^{-1}) and then Bivalvia (60-61 individuals L^{-1}) and there was no significant difference among the sampling sites (Figure 8). By the end of the culture period, the total number of individuals was reduced by 47% at the cage site (Fig. 8a) while the total numbers and composition of the macro-benthic fauna did not change at other locations (Figures 8b, 8c and 8d). On day 180 all Diptera, (Ephemeroptera, Plecoptera and

Trichoptera (EPT), Hemiptera, Hirudinae and Odonata had disappeared at the cage site (Fig. 8a) and the fauna consisted only of Bivalvia (52%), Gastropoda (39%) and Oligochaeta (9%).

At the beginning of the production period, there were 18 species of zoobenthos found underneath the cages and 22 species at the reference site (Appendix 2). By the end of the production cycle, only three species (*Physella* spp*, Sphaerium* spp *and Tubifex* spp.) were found underneath the cage, and 18 at the reference site (Appendix 2). Kruskal-Wallis test showed no significant differences ($H = 2$; $p = 0.399$) in the Shannon-Wiener mean diversity index of macroinvertebrate genera among the sites at the beginning of the study (Table 1). At the end of the study, the lowest mean Shannon-Weiner diversity was recorded at the cage site which was significantly different from the other sampling sites ($H = 2$; $p < 0.001$).

The composition of the macro-benthic fauna at the cage site did not recover to preproduction levels during the four-month fallowing period and on day 300 it was still dominated by gastropods (28%) and bivalves (36%) (Figure 8a). Diptera, EPT, and Odonata had reappeared in the samples at the end of the fallowing period but not to the previous abundance while Hemiptera was still absent. After four months of fallowing, the Shannon-Weiner diversity index remained lower at the cage site (Table 1).

4 DISCUSSION

The present study is the first of its kind that we are aware of to assess the environmental effects of cage aquaculture in tropical/subtropical waters, both during the production cycle and the subsequent fallowing period until the next production cycle commences. Cage aquaculture has significant effects on both the limnetic and benthic zones of the lake both with regard to water chemistry and with respect to species abundance, distribution and richness. However, these effects are restricted to the cage sites and dissipate quickly with distance from the cages such that at 50 m there was no evidence of changes. The changes at the cage site during production are largely

reversed in the limnetic zone during the four-month fallowing period. However, the effects of cage aquaculture on the benthic zone were not entirely reversed and suggest additive effects of subsequent production cycles that could lead to future disasters. These findings are now discussed in turn.

4.1. Limnetic effects

The present study shows that the effects of the cage aquaculture on the limnetic zone in the lake are primarily mediated through the increased concentrations of TN and TP (Figure 2). Unlike in conventional land-based aquaculture pond systems, cage systems do not use organic or inorganic fertilizers with high N and P content. Yet, they are essential elements for organismal development. Consequently, fish feeds for cages have been reported to contain higher P content than required by fish (Ackefors & Enell,1994; Von Sperling & Chernicharo, 2005; Musa et al., 2021b). Therefore, the observed highest level of TN (423.2 ± 1.4 µg L^{-1}) and TP (162.7 ± 5.6 µg L^{-1}) at the cage station by the end of the culture period could be from leaching from fish feeds and fecal matter, as well as metabolites. Previous research reported poor FCR (2.6) for fish feeds used in the study area (Musa et al., 2021b), that could have caused disproportionate increase in total P and N loadings. Hence, fish cage culture in freshwater lakes such as Lake Victoria raises concerns about water quality deterioration due to solid waste (Ngupula et al., 2012; Aura et al., 2018b) and soluble waste, especially nitrogen and phosphorus compounds. In this study, the progressive increase in chlorophyll *a* concentration, is an indication of increased algal biomass, found at the cage site during the production cycle followed the same pattern as the increased N and P concentrations (Figure 2), suggesting that the increased N and P concentrations at the cage site promoted the growth of phytoplankton.

The TP (62-69 $\mu g \cdot l^{-1}$), TN (218-220 $\mu g \cdot l^{-1}$) and chlorophyll *a* (7.6-8.4 $\mu g \cdot l^{-1}$) concentration recorded at all sampling sites before the production cycle started (Figure 2) are within the range of values reported for nearshore waters on Lake Victoria (Mwamburi et al., 2020; Simiyu et al., 2021; Deirmendjian et al., 2021). The observed N:P ratio of 7.5 at the cage site before production started and after two-month fallowing, in the present study, is similar to those reported in other studies (Guildford & Hecky, 2000; Mwamburi et al., 2020; Deirmendjian et al., 2021). The observed decrease in N:P molar ratio at the cage station by the end of culture period is at levels where phytoplankton production is limited by N rather than P (Guildford & Hecky, 2000; Mwamburi et al., 2020). These conditions favor heterocystous N-fixing cyanobacteria (Gikuma-Njuru & Hecky, 2005) and the decreased N:P molar ratio at the cage site during production may exacerbate this effect. Cyanobacterial bloom is a potential health risk and long-term exposure of Nile tilapia to cyanobacteria could accumulate the cyanotoxins in the fish tissue to be transferred to higher trophic levels (Mohamed et al., 2019). Even before commencement of fish cage culture, Lake Victoria has been reported to be highly eutrophic (Ochumba & Kibaara, 1989, Lungáayia et al., 2000, Kling et al., 2001). Despite the burgeoning industry within the lake, the fate and quantitative contribution of the new N and P sources emanating from cage aquaculture in Lake Victoria has yet to be understood.

There are six main influent rivers in the catchment of Lake Victoria, Kenya: Sio, Nzoia, Yala, Nyando, Sondu-Miriu and Kuja. Previous studies estimate the mean water discharge from the six rivers at 456.16 m^3s^{-1}, with TN and TP loading at 11.61 and 1.69 mgL^{-1}, respectively (LVEMP, 2005; Aura et al., 2021). Hence, agro-industrial and municipal sewerage discharges of TP and TN through the major rivers stands at 2,113,000 and 12,193,000 kg yr^{-1}, respectively. On the other hand, Anyanga cage culture site, the epicenter of cage aquaculture in Lake Victoria, has

been estimated to produce 20,480 kg of N and 970.7 kg of P each fish production cycle (Musa et al., 2021b). Therefore, agro-industrial and sewerage discharges contribute more than 2000 times the amount of P and almost 600 times the amount of N into the lake as compared to fish cage culture. These figures may even be higher if other seasonal rivers and streams are considered. With the current production levels, fish cage culture in Lake Victoria seems to contribute to increased nutrient loading to the lake ecosystem. However, with regard to nutrient loading in the lake, aquaculture-derived nutrients may tend to account for only a relatively small proportion (<1% of P or N) compared with agro-industrial and sewerage sources.

The present results reveal that the N and P concentrations dissipate quickly with increasing distance from the cages. In fact, the concentration of N and P did not change significantly during the production cycle in other locations, even as close as 50 m from the cages. A number of factors could contribute to this such as dilution, limited water exchange in and around the cages (due to presence of fish and clogged nets) and N and P being rapidly sequestered into algae. Contrary to best practices, the majority of cage farmers in Lake Victoria do not clean the cage nets to reduce clogging and fouling (Aura et al., 2018a), further limiting the water exchange around the cages.

In this study, increased phytoplankton density during the production cycle affected the diurnal fluctuations in DO and pH (Figure 5). At the beginning of the growth cycle, the diurnal fluctuations in DO and pH at the cage site were similar in magnitude to those at the reference site 500 m from the cages although the DO concentration was consistently about 1 $mg \cdot l^{-1}$ higher and pH about 0.16 units lower at the latter location (Figure 5a). The amplitude of DO and pH increased with time and by the end of the production cycle, increased phytoplankton density at the cage station (Figure 2a) contributed to larger amplitudes in DO and pH fluctuations (Figure 5b). The DO concentration was maximal during the afternoon due to photosynthesis and reached a

minimum just before sunrise. Diurnal fluctuations of pH were in phase with oxygen as CO_2 is consumed to produce O_2 (Figure 5) and the removal of CO_2 in turn increased pH due to the carbonate equilibrium. At the end of the production period (Day 180) diurnal variations in algae respiration and photosynthesis caused fluctuation in oxygen concentrations to reach minimum mean levels of 1.5 $mg \cdot L^{-1}$ (19% of air saturation) at 2 am and it is likely that the oxygen levels may have fallen even further until dawn. During the day, oxygen concentration came up to 7.8 $mg \cdot L^{-1}$ (118% of air saturation) at the cage site. The BOD increased (Figure 4b) as the algal density increased (Figure 2a), although an increased bacterial activity in the water may also have contributed to the BOD (Boyd and Tucker, 1998). The high BOD resulted in nearly 50% reduction in morning DO at the cage site from the beginning to the end of the production cycle (Figure 4a).

Growth, feed intake, disease resistance and survival of Nile tilapia is significantly reduced when the oxygen saturation falls below 50% of air saturation (Kolding et al., 2008; Tran-Duy et al., 2012; Abdel-Tawwab et al., 2014). Large diurnal fluctuations in O_2 levels such as those observed in the current study may also cause a reduction in growth even if the oxygen saturation remains above 100% for most of the hours of daylight (Tsadiki & Kutty, 1987). At the beginning of the production cycle, the minimum DO values at night fell just below 49% saturation (Figure 5a). However, by the end of the production cycle the oxygen saturation was below 50% for more than 10 hours each night (Figure 5b) and near or below 20% saturation for several hours. This suggests that the nightly fall in oxygen levels would have reduced growth, feed efficiency and survival of the fish which in turn would have reduced production and increased juvenile and feed costs. In contrast, the estimated maximum CO_2 concentration (~5 $mg \cdot l^{-1}$) is well below the tolerable levels of 10 $mg \cdot l^{-1}$ for warm water species (Timmons et al., 2018).

Increased phytoplankton production can promote the growth of zooplankton (Sládeček, 1983; Tasevska et al., 2010). In the present study, the abundance of rotifers increased more than six-fold during the production cycle while the abundance of Cladocera and Copepoda was reduced by 47% and 57%, respectively (Figure 3). There were primarily two species of Rotifera that increased in abundance, *B. angularis,* and *B. calyciflorus*. Rotifers, with their relatively short life cycle, are known to respond more quickly to increased eutrophication than other species of zooplankton, in particular those of the genus *Brachionus* (Sládeček, 1983; Radwan & Popiolek, 1989; Tasevska et al., 2010).

Previous studies in the Lake Victoria basin have also found that the numbers and biomass of rotifers increase in response to eutrophication (Vincent et al., 2012), especially *B. angularis*, as was observed in the present study. Eutrophication in Lake Victoria is increasing and this may increase the background levels of rotifers at all sampling locations which are close to shore in a protected bay (Ngupula, 2013). However, the observed increased abundance of rotifers at the cage site was likely primarily due to the phytoplankton bloom caused by the leaching of nutrients from the fish farming. Copepoda and Cladocera are more sensitive to reduced water quality than Rotifers (Vincent et al. 2012; Dias et al., 2012) and this may in part explain why their numbers were reduced. The shift in the zooplankton community composition at the cage site may also be due to increased predation by the growing biomass of fish. Due to their small size, predation is likely to affect the abundance of rotifers less than the other two groups (Dumont et al., 1975; Mwebaza-Ndawula et al., 2001, 2004; Lars-Anders et al., 2004).

The effects on the limnetic zone had disappeared after four months of fallow. Two months after the production cycle ended (Day 240), both the N and P concentrations had returned to baseline levels. Similarly, as the TN and TP levels decreased during the fallowing period, so did

algal density. As a result, the zooplankton community recovers, particularly reaffirmed by the reduction in the relative contribution of copepod nauplii and reappearance of Calanoida (see Appendix 1), suggesting that copepod nauplii could represent an important bioindicator of organic loading. Dias et al. (2012) affirms that higher proportions of calanoids in freshwaters indicates low eutrophy while nauplii are an indicator of a more productive habitat. The reappearance of calanoids indicate that the water quality at the cage site had completely recovered after 4 months fallow period. Notably, the low relative density of rotifers (14%) at the cage site by end of 4 months fallow period as compared to harvesting time (70%), confirms that water quality had recovered as rotifers are more responsive to water quality changes, hence are good indicators of trophic conditions (Gannon & Stemberger, 1978; Sladecek, 1983; Baranyi et al., 2002; Tasevska et al., 2010). The recovery of the environment (water) is more rapid, probably due to the small spatial scale of the impact (< 50 m). It could also be due to good water circulation caused by the absence of fish in cages after harvesting (Kutti et al., 2007). In summary, our results show that all effects of cage aquaculture on the limnetic zone dissipate after a four-month fallowing period. Hence, the limnetic zone in Lake Victoria is able to absorb and dilute perturbations within four months fallowing due to periodical lake turnover.

4.2. Benthic effects

The high TOC recorded under the cages by the time of harvest indicate high organic matter accumulation, mainly from food waste and fish excrement which have high P and N content (Figure 7). It is likely that the loss of P from the sediment is minimal (Holby & Hall, 1991; Von Sperling & Chernicharo, 2005) contributing to increased P accumulation under the cages. The high P content in the sediment under the cages reduced the N:P molar ratio from 2.3 to 0.6. Similar findings have been reported from Hong Kong where the N:P molar ratio was reduced from 8.75 at

the reference site to 1.83 at the cage station (Gao et al., 2005). Low TN:TP molar ratio in sediments is associated with increased phosphorous loading from the fish feeds, raising concerns of eutrophication.

The accumulated organic matter on the bottom is a favorable substrate for various organism and, hence, in the current study, BOD increased in the sediment (Nickel et al., 2003) resulting in reduced oxygen levels. This is confirmed by the progressively more negative ORP in the sediment below the cages during the production period (Figure 7) which indicates anaerobic bacterial metabolism. One result of anaerobic bacterial metabolism is the build-up of hydrogen sulphide and methane which is highly toxic to fish. These effects are expected to be more pronounced in cages sited in shallower waters, similar to the study area. Indeed, incidences of isolated fish kills have been reported in fish cages at Nyenye Got, Honge and Anyanga beaches in Lake Victoria, Kenya. Although preliminary results indicated low dissolved oxygen concentrations (0.64 mgL^{-1}) as the key cause of the fish kills (Njiru et al., 2018), hydrogen sulphide toxicity may have also been one of the main contributors to mass mortalities. This calls for further investigations into the effects of hydrogen sulfide on fish performance, especially in African inland waters where most cages are sited in shallow areas, with no fallowing periods.

The large amounts and deposition of organic matter beneath the cages in the current study may have contributed to changes in the benthic macroinvertebrate communities (Schmidlin & Baur, 2007). The reduced oxygen levels recorded at the cage site by the end of the culture period will have favored certain species and the increased amount of silt/clay on the bottom is potential food that can attract macroinvertebrates. This could in part have influenced the community composition and diversity of macroinvertebrates (Kalantzi & Karakassis, 2006; Nabirya et al., 2016). Certainly, the shift from arthropods to mollusks (bivalves and gastropods) and annelids

(oligochaetes) at cage site by the end of the culture period is consistent with organic enrichment (Mavuti & Litterick, 1991; Ngupula et al., 2012). Oligochaete annelids have often been cited as thriving in freshwaters receiving organic waste (Dobrowolski, 1987; Camargo, 1992; Miserendino & Pizzolon, 2000), an indication of negative effect of cage culture on the lake environment. Besides, the reduction in number of taxa and the dominance by the opportunistic species *Physella* spp, *Sphaerium* spp and *Tubifex* sp*p.*, at the cage sites indicates disturbance of the benthic faunal community in the immediate vicinity of the cages. These opportunistic species i.e. *Physella* spp, *Sphaerium sp* and *Tubifex* spp., are known for their high tolerance to pollution (Buss et al., 2002). Moreover, the disappearance of sensitive taxa such as EPT (Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies)) at the cage site by the end of the study indicated an ecologically impaired site, attributable to degradation from cage culture activities (Johnson et al., 1993). This is reaffirmed by the low Shannon-Wiener values (0.82) recorded at the cage site by the end of the culture period, an indication of loss of diversity.

The present study indicates that the effect of cage aquaculture on the benthic communities is fairly localized suggesting that the impact from cage fish culture is restricted to an area within 50 m radius of the cages. Guo & Li (2003) and Srithongouthai & Tada (2017) reported that the impact of cage culture extended up to 20 m and 10 m, respectively, outside the cage area in lakes in China and Japan, which is line with the findings of the current study. The extent of impact of aquaculture effluents is dependent on a number of factors, including the area used for culture, depth of site, age of the farm, stocking densities, hydrodynamics, sediment adsorption, current speed, production volume of the farm and management. The localized impact of aquaculture in the study area, may, in part be due to the shallow waters (< 5 m) under the cages and concentration of cages in one site in an enclosed bay. High proportion of silt/clay under the cages has been reported

to decrease the footprint of cage aquaculture (Mazzola et al., 2000; Kakantzi & Karakassis, 2006). The localized impact in the current study could also be due to the high silt/clay contents recorded underneath the cages by the end of the culture period.

In contrast to the limnetic zone, the findings indicate that the benthic zone under the cages does not recover fully during the four-month fallowing period. The organic material that accumulated over the production cycle had not disappeared after the fallowing period (Figure 6). Similarly, the levels of BOD, TN, ORP and TP at the cage site had not returned to preproduction levels after four-month fallowing (Figure 7). The composition of the meiofaunal had not returned to the levels recorded prior to commencement of cage fish farming four months after the end of the previous production cycle (Figure 8). However, other orders such as EPT, reappeared in some replicates after 4 months fallow period, comprising only 0.9% under cage site, which probably highlights their limited chances of survival in such areas, especially if culture continues. However, the reappearance of EPT, albeit in small numbers, could indicate that the system was on its way to recovery as this group is an important bioindicator of organic pollution. Nonetheless, low diversity recorded at the cage site, reaffirms that the cage site had not completely recovered after 4 months. Hence, the benthic zone in Lake Victoria is not able to absorb and dilute perturbation within 4 months fallowing period. Continued production at the same locations will result in increased accumulation of organic material that may eventually have dire consequences for the fish due to release of hydrogenated sulfur from sediments beneath the cages. Mass mortalities of tilapia have been reported in the study area in 2016 (Njiru et al., 2018), confirming the risks associated with such enterprise. Hence, with the current management practices, cage fish farming in Lake Victoria could be a disaster in waiting. In order to reduce the risk of catastrophes, the fallowing period must be extended which requires the cages to be relocated between production cycles. These results also

show that cage aquaculture in Lake Victoria, a system that is already under severe environmental stress, is highly questionable.

CONCLUSION AND RECOMMENDATIONS

With rapid growth of fish cage culture in African inland waters, it is important to understand the quantity, impact and the fate of aquaculture derived nutrients. Nile tilapia cage culture in the lake have significant effects on water and bottom sediment quality, especially with respect to nutrients, planktons and macroinvertebrates, although it is restricted to close vicinity of the cages, with no broader ecosystem impact. The impacts on water at the cage sites are neutralized during the four-month fallowing period. However, the findings suggested that sediment and meiofaunal recovery were far from complete after four months fallow period, an indication that the system is not able to assimilate the nutrients quickly enough and this may turn into an environmental disaster. Moving the cages slightly before the start of a new cycle by 50-100 m may allow the benthic communities to recover and alleviate the problem. In addition, the fallowing period should be six months, contrary to the current practice. Intensive and unchecked cage culture practices in the African inland lakes will highly likely result in negative responses in lake environments. Hence, the current efforts to promote commercial cage fish culture enterprises in Lake Victoria and the Great Lakes Region must proceed with caution especially regarding the location of cages within each site to minimize loss of environment quality, which can cause undesirable changes in natural biological productivity processes. In any case, regular environmental monitoring programs should be strictly implemented for all cage fish culture enterprises.

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ETHICAL APPROVAL All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

DATA AVAIL ABILITY STATEMENT

The data for this manuscript will be available upon request.

REFERENCES

Abdel-Tawwab, M., Hagras, A.E., Elbaghdady, H.A.M., & Monier, M.N. (2014). Dissolved oxygen level and stocking density effects on growth, feed utilization, physiology, and innate immunity of Nile tilapia, *Oreochromis niloticus*. *Journal of Applied Aquaculture*, 26, 340–355.

Ackefors, H., & Enell, M. (1994). The release of nutrients and organic matter from aquaculture systems in Nordic countries. *Journal of Applied Ichthyology* 10, 225–241.

Akintola, S. L., Brown, A., Bakare, A., Osowo, O. D., & Omolola, B. (2013). Effects of Hot Smoking and Sun Drying Processes on Nutritional Composition of Giant Tiger Shrimp (*Penaeus monodon*, Fabricius, 1798). *Polish Journal of Food and Nutrition Sciences*, 63(4), 227–237. https://doi.org/10.2478/v10222-012-0093-1.

Anderson, J.L., Asche, F., Garlock, T., & Chu, J. (2017). Aquaculture: Its role in the future of food. In *Frontiers of Economics and Globalization*; Emerald Publishing Limited: Bradford, UK, Volume 17, pp. 159–173.

APHA (2005). American Public Health Association Standard Methods for the Examination of Water and Wastewater, 21st edn. Washington, D.C., APHA-AWWA-WEF, ISBN 0875530478

Aura, M.C., Musa, S., Yongo, E., Okechi, J., Njiru, J.M., Ogari, Z. et al. (2018a). Integration of mapping and socio-economic status of cage culture: Towards balancing lake-use and culture fisheries in Lake Victoria, Kenya. *Aquaculture Research*, 49(1), 532–545. https://doi.org/10.1111/are.13484.

Aura, C. M., Nyamweya, C., Njiru, J.M., Musa, S., Ogari, Z., & Wakwabi, E. (2018b). Exploring the demarcation requirements of fish breeding and nursery sites to balance the exploitation, management and conservation needs of Lake Victoria ecosystem. *Fisheries Management and Ecology,* 26, 451-459.

Aura, C.M., Nyamweya, C.S., Njiru, J.M., Omondi, R., Manyala, J., Musa, S. et al. (2021). Using the Multi-metric Index of Biotic Integrity methodological approach to determine the major river catchment that most pollutes a lake. *Aquatic Ecosystem Health and Management Society*, 24(1), 12–20.

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*ogy, 47, 473–82.

Bondad-Reantaso, M. G., Subasinghe, R. P., Arthur, J. R., Ogawa, K., Chinabut, S., Adlard, R. et al. (2005). Disease and health management in Asian aquaculture. *Veterinary Parasitology*, 132(3-4), 249-72. https://doi.org/10.1016/j.vetpar.2005.07.005.

Boyd, C. E., Lim, C., Queiroz, J., Salie, K., & de Wet, L. (2008). Best management practices for responsible aquaculture. Report. 24 pp.

Boyd, C. E., & Tucker, C.S. (1998). Pond aquaculture water quality management. Kluwer Academic Publishers, New York. 711 pp.

Braaten, R. (2007). Cage aquaculture and environmental impacts. In A. Bergheim (Ed.). *Aquacultural engineering and environment* (Vol. 661, pp. 49–91). Research Signpost: Kerala.

Buss, D.F., Silva, M.M., Darcilio, B., & Nessimian, J. (2002). Erratum: Influence of water chemistry and environmental degradation on macroinvertebrate assemblages in a river basin in south-east Brazil. *Hydrobiologia*, 481, 125-136.

