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ORIGINAL ARTICLE

Impacts of Nile tilapia cage culture on water and bottom sediment quality: The ability of an eutrophic lake to absorb and dilute perturbations

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Abstract

Environmentally sustainable aquaculture depends on accurate understanding of the impacts of aquaculture-derived organic matter (AOM) and the ability of aquaculture systems to absorb and dilute perturbations. To this end, the present study assessed the impacts of AOM from cage culture of Nile tilapia on the ecology of Lake Victoria, Kenya, using fish cages near Anyanga Beach in Siaya County from December 2018 to October 2019. Four locations were surveyed for organic loadings from cage cultures, located 0, 50, 150 and 500 m (as a control site) away from the cages. The cage aquaculture produced increased P and N concentrations near the cages and a decreased N:P molar ratio. These changes stimulated algal growth which, in turn, affected the water quality. The organic material accumulated on the bottom under the cages, increasing the benthic BOD (BOD, >10 mg/g), a sensitive indicator of the ecological footprint of the cage aquaculture. Further, the negative ORP observed in the benthic layer suggested anoxic bacterial metabolism, possibly causing build-up of sulphides and methane. These changes altered the abundance and composition of both limnetic and benthic communities. At the beginning of the study, 22 zoobenthic taxa existed 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. The 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. The water quality recovery after cage disturbance is rapid (<4 months), noting there was no significant difference in the water quality recorded at the cage site and the other sampling sites after a fallow period of 4 months. However, the recovery of the sediment and meiofauna was far from complete at the end of this period. Moving the cages slightly (50–100 m) away from the former location may allow the benthic communities to recover and alleviate the problem. Further, the fallowing period, particularly for the Anyanga Beach site, should be extended from four to at least 5 months to allow for the environment to recover. With the rapid increase of cage fish farming in the African Great Lakes Region and with the potential for its occurrence in other lakes, there is a need to develop regulations to guide the industry, as well as the need

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for continuous monitoring of the environment, in order to provide information to guide investments and ensure sustainable cage farming.

KEYWORDS
aquaculture, benthos, fallowing, redox, pollution

1 | INTRODUCTION

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

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

Accordingly, concerns have been raised about the environmental impacts of cage aquaculture (Bondad-Reantaso et al., 2005; Boyd et al., 2008; Kashindye et al., 2015). The primary concern for African inland water systems is eutrophication attributable to the discharge of particulate and dissolved nutrients such as uneaten waste feed, metabolites and faecal matter (Dauda et al., 2019; Garcia de Souza et al., 2015). The accumulation of organic material in sediments increases the metabolic activity of bacteria which, in turn, can create anoxic conditions in the sediments (Henderson et al., 1997; Karakassis et al., 1998; Porrello et al., 2005). Changes in sediment chemistry resulting from organic loadings can alter the species abundance and biomass of macroinvertebrates (Braaten, 2007; Egessa et al., 2018; Kashindye et al., 2015; Ngupula & Kayanda, 2010; Villnas et al., 2011). Cage aquaculture can also affect water quality by reducing the dissolved oxygen concentration in the water column (Kashindye et al., 2015), elevating the ammonia and CO_2 levels (Aura, Musa, et al., 2018) and increasing the risk of algal blooms (Aura, Nyamweya, et al., 2018; Mwamburi et al., 2020). These ecological changes can affect the production of wild fish 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, the area under consideration, the depth of the lake and the water exchange rate (Huang, 1997; Phillips et al., 1985). The environmental effects of nutrient enrichment are also site-specific and depend on local chemical characteristics (Wu, 1995). Freshwater systems are often more vulnerable to nutrient loads than marine systems because of their smaller size and typically lower ecological carrying capacity. Lake Victoria, just like many other African inland waters, has suffered from severe eutrophication for many decades (Mwamburi et al., 2020; Verschuren et al., 2002), with regular and massive algal blooms occurring for at least the last 30 years (Mwamburi et al., 2020; Ochumba & Kibaara, 1989). The lake has seen a fivefold increase in turbidity since the early-1930s (Mwamburi et al., 2020) with Secchi disc measurements <1-m, specifically in shallow waters <25-km from shoreline, bays and gulfs, as well as other semi-enclosed inshore areas of the lake (Lung'ayia et al., 2001; Mwamburi et al., 2020). Further, the long water retention time of Lake Victoria (i.e. water residence time of 23 years; flushing time of 123 years), means pollutants entering the lake can accumulate in it. The regulatory framework for cage aquaculture in Lake Victoria is inadequate, and therefore, uncontrolled growth of this sector may degrade the environment, further threatening the future of capture fisheries. Almost all fish cages in African inland lakes are located in shallow waters (4–8 m) (Musinguzi et al., 2019) despite recommendations they should be placed in deeper waters exceeding 10-m (Kamadi, 2018). Further, cage aquaculture installations in African inland lakes are commonly inappropriately located near protected areas in eutrophic and hypertrophic waters, and close to the shoreline, in which important nursery grounds for wild fish are typically found (Musinguzi et al., 2019).

There is a paucity of information on the impacts of cage aquaculture on enrichment in tropical/sub-tropical waters. Several studies on aquaculture in African inland waters (Egessa et al., 2018; Kashindye et al., 2015; Mwebaza-Ndawula et al., 2013; Nabirye et al., 2016) have only evaluated the impacts occurring during the culture periods, with none of the studies addressing recovery of the water system during fallowing periods or the long-term effects. Accordingly, the primary objective of the current study was to assess the environmental consequences of cage culture in Lake Victoria, as well as the ability of the ecosystem to absorb and dilute perturbations, as a means of guiding the sustainable development of cage culture in the Great Lakes region.

2 | MATERIALS AND METHODS

2.1 | Study area

The present study was conducted at Anyanga Beach, Kadimo Bay, Lake Victoria, Kenya (Figure 1) from December 2018 to October 2019. Kadimo Bay was chosen for this study because it is the main

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aquaculture centre for Lake Victoria, Kenya (Aura, Musa, et al., 2018; Hamilton et al., 2020). The farm had fish in 600 cages (2×2×2 m) stocked with 2000 tilapia (15-g average initial body mass), with a 6-month production cycle. Prior to the present study, the farm had been operating for 3 years with a fallow period of 4 months between production cycles. The sampling sites were located at the edge of the cages (0-m) and then at 50-m and 150-m intervals away from the cages towards the centre of the bay (Figure 1). A reference site was located 500-m from the cages. The sampling sites were geo-referenced for future comparisons using Garmin, 78S, IC; 1792A-01664, FCC ID: IPH-01664 Global Positioning System (GPS). The mean cage depths were 3 m at the shoreline edge, 3.2 m at the 50-m interval and 3.5 m at the 50-m interval. The reference site had a depth of 4.6 m.

