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Water hyacinth (*Eichhornia crassipes*) infestation cycle and interactions with nutrients and aquatic biota in Winam Gulf (Kenya), Lake Victoria

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Abstract

Lake Victoria, like many other lakes in Africa, is affected by water hyacinth that reside in several bays for the majority of the year. The weed affects several economic activities of the local communities and denies revenue to the government from blue economic activities related to the lake. The present study examined the interaction of water hyacinth with biotic and abiotic factors and the efficiency of introduced weevils to better control this invasive weed. Water quality samples were collected and compared from the time of water hyacinth re-emergence and sinking within the Winam Gulf of Lake Victoria. The present study was divided into three phases with an interval of 2 months. Water hyacinth was collected, and the damages resulting from the weevils to the hyacinth, as well as the number of weevils, was recorded and analysed. Fish samples were collected with experimental gill nets. The collected water samples was analysed for the aquatic plant nutrient ammonium, soluble reactive phosphorus, nitrates and nitrites. Data were analysed using R package. The results of the present study indicated that the weevils inhibited nutrient uptake by hyacinth by 17% within the first 4 weeks. The hyacinth subsequently increased the nutrient levels in the gulf by threefold after their decay and sinking. Weevils also increased the sinking rate of water hyacinth through the destruction of their petioles and leaves. One hundred and ninety-four more fish were observed in the experimental nets during the weed infestation, compared to periods when the weed was absent within the gulf. The major conclusions were that water hyacinth impacts both biotic and abiotic factors, and that the weevils alone are unable to eradicate the weed.

KEYWORDS
abiotic factors, biotic factors, *Neochetina eichhorniae*, nutrient dynamics, water quality

1 | INTRODUCTION

Lake Victoria, the largest freshwater lake in Africa, supports local livelihoods through the provision of food, energy, drinking, irrigation water, transport and as a sink for human and industrial waste (Gichuru et al., 2019; Odoli et al., 2019). Over the past decades, however, the lake has faced major challenges because of an increase in human population in its basin, leading to an increased discharge of industrial and municipal effluents into the lake, poor land-use systems, mismanagement and destruction of wetlands. This situation has resulted in eutrophication of the lake, encouraging an infestation of water hyacinth (*Eichhornia crassipes*) and other aquatic plants in it (Twesigye et al., 2011). The introduction of water hyacinth into Lake Victoria has been a subject of debate among researchers over time. One of the most accepted theories is that the weed escaped from an ornamental pond in the 1980s in Rwanda and entered the Kagera River, one of the major rivers draining into Lake Victoria (Albright et al., 2004). Since its introduction, the weed has rapidly spread to the point of being a threat to aquatic life within the lake and to those that depend on it (Gichuki et al., 2012). Prolific spreading of this exotic weed in the lake is adversely impacting its biological diversity, fish breeding and access to fishermen's landing sites, water supply, lake transport and hydropower generation (Mailu, 2001; Outa et al., 2019).

In response to the associated problems, several attempts have been made by both governments and scientists to control water hyacinth. These attempts have included mechanical and biological weed control methods. One of the biological attempts was the introduction of weevils (*Neochetina eichhorniae* and *Neochetina bruchi*) (Wilson et al., 2007). Data on the efficiency of these weevils in controlling the weed are scanty, particularly for the Winam Gulf of Lake Victoria. Water hyacinth reproduces from both seed and vegetative growth. Under favourable nutrient conditions, temperature and minimal disturbance by pests and disease, it is capable of growth and reproduction throughout the year (Gutiérrez et al., 2001; Pérez et al., 2011). Thus, growth and reproduction of the weed are accelerated in areas exhibiting high nutrient concentrations. To this end, Winam Gulf receives nutrients from domestic sources, influent rivers, and industries around the city of Kisumu. Thus, the gulf is highly enriched with nutrients, therefore being an ideal area for the growth and reproduction of water hyacinth (Yongo et al., 2017). Data on the nutrient dynamics within the gulf, however, and its relationship with the hyacinth infestation cycle are largely lacking.

The objective of the present study, therefore, was to investigate the relationship between nutrients and water hyacinth within the gulf, as well as the interactions between the weed and the lake biota. It also generated data on the efficiency of the weevils in controlling the growth of hyacinth within the Winam Gulf (Kenya) of Lake Victoria.

2 | MATERIALS AND METHODS

2.1 | Study area

Fresh water hyacinth and water samples were collected from around the Winam Gulf (0°15′S, 4°35′E) of Lake Victoria (Figure 1). The gulf stretches about 100 km east to west and 50 km north to south, having about 550 km of shoreline. It is shallow, with an average and maximum depth of 6 and 37 m, respectively (Okely et al., 2010). The gulf is semi-isolated from the main lake, receiving nutrient loads from the surrounding towns and agricultural lands. The surface water temperatures range between 23.5 and 29.0°C. These conditions are ideal for the establishment and growth of water hyacinth. The area also is sheltered from strong winds and serves as a breeding zone for many fish species, including Nile perch and Nile tilapia.

2.2 | Study design

Water hyacinth samples were collected by hand uprooting and observed for the presence of the weevils and the number recorded. The damages caused by the weevils to the leaves were ranked from 1 to 4: 1, leaves with one fourth of the leaf surface damaged; 2, leaves with half of their surface damaged; 3, plants exhibiting both leave and petiole damage; and 4, leaves damaged to the extent that they were dry and the petioles rotting. Leaves from all the ranks were set to drift over a distance of 20 m, with the time taken to reach the mark recorded, mainly to determine how the weevil damage to the leaf affected the drifting speed and the vertical orientation of the water hyacinth in the water column, thereby affecting its floating and sinking. Flowers were also observed for the presence of weevils and damage. The water nutrient concentrations were determined using the Standard Methods (AOAC, 2005).