Camago, J.A. (1992). Temporal and spatial variations in dominance, diversity and biotic indices along a limestone stream receiving a trout farm effluent. Water Air Soil Pollution, 63, pp. 343-359.

Carrol, M.L., Cochrane, S., Fieler, R., Velvin, R., & White, P. (2003). Organic enrichment of sediments from salmon farming in Norway: environmental factors, management practices and monitoring techniques. *Aquaculture,* 226, 165–180.

Dauda, A.B., Ajadi, A., Tola-Fabunmi, A.S., & Akinwole, A.O. (2019). Waste production in aquaculture: Sources, components and managements in different culture systems. *Aquaculture and Fisheries*, 4(3), 81-88.

Deirmendjian, L., Descy, J., Morana, C., Okello, W., Stoyneva-Gartner, M.P., Bouillon, S. et al. (2021). Limnological changes in Lake Victoria since the mid-20th century. *Freshwater Biology*, 66(8): 1630-1647.

Dias, J. D., Simões, N. R., & Bonecker, C. C. (2012). Net cages in fish farming: a scientometric analysis. *Acta Limnologica Brasiliensia*, 24(1), 12–17. https://doi.org/10.1590/S2179-443 975X2012005000022.

Dobrowolski, Z. (1987). The effect of cage culture of Rainbow trout on the distribution and stability of macrobenthos in eutrophic Lake Letowskie. *Ekologia Polska*, 35, 611-638.

Dumont, H. J., Van De Velde, I. & Dumont, S. (1975). The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia*, 19, 75–97.

Dussart, B.H., & Defaye, D. (1995). Introduction to the Copepoda. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World**.** SPB Academic Publishing, 277pp.

Egessa, R., Pabire, G.W., & Ocaya, H. (2018). Benthic macroinvertebrate community structure in Napoleon Gulf, Lake Victoria: effects of cage aquaculture in eutrophic lake. *Environmental Monitoring and Assessment,* 190, 112.

FAO. (2020). The State of the World Fisheries and Aquaculture. Sustainability in action. Rome. https://doi.org/10.4060/ca9229en

FAO. (2016) The State of the World Fisheries and Aquaculture. http://www.fao.org/3/i5555e/i5555e.pdf.

Gannon, J. E. & Stemberger, R. S. (1978). Zooplankton (especially crustaceans and rotifers) as indicators of water quality. *Transactions of the American Microscopical Society*, 97, 16–35.

Gao, Q., Cheung, K., Cheung, S., & Shin, P. (2005). Effects of nutrient enrichment derived from fish farming activities on macroinvertebrate assemblages in a subtropical region of Hong Kong. *Marine Pollution Bulletin*, 51, 994−1002.

Garcia de Souza, J. R., Solimano, P. J., Maiztegui, T., Baigun, C. R. M., & Colautti, D. C. (2015). Effects of stocking density and natural food availability on the extensive cage culture of

pejerrey (*Odontesthes bonariensis*) in a shallow Pampean lake in Argentina. *Aquaculture Research*, 46, 1332–1344. https://doi.org/10.1111/are.12286

Gikuma-Njuru, P., & Hecky, R. E. (2005). Nutrient concentrations in Nyanza Gulf, Lake Victoria Kenya: Light limits algal demand and abundance. *Hydrobiologia*, 534, 131–140.

Greenberg, A.F., Clesceri, L.S., & Eaton, A.D. (1992). Standard methods for examination of water and waste water. 18th edition. American Public Health Association, Washington, D.C. USA.

Guildford, S.J. & Hecky, R.E. (2000). Total nitrogen, total phosphorus and nutrient limitation in lakes and oceans: is there a common relationship? *Limnology and Oceanography*, 45, 1213–1223.

GUO, L., & LI, Z. (2003). Effects of nitrogen and phosphorus from fish cage-culture on the communities of a shallow lake in middle Yangtze river basin of China. *Aquaculture*, 226 (1-4), 201-212.

Hamilton, S.E., Gallo, S.M., Krach, N., Nyamwea, C.S., Okechi, J.K., Aura, C.M. et al. (2020). The use of unmanned aircraft systems and high resolution satellite imagery to monitor tilapia fish cage aquaculture expansion in Lake Victoria, Kenya. *Bulletin of Marine Science*, 96, 71-93.

Henderson, R. J., Forrest, D. A. M., Black, K. D., & Park, M. T. (1997). The lipid composition of sea loch sediments underlying salmon cages. *Aquaculture*, 158(1-2), 69–83. https://doi.org/10.1016/S0044-8486(97)00207-X.

Holby, O., & Hall, P.O.J. (1991). Chemical fluxes and mass balances in a marine fish. *Marine Ecology Progress Series*, 70(3), 263-272.

Huang, X.F. (1999). Survey, observation and analysis of lake ecology. In: Sun HL, Liu GS (eds) Standard methods for observation and analysis in Chinese Ecosystem Research Network, Series V. Standards Press of China, Beijing (in Chinese)

Huang, C.H. (1997). Aquaculture and the endogenous damage cost of water pollution: the case of Taiwan. *Aquaculture Economics and Management*, 1, 99–108.

Institute of Fisheries & Macroinvertebrate Identification, IFM (2006). Aquatic Ecology. Department of Biology, Sweden: Linkoping University Press. 21pp.

Jeffrey, S.W., & Humphrey, G.F. (1975). New spectrophotometric equations for determining chlorophyll a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochemie und Physiologie der Pflanzen*, 167, 191-194.

Johnson, R. K., Wiederholm, T., & Rosenberg, D. M. (1993). Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. In Rosenberg, D. M. & Resh, V. H. (eds), Freshwater Biomonitoring and Benthic Macroinvertebrates. Chapman & Hall, New York: 488 pp.

Kakantzi, I., & Karakassis, I. (2006). Benthic impacts of fish farming: Meta-analysis of community and geochemical data. *Marine Pollution Bulletin,* 52, 484– 493.

Kamadi, G. (2018). Floating Fish Farms Become a Threat to Lake Victoria. Business Today. https://businesstoday.co.ke/floating-fish-farms-become-threat-lake-victoria/. Accessed 15 May 2019.

Karakassis, I., Tsapakis, M., & Hatziyanni, E. (1998). Seasonal variability in sediment profiles beneath fish farm cages in the Mediterranean. *Marine Ecology Progress Series*, 162, 243–252. https://doi.org/10.3354/meps162243.

Kashindye, B. B., Nsinda, P., Kayanda, R., Ngupula, G. W., Mashafi, C. A., & Ezekiel, C. N., (2015). Environmental impacts of cage culture in Lake Victoria : the case of Shirati Bay - Sota , Tanzania. *SpringerPlus*. https://doi.org/10.1186/s40064-015-1241-y.

Kifuko, R. (2015). The state of cage fish farming in Uganda: actors, enabling environment, challenges and way forward. *International Journal of Education and Research*, 3(3), 483–488.

Kling, H.J., Mugidde, R., & Hecky, R.E. (2001). Recent changes in the phytoplankton community of Lake Victoria in response to eutrophication. In: M. Munawar, R.E. Hecky (Eds.), Great Lakes of the World: Food Webs, Health and Integrity, Backhuys, Leiden (2001), pp. 47-66.

Kolding, J., Haung, L., & Stefansson, S. (2008). Effect of ambient oxygen on growth and reproduction in Nile tilapia (*Oreochromis niloticus*). *Canadian Journal of Fisheries and Aquatic Sciences*, https://doi.org/10.1139/F08-059

Korovchinsky, N. M. (1992). Sididae and Holopediidae. Guides to the identification of the Microinvertebrates of the Continental Waters of the World. SPB Acad. Publ., The Hague, 82 pp.

Koste, W., & Shiel, R. J. (1987). Rotifera from Australian inland waters. 11. Epiphanidae and Brachionidae (Rotifera : Monogononta). *Invertebrate Taxonomy*, 7, 949-1021.

Kutti, T., Hansen, P.K., Ervik, A., & Hoisaeter, T. (2007). Effects of organic effluents from a salmon farm on a fjord system. II. Temporal and spatial patterns in infauna community composition. *Aquaculture,* 262, 355-366.

Lars-Anders, H. A., Gyllstrom, M., Stahl-Delbanco, A. & Svensson, M. (2004). Responses to fish predation and nutrients by plankton at different levels of taxonomic resolution. *Freshwater Biology,* 49, 1538–50.

Lung'ayia H., Sitoki, L., & Kenyanya, M. (2001). The nutrient enrichment of Lake Victoria (Kenyan waters). *Hydrobiologia*, 458,75–82. https://doi.org/10.1023/A:1013128027773

LVEMP (2005). Lake Victoria Environmental Management Project. National Water Quality Synthesis Report, Kisumu (Kenya), p. 431. https://www.semanticscholar.org/paper/National-water-quality-synthesis-report%2C-Kenya.-Gikuma-Njuru-Abuodha/7ac0693da5dd211825382da4bda8a41f66886ca8. Accessed on 21/6/22.

Mavuti, K. M. & Litterick, M. R. (1991). Composition, distribution and ecological role of zooplankton community in Lake Victoria, Kenya waters. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen*, 24, 1117–22.

Mazzola, A., Mirto, S., La Rosa, T., Fabiano, M., & Danovaro, R. (2000). Fish-farming effects on benthic community structure in coastal sediments: analysis of meiofaunal recovery. *ICES Journal of Marine Science,* 57(5), 1454–1461. https://doi. org/10.1006/jmsc.2000.0904.

Merritt, R.W., & Cummins, K.W. (1978). An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publishing Company, Iowa. USA.

Miserendino, M.L & Pizzolon, L.A. (2000). Macroinvertebrates of a fluvial system in Patagonia: Altitudinal zonation and functional structure. *Hydrobiologia*, 150, 55-83.

Mohamed, Z., Ahmed, Z., & Bakr, A. (2019). Assessment of phytoplankton species in gut and feces of cultured tilapia fish in Egyptian fishponds: Implications for feeding and bloom control. *Acta Limnologica Brasiliensa*, 31, e27. DOI: 10.1590/s2179-975x8418.

Musa, S., Aura, C.M., & Okechi, J.K. (2021a). Economic analysis of tilapia cage culture in Lake Victoria using different cage volumes. *Journal of Applied Aquaculture*, https://doi.org/10.1080/10454438.2021.1884632.

Musa, S., Aura, C.M., Tomasson, T., Sigurgeirsson, O., Thorarensen, H. (2021b). A comparative study of the effects of pelleted and extruded feed on growth, financial revenue and nutrient loading of Nile tilapia (Oreochromis niloticus L.) cage culture in a lacustrine environment. Journal of applied Aquaculture. DOI: 10.1080/10454438.2021.2011528

Musinguzi, L., Lugya, J., Rwezaula, P., Kamya, A., Nuwahereza, C., Halafo, J. et al. (2019). The extent of cage aquaculture, adherence to best practices and reflections for sustainable aquaculture on African inland waters. *Journal of Great Lakes Research,* https://doi:10.1016/j.jglr.2019.09.011.

Mwamburi, J., Basweti, G., Owili, M., Babu, J., & Wawiye, P. (2020). Spatio-temporal trends of nutrients and physico-chemical parameters on lake ecosystem and fisheries prior to onset of cage farming and re-opening of the Mbita passage in the Nyanza Gulf of Lake Victoria. *Lakes and Reservoirs Research and Management for Sustainable Use*, 25:292–313. https://doi.org/10.1111/lre.12329

Mwebaza-Ndawula, L., Kiggundu, V., & Pabire, G. (2001). Invertebrate communities of Nabugabo lakes: avital support resource for the fisheries and ecosystem diversity. In: A Compilation of Scientific Information on Nabugabo Ramsar Site (eds H. Busulwa, P. G. Mafabi & L. Mwebaza-Ndawula), pp. 20–30. JOSU Links (U) Ltd Kampala, Nabugabo, Uganda.

Mwebaza-Ndawula, L., Kiggundu, V. & Pabire Ghandhi, W. (2004). The status and significance of invertebrate communities. In: Challenges for Management of the Fisheries Resources,

Biodiversity and Environment of Lake Victoria, 1st edn (eds J. S. Balirwa, R. Mugidde & R. Ogutu-Ohwayo), pp. 153–71. Fisheries Resources Research Institute, Jinja.

Mwebaza-Ndawula, L., Kiggundu, V. Magezi, G., Naluwayiro, J., Gandhi-Pabire, W., & Ocaya, H. (2013). Effects of cage fish culture on water quality and selected biological communities in northern Lake Victoria, Uganda. *Uganda Journal of Agricultural Sciences*, 14(2), 61 – 75.

Nabirye, H., Mwebaza-Ndawula, L., Bugenyi, F. W. B., & Jones, F. (2016). The evaluation of cage fish farming effects on water quality using selected benthic macro-invertebrate community parameters in the Napoleon gulf, northern Lake Victoria. *International Journal of Fisheries and Aquatic Sciences*, 4(1), 42–50.

Ngupula, G.W. (2013). How Does Increased Eutrophication and Pollution in the Lake Victoria Waters Impacts Zooplankton? *Journal of Environment and Ecology,* 4(2):151. DOI: 10.5296/jee.v4i2.4397.

Ngupula, G.W., & Kayanda, R. (2010). Benthic macrofauna community composition, abundance and distribution in the Tanzanian and Ugandan inshore and offshore waters of Lake Victoria. *African Journal of Aquatic Science,* 35(2), 185–192.

Ngupula, G.W., Ezekiel, C.N., Kimirei, I. A., Mboni, E., & Kashindye, B.B. (2012). Physical and chemical characteristics of the Tanzanian inshore and offshore waters of Lake Victoria in 2005–2008. *African Journal of Aquatic Science*, 37(3), 339-345.

Nickell LA, Kenneth DB, Hughes D, Overnell J, Brand T, Nickell TD, Breuer E, Harvey SM (2003). Bioturbation, sediment fluxes and benthic community structure around a salmon cage farm in Loch Creran, Scotland. J Exp Mar Biol Ecol 285–286:221–233.

Njiru, J.M., Aura, C.M., & Okechi, J.K. (2018). Cage fishing culture in Lake Victoria: A boon or disaster in waiting? *Fisheries Management and Ecology*, Review Article: 1 – 9.

Njiru, J., & Aura, C.M. (2019). Cage farming can protect Lake Victoria's fish. But regulations need tightening. The Conversation. https://theconversation.com/cage-farming-can-protectlake-victorias-fish-but-regulations-need-tightening-112641. Accessed 20 March 2019.

Obiero, K.O., Meulenbroek, P., Drexler, S., Dagne, A., Akoll, P., Oding, R. et al. (2019). The Contribution of Fish to Food and Nutrition Security in Eastern Africa: Emerging Trends and Future Outlooks. *Sustainability*, 11:1636. doi:10.3390/su11061636

Ochumba, P.B.O., & Kibaara, D.I. (1989). Observations on blue-green algal blooms in the open waters of Lake Victoria, Kenya. *African Journal of Ecology,* 27(1), 23–34. https://doi.org/10.1111/j.1365-2028.1989.tb00925.x

Perez, O.M., Telfer, T.C. & Ross, L.G. (2005). Geographical Information Systems-based models for offshore floating marine fish cage aquaculture site selection in Tenerife, Canary Islands. *Aquaculture Research*, 36, 946-961.

Phillips, M.J., Beveridge, M.C.M., & Ross, L.G. (1985). The environmental impact of salmonid cage culture on inland fisheries: present status and future trends. *Journal of Fish Biology*, 27 (Suppl. A), 123–127.

Pielou, E. C. (1975). Ecological diversity. John Wiley & Sons, New York, 165 pp.

Porrello, S., Tomassetti, P., Manzueto, L., Finoia, M. G., Persia, E., Mercatali, I., & Stipa, P. (2005). The influence of marine cages on the sediment chemistry in the Western Mediterranean Sea. *Aquaculture*, 249(1-4), 145–158. https://doi.org/10.1016/j.aquaculture.2005.02.042.

Quiley, M. (1977). Invertebrates of Streams and Rivers. Key to Identification. Bedford Square, London: Academic Press. 21pp.

Radwan, S., & Popiolek, B. (1989). Percentage of rotifers in spring zooplankton in lakes of different trophy. *Hydrobiologia*, 186/187, 235–386.

Schmidlin, S., & Baur, B. (2007). Distribution and substrate preference of the invasive clam Corbicula fluminea in the river Rhine in the region of Basel (Switzerland, Germany, France). *Aquatic Sciences*, 69(1), 153–161. https://doi.org/10.1007/s00027-006-0865y.

Segers, H.H. (1995). A reappraisal of the Scaridiidae (Rotifera, Monogononta). *Zoologica Scripta*, Vol. 24, No. 2, pp. 91-100.

Sladecek, V. (1983). Rotifers as indicators of water quality. *Hydrobiologia,* 100, 169–201.

Smirnov, N.N. (1996). Cladocera: the Chydorinae and Sayciinae (Chydoridae) of the world. Guides to the identification of the microinvertebrates of the continental waters of the world II. Amsterdam: SPB Academic Publishing, 197 pp.

Srithongouthai, S., & Tada, K. (2017). Impacts of organic waste from a yellowtail cage farm on surface sediment and bottom water in Shido Bay (the Seto Inland Sea, Japan). *Aquaculture*, 471: 140-145.

Simiyu, B.M., Amukhuma, H.S., Sitoki, L., Okello, W., Kurmayer, R. (2021). Interannual variability of water quality conditions in the Nyanza Gulf of Lake Victoria, Kenya. *Journal of Great Lakes Research*, 48(1), 97-109.

Tasevska, O., Kostoski, G., & Guseska, D. (2010). Rotifers Based Assessment of the Lake Dojran Water Quality. Balwois, Ohrid.

Timmons, M.B., Guerdat, T., Vinci, B.J. (2010). Recirculating Aquaculture, 4th edition. Ithaca Publishing Company, Ithaca, NY. 700 pp.

Tran-Duy, A., van Dam, A.A., & Schrama, J.W. (2012). Feed intake, growth and metabolism of Nile tilapia (*Oreochromis niloticus*) in relation to dissolved oxygen concentration. *Aquaculture Research*, 43, 730–744.

Tsadiki, G.G. & Kutty, M.M. (1987). Influence of ambient oxygen on feeding and growth of the tilapia *Oreochromis niloticus* (Linnaeus). Working paper, ARAC/87/WP/10

Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N. Leavitt, P.R., Brown, E.T., Talbot, M.R. & Hecky, R.E. (2002). History and timing of human impact on Lake Victoria, East Africa. *Proceedings of the Royal Society B*, 269, 289-294.

Villnas, A., Perus, J., & Bonsdorff, E. (2011). Structural and functional shifts in zoobenthos induced by organic enrichment - Implications for community recovery potential. *Journal of Sea Research*, 65: 8−18.

Vincent, K., Mwebaza-Ndawula, L., Makanga, B., & Nachuha, S. (2012). Variations in zooplankton community structure and water quality conditions in three habitat types in northern Lake Victoria. *Lakes & Reservoirs: Research and Management*, 17, 83–95.

Von Sperling, M. & Chernicharo C.A.L. (2005). Biological Wastewater Treatment in Warm Climate Regions. IWA Publishing, London, UK.

Wu, R.S.S. (1995). The environmental impact of marine fish culture: Towards a Sustainable Future. *Marine Pollution Bulletin*, 31, 159–166.

APPENDIX I Zooplankton species, relative contribution (%) and mean densities (parentheses) ind L^{-1} (± SEM) across cage culture sampling sites

	Day0 (Beginning of culture period)				Day 180 (End of culture period)				Day 300 (End of fallow period)			
	0 m	50 m	150 m	500 m	0 m	50 m	150 m	500 m	0 m	50 m	150 m	500 m
Rotifera												
B. falcatus	13.7 (3.7±0.7)	13.7 (3.7±0.3)	10.7(2.8±0.3)	16.7(1.6±0.3)	0.0(0.0±0.0)	12.5(5.2±0.0)	16.7(3.3±0.3)	33.3(3.3±0.3)	9.2(11.6±0.0)	12.5(5.2±0.0)	0.0(0.0±0.0)	10.3(1.6±0.0)
B. angularis	8.5 (2.3±0.3)	5.9 (1.6±0.3)	25.2(6.6±0.3)	16.7(1.6±0.3)	53.4(208.2±5.3)	16.7(6.9±0.3)	14.6(2.9±0.3)	0.0(0.0±0.0)	10.8(13.6±0.1)	12.5(5.2±0.0)	5.0(1.4±0.0)	0.0(0.0±0.0)
B. calciflrus	11.1 (3.0±0.6)	13.7 (3.7±0.3)	10.7(2.8±0.3)	0.0(0.0±0.0)	46.6(181.7±3.3)	12.5(5.2±0.6)	8.3(1.7±0.3)	33.3(3.3±0.3)	10.8(13.6±0.1)	12.5(5.2±0.0)	16.7(4.7±0.0)	10.3(1.6±0.0)
Filinia spp	13.7 (3.7±0.3)	13.7 (3.7±0.3)	10.7(2.8±0.3)	16.7(1.6±0.3)	0.0(0.0±0.0)	8.3(3.4±0.3)	8.3(1.7±0.3)	0.0(0.0±0.0)	10.8(13.6±0.0)	12.5(5.2±0.0)	16.7(4.7±0.0)	0.0(0.0±0.0)
Asplanchna spp	10.0 (2.7±1.1)	5.9 (1.6±1.1)	10.7(2.8±1.3)	0.0(0.0±0.0)	0.0(0.0±0.0)	16.7(6.9±1.0)	20.5(4.1±1.2)	0.0(0.0±0.0)	12(15.1±0.3)	12.5(5.2±0.0)	16.7(4.7±0.0)	0.0(0.0±0.0)
Lecane spp	11.1 (3.0±0.6)	13.7 (3.7±0.3)	10.7(2.8±0.3)	16.7(1.6±0.3)	0.0(0.0±0.0)	8.3(3.4±0.3)	15.0(3.0±0.0)	16.7(1.7±0.3)	15.9(20.0±0.4)	12.5(5.2±0.0)	16.7(4.7±0.0)	34.5(5.5±0.0)
Euchlanis spp	15.9 (4.3±0.3)	20.0 (5.4±0.0)	10.7(2.8±0.3)	16.7(1.6±0.3)	0.0(0.0±0.0)	12.5(5.2±0.0)	8.3(1.7±0.3)	0.0(0.0±0.0)	14.7(18.5±0.2)	12.5(5.2±0.0)	16.7(4.7±0.0)	10.3(1.6±0.0)
K. tropica	15.9 (4.3±0.3)	13.7 (3.7±0.3)	10.7(2.8±0.3)	16.7(1.6±0.3)	0.0(0.0±0.0)	12.5(5.2±0.0)	8.3(1.7±0.3)	16.7(1.7±0.3)	15.9(20.0±0.0)	12.5(5.2±0.0)	11.7(3.3±0.2)	34.5(5.5±0.0)
Cladocera												
Moina micrura	25 (13.3±1.0)	27.3 (14.7±0.6)	27.3(14.7±0.6)	17.7(11.8±0.3)	100.0(35.0±0.0)	28.6(20.1±0.0)	21.4(15.0±0.0)	25.0(20.0±0.0)	27.4(38.6±1.2)	27.5(23.8±2.3)	25.0(19.7±0.0)	25.8(28.0±2.4)
Bosmina longirostris	26.3 (13.8±0.7)	18.2 (9.8±0.0)	24.5(13.2±0.7)	28.4(19.0±0.3)	0.0(0.0±0.0)	28.6(20.1±0.0)	28.6(20.0±0.0)	25.0(20.00.0)	23.8(33.5±2.2)	21.6(18.7±1.2)	25.0(19.7±0.0)	22.6(24.5±1.2)
Daphnia lumhortzi	25.0 (13.3±0.0)	30.3 (16.4±0.3)	27.3(14.7±0.6)	30.8(20.6±0.0)	0.0(0.0±0.0)	21.4(15.0±0.0)	28.6(20.0±0.0)	25.0(20.0±0.0)	27.4(38.6±1.1)	27.5(23.8±0.2)	25.0(19.7±0.0)	25.8(28.0±2.2)
Chydorus spp.	23.8 (12.6±0.3)	24.5 (13.2±0.3)	20.9(11.3±0.3)	23.1(15.4±0.6)	0.0(0.0±0.0)	21.4(15.0±0.0)	21.4(15.0±0.0)	25.0(20.0±0.0)	21.4(30.1.0±0.4)	23.4(20.2±1.2)	25.0(19.7±0.0)	25.8(28.0±2.2)
Copepoda												
Copepoid nauplii	33.3 (34.0±0.0)	37.1 (37.8±0.7)	43.3(44.2±0.9)	22.2(9.6±0.6)	100.0(22.0±0.0)	30.0(14.5±0.0)	20.0(10.0±0.0)	16.7(10.0±0.0)	30.0(31.0±0.5)	28.6(20.6±0.2)	33.3(24.2±0.2)	30.7(21.6±1.2)
Cyclopoida	33.3 (34.0±0.0)	37.1 (37.8±0.7)	30.0(30.6±0.6)	37.0(16.0±0.7)	0.0(0.0±0.0)	40.0(19.3±0.0)	40.0(20.0±0.0)	33.3(20.0±0.0)	33.3(34.4.0±3.3)	35.7(25.7±0.4)	33.3(24.2±0.2)	33.6(23.7±1.1)
Calanoida	33.3 (34.0±0.0)	25.8 (26.3±0.9)	26.7(27.2±0.3)	40.7(17.6±0.9)	0.0(0.0±0.0)	30.0(14.5±0.0)	40.0 (20.0±0.0)	50.0(30.0±0.0)	36.7(37.9±3.3)	35.7(25.7±2.1)	33.3(24.2±0.2)	35.7(25.1±2.2)