2.2 | Water quality

Temperature, dissolved oxygen (DO) concentration, pH and alkalinity were monitored with a multi-parameter meter (Hanna Instruments, Model 8519 N, Singapore). The Secchi depth was measured using a standard Secchi disk. Diurnal DO and pH fluctuations were monitored at the cage and reference sites with a multi-parameter meter (Hanna Instruments, Model 8519 N, Singapore) from 0600 hours till 0600 hours of the following day at 4-h intervals. Water samples for chemical analysis were collected in triplicate at a depth of 1-m from the water surface using a Van Dorn water sampler. Pre-cleaned 1-L sample bottles were used to hold the water samples, which were preserved on ice and transported on the same day to the Kenya Marine and Fisheries Research Institute (KMFRI) Kisumu laboratory for analyses. Total phosphorus (TP), total nitrogen (TN) and total ammonia-N and Biochemical Oxygen Demand (BOD) concentrations were determined using photometric methods adopted from APHA (2005). The carbon dioxide (CO_2) concentration was measured using CO2sys and adjusted for temperature, pH and alkalinity (https://cdiac.ess-dive.lbl.gov/ftp/co2sys/). The 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.

2.3 | Plankton

Water samples for zooplankton and chlorophyll-*a* concentration (the latter as an indicator of phytoplankton) were collected in triplicates and analysed using the methods described by Greenberg et al. (1992). Zooplankton samples were collected with a conical plankton net (Nansen type; 60-µm mesh size; 0.25-m mouth diameter) towed vertically through the water column, as described by Mwebaza-Ndawula et al. (2013). The samples were preserved in a 5% formalin solution. Each sample was made to a known volume in the laboratory, thoroughly shaken to ensure uniform distribution. A sub-sample was placed in a counting chamber and examined with an inverted microscope (100X magnification) for taxonomic determination and at 40X for counting. Zooplankton were identified to genus and, where possible, to species level. Rotifers were sorted out using a fine glass capillary tube onto slides with glycerine mixed with distilled water and examined under a compound microscope (100X magnification). Identification keys of Dussart and Defaye (1995) were used for copepods. The identification keys of Korovchinsky (1992) and Smirnov (1996) were used for Cladocera identification, while Koste and Shiel (1987) and Segers (1995) keys were used for identifying rotifers.

Water samples (2-L) for quantification of total chlorophyll-*a* were collected in triplicate at the surface (photic zone) at each site using sampling bottles that were filtered on site using Whatman GF/C filters. The filter, together with the seston, was folded, covered with

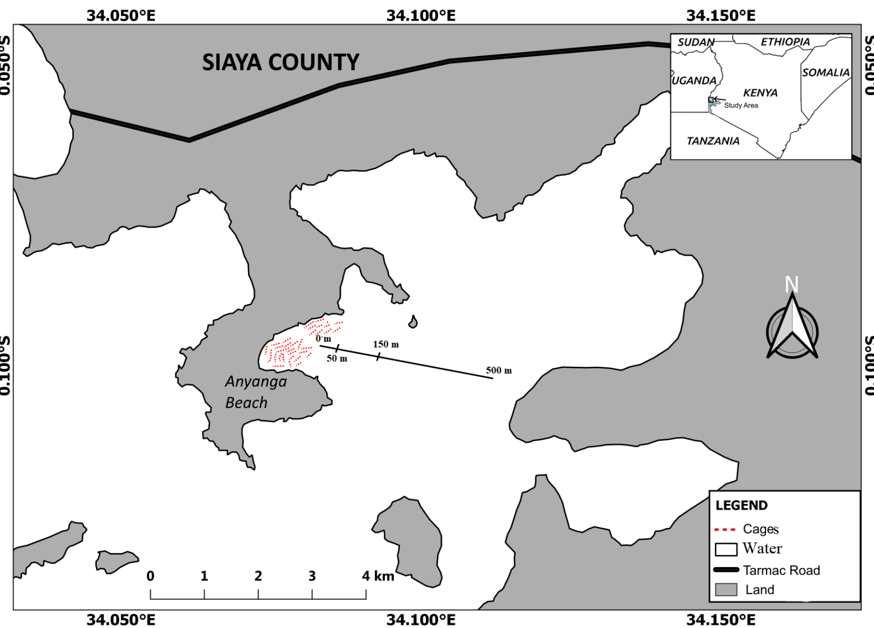

FIGURE 1 Map of study area showing Anyanga Beach, Kadimo Bay, Lake Victoria, Kenya, and sampling points (0, 50, 150 and 500-m away from cages)

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aluminium 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 one minute and covered with 5 ml of 90% aqueous acetone. The samples were transferred into screw-cap vial/centrifuge tubes, 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 h in the dark at 4°C for chlorophyll-*a* extraction. After incubation, the sample was centrifuged for 10 min and the clarified extract decanted into a clean test tube. Light absorbance of the chlorophyll-*a* extract was measured with a UV–visible Beckman DU64OB spectrophotometer at 750 nm and 663 nm, with the sample placed in 1-cm cell cuvettes. Chlorophyll-*a* concentrations were subsequently estimated using the equations of Jeffrey and Humphrey (1975), after subtracting absorbance at 750 nm from all absorbance values to account for turbidity, as follows:

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

where V = volume of acetone 90%; L = volume of water sample; E664 = absorbance value at 664-nm wavelength; E647 = absorbance value at wavelength 647-nm wavelength; and E630 = absorbance value of absorbance at 630-nm wavelength.

2.4 | 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) concentrations were collected with a Ponar grab (238-cm^2 open jaw area) by taking three vertical sediment hauls at each sampling site. Sediment samples were collected at the beginning and end of the culture period, and also during fallowing 2 and 4 months following the culture period. The samples were placed in clean labelled sample bags and transported to the KMFRI laboratory for analyses. The TN and TP contents in the sediments were analysed on the basis of the methods of Huang (1999). The Oxidation–Reduction Potential (ORP) was measured using a multi-parameter meter (Hanna Instruments, Model 8519 N, Singapore).

The sediment grain size analyses were performed as described by Egessa et al. (2018). A wet sediment sample (15-ml) from each sampling site was digested overnight in 30 ml of 30% hydrogen peroxide (H_2O_2) to remove organic matter. The excess H_2O_2 was 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 the ash weight. The quantity of organic matter in a sample was estimated as the difference between dry and ash weight.

2.5 | Community composition and abundance of macrobenthic fauna

Macroinvertebrate samples were collected using a Ponar grab by taking three vertical sediment hauls at each sampling site, followed by sieving through a 400-μm mesh to concentrate the sample. The concentrated samples were placed in clean, labelled sample bottles and preserved in 70% alcohol for taxonomic identification and enumeration in the laboratory. Macroinvertebrates were identified with the aid of the keys of Merritt and Cummins (1978), Quiley (1977) and IFM (2006). The composition and density of macrobenthic fauna was monitored at the beginning of the study, and on Days 90 and 180 of the culture period. They were also monitored on Day 240 and 300 during the fallowing period.

The macroinvertebrate assemblage composition was determined on the basis of the 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:

$$H' = \sum_{i=1}^{R} p_i \ln p_i \quad (2)$$

Where p_i = proportion of individuals belonging to i^{th} species. An associated evenness H'/H' max (Pielou, 1975) was also calculated.