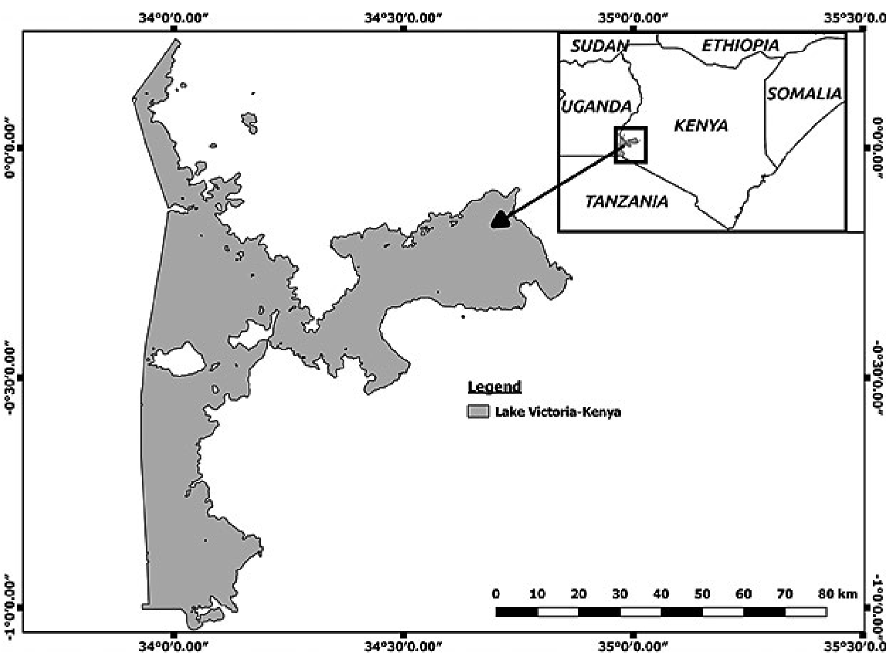

FIGURE 1 Map of Lake Victoria showing Kenyan sector and Winam Gulf

Experiments under controlled fertilization were carried out to determine the lowest nutrient level that would support hyacinth growth and how the weevils affected nutrient uptake by the hyacinth. Water was collected from the gulf during the third phase (i.e., the period characterized with massive sinking and decayed hyacinth), and the nutrient concentrations were determined at the beginning. The sample was then separated evenly into four setups, with the first setup being the lake water control. The second setup was diluted water at a ratio of 2:1 distilled to lake water, with 10 plants of freshly collected hyacinth of approximately the same age and size immersed in each setup. This second setup was used to determine how the nutrient concentrations influenced the growth of water hyacinth. The third setup comprised lake water and 10 hyacinth plants, being used to determine the optimum nutrient required to support growth and reproduction of the hyacinth. This setup was left to stand in an open area for 4 weeks. Six weevils were introduced in the fourth setup, which contained the same number of hyacinth plants and lake water in order to study the effects of the weevil under constant nutrient conditions. The nutrient levels were again determined for each setup and observations made at the end of the fourth week.

Data on fish abundance were determined on the basis of samples collected with a 0.75-in. monofilament experimental net for 2 h within a 5-week period during the water hyacinth infestation and a period in which the hyacinth were absent within the gulf. The stomach content of the fish sampled was studied using an inverted microscope (Leica S9E) to determine the feeding niche of the fish caught during the two periods.

2.3 | Data analysis

Statistical analysis was conducted using R-data analysis software. For places exhibiting significant differences, Tukey's Multiple Range Test was used to separate the mean. Student *t*-tests were used in analysing of two-group parameters.

3 | RESULTS

3.1 | Water hyacinth infestation cycle in Winam Gulf

The water hyacinth cycle begins from the time of its re-emergence within the gulf, the support systems and resources for its thriving, its 6–8 months lifespan within the gulf, its eventual death and sinking, and repeating the cycle in the next generation. The infestation cycle is presented in Figure 2.

3.2 | Macrophyte succession in the gulf

The first phase, encompassing the first 2 months after hyacinth re-emergence, was characterized by green mats of water hyacinth occurring in small patches amidst a bloom of blue-green algae. The mats move to different positions within the gulf, depending on the wind direction and strength. Most of the leaves were not significantly damaged by the weevils. Of the total, 90% were within rank 1 (one fourth of the total leaf surface damaged) and 68% not damaged at all. The phase is characterized by aggressive vegetative reproduction, with sexual reproduction being common during the mid-first phase to the early second phase. Algae are outcompeted towards the end of the first phase, leading to hyacinth dominance. Water samples taken from below the hyacinth mat were clear and had lost its green appearance.

The second phase, during the third and fourth months, was characterized by a continuous dense mat of water hyacinth with overgrown floating islands of macrophytes. The mats are so thick and heavy during this phase that economic activities in the lake were significantly reduced, with most fishermen possessing small fishing boats hardly able to access their fishing grounds within the gulf. The late second phase, however, was characterized by reduced sexual and vegetative reproduction with increasing numbers of weevils. The mats were still green but had begun to lose their deep green color towards the end of the second phase. The water hyacinth mat during this phase was damaged by the weevils' feeding activities, both on the leaves and the petioles, implying reduced efficiency of nutrient uptake and reproduction. Most of the plants towards the end of this phase had stopped reproducing, compared to the first and early second phases in which daughter plants were common. Data on wind speed that facilitated the drifting of hyacinth mat within the gulf are summarized in Table 1.

The third phase, from the fifth month to the hyacinth sinking time, was characterized by brown patches amidst overgrown macrophytes from the former green extensive 'field.' The remaining hyacinth were just petioles with small, withered leaves toward the end of this phase. The dead rotting mat began to sink toward the end of the sixth month. The macrophytes that had previously relied on water hyacinth as substrates for anchorage also begin to sink, leaving the lake surface open. Various activities such as fishing resumed on a full-time basis in most parts of the gulf with increasing accessibility of the fishing grounds. Nevertheless, gill nets still entangled debris of sinking hyacinth, thereby making it difficult to fish during the first few weeks after the sinking of the hyacinth mats, a situation that persisted until all the debris sank to the lake bed. What follows after a few months is a bloom of cyanobacteria that covered a larger part of the gulf.