APPENDIX 2 Species composition of zoobenthos sampled at cage culture site in Anyanga beach, Lake Victoria, Kenya during the study period

Order	Family	Genus	Day0 (beginning of culture period)				Day180 (end of culture period)				Day300 (end of fallow period)			
			0 m	50 m	150 m	500 m	0 m	50 m	150 m	500 m	0 m	50 m	150 m	500 m
		Aquatic insects												
Ephemeroptera	Baetidae	*Baetis* spp	+	+	+	+		+	+	+	+	+	+	+
	Heptagenidae	*Heptagenia* spp				+							+	+
	Caenidae	*Caenis* spp	+	+	+	+		+	+	+		+	+	+
	Ephemerellidae	*Ephemerella* spp			+	+				+			+	+
Plecoptera	Nemouridae	*Nemoura* spp	+	+	+	+		+	+	+	+	+	+	+
	Leuctridae	*Leuctra* spp				+				+			+	+
Trichoptera	Polycentropodidae	*Polycentropus* spp	+	+	+	+		+	+	+		+	+	+
Diptera	*Chironomidae*	*Brillia* spp	+	+	+	+		+	+	+	+	+	+	+
	Culicidae	*Culicida* spp	+	+	+	+		+	+	+	+	+	+	+
Odonata	*Gomphidae*	*Lanthus* spp	+	+	+	+		+	+	+	+	+	+	+
		Stylogomphus spp		+	+	+		+	+	+		+	+	+
	Aeshnidae	*Basiaeschna* spp	+	+	+	+		+	+		+	+	+	+
Hemiptera	*Corixidae*	*Corixa* spp		+		+				+		+	+	+
	Gerridae	*Gerris* spp	+	+	+					+	+	+	+	+
	Veliidae	*Velia* spp			+	+			+				+	+
	Notonectidae	*Notonecta* spp	+	+		+			+		+	+	+	+
	Nepididae	*Nepus* spp			+	+			+	+			+	+

	Belostomatidae	*Belostoma* spp		+	+	+			+			+			+	+
		Molluscs														
Gastropoda	*Physidae*	*Physella* spp	+	+	+			+	+	+			+	+	+	+
	Lymnaeidae	*Fossaria* spp	+	+	+	+			+	+			+	+	+	+
Bivalvia	*Sphaeniidae*	*Pisidium* spp	+	+	+	+			+	+	+		+	+	+	+
	Sphaeniidae	*Sphaerium* spp	+	+	+	+		+	+	+			+	+	+	+
		Annelids														
Oligochaeta	*Tubificiidae*	*Tubifex* spp	+	+	+			+	+	+			+	+	+	+
	Lumbricus	*Eclipidrulus* spp	+	+	+	+			+	+	+		+	+	+	+
Hirudinea	*Glossiphomiidae*	*Batracobdella* spp	+	+	+	+			+	+			+	+	+	+
		Helobdela spp	+	+	+	+			+	+	+		+	+	+	+

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FIGURE LEGENDS

FIGURE 1 Map of the study area showing Anyanga Beach**,** Kadimo Bay, Lake Victoria, Kenya, and the sampling points (0 m, 50 m, 150 m and 500 m away from cages)

FIGURE 2 Dissolved nutrients (mean ± SEM) at a cage culture site at Anyanga beach, Lake Victoria, Kenya showing **a)** chlorophyl *a*; **b)** Total phosphorus (TP); **c)** Total nitrogen (TN); and d) N:P molar ratio during culture and fallow period

FIGURE 3 Abundance (mean ± SEM) of zooplankton at a cage culture site at Anyanga beach, Lake Victoria, Kenya showing **a)** Rotifera, **b)** Cladocera and **c)** Copepoda during culture and fallowing periods

FIGURE 4 Water quality (mean ± SEM) at a cage culture site at Anyanga beach, Lake Victoria, Kenya showing **a)** Dissolved oxygen, **b)** BOD and **c)** Secchi depth **d)** NH_3 during culture and fallow periods

FIGURE 5 Diurnal variation in DO and pH at the cage and reference sites at the beginning and end of the culture period at Anyanga beach, Lake Victoria, Kenya

FIGURE 6 Proportions of grain size of surface sediment at a cage culture site at Anyanga beach, Lake Victoria, Kenya

FIGURE 7 The sediment composition (mean ± SEM) of **a)** total organic carbon TOC; **b)** Total phosphorous (TP); **c)** Total Kjeldahl nitrogen (TN); **d)** biological oxygen demand (BOD); and **e)** Oxidation-reduction potential during culture and fallowing periods

FIGURE 8 The structure of the macro-benthic invertebrate community (as mean number of individuals L^{-1}) during culture and fallow periods at Anyanga beach, Lake Victoria, Kenya

TABLE 1 Average Shannon index values (± SEM) for different sampling stations and time for Nile tilapia cage culture at Anyaga beach, Lake Victoria, Kenya. Significant differences are indicated with superscripted letters (Kruskal-Wallis test)

Day	Distance from cage	Shannon-Wiener diversity (*H'*)
Day 0 (Beginning of culture period)	0 m	2.38 ± 0.02[a]
	50 m	2.42 ± 0.02[a]
	150 m	2.40 ± 0.04[a]
	500 m	2.44 ± 0.07[a]
Day 180 (End of culture period)	0 m	0.82 ± 0.01[b]
	50 m	2.38 ± 0.01[a]
	150 m	2.40 ± 0.06[a]
	500 m	2.41 ± 0.05[a]
Day 300 (End of fallow period)	0 m	1.56 ± 0.03[b]
	50 m	2.41 ± 0.04[a]
	150 m	2.41 ± 0.02[a]
	500 m	2.43 ± 0.03[a]

Figures

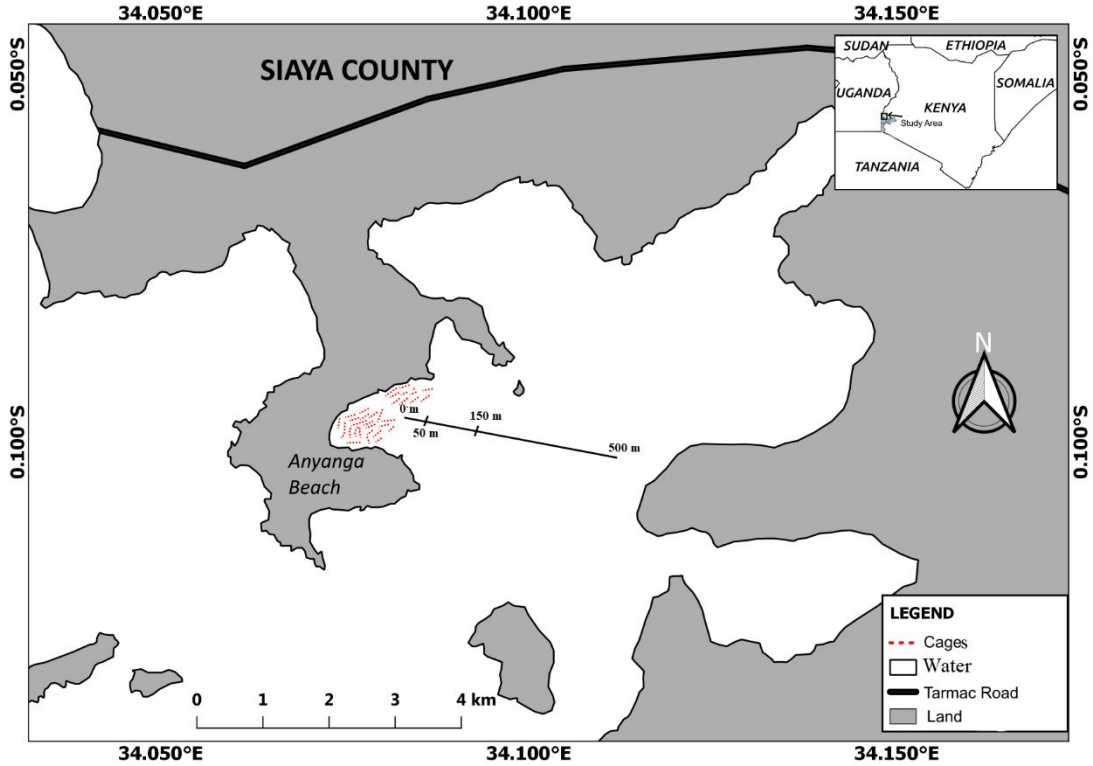
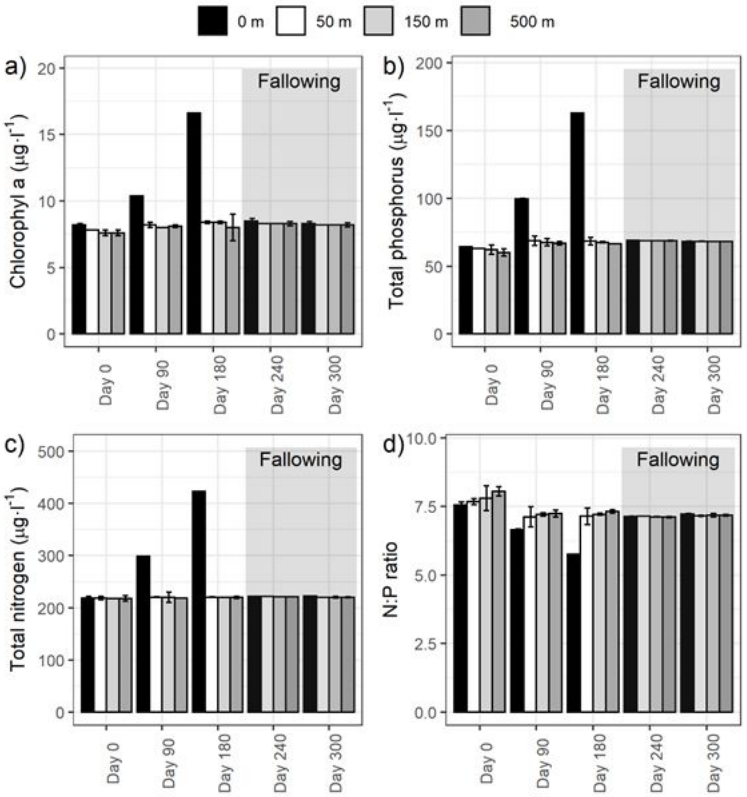


FIGURE 1



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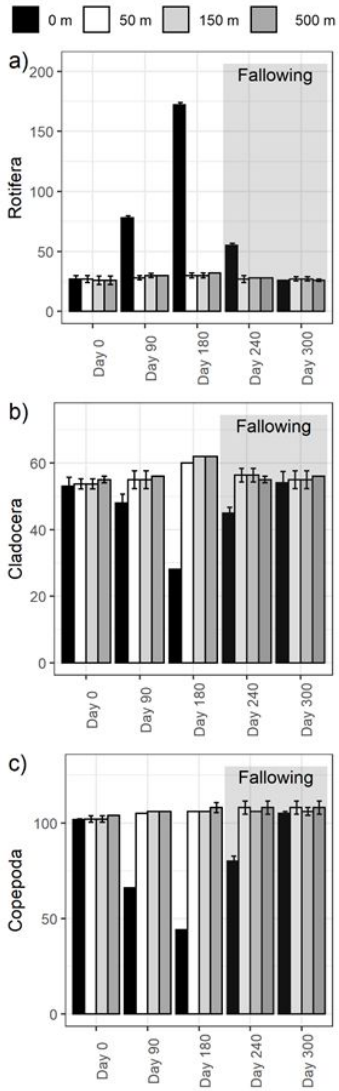
892 **FIGURE 2**



893

894 **FIGURE 3**

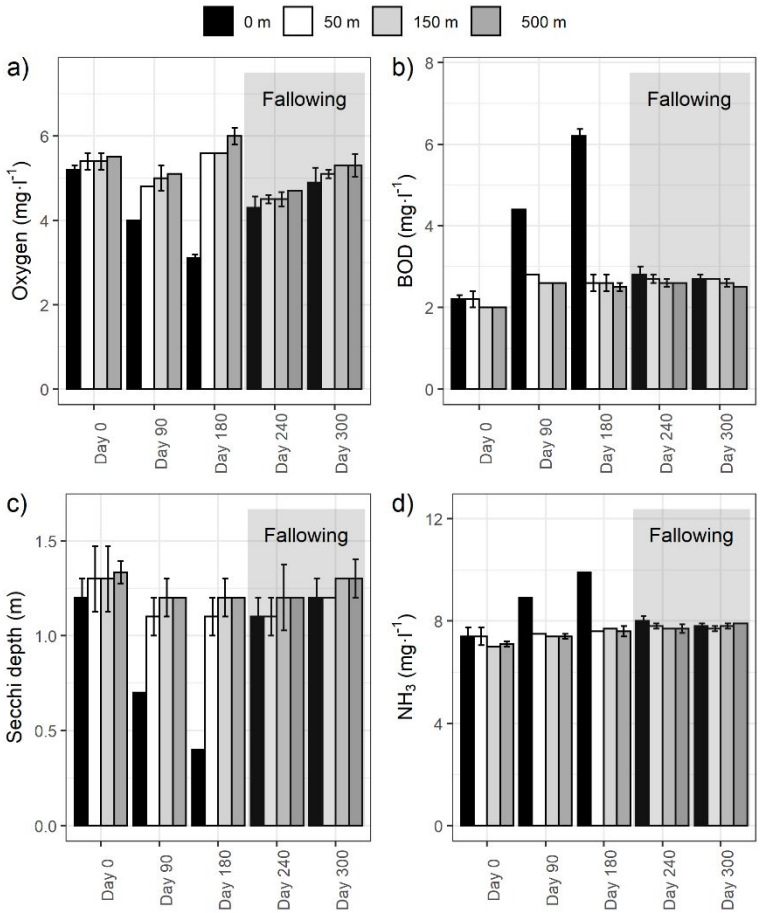
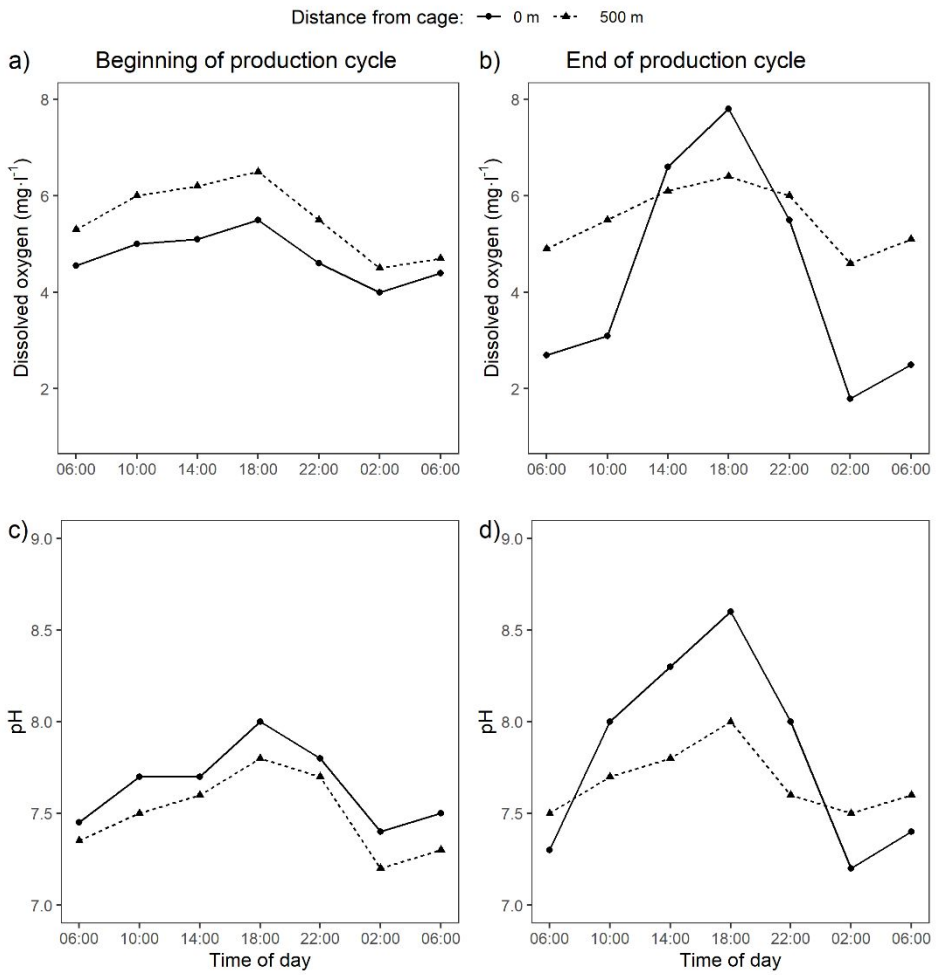
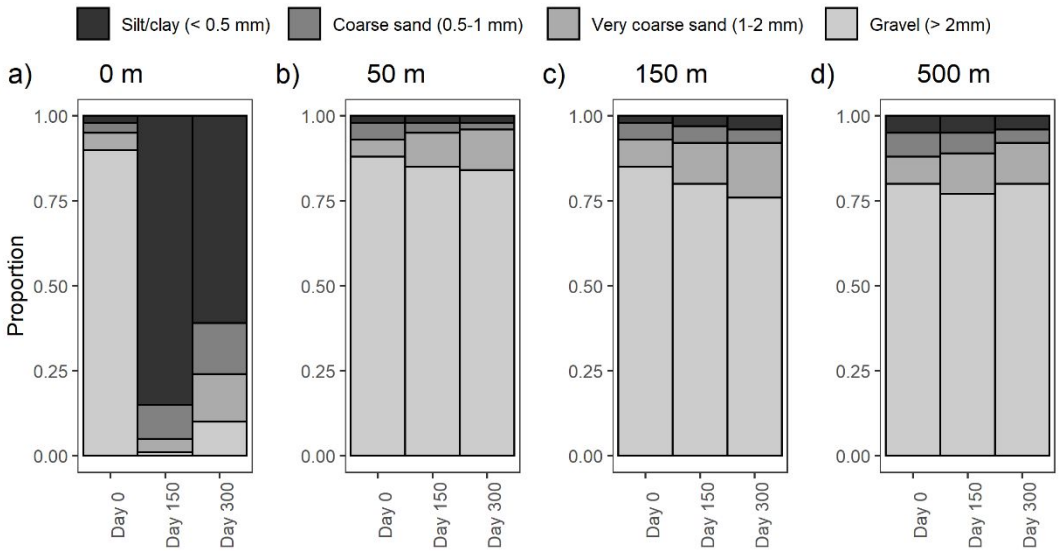

0 m
50 m
150 m
500 m
a)
b)
c)
d)
Fallowing
Oxygen (mg·l-1)
BOD (mg·l-1)
Secchi depth (m)
NH3 (mg·l-1)
Day 0
Day 90
Day 180
Day 240
Day 300

FIGURE 4



898

899 **FIGURE 5**

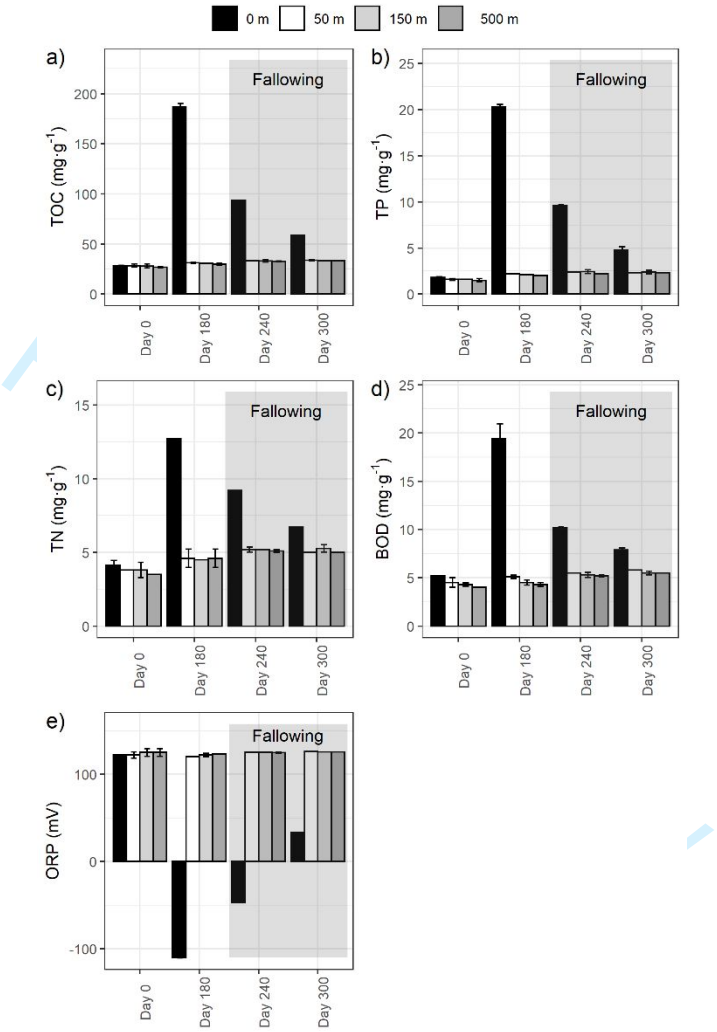


900

901 **FIGURE 6**

902

903



904

905

906 **FIGURE 7**

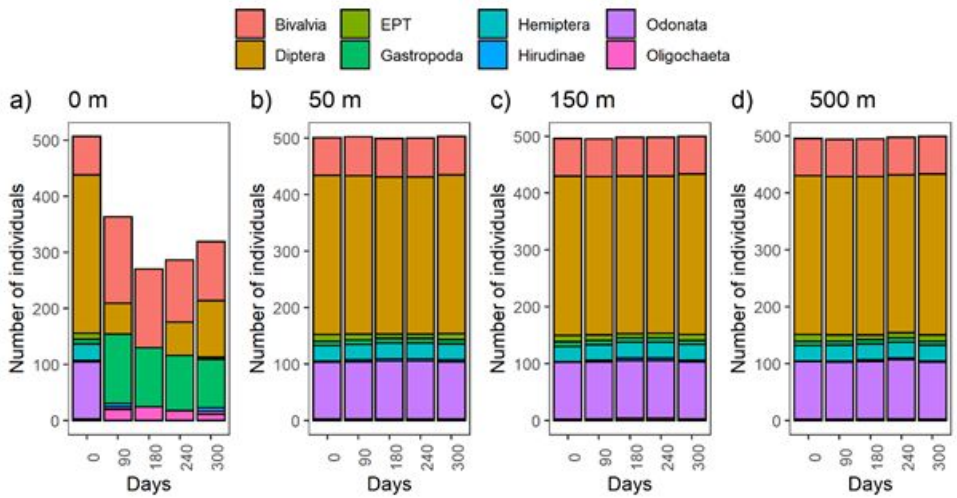


FIGURE 8

Impact of Nile tilapia Cage Culture on Water and Bottom Sediment Quality: The ability of a Eutrophic Lake to Absorb and Dilute Perturbations