2.6 | 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 at sampling sites and for sampling dates was conducted. One-way analysis of variance (ANOVA) was used to test for statistical significance in the mean variation of water and sediment quality parameters between sampling sites and time. The diversity of macrobenthic invertebrates was calculated by means of the Shannon–Wiener Index (Shannon & Weaver, 1949). Due to the small sample size, however, the data did not conform to assumptions of ANOVA. Accordingly, significant differences in the Shannon Diversity Index (H') between sampling sites 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 sites to support interpretation of the bottom faunal data. The Anderson–Darling test and histogram plots were used to evaluate the data for normal distribution and homogeneity of variance by assessing residual plots and employing Bartlett's and Levene's tests. The level of significance was estimated at $p < .01$.

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3 | RESULTS

3.1 | Effects of cage aquaculture on nutrients and chlorophyll-*a* concentrations

At the beginning of the production cycle, there were no significant differences in chlorophyll-*a* ($F[3] = 0.056$, $p = .826$), TP ($F[3] = 0.345$, $p = .782$), TN ($F[3] = 0.039$, $p = .883$) and N:P molar ratio ($F[3] = 0.432$, $p = .746$) among the different sampling sites (Figure 2). At the harvest time, however, chlorophyll-*a* ($F[3] = 5434.75$, $p < .0001$), TP ($F[3] = 3468.93$, $p < .0001$) and TN ($F[3] = 39{,}572.24$, $p < .0001$) had all increased significantly by 108%, 93% and 100%, respectively, by the cages (Figure 2a–c). The N:P molar ratio decreased by more than 40% by the cages, being significantly lower than at the other sampling sites at the time of harvest (Figure 2d). In contrast, there was no significant change in the nutrient concentrations at any other sampling sites during the production and fallowing periods (Figure 2). During the 4-month fallowing period, the chlorophyll-*a*, TP, TN, and N:P molar ratios by the cages recovered, with concentrations comparable to those observed at the other sampling sites.

3.2 | Effects of cage aquaculture on zooplankton

The production cycle had significant effects on the zooplankton community composition at the cage site, but not at the other locations (Figure 3). The zooplankton community consisted mainly of three taxonomic groups; namely, Rotifera, Cladocera and Copepoda (Figure 3). A total of 14 zooplankton species were identified in the collected samples. 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 A).

At the beginning of the production cycle, there was no significant differences ($p > .05$) in the abundance of the different taxonomic groups among the sampling sites (Figure 3). During the production cycle, however, the abundance of rotifers at the cage site increased significantly ($p < .001$) over sixfold, while the abundance of Cladocera and Copepoda decreased ($p < .001$) by 47% and 58%, respectively. No significant changes in abundance during the production cycle were found at the other sampling sites (Figure 3; Appendix A).

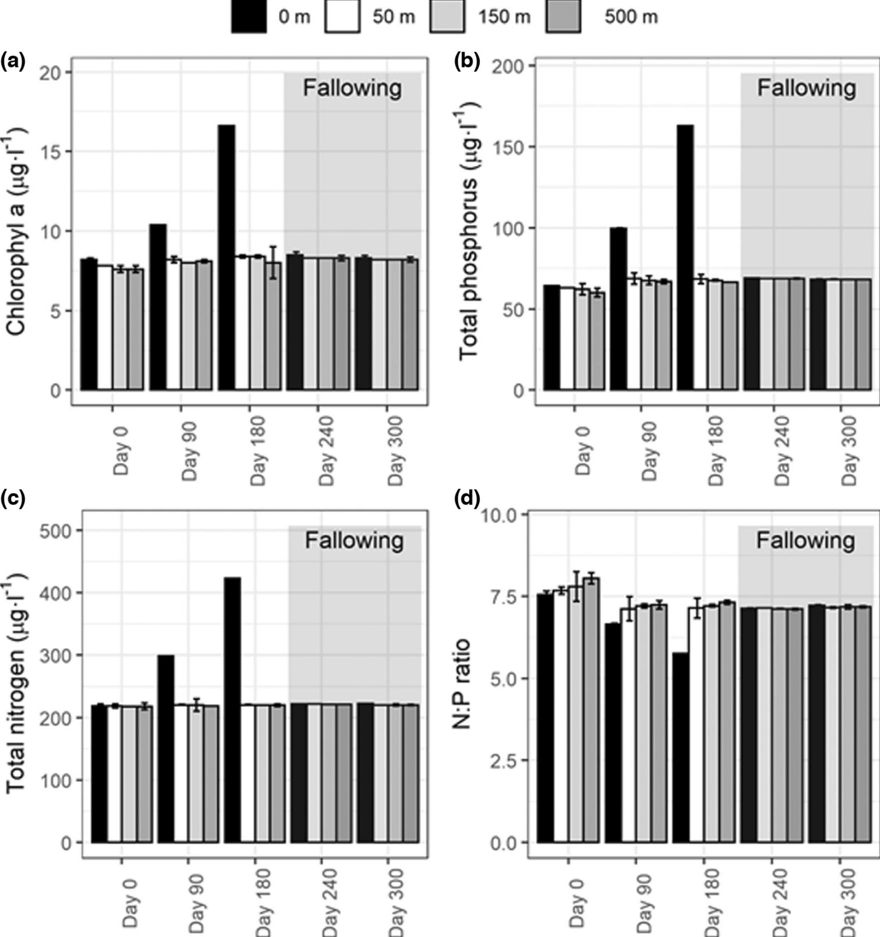

FIGURE 2 Dissolved nutrients (mean ± SEM) at cage culture site at Anyanga beach, Lake Victoria, Kenya (a) chlorophyl-*a*; (b) total phosphorus (TP); (c) total nitrogen (TN); and (d) N:P molar ratio during culture and fallow periods

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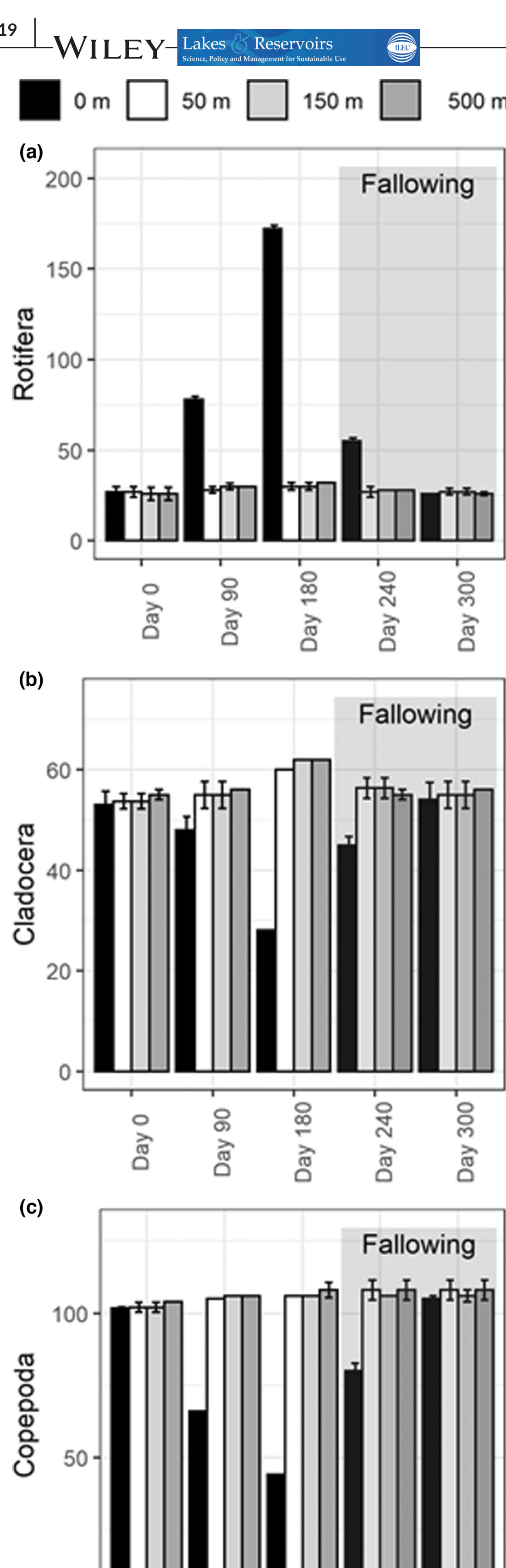