3.3 | Weevil infestation of water hyacinth within the gulf

The number of weevils increased linearly from the time the weed re-emerged, and by the end of the first and fifth months, a modal of 6 and 8 weevils and a mean of 4 and 5 weevils, respectively, were recorded per sampled plant. The fifth month was characterized by brown patches amidst overgrown macrophytes from the former

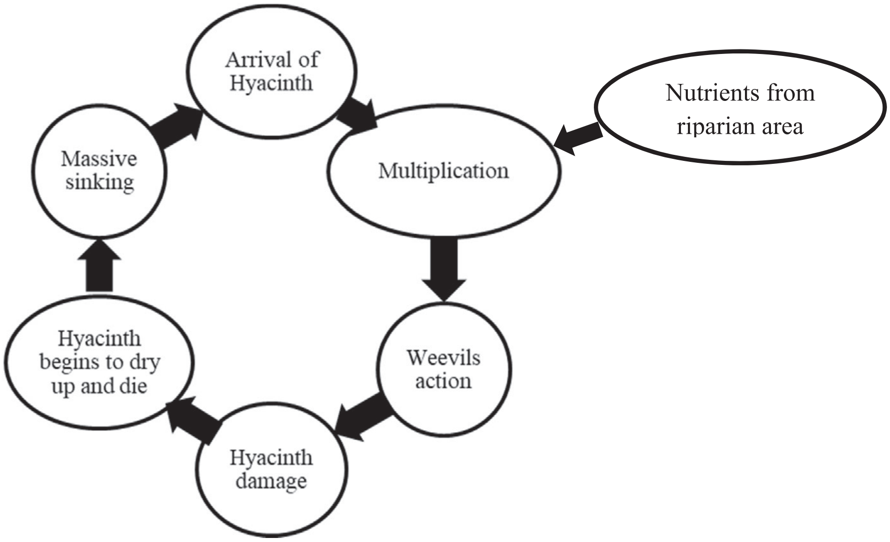

FIGURE 2 Flow diagram of water hyacinth infestation cycle in Winam Gulf, Lake Victoria

extensive green field. By the end of the sixth month, the remaining hyacinth were just petioles with small, withered leaves. Accordingly, the weevils are left with no food source, resulting in their beginning to fly away to seek refuge, if any, from the terrestrial environment. More weevils were sampled in the terrestrial environment, compared to the hyacinth mats, during this phase. Some weevils flew as far away as a kilometer from the lake, with a number being located on the rooftops of vehicles packed in Kisumu and other riparian residential areas.

3.4 | Impacts of water hyacinth on fish and other aquatic biota

The results of the present study indicated there were more fish (Table 2) present during the water hyacinth infestation than the periods when hyacinth was absent in the gulf. Catfish and lungfish exhibited the greatest increased in number of all the fishes caught in the experimental nets, whilst Haplochromines were the least increased. There was a general downward trend in the numbers of fish during the five-week sampling period, however, when hyacinth was present. Haplochromines and *Synodontis* spp exhibited little fluctuation in their numbers during the two periods of water hyacinth presence and absence.

Other than the macroinvertebrates isolated from the roots during the present study (Table 3), Orb snail and may fly remains were identified in the stomach content analyses of Haplochromines and *Synodontis* spp. caught in the gulf during the water hyacinth infestation. The roots, and the petiole connecting at the base of the drifting water hyacinth, also provided a substrate for different seeds of other macrophytes, which was noted during the second phase when patches of the floating island started to appear. Small patches of hippo grass (*Vossia cuspidata*), large islands of *Typha* spp and small patches of *Ipomoea aquatic* and other species of aquatic macrophytes were also observed during this phase.

3.5 | Impacts of the weevil on reproduction and distribution of water hyacinth

The third phase was characterized by small hyacinth plants with reduced physiological activities and which exhibited significant damage both on the leaves and petioles. Most of the plants during this phase had ceased vegetative reproduction, and the stolons, leaves and petioles were damaged and waterlogged. The plants also lost the chlorophyll pigmentation essential for photosynthesis, thereby limiting their ability to synthesize energy requirements for metabolism and physiological activity. Most of the sampled plants were in rank 4 and exhibited a reduced floating ability, compared to the first phase plants. Their vertical orientation had been lost, with petioles being waterlogged and bent deep into the water. It is also important to note there were no indications of weevil damage to the flowers of all the sampled plants during all three phases.

The results also indicated the weevils impacted the movement and distribution of the water hyacinth. As a demonstration of this observation, the experiment sampled plants in rank 1 (i.e., plants exhibiting very little damage on the leaves) and in rank 4 (i.e., plants damaged both on the leaves and petioles) were exposed to natural drifting over a distance of 20 m. The rank 1 plants reached the 20-m mark after 4 min and 9 s, whilst the rank 4 plants reached the mark after 6 min and 43 s. The other plants in ranks 2 and 3 reached the set mark in intermediate times, as highlighted in Figure 3. This suggests a possible model and indicator of a conclusion that the weevils play an important role in immobilizing the drifting of the water hyacinth in the lake.