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Abstract

Environmentally sustainable aquaculture depends on sound understanding of the impact of aquaculture derived organic matter (AOM) and the ability of aquaculture systems to absorb and dilute perturbations. We assessed the impact of AOM from cage culture of Nile tilapia on the ecology of Lake Victoria, Kenya using cages near Anyanga beach in Siaya County from December 2018 to October 2019. Four locations were surveyed for organic loading from cage culture: 0 m, 50 m, 150 m and 500 m (as a control site) away from the cages. The cage aquaculture caused increased P and N concentration near the cages and a decreased N:P molar ratio. These changes stimulated algal growth which, in turn, affected water quality. Organic material accumulated on the bottom under the cages, increasing benthic BOD (BOD, >10 mg g-1), a sensitive indicator of the ecological footprint of the cage aquaculture. Furthermore, the negative ORP in the benthic layer suggested anoxic bacterial metabolism, possibly causing buildup of sulphides and methane. These changes caused changes in the abundance and composition of both limnetic and benthic communities. At the beginning of the study, there were 22 zoobenthic taxa around the cages and 18 at the reference sites. Only 3 saprophilous taxa, chiefly gastropods (*Physella* spp.), bivalves (*Sphaerium* spp.) and oligochaetes (*Tubifex* spp.) were present at the cage site and 17 at the reference site at the end of the culture period. Shannon diversity index exhibited a declining tendency with the length of culture period at the cage site, signifying a negative impact of aquaculture on biodiversity. Water quality recovery after cage disturbance is rapid (<4 months) as there was no significant difference in the water quality recorded at the cage site and the other sampling sites after a fallow period of four months. However, sediment and meiofaunal recovery were far from complete. Moving the cages slightly (50-100 m) away from the former location may allow the benthic communities to recover and alleviate the problem. In addition, fallowing period, for the Anyanga site in particular, should be extended from 4 to at least 5 months to allow for the environment to recover. With the rapid increase of cage fish farming in the Great Lake's Region and with potential in other lakes, there is a need to develop regulations to guide the industry and continuous monitoring of the environment as to provide information to guide investment and to ensure sustainable cage farming.

KEYWORDS Benthos; fallowing; aquaculture; redox, pollution.

1 INTRODUCTION

Natural fish stocks in African inland waters are declining while the demand for fish protein is increasing because of rapid human population growth and growing awareness of nutritional and health benefits associated with fish consumption (Akintola et al., 2013; FAO, 2016; Anderson et al., 2017). Decreased catches have increased the interest in cage culture as an alternative source of fish (Aura et al., 2018a; Musinguzi et al., 2019; Hamilton et al., 2020; Musa et al., 2021a) and aquaculture will necessarily play a central role in bridging the widening gap between fish demand and supply (Obiero et al., 2019; FAO, 2020).

Large-scale culture of fish in cages is a common practice in different parts of the world (Carrol et al., 2003; Perez et al., 2005; Garcia, de Souza et al., 2015). In African inland waters, cage aquaculture is growing (Kifuko, 2015; Njiru et al., 2018; Aura et al., 2018a; Musinguzi et al., 2019; Hamilton et al., 2020). For example, between 2016 and 2019 the total number of cages in the Kenyan part of Lake Victoria increased from 1663 to more than 4537 and further growth is expected (Hamilton et al., 2020).

Concerns have been raised about the environmental impact of cage aquaculture (Bondad-Reantaso et al., 2005; Boyd et al., 2008; Kashindye et al., 2015). In African inland waters, the primary concern is eutrophication due to discharge of particulate and dissolved nutrients such as uneaten waste feed, metabolites and fecal matter (Garcia de Souza et al., 2015; Dauda et al., 2019). The accumulation of organic material in sediments increases the metabolic activity of bacteria which, in turn, can create anoxic conditions in sediments (Henderson et al., 1997; Karakassis et al., 1998; Porrello et al., 2005). Changes in sediment chemistry due to organic loading alters species abundance and biomass of macroinvertebrates (Braaten, 2007; Ngupula & Kayanda, 2010; Villnas & Bonsdorff, 2011; Kashindye et al., 2015; Egessa et al., 2018). Cage aquaculture can also affect the water quality by reducing dissolved oxygen in the water column (Kashindye et al.,

2015), elevating the levels of ammonia and CO_2 (Aura et al., 2018a) and increase the risk of algal blooms (Aura et al., 2018b; Mwamburi et al., 2020). These ecological changes can affect the production of wild populations in the area and may also create conflicts between cage culture and fisheries (Njiru & Aura, 2019).

The ecological effects of cage aquaculture depend primarily on the biomass produced, area, depth of the lake and water exchange rate (Phillips et al., 1985; Huang, 1997). The environmental effects of nutrient enrichment are also site-specific and depend on local chemical features (Wu, 1995). Freshwater systems are often more vulnerable than marine systems to nutrient loads due to smaller size and in essence low ecological carrying capacity. For many decades, Lake Victoria, just as many other African inland waters, has suffered from severe eutrophication (Verschuren et al., 2002; Mwamburi et al., 2020), with regular and massive algal blooms occurring for at least the last 30 years (Ochumba & Kibaara, 1989; Mwamburi et al., 2020). The lake has seen a five-fold increase in turbidity since the early 1930s (Mwamburi et al., 2020) with Secchi disc measurements below 1 m, specifically in shallow waters < 25 km from shoreline, bays and gulfs as well as the other semi-enclosed inshore areas of Lake Victoria (Lung'ayia et al., 2001; Mwamburi et al., 2020). In addition, the long retention time of Lake Victoria (residence time: 23 years; flushing time 123 years), means that pollutants entering the lake can accumulate. A regulatory framework for cage aquaculture in Lake Victoria is inadequate and, therefore, uncontrolled growth of the sector may degrade the environment and threaten the future of capture fisheries even more. Almost all cages in African inland lakes are located in shallow waters (4-8 m) (Musinguzi et al., 2019) despite recommendations that cages should be placed in deeper waters (> 10 m) (Kamadi, 2018). Furthermore, cage aquaculture installations in African inland lakes are commonly located -

inappropriately - near protected areas, in eutrophic and hypertrophic waters and close to the shoreline, where important nursery grounds for wild fish are to be found (Musinguzi et al., 2019).

There is a paucity of information on the impact of cage aquaculture on enrichment in tropical/subtropical waters. Several published studies on aquaculture in African inland waters (Mwebaza-Ndawula et al., 2013; Kashindye et al., 2015; Nabirye et al., 2016; Egessa et al., 2018) have only evaluated the impacts during the culture periods while none of these studies addressed recovery during fallowing periods and long-term effects. The primary objective of the current study was to assess environmental consequences of cage culture in Lake Victoria and the ability of the ecosystem to absorb and dilute perturbations to guide the development of cage culture in the Great Lakes region.

2 MATERIALS AND METHODS

2.1. Study Area

The study was conducted at Anyanga beach, Kadimo Bay, Lake Victoria, Kenya (Figure 1) from December 2018 to October 2019. Kadimo Bay was chosen for study as it is the main center of aquaculture in Lake Victoria, Kenya (Aura et al., 2018a; Hamilton et al., 2020). The farm had fish in 600 cages (2 m × 2 m × 2 m), stocked with 2000 tilapia (average initial body mass 15 g), with 6 months production cycle. Prior to the study, the farm had been in operation for three years with a fallow period of 4 months between production cycles. The sampling stations were located at the edge of the cages (0 m) and then 50 m and 150 m away from the cages towards the center of the bay (Figure 1). A reference station was located 500 m away from the cages. The sampling stations were geo-referenced for future comparisons using Garmin, 78S, IC; 1792A-01664, FCC ID: IPH-01664 Global Positioning System (GPS). Mean depth at cages was 3.0 m; 50 m = 3.2; 150= 3.5 and reference site had a depth of 4.6 m

2.4. Water quality

Temperature, dissolved oxygen (DO), pH and alkalinity were monitored using a multi-parameter meter (Hanna Instruments, Model 8519N, Singapore). Secchi depth was measured using a standard Secchi disk. Diurnal fluctuations of DO and pH were monitored at the cage and reference stations using a multi-parameter meter (Hanna Instruments, Model 8519N, Singapore) from 0600 hours till 0600 hours of the following day at an interval of 4h. Water samples for chemical analysis were collected in triplicate at a depth of 1 m from the surface using a Van Dorn water sampler. Pre-cleaned 1-litre sample bottles were used and the samples preserved on ice and transported the same day to Kenya Marine and Fisheries Research Institute (KMFRI) Kisumu laboratory for analyses. Total phosphorus (TP), total nitrogen (TN) and total ammonia-N and BOD were determined using photometric methods adopted from APHA (2005). Concentration of CO_2 was measured using CO2sys and adjusted for temperature, pH and alkalinity (https://cdiac.ess-dive.lbl.gov/ftp/co2sys/). Water quality was measured at the beginning of the culture period (day 0), at days 90 and 180 of the culture period and twice during the fallowing period, at day 240 and day 300. The diurnal fluctuations were monitored at day 0 and day 180

2.5. Plankton

Water samples for zooplankton and chlorophyll *a* (as an indicator of phytoplankton) were collected in triplicates and analyzed using the methods described by Greenberg et al. (1992). Zooplankton samples were collected with a conical plankton net (Nansen type; mesh size 60 µm; mouth diameter 0.25 m), towed vertically through the water column, as described by Mwebaza-Ndawula (2013). The samples were preserved in a 5% formalin solution. In the laboratory, each sample was made to a known volume, thoroughly shaken for uniform distribution and a sub-sample taken, placed in a counting chamber and examined under inverted microscope at 100X magnification for

taxonomic determination, and at 40X for counting. Zooplankton were identified to genus and where possible to the species level. Rotifers were sorted out using a fine glass capillary tube onto slides with glycerin mixed with distilled water and examined under a compound microscope at 100X. For copepods, identification keys by Dussart & Defaye (1995) were used. The keys by Korovchinsky (1992) and Smirnov (1996) were used for Cladocera identification while Koste & Shiel (1987) and Segers (1995) were used for the identification of rotifers.

Water samples (2 L) for the quantification of total chlorophyll-*a* were collected at the surface (photic zone) in triplicate at each station using sampling bottles, filtered on site, using Whatman GF/C filters. The filter together with the seston was folded and then covered by aluminum foil and stored in a freezer overnight to aid in the bursting of the cells. Chlorophyll-*a* was extracted using reagent-grade acetone under subdued light. The seston and the filter were homogenized in a tissue grinder at around 5000-rpm for about 1 minute, covered with 5 ml of 90% aqueous acetone. The samples were transferred into screw-cap vial/centrifuge tube, the grinder rinsed with 90% acetone and the rinse added to the extraction slurry. The volume was adjusted to 10 ml with 90% acetone and the sample left for at least 8 hours in the dark at 4°C for chlorophyll-*a* extraction. After incubation, the sample was centrifuged for 10 minutes and the clarified extract was decanted into a clean test tube. Light absorbance of the Chlorophyll-*a* extract was measured with a UV-visible Beckman DU64OB spectrophotometer with the sample placed in 1-cm cell cuvettes, at 750 nm and 663 nm. Subsequently, concentrations were estimated, using the equations of Jeffrey & Humphrey (1975) after subtracting absorbance at 750 nm from all absorbance values to account for turbidity:

$$Chlorophyll\ a\ (mg \cdot l^{-1}) = \frac{11.85 \times E664 - 1.54 \times E647 - 0.08 \times E630}{L} \times V$$

In which:

V = Volume of acetone 90%

L= Volume of water sample

E664 = Value of absorbance at wavelength 664 nm

E647 = Value of absorbance at wavelength 647 nm

E630 = Value of absorbance at wavelength 630 nm

2.6. Surface sediment (0-2 cm) granulometry and nutrient parameters

Sediment samples for analysis of total nitrogen (TN), total phosphorus (TP), total organic carbon (TOC), and biological oxygen demand (BOD) were collected using a Ponar grab (238-cm^2 open jaw area) by taking three vertical hauls of sediment at each sampling point. Sediment samples were collected at the beginning and the end of the culture period and then during fallowing two and four months following the culture period. The samples were placed in clean labelled sample bags and transported to KMFRI laboratory for analyses. Total nitrogen and TP in sediments were analyzed based on methods by Huang (1999). Oxidation Reduction potential (ORP) was measured using a multi-parameter meter (Hanna Instruments, Model 8519N, Singapore).

Analyses of grain size in sediments were performed as described by Egessa et al. (2018). A sample of wet sediment (15 ml) from each station was digested overnight in 30 ml of 30% H_2O_2 to remove organic matter. The excess H_2O_2 was then removed by boiling the sample. The soil particles were then dispersed using 5 ml of 10% sodium hexametaphosphate, agitated, and allowed to settle overnight, followed by wet sieving using 2, 1, and 0.5-mm diameter test sieves. The grain size fractions for each sample were put into weighed crucibles and oven-dried at 105°C to a constant dry weight followed by heating at 550 °C in a furnace for 4 h to obtain ash weight. The

amount of organic matter in a sample was then estimated as the difference between dry and ash weight.

2.7. Community composition and abundance of macro-benthic fauna

Macro invertebrate samples were collected using a Ponar grab by taking three vertical hauls of sediment at each sampling point, followed by sieving through a 400-µm mesh, to concentrate the sample. The concentrated samples were placed in clean, labeled sample bottles and preserved in 70% alcohol for taxonomic identification and enumeration in the laboratory. Macroinvertebrates were identified with the aid of different keys: Merrit & Cummins (1978); Quigley (1977); IFM (2006). Composition and density of macro-benthic fauna was monitored at the beginning of the study, on day 90 and day 180 of the culture period. They were also monitored on day 240 and 300 during the fallowing period.

The macroinvertebrate assemblage composition was determined using number of taxa (*S*), total number of individuals, and relative abundance of each taxon. The Shannon-Wiener diversity index (*H'*) was used to assess diversity as follows:

$$H' = \sum_{i=1}^{R} p_i \ln p_i$$

where p_i is the proportion of individuals belonging to the *i*th species. An associated evenness *H'*/*H'* max (Pielou, 1975) was also calculated.

2.9. Data analyses

Microsoft Excel 2016 was used for data entry and cleaning while STATISTICA version 6.0 was used for statistical analyses. Descriptive analysis of mean and Standard Error of the mean for water quality, order and genera abundance in stations and for sampling dates were carried out. One-way analysis of variance (ANOVA) was used to test for statistical significance in the mean variation of

water and sediment quality parameters between stations and time. Diversity of macro-benthic invertebrates was calculated by means of Shannon-Wiener index (Shannon and Weaver 1949) but due to small sample size, the data did not conform to assumptions of ANOVA, hence significant differences in Shannon diversity index (H') between station and time were determined using Kruskal-Wallis tests. The percentages of gravel (> 2 mm), very-coarse sand (1–2 mm), coarse sand (0.5–1 mm), and fine sand/silt/clay (< 0.5 mm) were computed for the stations to support interpretation of bottom faunal data. Anderson-Darling test and histogram plots were used to evaluate the data for normal distribution, and for homogeneity of variance, by assessing residual plots and employing Bartlett's and Levene's tests. The level of significance was estimated at $p < 0.01$.

3 RESULTS

3.1. Effects of cage aquaculture on nutrients and chlorophyll *a*

At the beginning of the production cycle, there were no significant differences in chlorophyll *a* ($F(3) = 0.056$, $P = 0.826$), TP ($F(3) = 0.345$, $P = 0.782$), TN ($F(3) = 0.039$, $P = 0.883$) and N:P molar ratio ($F(3) = 0.432$, $P = 0.746$) among different sampling stations (Figure 2). However, at the time of harvest, chlorophyll *a* ($F(3) = 5434.75$, $P < 0.0001$) , TP ($F(3) = 3468.93$, $P < 0.0001$) and TN ($F(3) = 39572.24$, $P < 0.0001$) had all increased significantly by 108%, 93% and 100% respectively by the cages (Figures 2a, b, c). The N:P molar ratio decreased by more than 40% by the cages and was significantly lower than at the other sampling stations at the time of harvest (Figure 2d). In contrast, there was no significant change in nutrient concentrations at any other sampling location during the production and fallowing periods (Figure 2). During the four-month

fallowing period, chlorophyll *a,* TP, TN, and N:P molar ratio by the cages recovered, with concentrations comparable to those observed at the other sampling stations.

3.2. Effects of cage aquaculture on zooplankton

The production cycle had significant effects on the composition of the zooplankton community at the cage station, but not at other locations (Figure 3). The zooplankton community consisted mainly of three taxonomic groups: Rotifera, Cladocera and Copepoda (Figure 3). A total of 14 species of zooplankton were identified in the samples collected. Eight species of Rotifera (*Brachionus falcatus, Brachionus angularis, Brachionus calyciflorus, Filinia* spp., *Asplanchna* spp., *Lecane* spp., *Euchlanis* spp., *Keratella tropica*), four species of Cladocera (*Moina micrura, Bosmina longirostris, Daphnia lumholtzi, Chydorus* spp.) and two species of Copepoda and nauplii (Copepod nauplii, *Cyclopoida* spp., *Calanoida* spp.) were identified (Appendix 1).

At the beginning of the production cycle, there was no significant difference ($P > 0.05$) in the abundance of the different taxonomic groups among the sampling sites (Figure 3). However, during the production cycle, the abundance of rotifers at the cage site increased significantly ($P < 0.001$) over six-fold while the abundance of Cladocera and Copepoda decreased ($P < 0.001$) by 47% and 58%, respectively. No significant changes in abundance during the production cycle were found at other sampling locations (Figure 3, Appendix I).

In addition to changes in total abundance, the abundance of species within each taxonomic group changed. At the beginning of the production cycle all the eight Rotifera species were present at the cage station, though not in similar proportions (8.5-15.9%). However, at the end of the culture period, when the total abundance of Rotifera was at a maximum (Figure 3), a total of six species (*B. falcatus, Filinia* spp, *Asplanchna* spp, *Lecane* spp., *Euchlanis* spp., *K. tropica*) out of the eight initially present at the cage station had disappeared from the samples. Dominating at the

cage site was *B. angularis* and *B. calyciflorus* that had increased in numbers at the cage station on day 180 (Appendix I). After fallowing period of 4 months the Rotifera returned to similar composition as before the production cycle began, with all the eight species present, though still not in similar proportions.

The composition of Cladocera at the cage site changed during the production cycle, while at other locations the composition did not change (Appendix I). On day 0, all four species were present in similar proportions (23.8-26.3%) at all sampling locations. At the end of the production cycle, only *Moina micrura* (100%) was present in the samples at the cage station and had nearly trebled in numbers. After fallowing, the composition of Cladocera returned to pre-production conditions, with all four species present.

The composition of Copepoda changed at the cage site during the production cycle but not at other locations (Appendix I). The initial composition of Copepoda was about equal numbers of Copepod nauplii, Calanoids and Cyclopoida. However, both Calanoids and Cyclopoida had disappeared from the cage site samples by day 180, with only Copepod nauplii dominating the cage site (100%). However, the species composition of Copepoda was restored to pre-production levels after 90 days of fallowing.

3.3. Effects of cage aquaculture on water quality

There was no significant difference in DO ($F(3) = 0.5454$ $P = 0.688$) (measured at 10 am), BOD ($F(3) = 0.036$, $P = 0.889$), Secchi depth ($F(3) = 0.356$, $P = 0.779$), and NH_3 ($F(3) = 0.045$, $P = 0.965$) (Figure 4) among sampling locations at the beginning of the production cycle. However, both DO ($F(3) = 424.6$, $P < 0.001$) and Secchi disk readings ($F(3) = 89.5$, $P < 0.0001$) decreased over time while BOD ($F(3) = 330.3$, $P < 0.0001$) and NH_3 ($F(3) = 386.0$, $P < 0.001$) increased progressively at the cage site (Figure 4). On day 180, the DO was reduced by 48.3%, Secchi depth

by 66.7% and the BOD and NH_3 increased by 181% and 35% respectively. During the fallowing period, the DO, BOD, Secchi depth, and NH_3 at the cage site recovered. Four months after harvesting there was no significant difference in DO ($F(3) = 0.048$, $P = 0.898$), BOD ($F(3) = 0.045$, $P = 0.899$), Secchi depth ($F(3) = 0.354$, $P = 0.789$), and NH_3 ($F(3) = 0.038$, $P = 0.969$) at different sampling sites (Figure 4). The DO ($F(3) = 0.046$, $P = 0.888$), BOD ($F(3) = 0.039$, $P = 0.989$), Secchi depth ($F(3) = 0.044$, $P = 0.889$) and NH_3 ($F(3) = 0.043$, $P = 0.899$) did not change significantly during the production cycle and fallowing period at any other sampling location. There were no significant differences in mean temperature (26.46 ± 1.22; $F(3) = 0.034$, $P = 0.973$), pH (7.96 ± 0.24; $F(3) = 0.041$, $P = 0.983$) and alkalinity (51.03 ± 1.45; $F(3) = 0.456$, $P = 0.749$) among the sampling sites at the beginning and at the end of the culture period. The estimated concentration of CO_2 never exceeded 5 $mg \cdot l^{-1}$.