FIGURE 3 Zooplankton abundance (mean ± SEM) at cage culture site at Anyanga beach, Lake Victoria, Kenya (a) Rotifera; (b) Cladocera; and (c) Copepoda during culture and fallowing periods

In addition to changes in total abundance, the abundance of species within each taxonomic group also changed. At the beginning of the production cycle, all the eight Rotifera species were present at the cage site, although not in similar proportions (8.5–15.9%). At the end of the culture period, however, 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 initial eight species present at the cage site had disappeared from the samples. Dominating at the cage site was *B. angularis* and *B. calyciflorus*, which had increased in numbers at the cage site on Day 180 (Appendix A). After a fallowing period of 4 months, the Rotifera returned to composition similar to that existing before the production cycle began, with all eight species present, although still not in similar proportions.

The composition of Cladocera at the cage site changed during the production cycle, although not at any other locations (Appendix A). On Day 0, all four species were present in similar proportions (23.8–26.3%) at all sampling sites. At the end of the production cycle, however, only *Moina micrura* (100%) was present in the samples at the cage site, having nearly trebled in number. After fallowing, the Cladocera composition 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 A). The initial Copepoda composition comprised approximately equal numbers of Copepod nauplii, Calanoids and Cyclopoida. However, both Calanoids and Cyclopoida disappeared from the cage site samples by day 180, with only Copepod nauplii dominating the cage site (100%). The Copepoda species composition, however, returned to pre-production levels after 90 days of fallowing.

3.3 | Effects of cage aquaculture on water quality

There were no significant differences in the DO ($F[3] = 0.5454$, $p = .688$; measured at 1000 Hr), BOD ($F[3] = 0.036$, $p = .889$), Secchi depth ($F[3] = 0.356$, $p = .779$) or NH_3 ($F[3] = 0.045$, $p = .965$) among sampling locations at the beginning of the production cycle (Figure 4). However, both the DO ($F[3] = 424.6$, $p < .001$) and Secchi disk readings ($F[3] = 89.5$, $p < .0001$) decreased over time, while the BOD ($F[3] = 330.3$, $p < .0001$) and NH_3 ($F[3] = 386.0$, $p < .001$) increased progressively at the cage site (Figure 4). The DO was reduced by 48.3%, Secchi depth by 66.7%, while the BOD and NH_3 increased by 181% and 35%, respectively, on Day 180. During the fallowing period, the DO, BOD, Secchi depth and NH_3 at the cage site recovered. Four months after harvesting there were no significant differences in the DO ($F[3] = 0.048$, $p = .898$), BOD ($F[3] = 0.045$, $p = .899$), Secchi depth ($F[3] = 0.354$, $p = .789$) or NH_3

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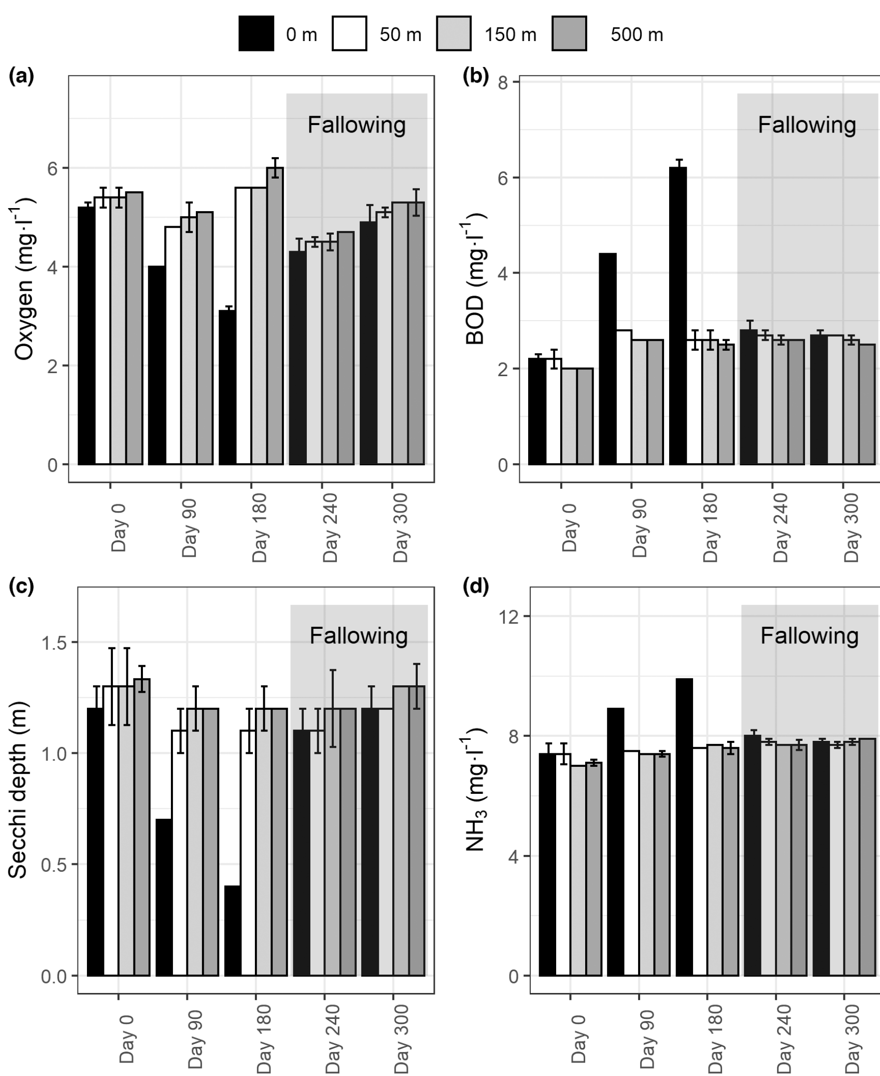

FIGURE 4 Water quality (mean ± SEM) at cage culture site at Anyanga beach, Lake Victoria, Kenya (a) dissolved oxygen; (b) BOD; (c) Secchi depth; and (d) NH_3 during culture and fallow periods

(F[3] = 0.038, p = .969) at the different sampling sites (Figure 4). The DO (F[3] = 0.046, p = .888), BOD (F[3] = 0.039, p = .989), Secchi depth (F[3] = 0.044, p = .889) and NH_3 (F[3] = 0.043, p = .899) did not change significantly during the production cycle and fallowing period at any other sampling site. There were no significant differences in the mean temperature (26.46 ± 1.22; F[3] = 0.034, p = .973), pH (7.96 ± 0.24; F[3] = 0.041, p = .983) or alkalinity (51.03 ± 1.45; F[3] = 0.456, p = .749) among the sampling sites at the beginning and end of the culture period. The estimated concentration of CO_2 never exceeded 5 mg/L.