3.6 | Nutrient dynamics

The third phase exhibited the highest nutrient concentrations, with a mean of 188.99 μg/L, ammonium and SRP levels being the highest. The average nutrient concentrations during the first and the second

TABLE 1 Data on wind speed, rainfall and temperature during the first study phase, characterized by re-emergence and drifting of water hyacinth mat within Winam Gulf as dictated by wind direction (unpublished data from Kenya Metrological Department)

	2018 October				2018 November				2018 December			
	Rain	Temperature (°C)		Wind	Rain	Temperature (°C)		Wind	Rain	Temperature (°C)		Wind
	mm	max	min	km/day	mm	max	min	km/day	mm	max	min	km/day
1	0.0	32.5	16.9	152.5	0.0	29.1	18.3	83.4	0.0	31.5	18.5	113.1
2	9.0	32.5	19.1	160.8	TR	28.8	19.7	94.3	2.8	30.6	17.3	88.8
3	26.6	32.5	17.5	172.3	1.6	30.2	18.7	99.8	0.0	31.6	19.1	106.0
4	27.2	31.0	17.4	143.3	TR	29.6	16.8	149.8	0.0	29.4	18.3	101.8
5	0.0	32.1	16.7	136.5	0.0	29.5	17.5	108.6	19.2	31.1	19.1	135.2
6	0.0	32.1	19.0	129.1	0.0	30.2	17.9	99.5	0.0	30.2	16.7	72.7
7	0.0	31.2	20.8	144.3	0.0	32.1	17.6	109.8	0.0	30.7	16.7	103.8
8	2.4	29.7	20.6	119.0	3.8	30.3	19.5	146.3	0.0	29.0	19.1	93.9
9	2.2	29.9	16.5	119.0	13.6	29.5	19.0	128.5	12.4	27.1	17.8	160.2
10	3.2	28.4	18.5	123.3	5.4	28.9	19.3	112.3	6.2	25.9	17.1	77.0
11	0.0	30.4	18.4	97.6	48.8	28.5	19.1	112.7	22.0	26.3	17.9	80.8
12	6.6	29.8	19.3	210.0	TR	30.7	16.5	115.6	0.0	27.0	17.5	64.3
13	0.1	30.7	17.8	119.0	TR	29.0	17.6	84.0	4.4	28.3	17.5	116.0
14	25.6	27.5	19.9	168.1	0.0	31.3	17.1	82.7	0.0	29.0	18.5	68.4
15	1.9	28.9	16.4	111.4	0.0	30.6	18.4	113.7	18.6	28.5	18.6	110.9
16	0.0	29.1	16.7	147.0	0.0	30.9	19.1	108.0	14.2	28.7	16.6	101.2
17	0.0	31.1	20.4	84.8	19.6	30.2	19.5	112.8	0.0	28.8	18.1	107.8
18	3.6	28.4	18.4	113.4	24.4	28.9	19.0	132.9	0.0	29.3	16.6	103.3
19	5.8	29.2	18.8	129.3	6.0	29.4	16.3	88.5	TR	26.4	21.0	93.4
20	0.0	27.9	17.1	109.7	2.0	30.1	17.8	108.8	1.0	28.7	19.2	66.2
21	10.2	30.3	18.2	119.9	0.2	28.7	18.2	107.6	4.0	29.1	19.3	115.2
22	0.0	30.0	16.4	109.7	0.0	28.9	19.3	81.9	16.2	29.5	18.7	124.2
23	0.0	28.8	16.3	96.9	TR	28.9	18.7	114.1	9.8	28.9	17.1	92.0
24	0.0	30.1	16.4	88.1	0.0	30.3	18.7	96.9	0.0	29.3	18.3	100.2
25	4.0	30.1	19.5	85.8	0.0	32.1	18.5	107.9	0.0	30.7	16.9	75.8
26	5.0	29.9	16.9	141.6	TR	31.8	19.3	98.8	0.0	30.0	16.5	101.2
27	0.8	29.1	18.6	119.2	0.0	32.4	17.9	108.0	0.0	31.0	16.8	83.0
28	0.8	28.0	18.1	115.3	0.0	32.4	19.4	103.3	1.4	30.5	17.3	123.1
29	14.4	30.3	17.0	112.3	TR	33.0	20.1	115.1	7.0	30.2	17.8	119.8
30	16.6	28.8	19.6	110.0	0.0	32.3	19.4	115.8	0.0	29.4	17.7	99.4
31	TR	28.0	19.3	93.2					0.0	29.1	17.3	81.7

Abbreviations: max, maximum value; min, minimum value; mm, millimeters; TR, traces of unmeasurable rainfall.

phases were 40.69 and 29.13 μg/L, respectively. The ammonium and SRP concentrations exhibited a sharp fluctuation during the third phase. The nitrate and nitrite levels remained relatively stable during all three phases (Figure 4).

3.7 | Nutrient impacts on water hyacinth growth and multiplication

The four experimental setups for investigating the impacts of the studied stressors (nutrients and weevils) on hyacinth growth and multiplication exhibited variable responses. The second setup (i.e., lake water diluted with distilled water and hyacinth plant) exhibited no growth of daughter plants nor flowers, whilst there was growth of daughter plants and a flower in the third setup (i.e., lake water plus hyacinth plant). The fourth setup (i.e., lake water with introduced weevil and hyacinth plant) exhibited a growth of daughter plants but no flower. The nutrient levels in each stand were compared to the control (i.e., lake water during the third phase) at the end of the experiment. The results indicated that, for the studied nutrient, an average concentration below 24.45 μg/L did not encourage multiplication of the hyacinth. However, hyacinth comfortably undergoes

TABLE 2 Number of fish sampled during presence and absence of water hyacinth in Winam Gulf, Lake Victoria

	Water hyacinth absent					Water hyacinth present				
Fish species	Week 1	Week 2	Week 3	Week 4	Week 5	Week 1	Week 2	Week 3	Week 4	Week5
Nile perch	4	6	7	3	10	17	13	11	8	9
Tilapia	5	12	11	9	8	24	21	19	22	16
Haplochromine	11	8	17	10	15	33	27	18	19	15
Catfish	1	3	2	—	—	3	5	2	4	2
Synodontis spp.	5	17	9	6	13	25	29	20	12	7
Lungfish	—	1	2	—	—	1	4	2	—	1

TABLE 3 Biota living in association with water hyacinth in Winam Gulf, Lake Victoria during first phase (first 2 months after re-emergence of water hyacinth)