Both DO and pH showed diurnal fluctuations, increasing during the day and decreasing at night (Figure 5). At the beginning of the production cycle, DO was consistently about 1 $mg \cdot L^{-1}$ lower and the pH about 0.1-0.2 units higher at the cage site than 500 m from the cages, otherwise the amplitude was similar. By the end of the culture period, the amplitudes of the diurnal fluctuations of DO and pH at the cage site were much larger than at the reference site. The lowest level of oxygen (1.5 mg L^{-1}) was recorded at 2 am in the morning at the cage site and corresponds to 21% oxygen saturation.

3.4. Surface sediment (0-2 cm) granulometry.

The surface sediment was mainly (> 85%) composed of gravel at all the sampling sites (Figure 6) and silt/clay was only 2-3%. This changed during the production cycle and, by the time of harvest, the bottom by the cages consisted mainly of silt/clay (85%) while gravel accounted for only 1% (Figure 6) which is consistent with the accumulation of organic matter on the bottom. No

significant changes in the composition of the surface layer were observed at other sampling sites during the production cycle. Following the 4-month fallowing period, the proportion of silt/clay decreased to 61% at the cage site, though still significantly lower ($P < 0.01$) than at other sampling sites.

At the beginning of the production cycle, there were no significant differences (P =0.7-0.9) in the mean concentrations of TOC, TP, and TN, or the levels of BOD and ORP in the bottom layer among the sampling sites (Figure 7). At the end of the production cycle, TOC ($F(3) = 5519.95$, $P < 0.0001$), TP ($F(3) = 14197.14$, $P < 0.0001$), TN ($F(3) = 254.46$, $P < 0.0001$) and BOD ($F(3) = 232.48$, $P < 0.0001$) had all increased at the cage station by 386.5%, 745.8%, 176.1% and 252.7%, respectively (Figure 7). The ORP at the cage site decreased from 122 mV to -110.4 mV during the production cycle, while remaining unchanged at other sampling locations. During the fallowing period, the chemical composition and ORP recovered partly but did not reach pre-production levels ($F(3) = 2542.35$, $P < 0.001$) (Figure 7).

3.5. Community composition and abundance of macro-benthic fauna

The macro-benthic fauna was composed of members from three phyla: Arthropoda, Annelida and Mollusca. Arthropoda was the richest phylum consisting of the class Insecta that had six orders (Ephemeroptera, Diptera, Trichoptera, Plecoptera, Odonata and Hemiptera). At the beginning of the production cycle, the most abundant group in all benthic samples was Diptera (300-305 individuals L^{-1}), followed by Odonata (100-102 individuals L^{-1}) and then Bivalvia (60-61 individuals L^{-1}) and there was no significant difference among the sampling sites (Figure 8). By the end of the culture period, the total number of individuals was reduced by 47% at the cage site (Fig. 8a) while the total numbers and composition of the macro-benthic fauna did not change at other locations (Figures 8b, 8c and 8d). On day 180 all Diptera, (Ephemeroptera, Plecoptera and

Trichoptera (EPT), Hemiptera, Hirudinae and Odonata had disappeared at the cage site (Fig. 8a) and the fauna consisted only of Bivalvia (52%), Gastropoda (39%) and Oligochaeta (9%).

At the beginning of the production period, there were 18 species of zoobenthos found underneath the cages and 22 species at the reference site (Appendix 2). By the end of the production cycle, only three species (*Physella* spp*, Sphaerium* spp *and Tubifex* spp.) were found underneath the cage, and 18 at the reference site (Appendix 2). Kruskal-Wallis test showed no significant differences ($H = 2$; $p = 0.399$) in the Shannon-Wiener mean diversity index of macroinvertebrate genera among the sites at the beginning of the study (Table 1). At the end of the study, the lowest mean Shannon-Weiner diversity was recorded at the cage site which was significantly different from the other sampling sites ($H = 2$; $p < 0.001$).

The composition of the macro-benthic fauna at the cage site did not recover to preproduction levels during the four-month fallowing period and on day 300 it was still dominated by gastropods (28%) and bivalves (36%) (Figure 8a). Diptera, EPT, and Odonata had reappeared in the samples at the end of the fallowing period but not to the previous abundance while Hemiptera was still absent. After four months of fallowing, the Shannon-Weiner diversity index remained lower at the cage site (Table 1).

4 DISCUSSION

The present study is the first of its kind that we are aware of to assess the environmental effects of cage aquaculture in tropical/subtropical waters, both during the production cycle and the subsequent fallowing period until the next production cycle commences. Cage aquaculture has significant effects on both the limnetic and benthic zones of the lake both with regard to water chemistry and with respect to species abundance, distribution and richness. However, these effects are restricted to the cage sites and dissipate quickly with distance from the cages such that at 50 m there was no evidence of changes. The changes at the cage site during production are largely

reversed in the limnetic zone during the four-month fallowing period. However, the effects of cage aquaculture on the benthic zone were not entirely reversed and suggest additive effects of subsequent production cycles that could lead to future disasters. These findings are now discussed in turn.

4.1. Limnetic effects

The present study shows that the effects of the cage aquaculture on the limnetic zone in the lake are primarily mediated through the increased concentrations of TN and TP (Figure 2). Unlike in conventional land-based aquaculture pond systems, cage systems do not use organic or inorganic fertilizers with high N and P content. Yet, they are essential elements for organismal development. Consequently, fish feeds for cages have been reported to contain higher P content than required by fish (Ackefors & Enell,1994; Von Sperling & Chernicharo, 2005; Musa et al., 2021b). Therefore, the observed highest level of TN (423.2 ± 1.4 µg L^{-1}) and TP (162.7 ± 5.6 µg L^{-1}) at the cage station by the end of the culture period could be from leaching from fish feeds and fecal matter, as well as metabolites. Previous research reported poor FCR (2.6) for fish feeds used in the study area (Musa et al., 2021b), that could have caused disproportionate increase in total P and N loadings. Hence, fish cage culture in freshwater lakes such as Lake Victoria raises concerns about water quality deterioration due to solid waste (Ngupula et al., 2012; Aura et al., 2018b) and soluble waste, especially nitrogen and phosphorus compounds. In this study, the progressive increase in chlorophyll *a* concentration, is an indication of increased algal biomass, found at the cage site during the production cycle followed the same pattern as the increased N and P concentrations (Figure 2), suggesting that the increased N and P concentrations at the cage site promoted the growth of phytoplankton.

The TP (62-69 µg·l^{-1}), TN (218-220 µg·l^{-1}) and chlorophyll *a* (7.6-8.4 µg·l^{-1}) concentration recorded at all sampling sites before the production cycle started (Figure 2) are within the range of values reported for nearshore waters on Lake Victoria (Mwamburi et al., 2020; Simiyu et al., 2021; Deirmendjian et al., 2021). The observed N:P ratio of 7.5 at the cage site before production started and after two-month fallowing, in the present study, is similar to those reported in other studies (Guildford & Hecky, 2000; Mwamburi et al., 2020; Deirmendjian et al., 2021). The observed decrease in N:P molar ratio at the cage station by the end of culture period is at levels where phytoplankton production is limited by N rather than P (Guildford & Hecky, 2000; Mwamburi et al., 2020). These conditions favor heterocystous N-fixing cyanobacteria (Gikuma-Njuru & Hecky, 2005) and the decreased N:P molar ratio at the cage site during production may exacerbate this effect. Cyanobacterial bloom is a potential health risk and long-term exposure of Nile tilapia to cyanobacteria could accumulate the cyanotoxins in the fish tissue to be transferred to higher trophic levels (Mohamed et al., 2019). Even before commencement of fish cage culture, Lake Victoria has been reported to be highly eutrophic (Ochumba & Kibaara, 1989, Lungáayia et al., 2000, Kling et al., 2001). Despite the burgeoning industry within the lake, the fate and quantitative contribution of the new N and P sources emanating from cage aquaculture in Lake Victoria has yet to be understood.

There are six main influent rivers in the catchment of Lake Victoria, Kenya: Sio, Nzoia, Yala, Nyando, Sondu-Miriu and Kuja. Previous studies estimate the mean water discharge from the six rivers at 456.16 m^3s^{-1}, with TN and TP loading at 11.61 and 1.69 mgL^{-1}, respectively (LVEMP, 2005; Aura et al., 2021). Hence, agro-industrial and municipal sewerage discharges of TP and TN through the major rivers stands at 2,113,000 and 12,193,000 kg yr^{-1}, respectively. On the other hand, Anyanga cage culture site, the epicenter of cage aquaculture in Lake Victoria, has

been estimated to produce 20,480 kg of N and 970.7 kg of P each fish production cycle (Musa et al., 2021b). Therefore, agro-industrial and sewerage discharges contribute more than 2000 times the amount of P and almost 600 times the amount of N into the lake as compared to fish cage culture. These figures may even be higher if other seasonal rivers and streams are considered. With the current production levels, fish cage culture in Lake Victoria seems to contribute to increased nutrient loading to the lake ecosystem. However, with regard to nutrient loading in the lake, aquaculture-derived nutrients may tend to account for only a relatively small proportion (<1% of P or N) compared with agro-industrial and sewerage sources.

The present results reveal that the N and P concentrations dissipate quickly with increasing distance from the cages. In fact, the concentration of N and P did not change significantly during the production cycle in other locations, even as close as 50 m from the cages. A number of factors could contribute to this such as dilution, limited water exchange in and around the cages (due to presence of fish and clogged nets) and N and P being rapidly sequestered into algae. Contrary to best practices, the majority of cage farmers in Lake Victoria do not clean the cage nets to reduce clogging and fouling (Aura et al., 2018a), further limiting the water exchange around the cages.

In this study, increased phytoplankton density during the production cycle affected the diurnal fluctuations in DO and pH (Figure 5). At the beginning of the growth cycle, the diurnal fluctuations in DO and pH at the cage site were similar in magnitude to those at the reference site 500 m from the cages although the DO concentration was consistently about 1 $mg \cdot l^{-1}$ higher and pH about 0.16 units lower at the latter location (Figure 5a). The amplitude of DO and pH increased with time and by the end of the production cycle, increased phytoplankton density at the cage station (Figure 2a) contributed to larger amplitudes in DO and pH fluctuations (Figure 5b). The DO concentration was maximal during the afternoon due to photosynthesis and reached a

minimum just before sunrise. Diurnal fluctuations of pH were in phase with oxygen as CO_2 is consumed to produce O_2 (Figure 5) and the removal of CO_2 in turn increased pH due to the carbonate equilibrium. At the end of the production period (Day 180) diurnal variations in algae respiration and photosynthesis caused fluctuation in oxygen concentrations to reach minimum mean levels of 1.5 $mg \cdot L^{-1}$ (19% of air saturation) at 2 am and it is likely that the oxygen levels may have fallen even further until dawn. During the day, oxygen concentration came up to 7.8 $mg \cdot L^{-1}$ (118% of air saturation) at the cage site. The BOD increased (Figure 4b) as the algal density increased (Figure 2a), although an increased bacterial activity in the water may also have contributed to the BOD (Boyd and Tucker, 1998). The high BOD resulted in nearly 50% reduction in morning DO at the cage site from the beginning to the end of the production cycle (Figure 4a).

Growth, feed intake, disease resistance and survival of Nile tilapia is significantly reduced when the oxygen saturation falls below 50% of air saturation (Kolding et al., 2008; Tran-Duy et al., 2012; Abdel-Tawwab et al., 2014). Large diurnal fluctuations in O_2 levels such as those observed in the current study may also cause a reduction in growth even if the oxygen saturation remains above 100% for most of the hours of daylight (Tsadiki & Kutty, 1987). At the beginning of the production cycle, the minimum DO values at night fell just below 49% saturation (Figure 5a). However, by the end of the production cycle the oxygen saturation was below 50% for more than 10 hours each night (Figure 5b) and near or below 20% saturation for several hours. This suggests that the nightly fall in oxygen levels would have reduced growth, feed efficiency and survival of the fish which in turn would have reduced production and increased juvenile and feed costs. In contrast, the estimated maximum CO_2 concentration (~5 $mg \cdot l^{-1}$) is well below the tolerable levels of 10 $mg \cdot l^{-1}$ for warm water species (Timmons et al., 2018).

Increased phytoplankton production can promote the growth of zooplankton (Sládeček, 1983; Tasevska et al., 2010). In the present study, the abundance of rotifers increased more than six-fold during the production cycle while the abundance of Cladocera and Copepoda was reduced by 47% and 57%, respectively (Figure 3). There were primarily two species of Rotifera that increased in abundance, *B. angularis,* and *B. calyciflorus*. Rotifers, with their relatively short life cycle, are known to respond more quickly to increased eutrophication than other species of zooplankton, in particular those of the genus *Brachionus* (Sládeček, 1983; Radwan & Popiolek, 1989; Tasevska et al., 2010).

Previous studies in the Lake Victoria basin have also found that the numbers and biomass of rotifers increase in response to eutrophication (Vincent et al., 2012), especially *B. angularis*, as was observed in the present study. Eutrophication in Lake Victoria is increasing and this may increase the background levels of rotifers at all sampling locations which are close to shore in a protected bay (Ngupula, 2013). However, the observed increased abundance of rotifers at the cage site was likely primarily due to the phytoplankton bloom caused by the leaching of nutrients from the fish farming. Copepoda and Cladocera are more sensitive to reduced water quality than Rotifers (Vincent et al. 2012; Dias et al., 2012) and this may in part explain why their numbers were reduced. The shift in the zooplankton community composition at the cage site may also be due to increased predation by the growing biomass of fish. Due to their small size, predation is likely to affect the abundance of rotifers less than the other two groups (Dumont et al., 1975; Mwebaza-Ndawula et al., 2001, 2004; Lars-Anders et al., 2004).

The effects on the limnetic zone had disappeared after four months of fallow. Two months after the production cycle ended (Day 240), both the N and P concentrations had returned to baseline levels. Similarly, as the TN and TP levels decreased during the fallowing period, so did

algal density. As a result, the zooplankton community recovers, particularly reaffirmed by the reduction in the relative contribution of copepod nauplii and reappearance of Calanoida (see Appendix 1), suggesting that copepod nauplii could represent an important bioindicator of organic loading. Dias et al. (2012) affirms that higher proportions of calanoids in freshwaters indicates low eutrophy while nauplii are an indicator of a more productive habitat. The reappearance of calanoids indicate that the water quality at the cage site had completely recovered after 4 months fallow period. Notably, the low relative density of rotifers (14%) at the cage site by end of 4 months fallow period as compared to harvesting time (70%), confirms that water quality had recovered as rotifers are more responsive to water quality changes, hence are good indicators of trophic conditions (Gannon & Stemberger, 1978; Sladecek, 1983; Baranyi et al., 2002; Tasevska et al., 2010). The recovery of the environment (water) is more rapid, probably due to the small spatial scale of the impact (< 50 m). It could also be due to good water circulation caused by the absence of fish in cages after harvesting (Kutti et al., 2007). In summary, our results show that all effects of cage aquaculture on the limnetic zone dissipate after a four-month fallowing period. Hence, the limnetic zone in Lake Victoria is able to absorb and dilute perturbations within four months fallowing due to periodical lake turnover.

4.2. Benthic effects

The high TOC recorded under the cages by the time of harvest indicate high organic matter accumulation, mainly from food waste and fish excrement which have high P and N content (Figure 7). It is likely that the loss of P from the sediment is minimal (Holby & Hall, 1991; Von Sperling & Chernicharo, 2005) contributing to increased P accumulation under the cages. The high P content in the sediment under the cages reduced the N:P molar ratio from 2.3 to 0.6. Similar findings have been reported from Hong Kong where the N:P molar ratio was reduced from 8.75 at

the reference site to 1.83 at the cage station (Gao et al., 2005). Low TN:TP molar ratio in sediments is associated with increased phosphorous loading from the fish feeds, raising concerns of eutrophication.

The accumulated organic matter on the bottom is a favorable substrate for various organism and, hence, in the current study, BOD increased in the sediment (Nickel et al., 2003) resulting in reduced oxygen levels. This is confirmed by the progressively more negative ORP in the sediment below the cages during the production period (Figure 7) which indicates anaerobic bacterial metabolism. One result of anaerobic bacterial metabolism is the build-up of hydrogen sulphide and methane which is highly toxic to fish. These effects are expected to be more pronounced in cages sited in shallower waters, similar to the study area. Indeed, incidences of isolated fish kills have been reported in fish cages at Nyenye Got, Honge and Anyanga beaches in Lake Victoria, Kenya. Although preliminary results indicated low dissolved oxygen concentrations (0.64 mgL^{-1}) as the key cause of the fish kills (Njiru et al., 2018), hydrogen sulphide toxicity may have also been one of the main contributors to mass mortalities. This calls for further investigations into the effects of hydrogen sulfide on fish performance, especially in African inland waters where most cages are sited in shallow areas, with no fallowing periods.

The large amounts and deposition of organic matter beneath the cages in the current study may have contributed to changes in the benthic macroinvertebrate communities (Schmidlin & Baur, 2007). The reduced oxygen levels recorded at the cage site by the end of the culture period will have favored certain species and the increased amount of silt/clay on the bottom is potential food that can attract macroinvertebrates. This could in part have influenced the community composition and diversity of macroinvertebrates (Kalantzi & Karakassis, 2006; Nabirya et al., 2016). Certainly, the shift from arthropods to mollusks (bivalves and gastropods) and annelids

(oligochaetes) at cage site by the end of the culture period is consistent with organic enrichment (Mavuti & Litterick, 1991; Ngupula et al., 2012). Oligochaete annelids have often been cited as thriving in freshwaters receiving organic waste (Dobrowolski, 1987; Camargo, 1992; Miserendino & Pizzolon, 2000), an indication of negative effect of cage culture on the lake environment. Besides, the reduction in number of taxa and the dominance by the opportunistic species *Physella* spp, *Sphaerium* spp and *Tubifex* spp., at the cage sites indicates disturbance of the benthic faunal community in the immediate vicinity of the cages. These opportunistic species i.e. *Physella* spp, *Sphaerium sp* and *Tubifex* spp., are known for their high tolerance to pollution (Buss et al., 2002). Moreover, the disappearance of sensitive taxa such as EPT (Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies)) at the cage site by the end of the study indicated an ecologically impaired site, attributable to degradation from cage culture activities (Johnson et al., 1993). This is reaffirmed by the low Shannon-Wiener values (0.82) recorded at the cage site by the end of the culture period, an indication of loss of diversity.

The present study indicates that the effect of cage aquaculture on the benthic communities is fairly localized suggesting that the impact from cage fish culture is restricted to an area within 50 m radius of the cages. Guo & Li (2003) and Srithongouthai & Tada (2017) reported that the impact of cage culture extended up to 20 m and 10 m, respectively, outside the cage area in lakes in China and Japan, which is line with the findings of the current study. The extent of impact of aquaculture effluents is dependent on a number of factors, including the area used for culture, depth of site, age of the farm, stocking densities, hydrodynamics, sediment adsorption, current speed, production volume of the farm and management. The localized impact of aquaculture in the study area, may, in part be due to the shallow waters (< 5 m) under the cages and concentration of cages in one site in an enclosed bay. High proportion of silt/clay under the cages has been reported

to decrease the footprint of cage aquaculture (Mazzola et al., 2000; Kakantzi & Karakassis, 2006). The localized impact in the current study could also be due to the high silt/clay contents recorded underneath the cages by the end of the culture period.

In contrast to the limnetic zone, the findings indicate that the benthic zone under the cages does not recover fully during the four-month fallowing period. The organic material that accumulated over the production cycle had not disappeared after the fallowing period (Figure 6). Similarly, the levels of BOD, TN, ORP and TP at the cage site had not returned to preproduction levels after four-month fallowing (Figure 7). The composition of the meiofaunal had not returned to the levels recorded prior to commencement of cage fish farming four months after the end of the previous production cycle (Figure 8). However, other orders such as EPT, reappeared in some replicates after 4 months fallow period, comprising only 0.9% under cage site, which probably highlights their limited chances of survival in such areas, especially if culture continues. However, the reappearance of EPT, albeit in small numbers, could indicate that the system was on its way to recovery as this group is an important bioindicator of organic pollution. Nonetheless, low diversity recorded at the cage site, reaffirms that the cage site had not completely recovered after 4 months. Hence, the benthic zone in Lake Victoria is not able to absorb and dilute perturbation within 4 months fallowing period. Continued production at the same locations will result in increased accumulation of organic material that may eventually have dire consequences for the fish due to release of hydrogenated sulfur from sediments beneath the cages. Mass mortalities of tilapia have been reported in the study area in 2016 (Njiru et al., 2018), confirming the risks associated with such enterprise. Hence, with the current management practices, cage fish farming in Lake Victoria could be a disaster in waiting. In order to reduce the risk of catastrophes, the fallowing period must be extended which requires the cages to be relocated between production cycles. These results also

show that cage aquaculture in Lake Victoria, a system that is already under severe environmental stress, is highly questionable.

CONCLUSION AND RECOMMENDATIONS

With rapid growth of fish cage culture in African inland waters, it is important to understand the quantity, impact and the fate of aquaculture derived nutrients. Nile tilapia cage culture in the lake have significant effects on water and bottom sediment quality, especially with respect to nutrients, planktons and macroinvertebrates, although it is restricted to close vicinity of the cages, with no broader ecosystem impact. The impacts on water at the cage sites are neutralized during the four-month fallowing period. However, the findings suggested that sediment and meiofaunal recovery were far from complete after four months fallow period, an indication that the system is not able to assimilate the nutrients quickly enough and this may turn into an environmental disaster. Moving the cages slightly before the start of a new cycle by 50-100 m may allow the benthic communities to recover and alleviate the problem. In addition, the fallowing period should be six months, contrary to the current practice. Intensive and unchecked cage culture practices in the African inland lakes will highly likely result in negative responses in lake environments. Hence, the current efforts to promote commercial cage fish culture enterprises in Lake Victoria and the Great Lakes Region must proceed with caution especially regarding the location of cages within each site to minimize loss of environment quality, which can cause undesirable changes in natural biological productivity processes. In any case, regular environmental monitoring programs should be strictly implemented for all cage fish culture enterprises.

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ETHICAL APPROVAL All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

DATA AVAIL ABILITY STATEMENT

The data for this manuscript will be available upon request.

REFERENCES

Abdel-Tawwab, M., Hagras, A.E., Elbaghdady, H.A.M., & Monier, M.N. (2014). Dissolved oxygen level and stocking density effects on growth, feed utilization, physiology, and innate immunity of Nile tilapia, *Oreochromis niloticus*. *Journal of Applied Aquaculture*, 26, 340–355.

Ackefors, H., & Enell, M. (1994). The release of nutrients and organic matter from aquaculture systems in Nordic countries. *Journal of Applied Ichthyology* 10, 225–241.

Akintola, S. L., Brown, A., Bakare, A., Osowo, O. D., & Omolola, B. (2013). Effects of Hot Smoking and Sun Drying Processes on Nutritional Composition of Giant Tiger Shrimp (*Penaeus monodon*, Fabricius, 1798). *Polish Journal of Food and Nutrition Sciences*, 63(4), 227–237. https://doi.org/10.2478/v10222-012-0093-1.

Anderson, J.L., Asche, F., Garlock, T., & Chu, J. (2017). Aquaculture: Its role in the future of food. In *Frontiers of Economics and Globalization*; Emerald Publishing Limited: Bradford, UK, Volume 17, pp. 159–173.