Both the DO and pH exhibited diurnal fluctuations, increasing during the day and decreasing at night (Figure 5). At the beginning of the production cycle, the DO was consistently about 1 mg/L lower and the pH about 0.1–0.2 units higher at the cage site than 500 m from the cages. The amplitude was otherwise 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 DO level (1.5 mg/L) was observed at 0200 Hr at the cage site, corresponding 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), with only 2–3% of silt/clay. This level changed during the production cycle, with the bottom sediment by the cages by the time of harvest at the consisting mainly of silt/clay (85%), with gravel accounting for only 1% (Figure 6), consistent with the accumulation of organic matter on the bottom of the lake. 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, although still significantly lower (p < .01) than at other sampling sites.

There were no significant differences (p = .7–.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 at the beginning of the production cycle (Figure 7). At the end of the production cycle, the TOC (F[3] =5519.95, p < .0001), TP (F[3] = 14197.14, p < .0001), TN (F[3] = 254.46, p < .0001) and BOD (F[3] = 232.48, p < .0001) had all increased at the cage site by 386.5%, 745.8%, 176.1% and 252.7%,

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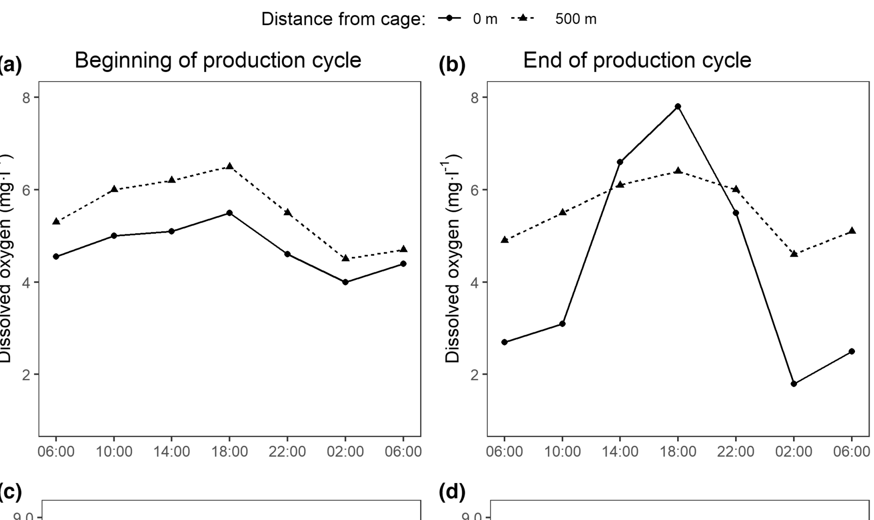

FIGURE 5 Diurnal DO and pH variations at cage and reference sites at the beginning and end of the culture period at Anyanga beach, Lake Victoria, Kenya

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 sites. During the fallowing period, the chemical composition and ORP recovered partly, although not reaching the pre-production levels (F[3] =2542.35, $p < .001$) (Figure 7).

3.5 | Community composition and abundance of macrobenthic fauna

The macrobenthic fauna was composed of members of three phyla, including Arthropoda, Annelida and Mollusca. Arthropoda was the richest phylum, consisting of the class Insecta with six orders (Ephemeroptera; Diptera; Trichoptera; Plecoptera; Odonata; Hemiptera). At the beginning of the production cycle, the most abundant group within all benthic samples was Diptera (300–305 individuals/L), followed by Odonata (100–102 individuals/L) and Bivalvia (60–61 individuals/L). There were no significant differences 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 (Figure 8a), while the total numbers and composition of the macrobenthic fauna did not change at the other locations (Figure 8b–d). On Day 180, all the Diptera, (Ephemeroptera, Plecoptera and Trichoptera (EPT)), Hemiptera, Hirudinae and Odonata had disappeared at the cage site (Figure 8a), and the fauna consisted only of Bivalvia (52%), Gastropoda (39%) and Oligochaeta (9%).

At the beginning of the production period, 18 species of zoobenthos were found underneath the cages, and 22 species were found at the reference site (Appendix B). By the end of the production cycle, only three species (*Physella* spp.; *Sphaerium* spp.; *Tubifex* spp.) were found underneath the cages, and 18 were found at the reference site (Appendix B). A Kruskal–Wallis test indicated no significant differences ($H = 2$; $p = .399$) in the Shannon–Wiener mean diversity index of macroinvertebrate genera among the sites at the beginning of the study (Table 1). The lowest mean Shannon–Weiner diversity at the end of the study was observed at the cage site, being significantly different from the other sampling sites ($H = 2$; $p < 0.001$).

The composition of the macrobenthic fauna at the cage site did not recover to pre-production levels during the 4-month fallowing period, still being dominated by gastropods (28%) and bivalves (36%) (Figure 8a) on Day 300. Diptera, EPT and Odonata had reappeared in the samples by the end of the fallowing period, but not to the previous level, while the Hemiptera was still absent. After 4 months of fallowing, the Shannon–Weiner diversity index remained lower at the cage site (Table 1).

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

4 | DISCUSSION

The present study may be the first of its kind to assess the environmental effects of cage aquaculture in tropical/sub-tropical water systems, both during the production cycle and the subsequent fallowing period prior to the commencement of the next production cycle. Cage aquaculture has significant effects on both the limnetic and benthic zones of the lake with regard to water chemistry and species abundance, distribution and richness. These effects, however, appear to be restricted to the cage sites, dissipating quickly with distance from the cages to the point there was no evidence of changes at a distance of 50 m from the cage. The changes at the cage site during the production period were largely reversed in the limnetic zone during the 4-month fallowing period. The effects of cage aquaculture on the benthic zone were not entirely reversed, however, suggesting additive effects of subsequent production cycles that could lead to future disasters, as discussed further in the following sections.

4.1 | Limnetic effects

The present study indicates the effects of the cage aquaculture on the limnetic zone in the lake are manifested primarily through increased TN and TP concentrations (Figure 2). In contrast to conventional land-based aquaculture pond systems, cage systems do not use organic or inorganic fertilizers with high N and P contents, even though they are essential elements for organismal development. Accordingly, fish feed for cages have been reported to contain higher P contents than required by the fish (Ackefors & Enell, 1994; Musa, Aura, Tomasson, et al., 2021; Von Sperling & Chernicharo, 2005). Thus, the highest levels of TN (423.2 ± 1.4 µg/L) and TP (162.7 ± 5.6 µg/L) observed at the cage site at the end of the culture period could be attributable to nutrient leaching from fish feed and faecal matter, as well as metabolites. Previous research reported poor FCR (2.6) for fish feeds used in the study area (Musa, Aura, Tomasson, et al., 2021) which could have caused disproportionate increases in the TP and TN loadings. This suggests that fish cage culture in freshwater lakes such as Lake Victoria raises concerns about water quality deterioration attributable to both solid (Aura, Nyamweya, et al., 2018; Ngupula et al., 2012) and soluble wastes, especially nitrogen and phosphorus compounds. The progressive increased chlorophyll-*a* concentrations observed during the present study is an indication of increased algal biomass. This effect being found at the cage site during the production cycle followed the same pattern as the increased N and P concentrations (Figure 2), suggesting the increased N and P concentrations at the cage site promoted phytoplankton growth.