Order	Family	Genus/spp	Common name	Counts
Hirudinea	Hirudinidae	*Hirudo medicinalis*	Leach	6
Prosobranchiata	Valvatidae	*Valvata cristata*	Orb snail	7
Pulmonata	Physidae	*Physa sayi*	Trumpet snail	1
Ephemeroptera	Ephemeridae	*Hexagenia bilineata*	May fly	1
Haplotaxida	Tubificidae	*Tubifex*	Sewerage worm	1
Hemiptera	Belostomatidae	*Lethorus americanus*	Giant water bug	1
Coleoptera	Dryopidae	*Dryopid* spp	Long toed water beetle	5

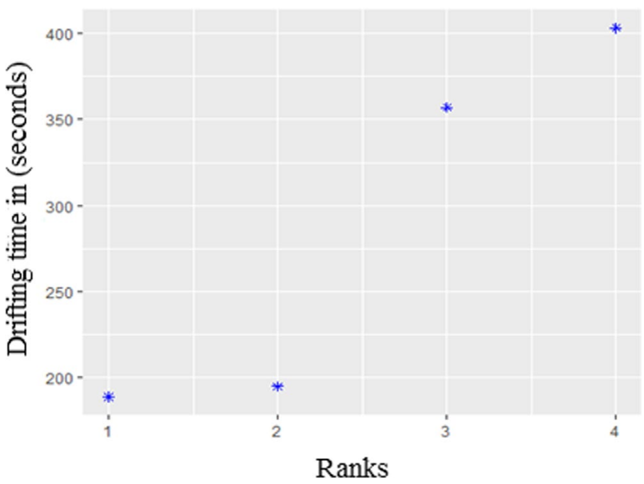

FIGURE 3 Scatter plot illustrating drifting time of water hyacinth exhibiting different severity of damage from weevils

both sexual and asexual reproduction when the mean of the studied nutrient is 107.945 μg/L. At this concentration, however, the weevils can interfere with sexual reproduction that produces seeds for future generations, whilst the vegetative reproduction continues. There was a 17% decrease in the nutrient uptake when weevils were introduced for 4 weeks. However, this percentage increased linearly until a level at which no uptake at all occurred, with the absorbed nutrient being returned into the water column.

Experiment 3 exhibited the highest growth of water hyacinth at the end of the 4 weeks, while experiment 2 exhibited the least growth for both petiole length and horizontal length of the leaf. In contrast, the longitudinal length did not exhibit any positive growth. There was a reduced nutrient concentration, except for ammonium, in the fourth experiment, which exhibited a positive increase (Figure 5).

The interrelationships between water hyacinth growth and nutrient concentrations are summarized in Figure 6. There was a strong correlation ($p < .05$) between petiole length and the longitudinal and horizontal lengths of the hyacinth leaves. In contrast, the hyacinth growth exhibited a negative correlation with nitrates.

4 | DISCUSSION

Water hyacinth re-emergence within Winam Gulf originates from vegetative and sexual reproduction of assemblages along the fringes and rivers draining into the gulf (Fusilli et al., 2013). During the first weeks of re-emergence, water hyacinth experiences little interference from the biological control agents (weevils) due to their limited numbers. Thereafter, the hyacinth mats are sustained by a rich nutrient supply dominated by organic nutrients from municipal areas, river discharges, atmospheric inputs and nutrients in the water column. There was limited nutrient input via floods during this period, however, because of little rainfall (Table 3). It is noted that the nutrient budget of Lake Victoria is dominated by direct atmospheric inputs, which contributes 55% of the total phosphorus (TP) and 65% of the total nitrogen (TN) load (Tamatamah et al., 2005).

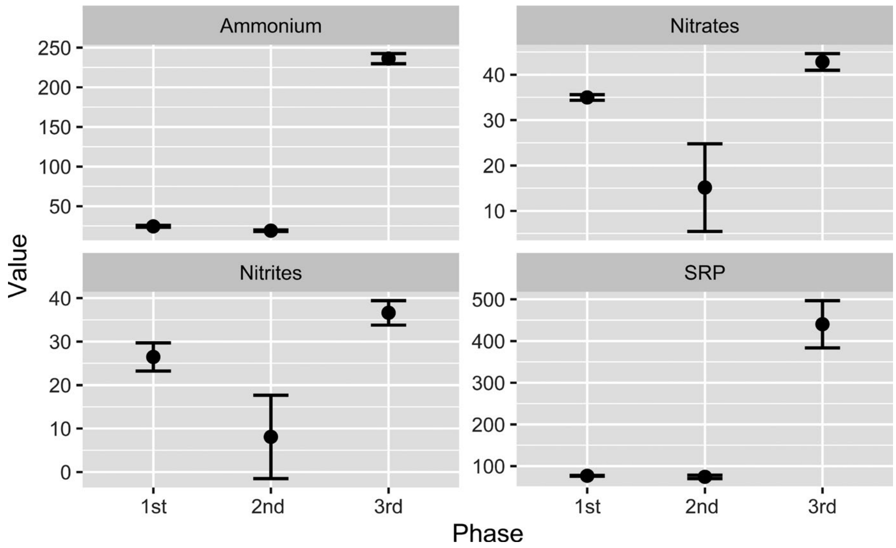

FIGURE 4 Nutrient concentrations (μg/L) during three phases of water hyacinth in Lake Victoria (1st phase, two months after reemergence of hyacinth; 2nd phase, third and fourth month after reemergence; 3rd phase, fifth and sixth month after reemergence of hyacinth mat)