APHA (2005). American Public Health Association Standard Methods for the Examination of Water and Wastewater, 21st edn. Washington, D.C., APHA-AWWA-WEF, ISBN 0875530478

Aura, M.C., Musa, S., Yongo, E., Okechi, J., Njiru, J.M., Ogari, Z. et al. (2018a). Integration of mapping and socio-economic status of cage culture: Towards balancing lake-use and culture fisheries in Lake Victoria, Kenya. *Aquaculture Research*, 49(1), 532–545. https://doi.org/10.1111/are.13484.

Aura, C. M., Nyamweya, C., Njiru, J.M., Musa, S., Ogari, Z., & Wakwabi, E. (2018b). Exploring the demarcation requirements of fish breeding and nursery sites to balance the exploitation, management and conservation needs of Lake Victoria ecosystem. *Fisheries Management and Ecology,* 26, 451-459.

Aura, C.M., Nyamweya, C.S., Njiru, J.M., Omondi, R., Manyala, J., Musa, S. et al. (2021). Using the Multi-metric Index of Biotic Integrity methodological approach to determine the major river catchment that most pollutes a lake. *Aquatic Ecosystem Health and Management Society*, 24(1), 12–20.

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*ogy, 47, 473–82.

Bondad-Reantaso, M. G., Subasinghe, R. P., Arthur, J. R., Ogawa, K., Chinabut, S., Adlard, R. et al. (2005). Disease and health management in Asian aquaculture. *Veterinary Parasitology*, 132(3-4), 249-72. https://doi.org/10.1016/j.vetpar.2005.07.005.

Boyd, C. E., Lim, C., Queiroz, J., Salie, K., & de Wet, L. (2008). Best management practices for responsible aquaculture. Report. 24 pp.

Boyd, C. E., & Tucker, C.S. (1998). Pond aquaculture water quality management. Kluwer Academic Publishers, New York. 711 pp.

Braaten, R. (2007). Cage aquaculture and environmental impacts. In A. Bergheim (Ed.). *Aquacultural engineering and environment* (Vol. 661, pp. 49–91). Research Signpost: Kerala.

Buss, D.F., Silva, M.M., Darcilio, B., & Nessimian, J. (2002). Erratum: Influence of water chemistry and environmental degradation on macroinvertebrate assemblages in a river basin in south-east Brazil. *Hydrobiologia*, 481, 125-136.

Camago, J.A. (1992). Temporal and spatial variations in dominance, diversity and biotic indices along a limestone stream receiving a trout farm effluent. Water Air Soil Pollution, 63, pp. 343-359.

Carrol, M.L., Cochrane, S., Fieler, R., Velvin, R., & White, P. (2003). Organic enrichment of sediments from salmon farming in Norway: environmental factors, management practices and monitoring techniques. *Aquaculture,* 226, 165–180.

Dauda, A.B., Ajadi, A., Tola-Fabunmi, A.S., & Akinwole, A.O. (2019). Waste production in aquaculture: Sources, components and managements in different culture systems. *Aquaculture and Fisheries*, 4(3), 81-88.

Deirmendjian, L., Descy, J., Morana, C., Okello, W., Stoyneva-Gartner, M.P., Bouillon, S. et al. (2021). Limnological changes in Lake Victoria since the mid-20th century. *Freshwater Biology*, 66(8): 1630-1647.

Dias, J. D., Simões, N. R., & Bonecker, C. C. (2012). Net cages in fish farming: a scientometric analysis. *Acta Limnologica Brasiliensia*, 24(1), 12–17. https://doi.org/10.1590/S2179-443 975X2012005000022.

Dobrowolski, Z. (1987). The effect of cage culture of Rainbow trout on the distribution and stability of macrobenthos in eutrophic Lake Letowskie. *Ekologia Polska*, 35, 611-638.

Dumont, H. J., Van De Velde, I. & Dumont, S. (1975). The dry weight estimate of biomass in a selection of Cladocera, Copepoda and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia*, 19, 75–97.

Dussart, B.H., & Defaye, D. (1995). Introduction to the Copepoda. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World**.** SPB Academic Publishing, 277pp.

Egessa, R., Pabire, G.W., & Ocaya, H. (2018). Benthic macroinvertebrate community structure in Napoleon Gulf, Lake Victoria: effects of cage aquaculture in eutrophic lake. *Environmental Monitoring and Assessment,* 190, 112.

FAO. (2020). The State of the World Fisheries and Aquaculture. Sustainability in action. Rome. https://doi.org/10.4060/ca9229en

FAO. (2016) The State of the World Fisheries and Aquaculture. http://www.fao.org/3/i5555e/i5555e.pdf.

Gannon, J. E. & Stemberger, R. S. (1978). Zooplankton (especially crustaceans and rotifers) as indicators of water quality. *Transactions of the American Microscopical Society*, 97, 16–35.

Gao, Q., Cheung, K., Cheung, S., & Shin, P. (2005). Effects of nutrient enrichment derived from fish farming activities on macroinvertebrate assemblages in a subtropical region of Hong Kong. *Marine Pollution Bulletin*, 51, 994−1002.

Garcia de Souza, J. R., Solimano, P. J., Maiztegui, T., Baigun, C. R. M., & Colautti, D. C. (2015). Effects of stocking density and natural food availability on the extensive cage culture of

pejerrey (*Odontesthes bonariensis*) in a shallow Pampean lake in Argentina. *Aquaculture Research*, 46, 1332–1344. https://doi.org/10.1111/are.12286

Gikuma-Njuru, P., & Hecky, R. E. (2005). Nutrient concentrations in Nyanza Gulf, Lake Victoria Kenya: Light limits algal demand and abundance. *Hydrobiologia*, 534, 131–140.

Greenberg, A.F., Clesceri, L.S., & Eaton, A.D. (1992). Standard methods for examination of water and waste water. 18th edition. American Public Health Association, Washington, D.C. USA.

Guildford, S.J. & Hecky, R.E. (2000). Total nitrogen, total phosphorus and nutrient limitation in lakes and oceans: is there a common relationship? *Limnology and Oceanography*, 45, 1213–1223.

GUO, L., & LI, Z. (2003). Effects of nitrogen and phosphorus from fish cage-culture on the communities of a shallow lake in middle Yangtze river basin of China. *Aquaculture*, 226 (1-4), 201-212.

Hamilton, S.E., Gallo, S.M., Krach, N., Nyamwea, C.S., Okechi, J.K., Aura, C.M. et al. (2020). The use of unmanned aircraft systems and high resolution satellite imagery to monitor tilapia fish cage aquaculture expansion in Lake Victoria, Kenya. *Bulletin of Marine Science*, 96, 71-93.

Henderson, R. J., Forrest, D. A. M., Black, K. D., & Park, M. T. (1997). The lipid composition of sea loch sediments underlying salmon cages. *Aquaculture*, 158(1-2), 69–83. https://doi.org/10.1016/S0044-8486(97)00207-X.

Holby, O., & Hall, P.O.J. (1991). Chemical fluxes and mass balances in a marine fish. *Marine Ecology Progress Series*, 70(3), 263-272.

Huang, X.F. (1999). Survey, observation and analysis of lake ecology. In: Sun HL, Liu GS (eds) Standard methods for observation and analysis in Chinese Ecosystem Research Network, Series V. Standards Press of China, Beijing (in Chinese)

Huang, C.H. (1997). Aquaculture and the endogenous damage cost of water pollution: the case of Taiwan. *Aquaculture Economics and Management*, 1, 99–108.

Institute of Fisheries & Macroinvertebrate Identification, IFM (2006). Aquatic Ecology. Department of Biology, Sweden: Linkoping University Press. 21pp.

Jeffrey, S.W., & Humphrey, G.F. (1975). New spectrophotometric equations for determining chlorophyll a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochemie und Physiologie der Pflanzen*, 167, 191-194.

Johnson, R. K., Wiederholm, T., & Rosenberg, D. M. (1993). Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. In Rosenberg, D. M. & Resh, V. H. (eds), Freshwater Biomonitoring and Benthic Macroinvertebrates. Chapman & Hall, New York: 488 pp.

Kakantzi, I., & Karakassis, I. (2006). Benthic impacts of fish farming: Meta-analysis of community and geochemical data. *Marine Pollution Bulletin,* 52, 484– 493.

Kamadi, G. (2018). Floating Fish Farms Become a Threat to Lake Victoria. Business Today. https://businesstoday.co.ke/floating-fish-farms-become-threat-lake-victoria/. Accessed 15 May 2019.

Karakassis, I., Tsapakis, M., & Hatziyanni, E. (1998). Seasonal variability in sediment profiles beneath fish farm cages in the Mediterranean. *Marine Ecology Progress Series*, 162, 243–252. https://doi.org/10.3354/meps162243.

Kashindye, B. B., Nsinda, P., Kayanda, R., Ngupula, G. W., Mashafi, C. A., & Ezekiel, C. N., (2015). Environmental impacts of cage culture in Lake Victoria : the case of Shirati Bay - Sota , Tanzania. *SpringerPlus*. https://doi.org/10.1186/s40064-015-1241-y.

Kifuko, R. (2015). The state of cage fish farming in Uganda: actors, enabling environment, challenges and way forward. *International Journal of Education and Research*, 3(3), 483–488.

Kling, H.J., Mugidde, R., & Hecky, R.E. (2001). Recent changes in the phytoplankton community of Lake Victoria in response to eutrophication. In: M. Munawar, R.E. Hecky (Eds.), Great Lakes of the World: Food Webs, Health and Integrity, Backhuys, Leiden (2001), pp. 47-66.

Kolding, J., Haung, L., & Stefansson, S. (2008). Effect of ambient oxygen on growth and reproduction in Nile tilapia (*Oreochromis niloticus*). *Canadian Journal of Fisheries and Aquatic Sciences*, https://doi.org/10.1139/F08-059

Korovchinsky, N. M. (1992). Sididae and Holopediidae. Guides to the identification of the Microinvertebrates of the Continental Waters of the World. SPB Acad. Publ., The Hague, 82 pp.

Koste, W., & Shiel, R. J. (1987). Rotifera from Australian inland waters. 11. Epiphanidae and Brachionidae (Rotifera : Monogononta). *Invertebrate Taxonomy*, 7, 949-1021.

Kutti, T., Hansen, P.K., Ervik, A., & Hoisaeter, T. (2007). Effects of organic effluents from a salmon farm on a fjord system. II. Temporal and spatial patterns in infauna community composition. *Aquaculture,* 262, 355-366.

Lars-Anders, H. A., Gyllstrom, M., Stahl-Delbanco, A. & Svensson, M. (2004). Responses to fish predation and nutrients by plankton at different levels of taxonomic resolution. *Freshwater Biology,* 49, 1538–50.

Lung'ayia H., Sitoki, L., & Kenyanya, M. (2001). The nutrient enrichment of Lake Victoria (Kenyan waters). *Hydrobiologia*, 458,75–82. https://doi.org/10.1023/A:1013128027773

LVEMP (2005). Lake Victoria Environmental Management Project. National Water Quality Synthesis Report, Kisumu (Kenya), p. 431. https://www.semanticscholar.org/paper/National-water-quality-synthesis-report%2C-Kenya.-Gikuma-Njuru-Abuodha/7ac0693da5dd211825382da4bda8a41f66886ca8. Accessed on 21/6/22.

Mavuti, K. M. & Litterick, M. R. (1991). Composition, distribution and ecological role of zooplankton community in Lake Victoria, Kenya waters. *Internationale Vereinigung für Theoretische und Angewandte Limnologie: Verhandlungen*, 24, 1117–22.

Mazzola, A., Mirto, S., La Rosa, T., Fabiano, M., & Danovaro, R. (2000). Fish-farming effects on benthic community structure in coastal sediments: analysis of meiofaunal recovery. *ICES Journal of Marine Science,* 57(5), 1454–1461. https://doi. org/10.1006/jmsc.2000.0904.

Merritt, R.W., & Cummins, K.W. (1978). An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publishing Company, Iowa. USA.

Miserendino, M.L & Pizzolon, L.A. (2000). Macroinvertebrates of a fluvial system in Patagonia: Altitudinal zonation and functional structure. *Hydrobiologia*, 150, 55-83.

Mohamed, Z., Ahmed, Z., & Bakr, A. (2019). Assessment of phytoplankton species in gut and feces of cultured tilapia fish in Egyptian fishponds: Implications for feeding and bloom control. *Acta Limnologica Brasiliensa*, 31, e27. DOI: 10.1590/s2179-975x8418.

Musa, S., Aura, C.M., & Okechi, J.K. (2021a). Economic analysis of tilapia cage culture in Lake Victoria using different cage volumes. *Journal of Applied Aquaculture*, https://doi.org/10.1080/10454438.2021.1884632.

Musa, S., Aura, C.M., Tomasson, T., Sigurgeirsson, O., Thorarensen, H. (2021b). A comparative study of the effects of pelleted and extruded feed on growth, financial revenue and nutrient loading of Nile tilapia (Oreochromis niloticus L.) cage culture in a lacustrine environment. Journal of applied Aquaculture. DOI: 10.1080/10454438.2021.2011528

Musinguzi, L., Lugya, J., Rwezaula, P., Kamya, A., Nuwahereza, C., Halafo, J. et al. (2019). The extent of cage aquaculture, adherence to best practices and reflections for sustainable aquaculture on African inland waters. *Journal of Great Lakes Research,* https://doi:10.1016/j.jglr.2019.09.011.

Mwamburi, J., Basweti, G., Owili, M., Babu, J., & Wawiye, P. (2020). Spatio-temporal trends of nutrients and physico-chemical parameters on lake ecosystem and fisheries prior to onset of cage farming and re-opening of the Mbita passage in the Nyanza Gulf of Lake Victoria. *Lakes and Reservoirs Research and Management for Sustainable Use*, 25:292–313. https://doi.org/10.1111/lre.12329

Mwebaza-Ndawula, L., Kiggundu, V., & Pabire, G. (2001). Invertebrate communities of Nabugabo lakes: avital support resource for the fisheries and ecosystem diversity. In: A Compilation of Scientific Information on Nabugabo Ramsar Site (eds H. Busulwa, P. G. Mafabi & L. Mwebaza-Ndawula), pp. 20–30. JOSU Links (U) Ltd Kampala, Nabugabo, Uganda.

Mwebaza-Ndawula, L., Kiggundu, V. & Pabire Ghandhi, W. (2004). The status and significance of invertebrate communities. In: Challenges for Management of the Fisheries Resources,

Biodiversity and Environment of Lake Victoria, 1st edn (eds J. S. Balirwa, R. Mugidde & R. Ogutu-Ohwayo), pp. 153–71. Fisheries Resources Research Institute, Jinja.

Mwebaza-Ndawula, L., Kiggundu, V. Magezi, G., Naluwayiro, J., Gandhi-Pabire, W., & Ocaya, H. (2013). Effects of cage fish culture on water quality and selected biological communities in northern Lake Victoria, Uganda. *Uganda Journal of Agricultural Sciences*, 14(2), 61 – 75.

Nabirye, H., Mwebaza-Ndawula, L., Bugenyi, F. W. B., & Jones, F. (2016). The evaluation of cage fish farming effects on water quality using selected benthic macro-invertebrate community parameters in the Napoleon gulf, northern Lake Victoria. *International Journal of Fisheries and Aquatic Sciences*, 4(1), 42–50.

Ngupula, G.W. (2013). How Does Increased Eutrophication and Pollution in the Lake Victoria Waters Impacts Zooplankton? *Journal of Environment and Ecology,* 4(2):151. DOI: 10.5296/jee.v4i2.4397.

Ngupula, G.W., & Kayanda, R. (2010). Benthic macrofauna community composition, abundance and distribution in the Tanzanian and Ugandan inshore and offshore waters of Lake Victoria. *African Journal of Aquatic Science,* 35(2), 185–192.

Ngupula, G.W., Ezekiel, C.N., Kimirei, I. A., Mboni, E., & Kashindye, B.B. (2012). Physical and chemical characteristics of the Tanzanian inshore and offshore waters of Lake Victoria in 2005–2008. *African Journal of Aquatic Science*, 37(3), 339-345.

Nickell LA, Kenneth DB, Hughes D, Overnell J, Brand T, Nickell TD, Breuer E, Harvey SM (2003). Bioturbation, sediment fluxes and benthic community structure around a salmon cage farm in Loch Creran, Scotland. J Exp Mar Biol Ecol 285–286:221–233.

Njiru, J.M., Aura, C.M., & Okechi, J.K. (2018). Cage fishing culture in Lake Victoria: A boon or disaster in waiting? *Fisheries Management and Ecology*, Review Article: 1 – 9.

Njiru, J., & Aura, C.M. (2019). Cage farming can protect Lake Victoria's fish. But regulations need tightening. The Conversation. https://theconversation.com/cage-farming-can-protectlake-victorias-fish-but-regulations-need-tightening-112641. Accessed 20 March 2019.

Obiero, K.O., Meulenbroek, P., Drexler, S., Dagne, A., Akoll, P., Oding, R. et al. (2019). The Contribution of Fish to Food and Nutrition Security in Eastern Africa: Emerging Trends and Future Outlooks. *Sustainability*, 11:1636. doi:10.3390/su11061636

Ochumba, P.B.O., & Kibaara, D.I. (1989). Observations on blue-green algal blooms in the open waters of Lake Victoria, Kenya. *African Journal of Ecology,* 27(1), 23–34. https://doi.org/10.1111/j.1365-2028.1989.tb00925.x

Perez, O.M., Telfer, T.C. & Ross, L.G. (2005). Geographical Information Systems-based models for offshore floating marine fish cage aquaculture site selection in Tenerife, Canary Islands. *Aquaculture Research*, 36, 946-961.

Phillips, M.J., Beveridge, M.C.M., & Ross, L.G. (1985). The environmental impact of salmonid cage culture on inland fisheries: present status and future trends. *Journal of Fish Biology*, 27 (Suppl. A), 123–127.

Pielou, E. C. (1975). Ecological diversity. John Wiley & Sons, New York, 165 pp.

Porrello, S., Tomassetti, P., Manzueto, L., Finoia, M. G., Persia, E., Mercatali, I., & Stipa, P. (2005). The influence of marine cages on the sediment chemistry in the Western Mediterranean Sea. *Aquaculture*, 249(1-4), 145–158. https://doi.org/10.1016/j.aquaculture.2005.02.042.

Quiley, M. (1977). Invertebrates of Streams and Rivers. Key to Identification. Bedford Square, London: Academic Press. 21pp.

Radwan, S., & Popiolek, B. (1989). Percentage of rotifers in spring zooplankton in lakes of different trophy. *Hydrobiologia*, 186/187, 235–386.

Schmidlin, S., & Baur, B. (2007). Distribution and substrate preference of the invasive clam Corbicula fluminea in the river Rhine in the region of Basel (Switzerland, Germany, France). *Aquatic Sciences*, 69(1), 153–161. https://doi.org/10.1007/s00027-006-0865y.

Segers, H.H. (1995). A reappraisal of the Scaridiidae (Rotifera, Monogononta). *Zoologica Scripta*, Vol. 24, No. 2, pp. 91-100.

Sladecek, V. (1983). Rotifers as indicators of water quality. *Hydrobiologia,* 100, 169–201.

Smirnov, N.N. (1996). Cladocera: the Chydorinae and Sayciinae (Chydoridae) of the world. Guides to the identification of the microinvertebrates of the continental waters of the world II. Amsterdam: SPB Academic Publishing, 197 pp.

Srithongouthai, S., & Tada, K. (2017). Impacts of organic waste from a yellowtail cage farm on surface sediment and bottom water in Shido Bay (the Seto Inland Sea, Japan). *Aquaculture*, 471: 140-145.

Simiyu, B.M., Amukhuma, H.S., Sitoki, L., Okello, W., Kurmayer, R. (2021). Interannual variability of water quality conditions in the Nyanza Gulf of Lake Victoria, Kenya. *Journal of Great Lakes Research*, 48(1), 97-109.

Tasevska, O., Kostoski, G., & Guseska, D. (2010). Rotifers Based Assessment of the Lake Dojran Water Quality. Balwois, Ohrid.

Timmons, M.B., Guerdat, T., Vinci, B.J. (2010). Recirculating Aquaculture, 4th edition. Ithaca Publishing Company, Ithaca, NY. 700 pp.

Tran-Duy, A., van Dam, A.A., & Schrama, J.W. (2012). Feed intake, growth and metabolism of Nile tilapia (*Oreochromis niloticus*) in relation to dissolved oxygen concentration. *Aquaculture Research*, 43, 730–744.

Tsadiki, G.G. & Kutty, M.M. (1987). Influence of ambient oxygen on feeding and growth of the tilapia *Oreochromis niloticus* (Linnaeus). Working paper, ARAC/87/WP/10

Verschuren, D., Johnson, T.C., Kling, H.J., Edgington, D.N. Leavitt, P.R., Brown, E.T., Talbot, M.R. & Hecky, R.E. (2002). History and timing of human impact on Lake Victoria, East Africa. *Proceedings of the Royal Society B*, 269, 289-294.

Villnas, A., Perus, J., & Bonsdorff, E. (2011). Structural and functional shifts in zoobenthos induced by organic enrichment - Implications for community recovery potential. *Journal of Sea Research*, 65: 8−18.

Vincent, K., Mwebaza-Ndawula, L., Makanga, B., & Nachuha, S. (2012). Variations in zooplankton community structure and water quality conditions in three habitat types in northern Lake Victoria. *Lakes & Reservoirs: Research and Management*, 17, 83–95.

Von Sperling, M. & Chernicharo C.A.L. (2005). Biological Wastewater Treatment in Warm Climate Regions. IWA Publishing, London, UK.

Wu, R.S.S. (1995). The environmental impact of marine fish culture: Towards a Sustainable Future. *Marine Pollution Bulletin*, 31, 159–166.