The TP (62–69 µg/L), TN (218–220 µg/L) and chlorophyll-*a* (7.6–8.4 µg/L) concentrations observed at all sampling sites before the production cycle began (Figure 2) are within the range of other values reported for Lake Victoria nearshore waters (Deirmendjian et al., 2021; Mwamburi et al., 2020; Simiyu et al., 2021). The observed N:P ratio of 7.5 at the cage site before the beginning of the production and after the two-month fallowing period in the present study is similar to those reported for other studies (Deirmendjian et al., 2021;Guildford & Hecky, 2000 ; Mwamburi et al., 2020). The observed decreased N:P molar ratio at the cage site by the end of culture period indicates phytoplankton production is limited by N rather than P (Guildford & Hecky, 2000; Mwamburi et al., 2020). These conditions favour

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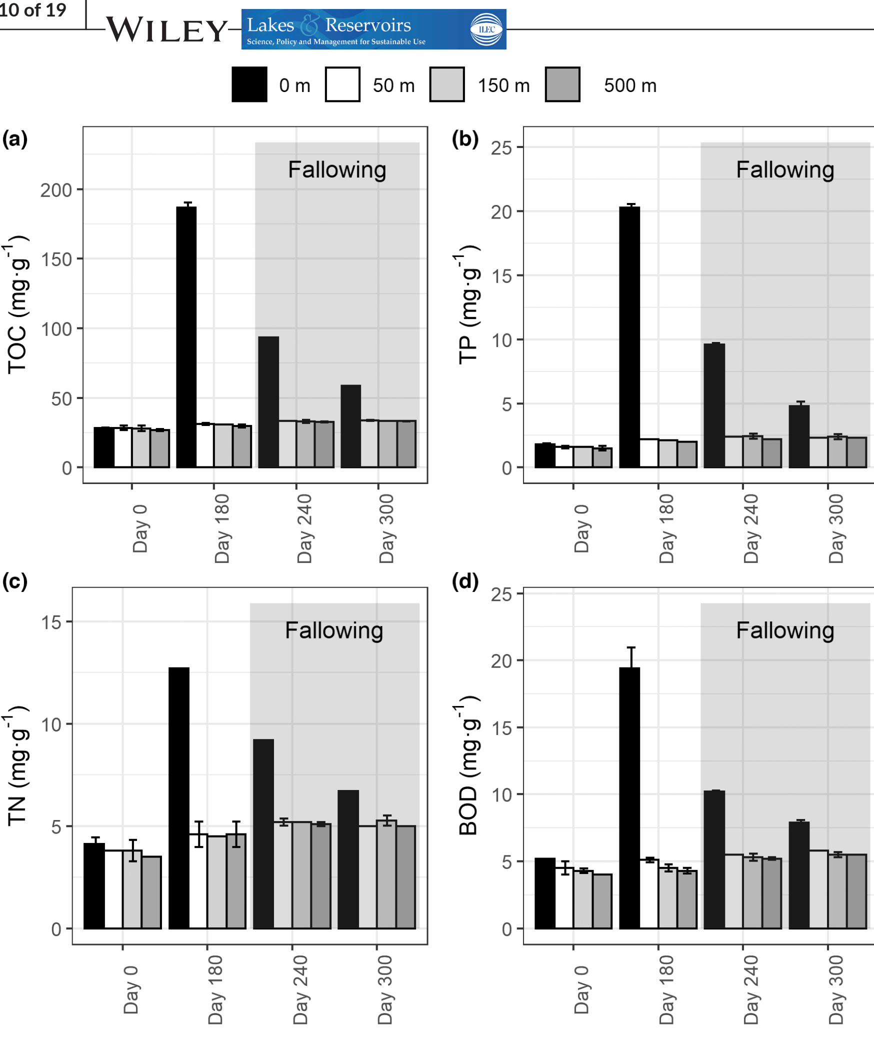

FIGURE 7 Sediment composition (mean ± SEM) of (a) total organic carbon, TOC, (b) total phosphorous (TP), (c) total Kjeldahl nitrogen (TN), (d) biological oxygen demand (BOD), and (e) oxidation–reduction potential during culture and fallowing periods

heterocystous N-fixing cyanobacteria (Gikuma-Njuru & Hecky, 2005), with the decreased N:P molar ratio at the cage site during production possibly exacerbating this effect. Cyanobacterial blooms are a potential health risk, and long-term exposure of Nile tilapia to cyanobacteria could result in an accumulation of cyanotoxins in the fish tissue that could transferred to higher trophic levels (Mohamed et al., 2019). Even before commencement of fish cage culture, Lake Victoria was reported to be highly eutrophic (Kling et al., 2001; Lung'ayia et al., 2001; Ochumba & Kibaara, 1989). Despite the burgeoning cage aquaculture industry within the lake, the fate and quantitative contribution of the new N and P sources emanating from this aquaculture in Lake Victoria has yet to be understood.

There are six main influent rivers in the Kenyan portion of the Lake Victoria catchment, including the Sio, Nzoia, Yala, Nyando, Sondu-Miriu and Kuja rivers. Previous studies estimated the mean water discharge from the six rivers to be approximately 456.16 m^3/s, with TN and TP loadings of 11.61 and 1.69 mg/L, respectively (Aura et al., 2021; LVEMP, 2005). Thus, the agro-industrial and municipal sewerage TP and TN discharges through the major rivers is estimated to be 2,113,000 and 12,193,000 kg/year, respectively. On