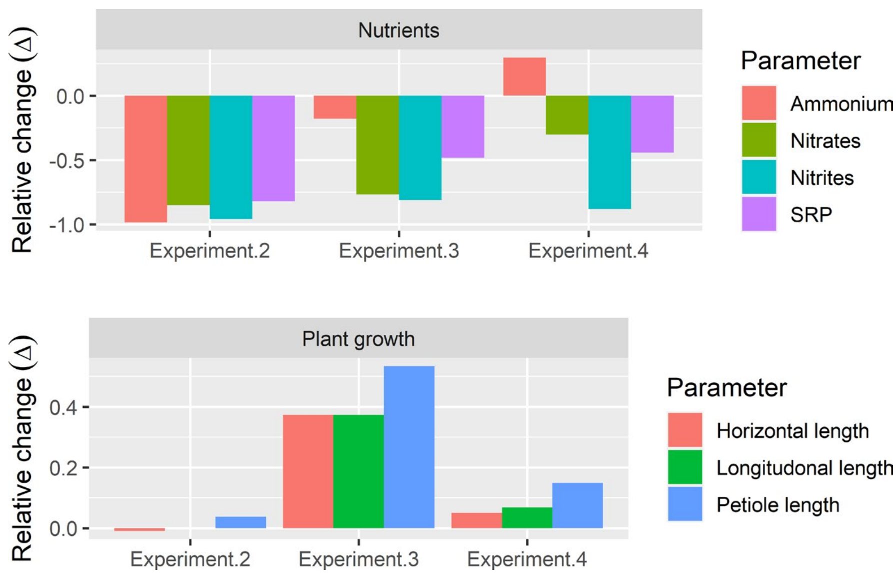

FIGURE 5 Diagram illustrating hyacinth growth and nutrient concentration changes during set experiment determining the effects of hyacinth stressors (nutrient and weevils) on its growth and multiplication (experiment 2 = lake water diluted with distilled water and hyacinth plant experiment 3 = lake water plus hyacinth plant; experiment 4, lake water, introduced weevil and hyacinth plant)

Nyanza Gulf is large and shallow, with a surface area of 1400 km^2 and a mean depth of 6 m. It is semi-isolated from the main lake and experiences high pollution from riparian towns such as Kisumu, with about 10% of the total river flowing into Lake Victoria through Nyanza Gulf. The gulf is connected to the main lake through the narrow, deep Rusinga Channel, the primary exchange between the gulf and the lake (Hecky, 2005). The channel is a physically active area characterized by strong vertical mixing and horizontal exchange of water and nutrients between the gulf and the lake (Gikuma-Njuru, 2008; Romero et al., 2006), resulting in persistent physicochemical gradients and the potential for spatial variability in biogeochemical processes. These conditions in the gulf along with the nutrient status sustain the hyacinth for 6–8 months. The death and eventual sinking of hyacinth mats is attributed to the increasing number of weevils during the late second phase, with their feeding damaging the hyacinth.

Macrophyte succession is a function of the nature of the gulf and the cyclic pattern of water hyacinth. Winam Gulf has a sheltered bay which is likely to create calmness, compared to open and exposed shorelines (Ongore et al., 2018). This protects the hyacinth mats from being swept away by the wind into the open water, thereby giving it sufficient time to grow and reproduce in this remote gulf. Water hyacinths have broad leaves that limit light penetration to the lake bottom, especially during a full infestation, which in turn results in inadequate photosynthesis to provide cyanobacteria with essential energy for physiological functions (Kim & Kim, 2000). The result is the death of the cyanobacteria and subsequent dominance of water hyacinth. The hyacinth dominance, however, is challenged during the second phase, when other macrophytes begin to appear as floating islands, resulting in stiff competition for nutrients as well as shading of the hyacinth mat by these large macrophytes. The hyacinth further suffers the consequences of weevils feeding on them. This reduces its ability to absorb the needed nutrients especially during the phase in which there is stiff competition from the emergent and floating macrophytes for nutrients. The damage caused by the feeding scar render the hyacinth physiologically inefficient and