APPENDIX I Zooplankton species, relative contribution (%) and mean densities (parentheses) ind L^{-1} (± SEM) across cage culture sampling sites

	Day0 (Beginning of culture period)				Day 180 (End of culture period)				Day 300 (End of fallow period)			
	0 m	50 m	150 m	500 m	0 m	50 m	150 m	500 m	0 m	50 m	150 m	500 m
Rotifera												
B. falcatus	13.7 (3.7±0.7)	13.7 (3.7±0.3)	10.7(2.8±0.3)	16.7(1.6±0.3)	0.0(0.0±0.0)	12.5(5.2±0.0)	16.7(3.3±0.3)	33.3(3.3±0.3)	9.2(11.6±0.0)	12.5(5.2±0.0)	0.0(0.0±0.0)	10.3(1.6±0.0)
B. angularis	8.5 (2.3±0.3)	5.9 (1.6±0.3)	25.2(6.6±0.3)	16.7(1.6±0.3)	53.4(208.2±5.3)	16.7(6.9±0.3)	14.6(2.9±0.3)	0.0(0.0±0.0)	10.8(13.6±0.1)	12.5(5.2±0.0)	5.0(1.4±0.0)	0.0(0.0±0.0)
B. calciflrus	11.1 (3.0±0.6)	13.7 (3.7±0.3)	10.7(2.8±0.3)	0.0(0.0±0.0)	46.6(181.7±3.3)	12.5(5.2±0.6)	8.3(1.7±0.3)	33.3(3.3±0.3)	10.8(13.6±0.1)	12.5(5.2±0.0)	16.7(4.7±0.0)	10.3(1.6±0.0)
Filinia spp	13.7 (3.7±0.3)	13.7 (3.7±0.3)	10.7(2.8±0.3)	16.7(1.6±0.3)	0.0(0.0±0.0)	8.3(3.4±0.3)	8.3(1.7±0.3)	0.0(0.0±0.0)	10.8(13.6±0.0)	12.5(5.2±0.0)	16.7(4.7±0.0)	0.0(0.0±0.0)
Asplanchna spp	10.0 (2.7±1.1)	5.9 (1.6±1.1)	10.7(2.8±1.3)	0.0(0.0±0.0)	0.0(0.0±0.0)	16.7(6.9±1.0)	20.5(4.1±1.2)	0.0(0.0±0.0)	12(15.1±0.3)	12.5(5.2±0.0)	16.7(4.7±0.0)	0.0(0.0±0.0)
Lecane spp	11.1 (3.0±0.6)	13.7 (3.7±0.3)	10.7(2.8±0.3)	16.7(1.6±0.3)	0.0(0.0±0.0)	8.3(3.4±0.3)	15.0(3.0±0.0)	16.7(1.7±0.3)	15.9(20.0±0.4)	12.5(5.2±0.0)	16.7(4.7±0.0)	34.5(5.5±0.0)
Euchlanis spp	15.9 (4.3±0.3)	20.0 (5.4±0.0)	10.7(2.8±0.3)	16.7(1.6±0.3)	0.0(0.0±0.0)	12.5(5.2±0.0)	8.3(1.7±0.3)	0.0(0.0±0.0)	14.7(18.5±0.2)	12.5(5.2±0.0)	16.7(4.7±0.0)	10.3(1.6±0.0)
K. tropica	15.9 (4.3±0.3)	13.7 (3.7±0.3)	10.7(2.8±0.3)	16.7(1.6±0.3)	0.0(0.0±0.0)	12.5(5.2±0.0)	8.3(1.7±0.3)	16.7(1.7±0.3)	15.9(20.0±0.0)	12.5(5.2±0.0)	11.7(3.3±0.2)	34.5(5.5±0.0)
Cladocera												
Moina micrura	25 (13.3±1.0)	27.3 (14.7±0.6)	27.3(14.7±0.6)	17.7(11.8±0.3)	100.0(35.0±0.0)	28.6(20.1±0.0)	21.4(15.0±0.0)	25.0(20.0±0.0)	27.4(38.6±1.2)	27.5(23.8±2.3)	25.0(19.7±0.0)	25.8(28.0±2.4)
Bosmina longirostris	26.3 (13.8±0.7)	18.2 (9.8±0.0)	24.5(13.2±0.7)	28.4(19.0±0.3)	0.0(0.0±0.0)	28.6(20.1±0.0)	28.6(20.0±0.0)	25.0(20.00.0)	23.8(33.5±2.2)	21.6(18.7±1.2)	25.0(19.7±0.0)	22.6(24.5±1.2)
Daphnia lumhortzi	25.0 (13.3±0.0)	30.3 (16.4±0.3)	27.3(14.7±0.6)	30.8(20.6±0.0)	0.0(0.0±0.0)	21.4(15.0±0.0)	28.6(20.0±0.0)	25.0(20.0±0.0)	27.4(38.6±1.1)	27.5(23.8±0.2)	25.0(19.7±0.0)	25.8(28.0±2.2)
Chydorus spp.	23.8 (12.6±0.3)	24.5 (13.2±0.3)	20.9(11.3±0.3)	23.1(15.4±0.6)	0.0(0.0±0.0)	21.4(15.0±0.0)	21.4(15.0±0.0)	25.0(20.0±0.0)	21.4(30.1.0±0.4)	23.4(20.2±1.2)	25.0(19.7±0.0)	25.8(28.0±2.2)
Copepoda												
Copepoid nauplii	33.3 (34.0±0.0)	37.1 (37.8±0.7)	43.3(44.2±0.9)	22.2(9.6±0.6)	100.0(22.0±0.0)	30.0(14.5±0.0)	20.0(10.0±0.0)	16.7(10.0±0.0)	30.0(31.0±0.5)	28.6(20.6±0.2)	33.3(24.2±0.2)	30.7(21.6±1.2)
Cyclopoida	33.3 (34.0±0.0)	37.1 (37.8±0.7)	30.0(30.6±0.6)	37.0(16.0±0.7)	0.0(0.0±0.0)	40.0(19.3±0.0)	40.0(20.0±0.0)	33.3(20.0±0.0)	33.3(34.4.0±3.3)	35.7(25.7±0.4)	33.3(24.2±0.2)	33.6(23.7±1.1)
Calanoida	33.3 (34.0±0.0)	25.8 (26.3±0.9)	26.7(27.2±0.3)	40.7(17.6±0.9)	0.0(0.0±0.0)	30.0(14.5±0.0)	40.0 (20.0±0.0)	50.0(30.0±0.0)	36.7(37.9±3.3)	35.7(25.7±2.1)	33.3(24.2±0.2)	35.7(25.1±2.2)

APPENDIX 2 Species composition of zoobenthos sampled at cage culture site in Anyanga beach, Lake Victoria, Kenya during the study period

Order	Family	Genus	Day0 (beginning of culture period)				Day180 (end of culture period)				Day300 (end of fallow period)			
			0 m	50 m	150 m	500 m	0 m	50 m	150 m	500 m	0 m	50 m	150 m	500 m
		Aquatic insects												
Ephemeroptera	Baetidae	*Baetis* spp	+	+	+	+		+	+	+	+	+	+	+
	Heptagenidae	*Heptagenia* spp				+							+	+
	Caenidae	*Caenis* spp	+	+	+	+		+	+	+		+	+	+
	Ephemerellidae	*Ephemerella* spp			+	+				+			+	+
Plecoptera	Nemouridae	*Nemoura* spp	+	+	+	+		+	+	+	+	+	+	+
	Leuctridae	*Leuctra* spp				+				+			+	+
Trichoptera	Polycentropodidae	*Polycentropus* spp	+	+	+	+		+	+	+		+	+	+
Diptera	*Chironomidae*	*Brillia* spp	+	+	+	+		+	+	+	+	+	+	+
	Culicidae	*Culicida* spp	+	+	+	+		+	+	+	+	+	+	+
Odonata	*Gomphidae*	*Lanthus* spp	+	+	+	+		+	+	+	+	+	+	+
		Stylogomphus spp		+	+	+		+	+	+		+	+	+
	Aeshnidae	*Basiaeschna* spp	+	+	+	+		+	+		+	+	+	+
Hemiptera	*Corixidae*	*Corixa* spp		+		+				+		+	+	+
	Gerridae	*Gerris* spp	+	+	+					+	+	+	+	+
	Veliidae	*Velia* spp			+	+			+				+	+
	Notonectidae	*Notonecta* spp	+	+		+			+		+	+	+	+
	Nepididae	*Nepus* spp			+	+			+	+			+	+

	Belostomatidae	*Belostoma* spp		+	+	+			+			+			+	+
		Molluscs														
Gastropoda	*Physidae*	*Physella* spp	+	+	+			+	+	+			+	+	+	+
	Lymnaeidae	*Fossaria* spp	+	+	+	+			+	+			+	+	+	+
Bivalvia	*Sphaeniidae*	*Pisidium* spp	+	+	+	+			+	+	+		+	+	+	+
	Sphaeniidae	*Sphaerium* spp	+	+	+	+		+	+	+			+	+	+	+
		Annelids														
Oligochaeta	*Tubificiidae*	*Tubifex* spp	+	+	+			+	+	+			+	+	+	+
	Lumbricus	*Eclipidrulus* spp	+	+	+	+			+	+	+		+	+	+	+
Hirudinea	*Glossiphomiidae*	*Batracobdella* spp	+	+	+	+			+	+			+	+	+	+
		Helobdela spp	+	+	+	+			+	+	+		+	+	+	+

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FIGURE LEGENDS

FIGURE 1 Map of the study area showing Anyanga Beach**,** Kadimo Bay, Lake Victoria, Kenya, and the sampling points (0 m, 50 m, 150 m and 500 m away from cages)

FIGURE 2 Dissolved nutrients (mean ± SEM) at a cage culture site at Anyanga beach, Lake Victoria, Kenya showing **a)** chlorophyl *a*; **b)** Total phosphorus (TP); **c)** Total nitrogen (TN); and d) N:P molar ratio during culture and fallow period

FIGURE 3 Abundance (mean ± SEM) of zooplankton at a cage culture site at Anyanga beach, Lake Victoria, Kenya showing **a)** Rotifera, **b)** Cladocera and **c)** Copepoda during culture and fallowing periods

FIGURE 4 Water quality (mean ± SEM) at a cage culture site at Anyanga beach, Lake Victoria, Kenya showing **a)** Dissolved oxygen, **b)** BOD and **c)** Secchi depth **d)** NH_3 during culture and fallow periods

FIGURE 5 Diurnal variation in DO and pH at the cage and reference sites at the beginning and end of the culture period at Anyanga beach, Lake Victoria, Kenya

FIGURE 6 Proportions of grain size of surface sediment at a cage culture site at Anyanga beach, Lake Victoria, Kenya

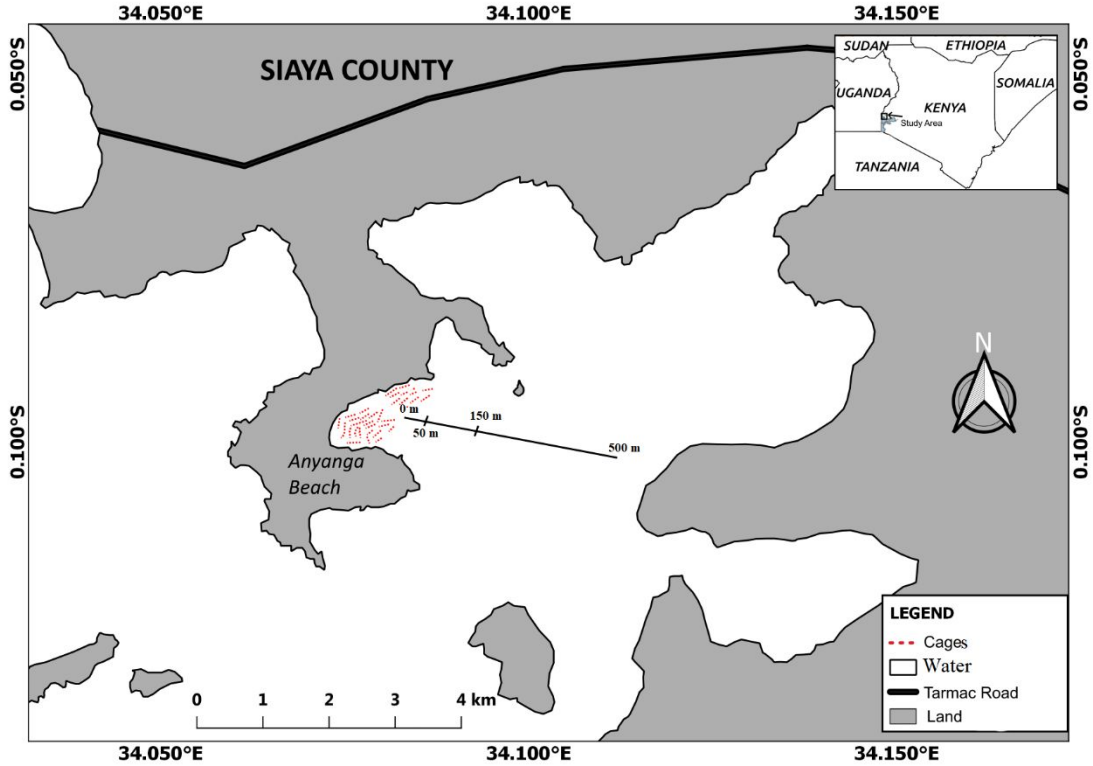
FIGURE 7 The sediment composition (mean ± SEM) of **a)** total organic carbon TOC; **b)** Total phosphorous (TP); **c)** Total Kjeldahl nitrogen (TN); **d)** biological oxygen demand (BOD); and **e)** Oxidation-reduction potential during culture and fallowing periods

FIGURE 8 The structure of the macro-benthic invertebrate community (as mean number of individuals L^{-1}) during culture and fallow periods at Anyanga beach, Lake Victoria, Kenya

TABLE 1 Average Shannon index values (± SEM) for different sampling stations and time for Nile tilapia cage culture at Anyaga beach, Lake Victoria, Kenya. Significant differences are indicated with superscripted letters (Kruskal-Wallis test)

Day	Distance from cage	Shannon-Wiener diversity (*H'*)
Day 0 (Beginning of culture period)	0 m	2.38 ± 0.02[a]
	50 m	2.42 ± 0.02[a]
	150 m	2.40 ± 0.04[a]
	500 m	2.44 ± 0.07[a]
Day 180 (End of culture period)	0 m	0.82 ± 0.01[b]
	50 m	2.38 ± 0.01[a]
	150 m	2.40 ± 0.06[a]
	500 m	2.41 ± 0.05[a]
Day 300 (End of fallow period)	0 m	1.56 ± 0.03[b]
	50 m	2.41 ± 0.04[a]
	150 m	2.41 ± 0.02[a]
	500 m	2.43 ± 0.03[a]

884 **Figures**



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886 **FIGURE 1**

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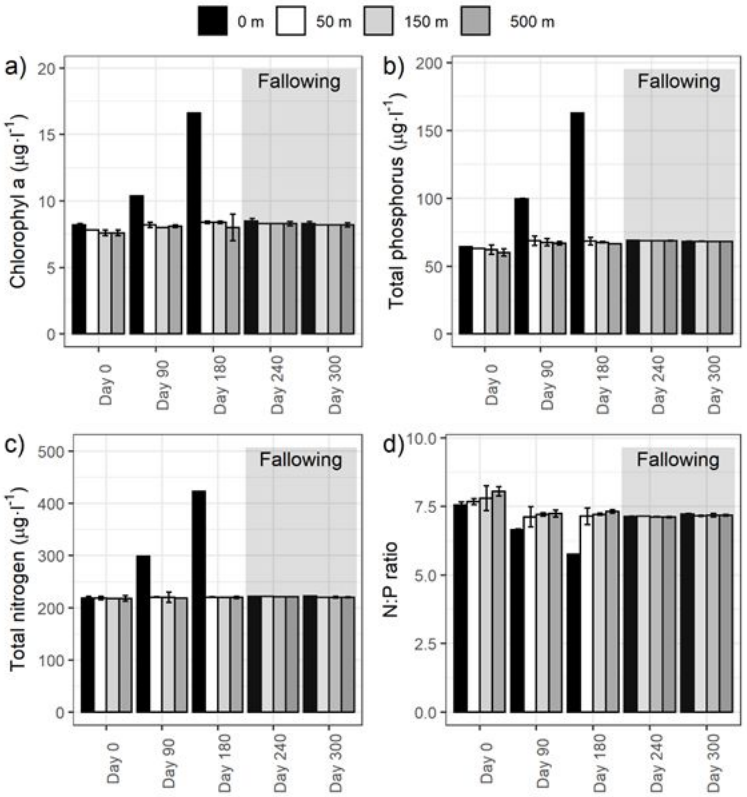
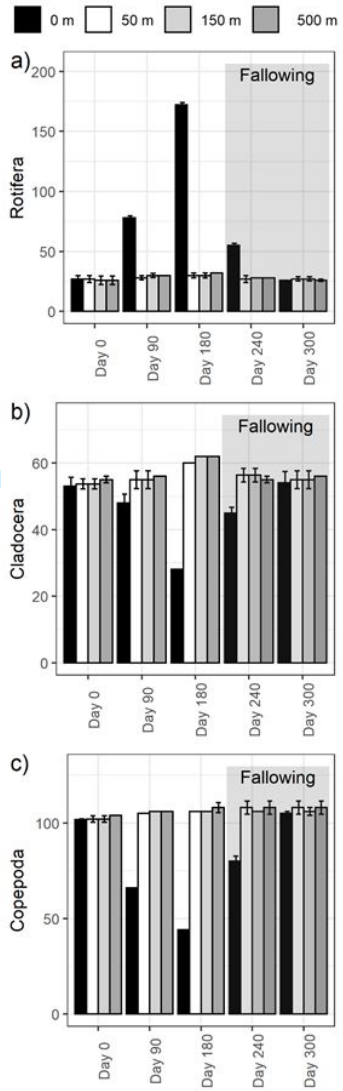

0 m
50 m
150 m
500 m
a)
Chlorophyl a (µg·l-1)
Fallowing
b)
Total phosphorus (µg·l-1)
Fallowing
c)
Total nitrogen (µg·l-1)
Fallowing
d)
N:P ratio
Fallowing
Day 0
Day 90
Day 180
Day 240
Day 300

FIGURE 2



893

894 **FIGURE 3**

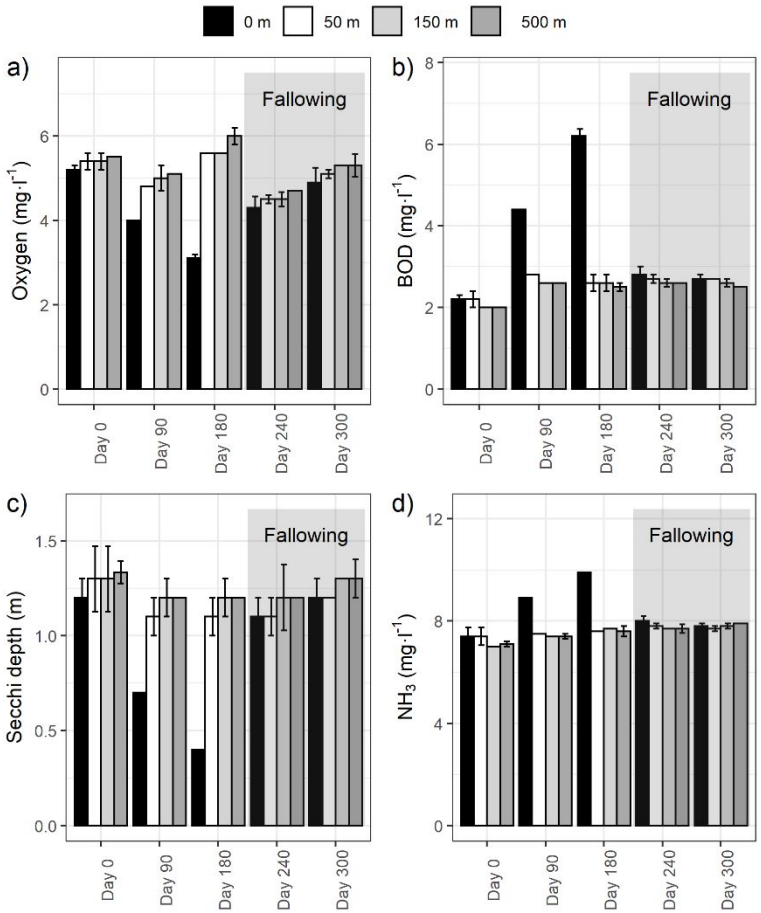
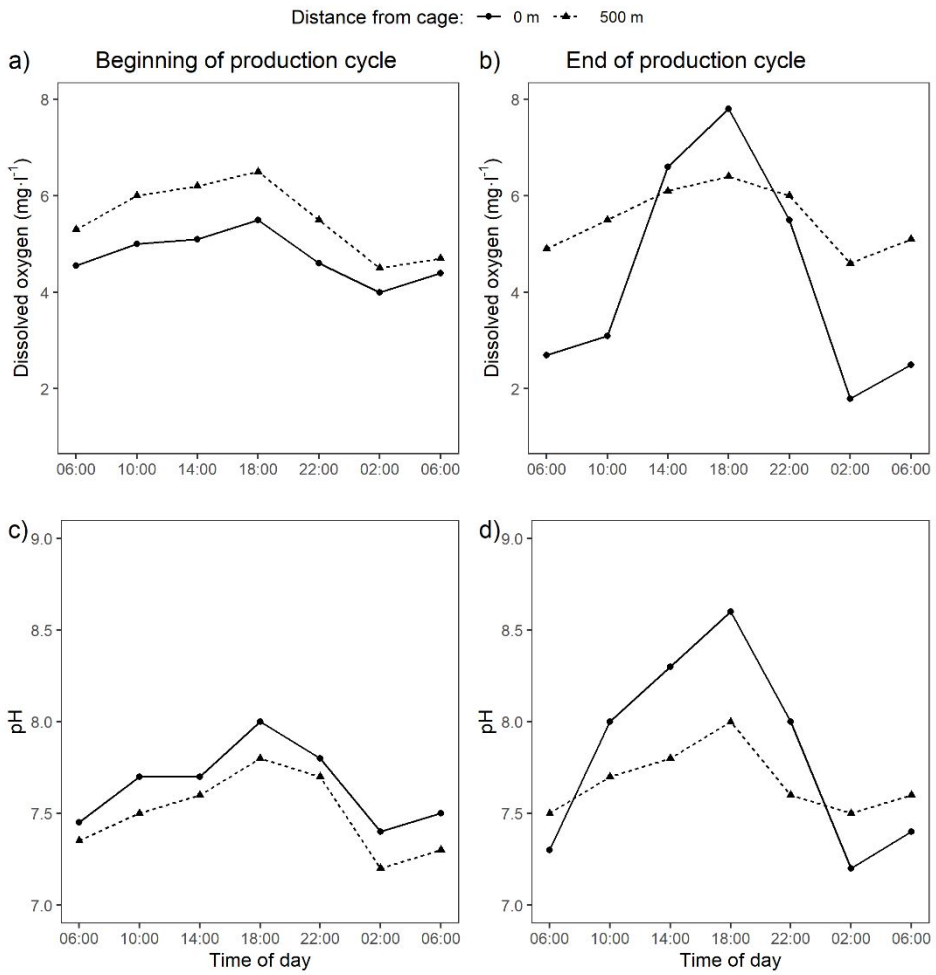

0 m
50 m
150 m
500 m
a)
b)
c)
d)
Fallowing
Oxygen (mg·l-1)
BOD (mg·l-1)
Secchi depth (m)
NH3 (mg·l-1)
Day 0
Day 90
Day 180
Day 240
Day 300