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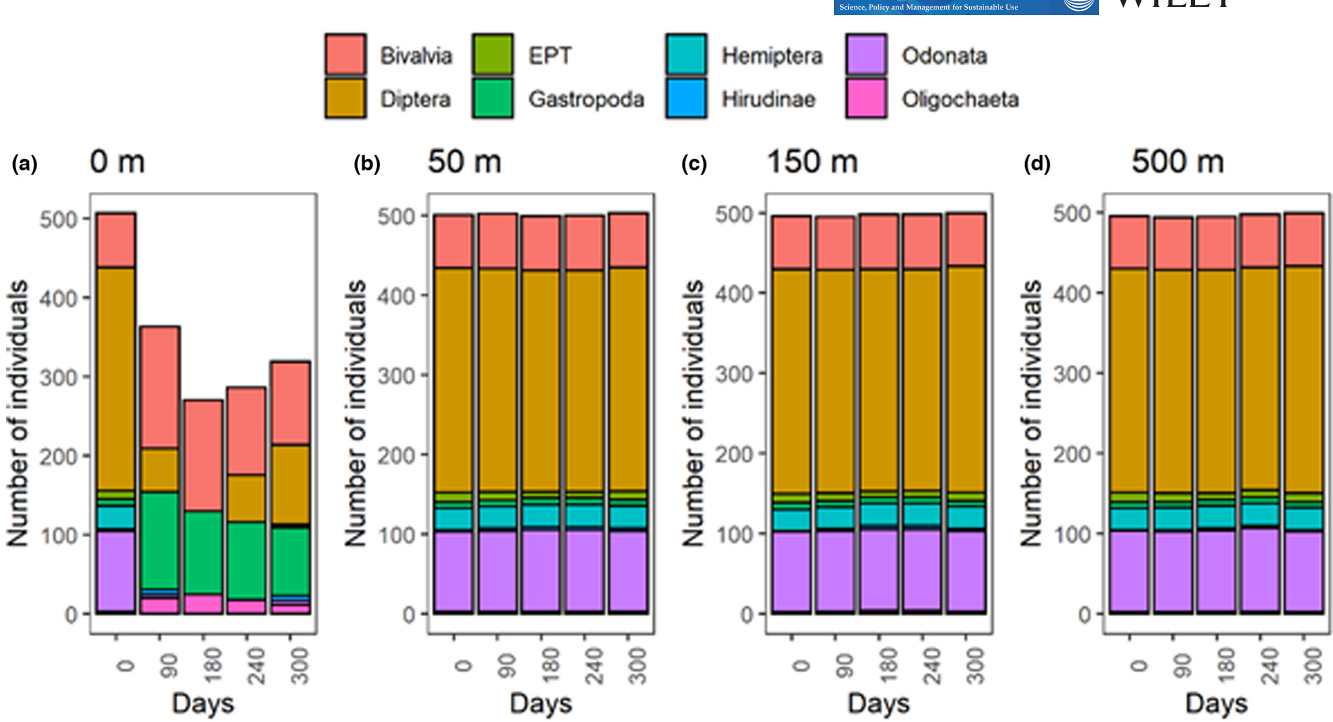

FIGURE 8 Macrobenthic invertebrate community structure (as mean number of individuals/L) during culture and fallow periods at Anyanga beach, Lake Victoria, Kenya

TABLE 1 Average Shannon index values (±SEM) for different sampling sites and times for Nile tilapia cage culture at Anyaga beach, Lake Victoria, Kenya (significant differences 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

the contrary, it estimated that the Anyanga cage culture site, the epicentre of cage aquaculture in Lake Victoria, produces 20,480 kg of N and 970.7 kg of P per each fish production cycle (Musa, Aura, Tomasson, et al., 2021). Thus, the agro-industrial and sewerage discharges contribute more than 2000 and almost 600 times the quantity of P and N into the lake, compared with fish cage culture contributions. These loads may even be higher if other seasonal rivers and streams are considered. Considering the current production levels, fish cage culture in Lake Victoria appears to contribute to increased nutrient loadings to the lake ecosystem. With regard to the nutrient loading in the lake, however, aquaculture-derived nutrients may only account for a relatively small proportion (<1% of P or N), compared with the agro-industrial and sewerage sources.

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

The increased phytoplankton density during the production cycle observed in the present study affected the diurnal DO and

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pH fluctuations (Figure 5). At the beginning of the growth cycle, the diurnal DO and pH fluctuations at the cage site were similar in magnitude to those at the reference site located 500 m from the cages, although the DO concentration was consistently about 1 mg/L higher and pH about 0.16 units lower at the latter location (Figure 5a). The amplitude of the DO and pH increased with time and, by the end of the production cycle, increased the phytoplankton density at the cage site (Figure 2a) contributed to larger amplitudes in the DO and pH fluctuations (Figure 5b). The DO concentration was maximal during the afternoon due to photosynthesis, reaching a minimum just before sunrise. The diurnal pH fluctuations were in phase with the DO as O_2 is consumed to produce CO_2 (Figure 5), and the removal of CO_2 in turn increased the pH due to the carbonate equilibrium. At the end of the production period (Day 180), diurnal variations in algae respiration and photosynthesis caused DO concentrations to reach minimum mean levels of 1.5 mg/L (19% of air saturation) at 0200 Hr, and it is likely the oxygen levels may have fallen even further until dawn. During the day, oxygen concentration increased up to 7.8 mg/L (118% of air saturation) at the cage site. The BOD increased (Figure 4b) with the increasing algal density (Figure 2a), although increased bacterial activity in the water may also have contributed to the BOD (Boyd & Tucker, 1998). The high BOD resulted in nearly 50% reduction in morning DO concentrations at the cage site from the beginning to the end of the production cycle (Figure 4a).

Growth, food intake, disease resistance and survival of Nile tilapia is significantly reduced when the oxygen saturation level decreases to <50% of air saturation (Abdel-Tawwab et al., 2014; Kolding et al., 2008; Tran-Duy et al., 2012). Large diurnal O_2 fluctuations levels such as those observed in the current study may also cause reduced growth even if the oxygen saturation remains above 100% for most of the daylight hours (Tsadiki & Kutty, 1987). At the beginning of the production cycle, the minimum DO levels at night fell just below a 49% saturation value (Figure 5a). By the end of the production cycle, however, the oxygen saturation was below 50% for >10 h each night (Figure 5b) and near or below 20% saturation for several hours. This observation suggests the nightly decrease in oxygen levels would have reduced growth, feed efficiency and survival of the fish which, in turn, could reduce production and increase juvenile and feed costs. In contrast, the estimated maximum CO_2 concentration (~5 mg/L) is well below the tolerable levels of 10 mg/L for warm water species (Timmons et al., 2010).

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

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

The effects of the cage aquaculture on the limnetic zone disappeared after 4 months of fallow. Two months after the production cycle ended (Day 240), both the TN and TP concentrations, as well as the algal density, returned to baseline levels. The zooplankton community recovered as a result, reaffirmed by the reduced relative contribution of copepod nauplii and the reappearance of Calanoida (see Appendix A), suggesting copepod nauplii could represent an important bioindicator of organic loading. Dias et al. (2012) affirms that higher proportions of calanoids in freshwaters indicate low eutrophy, while nauplii indicate a more productive habitat. The reappearance of calanoids indicate the water quality at the cage site had completely recovered after a 4-month fallow period. Noteworthy is that low relative density of rotifers (14%) at the cage site at the end of the 4-month fallow period, compared with the harvesting time (70%), confirms water quality had recovered since rotifers are more responsive to water quality changes, thereby being good indicators of trophic conditions (Baranyi et al., 2002; Gannon & Stemberger, 1978; Sladecek, 1983; Tasevska et al., 2010). The recovery of the environment (i.e. water) is more rapid, probably due to the small spatial scale of the impacts (<50 m). It could also be attributable to good water circulation caused by the absence of fish in cages after harvesting (Kutti et al., 2007). In summary, the results of the present study indicate that all the effects of cage aquaculture on the limnetic zone dissipate after a 4-month fallowing period. Thus, it is concluded that the limnetic zone in Lake Victoria is able to absorb and dilute perturbations within 4 months fallowing due to a periodical lake turnover.