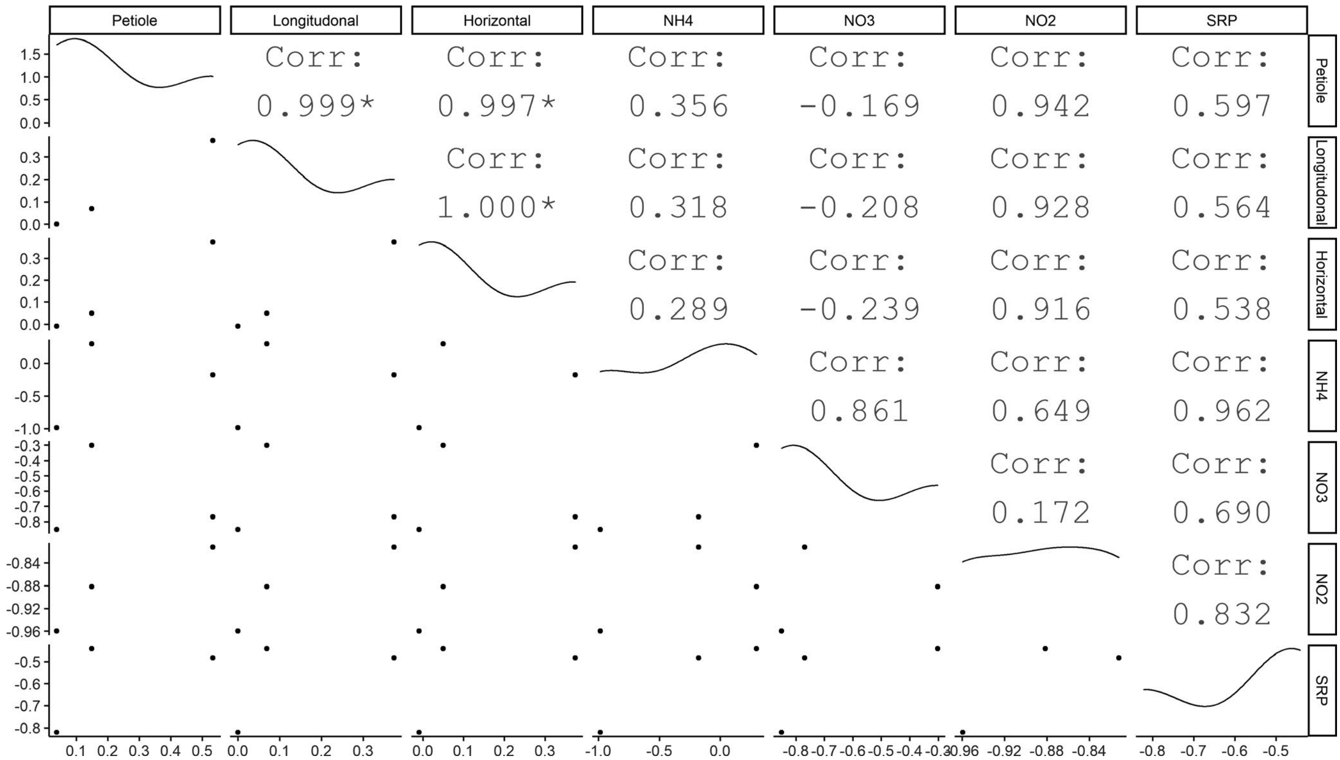

FIGURE 6 Correlation between water hyacinth growth and nutrient concentrations (significance difference at $p < .05$; numbers represent correlation coefficient values, with significant pairs indicated with*; Pearson correlation used, rather than ranked values, since raw data were used to evaluate linear relationship between continuous variables)

waterlogged. It then begins to rot, die and sink, signifying the end of its dominance. The floating macrophytes lose the substrate firmness previously provided by the hyacinth mat and also sink (Ouma et al., 2005). All the nutrients that had been absorbed by the macrophytes eventually return to the water. What follows is a nutrient stock in the sediment and the water column for the next future generation of the weed, explaining the blooming of the cyanobacteria after a few months. This situation, therefore, represents a circular use and reuse of the nutrients to sustain the flourishing of water hyacinth during the next generation.

The increased numbers of weevils result from the reproduction of the two species, which requires a period of between 72 and 120 days to complete the reproduction cycle and start feeding on the hyacinth mat (DeLoach & Cordo, 1976). The female *N. eichhorniae* lay between 5 and 7 eggs per week, with the larvae going through three development stages. Adults emerge from the cocoon after about 20 days and start to feed on the youngest succulent leaves within 24 h (Grodowitz et al., 1997). The feeding scars cause damage to the transport tissues, thereby denying the water hyacinth an essential supply of nutrients from the roots to the leaves, and photosynthates from the leaves. High weevil infestation results in small hyacinth plants with reduced physiological activity, therefore not producing flowers nor set seeds (Pérez et al., 2011). The tropical sun worsens the situation by facilitating evapotranspiration, which leads to withering of the leaves to result in the brown extensive mat observed during the third phase in the present study. The departure of the weevils from the weathered hyacinth mat is attributable to a lack of food source. Weevils feed purely on water hyacinth (Julien et al., 1999) and, therefore, move away from the drying mats to seek their death beds in the terrestrial environment, rather than waiting and drowning together with what was once their food.

The high and low numbers of fish during the presence and absence of water hyacinth, respectively (Table 1), was attributable to the physical blockage of the water surface within the gulf. This blockage is created by the availability of water hyacinth that dictated the accessibility of the fishing ground during these two periods (Kateregga & Sterner, 2009; Villamagna & Murphy, 2010). Water hyacinth mats create a natural control on fishing activities since it blocks most fishing grounds during full hyacinth infestations, thereby keeping fishermen at bay and giving time for the fish to replenish their stock (Ongore et al., 2018). Catfish and lungfish are bottom feeders, therefore requiring little illumination to capture prey. The presence of water hyacinth mats that reduce light penetration into the water column might have favoured their population, resulting in the observed increase during hyacinth infestation periods. The progressive decline of fish sampled during the presence of water hyacinth is also attributable to the inaccessibility of the gulf because of blockage by water hyacinth mats, thereby limiting access to the fishing grounds, noting the coverage of the mats increased with time over the five-week sampling period. Lake Victoria, like many African lakes, exhibits open access to fishing activities (Njiru et al., 2018). Thus, many fishermen seek to explore the fisheries resources within this remote gulf, thereby overstretching its capacity, with the result being increasing fishing pressures on the limited resource (the lake) against an ever-increasing population of the riparian neighbourhoods (Aura et al., 2013; Nyamweya et al., 2018). The fishing pressure experienced during periods when water hyacinth are absent and the lake is accessible also explains the reduced number of fish sampled during this period.

The macroinvertebrates isolated from water hyacinth were aquatic and would likely spend their life cycles in a damp or aquatic environment, explaining why they seek substrate in damp environments such as in water hyacinth roots and petioles. The stomach content analysis of the fish caught in Winam Gulf with experimental nets comprised some of the biota found in the roots of hyacinth from the stomach of tilapia (*Synodontis* spp.) and Haplochromines. Thus, one could hypothetically conclude that the hyacinth mat provides a food source for the said fishes, thereby positively impacting their population. However, the mats also outcompete algae that represent a direct food source for algivorous fish. Further, leeches also present on the roots are parasites to most cultured and wild fishes, making it very difficult to determine if the water hyacinth mats are a safe haven for fish, based on Odum's food abundance and predator theory, respectively (Odum & Brown, 1975; Odum & Collins, 2003). The findings of the present study indicate hyacinth lives in association with biota that hypothetically also influence the fish stock. However, the macrophytes seeds might have gotten access to the hyacinth, since hyacinth mats are common on the lake fringes before they are pushed and drifted into the open waters by the wind. Since these macrophytes are attached to soil substrates along the fringes, they might have dropped their seed on the vegetative parts of hyacinth, later germinating into the floating islands observed during the late second and third growth phases.