FIGURE 4



898

899 **FIGURE 5**

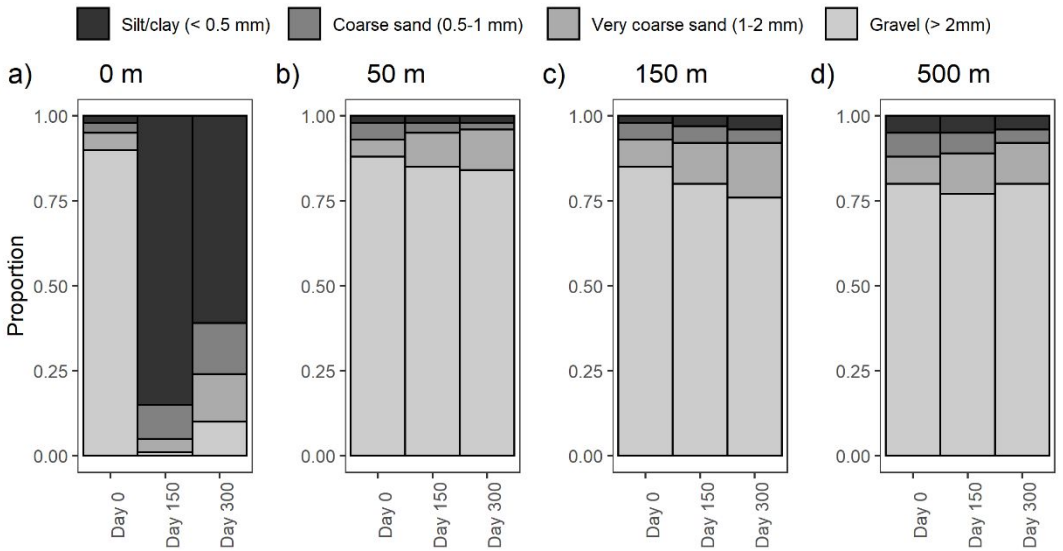
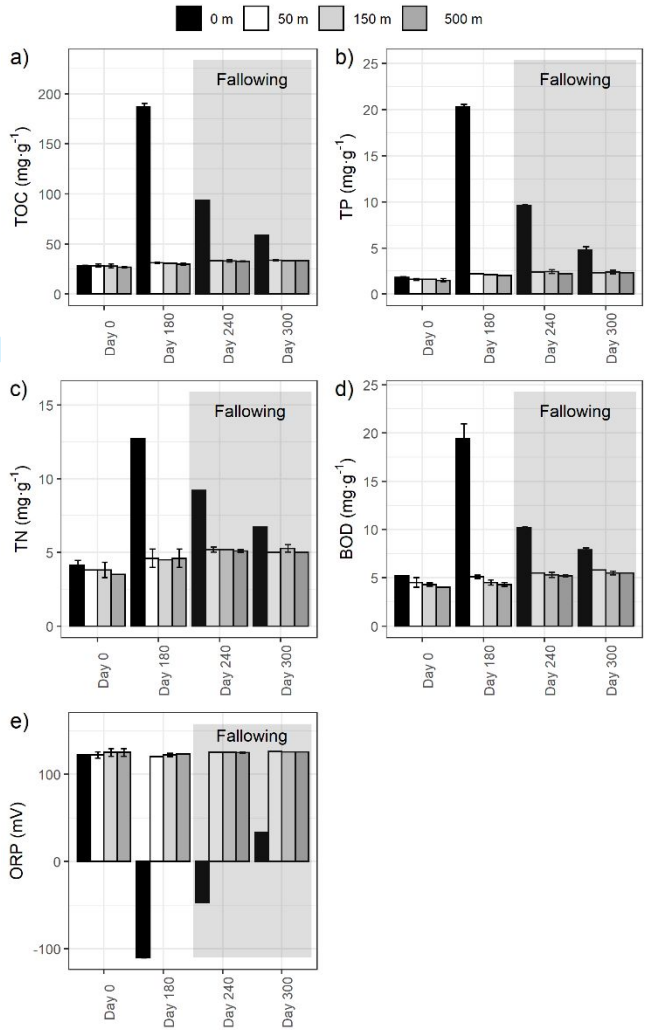


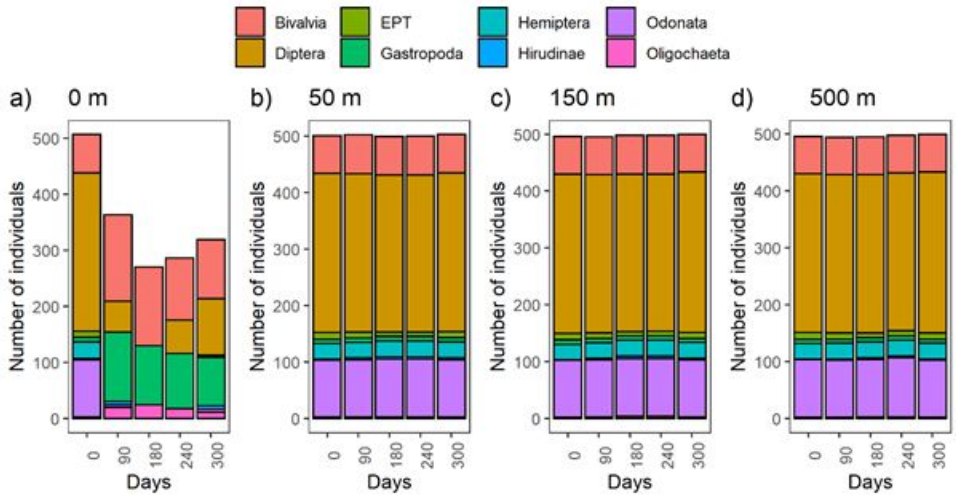
FIGURE 6



904

905

906 **FIGURE 7**



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908

909 **FIGURE 8**

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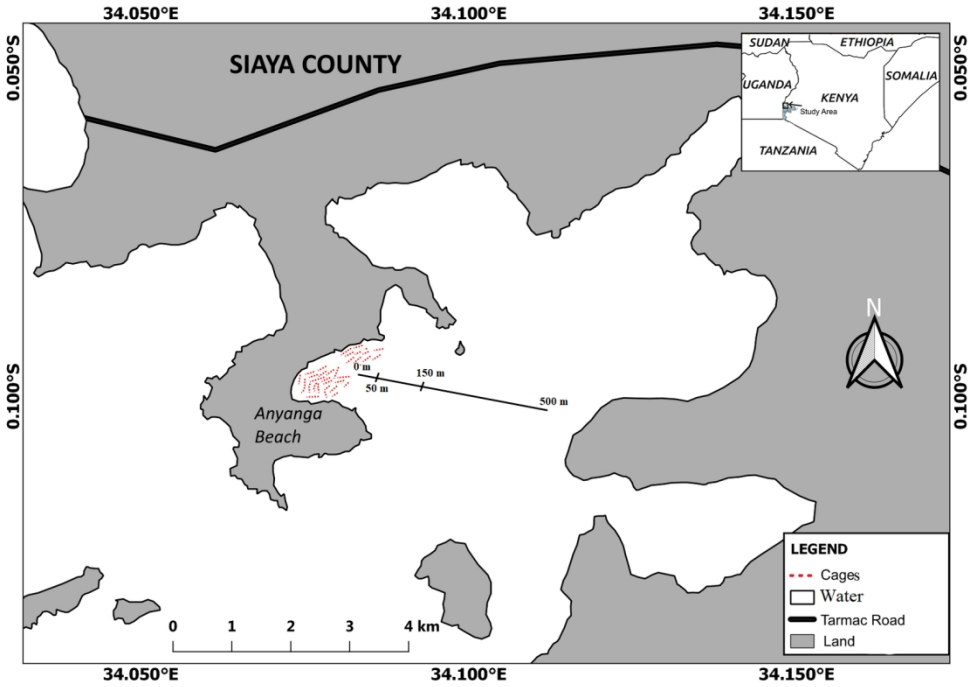
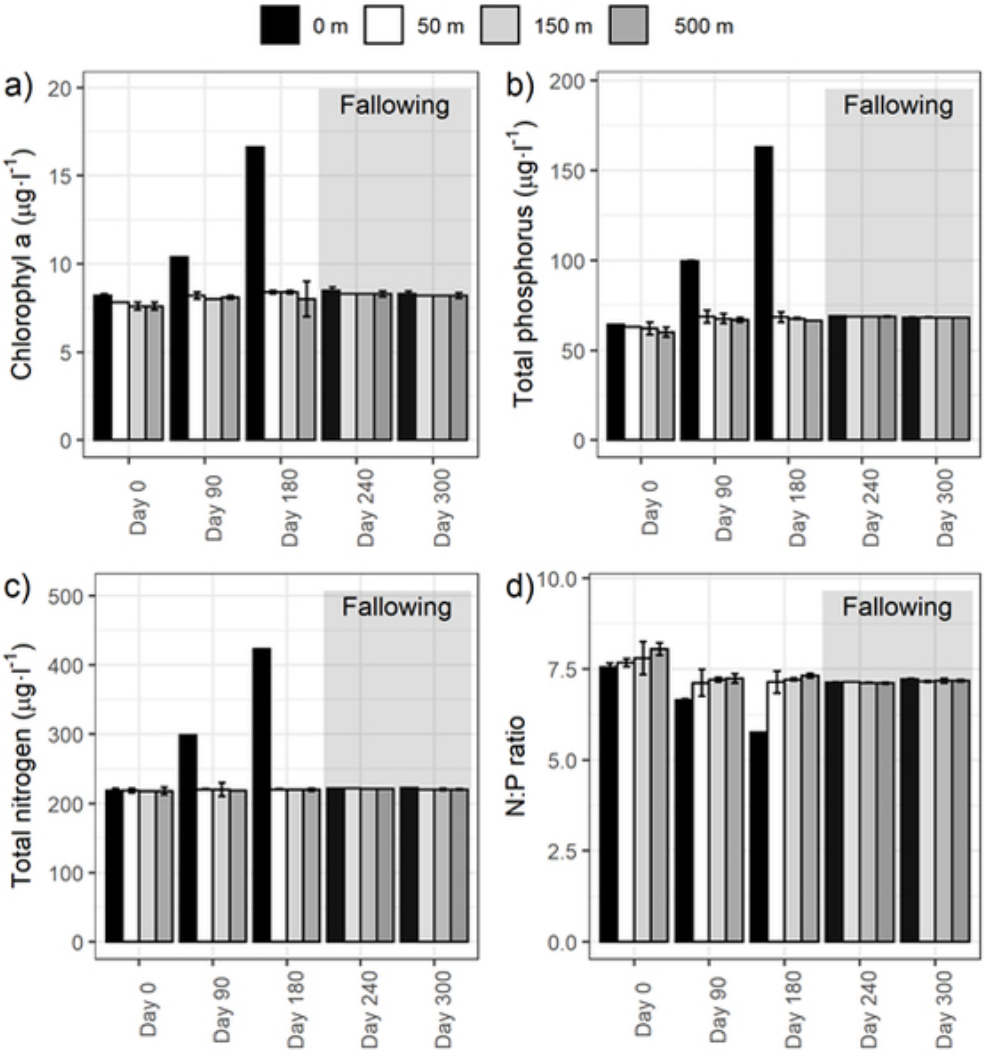
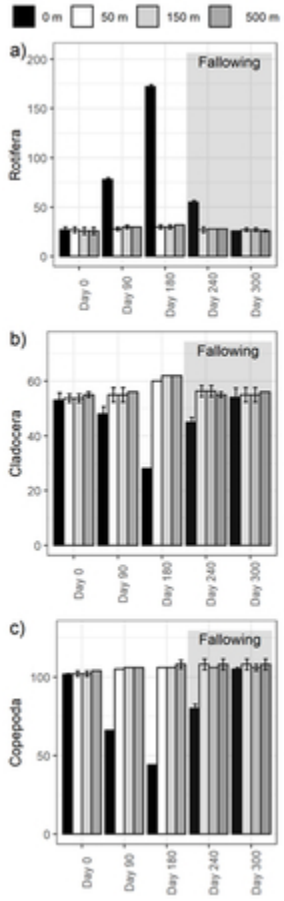
911



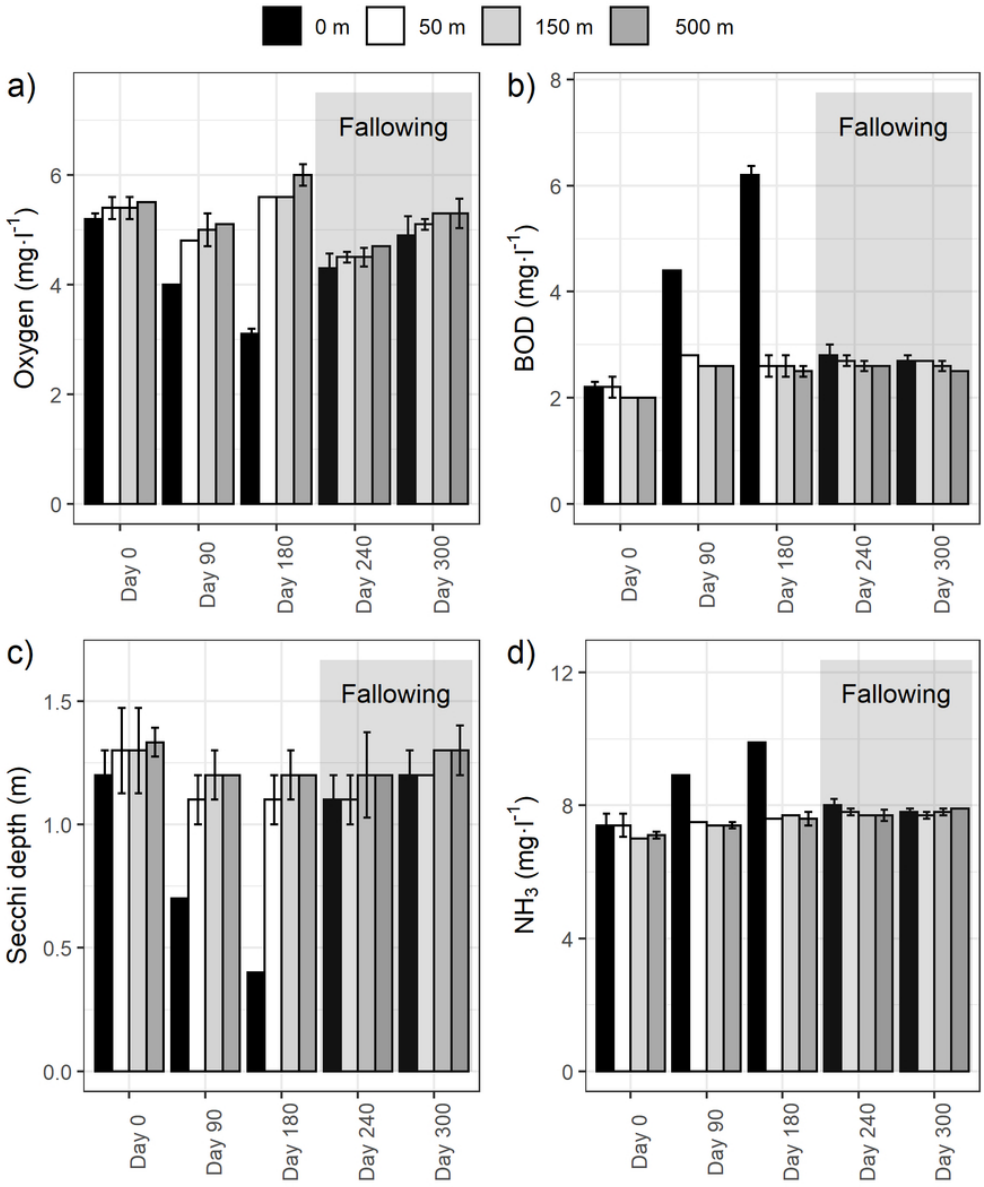
74x52mm (600 x 600 DPI)



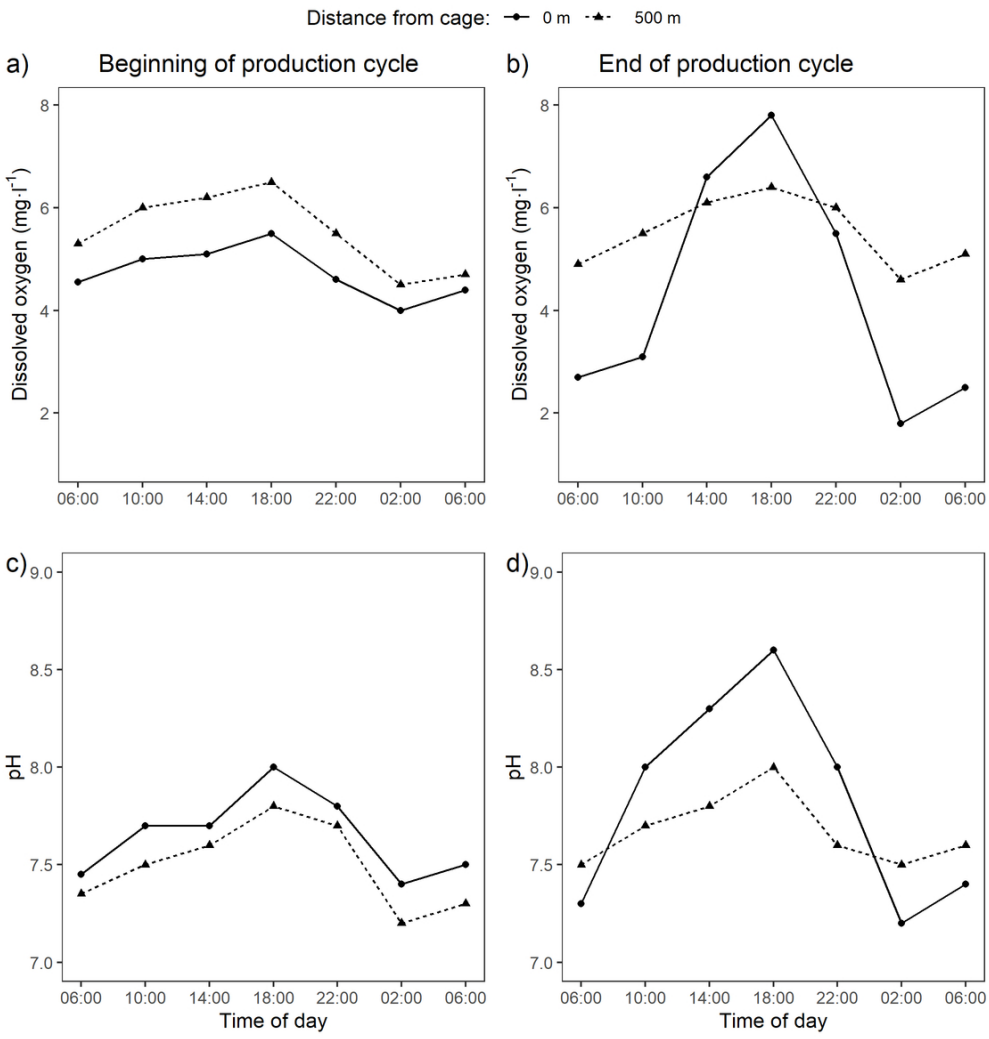
23x25mm (600 x 600 DPI)



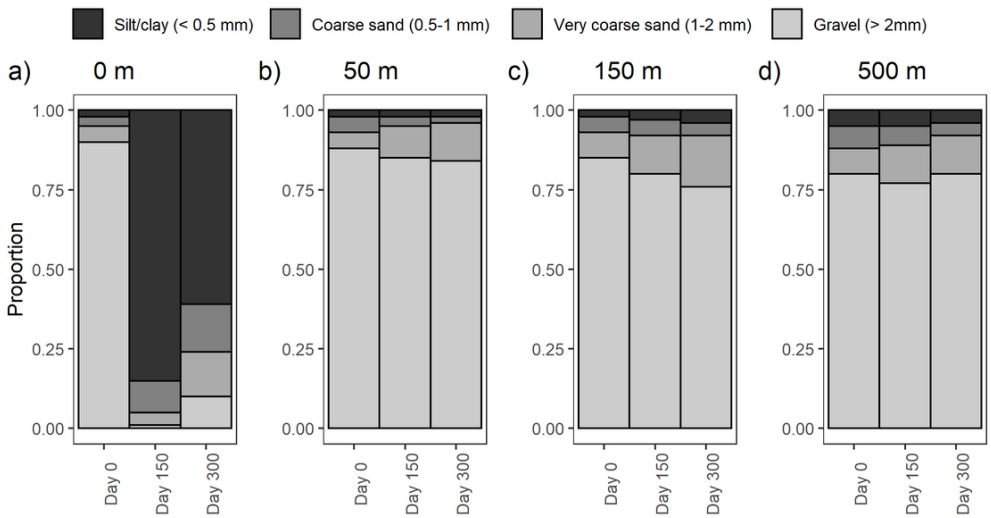
12x38mm (300 x 300 DPI)



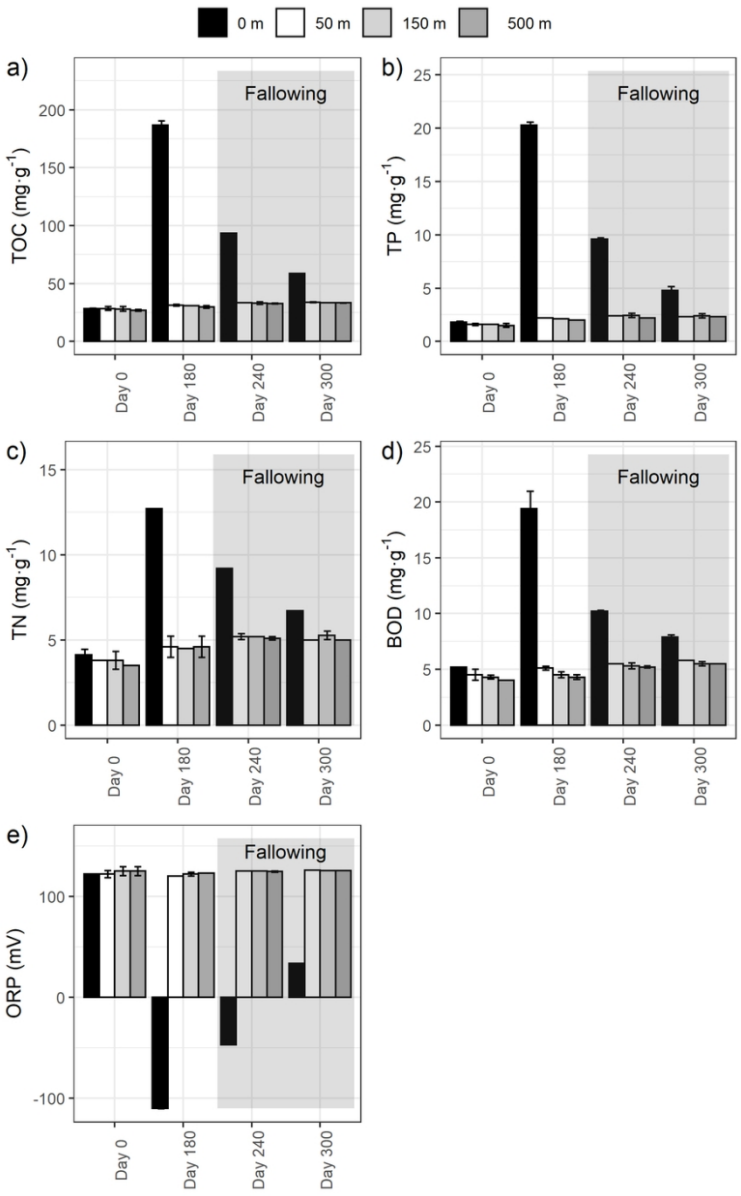
74x89mm (300 x 300 DPI)



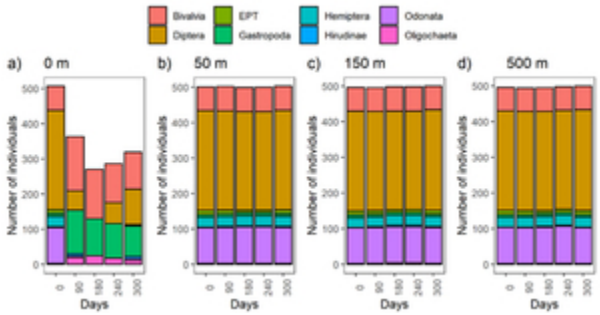
94x99mm (300 x 300 DPI)



94x49mm (300 x 300 DPI)



74x119mm (300 x 300 DPI)



25x13mm (300 x 300 DPI)