4.2 | Benthic effects

The high TOC concentration observed under the cages by the time of harvest indicates a high accumulation of organic matter, mainly from food wastes and fish excrement with high P and N content (Figure 7). It is likely the loss of P from the sediment is minimal (Holby & Hall, 1991; Von Sperling & Chernicharo, 2005), thereby contributing

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to the increased P accumulation under the cages. The sediment high P content under the cages reduced the N:P molar ratio from 2.3 to 0.6. Similar findings were 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 site (Gao et al., 2005). Low sediment TN:TP molar ratios are associated with increased phosphorous loadings from the fish feed, raising eutrophication concerns.

The accumulated organic matter on the bottom of the water body is a favourable substrate for various organism. According, as observed in the present study, the sediment BOD increased (Nickell 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), indicating 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 present study area. Indeed, incidences of isolated fish kills have been reported in fish cages at Nyenye Got, Honge and Anyanga beaches in the Kenyan portion of Lake Victoria. Although preliminary results suggested low DO concentrations (0.64 mg/L) as the main cause of the fish kills (Njiru et al., 2018), hydrogen sulphide toxicity may also have been a main contributor to the mass mortalities. This possibility warrants further investigations into the effects of hydrogen sulphide on fish performance, especially in African inland waters in which most cages are sited in shallow areas, with no fallowing periods.

The large quantities 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 would favour certain species, and the increased quantity of silt/clay on the bottom is potential food to attract macroinvertebrates. This situation could have partly influenced the macroinvertebrate community composition and diversity (Kakantzi & Karakassis, 2006; Nabirye et al., 2016). In fact, the shift from arthropods to molluscs (bivalves and gastropods) and annelids (oligochaetes) at the 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 reported as thriving in freshwaters receiving organic wastes (Camago, 1992; Dobrowolski, 1987; Miserendino & Pizzolon, 2000), representing an indication of negative effects of cage culture on the lake environment. In addition, the reduced number of taxa, and the dominance by the opportunistic species *Physella* spp, *Sphaerium* spp and *Tubifex* spp. at the cage sites indicates possible disturbance of the benthic faunal community in the immediate vicinity of the cages, with these opportunistic species known for their high pollution tolerance (Buss et al., 2002). Moreover, the disappearance of sensitive taxa such as Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies) at the cage site by the end of the present study indicated an ecologically impaired site, attributable to degradation from cage culture activities (Johnson et al., 1993), a possibility reaffirmed by the low Shannon–Wiener values (0.82) recorded at the cage site by the end of the culture period, which indicates a loss of diversity.

The present study indicates that the effects of cage aquaculture on the benthic communities are fairly localized, suggesting the cage fish culture is restricted to an area within a 50-m radius of the cages. GUO and LI (2003) and Srithongouthai and Tada (2017) reported the impacts of cage culture extended up to 20 and 10 m, respectively, outside the cage area in lakes in China and Japan, consistent with the findings of the current study. The extent of the impacts of aquaculture effluents is dependent on a number of factors, including the area used for culture, site depth, age of the farm, stocking densities, hydrodynamics, sediment adsorption, current speed, production volume of the farm and management efforts. The localized aquaculture impacts in the current study area may be partly attributable to the shallow waters (<5 m) under the cages, as well as the concentration of cages in one site in an enclosed bay. A high proportion of silt/clay under the cages has been reported to decrease the footprint of cage aquaculture (Kakantzi & Karakassis, 2006; Mazzola et al., 2000). Thus, the localized impacts observed in the current study could also be attributable 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 of the current study indicate the benthic zone under the cages did not recover fully during the 4-month fallowing period. The organic material accumulated over the production cycle had not disappeared after the fallowing period (Figure 6). Similarly, the BOD, TN, ORP and TP levels at the cage site had not returned to pre-production levels after the 4-month fallowing period (Figure 7). The meiofaunal composition also had not returned to the levels recorded prior to commencement of cage fish farming 4 months after the end of the previous production cycle (Figure 8). However, other orders such as Ephemeroptera reappeared in some replicates after the 4-month fallow period, comprising only 0.9% under the cage site, likely highlighting their limited survival chances in such areas, especially if culture continues. However, the reappearance of Ephemeroptera, albeit in small numbers, could indicate the system was on its way to recovery since this group is an important bioindicator of organic pollution. Nevertheless, the low diversity observed at the cage site reaffirms that the cage site had not completely recovered after the 4-month fallowing period. Thus, it appears the benthic zone in Lake Victoria is not able to absorb and dilute perturbation within the fallowing period. Continued production at the same locations will result in increased accumulation of organic material, with potentially dire consequences for the fish attributable to the release of hydrogenated sulphur from sediments beneath the cages. Mass tilapia mortalities were reported in the study area in 2016 (Njiru et al., 2018), confirming the risks associated with such enterprises. Thus, the current management practices regarding cage fish farming in Lake Victoria could be a disaster in waiting. In order to reduce the risk of catastrophes,

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therefore, the fallowing period should be extended, requiring the cages to be relocated between production cycles. The results of the current study also suggest that cage aquaculture in Lake Victoria, a water body already experiencing severe environmental stress, is highly questionable.

5 | CONCLUSION AND RECOMMENDATIONS

With the rapid growth of fish cage culture in African inland waters, it is important to better understand the quantity, impacts and fate of aquaculture-derived nutrients. The present study indicates Nile tilapia cage culture in the lake have significant effects on water and bottom sediment quality, especially with respect to nutrients, planktons and macroinvertebrates. It is, however, restricted to a close vicinity around the cages, exhibiting with no broader ecosystem impacts. The impacts on water at the cage sites are neutralized during the 4-month fallowing period. The findings, however, also suggested the sediment and meiofaunal recovery were far from complete after the 4 months fallow period. This is an indication that the water system is not able to quickly assimilate the nutrients, which could signal a serious pending environmental problem. Moving the fish cages slightly before the start of a new cycle by approximately 50–100 m may allow the benthic communities to recover and alleviate the problem. Further, the fallowing period should be 6 months, contrary to the current practice. In fact, intensive and unchecked cage culture practices in the African inland lakes have the serious potential for negative responses to the lake environment. Thus, current efforts to promote commercial cage fish culture enterprises in Lake Victoria, and the Great Lakes Region in general, should proceed with caution, especially in regard to locating cages within each site in order to minimize the loss of environment quality which can cause undesirable changes in the natural biological productivity processes. Finally, regular environmental monitoring programs should be strictly implemented for all cage fish culture enterprises in order to oversee and manage their impacts on Lake Victoria and other water systems in the Great Lakes region.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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APPENDIX A

ZOOPLANKTON SPECIES, RELATIVE CONTRIBUTION (%) AND MEAN DENSITIES (PARENTHESES) (IND./L) (±SEM) ACROSS CAGE CULTURE SAMPLING SITES

	Day 0 (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												
Brachionus 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)
Brachionus 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)
Brachionus calyciflorus	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)
Keratella 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)

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APPENDIX B

SPECIES COMPOSITION OF ZOOBENTHOS SAMPLED AT CAGE CULTURE SITE IN ANYANGA BEACH, LAKE VICTORIA, KENYA, DURING THE STUDY PERIOD

			Day 0 (beginning of culture period)				Day 180 (end of culture period)				Day 300 (end of fallow period)			
Order	Family	Genus	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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