Although the distribution of water hyacinth is mainly a function of wind direction and strength, some plants are brought into the lake by flowing rivers during flood periods (Gichuki et al., 2012). As a major player in the distribution of the weed by creating currents and waves on the water surface that drift the plant, the wind also acts on the vegetative parts, thereby leading to a 'push' of the weed and subsequent drifting. A reduced size of the vegetative part of the hyacinth, therefore, will result in a reduced speed of drifting of the plant across the lake. This could explain why plants damaged by the weevil's feeding activities at different ranks responded with different drifting speeds when exposed to natural drifting phenomenon by wind action on the water surface. The zero impact of the weevils on the flowers could be a result of feeding selectivity (Heard & Winterton, 2000), which indicates the weevil only feeds on the leaves and petiole but not the flowers. Thus, any plant that managed to flower would proceed to produce seeds to sustain the future generations of the plant.

The low nutrient concentration observed during the second growth phase (Figure 3) is a result of the massive water hyacinth biomass from vegetative and sexual reproduction observed during this phase. The high biomass assimilates the nutrients from the water column, leading to a significant reduction in the nutrient content (Blackmore & Sullivan, 2009; Wang et al., 2012). The differences in the nutrient levels observed during the three phases were a result of different activities and processes taking place during each phase. The first phase was characterized by small patches of hyacinth, indicating limited nutrient uptake from the water. The second phase exhibited massive nutrient uptake as evidenced by the extensive hectares of hyacinth mats. The third phase was characterized by weevil activities that decreased the nutrient uptake, resulting in dead and decaying water hyacinth that subsequently led to leaching of the absorbed nutrients back into the water column. This latter phenomenon is accompanied by very aggressive decomposition that utilizes dissolved oxygen, thereby reducing its concentration in the water column.

The sharp resurgence of ammonium and SRP during the third phase resulted from the transformation of organic phosphorus and nitrogen to their inorganic forms during the death and decomposition of the hyacinth mats as a consequence of the weevils' damage. The sampling for nutrient analysis during the third phase was done before the lake circulation that usually occurs during the months of July and August. This period also experienced little rainfall, suggesting the significant nutrient resurgence in the water column was largely attributable to its leaching from the dead and decaying hyacinth mats.

The effects of the stressors (weevils and nutrients) on the growth and multiplication of hyacinth result from the damages that impact the efficiency of nutrient uptake and the quantity of available nutrients available in the aquatic system to support its growth and multiplication, respectively (Opande et al., 2004). The inability of the hyacinth to produce a daughter plant or a flower, as observed in the second experimental setup, was due to limited nutrients, noting that diluting the experimental water with distilled water reduced the nutrients to levels that could not provide adequate nourishment for hyacinth growth and reproduction. The third experimental setup that resulted in both vegetative and sexual reproduction provided the optimum nutrient availability for metabolism and reproduction. Introducing the weevils to the hyacinth under the conditions of experiment 4, however, stopped sexual reproduction, thereby explaining the lack of a flower, but did allow a daughter plant. This phenomenon may be attributable to damage caused by the feeding scar, reducing the ability of the hyacinth to uptake nutrients, as well as secondary infections from bacteria and fungi (Centre et al., 1999).

The positive increase of ammonium in experiment 4 (Figure 4) was attributed to the decomposition of hyacinth tissues and the eventual return of their absorbed nutrients back into the water column, caused by the six weevils introduced in the experiment. The feeding scars resulted in damage to some older leaves and had begun decaying at the end of the fourth week of the experiment.

Water hyacinth can easily assimilate inorganic nitrogen and phosphorus and incorporate them into the tissues for different physiological functions and plant growth, thereby explaining the correlation observed between these nutrients and the hyacinth growth (Figure 5). Plants also grow through a combination of cell growth and cell division, which increases the size of the plant at varied rates when nutrient availability is optimal (Dhondt et al., 2010) and which explains the strong, significant correlation observed in the growth of different parts of the hyacinth plant. Organic nitrogen may be assimilated, for example, with the cooperation of microorganisms in co-existence with blue-green algae that can fix molecular nitrogen and release inorganic nitrogen into the water column upon their death and decomposition (Zhou et al., 2015). Water hyacinth can then simultaneously, quickly and efficiently absorb ammonium and nitrate from the water, although it has a preference for ammonium. The negative correlation observed between hyacinth growth and nitrates, therefore, may be a consequence of the two pathways of nitrate utilization wherein it can be absorbed directly or transformed through the nitrogen cycle. Absorbed nitrate, however, must be reduced to ammonium in the plant tissues, in contrast to absorbed ammonium, which is immediately incorporated into metabolism (Fang et al., 2007; Snow & Ghaly, 2008).

5 | CONCLUSIONS AND RECOMMENDATIONS

Water hyacinth impacts water quality from the time of its arrival into a waterbody by assimilating nutrients from the water column. It eventually returns all the nutrients back into the water, however, after death and eventual sinking. Water hyacinth growth and multiplication ceases when the mean concentration of the studied nutrient is 24.45 μg/L. Although their growth and multiplication is halted, the weeds do not die at this nutrient level. Additionally, the weevils do not feed on the water hyacinth flowers. Thus, those that manage to produce flowers within the first 2 weeks when the weevil numbers are still low will form seeds to sustain the future generation through sexual reproduction. The impacts of the weevils on the distribution of water hyacinth result from their feeding on the vegetative parts, which significantly reduces the air spaces in the mats as the plants rot and become waterlogged.

Controlling water hyacinth within the gulf should involve a mechanism that disrupts the circular uptake and return of nutrients to the water column since the nutrients in the water and bottom sediments sustain the next generation of incoming water hyacinth. Future models for controlling the growth of water hyacinth based on nutrient resurgence into the waterbodies or wetland approach should maintain a minimum of 24.45 μg/L for successful management of the weed. If weevils are to continue to be used in the future as agents of control, accurate and continuing monitoring of the hyacinth would play a major role in introducing them in young emerging weeds before their flowering.

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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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